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Han, Jiaxin; Wang, Ruzhen; Sardans i Galobart, Jordi; [et al.]. «Gradient variations in rhizospheric soil exchangeable cations across a forest-steppe transect». CATENA, Vol. 245 (October 2024), art. 108330. DOI 10.1016/j.catena.2024.108330

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Gradient variations in rhizospheric soil exchangeable cations across a forest-steppe transect

Jiaxin Han [a b c], Ruzhen Wang [a], Jordi Sardans [d e], Heyong Liu [a], Peng He [f], Huanhuan Deng [a], Weiyi Ma [a], Josep Peñuelas [d e], Xingguo Han [a], Yong Jiang [a]

[a] School of Life Sciences, Hebei Basic Science Center for Biotic Interaction, Hebei University, Baoding 071002, China
[b] College of Environment, Shenyang University, Shenyang 110044 China
[c] Erguna Forest-Steppe Ecotone Ecosystem Research Station, Institute of Applied Ecology, Chinese Academy of Sciences, Shenyang 110016, China
[d] CSIC, Global Ecology Unit CREAF-CSIC-UAB, 08913 Bellaterra, Catalonia, Spain
[e] CREAF, 08913 Cerdanyola del Vallès, Catalonia, Spain
[f] Tianjin Key Laboratory of Animal and Plant Resistance, College of Life Sciences, Tianjin Normal University, Tianjin 300387, China

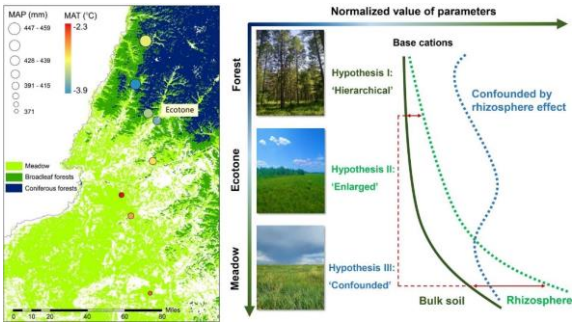
[*] Author for correspondence:

Professor Ruzhen Wang, College of Life Sciences, Hebei University, Baoding 071002, China. E-mail: ruzhenwang@hbu.edu.cn, Tel: +86 24 83970603

Abstract

The forest-steppe ecotone (FSE) is vulnerable to climate change and valuable to predict ecosystem succession. Although species diversity covaries with climatic factors and changes gradually across FSE transects, aligning with "Whittaker's hierarchy theory", whether soil nutrients follow a similar distribution pattern remains unclear. We studied the ecological gradient changes in effective cation-exchange capacity (ECEC, sum of exchangeable Ca2+, Mg2+, K+ and Na+) in the near-neutral-pH rhizosphere and bulk soils along the north–south zonal transect of the Hulunbuir FSE, China. The 230-km transect includes hierarchical transitions from two closed forests through two FSE to four meadow steppes. For both rhizosphere and bulk soils, soil ECEC were the highest in meadow steppes followed by closed forests and FSE area. ECEC were inversely correlated with soil water content but positively with soil pH. Therefore, the distribution of ECEC along the forest-steppe transect did not conform to a hierarchical distribution and decoupled from vegetation transitions, possibly due to the fact that the distribution of soil pH, plant uptake and leaching break the uniformity of ECEC variation along the gradient. In closed forests and FSE ecosystems, the ECEC and exchangeable Ca2+ in rhizosphere soils were higher than those in bulk soil, indicating that rhizosphere processes may alleviate cation limitation in these ecosystems. The study substantially improves our understanding of soil nutrient mobilization and soil fertility across forest-steppe ecotones which helps projecting ecosystem succession. It further highlights the critical role of rhizosphere processes in modulating hierarchical vegetation transition along environmental gradients and provides avenues for future research opportunities.

Graphical abstract



Keywords cation exchange capacity, rhizosphere, ecotone, forest-steppe transect, environmental gradient, plant nutrient uptake

1 Introduction

Forest-steppe ecotone (FSE), as the transitional area along a zonal transect of plant communities from forests to steppes (You *et al.*, 2021), is characterized by strong environmental heterogeneity and high sensitivity to global climate changes (Li *et al*., 2023). Its unique and highly heterogeneous habitats leading to the formation of some endemic species, concomitant with strong edge effects (Érdos *et al*., 2019). Meanwhile, the plant species and community structure are often more complex in the transitional area comparing with the forest or steppe side (He *et al*., 2023). The large environmental gradient across the forest-steppe transect underscore obvious changes in biological and non-biological elements, which is conducive to the coexistence of diverse species.

In the 1960s, Robert Whittaker proposed the hierarchical theory to explain the scale-dependence of species richness distribution and gradual increases in dissimilarity of community composition along environmental gradient (Whittaker, 1967). As claimed by the "Whittaker hierarchical theory", plant communities interrelate with the sum of environmental factors, *i.e.* environmental complex, to constitute an ecosystem gradient, which is structured progressively or hierarchically along a topographic or environmental transect (Whittaker, 1967). Moreover, changes in environmental factors along an environmental gradient are not only reflected in space, but also manifested in time (Okie *et al*., 2015; Zhang *et al*., 2020; Zhang *et al*., 2021; Feng *et al*., 2022). Numerous studies have revealed that carbon cycle rates, plant community composition and phytochemical elements also show a gradient of changes with environmental variations, fitting into the Whittaker hierarchical theory (Okie *et al*., 2015; Zhang *et al*., 2020; Zhang *et al*., 2021). Environmental gradients can be constituted by various factors in various forms, such as temperature gradients from hot to cold, precipitation gradients from rainy to arid, and soil gradients from infertile to fertile, or by their combinations (Feng *et al*., 2022). However, as a gauge of plant community composition and climatic variations along forest-steppe transects, soil fertility are expected to conform to the Whittaker hierarchical theory, although empirical evidence is still lacking.

Therefore, FSE transects naturally form unique environmental gradients in connection with gradual and concomitant shifts in physical habitat factors and life forms. A study conducted along a transect from alpine desert ecosystem to alpine grassland ecosystem found that soil moisture, concentrations of carbon, nitrogen (N) and phosphorus in plant-soil systems, and plant species

richness all them increased with increasing altitude (Zhang *et al*., 2021). Consistent with these gradient variations, soil decomposers of bacterial communities have been observed to show decreases in α-diversity, niche widths, and niche occupancies but an increase in β-diversity with increasing elevation and decreasing air temperature (Okie *et al*., 2015). Furthermore, a recent study found that functional diversity of waterbirds increased remarkably with temperature and precipitation (Zhang *et al*., 2020). All the above-mentioned cases follow the Whittaker hierarchical theory, where the diversity and composition of species within a community or ecosystem change in predictable ways along environmental gradients. However, whether abiotic habitat factors, such as exchangeable base cations that receive less attention than soil carbon, N and phosphorus (Ge *et al.*, 2021; Hong *et al.*, 2023), are in concert with life forms to follow the Whittaker hierarchical theory in an FSE has never been assessed. Addressing this uncertainty would facilitate better predictions of ecosystem processes on a whole-system angle.

Soil effective cation exchange capacity (ECEC) helps hold nutrients and buffer pH changes of soils, making it vital for maintaining basic functions of terrestrial ecosystems (Fang *et al*., 2017). In calcareous soils, ECEC is to a large extent equivalent to exchangeable base cations of calcium (Ca^{2+}), magnesium (Mg^{2+}), potassium (K^{+}), and sodium (Na^{+}) (Zhang *et al*., 2013; Wang *et al.*, 2017). These cations are predominant pH buffering substances and play an important role in maintaining soil stability under atmospheric acid deposition (Lucas *et al*., 2011; Cai *et al*., 2017). Therefore, ECEC can serve as good indicators of soil fertility (Zhang *et al*., 2013), and base cations themselves are critical nutrients for both plant and microbial metabolism (Cheng *et al*., 2010). Meanwhile, the gradient variations in soil bases cations are expected to play substantial roles in shaping plant local adaption to each concrete environmental circumstance (Cheng *et al*., 2010). This could be especially true in areas with high precipitation or N deposition, making soil base cations prone to leach (Wu *et al*., 2020). As consequence under moderate acidification of calcareous soils, the lower levels of ECEC (*i.e.*, the sum of Ca^{2+}, Mg^{2+}, K^{+} and Na^{+}) inhibits the plant uptake of mineral cations, and thus a loss of plant biodiversity and plant biomass have been frequently observed (Van Den Berg *et al*. 2005; Bowman *et al*. 2008). Moreover, the loss of exchangeable base cations, as a result of structural damage of colloids with soil acidification, could also undermine plant productivity (Liu *et al*., 2019). Only very few studies considered soil ECEC across the transect of FSE and found that

it sharply decreased from forests through forest-steppe transitional zone to steppes with the reasons being largely unexplored (Munroe, 2012; Lloyd *et al*., 2015).

To maintain the supply of base cations under different conditions, plants strategically regulate the secretion of organic acids to acidify the rhizosphere soil for the mobilization of base cations (Rengel and Marschner, 2005). Additionally, rhizosphere effect enhances soil nutrient availability via promoting exoenzyme activity, microbial proliferation and therefore organic matter mineralization (Gan *et al*., 2021, 2022). The magnitude of this rhizosphere effect could vary considerably along the FSE, which is still little known. One previous study suggested that the compositions of tree, shrub and herb species had relatively contradictory effects on base cations; for example, tree species had negative effect while both shrub and herb species demonstrated positive effects on soil Mg^{2+} (Wu *et al*., 2020). Therefore, the rhizosphere effects of steppes are hypothesized to be considerably different from that of forests, due to the differences in root morphology and physiology among different plant life forms (Gan *et al*., 2022). Overall, rhizosphere is a hot spot for soil nutrient turnover, and root stimulation of soil nutrient turnover is an effective way to supply the needed nutrients for plants (Kuzyakov and Blagodatskaya, 2015).

In this study, we determined gradient changes of soil ECEC along the north-south zonal transect of Hulunbuir forest-steppe ecotone. We addressed two questions in this study: i) Does the change of soil ECEC, possibly as a gauge of gradient variations in climatic factors, conform to the Whittaker hierarchical theory across the transect of forest-steppe ecosystems? ii) Does rhizosphere effects, that are deeply divergent among plant life forms (*e.g*., trees and herbs), alter the hierarchical distribution of soil ECEC across the transect? To address these questions, we measured the concentrations of soil exchangeable Ca^{2+}, Mg^{2+}, K^{+}, and Na^{+} in both rhizosphere and bulk soils along a transect of forest-steppe ecosystems, including three forest ecosystems, a forest-steppe transitional ecosystem and four steppe ecosystems. Meanwhile, we measured the soil water content (SWC) and collected data of mean annual temperature (MAT), mean annual precipitation (MAP), solar radiation (SR) to validate whether the variations in soil ECEC were due to environmental gradient changes. Correspondingly, three hypotheses were tested. Firstly, soil exchangeable Ca^{2+}, Mg^{2+}, K^{+} and Na^{+} concentrations would show a gradual increase from forest to steppe ecosystems with decreases in plant-community biomass and interspecific competition and thus lower plant nutrient demands.

Secondly, concentrations of soil exchangeable base cations in the rhizosphere would be higher than that in the bulk soil due to lower soil pH therein, with the magnitude of the difference in base cations between rhizosphere and bulk soils being increasingly prominent from forest to steppe ecosystems as a result of decreasing plant nutrient demands. Furthermore, rhizosphere effects on soil ECEC might substantially confound the hierarchical distribution of soil ECEC along the transect from closed canopy forests via forest-steppe ecotones to meadow steppes, given that the magnitude of rhizosphere pH drop depends on a variety of factors such as plant life forms, plant nutrient foraging strategy, and soil acid buffering capacity.

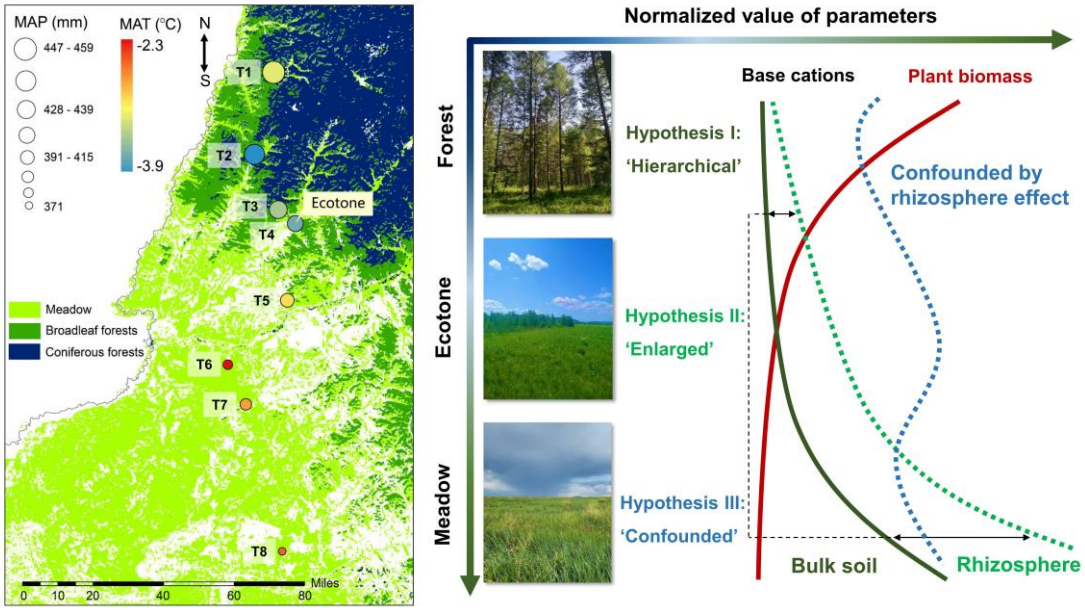


Fig. 1 Sampling sites (T1-T8) along the north-south zonal transect of Hulunbuir forest-steppe ecotone and hypothesized patterns of variations in soil base cations along the forest-steppe ecotone. The transect roughly include coniferous forests, mixed coniferous and broad-leaved forests, broad-leaved forests and meadow steppes. Hypothesis I: Soil base cations would increase gradually from forest to steppe ecosystems, showing an opposite trend with plant biomass ('hierarchical'). Hypothesis II: Rhizosphere effect would mobilize soil base cations with a higher magnitude in the meadow steppes where plant nutrient demand is lower than that of the forests ('enlarged'). Hypothesis III: Rhizosphere effect might vary across the forest-steppe ecotone, thus potentially confounding the hierarchical distribution of soil base cations ('confounded'). For each site, mean annual precipitation (MAP) was proportional to the size of circle and mean annual temperature

(MAP) was labelled with colors ranging from blue (low) to red (high).

2 Materials and methods

2.1 Study site and experimental design

The experimental site is located in the central part of Hulunbuir region (46°94′-51°50′N, 118°30′-122°55′E) of northeastern Inner Mongolia, China. Eight temperate sites (T1-T8) were selected along a transect from closed canopy forests, FSE and then to meadow steppes in northeastern China. Across these eight sites, T1-T3 has distinct tree and shrub species, which are classified as coniferous forests (T1), mixed coniferous and broad-leaved forests (T2), and broad-leaved forests (T3), respectively. We therefore define them as closed canopy forest (CF hereafter) ecosystems. The T4 site contains less trees but more shrubs and herbs with rich vegetation types, which is obviously an ecosystem of forest-steppe ecotone (FSE hereafter). Although we noted that the T3 site was categorized as FSE in He *et al.* (2023), it is understandable for the variations in ecosystem categorization depending on specific observational data. Sites T5-T8 are meadow steppe (MS) ecosystems composed of herbaceous plant species. Information on plant life forms and dominant species was listed in Table 1 for eight sites, which would be useful for understanding the uptake intensity of soil base cation by plants.

Biomass of N-fixing species was negligible across the transect as confirmed by plant community surveys and therefore show very limited effect on ecosystem N supply. The climatic conditions, including MAT, MAP and SR, at each sampling site were collected from climate stations of the China Meteorological Administration by extracting at 1 × 1 km spatial resolution using the interpolation software ANUSPLIN (He *et al*., 2014). Soil type of all selected sites is Chernozem (IUSS Working Group WRB, 2015).

Table 1 Characteristicss of the sampling sites regarding vegetation composition along the transect of forest-steppe ecotone in Northeast China. Ecosystem types include coniferous forest (T1), mixed coniferous and broad-leaved forest (T2), broad-leaved forest (T3), forest-steppe ecotone, and meadow. Abbreviations: CF, Canopy forests; FSE, Forest-steppe ecotone; MS, Meadow steppes.

Ecosystem	Type	Site	Plant life forms	Dominant species
CF	Coniferous	T1	Tree, shrub and herb	*Larix gmelinii*
	Mixed	T2	Tree, shrub and herb	*Larix gmelinii, Betula platyphylla, Spiraea salicifolia*
	Broad-leaved	T3	Tree and herb	*Betula platyphylla, Polygonatum odoratum, Carex pediformis*
FSE	Ecotone	T4	Tree, shrub and herb	*Betula platyphylla, Salix koreensis, Sanguisorba officinalis, Calamagrostis pseudophragmites, Rhamnus arguta*
MS	Meadow	T5	Herb	*Leymus chinensis, Bupleurum chinense, Koeleria cristata, Carex pediformis*
	Meadow	T6	Herb	*Leymus chinensis, Astragalus scaberrimus, Vicia cracca, Equisetum arvense, Carex korshinskyi*
	Meadow	T7	Herb	*Leymus chinensis, Polygonum divaricatum, Artemisia tanacetifolia, Carex pediformis*
	Meadow	T8	Herb	*Leymus chinensis, Pedicularis sylvatica, Thalictrum aquilegiifolium var. sibiricum, Stipa capillata, Carex korshinskii*

2.2 Sample collection and analysis

In August 2019, eight replication plots with size of 20 × 20 m were randomly established for plant community surveys as well as soil sampling at each site. To better represent the characteristics of a given habitat, any two adjacent sampling plots as selected were at least 200 m apart with relatively uniform and continuous vegetation. Although soil ECEC could change along with time, plant and soil samples were only collected once as we were interested in variational trend of ECEC across the FSE transect instead of across time scale. Moreover, it would be challenging to conduct sampling and measurements across time scales, given the relatively long distance and abundant samples of the FSE transect.

Within each sampling plot, five soil cores (0-30 cm deep) were randomly collected using an auger with a diameter of 8 cm. The rhizosphere soil from each soil core was collected by gently hand shaking according to Riley's protocol, where the shaken-offs were bulk soils and soils attached to the roots were rhizosphere soils (Riley & Barber, 1969). Rhizosphere soils, which are usually less than 2 mm in thickness on root surface, were brushed off from the roots and then collected. Isolated soils from the five soil cores were homogenized into one single sample for bulk soil or rhizosphere soil separately. Immediately after soil sampling, moisture was determined as mass losses for the bulk soils after drying at 105 °C for 24 h.

Soil pH values were measured with a pH meter (FE28; Mettler Toledo; Shanghai, China) after the soil samples being mixed with deionized water (w: v = 1:5). Soil inorganic N (NO_3^- and NH_4^+) were determined by weighing 10.0 g of fresh soil and mixed 50 mL 2*M* KCl solution. The mixture was shaken at 150 rpm for 1 hour at a constant temperature before filtration. Concentrations of NO_3^-, NH_4^+ in soil filtrate were determined using an AutoAnalyser III Continuous Flow Analyzer (Bran & Luebbe, Norderstedt, Germany). Soil exchangeable Ca^{2+}, Mg^{2+}, K^+ and Na^+ were extracted with 1*M* ammonium acetate (NH_4OAc, pH 7.0), and the extracts were then analyzed at the wavelengths of 422.7 nm, 285.2 nm, 766.5 nm and 589.0 nm, for the determination of the four analytes, respectively, using an atomic absorption spectrophotometer (AAS, Shimadzu, Japan) (Zhang *et al*., 2013). Soil ECEC was defined as the sum of exchangeable Ca, Mg, K and Na (Wang et al., 2017).

In the CF (T1-T3) and FSE (T4) plots, all species (including trees and shrubs) with a diameter ≥5 cm at breast height were measured and recorded for the species names, height, and diameter. The

biomass was calculated by the empirical biomass equations (Xie *et al*., 2018; Zhou *et al*., 2018):

D Equation $W = aD^b$ (1)

D^2H Equation: $\mathrm{W} = \mathrm{a}(D^2H)^b$ (2)

where W is plant biomass, a and b are the coefficients of the equation, D is the plant diameter at breast height, and H is the plant height.

Biomass of herbaceous species was determined for each sampling site of all ecosystem types. Briefly, 1 × 1 m quadrats were randomly selected in each plot to collect biomass samples of all plants and dried them in the oven at 65 ºC for 48 hours and weighed.

2.3 Statistical analysis

To clearly illustrate the differences in soil exchangeable base cations among three ecosystem types, presented values were means clustered from three forest ecosystems for CF (*i.e*., 24 plots) and four meadow steppe ecosystems for MS (*i.e*., 32 plots) given by eight replicates (n = 8) for each ecosystem. In detail, the values of CF and MS were obtained by averaging 24 plots from the three sites in CF, 8 plots for one site in FSE and 32 plots from the four sites in MS. The normality of data was verified using the Kolmogorov-Smirnov test, and the homogeneity of variances were determined using Levene's test. Linear mixed model with Duncan's multiple range tests were performed to determine the main effects from two studied fixed factors: rhizosphere/bulk soil and three ecosystem types (CF, FSE and MS) on soil exchangeable base cations and other measured soil variables, where plot replication was assigned as a random factor. The linear mixed model was executed with Origin 2021.Correlation analysis was performed to illustrate the relationships between soil pH, soil moisture, base cations and ECEC for rhizosphere and bulk soil separately, using *corrplot* package in R, version 4.1.2 (R Development Core Team, 2020; Wei & Simko, 2021). Statistical significance was accepted at $p < 0.05$. Redundancy analysis (RDA) was used to further assess the multiple correlations among soil exchangeable base cations, ECEC and environmental factors (*i.e.*, climatic factors, soil properties and plant biomass) and run separately for rhizosphere and bulk soils. Interpretability was also presented for each environmental factor (*i.e.*, climatic factors, soil properties and plant biomass) on soil exchangeable base cations. The RDA analyses were executed using CANOCO (version 5.0).

3 Results

3.1 Changes in climatic factors across study sites

Along the forest-steppe transect, MAT and SR increased while MAP decreased from sampling site T1 to T8 (Fig. 2a, b). Soil water content increased and then decreased from T1 to T8, showing the highest value at the site T4, *i.e.*, forest-steppe ecotone (Fig. 2b).

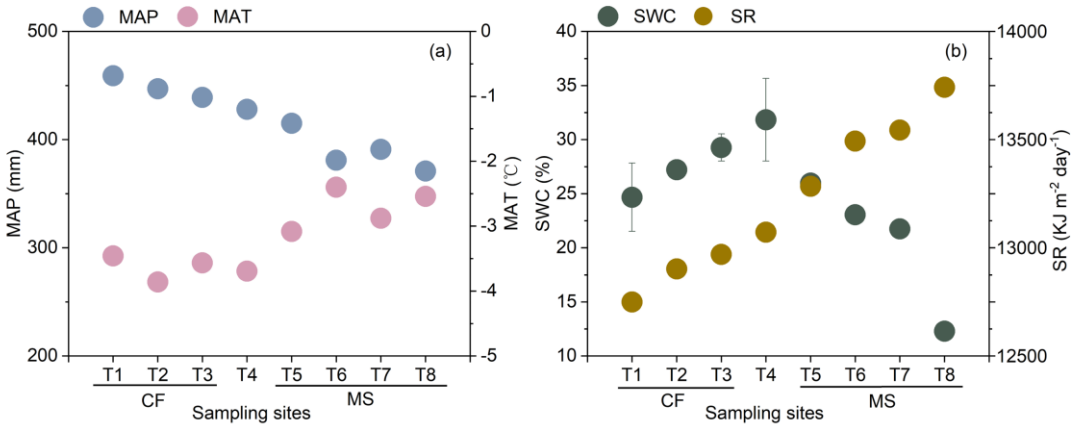


Fig. 2 Changes in environmental factors, including soil water content (SWC) and solar radiation (SR) as shown in panel (a) and mean annual temperature (MAT) and mean annual precipitation (MAP) in panel (b) across sampling sites along the transect of forest-steppe ecotone in Northeast China.

3.2 Exchangeable base cations along forest-steppe ecotone

Concentrations of exchangeable base cations changed significantly along the FSE, ranging from 35.2 to 44.3 cmol kg^{-1} for exchangeable Ca^{2+}, from 3.3 to 3.5 cmol kg^{-1} for exchangeable Mg^{2+}, and from 0.9 to 1.6 cmol kg^{-1} for exchangeable K^{+} across the transects (Fig. 3). Specifically, soil exchangeable Ca^{2+}, Mg^{2+} and K^{+} showed a concave-down parabolic trend from forest to steppe (Fig. 3a-c). On the contrary, exchangeable Na^{+} significantly increased from CF to MS (Fig. 3d). It was unexpected that exchangeable Ca^{2+} and K^{+} was higher in the rhizosphere than that of the bulk soil (p = 0.004 and 0.001, respectively; Fig. 3a, c).

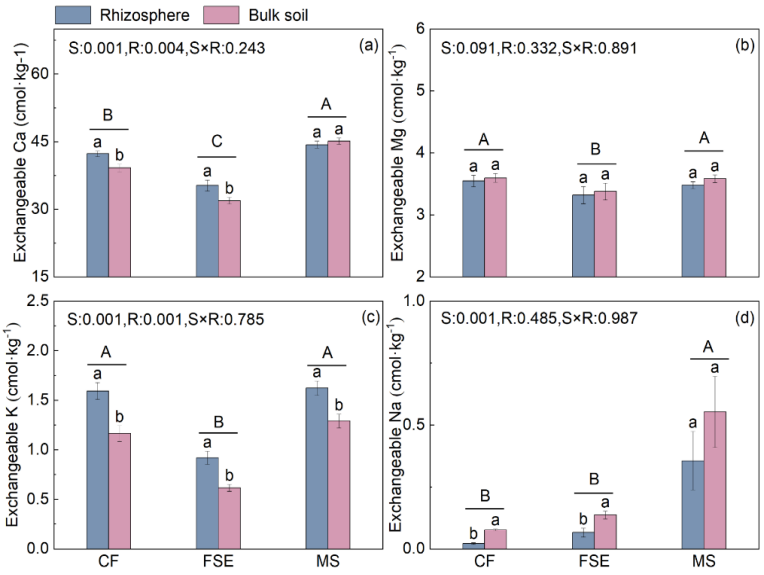


Fig. 3 Responses of (a) exchangeable Ca^{2+}, (b) exchangeable Mg^{2+}, and (c) exchangeable K^{+} and (d) exchangeable Na^{+} from CF to MS in the rhizosphere and bulk soils. Error bars are standard deviations of the mean. Different lowercase letters indicate significant differences among treatments as determined with Duncan's multiple-range test for rhizosphere and bulk soils separately. Abbreviations: CF, Canopy forests; FSE, Forest-steppe ecotone; MS, Meadow-steppes.

Soil pH was the highest in MS ecosystems for both rhizosphere and bulk soils (Fig. 4a). Soil ECEC showed a concave-down parabolic trend from CF via FSE to MS (Fig. 4b) but not exactly followed the variations of pH for rhizosphere and bulk soils (both $p < 0.01$; Fig. 4c, d). Across the three ecosystems, mean value of soil ECEC showed a positive correlation with soil pH for both rhizosphere and bulk soils (Fig. 4c, d, R^2=0.37, p<0.01).

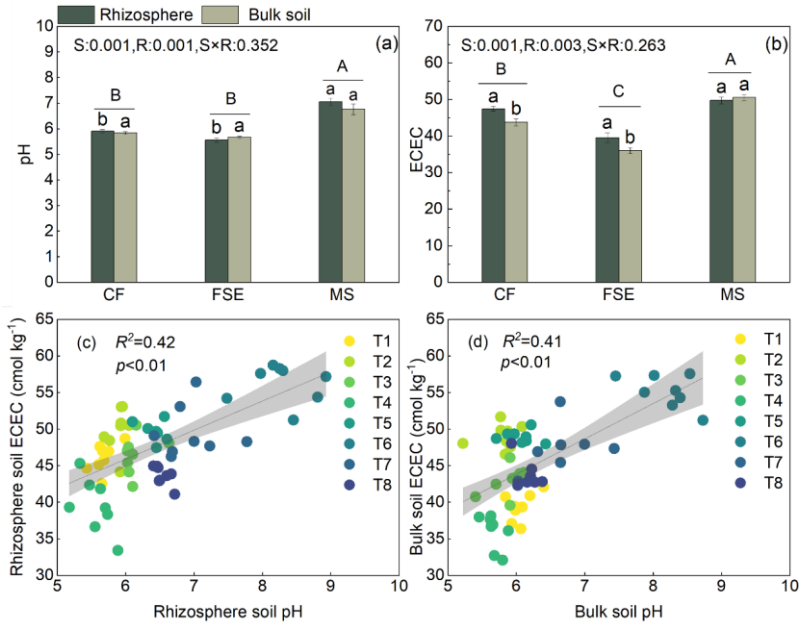


Fig. 4 (a) Change in average values of soil pH from CF to MS in the rhizosphere and bulk soils. Different letters indicate significant differences at $p < 0.05$. Error bars are standard deviations of the mean. (b) Change in average values of effective cation exchange capacity (Ca^{2+}, Mg^{2+}, K^+ and Na^+) from CF to MS in the rhizosphere and bulk soils. Different lowercase letters indicate significant differences among treatments as determined with Duncan's multiple-range test for rhizosphere and bulk soils separately. ECEC: Effective cation exchange capacity. Relationship between soil pH and the average values of the soil exchangeable cations in the (c) rhizosphere and (d) bulk soils in all the site. The shading represents 95% confidence intervals.

3.3 Soil mineral N and biomass of plant life forms

From CF to MS, soil inorganic N concentrations range from 8.3 to 105.3 mg kg^{-1} (Fig. 5a). Specifically, soil inorganic N first increased and then decreased from forest to grassland, as mainly driven by the distribution pattern of NH_4^+ (Fig. 5a). This followed the variational trend of soil water content as mentioned above that could favor soil organic matter mineralization. Herbaceous biomass showed a gradual increase from forest to grassland, ranging from 0.23 to 1.32 t hm^{-2} (Fig. 5b). Shrub biomass was higher at FSE than CF, while tree biomass showed the opposite (Fig. 5c, d).

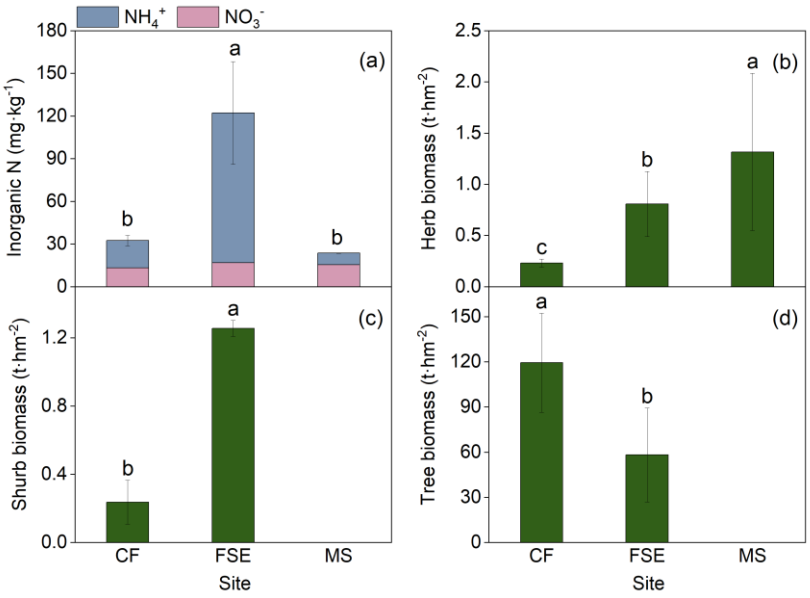


Fig. 5 Change in (a) soil inorganic N concentration and biomass of (b) herbs, (c) shrubs and (d) trees from CF to MS along the transect. Please note that no shrub or tree presented at the MS site. Different letters indicate significant differences among ecosystems as determined with Duncan's multiple-range test.

3.4 Correlation analyses between soil exchangeable base cations and physicochemical properties

Soil pH positively correlated with exchangeable Mg^{2+} and K^{+} in the rhizosphere, and with exchangeable Ca^{2+}, K^{+} and Na^{+} in the bulk soil (Fig. 6a, b). Only for the rhizosphere soil, exchangeable Na^{+} negatively correlated with MAP but positively correlated with MAT and SR (Fig. 6a).



Fig. 6 Correlation analyses between soil properties and exchangeable base cations. In panel, blue

and red colors represent positive and negative correlations, respectively. Larger squares and darker colors indicate proportionally stronger correlations.

Redundancy analysis (RDA) showed that the first axis explained 78.3% and 71.1% of base cation-environment variations for the rhizosphere and bulk soils, respectively, while the second axis explained 12.6% and 18.0%, respectively. On the first major axis, ECEC of the rhizosphere soil increased in parallel to soil pH, SWC and plant biomass (Fig. 7a), but increased inversely with respect to MAT, SR, and inorganic N (Fig. 7a). For the bulk soil, ECEC increased in parallel with MAT, SR and pH but increased inversely with respect to inorganic N, SWC and plant biomass (Fig. 7b).

Particularly, plant biomass and soil pH were the most explanatory factors of soil ECEC for the rhizosphere and bulk soils, respectively (Fig. 7c, d). Solar radiation followed by soil inorganic N were secondary factors contributing to the variations in ECEC for the rhizosphere soil, while they were plant biomass and then SWC for the bulk soil (Fig. 7c, d).

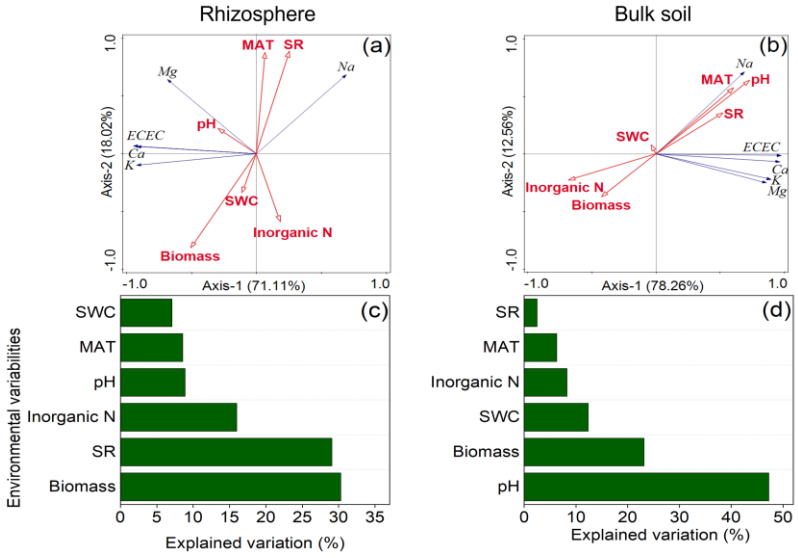


Fig. 7 Ordination plots of the results from the redundancy analysis (RDA) to identify the relationships among exchangeable base cations (Ca^{2+}, Mg^{2+}, K^{+} and Na^{+}), climatic factors, and plant and soil properties as performed for (a) rhizosphere and (b) bulk soils. Main explanatory factors and related explained variations (%) were also shown for (c) rhizosphere and (d) bulk soils. Note that plant biomass was the sum of biomass from trees, shrubs and herbs.

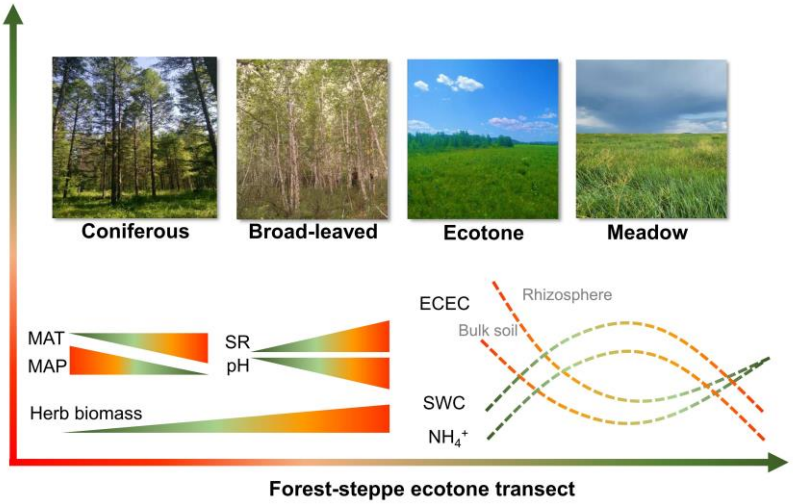


Fig. 8 A conceptual framework depicting the variation and drivers of soil exchangeable base cations along the forest-steppe ecotone transect. MAT, mean annual temperature; MAP, mean annual precipitation; SR, solar radiation; ECEC, exchangeable base cation; SWC, soil water content.

4. Discussion

4.1 Differences in exchangeable base cation from forests to steppes

Our first hypothesis of an increasing trend in soil base cations from CF through FSE to MS was not observed and therefore the environmental gradient theory from Robert Whittaker is not applicable for soil base cations in the studied transect. This finding is not in agreement with a previous study, observing that soil nutrient concentrations in FSE was intermediate across the transect from forests to grasslands in a forest-steppe ecotone of the Samobor Mountains (Croatia) (Érdos *et al*., 2019). This disagreement could be explained by the following reasons.

The main cause underlying the fact of base cations not changing linearly across the gradient was very likely underlying the fact that SWC was the highest in the middle of the gradient, *i.e.*, FSE (Fig. 8). In specific, the highest SWC in FSE that can contribute to a strong displacement of fixed cations in the ECEC with greater potential to be uptaken by plants and also being leached in sites with certain degrees of slope (Wu *et al*., 2020). This suggested that SWC was the unique physicochemical variability that clearly broke the uniformity of variation in ECEC along the transect. Although background N-deposition data for each studied site were not found, the regional area of northeast China, where the transect is located, has experienced a one-fold increase in acid deposition

from 1980s to 2010s (Yu *et al.*, 2017). Relatively low soil pH and possibly associated acid buffering capacity of soil exchangeable complex with consequent base cations mobilization in the FSE fostered the ecosystem to be more prone to leaching loss of base cations, especially under conditions of increasing acid deposition and overuse of N fertilizers (Wang *et al*., 2010; Nkoh *et al*., 2020). Leaching showed little explanatory power for the higher soluble inorganic N in FSE soils, which could be a result of inorganic N input from soil N mineralization outweighing the importance of leaching under favorable soil moisture (Abera *et al.*, 2012). Under high SWC in FSE, soil nitrification process and ammonium volatilization could be inhibited (Clay et al., 1990), favoring the high observed NH_4^+ accumulation in soil (Fig. 5a). This accumulated NH_4^+ could compete with cations for the positions in soil exchangeable complex, making that more cations remained free in soil solution and thus favoring both uptake by plants and losses by leaching (Wang et al., 2017).

In line with this viewpoint of leaching, a decline in soil pH as caused by nine-year N addition depleted soil base cations, especially Ca^{2+}, in a calcareous Eurasian grassland (Cai *et al*., 2017). A global meta-analysis also suggested decreases in soil exchangeable Ca^{2+}, Mg^{2+} and K^+ in boreal forests, temperate forests, and grassland biomes by an overall 24% following N-fertilization-induced soil acidification (Lucas *et al*., 2011). Due to increases in atmospheric acid deposition and N fertilization, soil acidification is becoming more pervasive across global terrestrial ecosystems (Nkoh *et al*., 2020), and this could be more obvious in forest-steppe ecotones given by their low levels of soil base cations. Indeed, it is recognized that anthropogenic activities involved in mining operations, coal-fired power plants, and urban expansion are increasing in this area, especially around MS side (Bardgett *et al*., 2021).

In the current study, one-unit drop of soil pH resulted in decreases in 3.97 cmol kg^{-1} and 4.82 cmol kg^{-1} of soil ECEC in the rhizosphere and bulk soils, respectively, as interpreted from the linear correlations between soil pH and ECEC. Meanwhile, the loss of base cations might restrain plant growth and increase the susceptibility of the ecosystem to other stresses (He *et al*., 2021). In addition, varieties in plant life forms (*e.g*., trees, shrubs and herbs) and species diversity have strong effects on soil nutrient availability (Érdos *et al*., 2019). Particularly with the increase in diversity of herbs from CF to FSE, plant interspecific interactions profoundly decreased soil mineral nutrients concurrent with the enhanced plant competition and probably a more efficient soil exploitation due

to niche differentiation (Wu *et al*., 2020). At the same time, with the increase of interspecific plant competition, the competition between plants and microorganisms would also increase, resulting in less available nutrients left over in soils (Wang *et al*., 2020). Nonetheless, we concluded that the FSE, due to its high SWC and complex vegetation composition and therefore higher inter-specific nutrient competition was lower in soil exchangeable base cations compared with adjacent forest and steppe ecosystems. However, attention was rarely paid to the effect of vegetation composition on soil exchangeable base cations along the transect of FSEs.

4.2 Differences in exchangeable base cation between the rhizosphere and bulk soil

Soil physicochemical properties (*e.g*., pH and SWC) were important for the mobilization of soil exchangeable base cations (Ca^{2+}, Mg^{2+}, K^{+} and Na^{+}). This was evidenced by the conditionally lower pH but higher ECEC (*e.g.*, FSE site) in rhizosphere than bulk soils (Fig. 8). Additionally, higher ECEC in the rhizosphere soil was likely due to soil moisture and plant growth. Under lower soil moisture conditions, drought-induced reduction in soil nutrient uptake by roots could contribute to enrichment of base cations in the rhizosphere (Ge *et al*., 2012). However, higher vegetation biomass increases the nutrient demand of plants especially N and phosphorus from the rhizosphere, thus stimulating the decomposition of soil organic matter and release of base cations (Hong *et al*., 2023). Therefore, significantly higher ECEC in the rhizosphere of CF and FSE than in the bulk soil could be due to the fact that tree roots cause strong and positive priming rhizosphere effect and increase the mineralization rate of soil organic matter by up to four-fold with respect to control soils without living roots (Yin *et al*., 2018). Consistently, a previous study collected 1043 samples from New Zealand soils, found that most variations of the ECEC arose from soil organic matter (Parfitt *et al*., 1995). Moreover, tree roots might release more carboxylates to mobilize mineral-bound nutrients from organic pools to maintain higher concentrations of exchangeable Ca^{2+} and K^{+} in the rhizosphere of CF and FSE ecosystems comparing with grassy biomes (Rengel and Marschner, 2005). Soil originally with high fertility (*e.g*., high contents of soil organic matter) provides sufficient available nutrients for both plant and microbial communities (Tang *et al*., 2021; Tian *et al*., 2020). In contrast, when soil is less fertile, the mass flow from the bulk soil to the rhizosphere is low and consequently shows very limited effects on the differences in base cation concentrations

between the rhizosphere and bulk soil (Tian *et al*., 2020). This might be the case in the meadow steppe. Overall, our results clearly demonstrated that rhizosphere showed a greater capacity of soil nutrient accumulation than that of bulk soil.

As we expected, higher soil exchangeable base cations in the rhizosphere than that of the bulk soil might be also partially caused by the variations in climatic factors. For instance, we found that exchangeable base cations were to a large extent to be affected by SR for both the rhizosphere soil bulk soils. Habitats with higher SR and temperature would show a reduced temperature sensitivity of soil organic matter mineralization through microbial acclimation (Zhou *et al*., 2012). This might partially explain the minor differences in ECEC and exchangeable Ca^{2+} between rhizosphere and bulk soils in MS ecosystems, where plants receive relatively more SR and surface soils showed higher temperature comparing to forests with greater light shading (Bader *et al.*, 2007). A comprehensive meta-analysis found that rhizosphere effects on microbial-driven nutrient cycling were enhanced with the increase of MAT (Lü *et al*., 2023), which was only consistent with our findings of Na^{+} tending to differentiate more between the rhizosphere and bulk soils and being positively correlated with MAT.

5 Conclusions

Instead of showing a gradual increase from forest to steppe ecosystems, soil exchangeable Ca^{2+}, Mg^{2+} and K^{+} concentrations were significantly lower in the FSE ecosystem than CF and MS ecosystems, and thus "Whittaker hierarchical theory" was not accomplished. Lower soil base cations in this FSE might be due to the fact that the FSE has higher soil SWC and more complex vegetation composition, obvious plant stratification and diverse complementary strategies for nutrient utilization as compared to the CF and MS ecosystems. In turn, these conditions of FSE reduces soil base cations, possibly because of strong biological retention and leaching losses associated with higher soil water content. The higher soil ammonium concentration in FSE soil could also contribute to more displacement of cations from soil exchangeable complex to a free position in soil water favoring both cation plant uptake and leaching.

Our study also showed that soil base cations of Ca^{2+} and K^{+} were averagely higher in the rhizosphere than bulk soil across the three ecosystem types, in concert with our hypothesis II.

Rhizosphere effects indeed increased soil exchangeable base cations, but maintained the concave-down parabolic distribution trend of base cations along closed CF to MS. Overall, this study provides new insights into the role of rhizosphere effects with deep differences between plant life forms (such as trees and herbaceous plants) on soil base cations, which has important implications for soil nutrient management and restoration in various ecological transition zones. It also further verified that the changes of soil base cations did not conform to Whittaker's hierarchical theory of transitional zones across forest-steppe ecosystems, which may be helpful to broaden the concept and feasibility of the theory to provide avenues for future research opportunities.

Acknowledgements

This work was supported by the National Natural Science Foundation of China (32222056 and 32071563) and Hebei Natural Science Foundation (C2022201042). Ruzhen Wang would like to acknowledge the support from Youth Innovation Promotion Association of Chinese Academy of Sciences. Josep Peñuelas and Jordi Sardans were supported by the Spanish Government grants PID2020115770RB-I, TED2021-132627 B–I00 and PID2022-140808NB-I00, funded by MCIN, AEI/10.13039/ 501100011033 European Union Next Generation EU/PRTR, and the Fundación Ramón Areces grant CIVP20A6621.

Competing interests

The authors declare that they have not financial or other competing interests.

Data Availability

Data (Han *et al.*, 2023) supporting the findings of this study are available in the Science Data Bank at https://doi.org/10.57760/sciencedb.11163.

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