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## Functional and habitat characteristics associated with nativeness, rarity, and invasiveness in the aquatic vascular flora of Sardinia

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### ABSTRACT

Mediterranean wetlands are of great conservation concern given their high biodiversity, functional value, societal importance, and significant decline during recent decades. Within the contexts of species protection and functional resilience, understanding the biological and environmental factors that influence the composition and diversity of wetland plant communities could help to inform management of these critical systems. To examine such factors, we considered 13 functional and habitat characteristics in explanatory models of the nativeness, rarity, and invasiveness of a comprehensive flora of 224 vascular plant species associated with wetlands in Sardinia. We categorised 59 of the 184 native species as rare and 21 of the 40 non-native species as invasive. Our models revealed some functional and habitat characteristics that are significantly associated with plant species' nativeness, rarity, and invasiveness in Sardinian wetlands. Specifically, native species generally have smaller flowers than non-native species, while non-native species tend to flower later and reproduce more vegetatively. Rare native species typically occur across a narrower elevation range, have shorter flowering duration, and are less likely to reproduce vegetatively than common species, while invasive species tend to have larger flowers than non-invasive species. The relatively high incidences of rarity and invasiveness in Sardinian wetlands are likely influenced by the intrinsic fragmentation of freshwater environments and profound anthropogenic modifications in the region. In addition, we suggest that differences in reproductive traits may further contribute to species' rarity and invasiveness in these systems.

### 1. Introduction

Wetlands support exceptionally high levels of biodiversity, productivity, and important ecosystem functions (Mitra et al., 2003; Kingsford et al., 2016; Taylor et al., 2021). However, these unique systems are among the most threatened by human activities associated with economic development, agriculture, and urbanization, and their impacts on climate (Gong et al., 2013; Xiong et al., 2023). Globally, it has been estimated that at least one-third of all wetlands have been already destroyed, largely due to human activities (Hu et al., 2017), although rates of decline have varied across continents. Europe has experienced the greatest percentage of wetland loss worldwide, which has been attributed to its relatively high human population density (Hu et al., 2017). In the

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Mediterranean Basin, in particular, wetlands are of major conservation concern as they have already experienced a 50 % decline during the past century (Geijzendorffer et al., 2018; Leberger et al., 2020) and occur within both a biodiversity and climate hotspot (Giorgi, 2006; Myers et al., 2000) that is projected to experience continued anthropogenic pressures (Bradshaw and Brook, 2014).

Given their multifaceted importance, wetland assessment and conservation efforts have focused on components of both biodiversity and ecosystem function (Kingsford et al., 2016) – factors that are often connected in ways that determine wetland multifunctionality (Van der Plas, 2019; Moi et al., 2022). Plant community composition, as a component of biodiversity, can be an especially strong predictor of wetland function (Schultz et al., 2011). For example, some plant species that are dependent on wetland habitats (hereafter wetland plants) have been shown to strongly influence both water chemistry and water quality through their absorption of nutrients, metals, and other contaminants (Kao et al., 2003; Webb et al., 2012; Cuena-Lombrana et al., 2021), thereby enhancing the provision of services, such as carbon sequestration (Cardinale et al., 2012), and resilience to several pressures, like pathogens, herbivory or aridity (Hambäck et al., 2014; Fraixedas et al., 2019). As such, changes in wetland plant diversity and community composition can have drastic effects on wetland functions (Bolpagni et al., 2018; Cuena-Lombrana et al., 2021), that can be weakened by human influences that impact wetland communities (Moi et al., 2022). However, the diversity of plants in wetland systems in many areas of the world often has been overlooked in considerations of wetland conservation (Flinn et al., 2008; Fois et al., 2021; Sun et al., 2024) relative to the biodiversity of more charismatic vertebrate species, including waterfowl, amphibians, and fishes (Geijzendorffer et al., 2018; Cuena-Lombrana et al., 2021; Ferrarini et al., 2023).

The diversity and composition of wetland communities can be impacted by a variety of factors – both intrinsic and extrinsic. For example, many coastal wetland species are found in dense occurrences across broad ranges, a pattern documented as early as the mid 1800s (De Candolle, 1855), as well as more recently (e.g. Murphy et al., 2019; Fois et al., 2024). This pattern may be influenced by prolific clonal propagation or perennation within occurrences, often in association with limited sexual reproduction (Barrett et al., 1993; Santamaría, 2002). But across fragmented wetland landscapes, evolutionary pressures may select for increased long-distance dispersal, especially by water (i.e., hydrochory; Cuena-Lombrana et al., 2024; Nilsson et al., 2010), or through close interaction with birds (i.e. ornithochory; Van Leeuwen et al., 2012; Fois et al., 2022a). In coastal areas, wetlands are subject to regular intermingling of freshwater and saline/brackish conditions, offering a broad availability of habitats and niches that could promote species diversity (Grillas et al., 1993; Santamaría, 2002). In Mediterranean wetlands, which experience particularly strong temporal variation in salinity and inundation, wetland plants can evolve high levels of plasticity that allow them to acclimate across conditions (Santamaría, 2002; Dalla Vecchia et al., 2020). In highly fragmented and/or ephemeral inland wetlands, plant species may be constrained to especially narrow ranges. These native rare or narrow-range endemics can be of special conservation concern (Bagella, 2023; Van den Broeck et al., 2015).

At the extreme opposite end of the spectrum of rarity and commonness are the human-introduced invasive plant species associated with wetland systems (Brundu, 2015; Mayoral et al., 2018), many as a direct consequence of the rapid growth of transport, trade and tourism (Pyšek et al., 2017; Seebens et al., 2017). The rates of such introductions are greater for wetlands in Europe than any other region of the world (Genovesi, 2007). Currently, many of the estimated > 250 introduced vascular plant species of European wetlands are of Union concern (Bolpagni, 2021; Ghiani et al., 2023; Mayoral et al., 2018). Given its high rates of endemism (as biological hotspot) combined with increasing regional anthropogenic pressures, the Mediterranean Basin is especially threatened by the potential for introduced plant species to outcompete native flora (Brunel et al., 2010). Yet, assessments of the region have highlighted knowledge gaps about the extent and characteristics of invasive plant species, especially for inland wetlands (Troia et al., 2020).

Sardinia is highly representative of the wetland richness of the Mediterranean region as a relatively large island with wetlands ranging from coastal to inland and permanent to seasonal, the latter largely owing to a Mediterranean climate of hot, dry summers and warm, rainy winters (Skoulikidis et al., 2017; Fois et al., 2021; Palmas et al., 2022). A recent inventory of Sardinian wetlands included ~2500 distinct lentic wetlands, covering 494 km<sup>2</sup> (Fois et al., 2021), as well as ~11,000 km of rivers and streams (Regione Sardegna, 2015). Most botanical investigations on the island have focused on large coastal wetlands of established conservation interest (such as Ramsar or Natura 2000 sites). Studies of smaller and often ephemeral inland wetlands of Sardinia have been more limited (Cuena-Lombrana et al., 2021; Fois et al., 2021), and this could lead to an underestimation of the already detected presence of rare, threatened and endemic taxa (Bagella et al., 2010; Bagella and Caria, 2012).

To address gaps in our knowledge of the taxonomic diversity of Sardinian wetlands as representative of the Mediterranean region, we compiled an updated and comprehensive list of vascular plant species for these systems. To elucidate potential changes in ecosystem functioning that could be influenced by changes in species composition involving invasive and rare species, as especially dynamic components of both taxonomic and functional diversity, we also inventoried the available functional and habitat characteristics of native and non-native plant species in Sardinian wetlands. Our main research questions were: (1) how many vascular aquatic plants are present in Sardinia? (2) How many of the native ones are rare and, among the non-native ones, invasive? (3) Can we find differences among functional and habitat characteristics of native versus non-native, rare versus common, and invasive versus non-invasive species? (4) Can we use such information to prevent threats to rare native plants and invasion of non-native ones? We discuss our results in the view of a more effective management of wetlands in the Mediterranean region.

## 2. Materials and methods

### 2.1. Compilation of species

To identify Sardinian wetland plant species, we compiled a list of all vascular aquatic plant species reported for Italy (Bolpagni et al., 2018) and for the Palearctic realm (Murphy et al., 2019). We then added to this list all species with Ellenberg moisture indicator

values reported as  $> 8$  by Pignatti et al. (2005), Domina et al. (2018), and Tichý et al. (2023). Such values indicate species with an obligatory requirement of saturated soils during at least part of their life cycle (Bolpagni et al., 2018). The resulting list of vascular plant species associated with Sardinian wetlands was then revised to include more recent reports or taxa descriptions reported in the Portale della Flora d'Italia (Portal of the Flora of Italy, 2024).

Taxonomy of species and subspecies (henceforth, species) across our data sources were unified according to checklists of native and non-native plants of Italy (Bartolucci et al., 2024; Galasso et al., 2024).

## 2.2. Species categorization and characteristics

We categorized each species in our resulting dataset as native or non-native. Native species were then further categorized as rare or common within Sardinia based on descriptions by Arrigoni (2006) with some revisions based on expertise. We defined 'rare' species as those known from  $\leq 5$  locations in Sardinia, with a location defined as a contiguous territory of  $\leq 20$  km<sup>2</sup>. This assessment of rarity aligns with those used previously for Sardinian flora (Arrigoni, 2006) and Rabinowitz's (1981) descriptions of rarity defined by restricted geographic range (if locations are spatially constrained rather than patchy across a broader area) and/or low local abundance (if the case of single or very few locations). Non-native species were further categorized as invasive or non-invasive to Sardinia based on Galasso et al. (2018) and Mayoral et al. (2018), with updates sourced from the Portale della Flora d'Italia (Portal of the Flora of Italy, 2024).

For each species in our dataset, we also compiled categorical and continuous measures of 13 functional and habitat characteristics as potential explanatory factors of nativeness, rarity and invasiveness from multiple sources (see Table 1). The selection of functional and habitat characteristics was based on assumptions raised by previous research with adjustments to align with the information available in open-access databases. Specifically, rare native species are more susceptible to extinction than their common counterparts (Enquist et al., 2019; Boyd et al., 2022). These species tend to be shorter in stature, produce fewer but larger seeds, and are less capable of vegetative reproduction compared to more common species. These traits may limit their ability to effectively disperse and establish in new habitats (Lavergne et al., 2004; Farnsworth, 2007; Boyd et al., 2022). Other studies indicate that rarity may be related to narrow geographic distribution and habitat specificity (Rabinowitz, 1981), and this information can be extrapolated from their altitudinal ranges (Casazza et al., 2014; Buira et al., 2020). Instead, invasiveness-related characteristics, and the hypothesis that invasive species possess superior competitive abilities given their prolific establishment and growth, can be assessed by measuring, among other things, life form, flower types, flowering duration and the opposite ability than rare ones to colonize a wide range of environments (Sikkema and Boyd, 2015). Flower size, colour, and type can also affect reproductive success by influencing plant-pollinator interactions (Bauer

**Table 1**

Species characteristics considered as explanatory factors in our analyses of rarity and invasiveness of Sardinian wetland plant species with constraints as noted in parentheses. Traits were recorded as categorical or continuous data as appropriate. The last column (Sources) includes the references from which the information was gathered. For websites, see the last accessions in the reference list.

Factor	Data type	Description	Sources
Vulnerability (for native species only)	Categorical	Yes = assessed at a global or regional scale as VU, EN, or CR by IUCN; No = not assessed as VU, EN, or CR by IUCN; Unknown = not assessed at the Mediterranean scale and/or suspected to be threatened at the Sardinian scale	(IUCN, 2022; Orsenigo et al., 2021)
Wetland preference	Categorical	Running = predominantly present in running waters; Standing = predominately present in standing waters; All = no preference for running or standing waters	(ItisWet, 2023)
Chorology (for native species only)	Categorical	Endemic = exclusive to Sardinia; Mediterranean = exclusive to the Mediterranean biogeographic region, Palearctic = exclusive to the Palearctic realm, (Sub)cosmopolitan = in more than one realm.	(Acta plantarum, 2024; Arrigoni, 2006; Fois et al., 2022b; Pignatti et al., 2017)
Origin (for introduced species only)	Categorical	Biogeographic region where species is native: Holarctic = Europe, Eurasia, N. America; Neotropical = Tropical America (C.-S. America); Palearctic = S. Africa, Red Sea, India, Asia	(Acta plantarum, 2024; Arrigoni, 2006; Pignatti et al., 2017)
Elevation range	Categorical	Small = $< 500$ m; Large $> 500$ m; calculated for the distribution of each species in the Mediterranean region	(Acta plantarum, 2024; Arrigoni, 2006; Pignatti et al., 2017)
Life form	Categorical	Therophytes (T); Hemicryptophytes (H); Geophytes (G); (nano-)phanerophytes (NP/P); Helophytes (He), Hydrophytes (Hy)	(Acta plantarum, 2024; Arrigoni, 2006; Pignatti et al., 2017)
Floral colour	Categorical	Yellow; White; Violet-Purple-Red; Blue; Green (including 'green-like' reproductive organs of pteridophytes) (Stefanaki et al., 2015)	(Acta plantarum, 2024; Arrigoni, 2006; Pignatti et al., 2017)
Floral type	Categorical	Single flower; Spikes/Raceme	(Acta plantarum, 2024; Arrigoni, 2006; Pignatti et al., 2017)
Floral size	Categorical	Small = $< 5$ mm; Large = $> 5$ mm)	(Acta plantarum, 2024; Arrigoni, 2006; Pignatti et al., 2017)
Flowering season	Categorical	Spring; Spring-Summer; Summer; Summer-Autumn; Autumn-Winter	(Acta plantarum, 2024; Arrigoni, 2006; Pignatti et al., 2017)
Flowering duration	Continuous	Total number of months during species has been reported to be in flower	(Acta plantarum, 2024; Arrigoni, 2006; Pignatti et al., 2017)
Asexual reproduction	Categorical	Yes = can reproduce by vegetative means (e.g. bulbs, tubers, corms, rhizomes, stolons, suckers); No = cannot reproduce vegetatively	(Acta plantarum, 2024; Arrigoni, 2006; Pignatti et al., 2017)
Seed weight (of 1000 seeds)	Categorical	Very Small = $< 0.10$ g; Small = $0.11-0.50$ g; Intermediate = $0.51-1$ g; Large = $1.01-2$ g; Very Large = $> 2.01$ g	(Acta plantarum, 2024; Society for Ecological Restoration SER, 2023)

et al., 2017). Human-mediated propagule pressure can be facilitated by small seeds, which are usually produced in large numbers and can be easily or accidentally transported (Von der Lippe and Kowarik, 2012), by ornamental value, such as bright flower colour or large flower size (Hu et al., 2023), and by their efficient commercial production, for example through vegetative propagation (Dong et al., 2024).

### 2.3. Data analysis

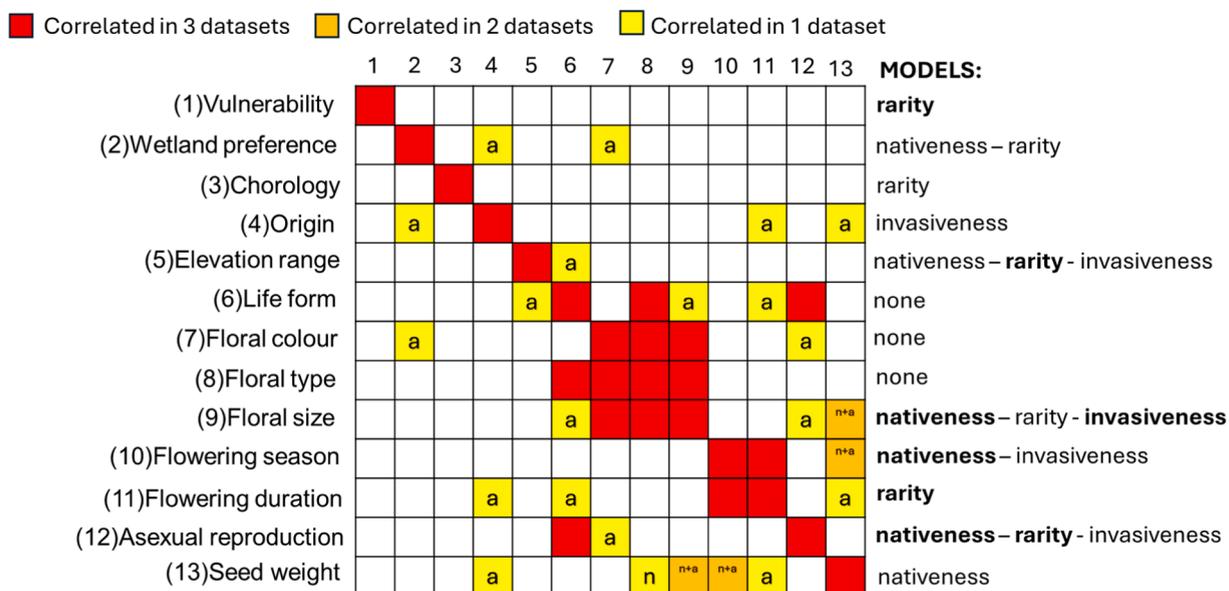
To resolve multicollinearity (Zuur and Ieno, 2016), we assessed associations between functional and habitat characteristics as independent variables prior to using them as predictors of plant categories in three logistic regression models: Nativeness (native vs. non-native species), Rarity (rare vs. common species), and Invasiveness (invasive vs. non-invasive species). Correlation between categorical and the only one continuous predictor (flowering duration) was explored with analysis of variance (ANOVA) with classical eta-squared values (Pierce et al., 2004) in R package *lsr* (Navarro, 2021). Eta-squared ( $\eta^2$ ) ranges from 0 to 1, and values > 0.14 indicate strong associations between variables (Cohen, 1988). We assessed correlations between categorical predictors with Cramer's V tests in R package *DescTools* (Signorell et al., 2023). The value of Cramer's V ranges from 0 to 1, and values > 0.4 indicate strong associations between variables (Omer et al., 2023; Yonaba et al., 2021). The choice to keep one of the two correlated variables followed the following process: either eliminate the one correlated with more other factors or compare the fitting of the two models with either variable.

We used a logistic regression model with Firth's (1993) bias reduction method to explore differences in the functional and habitat characteristics of native vs. non-native, rare vs. common (as subcategories of the native species), and invasive vs. non-invasive (as subcategories of the non-native species) Sardinian wetland plant species with the R package *logistf* (Heinze et al., 2013). We started with all independent predictors, and used backward elimination to identify the best fit model in terms of characteristics as exploratory of plant categories (i.e., native, non-native, rare, common, invasive, non-invasive). All statistical analyses were performed with R ver. 4.3.1 (R Core Team, 2019)

## 3. Results

### 3.1. Sardinian wetland plant species

In total, 224 wetland vascular plant species have been reported to occur in Sardinia. Of these, 83 % are native species ( $n=184$ ), and 26 % of these native species are rare ( $n=59$ ). Of the 40 non-native species, 52 % are described as invasive ( $n=21$ ). The three families most represented by native plant species in Sardinian wetlands included Cyperaceae ( $n= 29$  species), Ranunculaceae ( $n=15$ ), and



**Fig. 1.** Correlogram depicting strong associations between functional characteristics as predictor variables of plant species nativness, rarity, and invasiveness in logistic regression models. Numbers on the top of the graph correspond to the numbers of each functional characteristic listed on the left. Associations were determined by ANOVA with classical eta-squared or Cramer's V as appropriate. Colours refer to correlations detected in the three datasets, in two or just one of them (a = sub-dataset of only non-native species; n = of only natives; there are no cases of correlations detected only for the entire dataset). It is also reported in which of the three models (nativness, rarity and invasiveness) each variable was retained for the absence of collinearity issues. In bold those that were finally retained based on the backward model selection based on penalised likelihood ratio test (for further details, see Appendix B, Section 1). The numbers on the x-axis indicate the same functional characteristics as those reported in the y-axis.

Potamogetonaceae ( $n= 15$ ). Poaceae ( $n= 8$ ), Asteraceae ( $n= 6$ ), and Araceae ( $n= 5$ ) were the three families most represented by non-native species. A complete list of Sardinian wetland plant species, their categorization, and their functional and habitat characteristics are reported in the [supplementary material](#) (Appendix Information A).

### 3.2. Model development

We found strong associations between some of the functional and habitat characteristics that we evaluated. Specifically, flowering duration and flowering season were strongly correlated across the entire dataset and across the subset of native species. Flowering duration also was highly correlated with life form, seed weight, and origin across the subset of non-native species. Consequently, we decided to exclude flowering duration from our analyses of the entire dataset and of non-native species, while excluding flowering season from our analysis of native species. We also excluded life form and floral type from our analyses of all species, native species, and non-native species and both floral color and seed weight from analyses of non-native species due to strong correlations between these characteristics with others (Fig. 1; for details, see [Appendix Information B, Section 1](#)).

We ultimately developed the following logistic regression models for species nativeness (Eq. 1), rarity (Eq. 2), and invasiveness (Eq. 3) using selected factors after backward model selection (the equations are in R notation):

$$\text{Nativeness} \sim \text{Floral\_size} + \text{Flowering\_season} + \text{Asexual\_reproduction} \quad (1)$$

$$\text{Rarity} \sim \text{Vulnerability} + \text{Elev\_range} + \text{Asexual\_reproduction} + \text{Flowering\_duration} \quad (2)$$

$$\text{Invasiveness} \sim \text{Floral\_size} \quad (3)$$

### 3.3. Species nativeness, rarity, and invasiveness

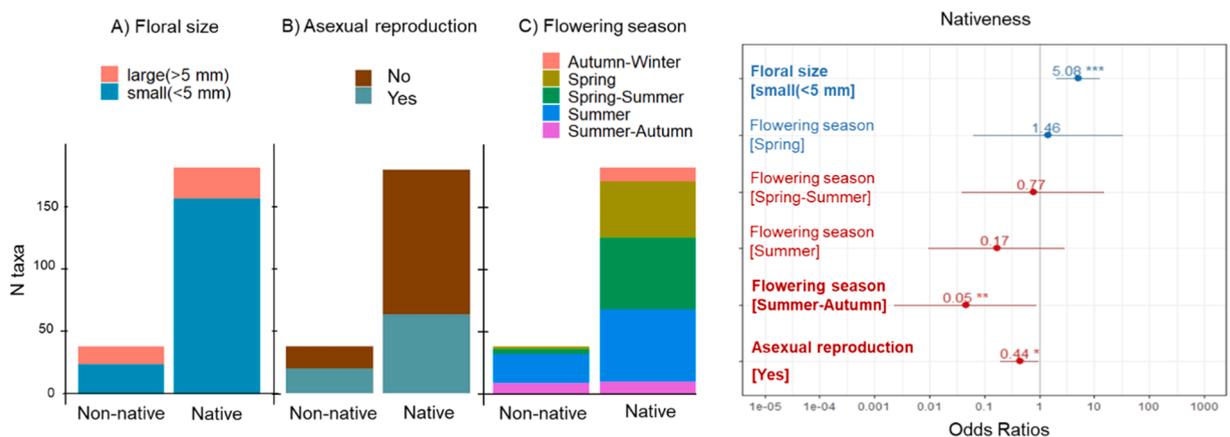
Our Nativeness model revealed that the most significant predictor of nativeness of Sardinian wetland plant species was floral size ( $p < 0.001$ ), with native species having smaller flowers than non-native species. Native species were also less likely than non-native species to flower during summer-autumn ( $p < 0.01$ ) and to reproduce vegetatively ( $p < 0.05$ ; Fig. 2).

Our Rarity model revealed that rare native plant species of Sardinian wetlands are not more likely to be classified as vulnerable than common plants species, but that rare species are more likely to have unknown conservation status ( $p < 0.001$ ). Relative to common native species, rare species also have a more restricted elevation range ( $p < 0.001$ ), are less likely to reproduce vegetatively ( $p < 0.05$ ), and exhibit shorter flowering duration ( $p < 0.05$ ; Fig. 3).

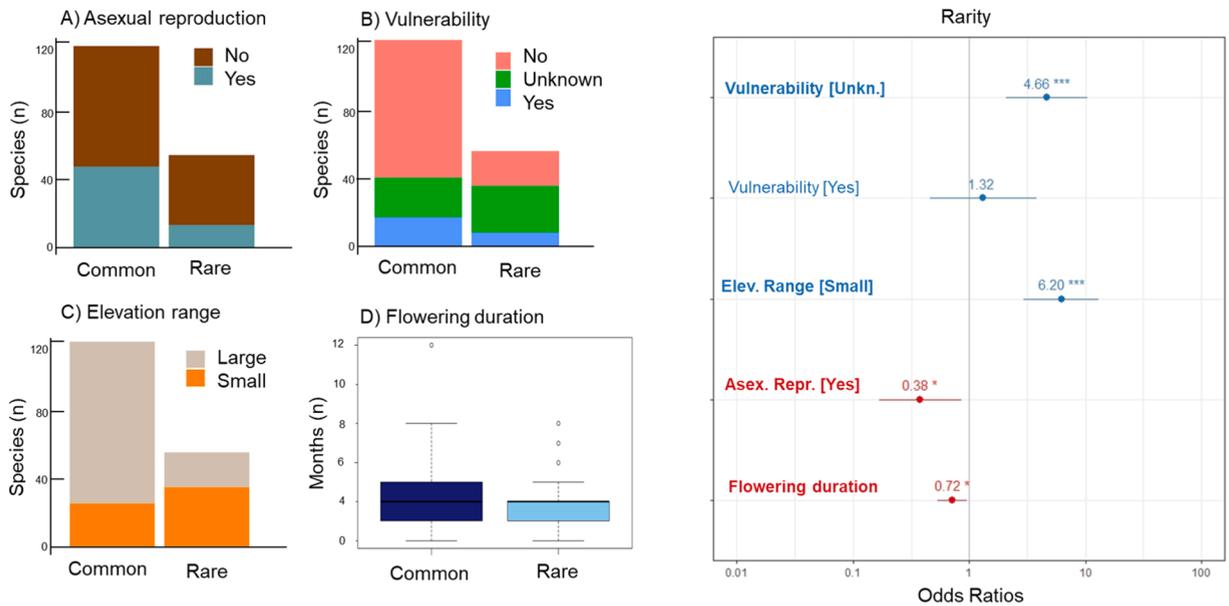
In contrast to the Nativeness and Rarity models, our Invasiveness model revealed just one functional characteristic that was associated with plant species invasiveness. Specifically, invasive plant species had observably larger flowers than non-invasive species; however, this trend was marginally insignificant ( $p > 0.05$ ; Fig. 4).

## 4. Discussion

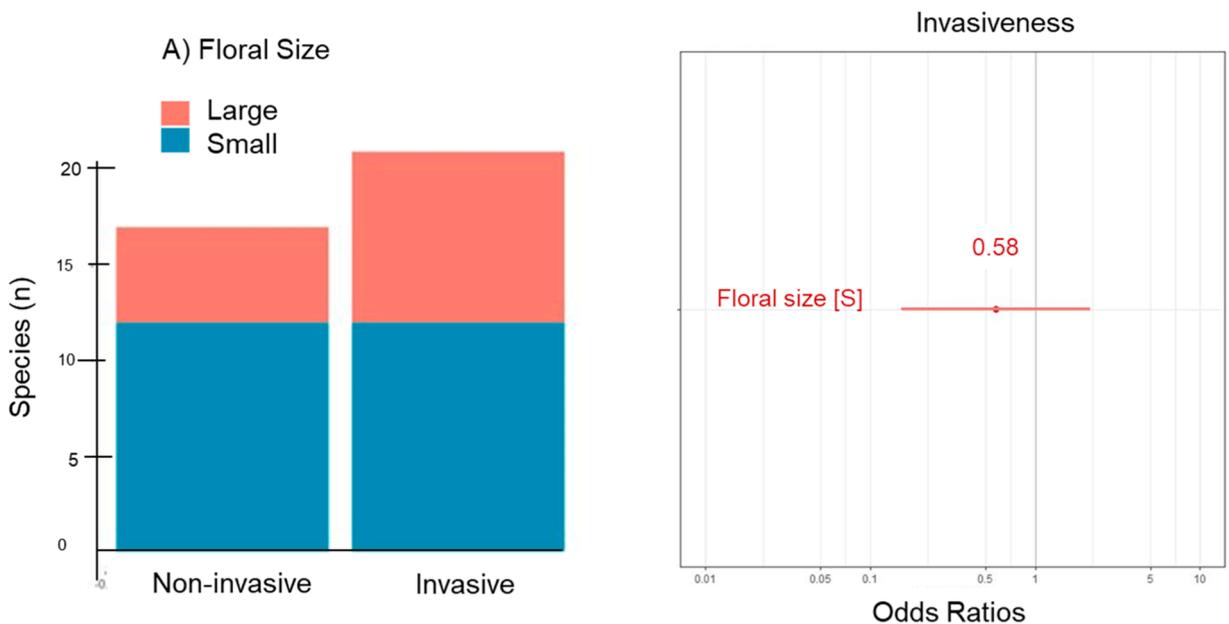
Our updated and comprehensive checklist of native and non-native wetland plant species of Sardinia (see [Appendix A](#)) is a novel contribution to our knowledge of biodiversity of the Island. Given that Sardinia is the second largest island in the Mediterranean Basin, the results of our analyses of this flora may be representative of the broader Mediterranean biogeographic region. The 224 wetland species included in our dataset represent  $\sim 7\%$  of the 2922 total plant species reported for Sardinia ([Galasso et al., 2018](#)). This



**Fig. 2.** Breakdown between native vs. non-native plants for the three significant parameters reported in the incidence rate ratios (in bold for significant, blue for positive and red for negative incidence) of the Nativeness model. Error bars indicate standard errors of mean values. Significance levels: \* $p < 0.05$ , \*\* $p < 0.01$ , \*\*\* $p < 0.001$ . Full parameters for regression models are reported in [Fig. 1](#) and [Appendix B \(Section 2.1\)](#).



**Fig. 3.** Breakdown between common and rare native plants for the four significant parameters reported in the incidence rate ratios (in bold for significant, blue for positive and red for negative incidence) of the final Rarity model. Error bars indicate standard errors of mean values. Significance levels: \* $p < 0.05$ , \*\* $p < 0.01$ , \*\*\* $p < 0.001$ ). Full parameters for regression models are available in Fig. 1 and Appendix B (Section 2.2).



**Fig. 4.** Breakdown between invasive and non-invasive plants for the only one significant parameter reported in the incidence rate ratios of the final Invasiveness model. Error bars indicate standard errors of mean values. Significance levels: \* $p < 0.05$ , \*\* $p < 0.01$ , \*\*\* $p < 0.001$ ). Full parameters for regression models are available in Fig. 1 and Appendix B (Section 2.3).

proportion of wetland species is greater than for Italy as a whole, in which 3 % of the flora are wetland species (Bolpagni et al., 2018), as well as for other Mediterranean territories, such as Peloponnesus or Palestine, in which 1 % of the native flora is comprised of wetland species (Ali-Shtayeh et al., 2022; Mermygkas et al., 2021).

Our finding that Cyperaceae was the predominant family represented by native wetland plants of Sardinia was predictable given that the Palearctic realm has been identified as the main center of diversification of associated taxonomic groups, including the genera *Carex* (Benítez-Benítez et al., 2021; Escudero et al., 2012) and *Isolepis* (Ito et al., 2016). The predominance of Poaceae, and especially species of Neotropical origin, among non-native Sardinian wetland plant species also was unsurprising, as grasses are among the most

common non-native aquatic plants in China (Wang et al., 2016). These similarities likely reflect that global trade is a major force driving change the spread of non-native species into new habitats (Bolpagni, 2021; Brundu, 2015; Hussner et al., 2017). The spread of many non-native grasses, and many of the same neotropical Poaceae species found in Sardinia, is likely facilitated by fire, eutrophication, and other human-related disturbances (Guarino et al., 2024; Praleskouskaya and Venanzoni, 2021). Although Fabaceae has been reported as the most dominant family among non-native flora in Sardinia across systems (Puddu et al., 2016), and legume species are more generally among some of the most prolific invasives in the world (Muresu et al., 2022; Richardson et al., 2000), no legume species were reported in the Sardinian aquatic flora, although there are some hygrophilous Fabaceae not considered here (Ellenberg moisture values = 7–8), such as *Sesbania punicea* (Cav.) Benth. Potentially, this could reflect habitat unsuitability and/or that associations with nitrogen-fixing bacteria are not particularly advantageous in these systems.

#### 4.1. Functional distinctions of native and non-native species

The proportion of Sardinian wetland plant species that are non-native (17 %) is similar to the proportion of non-native species previously reported in the Sardinian flora across systems (16 %; Galasso et al., 2018). The results of our analyses suggest that propagation pressure (also referred to as 'introduction effort') could explain why some introduced species fail to establish while others succeed, as has been previously reported for the Mediterranean biogeographic region (Fois et al., 2020; Lloret et al., 2005; Lozano et al., 2023) as well as more broadly (Lockwood et al., 2005). Specifically, the smaller flowers characteristic of native plant species relative to non-native plant species of Sardinian wetlands suggests that native species may be less successful in competing for pollinators (Lambdon et al., 2008). While it has been demonstrated that the effect of non-native plants on pollinator visitation and reproductive success may be more influenced by flower symmetry or colour than flower size (Morales and Traveset, 2009), we were not able to disentangle these traits in our analyses due to strong associations between floral characteristics in our datasets. We suggest that competition for pollinators between native and non-native plant species in Sardinian wetlands could be especially strong in summer/autumn given that flowering of non-native species is predominant during this time period (Rottenberg and Parker, 2004), probably due to aesthetic reasons given that summer/autumn is the peak of the tourist season in Sardinia (Lambdon et al., 2008; Lloret et al., 2005). Previous research in central Europe suggested that late flowering has contributed to the successful invasions of non-native plant species in that region (Guarino et al., 2021), and potentially, the Mediterranean climate could further facilitate invasiveness by enabling non-native species to fruit and germinate in milder winters than in climates at more northern latitudes.

Decreased fitness of native plant species in Sardinian wetlands due to reduced pollination associated with the floral characteristics of non-native species could be further exacerbated by the decreased capacity of native species for vegetative reproduction relative to non-native species. We suggest that the greater tendency of non-native species of Sardinia to reproduce vegetatively could facilitate their commercial production and spread (El-Barougy et al., 2021; Lloret et al., 2005), such as in the case of *Nymphaea mexicana* Zucc. or *Hydrocotyle ranunculoides* L.f. The potentially poor adaptability associated with the low genetic variability characteristic of clonal species is likely counterbalanced by introductions from multiple sources (Barbosa et al., 2019) or even by other possible processes that are more common than previously thought, such as mutation accumulation or genome rearrangement (Rottenberg and Parker, 2004).

#### 4.2. Functional distinctions of rare and common native species

Rarity has been reported to be relatively common among plants and other taxonomic groups (e.g. Enquist et al., 2019; García-Girón et al., 2021; Spitale, 2012). Our flora supports this trend in that nearly one-third of wetland plant species native to Sardinia are rare. The condition of rarity among Sardinian wetland plants could be exacerbated by potential reproductive limitations associated with relatively short flowering duration and limited capacity for vegetative reproduction, as elucidated by our analyses. At the other end of the spectrum of species prevalence, high reproductive capacity plays a crucial role in the prolific spread of common species like *Phragmites australis* (Cav.) Trin. ex Steud. and *Stuckenia pectinata* (L.) Börner, which can utilize vegetative reproduction when pollination is limited, allowing them to colonize open habitats and outcompete other plants with lower fitness. By contrast, non-colonial species such as rare *Damasonium bourgaei* (Coss.) Maire, *Isoetes* sp.pl., and *Juncus sorrentinii* Parl. may be constrained in their capacity to spread and compete or escape competition. We suggest that the high incidence of rarity in our flora may be influenced by numerous factors, including the intrinsic fragmentation of freshwater environments, such as temporary pools and ponds (Bagella, 2023; Latron et al., 2022), and the profound temporal oscillations of climatic conditions in the Mediterranean region, at least throughout the Tertiary and Quaternary Periods (Rodrigo-Gámiz et al., 2011; Tzedakis, 2007). As a result, many aquatic plants in the region are confined to small and fragmented habitats at the edge of their distributions and ecological ranges and are considered relicts (Tierno de Figueroa et al., 2013; Vargas et al., 2018).

While just eight of the 59 rare native species included in our flora of Sardinian wetlands have been designated as vulnerable, nearly half of the rare species in our flora (i.e., 28 species) have an unknown conservation status (IUCN, 2022), which highlights a knowledge gap that could include help to elucidate the association between rarity and vulnerability (Miranda Cebrián et al., 2022; Pironon et al., 2022). The unknown status of many rare species reflects often limited available knowledge of their functional characteristics, which can impede our ability to detect functional predictors of rarity. In this study, due to limited data availability, we had to lump many theoretically quantifiable measures into discrete categories that provided a coarse scale for analyses. For example, we had to simplify seed weights into two discrete range classes and then had to exclude seed weight from our models as it was highly associated with flower size, an association that may not have surfaced with finer scale data. Similarly, it occurred for dispersal syndromes, which were not finally included in the analyses despite being potentially informative (see the missing values of such functional characteristics in Appendix A).

### 4.3. Functional distinctions of invasive and non-invasive species

Particularly alarming in our findings is the high percentage of invasive plant species among non-native Sardinian wetland flora (~55 %) compared with the relatively low percentage of invasive species among the entire native Sardinian flora (i.e., of all habitat types; ~13 %), which is similar to the proportion of invasive species among non-native plant species globally (Bolpagni, 2021; Pyšek et al., 2017; Van Kleunen et al., 2010).

Potentially, the larger floral size of invasive wetland plant species in Sardinian wetlands compared with that of non-invasive plant species contributes to high propagule pressure that facilitates their spread in the region. Although our analyses revealed that floral size was the only explanatory factor of invasiveness of the functional characteristics that we considered, this variable was strongly associated with many others, such as life form, asexual reproduction, and seed weight. The latter and dispersal syndrome, for example, could be crucial traits to investigate, as they have been found to be important for regional abundance in non-native plants in Corsica and Majorca (Lloret et al., 2004). Overall, our limited findings of functional predictors of invasiveness in Sardinian wetland plant species echoed those previously reported for Mediterranean islands, which did not include a well-defined invasive syndrome (Lloret et al., 2005). This can be due to multiple factors, including the coarse scale of our data resolution and the possibility of unmeasured/underappreciated traits that can be more important or 'functional' than those most easily measured (Anderegg, 2023).

## 5. Conclusion: filling knowledge-practice gaps

Given the island's location, size and diversity of plant species in Sardinia, we consider this case study to be representative of the Mediterranean island context. Some differences across Mediterranean islands, particularly between the eastern and western Mediterranean, might be driven by different historical, current and future climate and land uses (Leberger et al., 2020), phylogeography (Médail, 2022), and geomorphology (Camilleri et al., 2024). Other differences could be related to the specific focus of aquatic plants, which may show different patterns to those of other floras. For example, as they are almost all accessible to many other species, the rarity of aquatic plants might be less related to their low ability to compete, as found for example in mountain plants (Casazza et al., 2005). In addition to providing a new checklist for Sardinian wetland flora, our findings about functional characteristics could provide a baseline for generating land-use and conservation practices that support native and rare species and control the spread of invasive species on the island. Specifically, we suggest that some functional characteristics predictive of rare or invasive plant species could help support the prioritisation of vulnerable native species or provide early detection of potentially invasive non-native species. For example, we found that floral size was a strong predictor of both rarity and invasiveness, but in different directions. As further research, we encourage investigations into plant-pollinator interactions in the context of nativeness, rarity, invasiveness, particularly between rare and common or invasive species, as this could be a critical issue for conservation. We also suggest some avenues for future investigation based on the limitations of existing data. These include more assessments of rare native species, for which data are especially limited and conservation statuses are often unknown, and more comprehensive investigations of functional characteristics, such as seed weight and dispersal syndromes, that could influence rarity and/or invasiveness. All functional characteristics should preferably not be deduced from indirect evidence-based, for instance, on other traits (e.g. dispersal syndrome from seed structure or weight) or plant habitat preferences (e.g. thalassochory for coastal plants). Only experimental approaches can sensibly the state of the art, sometimes leading to surprising findings. For instance, recent experiments have broadened the possibility of dispersal by the sea currents also for inland plants (Cuenca-Lombrana et al., 2024). Another recent research (Ciarle et al., 2024) found that the so-called island rule (small organisms become larger and large organisms become smaller after island colonization) was valid only for animal-pollinated flowers and not for wind-pollinated flowers. We would not exclude similar surprises if the nativeness, rarity, and invasiveness of Mediterranean island wetland plants were studied more thoroughly.

### Ethics statement

Not applicable: This manuscript does not include human or animal research.

### Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests.

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## Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.gecco.2025.e03482](https://doi.org/10.1016/j.gecco.2025.e03482).

## Data availability

General information about the study sites is available at the ItIsWet website (<https://italiaiswet.it/general/search.php?lang=en>). All data used for this research is available in Appendix A, but this and future updated versions are also available from the Zenodo Digital Repository (<https://doi.org/10.5281/zenodo.14582514>).

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