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Climate-Driven Effects on NPP in the Tibetan Plateau Alpine Grasslands Diminish with Increasing Elevation

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Abstract: Temperature and precipitation are important abiotic factors affecting net primary productivity (NPP) in grassland ecosystems. However, findings on how elevation influences the effects of these factors on NPP in alpine grasslands are not yet consistent. In addition, the impact of varied patterns of climate change on NPP sensitivity with elevation remain unclear. Therefore, alpine grassland on the Tibetan Plateau (TP) was selected to profile the spatial and temporal patterns of NPP from 2001 to 2022, and subsequently to reveal the effects of temperature and precipitation on the sensitivity of NPP with altitudinal gradient. The results showed that (1) 91% of the TP grassland experienced positive NPP trends, and the NPP trends followed a unimodal curve with elevation, with the largest mean value at 2500 m; (2) a positive correlation between precipitation and NPP dominated the grassland NPP up to an elevation of 3400 m, and a positive correlation between temperature and NPP dominated the grassland NPP above an elevation of 3400 m; (3) temperature, precipitation, and their interaction explained, on average, 21% of the temporal variation in the NPP of TP grassland, and the explanatory capacity decreased significantly with elevation; and (4) elevation, temperature, and precipitation variations together explained 35% of the NPP sensitivity of the TP grasslands. This study reveals the altitudinal characteristics of NPP in grasslands affected by climate, and reminds us to take elevation into account when carrying out grassland management.

Keywords: net primary productivity; climate change; elevation gradient; alpine grassland; Tibetan Plateau

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1. Introduction

Grassland is one of the Earth's three continental terrestrial ecosystems and a major carbon reservoir. It stores about 15.2% of the total carbon of terrestrial ecosystems and plays a pivotal role in the global carbon cycle [1,2]. However, grassland ecosystems possess a relatively simple community structure and are susceptible to external disturbances that affect vegetation growth [3,4]. In particular, dramatic environmental changes over the past decades have resulted in greater interannual variability of net primary productivity (NPP) in grassland ecosystems than in forest and desert ecosystems [5,6]. As an important component of the carbon cycle, NPP serves as a measure of vegetation productivity [7], and fluctuations in NPP would inevitably affect ecosystem composition, structure, and function [8]. Therefore, quantitatively revealing the spatial and temporal variations of grassland NPP and its relationship with climatic factors is crucial for an in-depth understanding of macro-scale plant–climate feedback processes and ecosystem management [9].

Among the numerous weather-related environmental variables, temperature and precipitation have been proven to be important factors influencing global patterns of vegetation productivity [3]. Studies have suggested that annual temperature and precipitation together explain 38–63% of the total variation in global primary productivity of terrestrial ecosystems [10,11]. The significance of temperature and precipitation on vegetation productivity at the regional scale is also well documented, e.g., temperature and precipitation together explain 48% of the variation in NPP in grassland ecosystems in Central Asia [12] and 24.3% of the variation in NPP in forest ecosystems in eastern China [13]. Alpine vegetation growing in harsh environments has been reported to be more susceptible to changes in temperature and precipitation [14,15]. The continuous rise in temperature in alpine regions has led to significant impacts on the growth and reproduction of alpine vegetation, for example, the advanced flowering of alpine plants and the reduction of their populations [7]. With regard to vegetation productivity, the dominant conclusion is that temperature increase enhances alpine vegetation productivity. However, recent studies have found that the response of alpine vegetation to increasing temperature is gradually weakening, and that increasing temperatures can even lead to a decrease in vegetation productivity by increasing water stress in plants [16,17]. There seems to be no consistent conclusion on whether increased precipitation promotes or suppresses vegetation productivity in alpine regions, and both findings have been reported [18,19]. Thus, it is urgent to clarify the effect of temperature and precipitation on the growth of alpine vegetation.

Climate effects on vegetation growth are related to specific environmental backgrounds [20]. This means that the effects of temperature and precipitation on vegetation growth are necessarily spatially variable, e.g., with latitude and with altitude. However, most of the current studies have only explored the spatial features of climate-influenced plant growth through vegetation indices such as NDVI and EVI, which give an indication of the vegetation status but do not quantitatively characterize vegetation productivity [1,21]. The remaining studies have mainly focused on how climate and factors such as slope and elevation affect vegetation productivity at small scales [22,23]. There is still a lack of regional characterization of climate impacts on grassland productivity, which limits our insights into climate–vegetation mechanisms in specific environments. In addition, it is not yet unanimously recognized whether the positive or negative influence of climatic factors on NPP depends on spatial location. For example, field control experiments have shown that the effect of temperature on NPP is negatively correlated with elevation, whereas regional remote sensing methods have come to the opposite conclusion [6,24]. It confounds our understanding of vegetation–climate processes, and more researches are needed to address this issue.

NPP sensitivity is another variable that deserves consideration in understanding the relationship between vegetation and climate. It reflects the extent to which NPP responds to changes in temperature and precipitation, and is a characteristic that determines the stability of vegetation in response to climatic disturbances [25]. Vegetation type and elevation are both important influences that alter the NPP sensitivity to climate. For example, a study of North American drylands found that human disturbance caused up to a fivefold increase in the sensitivity of NPP to interannual variation in precipitation [26], and another study in the Qilian Mountains of China revealed a decrease in the NPP sensitivity to temperature with increasing elevation in an alpine desert [6]. Most of the existing studies examined the effects of individual factors on NPP sensitivity, ignoring the combined effects of multiple factors. There is a need to explore the processes by which multiple factors combine to influence vegetation productivity.

The Tibetan Plateau (TP) occupies nearly one quarter of China's land area and possesses one third of China's grassland. With less human activity and stronger climate change in recent years than other regions [27], the TP has become an ideal area in which to study the response of grass growth to climate change. Different scholars have carried out NPP studies on the TP grassland from multiple perspectives, but the results are still subject to uncertainty due to the inconsistencies in study duration and data sources and analysis methods [28,29]. Findings such as the effect of temperature or precipitation on NPP increasing or decreasing with elevation have been reported [6,19,30]. However, the conclusions of these studies were simply determined by partial correlation coefficients, ignoring the combined effects of temperature and precipitation on vegetation. Moreover, these studies did not take into account spatial patterns in the explanatory capacity of temperature and precipitation for NPP, nor in altitudinal differences in the sensitivity of NPP to changes in temperature and precipitation.

In order to clarify these knowledge gaps, this study took the TP alpine grassland as the research object and used spatial analysis methods to reveal the effects of the climatic factors of temperature and precipitation on the variation of NPP with elevation. Specifically, we aimed to (1) reveal the spatial and temporal patterns of NPP variation in TP grassland during 2001–2022, (2) explore the elevational patterns of the temperature and precipitation effects on NPP, and (3) illustrate whether elevation affects the sensitivity of NPP to temperature and precipitation.

2. Materials and Methods

2.1. Study Area

The Tibetan Plateau (TP) occupies southwestern China, ranging from 73°18′52″ to 104°46′59″E in longitude and 26°00′12″ to 39°46′50″N in latitude (Figure 1). The terrain within the TP is undulating and generally decreases in elevation from northwest to southeast. The average elevation of the TP exceeds 4000 m, and a highland mountainous climate dominates most areas. It transitions from warm and humid in the southeast to arid and cold in the northwest. The annual mean temperature ranges from −3.1 °C to 4.4 °C, and the annual precipitation ranges from 350 mm to 700 mm. The TP is one of the most extensive regions of alpine grassland in the world, and the grassland area exceeds 1.25 million km^2. The main grassland types are alpine meadows and alpine steppes, which account for about 27% and 34% of the total area of the TP [31]. The extensive grassland distribution and sparse anthropogenic disturbance make it an excellent experimental site for studying grassland response to climate change.

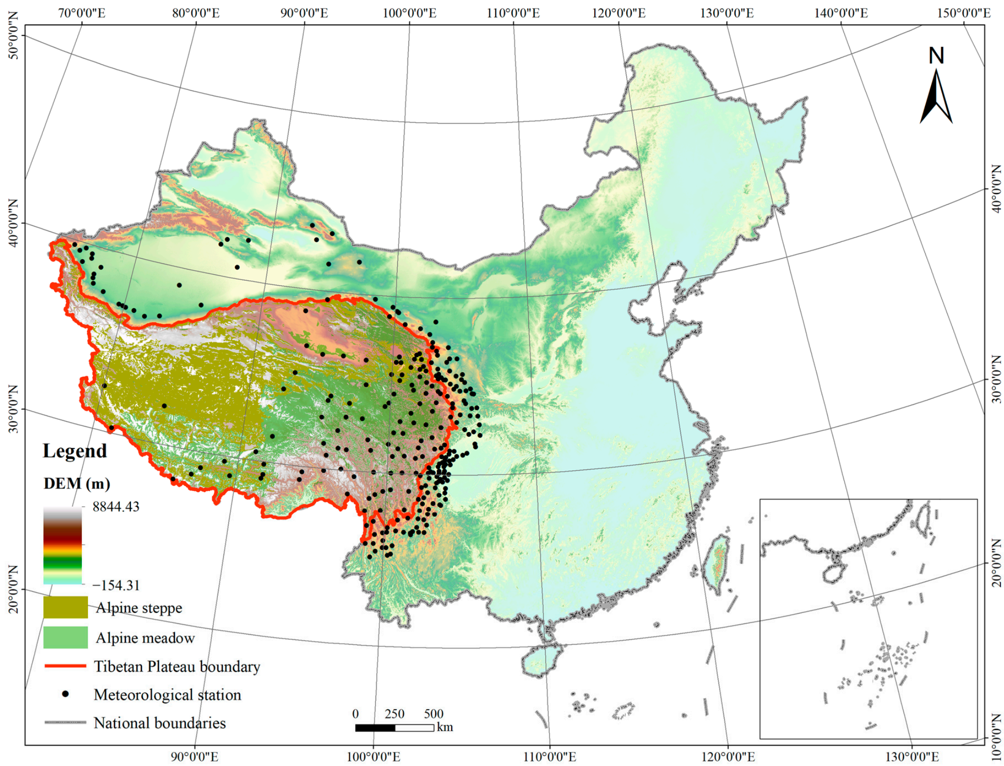

Figure 1. Location of the Tibetan Plateau (TP) and distribution of meteorological stations.

2.2. Extraction of Perennial Grassland Areas

The Normalized Difference Vegetation Index (NDVI) is an effective indicator of vegetation growth and has been proven to be effective in indicating the vegetation cover [32,33]. In this study, we utilized the NDVI to assist in determining the distribution of perennial grassland. First, we extracted the grassland boundary of the TP based on the 1:1,000,000 Vegetation Map of China released in 2001. Then, NDVI datasets with a temporal resolution of 16 days, a spatial resolution of 250 m, and a time span of 2001–2022 were extracted from the MOD13Q1 v061 product and downloaded from the NASA Earth Science Data System (available at https://search.earthdata.nasa.gov/ (accessed on 6 May 2024)). Maximum Value Composition (MVC) was used to extract areas where the maximum NDVI values were greater than 0.1 during the growing season (June–September) and greater than 0.15 during the peak growing season (July–August) for each year [34]. Areas meeting the above NDVI requirements for each year from 2001 to 2022 were extracted and considered as perennial vegetation cover areas. An overlapping analysis of the grassland boundary and perennial vegetation cover areas was carried out to obtain the intersections of the two landcover sources, which are considered to be the perennial grassland distribution area of alpine grassland on the Tibetan Plateau, and also the target region of this study.

2.3. Meteorological Data Production

In this study, daily meteorological records from 268 meteorological stations in and around the TP during 2001–2022 were collected from the China Meteorological Administration (Figure 1). We summarized the daily data to an annual scale and obtained the annual mean temperature and total annual precipitation for each weather station. A 30 m resolution digital elevation model (DEM) of the ASTER GDEM v2 dataset was downloaded from the USGS (http://earthexplorer.usgs.gov/ (accessed on 12 May 2024)) and then resampled to a spatial resolution of 1 km. Taking the annual-scale meteorological data, we hired the ANUSPLIN v4.2 meteorological interpolation software to expand temperature and precipitation point data into raster data. Although the relative lack of meteorological stations in the western part of the Tibetan Plateau brings some uncertainty to the interpolation process, the Thin-Plate Splines (TPS) interpolation method used in this ANUSPLIN software can fit the complex topography and meteorological element changes well to improve the accuracy of the interpolation results [35]. With longitude, latitude, and the DEM as covariate inputs, we obtained annual temperature raster data and annual precipitation raster data with a spatial resolution of 1 km per year.

2.4. NPP Data

Net primary productivity (NPP) characterizes vegetation vigor and is an important indicator of ecosystem productivity and energy conversion efficiency [26]. Currently, there are varied data products on NPP. According to existing studies, the model used for Moderate Resolution Imaging Spectroradiometer (MODIS) NPP data performs superiorly, as the model has been calibrated with large samples of data from around the globe and the product has been proven to retrieve grassland NPP on the TP with close to real values as well as a more stable performance [36,37]. Thus, we selected the NPP data from the MODIS product MOD17A3HGF dataset (at NASA Earth Science Data Systems, https://search.earthdata.nasa.gov/ (accessed on 12 May 2024)) to simulate grassland productivity on the TP.

The data were derived from the Terra satellite with a spatial resolution of 500 m. Key steps in the generation of the MODIS NPP include the calculation of each 8-day set of gross primary productivity (GPP) data based on the fraction of photosynthetically absorbed radiation (FPAR), incident solar radiation, minimum temperature, and daylight-averaged water vapor pressure difference (WVPD) data, as well as the calculation of annual maintenance respiration (MR) and growth respiration (GR) data based on the annual maximum leaf mass and temperature. NPP is the difference between the annual sum of 8-day GPP and MR and GR (https://modis-land.gsfc.nasa.gov/pdf/MOD17C61UsersGuideV11Mar112021.pdf (accessed on 12 May 2024)). This dataset has been improved by calibration changes and the use of climatological LAI/FPAR as a backup to the operational LAI/FPAR, improving data quality compared to previous versions. In addition, the dataset cleaned the poor-quality inputs from the 8-day Leaf Area Index and Fraction of Photosynthetically Active Radiation (LAI/FPAR) based on the quality control label for every pixel, and its value was replaced through linear interpolation, if any LAI/FPAR pixel did not meet the quality screening criteria. Prior to data processing and analyzing, we also resampled the NPP data to a 1 km resolution.

2.5. Data Analysis

To detect the trends in NPP over the period 2001 to 2022, the Mann–Kendall test and Sen's slope assessment were carried out on the time series data for the study period using the 'pyMannKendall' v1.4.3 package. We then obtained the grid-by–grid results of the trend and Sen's slopes of NPP, which we called NPP_{trend} and NPP_{slope}, respectively. We counted the mean values of NPP from 2001 to 2022 and the mean values of NPP_{slope} on elevation gradients at intervals of 100 m. Since vegetation response to elevation does not always follow the same pattern at different elevation gradients, and the number of grass raster cells varies greatly at different elevation gradients, we discussed the pattern of NPP and NPP_{slope} with elevation by using the segmentation function and unequal weights linear regression.

Climatic factors of temperature and precipitation were also analyzed using the Mann–Kendall test and Sen's Slope assessment to obtain the results of trends and Sen's slopes, referred to as $Temp_{trend}$, $Temp_{slope}$, Pre_{trend} and Pre_{slope}, respectively. Then, the NPP, temperature, and precipitation data for the years 2001–2022 were detrended using the least squares regression algorithm from the 'SciPy' v1.13.1 package to highlight the fluctuating characteristics of the data themselves. We obtained the NPP data, temperature data, and precipitation data for each year after detrending, and named them $NPP_{detrend}$, $Temp_{detrend}$, and $Pre_{detrend}$, respectively.

To explore the influence of temperature and precipitation on NPP, we performed a partial correlation analysis between $NPP_{detrend}$ and $Temp_{detrend}$ and $Pre_{detrend}$ using the 'pingouin' v0.5.4 package to account for the net correlation between NPP and each climatic factor. We further performed Ordinary Least Squares (OLS) analysis and Analysis of Variance (ANOVA) on these data using the 'statsmodels' v0.14.2 package to test the interpretation of NPP by means of temperature and precipitation. We also established a linear regression between R^2 of the explanation by temperature and precipitation on NPP and elevation to demonstrate whether the influence of temperature and precipitation on NPP is affected by elevation.

We further explored the extent to which NPP responds to changes in temperature and precipitation and its differences across the elevation gradient. The linear regression analyses in the 'scikit-learn' v1.5.1 package were used to investigate the NPP_{slope}, $Temp_{slope}$, and Pre_{slope} as a function of elevation based on the raster data. Finally, the effects of elevation and changes in temperature and precipitation on NPP sensitivity were investigated using a structural equation model (SEM). In this model, NPP_{slope} was defined as NPP sensitivity, and $Temp_{slope}$ and Pre_{slope} were defined as the changes in temperature and precipitation, respectively, as NPP_{slope} on each raster was the result of the combined response to $Temp_{slope}$, Pre_{slope}, and elevation.

The analysis by SEM was carried in Amos 26, and all the rest of the analyses were performed in Python 3.9.

3. Results

3.1. Spatial and Temporal Pattern of NPP

The NPP of grasslands on the TP generally decreased from east to west over the period 2001–2022, with NPP values exceeding 450 gC/m^2 on the eastern margins and less than 10 gC/m^2 in the western regions (Figure 2). NPP_{slope} varied between -30.2 and

15.8 gC/m^2/yr over the 22 years, with a mean value of 1.01 gC/m^2/yr. For 91.91% of the TP grasslands, NPP_{slope} was positive (Table 1). The eastern TP exhibited a predominantly positive slope in NPP, with the highest values at the eastern margin, while the southwestern TP exhibited a predominantly negative slope in NPP. Overall, NPP changed significantly in 51.84% of the grasslands. Among them, 51.47% exhibited a significantly increasing trend and 0.37% exhibited a significantly decreasing trend (Table 1).

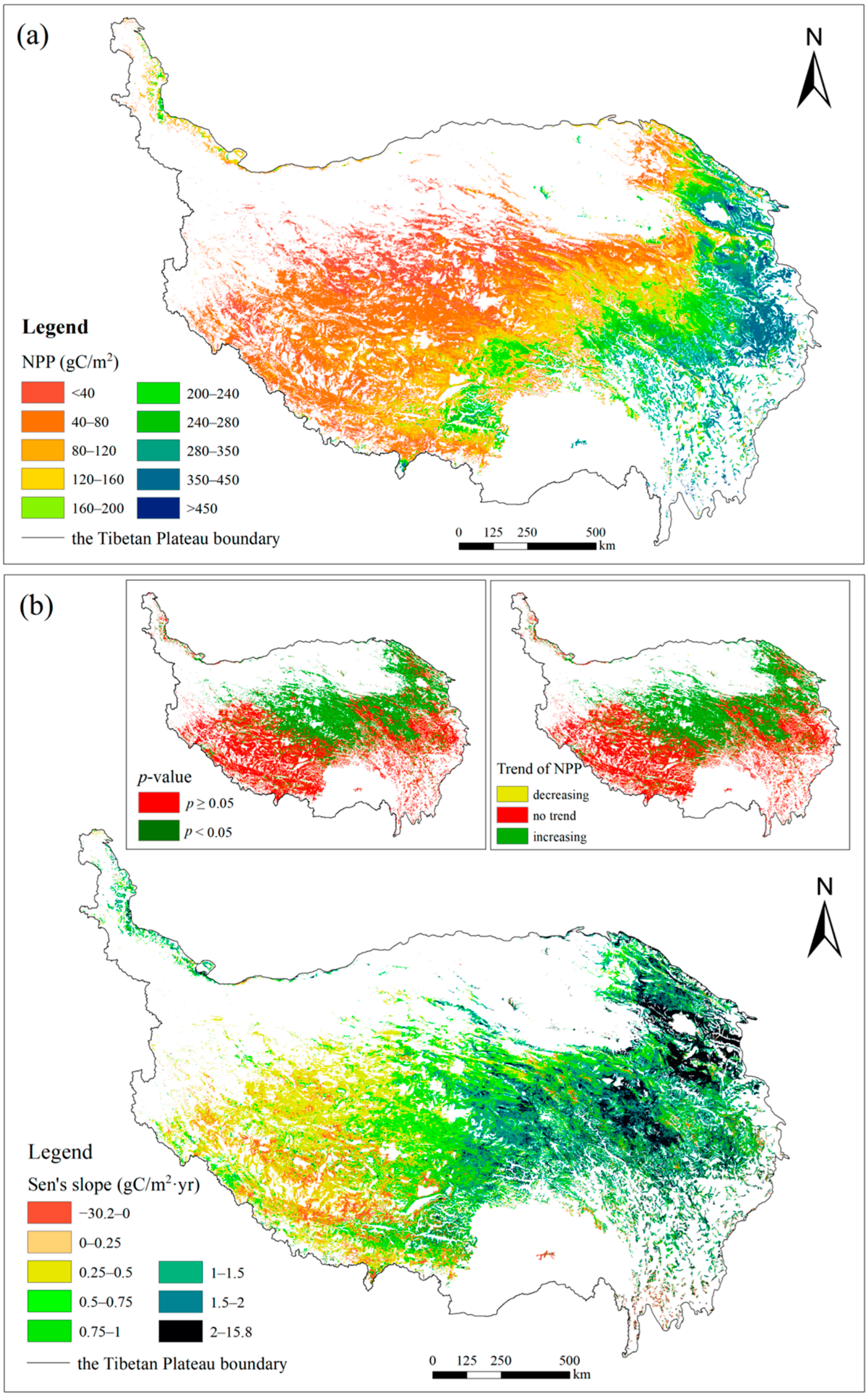

Figure 2. The average NPP of the Tibetan Plateau grassland during 2001 to 2022 (**a**) and the Sen's slope value of NPP after the Mann–Kendall test and Sen's slope assessment (**b**).

In addition to horizontal patterns, NPP and NPP_{slope} also exhibited vertical patterns across the TP grassland (Figure 3). NPP fluctuated and increased with rising elevation up to 3400 m ($r^2 = 0.23$, $p < 0.05$), and then decreased sharply with rising elevation above 3400 m ($r^2 = 0.70$, $p < 0.05$). NPP_{slope} also varied with elevation in a generally unimodal curve. Below 2500 m, the slope increased rapidly with elevation ($r^2 = 0.91$, $p < 0.05$). Above 2500 m, the slope gently declined with elevation ($r^2 = 0.89$, $p < 0.05$), except for a slight fluctuation between 3000 and 3200 m. At all elevation gradients, the mean value of NPP_{slope} was greater than 0, indicating an overall positive trend for the TP grassland.

Table 1. Statistics on NPP and its trends on the TP grassland.

	TP Grassland
NPP averages from 2001 to 2022 (gC/m^2/yr)	136.67
average NPP_{slope} (gC/m^2/yr)	1.01
proportion of slope < 0 (%)	7.66
proportion of slope = 0 (%)	0.43
proportion of slope > 0 (%)	91.91
decreasing trend	0.37
no trend	48.16
increasing trend	51.47

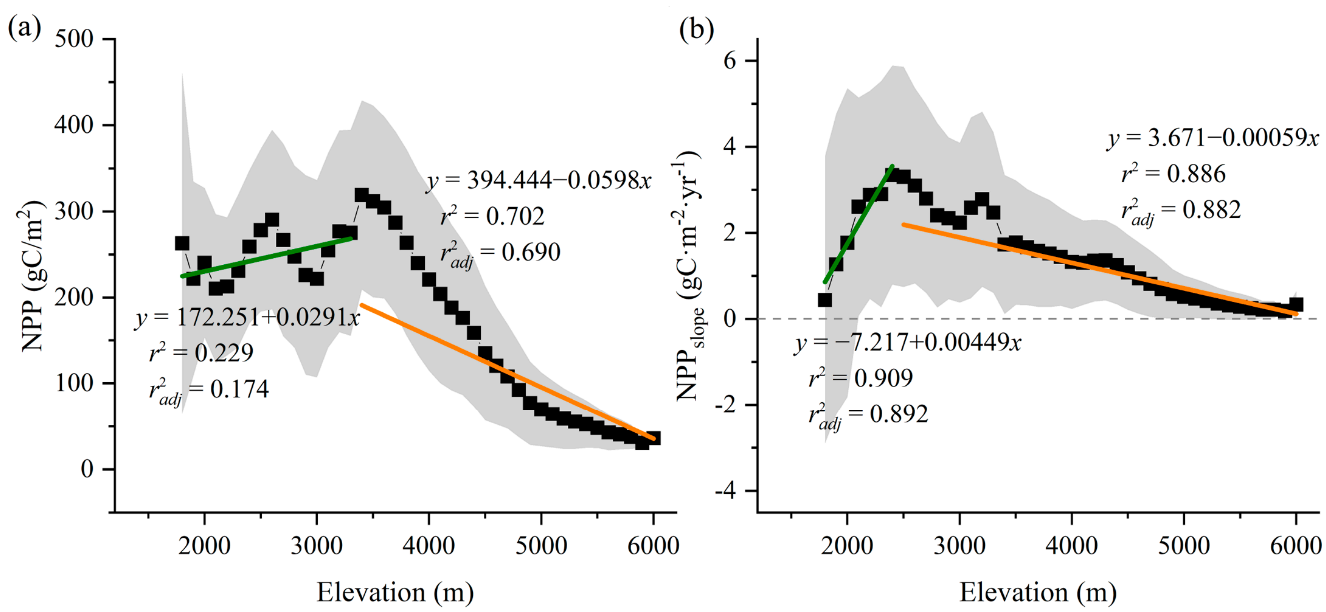

Figure 3. The mean value of NPP at 100 m intervals along with elevation (**a**) and the mean value of NPP_{slope} at 100 m intervals along with elevation (**b**). Note: Each point represents the mean of NPP or NPP_{slope} over the elevation gradient, and the shading represents the standard deviation of NPP or NPP_{slope} over the current elevation gradient.

3.2. Partial Correlation Between NPP and Climatic Factors

The partial correlation between temperature and NPP differed spatially from that between precipitation and NPP (Figure 4). A positive correlation between temperature and NPP was observed in 80.36% of the grasslands, out of which 20.68% reached a significant positive correlation. The high partial correlation coefficients were mainly concentrated in the central and northeastern TP, while the lower partial correlation coefficients were found on the southwestern margin. Precipitation was positively correlated with NPP in only 46.56% of the grasslands, and negatively correlated with NPP in the central, eastern, and northeastern parts of the TP.

We further counted the area proportions at various elevation gradients where NPP showed positive or negative correlations with both temperature and precipitation (Figure 5). A positive correlation between precipitation and NPP and a negative correlation between temperature and NPP dominated most of the area below 3400 m. Above 3400 m, a positive correlation between NPP and temperature dominated, and NPP was positively/negatively correlated with precipitation over a comparable area proportion.

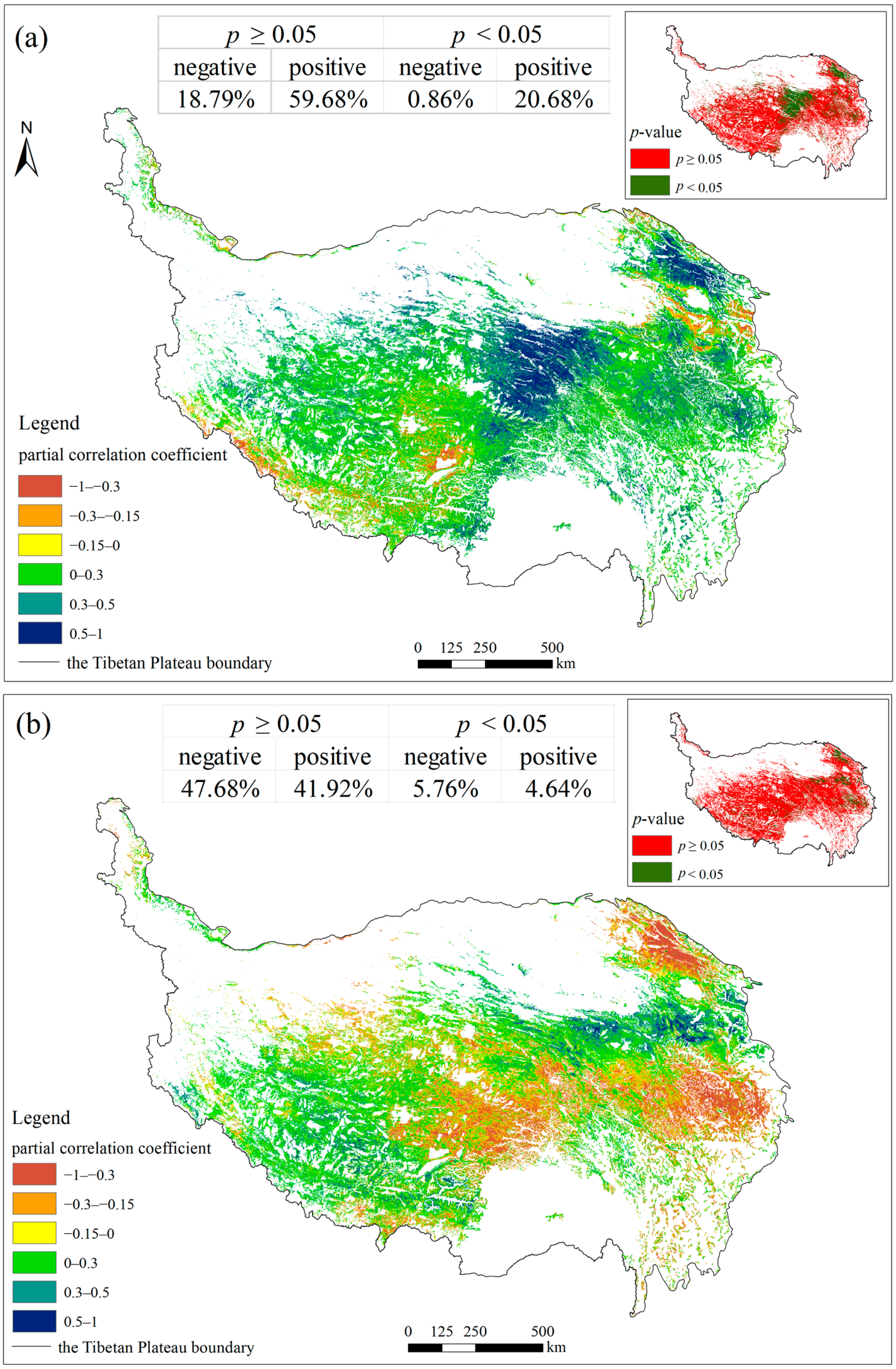

Figure 4. Partial correlations between NPP and climate factors: (**a**) partial correlation between $NPP_{detrend}$ and $Temp_{detrend}$; (**b**) partial correlation between $NPP_{detrend}$ and $Pre_{detrend}$.

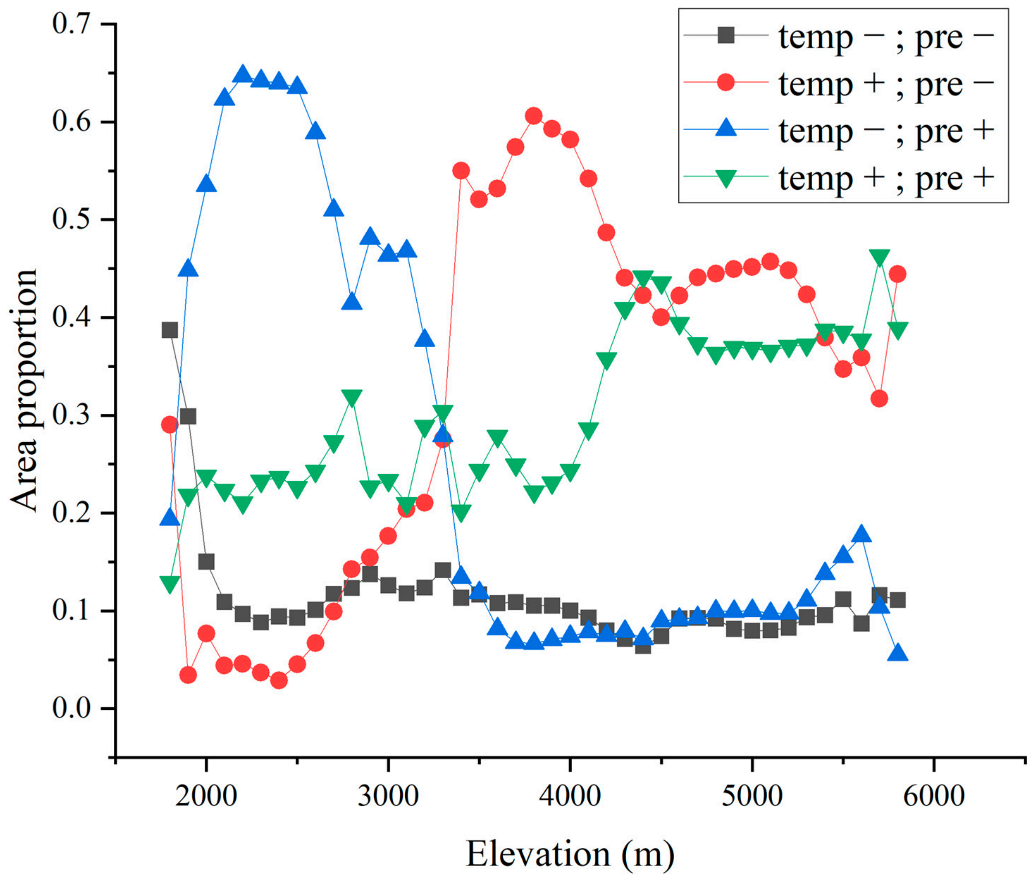

Figure 5. Area proportion of the partial correlation coefficients between temperature, precipitation, and NPP over the elevation gradient. Note: temp- indicates a negative correlation between temperature and NPP; temp+ indicates a positive correlation between temperature and NPP; pre- indicates a negative correlation between precipitation and NPP; pre+ indicates a positive correlation between precipitation and NPP.

3.3. The Effect of Climatic Factors on NPP Variation

The R^2 for the effect of temperature, precipitation. and their interaction on the temporal variation of NPP ranged from 0 to 0.87 with a mean value of 0.21 (Figure 6). The high values fell mainly in the central and eastern part of the TP. Decomposing the relative contributions of temperature, precipitation, and their interactions to NPP, 42.43% of the TP grasslands were primarily affected by temperature, mainly in the central and western areas of the TP. Precipitation dominated NPP in 35.35% of the grasslands, mainly distributed in the southwest and southeast of the TP. Temperature–precipitation interaction was the dominant factor for 22.22% of TP grassland NPP, mainly in the northeastern part of the TP.

The capacity of climatic factors to explain NPP weakened with elevation (Figure 7a). Considering the fact that vegetation types tend to be correlated with elevation, we further explored the effects of temperature and precipitation and their interactions on the NPP of different vegetation types (Figure 7b,c). The ability of temperature, precipitation, and their interactions to explain NPP was negatively correlated with elevation in both alpine meadows and alpine steppes. However, it did not reach the significance level in the alpine meadows, whereas the explanatory capacity of climate for NPP decreased significantly with increasing elevation ($r^2 = 0.64$, $p < 0.05$) in alpine meadows.

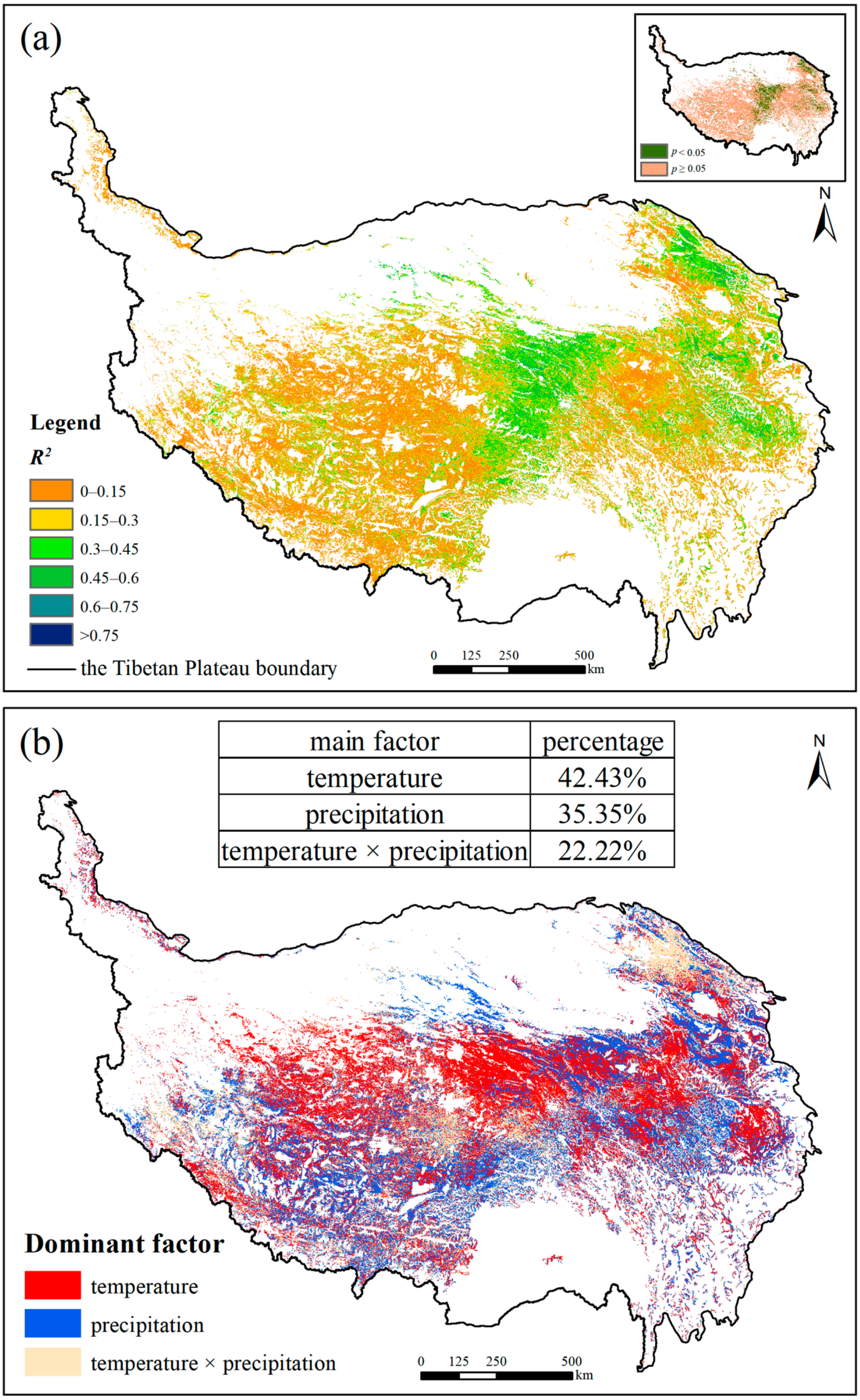

Figure 6. Spatial pattern of the explanation of temperature, precipitation, and their interactions on NPP (**a**) and the relatively dominant factor distribution of climate factors in the alpine grassland (**b**).

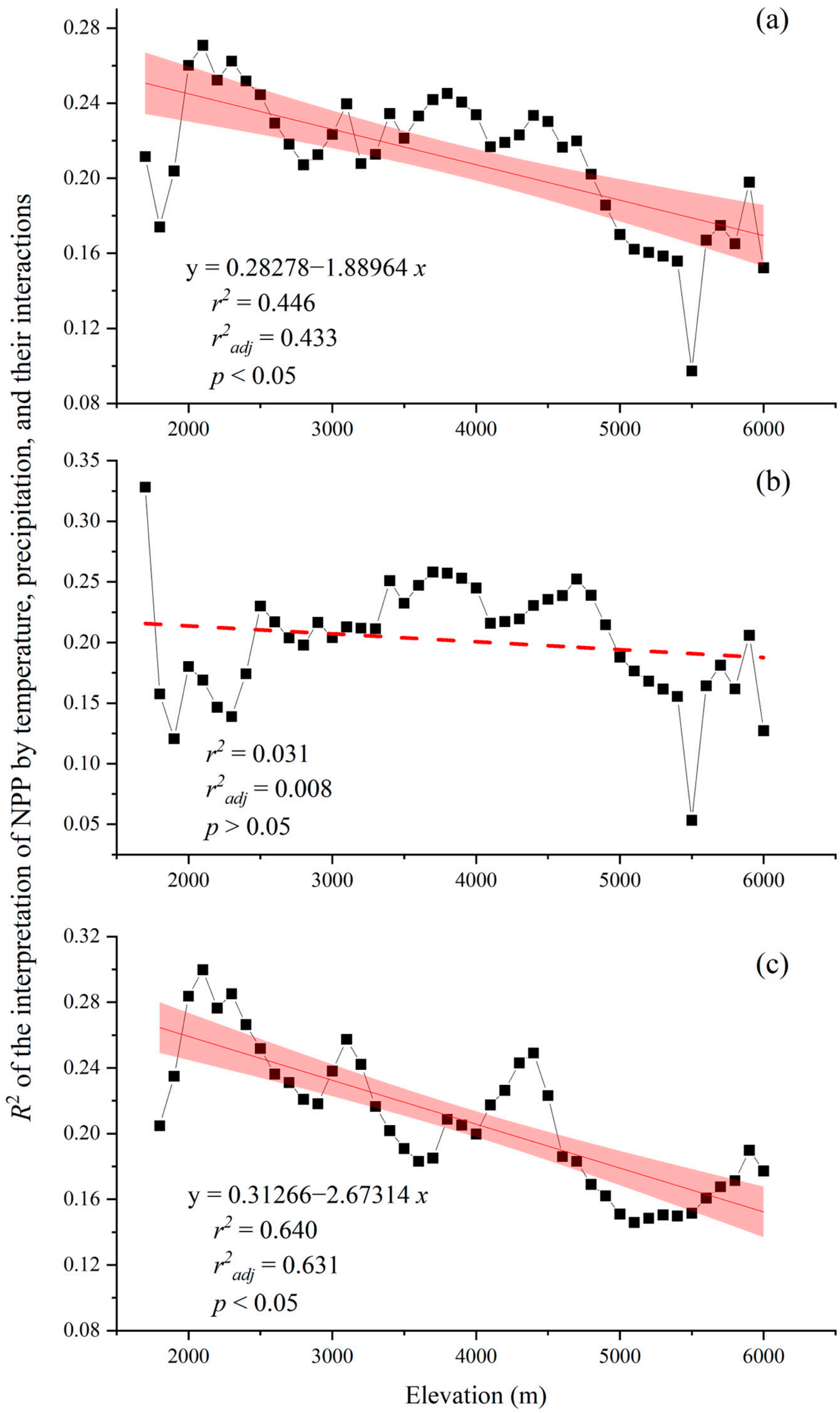

Figure 7. R^2 of the explanatory capacity for NPP of temperature, precipitation, and their interactions; NPP per 100 m interval of elevation (**a**) for the all the alpine grassland, (**b**) for all the alpine meadow, and (**c**) for all the alpine steppe. Note: Each point indicates the mean value of R^2 over a 100 m interval; The solid line indicates that the linear fit reaches the significance level, while the dashed line indicates that the linear fit does not reach the significance level; Shadows represent confidence bands with 95% confidence.

3.4. NPP Sensitivity in Response to Climate Change and Elevation

We conducted a partial correlation analysis of NPP_{slope} with $Temp_{slope}$, Pre_{slope}, and the DEM (Table 2). The results showed that $Temp_{slope}$, Pre_{slope}, and the DEM all significantly affected NPP_{slope}. Among them, NPP_{slope} was significantly positively correlated with

$Temp_{slope}$ and Pre_{slope}, while it was significantly negatively correlated with the DEM. The partial correlation coefficients between NPP_{slope} and $Temp_{slope}$ and between NPP_{slope} and Pre_{slope} were greater in alpine steppe than in alpine meadow, while the partial correlation coefficient between NPP_{slope} and the DEM was greater in alpine meadow.

Table 2. The partial correlation coefficients of NPP_{slope} with $Temp_{slope}$, Pre_{slope}, and the DEM.

	Alpine Grassland	Alpine Meadow	Alpine Steppe
Coefficient of partial correlation between NPP_{slope} and $Temp_{slope}$	0.266	0.182	0.262
Coefficient of partial correlation between NPP_{slope} and Pre_{slope}	0.221	0.118	0.208
Coefficient of partial correlation between NPP_{slope} and the DEM	−0.492	−0.608	−0.37

To verify the effects of elevation, temperature change, and precipitation change on the magnitude of NPP change, the SEM was used to explore the operation of these three factors on the magnitude of NPP change (Figure 8). The DEM ranked first in terms of influence (standard coefficient = −0.44, $p < 0.01$), as evidenced by a significant decrease in NPP_{slope} due to elevation gain. $Temp_{slope}$ ranked second (standard coefficient = 0.15, $p < 0.01$), as a greater trend of temperature enhanced the NPP_{slope}. Third, a greater trend of precipitation improved the NPP_{slope} (standard coefficient = 0.11, $p < 0.01$). The model indicated a smaller variability of NPP at higher elevations than at lower elevations for the same extent of temperature and precipitation change, implying that increasing elevation suppressed the sensitivity of NPP to temperature and precipitation, and that this suppression was stronger in alpine meadows than in alpine steppes.

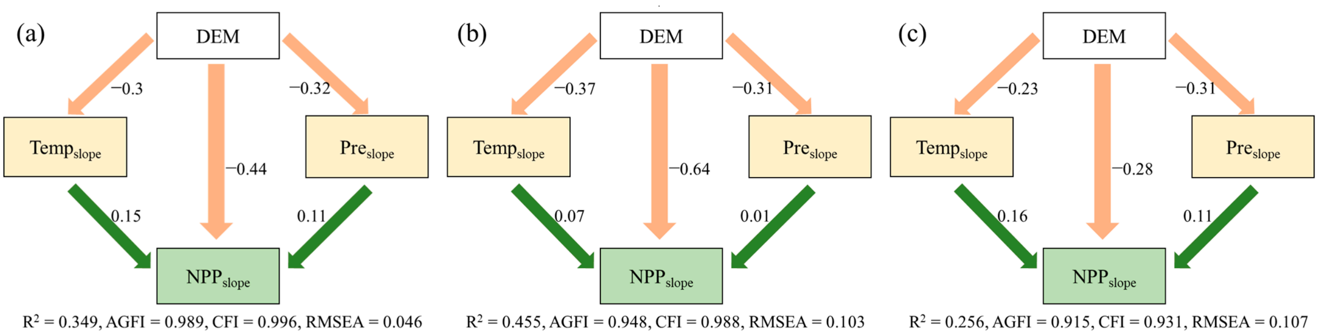

Figure 8. The effects of the DEM, $Temp_{slope}$, and Pre_{slope} on NPP_{slope} obtained using a structural equation model (SEM) (**a**) for all the alpine grassland, (**b**) for the alpine meadow, and (**c**) for the alpine steppe.

4. Discussion

4.1. Temporal and Spatial Patterns of NPP

NPP is an important characteristic of vegetation vigor and growth, and is susceptible to environmental impacts [20]. Influenced by zonal and other factors, the NPP of grasslands on the TP exhibited great elevational variability, i.e., increasing with elevation below 3400 m and decreasing with elevation above 3400 m. The difference between the mean values of grassland NPP according to elevation could reach more than 10 times, with the high values occurring in the eastern region. This may be due to a combination of vegetation types, climatic conditions, and human activities. The lower elevations of the TP are dominated by alpine meadows, and their productivity is significantly greater than that of alpine steppes distributed at higher elevations. As elevation increases, anthropogenic activities diminish, and disturbance to the grasslands decreases, resulting in an increase in grassland productivity. When the elevation exceeds the optimum height for vegetation growth, the climatic conditions gradually deteriorate to the point of being unsuitable for vegetation productivity [38]. The eastern TP is relatively low in elevation and located on the windward slopes of the Pacific monsoon, providing better thermal and hydrological conditions for vegetation growth [18,22], and thus is a high-value area for grassland NPP.

Over 90% of the grasslands on the TP experienced a positive trend in NPP over the past 22 years, with a mean value of 1.01 $gC/m^2/yr$, aligning with results from previous studies [29,39]. The large slopes were predominantly in the east of the plateau and coincided with the distribution of high values of temperature gains or precipitation gains (Figures S2 and S5). This implied a positive feedback of grassland vegetation vitality on climate change in the TP [40]. In terms of the elevation gradient, the positive trend of NPP ascended below 2500 m and declined above 2500 m with increasing elevation, which was associated mainly with the pattern of changes in temperature and precipitation. At low elevations, the increase of temperature in alpine meadows and the increase of precipitation in alpine steppes was enhanced with elevation (Figures S3 and S6), alleviating the limitations of temperature on meadow growth and water on steppe growth to support higher NPP_{slope} with elevation. Above 2500 m above sea level, the NPP_{slope} declined, although temperature and precipitation variations were still positive. On the one hand, the increase in temperature declined and the positive relationship between precipitation and NPP gradually weakened with elevation (Figure S7). On the other hand, the lower background values of temperature and precipitation above 2500 m weakened the activities of biological enzymes [41,42], and thus the NPP_{slope} declined with elevation. We also found that the positive trend of NPP was significantly higher in alpine meadows (1.16 $gC/m^2/yr$) than in alpine steppes (0.74 $gC/m^2/yr$) (Table S1). This was due to the fact that the average increase of temperature and precipitation in alpine meadows was 0.02 °C/yr and 6.23 mm/yr, respectively, whereas it was −0.01 °C/yr and 3.09 mm/yr, respectively, in alpine steppes during the last 22 years (Figures S2 and S5).

4.2. Driving Factors of NPP

Abiotic factors associated with temperature and precipitation are important factors affecting vegetation growth [43]. Numerous studies have revealed a significant positive correlation between temperature, precipitation, and NPP [20,44]. However, we found that NPP was only positively correlated with precipitation in no more than 50% of the grasslands in this study, but a positive correlation between temperature and NPP was found in more than 80% of the TP grasslands, implying that higher temperatures promote vegetation vigor, whereas increased precipitation inhibits vegetation growth at most sites on the plateau. This was because the areas with a negative correlation between precipitation and NPP were mainly located in the southeastern and northeastern TP (Figure 4), which are dominated by alpine meadows with abundant vegetation communities, sufficient precipitation, and high requirements for light conditions [45,46]. These regions also experienced the largest increase in precipitation (Figure S5), which inevitably led to a decrease in effective solar radiation [47,48], and consequently to a negative correlation between precipitation and NPP [49]. The negative correlation between temperature and NPP mainly occurred in the intermountain basins around Qinghai Lake, the suburban mountains of Lhasa, and the mountain valleys of the Brahmaputra River, where no significant changes in precipitation but significant changes in temperature were observed (Figures S2 and S5). An increase in temperature may limit vegetation growth due to water stress, while a decrease in temperature inhibits plant photosynthesis [50,51].

Our study suggested that climatic factors were not the main contributors to NPP variations in TP grasslands, with an R^2 of temperature, precipitation, and their interactions explaining NPP greater than 0.5 in less than 2% of the TP grasslands. Factors such as effective solar radiation, vegetation community characteristics, internal self-rhythms, and soil physicochemical properties may also affect grassland NPP [18]. In particular, we found a phenomenon rarely reported in previous studies, that the explanation of temperature, precipitation, and their interactions for NPP variation gradually decreased with increasing elevation (Figure 7). This may be due to the following reasons: (1) Vegetation at higher elevations is dominated by alpine steppes, and they tend to be more efficient with water use and able to maintain growth under arid conditions, which further weakens the aptness of precipitation in the interpretation of NPP in these areas [15,16]. (2) Temperature gradually decreases to near or below the physiological limit of vegetation growth with increasing elevation, and the explanatory capacity of temperature for NPP naturally weakens [6]. (3) Vegetation at higher elevation usually possesses strong adaptability to survive and reproduce under harsh climatic conditions. It relies more on its own physiological adaptive mechanisms to withstand harsh environments than on changes in temperature and precipitation alone. Such adaptability makes vegetation growth less dependent on a single climatic factor and thus reduces the explanatory power of temperature and precipitation on NPP [1,52]. (4) Vegetation growth is affected by a combination of environmental factors. At high elevations, climate factors such as wind speed, radiation, evaporation, etc., apart from temperature and precipitation, are highly variable and may also exert important influences on vegetation growth. Besides, soils in the alpine steppes are more infertile, and the lack of nutrients limits the positive response of alpine steppes to temperature and precipitation changes [31,39]. Compared with precipitation, temperature is the dominant influence on vegetation growth on the TP and mainly occurs at higher elevations, which is consistent with the findings of previous studies [53,54].

We further explored the relationship between the sensitivity of grassland NPP and elevation, temperature, and precipitation. The SEM indicated a promoting effect of elevated temperature and increased precipitation on NPP increase, yet the promotional effect diminished with elevation. This implies the conclusion that elevation inhibited the response of NPP to temperature and precipitation increases. On the one hand, higher temperature and increased precipitation promoted plant bioenzyme activity, lengthened plant season length, accelerated decomposition of organic matter in the soil, and facilitated plant growth [4,34,43]. On the other hand, elevation increase caused a rapid decrease in the environmental background values of temperature and precipitation, which counteracted the NPP increment promoted by increased temperature and precipitation. The lower elevations of the TP are mainly dominated by alpine meadows, where vegetation types are richer and more diverse, allowing the full use of different ecological niches for plant growth. When temperature and precipitation increase, the varied plants can jointly utilize these resources and optimize the use of resources through competition, symbiosis, and other ecological relationships, thus promoting NPP in the whole ecosystem [16,55]. In contrast, the vegetation communities at higher elevations are relatively simple and are dominated by cold- and drought-tolerant alpine native steppe plants. These plants have a narrower range of adaptation to environmental changes and are unable to fully utilize the resources through multiple ecological strategies when temperature and precipitation increase, resulting in a limited promotion of NPP [19,55]. The higher sensitivity of grassland NPP to temperature than to precipitation implied that grass growth on the TP was more susceptible to temperature regulation, which is consistent with findings that NPP on the TP is mainly temperature-limited [38,53]. Precipitation was generally lower at higher elevations on the TP (Figure S4), but it has increased more at higher elevations over the past 22 years (Figure S6), implying a greater mitigation of precipitation-induced inhibition of vegetation growth. Temperature increased less at higher elevations, and the inhibitory effect of temperature on vegetation growth was not well alleviated, resulting in temperature being the major constraint on plant growth. We also found a stronger effect of elevation on the sensitivity of NPP response to temperature and precipitation in alpine meadows than in alpine steppes. This is related to grassland distribution. Alpine meadows are distributed at lower elevations with better hydrothermal conditions. Elevation rise can cause rapid changes in environmental conditions (Figures S1 and S4), resulting in the rapid response of NPP changes to elevation. Alpine steppes are distributed at higher elevations, and the magnitude of change in hydrothermal conditions with elevation is smaller; hence, there is a smaller impact.

4.3. Uncertainties

Our study revealed the effects of temperature, precipitation, and their interactions on the variations of NPP in grasslands on the TP, as well as the impacts of changes in temperature, precipitation, and elevation on the sensitivity of grassland NPP. However, it is necessary to acknowledge the uncertainties of the study and therefore the limitations in the perception of the results. To reveal the influence of climatic factors on NPP, meteorological data for the period 2001–2022 were collected from 268 stations. However, these stations are mostly located in the eastern TP, and there is a lack of meteorological stations in the western plateau hinterland. Although the use of a DEM as a covariate eliminated the interpolation error of temperature and precipitation data to a certain extent, the uncertainty is difficult to eradicate due to the vastness of the Tibetan Plateau and the fact that there are other factors affecting climatic factors in addition to the topography. This created questionable authenticity of the interpolated meteorological data in the west. In addition, although previous studies have confirmed the high accuracy and applicability of MODIS NPP data in modeling grassland productivity on the TP, we did not undertake the step of validating the accuracy of the dataset used in this study due to the lack of measured data. The uncertainty in the accuracy of NPP data is somewhat detrimental to the subsequent conclusions about the relationship between NPP and temperature and precipitation. In addition, the SEM in this study well revealed relationships among multiple factors, but inevitably simplified the complex relationships between some of the factors into linear relationships. The SEM helped to identify the macroscopic patterns of vegetation–climate relationships on the TP, but the application of research results at local scales requires further analysis.

5. Conclusions

In this study, MODIS NPP data were combined with temperature and precipitation measurements from meteorological stations to reveal the spatial and temporal changes of grassland NPP on the Tibetan Plateau from 2001 to 2022, as well as to investigate the effects of temperature and precipitation on NPP variation and NPP sensitivity. From 2001 to 2022, the trend of grassland NPP on the TP varied spatially from -30.2 gC/m^2/yr to 15.8 gC/m^2/yr, with a mean value of 1.01 gC/m^2/yr. The trend of NPP was unimodal with elevation, and 91% of grassland exhibited an increase in NPP. Temperature and precipitation were not the main factors contributing to changes in grassland NPP, with their combined contribution to NPP change being 0–87% and significantly decreasing with elevation. It was also demonstrated that temperature was the dominant climatic factor for the variation of grassland NPP compared to precipitation. Temperature trend, precipitation trend, and elevation combined to influence NPP sensitivity, and elevation was the primary factor for the sensitivity of grassland NPP on the TP. In conclusion, our study contributes to a deeper understanding of the macro-spatial variations of alpine grassland NPP as influenced by climate, and supports site-specific policies for grassland management.

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