Hydrobiologia (2026) 853:1319–1336
https://doi.org/10.1007/s10750-025-05997-w

PRIMARY RESEARCH PAPER

Ecological niche dynamics across continents for aquatic plants native to South America and invasive aliens elsewhere

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Received: 4 February 2025 / Revised: 26 August 2025 / Accepted: 29 August 2025 / Published online: 25 September 2025

Abstract Understanding the niche dynamics of invasive non-native aquatic plants is limited by the insufficiency of freshwater-specific climatic environmental information. Specifically, non-native species are frequently not in equilibrium with environmental conditions in the introduced areas, allowing them to colonize environments absent from their native range. We investigated the niche dynamics of five South American aquatic non-native plants (*Egeria densa*, *Myriophyllum aquaticum*, *Pistia stratiotes*, *Pontederia crassipes*, and *Salvinia molesta*) considered invasive worldwide. The differences between the native and invaded niches were assessed using niche overlap, equivalence, and similarity indices. The dynamics of invasive niches were quantified by indices describing unfilled, stable, and expansion of niches. In general, the plants showed a moderate overlap, except for *S. molesta* (low overlap). North America showed the highest overlap values, while niche stability was high (mean = 0.726), but with potential expansion and unfilled, especially in Europe and Africa. Niche equivalency was mostly rejected, indicating significant climatic differences between native and invaded niches. This study showed species and continent-specific niche shifts, while niche expansion and unfilling were evident, most shifts occurred within the boundaries of the native niche.

Handling editor: Andre Andrian Padial.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10750-025-05997-w.

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The findings highlight limited niche conservatism, suggesting that dispersal events and introduction pathways facilitate invasions into novel conditions.

Keywords Hydroclimatic variables · Invasive macrophytes · Niche dynamics · Niche shift · Niche overlap

Introduction

According to the principle of niche conservatism, the species tend to preserve their ancestral fundamental niche requirements over time and space (Wiens et al., 2010; Qiao et al., 2024; Nzei et al., 2024). While niche could change slowly over time (Pearman et al., 2008, 2010), human-driven impacts could influence and shift the realized niche of a large number of species (Pearman et al., 2008; Guisan et al., 2014), affecting the suitable habitat area, posing challenge for biodiversity conservation (Barral, 2019; Bellard et al., 2018; Santamarina et al., 2023). For some species, greater niche conservatism may be narrowly associated with lower adaptation to environmental changes and smaller range expansions (Yang et al., 2022). Thus, invasive non-native species offer excellent model systems for examining niche conservatism during the invasion process (Sax et al., 2007; Peterson, 2011; Schulte et al., 2012), although increasing evidence regarding ecological and evolutionary adaptations over relatively short time periods suggests that niche shifts (i.e., species ability to occupy climate niches in a new range that differ substantially from those of the native range) might be more common than previously acknowledged, and especially frequent for invasive non-native species (Whitney & Gabler, 2008).

Different studies have examined whether invasive non-native plants experience climatic niche shifts between their native and introduced ranges. For example, Petitpierre et al. (2012) found that such shifts are relatively rare among 50 Holarctic invasive plant species, suggesting that models based on native range data can effectively predict potential invasions. However, Atwater et al. (2018) documented that some non-native plants could established in environments absent from their native range, indicating a shift. Overall, the extent of observed niche shifts probably depends on the studied organism as well as on the methods and data used (Guisan et al., 2014). Chapman et al. (2017a) showed that forward-mechanistic species distribution model can simulate potential niche shifts of invasive non-native plants, such as *Ambrosia artemisiifolia* L., by incorporating variation in phenological traits. Their study linked changes in functional traits to range expansions into cooler climates, suggesting rapid niche shift during the invasion process. Indeed, rapid evolution of non-native populations to different conditions is a common event that changes the phenotypic response exhibited by the species. Even if the niche is shifted, it could be narrower in the introduced than in the native range, this might be because the species is still spreading (Alexander & Edwards, 2010). In this context, niche expansion refers not necessarily to adaptation to novel environmental conditions but rather to the occupation of environmental conditions that exist within the species' fundamental niche yet remain inaccessible in the native range. Such conditions may become available in the invaded range, allowing the species to expand its realized niche without implying evolutionary novelty. Therefore, distinctions should be made between true niche shifts involving evolutionary changes and expansions resulting from increased environmental accessibility (Bates & Bertelsmeier, 2021). Anyway, having knowledge of these changes is very relevant because it allows us to evaluate the dynamics of the niches, helps us to clarify the distribution patterns and the adaptations of the species to different environmental conditions (Tingley et al., 2014), as well as to determine the rates of specialization and extinction (Sexton et al., 2017).

Developing niche models is useful to predict range shifts and assess the expansion risk of invasive non-native species. If species expand into novel environments, models may underestimate their potential spread (Holcombe et al., 2010; Parravicini et al., 2015). In this context, many studies focused on the distribution of terrestrial invasive non-native species and on quantifying their environmental niche through projection (e.g., Peterson et al., 2008; Lozano et al., 2020, 2023) and by ordination techniques related to climatic niche shifts (e.g., Thuiller et al., 2005; Early & Sax, 2014; Montagnani et al., 2022), but only few of them have used invasive non-native aquatic plant species as case study (e.g., Heikkinen et al., 2009;

Hoveka et al., 2016; Rodríguez-Merino et al., 2019). However, no actual study has investigated whether the niches of invasive non-native aquatic plants are conserved to a broader extent. Based on the niche conservatism principle, the niche of invasive non-native aquatic plants is then expected to remain similar in the native and invaded range.

The environmental niches of invasive species in the invaded range might change due to factors such as genetic evolution and plasticity (Wang et al., 2017; Guisan et al., 2014). The developed methodology to quantify the overlap of different environmental niches in geographical space has not yet been applied in the context of aquatic invasions (Yin et al., 2021; Robeck et al., 2024). Indeed, the detection of niche changes in invasive non-native aquatic plants could improve the prediction of their invasion process under climate change scenarios, providing the basis for future management plans and actions to contrast the impacts of these invasive non-native aquatic plants (Rodríguez-Merino et al., 2018).

Since freshwater environments are among the habitats most affected by invasive non-native species (Strayer, 2010), in this study, we focused on the climatic niche dynamics of five South American invasive non-native aquatic plants [i.e., *Egeria densa* (Planch.) Casp. (Hydrocharitaceae); *Myriophyllum aquaticum* (Vell.) Verdc. (Haloragaceae); *Pistia stratiotes* L. (Araceae); *Pontederia crassipes* Mart. (Pontederiaceae) and *Salvinia molesta* D.Mitch. (Salviniaceae)] that have very high impacts on their invaded ranges at global scale (Williams et al., 2008; Coetzee et al., 2017; Wang et al., 2017). These species occur in disturbed and natural freshwater ecosystems in both native and invaded ranges. Although they are sometimes considered as weeds in the native range, they rarely reach the high densities observed in the invaded range where they can behave as transformer species of aquatic habitats with significant impacts on biodiversity and ecosystem services (Lolis et al., 2020). Previous studies modeled the distribution of a subset of these species, but only at country level or based on a limited set of algorithms or bioclimatic variables useful mostly for terrestrial plants (Gallardo & Aldridge, 2013; Kelly et al., 2014). Considering the above, the main aim of this study was to quantify the niche dynamics in analogous climates (i.e., the climates that are available in both native and introduced extents) between the native (i.e., South America) and the invaded ranges (i.e., Asia, Africa, Australia, Europe, and North America) using ordination techniques for five invasive non-native aquatic plants: *E. densa*, *M. aquaticum*, *P. stratiotes*, *P. crassipes*, and *S. molesta*. In particular, our research aimed to address two primary questions: (i) Do selected invasive non-native aquatic plant species exhibit shifts in their climatic niche when comparing native to invaded ranges? and (ii) Do these species have achieved environmental equilibrium within the invaded regions, or is there potential for further expansion into environments analogous to those of their native niche?

Methods

Study species

Five aquatic invasive non-native plant species (*E. densa*, *M. aquaticum, P. crassipes, P. stratiotes,* and *S. molesta*) were selected for the analysis of niche dynamics across continents (Fig. 1). These plants are native to South America and renowned for their wide invasion ability outside the native range, mostly as a result of escape from cultivation, being used as ornamental species and for several other purposes (Coetzee et al., 2011). They were selected for the present study on niche dynamics based on their high level of invasiveness, as reported also by Lozano & Brundu (2018) in the risk assessment for aquatic species in South America. Two of them are submerged hydrophytes (*E. densa* and *M. aquaticum*), while the other three are free-floating (*P. crassipes*, *P. stratiotes*, and *S. molesta*). In introduced extents, these species grow vigorously in contaminated or degraded freshwater systems, allowing them to form dense monocultures and cause some negative impacts. Among these are impacts on ecosystem functioning and services (e.g., nutrient and water cycling), on native biodiversity (e.g., reduction in the size of native populations), and on socio-economic factors (e.g., reduction in aesthetic values; Hussner, 2014; Chapman et al., 2017a, b; Coetzee et al., 2017; Moffat et al., 2024).

Species occurrence data

Multiple data sources were used to collect occurrences of the investigated five invasive non-native

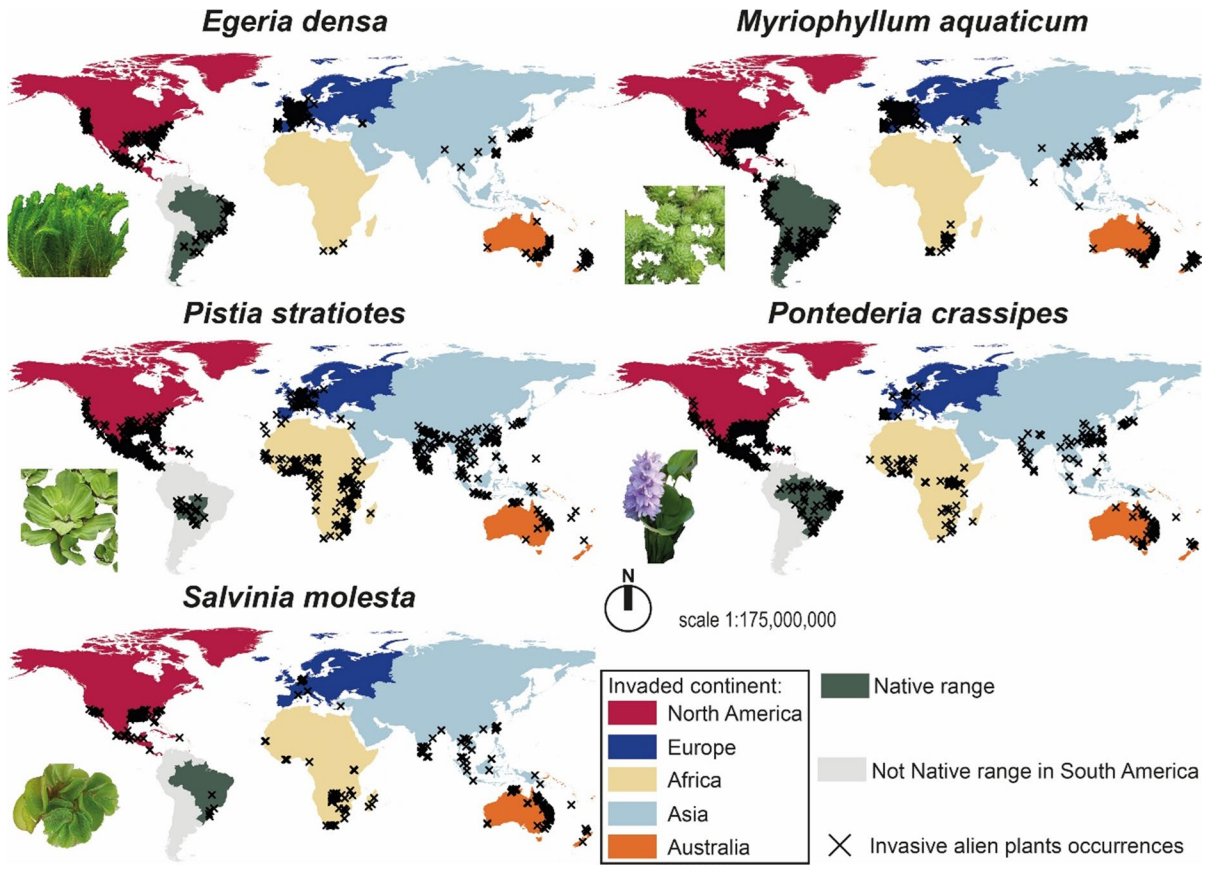

Fig. 1 Global occurrence records of *Egeria densa*; *Myriophyllum aquaticum*; *Pistia stratiotes*; *Pontederia crassipes,* and *Salvinia molesta*. Information on native range retrieved from EPPO Global Database (https://www.eppo.int)

aquatic plant species from their native and invaded ranges. Records were retrieved using the *occ* function of "Spocc" R package ver. 1.2.2 (Chamberlain, 2017). This package allows to download data of plant occurrence from the Global Biodiversity Information Facility (www.gbif.org), the Atlas of Living Australia (www.ala.org.au/), iNaturalist (www.inaturalist.org), and iDigBio (www.idigbio.org). All datasets were accessed on March 2024, and the total number of geographic records used to create the models is reported in Table S1.

Records with insufficient spatial accuracy (> 1 km), potential errors (duplicates of the same sample), and records that were outside of the coverage of the predictor layers (e.g., points occurring in the sea) were excluded, as well as records collected before 1950. After this, to reduce the effects of spatial autocorrelation and biases in the species occurrence data, only one record was retained within each pixel (1 km^2) containing multiple records to keep spatially independent records.

Furthermore, to further reduce the uncertainty in the data, we also removed occurrences that occupy climatically anomalous micro-habitats inhibiting the growth of the five invasive non-native aquatic plants, such as below the minimum growth temperature, prolonged exposure to lethal frosts, and prolonged drought periods (Table 1; Mitchell & Tur, 1975; Pieterse et al., 1981; Urbanic-Berčič & Gaberščik, 1989; Thiébaut et al., 2016; Wang et al., 2024). The filtered occurrences with climatically anomalous micro-habitats were based on high resolution, CHELSA climate data set v. 2.1, approximately 1 km (Karger et al., 2017, Table S1).

Table 1 Hydroclimatic variables used to define unsuitable conditions for establishment by the five study species

Species	Hydro 06	Hydro 10	Hydro 18	References
Egeria densa	< -2C; growth stops < 6°C; survival at 1°C under 15 cm ice	> 10°C; survives in waters with temperatures of 3–35°C	< 4 mm; drought can cause local extirpation where water levels fall	Williams et al., (2008); Yarrow et al., (2009); Kelly et al., (2014)
Myriophyllum aquaticum	< -2°C; frost limit growth and establishment	> 10°C; warmer temperatures boost establishment	< 4 mm; precipitation driest month limit growth	Millane & Caffrey (2014)
Pistia stratiotes	< 0 °C; prolonged exposure to lethal frosts	< 0°C; low temperature inhibiting seed germination	< 5 mm; seasonal drying reduces suitability	Hussner et al., (2014); EPPO, (2017)
Pontederia crassipes	< -2°C; frost events limit their spread	> 10°C; germination in 5–10°C	< 4 mm; germination occurs as substrates dry or are re-moistened; seeds survive in wet mud and are long-lived	Coetzee et al., (2017)
Salvinia molesta	< 0°C; buds die after > 2 h below -3°C frost	< 10°C; below the minimum growth temperature	< 4 mm; seasonal drying reduces suitability	Owens et al. (2004); EPPO, (2017)

Values of the variables were defined based on a combination of prior biological knowledge about key constraints and the extreme values of environmental limits (i.e., growth, germination and survival) for each species. Hydro 06 = Minimum Upstream Temperature of Coldest Month, Hydro 10 = Mean Upstream Temperature of Warmest Quarter, Hydro 18 = Upstream Precipitation of Warmest Quarter

Global environmental predictors for invasive non-native aquatic plants

Freshwater plants occupy azonal-habitats that are affected by environmental predictors only at specific scales (e.g., river flow can be affected by precipitation not at the local site of the occurrence but at catchment scale, Pfadenhauer & Klötzli, 2020). The water temperature and other features can significantly differ from neighboring terrestrial land even at a very short distance. Then, the use of those bioclimatic layers that are conventionally used for modeling terrestrial plants would only partially match the freshwater azonal-habitat and therefore provide only a partial estimate of the niche (Lo Parrino et al., 2023). In this study, freshwater-specific climatic data were collected from Near-Global Environmental Information for Freshwater Ecosystems (Domisch et al., 2015; www.earthenv.org/streams).

Domisch et al. (2015) report sub-catchment hydroclimatic variables and summarize the upstream environment for each grid cell along the hydrological network of the HydroSHEDS river layer (www.hydrosheds.org; Lehner & Grill, 2013; hereafter Hydro 1 to 19, spatial resolution 30 arcSec approximately 1 km). To improve the information for aquatic ecosystems, we collated the cells depicting lentic water bodies reported on the Global Lakes and Wetlands cover Database version 2 (GLWD, Lehner et al., 2004) to the above-mentioned river network. Hydroclimatic variables describing annual trends, seasonality, and climatic stress were considered, as these are key factors on regulating the distribution and the reproductive success of selected aquatic invasive non-native plants (Pouteau et al., 2021).

We selected a priori three hydroclimatic climatic variables capturing different aspects of the environmental niche, thought to be important for determining current range limits and based on natural historical data of each aquatic species (Coetzee et al., 2017; Lozano 2021). These species are largely tropical, with optimal growth occurring between 28°C and 30°C, while cold winter temperatures and frost events limit their spread (Coetzee et al., 2017). The main environmental limitations on plant distribution are mainly determined by temperature ranges between − 3 and 0°C (prolonged exposure to frost could be lethal, see Table 1). The following hydroclimatic and environmental variables that were chosen to model the species were as follows: Minimum Upstream

Temperature of Coldest Month (Hydro 06, reflecting exposure to frost), Mean Upstream Temperature of Warmest Quarter (Hydro 10, reflecting the growing season thermal regime), and the Upstream Precipitation of Warmest Quarter (Hydro 18, reflecting seasonal drying out of waterbodies). During warmer seasons, high temperatures can increase evaporation, and if there is little precipitation, water levels can drop or dry up completely. This can reduce the suitability of habitats that depend on stable water conditions. Therefore, including this factor helps predict where these plants are likely to survive and spread, depending on seasonal water availability. The last variable used in the analysis was the classes of GLWD (Table 1; Lozano, 2021). To avoid multicollinearity within variables, we used Variance Inflation Factor (VIF, Simoes et al., 2020) with a threshold of five (VIF < 5) to eliminate variables with multicollinearity problems (Table S2).

Assessing niche dynamics

We used the principal component analysis (PCA-env) as proposed by Broennimann et al. (2012) to analyze the niche dynamics of each species. Niche dynamics uses occurrences in invaded and native ranges (hereafter, native niche) to summarize the multivariate environmental space through PCA dimensionality reduction. To assess niche dynamics, it was considered the COUE framework (Centroid shift, Overlap, Unfilling, and Expansion), as defined by Guisan et al. (2014), which provides a structured approach for interpreting changes in species' niches across geographic ranges. This procedure allowed us to evaluate the hypothesis of niche shift between native and invaded ranges. For each PCA performed to compare the native niche with its niches estimated for each invaded range (i.e., Asia, Africa, Australia, Europe, and North America), we used the first two axes to define the environmental space (i.e., each cell corresponds to a unique set of hydroclimatic and environmental conditions) divided into 100×100 cells, and the occurrence points were converted into densities of occurrences, using a kernel smoothing function, correcting for sampling bias. The kernel smoothing function is a non-parametric multivariate technique that estimates a continuous probability density function by averaging nearby observed data (Broennimann et al., 2012). We will report the results of niche dynamics, visualized by PCA and calibrated on hydroclimatic/environmental availability within the native range extents.

Niche comparison in climate space

Niche dynamic metrics were used to test whether the niches estimated for each invaded region of the five invasive non-native plant species changed in comparison to the native one. We used Schoener's D to compare niche overlaps (i.e., the area shared between native and invaded niches). The D metric indicates the overall match between two niches over the whole climatic space (i.e., analogous, and non-analogous environments) and varies between 0 (no overlap) and 1 (complete overlap, Schoener, 1970; reviewed in Warren et al., 2008). We adopted the framework proposed by Rödder and Engler (2011) to support a more objective interpretation of the overlap metrics, following five categories: 0–0.2 (indicating no or very limited overlap), 0.2–0.4 (low overlap), 0.4–0.6 (moderate overlap), 0.6–0.8 (high overlap), and 0.8–1.0 (very high overlap).

To determine magnitude and orientation of niche shift in each invaded continent (i.e., Asia, Africa, Australia, Europe, and North America) and test any evidence of niche shift, we primarily used the test of niche similarity, while the niche equivalency test was applied to assess whether the niches were statistically identical (see Warren et al., 2008). Niche equivalency determines whether niches in two geographical ranges are equivalent (i.e., the niche overlap is constant when randomly reallocating the occurrences among the two ranges). The null hypothesis is rejected if $P < 0.05$ (niches are not identical, i.e., observed value of D falls outside the density of 95% of the simulated values). Niche similarity addresses whether the niche occupied in one range is more similar to the one occupied in the other range than would be expected by chance. The null hypothesis is rejected if $P < 0.05$ (i.e., niches are more similar than expected at random). For both tests, the effect size and significance were performed by 1000 randomizations in native and invaded ranges to produce the null distributions and were evaluated by measuring z-score.

Niche dynamic metrics

We investigated the niche dynamics of the five invasive non-native plant species by overlapping the native and invaded niches using three indices (see Petitpierre et al., 2012): 1) niche unfilling (*U*) the proportion of occurrence densities of the native range dropping outside of the invasive range but still in the analogous environment; 2) niche stability (*S*) the zone where species occurs in both ranges (similar to D, but considering only the analogous environment); and 3) niche expansion (*E*) the proportion of occurrence densities of the analogous invaded range are not shared with the native range and completely new niche space in the invasive range. While *S* quantifies the proportion of niche conserved, *E* values estimate the proportion of niche expanded (i.e., characterize true niche shifts). Expansion into new niche space can occur without a change of total niche breadth, while changes of niche breadth necessarily imply expansion into new niche space and the unfilling of native niche space in the invaded range may be a consequence of the non-native species niche not yet having reached equilibrium (Dellinger et al., 2016). The unfilled zone (*U*) represents the set of environmental conditions within the invaded range that fall within the potential niche of the species but is not currently occupied by the species. Since invasive species are unlikely to have reached hydroclimatic and environmental equilibrium in the invaded range, the unfilled zone may be very common and prove the future potential spread of the non-native species. These indices were measured in the hydroclimatic and environmental space shared between the native and invaded ranges to avoid detecting niche shifts due to hydroclimatic and environmental non-availability in the native range. Environmental equilibrium is reached when most of the species' niche falls within the stability zone, with minimal representation in the expansion and unfilling zones.

Using global occurrence records and the predictor layers at the global scale, we assessed niche shifts at the continental scale using the methods described above. Thus, occurrence records used to generate niche-based models were data from a broad geographic extent so that they approximate the fundamental niche as much as possible and niche shifts appear to be in the fundamental niche rather than the realized niche (Phillips et al., 2006).

Analyses were performed in R v4.3.2 (RCoreTeam, 2023) using scripts developed by Broennimann et al. (2012, 2021) and the R package "ecospat" (Di Cola et al., 2017) to conduct the niche dynamics analyses.

Results

We report the results of niche dynamics, quantified by PCA and calibrated on climate availability within the native range extents. In general, in the correlation circle, the arrow directions showed that the niche moved toward colder (Hydro 06) and the driest (Hydro 18) climates in all continents except in North America (Figs. S1-S4). The importance of climate and environmental variables varied strongly across the areas. Concerning climate variables, the minimum temperature of the coldest month (Hydro 06) had the highest effect on the species studied (Figs. S1-S4).

Niche comparison

For all invasive species, the native region exhibiting a broader niche breadth compared to any of the invaded regions. Niche overlap between native and invaded regions varied among species and continents, between 0.001 and 0.484, indicating low to moderate niche overlap (Table 2). Among the species studied, *M. aquaticum* had the highest average niche overlap (mean D = 0.180), with the highest value recorded in North America (D = 0.484), indicating a moderate overlap on that continent. While *S. molesta* showed the lowest average overlap (mean D = 0.034) across continents, reaching the minimum in Asia (D = 0.001), suggesting limited niche occupancy (Fig. 2; Table 2). North America was the continent with the highest niche overlap values for several species, and around 50% of the environmental space available in the invaded area is similar to that of the native area (Fig. 2; Table 2). *E. densa* and *P. stratiotes* also recorded their highest overlap in North America when compared with other continents, although the value remained below 0.3, indicating low overlap. In contrast, Europe and Africa generally exhibited low niche overlap values for most species, often below 0.05, e.g., *E. densa* (Europe D = 0.031, Africa D = 0.008) and *P. crassipes* (Europe D = 0.003, Africa D = 0.003). These results indicate that environmental suitability follows a species-continent pattern,

Table 2 Niche overlap index for the investigated aquatic invasive non-native plants across the continents where they have been introduced

Aquatic invasive plants	Index/Test	North America	Europe	Africa	Asia	Australia	Average
Egeria densa	D	**0.147**	0.031	*0.008*	0.125	0.098	0.081
	Equiv. z-score	− 0.957	− 15.074	− 0.400	− 3.698	− 8.936	
	Equiv. p value	> 0.05	< 0.001	0.049	< 0.001	< 0.001	
	Simil. z-score	4.108	1.446	− 0.075	2.830	3.075	
	Simil. p value	> 0.05	> 0.05	> 0.05	> 0.05	> 0.05	
Myriophyllum aquaticum	D	**0.484**	0.038	*0.006*	0.241	0.131	0.18
	Equiv. z-score	0.815	− 5.446	− 2.018	− 3.113	− 0.119	
	Equiv. p value	> 0.05	< 0.001	< 0.001	< 0.001	> 0.05	
	Simil. z-score	13.082	1.269	0.559	5.390	2.617	
	Simil. p value	> 0.05	> 0.05	> 0.05	> 0.05	> 0.05	
Pistia stratiotes	D	**0.272**	*0.006*	0.114	0.041	0.148	0.116
	Equiv. z-score	2.389	− 6.457	− 0.601	− 0.389	− 0.128	
	Equiv. p value	> 0.05	< 0.001	> 0.05	> 0.05	> 0.05	
	Simil. z-score	6.862	0.331	2.292	0.659	3.339	
	Simil. p value	> 0.05	> 0.05	> 0.05	> 0.05	> 0.05	
Pontederia crassipes	D	0.090	*0.003*	*0.003*	**0.110**	0.027	0.047
	Equiv. z-score	2.101	− 11.606	1591.9	0.859	− 6.982	
	Equiv. p value	> 0.05	< 0.001	> 0.05	> 0.05	< 0.001	
	Simil. z-score	1.424	1.194	0.068	3.818	0.662	
	Simil. p value	> 0.05	> 0.05	> 0.05	> 0.05	> 0.05	
Salvinia molesta	D	**0.070**	0.013	0.060	*0.001*	0.024	0.034
	Equiv. z-score	− 0.634	− 0.446	1.972	− 1.241	− 1.212	
	Equiv. p value	> 0.05	> 0.05	> 0.05	< 0.001	> 0.05	
	Simil. z-score	0.570	21.791	11.133	− 0.284	0.477	
	Simil. p value	> 0.05	> 0.05	> 0.05	> 0.05	> 0.05	

D: Schoener's D index, a measure of the overlap between native and invaded niche range. Bold values indicate the highest D values, while italicized values represent the lowest D values for each invasive non-native species. The effect sizes are shown in the table, measured by z-score, of niche equivalency test (Equiv. z-score) and of niche similarity test (Simil. z-score), and the p values of niche equivalency test (Equiv. p value) and of niche similarity test (Simil. p value)

and that *S. molesta* shows particularly poor overlap and minimal environmental niche occupation regardless of the invaded region (Fig. 2; Table 2).

The niche equivalency test was rejected for all species on at least one continent (Table 2). This means that the invaded niches are often not identical to the native niche (Figs. S5-S9). In Europe, the invaded niches of all species differed significantly from their native niches (z-score < − 0.4, $P < 0.001$), except for *S. molesta*. In Africa, niche divergence was detected for *E. densa* and *M. aquaticum* (z-score < − 0.4, $P < 0.05$), while *P. crassipes* and *S. molesta* showed no significant differences. In Asia, the niches of *E. densa*, *M. aquaticum*, and *S. molesta* were significantly different from their native niches (z-score < − 0.4, $P < 0.05$), whereas the other species were not. In Australia, niche equivalency was rejected for *E. densa* and *P. crassipes* (z-score < − 0.4, $P < 0.05$) but not for the remaining species. Finally, in North America, most species exhibited moderate overlap with the native niche (Table 2), but equivalency was not consistently rejected. The niche similarity test, in contrast, was not significant for any species on any continent, indicating that the realized niches in the invaded ranges do not converge toward those of the native range (Table 2, Figs. S10-S14). However, some species such as *M. aquaticum* rarely occur in new climates, and species like *P. crassipes* did not always occupy areas with similar climatic conditions to those found in their native range.

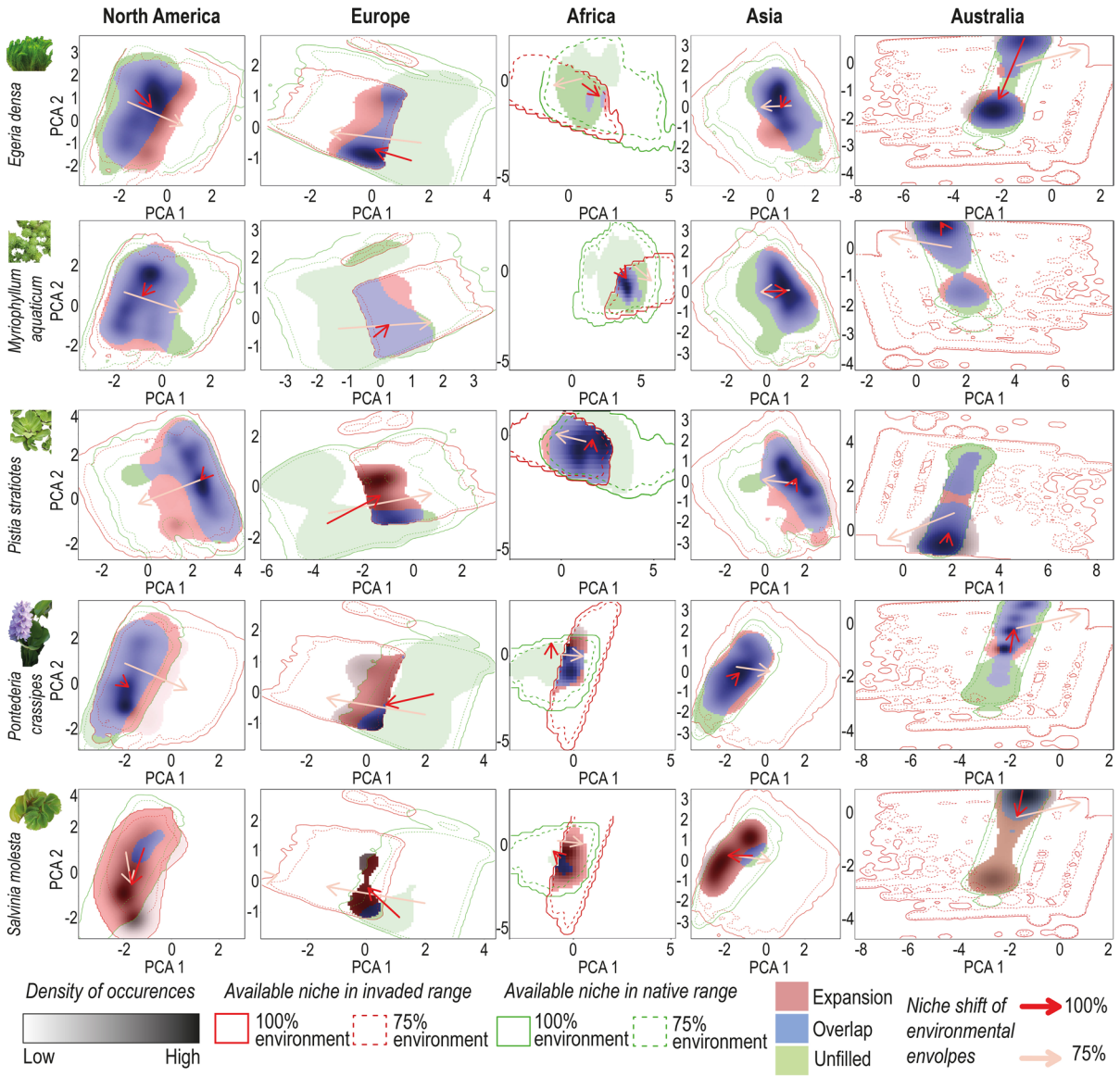

Fig. 2 Niche dynamic analysis between native and invaded ranges (i.e., Africa, Asia, Australia, Europe, and North America) of *Egeria densa*; *Myriophyllum aquaticum*; *Pistia stratiotes*; *Pontederia crassipes,* and *Salvinia molesta*. The contour lines delineate the available niche in its native range (green) and in its invaded range (red). The solid and dashed contour Lines illustrate, respectively, 100% and 75% of the available (background) environment. The density of occurrences is shown on a blue scale (light black = low density, black = high density). The colored areas correspond to the expansion zone (red), unfilled zone (green), and the overlap zone (blue), resulting from overlaying the native niche with the invaded niche. The arrows represent the direction of movement of the center of the species climatic niche (red) to available environment (pink)

Niche dynamic metrics

The analysis of niche dynamics showed a considerable stability (S) for all invasive aquatic non-native plants in all continents (general mean of $S = 0.726$), followed by expansion (general mean of $E = 0.274$) and a proportion of suitable environments in the introduced range not yet occupied (general mean of $U = 0.164$) (Table 3). In particular, Africa and Europe were the continents with the highest unfilled

Table 3 Niche indices for the investigated aquatic invasive non-native plants across the continents where they have been introduced. Niche expansion (*E*), stable niche (*S*), and unfilling (*U*) niche in the hydroclimatic and environmental space for each invasive non-native plant and for each invaded continent

Aquatic invasive plants		Native vs. North America	Native vs. Europe	Native vs. Africa	Native vs. Asia	Native vs. Australia
Egeria densa	*E*	0.196	0.204	**0.230**	0.087	*0.039*
	S	0.804	0.796	*0.770*	0.913	**0.961**
	U	0.090	*0.000*	**0.888**	0.111	0.121
Myriophyllum aquaticum	*E*	0.015	**0.130**	*0.000*	0.017	0.043
	S	0.985	*0.870*	**1.000**	0.983	0.957
	U	*0.043*	0.046	**0.253**	0.217	0.057
Pistia stratiotes	*E*	0.073	**0.665**	*0.008*	0.045	0.046
	S	0.927	*0.335*	0.992	**0.955**	0.954
	U	0.047	*0.000*	*0.000*	0.068	**0.220**
Pontederia crassipes	*E*	0.070	**0.769**	0.248	*0.051*	0.069
	S	0.930	*0.231*	0.752	**0.949**	0.931
	U	0.005	**0.965**	*0.004*	0.095	0.439
Salvinia molesta	*E*	0.883	0.750	0.742	**0.938**	*0.538*
	S	0.117	0.250	0.258	*0.062*	**0.462**
	U	*0.000*	0.168	*0.000*	**0.255**	*0.000*

Bold values indicate the highest values of *E*, *S*, and *U*, while italicized values represent the lowest values for each invasive non-native species

areas ($0.000 \leq$ Africa's $U \leq 0.888$; $0.000 \leq$ Europe's $U \leq 0.769$) of the predicted distribution. Niche expansion varied widely among invasive non-native plants between 0.883 and 0.015. The invaded niche was expanded, mostly in Europe for *P. stratiotes* ($E = 0.665$), *P. crassipes* ($E = 0.769$), while the niche expansion of *S. molesta* was high in all continents (mean of *E* in *S. molesta* = 0.770, Fig. 2; Table 3). The invaded occurrences were generally located within the limits of the native climatic niche, reflecting the broader niche breadth observed in the native region compared to each invaded continent. Only a few invaded occurrences were found in non-analog climatic conditions absent from the native range (Fig. 2). The studied species did not occupy the same environmental space as in their native range. However, only a small proportion of the environmental space differed between the native and introduced ranges (Fig. 2; Table 3). Then, slight evidence of shift is shown when the highest density of occurrences surpasses the limits of the native niche (Fig. 2).

Discussion

In this study, the use of niche metrics and indices to analyze niche dynamics allowed us to identify differences between the native and invaded niches and to detect changes across continents of *E. densa*, *M. aquaticum*, *P. stratiotes, P. crassipes,* and *S. molesta*, five invasive non-native aquatic plants from South America. The detected shifts were based on estimates of their ecological niches and the presence within their suitable hydroclimatic and environmental range. As far as we are aware, our study is one of the few approaches to identify the niche shifts between the invaded and native niches for invasive non-native aquatic plants at global scale.

Our findings reveal that shifts of the studied species are particularly toward colder and drier environments across continents, except for North America (see Figs. S1-S4). Species tend to evolve cold tolerance more frequently, suggesting that adaptation to cold climates has been a more common driver of niche evolution. Such temperature thresholds often act as physiological limits, constraining species' range boundaries (Araújo et al., 2013). The movement toward drier climates also supports the hypothesis

that species may exhibit increased tolerance or adaptation to water stress under changing climatic regimes (Weides et al., 2024). However, the lack of this trend in North America may reflect region-specific environmental heterogeneity or legacy effects of historical biogeography (Petitpierre et al., 2012).

Niche comparison

While niche shift has been documented in several invasive plant species worldwide (e.g., Hernández-Lambraño et al., 2017; Wang et al., 2017; Giulio et al., 2022), there is still considerable debate regarding the fundamental climatic niche conservatism of species (Liu et al., 2020; Vieira et al., 2021; Li et al., 2024). In our study, the five invasive non-native aquatic species exhibited low overlap between native and invaded niches, and in some cases, the invaded niches were nested within the native niche. These results are consistent with the idea that broader native niche breadth may limit the apparent extent of niche shifts (Li et al., 2014) but also suggest that the climatic conditions occupied in the invaded ranges are often suboptimal compared to those of the native distribution. This pattern supports the idea that climatic niches in the native range provide more environmental opportunities than those realized in invaded regions. Alahuhta et al. (2017) found Little evidence for niche conservatism in the distributions of the 11 macrophyte species on two continents (i.e., Europe and North America). They found that species were mostly affected by the same climate variables, as we reported in our study. Nevertheless, their main finding is that niches for some aquatic plants (mostly hydrophytes, i.e., physiologically adapted to grow in water-saturated environments) may not be conserved over space and time, which has several ecological implications. Similar to Alahuhta et al. (2017), we also detected cases of low or negligible overlap, particularly for *S. molesta*, supporting that niche shifts are species-specific and may depend on ecological or evolutionary factors such as phenotypic plasticity and genetic variation, which have been highlighted as key mechanisms facilitating niche differences across regions (Ackerly, 2003; Thiébaut et al., 2021). All these examples highlight that while niche shifts are not uniform across species or continents, aquatic plants show both evidence of niche conservatism and dissimilarity, reinforcing the complexity of predicting invasion dynamics across environmental gradients.

Our results suggest that the studied species were found to mainly occupy different climatic niches in their introduced ranges compared to their native habitats. Although the niches occupied are subsets of their native range, they represent only small subset of it with the climates experienced in the introduced range are suboptimal in the native range, leading to low niche overlapping. Thus, the invaded niche is in some cases nested in the native one.

The presence of these invasive non-native aquatic plants in novel hydroclimatic and environmental conditions suggest a slight lack of niche conservatism in invaded continents, especially for *S. molesta*. Therefore, these results suggested a greater capacity to invade new regions than previously thought. Our results revealed high expansion values for several species, suggesting that they are occupying climatic conditions in the invaded regions that were not available within their native ranges. This apparent niche expansion implies the potential use of novel environmental space, probably due to an ecological adaptation. However, the niche similarity tests were not significant, indicating that the observed differences in niche occupancy across regions could not exceed what would be expected by chance (Broennimann et al., 2012). Thus, it is difficult to attribute the observed expansion to a true niche shift, as it may simply reflect the availability of new climates in the invaded areas. However, the niche equivalency test was significant for most species, rejecting the hypothesis that native and introduced niches are identical. This supports the idea that species occupy different environmental conditions in the introduced area. Taken together, these results suggest a partial niche shift, where species do not fully conserve their native climatic niches, but also do not show strong evidence of adaptive expansion beyond what might occur under random environmental sampling. In accordance with this, the niches in the invaded and the native regions are not more similar than expected by chance, suggesting that the species' spread in the invaded range appears random and not driven by native niche requirements (Zhang et al., 2023).

We found that in Africa and Europe, the native ranges of *E. densa*, *M. aquaticum*, and *P. stratiotes* exhibited greater niche breadth, with their expansion in the introduced regions remaining largely within

the limits of their native ecological niches. Instead, *P. crassipes* and *S. molesta* expand beyond the limits of the native niche into novel hydroclimate and environmental conditions (Fig. 2). This tendency of species to expand toward new climates in the invaded range was related not only to climatic variables but also with aquatic habitat affinity, resident time in the invaded range, rapid evolution, biotic interactions, and changes in dispersal limitations (Pearman et al., 2008; Williams et al., 2022). In our study, the proportion of niche shifts in introduced ranges implies that the studied species only occupy, a part of the environment that is potentially suitable, due to dispersal limitations and changes in biological interactions (Atwater et al., 2018). *P. stratiotes* exhibit traits that allow it to survive in fluctuating water levels and salinity. In Europe, for instance, *P. crassipes* evolved traits to survive in habitats where desiccation and flooding are regular occurrences (Coetzee et al., 2017) invading a range of habitats, including the Pateira de Fermentelos a natural freshwater lagoon in the Iberian Peninsula of Portugal (Laranjeira & Nadais, 2008), the Guadiana and Júcar River Basins in Spain (Ruiz Téllez et al., 2008), and the river Mare'e Foghe, as well as the Pontine Marshes in Lazio, Italy (Brundu et al., 2013; Ghiani et al., 2023). Furthermore, in Djoudj National Park, Senegal, artificial flooding during the rainy season promotes the rapid growth of this aquatic plant (Den Hollander et al., 1999).

A common pattern exhibited across species and continents was shown when the environmental space occupied by invasive species was, for the most part, a subset of conditions in the native range. None of the five invasive non-native plants were identified as having native and invasive niches completely overlapping or disjunctive (see Fig. 2, Atwater et al., 2018). Furthermore, modeling the distributions of the five invasive non-native plants assumed to be responding to climate change is based on the idea that niches are conserved (Wiens & Graham, 2005; Wiens et al., 2010). Atwater et al. (2018) demonstrated, even in the absence of competitors and evolutionary processes, that diverse hydroclimates and environmental conditions will produce niche shifts.

Niche dynamic metrics

Salvinia molesta showed high niche expansion values in all continents, and the niche of species such as *E. densa*, *P. stratiotes*, *P. crassipes* was also expanded, particularly, in Europe and in North America. However, most of this expansion occurred within the environmental limits defined by the native niche, reflecting a broader native niche breadth compared to that of the invaded regions. Only a limited number of novel (non-analog) environments were identified in the invaded regions. Moreover, the studied species did not fully occupy the same environmental space as in their native range, and only a small portion of the environmental space showed no overlap between native and introduced ranges. As a result, evidence of niche shift was limited, though slight shifts were detected where the highest densities of occurrences extended beyond the boundaries of the native niche.

In some cases, like *E. densa* in Africa, *P. crassipes* in Europe, and *S. molesta* in Asia, the highest values of niche expansion coincided with the highest values of unfilled. This pattern may suggests that niche expansion was evident in regions where these species find environmental conditions with limited overlap with their native niche. Our findings also revealed the presence of suitable but currently unoccupied environments in the introduced ranges. Notably, Africa and Europe exhibited the largest proportions of unfilled suitable areas, indicating a significant potential for further spread.

Our results demonstrated a change in the density of occurrences between native and invasive niches (centroid position shift, see Fig. 2) with niche envelope displacement (i.e., change in borders compressing each niche space, Fig. 2) caused by niche unfilling and expansion. High values of unfilling (e.g., *E. densa*, *M. aquaticum*, *P. stratiotes,* and *P. crassipes* in Africa and Europe, and *S. molesta* in Europe) indicate that these species have not filled all the environmental conditions inside invaded continents (Ahmad et al., 2019; Dreyer et al., 2019). Niche unfilling has been associated with early stages of invasion for terrestrial invaders (Adelino & Lima 2023). Therefore, these large unfilling ranges observed in this study may be an indicator of a recent and/or ongoing invasion process.

On the other hand, niche expansion reveals that the studied species have colonized novel environmental conditions that are available and unoccupied in the native area, or available in the invaded area and absent in the native area (Gallien et al., 2010). These expansion events verified for the five invasive

non-native aquatic plants could be partially due to the introduction history of the plants. For instance, *P. crassipes* occur on every continent and in more than 50 countries except Antarctica, as the result of anthropogenic spread (Cordeiro et al., 2020). In Mexico and North America, it is assumed that the finding of this species is due to repeated re-invasion from anthropogenic release by humans, rather than propagation by seed (Coetzee et al., 2017). The propensity to expand toward new environmental conditions is probably related to resident time in the invaded range after the introduction process (Ahmad et al., 2019).

As a final consideration, widespread species such as *P. crassipes* or *M. aquaticum* with multiple introductions across continents from different source populations in the native range could facilitate the mixture of previously native populations and increase the genetic variation in invading populations (Ghoussein et al., 2023). However, in the case of *P. crassipes*, this pattern is context-dependent, introductions can also lead to low genetic variation within a community and may vary according to introduction history, propagule pressure, and environmental conditions. Then, dispersal and gene flow may influence shifts, though this relationship is equivocal, as gene flow can both facilitate and constrain adaptation. While it can introduce beneficial alleles that favor adaptation to new environments, it can also homogenize populations and prevent the acquisition of locally adaptive traits. Consequently, the effect of gene flow on niche dynamics depends on the context (Garant et al., 2007). Such events may promote the capacity of the non-native plants to respond to selection in new hydroclimate and environment conditions, favoring the occurrence of niche shifts (Pearman et al., 2008).

This study highlights that niche shifts are both continent and species-specific, emphasizing the need for tailored research that incorporates regional contexts. This is particularly crucial for aquatic invasive non-native plants, as their niches are often shaped by unique ecological and hydroclimatic factors (Xian et al., 2023). Future studies should prioritize integrating continent-specific data with detailed environmental datasets to explore these dynamics further. Such research could help clarify whether observed differences in niche features under current climatic conditions stem from changes in the fundamental niche or shifts in the realized niche, which represents a subset of the fundamental niche limited by biotic interactions (Hutchinson, 1957).

Conclusion

In this study, the use of niche metrics (PCA) and indices (Schoener's D, niche equivalency, niche similarity, stability, expansion, and unfilling) to analyze niche dynamics facilitated the identification of shifts between native and invaded ranges for five invasive non-native aquatic plants (*E. densa*, *M. aquaticum*, *P. stratiotes*, *P. crassipes*, and *S. molesta*) at the global scale.

Our results provided insights into the hydroclimatic and environment niche dynamics, suggesting that due to a small niche shift across continents, the five aquatic invasive non-native plants studied expand into uncolonized areas, where these conditions mainly reflect those in their native range. The results of this study evidenced a significant niche shift in the hydroclimatic and environmental space for invasive populations of *P. crassipes* and *P. stratiotes* in Europe, and *S. molesta* in Asia. In addition, we need to pay more attention to freshwater environments with high climatic suitability for these aquatic invasive non-native species, as well as small niche shifts between native and invasive ranges. Furthermore, our results exemplify the importance of monitoring both exports of propagules from the native range and then from introduced ranges to prevent further expansion globally.

Acknowledgements This study was carried out with the partial support of the PON-AIM (Programma Operativo Nazionale ricerca e innovazione 2014–2020 ID DM1062AGR-IV6BRUNDU) and by the COST-Action TD1209 Short Term Scientific Mission. VL and FM were supported by the project National Recovery and Resilience Plan (NRRP), Mission 4 Component 2 Investment 1.4—Call for tender No. 3138 of 16 December 2021, rectified by Decree n.3175 of 18 December 2021 of Italian Ministry of University and Research funded by the European Union – NextGenerationEU. Project code CN_00000033, Concession Decree No. 1034 of 17 June 2022 adopted by the Italian Ministry of University and Research, CUP J83C22000870007, Project title "National Biodiversity Future Center—NBFC." This work was also supported by a grant from the Visiting Professor/Scientist Program (Call ID 314) of the University of Sassari 2024. We gratefully thank Brandon Brett Andrew of the UNISS for reviewing the English language in the main text. We are grateful to the team of the

Plant Ecology Laboratory of Roma Tre University, in particular Professor Alicia Teresa Rosario Acosta, Associate professor Marta Carboni, and the entire research team for their hospitality. We are grateful for the insightful comments from the anonymous reviewers that improved the manuscript.

Author contributions VL contributed toward conceptualization, methodology, data processing, data curation, writing—original draft, writing—review and editing, and formal analysis; IH contributed toward writing—review and editing; AG contributed toward writing—review and editing; and FM contributed toward methodology, data processing, data curation, writing—original draft, writing—review and editing, and formal analysis. All authors contributed critically to the drafts and gave final approval for publication.

Funding Open access funding provided by Università degli Studi di Sassari within the CRUI-CARE Agreement. The authors have not disclosed any funding.

Data availability Data will be made available on request.

Declarations

Conflict of interest The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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