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Variations in Soil Seed Banks in Sedge Peatlands across an Altitude Gradient

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Abstract: As a key component of the ecosystem, soil seed banks (SSBs) play a vital role in the evolution and renewal of plant communities. Although the pattern and mechanisms of influence of SSBs along the altitudinal gradient have been reported, most studies have focused on forest, grassland and alpine meadow ecosystems. The pattern and factors of SSBs across the altitudinal gradient in sedge peatlands remain largely unknown. Through vegetation surveys and seed germination experiments, we studied the changes in aboveground vegetation and SSBs in sedge peatlands at altitudes ranging from 300 m to 1300 m in the Changbai Mountains, China, and discussed the direct and indirect effects of climatic factors, soil properties and aboveground vegetation on SSBs. The results showed that the richness and density of the SSBs of sedge peatlands decreased with the altitude. Similarly, aboveground vegetation richness and density declined with altitude. A Spearman correlation analysis showed that SSB richness and density were mainly correlated with mean annual temperature, soil total phosphorus and ammonia nitrogen and the plant composition and richness of aboveground vegetation. A structural equation model analysis showed that climatic factors and aboveground vegetation directly affected seed bank richness, while soil properties indirectly affected it by directly affecting aboveground vegetation. Climatic factors, soil properties and aboveground vegetation directly affected SSB density, and soil properties indirectly affected it by directly affecting aboveground vegetation. This finding enhances our understanding of the altitude patterns of the SSBs in sedge peatlands and the response to future climate and environmental changes.

Keywords: sedge peatlands; altitude; soil seed bank; aboveground vegetation; climatic factors; soil properties

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1. Introduction

Climate change has far-reaching effects on the distribution and regeneration of vegetation, and these effects may depend on the ability of the regenerating species to cope with the changing climate and environment [1]. Soil seed banks (SSBs) constitute an important part of plant regeneration strategies, facilitating the resilience of aboveground plant communities that are resistant to external disturbances and harsh environments [2]. However, the flexibility of SSBs to respond to climate and environmental changes may vary significantly across geographical regions, ecosystem types and vegetation zones [1,3,4]. Further insight into the responses of SSBs across their distributional ranges could assist in improving the accuracy of climate and environmental change predictions.

The climate factors, soil environment and vegetation change regularly with the altitude in mountains [5,6], which provides an ideal experimental condition for studying the dynamics of SSBs across climatic and environmental gradients. Former studies which focused on SSB dynamics across the altitude gradient presented conflicting conclusions. Several studies have shown that the richness and density of SSBs increase with altitude [7,8], partly because lower temperatures, fewer predators [9], fewer pathogenic fungi [10] and lower seed embryo metabolic rates [11] were more favorable for seed preservation at higher altitudes. In addition, the vegetation types changed with the altitude, which affected the SSB size via seed input from vegetation [3,12]. However, other studies have shown that the richness and density of SSBs decrease with altitude [13–15]. The harsh environment at high altitudes may reduce seed production and vegetation richness [15,16]. The discrepancy in these findings is due to the differences in vegetation types or ecosystems. Most previous studies on changes in SSBs along altitudinal gradients have focused on forest [6,12], grassland [7,13] and alpine meadow ecosystems [3,15]. In peatlands, as one of the most important terrestrial ecosystems, the distribution of vegetation types is non-zonal, which may have some influence on SSBs [17–19]. However, the dynamics of SSB in relation to altitudes in peatlands remain unknown.

Previous studies have shown that the unique environmental conditions of peatlands, such as higher humidity and SOC and lower nutrients, have an important influence on the establishment and maintenance of SSBs [17–19]. Higher SOC storage has a positive feedback effect on vegetation type and productivity by increasing the soil water holding capacity and maintaining soil fertility, which can be beneficial for an SSB [17,18]. Although low nutrient environments limit the growth of plant species, they can promote the reproduction of certain species, such as sedges [17,20,21]. Climate change is also an important factor affecting SSBs. Rising temperatures can stimulate seed dormancy and increase seed germination rates, while precipitation can not only stimulate seed germination but also accelerate seed mortality by increasing the activity of pathogenic fungi [1,3,15]. Aboveground vegetation is the main source for SSBs. Typically, changes in species composition and the cover of aboveground vegetation will have a significant impact on SSBs [2–4]. Although these studies have revealed the influence mechanism of SSBs, existing research is still not systematic and comprehensive. The formation and maintenance of SSBs is a complex ecological process involving the interaction of many biotic and abiotic factors. Further research is required to elucidate the ways in which the peatland climate, soil and vegetation characteristics change with altitude, and the ways in which these factors interact drive changes in SSBs.

The Changbai Mountain range is one of the largest peatland distribution areas in China. Sedge peatlands cover over 70% of the peatlands in this region. Tussock-forming *carex* species, such as *Carex meyeriana*, *C. schmidtii*, *C. limosa* and *C. lasiocarpa*, are the dominant species in these peatlands [22]. The purpose of this study was to understand SSB changes with altitude and their influencing factors in sedge peatlands. We explored SSBs, aboveground vegetation, climate and soil properties across an altitude gradient from 300 m to 1300 m in sedge peatlands. We wanted to explore the following: (1) How do the richness and density of SSBs change with altitude? (2) How do climatic factors, soil properties and aboveground vegetation drive SSB changes in peatlands across the altitudinal gradient?

2. Materials and Methods

2.1. Soil Sampling and Aboveground Vegetation Survey

Peatlands are widely distributed in the area of 300–1200 m above sea level in the Changbai Mountains, of which 70% are sedge peatlands dominated by tussock-forming *Carex* [22]. The region is of a temperate continental humid climate, with a mean annual temperature (MAT) and mean annual precipitation (MAP) range of 0.9–3.3 °C and 560–790 mm.

In April 2023, six study sites were selected across an altitude gradient (327, 540, 615, 900, 1005, 1280 m) along the Changbai Mountain range (Figure 1). Three plots (10 m × 10 m) were set up on each site, with the adjacent plots being > 20 m apart. Five quadrats

(25 cm × 25 cm × 10 cm) were randomly collected in each plot, and 90 samples were taken (6 sites × 3 plots/site × 5 samples/plot). The vegetation survey was conducted in August 2023. Three 1 m × 1 m points near the SSB sampling locations were set up at each of the three plots in each site. The species name, density, the coverage and height of each individual species, and the total coverage of the standing vegetation were recorded at each point. The vegetation in the quadrat was identified according to the description in 'Wild Vascular Plants of Wetlands in Northeast China' [23]. Vegetation species richness refers to the number of different vegetation species that exist in a specific area. It reflects the degree of vegetation species diversity in the ecosystem [24]. Vegetation density refers to the number of individuals of a given vegetation species per unit area (or volume) at a given time. It reflects the distribution of the vegetation species in the ecosystem and the size of the population [18]. The richness (VR) and density (VD) of the aboveground vegetation were calculated for each site. During the seedling germination experiment, the mean value of species and seedlings germinated from the 30 pots for each site were calculated as SSB richness (SR) and density (SD), respectively [3,4].

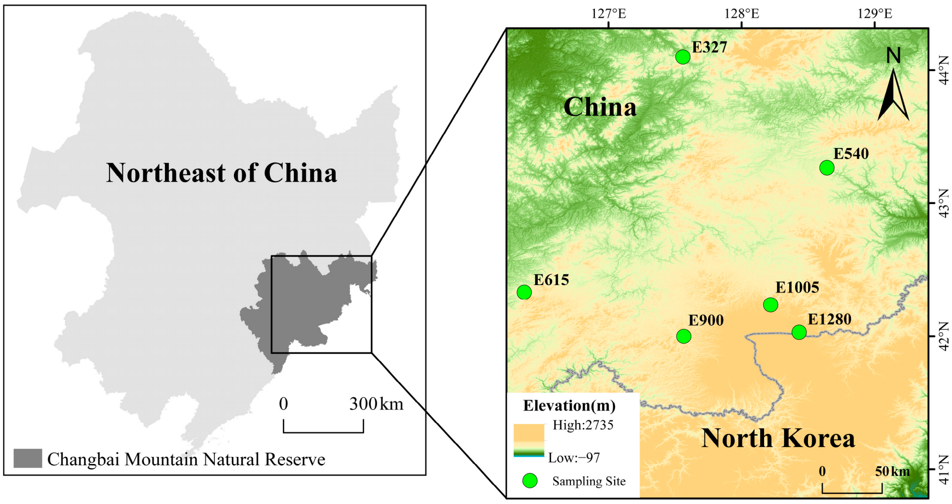

Figure 1. Location of the study sites along an altitudinal gradient on the Changbai Mountains, China.

2.2. Germination of Soil Seed Bank

Soil samples taken from each plot were mixed evenly and then were evenly spread with a thickness of 2 cm in 10 pots (25 cm× 25 cm) in the greenhouse. The bottoms of the pots were filled with sand. The pots were placed in a tank, and freshwater was added to the tank regularly to keep the soil moist. During the germination experiment, the emergedemerging seedlings were recorded and cut from each pot every two weeks. Seedlings germinated in greenhouses were identified according to the description in 'Wild Vascular Plants in Wetlands of Northeast China' [23]. The experiment lasted for 5 months.

2.3. Soil Properties Measurement

When SSB samplings were taken in April 2023, 6 soil cores (depth: 10 cm; diameter: 5 cm) were randomly collected in each plot. Soil organic carbon (SOC) was determined with the dichromate digestion method [25]. Soil water content (SWC) was determined with a gravimetric method [26]. Soil pH was measured with an acidity meter with a soil to water ratio of 1:5. Total nitrogen (TN) was measured with the semi-microKelvin method. Total phosphorus (TP) was determined by the concentrated sulfuric acid oxidation-molybdenum anti-colorimetric method [27]. Nitrate nitrogen (NO_3^--N) and ammonium nitrogen NH_4^+-N) were measured with a Continuous Flow Analyzer (SKALAR SAN++, The Netherlands). Available phosphorus (AP) was measured with an Olsen method [28].

2.4. Statistical Analysis

One-way ANOVA was used to compare the differences in soil environmental factors between the six sites in SPSS 25.0. The data were log-transformed to satisfy the test of homogeneity and normality. The linear regression in SPSS 25.0 was employed to find the relationships of SSB oil seed bank richness and density, standing vegetation richness and density, and the altitude. The dependent variables and residuals were tested for normality to meet the preconditions of the regression analysis.

Non-metric multidimensional scaling (NMDS) was conducted to study species composition similarities between the standing vegetation and SSB. The 'vegan' package was used for the NMDS analysis in R 4.3.2 [29]. A Spearman correlation was conducted to evaluate the correlation between SSBs and climatic factors, soil environmental factors, and aboveground vegetation with the package 'Corrplot' in R 4.3.2 [30]. The partial least squares path model (PLS-PM) was conducted to elucidate the direct and indirect contributions of climate, soil properties and aboveground vegetation to the SSB. Variables with strong correlations in the Spearman correlation analysis were incorporated into the structural equation model. The analysis was conducted using a 'plspm' package in R 4.3.2 [31].

3. Results

3.1. Climate and Soil Property Change with the Altitude

As the altitude increased from 327 m to 1280 m, the MAT declined from 3.34 °C to 0.96 °C and the MAP rose from 561.25 mm to 793 mm. TP had a decreasing trend with the altitude (Table 1). The SWC was the highest at 900 m (90.18%) and lowest in 327 m (82.36%). The soil was acidic at all sites, with the highest pH (6.01) at 540 m and the lowest pH (4.66) at 900 m. The SOC was high (≥30%) at all sites. TN (21.01 mg/g) and NO_3^--N (2.26 mg/g) were higher at 540 m than other sites. The AP was the highest at 900 m (14.89 mg/kg) and lowest in 1005 m (5.98 mg/kg).

3.2. Vegetation and Soil Seed Bank Change with the Altitude

The vegetation survey recorded 51 species belonging to 29 families and 39 genera. Among them, Cyperaceae species are dominant, mainly including *C. meyeriana*, *C. schmidtii*, *C. lasiocarpa* and *C. limosa* (Table S1). The richness and species density of aboveground vegetation declined with altitude (Figure 2). As the dominant functional group, the density of sedge species decreased with the altitude.

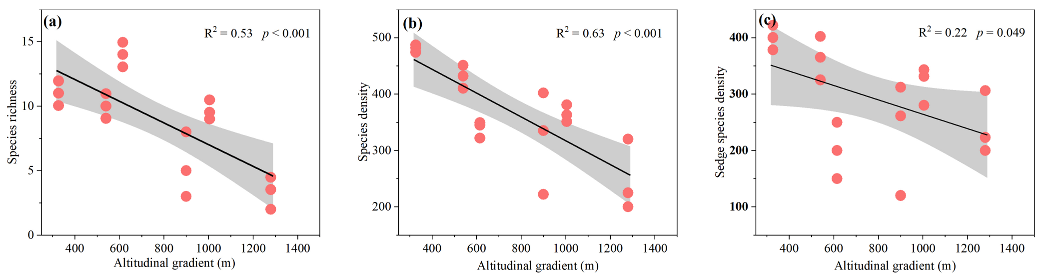

Figure 2. The relationship between species richness (**a**), species density (**b**), sedge species density (**c**) of aboveground vegetation and the altitude in the sedge peatlands of the Changbai Mountains. A linear regression was shown with the 95% confidence interval of the fit. The red dot represents the average of each plot.

A total of 46 species were identified from the seedlings germinated in the greenhouse, belonging to 25 families and 36 genera. Among them, the Cyperaceae species and Juncusiaceae species are dominant, mainly including *C. meyeriana*, *C. schmidtii*, *Juncus effusus*, *Eleocharis dulcis* and so on (Table S2). SSB richness and density declined with the altitude (Figure 3). The seed density of dominant sedge species decreased with the altitude.

Table 1. Site information and general climate and soil characteristics in the sedge-dominated peatlands of the Changbai Mountains, China.

Site Name	Site Location	Altitude (m a.s.l)	MAT (°C)	MAP (mm)	SWC (%)	pH	SOC (%)	TN (mg/g)	TP (mg/g)	AP (mg/kg)	NH_4^+-N (mg/kg)	NO_3^--N (mg/kg)
E327	44°6′1.73″ N, 127°33′33″ E	327	3.34	561.25	82.36 ± 0.46 c	5.94 ± 0.13 a	31.34 ± 0.22 b	20.30 ± 0.79 ab	1.28 ± 0.07 b	7.08 ± 2.19 bc	53.84 ± 0.96 bc	1.43 ± 0.48 b
E540	43°16′4.31″ N, 128°38′29″ E	540	3.25	564.42	85.43 ± 0.44 b	6.01 ± 0.12 a	38.89 ± 1.31 a	21.01 ± 0.51 a	1.65 ± 0.01 a	7.42 ± 0.08 bc	42.63 ± 5.20 bcd	2.26 ± 0.03 a
E615	42°20′ N, 126°22′ E	615	4.00	823.00	82.98 ± 0.99 c	5.77 ± 0.33 ab	31.13 ± 2.86 b	15.50 ± 5.05 b	1.25 ± 0.04 b	10.13 ± 4.85 abc	91.91 ± 14.40 a	0.84 ± 0.09 b
E900	42°00′03″ N, 127°33′57″ E	900	2.50	693.50	90.18 ± 0.64 a	4.66 ± 0.07 c	38.81 ± 0.57 a	17.02 ± 2.08 ab	0.94 ± 0.05 c	14.89 ± 0.68 a	62.34 ± 13.16 b	1.33 ± 0.27 b
E1005	42°14′21″ N, 128°13′07″ E	1005	2.21	706.00	89.19 ± 1.79 a	5.88 ± 0.02 a	41.01 ± 0.82 a	14.97 ± 0.42 b	0.79 ± 0.04 d	5.98 ± 0.06 c	38.77 ± 9.17 cd	1.17 ± 0.02 b
E1280	42°01′55″ N, 128°25′58″ E	1280	0.96	793.00	83.86 ± 0.46 bc	5.45 ± 0.05 b	33.56 ± 1.40 b	19.56 ± 0.16 ab	0.73 ± 0.00 d	11.96 ± 0.88 ab	28.69 ± 8.83 d	1.13 ± 0.36 b

Note: MAT, mean annual temperature; MAP, mean annual precipitation; SWC, soil water content; SOC: soil organic carbon; TN, total nitrogen; TP, total phosphorus; AP, available phosphorus; NH_4^+-N, ammonium nitrogen; NO_3^--N, nitrate nitrogen. Different letters within each column indicate significant differences among study sites based on one-way ANOVA and Tukey's test ($p < 0.05$).

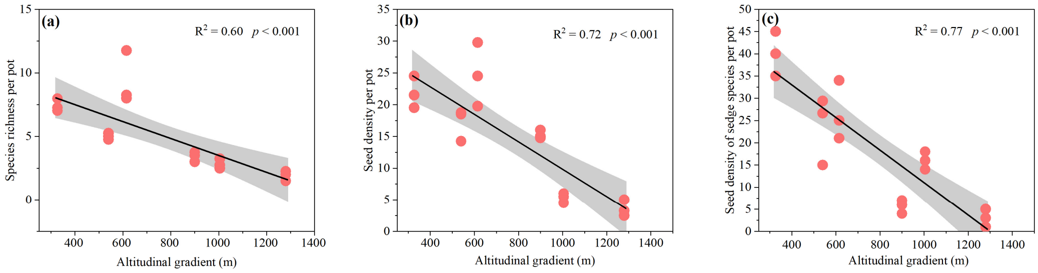

Figure 3. The relationship between species richness (**a**), total seed density (**b**) and seed density of sedge species (**c**) of soil seed banks and the altitudes of sedge peatlands in the Changbai Mountains. A linear regression was shown with the 95% confidence interval of the fit. The red dot represents the average of each plot.

3.3. Relationship between Climate, Soil Property, Aboveground Vegetation, and Soil Seed Bank

SSBs demonstrate significant correlations with climatic conditions, soil characteristics, and aboveground vegetation. Specifically, species richness in an SSB is positively correlated with the MAT, TP, NH_4^+-N, VR, and species composition (NMDS1; Figure 4). Conversely, it shows a negative correlation with the SWC and SOC. Furthermore, the density of the SSB shows a significant positive correlation with MAT, TP, NH_4^+-N, VR, VD, and species composition (NMDS1).

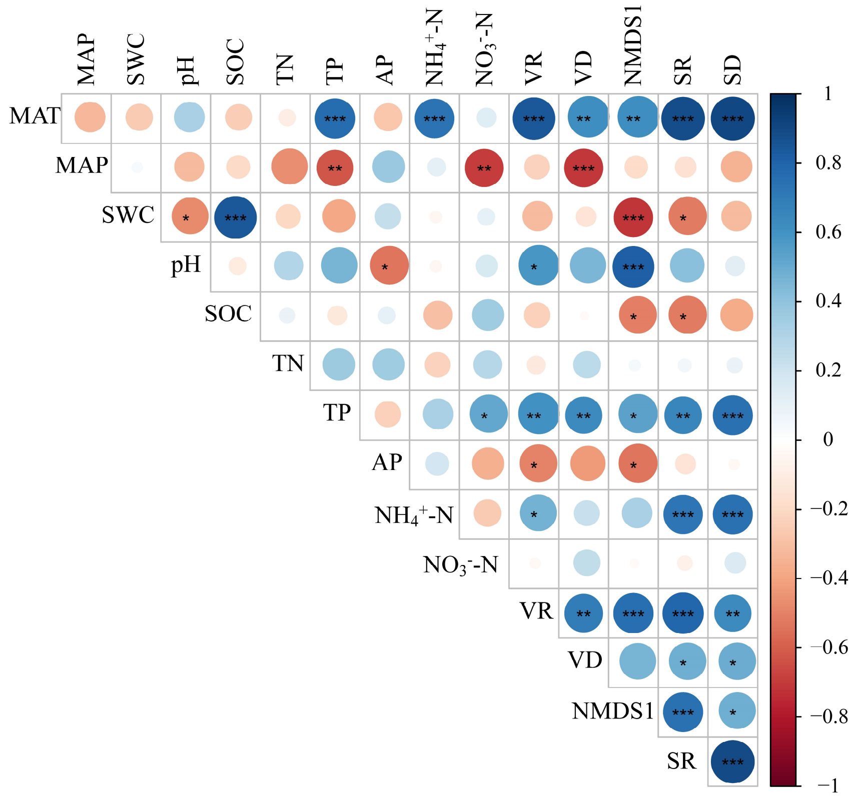

Figure 4. The relationship between climate, soil properties, aboveground vegetation and soil seed banks in sedge peatlands of the Changbai Mountains. The pairwise correlation of these variables is represented by the color gradient, which represents the spearman correlation coefficient. Red indicates negative correlation, blue indicates positive correlation. *** means $p < 0.001$, ** means $p < 0.01$, * means $p < 0.05$. SD, seed density of soil seed banks; SR, species richness of soil seed banks; VR, species richness of aboveground vegetation; VD, species density of aboveground vegetation; NMDS1, NMDS1 score of vegetation species composition; SWC, soil water content; SOC, soil organic carbon; TN, total nitrogen; TP, total phosphorus; AP, available phosphorus; NH_4^+-N, ammonium nitrogen; NO_3^--N, nitrate nitrogen.

3.4. Effects of Climate, Soil Property, Aboveground Vegetation on Soil Seed Bank

The SEM adequately fit our data (GoF = 0.65; Figure 5). SEM analysis showed that climatic factors and aboveground vegetation directly affected SSB richness, while soil properties indirectly affected SSB richness by directly affecting the aboveground vegetation. Climate factors, aboveground vegetation, and soil properties directly influenced seed density. Additionally, soil properties indirectly affected SSB density by influencing aboveground vegetation.

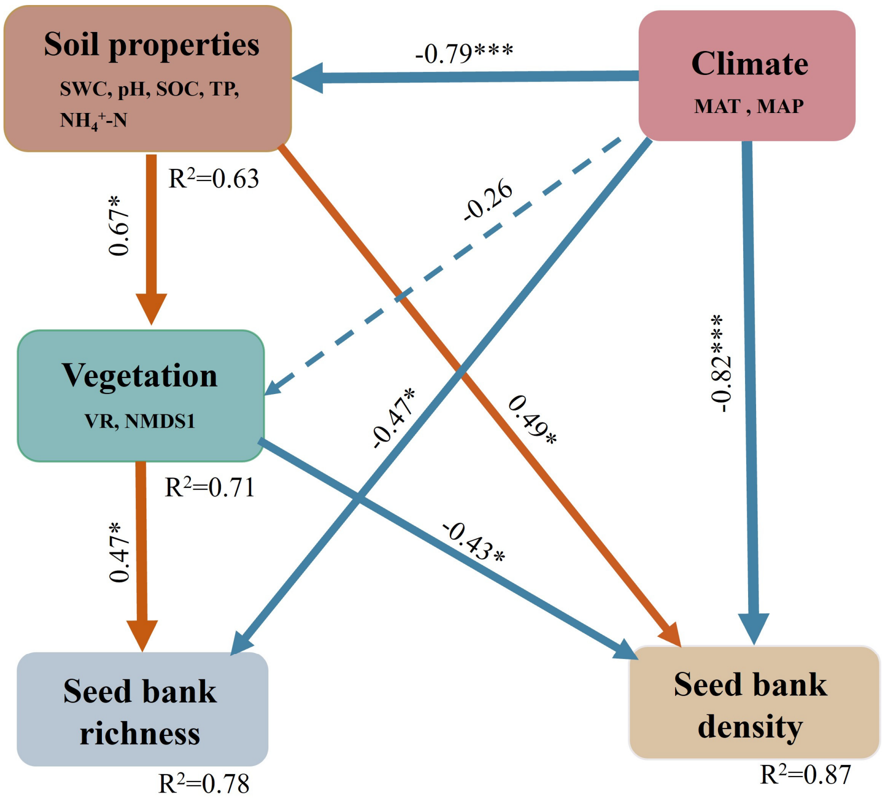

Figure 5. Partial least squares structural equation model (PLS-SEM) for the effects of climate factors (MAT, MAP), soil properties (SWC, pH, SOC, $NH_4{}^+$-N, $NO_3{}^-$-N) and aboveground vegetation (VR, NMDS1) on the species richness and seed density of soil seed banks. The red line and the blue line indicate positive and negative effects, respectively, and the dotted line indicates no significant effect. The linewidth is proportional to the effect intensity. *** means $p < 0.001$, * means $p < 0.05$. VR, species richness of aboveground vegetation; NMDS1, NMDS1 score of vegetation species composition; SWC, soil water content; SOC, soil organic carbon; TP, total phosphorus; $NH_4{}^+$-N, ammonium nitrogen.

4. Discussion

4.1. Variations in Soil Seed Bank Richness in Sedge Peatlands across the Altitude Gradient

Former studies have found that climate factors along the altitude gradient significantly affect SSB composition and richness [3,11]. SSB richness increased with altitudes because the suitable temperature condition at lower altitudes helped break dormancy and promoted seed germination of various species, thus decreased seed storage in soils [11]. The colder environment at higher altitudes generally has fewer predators [9] and pathogenic fungi [10], as well as lower metabolic rates of seed embryos [11], making it more conducive to the persistence of seeds in soils. However, our results showed that SSB richness correlated positively with MAT (Figure 4). The reason might be that the change in MAT along the altitude significantly affects seed production in peatlands. The higher MAT at lower altitudes can promote seed production by advancing the phenology of flowering and fruiting [32]. The richness of the seed rain at lower altitudes in *Carex* peatlands was higher than higher altitudes [17]. In addition, the increase in precipitation may directly reduce SSB richness by promoting seed germination and increasing pathogenic fungi in grasslands [15]. However, the MAP was not related with SSBs in our study (Figure 4); the reason may be that peatlands are usually wetting and seeds in soils are, relatively, not sensitive to precipitation.

Soil properties play an important role in vegetation establishment and SSB recruitment [4,33]. The changes in climate factors with altitude influence the rate of enzymatic hydrolysis reaction and organic matter decomposition [34–36], as well as nutrient transport and transformation [37], which create large variations in soil environments along the altitude. The vegetation richness correlated with soil pH, NH_4^+-N and TP in our study. Soil pH regulated species composition and richness in mountain grasslands and forests, as well as the arctic tundra [38,39]. The peatland soils in our study were acidic, and the vegetation richness increased with soil pH (Table 1, Figure 4). Although certain sedge species could survive in sites with a lower soil pH, diverse species from different functional groups were found in neutral and weakly acidic soils. N and P are considered to be the main factors limiting the growth of plants in terrestrial ecosystems [40,41]. Plant growth and litter decomposition are usually faced with N and/or P limitation in peatlands [21,33,42]. The higher levels of NH_4^+-N and TP increased the species richness of aboveground vegetation in our study (Figure 4), especially the dominant sedge species, which is consistent with other studies [20,43–45]. In our study, the variations in vegetation composition and richness caused by climate and soil environmental change significantly affected SSB richness (Figure 5 and Figure S1). The lower MAT and soil nutrients at higher altitudes decreased aboveground vegetation richness so that seed input and SSB richness were expected to decrease (Figures 4 and 5). This finding highlights the direct and indirect roles of climate and environmental change and aboveground vegetation dynamics in regulating SSB richness in peatlands.

4.2. Variations in Soil Seed Bank Density in Sedge Peatlands along the Altitude Gradient

SSB size is determined by seed input, the external environment, to maintain seed longevity, and the persistence of seeds themselves [46]. The input process of SSBs includes flower production, seed setting, seed dispersal and seed incorporation into the soil [47], which could be regulated by climate. Colder and wetter climatic conditions may reduce flowering and seed setting [48]. Temperature shifts affect the hormone level and gene expression in plants, which regulate the time of flowering and fruiting [49]. Temperature also influences the plant–pollinator interactions, which strongly affects seed production [50]. Increased precipitation may increase the presence of pathogens in soils, thereby reducing seed longevity [10]. Our study found that SSB density decreased with the altitude, which is directly affected by the MAT (Figures 2b and 3). The main reason is that a higher MAT at lower altitudes may increase seed production, especially the dominant sedge species [51], although the increase in temperature may also reduce the size of SSBs by promoting seed germination [15].

Soil environment is closely related to SSB recruitment and aboveground vegetation regeneration. In our study, TP and NH_4^+-N directly affected SSB density (Figures 3 and 4). N and P are commonly limited nutrients in peatland ecosystems [51]. Former studies found that nutrient addition significantly reduced the number of seedlings germinated from soils, and the response is species specific [52–54]. For example, nitrogen enrichment could promote seed production and seedling germination of certain species and increase plant growing in a freshwater wetland [55], while another study found that nitrogen addition inhibited seed germination of Nymphaea but had no effect on other wetland species in the Okefenokee Swamp [52]. In our study, the site with higher N and P nutrients had higher seed density in soils (Figure 3), which maybe because high soil nutrients promote seed production and seedling growth in sedge peatlands. In addition, soil properties, including soil pH and SWC, regulated vegetation composition and richness, which directly affected SSB density in our study (Figures 3 and 4). Many studies have shown that the species composition in peatlands is closely related to pH [56,57]. Peatland soils in the Changbai

Mountains are acidic, and sedge species could survive in soils with low pH levels. However, other species, including grass, forb and rush species, tend to grow in weakly acidic or neutral soil environments, which further influence seed production and germination. Thus, the change in aboveground vegetation composition and richness across the environmental gradient significantly affects SSB size in peatlands.

5. Conclusions

This study first investigated the pattern of SSB changes in relation to altitude in sedge peatlands. SSB richness and density decreased significantly as the altitudes increased. Climatic conditions and aboveground vegetation directly affected SSB richness and density along the altitude gradient. Climate and soil properties indirectly affected the SSBs by influencing vegetation composition and richness.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/d16090571/s1, Figure S1: Nonmetric multidimensional scaling (NMDS) ordination of the species composition of the sedge peatland based on relative density data for the soil seed bank and aboveground plant community (stress value = 0.141) along an altitudinal gradient on the Changbai Mountain. Blue circles and triangles represent the soil seed banks and aboveground plant communities of the sedge peatland, respectively. Coloration from dark blue to light blue represents an increase in altitude. Table S1: Species and their densities in vegetation plots at six altitudes in the Changbai Mountain area (mean ± standard error). Table S2: List of species of germinated seedlings and their seed density in each pot in the greenhouse germination experiment (mean ± standard error).

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Institutional Review Board Statement: Not applicable.

Data Availability Statement: The datasets used and/or analyzed during the current study are available from the corresponding author on reasonable request.

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Conflicts of Interest: The authors declare no conflicts of interest.

References

1. Middleton, B.; McKee, K. Soil warming alters seed-bank responses across the geographic range of freshwater Taxodium distichum (Cupressaceae) swamps. *Am. J. Bot.* **2011**, *98*, 1943–1955. [CrossRef]
2. Ooi, M.K.J. Seed bank persistence and climate change. *Seed Sci. Res.* **2012**, *22*, S53–S60. [CrossRef]
3. Ma, M.; Collins, S.L.; Du, G. Direct and indirect effects of temperature and precipitation on alpine seed banks in the Tibetan Plateau. *Ecol. Appl.* **2020**, *30*, e02096. [CrossRef] [PubMed]
4. Zhao, Y.; Wang, G.; Zhao, M.; Wang, M.; Liu, B.; Jiang, M. How soil salinization and alkalinization drive vegetation change in salt-affected inland wetlands. *Plant Soil* **2022**, *480*, 571–581. [CrossRef]
5. Kharkwal, G.; Mehrotra, P.; Rawat, Y.S.; Pangtey, Y.P.S. Phytodiversity and growth form in relation to altitudinal gradient in the Central Himalayan (Kumaun) region of India. *Curr. Sci.* **2005**, *89*, 873–878.
6. Sharma, C.M.; Suyal, S.; Gairola, S.; Ghildiyal, S.K. Species richness and diversity along an altitudinal gradient in moist temperate forest of Garhwal Himalaya. *Am. J. Sci.* **2009**, *5*, 119–128.
7. Funes, G.; Basconcelo, S.; Díaz, S.; Cabido, M. Seed bank dynamics in tall-tussock grasslands along an altitudinal gradient. *J. Veg. Sci.* **2003**, *14*, 253–258. [CrossRef]
8. Espinosa, C.I.; Luzuriaga, A.L.; De La Cruz, M.; Montero, M.; Escudero, A. Co-occurring grazing and climate stressors have different effects on the total seed bank when compared to the persistent seed bank. *J. Veg. Sci.* **2013**, *24*, 1098–1107. [CrossRef]

9. Noroozi, S.; Alizadeh, H.; Mashhadi, H.R. Temperature influences postdispersal predation of weed seeds. *Weed Biol. Manag.* **2016**, *16*, 24–33. [CrossRef]
10. Blaney, C.S.; Kotanen, P.M. Effects of fungal pathogens on seeds of native and exotic plants: A test using congeneric pairs. *J. Appl. Ecol.* **2001**, *38*, 1104–1113. [CrossRef]
11. Murdoch, A.J.; Ellis, R.M. Dormancy, viability and longevity. In *Seeds, the Ecology of Regeneration in Plant Communities*; Fenner, M., Ed.; CABI: London, UK, 2000; pp. 183–214.
12. Luo, X.; Cao, M.; Zhang, M.; Song, X.; Li, J.; Nakamura, A.; Kitching, R. Soil seed banks along elevational gradients in tropical, subtropical and subalpine forests in Yunnan Province, southwest China. *Plant Divers.* **2017**, *39*, 273–286. [CrossRef] [PubMed]
13. Ortega, M.; Levassor, C.; Peco, B. Seasonal dynamics of Mediterranean pasture seed banks along environmental gradients. *J. Biogeogr.* **1997**, *24*, 177–195. [CrossRef]
14. Ma, M.; Zhou, X.; Wang, G.; Ma, Z.; Du, G. Seasonal dynamics in alpine meadow seed banks along an altitudinal gradient on the Tibetan Plateau. *Plant Soil* **2010**, *336*, 291–302. [CrossRef]
15. An, H.; Zhao, Y.; Ma, M. Precipitation controls seed bank size and its role in alpine meadow community regeneration with increasing altitude. *Glob. Chang. Biol.* **2020**, *26*, 5767–5777. [CrossRef] [PubMed]
16. Jalili, A.; Hamzeh'ee, B.; Asri, Y.; Shirvany, A.; Yazdani, S.; Khoshnevis, M.; Zarrinkamar, F.; Ghahramani, M.-A.; Safavi, R.; Shaw, S.; et al. Soil seed banks in the Arasbaran Protected Area of Iran and their significance for conservation management. *Biol. Conserv.* **2003**, *109*, 425–431. [CrossRef]
17. Wang, M.; Han, Y.; Xu, Z.; Wang, S.; Jiang, M.; Wang, G. Hummock-hollow microtopography affects soil enzyme activity by creating environmental heterogeneity in the sedge-dominated peatlands of the Changbai Mountains, China. *Ecol. Indic.* **2021**, *121*, 107187. [CrossRef]
18. Wang, M.; Wang, S.; Wang, G.; Jiang, M. Soil seed banks and restoration potential of tussock sedge meadows after farming in Changbai Mountain, China. *Mar. Freshw. Res.* **2020**, *71*, 1099–1106. [CrossRef]
19. Benavides, J.C.; Vitt, D.H.; Cooper, D.J. The high-elevation peatlands of the northern Andes, Colombia. *Plants* **2023**, *12*, 955. [CrossRef]
20. Welker, J.M.; Jónsdóttir, I.S.; Fahnestock, J.T. Leaf isotopic (δ 13 C and δ 15 N) and nitrogen contents of Carex plants along the Eurasian Coastal Arctic: Results from the Northeast Passage expedition. *Polar Biol.* **2003**, *27*, 29–37. [CrossRef]
21. Wang, M.; Moore, T.R.; Talbot, J.; Richard, P.J.H. The cascade of C:N:P stoichiometry in an ombrotrophic peatland: From plants to peat. *Environ. Res. Lett.* **2014**, *9*, 024003. [CrossRef]
22. Wang, M.; Wang, G.; Wang, S.; Jiang, M. Structure and Richness of Carex meyeriana Tussocksin Peatlands of Northeastern China. *Wetlands* **2018**, *38*, 15–23. [CrossRef]
23. Yi, F. *Wild Vascular Plants in Wetlands of Northeast China*; Science Press: Beijing, China, 2008.
24. Granot, I.; Belmaker, J. Niche breadth and species richness: Correlation strength, scale and mechanisms. *Glob. Ecol. Biogeogr.* **2020**, *29*, 159–170. [CrossRef]
25. Kalembasa, S.J.; Jenkinson, D.S. A comparative study of titrimetric and gravimetric methods for the determination of organic carbon in soil. *J. Sci. Food Agric.* **1973**, *24*, 1085–1090. [CrossRef]
26. Jackson, R.B.; Anderson, L.J.; Pockman, W.T. Measuring Water Availability and Uptake in Ecosystem Studies. In *Methods in Ecosystem Science*; Sala, O.E., Jackson, R.B., Mooney, H.A., Howarth, R.W., Eds.; Springer: New York, NY, USA, 2000; pp. 199–214. [CrossRef]
27. Parkinson, J.A.; Allen, S.E. A wet oxidation procedure suitable for the determination of nitrogen and mineral nutrients in biological material. *Commun. Soil Sci. Plant Anal.* **1975**, *6*, 1–11. [CrossRef]
28. Zhou, Q.; Gibson, C.E.; Zhu, Y. Evaluation of phosphorus bioavailability in sediments of three contrasting lakes in China and the UK. *Chemosphere* **2001**, *42*, 221–225. [CrossRef]
29. Oksanen, J.; Blanchet, F.G.; Kindt, R.; Legendre, P.; Minchin, P.R.; O'Hara, R.B.; Wagner, H.H. Community Ecology Package Version 2.6-4. 2022. Available online: https://cran.rproject.org/web/packages/vegan/vegan.pdf (accessed on 21 December 2023).
30. Wei, T.Y.; Simko, V. R Package 'Corrplot': Visualization of a Correlation Matrix. R Package Version 0.92. 2021. Available online: https://cran.rproject.org/web/packages/corrplot/corrplot.pdf (accessed on 23 December 2023).
31. Sanchez, G.; Trinchera, L.; Russolillo, G. Plspm: Tools for Partial Least Squares Path Modeling (PLS-PM). R Package Version 0.5.0. 2023. Available online: https://CRAN.R-project.org/package=plspm (accessed on 27 December 2023).
32. Piao, S.; Liu, Z.; Wang, T.; Peng, S.; Ciais, P.; Huang, M.; Ahlstrom, A.; Burkhart, J.F.; Chevallier, F.; Janssens, I.A.; et al. Weakening temperature control on the interannual variations of spring carbon uptake across northern lands. *Nat. Clim. Chang.* **2017**, *7*, 359–363. [CrossRef]
33. Wang, M.; Wang, Y.; Wang, S.; Jiang, M.; Wang, G. The type of soil amendment during farming affects the restorability of peatlands. *Ecol. Eng.* **2023**, *189*, 106916. [CrossRef]
34. Kirschbaum, M. The temperature dependence of organic-matter decomposition—Still a topic of debate. *Soil Biol. Biochem.* **2006**, *38*, 2510–2518. [CrossRef]
35. Lawrence, C.R.; Neff, J.C.; Schimel, J.P. Does adding microbial mechanisms of decomposition improve soil organic matter models? A comparison of four models using data from a pulsed rewetting experiment. *Soil Biol. Biochem.* **2009**, *41*, 1923–1934. [CrossRef]
36. Wallenstein, M.; Allison, S.D.; Ernakovich, J.; Steinweg, J.M.; Sinsabaugh, R. Controls on the temperature sensitivity of soil enzymes: A key driver of in situ enzyme activity rates. *Soil Enzymol.* **2011**, *22*, 245–258. [CrossRef]

37. Reich, P.B.; Oleksyn, J. Global patterns of plant leaf N and P in relation to temperature and latitude. *Proc. Natl. Acad. Sci. USA* **2004**, *101*, 11001–11006. [CrossRef] [PubMed]
38. Peet, R.K.; Fridley, J.D.; Gramling, J.M. Variation in species richness and species pool size across a pH gradient in forests of the southern Blue Ridge Mountains. *Folia Geobot.* **2003**, *38*, 391–401. [CrossRef]
39. Ma, M.; Dalling, J.W.; Ma, Z.; Zhou, X. Soil environmental factors drive seed density across vegetation types on the Tibetan Plateau. *Plant Soil* **2017**, *419*, 349–361. [CrossRef]
40. Fay, P.A.; Prober, S.M.; Harpole, W.S.; Knops, J.M.H.; Bakker, J.D.; Borer, E.T.; Lind, E.M.; MacDougall, A.S.; Seabloom, E.W.; Wragg, P.D.; et al. Grassland productivity limited by multiple nutrients. *Nat. Plants* **2015**, *1*, 15080. [CrossRef]
41. Xiong, J.; Lin, C.; Ma, R.; Zheng, G. The total P estimation with hyper-spectrum—A novel insight into different P fractions. *Catena* **2020**, *187*, 104309. [CrossRef]
42. Damman, A.W.H. Regulation of Nitrogen Removal and Retention in Sphagnum bogs and Other Peatlands. *Oikos* **1988**, *51*, 291. [CrossRef]
43. Clarke, E.; Baldwin, A.H. Responses of wetland plants to ammonia and water level. *Ecol. Eng.* **2002**, *18*, 257–264. [CrossRef]
44. Elo, M.; Alahuhta, J.; Kanninen, A.; Meissner, K.K.; Seppälä, K.; Mönkkönen, M. Environmental Characteristics and Anthropogenic Impact Jointly Modify Aquatic Macrophyte Species Diversity. *Front. Plant Sci.* **2018**, *9*, 1001. [CrossRef]
45. Das Gupta, S.; Pinno, B.D. Drivers of understory species richness in reconstructed boreal ecosystems: A structural equation modeling analysis. *Sci. Rep.* **2020**, *10*, 11555. [CrossRef]
46. Hill, N.M.; Kloet, S.P.V. Longevity of Experimentally Buried Seed in Vaccinium: Relationship to Climate, Reproductive Factors and Natural Seed Banks. *J. Ecol.* **2005**, *93*, 1167–1176. [CrossRef]
47. Pakeman, R.J.; Cummins, R.P.; Miller, G.R.; Roy, D.B. Potential climatic control of seedbank density. *Seed Sci. Res.* **1999**, *9*, 101–110. [CrossRef]
48. Miller, G.R.; Cummins, R.P. Role of Buried Viable Seeds in the Recolonization of Disturbed Ground by Heather (*Calluna vulgaris* [L.] Hull) in the Cairngorm Mountains, Scotland, U.K. *Arct. Alp. Res.* **1987**, *19*, 396. [CrossRef]
49. Jagadish, S.V.K.; Bahuguna, R.N.; Djanaguiraman, M.; Gamuyao, R.; Prasad, P.V.V.; Craufurd, P.Q. Implications of High Temperature and Elevated CO2 on Flowering Time in Plants. *Front. Plant Sci.* **2016**, *7*, 913. [CrossRef] [PubMed]
50. Hegland, S.J.; Nielsen, A.; Lázaro, A.; Bjerknes, A.; Totland, Ø. How does climate warming affect plant-pollinator interactions? *Ecol. Lett.* **2009**, *12*, 184–195. [CrossRef]
51. Wang, M.; Li, X.L.; Dong, Y.M.; Wang, S.Z.; Liu, B.; Jiang, M.; Wang, G.D. Plant species diversity of Carex peat mire in Changbai Mountains, China. *Chin. J. Appl. Ecol.* **2021**, *32*, 2138–2146. [CrossRef]
52. Gerritsen, J.; Greening, H.S. Marsh Seed Banks of the Okefenokee Swamp: Effects of Hydrologic Regime and Nutrients. *Ecology* **1989**, *70*, 750–763. [CrossRef]
53. Gao, S.; Wang, J.; Knops, J.M.H.; Wang, J. Nitrogen addition increases sexual reproduction and improves seedling growth in the perennial rhizomatous grass Leymus chinensis. *BMC Plant Biol.* **2020**, *20*, 106. [CrossRef]
54. Johnson, S. Effects of water level and phosphorus enrichment on seedling emergence from marsh seed banks collected from northern Belize. *Aquat. Bot.* **2004**, *79*, 311–323. [CrossRef]
55. Ket, W.A.; Schubauer-Berigan, J.P.; Craft, C.B. Effects of five years of nitrogen and phosphorus additions on a Zizaniopsis miliacea tidal freshwater marsh. *Aquat. Bot.* **2011**, *95*, 17–23. [CrossRef]
56. Bridgham, S.D.; Pastor, J.; Janssens, J.A.; Chapin, C.; Malterer, T.J. Multiple limiting gradients in peatlands: A call for a new paradigm. *Wetlands* **1996**, *16*, 45–65. [CrossRef]
57. Chapin, C.T.; Bridgham, S.D.; Pastor, J. pH and nutrient effects on above-ground net primary production in a Minnesota, USA bog and fen. *Wetlands* **2004**, *24*, 186–201. [CrossRef]