Spatiotemporal evolution of net ecosystem productivity and the driving mechanisms in Horqin Sandy Land, China (postprint)

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Abstract

Vegetation in terrestrial ecosystems functions as a major carbon sink and is a critical component in mitigating global warming and achieving carbon neutrality targets; however, the drivers of net ecosystem productivity (NEP) under the combined influence of anthropogenic and environmental pressures remain insufficiently understood. In this study, we examined the spatiotemporal dynamics of NEP in the Horqin Sandy Land, China, from 2000 to 2020, and investigated NEP variations across different land-use types. We further identified and quantified the effects of human activities, topographic features, climatic conditions, and soil properties on NEP by applying structural equation modeling (SEM) and boosted regression trees (BRT). The results showed that the multi-year average NEP in the Horqin Sandy Land ranged from -137.79 to 461.96 g C/m^2, with 88.21% of the area exhibiting a significantly increasing trend. Among the different land-use types, forest land had the highest NEP values, followed by cropland, grassland, impervious surfaces, and unused land. In carbon sink areas, NEP was primarily regulated by potential evapotranspiration (negative correlation) and precipitation (positive correlation), whereas slope was identified as the most important positive determinant in carbon source areas. Forest land exhibited climate-topography interactions as the dominant drivers of NEP, while cropland and grassland were predominantly influenced by temperature; unused land and impervious surfaces were more susceptible to land-use/land-cover change and human footprint. These findings have important implications for sustaining carbon sink functions and for guiding ecological engineering programs aimed at enhancing terrestrial carbon sink capacity in semi-arid agro-pastoral ecotones.

Full Text

Preamble

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Spatiotemporal Evolution of Net Ecosystem Productivity and the Driving Mechanisms in Horqin Sandy Land, China

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Abstract: Vegetation in terrestrial ecosystems as a carbon sink is a crucial factor in mitigating global warming and reaching carbon neutrality targets, although the drivers of net ecosystem productivity (NEP) under combined human and environmental pressures remain poorly understood. In this study, we analyzed the spatiotemporal evolution of NEP in the Horqin Sandy Land, China from 2000 to 2020, and observed the variation in NEP across different land use types. We further identified and quantified the effects of human activities, topographical features, climatic conditions, and soil properties on NEP through the application of structural equation modeling (SEM) and boosted regression trees (BRT). The results showed that the multi-year average NEP ranged from -137.79 to 461.96 g C/m^2 in the Horqin Sandy Land, with 88.21% of the area showing a significant increasing trend. Among different land use types, forestland exhibited the highest NEP values, followed by cropland, grassland, impervious land, and unused land. The NEP in carbon sink areas was primarily regulated by potential evapotranspiration (negatively correlated) and precipitation (positively correlated). Slope was identified as the most significant positive determinant in carbon source areas. Forestland exhibited climate-topography interactions driving NEP, whereas cropland and grassland relied on temperature; unused land and impervious land were susceptible to land use/cover change and human footprint. This study has significant implications for maintaining the carbon sink function and promoting ecological engineering programs that aim to enhance the capacity of terrestrial carbon sinks in the semi-arid agro-pastoral ecotone.

Keywords: net ecosystem productivity (NEP); land use/cover change (LUCC); carbon sink; climate change; human activities; structural equation modeling (SEM); semi-arid agro-pastoral ecotone

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1 Introduction

Carbon sinks, defined as processes, activities, or mechanisms that can absorb and store carbon from the atmosphere, encompass forests, oceans, and other natural ecosystems. Notably, carbon sinks perform crucial functions in mitigating global warming and reaching carbon neutrality targets (Qiu et al., 2023; Jia et al., 2024). According to the worldwide carbon program, the proportion of CO_2 absorbed by terrestrial ecosystems between 2010 and 2019 accounted for 31.00% of total human emissions (Piao et al., 2022). Terrestrial ecosystems are capable of absorbing CO_2 through the natural process of photosynthesis, thereby effectively combating global warming (Sun et al., 2022; Nzabarinda et al., 2025). Net ecosystem productivity (NEP) indicates the net difference in an ecosystem between carbon fixation through photosynthesis and carbon loss through plant respiration (Dong et al., 2024). The value of NEP indicates the net state of carbon accumulation in ecosystems, and measuring this parameter is essential for assessing whether ecosystems can effectively absorb and store carbon (Guo et al., 2024). Further exploration of the carbon sink function enhances our understanding of the carbon cycle, leading to improved carbon storage capacity and optimal ecosystem management and conservation measures (Li et al., 2024a; Wei et al., 2024). The mechanisms that form carbon sinks (e.g., forests or recovering grasslands) and carbon sources (e.g., degraded grasslands or intensively cultivated croplands) reflect distinct equilibrium states in ecosystem carbon cycling. Identifying their differential driving factors can reveal the critical regulatory mechanisms of both anthropogenic disturbances and natural processes toward the carbon cycle balance, thereby providing a theoretical foundation for targeted ecological restoration projects.

In recent years, the dynamics of NEP and its driving mechanisms have been the subject of intensive research. NEP has experienced a significant improvement in China, and this phenomenon is not only strongly linked to changes in both precipitation and temperature (Wang et al., 2022; Qu et al., 2024) but also to fluctuations in solar radiation (Teng et al., 2024). Altitude (Chen et al., 2016; Li et al., 2017) and soil (Gielen et al., 2013; Tang et al., 2021) are equally important in determining the variation in NEP in addition to the effects of climate. Huang et al. (2023) demonstrated that the increase in atmospheric CO_2 concentration and vegetation changes also contribute to the growth in NEP in China, and the altered vegetation appears to be a critical driving factor behind NEP increase. Current research on the driving mechanisms of NEP primarily focuses on the isolated effects of individual environmental factors while overlooking complex, multifactorial synergistic interactions. However, the dynamics of NEP are not governed by a single dominant factor, but emerge from the coordinated regulation of multiple factors across different dimensions that exhibit intricate interrelationships (Wu et al., 2025). Therefore, a comprehensive assessment of the multifaceted combined effects would provide a more realistic representation of the coupled mechanisms among multiple driving factors in natural ecosystems, effectively overcoming the limitations inherent in single-factor analyses.

Certainly, NEP in different ecosystems is affected by a variety of factors that vary across ecosystems. For example, in cropland ecosystems, NEP is extremely sensitive to climate fluctuations, and the impacts of these fluctuations on crop growth vary widely across regions (Dold et al., 2017; Li et al., 2020a). In subtropical forests, temperature is a key environmental factor in young forests, significantly influencing the carbon sequestration capacity of trees, while in middle-aged and mature forests, precipitation is the dominant factor (Mao et al., 2022). Zhang et al. (2014) found that NEP is a function of the grassland type and several environmental factors in a northern temperate grassland with significant capacity for carbon sequestration; in particular, extreme climate phenomena can significantly reduce the net carbon sink. Between 1990 and 2019, China's urbanization increased dramatically in 31 provincial capitals, which negatively impacted the NEP of vegetation in developed land (Wang et al., 2024b). These studies demonstrated that various types of ecosystems exhibit marked differences in their responses to environmental changes. Different ecosystems possess distinct vegetation structures, soil carbon pool characteristics, and microclimatic conditions, resulting in significant differences in their responses to climate fluctuations, anthropogenic disturbances, and soil properties (Liang and Hurteau, 2023; Heim et al., 2025; Johnson et al., 2025). Clarifying these differences is crucial for developing more accurate models of the ecosystem carbon cycle and improving the reliability of regional-to-global carbon sink assessments. However, significant gaps remain in current research, with most studies focusing on single ecosystem types. The lack of comparative analyses across different ecosystems hinders the identification of the universality and specificity of driving mechanisms.

Structural equation modeling (SEM) has been widely applied in ecological research owing to its systematic advantages in analyzing multifaceted interactions, making it an essential analytical tool (Ren et al., 2025; Zhang et al., 2025a). This approach is especially suitable for ecosystems, such as the Horqin Sandy Land in China, which is experiencing the combined stress of environmental factors and human activities. In such contexts, SEM, which can effectively distinguish between direct and indirect effects and thus overcome the limitations of conventional statistical approaches, is particularly valuable (Zhu et al., 2025). Notably, studies employing SEM remain scarce in this ecologically vulnerable region.

The Horqin Sandy Land, as a typical agro-pastoral ecotone in northern China, represents a fragile ecological zone (Lian et al., 2017; Yuan et al., 2023). Its desertification has resulted from the synergistic effects of human activities, climate change, and vulnerable ecological conditions (Yang et al., 2023). First, the region is located in a semi-arid to arid transition zone, and its unique geographical position makes it highly sensitive to climate variability (Kang et al., 2022). Second, its inherent ecological vulnerability stems from its distinctive transitional characteristics: it lies at the margin of the East-Asian monsoon, experiencing high variation and uneven seasonal distribution in precipitation (Yao et al., 2013; Liu et al., 2016). The region' s sandy soils have a loose structure with poor water and nutrient retention (Niu et al., 2025), and the native vegetation exhibits a relatively simple ecosystem structure (Zuo et al., 2009; Zhao and Feng, 2019). These inherent weaknesses in the climate-soil-vegetation system result in a limited capacity to buffer against external disturbances. The inherent ecological fragility, compounded by anthropogenic disturbances, such as population growth, cropland expansion, and other unsustainable land-use practices, has further accelerated the desertification (Li et al., 2020b). This has led to a marked decline in ecosystem productivity and intensified sand mobilization, rendering the region a critical priority for desertification control in northern China. Consequently, continuous monitoring of this area, along with a comprehensive analysis of the spatiotemporal patterns and governing factors of NEP in desertified regions, is essential for developing sound and effective mitigation strategies.

Focusing on the Horqin Sandy Land, this study aimed to: (1) investigate the spatiotemporal variation in NEP and land use/cover change (LUCC) between 2000 and 2020; and (2) identify the underlying mechanisms regulating NEP in the Horqin Sandy Land and across different land use types based on SEM and boosted regression trees (BRT). The results will have implications for management strategies across diverse ecosystems to enhance ecosystem resilience and ensure the sustainable delivery of ecological services.

2.1 Study Area

The Horqin Sandy Land (117°49′-123°09′E, 41°41′-46°09′N) is situated in the eastern part of Inner Mongolia Autonomous Region, China. The region shows higher elevation in the northwest and a gradual decrease towards the southeast (Fig. 1a [Figure 1: see original paper]). Precipitation in the region decreases from northwest to southeast, ranging from 300.00 to 600.00 mm (Fig. S1). The average annual potential evapotranspiration (PET) ranges from 700.77 to 1042.03 mm, while the average annual temperature varies from -0.26°C to 9.00°C (Fig. S1). The Horqin Sandy Land, characterized by fragile ecosystem with low vegetation cover (Figs. 1b and S2), serves as a crucial ecological transition zone in China (Chen et al., 2024a; Zhang et al., 2025b).

2.2 Data Sources

The net primary productivity (NPP) datasets spanning from 2000 to 2020 were obtained from the MOD17A3 product released by the National Aeronautics and Space Administration. These data are commonly used in fields such as ecology and environmental science (Lyu et al., 2023; Shi et al., 2025). The data were converted using the Moderate Resolution Imaging Spectroradiometer (MODIS) reprojection software for splicing and projection transformation. After removing the outliers, the valid values were multiplied by a conversion coefficient to attain the final NPP data.

In this study, the climate variables of temperature, PET, and precipitation were accurate to approximately 1 km (0.0083333°). The data were obtained from the

National Tibetan Plateau Data Centre (https://www.tpdc.ac.cn/). The topographical variables were derived from a 90-m resolution digital elevation model (DEM) obtained through the Shuttle Radar Topography Mission (SRTM). Slope and aspect parameters were subsequently calculated from this DEM dataset. Soil properties, including pH, total phosphorus (TP), total nitrogen (TN), total potassium (TK), and soil organic matter (SOM), were acquired from the China dataset of soil properties for land surface modeling (with spatial resolution of 30 arc-seconds) published by the National Tibetan Plateau Data Centre (https://www.tpdc.ac.cn/). This dataset was developed based on the soil survey data from the second national soil survey of China, incorporating a 1:1,000,000 soil map and nationwide soil profile measurements.

Human activity data comprised gross domestic product (GDP), LUCC, and human footprint (HFP) data. The HFP data were acquired from the annual Global Human Footprint dataset (https://github.com/HaoweiGis/humanFootprintMapping/), which features a 1-km spatial resolution. This composite index quantifies anthropogenic pressures on natural ecosystems by integrating eight critical dimensions: built environment, cropland, pasture, nighttime lights, roads, population density, railways, and navigable waterways. The LUCC data were based on the land-use transfer matrix calculated from the first 30-m annual land cover product in China, generated using Landsat data (https://doi.org/10.5281/zenodo.4417810). The 1-km resolution GDP data were acquired from the Centre for Resources and Environmental Sciences (https://www.resdc.cn/).

To ensure compatibility for subsequent computations, we uniformly resampled all data to a 1-km grid.

2.3.1 Assessment of Carbon Sequestration

NEP is a prominent indicator of the net accumulation of carbon in ecosystems over time (Hou et al., 2024; Pow et al., 2024). A NEP value greater than zero indicates that the ecosystem acts as a carbon sink, serving as a net absorber of atmospheric CO_2. When NEP is less than zero, the ecosystem acts as a carbon source, representing a net releaser of CO_2 into the atmosphere. NEP (g C/m^2) was calculated by subtracting the soil heterotrophic respiration consumption (Rh; g C/m^2) of heterotrophic organisms (e.g., soil microorganisms) in the ecosystem from NPP (g C/m^2):

$$\mathrm{NEP} = \mathrm{NPP} - \mathrm{Rh}$$

The Rh was calculated using the exponential equation proposed by Pei et al. (2009) that established the relationship among temperature, precipitation, and soil carbon emissions. This approach has been extensively applied and verified in ecosystem studies across arid and semi-arid areas of China (Shi et al., 2024; Zhi et al., 2024), demonstrating particular suitability for assessing NEP. The calculation formula is as follows:

$$\mathrm{Rh} = 0.22 \times \exp(0.0913 \times \mathrm{TEM}) \times \ln(0.3145 \times \mathrm{PRE} + 1)$$

where TEM indicates the average monthly temperature (°C); and PRE denotes the monthly precipitation (mm).

2.3.2 Trend Analysis of NEP

The Theil-Sen median trend and the Mann-Kendall test are extensively employed non-parametric approaches in analyzing time series data (Xiao et al., 2024; Feng et al., 2025). Theil-Sen estimation is primarily used to estimate the magnitude and direction of the trend, while the Mann-Kendall test is employed to detect the existence of a trend and determine statistical significance. These statistics are often used together to provide a comprehensive analysis of trends within time series data. The calculation formula is as follows:

$$\beta = \mathrm{Median}\left(\frac{\mathrm{NEP}_j - \mathrm{NEP}_i}{j - i}\right), \quad \forall i < j$$

where β denotes the Sen' s slope (g C/(m^2 · a)); and NEP (g C/m^2) and NEP (g C/m^2) denote the NEP in years m and n, respectively.

$$S = \sum_{i=1}^{K-1} \sum_{j=i+1}^{K} \mathrm{sgn}(\mathrm{NEP}_j - \mathrm{NEP}_i)$$

$$\mathrm{var}(S) = \frac{K(K-1)(2K+5)}{18}$$

$$Z = \begin{cases} \frac{S-1}{\sqrt{\mathrm{var}(S)}} & \text{if } S > 0 \\ 0 & \text{if } S = 0 \\ \frac{S+1}{\sqrt{\mathrm{var}(S)}} & \text{if } S < 0 \end{cases}$$

where Z is the standardized test statistic; S is the test statistic; var(S) is the variance of S; K represents the length of the year; and NEP and NEP denote the NEP in years j and i, respectively.

A value of |Z| > 1.96 indicates a significant trend in NEP at the 0.05 significance level (Table 1).

2.3.3 BRT

We employed the BRT to assess the relative importance ranking of different factors, including climate, soil, topography, and human activities. This analysis is on the basis of a categorical regression tree algorithm and represents an integrated self-learning method with the ability to adapt to complex non-linear relationships (Nosetto et al., 2024; Wang et al., 2024a). BRT is widely used in fields such as environmental sciences and ecology (De' ath 2007; Shabani et al., 2020; Ren et al., 2024). During the construction of the BRT model, 70.00% of the data was allocated for the model's training phase, and the remaining 30.00% for the validation phase, with the entire model undergoing 10-fold cross-validation to ensure its robustness. Model uncertainty was reduced by optimizing four core parameters of tree complexity, bag fraction, the number of decision trees, and the learning rate. All statistical analyses were performed with the 'gbm' and 'caret' packages in the R 4.4.0 statistical software.

2.3.4 SEM

As a method for studying causality, SEM focuses on exploring the complex relationships between variables (He et al., 2024; Li et al., 2024b), especially how latent variables affect the observable dependent variables (Fan et al., 2016). Our aim was to quantify the effect of key drivers on NEP between 2000 and 2020. In SEM, path coefficients represent the direct relationship between two variables, indicating the direct effect of one variable on the other. Furthermore, when multiple factors interact to affect NEP, we can determine the indirect effect by multiplying the path coefficients in the relevant pathways. We therefore consider that a single direct pathway as well as the aggregated impacts of all possible indirect pathways can obtain a comprehensive assessment of the effects. This combined consideration of direct and indirect effects facilitates a deeper understanding of how various factors interact to influence NEP.

We first selected climate, soil, topography, and human activities as latent influencing factors, while other relevant factors were used as observed factors. Then, we constructed a preliminary SEM aimed at exploring the main factors affecting NEP, adjusted and optimized the model using the 'PiecewiseSEM' package in R 4.4.0, and assessed the validity of the model using Fisher' s C test. If the associated P-value lies between 0.050 and 1.000, and the ratio of the model' s Fisher' s C statistic to the degree of freedom (df) falls within the range of 0–2, this suggests that the model is suitable for the data. Once the model was acceptable, we constructed the final SEM based on these criteria for subsequent analyses.

3.1 Characteristics of the Variation in NEP

The spatial distribution of NEP indicated that higher values occurred in the marginal areas, while lower values were observed in the central areas, and the multi-year average NEP ranged from -137.79 to 461.96 g C/m^2 (Fig. 2 [Figure

2: see original paper]). The trend analysis showed that 88.21% of the total area demonstrated a significant increase in NEP. Regions with a significant decrease accounted for only 0.09% of the study area. In particular, the northeastern and southwestern regions exhibited the highest increases in NEP, while in regions with the steepest declines in NEP, the trends were nonsignificant. The long-term trend analysis revealed that the overall growth rate of NEP was 4.76 g C/($m^2 \cdot a$).

The results demonstrated that all land use types had a significant upward trend in NEP, with distinct variation in growth rates during 2000–2020 (Fig. 3 [Figure 3: see original paper]). Specifically, forestland exhibited the highest rate of NEP growth (6.15 g C/($m^2 \cdot a$)), significantly higher than cropland (4.94 g C/($m^2 \cdot a$)), grassland (4.70 g C/($m^2 \cdot a$)), impervious land (4.73 g C/($m^2 \cdot a$)), and unused land (3.47 g C/($m^2 \cdot a$)).

Analyses of NEP showed that the NEP values for forestland (194.83 g C/m^2) were higher than those of cropland (58.50 g C/m^2), grassland (62.69 g C/m^2), and impervious land (35.93 g C/m^2) (Fig. S3). The unused land had the lowest NEP values (-60.34 g C/m^2), indicating its characteristics as a carbon source. Approximately 12.17% of the cropland areas exhibited no significant change or a decreasing trend in NEP and were primarily located in the northwestern region. Similarly, approximately 10.66% of the grassland areas exhibited the same characteristics and were concentrated in the southeastern region. In particular, 96.20% of the forestland areas showed a significant increasing trend and were located in the northern region. Areas with the NEP showing a significant decrease accounted for 0.19% for impervious land and 0.04% for unused land.

3.2 LUCC

Figure 4a [Figure 4: see original paper] illustrates the variation in land use area for each type from 2000 to 2020 in the study area, where the dominant land use types were grassland and cropland. In 2020, these two land use types comprised 62,257 and 47,544 km^2, accounting for 49.54% and 37.83%, respectively. The smallest areas among land use types were water body and impervious land, with respective areas of 8266 and 3399 km^2, representing 0.23% and 2.70%. The areas of forestland and impervious land had been continuously increasing. The conversion area from cropland to grassland primarily occurred in the northern region, while the conversion from grassland to cropland was concentrated in the southern region (Fig. 4b). The area shifting from unused land to grassland predominantly occurred in the southwestern region.

The land use transfer matrix was based on land use in 2000 and 2020 (Table 2 ; Fig. S2), highlighting the conversion between cropland and grassland during 2000–2020. During this period, a total of 27,880 km^2 of land was converted in terms of land use type. Most land use conversions occurred in cropland (11,938 km^2) and grassland (12,387 km^2). Cropland was primarily converted to grassland (10,999 km^2) and impervious land (606 km^2). Grassland was primarily converted to cropland (9868 km^2) and unused land (1060 km^2).

3.3 Relative Contributions of Factors Influencing NEP

The BRT method was employed to identify and quantify the key drivers influencing NEP (Fig. 5 [Figure 5: see original paper]). The model demonstrated strong predictive performance, with R^2 values of 0.89 and 0.58 for carbon sink and source areas, respectively. The NEP in carbon sink areas was primarily driven by climatic factors (relative contribution of 82.86%), with temperature being the most influential factor (53.79%). The NEP in the carbon source areas was dominated by topographical factors (32.12%), with DEM accounting for the largest proportion (25.13%).

The BRT showed good performance, with R^2 values of 0.75 for cropland, 0.86 for forestland, 0.91 for grassland, 0.70 for unused land, and 0.59 for impervious land (Fig. 6 [Figure 6: see original paper]). Climate consistently dominated the NEP in forestland, cropland, and grassland, with contributions of 74.15%, 58.01%, and 80.29%, respectively. Among these, temperature and PET made the highest relative contributions. In contrast, for unused land and impervious land, NEP was affected by human activities (relative contributions of 38.62% and 33.13%, respectively), climate, and topography, but the differences in their impacts were minimal. GDP and HFP were more important drivers in human activities compared to LUCC, while precipitation and DEM were the most important climatic and topographical factors, respectively.

3.4 SEM for NEP Variation

This study analyzed the driving mechanisms of NEP based on the SEM for carbon sink/source areas and various land use types to identify the indirect and direct effects of driving factors on NEP (Fig. 7 [Figure 7: see original paper]; Table S1). We excluded all nonsignificant factors. In carbon sink areas, climate was a significant factor influencing NEP. PET and precipitation had significant effects on NEP, with respective coefficients of -0.87 and 0.15. In carbon source areas, the positive impact of topography on NEP was largely due to slope, with respective coefficient of 0.37. However, DEM had a significant negative effect on NEP, with coefficient of -0.43.

NEP for each land use type was significantly associated with climate, soil, topography, and human activities (Fig. 8 [Figure 8: see original paper]; Table S1). In cropland, climate was the dominant factor affecting NEP (total effect coefficient of 0.48), with temperature (coefficient of -0.54) exhibiting a significant negative correlation with NEP, while precipitation (coefficient of 0.31) had a positive effect on NEP. The total effect coefficient of topography on NEP was 0.22, less than those of climate (0.48) and human activities (0.32). HFP was a significant factor in human activities, and it had a significant positive effect on NEP (coefficient of 0.25). In forestland, climate had the greatest impact on NEP, with PET (coefficient of -0.86) and precipitation (coefficient of -0.16) serving as good indicators of climate. Topography and human activities primarily influenced the NEP through indirect pathways, with total effect coefficients of 0.66 and 0.43, respectively. The impact of soil on NEP was minimal compared to other environmental factors. In grassland, NEP was positively affected by precipitation (coefficient of 0.15) and negatively affected by temperature (coefficient of -0.91). Among topographical factors, DEM exerted a positive impact on NEP, and this was primarily an indirect effect (0.48). The significant indirect effect (0.55) of human activities was more prominent compared to the direct effect (-0.14). For unused land, human activities had the greatest impact on NEP (total effect coefficient of 0.53), followed by topography (0.31), climate (0.15), and soil (0.12). Human activity factors all had positive impact on NEP, with LUCC being the most influential (coefficient of 0.40). For impervious land, HFP had a significant positive effect on NEP. The total effect coefficients of climate, topography, and soil on NEP were 0.14, 0.18, and 0.13, respectively.

4.1 Spatiotemporal Dynamics of NEP in the Horqin Sandy Land

The present study analyzed the interannual variation in NEP, yielding a growth rate of 4.76 g C/($m^2 \cdot a$) (Fig. 2). The Theil-Sen and Mann-Kendall trend analysis also revealed significant changes in NEP during 2000–2020, with a significant increase in 88.21% of the study area. Moreover, our findings are consistent with the results of Wang et al. (2022) in northern arid regions of China, Lyu et al. (2023) in the Weihe River Basin of China, and Huang et al. (2024) in northern China. These studies demonstrated that the carbon sinks in the respective ecosystems are enhanced, while the carbon stocks in these areas show an increasing trend. The 21-a average NEP ranged from -137.79 to 461.96 g C/m^2, with carbon sink areas accounting for 81.17% (Fig. 2). The Horqin Sandy Land was primarily characterized as a carbon sink, but its carbon sequestration capacity remained relatively low. Zhang et al. (2023) also found that NEP in China is dominated by carbon sinks. Liu et al. (2023) demonstrated that the carbon sink capacity of arid zones is relatively weak. Vegetation development in semi-arid areas has been limited by hydrothermal conditions, resulting in a relatively limited carbon sink function (Liang et al., 2023).

4.2 Drivers of Carbon Sink Capacity in the Horqin Sandy Land

Climate change has been shown to have profound effects on carbon sequestration in semi-arid areas, primarily through variation in temperature (Zhou et al., 2018; Chuai et al., 2022) and water availability (Yang et al., 2016; Ghimire et al., 2022). The results showed that NEP in the carbon sink areas is primarily driven by climate (Fig. 7a). PET and precipitation were the key factors influencing NEP in these areas. These findings are consistent with previous studies conducted in arid and semi-arid areas (Lü et al., 2011; Tariq et al., 2024), underscoring the pivotal role of water availability in regulating carbon stocks. Our study in the carbon source areas demonstrated that the topographical factor (DEM) constitutes the primary driver of spatial variation in NEP (Fig. 7b). This finding corroborates previous studies that topography, rather than climate, predominantly governs spatial patterns of carbon storage (Swetnam et al., 2017). Compared to other variables, topography exhibited superior explanatory power for the variation in NEP through its regulation of local hydrothermal redistribution, soil nutrient distribution, and vegetation patterns (Kong et al., 2023; Mishra et al., 2024). Specifically, low-lying depressions exhibited enhanced NEP due to the accumulation of water, whereas high-DEM regions tend to act as stronger carbon sources due to water limitation and intense evaporation.

The Horqin Sandy Land has a remarkable diversity of land use types, dominated by cropland, grassland, and forestland, as well as unused land and impervious land, all of which were influenced by different factors (Fig. 8). Previous studies demonstrated that both temperature and precipitation are primary regulators of the variation in NEP in cropland and grassland (Du and Liu, 2013; Li et al., 2017; Wu et al., 2021; Niu et al., 2022). Consistent with previous studies, our results confirmed that both temperature and precipitation are primary drivers of NEP variability in cropland and grassland ecosystems (Fig. 8a and e). More importantly, this study supports previous conclusions regarding the dominant role of temperature, demonstrating that temperature exerts a stronger influence on NEP dynamics than precipitation, primarily as an inhibitory factor (Wu et al., 2021). Existing research on the sensitivity of semi-arid ecosystems to climate warming found that temperature increases can reduce carbon sink capacity by enhancing respiration and inducing water stress (Stein et al., 2021; Moreira et al., 2023).

In forestland ecosystems, climate has long been recognized as a key driver of carbon dynamics (Hubau et al., 2020; Wang et al., 2021). However, some studies have suggested that topographical factors may exert a more pronounced influence on carbon sequestration than climatic factors (Swetnam et al., 2017). Topography directly regulates local climatic conditions by modifying temperature gradients and redistributing precipitation (Chen et al., 2024b; Rao et al., 2024). For example, in the karst region of southwestern China (Luo et al., 2024) and semi-arid forests in western United States (Adams et al., 2014), the variation in DEM at micro-topographic scales plays a key regulatory role in forest carbon sink function. Interestingly, our findings revealed that in the Horqin Sandy Land, topographical factor (DEM) and climatic factor (PET) exhibit nearly equal and synergistic effects on NEP (Fig. 8c). This phenomenon may be attributed to the unique micro-environmental patterns resulting from the overlapping distribution of topographic gradients and climatic zones in the Horqin Sandy Land, an area that serves as a characteristic ecotone. These results indicated that the interaction between topographical features and regional climatic conditions collectively constrains or enhances carbon uptake, rather than either factor dominating the process. This finding highlights the importance of considering both topographical and climatic factors when evaluating forest carbon sequestration in transitional ecoregions, such as the Horqin Sandy Land.

This study revealed the driving mechanisms of NEP in two distinct ecosystem types: unused land and impervious land. Human activities had a positive effect on NEP in unused land, with LUCC being the dominant factor (Fig. 8g). In long-neglected unused land, human-induced LUCC, particularly grassland restoration rather than afforestation, significantly enhanced NEP. This strategic selection simultaneously addressed moisture constraints in semi-arid areas (where woody vegetation aggravates water stress) while enhancing regional carbon sequestration through increased vegetation coverage (Xiao et al., 2024). For impervious land, the results indicated a positive influence of HFP on NEP (Fig. 8i). While extensive research has suggested that human activities typically reduce regional carbon storage capacity (Chen et al., 2022; Wang et al., 2022), our study revealed a contrasting pattern. This phenomenon may be attributed to well-planned, developed areas (e.g., optimized green space allocation) that have improved the local microclimates and generated a net positive effect (Li et al., 2021; Tao et al., 2023). These two findings collectively demonstrated that semi-arid ecosystems require specific management approaches, where enhancing carbon sequestration necessitates addressing climatic constraints (e.g., prioritizing grassland systems) and implementing regulation of human activities (e.g., ecological design in construction), moving beyond the simple application of humid-region models. Within ecological carrying capacity thresholds, adaptive land management can achieve both carbon sequestration and ecological restoration.

Based on the present findings, we proposed a set of differentiated carbon sequestration management strategies integrating the "nature-based precision management" concept. For forestland ecosystems, afforestation projects should be prioritized in mid-elevation areas with lower PET while avoiding low-lying waterlogged areas. For precipitation-dependent cropland and grassland, drought-resistant varieties (e.g., drought-tolerant maize) and rotational grazing systems should be promoted to mitigate the increased evapotranspiration caused by rising temperatures. The conversion of unused land should be strictly regulated, with priority given to restoration by natural vegetation and incorporation into the "ecological conservation redlines" regulatory system. For impervious land, a "green space ratio quota" policy combined with vertical greening measures is recommended to offset losses caused by HFP. These spatially explicit management strategies can not only enhance regional carbon sequestration resilience but also balance the dual objectives of ecological conservation and economic development.

4.3 Limitations and Prospects

The present study examined the complex causal relationship between NEP and its drivers, considering the combined effects of the natural environment and human activities, and provided new perspectives on variations in NEP. Despite the benefits of using the relationship between NPP and NEP, some uncertainties and limitations remain. Although temperature and precipitation are important factors influencing soil heterotrophic respiration, they do not fully represent all the factors affecting soil heterotrophic respiration. For example, other factors such as CO_2 concentration, variation in soil organic carbon, and the complexity of ecosystem structure can also impact soil heterotrophic respiration, leading to uncertainty in estimates of carbon sequestration capacity. Therefore, subsequent studies should consider these deficiencies to provide a more comprehensive assessment of NEP.

5 Conclusions

The present study examined the spatiotemporal evolution of NEP in the Horqin Sandy Land and explored the effects of various drivers on NEP, both direct and indirect, from the perspectives of carbon sinks/sources and land use types. It was found that NEP in the Horqin Sandy Land has significantly increased from 2000 to 2020. The areas experiencing a significant increase in NEP (88.21% of the study area) were considerably larger than those with a reduction or no significant change. The NEP in carbon sink areas was primarily regulated by PET (with a negative correlation) and precipitation (with a positive correlation). The central part of the Horqin Sandy Land was the most concentrated area for carbon sources, and the topographical factor of slope was identified as the most significant positive determinant. In forestland, the variation in NEP was predominantly regulated by the synergistic effects of PET (negative) and DEM (positive). Temperature, the dominant climate driver, negatively influenced NEP in both cropland and grassland. In impervious and unused lands, HFP and LUCC were the primary human activity factors enhancing NEP. These findings advance our understanding of carbon cycling in semi-arid ecosystems and provide actionable insights for land-use optimization, particularly the need for elevation-stratified forest management, water-conservation agricultural practices in precipitation-dependent systems, and regulation of human activities in vulnerable areas.

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

Conceptualization: ZHANG Huayong; Methodology: XU Xiaona, ZHANG Huayong; Formal analysis: XU Xiaona; Writing - original draft preparation: XU Xiaona; Writing - review and editing: XU Xiaona, ZHANG Huayong; Funding acquisition: ZHANG Huayong; Resources: ZHANG Huayong; Supervision: ZHANG Huayong. All authors approved the manuscript.

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Appendix

Fig. S1 Spatial distribution of multi-year average temperature (a), precipitation (b), and potential evapotranspiration (PET; c) in the Horqin Sandy Land during 2000–2020

Fig. S2 Land use distribution of the Horqin Sandy Land in 2005 (a), 2010 (b), 2015 (c), and 2020 (d)

Fig. S3 Violin plots of multi-year average net ecosystem productivity (NEP) across different land use types in the Horqin Sandy Land during 2000–2020. The violin shape outlines the probability density of the data. The small square inside the box indicates the mean value, while the upper and lower boundaries of the box correspond to the 25th and 75th percentiles, respectively. The box extends lines to 1.5 times the interquartile range.

Table S1 Detailed structural equation modeling (SEM) calculations (significant paths only) for the net ecosystem productivity (NEP) in carbon sink areas, carbon source areas, cropland, forestland, grassland, unused land, and impervious land

Area/Type	Effect Type	Pathway	Effect Coefficient
Carbon sink areas	Direct effect	NEP~Climate	–
	Direct effect	NEP~Soil	–
	Direct effect	NEP~Topography	–

Area/Type	Effect Type	Pathway	Effect Coefficient
	Direct effect	NEP~Human activities	–
	Indirect effect	Climate→Soil→NEP	
	Indirect effect	Topography→Climate→NEP	
	Indirect effect	Topography→Climate→Soil→NEP	
	Indirect effect	Topography→Soil→NEP	
	Indirect effect	Human activities→Climate→NEP	–
	Indirect effect	Human activities→Climate→Soil→NEP	–
	Indirect effect	Human activities→Topography→NEP	–
	Indirect effect	Human activities→Topography→Climate→NEP	–
	Indirect effect	Human activities→Topography→Climate→Soil→NEP	–
	Indirect effect	Human activities→Topography→Soil→NEP	–
Carbon source areas	Direct effect	NEP~Soil	–
	Direct effect	NEP~	

Note: Figure translations are in progress. See original paper for figures.

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