



RESEARCH ARTICLE

10.1029/2026MS005888

Key Points:

- Across 16 African flux towers, Joint UK Land Environment Simulator (JULES) captured seasonal carbon and water cycles but performance varied among ecosystems
- Mixed savannas showed the largest errors, often linked to unrealistic soil moisture, water stress, and canopy structure
- Aridity and rainfall anomalies explain much of the bias; JULES often underestimates interannual variability in gross primary productivity

Supporting Information:

Supporting Information may be found in the online version of this article.

Correspondence to:

E. F. Akhabue,
akhasfaith@gmail.com

Citation:

Akhabue, E. F., Cunliffe, A. M., Bett-Williams, K., Harper, A. B., Zhu, S., Holden, P., et al. (2026). Assessing JULES across bioclimatic domains through a pan-African flux tower evaluation: Insights into controls on gross primary productivity, ecosystem respiration, and evapotranspiration biases. *Journal of Advances in Modeling Earth Systems*, 18, e2026MS005888. <https://doi.org/10.1029/2026MS005888>

Received 26 FEB 2026

Accepted 12 SEP 2026

Author Contributions:

Conceptualization: Enimhien F. Akhabue, Andrew M. Cunliffe, Karina Bett-Williams, Anna B. Harper, Petra Holden
Data curation: Enimhien F. Akhabue, Songyan Zhu
Formal analysis: Enimhien F. Akhabue
Funding acquisition: Andrew M. Cunliffe

© 2026 The Author(s). Journal of Advances in Modeling Earth Systems published by Wiley Periodicals LLC on behalf of American Geophysical Union. This is an open access article under the terms of the [Creative Commons Attribution License](#), which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

Assessing JULES Across Bioclimatic Domains Through a Pan-African Flux Tower Evaluation: Insights Into Controls on Gross Primary Productivity, Ecosystem Respiration, and Evapotranspiration Biases

Enimhien F. Akhabue^{1,2} , Andrew M. Cunliffe¹ , Karina Bett-Williams^{2,3} , Anna B. Harper⁴ , Songyan Zhu⁵ , Petra Holden⁶ , Jonas Ardö⁷ , Mika Aurela⁸ , Jerome Demarty⁹ , Frederic C. Do^{10,11} , Jordi Etchanchu⁹ , Mangaliso Gondwe¹² , Carole Helfter¹³ , Laurent Kergoat¹⁴ , Giacomo Nicolini¹⁵ , Yann Nouvellon^{10,16} , Maria Carolina Duran Rojas¹⁷ , Olivier Roupsard^{10,11,18} , Torbern Tagesson⁷ , Ville Vakkari^{8,19} , Pieter VanZyl¹⁹ , and Aleksander Wieckowski⁷ 

¹Department of Geography, University of Exeter, Exeter, UK, ²Global Systems Institute, University of Exeter, Exeter, UK, ³Met Office, Exeter, UK, ⁴Department of Geography, University of Georgia, Athens, GA, USA, ⁵School of Geography and Environmental Science, University of Southampton, Southampton, UK, ⁶African Climate & Development Initiative, University of Cape Town, Cape Town, South Africa, ⁷Department of Earth and Environmental Sciences, Lund University, Lund, Sweden, ⁸Finnish Meteorological Institute, Helsinki, Finland, ⁹HydroSciences Montpellier (HSM), CNRS, IRD, University Montpellier, Montpellier, France, ¹⁰Eco&Sols, CIRAD, INRAE, IRD, Institute Agro, University Montpellier, Montpellier, France, ¹¹LMI IESOL, Centre IRD-ISRA de Bel Air, Dakar, Senegal, ¹²Okavango Research Institute, University of Botswana, Maun, Botswana, ¹³UK Centre for Ecology & Hydrology, Edinburgh, UK, ¹⁴Geosciences Environment Toulouse, CNRS/IRD/Université Toulouse, Toulouse, France, ¹⁵CMCC Foundation—Euro-Mediterranean Center on Climate Change—IAFES Division, Viterbo, Italy, ¹⁶CIRAD, UMR Eco&Sols, Montpellier, France, ¹⁷Department of Mathematics and Statistics, Faculty of Environment, Science and Economy, University of Exeter, Exeter, UK, ¹⁸CIRAD, UMR Eco&Sols, Dakar, Senegal, ¹⁹Atmospheric Chemistry Research Group, Chemical Resource Beneficiation, North-West University, Potchefstroom, South Africa

Abstract Land surface models are fundamental for simulating coupled carbon, water and energy exchanges in Earth system models, yet their performance remains poorly constrained across Africa's diverse hydroclimatic gradients. We evaluate the Joint UK Land Environment Simulator (JULES) using eddy covariance observations from 16 flux towers spanning major African ecosystem types. Model skill is assessed for gross primary productivity (GPP), ecosystem respiration (Reco), and evapotranspiration, and we examine how model bias and error vary along gradients of mean annual temperature, aridity index, and precipitation anomalies. JULES reproduced broad seasonal dynamics of carbon and water fluxes across several ecosystems but showed systematic limitations in simulating Reco and interannual variability of GPP. Model performance differed among ecosystem types, with wetlands exhibiting large model-observation mismatches and cropland sites showing GPP overestimation linked to excessive simulated leaf area index. To isolate environmental controls on performance, we applied linear mixed-effects modeling to partition site-level variability from climate-driven effects. Aridity and precipitation anomalies emerged as dominant predictors of model bias and error, with wetter and anomalously humid conditions associated with larger deviations from observations, indicating limitations in representing soil hydrology and vegetation water stress processes. By integrating an expanded African flux tower network, this study provides a comprehensive regional evaluation of JULES. The results identify hydroclimatic regimes where model development should be prioritized and emphasize the importance of strengthening benchmarking across underrepresented African ecosystems to improve model transferability and support reliable climate and land management decision support under environmental change.

Plain Language Summary Land surface models are computer programs that help scientists understand how land ecosystems exchange water and carbon with the atmosphere. They are widely used to study climate change and support land and water management. However, most testing of these models has been carried out in regions with extensive data, and their performance across Africa's varied ecosystems is less well understood. In this study, we evaluated the Joint UK Land Environment Simulator (JULES) using measurements from 16 eddy-covariance flux towers across Africa. These towers

Investigation: Enimhien F. Akhabue, Andrew M. Cunliffe, Karina Bett-Williams, Anna B. Harper, Songyan Zhu, Petra Holden, Jonas Ardö, Mika Aurela, Jerome Demarty, Frederic C. Do, Jordi Etchanchu, Mangaliso Gondwe, Carole Helfter, Laurent Kergoat, Giacomo Nicolini, Yann Nouvellon, Maria Carolina Duran Rojas, Olivier Rouspard, Torbern Tagesson, Ville Vakkari, Pieter VanZyl, Aleksander Wieckowski

Methodology: Enimhien F. Akhabue, Andrew M. Cunliffe, Karina Bett-Williams, Anna B. Harper, Petra Holden

Project administration: Enimhien F. Akhabue

Resources: Maria Carolina Duran Rojas

Software: Enimhien F. Akhabue, Songyan Zhu

Supervision: Andrew M. Cunliffe, Karina Bett-Williams, Anna B. Harper, Petra Holden

Visualization: Enimhien F. Akhabue, Andrew M. Cunliffe

Writing – original draft: Enimhien F. Akhabue

Writing – review & editing: Enimhien F. Akhabue, Andrew M. Cunliffe, Karina Bett-Williams, Anna B. Harper, Songyan Zhu, Petra Holden, Jonas Ardö, Mika Aurela, Jerome Demarty, Frederic C. Do, Jordi Etchanchu, Mangaliso Gondwe, Carole Helfter, Laurent Kergoat, Giacomo Nicolini, Yann Nouvellon, Maria Carolina Duran Rojas, Olivier Rouspard, Torbern Tagesson, Ville Vakkari, Pieter VanZyl, Aleksander Wieckowski

directly measure how much carbon ecosystems absorb through photosynthesis and release through respiration, and how much water returns to the atmosphere through evapotranspiration. We compared model simulations with these observations across a range of climates, from dry to wet regions and from cooler to warmer sites. JULES successfully reproduced seasonal patterns of carbon and water exchange at many locations. However, it struggled to accurately represent ecosystem respiration and year-to-year variation in photosynthesis. Using a statistical approach that accounts for differences between sites, we found that dryness and unusual rainfall conditions were the main causes of model errors. These results highlight the need to improve how this model represents soil water processes and vegetation responses to water availability.

1. Introduction

Africa has a broad range of ecosystem types, including tropical forest, deserts, semi-deserts, grasslands, coastal, coral reefs and mountain environments which all differ in climate and structure providing essential ecosystem services (Kapuka & Hlásny, 2021; Sintayehu, 2018). Ecosystems can act as carbon sinks by absorbing atmospheric CO₂ through photosynthesis, termed gross primary productivity (GPP), a key component of climate regulation (Nunes et al., 2020; O'Sullivan et al., 2020). They also influence the water cycle by affecting how precipitation is partitioned among evapotranspiration, soil and groundwater storage, and runoff (Gardiya Weligamage et al., 2023; Jasechko et al., 2013; Nedbal et al., 2025). Through evapotranspiration, water from soils and vegetation is returned to the atmosphere, contributing to atmospheric moisture recycling and, in some regions, precipitation locally and downwind (Nyasulu et al., 2024; Te Wierik et al., 2022; Van Der Ent et al., 2010). These processes consequently affect the water available to ecosystems and human societies (Oki & Kanae, 2006). Through these exchanges, ecosystems regulate energy exchange between the biosphere and atmosphere, shaping agricultural productivity, weather, air and water quality (Wang et al., 2007; Wright et al., 2004). Accurate GPP estimation is essential because carbon uptake is tightly coupled to transpiration and surface energy partitioning through stomatal regulation, meaning uncertainties in ecohydrological controls (e.g., stomatal conductance and water stress) can propagate across GPP, latent heat (LE), and sensible heat (H) fluxes (Oliver et al., 2022; Slevin et al., 2015; Zheng et al., 2020).

Land surface models (LSM) are useful for understanding terrestrial ecosystem dynamics and their ability to provide essential ecosystem services especially in the context of climate change. They simulate coupled exchanges of carbon, water, and energy between land and atmosphere, supporting climate prediction and environmental decision making (Fisher & Koven, 2020; Lawrence et al., 2019). Evaluating LSMs is essential for improving predictive accuracy, informing process-level understanding, and guiding targeted observational efforts, particularly for African landscapes where reliable data sets remain limited and urgently needed for informed decision-making (Dinku, 2019; Friedlingstein et al., 2014). However, LSM performance varies across ecosystems, and evaluations have historically focused on North America, Europe, and parts of Asia, with relatively few studies incorporating African observations (James et al., 2018), reflecting strong geographical biases in available flux data sets (Pastorello et al., 2020). In this study we focus on the Joint UK Land Environment Simulator (JULES), the land-surface scheme used within the Met Office Unified Model and UK Earth System Model (UKESM), which contributes to the global model intercomparison projects such as the Coupled Model Intercomparison Project assessed in IPCC reports (Wiltshire et al., 2020). Evaluating JULES performance over Africa helps constrain land-surface biases that may propagate into broader climate projections and Earth system assessments.

Flux tower measurements provide continuous, high temporal resolution records of carbon, water, and energy fluxes using eddy-covariance (EC) methods, offering direct insight into land-atmosphere interactions and serving as a primary benchmark for evaluating LSMs (Ukkola et al., 2022; Xiao et al., 2012). Alternative data sources such as satellite products offer broad spatial coverage but rely on indirect proxies and are affected by retrieval errors, atmospheric effects, and cloud interference (Yue et al., 2015). Expanding site-level evaluations across diverse African ecosystems is therefore critical for improving LSM accuracy and reducing the risk that model biases propagate into climate projections and policy decisions (Ukkola et al., 2022).

Carbon fluxes vary seasonally and inter-annually in response to temperature, precipitation, solar radiation, and plant life-cycle dynamics (Liu et al., 2017; Niu et al., 2017). Across Africa, the relative importance of these

controls differs among ecosystems and regions (Yun et al., 2025). Seasonal rainfall and incoming radiation drive much of the carbon flux dynamics in many African savanna and rangeland ecosystems, while temperature can further constrain productivity, particularly under drier conditions (Ardö et al., 2008; Lomax et al., 2024; Quansah et al., 2015). Interannual variability is especially pronounced in water-limited African ecosystems, where precipitation anomalies can alter productivity and respiration (Bell et al., 2012; Dunn et al., 2007; Poulter et al., 2014; S. Zhou et al., 2016). The effects may also persist beyond the season or year in which rainfall occurs, as preceding moisture conditions can influence subsequent ecosystem productivity and carbon balance. Such precipitation legacy effects have been documented in semiarid grasslands and seasonally dry tropical forests (Bell et al., 2012; Delgado-Balbuena et al., 2019; Nouvellon et al., 2001; Uuh-Sonda et al., 2018; Verduzco et al., 2015). These sensitivities are particularly relevant to Africa's arid and semi-arid ecosystems, which can contribute strongly to interannual variability in regional carbon fluxes during years characterized by substantial precipitation anomalies (Ahlström et al., 2015; Fawcett et al., 2022; Poulter et al., 2014). Drylands often respond quickly to wet conditions with increased carbon uptake, but gains may be rapidly lost through decomposition, respiration, or fire in subsequent dry years (Huxman et al., 2004). Evaluating how LSMs represent interannual variability in fluxes such as GPP helps constrain uncertainties in carbon-climate feedbacks, especially in Africa where these dynamics remain underrepresented. Climate change is altering vegetation composition with savannas already experiencing shifts in plant communities as warming and drought intensify (Fensham et al., 2015; Jones et al., 2022). In the Congo Basin, declining rainfall is increasing tree mortality and altering biodiversity, though high moisture levels maintain some resilience to warming (Bonal et al., 2016; Tao et al., 2022; Taylor et al., 2017; Q. Zhang et al., 2017). Arid and semi-arid regions are particularly vulnerable to changes in rainfall regime, affecting water availability and ecosystem productivity (Lomax et al., 2024; Lu et al., 2023), with cascading impacts on biodiversity, ecosystem services, and livelihoods (IPBES, 2018).

Precipitation and temperature are the key climatic controls on land-atmosphere exchanges, shaping ecosystem productivity, phenology, and terrestrial carbon storage (Davies et al., 2023; Liu et al., 2024; R. Zhang et al., 2019). We therefore examined three gradients central to ecosystem functioning: Mean Annual Temperature (MAT), aridity index, and precipitation anomalies, allowing assessment of JULES performance across diverse environmental conditions and ecosystem types. These gradients capture both long-term hydroclimatic constraints and short-term moisture variability that influence carbon and water fluxes (Thorne & Arain, 2015; Wang et al., 2016). Together, they provide diagnostic evaluation axes for JULES, which often shows biases in water-stressed tropical and semi-arid regions, making these gradients particularly relevant for evaluation across African ecosystems (Harper et al., 2016, 2020).

In this study, we evaluated the simulation of carbon and water with the JULES LSM across a range of ecosystems using EC flux tower observations from African sites, including newly available records that have not been previously used in model evaluations. This allows us to better understand the applicability and potential of this model for informing land management and environmental policies in Africa. We addressed the following research questions:

- (a) How does the accuracy of JULES simulations of GPP, ecosystem respiration (Reco), and evapotranspiration (ET) vary across ecosystem types and along environmental gradients of temperature, aridity index, and precipitation anomalies?
- (b) How well does JULES simulate inter-annual variability of GPP?

2. Materials and Methods

2.1. Focal Sites With Flux Tower Observations

We identified 52 locations (Figure S1 in Supporting Information S2) across Africa where flux tower observations had been collected by reviewing literature, database searches, and consultation with colleagues. We contacted principal investigators and data owners to request access and collaboration, and additional flux data were obtained from FLUXNET (<https://fluxnet.org/>) and AMMACATCH databases (<https://amma-catch.osug.fr>) (AMMA-CATCH, 1990; Galle et al., 2018; Pastorello et al., 2020) in accordance with their data use policies. Our final data set comprised 16 focal sites representing 110 site-years, selected based on availability and permission for use. These sites span diverse ecosystems including savannas, forests, wetlands, grasslands, and agricultural systems, and collectively sample broad precipitation and temperature gradients (Figure 1). Ecosystem classifications were

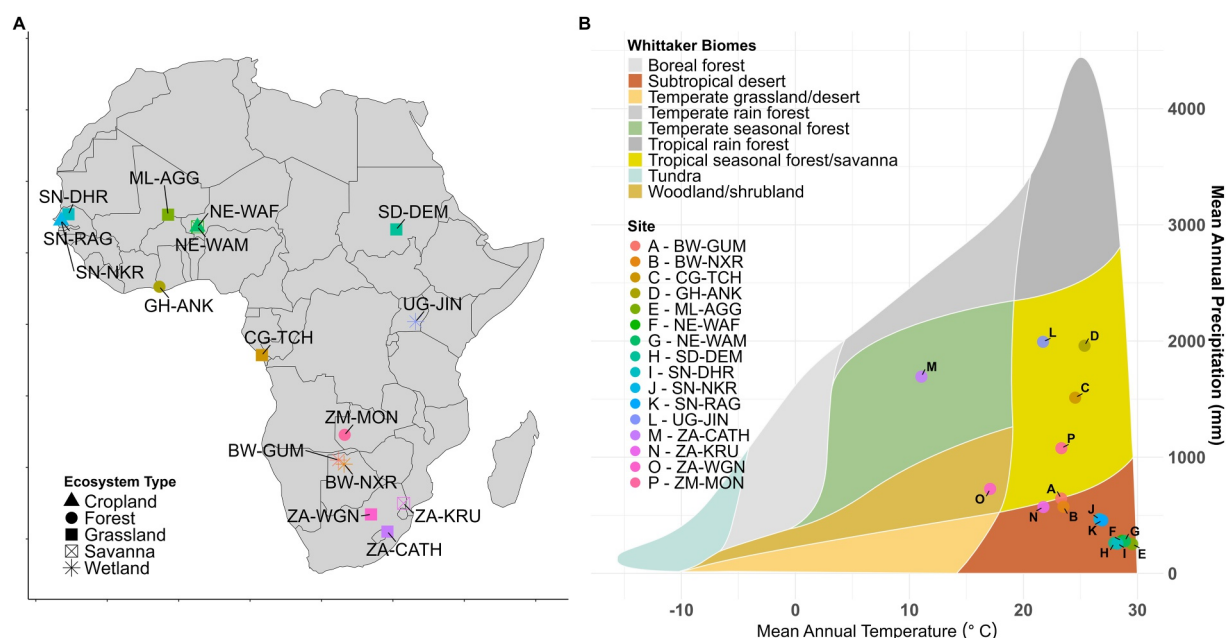


Figure 1. The flux data set sampled a wide range of geographic and climatic space across African Ecosystems. (a) The flux tower sites used in this study are unevenly distributed across Africa, with a concentration in Southern and West Africa, while Central and Northern areas remain relatively underrepresented. Points are shaped by ecosystem type including savanna, grassland, wetland, cropland, and evergreen forest using the International Geosphere–Biosphere Programme land-cover classification. (b) The colored regions show the Whittaker biome diagram (climate-based biome classes) for climatic context. Sites sample a wide range of climate space across mean annual temperature and precipitation, particularly warmer and drier areas in tropical seasonal forest/savanna and subtropical desert biomes.

simplified to align with global frameworks, with detailed site descriptions provided in Table S1 in Supporting Information S3.

The flux tower sites use the EC technique (Baldocchi, 2020; Burba, 2013) to quantify exchanges of energy, water and carbon between the terrestrial ecosystem and the atmosphere. These observations provide half-hourly measurements of land-atmosphere fluxes, including Net Ecosystem Exchange (NEE), H and LE. GPP and ecosystem respiration (Reco) were derived from NEE using the flux-partitioning procedure described in Section 2.4. ET was calculated from LE and air temperature following Equations S1 and S2 in Supporting Information S1. Some sites also recorded meteorological variables such as temperature, wind direction, wind velocity, relative humidity, precipitation, and surface radiation.

2.2. Experimental Design

For the first research question, we evaluated JULES against EC observations of GPP, Reco, ET, H, and LE across 16 African flux-tower sites spanning diverse ecosystems on a daily timescale. Model performance was assessed using mean bias error, hereafter referred to as Bias, defined as the mean difference between modeled and observed fluxes, root mean square error (RMSE), and Pearson correlation (r). These site-level performance metrics were subsequently used as response variables in the linear mixed-effects models (LMMs) to estimate how model performance varied across environmental gradients. To help interpret performance differences among sites and identify potential process-level explanations for carbon and energy flux errors, we analyzed JULES diagnostic outputs of leaf area index (LAI) and the gridbox soil moisture stress factor (f_{smc_gb} ; β). The β factor represents soil-moisture limitation on canopy gas exchange and downregulates potential photosynthesis, and, consequently stomatal conductance under water stress (Best et al., 2011). β is unitless and ranges from 0 (strong water stress, approaching the wilting point) to 1 (unstressed) (Harper et al., 2021). We used these diagnostics to assess whether differences in simulated carbon and energy fluxes were consistent with variation in simulated vegetation phenology or water limitation (Blyth et al., 2011; Harper et al., 2021).

To address our second research question, we repeated the evaluation with annual GPP across all sites. Daily-scale evaluation of GPP, Reco, and ET targets process representation across ecosystems, whereas the interannual variability analysis tests whether JULES captures year-to-year variability in ecosystem productivity, which is

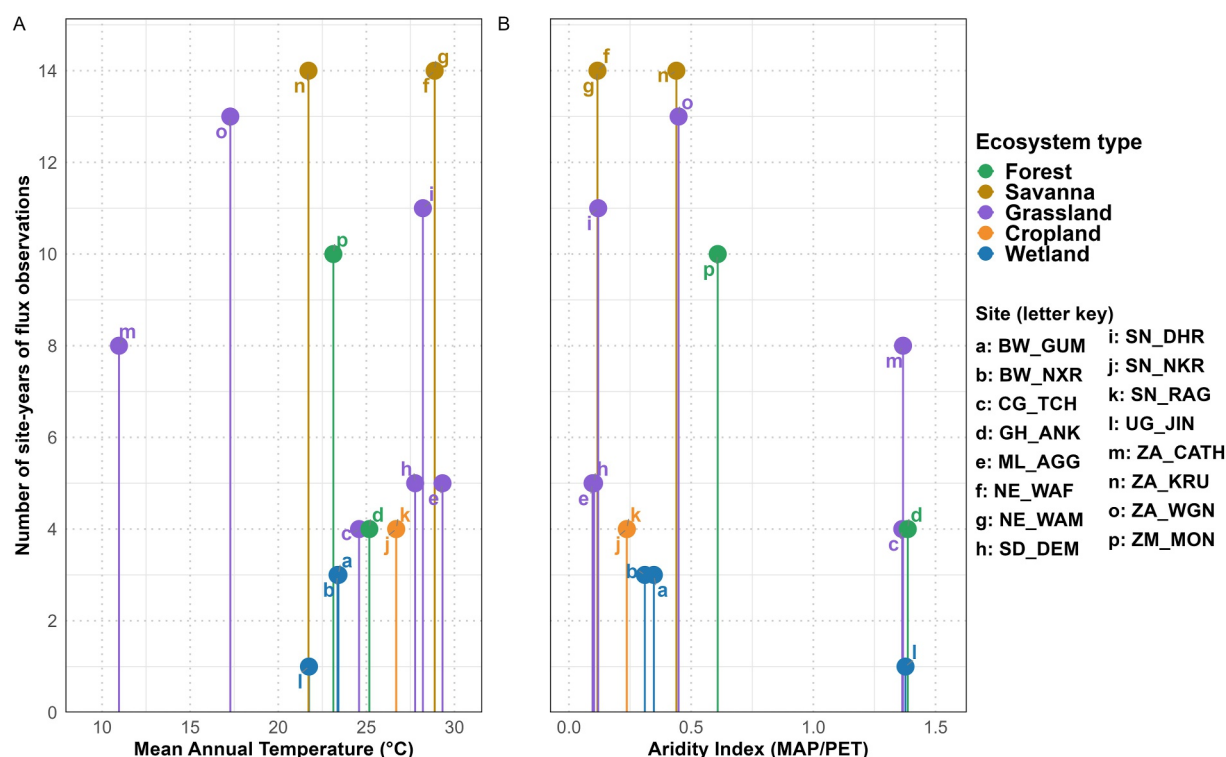


Figure 2. The flux data set unevenly sampled environmental gradients, indicating the necessity of using model-based inference including site-year to analyse these gradients. (a) Distribution of flux observation site-years across mean annual temperature. (b) Distribution of flux observation site-years across aridity index (MAP/PET). Most sites were concentrated in regions of warmer temperatures (23°C–30°C), in semi-arid to sub-humid zones (aridity index $\approx$ 0.2–0.6). There was limited representation of extremely arid or humid conditions.

most robustly assessed with GPP. We therefore restricted the interannual analysis to GPP because the second research question specifically examined whether JULES captures year-to-year variability in gross ecosystem productivity.

2.3. Climatic Gradients

To represent key climatic gradients influencing land-atmosphere exchanges, we derived MAT, aridity index, and annual precipitation anomaly for each site from ERA5-Land hourly data (Muñoz Sabater, 2019) over the period 1991–2020. ERA5-Land provides a spatially and temporally consistent baseline for 1991–2020, whereas comparable multi-decadal site meteorological observations are unavailable across most of the site network. MAT (°C) was used to represent long-term energy availability for plant growth and respiration (Sitch et al., 2008). The aridity index was used to integrate average precipitation and evaporative demand to indicate typical plant-available water (Fawcett et al., 2022; Huang et al., 2017; Salvati et al., 2013; Yao et al., 2024), which strongly affects water balance, ecosystem resilience, and productivity (J. Zhou et al., 2020). Annual precipitation anomalies, defined as deviations from the long-term mean, were included to capture short-term hydroclimatic variability that drives flux variability, especially in semi-arid systems (Lotsch et al., 2003; Yan et al., 2017).

We calculated MAT from the mean hourly air temperatures at 2 m above ground level. Annual precipitation anomaly was calculated as the percentage deviation of each year's total precipitation from the 30-year mean annual precipitation (MAP) baseline, providing a measure of interannual variability in rainfall. The aridity index was calculated as the ratio of MAP to annual potential evapotranspiration (PET), quantifying the balance between water supply and atmospheric demand, where lower values indicate drier conditions and higher values indicate more humid conditions. PET was obtained from the TerraClimate data set for 1991–2020 (Abatzoglou et al., 2018), although recent studies have highlighted alternative data sources for PET (Maes et al., 2019; Singer et al., 2021). These metrics were used to characterise long-term site-level climatic conditions and to support gradient-based evaluation of JULES performance (Figure 2).

2.4. Flux Data Processing

Flux data from each site underwent quality control and preprocessing to ensure consistency across data sets. Variables were standardized to uniform naming conventions and units. Data cleaning included identifying values outside physically plausible ranges and replacing them with missing values prior to gap filling.

We applied the Unified FLUXes (UFLUX) gap-filling algorithm (Zhu et al., 2022; Zhu, Quaife, & Hill, 2024), which extends EC flux measurements across unobserved periods (temporal gap filling) and supports spatial representativeness (Zhu et al., 2023; Zhu, Xu, et al., 2024). UFLUX has been globally validated for carbon, water, energy, and methane fluxes and shows stable performance even for gaps exceeding 1 month (Zhu et al., 2023). We evaluated performance using artificial gaps randomly imposed with predefined sizes and gap ratios: short gaps (24 hr, 20% of total gaps), long gaps (7 days, 30% of total gaps), and very-long gaps (30 days, 50% of total gaps) (Moffat et al., 2007; Zhu et al., 2022). The processing workflow comprised: (a) creating artificial gaps, (b) training the gap-filling model using EC fluxes and environmental forcings, (c) validating the model performance against artificial gaps, and (d) applying the trained model to real data gaps.

UFLUX is built upon SmartForest4D, a deep-layer XGBoost algorithm (T. Chen & Guestrin, 2016), a scalable gradient boosting algorithm selected for strong predictive performance, computational efficiency, and robustness to complex tabular and imbalanced data sets (T. Chen & Guestrin, 2016; Zhu, Quaife, & Hill, 2024). The implementation used here incorporates updates improving stability for EC applications and enabling uncertainty quantification. Gap-filling uncertainty was estimated using 10 ensemble members, each trained with 80% randomly sampled subsets of the flux and forcing time series. The ensemble mean was used as the gap-filled estimate, with ensemble spread representing uncertainty. The environmental forcings were derived from ERA5-Land (Muñoz Sabater, 2019) which has shown very close results to using local meteorological data (Zhu et al., 2023). The parameters include air temperature, solar radiation, longwave radiation, wind speed, and precipitation, along with temporal predictors (day of year and hour of day) to represent seasonal and diurnal vegetation dynamics (Zhu et al., 2022).

We partitioned ecosystem exchange (NEE) fluxes into GPP and Reco using the daytime partitioning approach. For the daytime-based approach we fitted a light-response curve (Michaelis–Menten function) to daytime NEE observations when photosynthetically active radiation exceeds a defined threshold (10 W m^{-2}) (Equation S3 in Supporting Information S1) (Lasslop et al., 2010; Reichstein et al., 2005). For the nighttime estimate a temperature-based Reco was used as an initial input and curve fitting was performed using non-linear least squares to derive key parameters: light-use efficiency (α), maximum GPP (GPP_{max}), and daytime Reco. The simplified partitioning workflow based on the general framework of Lasslop et al. (2010) was applied consistently across all sites. Our code for processing, gap filling, and flux partitioning is shared in the Open Research section.

2.5. Overview of the JULES Model

JULES is the terrestrial component of the Met Office Unified Model and is used within UKESM and the Hadley Center Global Environment Model (HadGEM) family for applications ranging from numerical weather prediction to climate simulations (Best et al., 2011; Burton et al., 2019; Martin et al., 2011). It simulates coupled exchanges of energy, water and carbon between land and atmosphere using a tiled representation of surface heterogeneity, with prognostic soil and vegetation states (Best et al., 2011; Clark et al., 2011). JULES is driven by meteorological forcing including precipitation, radiation, temperature, humidity, wind speed, snowfall and surface pressure (Best et al., 2011; Blyth et al., 2011).

Following Harper et al. (2016), we used nine Plant Functional Types (PFTs) (tropical broadleaf evergreen trees (BET-Tr), temperate broadleaf evergreen trees (BET-Te), broadleaf deciduous trees, needle-leaf evergreen trees, needle-leaf deciduous trees, C3 grasses, C4 grasses, evergreen shrubs, and deciduous shrubs) and four non-vegetation surface types (Urban, Inland water, Bare soil, Land-ice). In our simulations, each PFT in JULES is treated as existing on a separate tile within a grid box (Harper et al., 2016), but each grid box only has one soil column, meaning all PFT tiles share a common soil moisture and litterfall from each PFT contributes to a common soil carbon value. Vegetation carbon uptake in JULES is simulated using coupled leaf photosynthesis and stomatal conductance, with soil-moisture limitation represented by a grid-box soil moisture stress factor that downregulates potential photosynthesis under dry conditions and thereby reduces canopy gas exchange (Clark et al., 2011; Harper et al., 2020). Seasonal canopy dynamics are represented through LAI and phenology

Table 1
Data Sets Required to Drive Joint UK Land Environment Simulator

Variable	Data set	Temporal frequency	Source
Air temperature at 2 m	ERA5-Land	Half-hourly	https://cds.climate.copernicus.eu
Downward long-wave radiation (W/m^2)			
Downward short-wave radiation (W/m^2)			
Wind speed (m/s)			
Surface pressure (Pa)			
Precipitation ($\text{kg/m}^2/\text{s}$)			
Specific humidity (kg/kg)			
Soil texture	iSDAsoil/literature	Static	www.isda-africa.com
Soil parameters: Exponent in soil hydraulic characteristics, Dry heat capacity, Dry thermal conductivity, Hydraulic conductivity at saturation, soil matric suction at saturation, Volumetric soil moisture content, Volumetric soil moisture content at saturation, Volumetric soil moisture content at wilting point, Soil clay content	Calculated from fraction of sand, silt, and clay using the Cosby equation (Best et al., 2011; Chadburn et al., 2015; Cosby et al., 1984; Dankers et al., 2011; Farouki, 1981)	Static	
Albedo	MODIS		https://modis.gsfc.nasa.gov
Vegetation cover	Literature based and information from site PIs		

(prescribed or prognostic depending on the selected configuration), which control light interception, transpiration, and carbon uptake and are therefore central to evaluating simulated seasonal cycles. All simulations were run without nitrogen limitation (N-limitation option set to False), so photosynthesis and growth were not down-regulated by N availability. Further descriptions of the JULES model are in Best et al. (2011) and Clark et al. (2011).

2.6. Preparation of Driving Data for JULES

Meteorological, soil, and vegetation data were used to parameterize and drive JULES. Half-hourly meteorological data was resampled from ERA5-Land (Muñoz Sabater, 2019) (<https://cds.climate.copernicus.eu/datasets/>) (Table 1), providing spatially and temporally continuous, physically consistent inputs across all 16 sites. Site-based meteorological observations were incomplete for several towers and variables over the evaluation period, making a consistent observation-forced configuration impractical without introducing site-specific forcing biases. Using ERA5-Land therefore ensured uniform treatment across sites, aiding comparability of model performance patterns along ecosystem and climate gradients. Retrieved variables included air temperature at 2 m, dew point temperature, surface solar and thermal radiation, air pressure, precipitation, and wind speed. Specific humidity was calculated from vapor pressure (e , hPa) and air pressure (p , hPa). Description of the forcing, ancillary and evaluation data are provided below.

Soil texture fractions (sand, silt, and clay) for each site were obtained from published sources where available and otherwise from iSDA (www.isda-africa.com; Table S2 in Supporting Information S3). Relative to other global products, iSDAsoil is derived from a larger set of African soil observations and provides estimates at finer spatial resolution (30 m compared with 250 m to 1 km for SoilGrids), improving site-level representativeness for point-based studies (Hengl et al., 2021; Miller et al., 2021). As an open-access and continuously updated resource, iSDAsoil integrates improved modeling approaches, expanded training data, and satellite covariates (Eshetu et al., 2024; Lavarenne & Leroux, 2024).

Soil hydraulic and thermal parameters were derived from soil texture using established pedo-transfer functions (PTFs) (Best et al., 2011; Chadburn et al., 2015; Cosby et al., 1984; Dankers et al., 2011; Farouki, 1981). Although texture-based PTFs are widely applied in LSM studies, they do not always capture structural controls on infiltration and runoff such as surface crusting or soil compaction, which are frequently simplified or omitted in LSM representations (Vereecken et al., 2019). This limitation is particularly relevant for cultivated Sahelian systems, where thin, low-permeability surface crusts can substantially enhance runoff and restrict infiltration (Velluet et al., 2014).

The PFT fractional coverage for each site was prescribed using published site descriptions, information provided by site investigators, and available field surveys (Table S3 in Supporting Information S3). These prescribed fractions are subject to uncertainty because tower flux footprints vary spatially and temporally and may sample heterogeneous land cover (Cunliffe et al., 2022). Additional uncertainty arises because site descriptions and surveys often differ in spatial scale (e.g. plot, vs. landscape level) and observation period (Chu et al., 2021).

2.7. JULES Simulations

We extended the experimental configuration (“Rose suite”) described in Harper et al. (2021), (updated to JULES v7.1) by adding our 16 African sites, along with their PFT fraction, soil properties, and meteorological data. The Rose suite configuration, including all parameter settings and switches, is provided via the Open Research section. All other model settings followed Harper et al. (2021), including disabling vegetation competition and applying trait-based physiology. Simulations were conducted as single-point runs at 30-min time steps over multi-year periods corresponding to the available flux tower data.

A 1,000-year spin-up was applied prior to each simulation to equilibrate soil water and carbon pools, particularly for slow-turnover soil carbon reservoirs. Spin-up was achieved by repeatedly cycling the model through a defined meteorological forcing window until carbon and water pools stabilized (Figure S2 in Supporting Information S2). Model outputs were subsequently aggregated to daily resolution for each site-specific simulation period.

2.8. Evaluating JULES Performance Across Ecosystem Type and Environmental Gradients

For each of the 16 sites, model accuracy was evaluated at a daily time step using R (v4.1.2) (R Core Team, 2021). Agreement between simulated and EC-derived fluxes was quantified using three summary performance metrics: Bias (Equation S4 in Supporting Information S1), representing systematic over- or under-prediction; root mean square error (RMSE; Equation S5 in Supporting Information S1), representing overall error magnitude; and Pearson correlation coefficients (r ; Equation S6 in Supporting Information S1), representing the temporal correspondence between simulated and observed flux variability.

To examine how model performance varies among ecosystem types, sites were classified according to their dominant vegetation type. Different ecosystems exhibit distinct structural and physiological characteristics that influence carbon, water, and energy fluxes. Because JULES represents vegetation using PFTs, this classification allows evaluation of the model's ability to represent ecosystem-specific processes. We summarized model performance metrics (Bias, RMSE, and r) for GPP, Reco, and ET within each site-year, and subsequently summarized by ecosystem class.

To quantify how environmental gradients influence JULES performance for GPP, Reco, and ET, while accounting for covarying environmental drivers (Table S4 in Supporting Information S3), uneven sampling of climatic gradients, and variable record lengths among sites (Figure 2), we applied a LMM framework (Oberg & Mahoney, 2007). This statistical model-based inference enables estimation of the effects of multiple environmental drivers while also accounting for between-site variability and non-independence of repeated observations.

We calculated Bias, r , and RMSE for each site-year, with Bias and RMSE normalized by the mean observed flux for the corresponding site-year. These scaled metrics facilitate comparisons across sites and fluxes with differing magnitudes, reducing the disproportionate influence of high-flux ecosystems in the gradient analyses. All performance metrics were treated as continuous response variables.

We included MAT, annual precipitation anomaly, and aridity index as fixed effects, and site ID as a random effect to account for unobserved heterogeneity and the non-independence of observations within sites across years.

Because data record length varied among sites, we used site-year metrics rather than site means. LMM models were fitted using the *lme4* package (v1.1.32) (Bates et al., 2015).

We also fitted Flux Normalized Performance Indices (FNPI) for Bias and RMSE as continuous responses for separate models. FNPI rescales performance metrics to a 0–1 range (higher values indicate better performance), facilitating comparison across metrics. Fixed effects and random intercept structures were identical to those used in the primary LMMs. Scaled-bias models are presented in the main text because they retain an interpretable direction and magnitude without introducing an additional rescaling step. FNPI analyses produced consistent conclusions and are provided in Supporting Information S1 (Figure S3 in Supporting Information S2; Tables S5–S13 in Supporting Information S3).

LMM diagnostics and fit were evaluated using the R *performance* package, (v0.13.0) (Lüdtke et al., 2021). Standard diagnostic assessments, including residual patterns, leverage, and collinearity checks, did not indicate substantive violations of model assumptions. Posterior predictive densities closely matched observed distributions for scaled bias, RMSE, and *r*, indicating that the models capture the primary structure of the data (Figures S4–S18 in Supporting Information S2).

The results were visualized using R *ggeffects* package (v2.2.1) (Lüdtke, 2018) to generate marginal effect plots illustrating how model bias and error vary along each environmental gradient while holding other predictors at their mean values. Shaded ribbons represent 95% confidence intervals. The model structure for each flux was as follows:

$$\text{Bias} \sim \text{MAT} + \text{AI} + \text{Precip Anomaly} + (1 \mid \text{Site ID})$$

$$\text{RMSE} \sim \text{MAT} + \text{AI} + \text{Precip Anomaly} + (1 \mid \text{Site ID})$$

$$\text{Corr} \sim \text{MAT} + \text{AI} + \text{Precip Anomaly} + (1 \mid \text{Site ID})$$

We report effect directions and *p*-values as well as coefficients with unit-interpretable steps (e.g., +10% precipitation anomaly, +0.1 AI, +5°C) in Tables S14–S22 in Supporting Information S3.

2.9. Evaluating JULES Performance Across Time (Between Years)

To assess JULES' ability to simulate temporal patterns in ecosystem fluxes of GPP, we evaluated interannual variability across the sites to determine how well the model captures the timing and magnitude of GPP under different climatic and ecological conditions.

We calculated site-specific hydrological years, and for each year with full coverage we computed total GPP ($\text{kg C m}^{-2} \text{ yr}^{-1}$) within the hydrological year. Following Lomax et al. (2024), we calculated daily precipitation climatology Q_i for each day-of-year $i = 1 \dots 365$ using the mean over 1991–2020 and applied a 31-day running mean for smoothing. We formed the cumulative daily $C(d)$ rainfall anomaly curve (Equation S6 in Supporting Information S1) where $\bar{Q}$ is the mean of Q_i . Periods of below-average rainfall give a negative slope, and above-average rainfall a positive slope and the onset of the main rainy season is taken as the day after the minimum of $C(d)$. To ensure early onsets are captured, we defined the start of the hydrological year as 30 days prior to this onset. The same boundaries are applied to both EC GPP and JULES GPP before annual aggregation.

Quantitative assessment of interannual variability was restricted to sites with at least 5 years of data to ensure robust variance and correlation estimates. Model performance was evaluated using *r* to quantify temporal association, RMSE to characterize magnitude of deviation, and the coefficient of variation (CV; Equation S8 in Supporting Information S1). Together, these metrics provided an integrated assessment of JULES's ability to represent mean productivity and year-to-year variability.

3. Results

3.1. Evaluation of JULES Accuracy Against Eddy-Covariance Observations

3.1.1. Variation in Accuracy Across Vegetation Types

Model performance for GPP varied considerably across ecosystems (Figure 3). In croplands, JULES reproduced the observed dynamics reasonably well, with correlations of ($r = 0.77$ – 0.81) and negative biases of -1.3 and

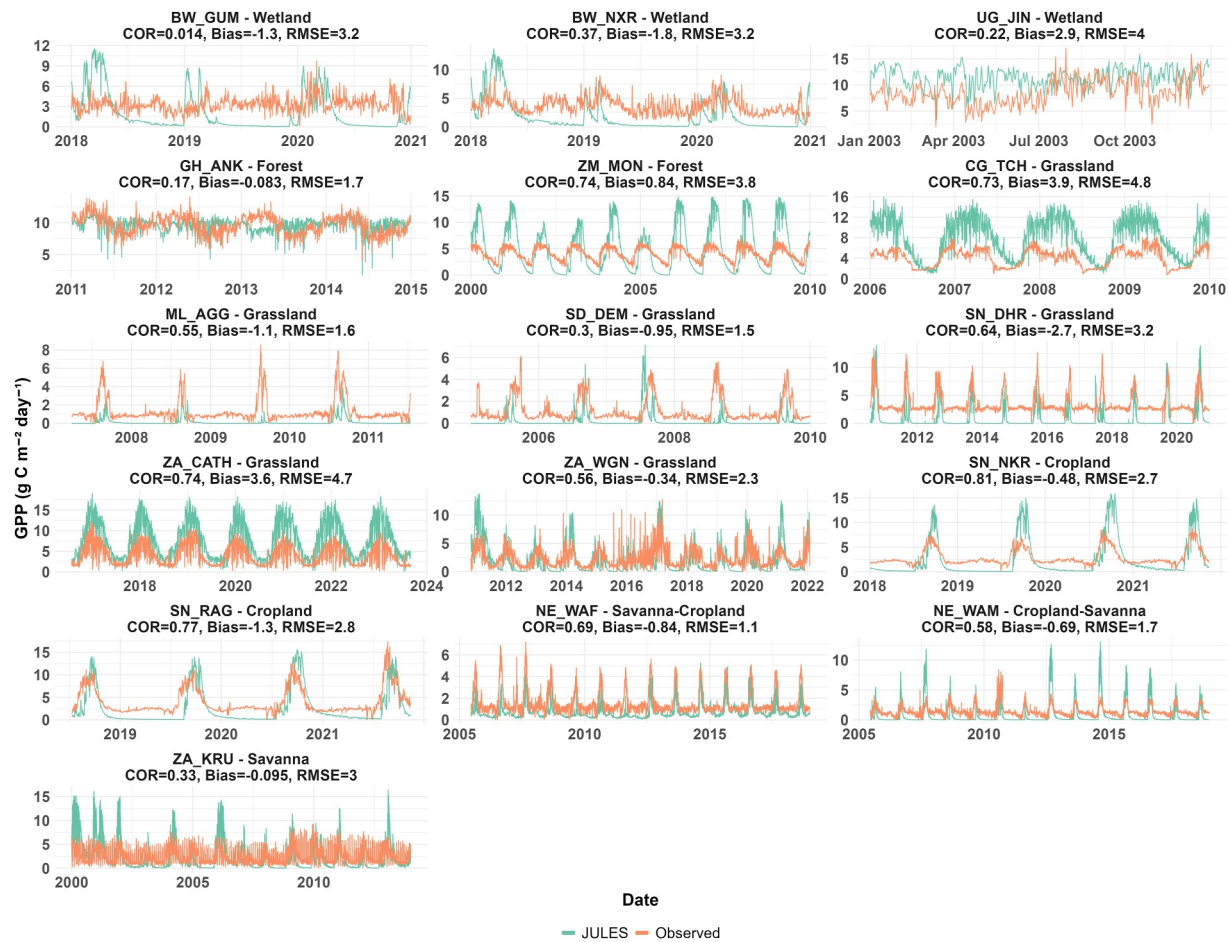


Figure 3. Joint UK Land Environment Simulator captures gross primary productivity dynamics reasonably in croplands and some grassland and forest sites, with performance declining in savannas and is poorest in wetlands with large underestimations.

$-0.48 \text{ g C m}^{-2} \text{ day}^{-1}$ at SN_RAG and SN_NKR, respectively, indicating systematic underestimation, although the magnitude and timing of individual seasonal peaks varied. Forest ecosystems showed contrasting outcomes. The deciduous forest site ZM_MON performed strongly ($r = 0.74$), with a positive bias of $0.84 \text{ g C m}^{-2} \text{ day}^{-1}$, whereas performance at the evergreen forest site GH_ANK was much weaker ($r = 0.17$). Although the overall bias at GH_ANK was small ($-0.083 \text{ g C m}^{-2} \text{ day}^{-1}$), JULES poorly reproduced the observed temporal variability. Grassland sites exhibited a broad performance range, from poor agreement at SD_DEM ($r = 0.30$) to strong agreement at ZA_CATH ($r = 0.74$). Biases occurred in both directions and ranged from $-2.7 \text{ g C m}^{-2} \text{ day}^{-1}$ at SN_DHR to $3.9 \text{ g C m}^{-2} \text{ day}^{-1}$ at CG_TCH, suggesting substantial variation among grassland sites. At the savanna–cropland site NE_WAF, JULES showed moderate agreement ($r = 0.69$) and underestimated GPP by $0.84 \text{ g C m}^{-2} \text{ day}^{-1}$. At the cropland–savanna site NE_WAM, agreement was weaker ($r = 0.58$), with a bias of $-0.69 \text{ g C m}^{-2} \text{ day}^{-1}$. The savanna site ZA_KRU also showed weak agreement ($r = 0.33$), although its mean bias was small ($-0.095 \text{ g C m}^{-2} \text{ day}^{-1}$), its RMSE was comparatively high. Wetland sites consistently showed the weakest performance, with correlations ranging from 0.014 to 0.37 and biases ranging from -1.8 to $2.9 \text{ g C m}^{-2} \text{ day}^{-1}$, indicating substantial errors in both the magnitude and temporal dynamics of simulated GPP.

Reco performance was generally poorer and more variable than GPP (Figure 4). At the two cropland sites, agreement was low ($r = 0.30$ – 0.34) although mean biases were small and positive, at 0.071 and $0.096 \text{ g C m}^{-2} \text{ day}^{-1}$ for SN_RAG and SN_NKR, respectively. Forest sites also showed weak performance, with correlations ranging from -0.027 to 0.29 and positive biases of $1.5 \text{ g C m}^{-2} \text{ day}^{-1}$ at ZM_MON and $3.1 \text{ g C m}^{-2} \text{ day}^{-1}$ at GH_ANK, indicating substantial overestimation. Grassland sites exhibited the widest

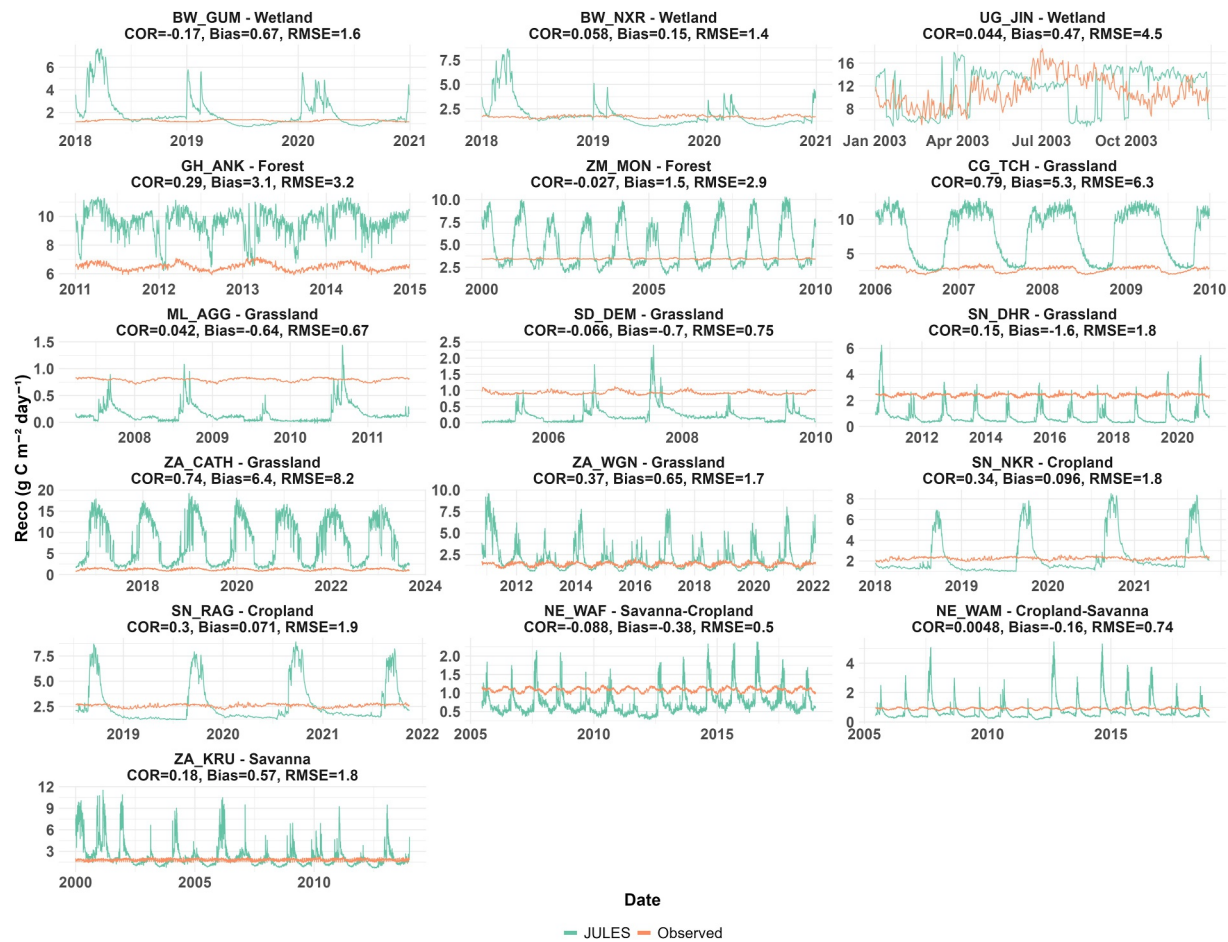


Figure 4. Joint UK Land Environment Simulator overestimated respiration across most ecosystems, with strongest agreement at grassland sites (CG_TCH, ZA_CATH) but weak to negligible correspondence in forests, savannas, and wetlands.

performance range, from weak agreement at SD_DEM and SN_DHR ($r = -0.066$ – 0.15) to strong temporal agreement at CG_TCH ($r = 0.79$) and ZA_CATH ($r = 0.74$). However, the two sites with the strongest correlations also showed the greatest overestimation, with biases of 5.3 and $6.4 \text{ g C m}^{-2} \text{ day}^{-1}$ at CG_TCH and ZA_CATH, respectively. In contrast, ML_AGG, SD_DEM, and SN_DHR showed negative biases of -0.64 , -0.70 , and $-1.6 \text{ g C m}^{-2} \text{ day}^{-1}$, respectively, while ZA_WGN showed a positive bias of $0.65 \text{ g C m}^{-2} \text{ day}^{-1}$. At the savanna–cropland site NE_WAF and the cropland–savanna site NE_WAM, correlations were near zero ($r = -0.088$ and 0.0048), with biases of -0.38 and $-0.16 \text{ g C m}^{-2} \text{ day}^{-1}$, respectively. The savanna site ZA_KRU also showed weak agreement ($r = 0.18$) and a positive bias of $0.57 \text{ g C m}^{-2} \text{ day}^{-1}$. Wetland sites showed similarly weak correspondence ($r = -0.17$ to 0.058), with positive biases ranging from 0.15 to $0.67 \text{ g C m}^{-2} \text{ day}^{-1}$. UG_JIN additionally showed a comparatively high RMSE of $4.5 \text{ g C m}^{-2} \text{ day}^{-1}$. Overall, JULES captured the temporal dynamics of Reco reasonably well at only a subset of grassland sites, but strong temporal correlations did not necessarily indicate accurate magnitude estimates, with the two strongest correlations accompanied by the largest positive biases. Performance was generally weaker in forests, croplands, mixed savanna–cropland systems, savanna, and wetlands, where temporal agreement was mostly weak and biases varied in direction and magnitude.

Model performance for ET was generally stronger than for the carbon fluxes but varied across ecosystems (Figure 5). Cropland sites showed strong agreement ($r = 0.81$ – 0.88) and slight underestimation, with mean bias error ranging from -0.055 to $-0.29 \text{ mm day}^{-1}$. Performance differed between the forest sites: ZM_MON showed strong agreement ($r = 0.82$) with a bias of 0.86 mm day^{-1} , whereas GH_ANK showed weaker agreement ($r = 0.23$) and greater overestimation, with a bias of 2.0 mm day^{-1} . Grassland sites showed variable performance,

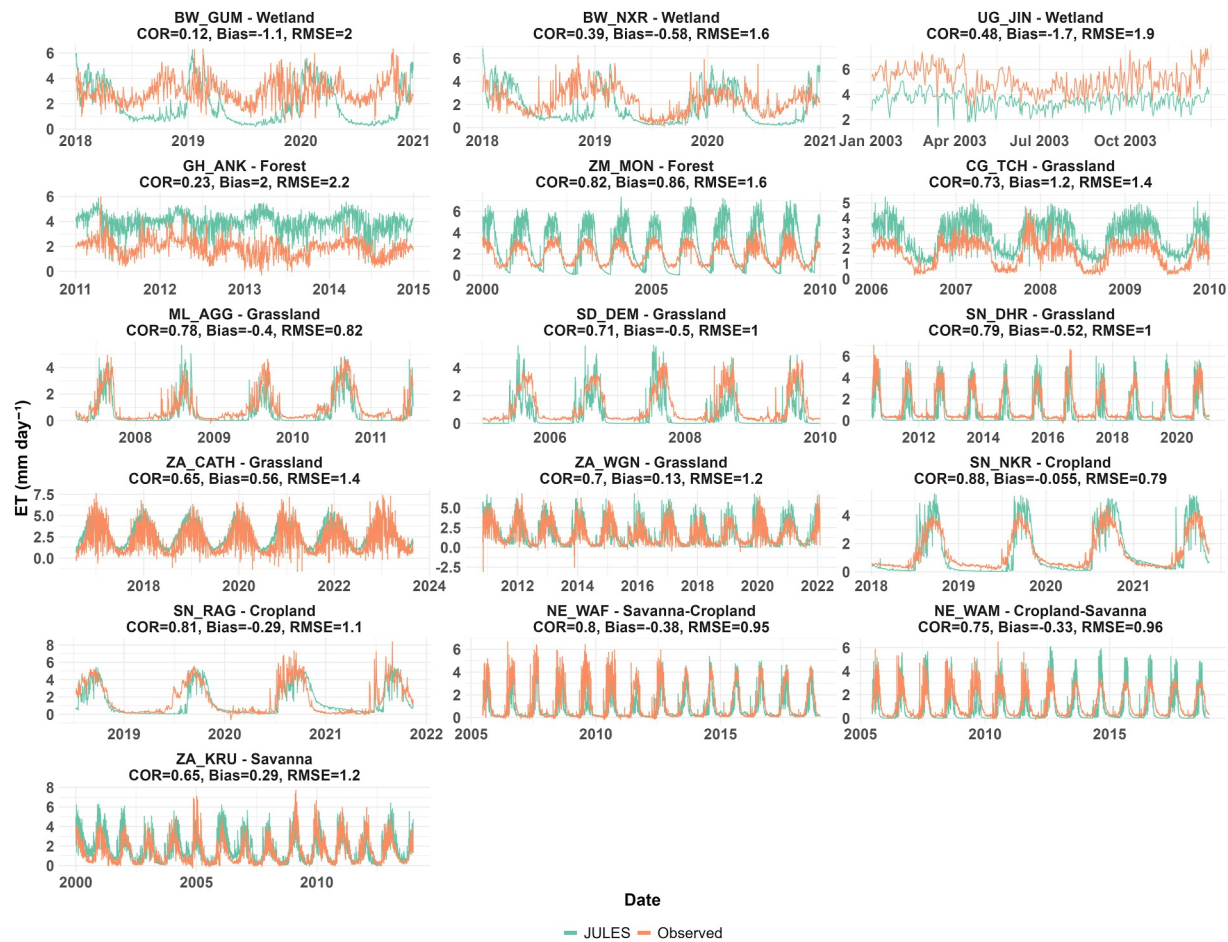


Figure 5. Evapotranspiration dynamics were best captured in croplands, savannas, and several grasslands, whereas wetlands showed weak agreement and higher errors.

with correlations ranging from 0.65 to 0.79 and biases from -0.52 to 1.2 mm day^{-1} . CG_TCH showed the greatest overestimation among the grassland sites (bias = 1.2 mm day^{-1}), while ML_AGG, SD_DEM, and SN_DHR underestimated ET with bias values of -0.40 , -0.50 , and -0.52 mm day^{-1} , respectively. The mixed savanna–cropland sites performed relatively well, with correlations of 0.75–0.80 and biases of -0.38 and -0.33 mm day^{-1} at NE_WAF and NE_WAM, respectively. At the savanna site ZA_KRU, agreement was more modest ($r = 0.65$), with a bias of 0.29 mm day^{-1} . Wetland sites remained the poorest performers, with correlations ranging from 0.12 to 0.48 and consistent underestimation. Biases were -1.1 mm day^{-1} at BW_GUM, -0.58 mm day^{-1} at BW_NXR, and -1.7 mm day^{-1} at UG_JIN.

The ecosystem comparison revealed clear and systematic differences in JULES performance. Croplands were consistently well-simulated, with strong correlations and relatively small biases across both carbon and energy fluxes. Forests, by contrast, exhibited high site-level variability, with ZM_MON closely aligning with observations across fluxes, whereas GH_ANK consistently underperformed. Grasslands showed intermediate performance, with some sites (e.g., CG_TCH, ZA_CATH) demonstrating strong correspondence, while others showed systematic overestimation or weak agreement. In savannas, JULES reproduced water and energy exchanges relatively well but struggled to capture GPP and Reco, highlighting persistent limitations in representing carbon processes under semi-arid conditions. Wetlands, as modeled, performed relatively poorly, with low correlations and large errors across all fluxes. Evaluation of H is provided in Supporting Information S1 (Figure S19 in Supporting Information S2) to document energy-flux behavior, whereas the main text focuses on GPP, Reco and ET. Sensible heat flux performance was variable among sites, with correlations ranging from approximately zero at several grassland, forest and wetland sites to 0.70–0.75 at other

sites (e.g., SN_DHR, SN_NKR, SN_RAG, and ZM_MON). Bias also varied among sites, although substantial underestimation occurred at various sites including GH_ANK, UG_JIN, ZA_CATH, ZA_KRU, ZA_WGN, and ZM_MON.

3.1.2. Process Diagnostics of Simulated Canopy Dynamics and Water Limitation

JULES-simulated grid-box LAI and the soil-moisture availability factor were examined alongside the carbon- and water-flux time series as process diagnostics (Figures S20–S23 in Supporting Information S2). At many seasonally varying sites, precipitation periods coincided with increases in simulated soil-moisture availability and LAI and with seasonal peaks in simulated GPP and ET. During drier periods, soil-moisture availability frequently declined toward zero, accompanied by reductions in simulated LAI, GPP, and ET. This behavior was particularly apparent at ML_AGG, SD_DEM, SN_DHR, SN_NKR, and SN_RAG. At these sites, prolonged periods of low simulated GPP occurred alongside negative mean GPP biases, even where some wet-season peaks were reproduced.

The relationship between the diagnostic variables and flux errors nevertheless differed among sites. At CG_TCH and ZA_CATH, seasonal increases in LAI occurred alongside large simulated GPP and Reco peaks and positive mean biases in GPP, Reco, and ET. ZM_MON maintained comparatively high LAI but showed strong seasonal soil-moisture limitation; positive mean biases were present for all three fluxes. In contrast, GH_ANK maintained nearly constant LAI and soil-moisture availability close to 1, with little mean GPP bias but positive Reco and ET biases. Thus, neither high LAI nor limited simulated water stress corresponded uniformly to improved flux performance.

The wetland sites showed particularly contrasting diagnostic behaviour. At BW_GUM and BW_NXR, simulated soil-moisture availability remained close to zero for much of each year and increased only during relatively short wet periods. These extended water-limited periods coincided with low simulated GPP and ET and negative mean biases in both fluxes. By contrast, UG_JIN maintained relatively stable LAI and soil-moisture availability close to 1 during its 1-year record, but JULES overestimated GPP on average while underestimating ET. The precipitation series therefore provided the temporal context for identifying wet and dry periods associated with changes in LAI, soil-moisture availability, GPP, and ET, while the temperature series documented the corresponding seasonal meteorological conditions.

3.2. Effects of Environmental Gradients on Model Performance (GPP, ET and Reco)

3.2.1. GPP

Predicted bias in GPP depended strongly on climate gradients (Figure 6a), showing greater sensitivity to aridity index and precipitation anomaly than to MAT. At cooler temperatures, predicted bias was close to zero and slightly positive, with confidence intervals overlapping zero. At higher MAT, predicted mean-normalized bias became increasingly negative, indicating stronger underestimation; each additional 1°C in MAT was associated with a 0.033 decrease in predicted bias ($p \approx 0.04$). Both drier and wetter-than-average years were associated with higher predicted bias, with the lowest bias occurring near intermediate moisture conditions (aridity index ≈ 0.75 ; precipitation anomaly $\approx +25\%$). A 0.1 increase in the aridity index corresponded to a 0.073 increase in scaled bias, and a +10% precipitation anomaly corresponded to a 0.1 increase. The marginal effect curves were approximately linear, with narrow uncertainty bands for aridity index and precipitation anomaly and a wider uncertainty for MAT, consistent with the coefficient estimates (Table S14 in Supporting Information S3), and indicating stronger support for moisture related effects than for temperature.

Predicted RMSE also exhibited clear climate dependency (Figure 6d). Anomalously wet periods were associated with higher predicted errors ($p < 0.001$). RMSE also decreased with increasing aridity index ($p = 0.06$), indicating larger errors under drier conditions. Predicted RMSE decreased with increase MAT ($p = 0.1583$) (Table S15 in Supporting Information S3).

Predicted r , exhibited a single robust gradient effect for GPP (Figure 6g). Correlation improves during above-normal rainfall ($p = 0.002$), while the effects of temperature and aridity were small and uncertain ($p = 0.822$ and $p = 0.55$, respectively) (Table S16 in Supporting Information S3).

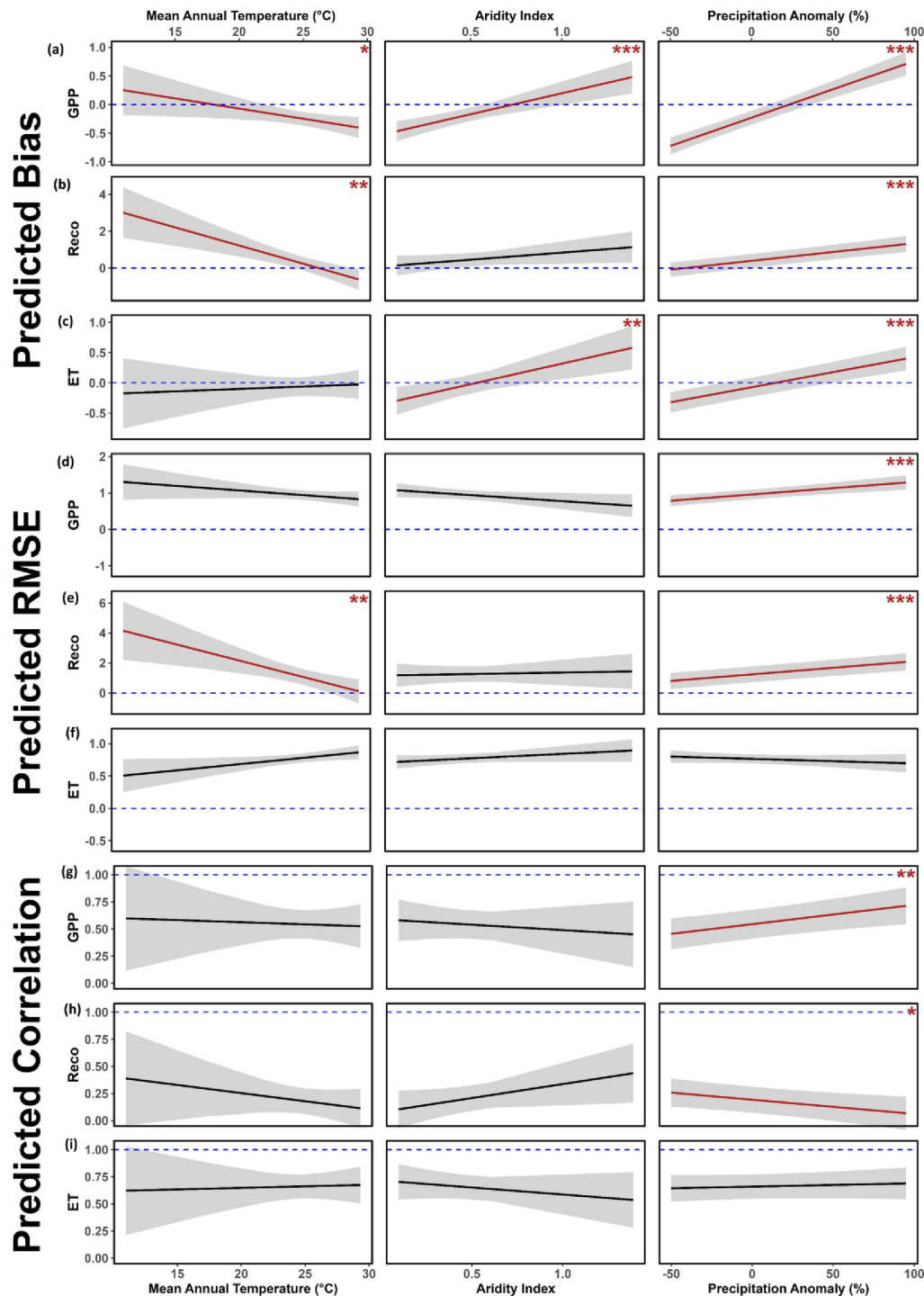


Figure 6. Predicted marginal effects of mean annual temperature, aridity index, and precipitation anomaly on Joint UK Land Environment Simulator bias, root mean square error (RMSE), and correlation indicate that precipitation anomaly was the environmental gradient most consistently associated with model performance, although the direction and strength of associations varied among fluxes and performance metrics. Rows represent performance metric and flux combinations as follows: (a) GPP predicted bias, (b) Reco predicted bias, (c) ET predicted bias, (d) GPP predicted RMSE, (e) Reco predicted RMSE, (f) ET predicted RMSE, (g) GPP predicted correlation, (h) Reco predicted correlation, and (i) ET predicted correlation. Higher aridity most strongly affected evapotranspiration (ET) and was associated with lower gross primary productivity (GPP) RMSE at more humid sites. Temperature rarely influenced correlation, but it reduced RMSE for Reco and increased RMSE for ET; its effect on Bias was weak for GPP, absent for ET, and negative for Reco. Curves show marginal effect partial predictions, with other covariates held at their means; ribbons are 95% CIs. The blue dashed line marks the “good” reference (0 for Bias and RMSE; 1 for Corr); red fitted lines indicate statistically significant fixed-effect slopes, while black lines indicate non-significant associations; stars indicate significance of the fixed-effect slope: *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$.

3.2.2. Ecosystem Respiration

The strongest and most consistent environmental association for ecosystem respiration was with precipitation anomaly, while warmer mean climates were generally associated with lower model error. After accounting for site-level heterogeneity, predicted scaled bias declined with MAT (Figure 6b; $p = 0.001$), indicating smaller bias in warmer mean climates, and increased with positive rainfall anomalies ($p < 0.001$); a +10% precipitation anomaly corresponding to an approximately +0.096 in bias. The aridity index showed no clear association with bias ($p = 0.1170$; 95% CI spans zero; Table S17 in Supporting Information S3). Similarly, predicted RMSE increased with positive precipitation anomalies ($p < 0.001$; 95% CI 0.064–0.112) and decreased with MAT ($p = 0.0066$), while aridity showed no clear effect ($p = 0.760$; Figure 6c; Table S18 in Supporting Information S3). Finally, precipitation anomaly was the only environmental predictor associated with predicted model–observation correlation, with positive anomalies corresponding to lower Reco r ($p = 0.01$); a +10% anomaly corresponded to an approximately –0.013 change in correlation (95% CI –0.023 to –0.003; Figure 6h; Table S19 in Supporting Information S3). Temperature and aridity showed no clear associations with correlation ($p = 0.346$ and 0.103, respectively). Overall, Reco performance was most consistently associated with precipitation anomalies, with wetter-than-average conditions linked to larger biases, higher RMSE, and weaker temporal agreement, whereas warmer climates were associated with lower bias and RMSE.

3.2.3. ET

ET predicted bias increased under wetter conditions and in more humid climates, with little evidence of a temperature effect (Figure 6c). In the mixed-effects model, positive precipitation anomalies were associated with higher bias ($p < 0.001$), with a +10% anomaly corresponding to a ca. +0.05 in the predicted metric (95% CI 0.038–0.062). Bias also increased with aridity index ($p = 0.0043$), where a +0.1 increase in aridity index corresponded to a ca. +0.067 (95% CI 0.2562–1.1006). In contrast, the temperature effect was small and uncertain ($p = 0.700$). The partial-effect lines are approximately linear, with the narrowest confidence intervals for precipitation anomaly, intermediate intervals for aridity index, and the widest for MAT, consistent with the coefficient uncertainties (Table S20 in Supporting Information S3).

Predicted RMSE for evapotranspiration increased with MAT ($p = 0.0626$), with a +5°C increase corresponding to ca. +0.12 in RMSE (95% CI –0.013 to +0.41). RMSE also increased with aridity index, by approximately +0.013 per +0.1 aridity index (95% CI –0.06 to +0.34). By contrast, positive precipitation anomalies showed a tendency toward lower RMSE, although this effect was weak and uncertain ($p = 0.2734$), with a +10% anomaly corresponding to a ca. –0.007 change in RMSE (95% CI –0.02 to +0.006) (Figure 6f). The summary of predicted RMSE across each environmental gradient is presented in Table S21 in Supporting Information S3, including the associated confidence intervals.

For correspondence in variability in evapotranspiration, the effects of temperature and precipitation anomaly were small and statistically indistinguishable from zero ($p = 0.84$, and 0.536, respectively). The aridity index shows a weak negative tendency ($p = 0.3673$; Figure 6i), indicating only a slight decline in r toward more humid conditions. The partial-effect lines are shallow with broad confidence intervals across the observed ranges, consistent with the high uncertainty in the coefficient estimates (Table S22 in Supporting Information S3).

3.3. Performance of JULES in Capturing Interannual Variability of GPP

Across the seven sites with at least five hydrological years of data, JULES consistently underestimated observed annual GPP and poorly represented interannual variability (Figures 7a–7g). Correlations with observations were weak to moderate (r : –0.49 to 0.55), and RMSE ranges from 0.31 to 1.32 kg C m^{–2} yr^{–1}, reflecting substantial model–data mismatch. In savanna sites (NE_WAF, ZA_KRU), JULES generally captured the mean state inconsistently, with correlations ranging from –0.08 to 0.55. At NE_WAM, the model failed to reproduce interannual variability altogether, while ZA_KRU showed the strongest agreement but still underestimated magnitude. Grassland sites showed systematic underestimation of annual GPP at two sites (SN_DHR, ZA_WGN) alongside large positive errors at ZA_CATH, where RMSE exceeded 1.3 kg C m^{–2} yr^{–1}, indicating poor representation of cross-site productivity differences. At the forest site ZM_MON, JULES misrepresented productivity, failing to capture both the direction and amplitude of interannual variability. Consistent with these findings, site-level mean annual biases (Figure 7h) reveal that JULES generally underestimated GPP at savanna and grassland sites, with ZA_CATH as the main exception, and overestimated GPP at ZM_MON. Overall, these

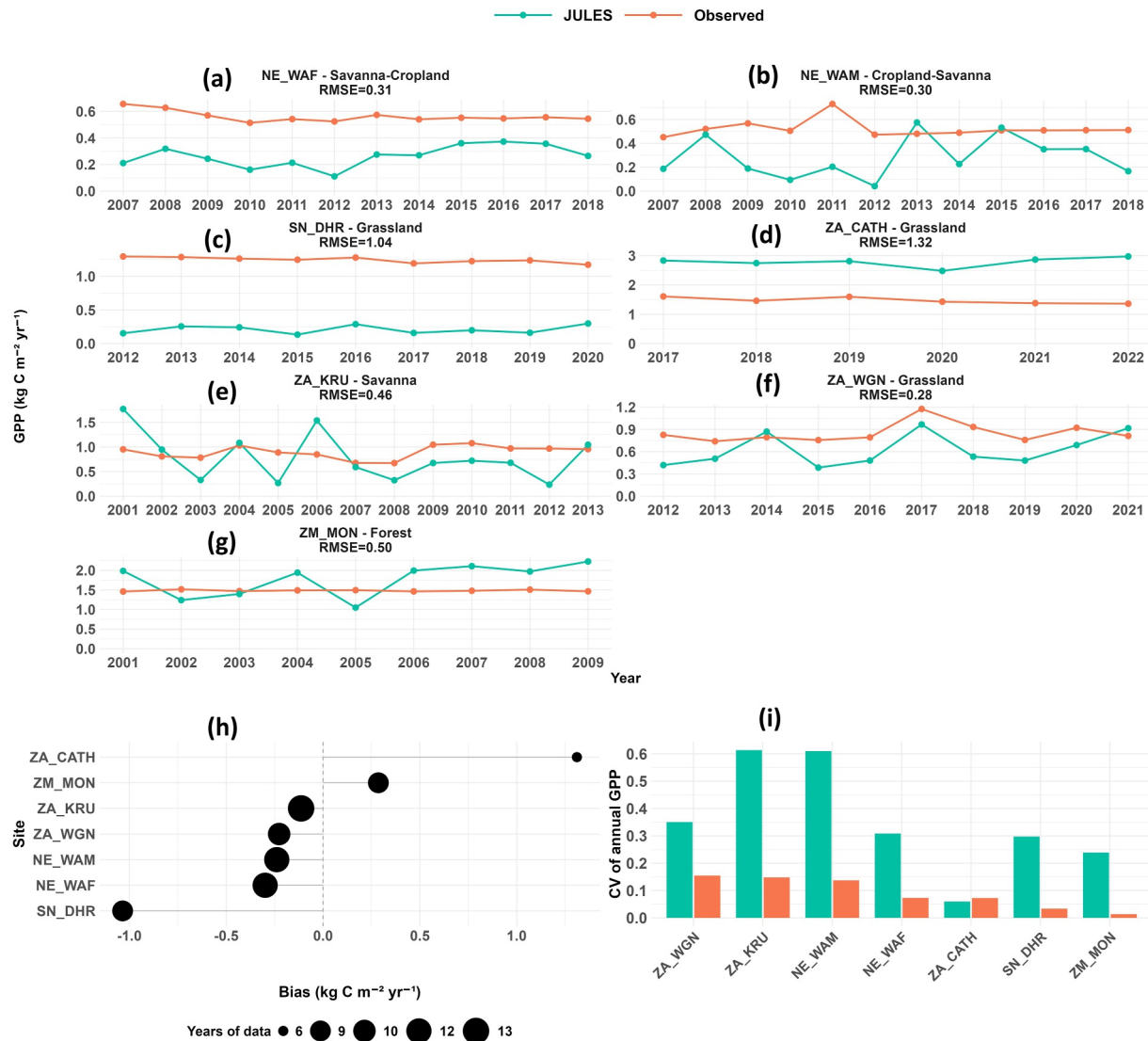


Figure 7. (a–g) Joint UK Land Environment Simulator (JULES) systematically underestimates annual gross primary productivity (GPP) and strongly overestimates interannual variability across most African savanna, grassland, and forest sites. Underestimation is strongest in grasslands (e.g., SN_DHR, ZA_WGN) and savannas (NE_WAF, ZA_KRU), and with high overestimation for ZA_CATH. (h) Mean annual bias (kg C m⁻² yr⁻¹) in GPP across African flux tower sites with ≥5 hydrological years of data. Positive values indicate JULES > observations, and negative values indicate underestimation by JULES. (i) JULES strongly overestimates interannual variability of GPP across African ecosystems, with coefficient of variation values up to six times higher than observations.

results demonstrate that JULES poorly reproduces both the magnitude and temporal dynamics of annual GPP across African savanna, grassland, and forest ecosystems.

The CV of annual GPP was consistently higher in JULES compared with observations across all sites (Figure 7i). At the savanna sites, simulated CVs were four to six times larger than observed, indicating substantial overestimation of year-to-year variability in productivity. Grassland sites also showed systematic overestimation, although with smaller magnitudes, while at the forest site, ZM_MON, JULES simulated much higher variability than observed.

4. Discussion

Our evaluation shows that JULES can reproduce broad seasonal patterns in carbon and water exchange across African ecosystems, but its performance varies substantially among sites, fluxes, and environmental conditions. The LMMs indicate that these differences are not explained by ecosystem type alone: precipitation anomalies,

aridity, and MAT were associated with model performance, although their effects differed among GPP, Reco, and ET. Together with the site-level comparisons and process diagnostics, these results indicate that model performance is particularly sensitive to how JULES represents vegetation dynamics, water availability, and the coupling between carbon and water fluxes.

Across the environmental gradients examined, precipitation anomaly was the most consistently associated predictor of model performance, although its effects differed among fluxes and performance metrics. For GPP, positive precipitation anomalies were associated with improved model–observation correlation but greater bias and RMSE, indicating that JULES captured the direction of precipitation-driven changes in productivity but not their magnitude. GPP bias also became more negative with increasing MAT, suggesting greater underestimation of photosynthesis at warmer sites. This may reflect limitations in the representation of photosynthetic capacity and stomatal responses across species adapted to contrasting thermal environments (Kattge & Knorr, 2007; Mercado et al., 2007). In particular, the parameterisation and temperature response of photosynthetic capacity, including V_{cmax} , may not adequately capture species-level thermal acclimation and adaptation in tropical and semi-arid ecosystems (Kattge & Knorr, 2007; Mercado et al., 2007). Photosynthesis can be strongly constrained when temperatures exceed species-specific optima, particularly in savannas and grasslands (Lomax et al., 2024), while heat stress can further suppress carbon assimilation through protective physiological responses (Way & Yamori, 2014). These findings are particularly relevant to drylands, where precipitation variability strongly regulates productivity and carbon exchange, and where ecosystem responses may persist beyond the year of a rainfall anomaly through precipitation legacy effects (Bell et al., 2012; Delgado-Balbuena et al., 2019; Poulter et al., 2014; Uuh-Sonda et al., 2018; Verduzco et al., 2015).

The interannual variability GPP analysis provides supporting evidence that JULES may not adequately represent the sensitivity of African ecosystem productivity to environmental variability. Across the seven sites with at least five hydrological years, JULES generally underestimated annual GPP and poorly represented interannual variability in almost all sites, with simulated coefficients of variation substantially exceeding those observed at many savanna, grassland, and forest sites. This contrasts with the broad seasonal agreement observed at many sites and suggests that JULES can capture the general timing of precipitation-driven productivity while misrepresenting the magnitude and persistence of year-to-year responses. Such discrepancies may reflect limitations in representing vegetation dynamics and soil-moisture feedbacks (Best et al., 2011; Harper et al., 2021). In highly seasonal ecosystems, interannual productivity is closely linked to rainfall onset, rooting depth, and plant recovery following dry periods (Lomax et al., 2024; Steiner et al., 2024), while errors in phenological timing and simplified phenology schemes can propagate into annual productivity estimates (Harper et al., 2016; Poulter et al., 2014). JULES has previously been reported to underestimate productivity variability (Slevin et al., 2015), although global dryland benchmarking found strong agreement between TRENDY land-surface models, including JULES, and the satellite-derived PML-v2 product in mean-normalized, detrended interannual GPP anomalies, despite disagreement in long-term trends and regional biases, including Sahelian overestimation (Fawcett et al., 2022). This apparent contrast suggests that JULES may capture broad, large-scale signals of interannual productivity variability while failing to reproduce the site-scale processes controlling their magnitude, timing, and persistence, particularly phenological responses, water-stress sensitivity, and the carry-over of dry-season conditions. In humid forests, where productivity often varies less among years because consistently high LAI and deep rooting maintain access to water (Freycon et al., 2015; Kanniah et al., 2013), the greater simulated variability may therefore indicate excessive sensitivity to short-term environmental forcing through the representation of canopy turnover, photosynthetic capacity, or water limitation.

Site-level comparisons provide further insight into the processes underlying these patterns. JULES performed relatively well at the cropland sites, reproducing broad seasonal dynamics despite the use of generic PFTs rather than the crop-specific JULES configuration and therefore without explicit representation of sowing, harvesting, crop rotation, or cultivar-specific phenology (Osborne et al., 2015). At the Sahelian sites, crop development was closely aligned with seasonal rainfall, which may explain why broad seasonal patterns were captured despite the simplified representation of crop processes. However, the diagnostic results suggest that this agreement was not necessarily mechanistically correct. Simulated peak LAI (2.0–2.5; Figure S20 in Supporting Information S2) exceeded reported values (LAI 0.6 at time of harvest) for SN_NKR and SN_RAG, as well as similarly low values reported from comparable Sahelian millet systems (Ibrahim et al., 2016; Roupsard, Audebert, et al., 2020; Velluet et al., 2014). Excessive simulated canopy development coincided with overestimated growing-season GPP and ET peaks. Lower simulated fluxes outside the growing season partly offset these peak-season errors, resulting in

relatively small whole-record mean biases. Similar LAI overestimation was observed at ZM_MON (simulated ~ 5.2 vs. reported ~ 1.6) (Merbold et al., 2009) and CG_TCH (simulated ~ 2.4 vs. reported ~ 0.9 –1) (Caquet et al., 2012), both associated with overestimation of GPP and ET, whereas the underestimated LAI at ML_AGG (simulated 0.9 vs. reported 1.2) (Merbold et al., 2009) coincided with negative GPP and ET biases. These comparisons should be interpreted cautiously because LAI observations differ in timing, measurement method, and spatial representativeness, but they nevertheless indicate that errors in canopy magnitude and phenological development can contribute to seasonal flux biases that may be obscured by whole-record mean metrics.

The crop–savanna transition sites provide an opportunity to examine whether changing land cover is reflected in model performance. NE_WAF and NE_WAM underwent opposing transitions around 2013, with NE_WAF changing from fallow/savanna to cropland and NE_WAM from cropland to fallow/savanna. However, comparison of model–observation relationships before and after these transitions (2005–2012 vs. 2013–2020; Figures S24 and S25 in Supporting Information S2) showed no systematic shift in performance, suggesting that persistent differences among sites, rather than land-cover change alone, dominated the observed patterns. NE_WAF showed moderate GPP agreement and NE_WAM weaker agreement, while Reco correspondence remained very weak at both sites. These results highlight the challenges of representing heterogeneous landscapes undergoing land-use change, where transitions can alter vegetation composition, canopy structure, rooting depth, phenology, and water use, but are not explicitly represented in the model configuration. They also caution against attributing site-level differences in model performance directly to land-cover, or land-cover transitions, where persistent differences in site characteristics, instrumentation, or ecosystem structure may be equally important.

The process diagnostics further indicate that vegetation dynamics and water availability interact to shape model performance. At many seasonally varying sites, precipitation periods coincided with increases in simulated soil-moisture availability and LAI and with seasonal increases in GPP and ET, whereas dry periods were associated with declining simulated water availability, LAI, GPP, and ET. At ML_AGG, SD_DEM, SN_DHR, SN_NKR, and SN_RAG, prolonged periods of low simulated GPP coincided with negative mean GPP biases, even where some wet-season peaks were reproduced. These patterns suggest that JULES may impose excessive water limitation during dry periods at some sites, where vegetation can maintain access to water and carbon uptake through adaptations including deeper rooting, contrasting phenological strategies, and physiological mechanisms that reduce water loss. In Sahelian savannas and agroforestry parklands, for example, woody vegetation can remain active after annual crops and grasses become dormant (Tagesson et al., 2015; Verbruggen et al., 2021); at SN_NKR, *Faidherbia albida* can maintain dry-season activity when the herbaceous layer is senescent (Gaglo et al., 2025; Rouspard et al., 1999). The ORCHIDEE simulation of an African agroforestry parkland illustrates the potential value of representing crop and tree layers separately and allowing differential groundwater access, producing realistic GPP for both vegetation layers in magnitude and seasonality (Gaglo et al., 2025). These examples suggest that representing soil-moisture stress through prescribed PFT-level rooting and stress-response parameters may not fully capture the contrasting water-use strategies of co-existing woody, crop, and herbaceous vegetation, particularly in seasonally dry and heterogeneous ecosystems.

The LMM results provide broader evidence that these water-related processes are important across climatic gradients. Aridity index and precipitation anomaly showed the strongest associations with ET bias and error, with more humid conditions and wetter-than-average years associated with higher ET bias. This suggests that JULES may allocate too much available energy to evapotranspiration when water is abundant, potentially through interactions among canopy conductance, LAI, soil-moisture limitation, and the partitioning of available energy between latent and sensible heat (Best et al., 2011; Blyth et al., 2010). The relatively weak influence of temperature on ET bias further suggests that moisture availability and surface energy partitioning are more important controls on the observed errors than thermal forcing alone. Temperature may also influence ET indirectly through vapour pressure deficit. At the same time, the lack of a consistent relationship between simulated LAI or water stress and flux performance across all sites indicates that neither variable alone provides a sufficient explanation. At CG_TCH and ZA_CATH, for example, seasonal increases in LAI coincided with large simulated GPP and Reco peaks and positive biases across several fluxes, whereas ZM_MON maintained relatively high LAI but experienced strong simulated seasonal water limitation. GH_ANK, by contrast, maintained relatively stable LAI and high simulated water availability but still showed positive Reco and ET biases. These contrasting cases highlight the importance of interactions among vegetation structure, hydrology, and flux processes rather than any single diagnostic variable.

Wetlands provide an especially clear example of the consequences of representing hydrological processes too simply. At BW_GUM and BW_NXR in the Okavango, simulated soil-moisture availability remained close to zero for much of the year and increased only during relatively short wet periods, coinciding with low simulated GPP and ET and negative mean biases in both fluxes. This contrasts with site conditions that maintain vegetation water access: BW_GUM is permanently flooded, while BW_NXR is a seasonal floodplain/lagoon where floating papyrus can access water, with inundation driven by riverine floods peaking in May–August and largely out of phase with local rainfall (October–April) (Helfter et al., 2021a, 2021b). These lateral water inputs and flood dynamics were not represented in the point-scale simulations, which relied primarily on vertical soil hydrology and consequently imposed prolonged, likely unrealistic, root-zone water limitation. By contrast, UG_JIN maintained relatively stable LAI and soil-moisture availability close to one during its 1-year record, yet JULES overestimated GPP while underestimating ET. The contrasting behaviour suggests that the particularly weak wetland performance reflects limitations in both site boundary conditions and the representation of wetland hydrological processes. JULES includes an optional hydrology scheme that estimates saturated and wetland fractions from simulated water-table depth and sub-grid topography (Gedney & Cox, 2003), but this was not used in our point simulations and would not, alone, capture vegetated inundation or delayed river-fed flood pulses. More appropriate site-scale evaluation would therefore require time-varying water-table or inundation constraints, lateral river inflows, and representation of vegetation growing under flooded conditions.

The forest sites further demonstrate that similar seasonal flux patterns can be reproduced through contrasting simulated mechanisms, reflecting limitations in how broad PFT classifications represent vegetation phenology, LAI dynamics, rooting depth, and access to soil water. At the deciduous miombo woodland ZM_MON, JULES reproduced seasonal GPP and ET dynamics comparatively well, although both fluxes were overestimated. Mongu, where ZM_MON is located, is strongly seasonal, with precipitation and soil-water availability important controls on carbon exchange (Merbold et al., 2009). Simulated soil-moisture availability declined strongly during dry periods, while LAI remained high and nearly invariant at approximately 5.1–5.2, suggesting that JULES reproduced the seasonal flux cycle primarily through water limitation rather than deciduous canopy dynamics; excessive LAI may also have contributed to the positive biases. At the evergreen GH_ANK site, high simulated LAI was broadly consistent with its classification, but weak GPP correlation indicated poor representation of shorter-term variability. Positive Reco and ET biases further indicated excessive simulated carbon release and water loss despite little sustained simulated water limitation. Although Ankasa experiences a distinct drier period from approximately December to April (Fattore et al., 2014), available site literature does not establish substantial drought stress or pronounced canopy leaf loss.

The environmental-gradient results also reveal distinct behaviour for ecosystem respiration. Reco bias and RMSE decreased with increasing MAT, while positive precipitation anomalies were associated with larger bias, higher RMSE, and weaker model–observation correlation. The stronger performance of Reco at warmer sites may partly reflect limitations in the temperature-response formulation used to represent respiration across contrasting biomes (Burke et al., 2017). Larger errors during unusually wet periods could also arise if JULES does not capture short-lived respiration pulses following rainfall. Rapid rewetting of dry soils can produce transient increases in CO₂ efflux through both enhanced biological respiration and the physical displacement of CO₂-rich soil air (S. Chen et al., 2008; Huxman et al., 2004). Although the half-hourly EC data used here provide substantially finer temporal resolution than daily data, such short-lived responses may still be difficult to isolate reliably from flux-partitioned Reco, particularly where precipitation affects EC measurement quality or where the observed signal is comparable to measurement uncertainty (Cunliffe et al., 2022; Zhu et al., 2023).

The contrasting positive and negative Reco biases among sites suggest that no single process explains the model errors. At ML_AGG, SD_DEM, and SN_DHR, Reco was underestimated, whereas other sites showed substantial overestimation. In seasonally dry grasslands, the absence of photodegradation in JULES may contribute to negative biases because exposed litter can lose carbon through solar degradation, subsequently also becoming more accessible to microbial decomposition (Austin et al., 2016; Berenstecher et al., 2020; Hewins et al., 2019; Méndez et al., 2019; Romich & King, 2026). However, this mechanism cannot explain the positive biases elsewhere. The contrasting errors instead point to broader uncertainty in litter inputs, autotrophic respiration, soil-carbon turnover, and their responses to temperature, drying, and rewetting. Excessive simulated LAI and productivity could increase plant respiration and litter inputs at some sites, whereas excessive water stress could suppress respiration at others.

Interpretation of Reco and GPP requires caution because they are not directly measured by the EC system, but are partitioned from, quality-controlled, and gap-filled EC-derived NEE. They should therefore be regarded as model-derived estimates constrained by EC data, rather than direct observations. The light-response-curve approach used here is widely applied and has been evaluated across diverse FLUXNET sites, including some African savanna ecosystems (Lasslop et al., 2010; Maluleke et al., 2024). However, our simplified implementation does not explicitly account for soil-moisture availability, water-table dynamics, or inundation, and may not capture differences in daytime and nighttime respiration responses to environmental conditions. These assumptions can introduce additional uncertainty, particularly under wetland or water-limited conditions. For example, allowing asymmetric daytime and nighttime temperature sensitivities and incorporating relative humidity can alter Reco estimates, with humidity-related differences particularly pronounced during dry periods (Li et al., 2022). Consequently, the Reco results provide useful evidence for evaluating model behaviour, but the magnitude and attribution of model–data mismatches should be interpreted alongside uncertainty in the EC-derived and subsequently partitioned benchmark.

Taken together, these results identify several priorities for improving JULES performance across African ecosystems. These include improving the representation of (a) African plant traits (LAI, phenology, rooting depth and access to deep soil water); (b) crop-specific growth, management, and land-use transitions; (c) interactions between heterogeneous woody, herbaceous and crop vegetation; (d) wetland water-table and inundation dynamics; and (e) respiration processes in seasonally dry ecosystems.

More broadly, these findings demonstrate the value of evaluating land-surface models across large networks spanning diverse climatic and ecological conditions. Although a handful of sites included here have featured in previous JULES calibration or evaluation studies, most provide new tests of model performance, and the substantial variation in model skill shows that evaluation against a small number of sites is unlikely to produce robust performance across Africa's diverse ecosystems. Importantly, recurring canopy, water-stress, and flux discrepancies across independent sites can reveal generalizable model deficiencies and provide a stronger basis for targeted model development and sensitivity experiments. Expanding African flux-tower networks and integrating them into model evaluation will therefore be important for identifying the vegetation, hydrological, and ecosystem processes that most consistently limit model performance, ultimately improving land-surface models and their capacity to represent African carbon and water cycles and project ecosystem responses to climatic and land-use change.

5. Conclusion

Our evaluation of JULES across African flux-tower sites shows that the model can reproduce broad seasonal patterns in carbon and water exchange, but that its performance varies substantially among sites, fluxes, and environmental conditions. JULES generally captured the timing of seasonal productivity and water fluxes at several sites but showed greater difficulty reproducing the magnitude and interannual variability of GPP and the dynamics of ecosystem respiration. These limitations were particularly evident in savanna and grassland ecosystems, where productivity and carbon exchange are strongly influenced by rainfall variability, phenological strategies, and plant access to water. Site-level diagnostics further indicate that errors in simulated LAI and water limitation can contribute to flux biases, while contrasting responses among woody, crop, and herbaceous vegetation highlight limitations in representing diverse plant functional strategies within heterogeneous landscapes.

Across environmental gradients, precipitation anomaly was the most consistently associated predictor of model performance, with wetter-than-average conditions generally associated with larger errors in GPP and Reco and weaker agreement for Reco, while aridity was strongly associated with ET performance. Increasing MAT was also associated with greater GPP underestimation, highlighting the potential importance of improving the representation of photosynthetic capacity and thermal responses across African vegetation. Together, these findings indicate that improving JULES performance will require more than broad ecosystem-specific calibration: it will require better representation of vegetation phenology and functional strategies, water availability and access, and the coupling of carbon and water processes.

Our expanded evaluation network provides a broader basis for identifying these limitations. Most sites included here have not featured prominently in previous multi-site LSM evaluations, and the substantial variation in model performance demonstrates the value of testing models across diverse African climates, ecosystems, and

hydrological conditions. Recurring discrepancies in canopy dynamics, water stress, and fluxes across independent sites provide opportunities to identify generalisable model deficiencies and prioritise targeted model development and sensitivity experiments. Addressing these limitations, alongside improved site characterisation of vegetation, soils, management, and hydrological dynamics, will strengthen land-surface models and their capacity to represent African carbon and water cycles and project ecosystem responses to climatic and land-use change.

Conflict of Interest

The authors declare no conflicts of interest relevant to this study.

Availability Statement

Data preparation, analysis code and the experiment-specific Rose suite configurations for JULES is available at <https://doi.org/10.5281/zenodo.17609933> (Akhabue & Cunliffe, 2026). The Google Earth Engine repository for data preprocessing can be accessed by registered Earth Engine users at https://earthengine.google.com/users/akhasfaith/ERA5_met_data. The JULES model source code is publicly available through the official Met Office GitHub repository at <https://github.com/MetOffice/jules>, with accompanying documentation available at <https://metoffice.github.io/jules>. The version of JULES used in this study is version 7.1 (https://jules-lsm.github.io/vn7.1/release_notes/JULES7-1.html). ERA5-Land are available at <https://cds.climate.copernicus.eu/datasets/reanalysis-era5-land?tab=overview> (Muñoz Sabater, 2019), TerraClimate data are available at http://developers.google.com/earth-engine/datasets/catalog/IDAHO_EPSCOR_TERRACLIMATE (Abatzoglou et al., 2018). While we do not have permission to redistribute the flux data sets used in this study, data obtained via FLUXNET and AMMA-CATCH remain available through their respective data portals <https://fluxnet.org/data/fluxnet2015-dataset/> (Pastorello et al., 2020) and <http://bd.amma-catch.org/main.jsf> (AMMA-CATCH, 1990; Galle et al., 2018) (subject to registration and their access conditions). For flux data sets provided directly by site data owners, we are happy to facilitate discussions between prospective users and the relevant data owners. Information on all sites are provided in the supplementary information, readers can also contact authors and data owners directly through the information provided. For the purpose of open access, the author has applied a Creative Commons Attribution (CC BY) licence to any author accepted manuscript version arising from this submission, in accordance with the University of Exeter's Rights Retention policy.

References

- Abatzoglou, J. T., Dobrowski, S. Z., Parks, S. A., & Hegewisch, K. C. (2018). TerraClimate, a high-resolution global dataset of monthly climate and climatic water balance from 1958–2015. *Scientific Data*, 5(1), 170191. <https://doi.org/10.1038/sdata.2017.191>
- Ahlström, A., Raupach, M. R., Schurgers, G., Smith, B., Arnett, A., Jung, M., et al. (2015). The dominant role of semi-arid ecosystems in the trend and variability of the land CO₂ sink. *Science*, 348(6237), 895–899. <https://doi.org/10.1126/science.aaa1668>
- Akhabue, E. F., & Cunliffe, A. (2026). TESS-Laboratory/Akhabue_et_al_evaluating_JULES_with_African_flux_sites: V0.04 (version v0.04) [Computer software]. *Zenodo*. <https://doi.org/10.5281/zenodo.18764959>
- AMMA-CATCH. (1990). AMMA-CATCH: A hydrological, meteorological and ecological observatory on West Africa. <https://doi.org/10.17178/AMMA-CATCH.all>
- Ardö, J., Mölder, M., El-Tahir, B. A., & Elkhidir, H. A. M. (2008). Seasonal variation of carbon fluxes in a sparse savanna in semi arid Sudan. *Carbon Balance and Management*, 3(1), 7. <https://doi.org/10.1186/1750-0680-3-7>
- Austin, A. T., Méndez, M. S., & Ballaré, C. L. (2016). Photodegradation alleviates the lignin bottleneck for carbon turnover in terrestrial ecosystems. *Proceedings of the National Academy of Sciences*, 113(16), 4392–4397. <https://doi.org/10.1073/pnas.1516157113>
- Baldocchi, D. D. (2020). How eddy covariance flux measurements have contributed to our understanding of *Global Change Biology*. *Global Change Biology*, 26(1), 242–260. <https://doi.org/10.1111/gcb.14807>
- Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67(1). <https://doi.org/10.18637/jss.v067.i01>
- Bell, T. W., Menzer, O., Troyo-Díquez, E., & Oechel, W. C. (2012). Carbon dioxide exchange over multiple temporal scales in an arid shrub ecosystem near La Paz, Baja California Sur, Mexico. *Global Change Biology*, 18(8), 2570–2582. <https://doi.org/10.1111/j.1365-2486.2012.02720.x>
- Berenstecher, P., Vivanco, L., Pérez, L. I., Ballaré, C. L., & Austin, A. T. (2020). Sunlight doubles aboveground carbon loss in a seasonally dry woodland in Patagonia. *Current Biology*, 30(16), 3243–3251.e3. <https://doi.org/10.1016/j.cub.2020.06.005>
- Best, M. J., Pryor, M., Clark, D. B., Rooney, G. G., Essery, R. L. H., Ménard, C. B., et al. (2011). The Joint UK Land Environment Simulator (JULES), model description—Part 1: Energy and water fluxes. *Geoscientific Model Development*, 4(3), 677–699. <https://doi.org/10.5194/gmd-4-677-2011>
- Blyth, E., Clark, D. B., Ellis, R., Huntingford, C., Los, S., Pryor, M., et al. (2011). A comprehensive set of benchmark tests for a land surface model of simultaneous fluxes of water and carbon at both the global and seasonal scale. *Geoscientific Model Development*, 4(2), 255–269. <https://doi.org/10.5194/gmd-4-255-2011>
- Blyth, E., Gash, J., Lloyd, A., Pryor, M., Weedon, G. P., & Shuttleworth, J. (2010). Evaluating the JULES land surface model energy fluxes using FLUXNET data. *Journal of Hydrometeorology*, 11(2), 509–519. <https://doi.org/10.1175/2009JHM1183.1>

Acknowledgments

We thankfully acknowledge the Oppenheimer Generations Research and Conservation (OGRC), Sarah Turvill, and the University of Exeter for funding this project as part of the Oppenheimer Programme in African Landscape Systems (OPALS; <https://opals-exeter.org/>). We acknowledge that flux tower measurements used in this study are from AMMA CATCH, FLUXNET 2015, South African Environmental Observation Network (SAEON), and directly sourced from data owners. We acknowledge Sue van Rensburg and Michele Toucher for providing flux data from Cathedral peak South Africa (which is part of SAEON), and Matthew Saunders for providing flux data from the UG_JIN site in Uganda. We also thank Guy Lomax and Hugh Graham for providing statistical advice. We acknowledge the ML-AGG and SN-RAG sites are supported by AMMA-CATCH SNO and maintained by F. Timouk. T.T. and the Dahra field site acknowledge funding from FORMAS (Dnr 2021-00644; 2023-02436), Carl Tryggers Stiftelse, Fysiografen, the Swedish National Space Agency (SNSA Dnr 2025-00108), and BECC. The EC sites in Senegal (SN_NKR and SN_RAG) are supported by the RIFT project of the exploratory research program FairCarboN that received government funding managed by the Agence Nationale de la Recherche under the France 2030 program, reference ANR-22-PEXF-0004; and by the Horizon Europe project GALILEO, funded by the European Union under Grant Agreement N° 101181623. M. C.D.R. is supported part by the H2020 4C project no. 821003 and part by the NetZeroPlus (NZ+) grant funded by UKRI-BBSRC award BB/V011588/1. A.B.H. was supported by the BBSRC NetZeroPlus award (BB/V011588/1) and the EPSRC ADD-TREES award (EP/Y005597/1). The EC sites in Botswana (BW_GUM and BW_NXR) are funded by the Gordon and Betty Moore Foundation through grant GBM11519, with previous support (2016–2021) from the UK Natural Environment Research Council (Grants NE/N015746/1 and NE/N015746/2). We also acknowledge the use of compute resources provided by the UK NERC and Met Office Monsoon High Performance Computing (HPC) facility, which supported model simulations for this work. The authors thank the reviewers and the editor for their constructive comments, which significantly improved the manuscript.

- Bonal, D., Burban, B., Stahl, C., Wagner, F., & Hérault, B. (2016). The response of tropical rainforests to drought—Lessons from recent research and future prospects. *Annals of Forest Science*, 73(1), 27–44. <https://doi.org/10.1007/s13595-015-0522-5>
- Burba, G. (2013). *Eddy covariance method for scientific, industrial, agricultural, and regulatory applications: A field book on measuring ecosystem gas exchange and areal emission rates*. LI-COR Biosciences.
- Burke, E. J., Chadburn, S. E., & Ekici, A. (2017). A vertical representation of soil carbon in the JULES land surface scheme (vn4.3_permafrost) with a focus on permafrost regions. *Geoscientific Model Development*, 10(2), 959–975. <https://doi.org/10.5194/gmd-10-959-2017>
- Burton, C., Betts, R., Cardoso, M., Feldpausch, T. R., Harper, A., Jones, C. D., et al. (2019). Representation of fire, land-use change and vegetation dynamics in the Joint UK Land Environment Simulator vn4.9 (JULES). *Geoscientific Model Development*, 12(1), 179–193. <https://doi.org/10.5194/gmd-12-179-2019>
- Caquet, B., De Grandcourt, A., Thongo M'bou, A., Epron, D., Kinana, A., Saint André, L., & Nouvellon, Y. (2012). Soil carbon balance in a tropical grassland: Estimation of soil respiration and its partitioning using a semi-empirical model. *Agricultural and Forest Meteorology*, 158–159, 71–79. <https://doi.org/10.1016/j.agrformet.2012.02.008>
- Chadburn, S., Burke, E., Essery, R., Boike, J., Langer, M., Heikenfeld, M., et al. (2015). An improved representation of physical permafrost dynamics in the JULES land-surface model. *Geoscientific Model Development*, 8(5), 1493–1508. <https://doi.org/10.5194/gmd-8-1493-2015>
- Chen, S., Lin, G., Huang, J., & He, M. (2008). Responses of soil respiration to simulated precipitation pulses in semiarid steppe under different grazing regimes. *Journal of Plant Ecology*, 1(4), 237–246. <https://doi.org/10.1093/jpe/rtn020>
- Chen, T., & Guestrin, C. (2016). XGBoost: A scalable tree boosting System. In *Proceedings of the 22nd ACM SIGKDD International Conference on Knowledge Discovery and Data Mining* (pp. 785–794). <https://doi.org/10.1145/2939672.2939785>
- Chu, H., Luo, X., Ouyang, Z., Chan, W. S., Dengel, S., Biraud, S. C., et al. (2021). Representativeness of Eddy-Covariance flux footprints for areas surrounding AmeriFlux sites. *Agricultural and Forest Meteorology*, 301–302, 108350. <https://doi.org/10.1016/j.agrformet.2021.108350>
- Clark, D. B., Mercado, L. M., Sitch, S., Jones, C. D., Gedney, N., Best, M. J., et al. (2011). The Joint UK Land Environment Simulator (JULES), model description—Part 2: Carbon fluxes and vegetation dynamics. *Geoscientific Model Development*, 4(3), 701–722. <https://doi.org/10.5194/gmd-4-701-2011>
- Cosby, B. J., Hornberger, G. M., Clapp, R. B., & Ginn, T. R. (1984). A statistical exploration of the relationships of soil moisture characteristics to the physical properties of soils. *Water Resources Research*, 20(6), 682–690. <https://doi.org/10.1029/WR020i006p0682>
- Cunliffe, A. M., Boschetti, F., Clement, R., Sitch, S., Anderson, K., Duman, T., et al. (2022). Strong correspondence in evapotranspiration and carbon dioxide fluxes between different Eddy covariance systems enables quantification of landscape heterogeneity in Dryland fluxes. *Journal of Geophysical Research: Biogeosciences*, 127(8), e2021JG006240. <https://doi.org/10.1029/2021JG006240>
- Dankers, R., Burke, E. J., & Price, J. (2011). Simulation of permafrost and seasonal thaw depth in the JULES land surface scheme. *The Cryosphere*, 5(3), 773–790. <https://doi.org/10.5194/tc-5-773-2011>
- Davies, R. W., Ryan, C. M., Harrison, R. D., Dexter, K. G., Ahrends, A., te Beest, M., et al. (2023). Precipitation gradients drive high tree species turnover in the woodlands of eastern and southern Africa. *Ecography*, 2023(10), e06720. <https://doi.org/10.1111/ecog.06720>
- Delgado-Balbuena, J., Arredondo, J. T., Loeschner, H. W., Pineda-Martínez, L. F., Carbajal, J. N., & Vargas, R. (2019). Seasonal precipitation legacy effects determine the carbon balance of a semiarid grassland. *Journal of Geophysical Research: Biogeosciences*, 124(4), 987–1000. <https://doi.org/10.1029/2018JG004799>
- Dinku, T. (2019). Challenges with availability and quality of climate data in Africa. In *Extreme hydrology and climate variability* (pp. 71–80). Elsevier. <https://doi.org/10.1016/B978-0-12-815998-9.00007-5>
- Dunn, A. L., Barford, C. C., Wofsy, S. C., Goulden, M. L., & Daube, B. C. (2007). A long-term record of carbon exchange in a boreal black spruce forest: Means, responses to interannual variability, and decadal trends. *Global Change Biology*, 13(3), 577–590. <https://doi.org/10.1111/j.1365-2486.2006.01221.x>
- Eshetu, S. B., Kipkulei, H. K., Koepke, J., Kächele, H., Sieber, S., & Löhr, K. (2024). Impact of forest landscape restoration in combating soil erosion in the Lake Abaya catchment, Southern Ethiopia. *Environmental Monitoring and Assessment*, 196(3), 228. <https://doi.org/10.1007/s10661-024-12378-8>
- Farouki, O. T. (1981). The thermal properties of soils in cold regions. *Cold Regions Science and Technology*, 5(1), 67–75. [https://doi.org/10.1016/0165-232X\(81\)90041-0](https://doi.org/10.1016/0165-232X(81)90041-0)
- Fattore, F., Bertolini, T., Materia, S., Gualdi, S., Thongo M'Bou, A., Nicolini, G., et al. (2014). Seasonal trends of dry and bulk concentration of nitrogen compounds over a rain forest in Ghana. *Biogeosciences*, 11(11), 3069–3081. <https://doi.org/10.5194/bg-11-3069-2014>
- Fawcett, D., Cunliffe, A. M., Sitch, S., O'Sullivan, M., Anderson, K., Brazier, R. E., et al. (2022). Assessing model predictions of carbon dynamics in global drylands. *Frontiers in Environmental Science*, 10, 790200. <https://doi.org/10.3389/fenvs.2022.790200>
- Fensham, R. J., Fraser, J., MacDermott, H. J., & Firn, J. (2015). Dominant tree species are at risk from exaggerated drought under climate change. *Global Change Biology*, 21(10), 3777–3785. <https://doi.org/10.1111/gcb.12981>
- Fisher, R. A., & Koven, C. D. (2020). Perspectives on the future of land surface models and the challenges of representing complex terrestrial systems. *Journal of Advances in Modeling Earth Systems*, 12(4), e2018MS001453. <https://doi.org/10.1029/2018MS001453>
- Freycon, V., Wonkam, C., Fayolle, A., Laclau, J.-P., Lucot, E., Jourdan, C., et al. (2015). Tree roots can penetrate deeply in African semi-deciduous rain forests: Evidence from two common soil types. *Journal of Tropical Ecology*, 31(1), 13–23. <https://doi.org/10.1017/S0266467414000595>
- Friedlingstein, P., Meinshausen, M., Arora, V. K., Jones, C. D., Anav, A., Liddicoat, S. K., & Knutti, R. (2014). Uncertainties in CMIP5 climate projections due to carbon cycle feedbacks. *Journal of Climate*, 27(2), 511–526. <https://doi.org/10.1175/JCLI-D-12-00579.1>
- Gaglo, E. K., Chaste, E., Luyssaert, S., Rouspard, O., Jourdan, C., Sow, S., et al. (2025). Sensitivity of a Sahelian groundwater-based agroforestry system to tree density and water availability using the land surface model ORCHIDEE (r7949). *Biogeosciences*. <https://doi.org/10.5194/egusphere-2025-1102>
- Galle, S., Grippa, M., Peugeot, C., Moussa, I. B., Cappelaere, B., Demarty, J., et al. (2018). AMMA-CATCH, a critical Zone observatory in West Africa monitoring a Region in transition. *Vadose Zone Journal*, 17(1), 1–24. <https://doi.org/10.2136/vzj2018.03.0062>
- Gardiya Weligamage, H., Fowler, K., Peterson, T. J., Saft, M., Peel, M. C., & Ryu, D. (2023). Partitioning of precipitation into terrestrial water balance components under a drying climate. *Water Resources Research*, 59(5), e2022WR033538. <https://doi.org/10.1029/2022WR033538>
- Gedney, N., & Cox, P. M. (2003). The sensitivity of global climate model simulations to the representation of soil moisture heterogeneity. *Journal of Hydrometeorology*, 4(6), 1265–1275. [https://doi.org/10.1175/1525-7541\(2003\)004<1265:tsogcm>2.0.co;2](https://doi.org/10.1175/1525-7541(2003)004<1265:tsogcm>2.0.co;2)
- Harper, A. B., Cox, P. M., Friedlingstein, P., Wiltshire, A. J., Jones, C. D., Sitch, S., et al. (2016). Improved representation of plant functional types and physiology in the Joint UK Land Environment Simulator (JULES v4.2) using plant trait information. *Geoscientific Model Development*, 9(7), 2415–2440. <https://doi.org/10.5194/gmd-9-2415-2016>

- Harper, A. B., Williams, K. E., McGuire, P. C., Duran Rojas, M. C., Hemming, D., Verhoef, A., et al. (2020). Improvement of modelling plant responses to low soil moisture in JULESv4.9 and evaluation against flux tower measurements [Preprint]. *Climate and Earth system modeling*. <https://doi.org/10.5194/gmd-2020-273>
- Harper, A. B., Williams, K. E., McGuire, P. C., Duran Rojas, M. C., Hemming, D., Verhoef, A., et al. (2021). Improvement of modeling plant responses to low soil moisture in JULESv4.9 and evaluation against flux tower measurements. *Geoscientific Model Development*, 14(6), 3269–3294. <https://doi.org/10.5194/gmd-14-3269-2021>
- Helfter, C., Gondwe, M., & Skiba, U. (2021a). *Methane and carbon dioxide fluxes from a permanent wetland in the Okavango Delta, Botswana, 2018–2020*. NERC Environmental Information Data Centre. <https://doi.org/10.5285/d366ed40-af8c-42be-86f2-bb90b11a659e>
- Helfter, C., Gondwe, M., & Skiba, U. (2021b). *Methane and carbon dioxide fluxes from a seasonal wetland in the Okavango Delta, Botswana, 2018–2020*. NERC Environmental Information Data Centre. <https://doi.org/10.5285/2170ebd0-7e6f-4871-97d9-1d42e210468f>
- Hengl, T., Miller, M. A. E., Križan, J., Shepherd, K. D., Sila, A., Kilibarda, M., et al. (2021). African soil properties and nutrients mapped at 30 m spatial resolution using two-scale ensemble machine learning. *Scientific Reports*, 11(1), 6130. <https://doi.org/10.1038/s41598-021-85639-y>
- Hewins, D. B., Lee, H., Barnes, P. W., McDowell, N. G., Pockman, W. T., Rahn, T., & Throop, H. L. (2019). Early exposure to UV radiation overshadowed by precipitation and litter quality as drivers of decomposition in the northern Chihuahuan Desert. *PLoS One*, 14(2), e0210470. <https://doi.org/10.1371/journal.pone.0210470>
- Huang, J., Li, Y., Fu, C., Chen, F., Fu, Q., Dai, A., et al. (2017). Dryland climate change: Recent progress and challenges. *Reviews of Geophysics*, 55(3), 719–778. <https://doi.org/10.1002/2016RG000550>
- Huxman, T. E., Snyder, K. A., Tissue, D., Leffler, A. J., Ogle, K., Pockman, W. T., et al. (2004). Precipitation pulses and carbon fluxes in semiarid and arid ecosystems. *Oecologia*, 141(2), 254–268. <https://doi.org/10.1007/s00442-004-1682-4>
- Ibrahim, A., Abaidoo, R. C., Fatondji, D., & Opoku, A. (2016). Determinants of fertilizer microdosing-induced yield increment of pearl millet on an acid sandy soil. *Experimental Agriculture*, 52(4), 562–578. <https://doi.org/10.1017/S0014479715000241>
- IPBES (2018). The IPBES regional assessment report on biodiversity and ecosystem services for Africa. In E. Archer, L. E. Dziba, K. J. Mulongoy, M. A. Maoela, & M. Walters (Eds.), *IPBES secretariat*. Zenodo. <https://doi.org/10.5281/ZENODO.3236177>
- James, R., Washington, R., Abiodun, B., Kay, G., Mutemi, J., Pokam, W., et al. (2018). Evaluating climate models with an African lens. *Bulletin of the American Meteorological Society*, 99(2), 313–336. <https://doi.org/10.1175/BAMS-D-16-0090.1>
- Jasechko, S., Sharp, Z. D., Gibson, J. J., Birks, S. J., Yi, Y., & Fawcett, P. J. (2013). Terrestrial water fluxes dominated by transpiration. *Nature*, 496(7445), 347–350. <https://doi.org/10.1038/nature11983>
- Jones, M. M., Fletcher, R., Kruger, L., Monadjem, A., Simelane, P., & McCleery, R. (2022). Drought limits large trees in African savannas with or without elephants. *Austral Ecology*, 47(8), 1668–1684. <https://doi.org/10.1111/aec.13244>
- Kanniah, K. D., Beringer, J., & Hutley, L. B. (2013). Response of savanna gross primary productivity to interannual variability in rainfall: Results of a remote sensing based light use efficiency model. *Progress in Physical Geography: Earth and Environment*, 37(5), 642–663. <https://doi.org/10.1177/0309133313490006>
- Kapuka, A., & Hlásny, T. (2021). Climate change impacts on ecosystems and adaptation options in nine countries in southern Africa: What do we know? *Ecosphere*, 12(12), e03860. <https://doi.org/10.1002/ecs2.3860>
- Kattge, J., & Knorr, W. (2007). Temperature acclimation in a biochemical model of photosynthesis: A reanalysis of data from 36 species. *Plant, Cell and Environment*, 30(9), 1176–1190. <https://doi.org/10.1111/j.1365-3040.2007.01690.x>
- Lasslop, G., Reichstein, M., Papale, D., Richardson, A. D., Arneeth, A., Barr, A., et al. (2010). Separation of net ecosystem exchange into assimilation and respiration using a light response curve approach: Critical issues and global evaluation. *Global Change Biology*, 16(1), 187–208. <https://doi.org/10.1111/j.1365-2486.2009.02041.x>
- Lavarenne, J., & Leroux, L. (2024). High-resolution mapping of available water content in Senegal using iSDA Africa dataset and USDA Rosetta3 model. *European Journal of Soil Science*, 75(2), e13461. <https://doi.org/10.1111/ejss.13461>
- Lawrence, D. M., Fisher, R. A., Koven, C. D., Oleson, K. W., Swenson, S. C., Bonan, G., et al. (2019). The community land model version 5: Description of new features, benchmarking, and impact of forcing uncertainty. *Journal of Advances in Modeling Earth Systems*, 11(12), 4245–4287. <https://doi.org/10.1029/2018MS001583>
- Li, N., Shao, J., Zhou, G., Zhou, L., Du, Z., & Zhou, X. (2022). Improving estimations of ecosystem respiration with asymmetric daytime and nighttime temperature sensitivity and relative humidity. *Agricultural and Forest Meteorology*, 312, 108709. <https://doi.org/10.1016/j.agrformet.2021.108709>
- Liu, X., Chen, X., Li, R., Long, F., Zhang, L., Zhang, Q., & Li, J. (2017). Water-use efficiency of an old-growth forest in lower subtropical China. *Scientific Reports*, 7(1), 42761. <https://doi.org/10.1038/srep42761>
- Liu, X., Wang, Z., Han, G., Cui, Y., Hou, D., & Wang, H. (2024). Increasing precipitation promotes carbon exchange in the *Stipa breviflora* desert steppe ecosystem. <https://doi.org/10.21203/rs.3.rs-4340518/v1>
- Lomax, G. A., Powell, T. W. R., Lenton, T. M., Economou, T., & Cunliffe, A. M. (2024). Untangling the environmental drivers of gross primary productivity in African rangelands. *Communications Earth & Environment*, 5(1), 500. <https://doi.org/10.1038/s43247-024-01664-5>
- Lotsch, A., Friedl, M. A., Anderson, B. T., & Tucker, C. J. (2003). Coupled vegetation-precipitation variability observed from satellite and climate records. *Geophysical Research Letters*, 30(14), 1774. <https://doi.org/10.1029/2003GL017506>
- Lu, T., Zheng, C., Zhou, B., Wu, J., Wang, X., Zhao, Y., et al. (2023). Response of liquid water and vapor flow to rainfall events in sandy soil of arid and semi-arid regions. *Agronomy*, 13(9), 2424. <https://doi.org/10.3390/agronomy13092424>
- Lüdecke, D. (2018). ggeffects: Tidy data frames of marginal effects from regression models. *Journal of Open Source Software*, 3(26), 772. <https://doi.org/10.21105/joss.00772>
- Lüdecke, D., Ben-Shachar, M., Patil, I., Waggoner, P., & Makowski, D. (2021). Performance: An R package for assessment, comparison and testing of statistical models. *Journal of Open Source Software*, 6(60), 3139. <https://doi.org/10.21105/joss.03139>
- Maes, W. H., Gentile, P., Verhoest, N. E. C., & Miralles, D. G. (2019). Potential evaporation at eddy-covariance sites across the globe. *Hydrology and Earth System Sciences*, 23(2), 925–948. <https://doi.org/10.5194/hess-23-925-2019>
- Maluleke, A., Feig, G., Brümmer, C., Rybachak, O., & Midgley, G. (2024). Evaluation of selected Sentinel-2 remotely sensed vegetation indices and MODIS GPP in representing productivity in semi-arid South African ecosystems. *Journal of Geophysical Research: Biogeosciences*, 129(4), e2023JG007728. <https://doi.org/10.1029/2023JG007728>
- Martin, G. M., Bellouin, N., Collins, W. J., Culverwell, I. D., Halloran, P. R., Hardiman, S. C., et al. (2011). The HadGEM2 family of Met Office Unified Model climate configurations. *Geoscientific Model Development*, 4(3), 723–757. <https://doi.org/10.5194/gmd-4-723-2011>
- Méndez, M. S., Martinez, M. L., Araujo, P. I., & Austin, A. T. (2019). Solar radiation exposure accelerates decomposition and biotic activity in surface litter but not soil in a semiarid woodland ecosystem in Patagonia, Argentina. *Plant and Soil*, 445(1–2), 483–496. <https://doi.org/10.1007/s11104-019-04325-1>

- Merbold, L. M., Ardo, J., Arneth, A., Scholes, R. J., Nouvellon, Y., de Grandcourt, A., et al. (2009). Precipitation as driver of carbon fluxes in 11 African ecosystems. *Biogeosciences*, 6(6), 1027–1041.
- Mercado, L. M., Huntingford, C., Gash, J. H. C., Cox, P. M., & Jögireddy, V. (2007). Improving the representation of radiation interception and photosynthesis for climate model applications. *Tellus B: Chemical and Physical Meteorology*, 59(3), 553. <https://doi.org/10.1111/j.1600-0889.2007.00256.x>
- Miller, M. A. E., Shepherd, K. D., Kisitu, B., & Collinson, J. (2021). iSDAsoil: The first continent-scale soil property map at 30 m resolution provides a soil information revolution for Africa. *PLOS Biology*, 19(11), e3001441. <https://doi.org/10.1371/journal.pbio.3001441>
- Moffat, A. M., Papale, D., Reichstein, M., Hollinger, D. Y., Richardson, A. D., Barr, A. G., et al. (2007). Comprehensive comparison of gap-filling techniques for eddy covariance net carbon fluxes. *Agricultural and Forest Meteorology*, 147(3–4), 209–232. <https://doi.org/10.1016/j.agrformet.2007.08.011>
- Muñoz Sabater, J. (2019). ERA5-Land monthly averaged data from 1950 to present. *Copernicus Climate Change Service (C3S) Climate Data Store (CDS)*. <https://doi.org/10.24381/cds.68d2bb30>
- Nedbal, V., Bernasová, T., Kobesová, M., Tesařová, B., Vácha, A., & Brom, J. (2025). Impact of landscape management and vegetation on water and nutrient runoff from small catchments for over 20 years. *Journal of Environmental Management*, 373, 123748. <https://doi.org/10.1016/j.jenvman.2024.123748>
- Niu, S., Fu, Z., Luo, Y., Stoy, P. C., Keenan, T. F., Poulter, B., et al. (2017). Interannual variability of ecosystem carbon exchange: From observation to prediction. *Global Ecology and Biogeography*, 26(11), 1225–1237. <https://doi.org/10.1111/geb.12633>
- Nouvellon, Y., Moran, M. S., Seen, D. L., Bryant, R., Rambal, S., Ni, W., et al. (2001). Coupling a grassland ecosystem model with Landsat imagery for a 10-year simulation of carbon and water budgets. *Remote Sensing of Environment*, 78(1–2), 131–149. [https://doi.org/10.1016/S0034-4257\(01\)00255-3](https://doi.org/10.1016/S0034-4257(01)00255-3)
- Nunes, L. J. R., Meireles, C. I. R., Pinto Gomes, C. J., & Almeida Ribeiro, N. M. C. (2020). Forest contribution to climate change mitigation: Management oriented to carbon capture and storage. *Climate*, 8(2), 21. <https://doi.org/10.3390/cli8020021>
- Nyasulu, M. K., Fetzer, I., Wang-Erlandsson, L., Stenzel, F., Gerten, D., Rockström, J., & Falkenmark, M. (2024). African rainforest moisture contribution to continental agricultural water consumption. *Agricultural and Forest Meteorology*, 346, 109867. <https://doi.org/10.1016/j.agrfor.2023.109867>
- Oberg, A. L., & Mahoney, D. W. (2007). Linear mixed effects models. In W. T. Ambrosius (Ed.), *Topics in biostatistics* (pp. 213–234). Humana Press. https://doi.org/10.1007/978-1-59745-530-5_11
- Oki, T., & Kanae, S. (2006). Global hydrological cycles and world water resources. *Science*, 313(5790), 1068–1072. <https://doi.org/10.1126/science.1128845>
- Oliver, R. J., Mercado, L. M., Clark, D. B., Huntingford, C., Taylor, C. M., Vidale, P. L., et al. (2022). Improved representation of plant physiology in the JULES-vn5.6 land surface model: Photosynthesis, stomatal conductance and thermal acclimation. *Geoscientific Model Development*, 15(14), 5567–5592. <https://doi.org/10.5194/gmd-15-5567-2022>
- Osborne, T., Gornall, J., Hooker, J., Williams, K., Wiltshire, A., Betts, R., & Wheeler, T. (2015). JULES-crop: A parametrisation of crops in the Joint UK Land Environment Simulator. *Geoscientific Model Development*, 8(4), 1139–1155. <https://doi.org/10.5194/gmd-8-1139-2015>
- O'Sullivan, M., Smith, W. K., Sitch, S., Friedlingstein, P., Arora, V. K., Haverd, V., et al. (2020). Climate-driven variability and trends in plant productivity over recent decades based on three global products. *Global Biogeochemical Cycles*, 34(12), e2020GB006613. <https://doi.org/10.1029/2020GB006613>
- Pastorello, G., Trotta, C., Canfora, E., Chu, H., Christianson, D., Cheah, Y.-W., et al. (2020). The FLUXNET2015 dataset and the ONEFlux processing pipeline for eddy covariance data. *Scientific Data*, 7(1), 225. <https://doi.org/10.1038/s41597-020-0534-3>
- Poulter, B., Frank, D., Ciais, P., Myneni, R. B., Andela, N., Bi, J., et al. (2014). Contribution of semi-arid ecosystems to interannual variability of the global carbon cycle. *Nature*, 509(7502), 600–603. <https://doi.org/10.1038/nature13376>
- Quansah, E., Mauder, M., Balogun, A. A., Amekudzi, L. K., Hingerl, L., Bliefernicht, J., & Kunstmann, H. (2015). Carbon dioxide fluxes from contrasting ecosystems in the Sudanian savanna in West Africa. *Carbon Balance and Management*, 10(1), 1. <https://doi.org/10.1186/s13021-014-0011-4>
- R Core Team. (2021). *R: A Language and environment for statistical computing*. R Foundation for Statistical Computing. Retrieved from <https://www.R-project.org/>
- Reichstein, M., Falge, E., Baldocchi, D., Papale, D., Aubinet, M., Berbigier, P., et al. (2005). On the separation of net ecosystem exchange into assimilation and ecosystem respiration: Review and improved algorithm. *Global Change Biology*, 11(9), 1424–1439. <https://doi.org/10.1111/j.1365-2486.2005.001002.x>
- Romich, T. L., & King, J. Y. (2026). Photodegradation increases solubility of grass litter carbon. *Journal of Geophysical Research: Biogeosciences*, 131(4), e2025JG009387. <https://doi.org/10.1029/2025JG009387>
- Roupsard, O., Audebert, A., Ndour, A. P., Clermont-Dauphin, C., Agbohossou, Y., Sanou, J., et al. (2020). How far does the tree affect the crop in agroforestry? New spatial analysis methods in a *Faidherbia* parkland. *Agriculture, Ecosystems & Environment*, 296, 106928. <https://doi.org/10.1016/j.agee.2020.106928>
- Roupsard, O., Ferhi, A., Granier, A., Pallo, F., Depommier, D., Mallet, B., et al. (1999). Reverse phenology and dry-season water uptake by *Faidherbia albida* (Del.) A. Chev. In an agroforestry parkland of Sudanese West Africa. *Functional Ecology*, 13(4), 460–472. <https://doi.org/10.1046/j.1365-2435.1999.00345.x>
- Salvati, L., Zitti, M., Di Bartolomei, R., & Perini, L. (2013). Climate aridity under changing conditions and implications for the agricultural sector: Italy as a case study. *Geography Journal*, 2013, 1–7. <https://doi.org/10.1155/2013/923173>
- Singer, M. B., Asfaw, D. T., Rosolem, R., Cuthbert, M. O., Miralles, D. G., MacLeod, D., et al. (2021). Hourly potential evapotranspiration at 0.1° resolution for the global land surface from 1981-present. *Scientific Data*, 8(1), 224. <https://doi.org/10.1038/s41597-021-01003-9>
- Sintayehu, D. W. (2018). Impact of climate change on biodiversity and associated key ecosystem services in Africa: A systematic review. *Ecosystem Health and Sustainability*, 4(9), 225–239. <https://doi.org/10.1080/20964129.2018.1530054>
- Sitch, S., Huntingford, C., Gedney, N., Levy, P. E., Lomas, M., Piao, S. L., et al. (2008). Evaluation of the terrestrial carbon cycle, future plant geography and climate-carbon cycle feedbacks using five dynamic Global Vegetation Models (DGVMs): Uncertainty in land carbon cycle feedbacks. *Global Change Biology*, 14(9), 2015–2039. <https://doi.org/10.1111/j.1365-2486.2008.01626.x>
- Slevin, D., Tett, S. F. B., & Williams, M. (2015). Multi-site evaluation of the JULES land surface model using global and local data. *Geoscientific Model Development*, 8(2), 295–316. <https://doi.org/10.5194/gmd-8-295-2015>
- Steiner, B., Scott, R. L., Hu, J., MacBean, N., Richardson, A., & Moore, D. J. P. (2024). Using phenology to unravel differential soil water use and productivity in a semiarid savanna. *Ecosphere*, 15(2), e4762. <https://doi.org/10.1002/ecs2.4762>
- Tagesson, T., Fensholt, R., Cropley, F., Guirio, I., Horion, S., Ehammer, A., & Ardo, J. (2015). Dynamics in carbon exchange fluxes for a grazed semi-arid savanna ecosystem in West Africa. *Agriculture, Ecosystems & Environment*, 205, 15–24. <https://doi.org/10.1016/j.agee.2015.02.017>

- Tao, S., Chave, J., Frison, P.-L., Le Toan, T., Ciais, P., Fang, J., et al. (2022). Increasing and widespread vulnerability of intact tropical rainforests to repeated droughts. *Proceedings of the National Academy of Sciences*, 119(37), e2116626119. <https://doi.org/10.1073/pnas.2116626119>
- Taylor, P. G., Cleveland, C. C., Wieder, W. R., Sullivan, B. W., Doughty, C. E., Dobrowski, S. Z., & Townsend, A. R. (2017). Temperature and rainfall interact to control carbon cycling in tropical forests. *Ecology Letters*, 20(6), 779–788. <https://doi.org/10.1111/ele.12765>
- Te Wierik, S. A., Keune, J., Miralles, D. G., Gupta, J., Artzy-Randrup, Y. A., Gimeno, L., et al. (2022). The contribution of transpiration to precipitation over African watersheds. *Water Resources Research*, 58(11), e2021WR031721. <https://doi.org/10.1029/2021WR031721>
- Thorne, R., & Arain, M. (2015). Influence of low frequency variability on climate and carbon fluxes in a temperate pine Forest in Eastern Canada. *Forests*, 6(8), 2762–2784. <https://doi.org/10.3390/f6082762>
- Ukkola, A. M., Abramowitz, G., & De Kauwe, M. G. (2022). A flux tower dataset tailored for land model evaluation [Preprint]. *Data, Algorithms, and Models*. <https://doi.org/10.5194/essd-2021-181>
- Uuh-Sonda, J. M., Gutiérrez-Jurado, H. A., Figueroa-Espinoza, B., & Méndez-Barroso, L. A. (2018). On the ecohydrology of the Yucatan Peninsula: Evapotranspiration and carbon intake dynamics across an eco-climatic gradient. *Hydrological Processes*, 32(18), 2806–2828. <https://doi.org/10.1002/hyp.13230>
- Van Der Ent, R. J., Savenije, H. H. G., Schaeffli, B., & Steele-Dunne, S. C. (2010). Origin and fate of atmospheric moisture over continents. *Water Resources Research*, 46(9), 2010WR009127. <https://doi.org/10.1029/2010WR009127>
- Velluet, C., Demarty, J., Cappelaere, B., Braud, I., Issoufou, H. B.-A., Boulain, N., et al. (2014). Building a field- and model-based climatology of local water and energy cycles in the cultivated Sahel—Annual budgets and seasonality. *Hydrology and Earth System Sciences*, 18(12), 5001–5024. <https://doi.org/10.5194/hess-18-5001-2014>
- Verbruggen, W., Schurgers, G., Horion, S., Ardö, J., Bernardino, P. N., Cappelaere, B., et al. (2021). Contrasting responses of woody and herbaceous vegetation to altered rainfall characteristics in the Sahel. *Biogeosciences*, 18(1), 77–93. <https://doi.org/10.5194/bg-18-77-2021>
- Verduzco, V. S., Garatuza-Payán, J., Yépez, E. A., Watts, C. J., Rodríguez, J. C., Robles-Morua, A., & Vivoni, E. R. (2015). Variations of net ecosystem production due to seasonal precipitation differences in a tropical dry forest of northwest Mexico. *Journal of Geophysical Research: Biogeosciences*, 120(10), 2081–2094. <https://doi.org/10.1002/2015JG003119>
- Vereecken, H., Weihermüller, L., Assouline, S., Šimůnek, J., Verhoef, A., Herbst, M., et al. (2019). Infiltration from the pedon to global grid scales: An overview and outlook for land surface modeling. *Vadose Zone Journal*, 18(1), 1–53. <https://doi.org/10.2136/vzj2018.10.0191>
- Wang, J., Yu, Q., & Lee, X. (2007). Simulation of crop growth and energy and carbon dioxide fluxes at different time steps from hourly to daily. *Hydrological Processes*, 21(18), 2474–2492. <https://doi.org/10.1002/hyp.6414>
- Wang, J., Zeng, N., & Wang, M. (2016). Interannual variability of the atmospheric CO₂ growth rate: Roles of precipitation and temperature. *Biogeosciences*, 13(8), 2339–2352. <https://doi.org/10.5194/bg-13-2339-2016>
- Way, D. A., & Yamori, W. (2014). Thermal acclimation of photosynthesis: On the importance of adjusting our definitions and accounting for thermal acclimation of respiration. *Photosynthesis Research*, 119(1–2), 89–100. <https://doi.org/10.1007/s11120-013-9873-7>
- Wiltshire, A. J., Duran Rojas, M. C., Edwards, J. M., Gedney, N., Harper, A. B., Hartley, A. J., et al. (2020). JULES-GL7: The Global Land configuration of the Joint UK Land Environment Simulator version 7.0 and 7.2. *Geoscientific Model Development*, 13(2), 483–505. <https://doi.org/10.5194/gmd-13-483-2020>
- Wright, I. J., Reich, P. B., Westoby, M., Ackerly, D. D., Baruch, Z., Bongers, F., et al. (2004). The worldwide leaf economics spectrum. *Nature*, 428(6985), 821–827. <https://doi.org/10.1038/nature02403>
- Xiao, J., Chen, J., Davis, K. J., & Reichstein, M. (2012). Advances in upscaling of eddy covariance measurements of carbon and water fluxes. *Journal of Geophysical Research*, 117(G1), 2011JG001889. <https://doi.org/10.1029/2011JG001889>
- Yan, D., Xu, T., Girma, A., Yuan, Z., Weng, B., Qin, T., et al. (2017). Regional correlation between precipitation and vegetation in the Huang-Huai-Hai River Basin, China.
- Yao, T., Liu, S., Hu, S., & Mo, X. (2024). Evaluation of ecosystem's response to flash drought in water-limited regions of China. *Environmental Research Letters*, 19(12), 124093. <https://doi.org/10.1088/1748-9326/ad8f4a>
- Yue, X., Unger, N., & Zheng, Y. (2015). Distinguishing the drivers of trends in land carbon fluxes and plant volatile emissions over the past 3 decades. *Atmospheric Chemistry and Physics*, 15(20), 11931–11948. <https://doi.org/10.5194/acp-15-11931-2015>
- Yun, J., Liu, J., Baker, D. F., Basu, S., Chevallier, F., Jiang, F., et al. (2025). Interannual variability in African regional ecosystem carbon fluxes and their drivers revealed by satellite observations. *Global Biogeochemical Cycles*, 39(7), e2025GB008597. <https://doi.org/10.1029/2025GB008597>
- Zhang, Q., Shao, M., Jia, X., & Wei, X. (2017). Relationship of climatic and Forest factors to Drought- and heat-induced tree mortality. *PLOS ONE*, 12(1), e0169770. <https://doi.org/10.1371/journal.pone.0169770>
- Zhang, R., Zhao, X., Zuo, X., Qu, H., Degen, A. A., Luo, Y., et al. (2019). Impacts of precipitation on ecosystem carbon fluxes in desert-grasslands in Inner Mongolia, China. *Journal of Geophysical Research: Atmospheres*, 124(3), 1266–1276. <https://doi.org/10.1029/2018JD028419>
- Zheng, Y., Shen, R., Wang, Y., Li, X., Liu, S., Liang, S., et al. (2020). Improved estimate of global gross primary production for reproducing its long-term variation (pp. 1982–2017).
- Zhou, J., Jiang, T., Wang, Y., Su, B., Tao, H., Qin, J., & Zhai, J. (2020). Spatiotemporal variations of aridity index over the Belt and Road region under the 1.5°C and 2.0°C warming scenarios. *Journal of Geographical Sciences*, 30(1), 37–52. <https://doi.org/10.1007/s11442-020-1713-z>
- Zhou, S., Zhang, Y., Caylor, K. K., Luo, Y., Xiao, X., Ciais, P., et al. (2016). Explaining inter-annual variability of gross primary productivity from plant phenology and physiology. *Agricultural and Forest Meteorology*, 226–227, 246–256. <https://doi.org/10.1016/j.agrformet.2016.06.010>
- Zhu, S., Clement, R., McCalmont, J., Davies, C. A., & Hill, T. (2022). Stable gap-filling for longer eddy covariance data gaps: A globally validated machine-learning approach for carbon dioxide, water, and energy fluxes. *Agricultural and Forest Meteorology*, 314, 108777. <https://doi.org/10.1016/j.agrformet.2021.108777>
- Zhu, S., McCalmont, J., Cardenas, L. M., Cunliffe, A. M., Olde, L., Signori-Müller, C., et al. (2023). Gap-filling carbon dioxide, water, energy, and methane fluxes in challenging ecosystems: Comparing between methods, drivers, and gap-lengths. *Agricultural and Forest Meteorology*, 332, 109365. <https://doi.org/10.1016/j.agrformet.2023.109365>
- Zhu, S., Quaife, T., & Hill, T. (2024). Uniform upscaling techniques for eddy covariance FLUXes (UFLUX). *International Journal of Remote Sensing*, 45(5), 1450–1476. <https://doi.org/10.1080/01431161.2024.2312266>
- Zhu, S., Xu, J., Zeng, J., He, P., Wang, Y., Bao, S., et al. (2024). UFLUX-GPP: A cost-effective framework for quantifying daily terrestrial ecosystem carbon uptake using satellite data. *IEEE Transactions on Geoscience and Remote Sensing*, 62, 1–17. <https://doi.org/10.1109/TGRS.2024.3439333>

References From the Supporting Information

- Archibald, S. A., Kirton, A., Van der Merwe, M. R., Scholes, R. J., Williams, C. A., & Hanan, N. (2009). Drivers of inter-annual variability in Net Ecosystem Exchange in a semi-arid savanna ecosystem, South Africa.
- Ardö, J. (2013). A 10-Year dataset of basic meteorology and soil properties in central Sudan. In *Dataset Papers in geosciences 2013* (pp. 1–6).
- Boulain, N., Cappelaere, B., Ramier, D., Issoufou, H., Halilou, O., Seghier, J., et al. (2009). Towards an understanding of coupled physical and biological processes in the cultivated Sahel—2. Vegetation and carbon dynamics. *Journal of Hydrology*, 375(1–2), 190–203. <https://doi.org/10.1016/j.jhydrol.2008.11.045>
- Cappelaere, B., Descroix, L., Lebel, T., Boulain, N., Ramier, D., Laurent, J. P., et al. (2009). The AMMA-CATCH experiment in the cultivated Sahelian area of south-west Niger—Investigating water cycle response to a fluctuating climate and changing environment. *Journal of Hydrology*, 375(1–2), 34–51. <https://doi.org/10.1016/j.jhydrol.2009.06.021>
- Chiti, T., Certini, G., Grieco, E., & Valentini, R. (2010). The role of soil in storing carbon in tropical rainforests: The case of Ankasa Park, Ghana. *Plant Soil*, 331(1–2), 453–461. <https://doi.org/10.1007/s11104-009-0265-x>
- Diongue, D. M. L., Rounsard, O., Do, F. C., Stumpp, C., Orange, D., Sow, S., et al. (2022). Evaluation of parameterisation approaches for estimating soil hydraulic parameters with HYDRUS-1D in the groundnut basin of Senegal. *Hydrological Sciences Journal*, 67(15), 2327–2343. <https://doi.org/10.1080/02626667.2022.2142474>
- Jaars, K., van Zyl, P. G., Beukes, J. P., Hellén, H., Vakkari, V., Josipovic, M., et al. (2016). Measurements of biogenic volatile organic compounds at a grazed savannah grassland agricultural landscape in South Africa. *Atmos. Chem. Phys.*, 16(24), 15665–15688. <https://doi.org/10.5194/acp-16-15665-2016>
- Ramier, D., Boulain, N., Cappelaere, B., Timouk, F., Rabanit, M., Lloyd, C. R., et al. (2009). Towards an understanding of coupled physical and biological processes in the cultivated Sahel—1. Energy and water. *Journal of Hydrology*, 375(1–2), 204–216. <https://doi.org/10.1016/j.jhydrol.2008.12.002>
- Räsänen, M., Aurela, M., Vakkari, V., Beukes, J. P., Tuovinen, J. P., Van Zyl, P. G., et al. (2017). Carbon balance of a grazed savanna grassland ecosystem in South Africa. *Biogeosciences*, 14(5), 1039–1054. <https://doi.org/10.5194/bg-14-1039-2017>
- Rounsard, O., Dô, F., Rocheteau, A., Jourdan, C., Orange, D., Tall, L., et al. (2020). More C uptake during the dry season? The case of a semi-arid agro-silvo-pastoral ecosystem dominated by *Faidherbia albida*, a tree with reverse phenology (Senegal). <https://doi.org/10.5194/egusphere-egu2020-11203>
- Tagesson, T., Fensholt, R., Guiro, I., Rasmussen, M. O., Huber, S., Mbow, C., et al. (2015). Ecosystem properties of semiarid savanna grassland in West Africa and its relationship with environmental variability. *Global Change Biology*, 21(1), 250–264. <https://doi.org/10.1111/gcb.12734>
- Timouk, F., Kergoat, L., Mougin, E., Lloyd, C., Ceschia, E., Cohard, J. M., et al. (2009). Response of surface energy balance to water regime and vegetation development in a Sahelian landscape. *Journal of Hydrology*, 375(1–2), 178–189. <https://doi.org/10.1016/j.jhydrol.2009.04.022>