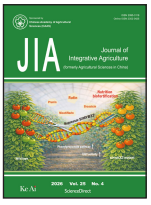
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RESEARCH ARTICLE

Plant community micronutrients mediate the soil carbon stock by altering plant growth, reproduction and survival trade-offs

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Highlights

- Plant communities tend to grow laterally and reproduce asexually over time.
- Community micronutrients show stronger coupling with trait trade-offs in the dry site.
- Community micronutrients mediate the soil carbon stock by altering trait trade-offs.

Abstract

Despite the essential role of micronutrients in plant metabolic processes and carbon cycle, the mechanisms by which micronutrients regulate plant community traits remain poorly understood. Here, we used a long-term experiment to explore the potential mechanisms of plant community micronutrients and traits along a precipitation gradient. Our results showed that plants shifted toward lateral growth and asexual reproduction over time. From 1985 to 2022, the plant community Fe content increased by 18.8% in the north but declined by 25.2% in the south of the typical steppe. Furthermore, plant community growth and reproduction were sensitive to both micronutrient contents and uptake efficiencies in the north of the typical steppe. While plant community Mn and Zn contents enhanced growth longitudinally, Zn and Fe uptake efficiencies hindered sexual reproduction. Furthermore, soil moisture and GDP per capita were the key drivers of micronutrient variation in the north and south of the typical steppe, respectively. Precipitation fluctuations primarily regulated community traits across all sites. In the arid site, micronutrient-driven shifts in reproduction stabilized the soil carbon stock by balancing biomass allocation. These findings can help us to better understand the coupling of plant micronutrients, traits, and soil carbon stocks, thereby providing the basis for a scientific grassland conservation strategy under global change scenarios.

Keywords: climate change, human activities, precipitation gradient, community morphological and structural traits, plant micronutrients, long-term monitoring

1. Introduction

Grasslands are one of the world's major ecosystems, covering 40% of the Earth's land surface and maintaining 34% of the carbon stock and 30% of net primary productivity in terrestrial ecosystems (Hou *et al.* 2021; Bai and Cotrufo 2022). In recent decades, increasing human populations, frequent climatic extremes and the expansion of agriculture have led to severe threats from the ongoing degradation of grasslands (Dong *et al.* 2012), thereby undermining their capacity to support biodiversity, ecosystem services and human well-being (Ren *et al.* 2024). The community-weighted mean trait, defined as the average of a trait value usually weighted by species abundance in terms of aboveground plant biomass (Miller *et al.* 2019), reflects plant community growth, reproduction and survival trade-offs. The expression of these traits ultimately influences ecosystem functions and can help researchers to predict the effects of climate change and human activities on ecosystem processes (Soudzilovskaia *et al.* 2013). For instance, increasing plant height at the community level can enhance the ecosystem carbon uptake,

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implying that ecosystems with higher plant communities would sequester more carbon under climate change (Quan *et al.* 2024). Recent studies also show that plant community trait trade-offs can explain ecosystem-level variation in soil carbon stocks and plant productivity (Everwand *et al.* 2014; Manning *et al.* 2015). Consequently, a better understanding of how trait-based associations in grasslands respond to climate change and human activities is critical for maintaining grassland functionality and sustainability.

Plant communities respond to environmental change by adjusting their growth, reproduction and survival strategies to maximize adaptation under limited resource conditions (Giesel 1976; Chen *et al.* 2024; Li G L *et al*. 2024). Plant height and crown diameter reflect the growth trade-off between competitive ability for obtaining light and biomass construction cost (Asigbaase *et al.* 2023). In resource-limited environments, plants adapt to global change by reducing height and increasing crown diameter, thereby balancing the allocation of assimilation products. In addition, trade-offs between reproductive branching and all branching are critical strategies for sexual reproduction during the plant life cycle (Mi *et al.* 2023). The branching patterns largely define the genetic diversity of plants and constitute a major determinant of productivity (Wang *et al.* 2015). Growth and reproductive trade-offs collectively affect plant survival by influencing resource allocation efficiency, adaptation, competition, and genetic diversity (Obeso 2002; Vincent and Ibáñez 2024). Previous studies have reported that seedling density also characterizes the potential for sexual reproduction and vegetative regeneration (Cao *et al*. 2018; Andivia *et al.* 2021). The trade-off between seedling and population density further reveals community renewal and seedling survival. Understanding the variations in community growth, reproduction and survival strategies caused by climate change and human activities can improve our predictions of ecosystem processes and contribute to the development of effective strategies for adapting to global change.

Plant micronutrients have vital biological functions as they are critical for redox homeostasis and cell growth, act as enzyme cofactors in common biochemical pathways, and are involved in the synthesis of vitamins and growth hormones (Bonanno *et al.* 2018; Yu *et al.* 2023). Small changes in plant micronutrients may significantly affect the trade-offs of plant growth, reproduction and survival (Mondal and Bose 2019; Tian *et al.* 2021; Xu *et al.* 2025), which in turn affect ecosystem functions such as carbon sequestration (De Deyn *et al.* 2008; Hanisch *et al.* 2020; Quan *et al.* 2024). On the one hand, most cells and enzymes involved in the biological processes of plant growth require plant micronutrients, such as iron and manganese for photosynthesis and copper and zinc for immunity (Welch and Shuman 2011; Dai *et al.* 2023). These micronutrients may influence plant light competition strategies, as their deficiencies can promote a "conservative strategy" (Hayes *et al.* 2013; Chen *et al.* 2024). Studies indicate that an elevated manganese content enhances the vertical growth tendency in plants (Mondal and Bose 2019). Micronutrients also play a crucial role in the development of plant reproductive trade-offs (Pandey 2010; Kaur *et al.* 2023). For instance, copper enhances the growth of floral organs, and its deficiency severely impacts reproductive growth in grasses (Mir *et al.* 2021). Similarly, deficiencies in zinc hinder seed formation and maturation, ultimately reducing the fruiting rate and seed fullness, thereby inhibiting sexual reproduction (Stanton *et al*. 2022). While the effects of plant macronutrients on plant trait trade-offs are well studied (Craine *et al.* 2002; Donovan *et al.* 2014; Zhang *et al.* 2018), trait trade-offs may be limited by micronutrient availability, as described by the law of the minimum and the theory of multiple resource limitation (Gleeson and Tilman 1992).

Plant community structure and function in grasslands are strongly modulated by climate change and human activities (Wang and Davidson 2007; Li L *et al.* 2024). Climate change can lead to soil moisture limitations (Berg and Sheffield 2018), which may affect plant growth and reproductive strategies by altering plant nutrient uptake and utilization (Nielsen *et al.* 2019), or indirectly by influencing root respiration and microbial activity (Bahn *et al.* 2006). In addition, the intensification of human activities has altered global precipitation patterns and warming trends (Xu *et al.* 2022), potentially increasing the risks posed by climate change. Some empirical studies have suggested that climate and human activities shape community traits simultaneously, leading to changes in ecosystem functions (Zhao *et al.* 2023; Liu *et al*. 2024). Thus, in ecologically fragile areas with varying water availability, there is an urgent need to better understand the collective responses of vegetation to climate change and human activities.

The Eurasian Steppe is the world's largest contiguous terrestrial habitat, and it stretches 8,000 km from the Mediterranean basin to eastern China (Ding *et al.* 2024). The impending rise in extreme climate events in the Eurasian Steppe grassland in the next few decades, coupled with intensified human activities, will have significant impacts on plant community structure and function (Zhou *et al.* 2025b). Grassland restoration and the sustainable management of grasslands in the context of global change are key priorities for both research and practice. Therefore, we selected an ecoregion within the Eurasian Steppe that is characterized by dramatic precipitation variability for this study. The aims of the present study were to: (1) assess the temporal variation patterns of plant community micronutrients and community trait trade-offs along a precipitation gradient; (2) determine the coupling and decoupling of community micronutrients and community trait trade-offs; (3) investigate the mechanisms underlying the responses of plant micronutrients and community trait trade-offs to climate, human activities and soil properties; and (4) reveal how key biotic and abiotic factors regulate the soil carbon stock and net primary productivity.

2. Materials and methods

2.1. Research areas

The study sites on the Chinese Loess Plateau, a part of the Eurasian Steppe, were located in typical steppe regions. Three sample sites were established along a precipitation gradient from north to south (36°23.5′–37°6.0′N, 106°50.3′–107°33.6′E). From 1967 to 2022, the mean annual

precipitation (MAP) levels were 266.9, 333.6 and 441.1 mm in the north, center and south, respectively. The mean annual temperatures (MAT) were 6.9, 7.1 and 7.5°C in the north, center, and south, respectively. These sites have sandy soils and are characterized by dominant plant species such as *Artemisia capillaris*, *Lespedeza davurica*, *Stipa bungeana*, *Potentilla bifurca*, *Heteropappus altaicus*, and *Cleistogenes songorica*.

2.2. Sampling and measurements

In 1985, we randomly established three long-term observation sampling plots (20 m×20 m) in each site and placed four quadrats (1 m×1 m) within each plot. In three sites, we collected soil and plant samples in mid-August of 1985, 2002 and 2022. Selected traits including plant height (PH), crown diameter (CD), seedling density (SD), population density (PD), reproductive branch density (RB) and all branch densities (AB) were investigated for all populations within each plot. The aboveground parts of all species in each quadrat were harvested, and roots were collected by sieving and washing through a 0.5 mm mesh screen. All plants were first sterilized at 105°C for 30 min and then dried at 65°C for 48 h until a constant weight. The aboveground and belowground biomasses of the community were obtained by weighing. Net primary productivity (NPP) was calculated as the sum of the dry weights of the above- and belowground parts in each plot.

Soils were sampled by using a 5 cm soil auger to collect three samples in each quadrat, which were then combined into a composite sample. The composite samples were air-dried for soil analysis. Soil organic carbon (SOC) content was determined using the potassium dichromate volumetric method. Soil moisture was determined by an oven-drying method. An acid meter was used to measure the soil pH, and soil salinity (SS) was assessed through conductivity analysis. The total contents of copper (Cu), iron (Fe), manganese (Mn) and zinc (Zn) in plant and soil samples were analyzed by inductively coupled plasma atomic emission spectrometry (ICP-AES) after digestion with H_2SO_4-$HClO_4$.

2.3. Driving factor data collection and processing

We aimed to assess the environmental drivers of community traits, micronutrients, soil carbon stock and NPP by selecting 12 factors related to climate, soil, and human activities (Table 1). Considering the combined effects of the past and current climates on community morphological and structural traits, micronutrients, soil carbon stock and NPP, we used climate fluctuations, long-term climate trends, and current climate indices. The meteorological data were obtained from 1 km monthly average temperature and precipitation datasets covering China from 1901 to 2023. These datasets, which were used to derive the climatic indices for all study sites, were obtained from the National Tibetan Plateau Data Center and the Big Earth Data Platform for Three Poles (Peng *et al.* 2017; Peng 2019, 2020). The comprehensive spatial and temporal coverage of these datasets ensured their suitability for detailed climatic analysis across the region. To evaluate the impact of human activities, we analyzed GDP per capita, cultivated area, and industrial output, with GDP and industrial output data sourced from the *Qingyang Statistical Yearbook* (Dai and Zhang 2023) and cultivated land area data obtained through rural household surveys. Finally, we also used data on soil properties.

Table 1 Description of the 12 driving factors

Class	Name	Unit
Climate	Temperature fluctuation	–
	Precipitation fluctuation	–
	Annual average temperature	°C
	Annual average precipitation	mm
	Current year's temperature	°C
	Current year's precipitation	mm
Human activities	GDP per capita	CNY
	Cultivated area	ha
	Industrial output	CNY
Soil properties	Soil moisture	%
	Soil pH	–
	Soil salinity	g kg^{-1}

2.4. Calculation of indicators

The community-weighted mean (CWM) can reflect the trade-offs between growth, reproduction and survival, as well as micronutrient variations, within plant communities. Here, the weights were determined based on the relative aboveground biomass (AGB) of each species. CWM was calculated as follows:

$$\mathrm{CWM}=\sum_{i}^{s} P_i \times t_i \quad (1)$$

where P_i represents the percent AGB of species i, t_i represents the micronutrients, PH, CD, RB, AB, SD and PD of species i, and S is the number of species in the community.

Micronutrient uptake efficiency is defined as the ability of plants to absorb micronutrients from the soil. The micronutrient uptake efficiency was calculated using the following equation:

$$\text{Micronutrient uptake efficiency}=\frac{C}{S} \quad (2)$$

where C and S represent the total micronutrient contents of the plant community and soil, respectively.

The temporal and spatial stability of community traits and micronutrients were calculated as follows:

$$\text{Stability index}=\frac{\mu}{\sigma} \quad (3)$$

where μ and σ represent the temporal or spatial mean and standard deviation, respectively, of community traits and micronutrients.

Climate fluctuation (CF) was used to study the inter-annual variations in precipitation and temperature. The calculation formula was as follows:

$$\mathrm{CF}=\frac{\alpha}{X} \quad (4)$$

where α and X represent the standard deviation and mean of precipitation or temperature.

The soil carbon stock was calculated as follows:

$$\text{C stock}=\frac{\mathrm{SOC}\times\mathrm{SBD}\times\mathrm{D}}{10} \quad (5)$$

where C stock represents the soil carbon stock, SOC represents the soil organic carbon content (g kg^{-1}), D

represents the soil layer thickness (cm), and SBD represents the soil bulk density (g cm^{-3}).

2.5. Calculations and statistical analyses

One-way ANOVA and the Tukey-Kramer test were used to analyze differences in community traits, as well as micronutrients, across the precipitation gradient in different years. Two-way ANOVA was used to explore the effects of year, site and their interaction on community traits, as well as on micronutrients. To further explore how the community traits changed with micronutrients, linear regression was used to analyze the relationships between the PH/CD, RB/AB, SD/PD ratios and community micronutrients along a precipitation gradient. These analyses were performed in SPSS 22.0 (SPSS Inc., Chicago, IL, USA). In addition, the relative importance of community micronutrients and uptake efficiency on the PH/CD, RB/AB, SD/PD ratios were analyzed using random forest ("vegan" package).

Furthermore, the potential driving mechanisms of variations in community traits and micronutrients were explored. Redundancy analysis (RDA) was used to examine the role of driving factors on community traits and micronutrients ("vegan" package). Principal component analysis (PCA) was employed for dimensional reduction of the climate, soil, human activities, community micronutrient contents and uptake efficiency indicators ("FactoMineR" package). Finally, structural equation model (SEM) was used to explore the effects of biotic and abiotic factors on the soil carbon stock and net primary productivity ("lavaan" package). The models exhibited a good fit to the data, as indicated by a non-significant Chi-square test (P>0.05), RMSEA was less than 0.05, and both GFI and AGFI were greater than 0.90.

3. Results

3.1. Temporal pattern of community trait trade-offs along the precipitation gradient

From 1985 to 2022, the plant communities generally tended to grow laterally. The PH/CD ratio declined by 15.5 and 16.4% in the north and south of the typical steppe, respectively. Meanwhile, the RB/AB ratio decreased by 16.3 and 19.0% in the north and south, respectively. In contrast, the SD/PD ratio increased significantly by 39.4% in the north. Linear regression analysis showed that the PH/CD and RB/AB ratios increased with higher precipitation, while the PD/SD ratio decreased. Finally, the temporal stabilities of the PH/CD, RB/AB, and PD/SD ratios were the lowest in the north, while the spatial stability was the lowest in 2022 (Fig. 1).

3.2. Temporal pattern of community micronutrients along the precipitation gradient

From 1985 to 2022, the community Fe content increased by 18.8% in the north but decreased by 25.2% in the south of the typical steppe. The community Cu content increased by 27.3, 26.1 and 9.0% in the north, center and south, respectively. Conversely, the community Zn content decreased by 23.4, 7.9 and 6.0% in the north, center and south, respectively. The community Mn content decreased by 19.9 and 11.9% in the north and south. In addition, the community Cu and Mn uptake efficiencies increased by 12.2 and 11.9% in the north, but increased by only 3.5 and 1.0% in the south, respectively. The community Zn uptake efficiencies increased by 9.0, 9.3

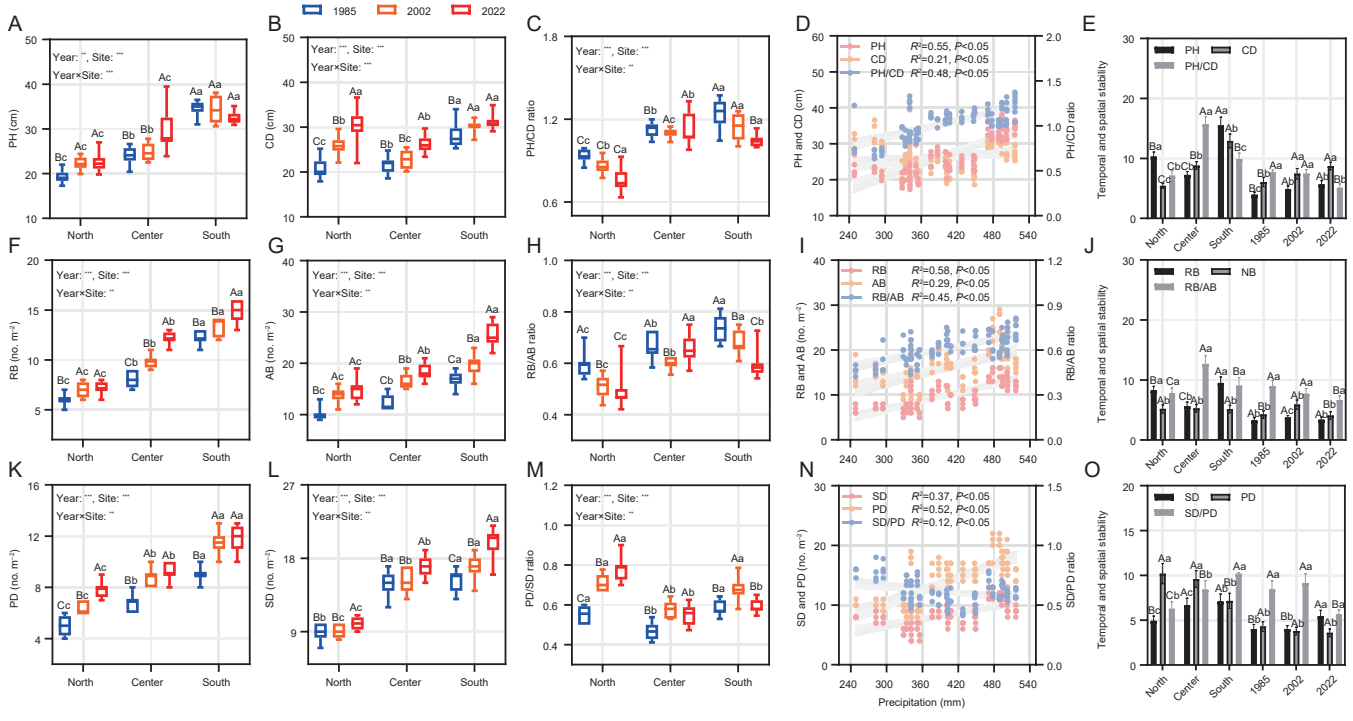


Fig. 1 Temporal variations of community trait trade-offs in the north, center and south of the typical steppe. PH, plant height; CD, crown diameter; SD, seedling density; PD, population density; RB, reproductive branch density; AB, all branch densities. Different uppercase and lowercase letters represent significant differences. **, P<0.01; ***, P<0.001.

and 5.5% in the north, center and south, respectively. The community Fe content, Fe uptake efficiency and Mn uptake efficiency increased with increasing precipitation, while the community Cu and Zn contents and their uptake efficiencies decreased. The temporal stability of the Fe, Cu and Mn uptake efficiencies were the highest in the south (Fig. 2).

3.3. Relationships between community trait trade-offs and micronutrients

The regression analysis results showed that community micronutrient content was more closely related to the PH/CD, RB/AB, and SD/PD ratios in the north than in the south and center of the typical steppe. Among these, the community Mn and Zn contents were significantly positively correlated with the PH/CD and RB/AB ratios, whereas the community Fe and Cu contents were significantly and positively correlated with the SD/PD ratio. In the south of the typical steppe, the Fe content showed significant positive correlations with the PH/CD and RB/AB ratios. By contrast, the Mn and Zn contents demonstrated significant negative correlations with the SD/PD ratio (Fig. 3).

In the north of the typical steppe, the PH/CD, RB/AB, and SD/PD ratios were most sensitive to community micronutrient uptake efficiency. Specifically, the Cu and Mn uptake efficiencies were significantly and positively correlated with the PH/CD and RB/AB ratios, but the PH/CD and RB/AB ratios decreased with increasing Fe and Zn. In contrast, the Cu and Mn uptake efficiencies were significantly negatively correlated with the SD/PD ratio. In the center and south, there were no significant linear relationships between the PH/CD and RB/AB ratios and community micronutrient uptake efficiencies. However, the SD/PD ratio increased significantly with increasing Fe and Cu uptake efficiencies (Fig. 4).

Random forest analysis showed that the effects of community micronutrient contents and uptake efficiencies on the PH/CD and SD/PD ratios became more homogeneous from north to south of the typical steppe. Conversely, the community Zn uptake efficiency explained a maximum of 34% of the RB/AB ratio in the south. The community Fe uptake efficiency had a greater effect on the SD/PD ratio, explaining 48, 78 and 19% of its variation in the north, center and south, respectively (Fig. 5).

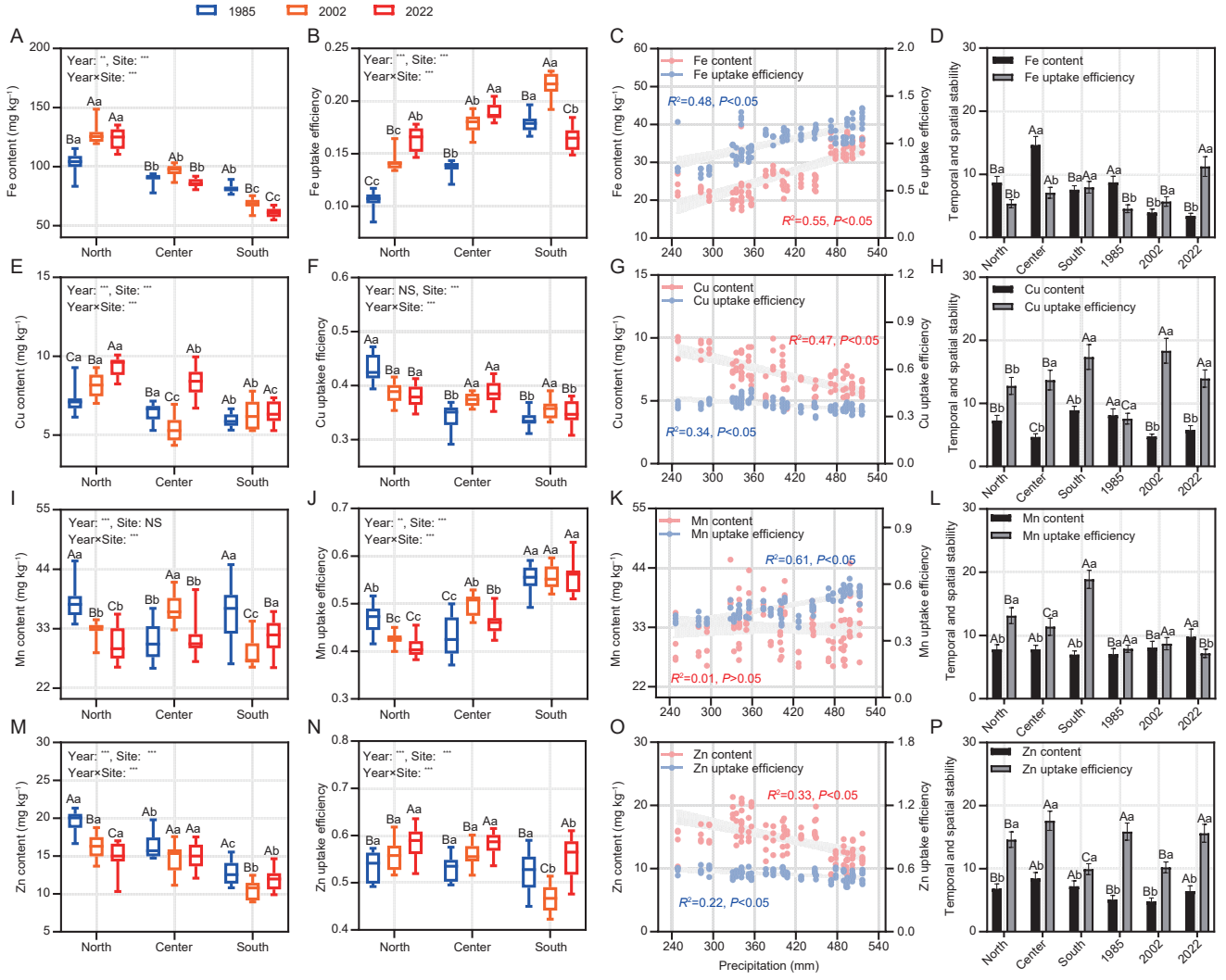


Fig. 2 Temporal variations of community micronutrient contents and uptake efficiencies in the north, center and south of the typical steppe. Different uppercase and lowercase letters represent significant differences. **, $P<0.01$; ***, $P<0.001$.

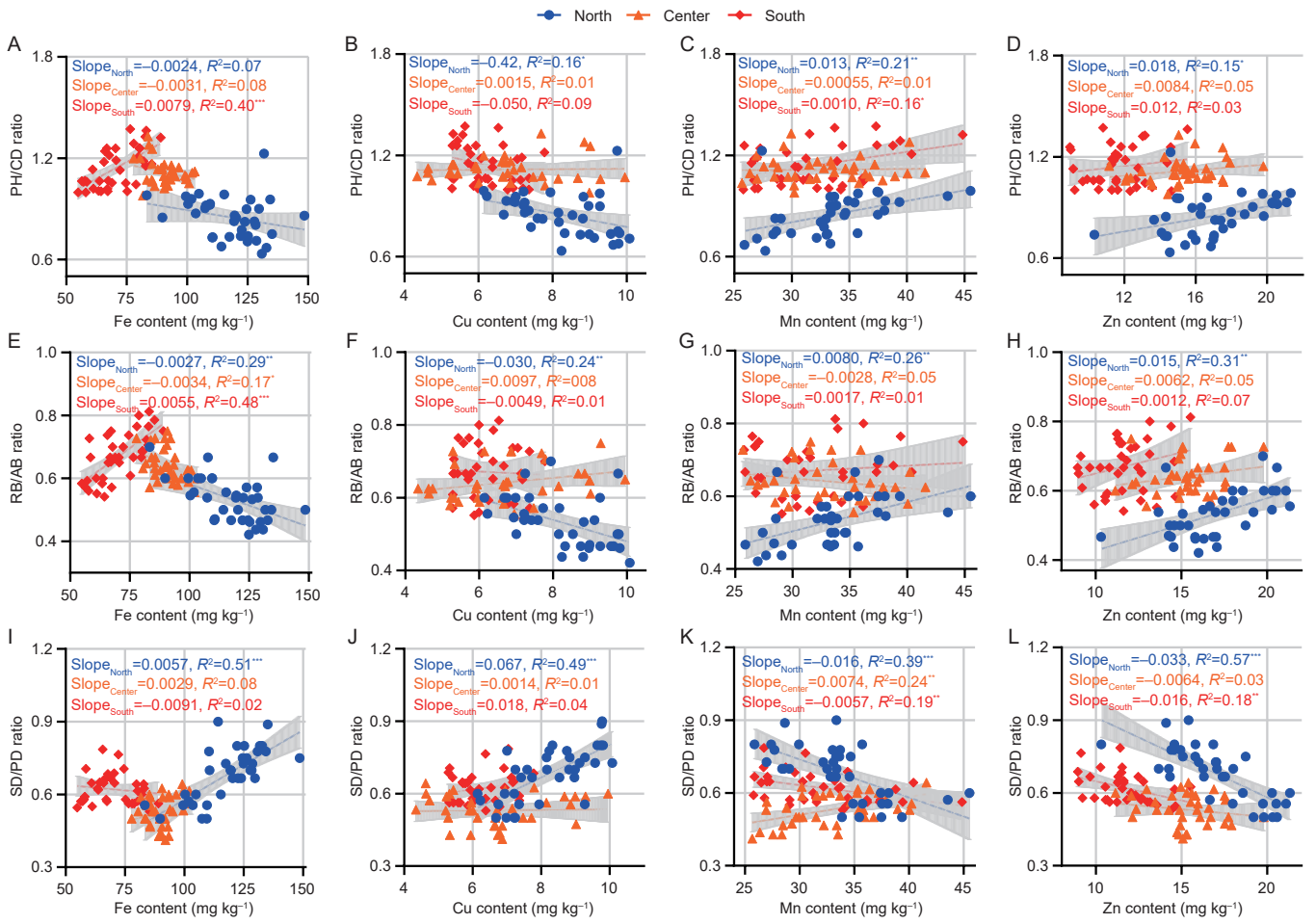


Fig. 3 Relationships between community micronutrient contents and the PH/CD, RB/AB, and SD/PD ratios in the north, center and south of the typical steppe. PH/CD, ratio of the plant height to the crown diameter of the plant community; RB/AB, ratio of the reproductive branch density to the all branch densities of the plant community; PD/SD, ratio of the population density to the seedling density of the plant community. *, $P<0.05$; **, $P<0.01$; ***, $P<0.001$.

3.4. The roles of environmental factors in community trait trade-offs and micronutrients

The RDA analysis showed that community functional traits and micronutrients were strongly linked to climate, human activities, vegetation and soil properties. Soil moisture, temperature fluctuation, and GDP per capita were the significant factors contributing to the variations in plant micronutrient contents and uptake efficiencies in the north, center, and south of the typical steppe, respectively. Specifically, soil moisture was closely and positively associated with the community Mn content and uptake efficiency but negatively correlated with the community Fe content and uptake efficiency in the north. In the center, temperature fluctuation was positively correlated with the Fe and Mn contents, but negatively correlated with the Cu content. GDP per capita was positively linked to the Zn content and uptake efficiency but negatively correlated with the Fe content and uptake efficiency in the south. Moreover, precipitation fluctuation primarily affected the growth and reproduction trade-offs in plant communities across the three sites. Precipitation fluctuation promoted vertical growth and sexual reproduction in the north but inhibited sexual reproduction in the south (Fig. 6).

3.5. The relative contributions of different factors to the soil carbon stock and NPP

Both the SEMs and variation partitioning analysis indicated the key drivers influencing the soil carbon stock and NPP, including environmental factors, community functional traits, and community micronutrients. In the north, shifts in plant micronutrient contents and uptake efficiencies in response to climate altered plant reproduction trade-offs, which in turn contributed to stabilizing the soil carbon stock. Climate had a direct negative effect on the soil carbon stock, explaining 49% of the variation. Conversely, the indirect effect of climate had a positive effect on the soil carbon stock, explaining 33% of the variation. In the center, soil and climate enhanced changes in NPP by reducing the community micronutrient contents. The interplay between vegetation, climate, human activities and soil accounted for 12% of the variability in the soil carbon stock and NPP. In the south, the direct and indirect effects of human activities accounted for 50% of the variance in the soil carbon stock. Human activities inhibited changes in the soil carbon stock by reducing the PH/CD ratio (Fig. 7).

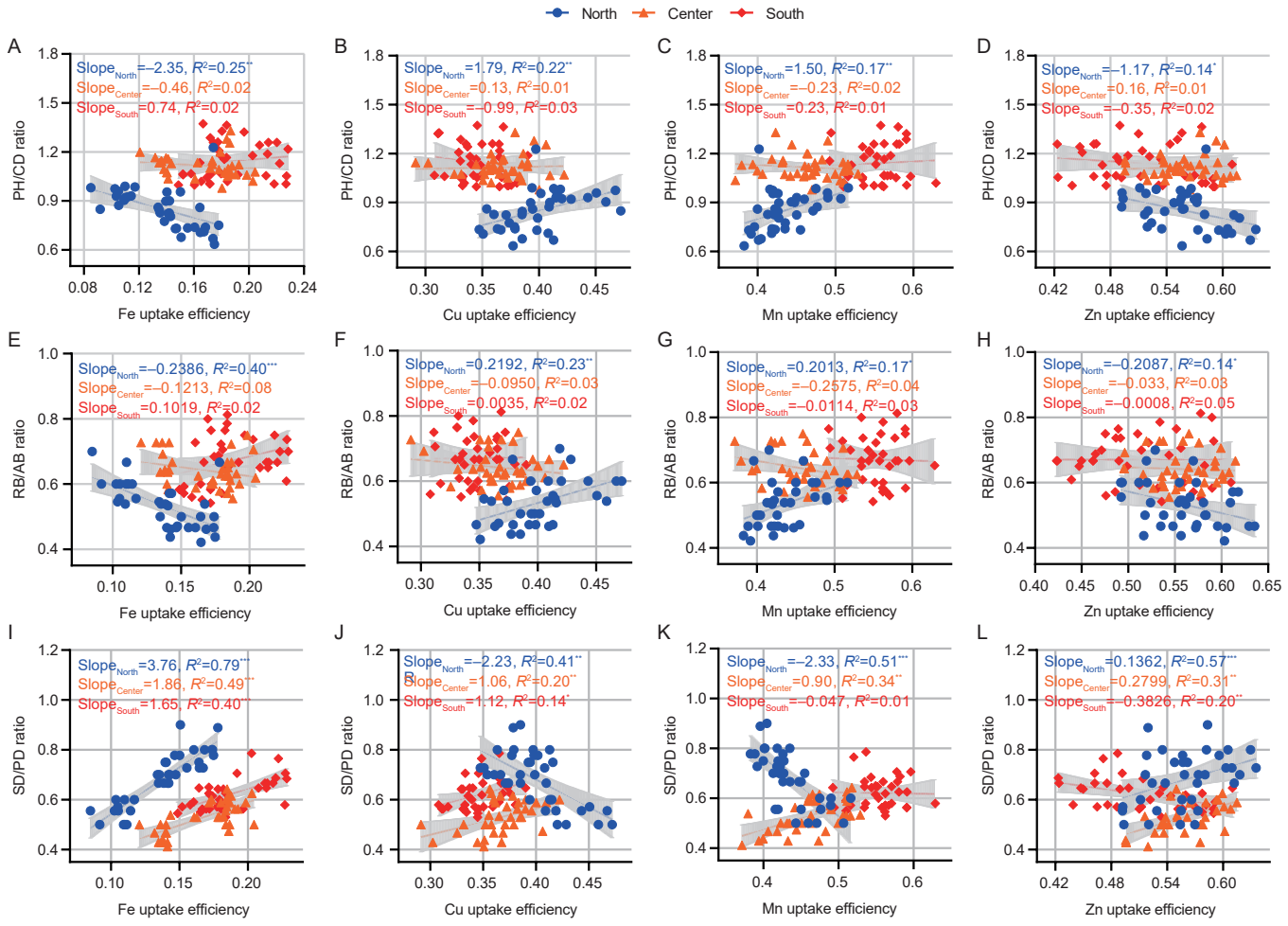


Fig. 4 Relationships between community micronutrient uptake efficiencies and the PH/CD, RB/AB, SD/PD ratios in the north, center and south of the typical steppe. PH/CD, ratio of the plant height to the crown diameter of the plant community; RB/AB, ratio of the reproductive branch density to the all branch densities of the plant community; PD/SD, ratio of the population density to the seedling density of the plant community. *, $P<0.05$; **, $P<0.01$; ***, $P<0.001$.

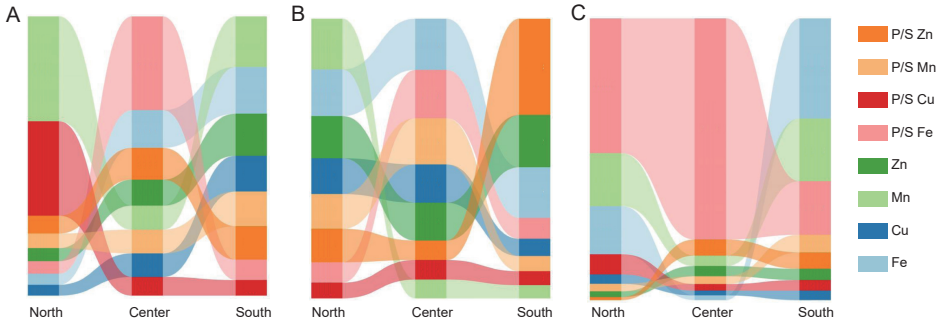


Fig. 5 Importance levels of micronutrient contents and uptake efficiencies on the PH/CD (A), RB/AB (B), SD/PD (C) ratios in the north, center and south of the typical steppe. P/S Zn, P/S Mn, P/S Cu and P/S Fe represent the uptake efficiencies of Zn, Mn, Cu, and Fe, respectively. PH/CD, ratio of the plant height to the crown diameter of the plant community; RB/AB, ratio of the reproductive branch density to the all branch densities of the plant community; PD/SD, ratio of the population density to the seedling density of the plant community.

4. Discussion

4.1. Changes in plant community micronutrients along the precipitation gradient over 37 years

Plant micronutrients are crucial for ecosystem functioning, material cycling, and the livestock supply in grassland ecosystems (Andrews *et al*. 1989). Understanding their temporal and spatial dynamics is key to addressing food security and human health issues. Our results showed that the temporal trends in plant community micronutrient contents

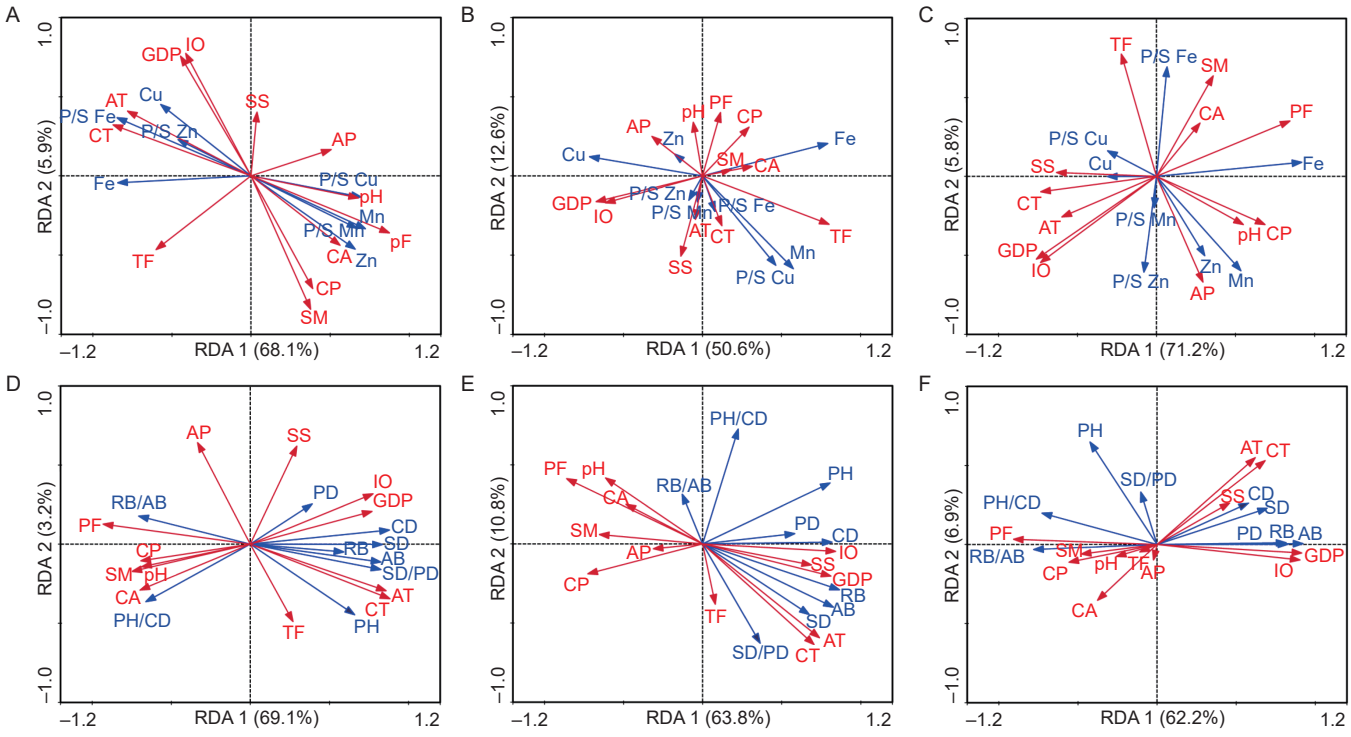


Fig. 6 Redundancy analysis (RDA) showing the impacts of soil, climate and human activity factors on community micronutrients in the north (A), center (B), and south (C) of the typical steppe, as well as community trait trade-offs in the north (D), center (E) and south (F) of the typical steppe.

and uptake efficiencies were dependent on local precipitation. This is similar to previous findings that local precipitation determines the sensitivity of community assembly to climate (Liu *et al.* 2021; Zhou *et al.* 2024). Specifically, from 1985 to 2022, the community Fe content increased by 18.8% in the north, which may have been due to the increase in aboveground biomass mediated by annuals in arid regions (Zhou *et al.* 2024), which results in the release of Fe during organic matter decomposition, thereby enhancing the soil Fe content. However, the community Fe content was negatively affected under humid conditions over the past 37 years, possibly due to the rainy and humid climate in the south, where prolonged precipitation may lead to the migration of iron from the surface soil to the underlying soil or water bodies through leaching. Such leaching may have reduced the amount of iron in the surface soil layer (Davies 1997; Yang *et al.* 2018). In addition, our results revealed that the Cu content increased and the Zn content decreased over time in the three sites, indicating that detrimental impacts of reduced plant community Zn availability in typical steppes may be exacerbated under climate change and human activities. This may limit the grazing suitability of many grasslands and their ability to sustain healthy plant and animal communities (Moreno-Jiménez *et al.* 2019).

Similarly, our results provide empirical evidence that the community Cu and Mn uptake efficiencies increased by 12.2 and 11.9% in the north but declined by 3.5 and 1.0% in south. These results might be associated with a few different mechanisms. First, in adapting to arid sites, some plants modify their roots to increase the root surface area (Kumar *et al.* 2019), ultimately resulting in the increased acquisition of Cu and Mn. Second, numerous studies have shown that increased temperatures in arid sites may enhance the bioavailability of soil nutrients to plants (Fotelli *et al.* 2004; Zhang *et al.* 2016). Higher temperatures also favor plant growth, which ultimately speeds up the processes of Cu and Mn uptake. Finally, climate change and human activities markedly affect the soil microbial communities in humid sites (Jansson and Hofmockel 2020; Zhou *et al.* 2025c), and their degradation potential consequently leads to nutrient deprived soil, resulting in reduced community Cu and Mn uptake. Meanwhile, our results provide empirical evidence that the temporal stability of the Fe, Cu and Mn uptake efficiencies was higher in the south compared to the north. This finding is consistent with long-term observations and controlled experimental studies (Liu *et al.* 2021; Zhou *et al.* 2024), and may be due to the adsorption and release of elemental Fe, Cu and Mn by more organic matter in the south.

4.2. Changes in plant community trait trade-offs along the precipitation gradient over 37 years

Trade-offs are essential for shaping life-history strategies in individual organisms, by influencing their growth patterns, reproductive investment, and lifespan. Based on a 37-year experiment in typical steppes, we observed that the plant community generally tended to grow laterally and reproduce asexually from 1985 to 2022, especially in the arid site. Some studies have found that under growth-limiting conditions, plants allocate more biomass to clonal propagation than to sexual reproduction (Zhou *et al.* 2021),

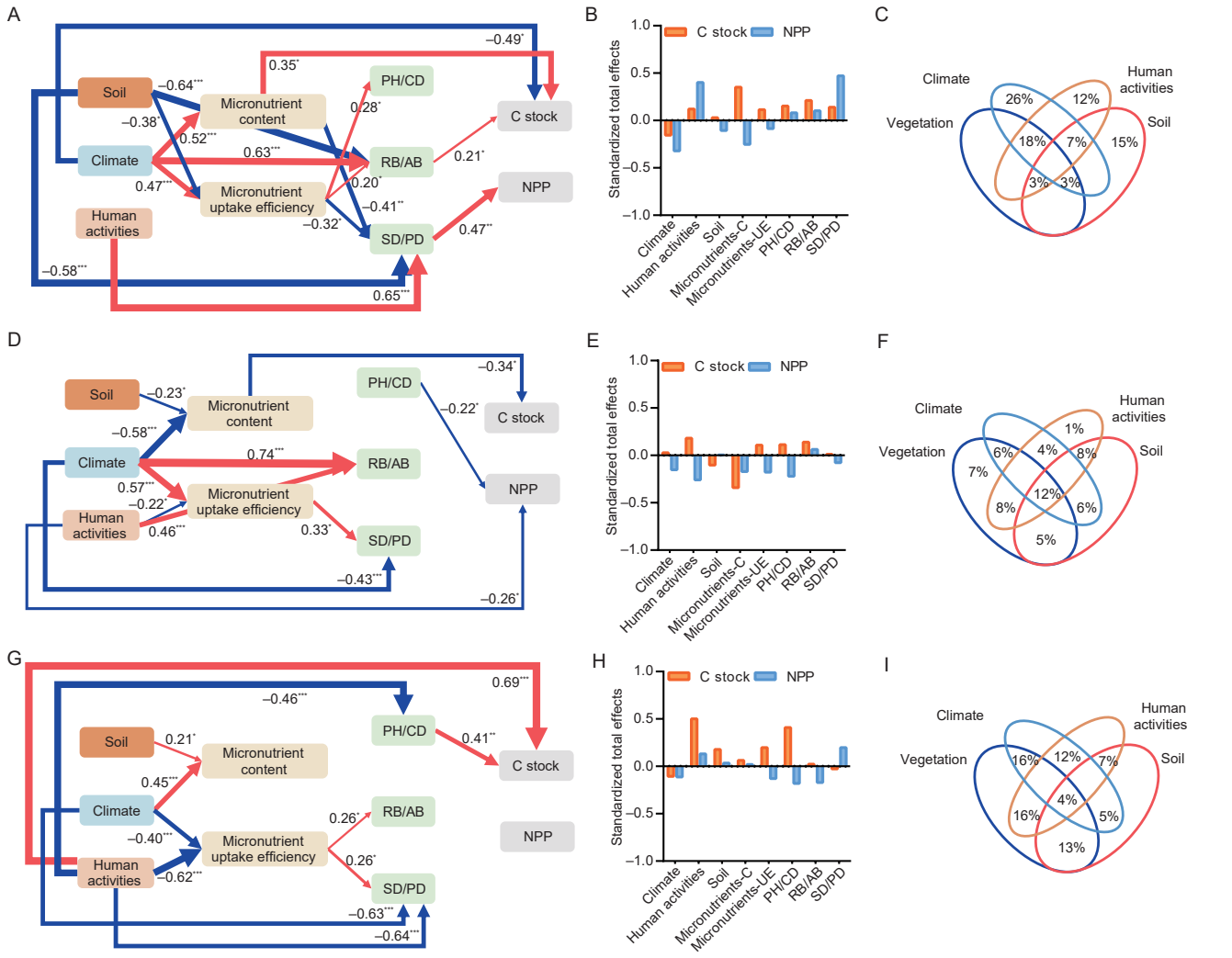


Fig. 7 The influence pathways and flux of the soil carbon stock and net primary productivity (NPP) according to the structural equation model analysis in the north (A–C), center (D–F), and south (G–I) of the typical steppe. Red and blue arrows indicate positive and negative relations, respectively. The width of an arrow indicates the strength of the relationship. Values adjacent to the arrows are standardized path coefficients. *, $P<0.05$; **, $P<0.01$; ***, $P<0.001$.

which is consistent with our findings. Lateral growth allows plants to increase their light competitiveness and ecological niche, enhancing their chances for survival (Asigbaase *et al.* 2023). Meanwhile, asexual reproduction can rapidly increase population size, improve genetic diversity, and increase resilience to climate change and human activities (Mi *et al.* 2023). At the same time, it is interesting to note that, the SD/PD ratio increased significantly in the north in our study. This phenomenon indicates that the plant community in the arid site increased its survival through sexual reproduction by adopting adaptive mechanisms. Furthermore, we also found that the temporal stabilities of the PH/CD, RB/AB, and PD/SD ratios were the lowest in the north. This may result from seasonal environmental changes, adjustments in plant growth strategies, genetic and physiological variations, and shifts in community dynamics and competition (Grossman 2023).

4.3. Coupling and decoupling of micronutrients and trait trade-offs in the plant community

Although micronutrients are known to be important regulators of plant community growth, reproduction and survival trade-offs, their interdependence makes estimating their relative importance challenging (Welch and Shuman 2011; Dai *et al.* 2023; Kaur *et al.* 2023). Our results indicate that plant community growth and reproduction trade-offs are sensitive to micronutrient contents and uptake efficiencies in the north. This suggests that variations in the micronutrient contents and uptake efficiencies of plant communities should be considered when predicting the impacts of climate change and human activities on community succession mechanisms in arid regions. In addition, we found that the community Mn and Zn contents enhanced longitudinal growth, but Zn and Fe uptake efficiencies hindered sexual reproduction in the north. Many authors have reported the positive influence of Zn on plant height (Ricachenevsky *et al.* 2015; Qiao *et al.* 2019). This may be because Zn is involved in the synthesis of chlorophyll and the process of photosynthesis, which contributes to an increase in plant community longitudinal growth (Qiao *et al.* 2019). On the other hand, Zn and Fe uptake in plant communities can be competitive. A high soil

Zn content may inhibit Fe absorption, leading to insufficient Fe in the plants, which can hinder sexual reproduction (Cao *et al.* 2018; Andivia *et al.* 2021). We found that the influence of plant micronutrient contents and uptake efficiencies on the PH/CD, RB/AB, and SD/PD ratios varied with local precipitation, with the effects on the PH/CD and SD/PD ratios becoming more homogeneous from north to south. This may result from the interactions of plant species, growth habits, and regional environmental conditions (Ahmed *et al.* 2024), and this information can aid in the development of more effective fertilization programs in arid regions.

4.4. Factors affecting micronutrients and trait trade-offs in the plant community

Micronutrients, growth, reproduction and survival trade-offs in the plant community were regulated by climate, human activities and soil properties, and the mechanism was associated with local precipitation. Our results showed evidence that soil moisture, temperature fluctuation, and GDP per capita were the significant factors contributing to the variations in plant micronutrient contents and uptake efficiencies in the north, center and south, respectively. These relationships might be associated with several mechanisms. First, soil moisture is crucial for nutrient uptake by plants, particularly in the arid northern site. Moderate moisture enhances the concentration of the soil solution, facilitating the absorption of micronutrients by roots. Moisture also influences soil structure and aeration, and drought-induced compaction can impede root growth and nutrient absorption. Second, temperature fluctuations affect microbial activity, which in turn influences the transformation and availability of soil nutrients in the center (Zhang *et al.* 2023). Finally, in the south, the high per capita GDP can lead to improved soil quality and enhanced nutrient availability through greater agricultural inputs, thereby benefiting the uptake of micronutrients by plants (Emenekwe *et al.* 2023). Our results also provide empirical evidence that precipitation fluctuations primarily affected the growth and reproduction strategies of plant communities across the three sites, which is consistent with previous findings (Campôa and Puhlick 2023; Zhou *et al.* 2024). Changes in water availability due to interannual variability in precipitation can lead to fluctuations in the abundances of various plant species within the community (Pearson and Carroll 1998), further influencing community adaptation strategies. These findings highlight the importance of both growth and reproduction trade-offs in community responses to altered precipitation fluctuations.

4.5. Mechanisms of biotic and abiotic factors on the soil carbon stock and NPP

Ecosystem carbon processes, such as NPP and the soil carbon stock, are generally known to be influenced by biotic and abiotic factors (Quan *et al.* 2019). Our study revealed that an increased plant micronutrient supply in response to climate altered plant reproduction trade-offs, which further stabilized the soil carbon stock in the north. On the one hand, numerous studies have shown that climate change, characterized by global warming and altered precipitation patterns, has a direct impact on the physical, chemical and biological properties of soil, which in turn affects the solubility and availability of micronutrients (Moreno-Jiménez *et al.* 2019; Yu *et al.* 2023; Zhang *et al.* 2023). On the other hand, greater micronutrient availability may allow plants to devote more resources to sexual reproduction processes, such as the development of sexual reproductive organs, pollen germination and pollen tube elongation (Pandey 2010; Kaur *et al.* 2023). Finally, sexual reproduction in plants allocates significant biomass to the reproductive organs, such as seeds and fruits, which eventually fall to the soil and contribute to the soil carbon stock. Conversely, in the south, human activity was the most important factor affecting the soil carbon stock, suppressing changes by indirectly reducing the PH/CD ratio. These results suggest that micronutrient-driven plant growth and reproduction trade-offs can improve predictions of ecosystem carbon dynamics under global change.

5. Conclusion

Our results suggest that climate change and human activities may limit sexual reproduction and vertical growth in plant communities by affecting micronutrient availability, which may further influence the carbon cycle. In addition, more pronounced relationships between micronutrients and the growth, reproduction, and survival trade-offs of plant communities were noted in the arid site compared to the humid site. Therefore, more attention should focus on the coupling processes of micronutrients with growth and reproduction trade-offs under drought conditions, particularly in the context of global change. While this study provides strong empirical evidence for the direction of plant community responses, our analyses did not account for continuous interannual observations. Thus, further long-term experimental *in situ* and controlled experiments based on our findings should account for the time-delayed effects of growing seasons or following extreme weather events.

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Declaration of competing interests

The authors declare that they have no conflict of interest.

Declaration of generative AI and AI-assisted technologies in the writing process

The authors declare that they did not use AI in the preparation and writing of this manuscript.

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