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Abstract

Understanding the drivers of gross primary production (GPP) is essential for assessing vegetation productivity dynamics under climate change, particularly across regions with strong climatic heterogeneity. China spans diverse climate zones and ecosystems, yet the relative importance of climatic, environmental, and anthropogenic factors regulating GPP has remained poorly resolved. In this study, we investigated the spatiotemporal patterns of GPP across China from 2001 to 2020 and quantified the contributions of multiple driving factors across different climate zones. We combined ridge regression with an interpretable machine learning framework based on Extreme Gradient Boosting (XGBoost) and SHapley Additive exPlanations (SHAP) to disentangle the long-term linear controls on and short-term nonlinear responses driving GPP. Ridge regression was employed to address multicollinearity among predictors and to quantify their interannual contributions, while SHAP analysis was used to quantify feature contributions in nonlinear model predictions. Our results indicated that leaf area index (LAI) and human footprint dominated the long-term variability of GPP in most climate zones, whereas temperature and solar radiation exerted stronger influences on instantaneous GPP responses. The relative importance of drivers varied markedly among climate zones, reflecting region-specific climatic constraints and vegetation physiological characteristics. In addition, the contribution of atmospheric CO₂ to GPP variability was notably limited in the alpine climate zone and showed a declining fertilization effect nationally, suggesting increasing constraints imposed by water availability and nutrient limitations. By integrating linear attribution and nonlinear interpretability, this study provides a comprehensive assessment of the controls on GPP dynamics across China and highlights the importance of accounting for climatic heterogeneity and temporal scales when evaluating vegetation productivity responses to environmental change.

Full Text

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Exploring the main driving factors of gross primary production in different climate zones of China using the XGBoost-SHAP model

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Abstract: Understanding the drivers of gross primary production (GPP) is essential for assessing vegetation productivity dynamics under climate change, particularly across regions with strong climatic heterogeneity. China spans diverse climate zones and ecosystems, yet the relative importance of climatic, environmental, and anthropogenic factors regulating GPP has remained poorly resolved. In this study, we investigated the spatiotemporal patterns of GPP across China from 2001 to 2020 and quantified the contributions of multiple driving factors across different climate zones. We combined ridge regression with an interpretable machine learning framework based on Extreme Gradient Boosting (XGBoost) and SHapley Additive exPlanations (SHAP) to disentangle the long-term linear controls on and short-term nonlinear responses driving GPP. Ridge regression was employed to address multicollinearity among predictors and to quantify their interannual contributions, while SHAP analysis was used to quantify feature contributions in nonlinear model predictions. Our results indicated that leaf area index (LAI) and human footprint dominated the long-term variability of GPP in most climate zones, whereas temperature and solar radiation exerted stronger influences on instantaneous GPP responses. The relative importance of drivers varied markedly among climate zones, reflecting region-specific climatic constraints and vegetation physiological characteristics. In addition, the contribution of atmospheric CO₂ to GPP variability was notably limited in the alpine climate zone and showed a declining fertilization effect nationally, suggesting increasing constraints imposed by water availability and nutrient limitations. By integrating linear attribution and nonlinear interpretability, this study provides a comprehensive assessment of the controls on GPP dynamics across China and highlights the importance of accounting for climatic heterogeneity and temporal scales when evaluating vegetation productivity responses to environmental change.

Keywords: gross primary production (GPP); ridge regression; Extreme Gradient Boosting-SHapley Additive exPlanations (XGBoost-SHAP) model; gravity migration model; leaf area index (LAI); carbon dioxide (CO₂); human footprint

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1 Introduction

Gross primary production (GPP), defined as the total amount of carbon assimilated by terrestrial vegetation through photosynthesis, is a fundamental indicator of vegetation productivity and ecosystem functioning. Variations in GPP directly reflect changes in plant growth and photosynthetic activity and have therefore been widely used to assess terrestrial ecosystem responses to climate variability and environmental change (Running et al., 2004; Beer et al., 2010; Xu et al., 2022). Under ongoing global warming, pronounced changes in temperature, precipitation, and radiation regimes have substantially altered vegetation productivity worldwide, underscoring the need to understand the dynamics of terrestrial carbon uptake and productivity across diverse climatic conditions (Nemani et al., 2003; Zhao and Running, 2010; Myhre et al., 2019; Robinson et al., 2021; Zhang et al., 2021). However, the responses of GPP to climate variability are highly heterogeneous across regions and ecosystems. Differences in climate regimes, dominant vegetation types, and limiting environmental factors lead to pronounced spatial contrasts in vegetation productivity and its sensitivity to climate change (Wu et al., 2010; Gao et al., 2017; Sun et al., 2018). Previous studies have shown that moderate warming can enhance vegetation productivity, whereas excessive warming may suppress GPP by intensifying soil moisture depletion and atmospheric drought stress, particularly in water-limited regions (Piao et al., 2014; Zhang et al., 2015). Moreover, the dominant climatic constraints on vegetation productivity shift across hydro-climatic gradients: precipitation exerts primary control in arid and semi-arid areas, while temperature becomes more influential in humid regions with sufficient water availability (Clifford et al., 2013). China, characterized by vast latitudinal and elevational gradients, encompasses multiple major climatic zones, including alpine, temperate continental, temperate monsoonal, and subtropical monsoonal zones. These zones host diverse ecosystems ranging from alpine grasslands and temperate grasslands to croplands and forest ecosystems, all governed by distinct thermal and hydrological constraints. Such strong climatic and ecological heterogeneity makes China an ideal natural laboratory for investigating GPP dynamics and their driving mechanisms across contrasting climate zones, which is essential for accurately characterizing regional vegetation productivity under climate change (Wu et al., 2010; Dong et al., 2022; Lu et al., 2024).

Remote sensing has become the primary approach for estimating GPP at large spatial and temporal scales. Most satellite-based GPP products are derived

from light-use efficiency (LUE) frameworks that integrate vegetation properties with meteorological constraints, such as the Moderate Resolution Imaging Spectroradiometer (MODIS) MOD17 algorithm (Running et al., 2004). In recent years, substantial methodological advances have been achieved by incorporating multi-source remote sensing observations, improved meteorological inputs, and data-driven approaches, thereby enhancing the ability to capture nonlinear responses of vegetation productivity to environmental drivers (Beer et al., 2010; Piao et al., 2020; Dong et al., 2022). Machine-learning techniques have been further introduced to explore complex interactions among climatic factors, vegetation characteristics, and human activities, providing new insights into the drivers of GPP variability at regional to national scales (Sun et al., 2018; Li et al., 2023).

Using these approaches, previous studies have documented significant spatiotemporal variations in GPP across China and explored the influences of climate change, atmospheric CO₂ concentration, vegetation dynamics, and human activities (Sun et al., 2018). In particular, elevated atmospheric carbon dioxide (CO₂) concentrations have been shown to enhance photosynthetic efficiency and vegetation productivity, although this fertilization effect is strongly constrained by water and nutrient availability and exhibits substantial spatial heterogeneity (McMurtrie et al., 2008; Cai and Prentice, 2020; Sun et al., 2020). Meanwhile, changes in vegetation structure, commonly represented by leaf area index (LAI), directly regulate canopy light absorption and photosynthetic capacity, thereby exerting a critical influence on GPP dynamics across ecosystems (Puma et al., 2013; Chen et al., 2023). Human activities, increasingly quantified using integrated human footprint indices, further modify vegetation productivity by altering land use, disturbance regimes, and resource availability (Mu et al., 2022). Nevertheless, several limitations remain. Many studies have focused on national averages or individual regions, which may obscure contrasting

GPP responses among different climatic zones. Moreover, traditional statistical methods are often affected by multicollinearity among explanatory variables, while data-driven models, despite their strong predictive power, often lack interpretability. A comprehensive framework that integrates climate-zone-specific analyses with both robust statistical methods and interpretable machine-learning approaches is still lacking.

To address these gaps, this study investigated the spatiotemporal variations and driving mechanisms of GPP in China's terrestrial ecosystems from 2001 to 2020 across four major climatic zones. Specifically, this study aims to: (1) characterize temporal trends, spatial patterns, and centroid migration of GPP at national and climatic-zone scales; (2) quantify the relative contributions of climatic factors, vegetation structure, atmospheric CO₂ concentration, and human activities to interannual GPP variability using pixel-wise ridge regression while accounting for multicollinearity; and (3) further explore nonlinear marginal effects and potential interactions among key drivers using an Extreme Gradient Boosting-SHapley Additive exPlanations (XGBoost-SHAP) framework. By ex-

PLICITLY considering climatic heterogeneity and methodological complementarity, this study aims to provide a more comprehensive and regionally differentiated understanding of vegetation productivity dynamics across China under ongoing climate change.

2 Study area and methodology

2.1 Study area

China (03°51'–53°33'N, 73°33'–135°05'E) is located in the eastern part of Asia, bordering the Pacific Ocean to the east. It spans nearly 50.00° of latitude from north to south, covering a vast geographical area with distinct topographical and climatic characteristics. In terms of terrain, China presents a clear west-east gradient: western regions feature high altitudes and steep slopes, while the terrain gradually descends eastward, transitioning from plateaus and mountains to plains. This topographical variation is directly associated with the diversity of climatic patterns across the country. Regarding vegetation and climate, China encompasses diverse vegetation types due to its broad latitudinal range and varied climate zones (Fig. 1). The complex terrain and geographical location have led to the formation of multiple distinct ecosystems. In this research, China's terrestrial ecosystems were categorized into four climatic zones to examine the factors influencing GPP in different areas, specifically: alpine climate zone, temperate continental climate zone, temperate monsoonal climate zone, and subtropical monsoonal climate zone (Zhang et al., 2025).

Fig. 1 Topographic (a) and vegetation type (b) distribution in China. DEM, digital elevation model.

2.2 Datasets

2.2.1 GPP data The GPP data, collected by MODIS, cover the period from 2001 to 2020. They have a spatial

resolution of 500 m and a temporal resolution of 8 d. The data are derived from the MOD17A2H dataset (Running and Zhao, 2021), which is made available by the United States' National Aeronautics and Space Administration (NASA; <https://search.earthdata.nasa.gov/search>). The GPP estimation model for these data is based on the BioGeoChemical Cycles (BIOME-BGC) model and the photosynthetic energy conversion efficiency model. It aims to simulate the daily GPP of terrestrial ecosystems and to calculate 8-day and annual GPP values accordingly. In the data, the interference effect of clouds on vegetation LAI and photosynthetically active radiation measurements is effectively eliminated, thus enhancing the accuracy of the data compared with those of the 8-day and annual GPP data provided by NASA (version 5). Currently, these data have been compared and verified against flux observation sites in multiple regions worldwide and have been widely applied in studies on global carbon cycles and global change.

2.2.2 Climate data

The climate dataset encompasses various meteorological parameters such as temperature, precipitation, solar radiation, wind speed, and soil moisture. In this research, temperature, precipitation, solar radiation, and wind speed data were obtained from the European Centre for Medium-Range Weather Forecasts (ECMWF) Reanalysis 5-Land (ERA5-Land) monthly mean climate reanalysis dataset provided by ECMWF (<https://cds.climate.copernicus.eu/>) (Muñoz Sabater, 2019). The ERA5 dataset has been evaluated from various perspectives and demonstrates excellent precision and reliability in numerous research endeavors. The data exhibit a spatial resolution of 0.10° and a temporal resolution of 30 d, encompassing a range of meteorological and climatic variables. In this work, temperature, precipitation, solar radiation, and wind speed data from 2001 to 2020 were selected as core meteorological drivers, since they control vegetation photosynthesis, energy supply, water balance, and aerodynamic conditions and have been proven to dominate terrestrial GPP variations across diverse climatic zones in existing studies. Soil moisture data were sourced from the Global Land Evaporation Amsterdam Model (GLEAM), with a spatial resolution of 0.25° and encompassing global coverage.

2.2.3 Vegetation data

The LAI data were obtained from the Global Leaf Area Index Mapping Project dataset (<https://zenodo.org/records/4700264>), which provides long-term time series LAI data globally since 1981 (Liu et al., 2012). Its temporal resolution is 8 d (from 2000 to present), and the spatial resolution is 8 km. In this study, LAI data from 2001 to 2020 were selected for analysis and research.

2.2.4 Human activity data

CO₂ data were obtained from the Open-Access Data Repository of Anthropogenic CO₂ Emissions (ODIAC) for the years 2001 to 2020 (Oda and Maksyutov, 2011), which provides a comprehensive set of greenhouse gas emissions data stemming from the combustion of fossil fuels worldwide. The data have a spatial resolution of 1 km and a temporal resolution of 30 d (https://db.cger.nies.go.jp/dataset/ODIAC/DL_odiac2022.html).

Human footprint data were derived from the Global Human Footprint (GHF) dataset (Mu et al., 2022), which was developed by the Urban Environmental Monitoring and Modelling (UEMM) group. This dataset incorporates eight variables that reflect various aspects of human pressure, including built environments, population density, nighttime light, croplands, pastures, roads, railways, and navigable waterways. The spatial resolution is 1 km, and human footprint data for the period 2001 to 2020 were used in this study.

All gridded datasets were resampled to a common spatial resolution of 0.05° using the GPP dataset as the spatial reference before analysis. Resampling was

conducted in ArcGIS Desktop v.10.8 (Environmental Systems Research Institute (ESRI), Redlands, USA) using the Resample tool: the nearest-neighbor method was used for discrete variables to preserve original values and avoid artificial smoothing, and bilinear interpolation was applied to continuous variables to maintain data continuity. All datasets were projected to the World Geodetic System 1984 (WGS84) coordinate system to ensure complete spatial consistency.

2.3 Methodology

2.3.1 Research framework overview

This study constructed a hybrid analytical framework, integrating ridge regression and XGBoost-SHAP, for the systematic investigation of the spatiotemporal dynamics and multi-scale driving mechanisms of terrestrial ecosystem GPP in China from 2001 to 2020. The research first synthesized multi-source datasets including MODIS GPP, ERA5 climate reanalysis, and GLOBMAP global Leaf Area Index since 1981 (GLOBMAP-LAI), employing the Theil-Sen median trend test and Mann-Kendall (M-K) significance test to reveal spatiotemporal patterns of GPP changes and utilizing the center of gravity migration model to analyze spatial displacement trajectories. Partial correlation analysis was then conducted to control for confounding variables and quantify the independent relationships between various factors and GPP. Furthermore, ridge regression was applied to quantify the relative contributions of climatic, vegetation, and anthropogenic factors at interannual scales, while the XGBoost-SHAP model was employed to capture nonlinear marginal effects and interactions among factors, ultimately revealing the divergence of driving mechanisms between long-term linear trends and short-term nonlinear responses (Fig. 2).

Fig. 2 visible schematic labels: Step 1: Data preparation; MODIS; ERA5; GLOBMAP-LAI. Step 2: Spatial variation analysis; Multi-year trend test analysis; Shift in center of gravity. Step 3: Partial correlation analysis; Control for confounding variables for correlation analysis; Partial correlation coefficient plot of partitions. Step 4: Analysis of the contribution of impact factors to GPP; Spatial distribution and percentage of regression coefficients; Relative contribution of the influencing factor. Step 5: XGBoost-SHAP model; Marginal contribution of factors to model predictions.

Fig. 2 Schematic of research framework. MODIS, Moderate Resolution Imaging Spectroradiometer; ERA5, European Centre for Medium-Range Weather Forecasts (ECMWF) Reanalysis 5; GLOBMAP-LAI, GLOBMAP global Leaf Area Index since 1981; GPP, gross primary production; XGBoost-SHAP, Extreme Gradient Boosting-Shapley Additive exPlanations.

2.3.2 Theil-Sen median analysis and the M-K significance test

The Theil-Sen median approach, alternatively referred to as Sen's Slope Estimation, is a resilient

non-parametric statistical technique used for trend analysis. This method evaluates all potential point pairs within a dataset, determines the slope for each pair, and then identifies the median slope to provide a robust estimation of the general trend. Owing to its high robustness, it is particularly suitable for situations with outliers or uneven data distributions (Sen, 1968). This study employed a linear regression model to characterize the trends in the time series of GPP for overall vegetation in China and its four climatic zones from 2001 to 2020. The trend can be expressed as follows:

$$\beta = \text{median} \frac{x_j - x_i}{j - i} (1 < i < j < n), \quad (1)$$

where β denotes the interannual trend in GPP; x_i and x_j are the annual averages of GPP in years i and j , respectively ($\text{g C}/(\text{m}^2 \cdot \text{a})$); and n represents the length of the time series. For $\beta > 0$, the overall primary productivity of vegetation increases; and for $\beta < 0$, the total primary productivity of vegetation decreases.

The M-K test is a non-parametric statistical method used for trend analysis, widely applied in the fields of hydrology, meteorology, and environmental science to detect trends in time-series data and to assess the significance of these trends (Cao et al., 2024). This method is defined as follows:

$$Z_{MK} = \begin{cases} \frac{S - 1}{\sqrt{\text{var}(S)}}, & S > 0, \\ 0, & S = 0, \\ \frac{S + 1}{\sqrt{\text{var}(S)}}, & S < 0, \end{cases} \quad (2)$$

$$S = \sum_{i=1}^{n-1} \sum_{j=i+1}^n \text{sgn}(x_j - x_i), \quad (3)$$

$$\text{sgn}(x_j - x_i) = \begin{cases} 1, & x_j - x_i > 0, \\ 0, & x_j - x_i = 0, \\ -1, & x_j - x_i < 0, \end{cases} \quad (4)$$

$$\text{var}(S) = \frac{n(n-1)(2n+5)}{18}, \quad (5)$$

where Z_{MK} represents the statistical test value for an individual data sequence. The S statistic, which is computed for the GPP data, incorporates $\text{var}(S)$ as the variance of the S statistic and uses sgn to denote the logical discriminant function. It is worth noting that a value of $|Z|$ exceeding 1.96 indicates a statistically significant increasing or decreasing trend at the 0.05 significance level, while a value of $|Z|$ exceeding 2.58 indicates a significant trend at the

99.00% confidence level ($P < 0.01$) (Table 1). The classification method used is as follows (Wang et al., 2024b):

Table 1 Utilized statistical significance levels for gross primary production (GPP) change

Category	GPP	S_{GPP}	Mann-Kendall (M-K) test ($ Z $)
Improvement	Highly	$S_{GPP} > 0$	$1.96 < Z \leq 2.58$
Improvement	Slight	$S_{GPP} > 0$	$ Z > 2.58$
Stable		$S_{GPP} = 0$	
Degradation	Slight	$S_{GPP} < 0$	$ Z > 2.58$
Degradation	Highly	$S_{GPP} < 0$	$1.96 < Z \leq 2.58$

Note: S_{GPP} denotes the slope of the linear trend of GPP over the study period, representing the annual rate of change in GPP.

2.3.3 Center of gravity migration model

The center of gravity migration model is a common method used to reveal the temporal variation

in the mean center of a group of elements in a region over time, and the dynamic spatial distribution and spatial evolution trend of specific elements can be analyzed with the help of indicators such as the center-of-gravity location and migration direction. Compared with the traditional static analysis method, the center-of-gravity migration model pays more attention to the spatiotemporal dynamic change characteristics of the elements in time and space. The model also employs the standard deviation ellipse, which takes the weighted center as its center, the principal trend direction as its azimuth, and the standard deviations in the X and Y directions as its axes, to further characterize the directional distribution and spatial extent of the elements. Assuming a region consists of n sub-regions, where the spatial geographic coordinates (or centroid coordinates) of the i^{th} research object are (x_i, y_i) , and ω_i represents the weight of the i^{th} research object, the average geographic center coordinates of the research object i can be obtained using the weighted average center (Wang et al., 2024a). The calculation formulae are as follows:

$$\bar{X}_\omega = \frac{\sum_{i=1}^n \omega_i f_i x_i}{\sum_{i=1}^n \omega_i f_i}, \quad (6)$$

$$\bar{Y}_\omega = \frac{\sum_{i=1}^n \omega_i f_i y_i}{\sum_{i=1}^n \omega_i f_i}. \quad (7)$$

In the formula, $\bar{X}_\omega$ and $\bar{Y}_\omega$ represent the longitude and latitude coordinates of the GPP centroid, respectively; ω_i is the area of the i^{th} pixel (m^2); f_i is the value of GPP for the i^{th} grid cell ($\text{g C}/(\text{m}^2\cdot\text{a})$); and x_i and y_i are the longitude and latitude coordinates of the center of the i^{th} pixel, respectively.

2.3.4 Partial correlation analysis method The partial correlation analysis technique is a statistical approach for evaluating the linear relationship association between two variables, which can control for the influence of one or more additional variables, thereby more accurately reflecting the true relationship between the two variables (Chen et al., 2024a). Thus, in this study, the partial correlation analysis was employed to evaluate the strength of relationship between the GPP and several influencing factors. For two variables X and Y , while controlling for variable Z , the calculation formula for the partial correlation coefficient can be expressed as:

$$r_{XY \cdot Z} = \frac{r_{XY} - r_{XZ} \times r_{YZ}}{\sqrt{(1 - r_{XZ}^2)(1 - r_{YZ}^2)}}, \quad (8)$$

where $r_{XY \cdot Z}$ denotes the first-order partial correlation coefficient between the target variables X and Y after controlling for the confounding variable Z ; in this study, it specifically represents the partial correlation coefficient between GPP (defined as Y) and a given influencing factor (defined as X) after controlling for the interference of the control variable Z ; r_{XY} represents the partial correlation coefficient between variable X and variable Y ; r_{XZ} represents the partial correlation coefficient between variable X and variable Z ; and r_{YZ} represents the partial correlation coefficient between variable Y and variable Z .

2.3.5 Attribution analysis The multivariate linear regression method can be employed to analyze the impact of various influencing factors on the GPP (Zhao et al., 2023). Specifically, it is as follows:

$$\text{GPP} = \sum_{j=1}^p \beta_j x_j + b, \quad (9)$$

where $j = 1, 2, \dots, p$; x_j denotes the independent variable; p is the number of independent variables; b is a constant intercept term; and β_j is the regression coefficient, which can be calculated via

the least squares method:

$$\beta = (X^T X)^{-1} X^T y, \quad (10)$$

where X is the $n \times (p + 1)$ design matrix composed of all independent variable samples; X^T is the transpose of matrix X ; and y is the n -dimensional column vector of the observed GPP values.

However, in this study, interactions among climate variables, environmental variables, and human activities introduced multicollinearity, which resulted in $\det(X^T X) \approx 0$ and unstable parameter estimates. To solve this problem, we introduced a disturbance perturbation term λI into the matrix to construct ridge regression, which can efficiently eliminate multicollinearity:

$$\beta_{\text{ridge}} = (X^T X + \lambda I)^{-1} X^T y, \quad (11)$$

where β_{ridge} is the vector of ridge regression coefficients; λ is the coefficient of the disturbance perturbation term; and I is a matrix of the same dimension as $X^T X$.

In this study, ridge regression was employed to quantify the relationships between the GPP and its influencing factors. First, each set of data was normalized to facilitate the calculation of different variables with distinct units:

$$X_m = \frac{x - \min(x)}{\max(x) - \min(x)}, \quad (12)$$

where X_m denotes the normalized data of the impact factor.

Then, the GPP was fed into the ridge regression model, yielding the following:

$$Y_m = \sum_{j=1}^p a_j x_{jm} + d, \quad (13)$$

where Y_m is the normalized GPP value; a_j is the ridge regression coefficient for the j^{th} normalized influencing factor; x_{jm} is the normalized value of the j^{th} influencing factor for the m^{th} sample; and d is the intercept term of the normalized ridge regression model. Subsequently, the absolute contribution of each influencing factor to the GPP trend was calculated:

$$\eta_{cj} = a_j \times X_{js_trend}, \quad (14)$$

where η_{cj} is the absolute contribution of the j^{th} influencing factor to GPP change; and X_{js_trend} is the normalized interannual trend of the j^{th} influencing factor during the study period.

Finally, the absolute contributions were converted into relative contributions to compare the relative importance of each factor:

$$\eta_{rcj} = \frac{|\eta_{cj}|}{|\eta_{c1}| + |\eta_{c2}| + |\eta_{c3}| + \dots + |\eta_{cp}|}, \quad (15)$$

where η_{rcj} represents the relative contribution of the j^{th} influencing factor to GPP change (%); and η_{c1} , η_{c2} , and η_{c3} in the formula correspond to the absolute contribution terms of the 1st, 2nd, and 3rd influencing factors.

2.3.6 XGBoost-SHAP model

Extreme Gradient Boosting (XGBoost) is a robust machine learning algorithm with strong adaptability and the ability to efficiently identify the importance of latent variables, while also providing high predictive accuracy and interpretability (Fan et al., 2025). In this study, the XGBoost algorithm was employed to model the complex relationships between GPP and its influencing factors, and was integrated with SHAP to improve model interpretability.

SHapley Additive exPlanations (SHAP) was developed based on the Shapley value from game theory (Shapley, 1953), and can enhance the interpretability of machine learning models (Lundberg and Lee, 2017). By calculating the Shapley value for each feature, SHAP quantifies the contribution of each feature to the prediction results, thereby providing both global and local interpretability. The definition of the SHAP value is as follows:

$$\phi_j = \sum_{T \subseteq F \setminus \{j\}} \frac{|T|!(|F| - |T| - 1)!}{|F|!} (V(T \cup \{j\}) - V(T)). \quad (16)$$

In the equation, ϕ_j is the SHAP value of the j^{th} feature; F denotes the set of all features; T represents a subset that does not contain the j^{th} influencing factor; $F \setminus \{j\}$ is the set of all possible feature combinations excluding j ; $|T|$ is the number of features in the subset T ; $|F|$ is the total number of features in the set F ; $V(T \cup \{j\})$ represents the contribution of the subset $(T \cup \{j\})$, which includes the j^{th} influencing factor, to the model prediction output; and $V(T)$ denotes the contribution of subset T to the model prediction output.

In the XGBoost model, the key hyperparameters were specified to ensure model reproducibility. The number of trees was set to 100, with a maximum tree depth of 10 and a learning rate of 0.05. Both the subsample ratio and the column subsampling ratio were set to 1. Regularization was applied using L1 regularization (`reg_alpha=1.0`) and L2 regularization (`reg_lambda=1.0`) to reduce overfitting. Model training was conducted using all available Central Processing Unit cores (`n_jobs = -1`), and a fixed random seed (`random_state=42`) was applied.

3 Results

3.1 Spatiotemporal trends of GPP

3.1.1 Temporal variation characteristics of GPP The temporal trends of the vegetation GPP within the terrestrial ecosystems and the four major climate zones of China were analyzed. The results indicated that from 2001 to 2020, GPP in the terrestrial ecosystems and the four climate zones of China

showed significant increasing trends, all of which passed the significance test (Fig. 3), but there were fluctuations between different years. In general, the lowest point was observed in 2004, and the peak was recorded in 2019. In summary, the mean annual increment was $4.64 \text{ g C}/(\text{m}^2 \cdot \text{a})$ ($P < 0.01$). Specifically, the value increased from $702.76 \text{ g C}/(\text{m}^2 \cdot \text{a})$ in 2001 to $793.24 \text{ g C}/(\text{m}^2 \cdot \text{a})$ in 2020, with a total increase of $90.48 \text{ g C}/(\text{m}^2 \cdot \text{a})$. Among the four climate zones, the subtropical monsoonal climate zone exhibited the largest increase in GPP, reaching $8.65 \text{ g C}/(\text{m}^2 \cdot \text{a})$. Specifically, the value increased from $1030.51 \text{ g C}/(\text{m}^2 \cdot \text{a})$ in 2001 to $1186.02 \text{ g C}/(\text{m}^2 \cdot \text{a})$ in 2020, with a total increase of $155.52 \text{ g C}/(\text{m}^2 \cdot \text{a})$. The highest value of the GPP occurred in 2019, reaching $1233.83 \text{ g C}/(\text{m}^2 \cdot \text{a})$ (Fig. 3e). The temperate monsoonal climate zone also exhibited a notable increase in GPP, featuring a growth rate that was just behind the subtropical monsoonal climate zone, amounting to $7.94 \text{ g C}/(\text{m}^2 \cdot \text{a})$. The highest value of the GPP occurred in 2018, reaching $804.91 \text{ g C}/(\text{m}^2 \cdot \text{a})$ (Fig. 3d). The growth rate in the temperate continental climate zone was $2.44 \text{ g C}/(\text{m}^2 \cdot \text{a})$, increasing from $130.90 \text{ g C}/(\text{m}^2 \cdot \text{a})$ in 2001 to $190.35 \text{ g C}/(\text{m}^2 \cdot \text{a})$ in 2020, with a total increase of $59.44 \text{ g C}/(\text{m}^2 \cdot \text{a})$ (Fig. 3b). The growth rate in the alpine climate zone was the lowest, at $1.03 \text{ g C}/(\text{m}^2 \cdot \text{a})$ (Fig. 3c).

3.1.2 Spatial variation characteristics of GPP The Sen-M-K approach was used to analyze the spatiotemporal patterns of the GPP across China and its four climatic zones from 2001 to 2020 (Fig. 4). Overall, from 2001 to 2020, approximately 69.04% of the regions in China showed an increasing trend, among which the GPP in approximately 47.16% of the areas exhibited a significant upward trend ($S_{\text{GPP}} > 0$; $P < 0.05$). These areas were mostly located on the Loess Plateau and in the Northeast China Plain. A downward trend in GPP was noted in 5.39% of the overall areas, with a markedly declining trend in only 0.93% of the areas ($S_{\text{GPP}} < 0$; $P < 0.05$). The regions experiencing a decline in GPP values were scattered across the study area, predominantly in urban clusters like the Yangtze River Delta, which are heavily impacted by human activities. The decreasing trend in the GPP gradually weakened from the urban centers to the surrounding areas (Fig. 4).

Among the four climate zones, the region exhibiting a significant rise in GPP exceeded 25.00% of the study area. Among them, the temperate monsoonal climate zone encompassed the highest

Fig. 3

Legend: GPP; fitted y of GPP; 95% confidence band of GPP.

- (a) GPP in China ($\text{g C}/(\text{m}^2 \cdot \text{a})$): $y = 4.64x - 8583$; $R^2 = 0.69$; $P < 0.01$.
- (b) GPP in temperate continental climate zone ($\text{g C}/(\text{m}^2 \cdot \text{a})$): $y = 2.44x - 4738$; $R^2 = 0.74$; $P < 0.01$.
- (c) GPP in alpine climate zone ($\text{g C}/(\text{m}^2 \cdot \text{a})$): $y = 1.03x - 1905$; $R^2 = 0.29$; $P < 0.05$.
- (d) GPP in temperate monsoonal climate zone ($\text{g C}/(\text{m}^2 \cdot \text{a})$): $y = 7.94x -$

15257; $R^2 = 0.83$; $P < 0.01$.

- (e) GPP in subtropical monsoonal climate zone ($\text{g C}/(\text{m}^2 \cdot \text{a})$): $y = 8.65x - 16260$; $R^2 = 0.60$; $P < 0.01$.

Fig. 3 Interannual variation of GPP from 2001 to 2020 in China. (a), China; (b), temperate continental climate zone; (c), alpine climate zone; (d), temperate monsoonal climate zone; (e), subtropical monsoonal climate zone.

proportion of areas with a significant increase in the GPP, reaching 64.13%, and these areas were distributed mainly in the Northeast China Plain, North China Plain, and Loess Plateau. This was followed by the subtropical monsoonal climate zone, where the proportion of areas with a significant increase in the GPP reached 50.67%. These regions were predominantly located in the middle and lower stretches of the Yangtze River Plain and within the Sichuan Basin. In contrast, the alpine climate zone encompassed a smaller proportion of areas with a significant increase in the GPP (25.56%), which were largely distributed on the Qinghai-Xizang Plateau and in the Qilian Mountains, among other places. Among the four climate zones, the proportion of areas showing a significant GPP degradation trend was relatively small (not

exceeding 1.70%). Among them, the subtropical monsoonal climate zone exhibited the highest proportion of areas with a significant GPP degradation trend (1.69%), and these areas were predominantly concentrated in the Yangtze River Delta and other regions with dense populations and rapidly developing urban agglomerations. In the temperate continental climate zone, the proportion of areas with significant GPP degradation was the lowest, accounting for only 0.23% of the total area, and such areas were mainly distributed in provincial capitals.

Fig. 4 Spatial patterns (a) and significance distribution (b) of GPP in China. The white area represents desert bare land where GPP is close to 0 year-round in Figure 4a.

3.2 GPP center of gravity migration trajectory

Based on the center of gravity migration model, we counted the center of gravity coordinates of GPP in 2001, 2005, 2010, 2015, and 2020, and calculated the change trajectory of GPP center of gravity according to the center of gravity coordinates (Fig. 5), so as to describe the distribution of GPP spatially. The results showed that the standard deviation ellipse of GPP in China was generally oriented in the northeast-southwest direction, and its center of gravity was distributed between 33° - 34°N and 111° - 112°E , corresponding to the southern part of the North China Plain, and the center of gravity of GPP has migrated to the northwest in the past 20 a. From 2001 to 2005, the center of gravity of GPP also showed a significant shift from south to north, and gradually shifted to the southwest in the following decade, and then to the northwest in 2020.

From 2001 to 2020, GPP in different climatic zones of China showed significant spatiotemporal heterogeneity, and even within a single climatic zone, GPP

exhibited noticeable variations in both time and space. The standard deviation ellipse of GPP in the alpine climate zone was generally oriented in the northeast-southwest direction, with its centroid distributed between 31° – 32° N and 96° – 98° E, located in the southeastern part of the Qinghai-Xizang Plateau. Over the past 20 a, there has been a trend of northwestward migration of the GPP centroid (Fig. 6a). From 2001 to 2020, the center of gravity of GPP also migrated from southeast to northwest, gradually migrated from south to north from 2001 to 2010, turned southward from 2010 to 2015, and moved to northwest from 2015 to 2020. The GPP standard deviation ellipse in the temperate monsoonal climate zone was generally oriented in the northeast-southwest direction. The centroid was distributed between 42° – 43° N and 120° – 122° E. Over the past 20 a, the GPP standard deviation ellipse has shown a clear trend of migration towards the southwest (Fig. 6b). From the trajectory of centroid migration, the GPP centroid has moved overall in the southwest direction, with an accelerated pace after 2010, which may be greatly related to the afforestation policies of the Chinese government. In the temperate continental climate zone, the standard deviation ellipse of GPP was generally oriented in the west-east direction, and there was a contraction in the ellipse area, indicating that the distribution of local vegetation was becoming more concentrated (Fig. 6c). The centroid of GPP in the temperate continental climate

zone was distributed between 43° – 44° N and 105° – 107° E, and over the past 20 a, there has been a trend of GPP centroid migration towards the south. However, their centroid positions extend beyond the national border, into Mongolian People's Republic. This is because the temperate continental climate zone forms a narrow east-west arc in northern China; the southern side of the arc is covered by vast Gobi deserts, resulting in nearly zero GPP values (weights close to zero), while the northern side of the arc comprises grassland belts with relatively high GPP values, thus dominating the weighted average results. As a result, the centroid is strongly pulled northward and eventually crosses the border into Mongolia. From the trajectory of centroid migration, there was a trend of GPP centroid migration from the northwest to the southeast over the 20 a period. The GPP standard deviation ellipse in the subtropical monsoonal climate zone was generally oriented in the southeast-northwest direction. The centroid was distributed between $26^{\circ}00'$ – $27^{\circ}10'$ N and $110^{\circ}00'$ – $111^{\circ}00'$ E, and over the past 20 a, the distribution range of the GPP standard deviation ellipse has gradually moved towards the northwest direction (Fig. 6d). From the trajectory of centroid migration, during the period from 2001 to 2020, the centroid of GPP exhibited periodic oscillations between the southeast and northwest directions. Despite these fluctuations, the long-term trend of the centroid still clearly showed a migration towards the northwest direction, indicating that the long-term trend of GPP was gradually shifting towards the northwest. Overall, China's GPP showed a trend of convergence from the periphery towards central areas, which implied that the vegetation coverage and ecosystem productivity in the central regions of China have improved.

Fig. 5 GPP standard deviation ellipse and its center of gravity migration

trajectory in China. The white area represents desert bare land where GPP is close to 0 year-round.

3.3 Relationships between climatic factors and GPP

From 2001 to 2020, the relationships between GPP and different variables were quantified using partial correlation analysis (Fig. 7). The results showed that the associations between GPP and various variables exhibited clear spatial heterogeneity. Among them, LAI had the strongest association with GPP, and 99.60% of the regions showed a positive relationship, mainly in the western regions of the temperate monsoonal climate zone and the eastern regions of the temperate continental climate zone (Fig. 7f). In addition, in 87.63% of the regions, GPP was

Legend

Gravity center: 2001; 2005; 2010; 2015; 2020

Gravity trajectory: 2001; 2005; 2010; 2015; 2020

→ Migration track

GPP ($\text{g C}/(\text{m}^2 \cdot \text{a})$): 0, 200, 400, 600, 800, 1200, 1800, 2400, 3200

Fig. 6 Standard deviation ellipse of GPP and centroid migration trajectory in climate zones. (a), alpine climate zone; (b), temperate monsoonal climate zone; (c), temperate continental climate zone; (d), subtropical monsoonal climate zone. The white area represents desert bare land where GPP is close to 0 year-round.

positively correlated with soil moisture, predominantly in the central regions of the alpine climate zone, the eastern and northwestern sectors of the temperate continental climate zone, the northern sectors of the temperate monsoonal climate zone, and the southern part of the subtropical monsoonal climate zone (Fig. 7e). An inverse correlation trend was observed only in the southern regions of the alpine climate zone and the eastern regions of the subtropical monsoonal climate zone. In contrast, the correlation coefficient between GPP and wind speed was negative in most regions (69.45%), while positive correlations were mainly found in the central part of the temperate monsoonal climate zone, the central and eastern parts of the alpine climate zone, and the northwestern part of the temperate continental climate zone (Fig. 7d). The areas where temperature had a positive association with GPP accounted for 87.86% of the total area, mainly in the northern and central-western sections of the subtropical monsoonal climate zone, as well as in the eastern section of the alpine climate zone (Fig. 7a). The proportions of regions showing positive correlations between solar radiation and CO_2 with GPP reached

75.24% and 74.83%, respectively. The difference was that positive correlations between solar radiation and GPP were mainly in the southern regions of the subtropical monsoonal climate zone and the southeast of the alpine climate zone (Fig. 7c). Conversely, regions exhibiting a positive correlation between CO_2 and

GPP were primarily found in the temperate monsoonal climate zone and the northern section of the subtropical monsoonal climate zone (Fig. 7g). The areas where the human footprint demonstrated a positive relationship with GPP comprised 72.36% of the total area, primarily concentrated in the central regions of the alpine climate zone and the southeastern section of the temperate monsoonal climate zone (Fig. 7h); regions with negative correlations were scattered throughout the subtropical monsoonal climate zone and the warm temperate monsoonal climate zone. The areas where precipitation was positively correlated with GPP accounted for 58.56% of the total area, mainly distributed in the eastern sectors of the temperate continental climate zone, whereas regions with negative correlations were predominantly located in the southeastern parts of the alpine climate zone and the southwestern parts of the humid subtropical monsoonal climate zone. Overall, at the national scale, the influencing factors on GPP were ranked in the following order: LAI>human footprint>wind speed>soil moisture>temperature>solar radiation> CO_2 >precipitation. The proportion of areas where the GPP was positively correlated with temperature, precipitation, solar radiation, soil moisture, LAI, CO_2 , and human footprint was greater than that of areas with a negative correlation, indicating an overall positive correlation pattern. The proportion of areas with negative correlations between the GPP and wind speed was greater than that of areas with positive correlations, indicating an overall negative correlation pattern. Nevertheless, at the regional scale, the response of the GPP to the various climatic elements showed substantial spatial heterogeneity (Fig. 7).

Comparing the four climate zones, the correlations between temperature, solar radiation, wind speed, and CO_2 with GPP within the temperate continental climate zone were comparatively low, except for those in the northeastern and northwestern parts, where they were relatively higher. Positive correlations between precipitation and GPP were predominantly found in the eastern regions of the temperate continental climate zone. The effects of soil moisture and LAI on GPP in this area were predominantly positive, with these influences mainly concentrated in the northwestern and eastern regions. Notable impacts of the various driving factors in the alpine climate zone predominantly concentrated in the central and southern sectors, among which the impact of CO_2 on the local GPP was very low, with only sporadic distributions in the northeastern and southwestern parts. In the temperate monsoonal climate zone, notable impacts of soil moisture, LAI, and human footprint on GPP were widely distributed across the region, with positive influences prevailing, whereas notable effects of the other elements were mostly concentrated in the northeastern, southwestern, and southeastern parts. In the subtropical monsoonal climate zone, areas where solar radiation and soil moisture were positively correlated with GPP were predominant and were primarily located in the southern part of the region. Positive correlations between temperature and GPP were mainly concentrated in the northern and central-eastern parts, whereas positive correlations between CO_2 and GPP were primarily concentrated in the northern part. Negative correlations between wind speed and GPP were widely distributed across the entire

region, with relatively larger proportions observed in the northern, central, and southwestern parts. By contrast, LAI exhibited a strong positive correlation with GPP throughout the entire region, nearly covering the whole area.

The partial correlation coefficients between GPP and the driving factors across China and the four climate zones are presented (Fig. 8). At the national scale, LAI exhibited the strongest positive correlation with GPP (0.56), followed by the human footprint, whereas CO_2 and precipitation were negatively correlated overall. Significant regional differences were observed, with the effect of LAI being most pronounced in the temperate continental, alpine, and temperate monsoonal climate zones (0.95, 0.86, and 0.89, respectively). These results indicate that LAI serves as the dominant factor regulating vegetation productivity, and its influence exhibits distinct zonal differentiation.

- (a) Temperature (b) Precipitation (c) Solar radiation
 (d) Wind speed (e) Soil moisture (f) LAI
 (g) CO_2 (h) Human footprint

Partial correlation value: -1.00, -0.80, -0.60, 0.00, 0.60, 0.80, 1.00

Fig. 7 Spatial distribution of the partial correlation coefficients between GPP and driving factors in China. (a), temperature; (b), precipitation; (c), solar radiation; (d), wind speed; (e), soil moisture; (f), leaf area index (LAI); (g), carbon dioxide (CO_2); (h), human footprint. Blank areas comprise both raw-data gaps and computational nulls from invalid partial correlations.

Correlation coefficient: 0.95, 0.62, 0.30, -0.03, -0.35, -0.68

Matrix values shown in Fig. 8:

- Subtropical monsoonal climate zone: Temperature -0.173; Precipitation -0.384; Solar radiation 0.298; Wind speed -0.188; Soil moisture 0.344; LAI 0.785; CO_2 -0.676; Human footprint 0.789.
- Temperate monsoonal climate zone: Temperature -0.304; Precipitation 0.508; Solar radiation 0.461; Wind speed -0.002; Soil moisture 0.170; LAI 0.888; CO_2 -0.663; Human footprint 0.698.
- Temperate continental climate zone: Temperature -0.391; Precipitation 0.022; Solar radiation -0.148; Wind speed 0.463; Soil moisture -0.297; LAI 0.949; CO_2 -0.022; Human footprint -0.093.
- Alpine climate zone: Temperature 0.410; Precipitation -0.117; Solar radiation 0.137; Wind speed -0.052; Soil moisture 0.689; LAI 0.860; CO_2 -0.658; Human footprint 0.126.
- China: Temperature 0.001; Precipitation -0.323; Solar radiation -0.053; Wind speed 0.174; Soil moisture 0.125; LAI 0.563; CO_2 -0.298; Human footprint 0.398.

Fig. 8 Matrix diagram of partial correlation coefficients.

3.4 Contributions of the influencing factors to GPP

The spatial distribution and percentage statistics of the regression coefficients of the impact factors on GPP change in China from 2001 to 2020 are shown in Figure 9. Overall, LAI was the dominant factor at the national scale, accounting for 41.13%, followed by CO₂ (24.68%). LAI dominated all climate zones except the alpine climate zone, particularly in the temperate monsoonal climate zone where it reached 52.82%. In the temperate continental climate zone, LAI (42.38%) and CO₂ (32.03%) were the first and second dominant factors, respectively, with soil moisture ranking third at 9.90%. In the alpine climate zone, CO₂ replaced LAI as the primary driving factor, accounting for 40.26%, followed by LAI (20.02%) and soil moisture (13.30%). In the temperate monsoonal climate zone, soil moisture (8.31%) ranked as the third leading factor, whereas wind speed (0.81%) was the least influential. In the subtropical monsoonal climate zone, solar radiation ranked third (12.96%), followed by soil moisture (6.62%).

Fig. 9 Spatial distribution (a) and percentage statistics (b) of regression coefficients. The white area in Figure 9a represents desert bare land where GPP is close to 0 year-round.

After comprehensively considering the contributions, trends, and multicollinearity effects of multiple independent variables, the relative contributions of various driving factors to GPP are depicted in Figure 10. Notably, the relative contributions of these driving factors to GPP differed significantly across climatic zones. Overall, LAI was the most significant contributor to GPP in China's terrestrial ecosystems, accounting for 33.92%, followed by the human footprint at 17.39%. After controlling for multicollinearity, CO₂ exhibited the smallest relative contribution at the national scale (4.61%). In the alpine climate zone, the human footprint contributed the most to GPP (22.99%), followed by soil moisture (19.13%), whereas CO₂ showed the smallest contribution (0.36%). In the temperate continental climate zone, LAI contributed the most (34.61%), followed by soil moisture (16.99%) and the human footprint (15.74%), with CO₂ contributing the least (2.92%). In the temperate monsoonal climate zone, LAI ranked first (39.18%), followed by soil moisture (14.33%) and the human footprint (14.32%), while wind speed had the smallest contribution (4.34%). In the subtropical monsoonal climate zone, LAI also ranked first (38.23%), followed by the human footprint (17.77%) and solar radiation (10.77%), with wind speed contributing the least (4.37%).

Significant spatial heterogeneity was observed in the dominant environmental and human activity factors across the different climate zones. The spatial pattern of the main factors influencing interannual GPP trends at the pixel scale is shown in Figure 11. Specifically, temperature and wind speed mainly controlled the interannual GPP trends in the central and

western parts of the alpine climate zone. Precipitation dominated in the eastern regions of the temperate continental climate zone, the southeastern regions

of the alpine climate zone, and the western part of the subtropical monsoonal climate zone. Solar radiation primarily influenced GPP in the southern regions of the alpine climate zone and the southwestern and eastern parts of the subtropical monsoonal climate zone. Soil moisture mainly controlled the interannual GPP trends in the central and eastern sectors of the alpine climate zone, the northwestern and northeastern sectors of the temperate continental climate zone, and the northeastern sectors of the temperate monsoonal climate zone. CO₂ exerted relatively strong effects in the eastern and southern parts of the temperate monsoonal climate zone, but its contribution was minimal in the alpine climate zone. The human footprint primarily controlled the interannual GPP trends in the central and southern parts of the alpine climate zone, the eastern part of the temperate monsoonal climate zone, and the subtropical monsoonal climate zone. By contrast, LAI dominated in most climate zones, with only a minor influence in the alpine climate zone, and accounted for the majority of interannual GPP variability across China's terrestrial ecosystems.

Fig. 10 Relative contribution of each driving factor in different climate zones

3.5 XGBoost-SHAP model

The SHAP interpreter was employed to quantify the nonlinear marginal effects of each factor on GPP and their potential interactions ($R^2=0.84$). At the national scale, the global SHAP bar chart (Fig. 12a) showed that temperature had a marginal contribution to GPP that far exceeded other factors, indicating that temperature exerted the strongest marginal effect on the predicted national average GPP. The temperature-SHAP polynomial curve (Fig. 12b) further revealed that under low temperature conditions, the SHAP values of temperature were low and fluctuated significantly; as the temperature rose, the SHAP values gradually increased. This suggested that in cold environments, the promoting effect of temperature on vegetation productivity was weak and highly variable, whereas within the optimal temperature range, the promoting effect on GPP gradually strengthened. In Figure 12c, soil moisture, which showed the strongest interaction with temperature SHAP values, was selected as the interaction variable. Under low soil moisture conditions, the SHAP values of temperature fluctuated significantly and were generally low. As soil moisture increased, the SHAP values of temperature gradually rose and tended to stabilize.

In the alpine climate zone, Figure 12d showed that solar radiation had the strongest marginal effect on the predicted average GPP. Figure 12e further revealed that the SHAP values decreased sharply as solar radiation increased. Figure 12f, with wind speed as the interaction variable,

Fig. 11 Relative contributions of driving factors to interannual GPP in China from 2001 to 2020. (a), temperature; (b), precipitation; (c), solar radiation; (d), wind speed; (e), soil moisture; (f), LAI; (g), carbon dioxide (CO₂); (h), human footprint. The white area represents desert bare land where GPP is close to 0 year-round.

showed that under low wind speed conditions, the SHAP values of solar radiation fluctuated greatly, ranging from high to low values, whereas under high wind speed conditions, the SHAP values began to decrease. In the temperate continental climate zone, Figure 12g showed that solar radiation had the greatest impact on the model's prediction of GPP. Figure 12h illustrated the nonlinear effect of solar radiation on GPP; at lower solar radiation levels, the SHAP values were higher and more variable, while as solar radiation increased, the SHAP values gradually declined. This indicated that excessively high solar radiation may enhance the light suppression effect on vegetation. Figure 12i, with soil moisture as the interaction variable, showed that under low soil moisture and high solar radiation conditions, the SHAP values of solar radiation fluctuated greatly; as soil moisture increased, the SHAP values gradually decreased. In the temperate monsoonal climate zone, Figure 12j showed that solar radiation had the strongest effect on the model's predicted GPP. Figure 12k demonstrated the nonlinear effect of solar radiation on GPP, with SHAP values showing a downward trend as solar radiation increased. Figure 12l, with temperature as the interaction variable, showed that the SHAP value was highest when both temperature and solar radiation were at moderate levels, and that the SHAP value gradually decreased as temperature and solar radiation increased. In the subtropical monsoonal climate zone, the effect of temperature on model-predicted GPP remained the greatest (Fig. 12m). Figure 12n showed that as temperature increased, the SHAP values gradually rose, indicating that the increase in temperature continuously contributed positively to GPP. Figure 12o was colored using solar radiation as the interaction variable. The SHAP values reached their maximum under high temperature and high solar radiation conditions, and the SHAP values interacting with solar radiation sharply increased when the accumulated temperature reached a critical point.

Fig. 12 Global SHapley Additive exPlanations (SHAP) bar (a, d, g, j, and m), univariate polynomial SHAP dependence curve (b, e, h, k, and n), and dominant factor interaction SHAP (c, f, i, l, and o) graphs. The point colors in Figure 12c, f, i, l, and o indicate the magnitude of the interacting variable, and blue represents low values and red represents high values.

4 Discussion

4.1 Impact of long-term trends of factors on GPP

Climate factors are key variables affecting vegetation growth and substantially contribute to shaping the terrestrial carbon cycle (Peñuelas and Filella, 2001; Wang et al., 2001; Pearson et al., 2014; Wen et al., 2019). Since the Industrial Revolution, the global climate has undergone significant changes, and one of the most direct manifestations is the substantial shift in global precipitation patterns (Myhre et al., 2019; Robinson et al., 2021; Zhang et al., 2021). Coinciding with this change has been an increase in the frequency of extreme precipitation events (Li et al., 2024a). Soil moisture, which is directly influenced by precipita-

tion infiltration, also exhibits corresponding changes (Liu et al., 2022), thereby exerting diverse effects on vegetation across China's terrestrial ecosystems. Our results showed that from 2001 to 2020, environmental factors played a positive role in promoting GPP in China's terrestrial ecosystems. Our analysis using ridge regression revealed that LAI made the greatest contribution to GPP at the national scale from 2001 to 2020, followed by CO₂ (Fig. 9). Soil moisture and precipitation are important

factors that regulate water and carbon cycles within the soil-vegetation-atmosphere continuum, and they significantly affect vegetation growth and recovery processes (Yang et al., 2023). Reports indicated that since 2007, during the accelerated greening of vegetation in China, the main factor affecting vegetation has shifted from vapor pressure deficit to soil moisture, with soil moisture affecting approximately 61.00% of the global vegetation area (Yang et al., 2023). This further corroborated the findings of this study, where soil moisture was identified as a key factor influencing GPP. Over the past two decades, soil moisture ranked as the second leading contributor in the alpine, temperate continental, and temperate monsoonal climate zones, whereas its contribution in the subtropical monsoonal climate zone was relatively minor (Fig. 10). In the arid and cold alpine meadow and grassland regions of the Qinghai-Xizang Plateau, plants typically allocate more biomass to underground parts (Yun et al., 2024). This biomass allocation strategy highlights the importance of soil moisture for vegetation growth and development in alpine climate zones. Moreover, as the permafrost layer in these regions gradually thaws, soil nutrients are released, which can help alleviate water stress in plants (Li et al., 2024b). In this study, soil moisture was highly significantly positively correlated with GPP in the central regions of the alpine climate zone. Accordingly, the ridge regression results indicated that the contribution of soil moisture to GPP in the alpine climate zone ranked second only to human footprint, further confirming the important status of soil moisture in this region. In the temperate zones, the positive effects of temperature and solar radiation during the critical growing period of vegetation are key drivers for promoting plant growth (Sun et al., 2018), which is consistent with our research findings that moderate warming leads to an increase in GPP.

4.2 The instantaneous response of factors on GPP

Ridge regression is designed to address multicollinearity among predictors and to quantify their linear contributions to interannual GPP variability, whereas SHAP analysis focuses on explaining marginal effects embedded in nonlinear model predictions. Specifically, ridge regression stabilizes coefficient estimation under strong interdependence among climatic and environmental variables, providing a robust characterization of long-term linear controls on GPP, while the XGBoost-SHAP framework captures instantaneous and nonlinear response patterns. We applied SHAP analysis to investigate the marginal contributions of individual factors to the prediction of China's average GPP, and the results in-

indicated that temperature exhibited the strongest marginal influence (Fig. 12a). In addition, the interaction analysis with soil moisture shows that under conditions of high temperature and high soil moisture, the promoting effect of temperature on GPP is more pronounced (Fig. 12c). This suggests that in some regions of China, although water conditions limit vegetation growth in the long term, temperature changes can exert a more pronounced fluctuating impact on vegetation productivity in the short term, thereby reflecting the high marginal contribution of temperature in the SHAP analysis (Gao et al., 2017). At the national scale, differences in factor rankings between ridge regression and SHAP analyses primarily reflect their distinct analytical objectives, which operate at different temporal scales. Ridge regression emphasizes interannual trends in GPP from 2001 to 2020, a period during which widespread vegetation greening occurred across China, resulting in a dominant contribution of LAI to long-term GPP variability. By contrast, SHAP analysis highlights the sensitivity of model predictions to instantaneous environmental conditions, thereby emphasizing variables such as temperature at the national scale. At the regional scale, solar radiation dominated in the alpine climate, temperate continental climate, and temperate monsoonal climate zones, with SHAP values gradually decreasing as solar radiation increased (Fig. 12d, g, and j), indicating that excessive solar radiation may enhance the light suppression effect on vegetation. In the alpine climate zone, the divergence in rankings between ridge regression and SHAP results stems from the differentiation of spatiotemporal scales and stages of physiological constraints. At the interannual scale, the human footprint rapidly expanded along the valleys, becoming the primary driver of long-term GPP trends; meanwhile, permafrost degradation led to a linear declining trend in soil moisture, determining

the maximum carrying capacity of vegetation, hence the prominent ranking of soil moisture (Wang et al., 2024a). Conversely, within the instantaneous value framework, the plateau's characteristic of high radiation and short growing season causes solar radiation to frequently fall within the light saturation range, where its marginal effect on instantaneous GPP is maximized (Baptist and Choler, 2008). Human footprint and soil moisture tend to be averaged out at the interannual scale, leading to a corresponding decrease in their contributions in the SHAP analysis. Under low wind speed conditions, plants experience less drought stress and mechanical damage, allowing for faster water conduction in the plant xylem and higher growth rates. However, strong winds can reduce the resistance of the canopy and the boundary layer of plants, leading to drier plant surfaces and potential mechanical damage (He et al., 2025). In the subtropical monsoonal climate zone, as temperature increased, the SHAP values gradually rose (Fig. 12n). Moreover, under the interaction of high solar radiation and high temperature, the SHAP values reached their maximum, possibly because vegetation in the subtropical monsoonal climate zone possesses strong adaptability to high temperature and high humidity conditions. Under the combined effects of high temperature and high solar radiation, this vegetation could make full use of light and thermal energy for photosynthesis, demonstrating higher

productivity (Wang and Zhang, 2023). This reflects the efficient use of solar radiation by vegetation in the subtropical monsoonal climate zone under favorable growing conditions.

Ridge regression highlights the dominant role of LAI, reflecting the stable contribution of long-term vegetation cover to GPP; SHAP analysis emphasizes the importance of temperature at the national scale and solar radiation at the regional scale, revealing the direct drive of short-term environmental changes on GPP. It should be noted that SHAP values quantify the contribution of predictors to the XGBoost model outputs and are therefore dependent on the underlying model structure, rather than representing direct causal effects. In contrast, ridge regression is employed to obtain stable linear estimates under multicollinearity and to characterize the relative importance of drivers for interannual GPP variability. Consequently, differences between the two sets of results primarily reflect their distinct analytical perspectives and temporal scales, with ridge regression emphasizing long-term linear controls and SHAP highlighting short-term and nonlinear response patterns. Taken together, these two approaches provide complementary insights into the drivers of GPP dynamics across different temporal scales.

4.3 Impact of CO₂ on the GPP in China

Since the Industrial Revolution, the CO₂ concentration in the atmosphere has continuously increased, substantially stimulating plant photosynthesis. Studies have shown that elevated atmospheric CO₂ can substantially influence terrestrial photosynthetic processes (Schimel et al., 2015). The increasing trend in global productivity is due mainly to enhanced LAI driven by the increase in CO₂ concentration (de Kauwe et al., 2016; Zhu et al., 2016; Piao et al., 2020; Kang et al., 2025). However, recent studies have revealed that the positive effects of increased atmospheric CO₂ concentrations on vegetation photosynthetic activity have weakened due to widespread land drought and have turned into negative effects at the beginning of the 21st century, especially at high latitudes (Chen et al., 2024b). This reduction has led to a sharp decrease in the growth benefits of vegetation attributed to the CO₂ fertilization effect. Over the past 40 a, the CO₂ fertilization effect has exhibited a significant downward trend in most land areas globally, especially between 2001 and 2015, when the decline became more pronounced (Wang et al., 2020). This downward trend may suggest a weakening response of vegetation productivity to increasing atmospheric CO₂. The study results demonstrated that the contribution of CO₂ to GPP in China between 2001 and 2020 accounted for only 4.61%, which indicates that the impact of the CO₂ fertilization effect on vegetation productivity in China has significantly decreased. In particular, in the alpine climate zone, the contribution of CO₂ reached only 0.36% (Fig. 10). This may be attributed to the fact that the CO₂ fertilization effect is closely related to soil nitrogen content and available water, and when both precipitation and nitrogen levels are low, a rise in atmospheric CO₂ concentration does not lead to a corresponding increase

in plant biomass (Reich et al., 2014). In the barren and ecologically fragile alpine regions, the vegetation comprises mainly alpine meadow, and the soil contains relatively few nutrients, which cannot provide sufficient nourishment for plant growth. Moreover, after 1998, the positive effect of climate warming gradually decreased, and atmospheric drought overrode the fertilization effect of CO_2 , resulting in a decline in both the greening rate and the rate of GPP increase on the Qinghai-Xizang Plateau since 1998 (Ren et al., 2024). Global warming is causing the atmosphere to dry, which increases vegetation water demand. Concurrently, the increase in atmospheric CO_2 levels alters the sensitivity of vegetation photosynthetic responses to CO_2 across various regions (Zaitchik et al., 2023). The different levels of soil nutrients and available water result in varying trends in GPP across different climate zones under elevated atmospheric CO_2 conditions. Excluding the alpine climate zone, the contribution of CO_2 to GPP in the other three climate zones also decreased significantly.

4.4 Potential applications and limitations The climate-zone-specific patterns of GPP variability identified in this study have important implications for ecosystem management under climate change. The distinct dominant drivers across climatic zones suggest that region-specific management strategies are likely to be more effective than uniform approaches. For example, vegetation productivity in water-limited regions may benefit more from water-conservation-oriented management, whereas temperature-sensitive ecosystems may require adaptive strategies to mitigate warming impacts. At the policy level, incorporating climate zone heterogeneity into ecosystem management and climate adaptation planning could improve the effectiveness of regional mitigation and adaptation strategies.

In this study, MODIS GPP products were used to examine the spatiotemporal distribution pattern of GPP in terrestrial ecosystems of China. However, compared with observed GPP, MODIS GPP was underestimated to varying degrees in different regions, especially in corn cropland areas (Huang et al., 2018). In future research, products with higher accuracy should be used for GPP analysis. Furthermore, this study did not fully consider human activity factors, incorporating only CO_2 and human footprint data. In future research, a broader range of human activity factors should be incorporated to comprehensively assess the impact of human activities on GPP in China's terrestrial ecosystems.

Additionally, although this study incorporated atmospheric CO_2 concentration and human footprint as proxies for anthropogenic influence, other important human-related factors were not explicitly considered. Nitrogen deposition has been shown to modify ecosystem productivity by altering nutrient availability, forest microclimate, and community functional traits, thereby regulating vegetation growth responses under climate change (Reich et al., 2014; Zhang et al., 2024). Irrigation and other land management practices may further reshape vegetation productivity, particularly in intensively managed agricultural and semi-arid areas, by alleviating water limitation and modifying surface-atmo-

sphere interactions. Future studies integrating nitrogen deposition, irrigation intensity, and other management-related variables could further improve the attribution of anthropogenic impacts on GPP dynamics.

5 Conclusions

Based on the Theil-Sen median trend analysis and the center-of-gravity migration model, this study investigated the spatiotemporal variation characteristics of GPP in China's terrestrial ecosystems from 2001 to 2020, and systematically quantified the relative contributions of multi-scale driving mechanisms using partial correlation analysis, ridge regression, and the XGBoost-SHAP framework. Our findings revealed a significant increasing trend in national GPP with an annual growth rate of $4.64 \text{ g C}/(\text{m}^2 \cdot \text{a})$, characterized by a significant increase in northeastern and central regions, with localized degradation in major urban clusters, accompanied by a converging trajectory of the GPP centroid from the periphery toward the center. Driver analysis indicated that LAI (contributing 33.92%), human footprint (17.39%), and soil moisture were the

dominant factors regulating interannual GPP variability, with LAI as the integrated indicator of vegetation coverage governing regional GPP changes, while soil moisture served as the critical climatic constraint directly limiting GPP. Notably, dominant drivers exhibited substantial divergence across temporal scales: ridge regression identified long-term trends dominated by LAI, human footprint, and soil moisture, whereas SHAP analysis highlighted temperature (at the national scale) and solar radiation (at the climate zone scale) as having the strongest marginal effects on instantaneous GPP responses. Particularly noteworthy was that the CO_2 fertilization effect markedly attenuated during the study period, contributing merely 4.61% nationally and declining to 0.36% in the alpine climate zone, indicating that water and nutrient limitations have severely constrained the promoting effect of CO_2 on vegetation productivity. This study advances a dual-scale attribution framework integrating linear long-term trends and nonlinear instantaneous responses, deepening the understanding of mechanisms regulating vegetation productivity in climatically heterogeneous regions; the findings provide scientific support for developing climate-zone-specific adaptive management strategies and optimizing terrestrial ecosystem carbon sink management.

Conflict of interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Author contributions

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