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Increasing coldward shift of karst vegetation carbon sink driven by climate warming

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Abstract: Climate warming has reshaped the thermal and moisture environments for vegetation growth. Spatial heterogeneity in hydrothermal factors may alter vegetation ecological adaptation processes, thereby restricting carbon sink potential in relatively warm zones while enhancing it in relatively cold zones. As a result, vegetation carbon sink growth may exhibit a warm-to-cold shift. However, this potential shift remains unverified, and its spatial patterns and evolutionary mechanisms remain unclear. Karst trough valleys are characterized by a typical three-dimensional

surface–subsurface dual hydrogeological structure, pronounced elevational variations, and complex combinations of slope aspects, which respectively form contrasting warm–cold zones between the surface and subsurface, low and high elevations, and sunny and shady slopes, making them representative regions for investigating the coldward shift of vegetation carbon sinks under climate warming. Based on this, taking the karst trough valley as a representative case, a three-dimensional warm–cold pattern framework based on slope aspect, elevation, and spatial structure was constructed to reveal the historical and future characteristics of the coldward shift in vegetation carbon sinks and to analyze its climatic driving mechanisms. The results showed that vegetation carbon sinks exhibited a warm-to-cold shift across the dimensions of spatial structure, elevation, and slope aspect. In terms of spatial structure, belowground net primary productivity (BNPP)/total net primary productivity (TNPP) increased at rates of 0.00026 and 0.00011 yr⁻¹ during the historical period and under the SSP245 scenario, respectively, indicating a continued strengthening of the growth advantage of belowground carbon sinks. Along the elevational gradient, net primary productivity (NPP) growth gradually shifted from low-elevation regions toward high-elevation regions. Under the high-emission scenario (SSP585), the NPP growth rate at high elevations was approximately twice that at middle and low elevations. Along the slope-aspect dimension, NPP growth shifted from semi-sunny and semi-shady slopes toward shady slopes. Under all three future scenarios, shady slopes exhibited a pronounced growth-rate advantage, with the highest growth rate reaching 1.22 g C m⁻² yr⁻¹. In addition, the results indicated that moisture conditions dominated the shift in the growth advantage of vegetation carbon sinks toward colder zones, while soil CO₂ partial pressure (*p*CO₂) exerted a pronounced effect at low elevations. This study confirms the shift in vegetation carbon sink growth advantage from warmer to colder zones and provides a new perspective for understanding the spatial reorganization of vegetation carbon sinks under climate warming.

Keywords

Karst; Climate change; NPP; Vegetation carbon sink; Karst trough valley

1. Introduction

Climate warming is reshaping the thermal and moisture environments for vegetation growth. Limiting factors such as rising temperature, enhanced evapotranspiration, and drought have placed greater pressure on vegetation growth, nutrient uptake, and the maintenance of metabolic balance, thereby potentially weakening the carbon sink function of terrestrial ecosystems (Friedlingstein et al., 2025). However, vegetation growth does not respond to climate warming in a completely passive manner. Vegetation can partly adapt to changes in hydrothermal conditions by increasing its optimum physiological temperature (Wang et al., 2024), adjusting the carbon allocation structure between aboveground and belowground organs (Schindlbacher et al., 2025), altering phenological rhythms (Grossiord et al., 2022), and regulating water-use strategies (Querejeta et al., 2021). Therefore, revealing the spatial differences in vegetation carbon sink changes and their adaptive adjustment processes is of great significance for understanding the reorganization of carbon sink patterns under climate warming.

Existing studies generally regard the direct effects of climatic factors on photosynthesis, respiration, and water limitation as the main drivers of vegetation carbon sink responses. These studies have emphasized how warming and drought weaken plant carbon sinks or enhance respiratory carbon consumption (Wei et al., 2025; Yang et al., 2024), while also noting the potential growth advantages of vegetation in cold-temperate regions under moderate warming (Fernández-Martínez et al., 2019). However, such studies often treat vegetation as a passive responder to climate change, with insufficient attention paid to how vegetation forms spatial adaptive adjustments based on local thermal patterns. Karst trough valleys provide distinctive natural conditions for investigating such spatial adaptive adjustments. First, karst trough valleys are characterized by a distinctive three-dimensional dual surface–subsurface hydrogeological structure. Shallow soils, well-developed fractures, and extensive subsurface spaces facilitate the vertical migration of water, resulting in pronounced hydrothermal differences between the surface and subsurface. Second, the region is characterized by steep terrain and large elevational differences, forming a pronounced vertical hydrothermal gradient from valley bottoms to high-elevation areas. Third, the rugged terrain and complex slope-aspect configurations result in differences in the intensity and duration of solar radiation received by different slope aspects,

thereby producing pronounced warm–cold contrasts between sunny and shady slopes. Together, these characteristics constitute a three-dimensional warm–cold spatial pattern in karst trough valleys, making them representative regions for investigating the redistribution of vegetation carbon sinks from relatively warm zones toward relatively cold zones under climate warming. Under such terrain settings, vegetation in different regions is exposed to different levels of heat stress, water limitation, and energy availability. In relatively warm zones, rising temperature may cause vegetation to approach or exceed its optimum physiological thresholds, thereby inhibiting carbon fixation and enhancing respiratory carbon consumption (Tarvainen et al., 2022; Fernández-Martínez et al., 2019). In contrast, in relatively cold zones, improved thermal conditions may alleviate low-temperature stress and enhance vegetation carbon input capacity (White et al., 2000; Ruehr et al., 2023; D’Orangeville et al., 2018). Based on this, vegetation carbon sinks can be hypothesized to exhibit a progressive spatial shift from relatively warm zones toward relatively cold zones. However, this key process has not yet been confirmed in existing research, and its spatial pattern and intrinsic driving mechanisms remain to be systematically clarified.

Based on this background, the National Center for Ecological Analysis and Synthesis (NCEAS) model was used in this study to estimate the evolution of vegetation carbon sinks in the karst trough valley from 2000 to 2100. A three-dimensional warm–cold analytical framework integrating elevational gradients (low, middle, and high elevations), slope-aspect categories (shady, semi-shady, semi-sunny, and sunny slopes), and aboveground-belowground spatial structure (aboveground net primary productivity (ANPP) and belowground net primary productivity (BNPP)) was developed to identify the spatial characteristics of the coldward shift in vegetation carbon sinks under climate warming (Fig.1). This study mainly aimed to address three scientific issues: (1) to introduce a three-dimensional warm–cold analytical framework and systematically reveal the trend characteristics of the coldward shift in net primary productivity (NPP) in the karst trough valley from 2000 to 2100; (2) to clarify the scenario differences and dominant characteristics of the coldward shift in NPP during the historical period and under different future climate scenarios; and (3) to analyze the driving effects of climatic and environmental factors on the coldward shift in NPP. The findings provide a new analytical perspective for identifying the mechanism of spatial reorganization of vegetation carbon sinks in complex terrain regions, and

offer scientific support for vegetation carbon sink assessment and adaptive ecosystem management in karst regions under climate warming.

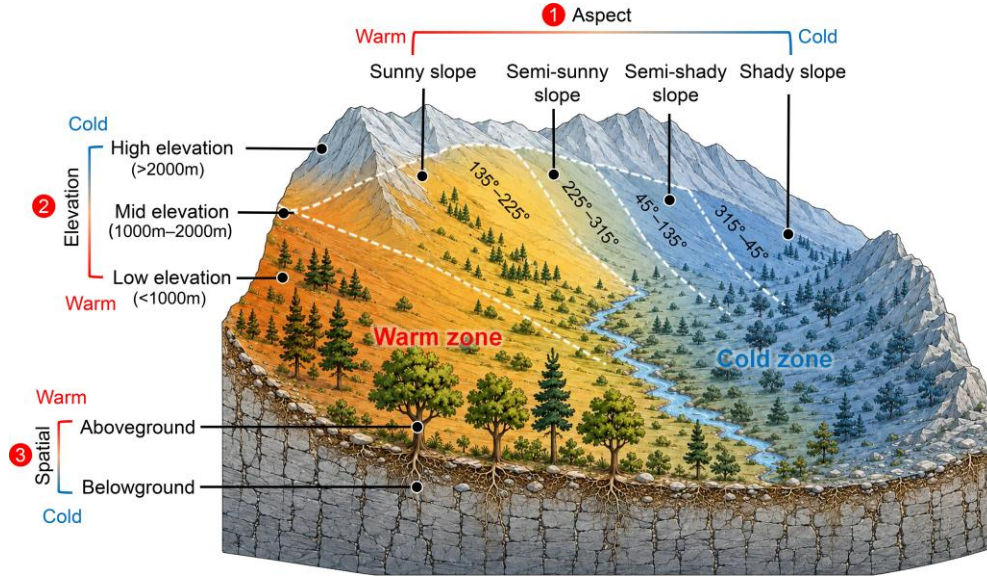


Fig. 1. Three-dimensional warm–cold spatial framework of the karst trough valley.

2. Study area

The karst trough valley is an important component of the karst area in southern China (Fig.2), covering approximately 286000 km². Exposed karst accounts for 46.06% of the total area within this region and 14.77% of the entire karst area in southern China (Cao et al., 2019; Jiang et al., 2014). The region spans seven provinces and municipalities, namely Hubei (HUB), Hunan (HUN), Henan (HN), Shaanxi (SAX), Chongqing (CQ), Sichuan (SC), and Guizhou (GZ), extending from 26°23' to 33°37' N and from 105°31' to 113°47' E. It serves as an important ecological security barrier in the upper and middle reaches of the Yangtze River (Bai et al., 2023). The region has a subtropical monsoon climate, with humid and mild climatic conditions. Precipitation is mainly concentrated from May to November, annual precipitation exceeds 800 mm, and the mean annual temperature ranges from approximately 11.54 to 18.83°C. The dominant soil types are yellow soil and calcareous soil.

The karst trough valley is characterized by the interbedding of multiple lithologies, steep mountains and slopes, large elevation differences, distinct two-wing and one-belt structures, and pronounced vertical three-dimensional features. The soil cover is discontinuous, and underground caves and fissures are well developed. Severe soil erosion has led to soil thinning and widespread rocky desertification, making the ecosystem extremely fragile (Xiong et al., 2009). The steep

trough valley terrain and unique binary three-dimensional spatial structure result in strong surface soil erosion and subsurface leakage (Li et al., 2017). The study area contains eight lithological types, including continuous limestone, continuous dolomite, mixed continuous limestone and dolomite, limestone interbedded with clastic rocks, dolomite interbedded with clastic rocks, interbedded limestone and clastic rocks, interbedded dolomite and clastic rocks, and non-carbonate rocks (Ma et al., 2018). Its unique binary three-dimensional spatial structure and open watershed characteristics make the redistribution of precipitation, surface water, and groundwater, as well as the processes of soil erosion and vegetation restoration, distinct from those in non-karst watersheds. The geological and geomorphological characteristics of the underlying surface also differ from those of specific karst landform types such as peak-cluster depressions, karst gorges, and karst plateaus, providing a typical regional basis for revealing vegetation carbon sink dynamics and their potential coldward shift process.

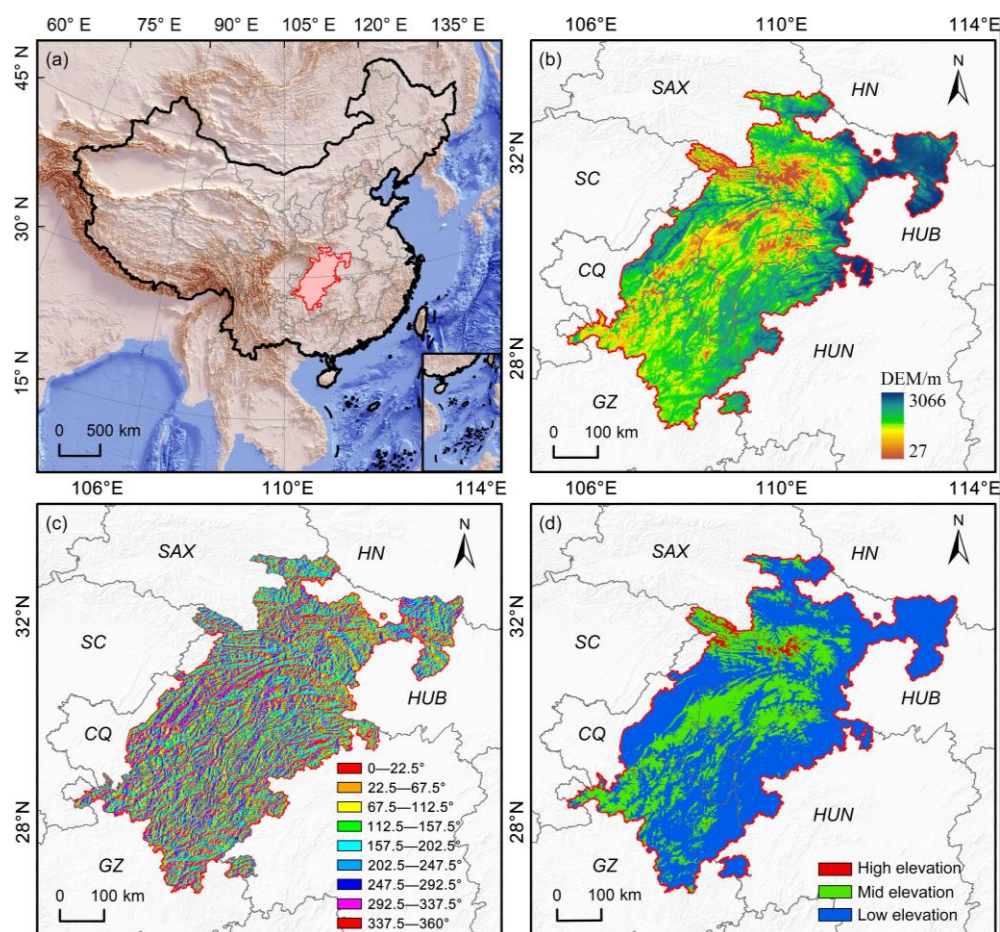


Fig. 2. Location and topographic characteristics of the karst trough valley. (a) Location of the karst trough valley in China; (b) spatial distribution of elevation based on the DEM; (c) spatial distribution of slope aspect; and (d) spatial distribution of low-, middle-, and high-elevation zones.

3. Materials and methods

3.1 Study design and analytical framework

A three-dimensional (3D) warm-cold analytical framework encompassing slope aspect, elevation, and aboveground-belowground structure was constructed in this study based on the vertical topographic characteristics of the karst trough valley. The study sequentially conducted NPP simulation and reliability validation for the historical period and different future scenarios, identification of three-dimensional coldward-shift characteristics across slope aspect, elevation, and aboveground-belowground structure, and analysis of climatic and environmental pathways, thereby establishing an integrated analytical framework progressing from the characterization of vegetation carbon sink evolution to the identification of spatial coldward shifts and ultimately to the elucidation of their driving mechanisms.

The specific methodological steps are detailed as follows (Fig.3): (1) Slope aspect and slope information were derived from the Digital Elevation Model (DEM), and total net primary productivity (TNPP), ANPP, and BNPP were simulated by integrating precipitation and temperature data with vegetation type data. (2) The predictive accuracy of the NCEAS-based simulated NPP was evaluated using percent bias (PB), coefficient of determination (R^2), and root mean square error (RMSE) as validation indicators. (3) Evolution trends and shift characteristics of NPP were assessed across the dimensions of slope aspect, elevation, and spatial structure. (4) Effective soil moisture (ESM) was estimated using the layer-weighted accumulation method, soil CO_2 partial pressure ($p\text{CO}_2$) was estimated via the semi-mechanistic NPP- $p\text{CO}_2$ model, and a structural equation model (SEM) was developed by integrating precipitation (P), solar radiation (SR), temperature (T), soil temperature (ST), CO_2 , ESM, $p\text{CO}_2$, and NPP across different dimensions. By decomposing the direct, indirect, and total effects of climatic and environmental factors on vegetation carbon sinks across different dimensions, the SEM was used to elucidate the potential pathways through which these factors are associated with the coldward shift of vegetation carbon sinks.

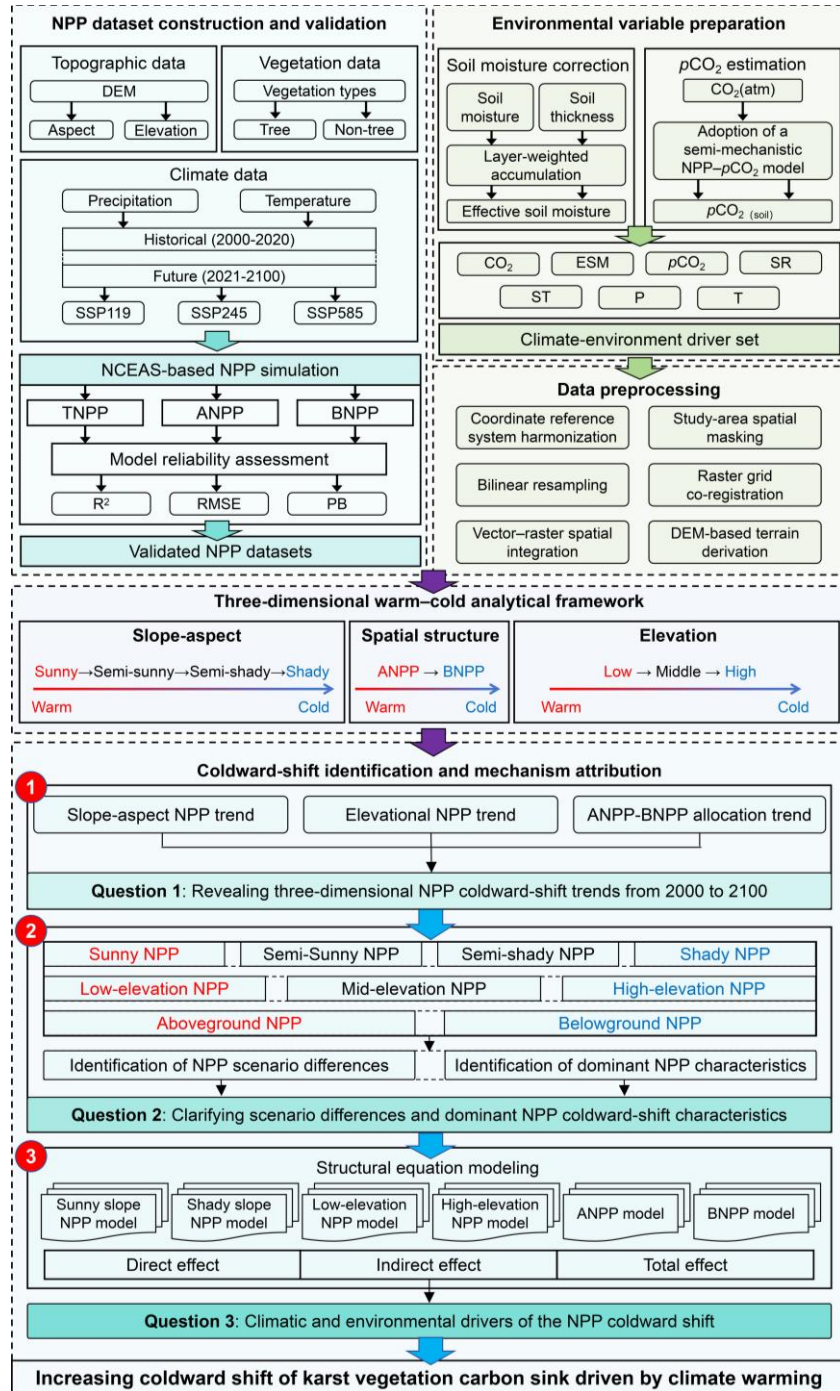


Fig. 3. Methodological framework for assessing the coldward shift of vegetation carbon sinks.

3.2 Data sources and preprocessing

3.2.1 Data sources

The data used in this study included DEM, climate, vegetation, soil, atmospheric CO₂, solar radiation, and NPP validation products (Table 1). The DEM data were derived from the SRTM v4.1 DEM dataset obtained through Google Earth Engine (<https://developers.google.com/earth-engine/datasets>), and were used to extract elevation, slope,

and aspect information. Historical T and P data from 2000 to 2020 were obtained from the National Earth System Science Data Center (<http://wdcrre.data.ac.cn>), and were used to simulate TNPP, ANPP, and BNPP during the historical period from 2000 to 2020. Future temperature and precipitation data from 2021 to 2100 were obtained from Coupled Model Intercomparison Project Phase 6 (CMIP6)-based downscaled climate products (<https://data.tpdc.ac.cn>). These data were generated by the EC-Earth3 climate model under the Shared Socioeconomic Pathway (SSP) scenarios (SSP119, SSP245, and SSP585), and were used to predict vegetation carbon sink dynamics under different emission pathways (Table 2).

Table 1. Summary of data sources.

Variable	Study period	Spatial resolution / scale	Data source	URL
DEM	Static	90 m	SRTM v4.1	https://developers.google.com/earth-engine/datasets
T, P	2000—2020	1 km	National Earth System Science Data Center	http://wdcrre.data.ac.cn
T, P	2021—2100	1 km	National Tibetan Plateau Data Center	https://data.tpdc.ac.cn
Vegetation type	Static	1:1,000,000	Plant Science Data Center	https://www.plantplus.cn/
ST, SR, SM	2000—2020	0.25°	GLDAS-2.1	https://ldas.gsfc.nasa.gov/gldas
SD	2010—2018	90 m	National Earth System Science Data Center	http://wdcrre.data.ac.cn/data/9a075
CO ₂	2000—2020	0.05°	EGG4	https://cis2.eea.europa.eu/product/752/
NPP	2000—2018	0.05°	GLASS AVHRR	http://www.glass.umd.edu
NPP	2000—2020	500 m	MOD17A3HGF	https://www.earthdata.nasa.gov

Vegetation classification data were derived from the 1:1,000,000 Vegetation Map of China (<https://www.plantplus.cn>). ST, SR, and soil moisture (SM) data were obtained from the Global Land Data Assimilation System (GLDAS) product released by NASA (<https://ldas.gsfc.nasa.gov/gldas>). Soil depth (SD) data were obtained from the National Earth System Science Data Center (<http://wdcrre.data.ac.cn/data/9a075>), and were combined with multilayer soil moisture data to estimate effective soil moisture (ESM). Atmospheric CO₂ data were obtained from the Copernicus Atmosphere Monitoring Service (CAMS) global greenhouse gas reanalysis (EGG4) product (<https://cis2.eea.europa.eu/product/752>), and were used for *p*CO₂

estimation. To ensure the reliability of the simulated data, two independent NPP products, namely GLASS AVHRR NPP (<http://www.glass.umd.edu>) and MOD17A3HGF NPP (<https://www.earthdata.nasa.gov>), were used to validate the simulated TNPP data.

Table 2. Future climate scenarios.

Climate model	Emission scenario	Scenario description
EC-Earth3	SSP119 (Low Emission)	Global emission cuts with clean energy transition
EC-Earth3	SSP245 (Neutral Emission)	Moderate growth with balanced emissions and development
EC-Earth3	SSP585 (High Emission)	Fossil fuel-driven rapid economic growth

3.2.2 Effective soil moisture estimation

Soils are shallow and unevenly distributed in the karst trough valley, which often leads to overestimation of actual effective soil moisture when using traditional soil moisture products. To improve estimation accuracy, this study corrected the original soil moisture data using a layer-weighted accumulation method. The calculation was performed using soil moisture information from four depth intervals (0–10 cm, 10–40 cm, 40–100 cm, and 100–200 cm) together with local soil depth data. The specific calculation formula is provided below:

$$ESM = \begin{cases} \theta_{0-10} \times \frac{H}{10}, & 0 < H \leq 10 \\ \theta_{0-10} + \theta_{10-40} \times \frac{H-10}{30}, & 10 < H \leq 40 \\ \theta_{0-10} + \theta_{10-40} + \theta_{40-100} \times \frac{H-40}{60}, & 40 < H \leq 100 \\ \theta_{0-10} + \theta_{10-40} + \theta_{40-100} + \theta_{100-200} \times \frac{H-100}{100}, & 100 < H \leq 200 \\ \theta_{0-10} + \theta_{10-40} + \theta_{40-100} + \theta_{100-200}, & H > 200 \end{cases} \quad (1)$$

where ESM is the actual effective soil moisture content (mm); θ_{0-10} , θ_{10-40} , θ_{40-100} , and $\theta_{100-200}$ represent the SM (mm) in the 0–10 cm, 10–40 cm, 40–100 cm, and 100–200 cm layers, respectively. H denotes the actual soil depth (cm). Since areas with soil depth greater than 200 cm are extremely limited in the study region and contribute minimally to profile moisture, the maximum soil depth was uniformly set to 200 cm in this study.

3.2.3 Soil CO₂ partial pressure estimation

To simulate the vertical distribution of pCO_2 within the soil profile, this study adopted a

semi-mechanistic NPP– $p\text{CO}_2$ model (Gaillardet et al., 2019) to estimate the maximum CO_2 partial pressure below the rooting zone. The model was developed based on large-scale statistical analyses of empirical data from 79 global sites (Raich et al., 1989), and assumes that approximately 75% of NPP is converted into CO_2 production within the root zone (Gwiazda et al., 1994). This model has been validated in numerous global studies and has demonstrated high applicability in simulating CO_2 enrichment processes in soils across different ecosystems and climatic conditions (Zeng et al., 2022; Bai et al., 2024; Li et al., 2022). The calculation formula is as follows:

$$p\text{CO}_{2(\text{soil})} = p\text{CO}_{2(\text{atm})} + \frac{A \times 0.75 \times \text{TNPP}}{T^2} \quad (2)$$

where $p\text{CO}_{2(\text{soil})}$ is the partial pressure of soil CO_2 (ppmv), $p\text{CO}_{2(\text{atm})}$ is the atmospheric CO_2 partial pressure (ppmv), which in this model can be directly replaced by atmospheric CO_2 concentration. T denotes the mean annual temperature (K). A is a unit conversion constant; following the settings of previous studies (Zeng et al., 2025), the annual-scale value of A in this study was set to 1.03×10^6 .

3.2.4 Data preprocessing

To ensure spatial consistency among data from different sources, all spatial datasets were standardized to EPSG:4326 and clipped according to the boundary of the karst trough-valley study area. Continuous raster datasets, including T, P, ST, SR, ESM, soil depth, CO_2 , and DEM, were resampled to a spatial resolution of 1 km using bilinear interpolation. Slope and aspect were derived from the processed DEM. Vegetation type data were provided in vector format and were matched with the study area and subsequent analytical units through spatial overlay. After preprocessing, all raster datasets used in the spatial analyses had consistent projection, spatial extent, resolution, and raster alignment.

3.3 NPP simulation and model validation

This study estimated TNPP, ANPP, and BNPP in the karst trough valley using the NCEAS model (Del Grosso et al., 2008). In this framework, distinct parameterizations are applied for tree-dominated and non-tree-dominated vegetation, allowing their contrasting sensitivities to precipitation and temperature to be represented. Relative to many commonly used NPP models, the NCEAS approach provides improved characterization of climate–NPP relationships across

different vegetation types (Sallaba et al., 2015; Liao et al., 2021; Zeng et al., 2025). The TNPP was calculated using the following method:

$$TNPP = 6116 \times [1 - \exp(-6.05 \times 10^{-5} \times P)] \quad (3)$$

tree

$$\text{Min}[F(P), F(T)] \quad (4)$$

non-tree

$$F(P) = 0.551 \times P^{1.055} / \exp(0.000306 \times P) \quad (5)$$

$$F(T) = 2540 / [1 + \exp(1.584 - 0.0622 \times T)] \quad (6)$$

The ANPP was calculated using the following method:

$$ANPP = 4000 \times [1 - \exp(-4.77 \times 10^{-5} \times P)] \quad (7)$$

tree

$$\text{Min}[F(P), F(T)] \quad (8)$$

non-tree

$$F(P) = 0.1665 \times P^{1.185} / \exp(0.000414 \times P) \quad (9)$$

$$F(T) = 3139 / [1 + \exp(2.2 - 0.0307 \times T)] \quad (10)$$

The BNPP was calculated using the following method:

$$BNPP = TNPP - ANPP \quad (11)$$

where *TNPP* represents the total NPP, *ANPP* represents the aboveground net primary productivity, and *BNPP* represents the belowground net primary productivity. *P* denotes the annual total precipitation, and *T* denotes the mean annual temperature.

To evaluate the reliability of TNPP simulated by the NCEAS model, two independent NPP products, namely GLASS AVHRR and MOD17A3HGF, were used for validation. Because the GLASS AVHRR NPP product is available through 2018, its validation period was set to 2000–2018, whereas the validation period for MOD17A3HGF was 2000–2020. After standardizing the spatial projection, extent, and resolution, 5,000 validation locations were randomly generated within the karst trough-valley region for each year. Simulated TNPP and NPP values from the corresponding validation product were then extracted at the same spatial locations to construct

paired validation samples. A total of 95000 paired validation samples were obtained for GLASS AVHRR during 2000–2018, and 105,000 paired validation samples were obtained for MOD17A3HGF during 2000–2020. Model performance was evaluated using percent bias (PB), coefficient of determination (R^2), and root mean square error (RMSE). PB reflects the overall bias of the simulated results, R^2 reflects the degree of consistency between the simulated values and the validation products, and RMSE reflects the overall magnitude of simulation errors. The calculation formulas are as follows:

$$PB = \frac{1}{n} \sum_{i=1}^n \left(\frac{Y_{i,rec} - Y_{i,obs}}{Y_{i,obs}} \times 100\% \right) \quad (12)$$

$$R^2 = 1 - \frac{\sum_{i=1}^n (Y_{i,obs} - \bar{Y}_{i,rec})^2}{\sum_{i=1}^n (Y_{i,obs} - \bar{Y}_{obs})^2} \quad (13)$$

$$RMSE = \sqrt{\frac{1}{n} \sum_{i=1}^n (Y_{i,rec} - Y_{i,obs})^2} \quad (14)$$

In these equations, n denotes the sample size, while the simulated and observed values are expressed as $Y_{i,rec}$ and $Y_{i,obs}$, respectively. The corresponding mean values of the simulated and observed data are indicated by $\bar{Y}_{i,rec}$ and $\bar{Y}_{i,obs}$.

3.4 Topographic classification and trend analysis

Terrain classification was conducted based on elevation, slope, and aspect information derived from the DEM data. To characterize aspect-related hydrothermal differences, slope aspects were divided into four categories according to azimuth: shady slopes (315° – 45°), semi-shady slopes (45° – 135°), sunny slopes (135° – 225°), and semi-sunny slopes (225° – 315°) (Table 3). In general, shady slopes receive less solar radiation and usually maintain relatively cool and moist environmental conditions, whereas sunny slopes receive stronger solar radiation and have higher heat accumulation. Semi-shady and semi-sunny slopes represent transitional aspect conditions between shady and sunny slopes. To avoid uncertainty in aspect classification for nearly flat areas, only areas with slopes greater than 6° were included in the aspect analysis, whereas areas with slopes less than or equal to 6° were regarded as flat areas and excluded from aspect classification (Fig.S2).

Elevation gradients were classified into three levels based on DEM data and regional

ecological characteristics, following the classification criteria of Li et al. (2008). These levels included low-elevation areas (<1000m), middle-elevation areas (1000–2000m), and high-elevation areas (>2000m). This classification was used to identify vertical differences in NPP dynamics.

Table 3. Basis for Slope Aspect Classification.

Category	Azimuth Range	Slope Orientation	Classification Basis Description
Shady slope	315°–45°	Northwest, North, Northeast	Receives the shortest duration of sunlight and has the lowest solar elevation; the coolest aspect
Semi-shady slope	45°–135°	Northeast, East, Southeast	Receives morning sunlight but limited overall solar radiation; transitional from shady to sunny
Sunny slope	135°–225°	Southeast, South, Southwest	Longest sunshine duration throughout the day; most solar radiation; the typical sunny aspect
Semi-sunny slope	225°–315°	Southwest, West, Northwest	Receives afternoon sunlight; slightly less heat than sunny slope; transitional from sunny to shady

3.5 SEM construction and analysis

To further identify the climatic and environmental pathways associated with the coldward shift of vegetation carbon sinks, SEM was used to examine the potential pathways through which climatic and environmental factors affected NPP across different warm–cold dimensions. Based on the three-dimensional warm-cold analytical framework, SEMs were constructed separately for slope-aspect classes, elevation zones, and aboveground-belowground productivity components. The model variables included P, T, SR, ST, CO₂, ESM, *p*CO₂, and NPP, with all data covering the period from 2000 to 2020. For the slope-aspect dimension, annual regional mean values of each variable were extracted within sunny and shady slope categories. For the elevation dimension, annual regional mean values of each variable were extracted within low- and high-elevation zones. For the aboveground-belowground dimension, ANPP and BNPP were used to represent the aboveground and belowground productivity systems, respectively. Before SEM construction, correlations among explanatory variables were examined to avoid the influence of strong multicollinearity on path coefficient estimation. Model fit was evaluated using the chi-square/degrees of freedom ratio (CMIN/DF), goodness-of-fit index (GFI), incremental fit

index (IFI), Akaike information criterion (AIC), root mean square error of approximation (RMSEA), and standardized root mean square residual (SRMR) (Table S1). Standardized path coefficients were used to compare the relative strengths of different pathways, and effect decomposition was further performed to distinguish direct, indirect, and total effects.

3.6 Trend analysis and identification of coldward shifts

Temporal trends in NPP and climatic variables were estimated using least-squares regression, with year as the independent variable and the corresponding variable as the dependent variable. The regression slope was used to represent the annual rate of change. Coldward shifts were identified based on changes in the NPP growth advantage among different warm-cold categories. In the aboveground-belowground dimension, an increase in BNPP/TNPP accompanied by a corresponding decrease in ANPP/TNPP indicated a shift in NPP growth toward belowground productivity. In the elevation and slope-aspect dimensions, changes in growth advantage were determined by comparing the rates of NPP change among different elevation zones and slope-aspect categories. When the NPP growth advantage at high elevations or on shady slopes increased relative to that at low elevations or on sunny slopes, NPP growth was considered to have shifted toward relatively colder zones.

4. Results

4.1 Validation of model performance

The performance of the NCEAS model was assessed by comparing the simulated TNPP with two independent validation products, GLASS AVHRR NPP (2000–2018) and MOD17A3HGF NPP (2000–2020), at the same spatial locations and for the corresponding years (Fig.4). By randomly sampling 5,000 points per year, a total of 95,000 validation samples were obtained for GLASS AVHRR and 105,000 validation samples for MOD17A3HGF. Model performance was comprehensively evaluated using the coefficient of determination (R^2), root mean square error (RMSE), and percent bias (PB). The validation results showed that, compared with GLASS AVHRR, the simulated TNPP yielded an R^2 of 0.83, an RMSE of 50.44 g C m⁻² yr⁻¹, and a PB of 2.51%. Validation against MOD17A3HGF showed higher consistency, with an R^2 of 0.86, an RMSE of 39.70 g C m⁻² yr⁻¹, and a PB of only 0.64%. Overall, the validation results from both independent NPP products showed high agreement and relatively low simulation errors, indicating

that the NCEAS model can accurately simulate TNPP in the study area and provide a reliable data basis for subsequent analyses of vegetation carbon sink changes and coldward shifts.

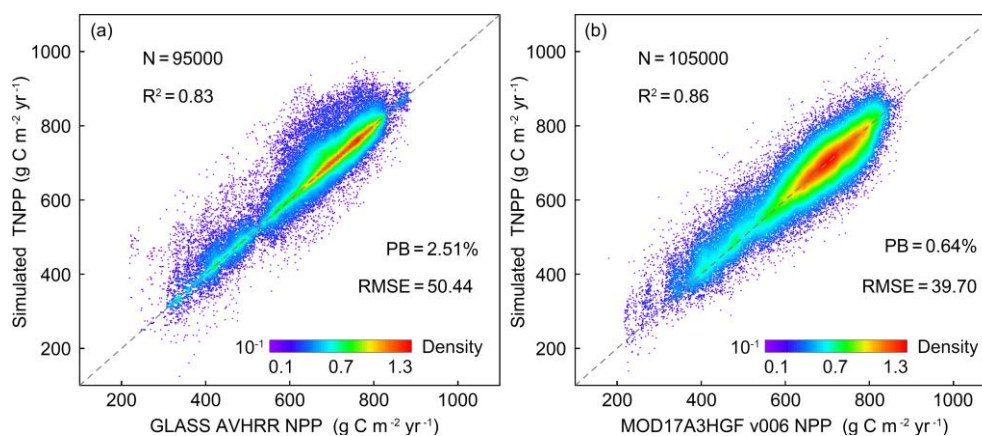


Fig. 4. Validation of simulated TNPP against independent NPP products. (a) Comparison between simulated TNPP and GLASS AVHRR NPP; (b) comparison between simulated TNPP and MOD17A3HGF NPP.

4.2 Future TNPP growth slowed under continued warming

The climate conditions in the karst trough valley showed a pattern of decreasing precipitation and increasing temperature during 2000-2020. Annual precipitation decreased at a rate of -6.62 mm yr^{-1} , whereas mean annual temperature increased slightly at a rate of $0.02^{\circ}\text{C yr}^{-1}$. In the future period, annual precipitation showed fluctuating increasing trends under different emission scenarios, with rates of 2.75, 3.18, and 2.49 mm yr^{-1} under SSP119, SSP245, and SSP585, respectively. Meanwhile, mean annual temperature continued to increase under all three emission scenarios, and the warming rate increased with emission intensity, reaching 0.002, 0.03, and $0.05^{\circ}\text{C yr}^{-1}$ under SSP119, SSP245, and SSP585, respectively (Fig.5). Spatially, future warming showed relatively consistent patterns across the different scenarios, whereas precipitation changes exhibited stronger spatial heterogeneity (Fig.S1).

Against the background of continued warming, TNPP in the karst trough valley showed a fluctuating increasing trend, with a mean annual growth rate of $1.44 \text{ g C m}^{-2} \text{ yr}^{-1}$ during 2000–2020 (Fig.5c). Compared with the historical period, the overall TNPP growth rate slowed under future scenarios. The mean annual growth rates were 1.01 and $0.63 \text{ g C m}^{-2} \text{ yr}^{-1}$ under SSP245 and SSP585, respectively, whereas TNPP decreased slightly at a rate of $-0.07 \text{ g C m}^{-2} \text{ yr}^{-1}$ under SSP119.

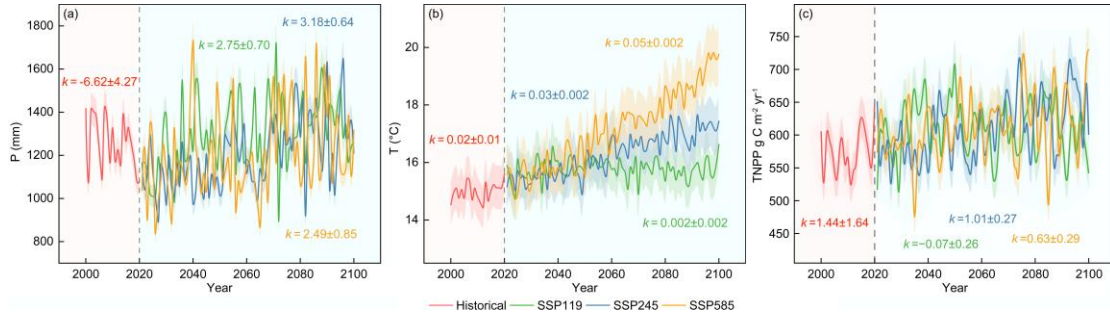


Fig. 5. Temporal trends in P, T, and TNPP from 2000 to 2100. (a) Precipitation trend; (b) temperature trend; and (c) TNPP trend.

4.3 Spatial coldward shift of vegetation carbon sinks became increasingly evident

4.3.1 Continuous shift from aboveground to belowground components

During the historical period, BNPP/TNPP in the karst trough valley showed a fluctuating upward trend at a rate of 0.00026 yr^{-1} , while ANPP/TNPP decreased at the same rate, indicating a pronounced shift in vegetation carbon sink allocation toward belowground productivity (Fig.6). During the future period, this shift persisted under the SSP245 scenario, with BNPP/TNPP continuing to increase at a rate of 0.00011 yr^{-1} and ANPP/TNPP decreasing at the same rate. In contrast, under the SSP119 and SSP585 scenarios, ANPP/TNPP increased at rates of 0.00011 and 0.000092 yr^{-1} , respectively, accompanied by corresponding decreases in BNPP/TNPP.

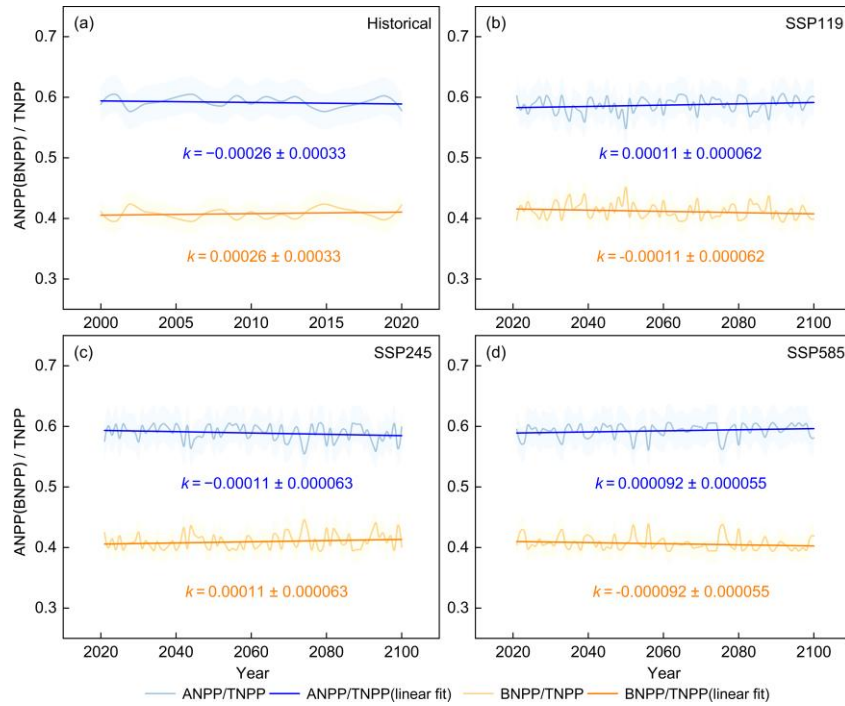


Fig. 6. Temporal trends in ANPP/TNPP and BNPP/TNPP during the historical period and under future climate scenarios. (a) Historical period (2000–2020); (b) SSP119 (2021–2100); (c) SSP245 (2021–2100); and (d) SSP585 (2021–2100).

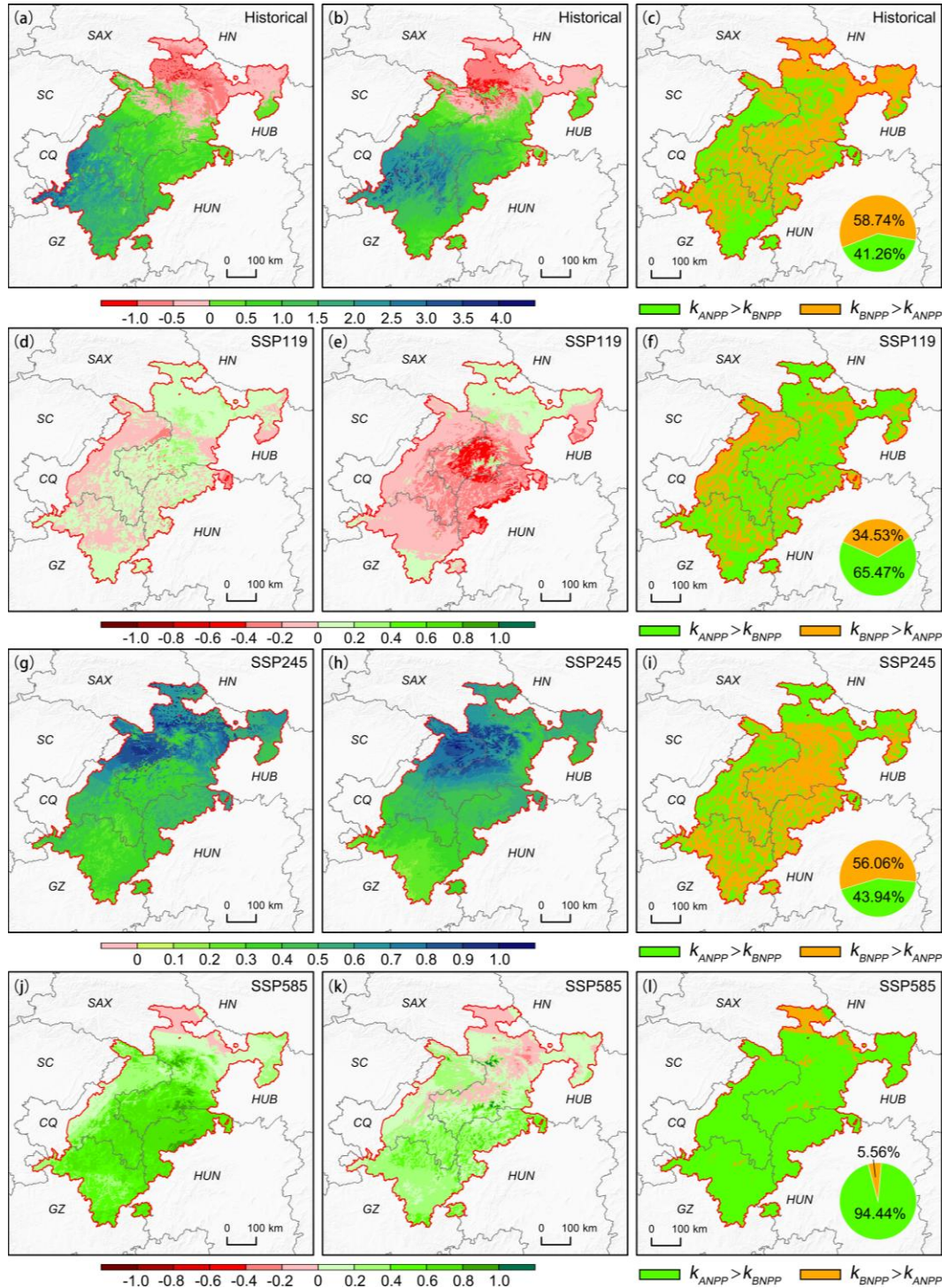


Fig. 7. Spatial distributions of ANPP and BNPP rates of change and their growth advantages during the historical period and under future scenarios. (a) Rate of change in ANPP during the historical period; (b) rate of change in BNPP during the historical period; (c) spatial distribution and area proportions of regions with ANPP and BNPP growth advantages during the historical period; (d) rate of change in ANPP under SSP119; (e) rate of change in BNPP under SSP119; (f) spatial distribution and area proportions of regions with ANPP and BNPP growth advantages under SSP119; (g) rate of change in ANPP under SSP245; (h) rate of change in BNPP under SSP245; (i) spatial distribution and area proportions of regions with ANPP and BNPP growth advantages under SSP245; (j) rate of change in ANPP under SSP585; (k) rate of change in BNPP under SSP585; and (l) spatial distribution and area proportions of regions with ANPP and BNPP growth advantages under SSP585.

Spatially, both the historical period and the SSP245 scenario showed a pronounced belowground NPP growth advantage (Fig.7), with areas where BNPP increased faster than ANPP accounting for 58.74% and 56.06% of the study area, respectively. In contrast, under the SSP119 and SSP585 scenarios, 65.47% and 94.44% of the study area, respectively, exhibited an ANPP growth advantage. Overall, vegetation carbon sinks in the karst trough valley exhibited a clear belowground growth advantage during the historical period, which was maintained under the SSP245 scenario, whereas the SSP119 and SSP585 scenarios showed different aboveground–belowground allocation responses.

4.3.2 Shift from low elevations toward high elevations was more pronounced

The shift of NPP growth advantage toward high elevations in the karst trough valley accelerated during 2000–2100 (Fig.8). During the historical period, NPP increased more rapidly in the middle- and low-elevation zones, with rates of 1.58 and 1.40 $\text{g C m}^{-2} \text{ yr}^{-1}$, respectively, whereas the high-elevation zone showed a much lower rate of only 0.41 $\text{g C m}^{-2} \text{ yr}^{-1}$, indicating that NPP enhancement in high-elevation areas was relatively constrained.

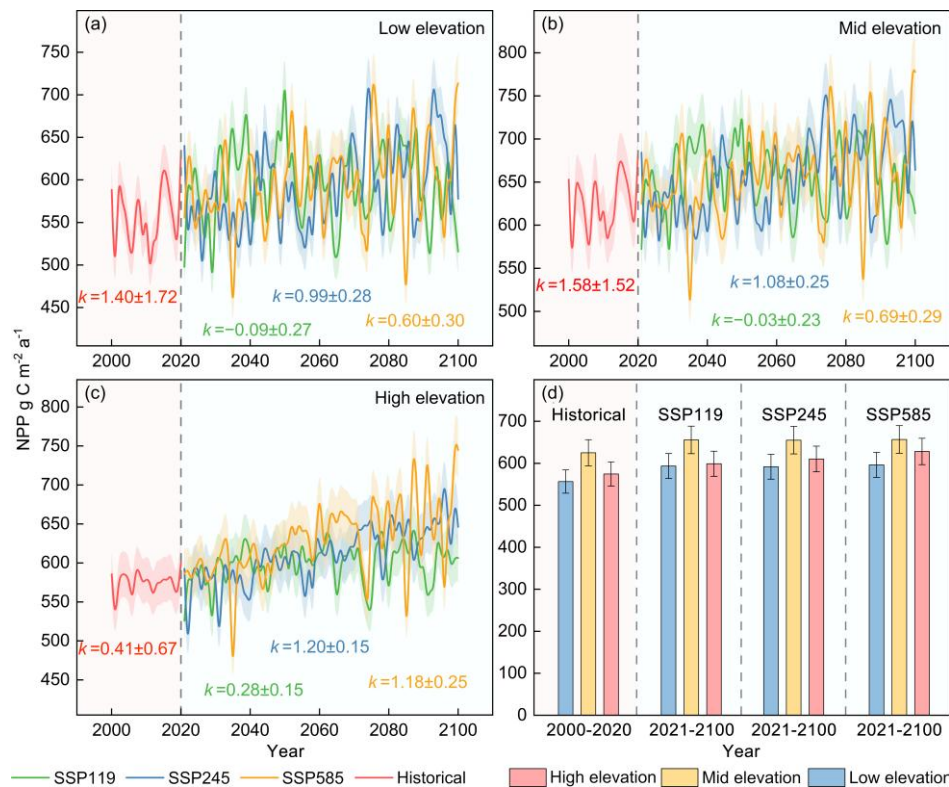


Fig. 8. Temporal trends and mean levels of NPP in low-, middle-, and high-elevation zones during the historical period and under future climate scenarios. (a) Temporal trend of NPP in the low-elevation zone; (b) temporal trend of NPP in the middle-elevation zone; (c) temporal trend of NPP in the high-elevation zone; and (d) mean NPP in the low-, middle-, and high-elevation zones during the historical period and under SSP119, SSP245, and SSP585.

Under future scenarios, however, this pattern changed markedly. Under SSP119, NPP in the low- and middle-elevation zones showed slight declining trends, with rates of -0.09 and -0.03 g C m^{-2} yr^{-1} , respectively, whereas the high-elevation zone still maintained an increasing trend of 0.28 g C m^{-2} yr^{-1} , indicating that the NPP growth advantage had shifted from the middle- and low-elevation zones toward the high-elevation zone. Under SSP245, the NPP growth rate in the high-elevation zone further increased to 1.20 g C m^{-2} yr^{-1} , exceeding those in the middle- and low-elevation zones, which were 1.08 and 0.99 g C m^{-2} yr^{-1} , respectively. Under SSP585, the NPP growth rate in the high-elevation zone reached 1.18 g C m^{-2} yr^{-1} , which was approximately twice that at the middle- and low-elevation zones. Overall, NPP growth advantage was mainly concentrated in the middle- and low-elevation zones during the historical period, whereas under all three future scenarios the high-elevation zone became the elevation belt with the fastest NPP growth, with the most pronounced high-elevation growth advantage occurring under SSP585.

4.3.3 Shift toward shady slopes was more pronounced under future scenarios

The NPP growth pattern in the karst trough valley showed an accelerated shift from relatively warm slopes toward cooler shady slopes during 2000-2100 (Fig.9). During the historical period, NPP increased most rapidly on semi-shady and semi-sunny slopes, reaching 1.87 and 1.76 g C m^{-2} yr^{-1} , respectively. In contrast, the growth rates on sunny and shady slopes were 1.43 and 1.18 g C m^{-2} yr^{-1} , respectively, indicating that the NPP growth advantage during the historical period was mainly concentrated on transitional slope aspects.

During the future period, differences in NPP growth rates among slope aspects narrowed markedly, but the growth advantage shifted steadily toward shady slopes. Under SSP119, SSP245, and SSP585, the NPP growth rates on shady slopes were 1.02 , 1.22 , and 1.01 g C m^{-2} yr^{-1} , respectively, all of which were the highest among the four slope-aspect categories. Under SSP119, the growth rate on shady slopes was slightly higher than those on sunny slopes (1.01 g C m^{-2} yr^{-1}) and semi-shady slopes (0.92 g C m^{-2} yr^{-1}). Under SSP245, the growth rates among slope aspects were the most similar, ranging from 1.20 to 1.22 g C m^{-2} yr^{-1} . Under SSP585, the growth rate on shady slopes remained higher than those on sunny slopes (0.99 g C m^{-2} yr^{-1}), semi-shady slopes (0.96 g C m^{-2} yr^{-1}), and semi-sunny slopes (0.94 g C m^{-2} yr^{-1}), indicating a renewed strengthening of the shady-slope growth advantage. Overall, the NPP growth advantage gradually shifted from semi-shady and semi-sunny slopes toward shady slopes, and shady slopes consistently showed the

highest growth rates under all three future scenarios, indicating an accelerated shift of vegetation carbon sinks from sunny slopes toward shady slopes in the karst trough valley.

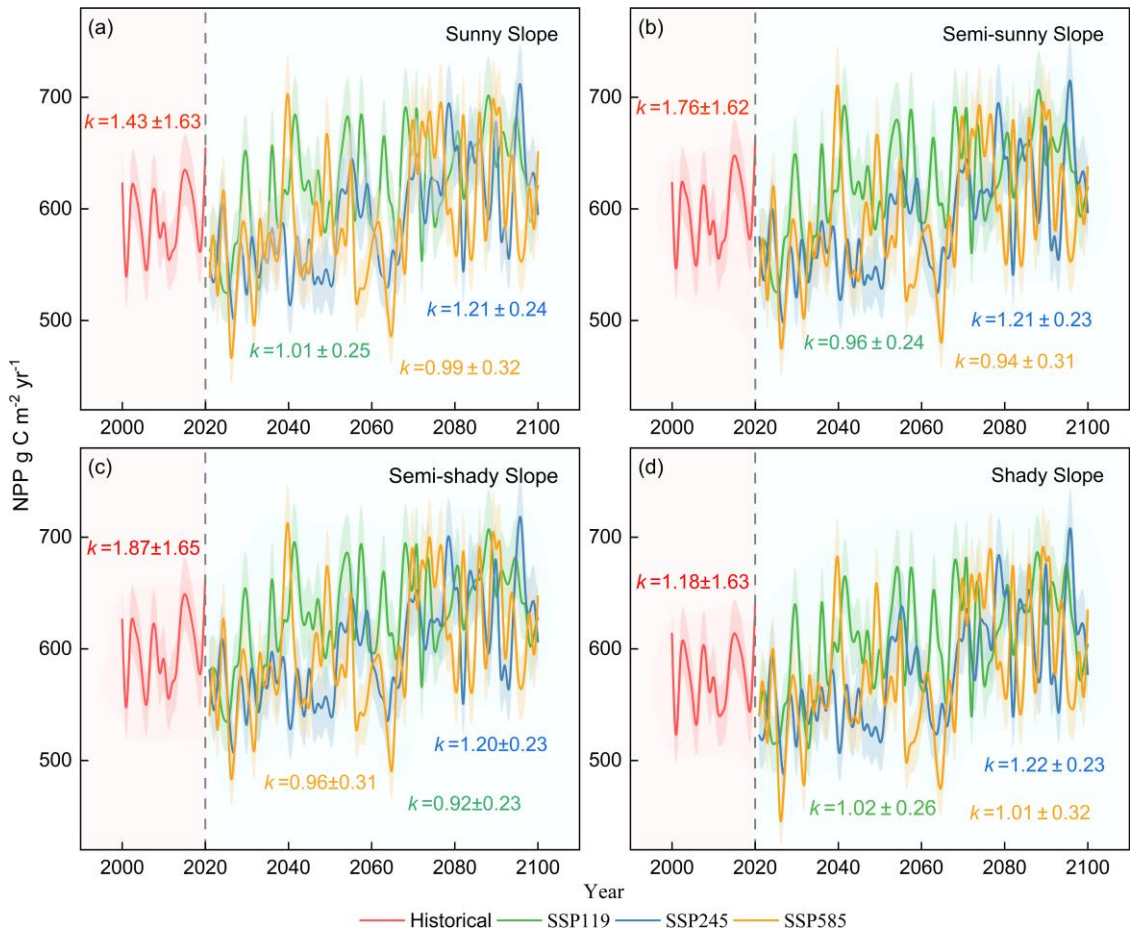


Fig. 9. Temporal trends of NPP on different slope aspects during the historical period and under future climate scenarios. (a) Sunny slopes; (b) semi-sunny slopes; (c) semi-shady slopes; and (d) shady slopes.

4.4 Water conditions dominated the coldward shift of vegetation carbon sinks

During 2000-2020, $p\text{CO}_2$, atmospheric CO_2 , and ST generally increased in the karst trough valley, whereas SR and ESM continued to decline (Fig.S3). The concurrent changes in light, heat, water, and soil environmental conditions altered the NPP response pathways across different topographic positions. Based on this, SEM was used to further examine the pathways through which climatic and environmental factors were associated with the coldward shift of vegetation carbon sinks (Fig.10).

In the slope-aspect dimension, sunny and shady slopes showed highly consistent moisture-driven path structures. P had a significant positive effect on NPP, with path coefficients of 0.54 and 0.58 on sunny and shady slopes, respectively. Meanwhile, P showed stronger positive effects on ESM, with path coefficients of 0.79 and 0.78, respectively. In contrast, the direct paths

from SR, T, and CO₂ to NPP were relatively weak across the different slope aspects. These results indicate that precipitation and its regulation of soil moisture constituted the major pathways affecting NPP across slope aspects, with NPP on shady slopes showing a slightly stronger direct response to P than that on sunny slopes.

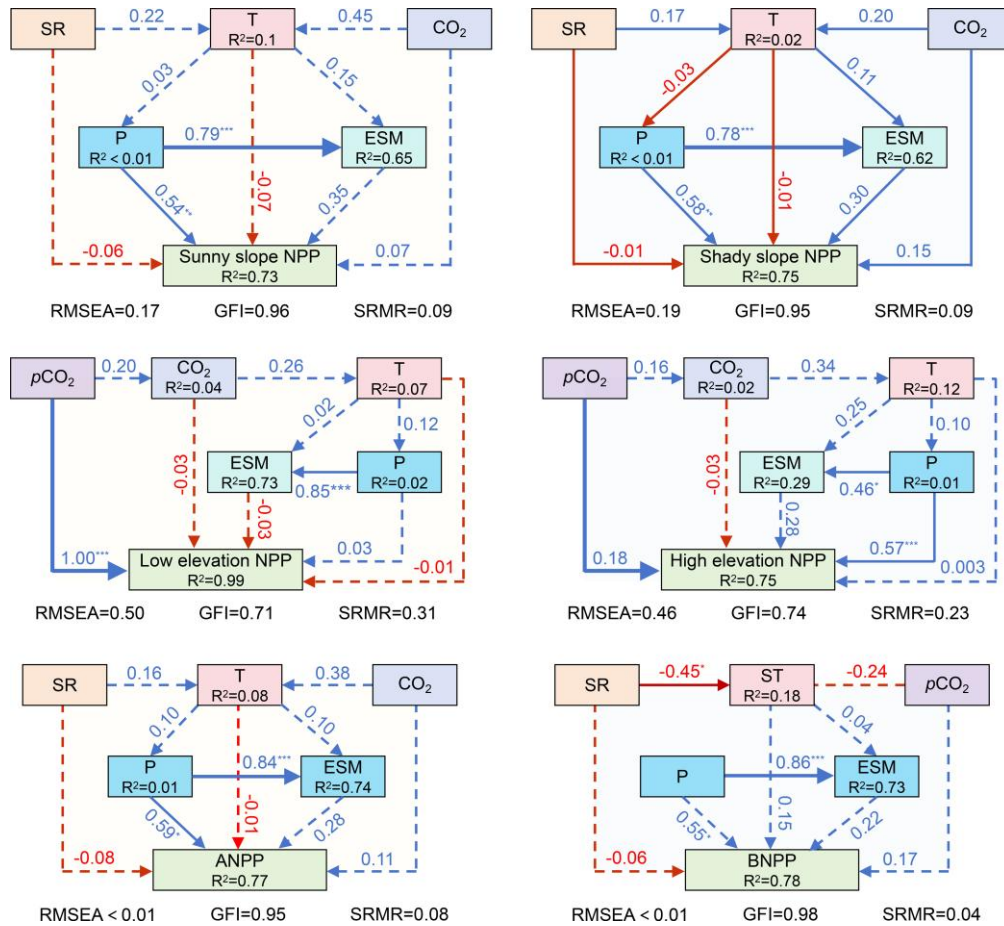


Fig. 10. Driving pathways of climatic and environmental factors affecting the coldward shift of NPP. “***” indicates a highly significant relationship ($P < 0.001$), “**” indicates a very significant relationship ($P < 0.01$), and “*” indicates a significant relationship ($P < 0.05$). Detailed SEM effect values are provided in Table S2.

In the elevational dimension, low-elevation NPP showed a significant positive response mainly to $p\text{CO}_2$, with a path coefficient of 1.00, while P exerted a strong positive effect on ESM, with a path coefficient of 0.85. In high-elevation areas, the direct effect of P was dominant, with a path coefficient of 0.57 for the P-NPP pathway. P also maintained a significant positive relationship with ESM, with a path coefficient of 0.46. Compared with low elevations, the direct linkage between NPP and precipitation was markedly strengthened at high elevations, whereas low-elevation NPP showed a more pronounced response to soil $p\text{CO}_2$.

In the aboveground–belowground dimension, both ANPP and BNPP showed significant positive responses to precipitation. The direct path coefficient from P to ANPP was 0.59, while

that from P to BNPP was 0.55. Meanwhile, P exerted strong positive effects on ESM in both the ANPP and BNPP models, with path coefficients of 0.84 and 0.86, respectively. For BNPP, the direct effects of ESM and $p\text{CO}_2$ were positive but relatively weak, with path coefficients of 0.22 and 0.17, respectively. In addition, SR had a significant negative effect on ST, with a path coefficient of -0.45. Overall, precipitation was the principal direct factor associated with both aboveground and belowground NPP, while also strongly regulating soil moisture conditions.

5. Discussion

5.1 Climate warming accelerated the coldward shift of karst vegetation carbon sinks

This study revealed a persistent reorganization of vegetation carbon sink growth advantages toward relatively cold zones across three dimensions: aboveground-belowground allocation, elevation gradients, and slope-aspect gradients. During the historical period, NPP growth at high elevations and on shady slopes was relatively constrained, whereas under all three future scenarios, high elevations and shady slopes became the areas with the highest NPP growth rates within their respective topographic gradients, showing a highly consistent spatial coldward shift. Aboveground-belowground allocation exhibited a similar structural adjustment. During the historical period, BNPP/TNPP continued to increase, and 58.74% of the study area showed a BNPP growth advantage, indicating an enhanced shift of vegetation carbon sink growth toward belowground components. The changes induced by climate warming were therefore reflected not only in increases in total NPP, but also in the reordering of growth advantages among different carbon sink components and topographic units. Relatively cold zones gradually transitioned from areas of relative growth disadvantage during the historical period to important areas of future carbon sink growth.

The stability of this coldward reorganization, however, differed among dimensions. Along the elevation and slope-aspect gradients, high elevations and shady slopes consistently maintained growth advantages under SSP119, SSP245, and SSP585, indicating that the spatial coldward shift was highly consistent across different future scenarios. In contrast, aboveground–belowground carbon allocation showed stronger scenario dependence. Under SSP245, BNPP/TNPP continued to increase, and 56.06% of the study area maintained a BNPP growth advantage, consistent with

the direction of change observed during the historical period, whereas under SSP119 and SSP585, the relative growth advantage shifted toward ANPP. Notably, SSP119 and SSP585 represent the lower and higher ends of future radiative forcing, respectively, whereas SSP245 represents an intermediate forcing level. The continuity of the belowground growth advantage from the historical period to SSP245 suggests that enhanced allocation of vegetation carbon sinks toward belowground components may exhibit stronger persistence under a non-extreme future pathway.

5.2 Topographic differentiation patterns of vegetation carbon sinks in relation to previous studies

The results indicated that, during the historical period, sunny slopes exhibited higher NPP growth rates than shady slopes. This pattern is consistent with the findings of Hua et al. (2023), which were based on allometric growth equations. Previous studies have shown that sunny slopes generally receive higher solar radiation and experience higher temperatures, but stronger evapotranspiration may limit soil moisture retention; therefore, their long-term mean NPP is not necessarily higher than that on relatively cool and shady slopes (Gao et al., 2013; Sun et al., 2015). Similarly, this study showed that, from 2000 to 2020, NPP on sunny slopes in the karst trough valley was slightly lower than that on semi-shady and semi-sunny slopes. With continued warming, this slope-aspect pattern changed further, with shady slopes shifting from the lowest NPP growth rate during the historical period to the highest growth rate under all three future scenarios. Similar slope-aspect responses have also been reported in other mountain ecosystems, where relatively cool and shady slopes often have more favorable moisture conditions and show greater potential for vegetation greening and productivity enhancement under continued warming (Yin et al., 2023; Zhang et al., 2024).

Regarding the elevational gradient, Chen et al. (2007) found that vegetation NPP peaked at approximately 1350 m and declined with further increases in elevation. A similar pattern was observed during the historical period in this study, with mean NPP in middle-elevation areas reaching $625.04 \text{ g C m}^{-2} \text{ yr}^{-1}$, higher than the $574.61 \text{ g C m}^{-2} \text{ yr}^{-1}$ observed at low elevations, indicating that productivity at high elevations remained constrained by low-temperature conditions. Under future scenarios, however, this relationship changed markedly. High-elevation areas became the elevation zone with the highest NPP growth rate under SSP119, SSP245, and SSP585. This finding is consistent with previous studies of mountain ecosystems showing that warming

can enhance vegetation growth and carbon uptake at high elevations by gradually alleviating low-temperature limitations, thereby resulting in a stronger productivity response to climate change in high-elevation vegetation (Guo et al., 2022; Kong et al., 2023).

Changes in aboveground and belowground productivity further indicated that increases in vegetation carbon sinks were accompanied by adjustments in internal carbon allocation. Previous studies have shown that ANPP and BNPP respond differently to climate change. Aboveground productivity is generally more sensitive to climatic variability, whereas belowground productivity is more closely associated with soil moisture, soil environmental conditions, and vegetation resource-acquisition strategies (Gherardi et al., 2020; Zheng et al., 2024). Warming experiments have shown that some cool ecosystems can adjust carbon allocation by increasing belowground productivity, thereby enhancing belowground resource acquisition capacity (Yang et al., 2020). In this study, BNPP/TNPP continued to increase during the historical period and maintained the same direction of change under SSP245, consistent with previous findings that belowground productivity has a relatively strong capacity to adjust to long-term environmental change.

5.3 Climatic mechanisms driving the coldward shift of vegetation carbon sinks

Under future climate scenarios, the growth advantage of vegetation carbon sinks in the karst trough valley generally shifted from relatively warm zones toward relatively cold zones, and this shift was reflected in the coordinated changes in slope aspect, elevation, and aboveground-belowground productivity structure (Fig.11). From the slope-aspect perspective, the results showed that NPP growth was relatively higher on semi-shady and semi-sunny slopes during the historical period, whereas shady slopes showed slightly higher growth under future scenarios. This shift may be related to the redistribution of hydrothermal advantages among different slope aspects under climate warming. Sunny slopes generally receive stronger solar radiation and have higher heat accumulation, making vegetation more susceptible to heat stress when temperature approaches or exceeds the suitable range for photosynthesis. Previous studies have shown that excessive radiation and high temperature can reduce photosynthetic efficiency and carbon fixation capacity by intensifying heat stress (Huang et al., 2019; Ge et al., 2017; Chou et al., 2012). In contrast, shady slopes are usually characterized by weaker radiation exposure, lower evaporative demand, and relatively higher soil moisture. Under climate warming, these conditions may allow vegetation on shady slopes to benefit from improved thermal availability

while avoiding excessive water loss (Kan et al., 2024; Fan et al., 2023; Jiang et al., 2020), thereby supporting photosynthetic performance and NPP enhancement (Sun et al., 2019; Jiang et al., 2022; Pan et al., 2017).

In the karst trough valley, widespread rock outcrops, shallow soil layers, discontinuous soil cover, and nutrient limitations can impose strong resource constraints on vegetation growth (Zhang et al., 2022). Under warming conditions, aboveground productivity may be more vulnerable to heat stress because excessive temperature can reduce Rubisco activity, inhibit photosynthesis, and increase respiratory carbon costs, thereby constraining aboveground biomass accumulation (Salvucci et al., 2004; Sage et al., 2008; Scafaro et al., 2021; Dijkstra et al., 2011). By contrast, belowground productivity may be more closely linked to soil hydrothermal regulation and nutrient acquisition processes. Previous studies have reported that soil warming can accelerate fine-root turnover (Kitajima et al., 2010; Leppälammi-Kujansuu et al., 2014), enhance soil phosphatase activity (Shaw et al., 2020), and promote organic phosphorus mineralization (Margalef et al., 2021), thereby improving nutrient availability for roots under nutrient-limited conditions. In this context, increased belowground allocation may help vegetation maintain root growth and resource uptake in shallow-soil karst environments. Litter input from aboveground biomass may also contribute to belowground carbon accumulation through top-down organic matter transfer (Staaf and Berg, 1981).

Along the elevation gradient, the NPP growth advantage also shifted from low-elevation areas toward middle- and high-elevation zones. NPP growth was highest in the middle-elevation zone during the historical period, whereas growth in the high-elevation zone was relatively limited. Under future scenarios, especially SSP585, NPP growth in high-elevation areas was stronger than that in low- and middle-elevation areas, suggesting that warming may gradually enhance the growth advantage of relatively cool high-elevation zones. In low-elevation areas, stronger heat accumulation under warming conditions may increase respiratory carbon consumption and physiological stress, thereby weakening vegetation carbon sink capacity (Sage et al., 2007; Bernacchi et al., 2001; Labate et al., 1988). In contrast, vegetation in middle- and high-elevation zones was more likely to be limited by low temperature during the historical period. Warming may alleviate this constraint by improving accumulated temperature conditions, expanding the thermal niche for vegetation growth, extending the growing season, and enhancing carbon assimilation

capacity (Wang et al., 2017; Fan et al., 2015; Xu et al., 2020). Elevated CO₂ may further promote carbon assimilation and water-use efficiency, although this effect may still be constrained by shallow soil layers, limited water availability, and nutrient deficiency in karst ecosystems. The SEM results showed that *p*CO₂ was positively associated with NPP in low-elevation regions, whereas precipitation showed a positive path to NPP in high-elevation regions. These differences indicate that the elevational shift in carbon sink growth may be regulated by differences in hydrothermal conditions and soil-mediated pathways across elevation zones.

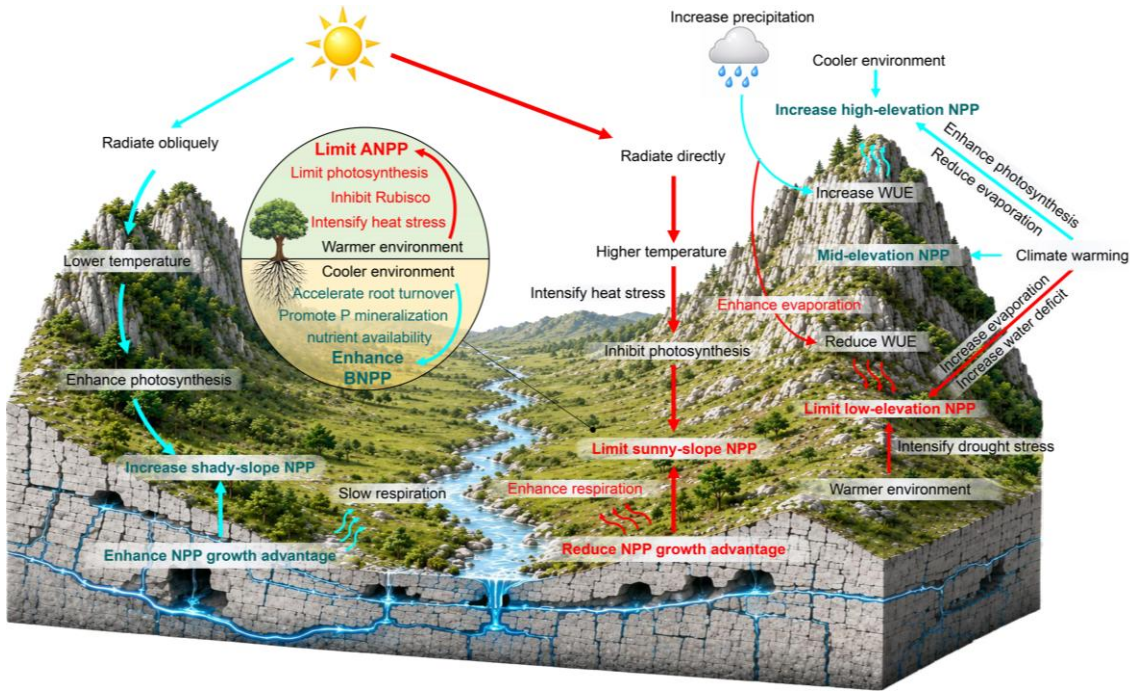


Fig. 11. Climatic mechanisms driving the coldward shift of vegetation carbon sinks across slope aspect, elevation, and spatial structure.

Overall, the shift of vegetation carbon sinks from relatively warm zones toward relatively cold zones in the karst trough valley can be understood as a coordinated response to the redistribution of topographic hydrothermal conditions under climate warming. Along the slope-aspect gradient, this shift reflects the increasing relative advantage of shady slopes under warming conditions. Along the elevation gradient, warming weakened low-temperature limitation in middle- and high-elevation vegetation while intensifying heat stress in low-elevation areas. In the aboveground-belowground structure, the increases in BNPP/TNPP during the historical period and under SSP245 indicate that belowground productivity became increasingly important for maintaining vegetation carbon sink growth in shallow-soil karst environments under these conditions. These patterns suggest that future carbon sink dynamics of karst vegetation are shaped

not only by regional climate warming, but also by local topographic regulation, soil moisture availability, soil CO₂ enrichment, and belowground resource acquisition processes.

5.4 Limitations and future research

This study developed a three-dimensional warm–cold analytical framework based on elevation gradients, slope-aspect differences, and aboveground–belowground productivity structure, and systematically revealed the spatial characteristics of the “coldward shift” of vegetation carbon sinks under climate warming. SEM was further used to analyze the pathways through which climatic and environmental factors influenced this shift. The findings provide scientific support for carbon sink assessment and ecological regulation in karst regions. However, several limitations remain. First, although the simulated TNPP was validated and showed good consistency with independent NPP products, the NCEAS model mainly estimates NPP based on temperature and precipitation. Other ecological factors, including soil properties, vegetation community composition, nutrient availability, disturbance processes, and land-use change, were not fully represented. In addition, the use of static vegetation-type data in future NPP projections may also introduce uncertainty. Therefore, the physiological and ecological mechanisms underlying the simulated productivity changes still require further investigation. Second, future projections in this study were based only on the EC-Earth3 climate model under SSP119, SSP245, and SSP585. Although these three scenarios represent different emission pathways, reliance on a single climate model cannot fully capture inter-model uncertainty in future climate projections. Therefore, the projected coldward shift should be interpreted as a scenario-dependent trajectory based on EC-Earth3 rather than a deterministic prediction. Future studies should incorporate multi-model climate ensembles and a broader range of emission scenarios to further evaluate the robustness of vegetation carbon sink redistribution under different climate-model structures. Third, the internal mechanisms underlying the shift of vegetation carbon sinks from warm zones toward cold zones remain to be further clarified. SEM was used to identify potential pathways among climatic factors, soil-related variables, and NPP, but it mainly reflects statistical associations rather than strict causal processes. Future research should combine long-term field observations, warming experiments, soil nutrient measurements, root trait monitoring, and plant physiological measurements to further clarify how vegetation adjusts carbon allocation processes and thermal adaptation strategies under climate warming.

6. Conclusion

In this study, a three-dimensional warm–cold analytical framework was constructed based on elevation gradients, slope-aspect differences, and aboveground–belowground productivity structure. This framework systematically revealed the spatial characteristics of the “coldward shift” of vegetation carbon sinks under different future scenarios, and SEM was further used to analyze the pathways through which climatic and environmental factors influenced this shift. The main conclusions are as follows.

1. Vegetation carbon sinks in the karst trough valley showed a shift toward belowground productivity. During the historical period, BNPP/TNPP continued to increase at a rate of 0.00026 yr^{-1} , and BNPP increased faster than ANPP across 58.74% of the study area. Under SSP245, BNPP/TNPP continued to increase at a rate of 0.00011 yr^{-1} , with areas showing a BNPP growth advantage accounting for 56.06% of the study area, indicating a continued increase in the relative contribution of belowground productivity to vegetation carbon sink growth. In contrast, under SSP119 and SSP585, BNPP/TNPP decreased at rates of 0.00011 and 0.000092 yr^{-1} , respectively, accompanied by an enhanced ANPP growth advantage.

2. The shift of vegetation carbon sink growth from middle- and low-elevation areas toward high-elevation areas accelerated. During the historical period, the middle-elevation zone showed the highest NPP growth rate of 1.58 $\text{g C m}^{-2} \text{yr}^{-1}$, followed by the low-elevation zone at 1.40 $\text{g C m}^{-2} \text{yr}^{-1}$, whereas the high-elevation zone showed the lowest rate of only 0.41 $\text{g C m}^{-2} \text{yr}^{-1}$. Under all three future scenarios, however, the high-elevation zone became the elevation belt with the highest NPP growth rate, reaching 0.28, 1.20, and 1.18 $\text{g C m}^{-2} \text{yr}^{-1}$ under SSP119, SSP245, and SSP585, respectively. The transition of high-elevation areas from the slowest NPP growth during the historical period to the fastest growth under future scenarios indicates a pronounced shift in vegetation carbon sink growth advantage toward high elevations.

3. Vegetation carbon sink growth accelerated its shift from relatively warm slopes toward cooler shady slopes. During the historical period, the highest NPP growth rate occurred on semi-shady slopes, reaching 1.87 $\text{g C m}^{-2} \text{yr}^{-1}$, followed by semi-sunny slopes at 1.76 $\text{g C m}^{-2} \text{yr}^{-1}$, whereas shady slopes showed the lowest rate of only 1.18 $\text{g C m}^{-2} \text{yr}^{-1}$. Under SSP119, SSP245, and SSP585, NPP growth rates on shady slopes reached 1.02, 1.22, and 1.01 $\text{g C m}^{-2} \text{yr}^{-1}$,

respectively, all of which were the highest among the four slope-aspect categories. The transition of shady slopes from the slowest NPP growth during the historical period to the fastest growth under all three future scenarios indicates a progressive shift in vegetation carbon sink growth advantage toward relatively cool and shady slopes.

4. Moisture conditions dominated the coldward shift of vegetation carbon sinks, while soil $p\text{CO}_2$ played a pronounced role at low elevations. SEM results showed that precipitation had significant positive effects on NPP on both sunny and shady slopes, with path coefficients of 0.54 and 0.58, respectively, and precipitation also exerted a major positive effect on NPP at high elevations. In contrast, low-elevation NPP was mainly associated with soil $p\text{CO}_2$. Within the aboveground–belowground structure, both ANPP and BNPP were primarily associated with precipitation, with significant positive path coefficients of 0.59 and 0.55, respectively. Overall, moisture conditions played a dominant role in NPP changes across slope aspects, at high elevations, and in both aboveground and belowground productivity, whereas soil $p\text{CO}_2$ showed a particularly strong association with NPP at low elevations.

The three-dimensional warm–cold framework proposed in this study provides a new analytical perspective for carbon sink assessment in complex karst terrain. It helps identify the spatial reorganization of carbon sink growth across different topographic positions and productivity components, and can provide scientific support for carbon sink assessment, ecological restoration zoning, vegetation restoration optimization, and climate-adaptive management in karst regions. It may also provide a methodological reference for identifying carbon sink spatial shifts and assessing future scenarios in fragile mountain ecosystems. It should be noted that the future projections in this study were based on a single climate model and static vegetation-type data. The SEM results mainly reflect pathway associations, and the related physiological processes and belowground mechanisms still require further verification through multi-model climate projections, long-term field observations, and controlled experiments.

Author contributions

Conceptualization, L.W.; methodology, H.W. and X.B.; software, H.W.; validation, D.Y. and J.D.; resources, L.W.; data curation, Y.L., L.X. and D.C.; writing—original draft preparation, H.W.; writing—review and editing, L.W. and X.B.; visualization, L.X., D.C., D.Y. and J.D.; table

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733 **Data Availability**

734 All data used in this study are publicly available. Digital elevation data were downloaded via
735 the Google Earth Engine platform ([https://developers.google.com/earth-engine/datasets/catalog/C](https://developers.google.com/earth-engine/datasets/catalog/C_GIAR_SRTM90_V4)
736 [GIAR_SRTM90_V4](https://developers.google.com/earth-engine/datasets/catalog/C_GIAR_SRTM90_V4)). Historical temperature and precipitation data were obtained from the
737 National Earth System Science Data Center of China ([http://wdcrre.data.ac.cn/data/9a072](http://wdcrre.data.ac.cn/data/9a072;);
738 <http://wdcrre.data.ac.cn/data/9a073>), while future climate data were accessed through the National
739 Tibetan Plateau Data Center ([https://data.tpdac.ac.cn/en/data/90a7b4b6-4009-463a-b34f-e8ebd0238](https://data.tpdac.ac.cn/en/data/90a7b4b6-4009-463a-b34f-e8ebd0238617)
740 [617; https://data.tpdac.ac.cn/en/data/169d91c0-c38f-4253-84ae-03f3e18ba643](https://data.tpdac.ac.cn/en/data/169d91c0-c38f-4253-84ae-03f3e18ba643)). Vegetation type
741 data were sourced from the 1:1,000,000 Vegetation Map of China (<https://www.plantplus.cn/en/do>

i/10.12282/plantdata.0155). Soil temperature, soil moisture, and solar radiation data were obtained from the NASA GLDAS-2.1 dataset via the Google Earth Engine platform (https://developers.google.com/earth-engine/datasets/catalog/NASA_GLDAS_V20_NOAH_G025_T3H). CO₂ data were downloaded from the Copernicus EGG4 greenhouse gas reanalysis dataset (<https://ads.atmosphere.copernicus.eu/datasets/cams-global-ghg-reanalysis-egg4>). Soil depth data were accessed from the National Earth System Science Data Center of China (<http://wdcrre.data.ac.cn/data/9a075>). NPP validation data were downloaded from the MOD17A3HGF dataset via the Google Earth Engine platform (https://developers.google.com/earth-engine/datasets/catalog/UMT_NTSG_v2_MODIS_NPP) and from the GLASS AVHRR dataset via <http://www.glass.umd.edu/Download.html>.

Declarations

Ethics and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare no competing interests.

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