ARTICLE

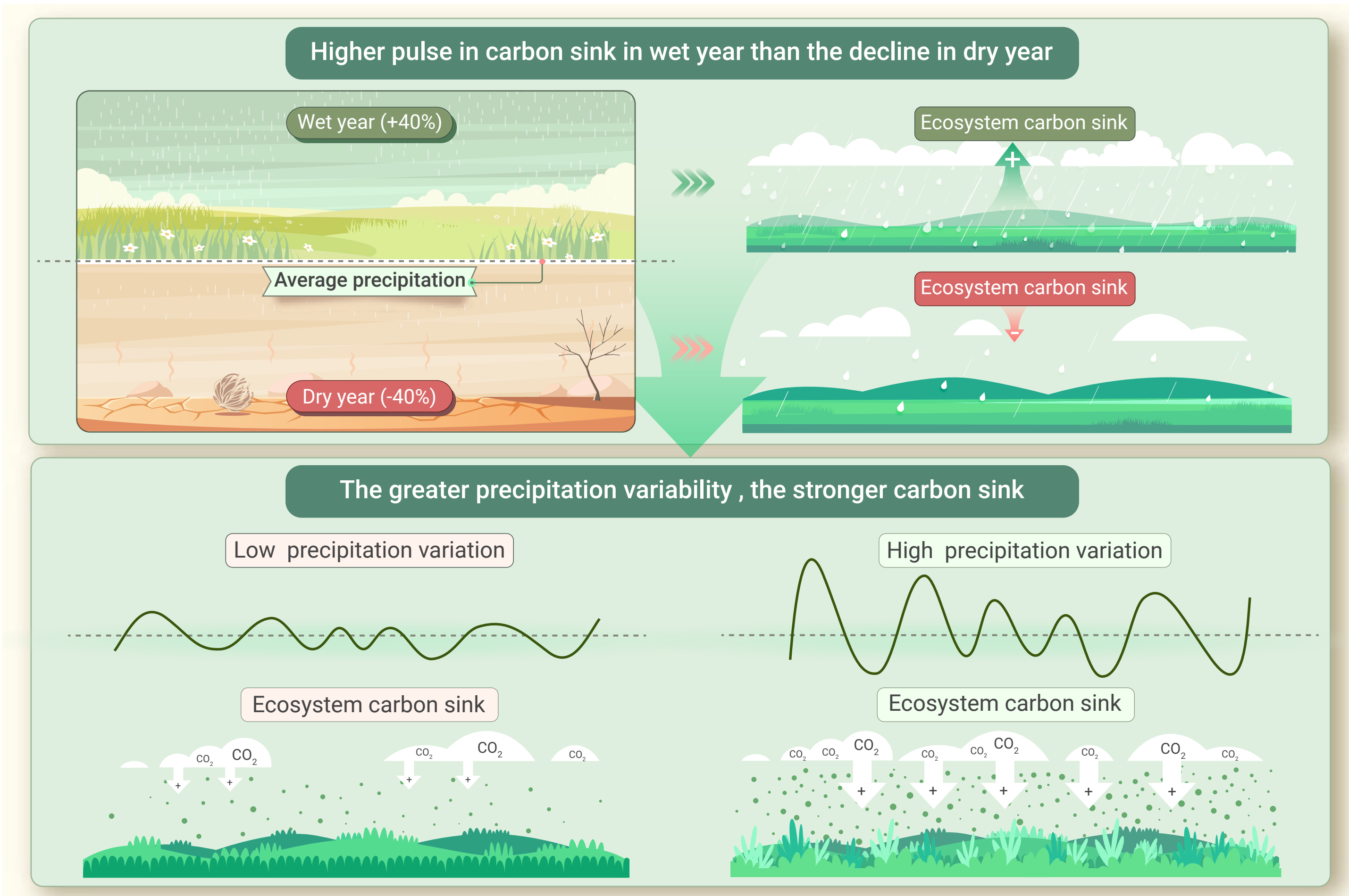
Positive asymmetric responses indicate larger carbon sink with increase in precipitation variability in global terrestrial ecosystems

Licong Dai,[1,2] Yue Yang,[1,2] Xuhui Wang,[3] Guojiao Yang,[1,2] Minqi Liang,[4] and Zhongmin Hu[1,2,*]

*Correspondence: huzm@hainanu.edu.cn

Received: September 6, 2023; Accepted: March 11, 2024; Published Online: March 14, 2024; https://doi.org/10.59717/j.xinn-geo.2024.100060

GRAPHICAL ABSTRACT



PUBLIC SUMMARY

- Increased carbon sink in wet years exceeds the reduction in dry years.
- Greater precipitation variability enhances carbon sink strength.
- Models display poor performance in ecosystem respiration responses.
- Improvements in simulating the soil water content responses could promote model performance.

Positive asymmetric responses indicate larger carbon sink with increase in precipitation variability in global terrestrial ecosystems

Licong Dai,[1,2] Yue Yang,[1,2] Xuhui Wang,[3] Guojiao Yang,[1,2] Minqi Liang,[4] and Zhongmin Hu[1,2,*]

[1]Hainan Baoting Tropical Rainforest Ecosystem Observation and Research Station, School of Ecology and Environment, Hainan University, Haikou 570228, China

[2]Key Laboratory of Agro-Forestry Environmental Processes and Ecological Regulation, School of Ecology and Environment, Hainan University, Haikou 570228, China

[3]Department of Ecology, College of Urban and Environmental Science, Key Laboratory for Earth Surface Processes of the Ministry of Education, Peking University, Beijing 100871, China

[4]School of Atmospheric Sciences, Sun Yat-sen University, Zhuhai 519082, China

*Correspondence: huzm@hainanu.edu.cn

Received: September 6, 2023; Accepted: March 11, 2024; Published Online: March 14, 2024; https://doi.org/10.59717/j.xinn-geo.2024.100060

Citation: Dai L., Yang Y., Wang X., et al., (2024). Positive asymmetric responses indicate larger carbon sink with increase in precipitation variability in global terrestrial ecosystems. The Innovation Geoscience **2(1)**: 100060.

Climate changes have caused high inter-annual variability in precipitation. However, how the terrestrial ecosystem responds to precipitation variability remains unclear. Using global remote sensing data and a meta-analysis by synthesizing 800 pairwise observations of experimental manipulations worldwide, we quantified the responses of the terrestrial ecosystem net carbon productivity (NEP) to precipitation variability. The results indicate that NEP displays a positive asymmetry in response to precipitation change, e.g., the magnitude of the increase in NEP (33.4%) under water-addition treatments is larger than that of the decline in NEP (-24.62%) under water-reduction treatments. The positive asymmetry of NEP in arid regions (< 500 mm) is larger than that in humid regions (> 500 mm). The former is mainly due to the positive asymmetry in vegetation productivity, while the latter results from the respiration process, i.e., the decrease in soil respiration in water-reduction treatments is stronger than in water-addition treatments. Furthermore, land models reproduce a positive NEP asymmetry in response to precipitation change, but display poor performance in ecosystem respiration (ER) responses owing to uncertainties in simulating soil water content (SWC). The positive asymmetry of NEP in this study implies that the increase in precipitation variability (except extreme anomalies) is conducive to high carbon sink in the global terrestrial ecosystem. Meanwhile, the performance of the models when simulating SWC in response to precipitation in humid regions needs to be further improved to better predict the carbon sink in the terrestrial ecosystem.

INTRODUCTION

Global warming has intensified hydrological processes over the past decades, altering precipitation regimes worldwide and inducing high inter-annual precipitation variability.[1,2] This amplification of precipitation variability in direction and magnitude is projected to continue at inter-annual and decadal scales under future climate change scenarios,[3] which can profoundly influence the carbon budget of the terrestrial ecosystem.[4] Therefore, for predicting the carbon sink of the ecosystem in response to future climate changes, it is critical to explore how the changes in precipitation variability affect the ecosystem's carbon budget or carbon sink.

Numerous field and model experiments have been conducted to clarify how terrestrial carbon budget responds to precipitation change,[5] with a special focus on the sensitivity of carbon processes to precipitation change, i.e., the relationship between precipitation variability and carbon fluxes.[6,7] Nevertheless, it is expected that precipitation variability will continuously increase with no obvious change in total precipitation under future climate scenarios.[3] Despite tremendous efforts in exploring the relationship between precipitation variability and land carbon sink variability,[8] how changes in precipitation variability affect the magnitude of carbon sink per se is still under debate, impeding the understanding of ecosystem responses and potential feedback of the global carbon budget to future climate variation.

The effect of precipitation variability on the ecosystem's carbon budget depends on the exact form of their relationship. Rudgers et al. (2018) elaborated on how vegetation productivity might change with precipitation variance, which was precipitation variability will not influence NEP because the pulse in NEP in a wet year is equal to the decline in NEP in a dry year with the same magnitude of precipitation variability.[9] However, NEP may have a nonlinear relationship with precipitation, resulting in asymmetric responses of NEP to precipitation variability and a decrease (Figure 1B) or increase (Figure 1C) in NEP. For example, a concave precipitation-NEP relationship (a negative asymmetry) represents that the magnitude of the increase in NEP in a wet year is lower than the magnitude of the decline in a dry year (Figure 1B), suggesting that the ecosystem's carbon sink will not benefit from increasing precipitation variability. In contrast, a convex precipitation-NEP relationship (a positive asymmetry) means that the increase in NEP in a wet year is larger than the decline in NEP in a dry year (Figure 1C), implying that increasing precipitation variability will favor promoting the carbon sink of the ecosystem.

NEP is the residual of two major ecosystem carbon processes, i.e., the carbon input process net primary productivity (NPP) and the carbon output process soil heterotrophic respiration (R_h).[10] This suggests that clarifying how asymmetric NPP and R_h respond to precipitation variability is the precondition for quantifying the responses of NEP to precipitation variability. Although the effect of precipitation variability on vegetation productivity in the grassland ecosystem has been extensively studied, both increased[11] and reduced productivities[12,13] under intensified precipitation variability have been found through in-situ observations and field experiments. Nevertheless, most studies focused on arid regions,[14,15] with little attention to humid areas. Furthermore, compared with vegetation productivity, how asymmetric the response of ecosystem respiration (ER) to precipitation change has been much less documented,[16,17] which further challenges the prediction of NEP under future climate scenarios.

To address these knowledge gaps and clarify the degree of asymmetry of the response of NEP to precipitation variability, we conducted a meta-analysis by synthesizing 800 pairwise observations of experimental precipitation manipulations in 145 globally published articles to address the following questions: (1) How asymmetric is the response of NEP to precipitation change? Which process (carbon input or carbon output) dominates the magnitude of the asymmetry? (2) How does the asymmetric NEP response to precipitation change vary with climate? Meanwhile, we also compared the observations with simulations of land models to clarify whether the models can capture the asymmetric responses of carbon fluxes to precipitation change. This study can provide new insight into predicting the response of the terrestrial carbon sink to precipitation variability in the background of global climate alternation.

MATERIALS AND METHODS

Data collection

This study collected peer-reviewed publications on the impact of precipitation change on the terrestrial carbon budget published before November 2021 using the Web of Science, Google Scholar, and the China Knowledge Resource Integrated Database (CNKI) that included cases of increased precipitation (+PPT) and decreased precipitation (−PPT). The search keywords and terms consisted of "climate change," "precipitation or rainfall increased/decreased," "water addition/removal," "irrigation," "drought," "aboveground biomass," "aboveground net primary productivity (ANPP)," "belowground net primary productivity (BNPP)," "biomass," "soil respiration (R_s)," "net ecosystem productivity (NEP)," "net carbon sink," and "carbon fluxes."

To minimize publication bias, the inclusion criteria included: (1) precipita-

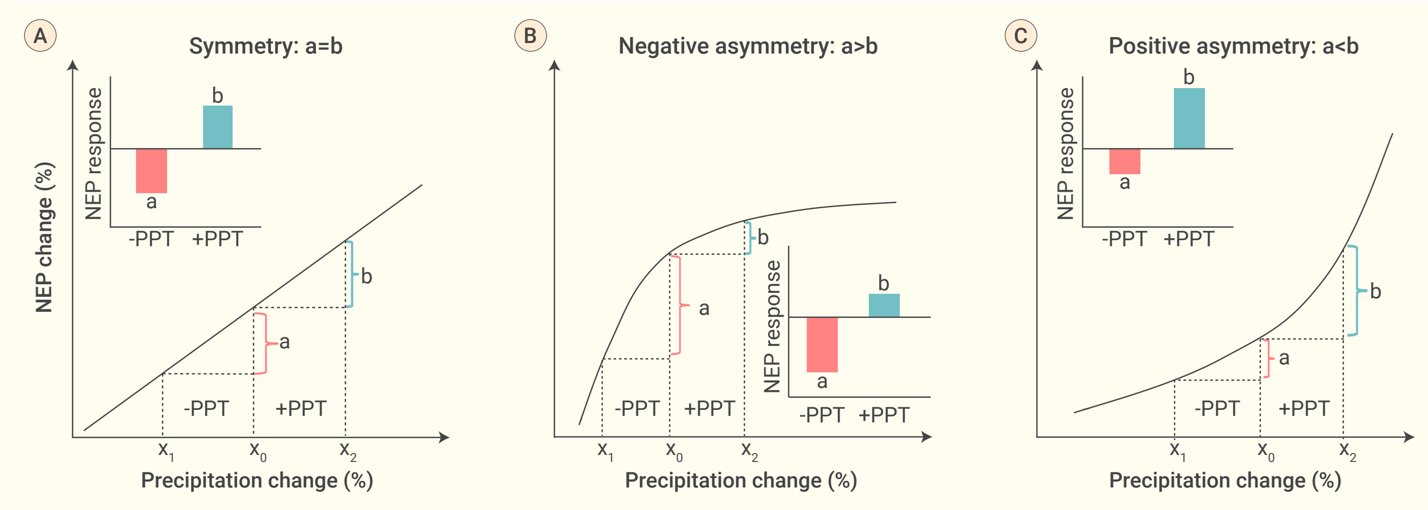


Figure 1. Schematic illustration of the response forms of NEP to precipitation variability (A) The symmetry response denotes that the pulse in NEP in wet years would equal to the decline in dry years with the same magnitude of changes in precipitation, (B) the negative asymmetry response denotes that the pulse in NEP in wet years is lower than the magnitude of decline in dry years, (C) and the positive asymmetry response denotes that the pulse in NEP in wet years is larger than the magnitude of decline in dry years. -PPT denotes in dry years, +PPT denotes in wet years.

tion experiments were manipulated in the field, including paired control and experimental treatment groups; each precipitation experiment had at least three replicates; (2) only control and experimental precipitation treatments were selected when multifactor and interactive effects of other factors existed in the study; (3) at least one growing season or an entire year was used as an experimental duration to avoid short-term noises; (4) the means, standard deviations (SDs) or standard errors (SEs), and sample size were provided directly or could be calculated; (5) only precipitation experiments were included, excluding snowfall addition/removal or increased/decreased snowfall or other multiple treatment experiments; (6) at least one of the selected variables (i.e., ANPP, aboveground biomass, BNPP, NEP, net carbon sink, and carbon flux) was included. In total, 800 pairwise observations from 145 published articles were selected across six biomes, i.e. boreal forests (4 sites), temperate seasonal forests (20 sites), tropical seasonal forests (1 site), tropical seasonal forests/savannas (20 sites), subtropical deserts (4 site), temperate grasslands/deserts (22 sites), woodlands/shrubland (45 sites) following the Whittaker vegetation classification, ANPP (31 sites), BNPP (41 sites), R_s (55 sites), and NEP (29 sites) (Figure S1).

From the selected publications, we used the Engauge Digitizer (Free Software Foundation, Inc., Boston, MA, USA) to extract means, SDs or SEs, sample size (N), table data, relevant variables (including the magnitude of the rainfall treatments, plant biomass, ANPP, BNPP, R_s, NEP, and SWC), and the site information (latitude, longitude, elevation, mean annual temperature, and mean annual precipitation).

Data analysis

We conducted a meta-analysis and meta-regression to explore the responses of carbon fluxes (ANPP, BNPP, R_s, and NEP) to precipitation change. The effects of the precipitation treatments were quantified using the natural log of the response ratio (RR). The effect size was calculated by the following equation: [18]

$$\mathrm{lnRR} = \ln\left(\frac{\overline{X}_T}{\overline{X}_c}\right) \tag{1}$$

The variance was obtained as follows:

$$V_{\mathrm{lnRR}} = \frac{SD_T^{\,2}}{n_t\overline{X}_T^{\,2}} + \frac{SD_c^{\,2}}{n_c\overline{X}_c^{\,2}} \tag{2}$$

Where $\overline{X}_T$ and $\overline{X}_c$ are the mean values of a given variable in the treatment and control groups, respectively; SD_T and SD_c represent standard deviation values; n_t and n_c denote the sample sizes of relevant variables in the treatment and control plots, respectively. For all meta-analyses and meta-regressions, we used inverse-variance weighted regressions and random-effect models to pool and compare RRs. The random-effect analyses employed a REML approach for estimating the between-study variance of each regression model. Non-zero effects were assessed with 95% confidential interval (CI).

The percentage of altered precipitation varies in published articles. For instance, the water-addition treatments ranged from 5% to 100% of the precipitation under the control treatment during the year, with a median of 40.5%, and the water-reduction treatments were between -3.8% and −100%, with a median of −39.5%. Therefore, we pooled all data to determine the absolute values of their manipulation levels, and the median was 40% of the precipitation under the control treatment. To quantify the asymmetry degree, this study normalized water-addition and water-reduction treatments to the same level (40%) of changes based on previous studies (Figure S2):[19]

$$\overline{X}_{NT} = \overline{X}_C + \frac{\overline{X}_T - \overline{X}_c}{P_c} \times 40 \tag{3}$$

Where $\overline{X}_{NT}$ is the normalized value under 40% above or below the MAP; P_c is the precipitation alteration level, expressed as a proportion of the local annual precipitation, and positive and negative values represent water-addition and water-reduction treatments, respectively. Considering that the temporal precipitation-carbon flux relationship can generally be fitted by a linear, concave, or convex function, the overall precipitation-carbon flux relationship is not undermined by normalizing water-addition and water-reduction treatments (Figure S2). In order to accurately determine the degree of asymmetry, this study selected treatments mostly adopted in field experiments (40%-50%, see Figure 2) and calculated their asymmetry degrees without normalization.

According to Hedges et al. (1999), the normalized effect size of the altered precipitation regime on was obtained from the natural log of the response ratio ($\mathrm{lnRR_{norm}}$), as shown in Eq. (4) :[18]

$$\mathrm{lnRR_{norm}} = \ln\left(\frac{\overline{X}_{NT}}{\overline{X}_C}\right) \tag{4}$$

Where $\overline{X}_{NT}$ and $\overline{X}_C$ are the mean values of a given variable in the treatment and control groups, respectively.

The variance (V_{lnRR}) of RR was computed using Eq. (3):

$$V_{\mathrm{lnRR_{norm}}} = \frac{SD_{NT}^{\,2}}{n_t\overline{X}_{NT}^{\,2}} + \frac{SD_c^{\,2}}{n_c\overline{X}_c^{\,2}} \tag{5}$$

Where SD_{NT} and SD_c represent standard deviation values, and n_t and n_c are the sample sizes of relevant variables in the treatment and control plots, respectively. When only SE was reported, it was converted to SD.

The overall effect of altered precipitation on the relevant variable was esti-

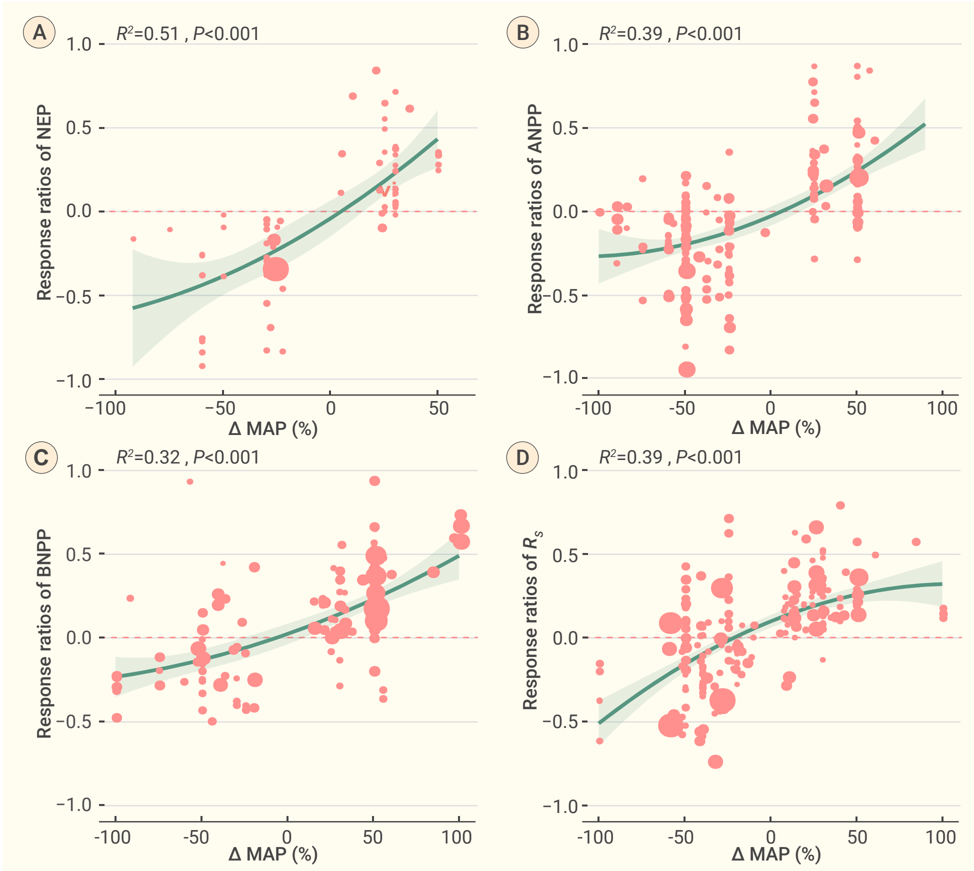


Figure 2. Relationships between precipitation changes and the response ratios of NEP (A), ANPP (B), BNPP (C), and R_s at all sites (D) The size of the bubble is proportionate to the weight of the effect size (RR) in the random-effects meta-regression. Larger bubbles indicate study outcomes that contributed to greater overall weight in the analyses. NEP, net carbon productivity; ANPP, aboveground net primary productivity; BNPP, belowground net primary productivity; R_s, soil respiration; ΔMAP, the magnitude of altered precipitation in percent (%) relative to the control the same below.

mated by the weighted random effect model in meta-analysis. The normalized weighted mean effect size ($lnRR_{++}$) and SE associated with $InRR_{++}$ were calculated by Eq. (4) and Eq. (5), respectively:

$$InRR_{++} = \frac{\sum_{i-1}^{m}\sum_{j-1}^{k} w_{ij} lnRR_{ij}}{\sum_{i-1}^{m}\sum_{j-1}^{k} w_{ij}} \tag{6}$$

$$SE_{lnRR_{++}} = \sqrt{\frac{1}{\sum_{i=1}^{m}\sum_{j=1}^{n} w_{ij}}} \tag{7}$$

Where m represents the number of groups (i.e., humid and arid regions), k denotes the number of observation variables in the i^{th} group, and w is the weighting factor of each observation variable, defined as the inverse of V_{lnRR}. This study used the 95% CI of $lnRR_{++}$, including zero or not, to examine the significance of the variation in each variable between the treatment and control groups. If the 95% CI of $lnRR_{++}$ did not include zero, it was considered to be significantly different from zero.[20] Moreover, the publication bias in the studies was evaluated by funnel plots, which were the scatter plots of the treatment effect size. The publication bias was absent when the studies were distributed symmetrically in a 'funnel' shape around a mean effect size. The results of the funnel plots with increased precipitation (IP) and decreased precipitation (DP) are provided in Supplementary Figures S3 and S4.

The categorical random model of meta-analysis was used to evaluate the significance of the categorical moderator. According to Eq. (6), the effect of altered precipitation on each variable was converted to the mean percentage change (P %) relative to the control plots to allow for comparing IP and DP.

$$P = (e^{lnRR_{++}} - 1) \times 100\% \tag{8}$$

If zero was not contained in 95% CI, the result was considered significant at $P < 0.05$; otherwise, the result was not significant.

To explore the relationship between precipitation changes and carbon fluxes for all sites, we selected two models: linear and quadratic. The response variables of the linear model were NPE, ANPP, BNPP, and R_s, and precipitation change were regarded as explanatory variables. The quadratic model allowed for concave-up and concave-down responses that were biologically possible. Other models, such as those explained by power functions, were excluded because they did not make biological sense. Then, the optimal fit was derived based on AIC and BIC scores.

All analyses and figure plotting were performed using R version 3.3.4 (R Core Team, 2016), and the meta-analysis was conducted by the "metafor" package with the restricted maximum likelihood "REML" method. Furthermore, the linear and non-linear mixed-effect models were fit using the "nlme" package to explore the relationship between the response ratio of carbon cycling variables and the precipitation change percentage.

Asymmetry

In this meta-study, the asymmetry index (AS) was adopted to characterize the asymmetry of carbon processes in response to precipitation change. Moreover, to explore the response of ecosystem carbon processes to precipitation variability in humid and arid regions, we defined the regions with a mean annual precipitation of less than 500 mm as arid areas and those with a mean annual precipitation of larger than 500 mm as humid areas.[21] The AS was calculated using Eq. (7):

$$AS = \frac{IP}{DP} \tag{9}$$

Where IP represents the overall increased percentage in variables under water-addition treatments, and DP denotes the overall decreased percentage in variables under water-reduction treatments. The values of IP and DP were calculated by Eq. (6), and water-addition and water-reduction precipitation were previously normalized to the same percentage (±40%). If AS was larger than 1 represented a positive asymmetry (i.e., the magnitude of the increase in carbon fluxes (ANPP, BNPP, Rs, and NEP) under water-addition treatments was larger than that of the decrease in ANPP under water-reduction treatments). If AS was lower than 1, it stood for a negative asymmetry (i.e., the magnitude of the increase in carbon fluxes under water-addition treatments was less than that of the decrease in ANPP under water-reduction treatments).

Terrestrial ecosystem models

To compare with the observed data from the meta-analysis and assess the performance of current terrestrial ecosystem models in simulating the carbon sink function to precipitation change, the TRENDY v6 models were employed to simulate the response of global ecosystem carbon fluxes (GPP, RE, and NEP). TRENDY (v6) is an ensemble of global dynamic vegetation models (DGVMs) forced by historical data,[22] including 12 models: CABLE (0.5°×0.5°), CLM4.5 (1.25°×0.94°), DLEM (0.5°×0.5°), ISAM(0.5°× 0.5°), LPX-Bern (1°×1°), LPJ-wsl (0.5°×0.5°), LPJ-GUESS (0.5°×0.5°), ORCHIDEE (0.5°×0.5°), JULES (1.88°×1.25°), ORCHIDEE-MICT (1°×1°), VEGAS (0.5°×0.5°), and VISIT (0.5°×0.5°). First, this study eliminated models without GPP in their outputs. Second, for consistency, the models with the same spatial resolution (0.5°) were selected, i.e., DLEM,[23] ISAM,[24] LPJ-wsl,[25] ORCHIDEE,[26] VEGAS,[27] VISIT,[28] CABLE,[29] and LPJ-GUESS.[30] It should be noted that the

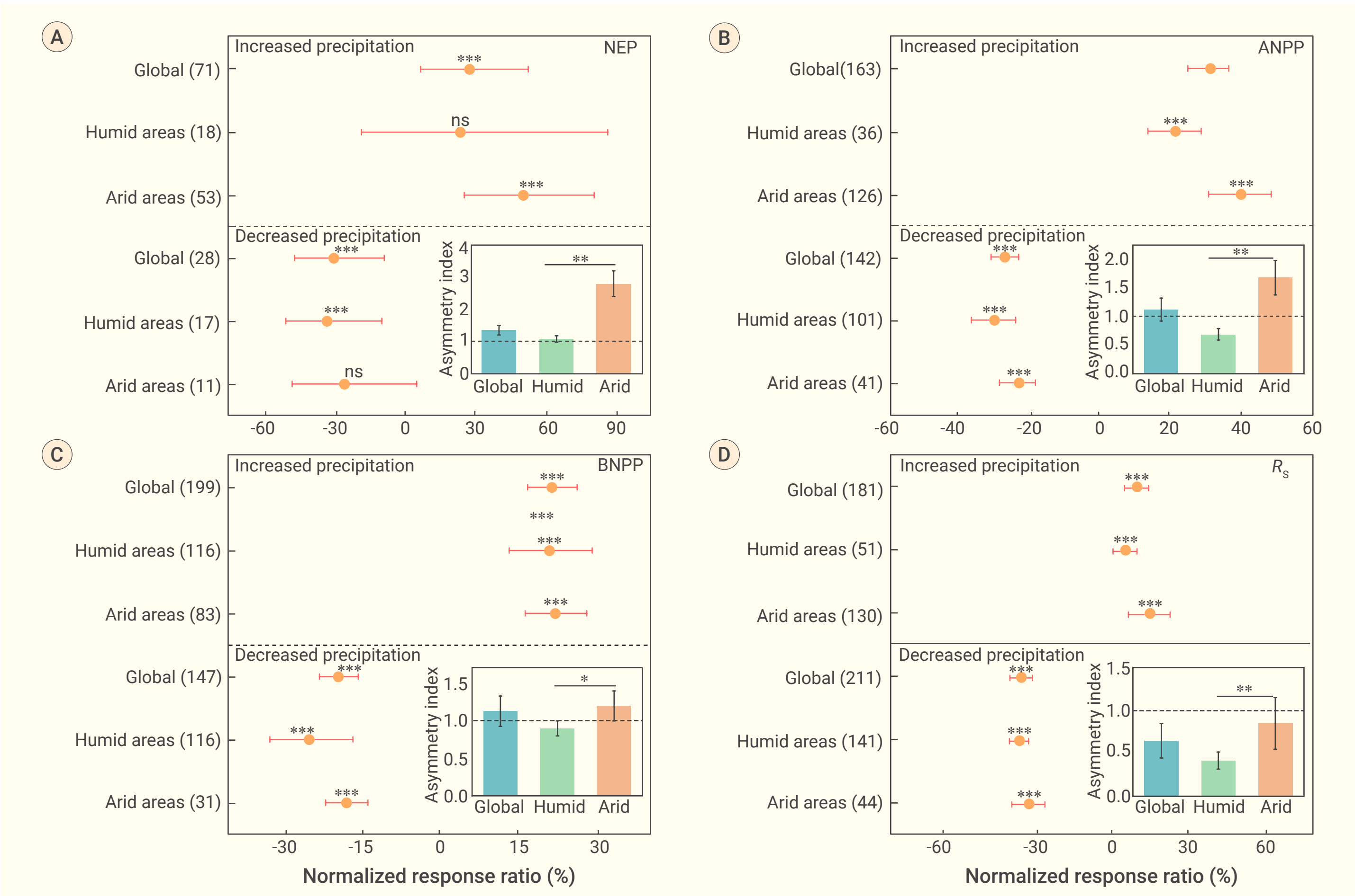


Figure 3. Changes in NEP, ANPP, BNPP, and R_s under the normalized precipitation change (40%) The effects of increased and decreased precipitation are significant when the 95% confident interval (CI) does not overlap 0. Values in parentheses indicate the means with CIs and the numbers of observations are shown in Y axis. *, ** and *** indicated significant differences at 0.05, 0.01 and 0.001 level, respectively. ns indicated no significant difference.

ORCHIDEE model only outputs GPP and does not output ER and NEP. Therefore, the ER and NEP data from ORCHIDEE were not included in this analysis. Besides, simulations under the S3 and S1 scenarios were compared with the data of the meta-analysis. Precipitation data with a spatial resolution of 0.5° came from the Climatic Research Unit (CRU) v4.03 dataset. This study extracted ecosystem carbon fluxes and precipitation data from 2000 to 2016. The yearly ecosystem carbon flux was the average value of monthly data over the whole year. The yearly precipitation was the sum of monthly precipitation over the whole year. The AS was computed as follows:

$$\mathrm{AS} = \frac{(f_{wet} - f_{normal})/f_{normal}}{(f_{normal} - f_{dry})/f_{normal}} \tag{10}$$

Where f_{normal} is the value of GPP, RE, or NEP corresponding to the year with a mean precipitation between 2000 and 2016; f_{wet} and f_{dry} are the values of GPP, RE, or NEP corresponding to the year with a precipitation increased or decreased by 10-15% compared with the mean annual precipitation in 2000-2016.

Satellite products

Satellite-retrieved solar-induced chlorophyll fluorescence (SIF) is widely used to reflect the GPP of the terrestrial ecosystem. This study calculated the AS of SIF in the selected sites and the global terrestrial ecosystem. The global spatially contiguous values of SIF (CSIF, 0.05°, 4-day, 2000-2018) were derived by Zhang et al. (2018) via training a neural network (NN) with the surface reflectance from the MODerate-resolution Imaging Spectroradiometer (MODIS) and SIF from Orbiting Carbon Observatory-2 (OCO-2).[31] Annual CSIF was obtained from the mean of 4-day data in one year. The spatial resolution was resampled to 0.5 degrees for global analysis. The AS was computed as follows:

$$\mathrm{AS} = \frac{(SIF_{wet} - SIF_{normal})/SIF_{normal}}{(SIF_{normal} - SIF_{dry})/SIF_{normal}} \tag{11}$$

Where SIF_{normal} is the value of SIF corresponding to the year with a mean precipitation in 2000-2018; SIF_{wet} and SIF_{dry} are the values of SIF corresponding to the year with a precipitation increased or decreased by 10-15% compared with the mean annual precipitation in 2000-2018.

RESULTS

Relationship between changes in precipitation and carbon fluxes

The relationship between precipitation changes and carbon fluxes was better fitted by a quadratic model than a linear model based on AIC and BIC scores (Table S1). Specifically, NEP showed a convex relationship with changes in annual precipitation (Figures 2A and S5A), indicating that the magnitude of the increase in NEP under water-addition treatments was larger than that under water-reduction treatments. Carbon input processes, i.e., ANPP and BNPP, exhibited a convex relationship with precipitation changes (Figures 2B and 2C), similar to the response function of NEP. However, the productivity-precipitation relationship varied between grassland and forest ecosystems. This study found a convex productivity-precipitation relationship in the grassland ecosystem and a concave productivity-precipitation relationship in the forest ecosystem (Figures S5B-C). Instead of R_h, soil respiration (R_s) was reported in most experimental studies. In this study, a concave response of R_s to precipitation changes (Figures 2D and S5D) was discovered, indicating that the magnitude of the increase in R_s under water-addition treatments was lower than that of the decrease in R_s under water-reduction treatments. Therefore, it can be considered that both input and output processes contributed to the convex precipitation-NEP relationship.

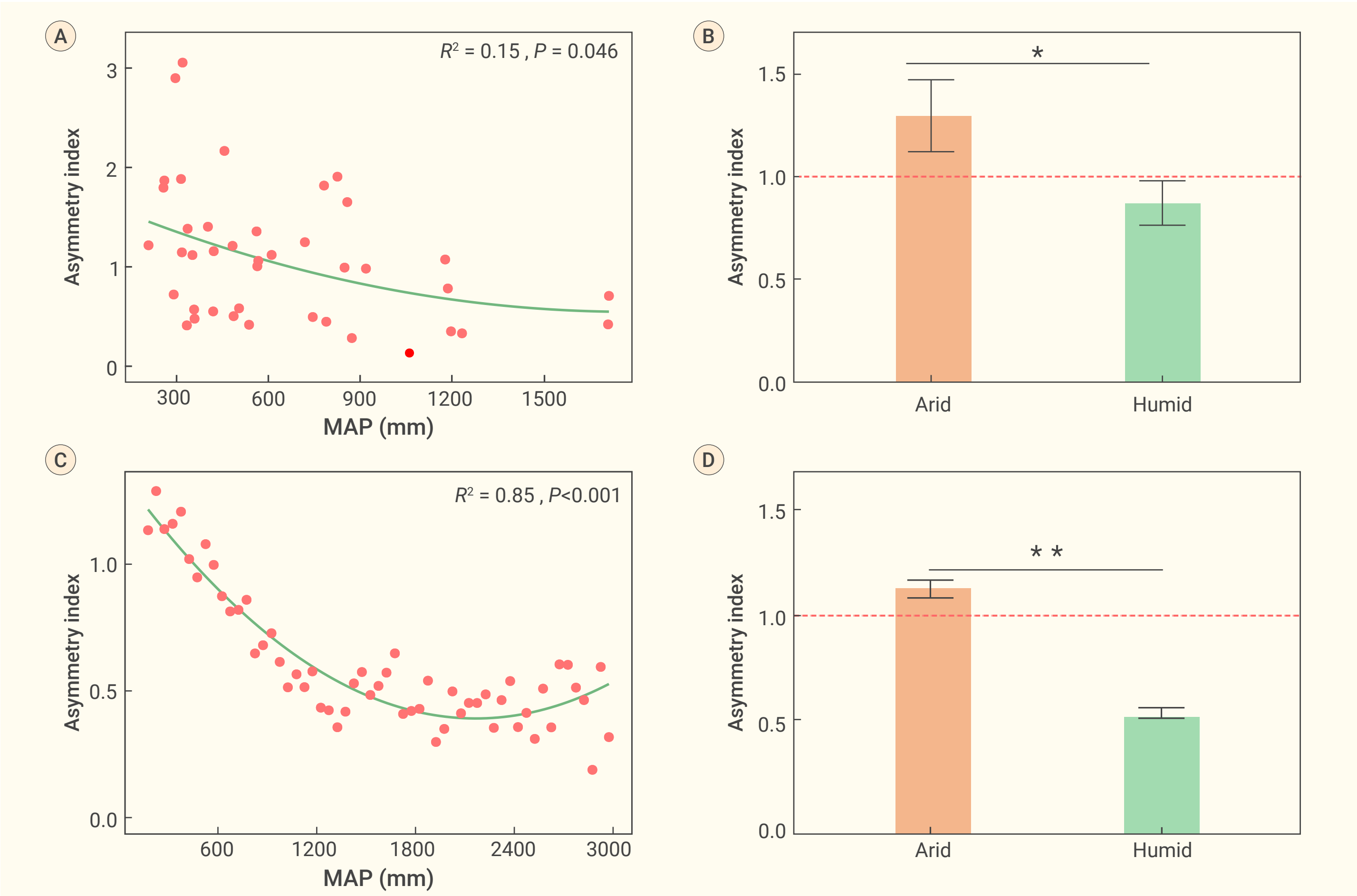


Figure 4. Spatial variations of the asymmetry index (AS) of solar-induced chlorophyll fluorescence (SIF) along precipitation gradient The comparison between arid and humid areas across the meta-analysis sites (A, B) and global terrestrial ecosystems (C, D). * and ** indicated significant differences at 0.05 and 0.01 level, respectively.

Asymmetric responses of carbon fluxes to precipitation changes

All treatments were normalized to the same level of 40% (water-addition and water-reduction treatments were normalized separately, as shown in Materials and Methods). NEP was significantly enhanced by 33.4% under water-addition treatments and reduced by 24.62% under water-reduction treatments (Figure 3A), indicating a positive asymmetry in response to precipitation change. This positive asymmetry was further confirmed (without normalization) using 40-50% of water-addition and water-reduction treatments, which was adopted in most field experiments (Figure S6A). The degree of the positive asymmetry in arid areas (MAP < 500 mm) and grasslands was larger than that in humid areas and forests (MAP > 500 mm) (P < 0.01, Figures 3A and S7A).

ANPP, BNPP, and R_s were enhanced by 39.72%, 21.35%, and 16.97% under water-addition treatments, respectively (P < 0.05, Figures 3B-D). The magnitudes of reductions in ANPP (27.60%) and BNPP (19.12%) under water-reduction treatments were smaller than that in R_s (28.84%) (P < 0.05), resulting in positive asymmetries in ANPP and BNPP and a negative asymmetry in R_s in response to precipitation change. These results were reproduced using 40-50% of water-addition and water-reduction treatment data (Figures S6B-D). However, the asymmetries of ANPP and BNPP differed profoundly among climate regions and ecosystems (P < 0.05), i.e., they were positive in arid areas and grasslands and negative in humid areas and forests (Figures 3B-C and S7B-C). In the dataset of global satellite-retrieved solar-induced chlorophyll fluorescence (SIF), a proxy of vegetation productivity, the same results were obtained, i.e., the asymmetry of SIF gradually declined with precipitation (P < 0.05, Figures 4A and C), high in arid regions and low in humid regions (P < 0.05, Figure 4B, D). Additionally, under water-addition treatments, the increased Rs in arid areas and forests was remarkably higher than in humid areas and forests (P < 0.01, Figures 3D and S7D). However, under water-reduction treatments, it reduced less than in humid areas and forests, leading to a higher negative asymmetry in arid areas and grasslands.

Mechanism of the asymmetric responses of carbon fluxes to precipitation change

Soil water content (SWC) was considered the key factor causing the asymmetric responses of NEP to precipitation change. Overall, SWC was enhanced by 29.55% under water-addition treatments and reduced by -24.44% under water-reduction treatments, presenting a positive asymmetry in response to precipitation change (Figure S8). It is consistent with the response pattern of NEP mentioned above (Figure 3A). In addition, the same magnitude of changes in SWC did not result in asymmetric responses for most carbon processes, suggesting that the precipitation change-induced asymmetry in SWC played a vital role in the asymmetric response of NEP (Figure S9). The paths through which SWC caused the NEP asymmetry differed between arid regions and humid regions (Figure 5). In arid regions, an apparently positive asymmetry in SWC in response to precipitation change was identified (P < 0.01, Figure S8), which resulted in positive asymmetric responses of vegetation productivity and NEP (Figure 5A). In contrast, SWC in humid regions displayed negative asymmetric responses to precipitation change: water-addition treatments caused an increase of 13% in SWC, and water-reduction treatments made SWC decline by 33% (Figure S8). This resulted in negative asymmetry of vegetation productivity and R_s. The negative asymmetry of R_s overweighed vegetation productivity, leading to a positive asymmetry of NEP (Figure 5B).

Performance of land models in simulating asymmetric responses of carbon fluxes

The model outputs under the S3 scenario (changing climate, CO_2, and land

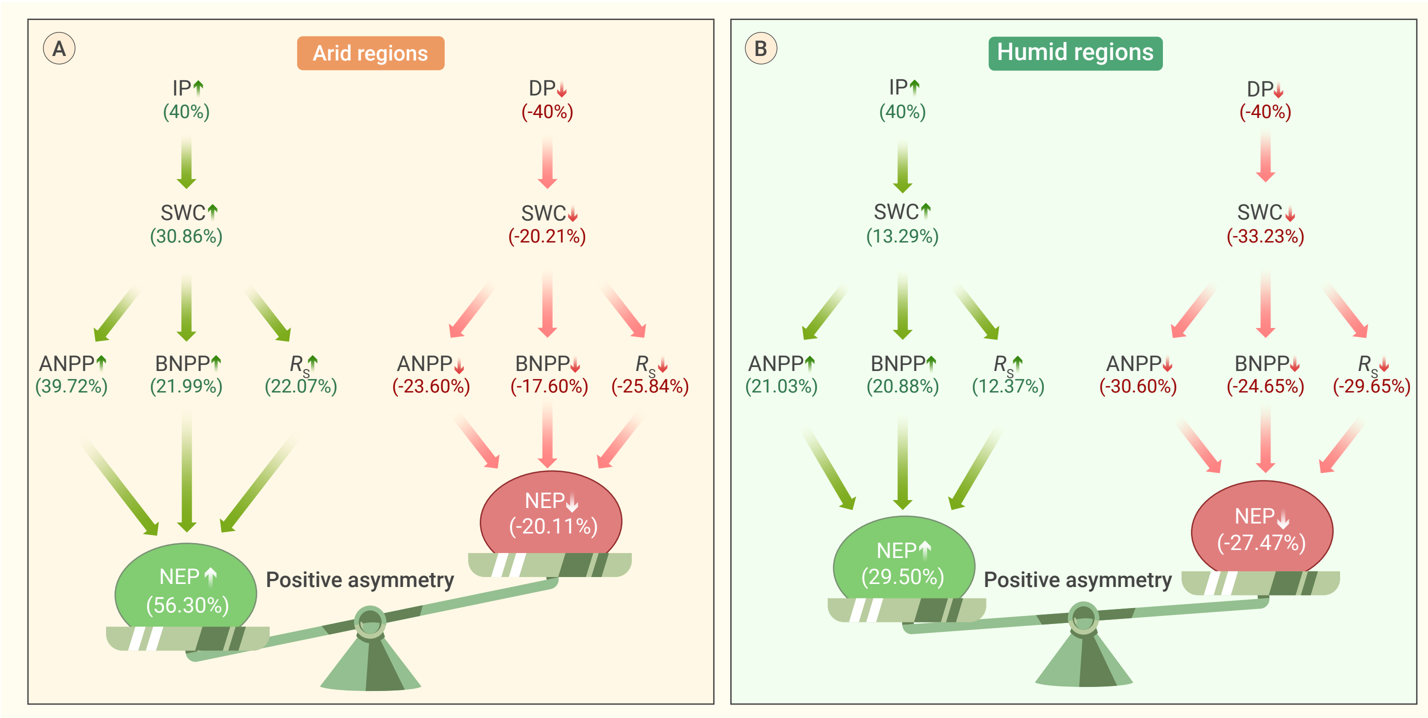


Figure 5. Mechanism of asymmetric responses of carbon budget to changes in precipitation in arid regions (A) and humid regions (B) IP: increased precipitation, DP: decreased precipitation, SWC: soil water content.

use) captured the overall positive asymmetry of NEP in response to global precipitation change (Figure 6A, see the performance of each model in Figures S10-17). Besides, the model outputs under the S1 scenario (changing CO_2 only) were consistent with the results under the S3 scenario (Figure S18A), suggesting that the simulated positive asymmetry in NEP was not attributed to asymmetry of climate factors. Notably, the models simulated the positive asymmetry of the ER in the carbon output process, which was opposite to the observations of soil respiration (Figures 6B and S18B). It was due to an overestimated pulse in wet years and an underestimated reduction in dry years, which was obvious at more humid sites (Figure 6B). Contrary to the observations, the models overestimated the positive asymmetry of GPP in humid regions (Figures 6C and S18C), because of which the simulated NEP in humid areas illustrated an obviously higher positive asymmetry (1.8) than the observation (1.1) ($P < 0.01$). The uncertainties of land models in simulating ER and GPP in humid regions were related to its poor performance in capturing SWC, i.e., the models overestimated the pulse in wet years and underestimated the reduction in dry years for SWC (Figure S19).

DISCUSSION

Asymmetric responses of carbon budget to precipitation change

Overall, the global synthesis in this study demonstrates that owing to the positive asymmetry of carbon input processes (ANPP and BNPP) and the negative asymmetry of the carbon output process (R_s), NEP shows a positive asymmetry in response to precipitation change (Figures 2 and 3), indicating that terrestrial carbon sink will benefit from the increase in precipitation variability under future climate scenarios. It has been reported that the interannual variability of precipitation will continue to increase in the context of global warming,[3] implying that the positive effect of precipitation variation caused by its positive asymmetry on carbon sink can offset the negative effect of climate anomalies on carbon sink under increasing precipitation variability.[32,33] Moreover, this study found that the positive asymmetry of NEP in arid regions was much higher than that in humid regions, representing that under increasing precipitation variability in arid regions, the carbon sink in arid areas will increase more than in humid areas.[34] It should be noted that the increasing precipitation variability in this study is limited to nominal precipitation variability that can favor carbon sink in the global terrestrial ecosystem. In contrast, carbon sink will drop under extreme precipitation variability.

Heterotrophic respiration, R_h, should be used to identify the reason for the NEP asymmetry (NEP=NPP- R_h). Instead, soil respiration R_s was used in this study due to data availability. This may introduce minor uncertainties to conclusions. It is widely acknowledged that R_h is the major part (55-70%) of R_s,[35,36] demonstrating that variations in NEP are mainly contributed by R_h. The previous meta-analysis disclosed that root respiration (the residual of R_s and R_h) remained the same under water-addition and water-reduction treatments.[19]

Mechanism of asymmetry in carbon budget under different climates

In arid regions, the positive asymmetric response of SWC and hence vegetation productivity contribute to the asymmetric response of carbon budget to precipitation change (Figure 5). The results agree with most studies, which reported a positive asymmetric response to precipitation fluctuations in grasslands.[15,37] The underlying mechanism might be that the increase in annual precipitation enhances the intensity of single rainfall events, which is conducive to recharging deeper soil layers and diminishing water loss via soil water evaporation, leading to higher than proportion increase in SWC.[38,39] Knapp et al. (2017) proposed a conceptual model depicting the response of NPP to precipitation change with a 'double asymmetry' function, displaying a positive asymmetry under nominal precipitation variation and a negative asymmetry at extreme precipitation levels.[14] In this study, the magnitude of manipulated precipitation change ranged from -70 to 70%, with an average of ca. ± 40% (Figure 2), belonging to moderate to high magnitude of changes and below the extreme conditions.

Notably, vegetation productivity illustrates a positive asymmetry even with a similar degree of SWC variability in arid regions (Figure 5A). Water plays a dominant role in controlling vegetation production.[40] In wet years, microbial activities and the increase in SWC enhance soil nutrient availability,[41] subsequently promoting plant photosynthesis.[42,43] Conversely, the reduction in precipitation affects vegetation productivity mildly because plants in arid regions have a strong drought resistance capacity.[44]

In contrary to the pattern in arid regions, SWC in humid regions presents a negative asymmetry in response to precipitation changes (Figure S8), resulting in a negative asymmetry in the carbon output flux and hence a positive asymmetry in carbon budget (Figure 6). Due to relatively high SWC in soil layers and steep slope topography in humid regions,[45] it is within the expectation that SWC changes less in wet years than in dry years. For example, the

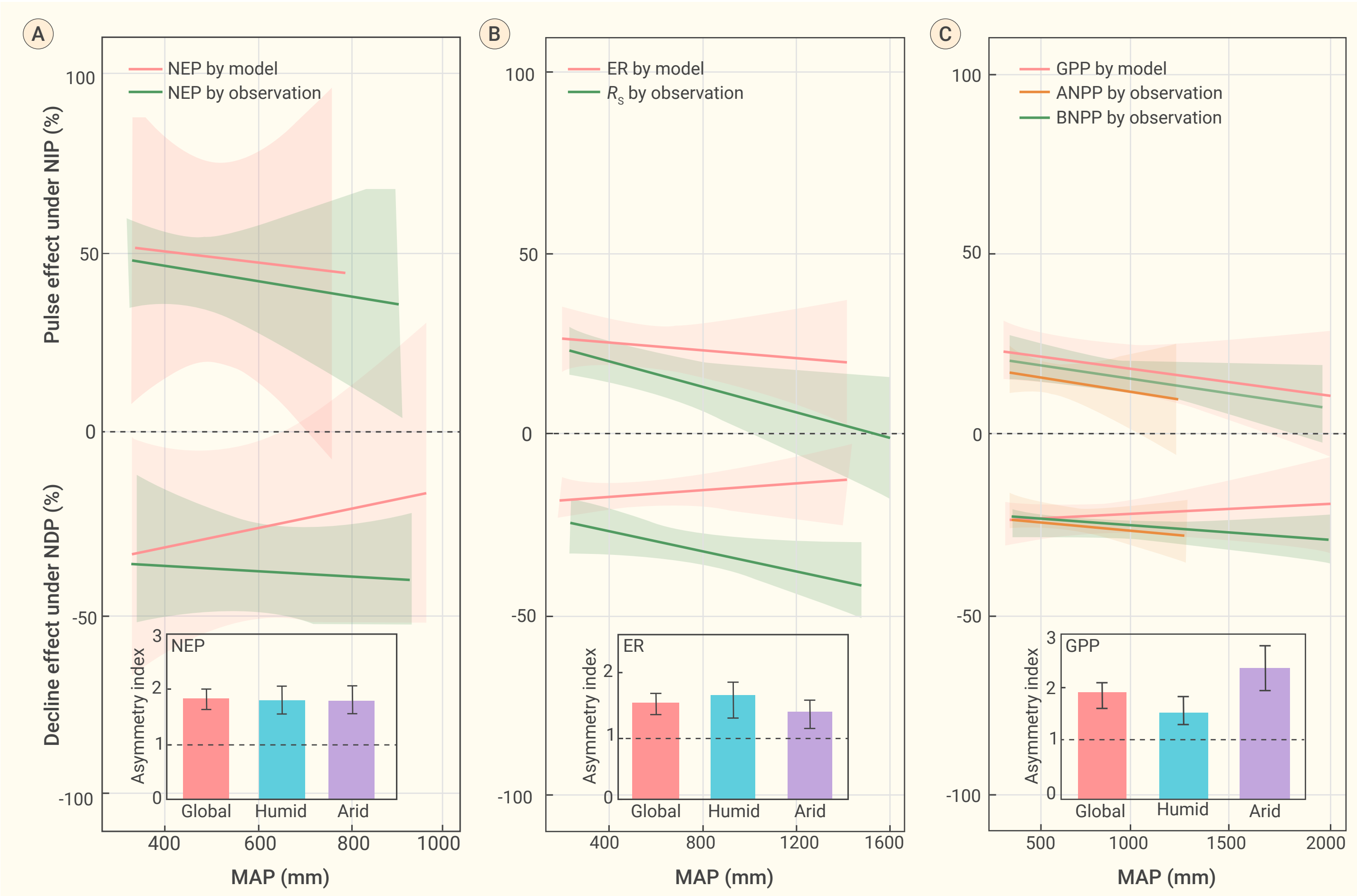


Figure 6. Comparison of responses of carbon fluxes to precipitation change between model simulations under the S3 scenario (changing climate, CO_2, and N deposition) and observations along precipitation gradient Linear regression is shown as solid line and 95% CIs are in the shaded area obtained, the error bars in represent 95% confidence intervals. NIP: normalized increased precipitation, NDP: normalized decreased precipitation. The inset panels indicate the average of the modeled asymmetry for NEP, ER, and GPP.

increase in precipitation will induce relatively minor growth in SWC with a large fraction of rainfall loss in the form of runoff.[46,47] In contrast, a reduction in rainfall in dry years can cause an obvious decline in SWC.[19] Furthermore, the vegetation productivity in humid regions exhibits a negative asymmetry in response to precipitation change (Figures 3B and C) because the increase in vegetation productivity is slight in wet years due to the limitation of nutrients and light.[48] The reduction in precipitation can significantly inhibit vegetation productivity because of its poor resistance to drought. Increasing evidence has shown that drought can drastically downgrade productivity even in the wettest rainforests, i.e., Amazon forests.[49,50]

Negative asymmetry of carbon output flux in response to precipitation change

The carbon output process R_s displays a negative asymmetry response to precipitation change in arid and humid regions, which contributes to the positive asymmetry in NEP, especially in humid regions (Figure 5). Obviously, the negative asymmetry of R_s in humid regions is caused by the negative asymmetric response in SWC (Figure 5). In comparison, R_s in arid regions exhibits a negative asymmetry despite the positive asymmetric response in SWC (Figure 3), which may be closely related to microbial activities.[51,52] For example, soil microbes in arid regions are constricted by SWC, and drought can trigger cell dehydration and even the death of soil microbes,[53] resulting in a significant decrease in heterotrophic respiration. In contrast, the increased R_s in wet years may be constrained or saturated owing to the limitation of oxygen and nutrients when increasing SWC.[19,54]

Soil temperature is another key factor controlling R_s. This study only investigated the effect of SWC because soil temperature was seldom documented in experimental studies. The role of soil temperature in the asymmetric response of R_s to precipitation change needs to be further clarified.

Merits and uncertainties in land carbon cycle models

The simulations of the models under the S3 scenario can capture the positive asymmetry of NEP in response to the increase in precipitation variability (Figure 6A). However, there are two uncertainties warranting more attention. First, the models simulated the positive asymmetry in ER. They overestimated the stimulus in wet years and underestimated the decline in dry years, especially in humid regions (Figure 6B). One reason might be that the models failed to reproduce the negative asymmetry in SWC in response to interannual precipitation anomalies (Figure S19). For example, in humid regions, the rainfall interception owing to the dense canopy can generate sharp declines in soil moisture in dry years.[55] However, the runoff from slope topography can lead to minor increases in soil moisture in wet years.[45] Another reason might be that the models fail to capture the mechanisms dominating ER in dry and wet years (see discussion above). The second uncertainty lies in the overestimation of the positive asymmetry in GPP in humid regions (Figure 6C). According to the data-model comparison, the reason is likely that the models underestimated the reduction in GPP in dry years (Figure 6C). Considering the similar phenomenon in ER (Figure 6B), one possible reason is the models underestimated the decline in SWC in dry years (Figure S19). Another mechanism might be that the reduction in precipitation abates nutrient availability and strengthens the constraint on plant growth, which the models usually fail to capture.[56,57] With the above two uncertainties, the prediction of carbon sink in response to changes in precipitation variability might be biased in humid regions. Further investigations on model performance in simulating SWC, especially in humid regions, and more data-model comparisons in the switch of controls on ER and plant growth in dry and wet years are essential.

CONCLUSIONS

Based on 800 pairwise observations of experimental precipitation manipulations, we found that NEP displayed a positive asymmetry in response to precipitation change, especially in arid regions. The underlying mechanism differs between arid and humid regions. The positive asymmetry of NEP in arid regions is mainly attributed to the increased carbon input process, whereas that of NEP in humid areas is mostly sourced from the reduced carbon output process. Furthermore, land models can capture the positive asymmetry of NEP in response to precipitation change at a global scale but exhibit poor performance at humid sites owing to uncertainties in simulating SWC and ER. The results suggest that intensified precipitation variability can stimulate terrestrial carbon sink (except extreme anomalies), especially at arid sites. Besides, it should be cautious when it is applied in humid areas due to the poor performance of the land carbon cycle model in simulating NEP in humid regions.

REFERENCES

1. Sloat, L.L., Gerber, J.S., Samberg, L.H., et al. (2018). Increasing importance of precipitation variability on global livestock grazing lands. Nature Climate Change 8(3):214-218. DOI: 10.1038/s41558-018-0081-5.
2. Smith, M.D. (2011). An ecological perspective on extreme climatic events: a synthetic definition and framework to guide future research. Journal of Ecology 99(3): 656–663. DOI: 10.1111/j.1365-2745.2011.01798.x.
3. Zhang, W., Furtado, K., Wu, P., et al. (2021). Increasing precipitation variability on daily-to-multiyear time scales in a warmer world. Science advances 7(31): eabf8021. DOI: 10.1126/sciadv.abf8021.
4. Poulter, B., Frank, D., Ciais, P., et al. (2014). Contribution of semi-arid ecosystems to interannual variability of the global carbon cycle. Nature 509(7502): 600–603. DOI: 10.1038/nature13376.
5. Hu, Z., Liang, M., Knapp, A., et al. (2022). Are regional precipitation–productivity relationships robust to decadal-scale dry period. Journal of Plant Ecology 15(4): 711–720. DOI: 10.1093/jpe/rtac008.
6. Piao, S., Sitch, S., Ciais, P., et al. (2013). Evaluation of terrestrial carbon cycle models for their response to climate variability and to CO2 trends. Global change biology 19(7): 2117–2132. DOI: 10.1111/gcb.12187.
7. Song, J., Wan, S., Piao, S., et al. (2019). A meta-analysis of 1,119 manipulative experiments on terrestrial carbon-cycling responses to global change. Nature ecology & evolution 3(9): 1309–1320. DOI: 10.1038/s41559-019-0958-3.
8. Ahlström, A., Raupach, M.R., Schurgers, G., 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. DOI: 10.1126/science.aaa1668.
9. Rudgers, J.A., Chung, Y.A., Maurer, G.E., et al. (2018). Climate sensitivity functions and net primary production: a framework for incorporating climate mean and variability. Ecology 99(3): 576–582. DOI: 10.1002/ecy.2136.
10. Shang, R., Chen, J.M., Xu, M., et al. (2023). China's current forest age structure will lead to weakened carbon sinks in the near future. The Innovation 4(6):100515. DOI: 10.1016/j.xinn.2023.100515.
11. Hou, E., Litvak, M.E., Rudgers, J.A., et al. (2021). Divergent responses of primary production to increasing precipitation variability in global drylands. Global change biology 27(20): 5225–5237. DOI: 10.1111/gcb.15801.
12. Gherardi, L.A., and Sala, O.E. (2015). Enhanced interannual precipitation variability increases plant functional diversity that in turn ameliorates negative impact on productivity. Ecology Letters 18(12): 1293–1300. DOI: 10.1111/ele.12523.
13. Gherardi, L.A., and Sala, O.E. (2015). Enhanced precipitation variability decreases grass-and increases shrub-productivity. Proceedings of the National Academy of Sciences 112(41): 12735–12740. DOI: 10.1073/pnas.1506433112.
14. Knapp, A.K., Avolio, M.L., Beier, C., et al. (2017). Pushing precipitation to the extremes in distributed experiments: recommendations for simulating wet and dry years. Global change biology 23(5): 1774–1782. DOI: 10.1111/gcb.13504.
15. Ru, J., Wan, S., Hui, D., et al. (2022). Increased interannual precipitation variability enhances the carbon sink in a semi‐arid grassland. Functional Ecology 36(4): 987–997. DOI: 110.1111/1365-2435.14011.
16. Jiang, H., Deng, Q., Zhou, G., et al. (2013). Responses of soil respiration and its temperature/moisture sensitivity to precipitation in three subtropical forests in southern China. Biogeosciences 10(6): 3963–3982. DOI: 110.5194/bg-10-3963-2013.
17. Miao, Y., Han, H., Du, Y., et al. (2017). Nonlinear responses of soil respiration to precipitation changes in a semiarid temperate steppe. Scientific Reports 7(1): 1–8. DOI: 10.1038/srep45782.
18. Hedges, L.V., and Olkin, I. (2014). Statistical methods for meta-analysis (Academic press).
19. Liu, L., Wang, X., Lajeunesse, M.J., et al. (2016). A cross‐biome synthesis of soil respiration and its determinants under simulated precipitation changes. Global change biology 22(4): 1394–1405. DOI: 10.1111/gcb.13156.
20. Koricheva, J., Gurevitch, J., and Mengersen, K. (2013). Handbook of meta-analysis in ecology and evolution (Princeton University Press).
21. Wang, B., Chen, Y., Li, Y., et al. (2021). Differential effects of altered precipitation regimes on soil carbon cycles in arid versus humid terrestrial ecosystems. Global Change Biology 27(24): 6348–6362. DOI: 10.1111/gcb.15875.
22. Sitch, S., Friedlingstein, P., Gruber, N., et al. (2015). Recent trends and drivers of regional sources and sinks of carbon dioxide. Biogeosciences 12(3): 653–679. DOI: 10.5194/bg-12-653-2015.
23. Tian, H., Chen, G., Lu, C., et al. (2015). North American terrestrial CO2 uptake largely offset by CH4 and N2O emissions: toward a full accounting of the greenhouse gas budget. Climatic Change 129(3): 413–426. DOI: 10.1007/s10584-014-1072-9.
24. Jain, A.K., Meiyappan, P., Song, Y., et al. (2013). CO2 emissions from land‐use change affected more by nitrogen cycle, than by the choice of land‐cover data. Global change biology 19(9): 2893–2906. DOI: 10.1111/gcb.12207.
25. Poulter, B., Frank, D., Hodson, E., et al. (2011). Impacts of land cover and climate data selection on understanding terrestrial carbon dynamics and the CO 2 airborne fraction. Biogeosciences 8(8): 2027–2036. DOI: 110.5194/bg-8-2027-2011.
26. Krinner, G., Viovy, N., de Noblet‐Ducoudré, N., et al. (2005). A dynamic global vegetation model for studies of the coupled atmosphere‐biosphere system. Global Biogeochemical Cycles 19(1). DOI: 10.1029/2003gb002199.
27. Zeng, N., Mariotti, A., and Wetzel, P. (2005). Terrestrial mechanisms of interannual CO2 variability. Global biogeochemical cycles 19(1). DOI: 10.1029/2004gb002273.
28. Kato, E., Kinoshita, T., Ito, A., et al. (2013). Evaluation of spatially explicit emission scenario of land-use change and biomass burning using a process-based biogeochemical model. Journal of Land Use Science 8(1): 104–122. DOI: 10.1080/1747423x.2011.628705.
29. Haverd, V., Smith, B., Nieradzik, L., et al. (2017). A new version of the CABLE land surface model, incorporating land-use change, woody vegetation demography and a novel optimisation-based approach to plant coordination of photosynthesis. arXiv preprint arXiv:1711.05351. DOI: 10.48550/arXiv.1711.05351.
30. Smith, B., Wårlind, D., Arneth, A., et al. (2014). Implications of incorporating N cycling and N limitations on primary production in an individual-based dynamic vegetation model. Biogeosciences 11(7): 2027–2054. DOI: 10.5194/bg-11-2027-2014.
31. Zhang, Y., Joiner, J., Alemohammad, S.H., et al. (2018). A global spatially contiguous solar-induced fluorescence (CSIF) dataset using neural networks. Biogeosciences 15(19): 5779–5800. DOI: 10.5194/bg-15-5779-2018.
32. Ciais, P., Reichstein, M., Viovy, N., et al. (2005). Europe-wide reduction in primary productivity caused by the heat and drought in 2003. Nature 437(7058): 529–533. DOI: 10.1038/nature03972.
33. Reichstein, M., Bahn, M., Ciais, P., et al. (2013). Climate extremes and the carbon cycle. Nature 500(7462): 287–295. DOI: 10.1038/nature12350.
34. Li, L., Kang, X., Biederman, J.A., et al. (2021). Nonlinear carbon cycling responses to precipitation variability in a semiarid grassland. Science of the Total Environment 781: 147062. DOI: 10.1016/j.scitotenv.2021.147062.
35. Graham, S.L., Millard, P., Hunt, J.E., et al. (2012). Roots affect the response of heterotrophic soil respiration to temperature in tussock grass microcosms. Annals of Botany 110(2): 253–258. DOI: 10.1093/aob/mcs073.
36. King, J.S., Hanson, P.J., Bernhardt, E., et al. (2004). A multiyear synthesis of soil respiration responses to elevated atmospheric CO2 from four forest FACE experiments. Global Change Biology 10(6): 1027–1042. DOI: 10.1111/j.1529-8817.2003.00789.x.
37. Gherardi, L.A., and Sala, O.E. (2019). Effect of interannual precipitation variability on dryland productivity: A global synthesis. Global Change Biology 25(1): 269–276. DOI: 10.1111/gcb.14480.
38. Guo, Q., Hu, Z., Li, S., et al. (2015). Contrasting responses of gross primary productivity to precipitation events in a water-limited and a temperature-limited grassland ecosystem. Agricultural and Forest Meteorology 214: 169–177. DOI: 10.1016/j.agrformet.2015.08.251.
39. Hao, Y., Zhou, C., Liu, W., et al. (2017). Aboveground net primary productivity and carbon balance remain stable under extreme precipitation events in a semiarid steppe ecosystem. Agricultural and Forest Meteorology 240: 1–9. DOI: 10.1016/j.agrformet.2017.03.006.
40. Jung, M., Reichstein, M., Schwalm, C.R., et al. (2017). Compensatory water effects link yearly global land CO2 sink changes to temperature. Nature 541(7638): 516–520. DOI: 10.1038/nature20780.
41. Knapp, A.K., Fay, P.A., Blair, J.M., et al. (2002). Rainfall variability, carbon cycling, and plant species diversity in a mesic grassland. Science 298(5601): 2202–2205. DOI: 10.1126/science.1076347.
42. Parton, W., Morgan, J., Smith, D., et al. (2012). Impact of precipitation dynamics on net ecosystem productivity. Global Change Biology 18(3): 915–927. DOI: 10.1111/j.1365-2486.2011.02611.x.
43. Shibata, H., Hasegawa, Y., Watanabe, T., et al. (2013). Impact of snowpack decrease on net nitrogen mineralization and nitrification in forest soil of northern Japan. Biogeochemistry 116(1): 69–82. DOI: 10.1007/s10533-013-9882-9.
44. Craine, J.M., Ocheltree, T.W., Nippert, J.B., et al. (2013). Global diversity of drought tolerance and grassland climate-change resilience. Nature Climate Change 3(1): 63–67. DOI: 10.1038/nclimate1634.
45. Ponce-Campos, G.E., Moran, M.S., Huete, A., et al. (2013). Ecosystem resilience despite large-scale altered hydroclimatic conditions. Nature 494(7437): 349–352. DOI: 10.1038/nature11836.

46. Du, Y., Han, H., Wang, Y., et al. (2018). Plant functional groups regulate soil respiration responses to nitrogen addition and mowing over a decade. Functional Ecology **32**(4): 1117–1127. DOI: 10.1111/1365-2435.13045.
47. Zhang, F., Quan, Q., Ma, F., et al. (2019). Differential responses of ecosystem carbon flux components to experimental precipitation gradient in an alpine meadow. Functional Ecology **33**(5): 889–900. DOI: 10.1111/1365-2435.13300.
48. Li, L., Zheng, Z., Biederman, J.A., et al. (2019). Ecological responses to heavy rainfall depend on seasonal timing and multi - year recurrence. New Phytologist **223**(2): 647–660. DOI: 10.1111/nph.15832.
49. Doughty, C.E., Metcalfe, D., Girardin, C., et al. (2015). Drought impact on forest carbon dynamics and fluxes in Amazonia. Nature **519**(7541): 78–82. DOI: 10.1038/nature14213.
50. Xu, L., Samanta, A., Costa, M.H., et al. (2011). Widespread decline in greenness of Amazonian vegetation due to the 2010 drought. Geophysical Research Letters **38**(7). DOI: 10.1029/2011gl046824.
51. Du, Y., Wang, Y.P., Su, F., et al. (2020). The response of soil respiration to precipitation change is asymmetric and differs between grasslands and forests. Global Change Biology **26**(10): 6015–6024. DOI: 10.1111/gcb.15270.
52. Wang, P., Huang, K., and Hu, S. (2020). Distinct fine - root responses to precipitation changes in herbaceous and woody plants: a meta - analysis. New Phytologist **225**(4): 1491–1499. DOI: 10.1111/nph.16266.
53. Unger, S., Máguas, C., Pereira, J.S., et al. (2010). The influence of precipitation pulses on soil respiration–Assessing the "Birch effect" by stable carbon isotopes. Soil Biology and Biochemistry **42**(10): 1800–1810. DOI: 10.1016/j.soilbio.2010.06.019.
54. Deng, Q., Hui, D., Zhang, D., et al. (2012). Effects of precipitation increase on soil respiration: a three-year field experiment in subtropical forests in China. PLoS One **7**(7): e41493. DOI: 10.1371/journal.pone.0041493.
55. He, L., Ivanov, V.Y., Bohrer, G., et al. (2013). Temporal dynamics of soil moisture in a northern temperate mixed successional forest after a prescribed intermediate disturbance. Agricultural and Forest Meteorology **180**: 22–33. DOI: 10.1016/j.agrformet.2013.04.014.
56. Cheng, K., Hu, Z., Li, S., et al. (2021). Improvement of predicting ecosystem productivity by modifying carbon–water–nitrogen coupling processes in a temperate grassland. Journal of Plant Ecology **14**(1): 10–21. DOI: 10.1093/jpe/rtaa072.
57. Knapp, A.K., and Smith, M.D. (2001). Variation among biomes in temporal dynamics of aboveground primary production. Science **291**(5503): 481–484. DOI: 10.1126/science.291.5503.481.

ACKNOWLEDGMENTS

We are grateful to the authors of the studies whose valuable field work provided the data for this meta-analysis. The study was financially supported by the National Natural Science Foundation of China (U23A2002), Second Tibetan Plateau Scientific Expedition and Research Program (2019QZKK0405), Key R&D Program of Hainan (ZDYF2022SHFZ042), and the start-up fund of Hainan University (KYQD(ZR)-22085, KYQD(ZR)21096).

AUTHOR CONTRIBUTIONS

L.D. and Z.H. initiated this study and led the writing of the manuscript. Y.Y., G.Y. , M.L., and X.Z. performed the data processing and analysis. All authors participated in the discussion and writing.

DECLARATION OF INTERESTS

The authors declare no competing interests.

DATA AND CODE AVAILABILITY

All meta data generated in this study and used to create the figures have been deposited the Dryad database: https://doi.org/10.5061/dryad.zs7h44jf8

SUPPLEMENTAL INFORMATION

It can be found online at https://doi.org/10.59717/j.xinn-geo.2024.100060

LEAD CONTACT WEBSITE

https://see.hainanu.edu.cn/info/1101/2711.htm