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Research article

Spatial mid-domain effect overrides climate, soil properties and microbes on a cosmopolitan non-native plant across elevation

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Climate warming and anthropogenic activities have led to an increase in the prevalence of non-native plants in mountainous regions that previously exhibited limited occurrences. This phenomenon has resulted in detrimental effects on endemic plants and ecosystem functions. However, the variation in traits of non-native plants that successfully spread to high elevations, as well as the underlying drivers of these changes, remains poorly understood. In this study, we use *Erigeron annuus*, a cosmopolitan non-native plant that has invaded high elevations, as our model to explore its individual biomass pattern along a 1900 m elevation gradient. We also contrast this pattern with that of the native *Artemisia lavandulifolia,* which has the same distribution range as *E. annuus*. We found that the biomass of *E. annuus* displayed a hump-shape pattern along elevation, while the biomass of the native *A. lavandulifolia* gradually decreased with increasing elevation. By evaluating the effects of climate variables, soil properties, rhizosphere fungal communities and its spatial mid-domain effect (i.e. geographic limitation) on plant biomass, we found that the biomass of *E. annuus* was primarily influenced by the spatial mid-domain effect, while the biomass of *A. lavandulifolia* resulted from a complex interplay of climatic variables and rhizosphere microbial communities. Our findings emphasize the importance of a spatial mid-domain effect on the growth of non-native *E. annuus* across elevation, indicating the impact of *E. annuus* probable be greatest at mid-elevations and thus, where management priority should be set. Further investigations considering more non-native plant species and species' traits will allow to scrutinize this vision.

Keywords: elevation gradient, non-native plant, spatial mid-domain effect, rhizosphere fungal community

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Introduction

Mountain ecosystems are recognized as critical refuges for biodiversity, encompassing approximately 25% of the Earth's land area while harboring over 85% of the planet's species (Rahbek et al. 2019). However, these ecosystems face significant threats from plant invasions exacerbated by climate warming and anthropogenic disturbances. Numerous studies have documented the upward migration of non-native plant populations to higher elevations as a direct response to climate warming (Dainese et al. 2017, Slodowics et al. 2018). Additionally, researches indicate that the expansion and establishment of non-native plants in mountainous regions are facilitated by the construction of roads and railways extending into mountain ecosystems (Rashid et al. 2021). Currently, more than 600 non-native plant species have been recorded in the mountains worldwide (Iseli et al. 2023), but not all of them have reached high elevation areas (Alexander et al. 2016). Previous investigations into non-native plant species in mountainous regions have predominantly focused on community-level assessments, revealing a global trend of decreasing non-native plant species richness with increasing elevation (Alexander et al. 2011, Guo et al. 2018, Haider et al. 2018). Nevertheless, there is a paucity of information regarding the population-level trait dynamics of non-native plant species which are successfully establishing themselves at high elevations. This information is crucial for evaluating invasion risks, predicting future spread, and informing targeted management interventions (Laeseke et al. 2020).

A steep environmental gradient over a short geographic distance, characterized by variations in abiotic (e.g. temperature, precipitation and soil nutrient availability) and biotic (e.g. microbial diversity and composition) factors across different elevations, is a defining feature of mountain ecosystems (Körner 2007, Salinas et al. 2011, Wang et al. 2022). These variations can lead to strongly divergent selection pressures, potentially resulting in alterations in plant traits, particularly in plant biomass. Main possible processes explaining the dynamic of plant biomass across elevation are: 1) the 'temperature–primary productivity relationship' stating temperature is the primary determinant for plant biomass, with higher temperatures at lower elevations promoting enhanced photosynthesis and plant growth, thereby leading to a decreasing trend in plant biomass with increasing elevation (Reich et al. 2014); 2) the 'water–energy hypothesis' suggesting that water availability (precipitation) and energy inputs (temperature and solar radiation) collectively influence plant biomass, with the effect of water diminishing while the impact of energy intensifying as elevation increases (Hawkins 2003); 3) the 'nutrient availability hypothesis' assuming soil nutrient availability declines with increasing elevation due to reduced mineralization rates and litter decomposition at higher elevations, resulting in a downward trend in plant biomass along elevation (Salinas et al. 2011); 4) the 'plant–microbe interactions' hypothesis highlights the important role of soil microorganisms in influencing plant biomass including growth promotion, nutrient uptake, disease suppression and stress tolerance (Trivedi et al. 2020). As elevation increases, environmental factors such as temperature, moisture, can influence the diversity and composition of soil microbial communities (Wang et al. 2022). These shifts in microbial communities can either enhance or inhibit plant biomass depending on microbial functions. Except these abiotic and biotic factors, a non-environmental factor known as the spatial mid-domain effect has been proposed as an alternative explanation for plant distribution patterns along elevation (Colwell and Lees 2000, Du et al. 2024). The spatial mid-domain effect refers to geographic constraints, assuming species are distributed randomly and species within a bounded domain are more frequently in the center of the domain than at the edges, without involving environmental gradients or biological interactions. Under the spatial mid-domain effect assumption, the lower species diversity at distribution boundaries is largely due to harsher environment conditions, geographical barriers and fewer ecological niches. Thus, plant biomass may be lower at the distribution boundaries when affected by the spatial mid-domain effect.

Affected by harsh abiotic factors, the biomass of native plants usually decreases linearly with elevation (Whittaker and Niering 1975, Wang et al. 2007, Ma et al. 2010, Qi et al. 2019, Lee et al. 2021). However, it remains uncertain whether the biomass of non-native plant species follows a similar declining trend with increasing elevation. As non-native species are intentionally or unintentionally introduced to a new region, their performance may be less influenced by local abiotic and biotic conditions compared to that of native plants (Alexander et al. 2011). This may be attributed to the inherent characteristics of non-native plants, including rapid growth rates, high phenotypic plasticity, broad environmental tolerances, strong dispersal abilities and minimal reliance on specialized mutualists (Richards et al. 2006). These traits not only contribute to their success in introduced ranges but also render them more resilient to environmental changes than native plants (Sorte et al. 2013, Liu et al. 2017). Previous common garden experiments contrasting the environmental sensitivity of native and non-native plant species indicated that non-native plant species were less sensitive to environment changes (Peng et al. 2019, Zettlemoyer et al. 2019). Thus, the biomass patterns of individual non-native plants are less correlated with abiotic (climate variables and soil properties) and biotic (soil microbial communities) factors.

Erigeron annuus (Asteraceae) is native to North America and has been introduced globally due to its rapid dispersal and strong reproductive ability (Huang et al. 2023). Even though most non-native species frequently occur in the lowlands because of stronger climatic constraints and fewer anthropogenic disturbances at higher elevations, *E. annuus* has been reported as a pioneer species in high elevations (Trtikova et al. 2011, Seipel et al. 2016). The species that thrive at high elevations often possess broad environmental and biotic niches, making them less dependent on specific environmental conditions and soil microorganisms. As a result, they pose a threat to the survival of endemic native plant species in these high elevations (Alexander et al. 2011, Buckley and Catford 2016).

To understand plant invasions in mountain areas, it is necessary to first consider patterns and mechanisms of non-native plants that had successfully spread to high elevations. Here, we surveyed the biomass of non-native *E. annuus* along a broad elevational gradient in the Qinling Mountains, China. We collected data on climatic variables, soil properties, rhizosphere fungal community and the spatial mid-domain effect to elucidate the influence of these factors on the elevational distribution of the non-native *E. annuus*. As the spatial mid-domain effect is assessed using community data, we utilized the spatial mid-domain effect on rhizosphere fungal community as a proxy for the spatial mid-domain effect on its host plants. There are two reasons that motivated us to extend the spatial mid-domain effect on rhizosphere fungal community to its host plant. First, space typically has similar effects on trophically interacting species, and the notion of the spatial mid-domain effect from species richness has been extended to trophically structured communities (von Prillwitz and Blasius 2020). Second, plants and their rhizosphere microbes, particularly the fungal community, are highly dependent on the exchange of nutrient resources and molecular signals (Phillips et al. 2003). The spatial mid-domain effect may cascade from the fungal community to its host plants. We hypothesized that 1) the biomass of non-native *E. annuus* will not decrease linearly with increasing elevation, and 2) the spatial mid-domain effect is more important than abiotic and biotic factors in influencing the biomass pattern of non-native *E. annuus*. In addition, we sampled the biomass of the native *Artemisia lavandulifolia* (Asteraceae), which shares the same distribution range as *E. annuus* along the elevational gradient in the Qinling Mountains for comparison.

Material and methods

Study area and plant species

The study was carried out in the Qinling Mountains, Shaanxi Province, China (32°22′–34°48′N, 105°13′–113°13′E), which is the physical geographical boundary between southern and northern China and climate boundary between the subtropical humid and warm temperate semi-humid climates. Due to their unique geological features, the Qinling Mountains are known as an international biodiversity hotspot, harboring several extant tertiary ancient plant species, a multitude of wild plants, and a high diversity of both flora and fauna (Zhang et al. 2017). The Qinling Mountains are characterized by mountains and hills, with the highest peak at 3767 m a.s.l. (Taibai Mountain). With the rapid economic development and population growth, the place has suffered from biological invasions threatening its native biodiversity (Liu et al. 2021).

Erigeron annuus (Asteraceae), a cosmopolitan annual or biennial herb (Supporting information), is one of the most serious alien invasive weeds in China reported by the Ministry of Ecology and Environment of China. This species is extensively distributed across warm temperate to subtropical areas of China (Huang et al. 2023). *Erigeron annuus* was first discovered in China from Shanghai in 1886 and progressively spread to Shaanxi Province by 1959 (Wang et al. 2010). Based on our previous field survey along the major roads traversing the Qinling Mountains at elevations ranging from 600 to 2700 m, we found *E. annuus* as the only non-native plant species that has reached 2400 m, exhibiting a continuous elevation distribution between 600 and 2400 m. Within the same elevation range, we also observed the presence of the native perennial herb, *Artemisia lavandulifolia* (Asteraceae), which is the dominant herbaceous species at the Qinling Mountains (Chen et al. 2023). Hence, we chose this native species for comparison.

Plot set up

Given the significant habitat heterogeneity and the relatively short distances within each elevation range, we referred to the MIREN (Mountain Invasion Research Network) protocol (Iseli et al. 2023) and established a 100 m transect through the monodominant stands of *E. annuus* based on the local condition such as terrain and plant distribution. Within the transect, we set five independent plots (1 m × 1 m) spaced evenly at 25 m intervals, with this setup repeated at each elevation during autumn 2021 (Fig. 1A). A total of 95 plots (19 elevations × 5 replicates) were characterized for *E. annuus*. We also applied the same set up for *A. lavandulifolia* at each elevation.

Climatic variables, soil properties and plant biomass data collection

At each elevation, we recorded geographic coordinates (longitude and latitude) using a handheld GPS device. We extracted the mean annual temperature (MAT) and mean annual precipitation (MAP) data from the WorldClim 2 dataset (www.worldclim.org/) at 1 km spatial resolution for the time period spanning 1970–2000. At each sampling plot, we selected three healthy target plant individuals of similar size and collected the tightly root-attached soil as rhizosphere soil. The rhizosphere soil samples of three plant individuals were pooled together as a single rhizosphere soil sample for each plot. The aboveground biomass of the target plants was weighted by cutting the plant shoots above the soil surface. A total of 190 rhizosphere soil samples (19 elevation × 5 plots × 2 plant species) were delivered to the lab and then sieved through a 2 mm mesh for soil biogeochemical properties and rhizosphere fungal community measurements. Soil pH was determined by a pH meter (Thermo Fisher Scientific) in a 1:5 soil-to-water ratio. Soil total carbon (TC), total nitrogen (TN) and TC:TN ratio were measured by an elemental analyzer (FXL950, Thermo Fisher Scientific).

Rhizosphere fungal community measurement

We extracted soil DNA using the PowerSoil DNA Isolation Kit (Qiagen) for the amplification of the ITS1 region of

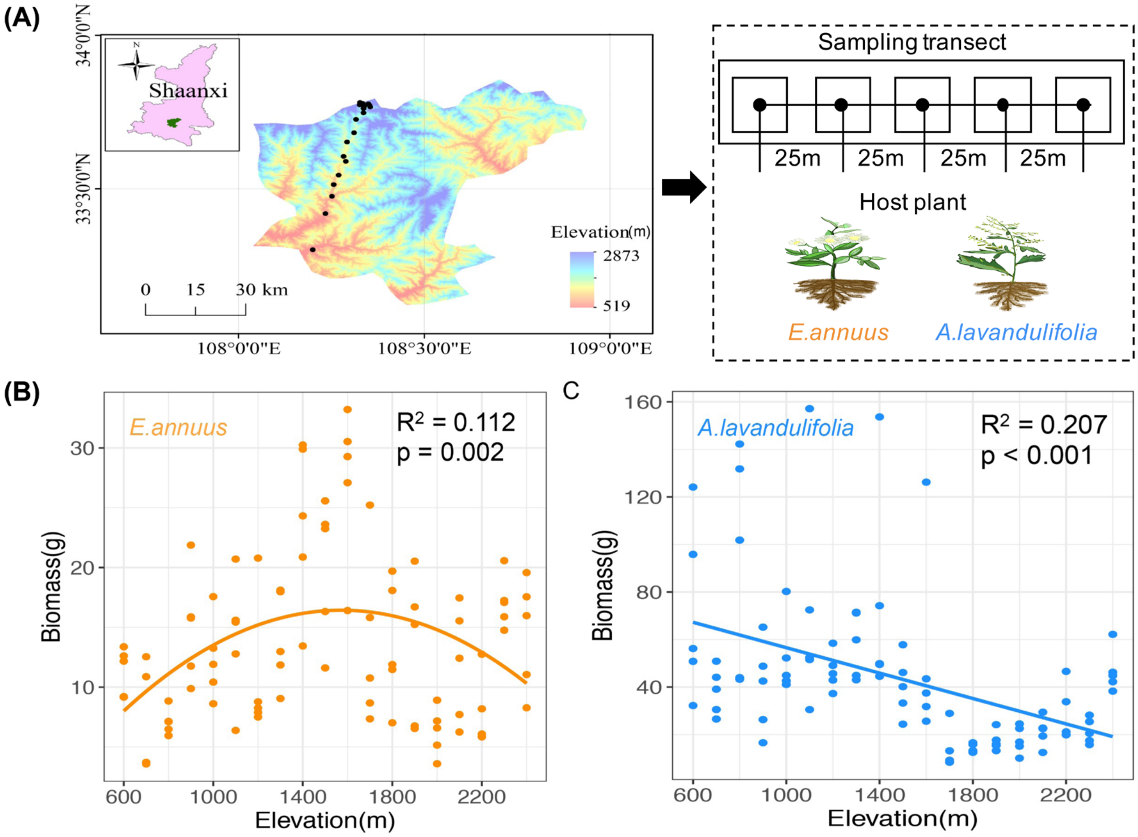

Figure 1. Sampling sites and plots of non-native *E. annuus* and native *A. lavandulifolia* across broad elevation gradient range on Qinling Mountains (A) and the aboveground biomass of non-native *E. annuus* (B) and native *A. lavandulifolia* (C) along elevation.

the fungal ribosomal RNA gene. A universal PCR primer pair ITS1F (CCTGGTCATTTAGAGGAAGTAA)/ITS2R (GCTGCGTTCTTCATCGATGC) (Walters et al. 2016) was applied. All PCR products were visualized by 2% agarose gel electrophoresis and subsequently purified with the AxyPrep DNA Gel Extraction Kit (AxyGen). The concentration of each PCR product was quantified using the QuantiFluor-ST Fluorometer (PromegaA), and the products were equivalently pooled for library construction and amplicon sequencing on the Illumina NovaSeq 6000 platform. We used QIIME2-2021.4 (Bolyen et al. 2019) to process the imported paired-end sequences, followed by Deblur algorithm to generate fungal ASVs (Amplicon sequence variant) table. ASVs with fewer than 10 sequences across all samples were excluded to minimize the impact of PCR and sequencing errors. We filtered the chimeric sequences using the vsearch uchime_denovo method. We delineated all 11 971 fungal ASVs using a pre-trained Naïve Bayes classifier based on the Unite developed dynamic sequences database (10 May 2021 release). We estimated the fungal diversity by diversity core-metrics pipeline at a sequence depth of 14 621. Based on the taxonomy of each fungal ASV, the fungal ASVs were further assigned to functional traits using FungalTraits which had better functional annotation quantity and quality than FunGuild (Tanunchai et al. 2023). The relative abundance of fungal functional traits was calculated using an unrarefied fungal ASVs table.

Spatial mid-domain effect estimation

The null model was used to examine the influence of the spatial mid-domain effect on the spatial distribution of rhizosphere fungal species richness along an elevation gradient (Peters et al. 2016). We reassigned the rhizosphere fungal richness in our study at random replacement for 999 times to generate a predicted pattern of rhizosphere fungal diversity that is controlled by the spatial mid-domain effect. The procedure was executed using the *rangemod1d* function from the ‘rangemodelR’ package (Marathe 2019). The predicted mean richness was used to evaluate the explanatory power of the spatial mid-domain effect on the rhizosphere fungal community along elevation and the spatial mid-domain effect on the rhizosphere fungal community was considered as a proxy of the spatial mid-domain effect on its host plant.

Statistical analysis

Data analysis was performed in R ver. 4.0.3 (www.r-project.org). We applied both quadratic and linear regression models to examine how plant biomass, climatic variables, soil properties and rhizosphere fungal diversity change with elevation. For each model, we calculated the AIC value and set the model with lower AIC value as the better fitting model. We used the ASVs richness and Shannon index to represent potential species pool and alpha diversity respectively. To reveal the variations in rhizosphere fungal community composition between different samples, we used the first axis of the PCoA based on the Bray–Curtis dissimilarity of fungal ASVs to represent the potential fungal beta diversity (Lei et al. 2024). The effect of elevation and plant species on the variation of rhizosphere fungal community composition was estimated by PERMANOVA analysis using the *adonis* function in the 'vegan' package (Oksanen et al. 2020).

To disentangle the effects of climatic variables, soil properties, rhizosphere fungal diversity and functional traits as well as the spatial mid-domain effect on the plant biomass across different elevations, we applied Spearman correlation and machine learning Boruta feature selection analyses. We conducted Spearman correlations between these factors using *corr.test* in the R-package 'psych' (Revelle 2022). The p-values were adjusted using false discovery rate (FDR, van Iterson et al. 2010). We further performed a feature selection with the *Boruta* algorithm in the 'Boruta' package (Kursa and Rudnicki 2010) to verify predictor variables (climatic variables, soil properties, rhizosphere fungal diversity, fungal functional traits and spatial mid-domain effect) responsible for plant biomass. Boruta iteratively compares the importance of each individual variable with a random variable by fitting random forest models. Variables that have significantly higher importance than random ones are classified as 'confirmed'; variables that have significantly lower importance than random ones are classified as 'rejected'; and variables that have no significant difference between random ones are classified as 'tentative'.

Results

Plant biomass of non-native *E. annuus* and native *A. lavandulifolia* along elevation

Biomass of non-native *E. annuus* displayed a significant hump-shape pattern across elevation ($R^2 = 0.112$, $p = 0.002$; Fig. 1B), while the biomass of native *A. lavandulifolia* showed a significant linearly decreasing trend with increasing elevation ($R^2 = 0.207$, $p < 0.001$; Fig. 1C).

Climatic variables, soil properties and rhizosphere fungal community along elevation

Through compiling MAT and MAP at various elevations, we observed significant correlations between these climatic variables and elevation. Specifically, the MAT decreased with increasing elevation changing from 12.18 to 4.72°C ($R^2 = 0.977$, $p < 0.001$; Fig. 2A), while the MAP increased with elevation varying from 766 to 834 mm ($R^2 = 0.748$, $p < 0.001$; Fig. 2B).

Rhizosphere soil properties also changed across elevation. The rhizosphere pH of non-native *E. annuus* ranged from 7.38 to 9.56 and pH of native *A. lavandulifolia* ranged from 7.41 to 9.20. The rhizosphere pH for both plant species exhibited a significant hump-shape pattern along elevation (*E. annuus*: $R^2 = 0.093$, $p = 0.005$; *A. lavandulifolia*: $R^2 = 0.187$, $p < 0.001$; Fig. 2C). In terms of total carbon (TC), the rhizosphere TC for *E. annuus* varied from 0.81% to 5.87%, whereas the TC for *A. lavandulifolia* ranged from 0.41% to 7.91%. The rhizosphere TC for both plant species showed an increasing trend with elevation (*E. annuus*: $R^2 = 0.035$, $p = 0.039$; *A. lavandulifolia*: $R^2 = 0.035$, $p = 0.039$; Fig. 2D). Regarding total nitrogen (TN), the rhizosphere TN for *E. annuus*, ranging from 0.05% to 0.31%, initially increased and then flattened out with elevation, while TN for *A. lavandulifolia*, ranging from 0.02% to 0.60%, showed an increasing trend with elevation (*E. annuus*: $R^2 = 0.213$, $p < 0.001$; *A. lavandulifolia*: $R^2 = 0.063$, $p = 0.008$; Fig. 2E). The rhizosphere TC:TN for *E. annuus* ranged from 10.1 to 21.1 and TC:TN for *A. lavandulifolia* ranged from 9.47 to 23.73. The rhizosphere TC:TN for both plant species initially decreased and then slightly increased again above 1800 m a.s.l. (*E. annuus*: $R^2 = 0.256$, $p < 0.001$; *A. lavandulifolia*: $R^2 = 0.198$, $p < 0.001$; Fig. 2F).

The diversity and composition of rhizosphere fungal community exhibited significant variations with elevation. The species pool (*E. annuus*: $R^2 = 0.559$, $p < 0.001$; *A. lavandulifolia*: $R^2 = 0.354$, $p < 0.001$; Fig. 3A) and alpha diversity (*E. annuus*: $R^2 = 0.343$, $p < 0.001$; *A. lavandulifolia*: $R^2 = 0.191$, $p < 0.001$; Fig. 3B) of both plant species displayed a significant hump-shape pattern along the elevation gradient. Conversely, the beta diversity of both plant species exhibited a decreasing trend as elevation increased (*E. annuus*: $R^2 = 0.805$, $p < 0.001$; *A. lavandulifolia*: $R^2 = 0.860$, $p < 0.001$; Fig. 3C). Notably, the composition of rhizosphere fungal community significantly differed between the two plant species and across different elevations (plant: $R^2 = 0.022$, $p < 0.001$; elevation: $R^2 = 0.093$, $p < 0.001$; plant × elevation: $R^2 = 0.011$, $p < 0.001$; Fig. 3D). We further categorized the overall fungal community composition into distinct functional guilds and identified that putative saprotrophs and plant pathogens were dominant at our study sites. In the rhizosphere of *E. annuus*, saprotrophs accounted for 54.57%, primarily represented by *Tetracladium* and plant pathogens make up 14.34%, predominantly *Fusarium*. In the rhizosphere of *A. lavandulifolia*, saprotrophs constituted 55.91%, mainly composed of *Mortierella* and plant pathogen represented 17.81%, primarily *Paraphoma* (Fig. 3E). The relative abundance of the putative saprotrophs in the rhizosphere of both plant species did not exhibit a clear trend across different elevations (*E. annuus*: $R^2 = 0.002$, $p = 0.277$; *A. lavandulifolia*: $R^2 = 0$, $p = 0.857$; Supporting information). Additionally, the relative abundance of putative ectomycorrhizal fungi (*E. annuus*: $R^2 = 0.030$, $p = 0.050$; *A. lavandulifolia*: $R^2 = 0$, $p = 0.389$; Supporting information) and arbuscular mycorrhizal fungi (*E. annuus*: $R^2 = 0$, $p = 0.769$; *A. lavandulifolia*: $R^2 = 0$, $p = 0.762$; Supporting information) remained relatively stable

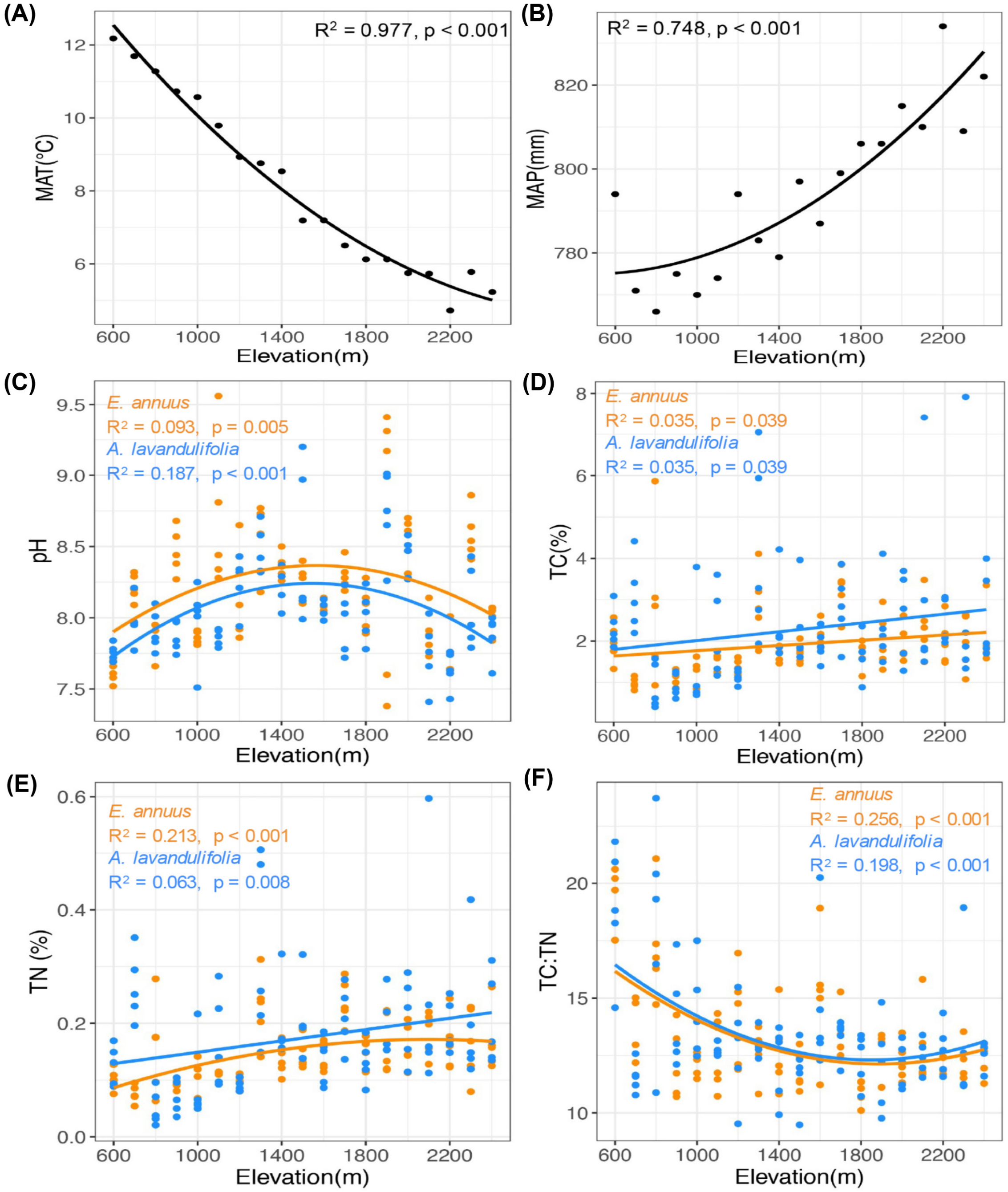

Figure 2. Climate variables MAT (A) and MAP (B) of each sampling site, and rhizosphere soil properties pH (C), TC (D), TN (E) and TC:TN (F) of the two plant species along elevation. MAT: mean annual temperature; MAP: mean annual precipitation; TC: total carbon; TN: total nitrogen.

across different elevations. The relative abundance of putative plant pathogens in the rhizosphere of *E. annuus* displayed a U-shape pattern across different elevations, while the rhizosphere of *A. lavandulifolia* showed a slightly decreasing trend with increasing elevation (*E. annuus*: $R^2 = 0.067$, $p = 0.007$; *A. lavandulifolia*: $R^2 = 0.311$, $p < 0.001$; Supporting information). The relative abundance of putative root endophytes in the rhizosphere exhibited an increasing trend with elevation for both species (*E. annuus*: $R^2 = 0.034$, $p = 0.041$; *A. lavandulifolia*: $R^2 = 0.127$, $p < 0.001$; Supporting information).

Estimated spatial mid-domain effect

Simulated by the spatial mid-domain null models, we found significant spatial mid-domain effects for both plant species. The predicted rhizosphere fungal species pool generated by

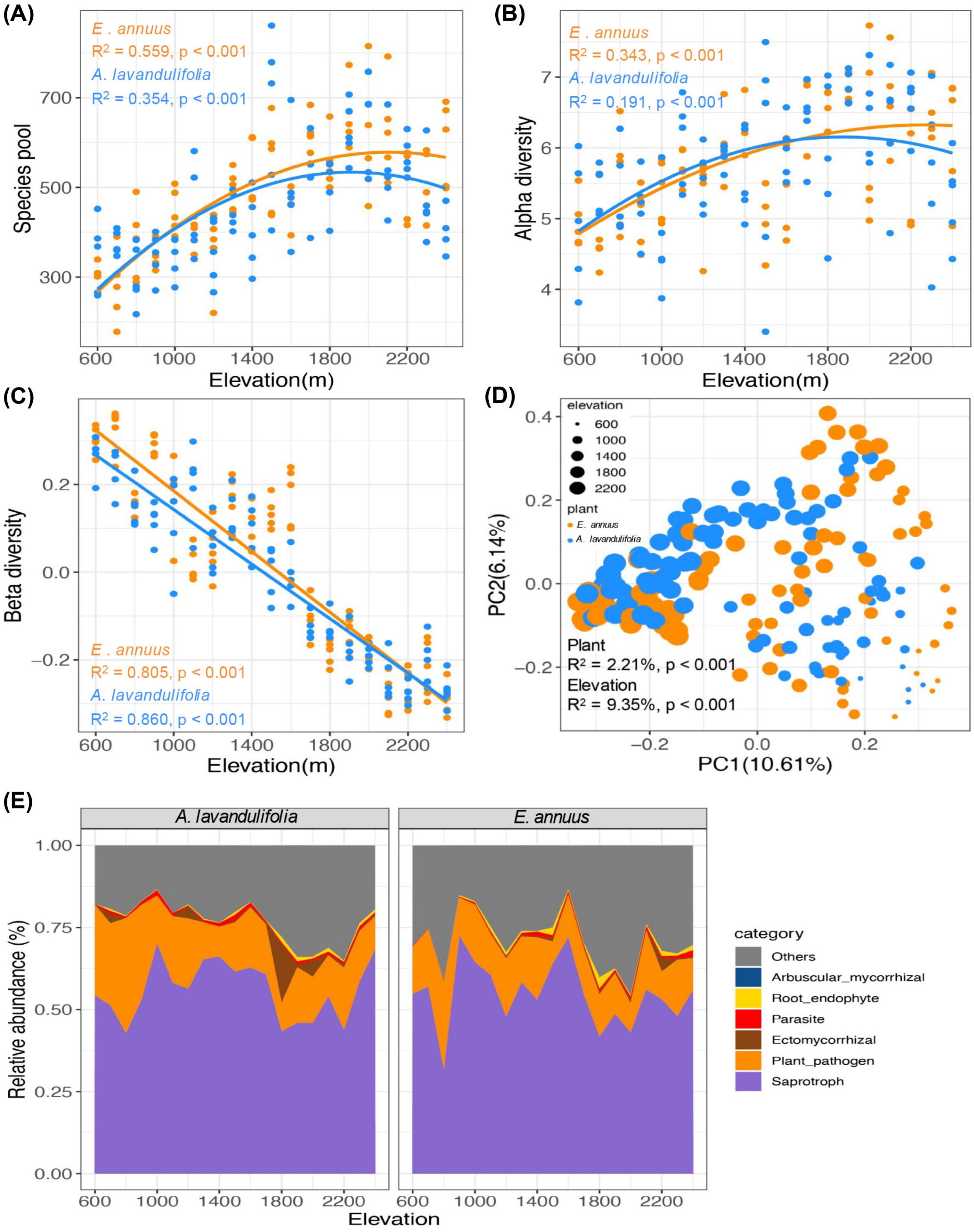

Figure 3. Rhizosphere fungal species pool (A), alpha diversity (B) and beta diversity (C) of the two plant species along elevation; the rhizosphere fungal community composition visualized by PCoA across elevation and the effects of plant species and elevation on the variance of fungal community composition were detected by PerManova (D); stacked area plots show the relative abundance of rhizosphere fungal functional guilds of two plant species (E).

randomized range placement falls within the 95% confidence limits at most individual sites within the elevation boundaries of *E. annuus* (Fig. 4A) and *A. lavandulifolia* (Fig. 4B) in the Qinling Mountains. We also detected significant positive correlations between the mid-domain predicted species pool and the observed species pool which verified the existence of spatial mid-domain effects for both plant species (Supporting information).

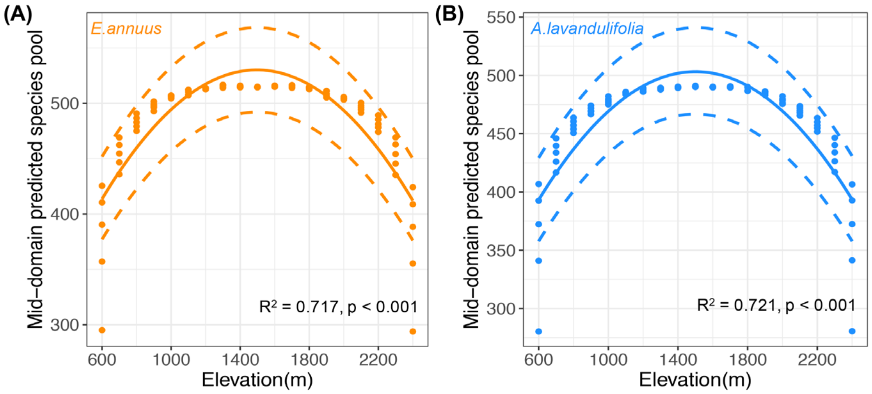

Figure 4. Predicted rhizosphere fungal species pool under the assumption of random range placement using mid-domain null models along elevation on Qinling Mountains for non-native *E. annuus* (A) and native *A. lavandulifolia* (B). The dash lines represent the upper and lower 95% CI limits.

Relative importance of climatic variables, soil properties, fungal community and spatial mid-domain effect on the elevation pattern of plant biomass

Using Boruta feature selection, we identified the spatial mid-domain effect as having a significantly high impact on the plant biomass of *E. annuus* followed by elevation, MAT and MAP (Fig. 5A). In contrast, for *A. lavandulifolia*, MAT, rhizosphere fungal beta diversity, elevation and MAP were found to exert considerable influence on plant biomass across different elevations (Fig. 5C). Using Spearman correlations, we determined that only the spatial mid-domain effect (rho = 0.379, $p < 0.001$) and putative saprotroph (rho = 0.213, $p = 0.039$) exhibited a significant positive relationship with the plant biomass of *E. annuus* (Fig. 5B). While for *A. lavandulifolia*, MAT (rho = 0.549, $p < 0.001$) and rhizosphere fungal beta diversity (rho = 0.590, $p < 0.001$) demonstrated significant positive correlations with plant biomass and elevation (rho = −0.539, $p < 0.001$), MAP (rho = −0.559, $p < 0.001$), putative ectomycorrhizal (rho = −0.467, $p < 0.001$), putative root endophyte (rho = −0.410, $p < 0.001$), rhizosphere fungal species pool (rho = −0.534, $p < 0.001$) and rhizosphere fungal alpha diversity (rho = −0.375, $p < 0.001$) were associated with significant negative relationships with plant biomass (Fig. 5D).

Discussion

Plant functional traits, particularly those associated with the competitive ability of non-native plants, such as biomass, play a crucial role in determining the severity of the impacts caused by these invasions (Ni et al. 2021). By accounting for variations in the traits of non-native plants, we can enhance our understanding of the consequences of such invasions (Gioria et al. 2023). Generally, it is anticipated that the biomass of native plants will decline with increasing elevation due to the unfavorable growth conditions, such as lower temperatures and reduced nutrient availability (Wang et al. 2007, Malhi et al. 2015). In alignment with this expectation, our study revealed a decreasing trend in the biomass of native *A. lavandulifolia* with increasing elevation. Conversely, the biomass of non-native *E. annuus* exhibited a hump-shaped pattern in relation to elevation, rather than a consistent linear decline.

We further conducted a comprehensive investigation into the factors influencing biomass at various elevations. Our findings indicate that the spatial mid-domain effect, rather than abiotic or biotic environmental factors, predominantly influences the biomass of *E. annuus* across different elevations. Conversely, this effect is not significant for *A. lavandulifolia*. The spatial mid-domain effect has been extensively used to elucidate the elevation gradient of species diversity among plants (Lee et al. 2013, Xu et al. 2021), animals (Chettri and Archarya 2020) and microorganisms (Miyamoto et al. 2014). Our research is pioneering in demonstrating that the spatial mid-domain effect can also drive the biomass of a non-native plant species along elevation gradients. The spatial mid-domain effect posits that a random replacement of species within a bounded geographic domain results in the highest species range overlap at the center of the domain without involving any environmental gradient (Colwell and Lees 2000). This concept postulates a continuous distribution range. Accordingly, the continuous elevation distribution of *E. annuus* may lead to peak biomass at mid-elevations, rather than at higher or lower elevations, under random replacement conditions, particularly when the species exhibits lower sensitivity to environmental gradients within the elevation domain. In contrast, the biomass of native *A. lavandulifolia* decreased linearly along elevation, with its biomass distribution along elevation being significantly influenced by climatic factors and rhizosphere fungal community. Therefore, despite *A. lavandulifolia* also possessing a continuous distribution range, the random effect is effectively overshadowed by other environmental factors. We acknowledge that it is difficult to draw conclusions about a direct impact of spatial mid-domain effect on the non-native plant biomass because

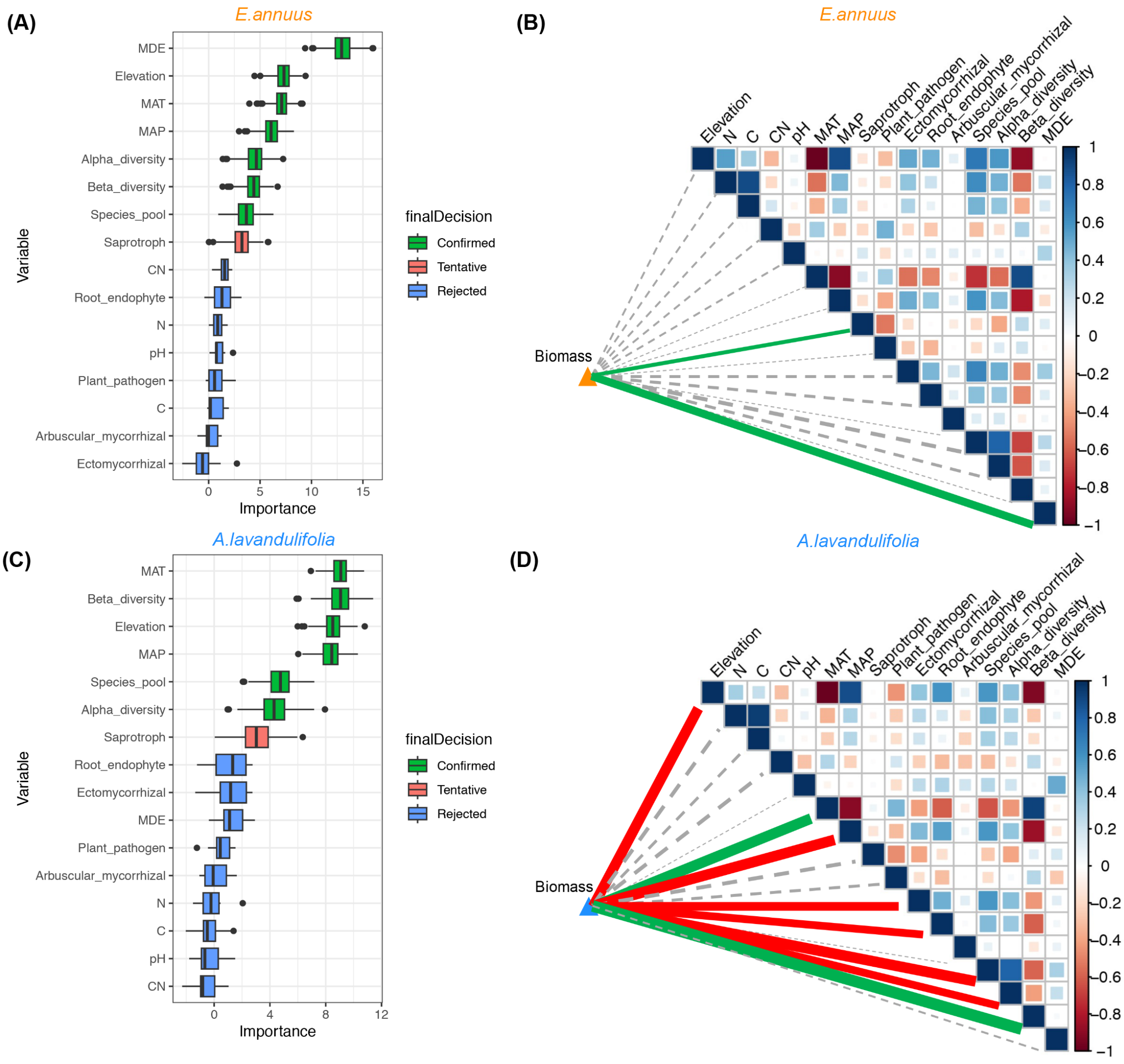

Figure 5. Boruta feature selection determining the importance of impact variables on plant aboveground biomass of non-native *E. annuus* (A) and native *A. lavandulifolia* (C), Spearman correlation of plant aboveground biomass of non-native *E. annuus* (B) and native *A. lavandulifolia* (D) with impact variables. The dash lines represent non-significant relationship ($p > 0.05$), the green lines represent positive significant relationship, the red lines represent negative significant relationship and the bold lines represent the strength of the correlation. MAT: mean annual temperature; MAP: mean annual precipitation; TC: total carbon; TN: total nitrogen; MDE: spatial mid-domain effect.

the spatial mid-domain effect on individual plant species in this study was assessed indirectly through its associated rhizosphere fungal community.

The possible explanation for the lower dependence on environmental factors of non-native *E. annuus* may be its broader range of environmental tolerance (Huang et al. 2023) compared to native *A. lavandulifolia*, allowing it to maintain high aboveground biomass at high elevations. The occurrence records of *E. annuus* based on GBIF database confirmed its worldwide distribution. Recent findings have also identified a hump-shaped relationship between biomass and elevation in tropical mountain forests when the trees were dominated by higher environmental tolerance temperate-affiliated clades (Venter et al. 2017, González-Caro et al. 2020). In addition, non-native plant species, which typically possess a shorter evolutionary history in newly introduced environments, often demonstrate enhanced phenotypic plasticity relative to native ones, enabling them to rapidly adjust their growth strategy in response to environmental changes (Richards et al. 2006). For example, some invasive Asteraceae plants showed stronger plastic root growth response that allowed them to maintain high performance under drought condition, which was not the case for native Asteraceae plants (Li et al. 2023). According to herbarium records, *E. annuus* first appeared in Shaanxi Province (where our sampling sites are located) in 1959 (Wang et al. 2010). The presence of *E. annuus* at Qinling Mountains is probably less than 65 years, a too short time-period to allow for population differentiation and local adaptation. Hence, higher phenotypic plasticity of *E. annuus* as compared to native *A. lavandulifolia* might have contributed to the different elevation trends between the non-native and native species in our study.

The generalizability of our findings should be interpreted with caution. Firstly, our investigation was limited to a single non-native plant species at a single elevation gradient, and it is noteworthy that only a few non-native plant species are capable of thriving at high elevations (Pyšek et al. 2011, Haider et al. 2018). The observed pattern may be confounded by species-specific effect or site-specific effect, as different species at different sites exhibit variability in their functional traits (Mudrák et al. 2019). Despite this significant limitation, we have elucidated the biomass dynamics of non-native plant species that are rarely able to reach up to high elevation across a gradient of 1900 m. From a methodological perspective, longer elevation gradients can provide a more comprehensive representation of elevation related changes; however, data on gradients exceeding 1000 m are scarce (Zvereva and Kozlov 2022). Our findings provide a relative complete elevation patterns of the biomass dynamic of both a native and a non-native plant species. Secondly, our study concentrated solely on plant aboveground biomass. This focus may undermine our ability to predict the overall impact of non-native plants on mountain ecosystems, as other functional traits, such as seed mass and total leaf area, are also anticipated to contribute to the invasion's impact (Liao et al. 2021, Ni et al. 2021). We acknowledge that future studies including more non-native and native plant species and more functional traits will be essential to enhance the inferential strength of our study. Besides, it is important to note that the rhizosphere fungal community in this study was measured using a general fungal ITS1 primers and ASV method, which may underestimate or overestimate fungal diversity because of primer bias, inefficient amplification of certain taxa and intraspecific variation in ITS region (Kauserud 2023). More specific primers or complementary methods can provide a more comprehensive view of the effects of rhizosphere fungal community.

Significance statement

Mountain ecosystems, critical refuges for biodiversity, are threatening by non-native plant invaders. Understanding the trait dynamics of non-native plant invaders which are successfully establishing themselves at high elevations is crucial for evaluating invasion risks and informing targeted management interventions. In this study, we integrated multiple mechanism underlying plant spatial distribution to uncover their role on elevation distribution of non-native plant. We found that non-native plant was primarily influenced by the spatial mid-domain effect, exhibited showed a hump-shape pattern along elevation gradient. In contrast, native plant was mainly affected by both abiotic and biotic factors, showing a decreasing trend with elevation. Our findings improved our understanding of ecological mechanisms underlying non-native plant invaders in mountain ecosystems.

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Speculations

While our study identifies the spatial mid-domain effect as a key factor driving the biomass pattern of non-native *Erigeron annuus* across different elevations, we could explore the genetic adaptation of non-native plants in relation to climate change resilience. Beyond our current findings, if non-native plants like *E. annuus* evolve rapidly and exhibit genetic diversity, their evolutionary dynamics could lead to novel traits not yet captured in our dataset, potentially making them better adapted to high-elevation environments. Additionally, if hybridization occurs between non-native plants and closely related native plants, the mixing of genes from different populations could accelerate the genetic adaptation process, complicating the assessment of non-native plants' performance in various environments. Furthermore, looking at aboveground interactions such as plant–pollinator interactions, plant–herbivore interactions along the elevation gradient could deepen our understanding. The presence of the non-native plants not only alters the soil and microbial dynamics but also changes the structure of the entire ecological network. Integrating the feedback loops between non-native plants and aboveground fauna could help understand the dynamic of non-native plants across diverse elevations.

Author contributions

Kaoping Zhang: Conceptualization (lead); Data curation (lead); Formal analysis (lead); Funding acquisition (supporting); Investigation (supporting); Methodology (lead); Project administration (lead); Validation (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **Yu Shi**: Methodology (supporting); Supervision (supporting); Writing – review and editing (supporting). **Pengdong Chen**: Investigation (lead). **Heinz Müller-Schärer**: Supervision (supporting); Writing – review and editing (supporting). **Wei Huang**: Conceptualization (supporting); Funding acquisition (lead); Supervision (supporting); Writing – review and editing (supporting).

Data availability statement

Raw sequencing data were deposited to the Genome Sequence Archive in National Genomics Data Center under the accession number GSA: CRA018063 (https://bigd.big.ac.cn/gsa/browse/CRA018063); Metadata including plant biomass, soil properties and climate variables are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.80gb5mm1d (Zhang et al. 2025)

Supporting information

The Supporting information associated with this article is available with the online version.

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