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RESEARCH ARTICLE

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Effect paths of environmental factors and community attributes on aboveground net primary productivity of a temperate grassland

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Abstract

Aboveground net primary productivity (ANPP) of grassland influenced by both environmental factors and structural plant community attributes indicates its growth situation and ability to provide ecosystem services. However, previous works have focused on the effects of either environmental factors or plant community attributes on ANPP, which makes it difficult to quantify the effect pathways of environmental factors and plant community attributes on ANPP. In our study, we took a temperate grassland in the agropastoral ecotone of northern China as the research area and quantified the effects of environmental factors and plant community attributes on grassland ANPP with a structural equation model, together with correlation and partial correlation analyses. We found that growing season precipitation is the most critical factor for grassland ANPP, and its direct effect (standardized direct positive effect, SDE $= 0.401$, $p < 0.05$) on ANPP was the main path. Temperature affected ANPP directly (SDE $= 0.230$, $p < 0.05$) and indirectly (standardized indirect positive effect SIE $= 0.110$, $p < 0.05$) mainly through community attributes in the area, such as tiller number and cover. The increase in soil sand content reduced tiller number and further affected ANPP (SIE $= 0.011$, $p < 0.05$). Human population influenced ANPP through species diversity (SIE $= -0.059$, $p < 0.05$), and the increase in livestock number worked on ANPP by degrading the soil. Our results imply that improving grassland community attributes, such as maintaining species diversity and increasing vegetation coverage, will effectively mitigate the negative effects of climate change.

KEYWORDS
aboveground net primary productivity of grassland (ANPP), climate change, environmental factors, structural equation model, structural plant community attributes

1 | INTRODUCTION

The aboveground net primary productivity (ANPP) of grassland is an important indicator that directly reflects grassland growth status and is used to evaluate grassland ecosystem services (Dieleman et al., 2012; Fang et al., 2001; Grime et al., 2000; Guo et al., 2012; Knapp & Smith, 2001). However, ANPP is also a sensitive indicator of grassland degradation.

Grassland ANPP is strongly determined by environmental factors such as climate and soil factors (Adams et al., 2017; Guo et al., 2017; Zhu et al., 2016). The increase in temperature can either effectively promote ANPP by enhancing the activities of enzymes in photosynthesis (Adams et al., 2017; Gu et al., 2017) or reduce ANPP by increasing evapotranspiration (Guo et al., 2017). As one of the important limiting factors of grassland growth in an arid area, precipitation also determines productivity (Guo et al., 2017). Soil texture can contribute to ANPP by changing the biomass allocation between belowground and aboveground organizations, with ANPP decreasing with increasing soil sand content (Sanaei et al., 2019). The aboveground biomass of forbs and grasses on sandy soil is less than that on clay soil (He et al., 2019; Sanaei et al., 2019). In addition, human activities, such as reclamation and grazing pressure, also affect ANPP (Liu et al., 2015; Sanaei et al., 2019).

ANPP is also directly related to structural plant community attributes, in addition to environmental factors (Barbehenn et al., 2004; Fehmi et al., 2001; Fridley, 2002; Rolim et al., 2005; Steudel et al., 2012). Species richness benefits the stabilization of productivity through compensation effects (Hector et al., 2010). In crop plant research, the biomass of stem and leaf from a grasses is positively correlated with the number of tillers (Barnaby et al., 2019; Cai et al., 2014). Moreover, the species composition of a plant community also affects ANPP (McLaren & Turkington, 2011); for example, grasslands with abundant annual plants have much higher productivity than that in grasslands dominated by perennials during the wet season (Yan et al., 2015).

Causal relationship exists between environmental factors and grassland community attributes, which may make community attributes act as an intermediate path to regulate the effects of environmental factors on ANPP. Climatic drought would reduce plant species richness, thus weaken the complementary effect between species and further reduce ANPP (Craven et al., 2016; Zhang et al., 2018). Previous studies have shown that temperature increase is conducive to the greening of grassland vegetation and the improvement of photosynthetic capacity, thus improves productivity (Adams et al., 2017; Li & Yang, 2014). Changes in climatic conditions can also lead to changes in the proportion of species in specific groups in grasslands (Qiu et al., 2016). It has been shown that low temperature promotes tiller number in crop experiments (Shimono & Okada, 2012), while precipitation increase can improve the species diversity of the grassland plant community and the vegetation coverage (Craven et al., 2016). The effects of grazing and human activities on grassland are evident (Cadotte, 2011), for example, grazing can affect soil texture through trampling, while human activities such as sowing may alter grassland species diversity. Overgrazing and inappropriate human activities can lead to grassland degradation with reduced vegetation cover, propagation of annual plants, and even coarsened soil through enhancing wind erosion of fine particles under reduced vegetation cover. Soil coarsening, in turn, may affect aboveground plant growth and thus tiller numbers.

Previous studies have focused more on the effect of changes in individual environmental factors on ANPP, but little attention has been paid to the influence path of environmental conditions on ANPP. Previous works on the effects of multiple factors on ANPP only focused on either environmental factors or plant community attributes, which made it difficult to quantify the effect pathways of environmental factors and plant community attributes on ANPP (Jin et al., 2014). To quantify the effect pathways, in particular those with strong pressure from human activities, we chose an agropastoral ecotone that had a significant climatic gradient and human activity gradient in the semiarid steppe region of northern China as our study area and tried to clarify the effect pathways with a structural equation model. We aimed to answer the following scientific questions: (1) How do environmental conditions and community attributes jointly affect the grassland ANPP in the agropastoral ecotone of northern China? (2) Which factors are the most critical ones to the grassland ANPP?

2 | MATERIALS AND METHODS

2.1 | Study area

The study area extends from Horqin Sandy Land in northeastern China to the Loess Plateau in northern China (100.47–124.28°E, 34.50–46.07°N). The altitude of the study area is 220–1750 m above sea level. This is the main area of temperate grasslands in China and is also an important part of the eastern Eurasian grasslands (Bai et al., 2008; Dai et al., 2016).

The region is dominated by a temperate continental monsoon climate. The mean annual temperature (MAT) is 0.4–9.1°C, and the mean annual precipitation (MAP) is 230–470 mm. The whole study area is located in a semi-arid region, precipitation and temperature have similar seasonal patterns in the study area. The growing season of grassland plants is from May to September. With a decrease in MAP, the soil in the study area changes from Chernozem and chestnut soil to brown calcic soil. Sandy soil exists in the vastly distributed sandy sheets. The vegetation changes from meadow steppe with abundant forbs to typical steppe dominated by grasses and desert steppe characterized by desert shrubs.

Previous studies in the agropastoral ecotone of northern China showed that the main change of land use types in this region was the mutual conversion of arable land and grassland. Although land use types changed frequently, there is no obvious change in land use structure, and grassland and arable land still occupy the dominant position (Li et al., 2018). In this context, agriculture and animal husbandry have been developing in a staggered way in the study area. From southeast to northwest along gradients of both mean annual precipitation and human population, the study area gradually changes from agriculture-dominated to animal husbandry-dominated. In the study area, the grazing management of the sampling site is varied, which in the pastoral area is mainly rotational grazing and nomadic, while in the agricultural area is mainly nomadic and herding in captivity. The livestock number decreases from pastoral area to agricultural area. Therefore, the influence of grazing management can be included in the livestock number.

2.2 | Field sampling and laboratory measurements

To rationally locate our sampling plots in the study area, we divided the agropastoral ecotone and surrounding region into 59 sampling areas according to climate, landform, surface soil texture, vegetation, and land use by self-organizing mapping neural network for unsupervised partition. In each sampling area, one sampling site was randomly selected with accessibility taken into account (Figure 1). Field surveys and sampling were conducted in the late growing season (late July to early August) of 2017 and 2018 as the aboveground biomass in the late growing season is widely used to indicate ANPP (Scurlock & Johnson, 2002).

At each site, three plots were set up for sampling, during which grounds with visible grazing were excluded when collecting samples. Plant species, species abundance, and coverage were recorded for each plot. Aboveground biomass was harvested in one randomly chosen 1 m × 1 m plot within each 2 m × 2 m sample plots where species covers and the number of tillers were estimated, and dead material and plant litter were removed. Aboveground biomass was then obtained as the dry weight after drying the samples at 65°C for 48 h.

For the community features, ANPP was related to the vegetation coverage, the plant species richness, and the species composition of plant community. Among the selected indexes, the number of aboveground tillers is a relatively new index that intuitively represents the number of plant individuals in the plots. We manually counted the number of aboveground tillers at the community level during the survey. In the grassland of the study area, annual and perennial plants tend to have different performances in aboveground biomass due to different reproduction patterns. Therefore, coverage, tiller number, species diversity index, and annual proportion were selected as indicators of community features.

The surface soil (0–20 cm) was sampled using a cutting ring. The soil texture was measured with a laser particle size analyzer (Mastersizer 2000, Malvern, UK). Soil texture was divided into three size fractions: clay (<0.002 mm), silt (0.002–0.2 mm), and sand (>0.2 mm). The content of sand (grain diameter > 0.063 mm) was used to indicate soil texture.

2.3 | Data processing

For data preprocessing, we calculated average cover and aboveground tiller number of each species in the site. The average aboveground biomass of each sample site was calculated as the aboveground biomass of three plots. According to the *Flora of China*

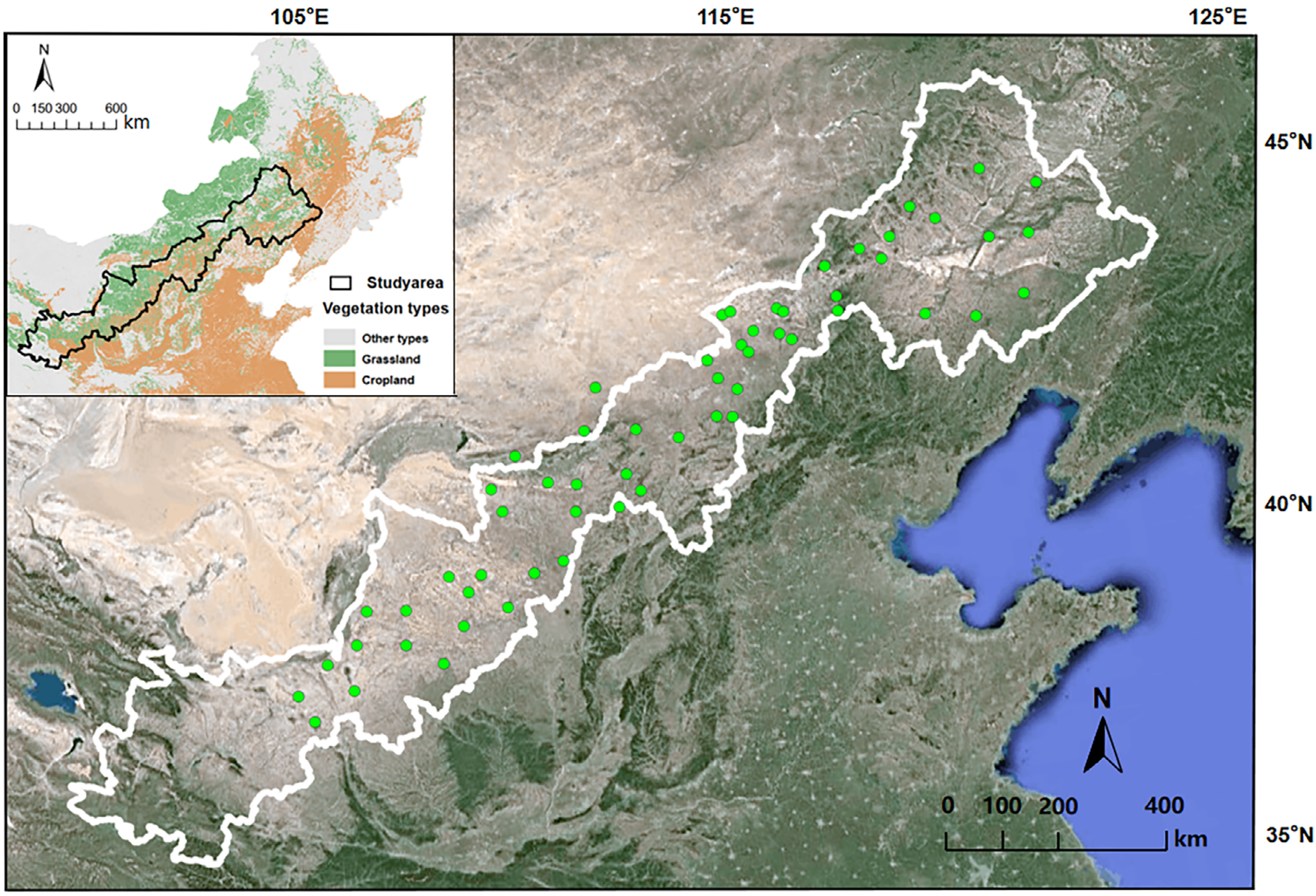

FIGURE 1 Overview of the area and sampling sites. The main plot shows the location of sampling sites, while the subplot shows the location of the agropastoral ecotone in northern China and the vegetation type within the ecotone. Green points in the main plot indicate the sampling sites [Colour figure can be viewed at wileyonlinelibrary.com]

(http://www.iplant.cn/), the existing species were categorized into annual and perennial, and annual proportion was quantified as weighted annual species abundance. The Shannon–Wiener index considering both species richness, and evenness was calculated for each plot (Shannon, 1948):

$$\text{The Shannon – Wiener index} = -\sum (P_i)\,(\ln P_i)$$

P_i is the abundance proportion of species i to the total abundance.

Among the environmental factors, temperature and precipitation have commonly been recognized as the most important influencing factors to grassland ANPP. For degraded grassland, soil coarsening can change both soil moisture and nutrient conditions that are critical to grassland ANPP, so we involved soil texture into our model. In the aspect of human influence, the human population and the quantity of livestock are the main factors affecting the grasslands in the ecotone of agriculture and pastoral. We downloaded existing meteorological station data from Climatic Research Unit (CRU) (https://sites.uea.ac.uk/cru/data) and extracted the temperature and precipitation in the growing season of the sample point by spatial interpolation. Human population and livestock numbers of the nearest township to each sample point were obtained from *China's Statistical Yearbook 2018*. We collected the data of cattle and sheep loading transferred cattle number into sheep number and adding them together as the total livestock number (Xu et al., 2014).

2.4 | Statistical analyses

The structural equation model (SEM) is now widely used to verify the complex causal relationship between variables (Fan et al., 2016; Grace & Irvine, 2020; Jonsson & Wardle, 2010). To quantify the effect path of environmental factors and community features on grassland ANPP with structural equation model, we used SPSS Amos version 22.0.0 software (IBM, Somers, NY, USA) to analyze the obtained data. We started with an initial model that contained all plausible interactions between all factors, based on the results of previous studies (Adams et al., 2017; Guo et al., 2017; Jacob et al., 2015; Fehmi et al., 2001; Rolim et al., 2005; Steudel et al., 2012) (Figure 4). Environmental data and grassland community data are continuous variables within the corresponding range. Nonnormally distributed data were transformed into normal distribution (Supplementary Table 1 and 2, Supplementary Figure 1 and 2). The maximum likelihood method is used to determine the path coefficient as standardized regression weights. Goodness of fit index (χ^2/DF, DF: degree of freedom), compare fit index (CFI), incremental fit index (IFI), root mean square error approximation (RMSEA), and significance level (p) were applied to test the model (Fan et al., 2016; Table 1). The model was reasonably modified at the modification indices (critical ratio), until the model passes the tests of selected indexes. The standardized direct effect (SDE) was expressed by standardized regression coefficient between the dependent variable and the independent variable, and the standardized indirect effect (SIE) is the product of the standardized regression coefficients of the dependent and independent variables, respectively, with the intermediate variables (Feßel et al., 2016). Then, we calculated the total standardized effect (SDE + SIE) of each factor on the ANPP.

We also analyzed the data through statistical methods of correlation analysis, in order to enhance the credibility of our conclusions. The aboveground biomass, environmental factors and plant community attributes were correlated. Partial correlation analyses were further conducted to remove the interactions between variables to obtain the potential correlation between variables. SPSS version 20.0 (SPSS Inc., Chicago) software was used to conduct the correlation analysis and partial correlation analysis.

3 | RESULTS

3.1 | Influence path of each factor on grassland ANPP of the initial model and the result fitted by SEM

Based on previous research studies, the initial SEM model was established as follows (Figure 2), which is named the influencing path on ANPP of grassland model. The initial model was modified until the selected index criteria were passed (Table 1).

The SEM results show that the effect path of the environmental factors on grassland ANPP are different, as well as the process and intensity of the effects on ANPP (Figure 3). The total standardized effect (SDE + SIE) of the environmental factors and community attributes to ANPP are calculated according to the standardized regression coefficients (Supplementary Table 3) of each path (Table 2).

The factors that have direct effects on ANPP are coverage, precipitation, tiller number, and temperature. Precipitation increase only directly affects ANPP, and the precipitation has the biggest effect (SDE = 0.401) during the environmental factors. Therefore, precipitation may be the most critical influencing factor for grassland ANPP in the study area. Temperature increasing on the one hand promotes ANPP directly (SDE = 0.230) and, on-the-other-hand, affects ANPP indirectly in regulating the number of tillers aboveground (SIE = −0.258). Compared with climatic conditions, soil texture,

TABLE 1 Fitting index for the structural equation modelling

Index name	χ^2/DF (χ^2/degree of freedom)	CFI (compare fit index)	IFI (incremental fit index)	RMSEA (root mean square error approximation)	p
Threshold of the fitting index	<3	>0.900	>0.900	<0.090	>0.050
Result	1.409	0.907	0.916	0.085	0.068

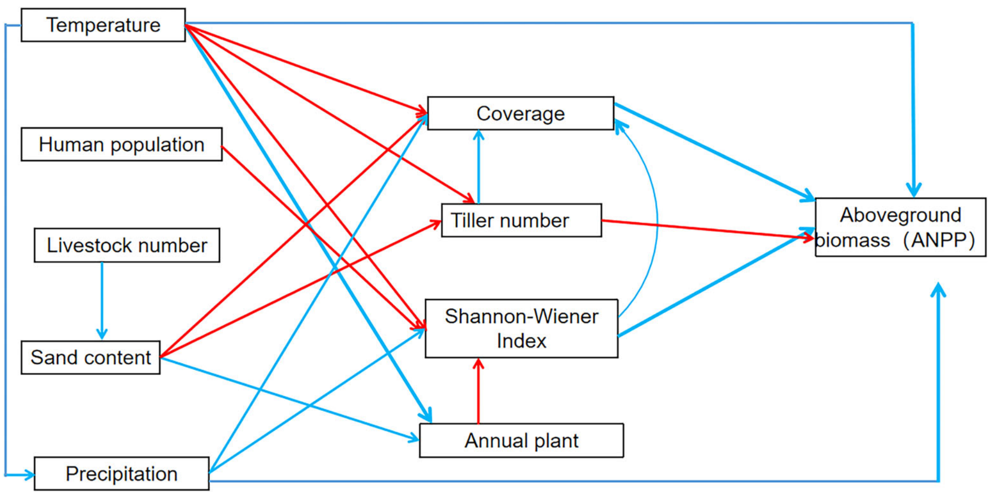

FIGURE 2 The initial SEM model is displayed in this figure, in which the red lines represent the paths of a negative relationship, and the blue lines represent the path of a positive relationship. Temperature: temperature of the growing season in the current year; Human population: human population of the nearest village or town of the sites; Livestock number: livestock number of the village or town of the sites; Sand content: soil sand content; Precipitation: precipitation of the growing season in the current year; Coverage: plant community coverage of the plots; Tiller number: tiller number on the ground per plot area; and Annual plant: the abundance proportion of annual plants [Colour figure can be viewed at wileyonlinelibrary.com]

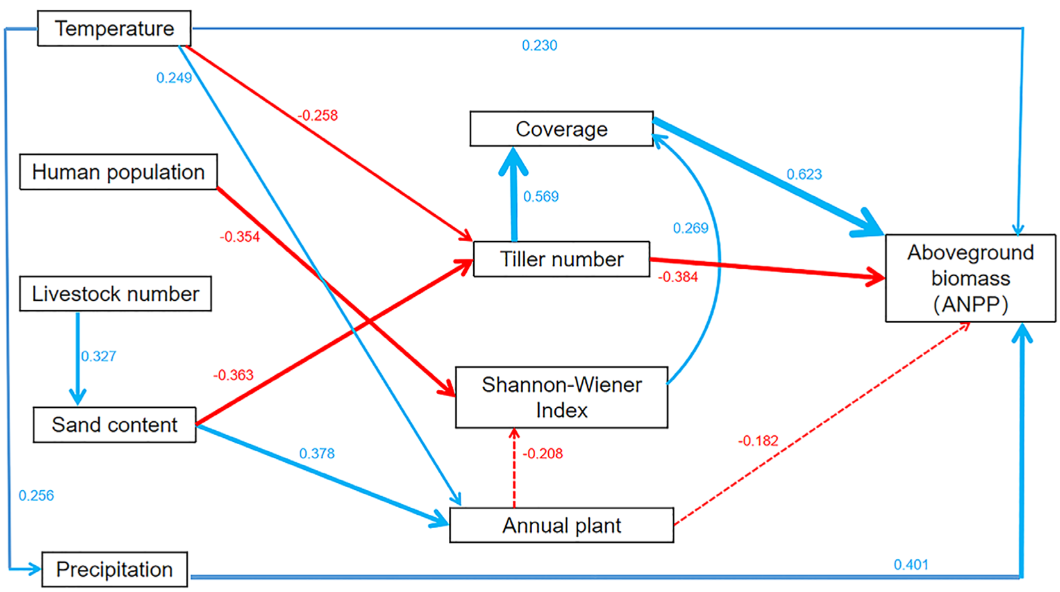

FIGURE 3 The fitted SEM model is displayed in this Figure ($p = 0.068$, $\chi^2/DF = 1.409$). The solid lines represent the significant influence paths ($p < 0.05$), and the dotted lines represent the paths that fail to pass the significance test. The red lines represent the paths of the negative relationship, and the blue lines represent the paths of positive correlation [Colour figure can be viewed at wileyonlinelibrary.com]

livestock number, and human population have less influence (SIE = 0.011, −0.059 and 0.004), and the increase in soil sand content can affect the ANPP of grassland by reducing the number of tillers. Human population reduces ANPP by reducing the Shannon–Wiener index. The increase in livestock number leads to the increase in soil sand content, which can reduce the tiller number and affect ANPP. All environmental factors can indirectly affect ANPP through community attributes except the precipitation. Therefore, plant community attributes play an important role in the process of environmental factors affecting ANPP. Among plant community attributes, coverage, the Shannon–Wiener index, aboveground tiller number are the important factors affecting ANPP, while the proportion of annual plants shows no significant effect. The levels of different community attributes in the ANPP impact path are different, and the order of the regression coefficients is coverage (SDE = 0.623), the Shannon–Wiener index (SIE = 0.168), and aboveground tiller numbers (SDE + SIE = −0.030). In terms of the total

TABLE 2 Standardized direct effect and the indirect effects of each impact factor on ANPP and the total standardized effect in SEM analysis

Influence factor	The standardized direct effect (SDE)	Indirect influence path	The standardized indirect effect (SIE)	Total standardized effect
Temperature	0.230	Tiller number - coverage; tiller number; precipitation	0.110	0.340
Precipitation	0.401	/	/	0.401
Sand content	/	Tiller number; tiller number - coverage;	0.011	0.011
Human population	/	Shannon – Wiener index - coverage	– 0.059	−0.059
Livestock number	/	Sand content	0.004	0.004
Coverage	0.623	/	/	0.623
Tiller number	−0.384	Coverage	0.354	−0.030
Shannon – Wiener index	/	Coverage	0.168	0.168
Annual plant	/	Shannon – Wiener index - coverage	−0.035 (nonsignificant)	−0.035 (nonsignificant)

Note: Slash means that the path does not exist.

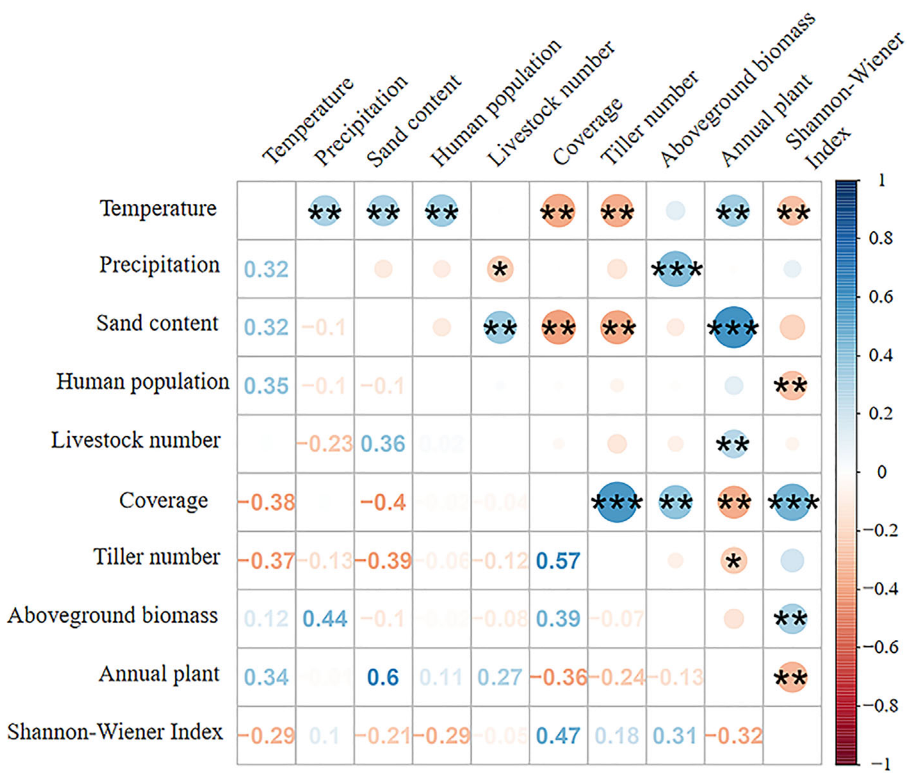

FIGURE 4 Correlations between variables. The circles' sizes represent the correlation coefficient. The circles in red represent the negative correlation, and the ones in blue represent the positive correlation. Stars represent show the significance level: *, $p < 0.10$; **, $p < 0.05$; and ***, $p < 0.01$ [Colour figure can be viewed at wileyonlinelibrary.com]

effect, among the environmental factors, the largest influence on ANPP is from precipitation (0.401), followed by temperature (0.340), human population (−0.059), soil sand content (0.011), and livestock number (0.004) (Table 2).

3.2 | Correlations between grassland ANPP and the impact factors

Correlation analysis shows that ANPP is significantly correlated with precipitation, coverage, and the Shannon–Wiener index ($R = 0.44$, 0.39, and 0.31, respectively) (Figure 4). Partial correlation analysis is to analyze the linear correlation between two variables under the condition of controlling the linear influence of other variables. When controlling the related common variables to carry partial correlation between each pair of factors, ANPP is still significantly correlated with precipitation and coverage (partial $R = 0.36$ and 0.49, respectively), while the correlation between Shannon–Wiener index and ANPP disappears ($p > 0.05$). In addition, ANPP becomes significantly correlated with tiller numbers in partial correlation analysis (partial $R = -0.32$) (Figures 4 and 5).

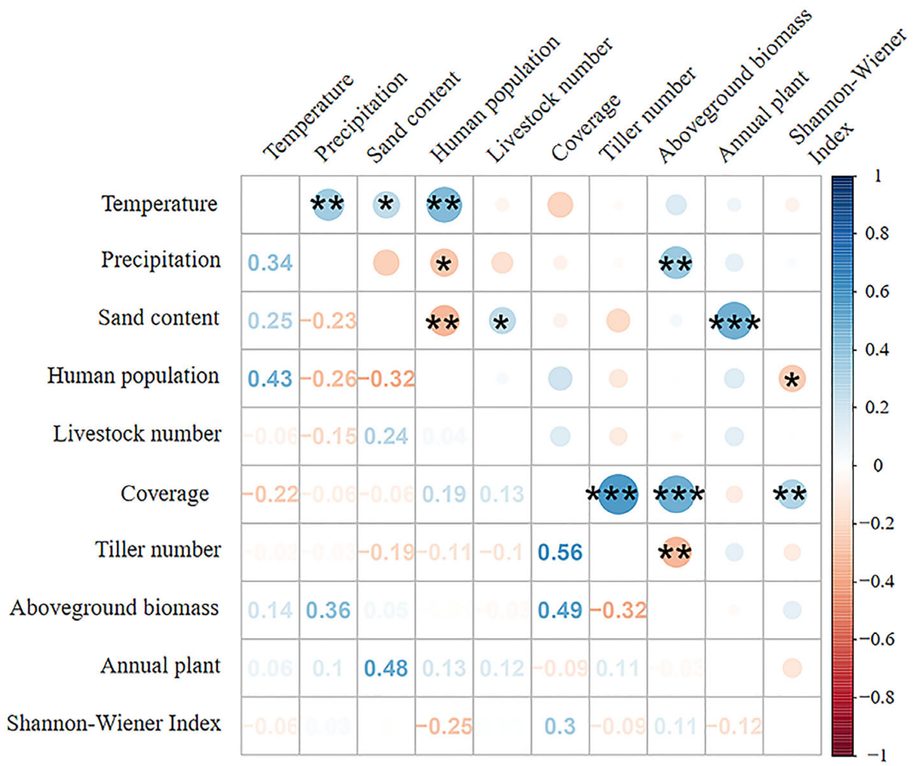

FIGURE 5 Partial correlation between variables. The circles' sizes represent the correlation coefficient. The circles in red represent the negative correlation, and the ones in blue represent the positive correlation. Stars represent show the significance level: *, $p < 0.10$; **, $p < 0.05$; ***, and $p < 0.01$ [Colour figure can be viewed at wileyonlinelibrary.com]

4 | DISCUSSION

Our results reveal the effect of individual plant community attributes on grassland ANPP. ANPP is positively correlates with vegetation coverage. The increase in species diversity indicated by the Shannon–Wiener index can improve the stability of the community structure and thus ANPP under environmental disturbance (Floder & Hillebrand, 2012; Tilman et al., 2006; Van Ruijven & Berendse, 2010), during which the complementary effect among species is a critical mechanism (Bai et al., 2004; Chi et al., 2019; Feßel et al., 2016; Gross et al., 2007; Ye et al., 2018). Our results can be confirmed by the previous work carried out in a semi-natural temperate grassland of central Germany, in which the increase in plant species diversity reduced the light transmittance of the plant community and improved coverage to obtain light capture (Feßel et al., 2016). The increase of tiller number has a positive effect on ANPP by improving grassland coverage. Meanwhile, tiller number increasing may also reduce ANPP, possibly because plants can allocate resources to new tillers to adapt to environmental changes, which may result in a decrease of the total biomass of all tillers, even though the total number of tillers increases. Unfortunately, more research is needed about this process.

Environmental factors have a series of complicated direct effects on ANPP, through community attributes. Among them, precipitation only has a direct effect, and temperature has both direct and indirect effects, while other factors have only indirect effects. Both methods suggest a correlation between temperature and precipitation, and we believe altitude to be a co-determinant of both ($R = -0.536$ and 0.259, respectively, $p < 0.05$). After controlling for altitude, the high correlation between temperature and precipitation still exists (partial $R = 0.559$), which may be because rising temperature increases surface evapotranspiration, thus increases precipitation (Chen, Chen, et al., 2020; Chen, Tang, et al., 2020).

In the SEM model (Figure 3), precipitation only directly affects ANPP, and its influence coefficient is the largest (SDE = 0.401). In the correlation analysis and partial correlation analysis, there is no variables were associated with both precipitation and ANPP, and the correlation coefficient between precipitation and ANPP is the largest among all environmental factors, which indicate that the direct positive effect of precipitation in growing season on ANPP is the most critical, which is consistent with the results of previous works (e.g., Hu et al., 2007; Lauenroth & Sala, 1992). Temperature is the second most important influencing factor of ANPP (SDE + SIE = 0.340). Its effects can be divided into both direct and indirect effects (Figure 3). Temperature can directly promote ANPP (SDE = 0.230) and its impact is secondary only to precipitation in environmental factors in the whole model. Temperature rise may promote productivity through plant physiological function; That is, warming in the growing season promotes enzyme activity and increases the photosynthesis rate within a certain range (Adams et al., 2017). The temperature also indirectly affects ANPP through community attributes. The increase in temperature can inhibit the increase in aboveground tillers in the temperature grassland, which is consistent with the results of a crop rice control experiment showing that low temperatures promoted tiller number (Shimono & Okada, 2012). However, for grasslands, there is still a lack of studies on the effect of temperature on ANPP based on the number of aboveground tillers.

Soil sand content increase inhibits the increase of aboveground tillers (Figure 3), further affects ANPP. It may be due to the limitation of soil aggregate structure on plant germination. Sandy soil has a larger aggregate size, which is not conducive to plant germination (Song et al., 2009). Soil texture also influence soil nutrients (Chen & Duan, 2009), which indirectly affect tiller numbers (Bauer & von Wiren, 2020; Chen, Chen, et al., 2020; Chen, Tang, et al., 2020).

Human population and livestock number affect ANPP through different community attribute paths (Figure 3). The increase in human population reduces the species diversity of the grassland and further increases the grassland vegetation cover and causes an ANPP reducing (−0.059). Previous studies suggested that human activities may alter grassland species diversity by sowing seeds and removing certain species (Valko et al., 2016). The increase in grazing pressure, such as livestock number, causes soil coarsening (Jacob et al., 2015; Sanaei et al., 2019). Sand content inhibits the increase of tillers number and then affects coverage and ANPP, which can partly explain how the soil degradation caused by the increase in livestock number causes grassland degradation (Su et al., 2005).

It should be admitted that we missed the significant relationship between temperature and ANPP in correlation analysis and partial correlation analysis, which could be caused by the climate difference between the two sampling years. We separated 2017 and 2018 and verified the initial model with SEM (Supplementary Figure 4). The relationship between environmental factors and ANPP could not be established through the modified model in the dry year (Supplementary Figure 4). This may be because of the extreme deficit of precipitation breaks such as influence mechanism. The potential extreme drought events in the future may make the grassland ANPP and the environment relationship become very uncertain (Volaire et al., 2009).

The results of correlation analysis and partial correlation analysis show no significant correlation between sand content, human population, livestock quantity, and ANPP. The results of SEM show that the indirect effect of these three factors on ANPP. This difference from two methods may be because there are many intermediate variables between the three factors and ANPP, but there is no direct effect (Figure 3). In the process of correlation analysis, the complex mediating effect leads to a large residual mean square, which leads to no significant correlation. In such a large sample area, these three factors have a very small impact on ANPP, SEM also shows the influence intensity of the three factors is far weaker than climate conditions (10–40-times). This result is confirmed with previous view that small variations in climate may have greater influence on multispecies occurrences than past and present human activities (Gang et al., 2014; Janssen et al., 2018). That also lead to it is difficult to show significant correlation just through correlation analysis in a complex mechanism process.

5 | CONCLUSIONS

With large-scale sampling of temperate grassland in northern China, we quantified the direct and indirect effects of environmental factors on grassland ANPP through plant community attributes. Precipitation as the most critical environmental factor has only direct effect on ANPP. Temperature is the second important environment factor, having both direct effects on ANPP and also indirect effects by regulating community attributes, with greater direct impacts than indirect ones. Soil texture and human activities have only significant indirect effects on ANPP. Climatic factors such as precipitation have a 10–40-times stronger impact on ANPP than soil texture and human activities. Therefore, in the context of climate change, research studies on grassland restoration should focus more on the extreme climate events influences, such as extreme drought and heat waves. During degraded grasslands restoration, improving species diversity and vegetation coverage can be an effective measure to increase grassland productivity rapidly.

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AUTHOR CONTRIBUTIONS

H.L., Z.P., L.J., J.D., and Z.C. collected samples and analyzed the data, Z.P. and L.J. did laboratory measurements. H.L and X.L. designed the project and this study area; Z.P. wrote the manuscript; all the authors discussed the results and commented on the manuscript.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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