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Research Article

Similar alpha yet varied beta functional diversities between invasive and native plant species along an elevational gradient

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Abstract

Illuminating the invasive strategies of alien species in mountainous regions is critical to preventing the increasing frequency of invasion events and enhancing our understanding of the vulnerability of these ecosystems. Here, we investigated differences in diversity between invasive and native species across an elevational gradient through field experiments conducted along a 1200 m range, combined with measurements of plant functional traits and environmental factors. Our results revealed significant distinctions in diversity patterns between invasive and native species when considering multiple aspects of taxonomic and functional diversity at both α and β levels. Native species showed clear species replacement along elevation, while invasive species at higher elevations tended to be a subset of those found at lower elevations. Although invasive and native species shared relatively similar functional α diversity, they exhibited more significantly different functional β diversity. Elevation-related environmental factors played a major role in shaping functional dissimilarity and species similarity across plots. In contrast, functional redundancy at both α and β levels was more influenced by species status. Our findings highlight that invasive species exhibit a dissimilar strategy compared to native species along the elevational gradient and emphasize the importance of decreasing the introduction of alien species to better manage and prevent plant invasions in mountainous regions.

Key words: Environmental changes, functional redundancy, invasive plants, mountainous invasion, multi-dimensional diversities

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Introduction

Biological invasions significantly undermine biodiversity and ecosystem services, posing substantial risks to the economy, food security, and human health (Pyšek and Richardson 2010; IPBES 2023). Mountain ecosystems, global hotspots of biodiversity, were once considered less vulnerable to invasions (Pauchard et al. 2009; Carboni et al. 2018), whereas recent evidence shows that a rapid increase in invasive species is now occurring even in the areas of high elevations (Guo et al. 2018a; Kueffer et al. 2013; Petitpierre et al. 2016; Zheng et al. 2024). This surge in invasions is drawing greater attention to their potential impacts on mountainous regions (Alexander et al. 2011; Pyšek et al. 2011; Alexander et al. 2016; Iseli et al. 2023), such as significant declines in native endemic species and thus species composition homogenization (Daehler 2005; Dainese et al. 2017; Haider et al. 2018; Haider et al. 2022).

As invasive species continue to spread upward, researchers are increasingly concerned with whether biodiversity patterns differ between native and invasive species (Arévalo et al. 2005; Haider et al. 2010; Guo et al. 2018a). Extensive evidence suggests a more pronounced negative trend with elevations in invasive species richness, in contrast to the unimodal or more negative patterns among native species (Guo et al. 2013; Guo et al. 2018a; Haider et al. 2018). Initially proposed to depict the compositional differences among different sites (Whittaker 1960, 1972), β diversity's variations along elevational gradients have been used to elaborate on the mechanisms of invasion in mountain regions (Kraft et al. 2011; Marini et al. 2013; Du et al. 2021). While debates persist regarding β diversity patterns along elevational gradients, numerous studies demonstrate a monotonic decrease for native species (Mori et al. 2013; Tello et al. 2015; Sabatini et al. 2018). Conversely, less emphasis has been placed on the β diversity patterns of invasive species in mountainous regions, although it is acknowledged that invasive species tend to display lower species replacement along elevation gradients (Alexander et al. 2011; Marini et al. 2013; Steyn et al. 2017; Rana et al. 2024).

Taxonomic diversity provides certain measurements of biodiversity, but it does not consider the differences among species, such as functional aspects (Jarzyna and Jetz 2016; Ricotta and Pavoine 2024). Functional diversity, which pertains to the scope and value of traits in the community and reflects disparities/similarities in ecological niches among species (Tilman 2001), holds significant implications for community relationships and the community's response to environmental change, and thus ecosystem functioning (Hillebrand et al. 2008; Hillebrand et al. 2008; Suding et al. 2008; de Bello et al. 2021). Investigating the functional difference between invasive and native species along elevational gradients can enhance our understanding of invasive strategies along the gradients (Ordonez et al. 2010; Divíšek et al. 2018). Studies have demonstrated that the native species are likely to show negative or unimodal functional α diversity-elevation patterns (Lee et al. 2013; Zhang et al. 2014; Thakur and Chawla 2019; Ratier Backes et al. 2023), and an upward tendency of functional β diversity with elevation (Swenson et al. 2011; Zhang et al. 2023; Lin et al. 2024). However, summarizing the patterns of functional diversity for invasive species along elevational gradients remains challenging due to the limited amount of research. Given the complexity and importance of functional diversity, a more comprehensive framework is needed to better evaluate the multiple biodiversity patterns across these gradients (Fukami et al. 2005; Cardoso et al. 2014; Bishop et al. 2015; Shen et al. 2024). More importantly, exploring the differences in diversity between native and invasive species aids in seeing the big picture of how invasive species take advantage of potentially stronger competitive capacity than native species along elevation to spread upward (Divíšek et al. 2018).

Recently, a novel framework has been proposed that integrates both taxonomic and functional diversity into mathematical algorithms and ecological theory, providing a comprehensive tool for examining each of the α and β biodiversity from multiple perspectives simultaneously (Ricotta et al. 2023; Ricotta and Pavoine 2024). Specifically, this framework decomposes traditional taxonomic α diversity (S, Simpson's diversity) into α functional diversity (Rao's Q, reflecting species' trait variations within sites) and α functional redundancy (R, representing the similarity between species pairs within sites), along with a complementary measure of taxonomic diversity, taxonomic similarity (D, Simpson's dominance, emphasizing dominant species within sites) (Rao 1982; de Bello et al. 2007). Together, these three indices form a unified framework, providing a more exhaustive and consistent approach to elaborating the complex mechanisms driving community assemblages and biological invasions. Similarly, traditional taxonomic β diversity (D_{BC}, classical Bray-Curtis dissimilarity) is decomposed into β functional dissimilarity (D_{KG}, algorithmic dissimilarity coefficient, reflecting functional dissimilarity between species pairs among sites) and β functional redundancy (R_{β}, quantifying shared functionality among species across sites), with species similarity (S_{BC}, reflecting compositional similarity among sites) (Bray and Curtis 1957; Ricotta et al. 2021; Ricotta and Pavoine 2024). Species dominance (D) and the similarity of species across different sites are indicative of taxonomic stability, and functional redundancy at both α (R) and β (R_{β}) levels suggests functional stability. These factors are closely linked to the overall stability of the ecosystem. Additionally, functional diversity (Q) and the dissimilarity between sites (D_{KG}) represent the distinct ecological strategies employed by native and invasive species along elevation gradients, reflecting changes in their fitness. These novel frameworks provide a more holistic perspective on both the compositional and functional dynamics within ecosystems. By highlighting differences in diversity, the framework underscores the strategies of invasive species in mountainous regions and sheds light on potential invasion mechanisms from multiple perspectives.

Here, we constructed an experiment in the West Tianmu Mountain National Nature Reserve, located in Hangzhou, Zhejiang Province, one of the economic centers in East China, where invasive species have been found across all elevations, posing a significant threat to the local environment and economy (Hasigerili et al. 2023). Using data collected from an elevational gradient exceeding 1200 m, we calculated decomposed α and β diversity indices following the methods of Ricotta and Pavoine (2023, 2024). By integrating multiple aspects of taxonomic and functional biodiversity, we aimed to address the following questions: (1) what are the biodiversity patterns of invasive and native species at high and low elevations? (2) how do species status (i.e., invasive vs. native) and environmental factors influence these biodiversity patterns? For both α and β diversities, we hypothesize that, compared to natives, invasive species exhibit lower taxonomic diversity and reduced functional diversity but higher functional redundancy. Moreover, we expect these differences to be more pronounced at higher elevations, likely due to dispersal limitations and stronger environmental filtering, which may restrict the establishment of invasive species lacking specific traits.

Material and methods

Study area and experimental design

The experiment was carried out at the West Tianmu National Natural Reserve. Located in a subtropical climate region (30°18'-30°21'N, 119°24'-119°27'E), the mountain's elevational gradient ranges from 300 m to 1,506 m a.s.l., with an average annual temperature of 8.8 °C at the summit and 14.8 °C at the foot of the hill (Jiang et al. 2023).

We established 1 m^2 plots being 1–3 m from the roadside at low (< 500 m) and high (> 1000 m) elevations, given the presence of either cliff or rocks alongside roads between 500 and 1000 m, rendering it unsuitable for setting up surveying plots. In total, we established 15 low-elevation plots and 22 high-elevation plots, with a minimum horizontal distance of 50 m between sample plots to reduce spatial autocorrelation.

Plot survey and trait measurement

We identified the species in the plots based on the "Flora of Tianmu Mountain" (Chen et al. 2010). All identifiable plant species were recorded in each plot and the abundance of each species was estimated. We defined invasive species in our plots based on records of "A dataset on catalogue of alien plants in China" (Ma 2020; Lin et al. 2022). Species for which the "dataset" has a record of invasive status were categorized as invasive, and species with no records of alien status were categorized as native. There were 77 native species and 12 invasive species in all investigated plots.

To capture the plant's functional information, we measured nine functional traits for every species. Ten mature and healthy individuals of each species were selected to measure their height (cm), ground diameter (mm), and leaf thickness (mm) in situ. Three mature leaves were collected from the measured individuals and brought back to the laboratory in a cooling box to measure leaf area (mm^2), fresh weight (mg), dry weight (mg) after drying, and leaf nitrogen content (%). For species with fewer than 10 individuals, trait information was measured for all mature and healthy individuals. In addition, we calculated specific leaf area (the ratio of leaf area and leaf dry weight, mm^2/mg) and leaf dry matter content (the ratio of leaf dry weight and leaf fresh weight, mg/mg). We further calculated the mean value of each trait for each species.

Environmental variables

For each plot, the temperature (°C) of soil (6 cm below ground, T.soil), ground (T. ground), air (15 cm above ground, T.air), and soil humidity (%) were obtained using a TMS-4 recorder (Wild et al. 2019). Canopy density and slope were measured on-site. A fisheye lens was used to shoot at a distance of one meter above the plot center, and the canopy density was calculated via "Canopeo" (Patrignani and Ochsner 2015). We measured the slope of each plot with an instrumental slope angle meter. We collected soil samples in each plot following the three-point sampling method in which three corners of the plot were randomly selected to collect soil cores with a diameter of 5 cm and a length of 10 cm and then well mixed. For each soil sample, soil pH, silt content (Silt, %), clay content (Clay, %), sand content (Sand, %), total phosphorus content (TP, g/kg), total nitrogen content (TN, g/kg), total carbon content (TC, g/kg), carbon to nitrogen ratio (C/N, %), carbon to phosphorus ratio (C/P, %), nitrogen to phosphorus ratio (N/P, %), nitrate nitrogen content (NH_4^+, mg/kg), ammonium nitrogen content (NO_3^-, mg/kg), nitrate-ammonium nitrogen ratio (NH_4^+/NO_3^-, %), electrical conductivity (SEC, %), and water content (SWC, %) were obtained (Bremner 1960; Bowman 1988; Liu et al. 2021).

Taxonomic diversity and composition

Species richness was calculated for native and invasive species separately in each plot. To demonstrate the differences in species composition among species status along the elevation, we performed the Nonmetric Multidimensional Scaling (NMDS) based on Bray-Curtis distances with the R package Vegan (Oksanen et al. 2024).

Functional α diversity

To compute native and invasive species' functional diversity per plot, we scaled the trait matrices and calculated the relative functional Euclidean distance (the ratio of the original functional distance to the maximum functional distance) between species within plots. Simpson's dominance (D) is the probability that two individuals randomly selected from a plot will belong to the same species and is a complementary index of Simpson's diversity. Functional diversity (Q), Rao's quadratic diversity, is the mean of the dissimilarities between each pair of species *i* and *j* (d_{ij}) within plots, weighted by the species abundance (Rao 1982). Functional redundancy (R) is the difference between the classical Simpson diversity and functional diversity (Q) (de Bello et al. 2007). Based on the transformed functional matrix, we calculated Simpson's dominance (D) and functional diversity (Q) using the "avid" package in R by Equations (1–2) and functional redundancy (R) by Equation (3) (Pavoine 2020).

$$D = \sum_{i=1}^{N} p_i^2 \tag{1}$$

$$Q = \sum_{i,j=1}^{N} p_i p_j d_{ij} \tag{2}$$

$$R = 1 - D - Q \tag{3}$$

where N is the number of species in each plot, p is the species' relative abundance in each plot, and d_{ij} is the distance function between the *i*-th and *j*-th species.

Functional β diversity

Species similarity S_{BC} is the complementary index of classical Bray-Curtis dissimilarity, which depicts the taxonomic similarity based on the species relative abundance between plots ($d_{ij=1}$, *i* and *j* denote two different species) (Bray and Curtis 1957; Kosman 2014; Ricotta and Pavoine 2024). Functional dissimilarity D_{KG} is the actual functional difference among plots based on functional distances between pairs of species i and j weighted by species relative abundances (Ricotta et al. 2021). Functional redundancy R_{β}, the difference between S_{BC} and D_{KG}, represents the functional similarities between plots (Ricotta and Pavoine 2024). S_{BC}, D_{KG} and R_{β} between plots in the high and low elevation were computed with the functions '*betaUniqueness*' of the R package "adiv" by Equations (4–6), respectively (Pavoine 2020; Ricotta and Pavoine 2024).

$$S_{BC} = \sum_{i=1}^{N} min\{p_{jh,} p_{jk}\} \tag{4}$$

$$D_{KG} = min_{\pi} \sum_{i=1}^{N} \sum_{j=1}^{N} \pi(i,j) \times d_{ij} \tag{5}$$

$$R_{\beta} = 1 - S_{BC} - D_{KG} \tag{6}$$

where N is the number of species in each plot, p_{jh} and p_{jk} are the *j*-th species' relative abundance in the *h*-th and *k*-th plot respectively $\pi(i,j)$ is the *i*-th species' relative abundance in the *h*-th plot matched with *j*-th species in the *k*-th plot, and d_{ij} is the functional distance between the *i*-th and *j*-th species.

Statistical analyses

The results of functional α and β diversity were illustrated on the ternary diagram by the R package "ggplot2" (Wickham et al. 2024). To compare the decomposed functional diversity of native and invasive species in different elevations, we applied one-way ANOVA for each decomposed functional α and β diversity index. Multiple comparisons were then performed using the "TukeyHSD" method by the R package "multcomp" and the results of the comparisons were corrected by the "holm" method (Hothorn et al. 2008).

To explore how species status and environmental factors affect the different aspects of functional α and β diversity, we first applied a principal component analysis (PCA) for all environmental factors with the R package "FactoMineR", and the first two PC axes that explained 61.6% variance of the environmental factors were used as the environmental variables (Appendix 1: Fig. A1) (Lê et al. 2008). We constructed linear mixed models with different diversity indices as response variables, environmental PC1 and PC2 as fixed effects, and the species status as a random intercept with the R package "lme4" (Bates et al. 2015). Alternatively, we fitted the model with environmental PC1 and PC2 as fixed effects and species status as random intercepts and slopes, but ultimately excluded it because model performance did not improve significantly. We then extracted the proportions explained by the different factors (environmental PC1, PC2, status, and residual) for those diversity indices from our models via the R package "glmm.hp" (Lai et al. 2022, 2023).

All data analyses were carried out in R version 4.3.1 (R Core Team 2023).

Results

Differences in species richness and community composition

Noticeably, all of the surveyed plots observed the presence of invasive species. Native plant species exhibited significantly higher species richness compared to invasive species, irrespective of elevation ($p < 0.05$). Additionally, there was no significant difference in species richness between low and high elevations for either native or invasive species (Fig. 1A). The species composition of native species varied significantly in the plots between low and high elevations (Fig. 1B). In contrast, the invasive species at high elevations were predominantly a subset of those at low elevations (Fig. 1C)

Functional α and β diversity

Overall, functional α and β diversity differed between invasive and native species, with especially pronounced distinctions in functional β diversity (Fig. 2). In terms of functional α diversity, invasive species tended to cluster in the lower left corner of the α ternary diagram (Fig. 2A), representing higher species dominance (D)

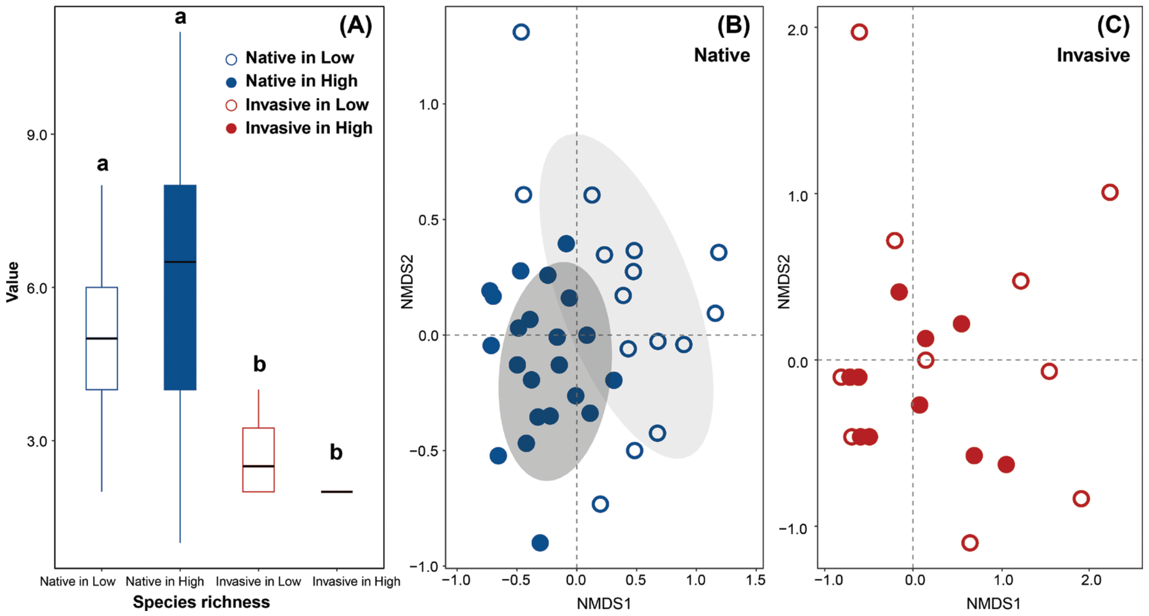

Figure 1. (**A**) Differences in species richness of native species (Native) and invasive species (Invasive) between the low and high elevations. Different letters indicate a significant difference ($p < 0.05$) from multiple post hoc comparisons with holm-adjustment of one-way ANOVA. Two-dimensional NMDS ordination of all plots showed differences in species composition of (**B**) Native and (**C**) Invasive species at different elevations (the stress values equal to 0.12 and 0.04, respectively). Shadow ellipses represent 95% confidence intervals around the centroids for the point types.

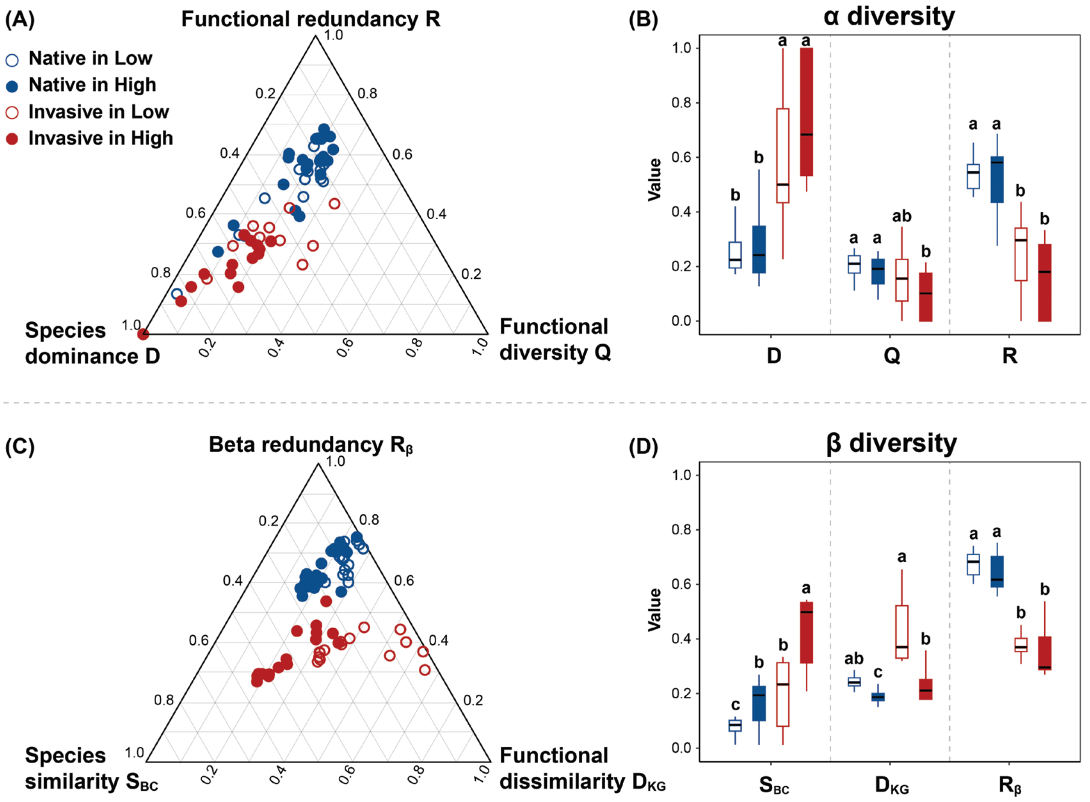

Figure 2. Ternary diagrams of functional (**A**) α diversity and (**C**) β diversity for native and invasive species at low and high elevations. One-way ANOVA with holm-adjusted multiple comparisons for each of the functional (**B**) α diversity and (**D**) β diversity components were shown in boxplots, with different letters indicating significant differences ($p < 0.05$). D, species dominance within plots; Q, functional diversity within plots; R, functional redundancy within plots; S_{BC}, species similarity among plots; D_{KG}, functional dissimilarity among plots; and R_{β}, functional redundancy among plots.

and lower functional redundancy (R) than natives (Fig. 2B). However, functional diversity (Q) did not differ significantly between invasive and native species, although invasive species at higher elevations exhibited considerably lower values. In addition, functional α diversity remained consistent across elevations for both invasive and native species (Fig. 2B). In contrast, differences in β diversity were more pronounced between the two groups. Specifically, invasive species tended to occupy the lower section of the β ternary diagram, indicating higher species similarity (S_{BC}) and reduced functional redundancy (R_{β}). At higher elevations, invasive species were more frequently positioned towards the left side of the β ternary, reflecting increased S_{BC} and decreased functional dissimilarity (D_{KG}) (Fig. 2C, D).

Status and environment effects on functional α and β diversity

Species status and the first two environmental PCs (PC1 and PC2) collectively explained a substantial portion of the variation in functional α and β diversity (Fig. 3), accounting for 56.06% to 92.42% of the total variation. However, this pattern did not extend to functional diversity Q, where 80.13% of the variation remained unexplained by factors included in the model. Notably, species status emerged as the dominant factor, contributing between 18.60% and 91.80% across all metrics, with the least influence on Q (18.60%) and the greatest impact on R_{β} (91.80%).

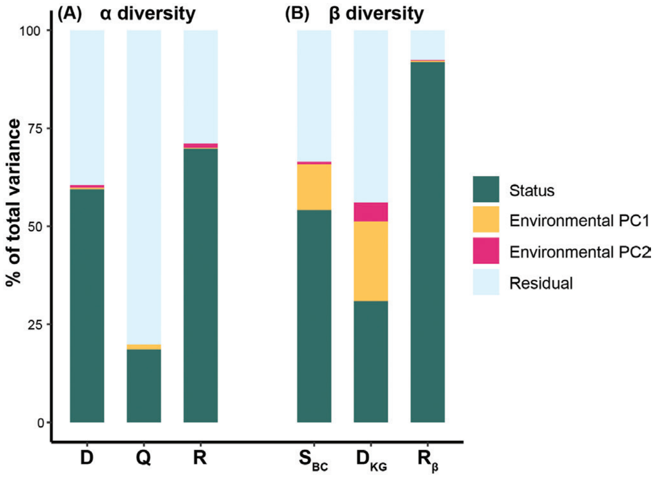

Figure 3. Stacked bar plots demonstrate the explained variation in functional α (**A**) and (**B**) β diversity. Each bar represents the contribution of species status (invasive/native), the first two PC axes derived from environmental factors, and residuals. D, species dominance within plots; Q, functional diversity within plots; R, functional redundancy within plots; S_{BC}, species similarity among plots; D_{KG}, functional dissimilarity among plots; and R_{β}, functional redundancy among plots.

Discussion

With the increasing frequency of invasion events in mountainous regions, the differences in multiple diversity patterns between invasive and native species deserve deeper exploration to reduce the consequential damage that would follow. Considering the complexity and lack of harmonization of multiple diversity, we integrated taxonomic and functional information via decomposed α and β diversity methods to reveal the differences in diversity patterns between invasive and native species along an elevational gradient. We found that species of distinct statuses at separate elevations held marked differences in patterns of multiple diversity, especially in β diversity, and the explanatory power of drivers was divergent among indices.

Consistent with our hypotheses, invasive species displayed higher species dominance (D) and species similarity (S_{BC}) compared to native species. Our observation revealed that invasive species found at higher elevations were a subset of the invasive species at lower elevations. Notably, invasive species at high elevations, *Erigeron annuus* (L.) Pers., *Conyza canadensis* (L.) Cronquist, *Bidens frondosa* L., *Solidago canadensis* L., *Crassocephalum crepidioides* (Benth.) S. Moore, all belonging to the Asteraceae family, predominantly adopted the ruderal strategy, characterized by traits like rapid dispersal and reproduction (Grime 1974; Hasigerili et al. 2023). These ruderal invasive species demonstrated stronger adaptability and greater abundance (Alexander et al. 2011), resulting in higher species dominance and species similarity at higher elevations. In contrast, native species showed greater species richness and lower species dominance, mainly due to the presence of numerous locally rare species with low abundance. Furthermore, native species showed a stronger elevational preference, with many species occurring only at specific elevations, unlike the invasive species at high elevations, which were generalists and distributed throughout the entire elevation range (Marini et al. 2013; Steyn et al. 2017). Our results align with previous findings of distinct community assembly mechanisms between invasive and native species, with the former initially establishing at lower elevations with a subset spreading upward, and the latter showing minimal overlap between low and high elevations (Marini et al. 2013; McDougall et al. 2011; Zhang et al. 2015; Yang et al. 2018).

The functional diversity differences between invasive and native species further clarified the competitive strategies of invasive species. At lower elevations, invasive species occupied functional niche widths comparable to those of native species, suggesting they had an equivalent advantage in colonization despite lower species richness and shorter residence time. Remarkably, at higher elevations, invasive species exhibited lower functional α diversity but higher functional β diversity compared to native species. The reduced functional diversity Q of invasive species at higher elevations was related to their lower species richness, though a substantial proportion remained unexplained. In our study, many invasive species from the same family exhibited significant trait dissimilarity across different plots. The greater trait dissimilarity of invasive species compared to native species across elevations indicates a stronger resistance of these ruderal-strategy invasive species to environmental filtering (Hasigerili et al. 2023). Furthermore, in line with previous findings that environmental filtering can reduce functional β diversity (Perez Rocha et al. 2018; Diniz et al. 2021), we found that environmental factors (environmental PC1 and PC2) had a relatively high explanatory power for functional dissimilarity. Specifically, elevation-related factors such as temperature and soil nutrients (environmental PC1, Appendix 1: Fig. A1) played a more significant role than other factors like soil pH and SEC (environmental PC2), highlighting the critical influence of elevation in shaping diversity patterns. Our findings indicate that intensified human disturbances associated with lowland tourism development lead to resource fluctuations, creating opportunities for invasive species colonization and promoting trait divergence in both invasive and native species (Blumenthal 2006; Grime 2006). As disturbance intensity declines with elevation, both invasive and native assemblages exhibit reduced functional dissimilarity. Notably, four out of five invasive species at high elevations originate from North America, which shares similarities in climate, vegetation types, and floristic composition with China (Qian et al. 2017). In our study, these similar environmental conditions between native and introduced ranges could facilitate the rapid establishment of ruderal invasive species with pre-adapted traits (e.g., higher SLA, nutrient-rich foliage, and taller plant heights) in recipient ecosystems (van Kleunen et al. 2010; Guo et al. 2018b; Hasigerili et al. 2023).

The observed pattern of functional redundancy in our study was counterintuitive, as invasive species, despite having greater species dominance (D) and species similarity (S_{BC}), showed lower functional α and β redundancy compared to native species. This can probably be explained by the limiting similarity hypothesis (MacArthur and Levins 1967), where functional niche differentiation and reduced trait redundancy minimize competition among closely related invasive species, thus promoting their coexistence (Grime 2006; Kraft et al. 2014). Furthermore, environmental differences between low and high elevations had minimal impact on functional α and β redundancy for both invasive and native species, indicating that biotic interactions may play a more dominant role than environmental conditions in shaping local community functional similarity. In addition, despite substantial changes in species composition, functional composition remained relatively stable, thus promoting community resilience (Biggs et al. 2020; Jarzyna et al. 2022). Communities with higher functional redundancy are likely more resistant to harsh conditions and are less susceptible to species loss or turnover (Hidasi-Neto et al. 2012; Gallagher et al. 2013; Ricotta et al. 2016). Nevertheless, a considerable proportion of variation in diversity patterns apart from the functional redundancy remains unexplained. Previous studies have demonstrated other potential factors influencing elevational diversity patterns, including anthropogenic drivers related to propagule pressure, such as reduced human activities and different land use types at higher elevations (Parks et al. 2005; Marini et al. 2013), water-energy dynamics (Jakobs et al. 2010) and area effects (Romdal and Grytnes 2007). Our results thus suggested the necessity of exploring other factors of the elevational gradient to better understand these patterns.

According to our results, the strong biological interactions generated by invasive species outweigh the environmental filtering effect and ultimately lead to invasive species' upward spread trend along elevation. In the context of dramatic global change, alien species are dispersing intentionally or accidentally at a rapid speed. Once they overcome geographical barriers and become invasive, biotic interactions would dominate the process of colonization even in mountainous areas with harsh environments (Cadotte et al. 2018). Thus, an effective prevention practice would be reducing anthropogenic disturbance and the introduction of alien species (Kueffer et al. 2013; Fertakos and Bradley 2024).

Conclusion

By thoroughly examining various aspects of taxonomic or functional α and β diversity, our study provides a more comprehensive exploration of both invasive and native plant diversity patterns in mountain regions, offering new insights into the mechanisms behind invasion events. We found distinct differences between invasive and native species in terms of distribution and diversity variation. Native species demonstrated a stronger elevational preference, with notable species replacement, whereas invasive species at higher elevations were largely subsets of those at lower elevations. While invasive and native species occupied relatively similar α diversity spaces, their β diversity spaces were more significantly differentiated, likely due to the strong adaptive capacity and more favorable competitive strategies of invasive species. Our study further confirms the utility of the novel diversity decomposition framework to provide a deeper understanding of the factors driving the distinct patterns between invasive and native species across environmental gradients.

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

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Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

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Appendix 1

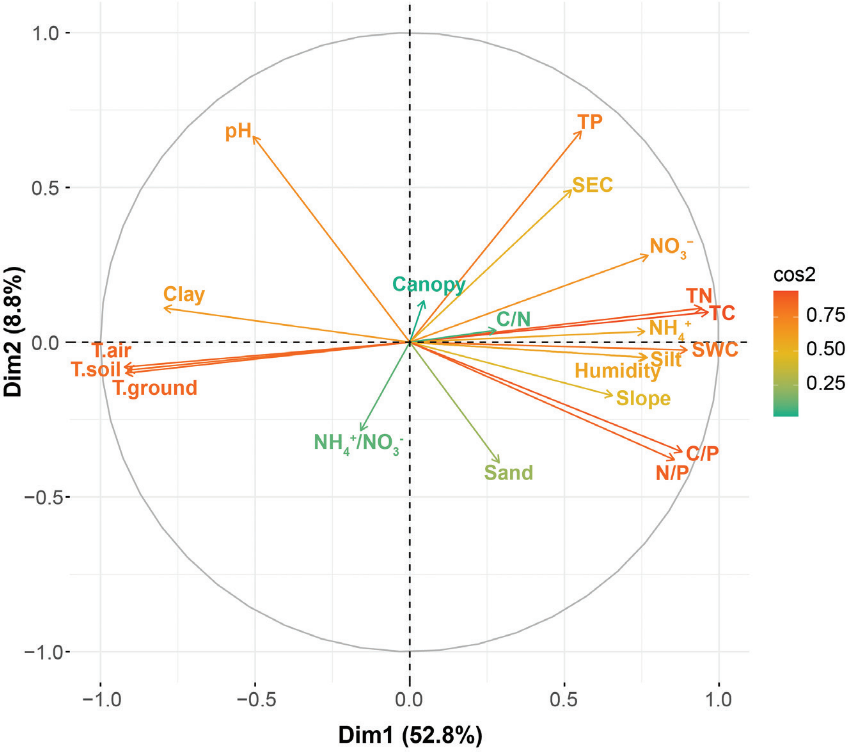

Figure A1. The result of the principal component analysis (PCA), with cos2 representing the magnitude of the correlation between the environmental factors and the principal component.

Supplementary material 1

Data utilized for the analysis

Authors: Yan-Yan Wang, Kun Guo, Rui-Ling Liu, Hasigerili, Miao-Miao Zheng, Yuan Gao, Ming-Shui Zhao, Jian Zhang, Wen-Yong Guo

Data type: xlsx

Link: https://doi.org/10.3897/neobiota.99.143495.suppl1