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Posted Date: 1 April 2025

doi: 10.20944/preprints202504.0022.v1

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Climate Change and Invasive Alien Plants Affect Native Plant Communities in the Ertix River Basin Wetlands

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Abstract: Climate change accelerates the competitive displacement of native plants by non-native plants in wetland ecosystems, critically affecting the diversity of wetland plant communities. However, it remains unclear how variation in climate change factors and non-native plants may impact the diversity of native plant communities in the Ertix River Basin wetland ecosystems. As a result, we selected 161 representative wetland plant communities for plot surveys and community classification, including the community structure, species diversity patterns, and the current status of non-native plant species in the Ertix River Basin wetlands, as the region faces serious plant invasion threats in recent decades. We also measured the elevation, mean annual precipitation, and mean annual temperature pattern to assess the impact of environmental factors on the dynamics of relationships between native plant communities and non-native plants. Results of Patrick richness, and Shannon-Wiener indices of native plant communities significantly increased with increasing temperature and elevation of the Ertix River Basin wetlands. The Patrick richness index, Pielou index and Shannon-Wiener index of native plant species positively correlated with the increasing number of naturalized individuals or species. Meanwhile, the number of casual plants, invasive plants, and naturalized plants negatively correlated with the importance value of native plant communities. Overall, results suggest that environmental variability and plant invasion can shift the diversity and distribution pattern of native plant communities in the Ertix River Basin wetlands.

Keywords: alien plants; elevational gradient; environmental factors; Ertix River Basin; native plant diversity; wetland plant communities

Introduction

Climate change accelerates the competitive displacement of native plants by invasive alien plants in many ecosystems, including wetlands [1,2], critically driving biodiversity loss in wetland habitats worldwide [3–5]. The colonization of non-native plants in wetland ecosystems has dramatically altered vital attributes of native plant diversity, i.e., species richness and evenness [5,6]. Such invasion-driven effects on native plants have been reported in many wetland ecosystems in China due to favorable and variable climatic conditions [7–9], causing enormous ecological and economic losses over the years [10]. For instance, biological invasion has been estimated to result in approximately USD 14.5 billion annual economic cost in China [11]. Despite these negative ramifications on wetland ecosystems in China, how climate change-driven impacts and invasive alien plants may affect the diversity of native plant communities in the Ertix River Basin wetlands remain unclear.

There is a growing awareness of the varying ecological impacts of non-native plants on species composition and diversity of native plant communities [12]. The mechanisms underpinning such ecological impacts of alien plants have been attributed to their superior competitive ability, resource use efficiency, and inherent environmental adaptability [13–15]. Additionally, non-native plants are known for their capacity to modify the biotic and abiotic characteristics of invaded soils through priority effects [16] and allelochemical inputs [17,18], creating favorable soil conditions for their growth and fitness. As a result, non-native plants can rapidly colonize, establish, and dominate native plant communities [19,20]. For instance, previous studies indicate that invasive alien plants alter soil biogeochemical processes and functional diversity of soil biota composition of the invaded ecosystems [21,22]. It is worth noting, however, that the resultant effects of the invasibility of native communities also depend on the diversity of native communities, resource availability, and the scale of the experimental study [23,24]. Thus, exhibiting the diversity-invasibility relationship and inconsistent or bi-directional effects of native and invasive plants in natural ecosystems [24–26]. While highly diverse native plant communities mediate biotic resistance to alien plant invasion at large scales, the opposite is true for low diverse plant communities at small scales [24–26]. Although significant advancements in mechanisms mediating the invasibility of local communities have been studied, how environmental variability contributes to the invasibility of native plant communities in wetland ecosystems remains understudied.

Plants show varying sensitivity and responses to environmental factors such as temperature and precipitation along elevational gradients [27,28], profoundly contributing to the distribution of plant communities [29]. Soil temperature and moisture are known to modulate key soil microbial processes, organic matter decomposition, and nutrient availability [30,31]. For example, Niu et al. found that decreased soil moisture content and increased soil temperature significantly reduced species richness of alpine plant communities [31]. Although climate warming promotes plant biomass [30,32], it significantly reduces species diversity across continental scales among wetland communities [30]. Indeed, as plants, either natives or non-natives, differ in their sensitivity to environmental variation [33,34], responses along elevational gradient may vary accordingly. While invasive plants are known to expand their range towards the north in response to climate warming [35,36], how climate change and invasive alien plants may interactively affect the diversity and distribution of native communities in wetland communities along elevational gradient remain inadequately explored.

Wetland ecosystems are usually located between elevational gradients where the aquatic and terrestrial ecosystems intersect [37], creating unique and distinct soil characteristics supporting the spatial distribution of diverse plant species [37]. The distinctive soil characteristics and favorable environmental conditions also attract many human activities, including agriculture, potentially modifying soil biogeochemical attributes [38,39]. As environmental disturbances are shown to mediate influxes and establishment of invasive species [40,41], human-driven modifications of the wetland ecosystems may likely initiate the interaction of invasive species and native plant communities [40,42]. Similarly, the wetland ecosystems of the Ertix River Basin, with its rich biodiversity, represent a conducive habitat for many plant species [43]. Therefore, under the ongoing rapidly changing global environment, the Ertix River Basin wetlands may be exposed to large influxes of non-native plants, ultimately posing a significant threat to native plant communities. However, the information regarding the magnitude and direction of impacts of non-native plant invasion on the diversity of native plant communities, distribution patterns, and invasion status in the Ertix River Basin wetlands remains limited.

We, therefore, conducted a field study to examine the impact of non-native plants on native plant communities in the Ertix River Basin wetland ecosystems. Specifically, we asked (1) whether non-native plant species affect native plant communities in the wetlands of the Ertix River Basin, (2) what the magnitude and direction of such non-native plants impact the diversity of native plants, (3) whether environmental factors, i.e., mean annual temperature and precipitation, drive non-native plant species impact along elevational gradients in the Ertix River Basin wetland ecosystems.

 doi:10.20944/preprints202504.0022.v1

Results

Results of the linear mixed-effects model (LMM) with importance value as the dependent variable indicate that the number of casual plants, invasive plants, and naturalized plants significantly affected the importance value of native plant communities, thus all showing a negative correlation (Table 1, Figure 2). Additionally, elevation was significantly and positively correlated with the importance value (Table 1, Figure 2). The linear mixed-effects model with the Patrick richness index of native plant communities as the dependent variable showed that increases in temperature, elevation, and number of naturalized species significantly enhanced the Patrick richness index of native plant communities (Table 2, Figure 3). The Pielou evenness index of native species communities also increased dramatically with rising number of naturalized plants (Table 3, Figure 4). In the linear mixed-effects model based on the Shannon-Wiener index of native species, elevation and number of naturalized plants were significantly and positively correlated with the Shannon-Wiener index (Table 4, Figure 5).

Table 1. Linear mixed-effects model analysis of the importance value of native plants in the sample plot with environmental factors, the number of alien plant species, and individuals. Adjusted R^2 of the model is 0.77. All continuous variables were natural-log transformed and then scaled. The individual R^2 for each variable and the percentage of R^2 were given.

Term	Estimate	SE	*t*-value	*P*-value	Ind. R^2	Ind. perc
Intercept	0.92	0.01	182.87	<0.001	/	/
Elevation	0.01	0.01	2.39	0.021	0.02	2.41
NCP	-0.02	0.01	-3.23	0.002	0.09	12.18
NIP	-0.06	0.01	-12.60	<0.001	0.22	29.23
NNP	-0.09	0.01	-16.08	<0.001	0.43	56.18

NCP represents the number of casual plants. NIP represents the number of invasive plants. NNP represents the number of naturalized plants.

Table 2. Linear mixed-effects model analysis of the richness of native plants in the sample plot with environmental factors, the number of alien plant species, and individuals. The adjusted R^2 of the model is 0.52. All continuous variables were natural-log transformed and then scaled. The individual R^2 for each variable and the percentage of R^2 were given.

Term	Estimate	SE	*t*-value	*P*-value	Ind. R^2	Ind. perc
Intercept	1.79	0.04	45.36	<0.001	/	/
Elevation	0.26	0.06	4.27	<0.001	0.16	72.29
MAT	0.12	0.06	2.02	0.048	0.03	14.23
NNS	0.07	0.03	2.40	0.018	0.03	13.48

MAT represents the mean annual temperature. NNS represents the number of naturalized species.

Table 3. Linear mixed-effects model analysis of the Pielou index of native plants in the sample plot with environmental factors, the number of alien plant species, and individuals. The adjusted R^2 of the model is 0.38. All continuous variables were natural-log transformed and then scaled.

Term	Estimate	SE	*t*-value	*P*-value
Intercept	0.58	0.02	23.92	<0.001
NNP	0.06	0.02	2.92	0.004

NNP represents the number of naturalized plants.

doi:10.20944/preprints202504.0022.v1

Table 4. Linear mixed-effects model analysis of the Shannon index of native plants in the sample plot with environmental factors, the number of alien plant species, and individuals. Adjusted R^2 of the model is 0.54. All continuous variables were natural-log transformed and then scaled. The individual R^2 for each variable and the percentage of R^2 were given.

Term	Estimate	SE	*t*-value	*P*-value	Ind. R^2	Ind. perc
Intercept	1.07	0.05	19.41	<0.001	/	/
Elevation	0.18	0.06	3.30	0.002	0.10	63.37
NNP	0.14	0.04	3.44	<0.001	0.06	36.63

NNP represents the number of naturalized plants.

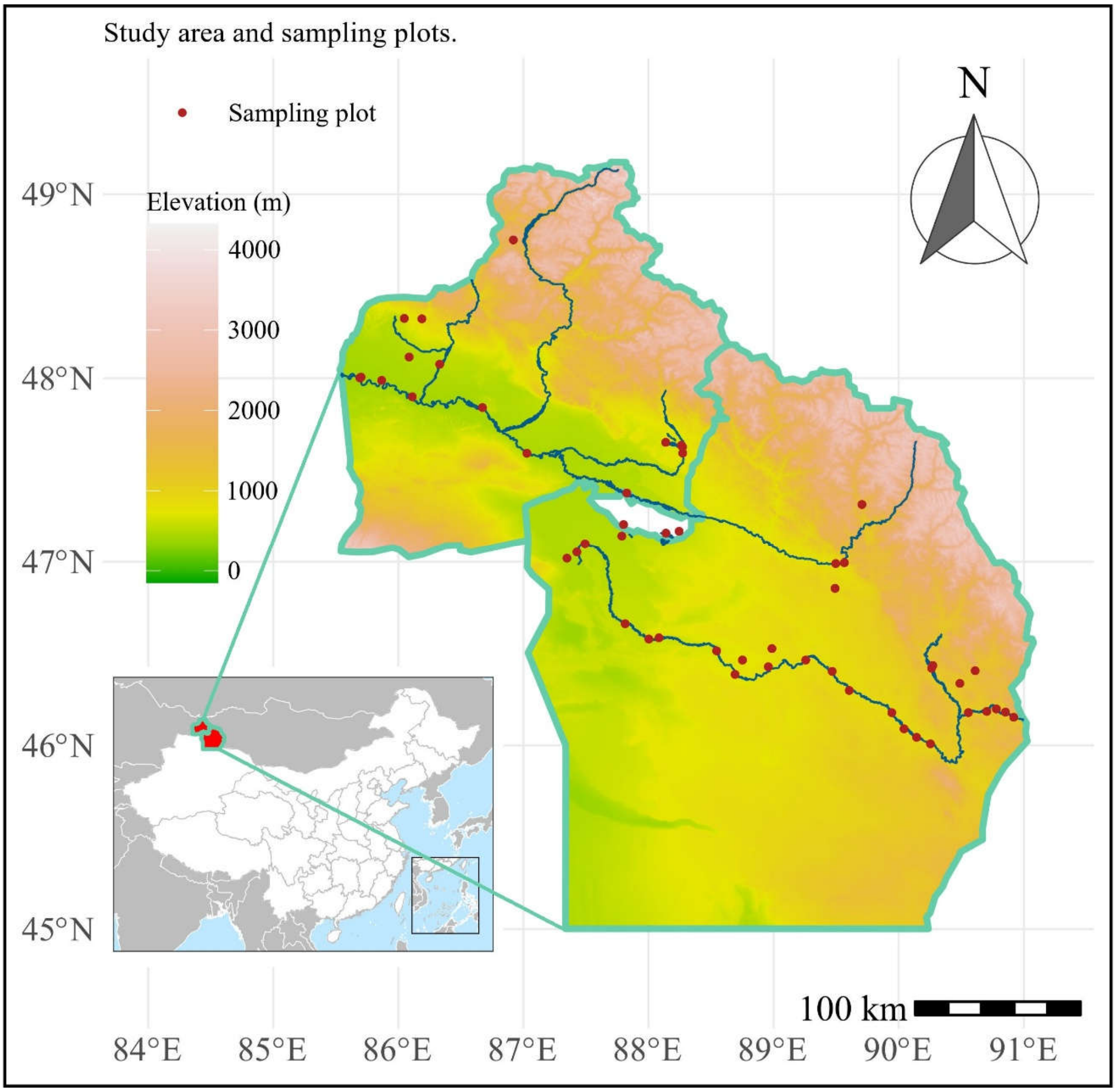

Figure 1. Study area and sampling plots. The sampling plots were selected primarily based on the geographical distribution of the Irtysh River Basin and natural vegetation community patterns, with a total of 54 transects established along moisture gradients.

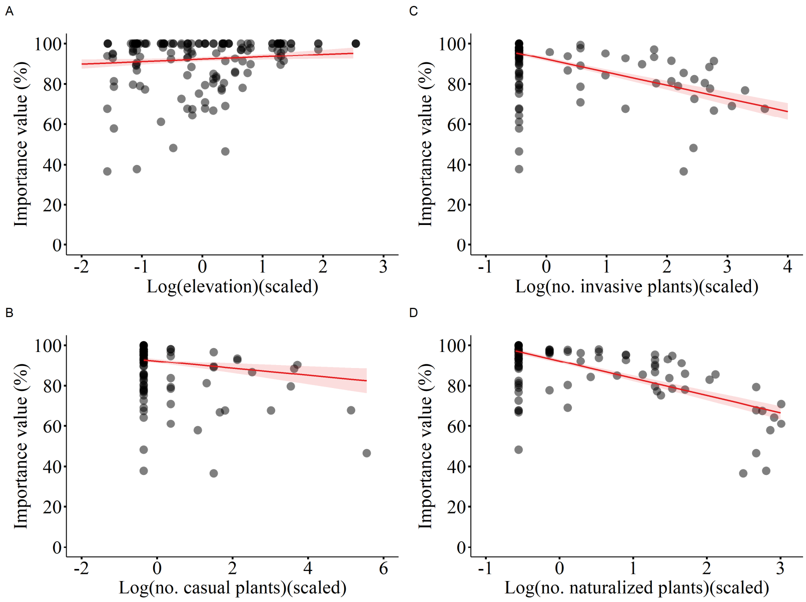

Figure 2. Importance value of native species in relation to (A) elevation, (B) number of casual plants, (C) number of invasive plants, and (D) number of naturalized plants. The fitted lines with 95% confidence intervals from the minimum adequate linear mixed model (LMM) model are shown.

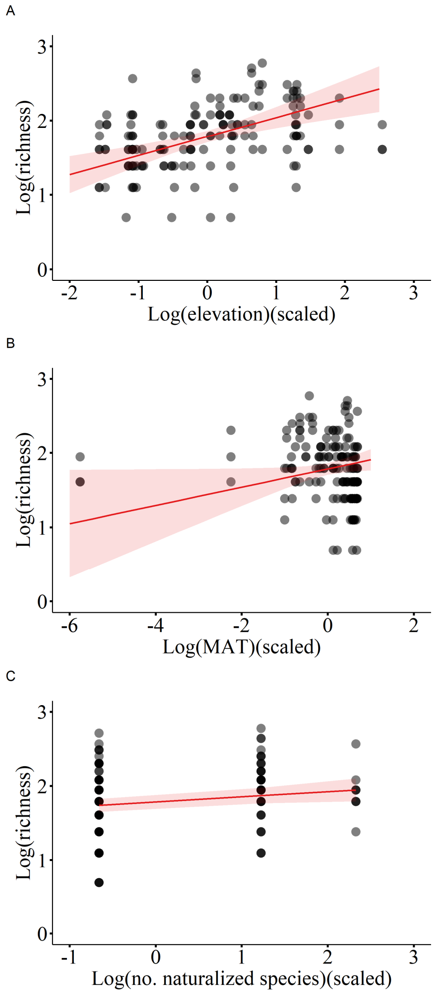

Figure 3. Richness of native species in relation to (A) elevation, (B) mean annual temperature, and (C) number of naturalized species. The fitted lines with 95% confidence intervals from the minimum adequate LMM model are shown.

 doi:10.20944/preprints202504.0022.v1

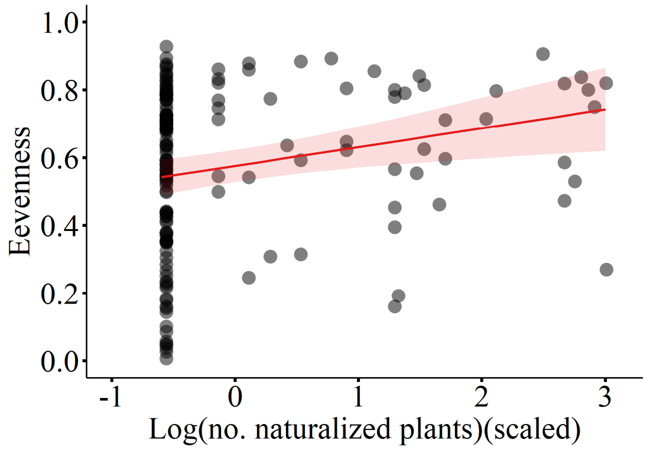

Figure 4. Evenness of native species in relation to number of naturalized plants. The fitted lines with 95% confidence intervals from the minimum adequate LMM model are shown.

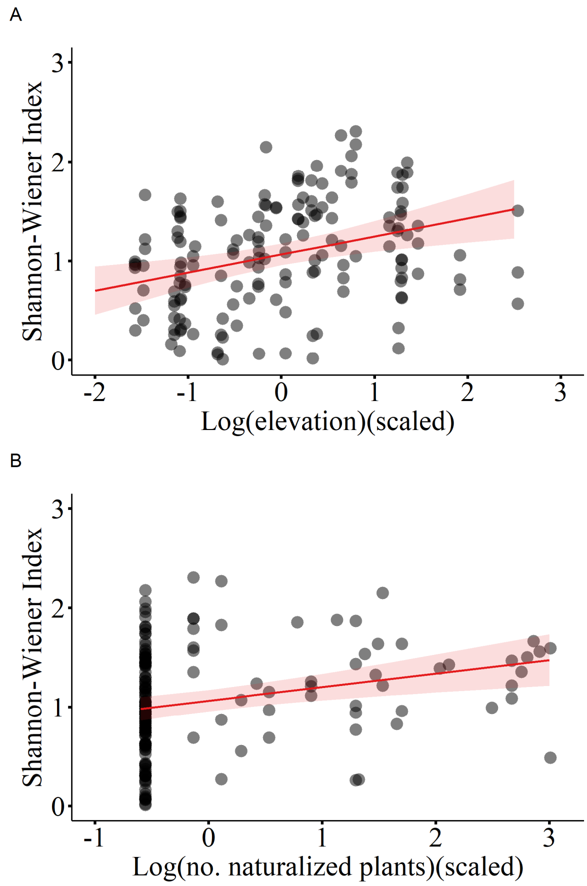

Figure 5. Shannon of native species in relation to (A) elevation, (B) number of naturalized plants. The fitted lines with 95% confidence intervals from the minimum adequate LMM model are shown.

Discussion

Historically, non-native plants are known to impact native plant communities in many ecosystems [5,12,14,15,44]. Common natural ecosystems that are mostly invaded include wetlands due to their unique and distinctive environmental conditions [7,45], favoring human activities such as agriculture [46]. Such disturbance-mediated influxes of non-native plants, especially under the ongoing climate change [47], induce negative ramifications on native plant diversity [48]. However,

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little is known about how climate change and non-native plants affect the diversity and distribution pattern of native plants [49,50] in the Ertix River Basin wetland ecosystems. Our results provide empirical evidence that non-native plants affect native plant communities of the Ertix River Basin wetlands via additive effects of environmental factors and alien plants.

Results indicate that non-native plants affect native plant communities in the Ertix River Basin wetlands as the increase in the number of casual, naturalized, and invasive plants significantly reduced the importance value of native species. These findings consistently confirmed most previously documented findings on the negative impacts of non-native plant invasions on native plants in terrestrial [51–53] and wetland ecosystems [1,5,6]. The widely recognized mechanisms underlying such destructive trends in their invaded communities revolved around their inherent superior competitive abilities, resource use dominance, and fast growth rate, usually outperforming the native plant communities [13–15].

Most previous studies fail to distinguish casual, naturalized, and invasive species and account for their respective roles in native ecosystems, limiting our capacity to predict their contributions to the invasion processes [54]. Regardless, the disruptive characteristics of non-native plants remain inevitable in many native plant communities [55]. In a meta-analysis of 21 habitat types, for example, two times greater negative impacts of non-native species on native communities and five times higher performance of non-native than native species [55]. Nevertheless, alien plants are reported to play facilitative or complementary roles in native plant communities [56]. For example, in the southern California ecosystem, the native *Cryptantha muricata* produced more than twice the flowers, reproductive biomass, and total biomass when grown in the presence of non-native grasses than in their absence [57].

Likewise, in the present study, an increasing number of naturalized species showed a significantly positive correlation with the richness of the native plant communities. Also, results showed that the number of naturalized plants was positively correlated with the evenness and Shannon index of native plant communities, which again highlights the promoting effect of alien plants on native plant communities. Similarly, an early-stage mild invasion of the invasive plant *Alternanthera philoxeroides* increased species richness and evenness among the native community [58]. Such promotional effects of non-native species on native communities have been reported in *Solidago canadensis* [59] and *Ambrosia trifida* [60]. Our results suggest that alien plants may promote multi-species coexistence by altering resource utilization or mediating the resistance of native plants against common disturbances within the Ertix River Basin wetland ecosystems.

Furthermore, results indicate that environmental factors (i.e., elevation and temperature) exhibit a more significant correlation with Shannon-Wiener and Patrick richness, than alien plants. The richness of native plants significantly increased with increasing temperature. These results replicate most previous studies that observed significant effects of MAT on the diversity and pattern of distribution of native plant communities [61]. For example, Li et al. found a significant correlation between temperature and the overall richness and abundance of shrubs and trees in montane forests [61].

Environmental factors, such as temperature and precipitation, directly and indirectly affect plants via modulating plant resource uptake and utilization, metabolic and physiological processes, and plant-microorganism interactions [62]. Thus, within the maximum temperature threshold, increasing temperatures can promote plant resource use efficiency and competitive interaction [63,64], critically shaping the life histories and dynamics of native plant communities [61]. Despite temperature and precipitation are vital predictors of plant performance [65,66], both are shown to hinder the migration capacity and adaptability of plants [61], otherwise alien plants, due to climatic variability consequences on species coexistences or interspecific relationships [67–69]. Therefore, the observed strong correlation between increasing native plant diversity and rising temperatures along an elevational gradient in the present study may ultimately limit the invasibility of the Ertix River Basin wetland ecosystems. Thus, exhibiting the positive diversity-invasibility or biotic resistance scenario [23,25,26] in the Ertix River Basin wetland ecosystem. As another potent predictor

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determining climatic impacts on plant growth, precipitation in our study had less effect on native plants than temperature. Such observation was not surprising, especially when the experimental or survey setting is within wetland communities, suggesting that precipitation may least limit native plant diversity [65,66,70].

Plants, natives or invasives, differ in their sensitivity to climatic variability [33,71], substantially exhibiting spatial-structuring patterns of plant diversity and distribution along elevational gradients [71–73]. Notably, plant species diversity increases with altitude, especially with the native taxa [71]. Such plants develop unique adaptation strategies, including thick leaves, specialized root systems, and shorter growth forms [74], facilitating their resistance to varying elevation-induced stressors. In the present study, a significant positive correlation between the diversity of native plant communities and increasing elevation was observed, which is consistent with most previous findings [75,76]. For example, as native species richness increased along an increasing gradient in the Mediterranean island, alien plants predominantly occupied the lower elevations [76], suggesting a facilitative role of invasive plants via shielding natives from harsh environmental forces [56].

As indicated earlier, with substantial climatic variability consequences on new arrival species (i.e., alien plants) in mountainous ecosystems [67–69,77], native plant diversity and environmental factors can interactively shape the coexistences of alien plants in the Ertix River Basin wetland ecosystems. Overall, results provide empirical evidence that native plants may occupy more ecological niches within the Ertix River Basin wetland communities, enhancing resource use efficiency and providing competitive resistance to alien plant invasions.

Materials and Methods

Study Area

The Ertix River Basin wetlands are located in the northern region of the Xinjiang Uygur Autonomous Region, China. It is bordered by the Altai Mountains to the north, the Sayram Mountains to the southwest, and the Gurbantunggut Desert to the south. The expansive alluvial plain of the Ertix River and the Ulungur River lies at the center of this region. The Ertix River is the second-largest river in Xinjiang and an international river within the Arctic Ocean watershed [78]. The Ertix River Basin spans 85°30′ to 90°30′ E and 46°55′ to 49°10′ N, with elevations ranging from 1,337 m to 3,846 m above sea level. The river system extends over an area of 1,640,000 km^2 with a length of 4,248 km, of which 633 km flows through China territory, encompassing a basin area of 52,730 km^2. Located in the northwest arid region of China, the basin is characterized by a temperate continental arid to semi-arid climate and receives an annual mean temperature of 3.3°C and an average annual precipitation of 93.9 mm. [78–80].

Field Survey

On 23 June 2022 and 28 July 2022, we conducted a field survey in the Ertix River Basin wetland ecosystems (see Figure 1). The survey site was primarily selected based on the geographical distribution of the Ertix River and natural plant community patterns. By employing a combination of transect and quadrat methods, we established 54 transects with three randomly placed 1 m × 1 m quadrats along each transect to capture different community types across moisture gradients, totaling 161 quadrants. We recorded geographic coordinates and the herbaceous plant species composition for each quadrat, including species names, abundance, and coverage. We calculated the average height of species by summing all individual species' heights and dividing them by their total number.

Species Name Standardization

Each plant species name was standardized, and their invasion status was determined through a multi-step process. Thus, (1) we identified the species on-site using the Flora of China (FOC; http://www.iplant.cn/) and subsequently verified by botanical experts' consideration and judgment. (2) We standardized further the names of the species through the Plants of the World Online (POWO;

https://powo.science.kew.org/), using the "*rWCVP*" package in R [81]. (3) For easy categorization, each standardized plant species was classified into four groups and defined as follows: native plants (i.e., the indigenous plant species), naturalized plants (i.e., introduced species that reproduce without human intervention but are not invasive), and casual plants (i.e., alien plants that are not naturalized), as well as those established and confirmed as invasive species. While the alien invasive plants were identified based on the checklist developed by Lin et al. [82], we identified the native plants based on the checklist developed by Lu et al. [83] and cross-checked via the POWO. Additionally, the naturalized and invasive plants were further identified based on the updated checklist from the Naturalized Plant of China (NPC; https://www.iplant.cn/npc/) and the Invasive Alien Species in China (IASC; https://www.plantplus.cn/ias/).

Environmental Factors

Elevation data were extracted from the National DEM dataset (1 km resolution) available through the Resource and Environmental Science Data Platform (https://www.resdc.cn/). We use the "*raster*" package in R to extract the elevation data for specific coordinate points based on the latitude and longitude of the sampling points. Moreover, the climate data, including monthly temperature and precipitation from 1901 to 2022 (1 km resolution) were obtained from the National Earth System Science Data Center (https://www.geodata.cn) [84]. We use the "*ncdf4*" package in R to extract the environmental factor data for specific coordinate points based on the latitude and longitude of sampling points. Both temperature and precipitation data from 2012 to 2022 were extracted for each year, and the mean annual temperature (MAT) was calculated by averaging the monthly temperatures. Likewise, we obtained the annual precipitation (MAP) by summing monthly precipitation values.

Species Diversity Metrics

From the field survey data, the relative height, relative abundance, and relative coverage of the native species in each plot were calculated (i.e., the proportion of the sum of the average heights, abundance, and coverage of native species relative to the sum of the average heights, abundance, and coverage of all species in the plot). Also, the importance value of species based on their relative heights, relative abundance, and relative coverage were calculated, further allowing us to determine the alpha diversity indices, i.e., the Patrick Richness Index, Shannon-Wiener Index, and Pielou Evenness Index [85,86]. All calculations were performed using the "*vegan*" package in R. The formulas are as follows:

$$\text{Importance value}, IV = \frac{rh+ra+rc}{3} \quad (1)$$

$$\text{Patrick Richness Index}, R = S \quad (2)$$

$$\text{Shannon} - \text{Wiener Diversity Index}, H = -\sum P_i ln(P_i) \quad (3)$$

$$\text{Pielou Evenness Index}, E = H/H_{max} \quad (4)$$

Where *IV* represents importance value，*rh* is relative height，*ra* is relative abundance, and *rc* is relative coverage. Moreover, *S* denotes the total number of species in the community. P_i is the proportion of individuals of species *i* to the total number of individuals in the community, calculated as $P_i = N_i / N$. N_i represents the number of individuals of species *i*.

Data Analysis

For each quadrant, we recorded the total number of biological species of casual, naturalized, or invasive plants (hereafter referred to as the "number of casual, naturalized, or invasive species") and the total number of individual casual, naturalized, or invasive plants (hereafter referred to as the "number of casual, naturalized, or invasive plants"). Prior to analysis, we log-transformed and scale-standardized all independent variables, and applied a log transformation to species richness. We used linear mixed-effects model (LMM) to examine the effect of environmental factors (elevation, MAT, and MAP), the number of non-native species (casual, naturalized, and invasive species), and

 doi:10.20944/preprints202504.0022.v1

the individual number of non-native plants (casual, naturalized, and invasive plants) on the Shannon index, species richness, importance value and evenness of the native plant community. The optimal model was obtained by manually retaining only significant factors, using the "lmer" function from the "*lme4*" package [87]. The individual marginal R^2 of each fixed factors was estimated using "glmm.hp" function from the "*glmm.hp*" package[88]. All analyses were performed using R v4.4.0 [89].

Conclusions

We conclude that the invasion of alien plants of the Ertix River Basin wetlands significantly affects the diversity−Shannon, richness and evenness of native plant communities. However, a strong positive correlation between rising temperatures with the diversity of native plant communities along elevational gradients observed in this study may hinder the invasibility of the Ertix River Basin wetland ecosystems. Ultimately, it provides an essential clue of the positive diversity-invasibility or invasion resistance scenario, underscoring the need to bolster the diversity of native plants as management strategies against plant invasions in the Ertix River Basin wetland ecosystems. One caveat is that we did not analyze the taxonomic functional identity (e.g., grasses, forbs, and legumes species) of the various native plant communities, and thus, we cannot provide information regarding species-specific responses to the environmental variability and plant invasions in the Ertix River Basin wetlands. To comprehensively understand the distribution pattern, life-history strategies, and adaptation dynamics of native plants in wetlands and mountainous plant communities, future studies may consider climate- and human-driven disturbances across variable environmental factors when exploring the relationships between alien and native plant species.

Author Contributions: Conceptualization, B.-C.D., J.-Q.G. and F.-H.Y.; methodology, B.-C.D., J.-Q.G. and X.-M.C.; data curation, B.-C.D. and X.-M.C.; formal analysis, B.-C.D. and X.-M.C.; writing-original draft preparation, X.-M.C.; writing-review & editing, B.-C.D., J.-Q.G., O.-A.M., X.-M.C. and F.-H.Y.; supervision, B.-C. D. and J.-Q.G.. All authors have read and agreed to the published version of the manuscript.

Funding: This work was supported by the National Natural Science Foundation of China (grant 31500331) and the Third Xinjiang Scientific Expedition Program (grant 2021xjkk0601).

Data Availability Statement: Raw data and R codes are available on request to the corresponding author.

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

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