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Climate-driven carbon exchange in German forests before, during and after the 2018 drought: implications of climate forcing uncertainty

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Abstract

Forest carbon exchange is strongly influenced by climatic conditions, yet its response to drought remains difficult to quantify because of complex interactions among climate, tree growth, and ecosystem processes. In this study, we use the process-based model LandscapeDNDC to investigate the spatial and temporal variability of carbon exchange processes across German forests between 2011 and 2023, encompassing the extreme drought year 2018. To isolate the direct climate signal, simulations exclude forest management, and disturbances, thereby representing the response of an undisturbed forest system to climatic variability. Using E-OBS climate forcing the model reproduces the overall magnitude and variability of carbon fluxes when compared to FLUXCOM (X-VIIRS), a machine-learning-based upscaling of eddy covariance observations. The 2018 drought emerges as the dominant disturbance, with a marked reduction in productivity and a strong weakening of the carbon sink strength (-46.3%) compared to the baseline period 2011–2017. Although carbon uptake partially recovered in subsequent years, reduced sink strength persisted in drought-prone regions, particularly in beech and pine-dominated forests in northern and northeastern Germany, whereas southern regions remained comparatively resilient. A sensitivity analysis comparing E-OBS with ERA5 climate forcing datasets reveals that carbon flux estimates are strongly dependent on climate inputs. Despite higher precipitation in ERA5, increased interception losses and evaporation associated with more frequent low-intensity rainfall events reduce transpiration and gross primary productivity (GPP), while higher minimum temperatures enhance ecosystem respiration, resulting in a systematically weaker net carbon sink. Overall, our results highlight both the spatial heterogeneity of drought impacts and the critical role of climate forcing uncertainty in shaping simulated forest carbon dynamics.

1. Introduction

Forest ecosystems play a central role in the global carbon cycle by acting as long-term sinks for atmospheric carbon dioxide (CO_2), thereby mitigating climate change (Dixon et al. 1994; Mitchard 2018; Nunes et al. 2019). In Europe, and particularly in Germany, forests cover a large fraction of the land surface and contribute substantially to national carbon budgets through biomass accumulation and ecosystem carbon exchange (Janssens et al. 2005; Ciais et al. 2008; Kilpeläinen et al. 2022; Vizzarri et al. 2022). Forest biomass and soils in Germany currently store approximately 2.5 billion tons of carbon (Wellbrock et al. 2017), highlighting the importance of forests not only as long-term carbon reservoirs but also as a critical component of national greenhouse gas mitigation strategies. Consequently, maintaining forest carbon uptake is essential for achieving Germany's climate neutrality target by 2045. However, forest carbon uptake and storage are increasingly affected by climate variability and extremes, such as heatwaves and droughts. These events have become more frequent and severe in recent decades (Reichstein et al. 2013; Seidl et al. 2014; Lloret and Batllori 2021) leading to a decline of the forest carbon sink strength (Migliavacca et al. 2025). Understanding how forest carbon dynamics respond to changing climatic conditions is therefore critical for reliable carbon accounting and for assessing future forest resilience.

Forest carbon exchange is sensitive to climatic drivers, including temperature, precipitation, and atmospheric demand for water. These drivers regulate photosynthesis, respiration, and allocation processes, while also interacting with soil water availability and nutrient cycling (Yalav et al. 2024). In particular drought events can substantially reduce carbon uptake. For example, losses of up to 0.5 PgC were reported during the European heat wave and drought 2003 (Sippel et al. 2018). Such reductions in carbon uptake arise from multiple interacting processes such as stomatal closure, growth limitation, accelerated senescence and increased mortality and may persist beyond the drought event through legacy effects on tree physiology and stand structure (Kannenberg et al. 2020). Because these responses are often nonlinear, temporally lagged, and strongly shaped by environmental conditions, they are difficult to represent with empirical forest growth models (Bloom et al. 2020).

Process-based models therefore offer a more suitable tool for analyzing climate-driven changes in forest carbon exchange by explicitly representing interactions among vegetation processes, soil biogeochemistry, and environmental drivers. One example is the process-based modeling framework LandscapeDNDC, which links vegetation dynamics, ecosystem gas exchange, and soil biogeochemistry (Haas et al. 2013)Its ability to simulate gas exchange and growth has been extensively evaluated for a variety of tree species and forest types (Grote et al. 2011; Molina-Herrera et al. 2015; Cade et al. 2021; Nadal-Sala et al. 2021). Applying such a model at regional scales, however, requires robust species-specific parameterization obtained from independent observations, together with spatially consistent information on climate, soil properties, and vegetation characteristics .

A major source of uncertainty in regional ecosystem modeling, particularly when assessing drought impacts, is the choice of climate forcing data. Gridded observational datasets such as E-OBS and reanalysis products such as ERA5-Land differ in spatial resolution, underlying data sources, and data assimilation approaches, which can result in systematic differences in temperature, precipitation, radiation, and atmospheric demand (Cornes et al. 2018; Muñoz-Sabater et al. 2021). These differences can propagate nonlinearly through process-based models, affecting simulated soil moisture dynamics, plant water stress, nutrient cycling, forest growth, and ultimately carbon fluxes. Evaluating the sensitivity of simulated forest carbon exchange to alternative climate forcing datasets is therefore essential for assessing the robustness of regional-scale simulations, particularly under drought conditions.

German forests are a central component of European temperate ecosystems and provide a sound basis for the analysis of carbon exchange depending on drought because they combine high ecological relevance with relatively good data availability. They are dominated by a limited number of major tree species with relatively well-investigated physiological traits, while soil properties and climate data are available from detailed spatial datasets. In this study, we apply LandscapeDNDC to forests across Germany for the period 2011–2023, including the severe 2018 drought and the following years of climate anomalies. with species-specific parameterization and spatially explicit initialization of forest composition, the simulations enable the evaluation of how carbon exchange of forests with different dominant tree species vary in their responses to drought conditions and how these responses depend on regional patterns of soil properties.

Because forest carbon dynamics are influenced not only by climate but also by management and disturbances, attributing changes in carbon fluxes to meteorological variability alone is difficult. To isolate the direct climate signal, we exclude these additional influences and simulate the response of forests with observation-based composition and structure to climate forcing only. This study therefore investigates climate-driven dynamics of a spatially realistic but idealized unmanaged and undisturbed forest system. Against this background, this study aims to quantify the spatial and temporal variability of forest carbon exchange across Germany, assess species- and region-specific drought responses, and evaluate the sensitivity of simulated carbon fluxes to the choice of climate forcing dataset by comparing E-OBS- and ERA5-Land-driven simulations.

2. Materials and Methods

2.1 Study Area: German Forests

Forests in Germany extend over approximately 11.5 million hectares, covering about one-third of the national territory. The climate is temperate with moderate rainfall distributed throughout the year. Mean annual precipitation ranges from less than 500 mm in parts of eastern Germany to more than 1500 mm in the southern uplands, while mean annual temperatures vary between 6–10°C depending on elevation and region.

Germany is home to almost 76 tree species which were summarized in 51 tree species or groups of tree species in the last National Forest Inventory (NFI; Riedel et al. 2024). However, 90% of the forest area is occupied by only eleven tree species or tree species groups. The major tree species account for about 71% of the total forested area and are dominated by pine (Pinus sylvestris), spruce (Picea abies), beech (Fagus sylvatica), and oak (Quercus spp.). According to the most recent NFI, pine is currently the most widespread species, covering roughly 2.4 million hectares (21.8%), closely followed by spruce at 2.3 million hectares (20.9%). Beech represents around 1.8 million hectares (16.6%), while oak covers approximately 1.3 million hectares (10.6%) (Riedel et al. 2024). The 11 dominant tree species were grouped into four main categories for simulations reasons. These are based on similarities in vegetation, physiology, and phenology and are characterized as beech, oak, Spruce, and pine groups (Fig. 1).

German forest soils reflect strong regional contrasts shaped by geology and glacial history. The National Forest Soil Inventory distinguishes eight main soil parent material groups: base-poor consolidated bedrock (42%), base-poor unconsolidated sandy sediments (21%), loamy lowland soils (13%), carbonate bedrock (9%), basic to intermediate bedrock (8%), and smaller fractions of alluvial (3%), organic (2%), and alpine soils (1%). These soil types correspond to Germany’s main physiographic regions. The North German Lowlands are dominated by nutrient-poor sandy sediments, favoring pine-dominated stands, whereas the Central Uplands consist largely of acidic bedrock and loess-derived soils supporting mixed spruce–beech–oak forests. In the southern Alpine foreland and mountains, carbonate and silicate bedrock give rise to shallow, stony soils, complemented by fertile alluvial deposits in major river valleys

(Wellbrock et al. 2019). Forest soils contained on average 117.1 ± 1.7 Mg ha^{-1} of organic C in the organic layer and the mineral soil to a maximum depth of 90 cm (Grüneberg et al. 2019).

2.2 Input Data and Comparison Data

2.2.1 Climate Data

Two independent climate datasets were used to force the model and evaluate the sensitivity of carbon flux simulations to different meteorological inputs. The first is the E-OBS gridded dataset (v30.0e; Cornes et al. 2018), providing daily observational data for Europe at ~ 0.1° (~ 11 km) resolution. The second is the ERA5-Land reanalysis (Muñoz-Sabater et al. 2021), offering hourly data at ~ 0.1° (~ 9 km) resolution, downscaled from ERA5 and optimized for land surface processes. For both datasets, the period 2011–2023 was considered, and daily aggregates of minimum and maximum temperature, precipitation, shortwave radiation, wind speed, and relative humidity were extracted. For each simulated 10 × 10 km forest grid cell, the nearest climate grid point to the cell centroid was selected. Because E-OBS is derived from interpolated station observations and showed the closest agreement with independent DWD precipitation data (Fig. S1), it was selected as the primary climate forcing dataset, while ERA5-Land was used for sensitivity analyses.

2.2.2 Soil Data

Soil properties were derived from the SoilGrids dataset (version 2.0; Poggio et al. 2021) at 250 m spatial resolution. Data were extracted at the sampling points (15 per species group within each 10 × 10 km grid cell; see Section 2.3.3) and for each of the standard depth intervals (0–5, 5–15, 15–30, 30–60, and 60–100 cm). The following variables were included: bulk density, soil organic carbon (SOC), total nitrogen, sand, silt and clay fractions, soil pH, and volumetric fraction of coarse fragments (cfvo).

2.2.3 Atmospheric Nitrogen Deposition and Carbon Dioxide Concentration

Mean atmospheric nitrogen (N) deposition for the period 2013–2015 was obtained from the PINETI-3 database (Schaap et al. 2017) of the German Environment Agency (Umweltbundesamt, Dessau-Roßlau, Germany). The dataset provides spatially explicit estimates of nitrate (NO_3^-) and ammonium (NH_4^+) deposition at 1 km × 1 km resolution, distinguishing between wet and dry deposition and between coniferous and deciduous forests. Values were extracted for each forest sampling point applying forest-type-specific deposition rates. For atmospheric CO_2 concentration, we used the average of the observed values for the simulation period (2011–2023)

2.2.4 Vegetation Data

Forest composition was derived from the dominant tree species map of Germany (Blickensdörfer et al. 2022), which provides wall-to-wall species coverage at 10 m resolution based on Sentinel-1/2 data and National Forest Inventory reference plots. Eleven dominant species or species groups are distinguished;

for modeling they were aggregated into four main groups: beech, oak, spruce, and pine. Structural attributes were initialized using the biomass and canopy height dataset from Kacic et al. (2023), which combines high-resolution satellite imagery with allometric models to provide above-ground biomass and height maps at 10 m resolution. These datasets together allowed for a spatially explicit initialization of species distribution and forest structure.

2.2.5 Comparative model analysis data

X-BASE is a global land–atmosphere flux product generated with the FLUXCOM-X framework (Nelson and Walther et al., 2024), which uses machine-learning algorithms trained on eddy covariance observations, satellite remote sensing, and ERA5 meteorological data to estimate spatially continuous carbon and water fluxes (Jung et al., 2020). The dataset provides high-resolution (0.05°, hourly) estimates of gross primary productivity (GPP), net ecosystem exchange (NEE), evapotranspiration (ET), and transpiration (ET_T). In this study, we use X-VIIRS, a pre-release extension of the FLUXCOM-X framework that replaces MODIS inputs with VIIRS-derived vegetation and surface products while maintaining the same machine-learning methodology. The dataset provides high-resolution estimates of carbon fluxes for the period 2012–2025 and is used here as an independent reference for comparison with LandscapeDNDC simulations.

2.3. LandscapeDNDC model

2.3.1. Model description and initialization

LandscapeDNDC (https://ldndc.imk-ifu.kit.edu, last access: August 15, 2025) is a modular terrestrial ecosystem model (Haas et al., 2013). It has been designed to reproduce atmosphere–biosphere exchange process of carbon, water, and nitrogen, including C and N trace gas exchanges. For this purpose, detailed microclimate, biogeochemical and physical soil process modules are provided to be coupled with vegetation modules that describe physiology and growth (Grote et al. 2011b). All vegetation processes are parameterized at the species level. The LandscapeDNDC model uses meteorological and air chemical inputs generally in daily temporal resolution. Soil as well as canopy are divided into multiple layers, with flexible extension, and properties which can be provided by available measurements or estimated from initialized soil types and ecosystem structure. In this configuration, LandscapeDNDC has been used to investigate carbon fluxes and budgets in various ecosystems (Nadal et al. 2021; Rahimi et al., 2021) including different European forest sites (Dirnböck et al., 2020; Magh et al., 2020; Cade et al., 2021; Mahnken et al., 2022).

Forest carbon uptake and loss are calculated within the physiological simulation model (PSIM) from the processes photosynthesis, respiration, allocation and senescence (Grote et al. 2009). Respiration is differentiated into autotrophic respiration, which in turn consists of growth (fixed fraction of carbon allocated to increase biomass), maintenance (in dependence on temperature and nitrogen concentration, according Cannell and Thornley (2000)) and nitrogen uptake (fixed rate related to nitrate uptake), and heterotrophic respiration related to microbial decomposition of organic matter driven by soil

moisture, pH and temperature. Photosynthesis is calculated according to the Farquhar model (Farquhar et al., 1980), which is linked to a soil water-limited stomatal conductance module to optimize gas exchange (Leuning, 1995). The water balance is based on explicit consideration of water fluxes interception, percolation, evaporation from various surfaces, and transpiration. The latter is defined by stomatal conductance and constrained by soil water availability. Interception capacity depends on leaf area, and evaporation from surfaces (including snow) is driven by potential evaporation determined by a modified Thornthwaite approach (Thornthwaite and Mather, 1957). For more details see descriptions in Holst et al. (2010).

LandscapeDNDC was initialized using the climate, soil, atmospheric, and vegetation datasets described in Section 2.2. The main analysis was based on E-OBS climate forcing for the period 2011–2023. Atmospheric CO_2 concentrations and nitrogen deposition were prescribed from the datasets described in Section 2.2.3. Soil profiles were initialized from SoilGrids-derived physicochemical properties, while soil hydraulic characteristics were estimated using the van Genuchten retention function (van Genuchten, 1980). Vegetation is characterized by key stand attributes, including tree species, canopy height, diameter at breast height (DBH), and stem density or volume per hectare. Species groups were assigned according to the dominant tree species in each grid cell, and DBH was derived from height and biomass using species-specific allometric functions.

2.3.2. Model parameterization and calibration

Forests dominated by spruces, beeches, pines or oaks have been simulated before with LandscapeDNDC or predecessor models, resulting in site-based parameterizations for these species (Holst et al. 2010; Grote et al. 2011a; Cade et al. 2021; Nadal et al. 2021; Moutahir et al. 2026). However, to ensure the applicability of these parameterizations, at the national scale, we recalibrated the most sensitive parameters controlling phenology, transpiration, and photosynthesis using long-term eddy covariance observations. Three European eddy covariance sites per forest group, each providing more than ten years of latent heat flux and net ecosystem exchange observations, were selected for calibration (Table S1).

We calibrated the most sensitive parameters for phenology, transpiration and photosynthesis in a stepwise optimization approach for each site as well as for each species separately. Best parameters were taken according to the least deviation in terms of regression as well as bias. Although the site-specific parameterization yielded the best results, species-specific parameterization showed to represent all sites reasonably well and has thus been used for all simulations provided here. Details of the calibration procedure and model performance are provided in the Supplementary Material (Tables S1 and S2; Figs. S2–S9).

2.3.3 Sampling Strategy and Simulation Setup

LandscapeDNDC simulations were conducted at the level of 10 × 10 km grid cells covering the forested area of Germany. To account for the different spatial resolution of the input data (climate ~ 11 km, soil 250 m, vegetation 30 m), a nested sampling approach was applied: within each grid cell, 15 points per

tree species group (beech, oak, spruce, pine) were randomly selected and used to extract climate, soil and vegetation attributes.

Two filtering steps were introduced to avoid simulations in cells with negligible forest cover. First, grid cells with < 1% forest cover were excluded, which removed 202 of the 3,857 forest grid cells (0.04% of German forest area). Second, within each remaining cell, species groups covering < 5% of the forest area were excluded from sampling. This filter primarily affected pine (excluded in 2060 cells), while oak and spruce were excluded in 1,010 and 929 cells, respectively, and beech in only 66 cells. Overall, this procedure led to the exclusion of < 1% of beech and spruce forest area, ~ 2.5% of pine, and ~ 5% of oak, while retaining the vast majority of forested area for simulations.

The resulting number of simulated grid cells and sampling points per tree group is summarized in Table S3. Across the 3857 forest grid cells in Germany, beech was simulated in 3589 cells (93%), spruce in 2,709 cells (70%), oak in 2629 cells (68%), and pine in 1464 cells (38%). Beech had the highest representation across German forest grid cells, whereas pine had the lowest and was mainly located in eastern Germany (fig. S10). Based on 15 sampling points per cell and per tree group, this corresponds to a total of 155865 simulations, distributed as 53835 for beech, 40635 for spruce, 39435 for oak, and 21960 for pine (Table S3).

2.4 Data analysis

Model outputs were aggregated from daily to annual time scales and analyzed at grid-cell scale (10 × 10 km), species, and national levels. Unless otherwise stated, all results are based on simulations driven by the E-OBS climate dataset. The impact of the 2018 drought was assessed by comparing a pre-drought period (2011–2017) with the drought year (2018) and the post-drought period (2019–2023). Differences in mean annual GPP, TER, and NEE were calculated to characterize temporal and spatial changes in forest carbon dynamics, both nationally and for the four main forest groups (beech, oak, spruce, and pine). In addition, a sensitivity analysis was conducted using ERA5-Land climate forcing to evaluate the influence of climate input uncertainty on simulated carbon fluxes.

3. Results

3.1 Comparison with FLUXCOM-X (X-VIIRS)

Simulated carbon fluxes were compared with the FLUXCOM X-VIIRS dataset to assess the performance of LandscapeDNDC (Fig. 2). Across all forest grid cells, LandscapeDNDC simulated systematically higher carbon fluxes than X-VIIRS. Mean GPP was about 26% higher in the model simulations (19806 kg C ha^{-1} yr^{-1}) than in X-VIIRS (15695 kg C ha^{-1} yr^{-1}). Consequently, LandscapeDNDC simulated a stronger carbon sink, with mean NEE of -4530 kg C ha^{-1} yr^{-1} compared with − 2941 kg C ha^{-1} yr^{-1} in X-VIIRS (Fig. 3a). When restricting the analysis to near-pure forest grid cells (> 95% forest cover), the agreement between the two datasets improved substantially (Fig. 3b). In these pixels, mean GPP in X-VIIRS increased markedly (to 17811 kg C ha^{-1} yr^{-1}), reducing the difference to LandscapeDNDC (20048 kg C

$ha^{-1}\ yr^{-1}$). A similar pattern was observed for NEE, with X-VIIRS indicating a stronger carbon sink (-4111 kg C $ha^{-1}\ yr^{-1}$) that is closer to the modeled estimate (-4596 kg C $ha^{-1}\ yr^{-1}$). The reduced discrepancy can be attributed to the coarse spatial resolution of the X-VIIRS product (0.05° × 0.05°), where individual grid cells often include a mixture of land-cover types.

3.2 Climate dynamics and species-specific exposure

Hydroclimatic conditions derived from E-OBS data indicate a predominantly water-surplus regime prior to the 2018 drought (Fig. 3). During the baseline period (2011–2017), mean annual precipitation across all forests was ~ 747 mm (spatial SD ≈ 230 mm), while potential evapotranspiration (PET) averaged ~ 663 mm (SD ≈ 58 mm), resulting in a positive climatic water balance (CWB) of approximately + 85 mm (SD ≈ 260 mm). Most pre-drought years exhibited surplus conditions, with maxima reaching + 181 mm in 2017, indicating generally non-limiting moisture availability despite substantial spatial heterogeneity.

The year 2018 represents a pronounced hydroclimatic extreme. Precipitation declined to 569 mm (24% relative to baseline), while PET increased to 736 mm (+ 11%), producing a strong deficit of − 167 mm, corresponding to an anomaly of roughly − 250 mm relative to baseline conditions. The magnitude of this imbalance exceeded typical interannual variability and was accompanied by substantial spatial heterogeneity in water balance (SD ≈ 235 mm), highlighting the severity of the compound drought event.

Post-drought conditions (2019–2023) were highly variable rather than persistently dry. While 2019–2020 remained near neutral to slightly negative balance, 2021 showed a clear recovery (+ 140 mm), followed by renewed deficit in 2022 (− 67 mm) and an exceptionally wet year in 2023 (+ 222 mm). Overall, the post-2018 period is best characterized by alternating wet and dry conditions, rather than a sustained shift toward drier climate conditions.

Species-specific hydroclimatic exposure reflects spatial distribution patterns. The aggregated forest signal closely resembles beech, consistent with its broad national distribution. Pine forests in eastern Germany exhibited systematically lower water balances and the strongest drought deficits (e.g., − 299 mm in 2018), whereas spruce forests in the wetter southern regions remained comparatively buffered (− 100 mm in 2018). Oak forests, distributed along a southwest–northeast axis in relatively drier areas, showed intermediate but consistently negative drought anomalies.

3.3 Temporal and spatial variability of carbon fluxes over Germany

At the national scale, Carbon fluxes across German forests showed clear interannual variability during 2011–2023, with a pronounced disturbance during the 2018 drought. For all forests combined, ecosystems acted as a persistent carbon sink over the study period, with mean annual GPP of ~ 19895.4 ± 1174.5 kg C $ha^{-1}\ yr^{-1}$ and TER of ~ 15570.7 ± 879.1 kg C $ha^{-1}\ yr^{-1}$, resulting in an average NEE of about − 4324.6 ± 1077.3 kg C $ha^{-1}\ yr^{-1}$. However, productivity and sink strength declined markedly in

2018, when GPP dropped to ~ 18140.1 kg C ha^{-1} yr^{-1} and the carbon sink weakened substantially (NEE ≈ − 2590.9 kg C ha^{-1} yr^{-1}), representing roughly a 40% reduction in sink strength relative to the long-term mean (Fig. 4).

Across forest types, spruce forests showed the highest productivity and strongest carbon uptake, with mean GPP exceeding 21342.1 kg C ha^{-1} yr^{-1} and NEE around − 5263.4 kg C ha^{-1} yr^{-1}. Beech forests, which are widely distributed across Germany, exhibited intermediate values. Oak forests showed slightly lower productivity, while pine forests had the weakest carbon sink (mean NEE around − 2754.0 kg C ha^{-1} yr^{-1}) and were the most sensitive to drought, temporarily shifting to a net carbon source in 2018 in some areas.

Clear spatial gradients in carbon fluxes were observed across Germany (Fig. 5). Higher GPP and stronger carbon sinks occurred in southern regions, particularly in mountainous areas such as the Black Forest and Bavarian uplands, where spruce- and beech-dominated forests prevail under cooler and wetter climatic conditions. In contrast, lower productivity and weaker carbon uptake characterized northern and especially north-eastern Germany, where pine forests dominate under comparatively drier conditions. Central Germany exhibited intermediate fluxes, reflecting mixed forest composition and moderate climatic conditions.

3.4 Drought Effects in Forest Carbon Fluxes

3.4.1 Immediate drought response

The 2018 drought caused a pronounced reduction in net ecosystem carbon uptake across most of Germany (Fig. 6b and c). Compared with the baseline period (2011–2017), NEE values in 2018 became substantially less negative, indicating a widespread weakening of the forest carbon sink. The magnitude of this decline, however, showed strong spatial variability. The largest reductions in sink strength occurred in north-eastern Germany, where pine-dominated forests are prevalent and drought conditions were most severe. In several areas of this region, NEE values became positive, indicating a temporary shift from a carbon sink to a net carbon source, with relative changes exceeding − 100% and locally approaching − 130% compared with baseline conditions. In contrast, southern upland regions, including mountainous areas characterized by spruce and beech forests, showed much smaller changes in NEE, with values remaining close to baseline levels.

3.4.2 Post-drought recovery

A comparison of the pre-drought (2011–2017) and post-drought (2019–2023) periods reveals persistent shifts in forest carbon fluxes (Fig. 6d and e). At the national scale, GPP shows no substantial change (+ 0.8%), in contrast, ecosystem respiration (TER) increases markedly (+ 4.5%), and as a result, NEE remains weakened (− 11.3%), indicating that forest ecosystems have not fully recovered their pre-drought carbon sink strength despite the partial recovery of productivity. Spatially, the recovery signal is

highly heterogeneous and strongly structured by forest composition. While many regions show partial stabilization of GPP, a widespread weakening of the carbon sink persists, particularly in northeastern Germany, where pine-dominated forests prevail. In these areas, NEE declines by more than 30% relative to the pre-drought period, reflecting the combined effect of increased TER and only limited compensation from GPP.

3.5 Sensitivity of Simulated Carbon Fluxes to Climate Forcing (ERA5 vs. E-OBS)

The comparison between ERA5 and E-OBS climate datasets reveals systematic but spatially variable differences in the meteorological drivers used in the simulations (Fig. 7, table S4). On average, ERA5 precipitation is about 20% higher than in E-OBS across most of Germany, although localized areas in the Black Forest, parts of central Germany, and the far north show slightly lower values. Mean air temperature is only marginally higher in ERA5, but the dataset exhibits substantially higher minimum temperatures (≈ + 17%) and lower maximum temperatures, resulting in a reduced diurnal temperature range compared with E-OBS. In addition, incoming radiation is generally higher in ERA5 over most of the country. Overall, these patterns indicate that ERA5 represents a wetter and more radiatively energetic climate with warmer nighttime conditions and reduced temperature extremes relative to E-OBS.

These differences in climate forcing propagate into the simulated carbon fluxes (upper panel of Fig. 8). Simulations driven by ERA5 produce slightly lower GPP (-0.5%) and higher TER (+ 0.8%) across most regions resulting in a slightly weaker carbon sink under ERA5, with NEE being about 5.3% lower (i.e., less negative) compared with simulations forced by E-OBS. The stronger increase in respiration is likely linked to the higher minimum temperatures in ERA5, which imply warmer nighttime conditions and therefore enhanced ecosystem respiration. Spatially, the relative differences in GPP and TER vary considerably across the country (approximately − 15% to + 15%), indicating heterogeneous ecosystem responses to the alternative climate forcing. Despite these regional variations, the overall effect remains small at the national scale, with slightly enhanced respiration and modest reduction in productivity under ERA5.

During the extreme drought year 2018, these differences become more pronounced and and exhibit strong spatial heterogeneity across Germany (lower panel of Fig. 8). GPP shows only a minor national reduction (− 0.4%), TER increases substantially (+ 1.5%) and as a result, NEE exhibits a much stronger divergence (− 11.8%). The spatial patterns further reveal that drought impacts are highly heterogeneous across Germany. GPP is reduced by more than 2500 kg C ha^{-1} in extended areas of northern and southwestern Germany. NEE decreases across most of the country, with widespread areas showing reductions exceeding 1,500 kg C ha^{-1}, particularly where strong GPP reductions coincide with increased TER.

4. Discussion

4.1 Carbon fluxes and Drought Impact

Overall, LandscapeDNDC simulated higher carbon fluxes than FLUXCOM X-VIIRS. Much of this discrepancy can be attributed to differences in spatial representation: LandscapeDNDC simulates forest-only areas, whereas X-VIIRS fluxes are derived for 0.05° grid cells that often contain a mixture of land-cover types and using eddy covariance observations from a wide range of ecosystem types (Jung et al., 2020; Nelson and Walther et al., 2024). The presence of non-forest areas within these cells lowers the apparent carbon fluxes in X-VIIRS. Consistent with this interpretation, agreement improved substantially when the comparison was restricted to grid cells with more than 95% forest cover, where differences in mean GPP decreased from about 26% to 13% and NEE estimates became much more consistent. Remaining differences likely reflect methodological differences and uncertainties associated with both approaches.

Spatial distribution of carbon and water fluxes are following in particular the distribution of species, soil and climate conditions. For NEE we can depict a strong gradient of increasing carbon sequestration (more negative values) from the north to the south and a less expressed decline of NEE from the west to the east. These trends are strongly correlated with deficits in water supply which is limiting carbon gain more strongly in the north/east (below 500 mm a-1 in central Brandenburg) than in the south/(west) (> 1000mm with peaks above 2000 mm a-1 close to the Alps) (McNamara et al. 2024). Smaller soil water holding capacities in the eastern regions, which are known for their sandy soils, exaggerate this effect because soil water reserves are not only less refilled but are also smaller, providing only minor reserves during dry periods.

The spatial distribution of NEE is also correlated with species abundance, which is due to the fact that pines are more adapted to dry conditions where spruces wouldn’t grow. In contrast, spruces are specifically planted in regions which are known for their better water supply. At such sites, spruces are considerably more productive than other species (Nord-Larsen & Pretzsch 2017). Interestingly, at sites with intermediate climate conditions as can be found in the west of Germany, higher shares of beeches and oaks can be found, showing medium carbon uptake but also – at least in case of the oaks – relatively high ecosystem respiration rates.

The pronounced reduction in carbon uptake during 2018 is consistent with numerous studies reporting a widespread weakening of the European forest carbon sink during the 2018 drought (e.g., Schuldt et al. 2020; Van Der Woude et al. 2023; Holtmann et al. 2024). In our simulations, NEE decreased by 46% relative to the pre-drought period, with the strongest impacts occurring in beech- and pine-dominated forests. These species-specific differences reflect contrasting drought sensitivities and regional distributions, as pine forests are concentrated in the dry northeastern lowlands, while beech forests are more concentrated in central Germany. In contrast, southern regions, characterized by higher precipitation and a larger proportion of spruce and mixed forests, maintained a comparatively stronger carbon sink throughout the study period.

The strong influence of dry conditions has been demonstrated by the temporal variability of carbon and water fluxes, too. Precipitation was particularly low the years 2018 and 2022 in almost all regions while

transpiration demand was high, leading to extensive periods of negative climatic water balance. Thus, net carbon uptake in these years is decreased (less negative NEE) for all investigated species similar to what was reported by Van Der Woude et al. (2023) for European forests. As supported by other studies, the response of spruce was particularly strong, while oak and pine carbon exchange were much less affected (Bouwman et al. 2025; Jiang et al. 2024; Ogana et al. 2024; Popa et al. 2024). Interestingly, NEE was also low in 2013, a year with sufficient precipitation but quite cool temperatures. Here, susceptibility was reversed between species, with oaks showing the highest reduction in NEE and spruces the least.

4.2 Sensitivity to Climate Forcing (ERA5-Land vs. E-OBS)

The spatially coherent but variable differences between ERA5-Land and E-OBS identified over Germany are consistent with previously documented characteristics of the two datasets. The widespread precipitation surplus in ERA5-Land (+ 19.8% on average) aligns with findings that ERA5 products tend to overestimate mean precipitation due to an excess of wet days (Bandhauer et al. 2022). While both ERA5 and E-OBS reproduce large-scale precipitation patterns well, E-OBS generally performs better in regions with dense station coverage. The temperature structure in ERA5-Land is characterized by slightly higher mean temperatures relative to E-OBS, systematically warmer minimum temperatures and lower maximum temperatures. Similar patterns have been reported across Europe, including pronounced topographic effects in alpine regions, where ERA5 exhibits larger deviations from E-OBS (Velikou et al. 2022).

The differences in carbon fluxes between ERA5-Land and E-OBS are not driven by precipitation totals alone, but by the combined effects of precipitation structure and temperature biases. Although ERA5-Land provides substantially higher total precipitation, this does not translate into increased productivity. A large fraction of the additional rainfall occurs as frequent low-intensity events, many of which fall below canopy storage capacity and are therefore intercepted and re-evaporated before reaching the soil (Pflug et al. 2021). Under these conditions, atmospheric evaporative demand is initially satisfied by evaporation from intercepted canopy water, temporarily suppressing transpiration and associated carbon uptake until canopy surfaces progressively dry. This mechanism is conceptually similar to transpiration suppression observed under dew deposition (Gerlein-Safdi et al. 2018). Consequently, despite wetter conditions, effective soil water recharge and plant transpiration remain limited, leading to reduced GPP.

At the same time, the reduced diurnal temperature range in ERA5-Land, characterized by higher minimum and lower maximum temperatures, further modifies ecosystem processes. Warmer night-time temperatures enhance ecosystem respiration (Lloyd and Taylor 1994; Davidson and Janssens 2006), while the dampened daytime temperatures limit peak photosynthetic rates. Consequently, ERA5-Land consistently simulates slightly increased TER and reduced net carbon uptake, despite higher precipitation. These effects are particularly pronounced during extreme conditions such as the 2018 drought, where differences in precipitation structure and temperature amplify water limitation and carbon flux responses. Overall, the results demonstrate that forest carbon exchange is strongly controlled not only by the magnitude of climate forcing, but also by precipitation timing and intensity as

well as temperature characteristics that regulate transpiration and respiration processes (Reichstein et al. 2013; Grossiord et al. 2020).

4.3 Model limitations and uncertainties

Simulation results are subject to a number of uncertainties related to parameterization, initialization, and driving forces. Parameterization of physiological processes is based on experimental results but each measurement comes with an uncertainty range. Therefore, the most sensitive parameters affecting carbon and water exchange (steering photosynthesis, transpiration and phenology) have been calibrated using three monculture forest sites in Europe for each species spanning a range of environmental conditions (see supplementary). Site specific parameter definition yielded in an overall better relation between simulated and measured ecosystem fluxes, indicating that gas exchange may be affected by conditions not fully covered in the model (e.g. other nutrient limitations than nitrogen, disturbances). In case of oak, an additional uncertainty is related to a significant contribution of other species at the calibration sites (ash, hornbeam, beech) that have been treated as oaks. Nevertheless, the small bias in the calibration over all sites still supports the assumption that the model is able to reflect species-specific responses at other sites too.

The initialization, derived from a combination of site information and remote sensing data, is necessarily simplified regarding stand structure. However, forest structure is known for affecting gas exchange in different ways, particularly if upper story trees are not completely covering the ground leading to increased vulnerability regarding drought and other stresses (Mathes et al. 2024). Depending on competition, single trees might be more vulnerable to drought events with no clearly depicted link to plant traits, although the responses seem to be species dependent (Pardos et al. 2021; Verdonck et al. 2025). As a result from the simulations, soil water holding capacity stands out as an important mitigating factor regarding drought stress. This is well reflected in the LandscapeDNDC model but the soil properties which define it (bulk density, soil texture, stoniness) and their distribution with depth are initialized with coarse soil maps, introducing additional uncertainties. Apart from the physical soil properties, also nutrient supply may have indirect impacts on growth responses to drought (Lévesque et al. 2016) that are difficult to consider since nutrient availability at a particular site is uncertain, influenced by long-term management and deposition history.

Another uncertainty regarding soil conditions is that we didn’t consider any possible groundwater access of the forests, which of course would influence/increase the gas exchange particularly during dry conditions (Skiadaresis et al. 2021). This is mostly because the large majority of sites have groundwater deeper than 2 m (BGR 2015), a level generally considered not plant accessible, but also because the accessible depth is variable (decreasing ground water level in summer) and species dependent (oaks are supposed to have a deeper rooting system). Groundwater levels closer to soil surfaces are supposed to concentrate on relatively small regions close to rivers, which are often not forested or composed of relatively rare species.

Finally, disturbance related to tree mortality could not be considered in the simulations. Disturbance related to drought was considerably after 2018 (Knapp et al. 2024; Thonfeld et al. 2022), concentrating in central Germany from northern North Rhine-Westphalia over southern Lower Saxony and Saxony-Anhalt to southern Brandenburg and eastern Saxony. This region is approximately covering the areas with highest NEE declines. It can be expected that the high mortality rates here which are not represented in the model may have led to an overestimation of gas exchange at least during the relatively well watered years in 2021 and 2023. This highlights the need for a mechanistic representation of drought related tree mortality, which is yet to be developed (Dukes et al. 2026).

5. Conclusions

This study provides a comprehensive assessment of climate-driven variability in forest carbon exchange across Germany during 2011–2023, with a particular focus on the extreme 2018 drought. The results demonstrate a pronounced and spatially heterogeneous reduction in carbon uptake during drought years, with the strongest impacts occurring in drought-prone regions of northeastern Germany, while southern forests showed greater resilience. The sensitivity analysis further revealed that simulated carbon fluxes are strongly influenced by climate forcing uncertainty, particularly through differences in precipitation characteristics and temperature. Because mortality, disturbances, and management were excluded, the simulations represent potential climate-driven carbon exchange rather than fully realized ecosystem responses. This interpretation is supported by the comparison with FLUXCOM-X (X-VIIRS), which showed a larger divergence from model results after 2018, suggesting that the simulated recovery mainly reflects climatic conditions, whereas the observationally constrained product captures additional effects of drought-induced mortality and disturbances. Overall, our findings highlight the strong spatial heterogeneity of drought impacts and emphasize the need to incorporate mortality and disturbance processes into future forest carbon modeling studies.

Declarations

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Author Contribution

H.M., R.G. and R.K. conceived the study, conducted the simulations and analyses, prepared the figures, and wrote the original manuscript draft. H.I. contributed to the acquisition and preparation of input datasets, interpretation of the results, and manuscript revision. P.L. contributed to model calibration and parameterization, and manuscript revision. E.H. and D.K. contributed to the simulation setup and methodological development, and manuscript revision. M.B. and C.M. provided and processed the eddy covariance data used for model calibration. All authors critically reviewed the manuscript and approved the final version.

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Data Availability

The LandscapeDNDC model source code for released versions of the model is permanently available online at the Radar4KIT database (https://doi.org/10.35097/438; Butterbach-Bahl et al., 2021). The published model version that has been used for the presented simulations can also be freely downloaded upon request from the website: https:// ldndc.imk-ifu.kit.edu/download/download-model.php (last access: 30 May 2026). All parameters needed to run the model are provided in the Supplement (soil properties, initial stand properties, and species-specific parameters). Forcing data will be provided on request. Furthermore, the data used for evaluation of beech sites are available from the ICOS data portal (https://www.icos-cp.eu/data-products/ecosystem-release) , except for the oak site at the UK (straits) this would be available on request from MB (or ‘the authors’).

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Figures

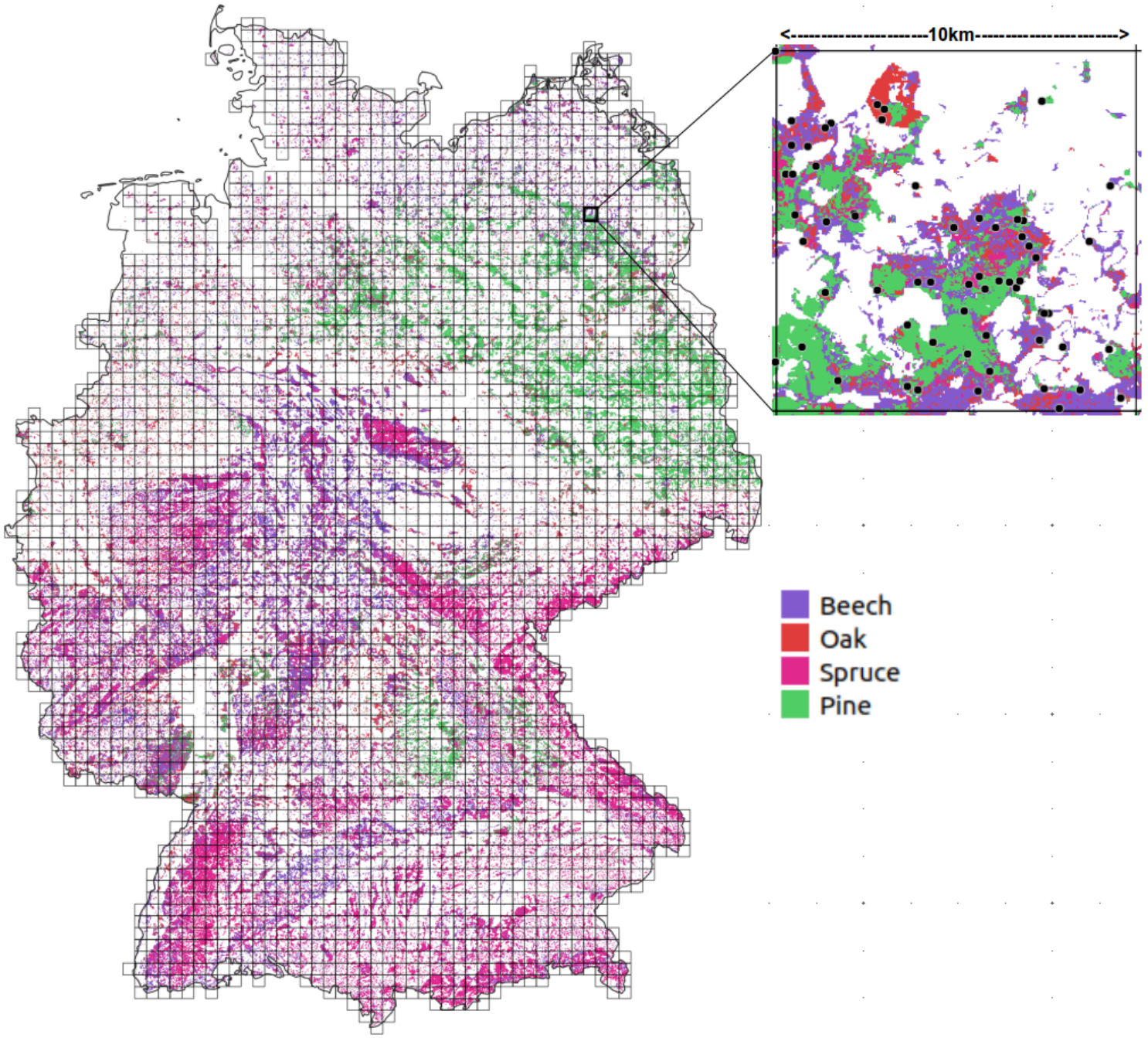


Figure 1

Distribution of the four main tree species according to the Blickensdörfer et al. (2022) dataset, overlaid with the simulation grid cells (10 x 10 km).

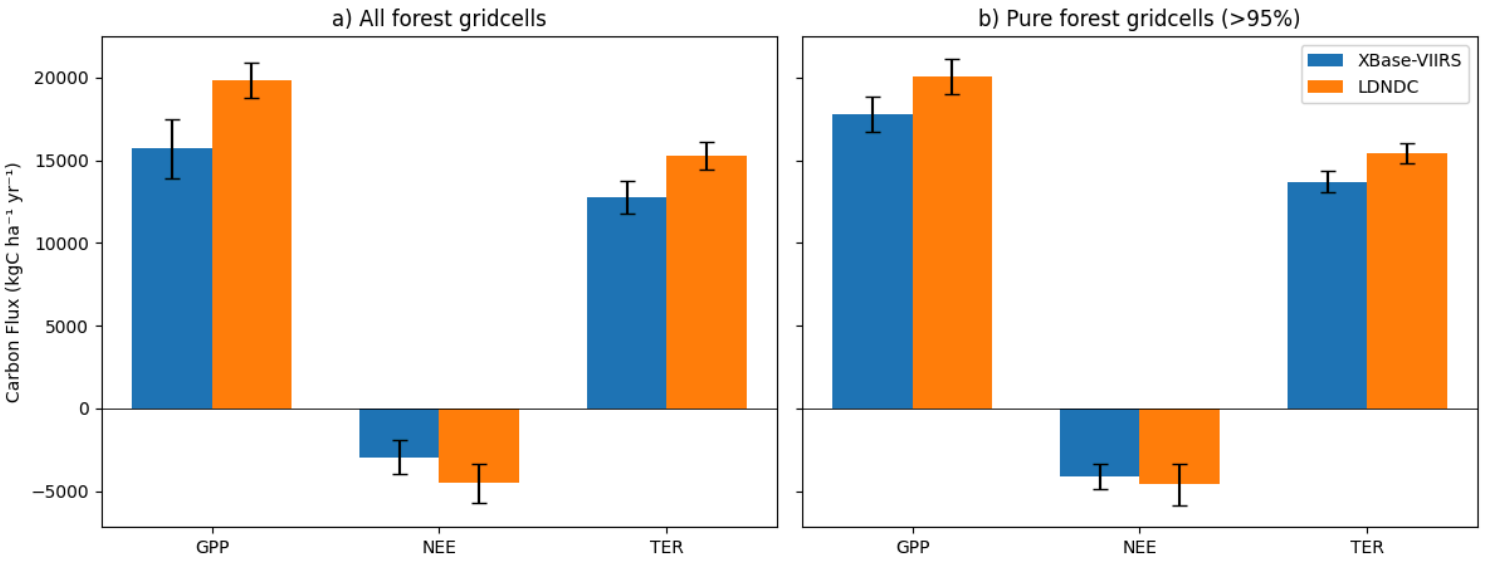


Figure 2

Comparison of modeled (LandscapeDNDC) and data-driven (X-VIIRS) carbon fluxes for German forests at two forest cover thresholds: a) all forest gridcells and b) pure forest gridcells (>95%). Mean GPP, TER, and NEE are shown for 2012–2023 (kg C ha⁻¹ yr⁻¹), aggregated at the national scale. Error bars denote spatial variability (standard deviation) across grid cell

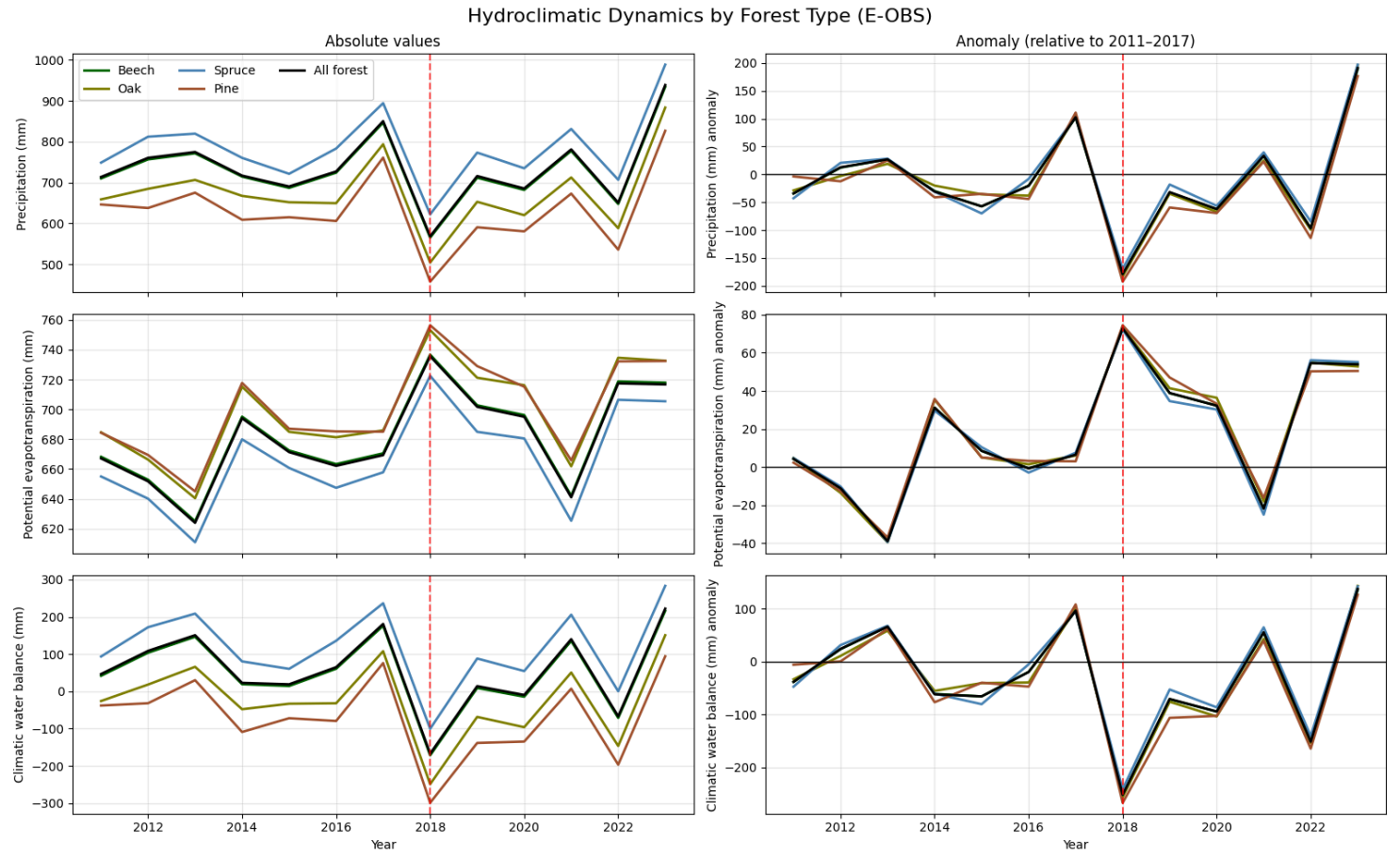


Figure 3

Hydroclimatic dynamics by forest type based on E-OBS data. Left column shows absolute annual precipitation, potential evapotranspiration (PET), and climatic water balance (P–PET). Right column shows anomalies relative to the 2011–2017 baseline period (pre-drought). The vertical dashed line marks the 2018 extreme drought year.

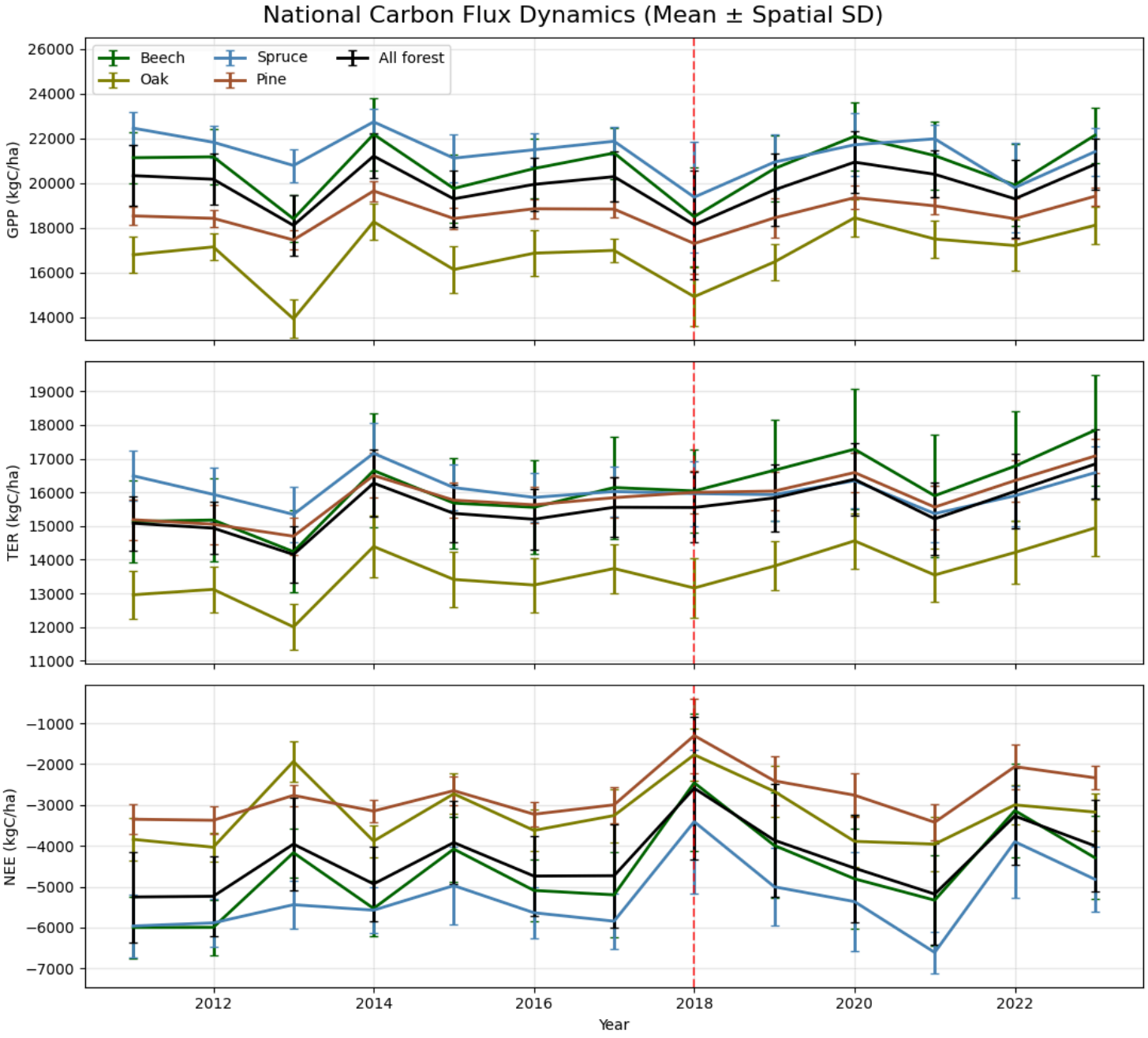


Figure 4

National annual gross primary production (GPP), total ecosystem respiration (TER), and net ecosystem exchange (NEE) for major forest types in Germany from 2011 to 2023 (mean ± spatial standard deviation across grid cells). The vertical dashed line marks the 2018 extreme drought year.

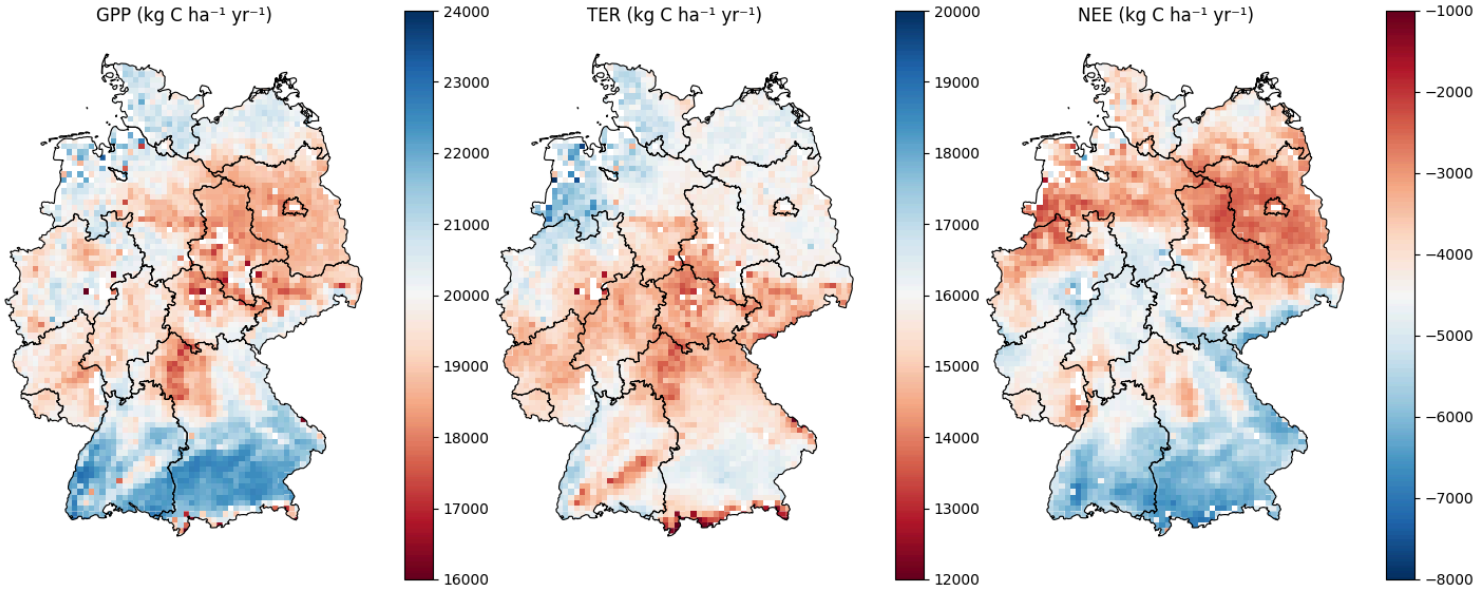


Figure 5

Spatial patterns of mean forest carbon fluxes in Germany (2011–2023).Maps show the spatial distribution of mean annual gross primary productivity (GPP), total ecosystem respiration (TER), and net ecosystem exchange (NEE) for all forests across Germany during the study period (2011–2023). Fluxes are expressed in kg C ha⁻¹ yr⁻¹ and aggregated at the 10 × 10 km grid level.

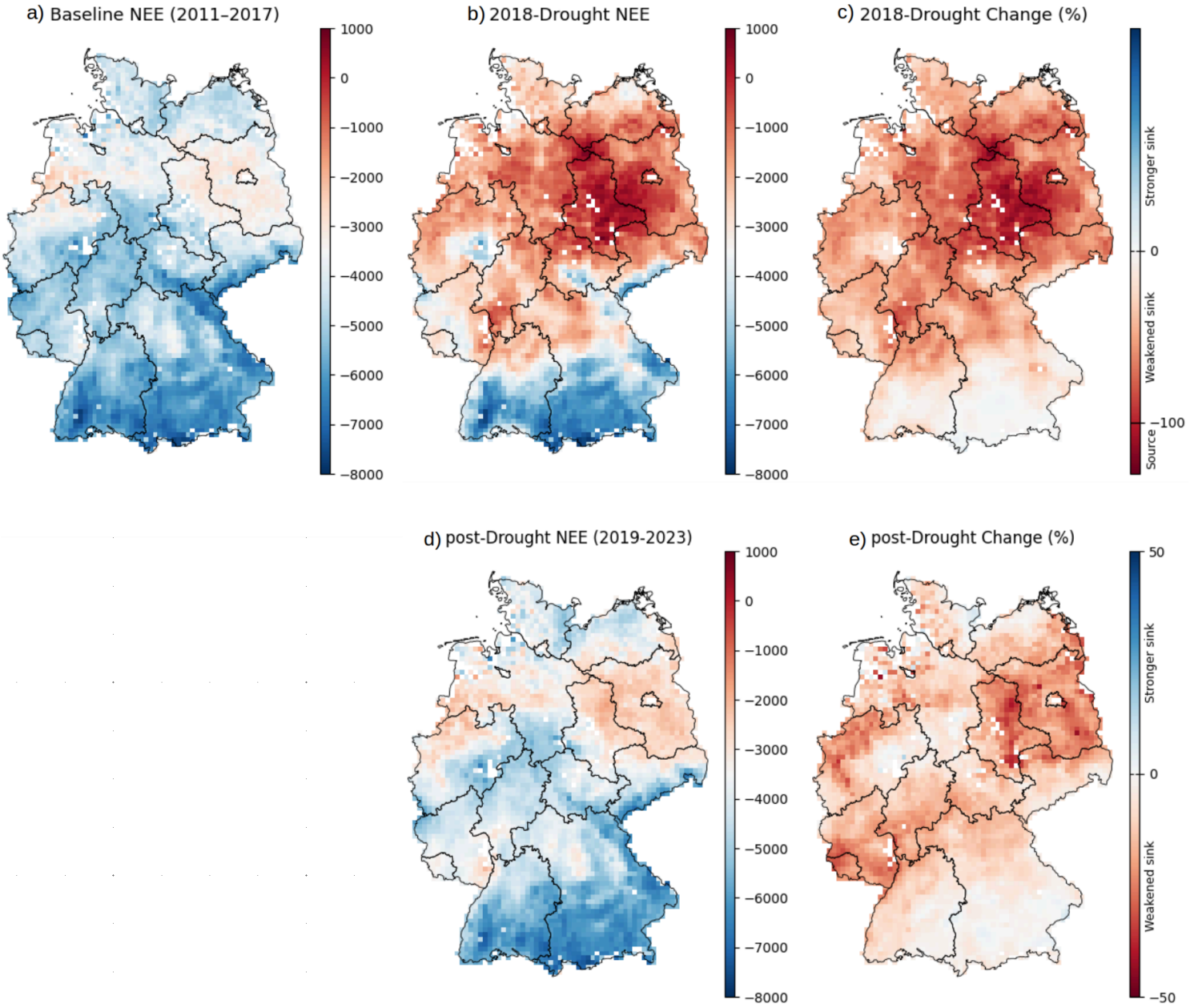


Figure 6

Response of forest net ecosystem exchange (NEE in kg C/ha) to the 2018-drought and in post-drought period in Germany. Maps show (a) the mean baseline NEE during the 2011–2017 period, (b) NEE during the 2018 drought year, (c) the relative change (%) in 2018 compared with the baseline, (d) NEE during the post drought period (2019-2023), and (e) the relative change (%) in the post-drought compared with the baseline. Negative NEE values indicate a carbon sink, while positive values indicate a net carbon source.

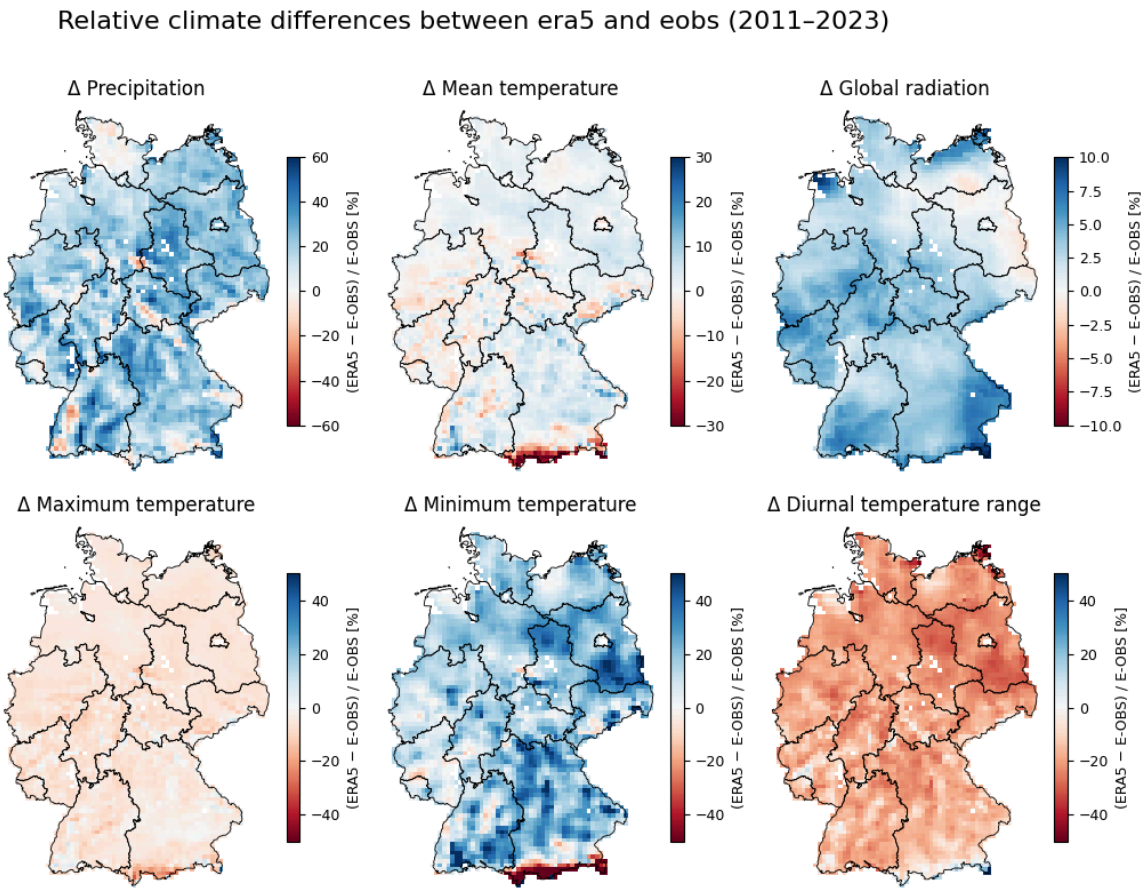


Figure 7

Relative differences between ERA5 and E-OBS climate variables over Germany for the period 2011–2023, expressed as (ERA5 – E-OBS) / E-OBS × 100. Positive values indicate higher ERA5 estimates relative to E-OBS, while negative values indicate lower ERA5 estimates.

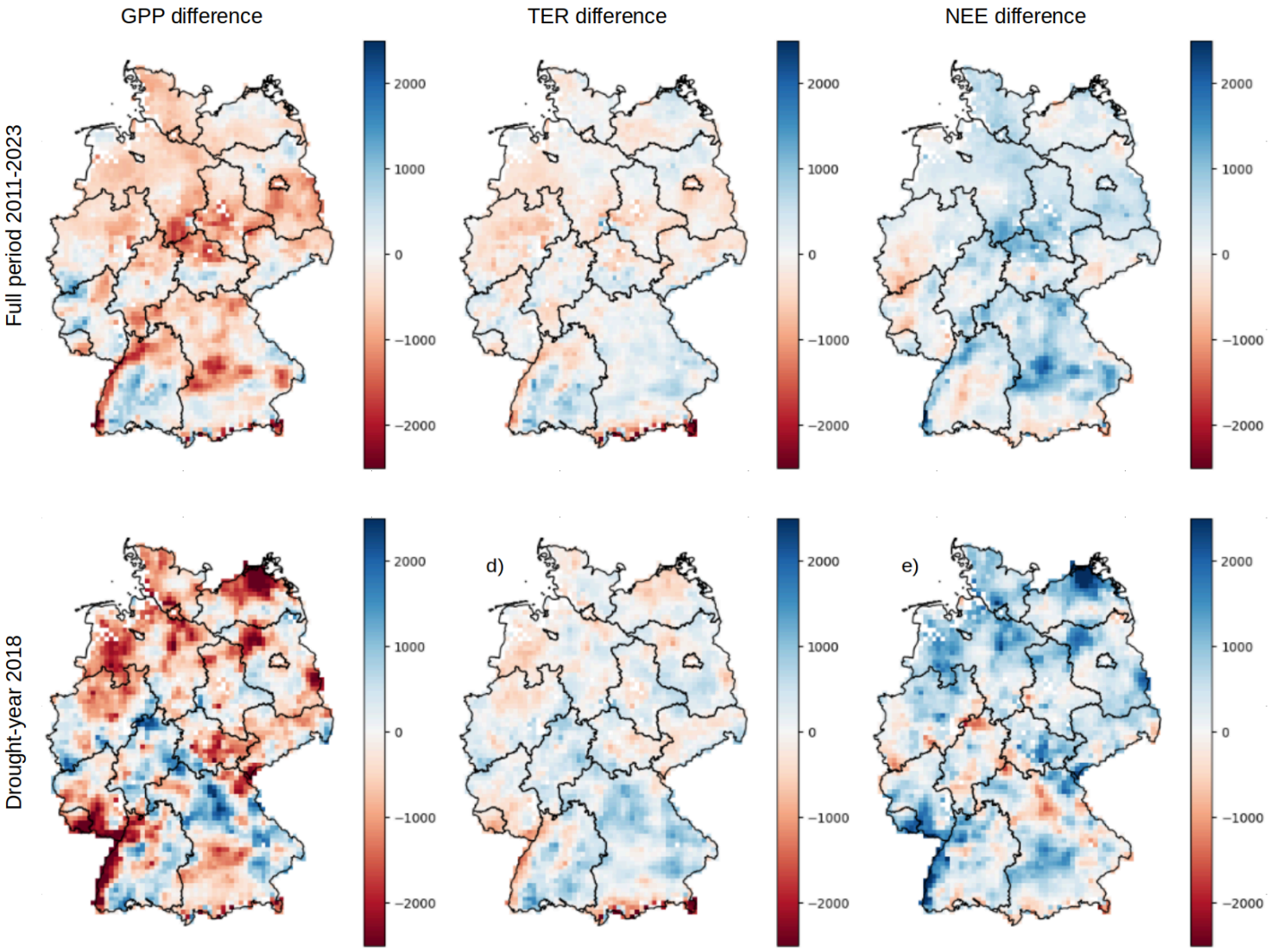


Figure 8

Absolute differences (kg C ha⁻¹) in GPP, TER, and NEE (ERA5-Land minus E-OBS) for the period 2011–2023 (upper panel) and for the drought-year 2018 (lower panel). NEE is expressed as negative for carbon uptake; thus, positive values in the difference map correspond to reduced carbon uptake (weakened sink strength).

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- MoutahiretalSupplements100626.pdf