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RECEIVED 06 January 2023

ACCEPTED 17 May 2023

PUBLISHED 23 June 2023

CITATION

Wang Y, Zhang J, Shen X, Ma R, Liu Y, Wu L,
Tong S, Jiang M and Lu X (2023)
Spatiotemporal variation of marsh vegetation
productivity and climatic effects in Inner
Mongolia, China.
Front. Ecol. Evol. 11:1138965.
doi: 10.3389/fevo.2023.1138965

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Spatiotemporal variation of marsh vegetation productivity and climatic effects in Inner Mongolia, China

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Net primary productivity (NPP) is a vital ecological index that reflects the ecological function and carbon sequestration of marsh ecosystem. Inner Mongolia has a large area of marshes, which play a crucial role in the East Asian carbon cycle. Under the influence of climate change, the NPP of Inner Mongolian marsh has changed significantly in the past few decades, but the spatiotemporal variation in marsh vegetation NPP and how climate change affects marsh NPP remain unclear. This study explores, for the first time, the spatiotemporal variation of marsh NPP and its response to climatic change in Inner Mongolia based on the MODIS-NPP and climate datasets. We find that the long-term average annual NPP of marsh is 339.85 g·C/m² and the marsh NPP shows a significantly increasing trend (4.44 g·C/m²/a; $p < 0.01$) over Inner Mongolia during 2000–2020. Spatially, the most prominent increase trend of NPP is mainly distributed in the northeast of the region (Greater Khingan Mountains). The partial correlation results show that increasing autumn and summer precipitation can increase the NPP of marsh vegetation over Inner Mongolia. Regarding the temperature effects, we observe a strong asymmetric effect of maximum (T_{max}) and minimum (T_{min}) temperature on annual NPP. A high spring T_{max} can markedly increase marsh NPP in Inner Mongolia, whereas a high T_{min} can significantly reduce it. In contrast to spring temperature effects on NPP, a high summer T_{max} can decrease NPP, whereas a high T_{min} can increase it. Our results suggest different effects of seasonal climate conditions on marsh vegetation productivity and highlight the influences of day-time and night-time temperatures. This should be considered in simulating and predicting marsh carbon sequestration in global arid and semi-arid regions.

KEYWORDS

marsh, net primary productivity, climate change, vegetation, Inner Mongolia

1. Introduction

As an important ecosystem, wetlands is crucial in supporting biodiversity conservation, climate change regulation and global biogeochemical cycle (Zedler and Kercher, 2005; Fossey and Rousseau, 2016; Gunderson et al., 2016; Savickis et al., 2016; Dinsa and Gameda, 2019; Pasut et al., 2021; Yang et al., 2022). Marsh is a major type of wetlands ecosystem and significantly affects global carbon cycle (Aukes et al., 2021; Luk et al., 2021;

Smith and Kirwan, 2021; Shen et al., 2021a,b, 2022a,b; Wang Y. et al., 2021, 2022). Vegetation is a vital component part of the marsh ecosystems and plays a crucial role in regulating ecosystem carbon balance. Net primary productivity (hereinafter referred to as NPP) is defined as the residual level of dry organic matter produced by photosynthesis after subtracting autotrophic respiration (Field et al., 1995; Imhoff et al., 2004; Haberl et al., 2007; Mu et al., 2013; Zhao et al., 2019), which represents the strength of an ecosystem in terms of its carbon sequestration capacity (Imhoff et al., 2004; Haberl et al., 2007; Keppeler et al., 2021; Saderne et al., 2021). There are many factors that affect marsh productivity, with the climate being one of the most important (Bai et al., 2008; Liang et al., 2015; Hu et al., 2021; Cai et al., 2022; Coleman et al., 2022). Over the past decades, global or regional climate has changed significantly (Shen et al., 2018, 2022c), leading to a significant impact on marsh ecosystem productivity. At present, many researches have explored the influence of climate change on marsh NPP across different areas (Bian et al., 2010; Yang et al., 2020; Molino et al., 2022; Wang Y. et al., 2022), but the potential responses of marsh NPP to climate change are still unknown. In recent years, the area of natural marsh wetlands decreased significantly, and the ecological functions severely degraded (Fluet-Chouinard et al., 2015; Hu et al., 2017; Rietl et al., 2021; Shen et al., 2022a, 2021b). In the context of global change, realizing the productivity changes in marsh vegetation and their driving factors is of great importance for the management and protection of regional marsh ecosystem.

Inner Mongolia ranks third in the total area of marsh in China (Zheng et al., 2019). Most of the Inner Mongolia has an arid to semi-arid climate with a fragile ecological environment and is sensitive to global climate change. Because of climatic change and intensive human activities, the degradation rate of marshes has shown an increasing trend (Shen et al., 2019). Several studies have assessed the changes of marsh NPP and its response to climate change on Inner Mongolia vegetation NPP (Zhu et al., 2005; Zhao et al., 2019). For example, Zhao et al. (2019) investigated the spatiotemporal variations of NPP and its potential influencing factors in Inner Mongolia over 2000–2014. Wang Y. et al., 2021 simulated the spatiotemporal changes of aboveground biomass (AGB) in the grasslands of Inner Mongolian. Zhao et al. (2014) estimated grassland aboveground biomass based on NPP in the Xilingol grassland under different environmental conditions. Ma et al. (2022) explored the spatiotemporal change in NPP and its response to climate change in temperate grasslands of China. Chun et al. (2020) analyzed the impacts of climate variability on the Daihai wetland of central Inner Mongolia. However, most of the studies concentrated on variations of grassland NPP and its response to climate change (Long et al., 2010; Zhang et al., 2011; Han et al., 2015; Lin and Dugarsuren, 2015; Yuan et al., 2015; Chi et al., 2018; Zhao et al., 2019; Wang G. et al., 2021), and the effect of climate change on NPP in the Inner Mongolia marshes remains largely unknown. Some studies demonstrated that marsh wetland has a unique environment, and the responses of marsh NPP to climate changes were different from other ecosystems (Wang Y. et al., 2021, 2022). As climate change could have a distinct impact on marsh NPP for different vegetation types, it is necessary to explore the changes of marsh NPP and its response to climate change in the Inner Mongolia marshes. In addition, previous research has shown the asymmetric effects of day-time and night time temperatures on marsh productivity in Tibet Plateau (Wang Y.

et al., 2021). Specifically, warming day-time temperature does not significantly affect marsh productivity, whereas night-time warming can markedly improve the productivity of marshes (Wang Y. et al., 2021). Compared with the Tibetan Plateau, an obvious dry and warm season has been documented in the Inner Mongolia (Hu et al., 2015). However, whether the increases in nighttime and daytime temperatures have an asymmetric impact on NPP of marsh vegetation in Inner Mongolia is still unclear. In view of global asymmetric warming, we need to further assess the influences of night and day temperatures on the NPP of marsh vegetation in Inner Mongolia in seasons.

Using the MODIS NPP and climate datasets from 2000 to 2020, this research assessed the spatial and temporal variation of marsh NPP and its association with climate change in Inner Mongolia. The objective of this paper is to clarify the spatial and temporal variation of marsh NPP and its responses to climate change in Inner Mongolia. The findings contribute to the further understanding of the changes of marsh vegetation and the understanding of the basic biological processes of marsh vegetation in arid and semi-arid regions.

2. Materials and methods

2.1. Study area

Inner Mongolia is located in the northern frontier of China with a total area of approximately 118×10^4 km². This area is flat, with the Yinshan Mountains and Henan Mountains in the south and the Greater Khingan Mountains in the east (Zhao et al., 2019). The altitude of this region is 1,000–1,200 m. The climatic characteristics vary significantly, from east to west across the sub-humid region, temperate humid region, semi-arid region, arid region and extreme arid region. The combined effect of geographical location and climatic conditions makes the marsh vegetation distribution in Inner Mongolia showing obvious zonal characteristics (Hang et al., 2015). The major marsh vegetation types in Inner Mongolia include *Phragmites australis*, *Carex appendiculata*, *Typha laxmannii*, *Acorus calamus*, and *Bolboschoenus planiculmis* (Chuai et al., 2013; Miao et al., 2015).

2.2. Datasets and methods

This study used the MOD17A3-NPP data from 2000 to 2020, which had a spatial resolution of 500 m and were provided by the NASA. Two raster marsh maps covering the Inner Mongolia in 2000 and 2015 (Shen et al., 2021b) were employed to analyze the unchanged marshes. The marsh distribution data was provided by the National Earth System Science Data Center. The meteorological data were obtained by the China Meteorological Data Service Network, including monthly accumulated precipitation and average temperature datasets during 2000–2020. According to previous studies (Peng et al., 2013; Shen et al., 2018), this study used the maximum and the minimum temperatures to represent the daytime and nighttime temperatures, respectively. The spatial distribution of the observation dataset of 45 weather stations throughout Inner Mongolia is shown in Figure 1.

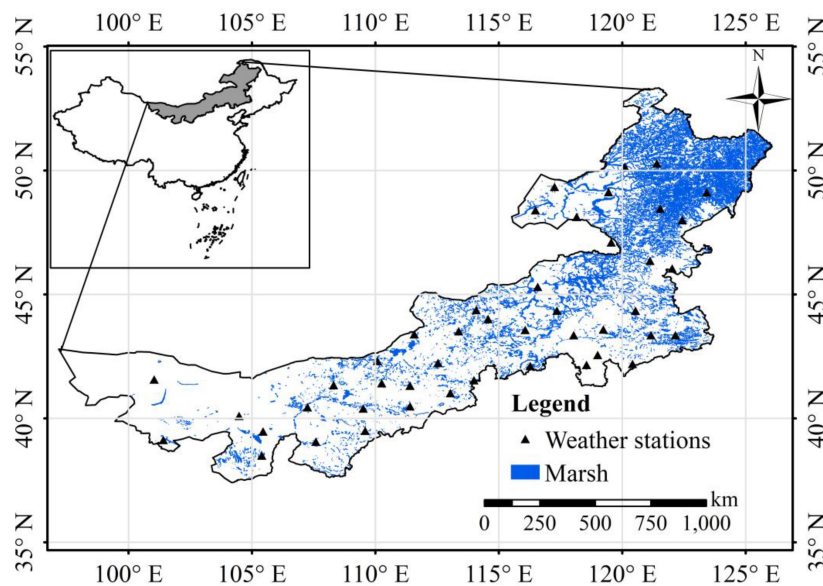


FIGURE 1
Marsh distributions and locations of the weather stations in Inner Mongolia.

2.3. Methods

The meteorological station data in Inner Mongolia were interpolated into the marsh distribution using the ordinary Kriging method (Shen et al., 2021b, 2022c,d). Subsequently, the data were resampled to a similar resolution as the NPP data. The mean value was corresponding mean values of all pixels in the marsh area of Inner Mongolia (Shen et al., 2022d). Partial correlation analysis was conducted to evaluate the relationship between annual NPP and meteorological variables (Piao et al., 2014; Guo et al., 2021). This method removes the influence of other related variables, so it can effectively evaluate the correlation between two variables (Wu et al., 2015; Li et al., 2021). The partial correlation coefficient ($R_{xy,z}$) is calculated as follows:

$$R_{xy,z} = \frac{R_{xy} - R_{xz} \times R_{yz}}{\sqrt{(1 - R_{xz}^2) \times (1 - R_{yz}^2)}}$$

where $R_{xy,z}$ is the partial correlation coefficient between x and y while removing the influence of z . R_{yz} , R_{xz} , and R_{xy} represent the partial correlation coefficients between y and z , x and z , and x and y , respectively. T -test was employed to demonstrate the statistical significance of the correlations.

3. Results

3.1. Spatial and temporal variations of NPP in the Inner Mongolia marshes

Spatial heterogeneity was observed for the temporal trend and long-term average of NPP in the Inner Mongolia marsh over the last 20 years (Figure 2). The long-term annual marsh NPP was about 339.85 g-C/m², increasing gradually from southwest

to northeast (Figure 3A). The region with higher marsh NPP was mainly in northeastern Inner Mongolia. Among them, about 41.74% of the average marsh NPP was greater than 400 g-C/m², and only 3.49% had an average of less than 100 g-C/m² (Figure 3A). With regard to temporal changes, although marshes in Inner Mongolia had undergone dramatic loss, the unchanged marsh NPP over the Inner Mongolia significantly increased by 4.44 g-C/m²/a ($p < 0.01$) between 2000 and 2020 (Figure 3B). Spatially, the most prominent increasing trend of NPP was observed in the northeast Inner Mongolia (Greater Khingan Mountains). On the contrary, a significant decline of marsh NPP was found in the southwest Inner Mongolia (Figure 3B).

3.2. Impact of climatic factors on marsh NPP in the study region

The partial correlation results demonstrated a significant positive correlation between annual NPP and annual precipitation, while a weak positive correlation between annual NPP and annual T_{mean} in Inner Mongolia (Table 1). Spatially, annual NPP was positively related to annual precipitation in most of the areas, and significant positive correlation was mostly distributed in the southeast Inner Mongolia regions (Figure 4A). A positive relationship between mean temperature and NPP was also found in the southeast Inner Mongolia regions (Figure 4B).

To further understand the potential effects of climate change on marsh NPP, partial correlation analysis was conducted between annual NPP and climate factors in different seasons (Table 1; Figures 5, 6). Table 1 shows that annual NPP was significantly positively correlated with summer and autumn precipitation ($p < 0.01$). For the effects of T_{max} and T_{min} on NPP, annual NPP had an inverse relationship with spring T_{max} and T_{min} . A positive correlation was found between annual NPP and spring

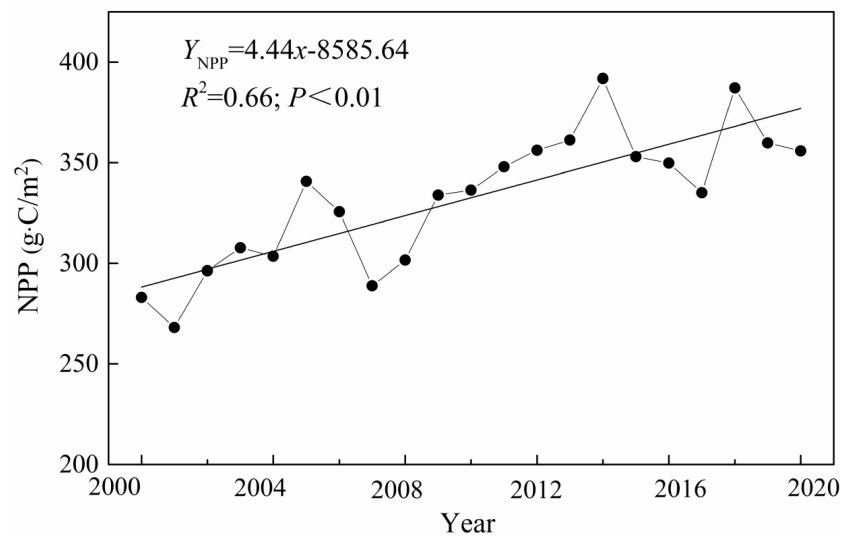


FIGURE 2 Temporal changes of marshes NPP in Inner Mongolia over 2000–2020.

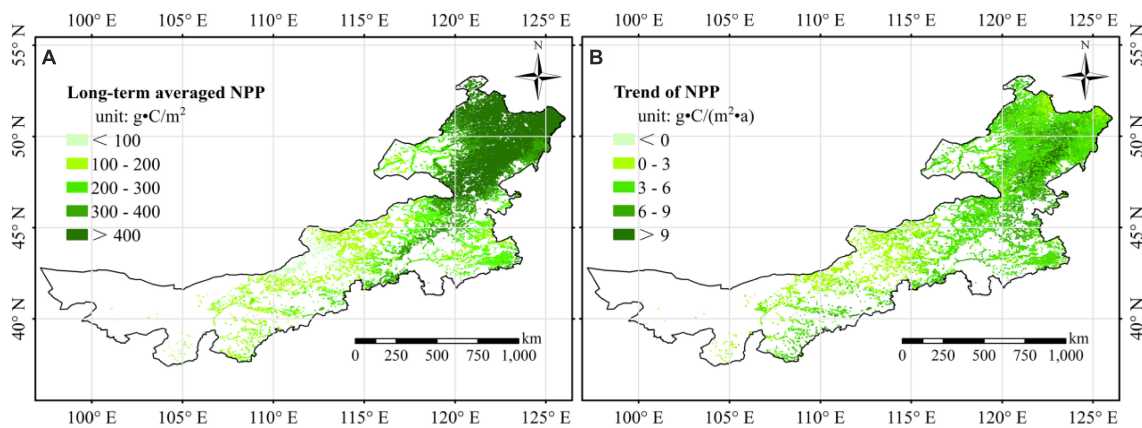


FIGURE 3 Spatial distributions of long-term average (A) and temporal trends (B) of NPP in Inner Mongolia marshes over 2000–2020.

TABLE 1 Partial correlations between NPP of marsh and seasonal climate variables (precipitation, T_{mean} , T_{max} , and T_{min}) in Inner Mongolia.

	Precipitation	T_{mean}	T_{max}	T_{min}
Annual	0.74**	0.03	0.16	-0.15
Spring	0.27	0.23	0.78**	-0.74**
Summer	0.62**	0.14	-0.27	0.36
Autumn	0.47*	0.23	0.22	-0.13
Winter	-0.04	-0.13	-0.15	0.14

Levels of significance are set at * $p < 0.05$ and ** $p < 0.01$.

T_{max} , whereas a negative correlation was detected between annual NPP and spring T_{min} (Table 1; Figure 5). Spatially, the positive association between productivity and T_{max} was mainly observed in the southwest Inner Mongolia regions (Figure 5C). It was found that the spatial correlation between annual productivity and summer T_{min} was moderately positive in the northeast Inner

Mongolia regions (Figure 6D). By contrast, the association between annual NPP and summer T_{max} was negative (Table 1; Figure 6C). Spatially, the asymmetrical effects of daytime and night-time on marsh NPP were mainly concentrated in the northeast Inner Mongolia regions (Figure 6).

4. Discussion

4.1. Change trend of marsh NPP in Inner Mongolia

During the last two decades, the long-term mean average of NPP was approximately 339.85 $g\cdot C/m^2$ (Figure 3A). The results were basically consistent with Zhu et al. (2005) who estimated that the annual NPP over Inner Mongolia marsh was approximately 376.8 $g\cdot C/m^2$. The average annual NPP over the Inner Mongolia

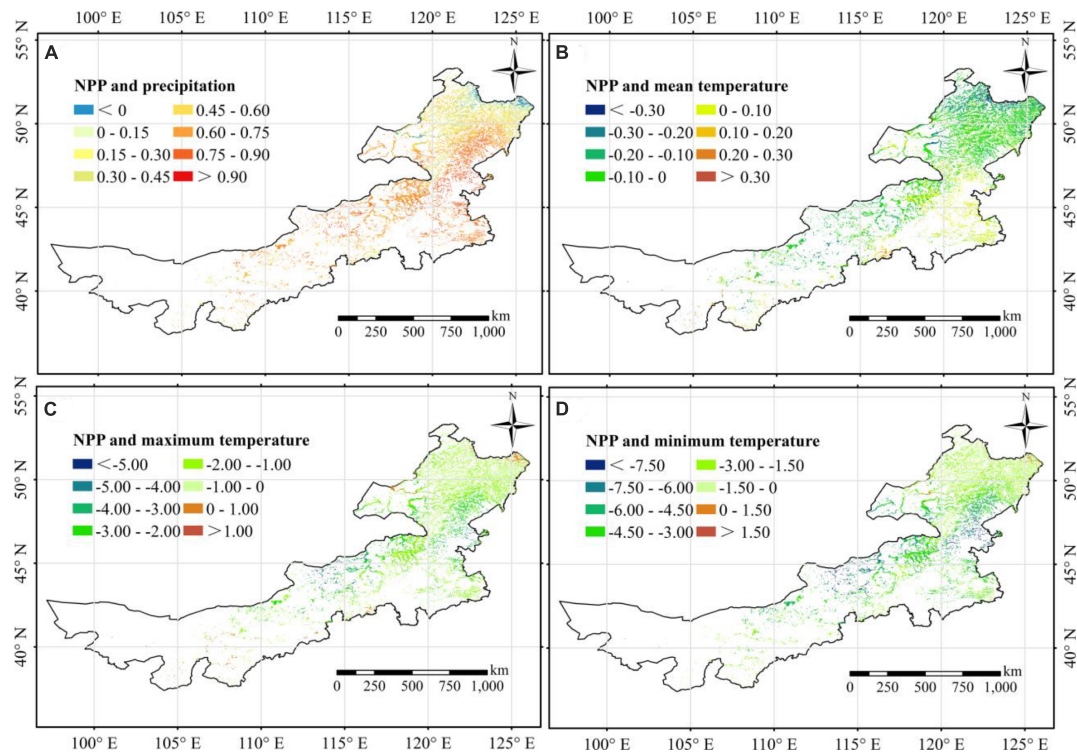


FIGURE 4 Spatial distributions of the partial correlation coefficients between annual NPP and annual meteorological variables [precipitation (A), mean (B), maximum (C), and minimum (D) temperatures] in the Inner Mongolia marshes during 2000–2020.

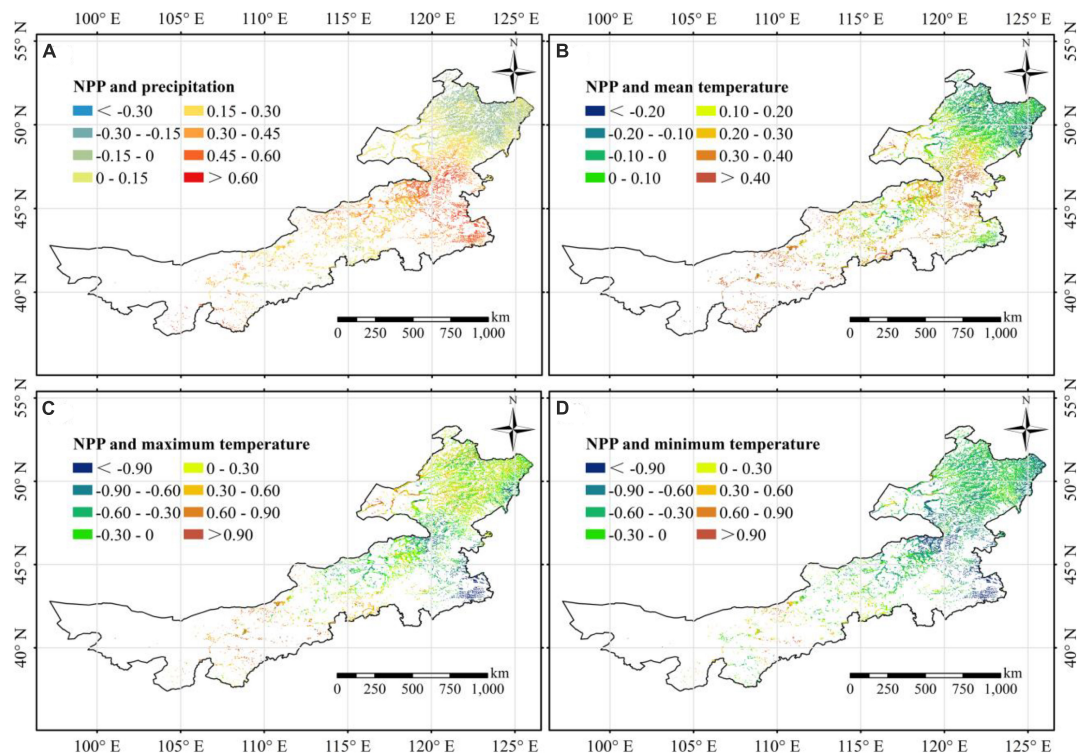


FIGURE 5 Spatial distributions of the partial correlation coefficients between annual NPP and spring meteorological variables [precipitation (A), mean (B), maximum (C), and minimum (D) temperatures] in the Inner Mongolia marshes during 2000–2020.

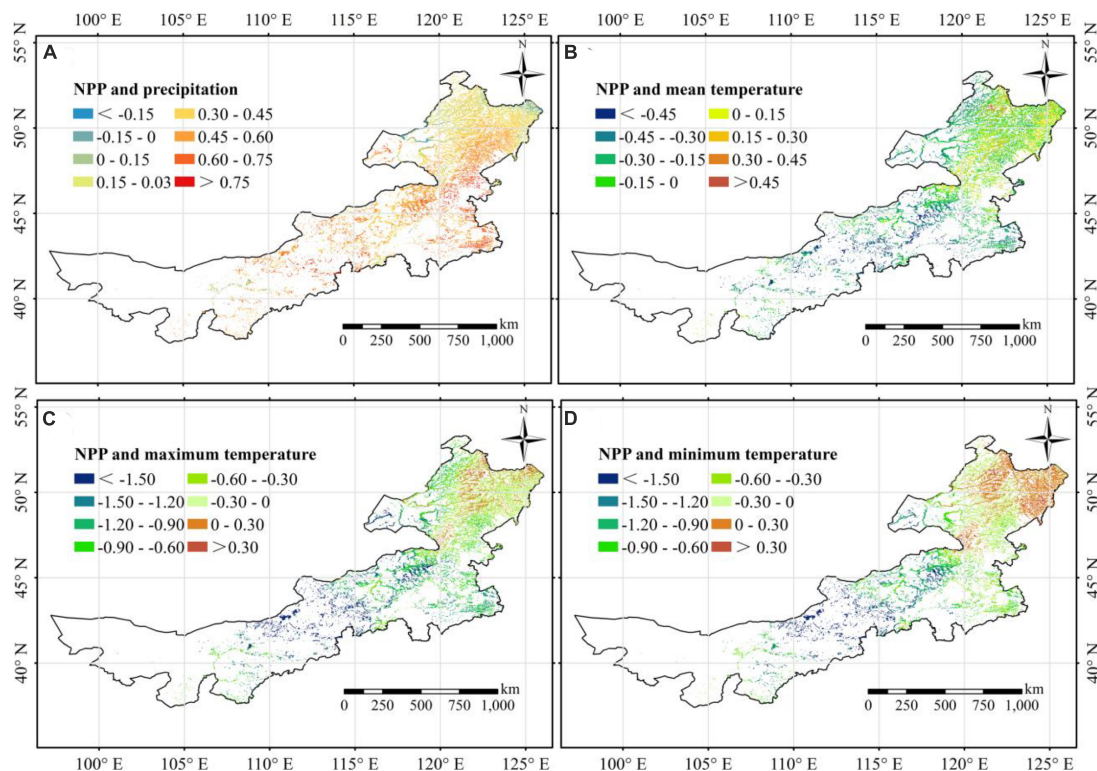


FIGURE 6 Spatial distributions of the partial correlation coefficients between annual NPP and summer meteorological variables [precipitation (A), mean (B), maximum (C), and minimum (D) temperatures] in the Inner Mongolia marshes during 2000–2020.

marshes increased significantly ($4.44 \text{ g}\cdot\text{C}/\text{m}^2/\text{a}$; $p < 0.01$) during the study period, confirming that the growth of marsh plants is getting better in China over the past 20 years (Shen et al., 2021b). Spatially, the highest long-term mean NPP was observed in the northeast Inner Mongolia regions (Figure 3A). The reason may be because that vegetation with high productivity tends to have a high capacity for productivity change caused by climate change (Shen et al., 2020; Wang Y. et al., 2022).

4.2. Factors affecting the vegetation NPP in Inner Mongolia marsh

To determine the responses of marsh vegetation NPP to climate change, the association between meteorological factors and NPP was investigated during 2000–2020. The partial correlation results demonstrated that annual NPP was significantly ($p < 0.05$) positively correlated with annual precipitation, while weakly ($p > 0.05$) positively correlated with T_{mean} in the Inner Mongolia marshes. This implies that increasing annual precipitation can enhance marsh vegetation growth over the Inner Mongolia marshes. Our results confirmed the conclusions of Shen et al. (2019) who have found that precipitation can significantly affect marsh vegetation growth in Inner Mongolia. As a crucial physical disturbance, precipitation can induce marsh vegetation growth in arid regions (Dunton et al., 2001). In different seasons, our findings showed that the increase in autumn and summer precipitation could increase NPP of marsh vegetation over Inner Mongolia

(Table 1; Figures 5, 6). Most of Inner Mongolia is relatively arid region, and the increased precipitation can improve the growth of marsh vegetation in Inner Mongolia by stimulating the carbon and water fluxes of the marsh ecosystem, thereby increasing the NPP of marshes (Shen et al., 2021b; Wang Y. et al., 2022). In summer, both temperature and evapotranspiration are the highest, and water demand for marsh vegetation growth is the largest. Therefore, the increase of summer precipitation can remarkably promote the NPP of marsh vegetation. However, it is noteworthy that the marsh distribution data employed in this work may include certain seasonal marsh. High precipitation can increase the distribution of marshes, which obviously increases the NPP of marshes within $500 \text{ m} \times 500 \text{ m}$ region. This could partially explain the positive impacts of precipitation on NPP over the Inner Mongolia marshes (Shen et al., 2021b, 2022b).

TABLE 2 Temporal variation trends of climate variables (precipitation, T_{mean} , T_{max} , and T_{min}) in the Inner Mongolia marshes from 2000 to 2020.

	Precipitation (mm/a)	T_{mean} ($^{\circ}\text{C}/\text{a}$)	T_{max} ($^{\circ}\text{C}/\text{a}$)	T_{min} ($^{\circ}\text{C}/\text{a}$)
Annual	7.01**	0.02	0.02	0.03
Spring	0.33	0.05	0.07	0.03
Summer	4.59*	-0.01	-0.04	0.03
Autumn	2.16*	0.02	-0.01	0.04
Winter	-0.06	0.05	0.05	0.04

Levels of significance are set at * $p < 0.05$ and ** $p < 0.01$.

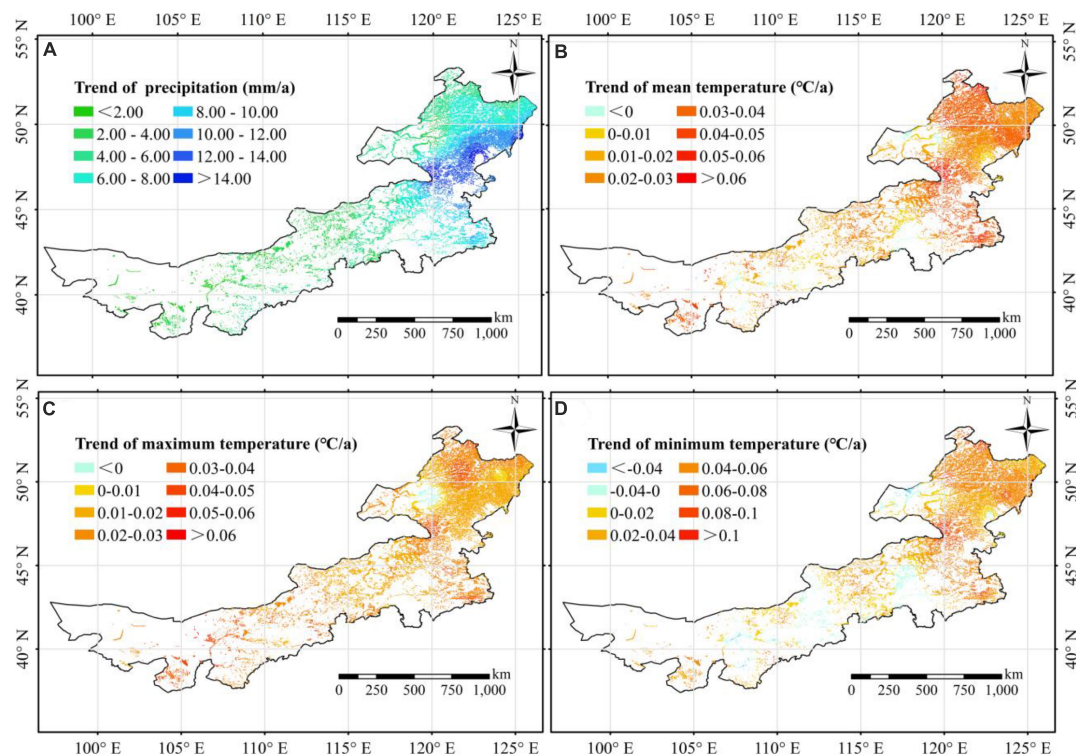


FIGURE 7

Change trends of annual climate variables [precipitation (A), mean (B), maximum (C), and minimum (D) temperatures] in the Inner Mongolia marshes from 2000 to 2020.

Regarding the temperature effects, we observed a strong asymmetric effect of spring T_{\max} and T_{\min} on annual NPP. A high spring T_{\max} could markedly increase marsh NPP, whereas a high T_{\min} could significantly reduce NPP in Inner Mongolia. This may be due to the fact that the warming day-time temperature in spring at the beginning of the growing season enhances the photosynthesis of plants to produce more organic matter, thereby facilitating the growth of marshes and increasing the NPP (Xu and Zhou, 2005; Sun and Mu, 2018). In spring, an increase in T_{\min} at night can lead to the consumption of more organic matter by respiration (Wang and Han, 2005). This will adversely affect the growth of marsh vegetation and reduce the NPP. In contrast to spring temperature effects on NPP, we found that a high summer T_{\max} could decrease NPP, whereas a high T_{\min} could increase NPP (Table 1). The negative effect of summer T_{\max} on NPP may be attributed to the highest temperature in summer. The continuous accumulation of high temperatures can aggravate soil water evaporation and reduce water consumption in the arid area (Xu and Zhou, 2005; De Boeck et al., 2006). Marsh plants consume more organic matter because of their better respiration rates at night. Hence, they can generate a larger amount of organic matter by promoting and compensating for photosynthesis in the next few days, leading to an improved plant growth (Wang Y. et al., 2022). It has been reported that the plants with adequate supplies of water and nutrients can exert high compensation or overcompensation effect (Belsky, 1986; Shen et al., 2021b). In summer, the Inner Mongolia marshes have good hydrothermal conditions and sufficient nutrition, which is the best period for their overcompensation effect (Li et al., 2018; Park et al., 2019; Wang et al., 2019). Thus, an increase in summer T_{\min} at night

can promote the growth of marsh plants via compensation effects, in which the plants produce more food than their consumption during respiration due to night warming. Such mechanism partially explains the positive association between NPP and summer T_{\min} in Inner Mongolia.

To understand the change of NPP in the Inner Mongolia marshes, the spatiotemporal alterations of meteorological factors in Inner Mongolia over 2000–2020 were analyzed (Table 2; Figures 7–9). The results showed that annual precipitation was significantly increased (7.014 mm/a) during 2000–2020, which reached an extremely significant level ($p < 0.01$). The annual temperature (including T_{mean} , T_{\max} , and T_{\min}) in most areas of Inner Mongolia showed an obvious increasing trend (Figure 7). In different seasons, the precipitation in summer and autumn exhibited obvious increasing trends (4.593 and 2.157 mm/a, respectively) (Figures 8, 9). According to the partial correlation data, an increase in autumn and summer precipitation may interpretation the increased vegetation NPP of the Inner Mongolia marsh. By contrast, an increase in spring T_{\max} may explain the increased NPP of vegetation NPP in the Inner Mongolia marsh. For spatial NPP changes, the most prominent increasing trend of NPP was mainly distributed in the northeast Inner Mongolia regions. It was found that spring T_{\max} and summer precipitation significantly increased in the northeast Inner Mongolia marshes (Figures 8, 9). Considering that summer precipitation and spring T_{\max} were significantly correlated with annual NPP in the northeast Inner Mongolia regions (Figure 4), it can be inferred that the increases in summer precipitation and spring temperature are indicative of marsh NPP elevation in this region.

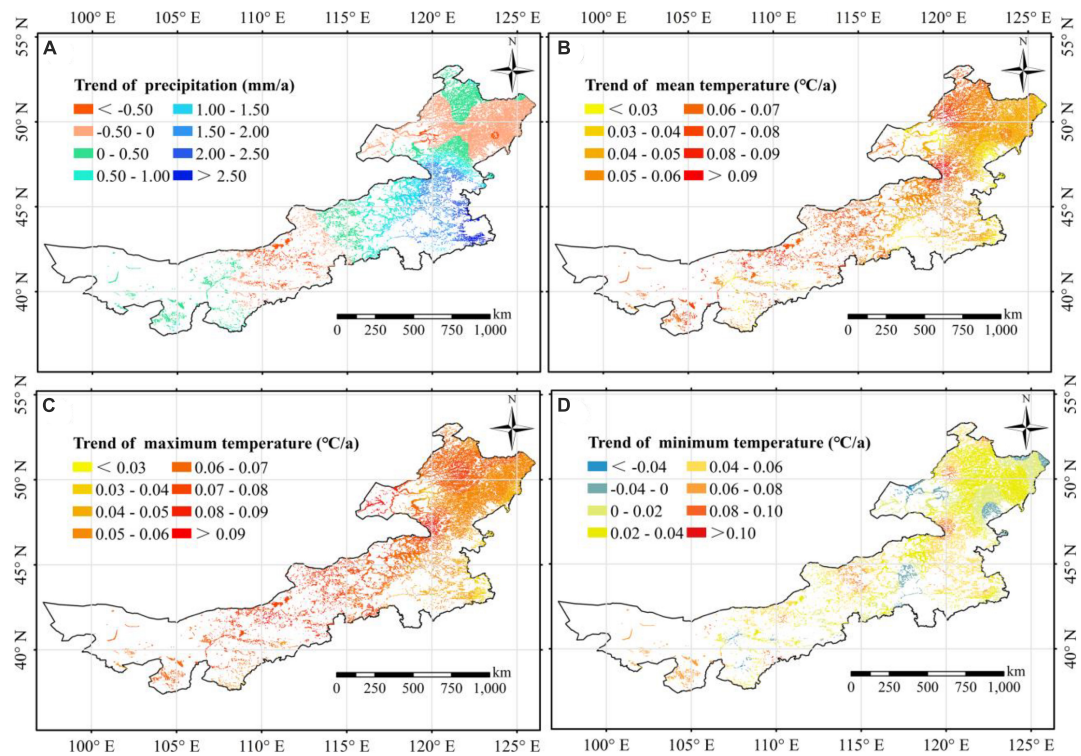


FIGURE 8
Change trends of spring climate variables [precipitation (A), mean (B), maximum (C), and minimum (D) temperatures] in Inner Mongolia from 2000 to 2020.

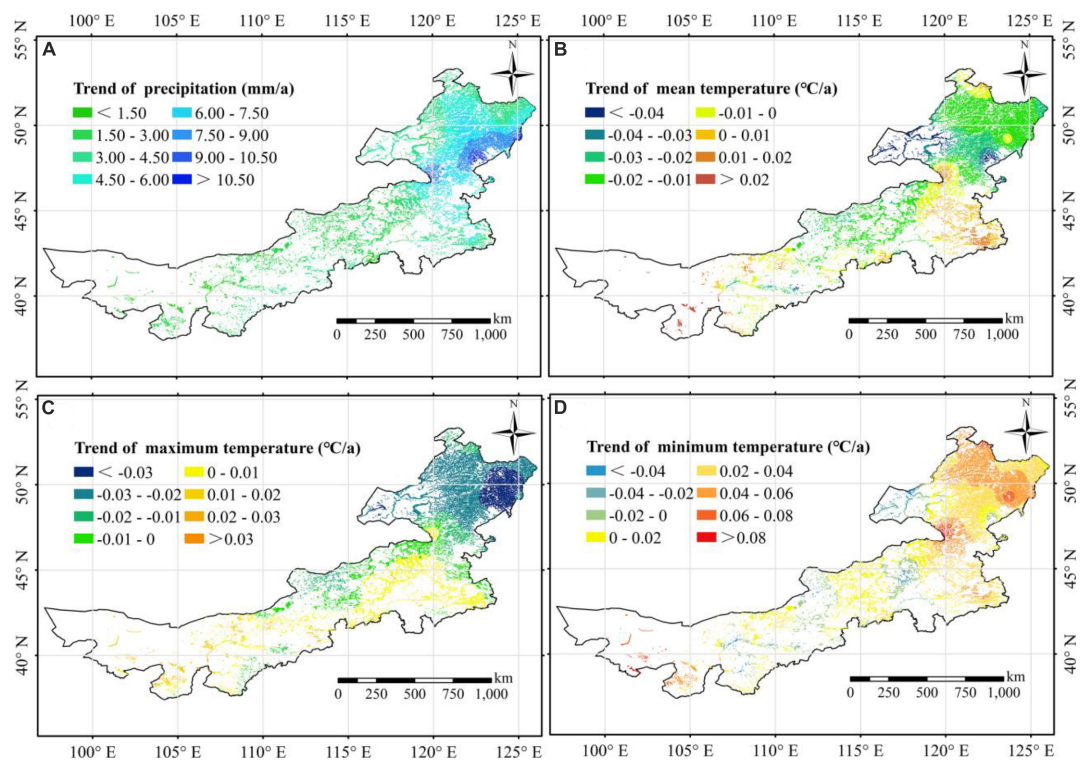


FIGURE 9
Change trends of summer climate variables [precipitation (A), mean (B), maximum (C), and minimum (D) temperatures] in Inner Mongolia from 2000 to 2020.

4.3. Uncertainty of this study

The limitations of this study should also be noted. First, the accuracy of marsh distribution data was relatively low, owing to the uncertainty in satellite remote sensing data. Second, the actual status of marsh vegetation in 500 m × 500 m regions could not be accurately reflected by the NPP data due to relatively low spatial resolution. Third, the marsh data used in this research might include seasonal marsh wetlands, possibly affecting the change in NPP and its response to climate factors. More accurate remote sensing and measured NPP data should be used to further confirm the results of this study. Finally, some other environmental factors and human activities, such as grazing and land-use change, could also affect vegetation productivity dynamics. Although unchanged marshes have been retrieved to eliminate the impact of human activities, the effects of human activities (such as grazing, farmland, etc.) may not be completely excluded. To further explore the mechanism of NPP changes in the Inner Mongolia marshes, further studies are needed to determine the effects of human activities and other environmental factors on marsh NPP in Inner Mongolia.

5. Conclusion

Based on the MODIS-NPP and climate datasets, this study explored the spatiotemporal variations of NPP and its influential factors in Inner Mongolia during 2000–2020. The results demonstrated that the NPP of Inner Mongolia marsh had a significantly increasing trend ($4.44 \text{ g-C/m}^2/\text{a}$; $p < 0.01$) between 2000 and 2020. The long-term annual mean NPP of marsh was about 339.85 g-C/m^2 . The most prominent increasing trend of NPP was found in the northeast Inner Mongolia (Greater Khingan Mountains). In terms of climate impacts, increases in spring and autumn precipitation could significantly increase marsh NPP in Inner Mongolia. We observed a strong asymmetric effect of T_{\max} and T_{\min} on annual NPP. Notably, a high spring T_{\max} could markedly increase marsh NPP, whereas a high T_{\min} could significantly reduce NPP in Inner Mongolia. In autumn, nighttime warming could moderately decrease NPP, while daytime warming could moderately increase the annual NPP of vegetation marsh in Inner Mongolia. In contrast to spring temperature effects on NPP, we found that a high summer T_{\max} could decrease NPP, whereas a high T_{\min} could increase NPP. This study highlights the different effects of seasonal climate conditions on marsh vegetation productivity and suggests that the influences of day-time and night-time temperatures should be considered in simulating and predicting marsh carbon sequestration in global arid and semi-arid regions, especially under the background of diurnal asymmetric warming.

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Data availability statement

The original contributions presented in this study are included in the article/supplementary material, further inquiries can be directed to the corresponding authors.

Author contributions

YW, JZ, XS, RM, YL, and LW: data curation and writing—original draft. XS: methodology and writing—review and editing. ST and MJ: supervision. ST: visualization and investigation. XL: conceptualization and methodology. All authors contributed to the article and approved the submitted version.

Funding

This work was funded by the National Natural Science Foundation of China (41971065), the Youth Innovation Promotion Association, CAS (2019235), the Natural Science Foundation of Jilin Province (20210101104JC), the Key Research Program of Frontier Sciences, CAS (ZDBS-LY-7019), the Innovation Team Project of Northeast Institute of Geography and Agroecology, CAS (2022CXTD02), the Key S&T Special Projects in Jilin Province (20230303005SF), and the Strategic Priority Research Program of the Chinese Academy of China (XDA23060402).

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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