



Drought thresholds shape divergent responses in ecosystem water use efficiency

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Abstract. Ecosystem water use efficiency (WUE), the ratio of gross primary productivity (GPP) to evapotranspiration (ET), couples the land carbon and water cycles and is a key indicator of water–carbon coupling and ecosystem resilience. Yet how WUE responds to intensifying drought has remained unresolved, with studies reporting both increases and decreases. Here, combining multi-source global satellite, reanalysis, and model-fusion datasets, we show that across 57.5% of vegetated land WUE first rises and then falls as drought deepens, reversing only once drought reaches extreme severity. This reconciles the apparent contradiction in earlier work, whose reported increases and decreases are the rising and falling limbs of one threshold response rather than competing outcomes. The reversal arises from an ecohydrological asymmetry, in which the early rise is driven by ET declining faster than GPP while continued GPP loss under severe drought overturns it. The depth of the threshold is not uniform but set by aridity, radiation, leaf area, and atmospheric dryness overlaid on vegetation type, so that denser, more productive ecosystems tolerate more severe drought before reversing. Because these thresholds cluster in the semi-arid and transitional biomes that dominate the variability of the land carbon sink, a rising WUE signals only transient coping rather than durable resilience, and the threshold marks an early indicator of where intensifying drought begins to erode ecosystem carbon uptake.

1 Introduction

Vegetation simultaneously fixes atmospheric carbon dioxide through photosynthesis and loses water through transpiration (Hatfield & Dold, 2019). Ecosystem water use efficiency (WUE) is the ratio of gross primary productivity (GPP) to evapotranspiration (ET) (Naeem et al., 2023). It couples the carbon and water cycles and offers a unique lens on how ecosystems respond to climatic stressors, especially drought (Keenan et al., 2013; Li et al., 2023a). Because the terrestrial biosphere takes up roughly a third of anthropogenic carbon emissions while returning most land precipitation to the atmosphere, the efficiency with which ecosystems trade water for carbon helps set the strength of the land carbon sink, the partitioning of water resources, and the trajectory of the coupled carbon–climate system (Friedlingstein et al., 2025). How this efficiency behaves as droughts intensify is therefore not merely an ecological question but a first-order control on the future of the land sink and on the water available to human and natural systems.



Driven by climate change, droughts have become more prolonged (L. Chen et al., 2025), frequent (Pokhrel et al., 2021), intense (Yin et al., 2023), and faster-developing (Yuan et al., 2023), posing severe threats to ecosystems and societies (Yichen Zhang et al., 2022). During drought, reduced ET can intensify atmospheric dryness (Mondal et al., 2024), whereas GPP shows a more complex, spatially heterogeneous response (Peng et al., 2024). Because ET and GPP respond in such intertwined ways, WUE remains highly uncertain and poorly constrained in current Earth system models (Dan Li & Wang, 2025), which limits confidence in projections of the land carbon sink and of ecosystem water demand under future warming. Understanding how WUE responds to drought is therefore essential for revealing ecosystem adaptation under intensifying water deficit and for anticipating where terrestrial carbon uptake is most vulnerable.

Conventionally, drought-stressed vegetation reduces stomatal conductance to limit ET and conserve water (Martínez-Sancho et al., 2022; Peters et al., 2018). Although this also suppresses GPP, the high temperatures that often accompany drought can stimulate photosynthesis (M. Huang et al., 2019), while elevated atmospheric CO₂ further enhances drought tolerance (De Kauwe et al., 2021) and photosynthetic capacity (Keenan et al., 2023). Together these effects tend to raise WUE during drought, widely interpreted as ecosystem resilience (Ponce-Campos et al., 2013). This “positive response pattern” is widely embedded in process-based models (De Kauwe et al., 2015; Medlyn et al., 2011). However, WUE has also been observed to decline during drought in cold-dry regions (L. Huang et al., 2017) and under extreme drought in southwestern China (M. Wang et al., 2021)—a “negative response pattern” that challenges the universality of a unidirectional WUE response. Recently, in the Yellow River basin of China (S. Chen et al., 2024), we documented a more complex “two-stage response pattern,” in which WUE first increases and then declines as drought intensifies, implying a “response threshold” in ecosystem adaptation (Berdugo et al., 2020). Similar threshold-like behavior has also been reported elsewhere (Hu et al., 2024; Xu et al., 2019), suggesting such nonlinear transitions may be widespread. Such a threshold is the hallmark of tipping-point behavior in the Earth system: once it is crossed, an ecosystem's water–carbon strategy switches abruptly from coping to declining, so the threshold itself is a measurable early-warning indicator of where vegetation is approaching the limits of its drought tolerance (Berdugo et al., 2020). Being nonlinear and stage-dependent, this behavior cannot be captured by conventional correlation metrics; if the positive response reflects resilience, the threshold could quantify resilience capacity and improve how drought–ecosystem interactions are represented in models. Yet the environmental controls that set the depth of this threshold, and the ecohydrological mechanism that drives the reversal, remain unquantified. No systematic, global characterization of WUE drought-response patterns exists, and whether consistent patterns emerge across regions and ecosystem types—and what drives them—remains unclear.

Here we hypothesize that ecosystem WUE responds to drought through a severity threshold marking an abrupt transition from a positive to a negative response. To test this globally over 35 years, we combined a drought severity index based on terrestrial water storage anomalies (TWSA-DSI) with monthly WUE relative anomalies (WUEA) to build a classification framework that identifies drought thresholds and delineates three response patterns—two-stage, positive, and negative—and maps their global distribution. Within this framework, we developed a threshold-detection method to quantify the spatial variability of thresholds in two-stage regions. We then applied an interpretable machine-learning approach (Deep Forest with



SHapley Additive exPlanations) to identify the dominant climatic, soil, and vegetation drivers of both the response patterns and the threshold magnitudes, and finally examined the underlying ecohydrological mechanism by tracking WUE, GPP, and ET throughout the drought. By resolving where, why, and how ecosystems cross this drought threshold, our results provide a globally consistent, mechanistic basis for representing vegetation–drought interactions and for anticipating the response of the land carbon sink to a more drought-prone future.

2 Materials and Methods

2.1 Data

We analyzed monthly GPP and ET over 1982–2016. GPP was compiled from three products: NIRv (Wang et al., 2021), FLUXCOM (Jung et al., 2020), and light-use-efficiency (LUE) GPP (Madani et al., 2017a). NIRv GPP estimates productivity from the near-infrared reflectance of vegetation, a remote-sensing proxy strongly correlated with photosynthetic activity, at 0.05° resolution; FLUXCOM GPP upscales eddy-covariance tower observations with remote-sensing and meteorological predictors using machine learning (0.083°); and LUE GPP combines flux-tower measurements, satellite observations, and a light-use-efficiency model (0.083°). ET was compiled from ERA5-Land (Muñoz-Sabater, 2019), FLUXCOM (Jung et al., 2019), and GLEAM v3.7a (Martens et al., 2017; Miralles et al., 2011), each providing monthly records over the same period. ERA5-Land ET is the evapotranspiration flux of the ECMWF land-surface reanalysis (0.1°); FLUXCOM provides latent heat flux, which we converted to grid-scale ET using the standard energy-to-water conversion (Allen et al., 1998); and GLEAM ET is produced by the Global Land Evaporation Amsterdam Model, which integrates satellite-derived soil moisture, vegetation optical depth, and radiation (0.25°). Vegetation types were taken from the MODIS MCD12Q1 IGBP product (Friedl and Sulla-Menashe, 2019) and reclassified into nine categories (ENF, EBF, DNF, DBF, MF, SAV, CRO, GRA, SHR; Fig S1).

2.2 Drought index

The Gravity Recovery and Climate Experiment (GRACE) mission provides a unique observation of terrestrial water storage (TWS), which integrates canopy water, snow and ice, surface water, soil moisture, and groundwater (Pokhrel et al., 2021; Zhang et al., 2023). Because the GRACE mission has operated only since 2002 and contains data gaps, we used a gap-free, GRACE-reconstructed TWSA dataset spanning the full study period (Humphrey and Gudmundsson, 2019a). This widely validated (Gu et al., 2023; Yin et al., 2023; Zhou et al., 2023) product statistically reconstructs TWSA by combining two GRACE/GRACE-FO solutions with three meteorological forcings into six ensemble members; we used the ensemble mean to obtain a robust, temporally complete global series. Drought severity was characterized by the drought severity index based on terrestrial water storage anomalies (TWSA-DSI) (Zhao et al., 2017):

$$TWSA - DSI_{i,j} = \frac{TWSA_{i,j} - \overline{TWSA_j}}{\sigma_j} \quad (1)$$



where $TWSA - DSI_{i,j}$ and $TWSA_{i,j}$ represent the TWSA-DSI and TWSA data for the i th year and j th month and $\overline{TWSA_j}$ and σ_j , respectively, denoting the average and standard deviation of TWSA for the j th month within the study period. Compared with conventional indices such as the Palmer Drought Severity Index (PDSI), the Standardized Precipitation Evapotranspiration Index (SPEI), the Soil Moisture Index (SMI), the Standardized Precipitation Index (SPI), and the Standardized Runoff Index (SRI), TWSA-DSI captures the integrated hydrological impact of drought and, unlike most indices, does not use ET as a direct input, thereby avoiding collinearity with WUE (Du et al., 2019; Zhao et al., 2017). TWSA-DSI < 0 denotes drought, with lower values indicating more severe conditions.

2.3 WUE anomalies

All datasets were resampled to a common 0.5° grid by bilinear interpolation. To reduce inter-product uncertainty, the three GPP and three ET products were each fused into a single ensemble using the Bayesian Combined Triangle Hat (BCTH) method (Lu et al., 2025; Zhang et al., 2024). BCTH extends the classical three-cornered-hat approach by estimating each product's relative uncertainty without assuming a reference "truth," and then assigns larger weights to products with lower uncertainty and stronger mutual consistency.

From the fused ensemble we computed monthly WUE (GPP/ET) on a 0.5° grid over 1982–2016, after excluding low-productivity months (GPP $< 20 \text{ gC m}^{-2} \text{ month}^{-1}$ or ET $< 10 \text{ mm month}^{-1}$) to avoid spurious ratios (Liu et al., 2025; Naeem et al., 2023). We then removed the climatological seasonal cycle to obtain relative WUE anomalies (WUEA):

$$WUEA_{i,j} = \frac{(WUE_{i,j} - \overline{WUE_j})}{\overline{WUE_j}} \quad (2)$$

where $WUEA_{i,j}$ denotes the relative anomaly for the i th year and j th month, $WUE_{i,j}$ is the raw WUE value, and $\overline{WUE_j}$ is the long-term mean WUE for the j th month over the entire study period. This treatment allows for the analysis of WUE responses across different regions and seasons. To obtain a robust per-cell signal, WUEA series were smoothed with a 5×5 spatial moving window over the surrounding neighborhood. GPP and ET relative anomalies (GPPA and ETA) were defined in the same way as WUEA (Equation 2), each computed as the departure from, and normalized by, its own long-term monthly mean ($\overline{GPP_j}$ and $\overline{ET_j}$).

2.4 Response-pattern classification and threshold detection

For cells under drought (TWSA-DSI < 0), WUEA was averaged within 0.05-wide TWSA-DSI bins using a three-bin moving average (Huang et al., 2019; Niu et al., 2024); cells with fewer than 20 valid bins were discarded. We hypothesized three patterns: a two-stage pattern, in which WUEA first rises then falls as drought intensifies (a negative followed by a positive slope, defining a drought threshold); a positive pattern (WUEA rises throughout; negative slope); and a negative pattern (WUEA falls throughout; positive slope). To detect them, we developed a three-step Fitting–Identification–Classification framework refining previous curve-identification methods (Berdugo et al., 2020; Manzoni et al., 2008).



In the Fitting step, each cell was fit with both a piecewise-linear model and a generalized additive model (GAM):

$$y = \beta_0 + f(x) + \varepsilon \quad (3)$$

$$f(x) = \sum_{i=1}^K \beta_i B_i(x) \quad (4)$$

where $f(x)$ is a smooth function of TWSA-DSI estimated from penalized B-splines (Eilers and Marx, 1996), ensuring a continuous, differentiable curve. The optimal model was selected by R^2 : (1) if the GAM fit better, we computed its derivative—if no zero-derivative point existed (no slope sign change), the piecewise-linear model was retained (Fig S4b); if a local extremum existed (derivative = 0), the GAM was retained and the zero-derivative point was taken as the "threshold candidate"; (2) otherwise the piecewise-linear model was optimal, with its breakpoint as the threshold candidate (Fig S4c). In the Identification step, bins between 0 and the candidate were assigned to Stage I and more-severe bins to Stage II, and a linear model was fit to each stage:

$$WUEA = \begin{cases} k_{\text{stageI}} \cdot TWSA - DSI + b_{\text{stageI}}, & TWSA - DSI \geq \text{threshold candidate} \\ k_{\text{stageII}} \cdot TWSA - DSI + b_{\text{stageII}}, & TWSA - DSI < \text{threshold candidate} \end{cases} \quad (5)$$

where k and b are the slope and intercept and the subscripts denote the two stages. In the Classification step, cells were labeled from the two slope signs: two-stage ($k_{\text{stageI}} < 0$, $k_{\text{stageII}} > 0$; threshold candidate was retained as the drought threshold), positive or negative (both slopes the same sign; threshold candidate was treated as a pseudo-threshold), or invalid. The mean optimal-fit R^2 was 0.78 and only 4.2% of cells were invalid (Fig S2), supporting the robustness of the framework.

2.5 Attribution based on interpretable machine learning

We attributed both the response patterns and the two-stage threshold magnitudes to environmental drivers using a Deep Forest model (Zhou and Feng, 2017). Deep Forest cascades layers of random forests so that each layer's outputs feed the next, improving predictive skill over a single random forest (Li et al., 2022) while requiring far less hyperparameter tuning than deep neural networks (Zhou and Feng, 2019). We trained separate classification (response pattern) and regression (threshold value) models on 30 climate, vegetation, and soil predictors (Table S2), optimizing hyperparameters by grid-search cross-validation. We computed SHapley Additive exPlanations (SHAP) values to quantify each predictor's marginal contribution independent of the others (Green et al., 2022). Following the principle of recursive feature elimination (Guyon et al., 2002), we retained the ten highest-SHAP predictors and recomputed SHAP for the final models (classification accuracy 72.6%, AUC > 0.8; threshold-regression $R^2 = 0.65$; Fig S3). Land cover, a categorical variable, was one-hot encoded for the classification model but excluded from the threshold regression, where its effect was instead examined separately by vegetation type (Fig 4b).

2.6 Mechanistic decomposition of the WUE response

To interpret the two-stage response mechanistically, for each two-stage cell we used the fitted models to predict the relative anomalies of WUE, GPP, and ET (WUEA, GPPA, ETA) at the drought threshold and at the most extreme observed drought.



We then decomposed the response in logarithmic space using the exact identity $\ln(1+WUEA) = \ln(1+GPPA) - \ln(1+ETA)$, which additively partitions the change in WUE into a GPP contribution ($+\ln(1+GPPA)$) and an ET contribution ($-\ln(1+ETA)$). Because this holds term-by-term along the entire drought gradient, it isolates at each stage whether the WUE change is driven by carbon uptake (GPP) or water loss (ET), revealing the ecohydrological mechanism underlying the threshold. For the aggregate view (Fig 7d), each cell's gradient was aligned to its own threshold, the three log terms were binned at 0.05 intervals of threshold-relative TWSA-DSI, and smooth GAM fits were computed over the well-sampled window.

3 Results

3.1 WUE response to drought

Over 1982–2016, the response of ecosystem WUE to intensifying drought, expressed as relative WUE anomalies (WUEA) plotted against TWSA-DSI, resolved into three distinct trajectories (Fig 1c–e). In the positive and negative patterns the WUEA–TWSA-DSI relationship was monotonic, with a slope that stayed negative or positive across the entire drought gradient. The two-stage pattern was fundamentally nonlinear: WUEA first increased as drought deepened (Stage I) and then reversed to decline once a drought threshold was surpassed (Stage II). In the representative cell of Fig 1c, for instance, this inflection occurred at a TWSA-DSI of -1.93 . The three-step Fitting–Identification–Classification framework reproduced these binned WUEA–drought curves well, achieving a mean optimal-fit R^2 of 0.78 across cells (Fig S2), with worked examples of each pattern shown in Fig 1c–e; only 4.2% of cells lacked a coherent structure, were labeled invalid, and were excluded from all subsequent analyses.

Globally, the two-stage pattern was overwhelmingly the most common, occupying 57.5% of vegetated land, ahead of the positive (27.1%) and negative (11.2%) patterns (Fig 1a). Stratifying the land surface into four latitudinal zones (Fig 1b) showed that the two-stage pattern prevailed in every zone, peaking in the low-latitudes (62.8%) and easing poleward to 56.0%, 53.0%, and 52.5% in the northern mid-, northern high-, and southern mid-latitudes. The positive pattern was broadly distributed, most frequent in the southern mid-latitudes (44.3%) and comparable elsewhere (26.6%, 25.3%, and 22.7% in the northern mid-, low-, and northern high-latitudes). The negative pattern was by far the most geographically confined: almost absent in the southern mid-latitudes (1.2%), it rose steadily northward from 8.1% in the low-latitudes to 13.2% and 17.0% in the northern mid- and high-latitudes, and clustered in the central North American plains, the western Amazon Basin, southwestern and northeastern China, eastern Siberia, and the Southeast Asian archipelago.

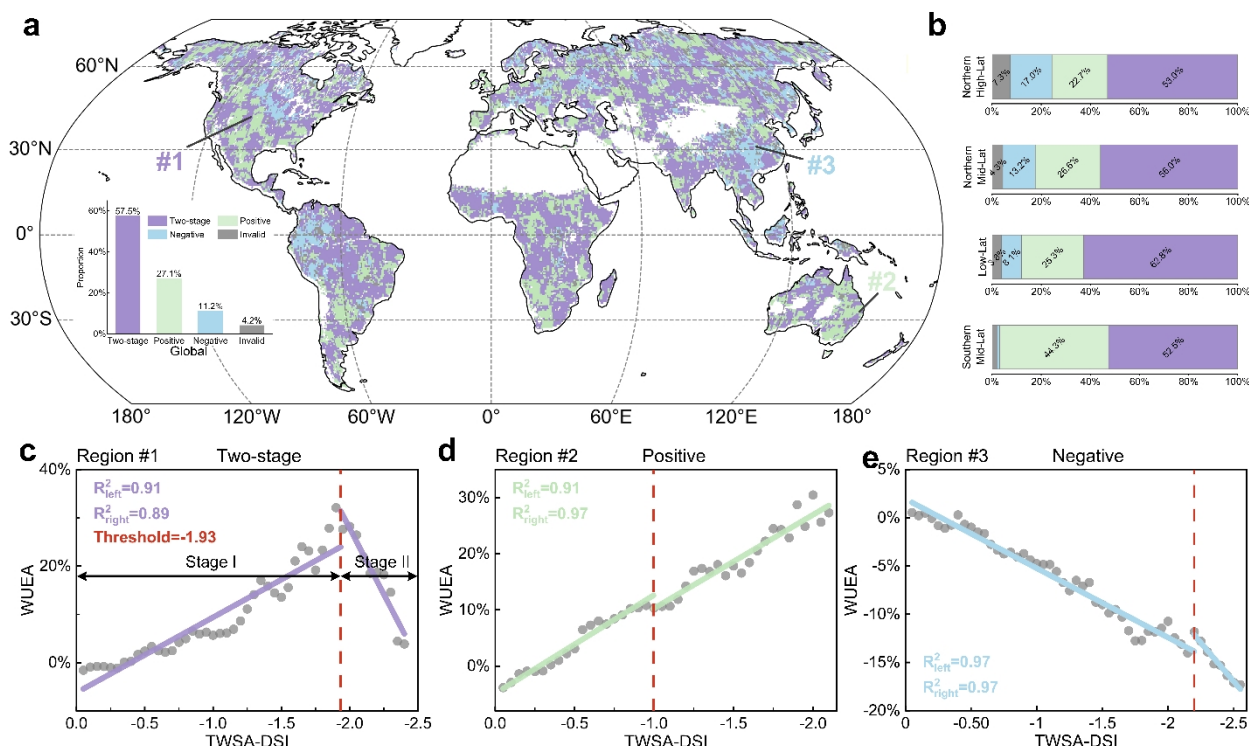


Figure 1: Global WUE response patterns to drought. (a) Spatial distribution of the three patterns; the bar chart gives each pattern's share of vegetated land (valid cells only), and labels #1-3 mark the examples in (c-e). (b) Latitudinal distribution across four zones (southern mid-, low-, northern mid-, and northern high-latitudes, bounded at 23.5° and 66.5°). (c-e) Examples of the (c) two-stage (41.5°N, 105.5°W), (d) positive (27°S, 152°E), and (e) negative (30.5°N, 110°E) patterns; gray dots are observations, solid lines the piecewise-linear fits, and dashed lines the threshold candidate.

3.2 Global thresholds of two-stage WUE response patterns

We next mapped, for every two-stage cell, the TWSA-DSI threshold at which WUE reverses from rising to falling (Fig 2a). Threshold magnitudes followed an approximately normal distribution but were spatially heterogeneous, averaging -1.67 ± 0.61 , corresponding to a D3-level extreme drought (Table S1), a severity that much of the vegetated land experiences. Shallow thresholds (small absolute values, roughly -0.6 to 0) bordered the negative-pattern zones—central Siberia, the midwestern United States, and northwestern South America—where WUE turns downward under only mild drought. Deep thresholds (more negative than -2.7) concentrated in the Ural Mountains of eastern Europe, the Brazilian and central African highlands, southeastern South America, and southwestern Australia, where WUE keeps rising until drought becomes severe. A clear latitudinal gradient emerged, with lower latitudes exhibiting more negative thresholds (Fig 2b). The pattern broke down only near 38°S, where two-stage land is sparse and a handful of deep thresholds in southeastern Africa inflate the zonal mean.

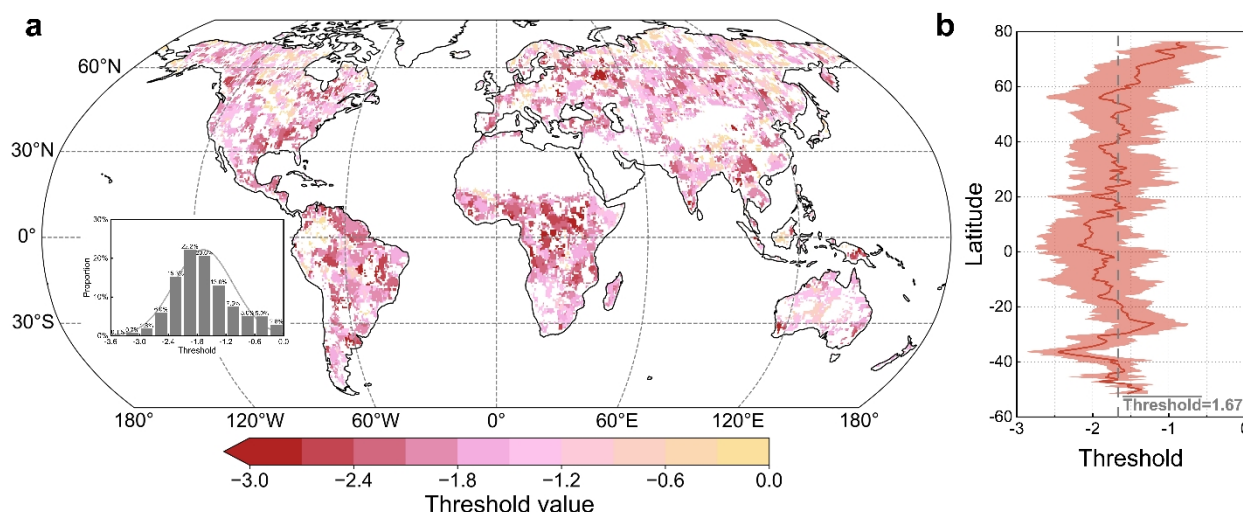


Figure 2: Drought thresholds under the two-stage pattern. (a) Spatial distribution of threshold values (TWSA-DSI) for two-stage cells, with the inset histogram showing their frequency distribution. (b) Latitudinal variation in the mean threshold (solid line) with one standard deviation (shading); the dashed line marks the global mean.

The slopes on either side of the threshold quantify how sharply the reversal unfolds (Fig 3). Averaged over two-stage cells, the Stage II decline was several times steeper than the Stage I rise, with slope magnitudes of about 0.39 versus 0.07 in WUEA per unit TWSA-DSI. Because drought severity increases as TWSA-DSI falls, these correspond to a negative slope in Stage I and a positive slope in Stage II under our convention. WUE thus climbs only gradually as mild drought conserves water but is shed abruptly once carbon limitation sets in past the threshold. The magnitude of the slope change across the threshold (Δk) averaged 0.46 and peaked in southwestern North America, eastern and southern South America, northwestern India, southeastern Africa, and Australia, pinpointing the regions where the physiological switch between stages is most abrupt.

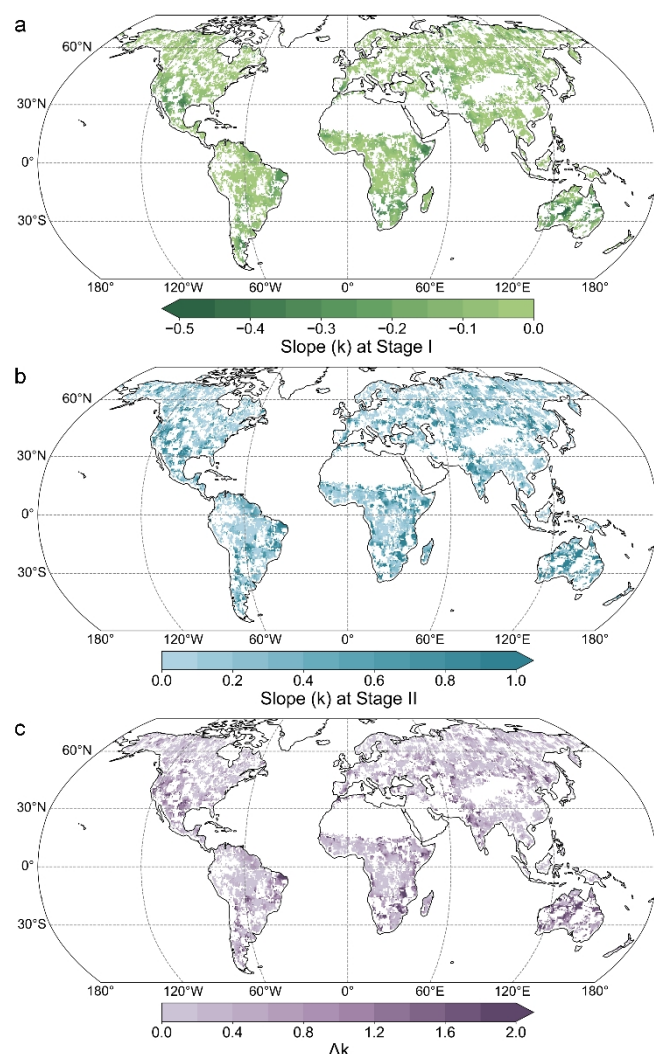


Figure 3: Slope variation in the two-stage response pattern. (a) and (b) show the spatial distribution of fitted slopes during Stage I (increasing WUEA with increasing drought severity) and Stage II (decreasing WUEA with increasing drought severity), respectively. (c) displays the difference in slopes between the two stages, calculated as $\Delta k = k_{stage II} - k_{stage I}$.

3.3 Drivers of response patterns and threshold values

To identify what governs these contrasting patterns, we trained a Deep Forest classification model on 30 climate, soil, and vegetation predictors, retained the ten most important by SHAP, and recomputed SHAP for the refined model (Fig 4a). The refined model was skilful, reaching an overall accuracy of 72.6% with an area under the ROC curve above 0.8 for all three patterns (Fig S3a), confirming that the predictors reliably discriminate the response types. Four variables dominated—land cover type (LCT), net shortwave radiation (Rad), the aridity index (AI), and vapor pressure deficit (VPD)—jointly

explaining 50.0% of the total importance (14.3%, 12.7%, 12.4%, and 10.6%), while the remaining predictors, led by
225 temperature, potential evapotranspiration, air pressure, and precipitation, each contributed 8–10%.

Because LCT was the single most important driver, we resolved the response behavior by vegetation type (Fig 4b). The two-
stage pattern was ubiquitous but its prevalence and threshold varied systematically. Savannas (SAV) had the highest two-
stage fraction (66.7%) and the lowest negative fraction (5.7%); grasslands showed the largest positive fraction (36.6%);
shrublands (SHR) combined a high positive fraction (31.2%) with the shallowest threshold (-1.42 ± 0.59); and evergreen

230 broadleaf forests (EBF) had the deepest threshold (-1.89 ± 0.65) together with a high proportion of negative responses
(17.6%), concentrated in the western Amazon. Across the continuous gradients (Fig 4c–e), the positive-response fraction
increased and the negative-response fraction decreased with rising AI and Rad, and the negative pattern all but disappeared
where AI exceeded 30 or Rad exceeded 150 W m^{-2} . The positive fraction instead rose and then fell with VPD. The two-stage
pattern therefore grew increasingly dominant under higher aridity, radiation, and atmospheric demand.

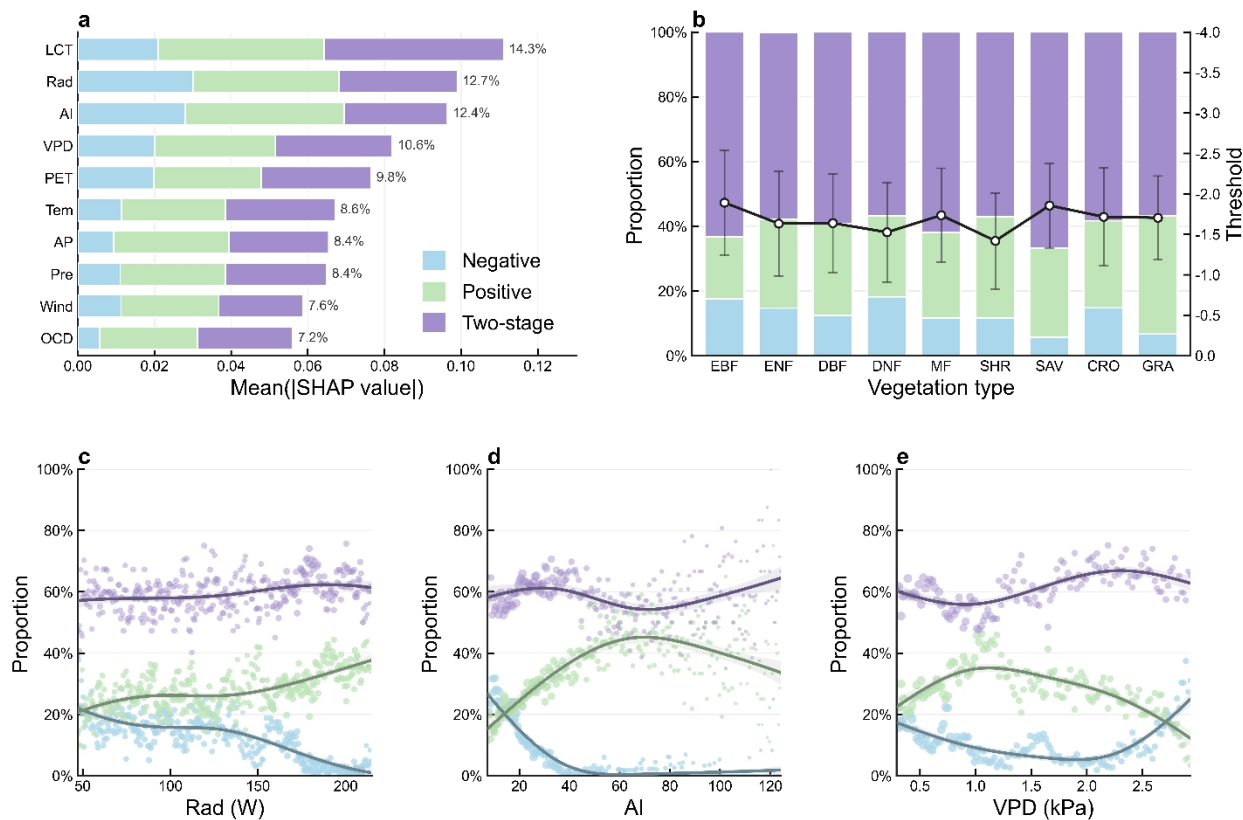


Figure 4: Drivers of WUE response patterns. (a) Predictor importance (mean absolute SHAP) for the negative (blue), positive (green), and two-stage (purple) patterns; percentages give each predictor's share of total importance. LCT, Rad, AI, VPD, PET, Tem, AP, Pre, Wind, and OCD denote land cover type, net shortwave radiation, aridity index, vapor pressure deficit, potential evapotranspiration, temperature, air pressure, precipitation, wind speed, and organic carbon density, respectively. (b) Proportions of the three patterns by vegetation type (bars) and the mean two-stage threshold (line with error bars, $\pm$ one standard deviation). (c–e) Pattern proportions versus net shortwave radiation (Rad), aridity index (AI), and vapor pressure deficit (VPD); solid lines are fitted trends.



We then trained a separate Deep Forest regression on the two-stage threshold magnitude, excluding LCT because its effect had already been resolved by vegetation type. The regression achieved an R^2 of 0.65 (Fig S3b) and singled out AI, Rad, leaf area index (LAI), and VPD as the four leading controls, with mean absolute SHAP values near 0.05 (Fig 5). A cluster of secondary contributors followed, namely potential evapotranspiration (PET), precipitation (Pre), temperature (Tem), and CO_2 at about 0.04, with wind speed and rooting depth weakest. Their SHAP dependences (Fig 6) exposed distinct functional forms. The threshold deepened approximately monotonically with LAI (Fig 6c). It varied nonmonotonically with AI, reaching its deepest values at intermediate moisture and becoming shallower toward both the arid and the humid extremes (Fig 6a). It responded more weakly, and largely toward deeper thresholds, to Rad and VPD (Fig 6b, d).

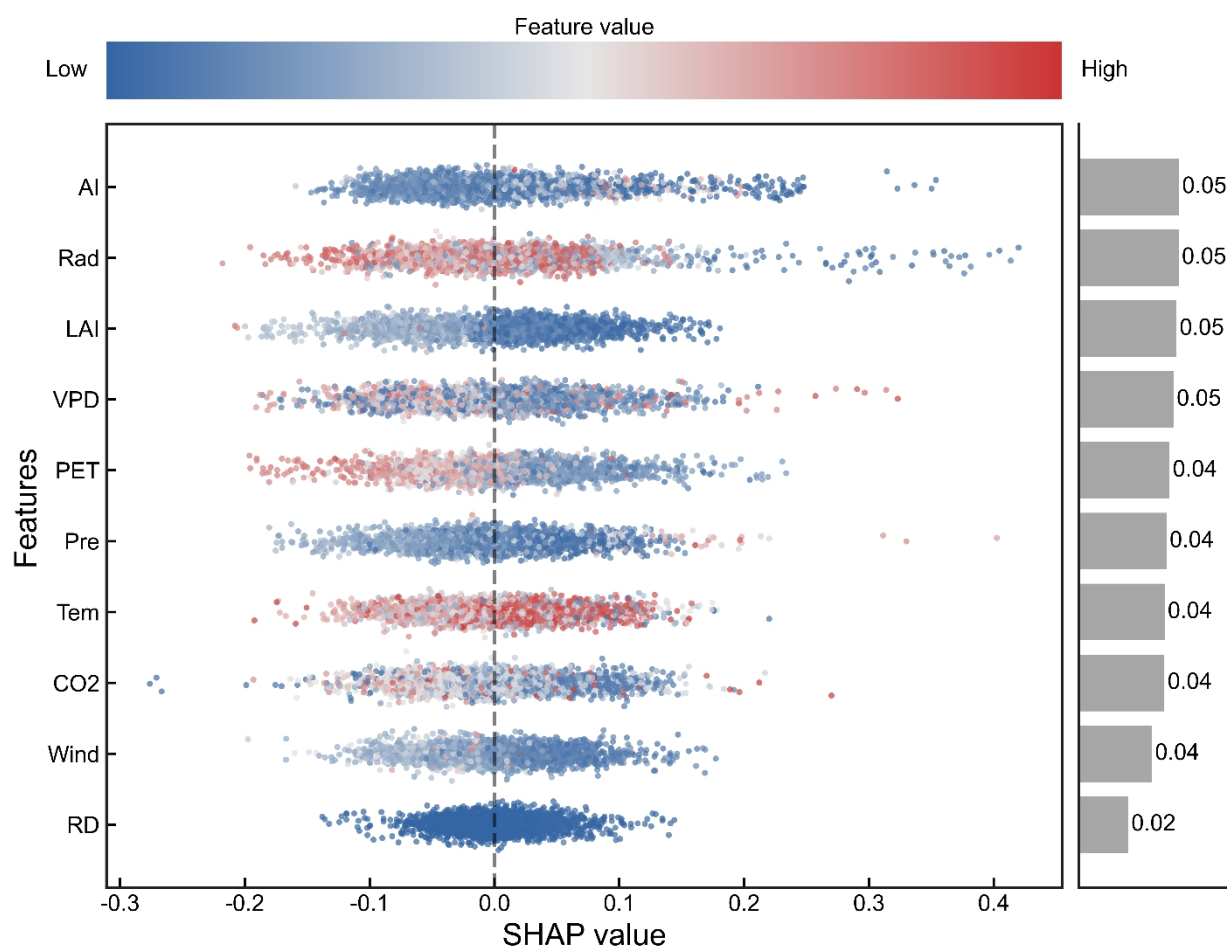


Figure 5: Drivers of the two-stage drought threshold. SHAP summary for the Deep Forest regression of the threshold magnitude. Each point is a grid cell; its color denotes the feature value (low to high) and its horizontal position the SHAP value, i.e., the predictor's contribution to the predicted threshold. Predictors are ordered from top to bottom by mean absolute SHAP, shown by the bars at right. Aridity index (AI), net shortwave radiation (Rad), leaf area index (LAI), and vapor pressure deficit (VPD) are the four leading controls, followed by potential evapotranspiration (PET), precipitation (Pre), temperature (Tem), atmospheric CO_2 concentration (CO_2), wind speed (Wind), and rooting depth (RD).

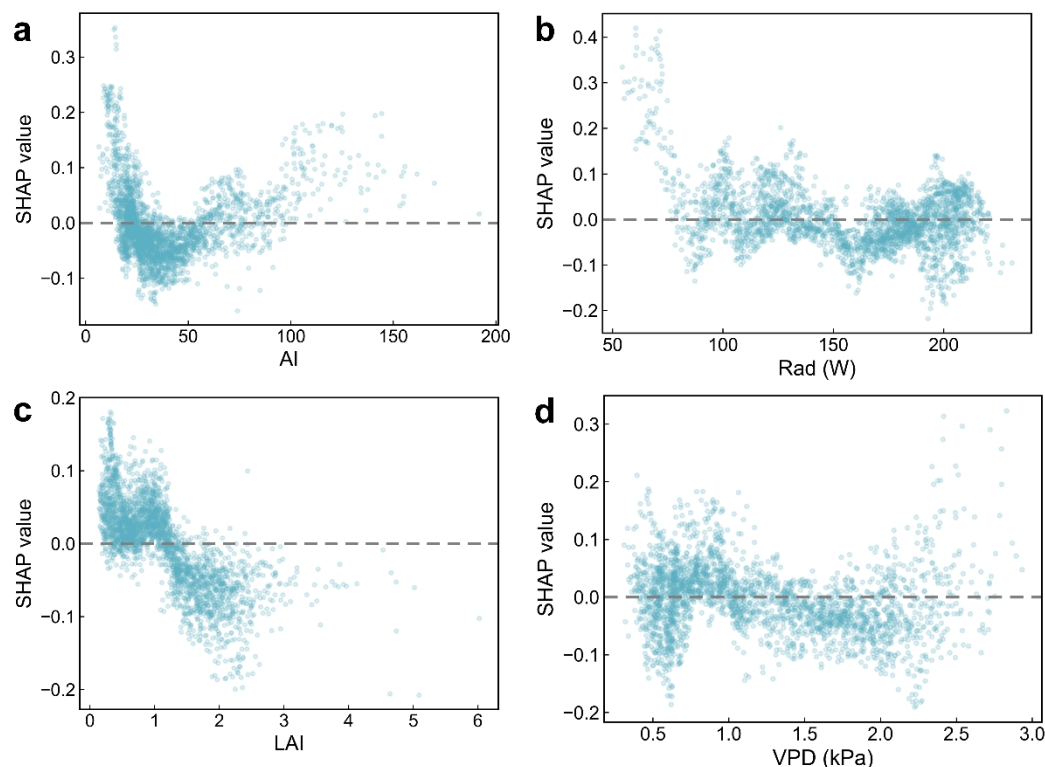


Figure 6: Effects of different factors on the threshold values in the two-stage response pattern. (a)–(d) illustrate the influence of aridity index (AI), net shortwave radiation (Rad), leaf area index (LAI), vapor pressure deficit (VPD), respectively. The x-axis represents the value of each factor, while the y-axis indicates the corresponding SHAP value. The dashed line denotes a SHAP value of zero.

3.4 Mechanisms underlying the two-stage response pattern

Finally, to expose the mechanism, we tracked the relative anomalies of WUE, GPP, and ET (WUEA, GPPA, ETA) for every two-stage cell at its threshold and at its most extreme observed drought. Over the record these cells sustained mean WUE, GPP, and ET of $1.9 \pm 0.7 \text{ gC kg}^{-1} \text{ H}_2\text{O}$, $90.9 \pm 64.4 \text{ gC m}^{-2}$, and $47.0 \pm 28.8 \text{ mm}$ (Fig 7a). At the threshold, 94.4% of regions registered a WUE increase averaging $14.8\% \pm 17.3\%$ (Fig 7b; Table S3). Under the most extreme drought, however, mean WUEA collapsed to $1.2\% \pm 12.1\%$ and the fraction of regions retaining a positive WUE anomaly fell to 42.9% (Fig 7c), so more than half of the area suffered a net WUE decline. This transition was spatially coherent (Fig 8). Threshold-point gains were near-ubiquitous (Fig 8a), but under the most extreme drought the regions still gaining WUE contracted toward the deeper-threshold, more resilient zones, while shallow-threshold regions flipped to net loss (Fig 8b).

Carbon uptake and water loss changed asymmetrically along the way. GPPA declined by $2.6\% \pm 7.5\%$ at the threshold and by $7.9\% \pm 10.5\%$ at the most extreme drought (Fig 7b, c). Even so, 36.8% of cells still gained GPP at the threshold and 21.5% during extreme drought, and in places GPP under extreme drought exceeded its threshold-point level (Fig S5; Table S3), indicating a non-monotonic productivity response. ETA fell by $9.8\% \pm 12.4\%$ at the threshold and by $8.7\% \pm 14.8\%$ at extreme drought (Fig 7b, c), and ET rose rather than fell in a subset of regions, 18.3% of cells at the threshold and 28.2% at



the most extreme drought (Fig S6; Table S3). The logarithmic decomposition of the WUE change (Fig 7d) resolves this asymmetry directly. Through Stage I the WUE rise was carried mainly by the reduction in ET while GPP was relatively maintained, so water savings outpaced carbon loss. As drought advanced into Stage II the ET reduction levelled off but GPP kept falling, and this sustained carbon loss overturned the WUE trajectory.

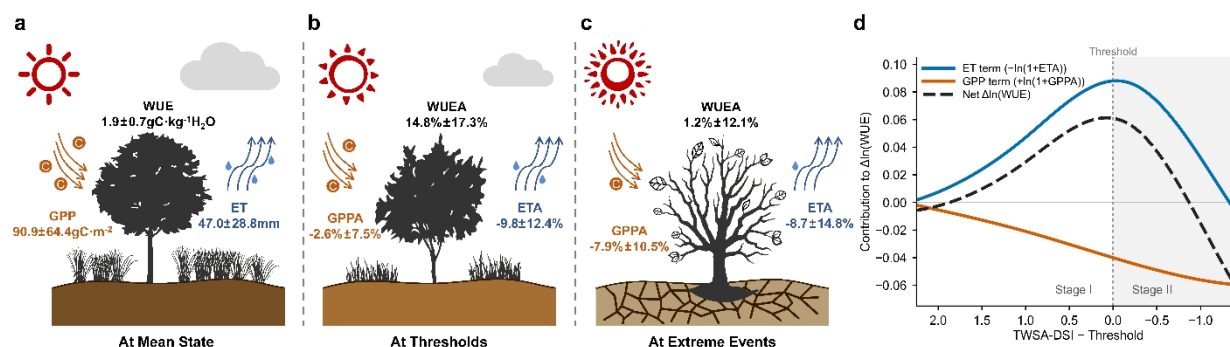


Figure 7: Mechanism of the two-stage response. (a) Long-term monthly means (1982–2016) of WUE, GPP, and ET for two-stage cells. (b, c) Mean WUEA, GPAA, and ETA at the threshold (b) and at the most extreme drought (c); values are mean $\pm$ standard deviation. (d) Logarithmic decomposition of the WUE response. For each two-stage cell, $\ln(1+WUE) = \ln(1+GPP) - \ln(1+ETA)$, so the net change in log-WUE (black) splits additively into a GPP term ($+\ln(1+GPAA)$, orange) and an ET term ($-\ln(1+ETA)$, blue). Each cell's gradient is aligned to its own threshold, so the x-axis is TWSA-DSI minus that threshold and the dashed line at zero marks the threshold, with the milder (Stage I) and more severe (Stage II, shaded) sides on either side. Curves are GAM fits to the three terms binned at 0.05 intervals of threshold-relative TWSA-DSI.

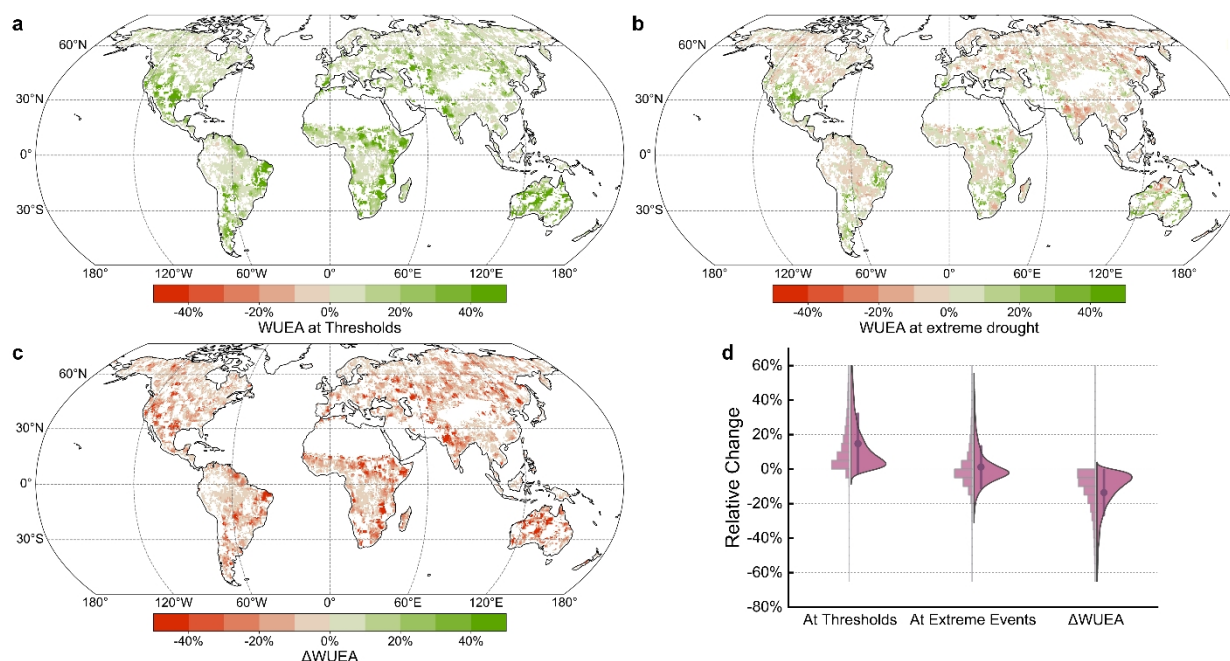


Figure 8: Spatial and statistical distribution of WUEA in the two-stage response pattern. (a) Global distribution of WUEA at the threshold point. (b) Global distribution of WUEA during the most extreme drought conditions. (c) Spatial distribution of $\Delta WUEA$, defined



290 as the difference between (b) and (a). **(d)** Statistical distributions of WUEA at the threshold point, WUEA under the most extreme drought, and their difference (Δ WUEA). In the violin plots, dots represent the mean values, and whiskers indicate one standard deviation.

4 Discussion

4.1 Physiological basis of the two-stage response

295 The two-stage response we identify across 57.5% of the vegetated land surface reflects a shift in which side of the carbon–water exchange limits water use efficiency. Under mild water deficits WUE rises. The threshold-aligned log decomposition (Fig 7) shows that in this first stage the ET term declines faster than the GPP term, so the ratio increases even though both fluxes weaken. Ecosystems in Stage I are behaving conservatively. Partial stomatal closure and reduced canopy conductance curtail transpiration while assimilation is initially maintained, the water–carbon trade-off that optimal stomatal theory predicts (Medlyn et al., 2011) and that drought physiology confirms (Gupta et al., 2020). This water-saving phase is the
 300 drought resilience that earlier work reported as rising WUE during dry spells (Ponce-Campos et al., 2013), a rise that global analyses find in water-limited ecosystems even where the sign reverses in more humid ones (Yang et al., 2016a).

Beyond the threshold the sign of the control reverses. In Stage II the GPP term falls steeply while the ET term flattens or rebounds, so WUE declines. Why the ET term stops falling is the less obvious half of the reversal. Once stomatal closure has suppressed transpiration, the residual flux is increasingly non-transpirational evaporation from soil and canopy surfaces that
 305 is insensitive to plant water status, and prolonged deficit can drive the canopy decline that follows structural overshoot (Zhang et al., 2021), shifting the balance further toward soil evaporation. At the same time, the reduced cloud cover, higher available energy, and rising vapor pressure deficit that accompany drought raise atmospheric demand even as supply declines (Miralles et al., 2019), so that total ET can hold steady or even rise rather than track the loss of carbon uptake (Zhao et al., 2022). Water loss therefore decouples from carbon gain, and the continuing decline in GPP is left to drive WUE down.
 310 The mean slope steepens from -0.07 in Stage I to $+0.39$ in Stage II, and the change in slope magnitude averages 0.46 across grid cells, so the loss after the threshold is markedly sharper than the preceding gain. This asymmetry is the signature of a nonlinear failure of carbon uptake rather than a smooth continuation of water saving. Photosynthesis declines sharply once soil moisture falls below the critical level that marks the shift from an energy-limited to a water-limited regime (Fu et al., 2022; Green et al., 2019), a decline set in motion because soil moisture dominates the dryness stress on production across
 315 most vegetated land (Liu et al., 2020). The underlying physiology follows a sequence in which stomatal and xylem regulation protect the plant early on (Choat et al., 2012) before prolonged deficit erodes the carbon balance toward carbon starvation (McDowell et al., 2008; Sevanto et al., 2014). The threshold therefore marks the point where ecosystems move from ET-limited water saving to GPP-limited carbon loss, and its depth sets how much drought a system absorbs before that reversal.



320 4.2 Environmental controls on pattern and threshold

Two questions follow from the two-stage response. Where does each response type occur, and how deep is the threshold where it turns. The classification analysis answers the first. Land cover type, radiation, aridity and VPD together account for roughly half of the predictive importance (Fig 4), with land cover the single strongest control. This points to plant hydraulic strategy, which differs among vegetation types, as the primary organizer of response type (Anderegg et al., 2018). Savanna shows the highest two-stage prevalence at 66.7%, consistent with its seasonally water-limited structure and its mix of trees and grasses that draw on soil water over different depths and timescales (Nippert and Holdo, 2015; Scholes and Archer, 1997). Grasslands more often follow the monotonic increase pattern at 36.6%, in line with their shallow rooting (Schenk and Jackson, 2002) and the tight stomatal and xylem regulation that lets grassland productivity down-regulate gradually rather than collapse (Konings et al., 2017).

330 The threshold regression answers the second question. Aridity, radiation, LAI and VPD dominate the control on threshold depth (Fig 5). Aridity acts nonmonotonically. The threshold first deepens and then shallows as conditions become drier, so ecosystems in transitional climates tolerate the most severe drought before reversing while both the wettest and the most arid systems reach their turning point sooner. Systems adapted to intermittent water stress carry structural and physiological buffers that delay collapse, yet the driest systems operate so close to their water-stress limit that little additional deficit is needed to cross it (Berdugo et al., 2020; Li et al., 2023c). Radiation and VPD shift the threshold through evaporative demand. Higher atmospheric demand strengthens stomatal limitation (Grossiord et al., 2020) and asymmetrically depresses the carbon gain that sets WUE, which is why ecosystem WUE saturates as VPD rises (Li et al., 2023a), together bringing the carbon-loss stage forward. Leaf area index deepens the threshold approximately monotonically (Fig 6c), so ecosystems with denser canopies keep saving water until drought grows more severe. This most likely reflects the greater carbon and water reserves of high-LAI, more productive ecosystems, which buffer them and postpone the reversal. The extra transpiration that dense canopies sustain works the other way, tending to deplete water sooner and shallow the threshold where structural overshoot leaves ecosystems exposed to later drought (Zhang et al., 2021). That the net effect is a monotonic deepening indicates the resource-buffering effect dominates. Rooting depth, regulated by local hydrology, reinforces this buffering as a separate control (Fan et al., 2017). Evergreen broadleaf forests hold the deepest threshold at -1.89 while shrublands turn at a shallower -1.42 . Where these limits fall may be set by hydraulic safety margins, the water-transport thresholds that govern how forests respond to drought (Brodribb et al., 2020; Choat et al., 2012).

4.3 Reconciling divergent findings in previous work

Reports of how WUE responds to drought have long disagreed. Some studies find that WUE rises as water becomes scarce and read this as evidence of drought resilience (Ponce-Campos et al., 2013). Others document that WUE falls under severe or prolonged deficit. Evapotranspiration frequently rises rather than falls during drought (Zhao et al., 2022), which drives the GPP/ET ratio down, and primary production is directly suppressed once soil moisture becomes limiting (Stocker et al., 2019).



A single global synthesis already contains both signs, with WUE increasing in water-limited ecosystems and decreasing in more humid ones (Yang et al., 2016a). Our results show that these are not competing outcomes but two stages of one response separated by a threshold. A study that samples mild to moderate drought captures the rising limb, while one that reaches severe drought captures the falling limb. The framework therefore reconciles the apparent contradiction and explains why the sign of the reported WUE trend has depended on the drought range analyzed.

Placing the threshold in a global and spatially resolved setting also extends earlier point-scale and flux-tower analyses. Site studies established the physiological mechanisms but could not map where the turning point sits across biomes and climates. The latitudinal and aridity structure we recover connects the WUE threshold to the broader family of ecological drought thresholds now being reported for productivity and vegetation state (Berdugo et al., 2020; Li et al., 2023c). It shows that the transition from water saving to carbon loss is a coherent global pattern rather than a set of isolated site behaviors, and it locates that transition most densely in the seasonally dry and transitional ecosystems that sit between energy and water limitation.

4.4 Implications and limitations

The two-stage threshold carries consequences for the land carbon sink. The ecosystems where the threshold is most common are the semi-arid and transitional biomes that dominate the trend and the interannual variability of the global terrestrial CO₂ sink (Ahlström et al., 2015). In these systems crossing the threshold turns a period of efficient carbon gain into one of rapid carbon loss, so the same drought that a resilient ecosystem would buffer becomes a strong negative forcing once the turning point is passed. As drought frequency and atmospheric demand continue to rise, more of these ecosystems will spend more time beyond their thresholds, which would sharpen the sensitivity of the sink to dry extremes and reduce its capacity to offset emissions. The behavior resembles the loss of resilience now detected in forest biomes through early-warning indicators (Boulton et al., 2022; Forzieri et al., 2022), and crossing the WUE threshold is itself an abrupt transition of the kind that aridity can drive (Berdugo et al., 2020). It argues for treating the WUE threshold as an early indicator of where ecosystems are moving toward drought-driven carbon loss.

These findings also expose a gap in how models represent the carbon–water link. Many land surface and Earth system models encode a smooth WUE response and do not reproduce a threshold beyond which efficiency falls, which contributes to the wide spread in simulated carbon and water fluxes under drought. Embedding the two-stage behavior and its environmental controls offers a route to constrain that spread and to improve projections of drought impacts on productivity and evapotranspiration.

A few limitations remain. The drought index derives from GRACE terrestrial water storage, which is coarse in space, so we apply a spatial moving window and the multi-product BCTH fusion of three GPP and three ET datasets to reduce input uncertainty. The analysis also works at the ecosystem scale and does not resolve the species-level hydraulic traits that fine-tune the threshold within a grid cell. Extending the observational record and validating the thresholds against eddy-covariance measurements would sharpen the picture further. None of these caveats affects the central result that the WUE



385 response to drought is organized into two stages around a threshold, and mapping where and when ecosystems cross that threshold would give an observationally grounded constraint on the future trajectory of the land carbon sink.

5 Conclusions

We mapped how ecosystem water use efficiency responds to drought across the global vegetated land surface and found that the response is not monotonic but organized into two stages around a threshold. Over 57.5% of vegetated land, WUE first
 390 rises as mild drought develops and then falls once drought passes a critical severity, with the turning point at a mean drought index of -1.67 . Purely monotonic responses are less common, a rising pattern covering 27.1% of the land and a declining pattern 11.2%.

The two stages reflect a shift in what limits the carbon and water exchange. In the first stage ecosystems conserve water because evapotranspiration falls faster than photosynthesis, so efficiency climbs. Beyond the threshold photosynthesis
 395 weakens faster than evapotranspiration can decline, so efficiency drops, and this decline is steeper than the preceding rise. The threshold therefore marks the point where an ecosystem moves from conserving water to losing carbon.

Where each response occurs and how deep its threshold sits are set by identifiable controls. Land cover, radiation, aridity and vapor pressure deficit together explain about half of where the two-stage pattern appears, with vegetation type the strongest single control. The depth of the threshold varies with aridity, radiation, leaf area and vapor pressure deficit, and aridity acts
 400 nonmonotonically so that transitional ecosystems tolerate the most severe drought before reversing. Savannas show the two-stage response most often, while grasslands more often grow steadily more efficient as they dry.

These thresholds concentrate in the semi-arid and transitional ecosystems that govern the trend and variability of the global land carbon sink. Crossing them converts efficient carbon uptake into rapid carbon loss, so the WUE threshold behaves as an early indicator of where drought is pushing ecosystems toward a carbon-losing state. As droughts intensify and the
 405 atmosphere grows drier, more of these ecosystems will spend more time beyond their thresholds. Representing the two-stage response and its controls in models would improve projections of how the land carbon sink will fare under a drier future.

Data and code availability

The NIRv GPP dataset is available at figshare (Wang et al., 2020). The FLUXCOM GPP and energy-flux (ET) products are available from the Max Planck Institute for Biogeochemistry data portal (Jung et al., 2018; Jung and FLUXCOM Team,
 410 2016). The optimum light-use-efficiency (LUE) GPP dataset is available from the Numerical Terradynamic Simulation Group (Madani et al., 2017b). ERA5-Land monthly averaged reanalysis, which provides evapotranspiration and the climatic predictors, is available from the Copernicus Climate Data Store (Muñoz-Sabater, 2019). The GLEAM evapotranspiration and potential evapotranspiration data are available at <https://www.gleam.eu/> (Martens et al., 2017; Miralles et al., 2011). The



reconstructed terrestrial water storage anomaly dataset (GRACE-REC) is available at figshare (Humphrey and
415 Gudmundsson, 2019b).

The additional predictor datasets (Table S2) are available as follows: the MODIS MCD12Q1 land-cover product (Friedl and Sulla-Menashe, 2019); TerraClimate vapor pressure deficit (Abatzoglou et al., 2017); SoilGrids 2.0 soil properties from the ISRIC Soil Data Hub (Poggio et al., 2021); the GIMMS LAI4g leaf area index (Cao et al., 2023); the PKU GIMMS NDVI (Li et al., 2023b); the global gridded atmospheric CO₂ concentrations (Cheng et al., 2021); the global effective plant rooting
420 depth (Yang et al., 2016b); the global plant hydraulic traits (Liu et al., 2021); and the global soil total phosphorus (He et al., 2021).

The analysis code is available from the corresponding author on reasonable request.

Author contributions

Conceptualization: S.C., YP.X., Y.G.; Methodology: S.C., YP.X., C.D.; Project administration: YP.X.; Writing – original
425 draft: S.C., C.D., Writing – review & editing: YP.X., Y.G., X.Y., H.G., A.K.

Competing interests

The authors declare that they have no conflict of interest.

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References

435 Abatzoglou, J. T., Dobrowski, S. Z., Parks, S. A., and Hegewisch, K. C.: Monthly climate and climatic water balance for global terrestrial surfaces from 1958-2015, Northwest Knowledge Network [data set], <https://doi.org/10.7923/G43J3B0R>, 2017.

Ahlström, A., Raupach, M. R., Schurgers, G., Smith, B., Arneth, A., Jung, M., Reichstein, M., Canadell, J. G., Friedlingstein, P., Jain, A. K., Kato, E., Poulter, B., Sitch, S., Stocker, B. D., Viovy, N., Wang, Y. P., Wiltshire, A., Zaehle, S., and Zeng, N.:



- 440 The dominant role of semi-arid ecosystems in the trend and variability of the land CO₂ sink, *Science*, 348, 895–899, <https://doi.org/10.1126/science.aaa1668>, 2015.
- Allen, R. G., Pereira, L. S., Raes, D., and Smith, M.: Crop evapotranspiration: Guidelines for computing crop water requirements, FAO Irrigation and Drainage Paper No. 56, Food and Agriculture Organization of the United Nations, Rome, Italy, ISBN 92-5-104219-5, <https://www.fao.org/4/x0490e/x0490e00.htm>, 1998.
- 445 Anderegg, W. R. L., Konings, A. G., Trugman, A. T., Yu, K., Bowling, D. R., Gabbitas, R., Karp, D. S., Pacala, S., Sperry, J. S., Sulman, B. N., and Zenes, N.: Hydraulic diversity of forests regulates ecosystem resilience during drought, *Nature*, 561, 538–541, <https://doi.org/10.1038/s41586-018-0539-7>, 2018.
- Berdugo, M., Delgado-Baquerizo, M., Soliveres, S., Hernández-Clemente, R., Zhao, Y., Gaitán, J. J., Gross, N., Saiz, H., Maire, V., Lehmann, A., Rillig, M. C., Solé, R. V., and Maestre, F. T.: Global ecosystem thresholds driven by aridity, *Science*, 367, 787–790, <https://doi.org/10.1126/science.aay5958>, 2020.
- 450 Boulton, C. A., Lenton, T. M., and Boers, N.: Pronounced loss of amazon rainforest resilience since the early 2000s, *Nat. Clim. Chang.*, 12, 271–278, <https://doi.org/10.1038/s41558-022-01287-8>, 2022.
- Brodribb, T. J., Powers, J., Cochard, H., and Choat, B.: Hanging by a thread? Forests and drought, *Science*, 368, 261–266, <https://doi.org/10.1126/science.aat7631>, 2020.
- 455 Cao, S., Li, M., Zhu, Z., Wang, Z., Zha, J., Zhao, W., Duanmu, Z., Chen, J., Zheng, Y., Chen, Y., Myneni, R. B., and Piao, S.: Spatiotemporally consistent global dataset of the GIMMS leaf area index (GIMMS LAI4g) from 1982 to 2020 (version 1.2), Zenodo [data set], <https://doi.org/10.5281/zenodo.7649107>, 2023.
- Cheng, W., Dan, L., Deng, X., Feng, J., Wang, Y., Peng, J., Tian, J., Qi, W., Liu, Z., Zheng, X., Zhou, D., Jiang, S., Zhao, H., and Wang, X.: Global monthly gridded atmospheric carbon dioxide concentrations under the historical and future scenarios, Zenodo [data set], <https://doi.org/10.5281/zenodo.5021361>, 2021.
- 460 Choat, B., Jansen, S., Brodribb, T. J., Cochard, H., Delzon, S., Bhaskar, R., Bucci, S. J., Feild, T. S., Gleason, S. M., Hacke, U. G., Jacobsen, A. L., Lens, F., Maherali, H., Martínez-Vilalta, J., Mayr, S., Mencuccini, M., Mitchell, P. J., Nardini, A., Pittermann, J., Pratt, R. B., Sperry, J. S., Westoby, M., Wright, I. J., and Zanne, A. E.: Global convergence in the vulnerability of forests to drought, *Nature*, 491, 752–755, <https://doi.org/10.1038/nature11688>, 2012.
- 465 Du, J., Kimball, J. S., Velicogna, I., Zhao, M., Jones, L. A., Watts, J. D., and Kim, Y.: Multicomponent Satellite Assessment of Drought Severity in the Contiguous United States From 2002 to 2017 Using AMSR-E and AMSR2, *Water Resources Research*, 55, 5394–5412, <https://doi.org/10.1029/2018WR024633>, 2019.
- Eilers, P. H. C. and Marx, B. D.: Flexible smoothing with B-splines and penalties, *Statist. Sci.*, 11, 89–99, <https://doi.org/10.1214/ss/1038425655>, 1996.
- 470 Fan, Y., Miguez-Macho, G., Jobbágy, E. G., Jackson, R. B., and Otero-Casal, C.: Hydrologic regulation of plant rooting depth, *Proc. Natl. Acad. Sci. U.S.A.*, 114, 10572–10577, <https://doi.org/10.1073/pnas.1712381114>, 2017.
- Forzieri, G., Dakos, V., McDowell, N. G., Alkama, R., and Cescatti, A.: Emerging signals of declining forest resilience under climate change, *Nature*, 608, 534–539, <https://doi.org/10.1038/s41586-022-04959-9>, 2022.
- Friedl, M. and Sulla-Menashe, D.: MCD12Q1 MODIS/Terra+Aqua Land Cover Type Yearly L3 Global 500m SIN Grid V006, NASA EOSDIS Land Processes DAAC [data set], <https://doi.org/10.5067/MODIS/MCD12Q1.006>, 2019.



- 475 Fu, Z., Ciais, P., Feldman, A. F., Gentine, P., Makowski, D., Prentice, I. C., Stoy, P. C., Bastos, A., and Wigner, J.-P.: Critical soil moisture thresholds of plant water stress in terrestrial ecosystems, *Sci. Adv.*, 8, eabq7827, <https://doi.org/10.1126/sciadv.abq7827>, 2022.
- Green, J. K., Seneviratne, S. I., Berg, A. M., Findell, K. L., Hagemann, S., Lawrence, D. M., and Gentine, P.: Large
480 influence of soil moisture on long-term terrestrial carbon uptake, *Nature*, 565, 476–479, <https://doi.org/10.1038/s41586-018-0848-x>, 2019.
- Green, J. K., Ballantyne, A., Abramoff, R., Gentine, P., Makowski, D., and Ciais, P.: Surface temperatures reveal the patterns of vegetation water stress and their environmental drivers across the tropical Americas, *Global Change Biology*, 28, 2940–2955, <https://doi.org/10.1111/gcb.16139>, 2022.
- Grossiord, C., Buckley, T. N., Cernusak, L. A., Novick, K. A., Poulter, B., Siegwolf, R. T. W., Sperry, J. S., and McDowell, N. G.: Plant responses to rising vapor pressure deficit, *New Phytologist*, 226, 1550–1566, <https://doi.org/10.1111/nph.16485>, 2020.
485
- Gu, H., Xu, Y.-P., Liu, L., Xie, J., Wang, L., Pan, S., and Guo, Y.: Seasonal catchment memory of high mountain rivers in the Tibetan Plateau, *Nat. Commun.*, 14, 3173, <https://doi.org/10.1038/s41467-023-38966-9>, 2023.
- Gupta, A., Rico-Medina, A., and Caño-Delgado, A. I.: The physiology of plant responses to drought, *Science*, 368, 266–269, <https://doi.org/10.1126/science.aaz7614>, 2020.
490
- Guyon, I., Weston, J., Barnhill, S., and Vapnik, V.: Gene selection for cancer classification using support vector machines, *Machine Learning*, 46, 389–422, <https://doi.org/10.1023/A:1012487302797>, 2002.
- He, X., Augusto, L., Goll, D. S., Ringeval, B., Wang, Y., Helfenstein, J., Huang, Y., Yu, K., Wang, Z., Yang, Y., and Hou, E.: A global dataset of soil total phosphorus concentration in (semi-)natural terrestrial ecosystems, *figshare* [data set], <https://doi.org/10.6084/m9.figshare.14583375>, 2021.
495
- Huang, M., Piao, S., Ciais, P., Peñuelas, J., Wang, X., Keenan, T. F., Peng, S., Berry, J. A., Wang, K., Mao, J., Alkama, R., Cescatti, A., Cuntz, M., De Deurwaerder, H., Gao, M., He, Y., Liu, Y., Luo, Y., Myneni, R. B., Niu, S., Shi, X., Yuan, W., Verbeeck, H., Wang, T., Wu, J., and Janssens, I. A.: Air temperature optima of vegetation productivity across global biomes, *Nature Ecology & Evolution*, 3, 772–779, <https://doi.org/10.1038/s41559-019-0838-x>, 2019.
- 500 Humphrey, V. and Gudmundsson, L.: GRACE-REC: a reconstruction of climate-driven water storage changes over the last century, *Earth Syst. Sci. Data*, 11, 1153–1170, <https://doi.org/10.5194/essd-11-1153-2019>, 2019a.
- Humphrey, V. and Gudmundsson, L.: GRACE-REC: A reconstruction of climate-driven water storage changes over the last century, *figshare* [data set], <https://doi.org/10.6084/m9.figshare.7670849>, 2019b.
- Jung, M. and FLUXCOM Team: FLUXCOM (RS+METEO) global land carbon fluxes using CRUNCEP climate data, Max Planck Institute for Biogeochemistry [data set], https://doi.org/10.17871/FLUXCOM_RS_METEO_CRUNCEPv6_1980_2013_v1, 2016.
505
- Jung, M., Koirala, S., Weber, U., Ichii, K., Gans, F., Camps-Valls, G., Papale, D., Schwalm, C., Tramontana, G., and Reichstein, M.: FLUXCOM global land energy fluxes, Max Planck Institute for Biogeochemistry [data set], https://doi.org/10.17871/FLUXCOM_EnergyFluxes_v1, 2018.



- 510 Jung, M., Koirala, S., Weber, U., Ichii, K., Gans, F., Camps-Valls, G., Papale, D., Schwalm, C., Tramontana, G., and Reichstein, M.: The FLUXCOM ensemble of global land-atmosphere energy fluxes, *Sci Data*, 6, 74, <https://doi.org/10.1038/s41597-019-0076-8>, 2019.
- Jung, M., Schwalm, C., Migliavacca, M., Walther, S., Camps-Valls, G., Koirala, S., Anthoni, P., Besnard, S., Bodesheim, P., Carvalhais, N., Chevallier, F., Gans, F., Goll, D. S., Haverd, V., Köhler, P., Ichii, K., Jain, A. K., Liu, J., Lombardozzi, D.,
515 Nabel, J. E. M. S., Nelson, J. A., O’Sullivan, M., Pallandt, M., Papale, D., Peters, W., Pongratz, J., Rödenbeck, C., Sitch, S., Tramontana, G., Walker, A., Weber, U., and Reichstein, M.: Scaling carbon fluxes from eddy covariance sites to globe: Synthesis and evaluation of the FLUXCOM approach, *Biogeosciences*, 17, 1343–1365, <https://doi.org/10.5194/bg-17-1343-2020>, 2020.
- Konings, A. G., Williams, A. P., and Gentine, P.: Sensitivity of grassland productivity to aridity controlled by stomatal and
520 xylem regulation, *Nature Geosci*, 10, 284–288, <https://doi.org/10.1038/ngeo2903>, 2017.
- Li, D., Liu, Z., Armaghani, D. J., Xiao, P., and Zhou, J.: Novel ensemble tree solution for rockburst prediction using deep forest, *Mathematics*, 10, 787, <https://doi.org/10.3390/math10050787>, 2022.
- Li, F., Xiao, J., Chen, J., Ballantyne, A., Jin, K., Li, B., Abraha, M., and John, R.: Global water use efficiency saturation due to increased vapor pressure deficit, *Science*, 381, 672–677, <https://doi.org/10.1126/science.adf5041>, 2023a.
- 525 Li, M., Cao, S., Zhu, Z., Wang, Z., Myneni, R. B., and Piao, S.: Spatiotemporally consistent global dataset of the GIMMS normalized difference vegetation index (PKU GIMMS NDVI) from 1982 to 2022 (version 1.2), Zenodo [data set], <https://doi.org/10.5281/zenodo.8253971>, 2023b.
- Li, X., Piao, S., Huntingford, C., Peñuelas, J., Yang, H., Xu, H., Chen, A., Friedlingstein, P., Keenan, T. F., Sitch, S., Wang, X., Zscheischler, J., and Mahecha, M. D.: Global variations in critical drought thresholds that impact vegetation, *Natl. Sci. Rev.*, 10, nwad049, <https://doi.org/10.1093/nsr/nwad049>, 2023c.
- 530 Liu, L., Gudmundsson, L., Hauser, M., Qin, D., Li, S., and Seneviratne, S. I.: Soil moisture dominates dryness stress on ecosystem production globally, *Nat Commun*, 11, 4892, <https://doi.org/10.1038/s41467-020-18631-1>, 2020.
- Liu, Y., Holtzman, N. M., and Konings, A. G.: Global ecosystem-scale plant hydraulic traits retrieved using model-data fusion, *figshare* [data set], <https://doi.org/10.6084/m9.figshare.13350713>, 2021.
- 535 Liu, Z., Ciais, P., Peñuelas, J., Xia, J., Zhou, S., Zhang, Y., and Fu, Y. H.: Enhanced vegetation productivity driven primarily by rate not duration of carbon uptake, *Nat. Clim. Chang.*, 15, 560–568, <https://doi.org/10.1038/s41558-025-02311-3>, 2025.
- Lu, J., Kong, D., Zhang, Y., Xie, Y., Gu, X., and Gulakhmadov, A.: Hotspots of global water resource changes and their causes, *Earth’s Future*, 13, e2024EF005461, <https://doi.org/10.1029/2024EF005461>, 2025.
- 540 Madani, N., Kimball, J. S., and Running, S. W.: Improving global gross primary productivity estimates by computing optimum light use efficiencies using flux tower data, *JGR Biogeosciences*, 122, 2939–2951, <https://doi.org/10.1002/2017JG004142>, 2017a.
- Madani, N., Kimball, J. S., and Running, S. W.: Optimum light-use-efficiency-based global gross primary productivity (GPP) dataset, Numerical Terradynamic Simulation Group [data set], http://files.nts.g.umd.edu/data/Optimum_LUE/, 2017b.
- 545 Manzoni, S., Jackson, R. B., Trofymow, J. A., and Porporato, A.: The global stoichiometry of litter nitrogen mineralization, *Science*, 321, 684–686, <https://doi.org/10.1126/science.1159792>, 2008.



- Martens, B., Miralles, D. G., Lievens, H., Van Der Schalie, R., De Jeu, R. A. M., Fernández-Prieto, D., Beck, H. E., Dorigo, W. A., and Verhoest, N. E. C.: GLEAM v3: Satellite-based land evaporation and root-zone soil moisture, *Geosci. Model Dev.*, 10, 1903–1925, <https://doi.org/10.5194/gmd-10-1903-2017>, 2017.
- 550 McDowell, N., Pockman, W. T., Allen, C. D., Breshears, D. D., Cobb, N., Kolb, T., Plaut, J., Sperry, J., West, A., Williams, D. G., and Yezpe, E. A.: Mechanisms of plant survival and mortality during drought: Why do some plants survive while others succumb to drought?, *New Phytologist*, 178, 719–739, <https://doi.org/10.1111/j.1469-8137.2008.02436.x>, 2008.
- Medlyn, B. E., Duursma, R. A., Eamus, D., Ellsworth, D. S., Prentice, I. C., Barton, C. V. M., Crous, K. Y., De Angelis, P., Freeman, M., and Wingate, L.: Reconciling the optimal and empirical approaches to modelling stomatal conductance, *Global Change Biology*, 17, 2134–2144, <https://doi.org/10.1111/j.1365-2486.2010.02375.x>, 2011.
- 555 Miralles, D. G., Holmes, T. R. H., De Jeu, R. A. M., Gash, J. H., Meesters, A. G. C. A., and Dolman, A. J.: Global land-surface evaporation estimated from satellite-based observations, *Hydrol. Earth Syst. Sci.*, 15, 453–469, <https://doi.org/10.5194/hess-15-453-2011>, 2011.
- Miralles, D. G., Gentine, P., Seneviratne, S. I., and Teuling, A. J.: Land–atmospheric feedbacks during droughts and heatwaves: state of the science and current challenges, *Annals of the New York Academy of Sciences*, 1436, 19–35, <https://doi.org/10.1111/nyas.13912>, 2019.
- 560 Muñoz-Sabater, J.: ERA5-Land monthly averaged data from 1950 to present, Copernicus Climate Change Service (C3S) Climate Data Store [data set], <https://doi.org/10.24381/cds.68d2bb30>, 2019.
- Naeem, S., Zhang, Y., Zhang, X., Rehman, A. U., Tang, Z., Xu, Z., Li, C., and Azeem, T.: Recent change in ecosystem water use efficiency in China mainly dominated by vegetation greening and increased CO₂, *Remote Sensing of Environment*, 298, 113811, <https://doi.org/10.1016/j.rse.2023.113811>, 2023.
- 565 Nippert, J. B. and Holdo, R. M.: Challenging the maximum rooting depth paradigm in grasslands and savannas, *Functional Ecology*, 29, 739–745, <https://doi.org/10.1111/1365-2435.12390>, 2015.
- Niu, S., Chen, W., Liang, L. L., Sierra, C. A., Xia, J., Wang, S., Heskell, M., Patel, K. F., Bond-Lamberty, B., Wang, J., Yvon-Durocher, G., Kirschbaum, M. U. F., Atkin, O. K., Huang, Y., Yu, G., and Luo, Y.: Temperature responses of ecosystem respiration, *Nat Rev Earth Environ*, 5, 559–571, <https://doi.org/10.1038/s43017-024-00569-3>, 2024.
- 570 Poggio, L., De Sousa, L. M., Batjes, N. H., Heuvelink, G. B. M., Kempen, B., Ribeiro, E., and Rossiter, D.: SoilGrids 2.0: Producing soil information for the globe with quantified spatial uncertainty, *SOIL*, 7, 217–240, <https://doi.org/10.5194/soil-7-217-2021>, 2021.
- Pokhrel, Y., Felfelani, F., Satoh, Y., Boulange, J., Burek, P., Gädeke, A., Gerten, D., Gosling, S. N., Grillakis, M., Gudmundsson, L., Hanasaki, N., Kim, H., Koutroulis, A., Liu, J., Papadimitriou, L., Schewe, J., Müller Schmied, H., Stacke, T., Telteu, C.-E., Thiery, W., Veldkamp, T., Zhao, F., and Wada, Y.: Global terrestrial water storage and drought severity under climate change, *Nat. Clim. Change*, 11, 226–233, <https://doi.org/10.1038/s41558-020-00972-w>, 2021.
- 575 Ponce-Campos, G. E., Moran, M. S., Huete, A., Zhang, Y., Bresloff, C., Huxman, T. E., Eamus, D., Bosch, D. D., Buda, A. R., Gunter, S. A., Scalley, T. H., Kitchen, S. G., McClaran, M. P., McNab, W. H., Montoya, D. S., Morgan, J. A., Peters, D. P. C., Sadler, E. J., Seyfried, M. S., and Starks, P. J.: Ecosystem resilience despite large-scale altered hydroclimatic conditions, *Nature*, 494, 349–352, <https://doi.org/10.1038/nature11836>, 2013.
- Schenk, H. J. and Jackson, R. B.: The global biogeography of roots, *Ecological Monographs*, 72, 311–328, [https://doi.org/10.1890/0012-9615\(2002\)072%5B0311:TGBOR%5D2.0.CO;2](https://doi.org/10.1890/0012-9615(2002)072%5B0311:TGBOR%5D2.0.CO;2), 2002.



- 585 Scholes, R. J. and Archer, S. R.: Tree-grass interactions in savannas, *Annual Review of Ecology and Systematics*, 28, 517–544, <https://doi.org/10.1146/annurev.ecolsys.28.1.517>, 1997.
- Sevanto, S., McDowell, N. G., Dickman, L. T., Pangle, R., and Pockman, W. T.: How do trees die? A test of the hydraulic failure and carbon starvation hypotheses, *Plant, Cell & Environment*, 37, 153–161, <https://doi.org/10.1111/pce.12141>, 2014.
- 590 Stocker, B. D., Zscheischler, J., Keenan, T. F., Prentice, I. C., Seneviratne, S. I., and Peñuelas, J.: Drought impacts on terrestrial primary production underestimated by satellite monitoring, *Nat. Geosci.*, 12, 264–270, <https://doi.org/10.1038/s41561-019-0318-6>, 2019.
- Wang, S., Zhang, Y., and Ju, W.: Long-term (1982–2018) global gross primary production dataset based on NIRv (version 2), figshare [data set], <https://doi.org/10.6084/m9.figshare.12981977.v2>, 2020.
- 595 Wang, S., Zhang, Y., Ju, W., Qiu, B., and Zhang, Z.: Tracking the seasonal and inter-annual variations of global gross primary production during last four decades using satellite near-infrared reflectance data, *Science of The Total Environment*, 755, 142569, <https://doi.org/10.1016/j.scitotenv.2020.142569>, 2021.
- Yang, Y., Guan, H., Batelaan, O., McVicar, T. R., Long, D., Piao, S., Liang, W., Liu, B., Jin, Z., and Simmons, C. T.: Contrasting responses of water use efficiency to drought across global terrestrial ecosystems, *Sci Rep*, 6, 23284, <https://doi.org/10.1038/srep23284>, 2016a.
- 600 Yang, Y., Donohue, R. J., and McVicar, T. R.: Global effective plant rooting depth, CSIRO Data Access Portal [data set], <https://doi.org/10.4225/08/5837b3aa9cb90>, 2016b.
- Yin, J., Gentile, P., Slater, L., Gu, L., Pokhrel, Y., Hanasaki, N., Guo, S., Xiong, L., and Schlenker, W.: Future socio-ecosystem productivity threatened by compound drought–heatwave events, *Nat Sustain*, 6, 259–272, <https://doi.org/10.1038/s41893-022-01024-1>, 2023.
- 605 Zhang, G., Xu, T., Yin, W., Bateni, S. M., Jun, C., Kim, D., Liu, S., Xu, Z., Ming, W., and Wang, J.: A machine learning downscaling framework based on a physically constrained sliding window technique for improving resolution of global water storage anomaly, *Remote Sensing of Environment*, 313, 114359, <https://doi.org/10.1016/j.rse.2024.114359>, 2024.
- Zhang, Y., Keenan, T. F., and Zhou, S.: Exacerbated drought impacts on global ecosystems due to structural overshoot, *Nat Ecol Evol*, 5, 1490–1498, <https://doi.org/10.1038/s41559-021-01551-8>, 2021.
- 610 Zhang, Y., Li, C., Chiew, F. H. S., Post, D. A., Zhang, X., Ma, N., Tian, J., Kong, D., Leung, L. R., Yu, Q., Shi, J., and Liu, C.: Southern Hemisphere dominates recent decline in global water availability, *Science*, 382, 579–584, <https://doi.org/10.1126/science.adh0716>, 2023.
- Zhao, M., A, G., Velicogna, I., and Kimball, J. S.: Satellite Observations of Regional Drought Severity in the Continental United States Using GRACE-Based Terrestrial Water Storage Changes, *J. Climate*, 30, 6297–6308, <https://doi.org/10.1175/JCLI-D-16-0458.1>, 2017.
- 615 Zhao, M., A, G., Liu, Y., and Konings, A. G.: Evapotranspiration frequently increases during droughts, *Nat. Clim. Change*, 12, 1024–1030, <https://doi.org/10.1038/s41558-022-01505-3>, 2022.
- Zhou, S., Yu, B., Lintner, B. R., Findell, K. L., and Zhang, Y.: Projected increase in global runoff dominated by land surface changes, *Nat. Clim. Chang.*, <https://doi.org/10.1038/s41558-023-01659-8>, 2023.



620 Zhou, Z.-H. and Feng, J.: Deep forest: Towards an alternative to deep neural networks, in: Proceedings of the Twenty-Sixth International Joint Conference on Artificial Intelligence, Twenty-Sixth International Joint Conference on Artificial Intelligence, 3553–3559, <https://doi.org/10.24963/ijcai.2017/497>, 2017.

Zhou, Z.-H. and Feng, J.: Deep forest, National Science Review, 6, 74–86, <https://doi.org/10.1093/nsr/nwy108>, 2019.