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Climate-driven distribution shifts and phytocoenological patterns of invasive and range-expanding aquatic macrophytes in the Danube Delta Biosphere Reserve, Romania

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Abstract

Aquatic macrophytes with invasive or range-expanding behaviour are a growing ecological concern, especially in vulnerable wetland habitats under pressure from climate change. The present study analyses the phytocoenological preferences and climate-influenced expansion potential of three macrophyte species in the Danube Delta Biosphere Reserve: two alien invasive species, *Azolla filiculoides* and *Elodea nuttallii*, and one non-native range-expanding macrophyte, *Vallisneria spiralis*.

The study was conducted during 2024–2025, in selected lakes from the Danube Delta Biosphere Reserve, Romania. For vegetation analysis, phytocoenological relevés were carried out, subsequently processed by cluster analysis and DCA ordering, in order to highlight floristic groupings and gradients of vegetation variation. Species presence data and environmental variables were used for spatial modelling.

The three aquatic species studied differed clearly in their current distribution, the factors controlling their occurrence and their response to future climate scenarios. *Azolla filiculoides* showed the highest current suitability and a generally stable to expanding trend under SSP3-7.0, although a reduction was projected under SSP5-8.5 by 2071–2100. *Elodea nuttallii* showed a reduction under most scenarios, but a late-century increase in suitable area was projected under SSP5-8.5. *Vallisneria spiralis* was more stable overall, although the models indicated an initial increase in suitable area, followed by a decline towards the end of the century, more pronounced under SSP5-8.5. Cluster analysis showed that each species was mainly linked to its characteristic vegetation type, while DCA revealed moderate to relatively strong floristic gradients between relevés.

In conclusion, climate change may increase the risk of invasion of some aquatic macrophytes in the Danube Delta, but the magnitude and direction of change differ depending on the species. *Azolla filiculoides* appears to benefit most from future conditions, *E. nuttallii* may become more restricted, and *V. spiralis* appears comparatively more stable. This species-specific response highlights the need for targeted monitoring and adaptive management in vulnerable wetland habitats. The qualitative hydromorphological assessment further indicates that differences in lake connectivity, water exchange and transparency may contribute to the ecological variation observed among the studied lakes and should be considered in future monitoring of submerged macrophyte development.

Key words: *Azolla filiculoides*, climate change impact, *Elodea nuttallii*, invasive aquatic plants, range-expanding species, species distribution modelling, *Vallisneria spiralis*

Introduction

Biodiversity is declining globally (Liu et al. 2025), but this is more significant in freshwater habitats compared to terrestrial habitats (Dudgeon et al., 2006; Albert et al. 2021). Freshwater habitats contain over 10% of all known species (Strayer and Dudgeon 2010) and provide ecosystem services, such as nutrient cycling, flood control and climate change mitigation, etc. (Moog et al. 2018; Lynch et al 2023; Liu et al. 2025). Wetlands have suffered a 35% loss of area between 1970 and 2015 (Gardner and Finlayson 2018). Approximately 65% of wetland habitats are under moderate to high levels of threat (Vörösmarty et al. 2010). Macrophytes play a fundamental role in the stability and dynamics of aquatic habitats (Lind et al. 2022), being strongly affected by pollution, eutrophication, habitat loss and climate change (Kundzewicz et al., 2008; Smith et al., 2014).

The distribution, species phenology, ecosystem productivity and interactions of aquatic species are undergoing significant changes due to the increase in greenhouse gas concentrations and global warming (Parmesan 2006; IPCC 2014; Lind et al., 2022). In this context, aquatic ecosystems are among the most vulnerable, being affected by increasing water temperatures, changing hydrological conditions, and the intensification of extreme events (Poff et al. 2002). Furthermore, these ecosystems are also affected by the spread of invasive species (Sayer et al. 2025), favored by international shipping, canal construction, accidental releases and deliberate introductions (Rahel 2007).

To respond to various human uses and interests, plants are transported to non-native areas (Hoveka et al. 2016), and some of these plants spread beyond the initial point of introduction (McGeoch et al. 2010). This spread has negative effects on the environment and economy (Hoveka et al. 2016). Once climate change facilitates the expansion of these invasive species, the effects will be amplified in the future (Willis et al. 2010). In this context, studies need to be carried out to assess the impact of climate change on the dynamics and invasive potential of these species. According to the literature (Andreu and Vilà 2010; Azan et al. 2015) aquatic plants have a higher probability of becoming invasive in new environments.

The Danube Delta is one of the largest wetlands in Europe (4,150 km²), hosting over 11,000 taxa (Covaliov et al. 2023) and 30 types of terrestrial, aquatic and marsh ecosystems (Gâștescu et al. 1996; Posea and Gâștescu 2005). These ecosystems provide important services at local and regional levels, such as freshwater supply, recreation and cultural values (Haines-Young and Potschin, 2013; Potschin and Haines-Young 2016). Despite its remarkable ecological and cultural value, the Danube Delta remains vulnerable to anthropogenic pressures and climate change. However, research on the effects of climate change on aquatic plant species in the Danube Delta remains limited, which underlines the need to understand how these processes may influence the distribution and invasive potential of selected aquatic macrophytes.

In the Danube Delta Biosphere Reserve, several aquatic macrophytes, including *E. nuttallii* and *V. spiralis*, can form locally abundant or dominant populations, potentially influencing the structure of submerged vegetation. Thus, *E. nuttallii* is known to spread rapidly in

stagnant or slow-flowing waters and may negatively affect native aquatic vegetation (Bučar et al. 2024). In contrast, based on our observations, *V. spiralis* exhibits increased tolerance to thermal and trophic variability. As for the *A. filiculoides*, it plays a role in nitrogen fixation, substrate shading and water oxygenation reduction (Pinero-Rodríguez et al. 2021).
Modelling the spatial distribution of plant species allows for the assessment of spread risks and supports management planning in vulnerable habitats. Recent research (Steen et al. 2019) has shown that combining climate data with species occurrence records can help identify areas potentially favourable for the establishment and expansion of invasive species according to their ecological niche.
The aim of the study is to analyse the current distribution and to project the future distribution of three aquatic macrophyte species (*Azolla filiculoides*, *Elodea nuttallii*, and *Vallisneria spiralis*) in the lakes of the Danube Delta, depending on the current climatic conditions and the predicted climate change scenarios. The objectives of the study were (i) to map the presence of the three target aquatic macrophyte species in representative lakes of the Danube Delta Biosphere Reserve, (ii) to analyze the climatic and environmental factors that determine their distribution, (iii) to model the current and future ecological distribution (SDM), and (iv) to compare the spread of the species and to delimit the areas with high ecological risk.

Materials and methods

Study area

The study was conducted in the Danube Delta Biosphere Reserve (Romania), during 2024–2025 (Fig. 1). The lakes and canals were characterised by shallow depths and relatively transparent waters. Physico-chemical data indicated an alkaline environment, with weakly mineralised freshwater and high temperatures in the warm season. Moreover, the analysed areas are influenced by a temperate continental climate, with hot summers and mild winters. The hydrological dynamics depend on the level of the Danube River and the precipitation input. In general, the lakes and canals are characterised by emergent vegetation (*Phragmites australis*, *Typha angustifolia*), floating and floating-leaved macrophytes (*Hydrocharis morsus-ranae*), which favours the formation of heterogeneous habitats.

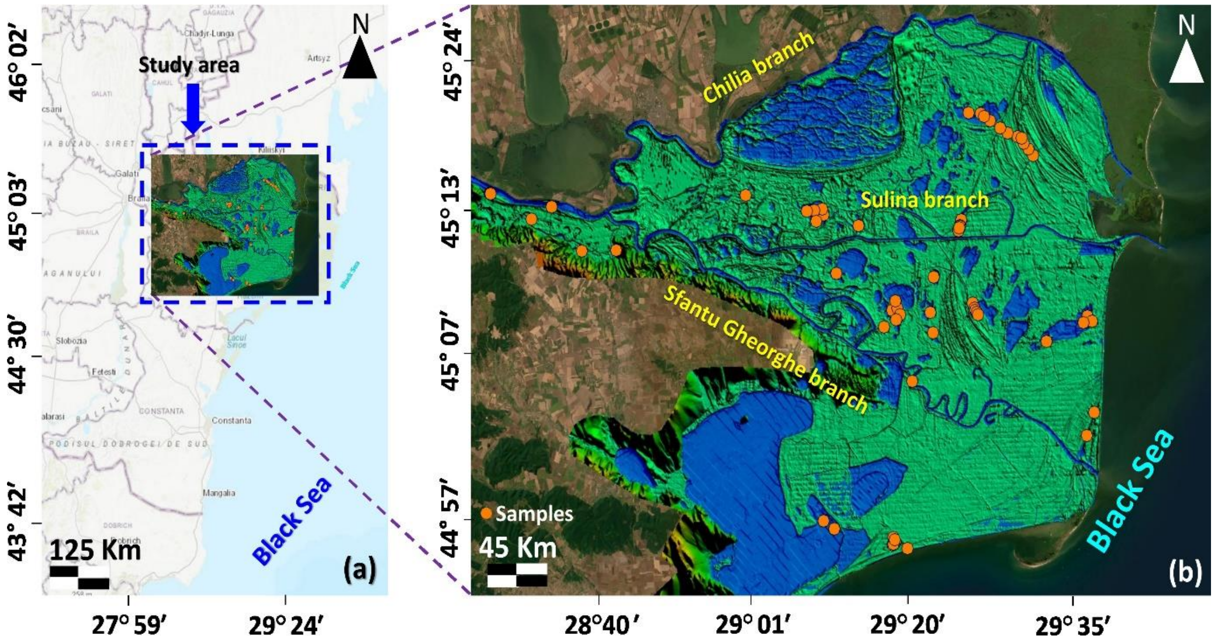

Figure 1. Study area (Map design: Alexandru Bănescu)

Study species

Azolla filiculoides Lam. is an annual species (Ciocârlan 2009) of the Salviniaceae family (Christenhusz and Raab-Straube 2013), native to North America (Sîrbu and Oprea 2011). *Elodea nuttallii* (Planch.) H. St. John is a perennial species (Ciocârlan 2009) of the Hydrocharitaceae family (Uotila 2009), native to North America (Cook and Urmi-König 1985). This species reproduces vegetatively through stem fragments and overwintering structures (Hussner 2017). The species spreads through stem fragments and winter buds (Wittenberg 2005; Sîrbu and Oprea 2011). *Vallisneria spiralis* L. is a submerged, dioecious, perennial plant native to southern Europe, northern Africa, the Middle East and southwestern Asia (Les et al. 2008; Hussner 2012). In Romania, however, the species is regarded as adventive (non-native) and of tropical origin (Ciocârlan 2009; Sîrbu and Oprea 2011), having been introduced as an ornamental and fodder plant; it is therefore treated here as a non-native, range-expanding macrophyte rather than as an invasive species. This species belongs to the Hydrocharitaceae family (Uotila 2009) and has fibrous roots, horizontal stolons (Rimac et al. 2021) and is fixed to the bottom of the water (Fig. 2; Grințescu et al. 1966).

Figure 2. *Azolla filiculoides* (A), *Elodea nuttallii* (B), and *Vallisneria spiralis* (C) (Photographs: Simona Chirilă)

Phytocoenological analysis

For the vegetation analysis, phytocoenological relevés were carried out in 4 m² plots. (Supplementary Material 1: phytocoenological relevé data). The data used were represented by mean percentage values of the Braun-Blanquet scale of cover abundance (Cristea et al. 2004): r (0.05%); + (0.5%); 1 (5%); 2 (17.5%); 3 (37.5%); 4 (62.5%); and 5 (87.5%). The vegetation classification was carried out in the GINKGO software from the VegAna package (Bouxin 2005), where the hierarchical agglomerative clustering method was applied (ß-flexible method, ß = -0.25, Bray-Curtis dissimilarity). Based on the Silhouette index, the optimal number of clusters was identified (Rousseeuw 1987). The synoptic table with the identified clusters was obtained from the Juice version 7.1 software (Tichý 2002), and the diagnostic species were identified using Indicator Value (IndVal; Dufrêne and Legendre 1997).

To statistically select only the associated species for each cluster, a permutation test was used (999 iterations; de Cáceres and Legendre 2009). The IndVal threshold was set at 0.500 (Legendre and Legendre 1998).

The classification of plant associations and their nomenclature followed the specialized literature (Chifu et al. 2014; Chifu and Irimia 2014). The nomenclature of plant species followed Euro+Med (2025), and for the higher-level syntax Mucina et al. (2016) was used. EUNIS habitats were identified based on alliances (Chytrý et al. 2020).

Hydromorphological characterization of lakes

The qualitative descriptors used in this study (connectivity class, water exchange, seasonal fluctuation, transparency/turbidity and sedimentation/clogging) were defined by the authors as an operational classification for the comparative characterization of some lakes in the Danube Delta. The assignment of qualitative classes was based on the main hydrological connection of each lake, its position in the channel-lake network and its hydromorphological framework. This is in line with previous studies (Coops et al. 1999; Oosterberg et al. 2000; Wantzen et al. 2008) showing that hydrological connectivity, water level dynamics, turbidity and sedimentation are important factors of ecological variation in deltaic lakes.

Spatial modelling

Species occurrence points were spatially filtered to avoid overfitting the model, setting a threshold of 1 km, so that all records located at a smaller distance were eliminated. The filtering was performed in ArcGIS Pro. Species distribution modeling (SDM) was based on the presence points resulting from the filtering and on environmental variables, represented by the 19 bioclimatic variables at 1 km resolution from CHELSA v2.1 (https://www.chelsa-climate.org/datasets/chelsa_bioclim) and a land-use variable. The land-use variable was obtained from the Copernicus Corine Land Cover dataset (100 m raster; DOI: https://doi.org/10.2909/960998c1-1870-4e82-8051-6485205ebbac). All environmental layers were resampled to a common spatial resolution of 100 m, which was used for the modelling. The raster datasets were cropped for the Dobrogea region and exported in ASCII format to be compatible with the MaxEnt program, used for modelling. The final suitability maps were subsequently clipped to the boundary of the Danube Delta Biosphere Reserve. Modelling was initially attempted at the scale of the Danube Delta alone; however, its surface is too small and the resolution of the available climate data too coarse to yield satisfactory results, so the modelling was carried out at the broader Dobrogea scale. As the available climate data are better suited to analyses over large spatial extents, the results for the Danube Delta should be interpreted with caution.

The selection of relevant variables was carried out in several stages. In a first phase, the distribution of each species was modeled using all 20 variables. Subsequently, Pearson correlations were calculated in R, applying an exclusion threshold $|r| > 0.8$ to eliminate strongly correlated variables. From the remaining set, variables with high contribution to the model and without significant correlations were retained.

The current distribution of each species was modelled using the filtered occurrence points and the selected environmental variables. For the future projections, CMIP6 climate scenarios available from CHELSA were used, corresponding to the periods 2040–2070 and 2071–2100. Two socio-economic scenarios were considered, SSP3-7.0 and SSP5-8.5, representing high and very high greenhouse gas concentration trajectories. The MaxEnt model calibration was performed using cloglog output format, ASCII files, a regularization multiplier of 0.5, a maximum of 5000 background points, ten replications and cross-validation. Finally, each species was modelled separately based on the relevant variables previously identified. Model settings and predictive performance (AUC) are summarised in Supplementary Table S1.

Results

Phytocoenological analysis

Azolla filiculoides was identified within phytocoenoses classified into two phytocoenological classes: *Lemnetea* and *Potamogetonetea*. In this context, the vegetation was grouped into two orders, four alliances and seven plant associations (Fig. 3).

Class *Lemnetea* O. de Bolòs et Masclans 1955
- **Order** *Lemnetalia minoris* O. de Bolòs et Masclans 1955
  - **All.** *Lemnion minoris* O. de Bolòs et Masclans 1955
    - **Ass.** *Lemneto-Azolletum filiculoidis* (Langendock 1935) Br.-Bl. 1952
    - **Ass.** *Lemnetum minoris* Soó 1927
    - **Ass.** *Lemnetum gibbae* Miyawaki et J. Tx. 1960
    - **Ass.** *Lemno-Salvinietum natantis* Miyawaki et J. Tx. 1960
  - **All.** *Stratiotion Den Hartog et Segal 1964*
    - **Ass.** *Ceratophylletum demersi* Hild 1956

Class *Potamogetonetea* Klika in Klika et Novák 1941
- **Order** *Potamogetonetalia* Koch 1926
  - **All.** *Potamogetonion* Libbert 1931
    - **Ass.** *Ceratophyllo demersi-Elodeetum nuttalii* Ciocârlan et al. 1997
  - **All.** *Nymphaeion albae* Oberd. 1957
    - **Ass.** *Nymphaeetum albae* Vollmar 1947

Azolla filiculoides was most associated with its own floristic cluster, namely *Lemneto-Azolletum filiculoides*. The species had a share of 37.5%, although it is represented by only two relevés. At the same time, *A. filiculoides* was identified in 63 relevés analysed from the lakes of the Danube Delta and was recorded in 13 lakes: Uzlina (seven relevés), Băclănești, Furtuna, and Matița (six relevés each), Cuibul cu Lebede, Isac, Meșteru, Puiu, Roșu and Trei Iezere (five relevés each), Merhei (four relevés), Gorgova (three relevés), and Isaccea (one relevé). The classification of relevés by cluster analysis, presented in the dendrogram, highlighted seven distinct floristic groups. In the other clusters, corresponding to the associations *Lemnetum minoris*, *Lemnetum gibbae*, *Ceratophyllo demersi-Elodeetum nuttalii*, *Lemno-Salvinietum natantis*, *Ceratophylletum demersi,* and *Nymphaeetum albae*, the participation of the *A. filiculoides* was much lower, of only 0.5%.

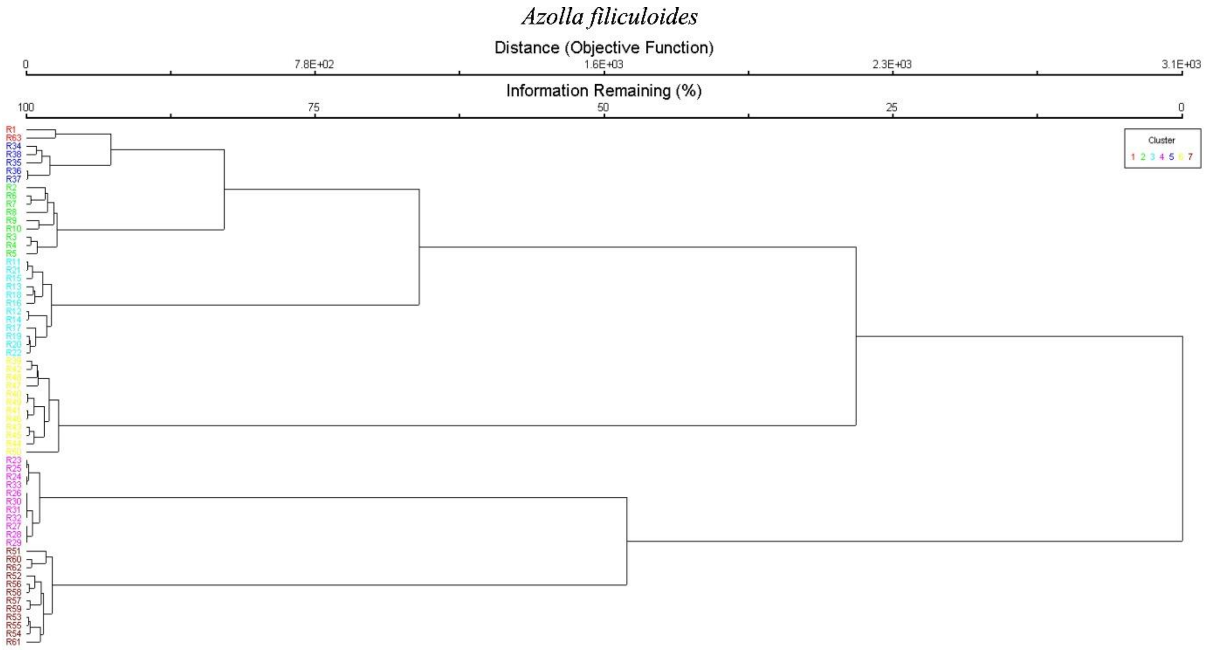

Figure 3. Dendrogram of relevés with *Azolla filiculoides* in Danube Delta

Elodea nuttallii was identified in three phytocoenological classes (*Lemnetea*, *Potamogetonetea*, and *Charetea intermediae*), four orders, seven alliances, and 14 plant associations (Fig. 4).

Class *Lemnetea* O. de Bolòs et Masclans 1955
Order *Lemnetalia minoris* O. de Bolòs et Masclans 1955
All. *Stratiotion Den Hartog et Segal 1964*
Ass. *Ceratophylletum demersi* Hild 1956
Ass. *Lemno-Hydrocharietum morsus-ranae* (Oberd.1957) Passarge 1978
All. *Lemnion minoris* O. de Bolòs et Masclans 1955
Ass. *Lemnetum minoris* Soó 1927
Ass. *Lemnetum gibbae* Miyawaki et J. Tx. 1960
Ass. *Lemno-Salvinietum natantis* Miyawaki et J. Tx. 1960
All. *Utricularion vulgaris* Passarge 1964
Ass. *Lemno-Utricularietum vulgaris* Soó (1928) 1947

Class *Potamogetonetea* Klika in Klika et Novák 1941
Order *Potamogetonetalia* Koch 1926
All. *Potamogetonion* Libbert 1931
Ass. *Ceratophyllo demersi-Elodeetum nuttalii* Ciocârlan et al. 1997
Ass. *Potametum perfoliati* W. Koch 1926 em. Passarge 1964
Ass. *Potametum lucentis* Hueck 1931
All. *Nymphaeion albae* Oberd. 1957
Ass. *Nymphaeetum albae* Vollmar 1947
Ass. *Trapetum natantis* V. Kárpáti 1963
Order *Zannichellietalia pedicellatae* Schaminée, Lanjouw et Schipper ex Mucina et Theurillat ined.
All. *Zannichellion pedicellatae* Schaminée, Lanjouw et Schipper ex Passarge 1996
Ass. *Potametum pectinati* Carstensen ex Hilbig 1971
Ass. *Potametum trichoidis* (Freitag, Markus & Schwippl 1959) Tüxen 1974

Class *Charetea intermediae* F. Fukarek 1961
Order *Charetalia intermediae* Sauer 1937
All. *Charion intermediae* Sauer 1937
Ass. *Nitellopsidetum obtusae* Sauer ex Dambska 1961

Elodea nuttallii was noted for its high representation in Cluster 1, corresponding to the *Ceratophyllo demersi-Elodeetum nuttalii* association, where it was recorded in 48 relevés, with values of 37.5–62.5–87.5%. The species' participation in the remaining clusters was much lower. Values of 0.5–5% were recorded in the associations with *Potametum pectinati*, *Potametum trichoidis*, *Nitellopsidetum obtusae* and *Ceratophylletum demersi*, and in the *Nymphaeetum albae* association, the value was 5%. In the other associations, namely those with *Lemnetum minoris*, *Lemnetum gibbae*, *Lemno-Salvinietum natantis*, *Lemno-Hydrocharietum morsus-ranae*, *Lemno-Utricularietum vulgaris*, *Potametum perfoliati*, *Potametum lucentis* and *Trapetum natantis*, the participation of the species was only 0.5%. *Elodea nuttallii* was widely distributed across the study area, with the highest numbers of relevés in Furtuna (24 relevés) and Uzlina (20 relevés), followed by Matița (13 relevés), Cuibul cu Lebede (13 relevés) Trei Iezere (12 relevés), Isac, Merhei and Roșu (11 relevés each), Băclănești, Meșteru and Puiu (ten relevés each), Gorgova (nine relevés), Rotund (five relevés), Gorgoștel (four relevés), Nebunu and Perișor (two relevés each), and Câșla, Chiril, Iacub and Plin (one relevé each).

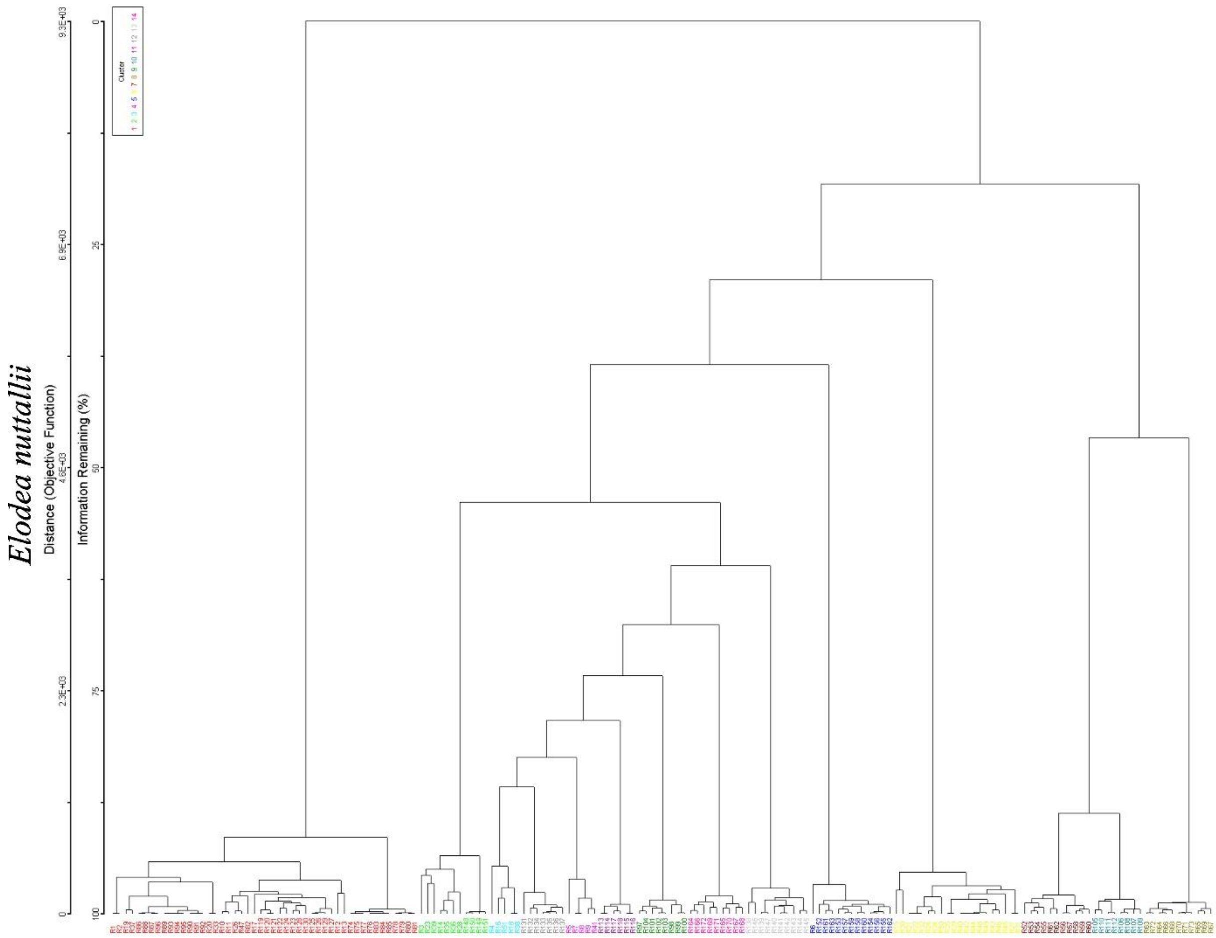

Figure 4. Dendrogram of relevés with *Elodea nuttallii* in Danube Delta

Vallisneria spiralis was identified in three phytocoenological classes (*Lemnetea*, *Potamogetonetea*, and *Charetea intermediae*), four orders, five alliances, and nine plant associations (Fig. 5).

Class *Lemnetea* O. de Bolòs et Masclans 1955
  Order *Lemnetalia minoris* O. de Bolòs et Masclans 1955
    All. *Stratiotion Den Hartog et Segal 1964*
      Ass. *Ceratophylletum demersi* Hild 1956

Class *Potamogetonetea* Klika in Klika et Novák 1941
  Order *Potamogetonetalia* Koch 1926
    All. *Potamogetonion* Libbert 1931
      Ass. *Ceratophyllo demersi-Vallisnerietum spiralis* Lazić 2006
      Ass. *Ceratophyllo demersi-Elodeetum nuttalii* Ciocârlan et al. 1997
      Ass. *Myriophyllo-Potametum lucentis* Soó 1934 subas. *myriophylletosum spicati* Soó 1957
      Ass. *Potametum lucentis* Hueck 1931
    All. *Nymphaeion albae* Oberd. 1957
      Ass. *Myriophyllo verticillati-Nupharetum luteae* W. Koch 1926
  Order *Zannichellietalia pedicellatae* Schaminée, Lanjouw et Schipper ex Mucina et Theurillat ined.
    All. *Zannichellion pedicellatae* Schaminée, Lanjouw et Schipper ex Passarge 1996
      Ass. *Potametum crispi* Soó 1927
      Ass. *Potametum pectinati* Carstensen ex Hilbig 1971

Class *Charetea intermediae* F. Fukarek 1961
  Order *Charetalia intermediae* Sauer 1937
    All. *Charion intermediae* Sauer 1937
      Ass. *Nitellopsidetum obtusae* Sauer ex Dambska 1961

Vallisneria spiralis was recorded in 75 relevés from 13 lakes in the Danube Delta. The species was most strongly associated with Cluster 2, corresponding to communities with the *Ceratophyllo demersi-Vallisnerietum spiralis* association, where it recorded the highest cover values (62.5–87.5%). In the other relevés, its presence was much lower, generally 0.5%, while in Cluster 5, corresponding to the *Ceratophylletum demersi* association, it reached 0.5–5%. The other relevés corresponded to the associations *Nitellopsidetum obtusae* (Cluster 1), *Ceratophyllo demersi-Elodeetum nuttalii* (Cluster 3), *Myriophyllo-Potametum lucentis* subas. *myriophylletosum spicati* (Cluster 4), *Potametum crispi* (Cluster 6), *Potametum lucentis* (Cluster 7), *Potametum pectinati* (Cluster 8) and *Myriophyllo verticillati-Nupharetum luteae* (Cluster 9). At the same time, the species was distributed across several lakes, with the highest number of relevés being recorded in Furtuna (13 relevés) and Uzlina (12 relevés), followed by Isac, Matița, Merhei Mare and Trei Iezere (six relevés each), Roșu (five relevés), Băclănești, Gorgova, Meșteru and Puiu (four relevés each), Cuibul cu Lebede (three relevés), and Roșuleț (two relevés).

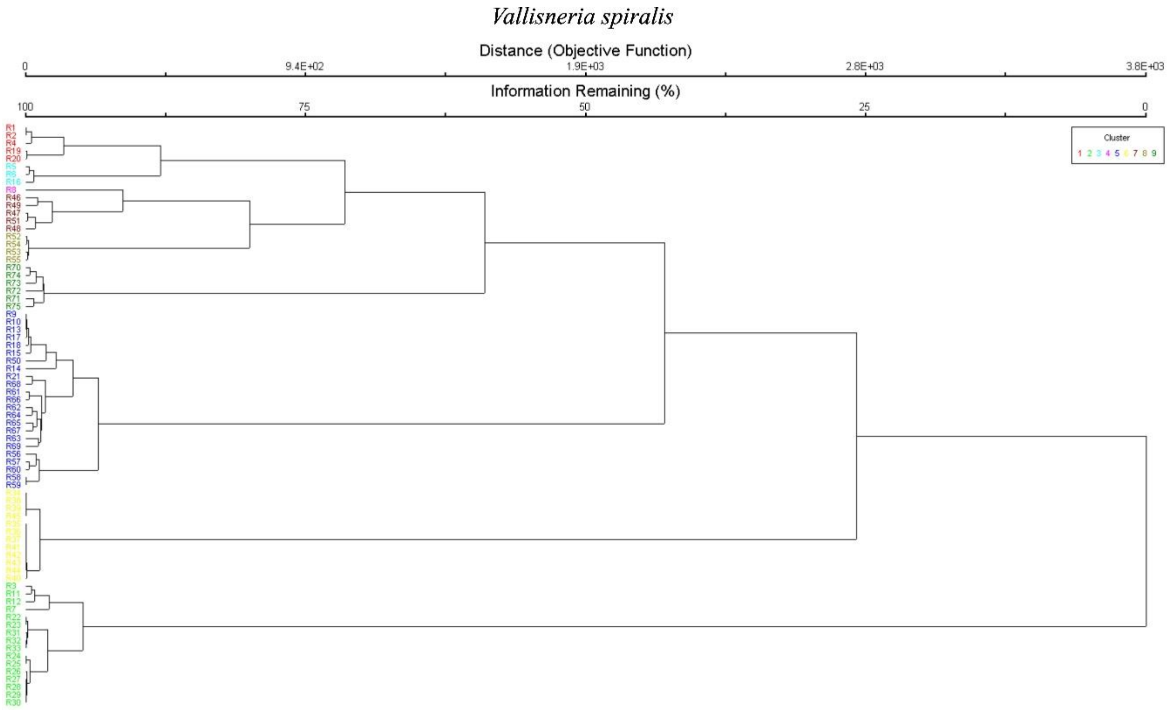

Figure 5. Dendrogram of relevés with *Vallisneria spiralis* in Danube Delta

The DCA ordination showed differences in the floristic structure of the relevés containing the three species (Fig. 6). For *A. filiculoides*, the gradient length was 3.2 SD on axis 1 and 1.8 SD on axis 2, and the two axes explained 25.83% and 11.38% of the total inertia, respectively. For *E. nuttallii*, the gradient length was 3.7 SD on axis 1 and 3.1 SD on axis 2, while for *V. spiralis* it was 3.8 SD on axis 1 and 3.5 SD on axis 2, with the first two axes explaining 16.09% and 13.73% of the total inertia. Overall, these values indicate moderate floristic gradients for all three species, with only slightly longer gradients observed for *E. nuttallii* and *Vallisneria spiralis* compared with *A. filiculoides*.

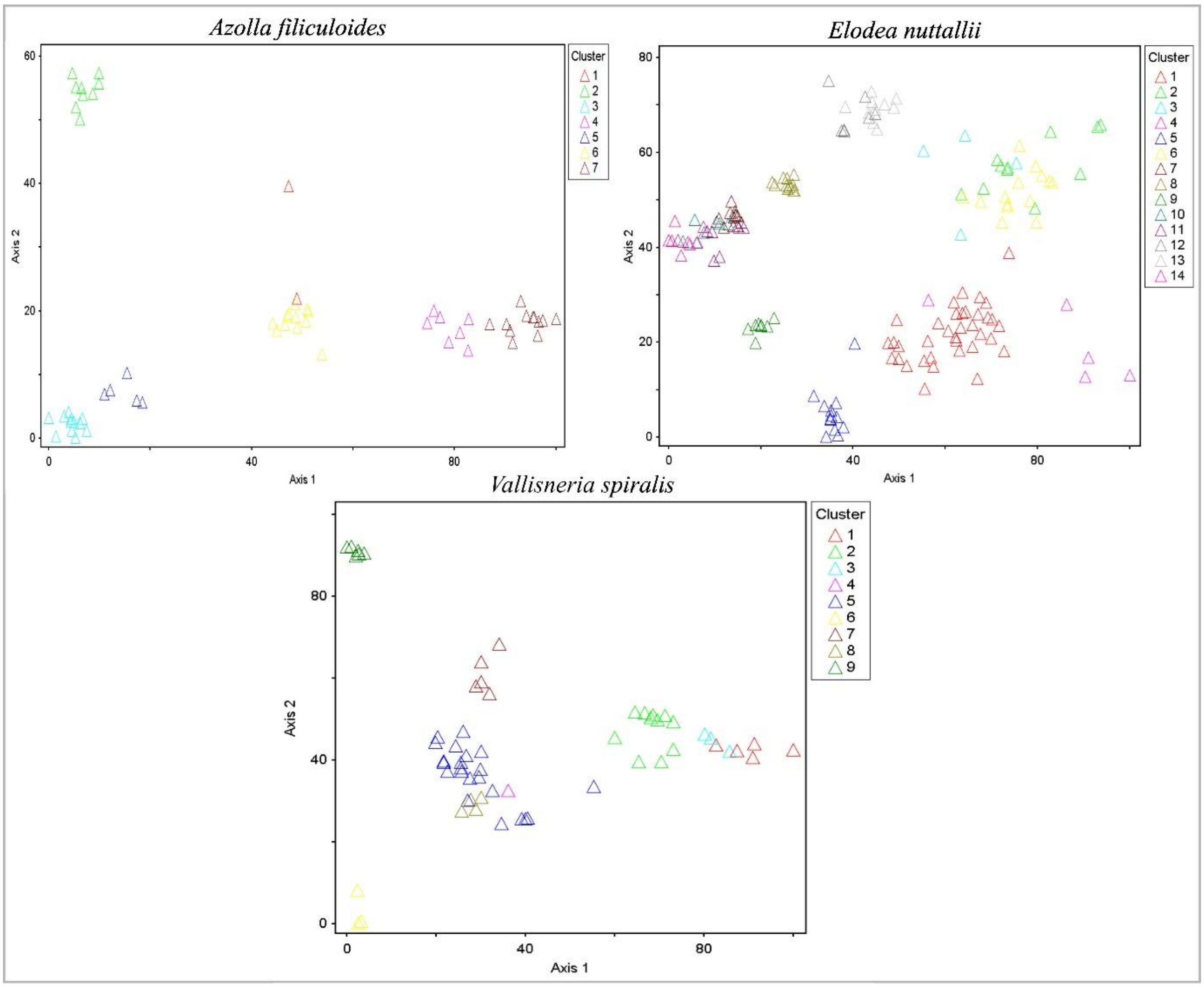

Figure 6. DCA ordination of relevés containing *Azolla filiculoides*, *Elodea nuttallii* and *Vallisneria spiralis*

EUNIS habitats

Azolla filiculoides therefore occurs in C1.32, C1.33 and C1.241 (predominantly C1.32, as the species itself is free-floating). *Elodea nuttallii* occurs in C1.32, C1.33, C1.241 and C1.25 (the widest range of habitats; its real nucleus, the *Ceratophyllo-Elodeetum* association, is C1.33). *Vallisneria spiralis* occurs in C1.32, C1.33, C1.241 and C1.25 (its nucleus, *Ceratophyllo-Vallisnerietum*, is C1.33).

Hydromorphological characterization of lakes

The results obtained for certain qualitative descriptors indicate that hydrological connectivity and turbidity are the main factors structuring the ecological differences between the studied lakes. Thus, lakes with high connectivity and active water exchange were generally interpreted as less favourable for submerged macrophytes. Lakes with lower connectivity and higher water transparency were considered potentially more suitable, although sedimentation and reduced circulation may act as local constraints. Most lakes with intermediate conditions were interpreted as moderately favourable for macrophytes (Table 1).

Table 1. Hydromorphological and ecological characteristics of the studied lakes

Lake	Complex	Main hydrological connection	Connectivity class	Water exchange	Mean depth (m) BS75	Seasonal fluctuation	Transparency/ turbidity	Sedimentation/ clogging	Relevance for macrophytes
Furtuna	Șontea–Furtuna	Sulina via Crânjală; secondary channels	High	Active	-0.37	high seasonal fluctuation	high turbidity during high-water periods	sediment-influenced	Likely constrained by high turbidity and strong hydrological exchange
Uzlina	Gorgova–Uzlina	Sf. Gheorghe via Uzlina channel; linked to adjacent lakes	High	Active	-0.21	high seasonal fluctuation	high turbidity during high-water periods	sediment-influenced	Likely constrained by high turbidity despite permanent connectivity
Băclănești	Șontea–Furtuna	Chilia via Stipoc; linked to adjacent channels	Moderate	Moderate	0.21	moderate fluctuation	variable transparency	local clogging near inlets	Moderately favourable under intermediate light and exchange conditions
Câșla	Somova-Parcheș	Danube river via Carpov; linked to adjacent channels	Low	Reduced	0.09	reduced fluctuation	relatively clear in low-water periods	reduced circulation due to sedimentation	Potentially favourable under relatively clear and stable conditions, but limited by sedimentation
Chiril	Gorgova–Uzlina	Sf. Gheorghe via Perivolovca channel; linked to adjacent lakes	Moderate	Moderate	0.11	moderate fluctuation	variable transparency	local clogging near inlets	Moderately favourable under intermediate hydrological conditions

Lake	Complex	Main hydrological connection	Connectivity class	Water exchange	Mean depth (m) BS75	Seasonal fluctuation	Transparency/ turbidity	Sedimentation/ clogging	Relevance for macrophytes
Cuibu cu Lebede	Gorgova–Uzlina	Sf. Sulina via Caraorman channel; linked to adjacent channels	High	Active	-0.07	high seasonal fluctuation	high turbidity during high-water periods	sediment-influenced	Likely constrained by high turbidity and active water exchange
Gorgoștel	Gorgova–Uzlina	Sf. Gheorghe via Perivolovca channel; linked to adjacent channels	High	Active	-0.37	high seasonal fluctuation	high turbidity during high-water periods	sediment-influenced	Likely constrained by high turbidity and strong hydrological forcing
Gorgova	Gorgova–Uzlina	Sf. Gheorghe via Litcov channel; linked to adjacent channels	Moderate	Moderate	-0.7	moderate fluctuation	variable transparency	local clogging near inlets	Moderately favourable, with possible local limitation near inlets
Iacub	Roșu-Puiu	Sf. Sulina via Caraorman channel; linked to adjacent channels and lakes	High	Active	-0.54	high seasonal fluctuation	high turbidity during high-water periods	sediment-influenced	Likely constrained by high turbidity despite high connectivity
Isac	Gorgova–Uzlina	Sf. Gheorghe via Uzlina channel; linked to adjacent channels and lakes	High	Active	-0.56	high seasonal fluctuation	high turbidity during high-water periods	sediment-influenced	Likely constrained by high turbidity and active exchange
Matita	Matița-Merhei	Sf. Sulina via Eracle channel; linked to adjacent lakes	Low	Reduced	-0.79	reduced fluctuation	variable transparency	local clogging near inlets	Potentially favourable, but possibly limited by reduced exchange and local clogging
Merhei	Matița-Merhei	Sf. Sulina via Eracle channel; linked to adjacent lakes	Moderate	Reduced	-0.33	moderate fluctuation	variable transparency	local clogging near inlets	Moderately favourable, with possible constraints from

Lake	Complex	Main hydrological connection	Connectivity class	Water exchange	Mean depth (m) BS75	Seasonal fluctuation	Transparency/ turbidity	Sedimentation/ clogging	Relevance for macrophytes
									reduced exchange
Mesteru	Șontea–Furtuna	Tulcea via Mila 35; linked to adjacent channels	Moderate	Moderate	0.33	moderate fluctuation	variable transparency	local clogging near inlets	Moderately favourable under intermediate connectivity and variable transparency
Nebunu	Șontea–Furtuna	Tulcea via Mila 35; linked to adjacent channels	Moderate	Moderate	0.51	moderate fluctuation	variable transparency	local clogging near inlets	Moderately favourable under intermediate connectivity and variable transparency
Perisor	Dunăvăț-Dranov	indirect connection through adjacent lakes/channels	Low	Reduced	-0.75	reduced fluctuation	relatively clear in low-water periods	unknown	Potentially favourable under relatively clear and stable conditions; uncertainty remains
Plin	Matița-Merhei	Sf. Sulina via I5c channel; linked to adjacent channels	Moderate	Moderate	-0.22	moderate fluctuation	variable transparency	local clogging near inlets	Moderately favourable under intermediate hydrological conditions
Puiu	Roșu-Puiu	Sf. Sulina via Caraorman channel; linked to adjacent lakes	Moderate	Moderate	-1.43	moderate fluctuation	variable transparency	local clogging near inlets	Moderately favourable, though depth and variable transparency may limit submerged

Lake	Complex	Main hydrological connection	Connectivity class	Water exchange	Mean depth (m) BS75	Seasonal fluctuation	Transparency/ turbidity	Sedimentation/ clogging	Relevance for macrophytes
									vegetation locally
Roșu	Roșu-Puiu	Sf. Sulina via Caraorman channel; linked to adjacent lakes	Moderate	Moderate	-1.22	moderate fluctuation	variable transparency	local clogging near inlets	Moderately favourable, though variable transparency may restrict submerged macrophytes
Roșuleț	Roșu-Puiu	Sf. Sulina via Caraorman channel; linked to adjacent channels and lakes	Moderate	Moderate	-0.96	moderate fluctuation	variable transparency	local clogging near inlets	Moderately favourable under intermediate connectivity and transparency conditions
Rotund	Somova-Parcheș	Danube river via Gârla nouă; linked to adjacent lakes	Moderate	Moderate	0.52	reduced fluctuation	relatively clear in low-water periods	reduced circulation due to sedimentation	Potentially favourable under relatively clear water, but constrained by sedimentation and reduced circulation
Trei Iezere	Matița-Merhei	Sf. Sulina via Trei Iezere channel; linked to adjacent lakes	Moderate	Moderate	-0.51	moderate fluctuation	variable transparency	local clogging near inlets	Moderately favourable under intermediate hydrological conditions

Spatial modelling

Pearson correlation

For the distribution modelling of *A. filiculoides*, 16 occurrence points were used, and six environmental variables were selected. The classification threshold established was "Maximum training sensitivity plus specificity cloglog threshold", with a value of 0.4. In the case of *E. nuttallii*, the modelling was carried out based on 25 occurrence points and seven selected variables, the classification threshold being 0.5. For *V. spiralis*, 35 occurrence points and eight variables were used, and the classification threshold was 0.3 (Fig. 7).

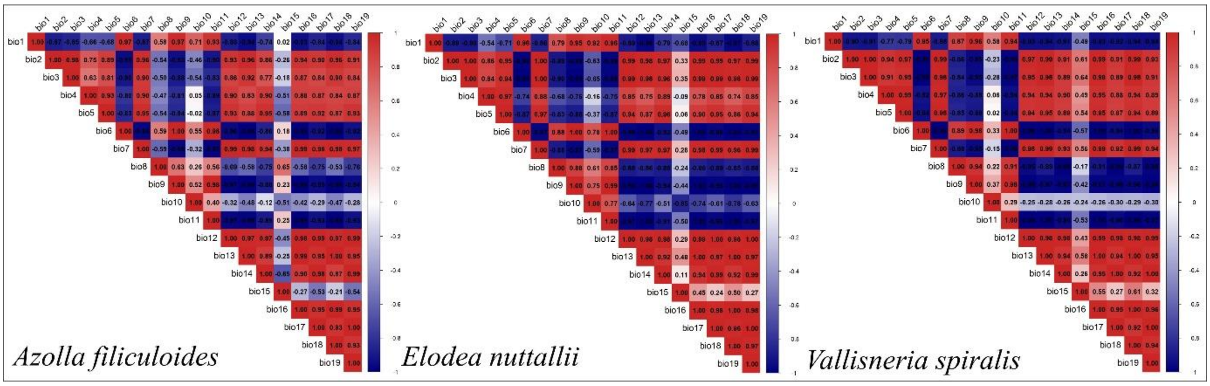

Figure 7. Pearson correlation matrix of bioclimatic variables (BIO1–BIO19)

Current Distribution Modelling

Azolla filiculoides had the largest area with high suitability, namely 2395.8 km^2, representing approximately 53.70% of the analysed area (Fig. 8; Table 2). This shows that the species has a high potential to occupy habitats in the Danube Delta, being adapted to a wider spectrum of favourable ecological conditions. In contrast, *E. nuttallii* presented a much lower potentially favourable distribution. Only 251.8 km2, i.e. approximately 5.64% of the analysed area, were classified as suitable. The majority of the area, 94.36%, was classified as unsuitable. This result shows that, under current conditions, the species has a lower probability of wide expansion in the Danube Delta. For *V. spiralis*, the results were similar to those observed for *E. nuttallii*. The suitable area was 231.1 km^2, representing approximately 5.18% of the total. This indicates a restricted potential distribution, with limited and fragmented favourable areas. Current and projected suitable areas for all scenarios are given in Supplementary Table S2.

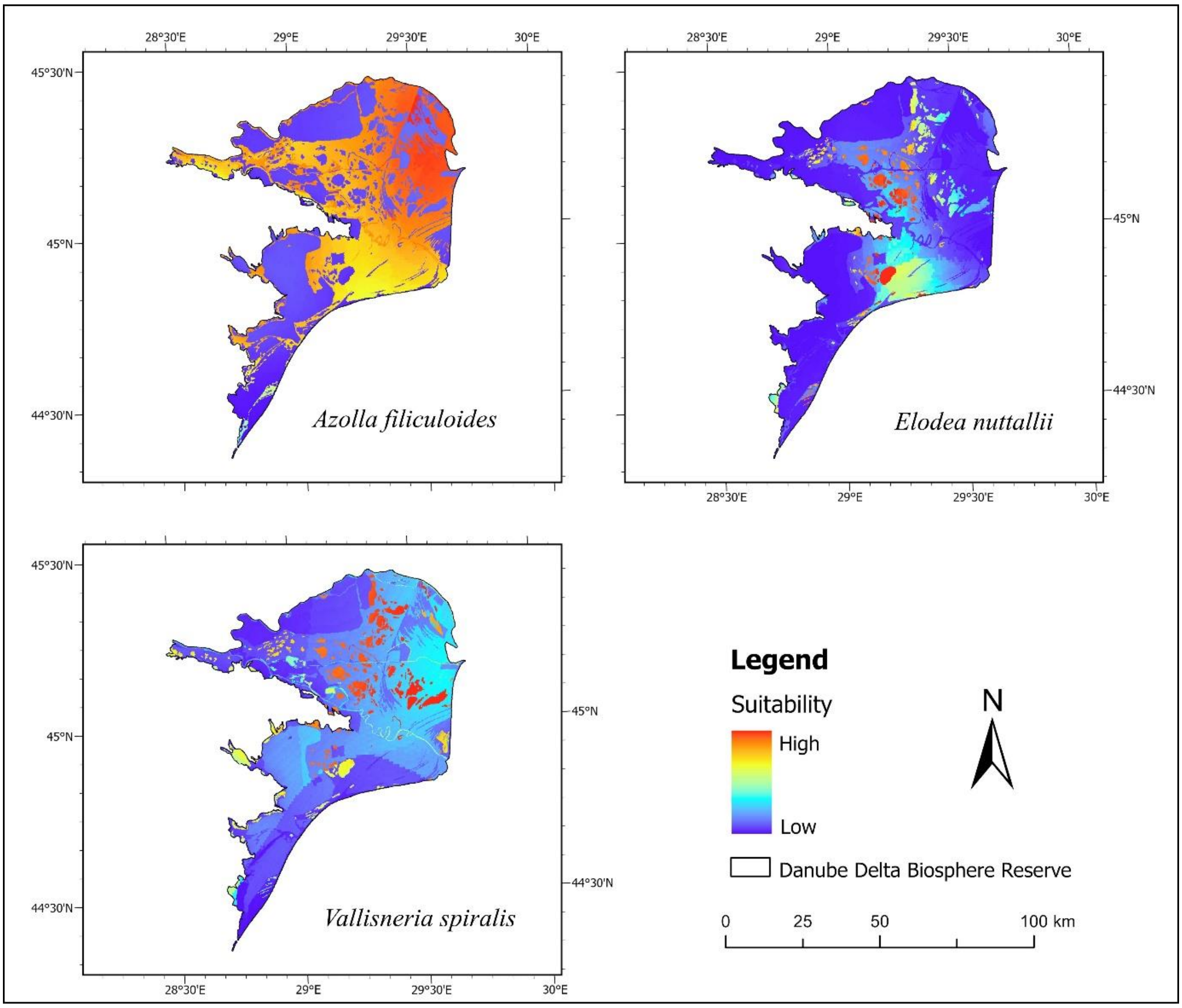

Figure 8. Current distribution of species in the Danube Delta Biosphere Reserve

Table 2. Estimated area of suitable and unsuitable habitats for the aquatic plant species analysed

Specia	Unsuitable (<0,5)	Suitable (>0,5)	Approximate total	Suitable (%)	Unsuitable (%)
Azolla filiculoides	2065,5	2395,8	4461,3	53,70%	46,30%
Elodea nuttallii	4210,1	251,8	4461,9	5,64%	94,36%
Vallisneria spiralis	4230,5	231,1	4461,6	5,18%	94,82%

Analysis of variable contributions

The LULC variable contributed the highest percentage to modelling the distribution of the three species analysed (Table 3; Fig. 9). The strongest influence was observed in *A. filiculoides*, where LULC had a contribution of 87.6% and a permutation importance of 76.3%. This indicated that land cover and land use are the main factors associated with the distribution of this species. For *E. nuttallii*, LULC had the highest percentage contribution (67.5%), but the permutation importance was higher for BIO12 (32%) and BIO15 (27.5%). This indicated that, although LULC contributed the most to building the model, precipitation-related variables had an important role in the stability of the prediction. In the case of the species *V. spiralis*, LULC remained the most important variable both in percentage contribution (67.7%) and in permutation importance (39.8%). However, BIO12 had an important influence, with a contribution of 22.5% and a permutation importance of 30%. The full set of variable contributions and permutation importance values is provided in Supplementary Table S4.

Table 3. Contribution of variables to the distribution of aquatic species

Variable	Percent contribution	Permutation importance
Azolla filiculoides		
LULC	87.6	76.3
BIO12	7.9	13.9
BIO4	4.1	4.1
BIO10	0.2	2.9
BIO15	0.1	0.1
BIO1	0.1	2.6
Elodea nuttallii		
LULC	67.5	24.7
BIO15	13.3	27.5
BIO12	9.6	32
BIO10	4.5	7.5
BIO1	3.2	3.3
BIO9	1.5	0.8
BIO14	0.4	4.2
Vallisneria spiralis		
LULC	67.7	39.8
BIO12	22.5	30
BIO8	6.7	7.6
BIO11	1.3	13.1
BIO3	1	7.2
BIO9	0.5	1.6
BIO15	0.3	0.2
BIO10	0.1	0.4

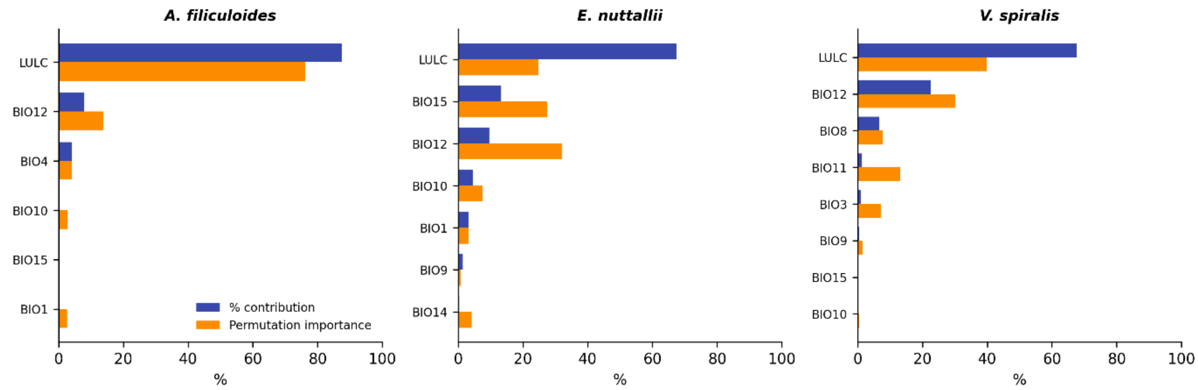

Figure 9. Environmental variable contributions (percent contribution and permutation importance) to the MaxEnt models for *A. filiculoides*, *E. nuttallii* and *V. spiralis*

Future distribution modelling

The three species analysed respond differently to future climate scenarios. For *A. filiculoides*, the suitable area remains high in most scenarios, increasing slightly in SSP3-7.0 to 2450.2

km² in the period 2071–2100. In contrast, in the SSP5-8.5 scenario for the same period, the suitable area decreases to 2239.6 km², below the current value of 2395.8 km², indicating a possible reduction in favourable habitat under more extreme climate conditions. For *E. nuttallii*, the suitable area is currently reduced to 251.8 km², and decreases in the period 2040–2070, especially in SSP5-8.5, where it reaches 118.9 km². For the period 2071–2100, the SSP5-8.5 scenario indicates a significant increase, to 397.9 km², suggesting a possible future expansion of favourable habitat. For *V. spiralis*, the suitable area increases between 2040 and 2070, reaching 441.9 km² in SSP3-7.0 and 470.5 km² in SSP5-8.5. However, towards the end of the century, the favourable area decreases, especially in SSP5-8.5, where it reaches only 117 km² (Figs. 10-12).

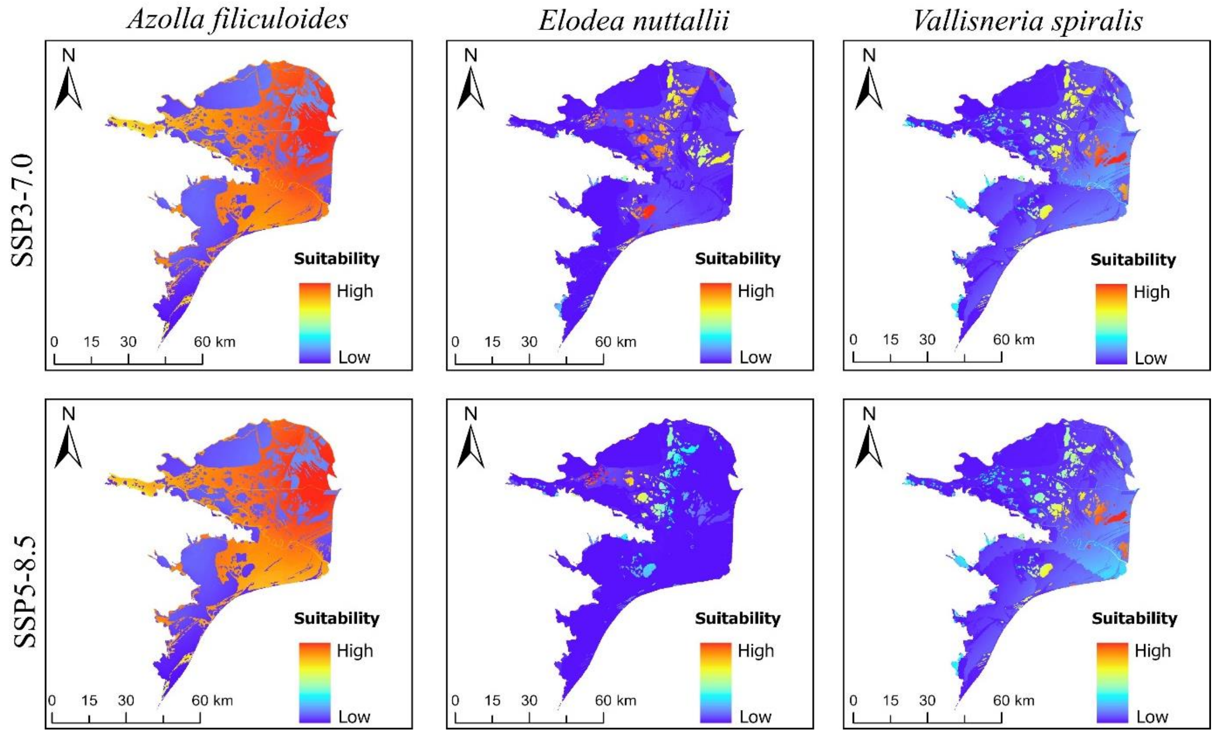

Figure 10. Future distribution of species in the Danube Delta Biosphere Reserve. Period 2040-2070

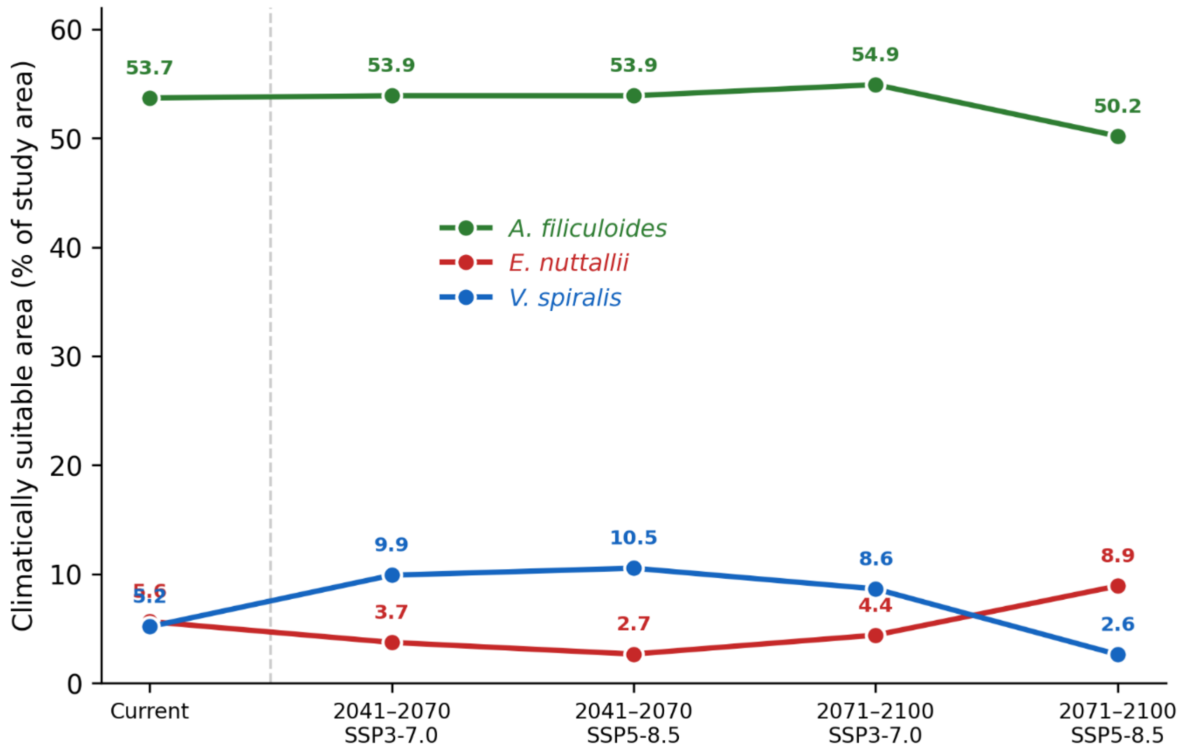

Figure 11. Projected change in suitable habitat area (% of study area) for the three species across current conditions and the future climate scenarios

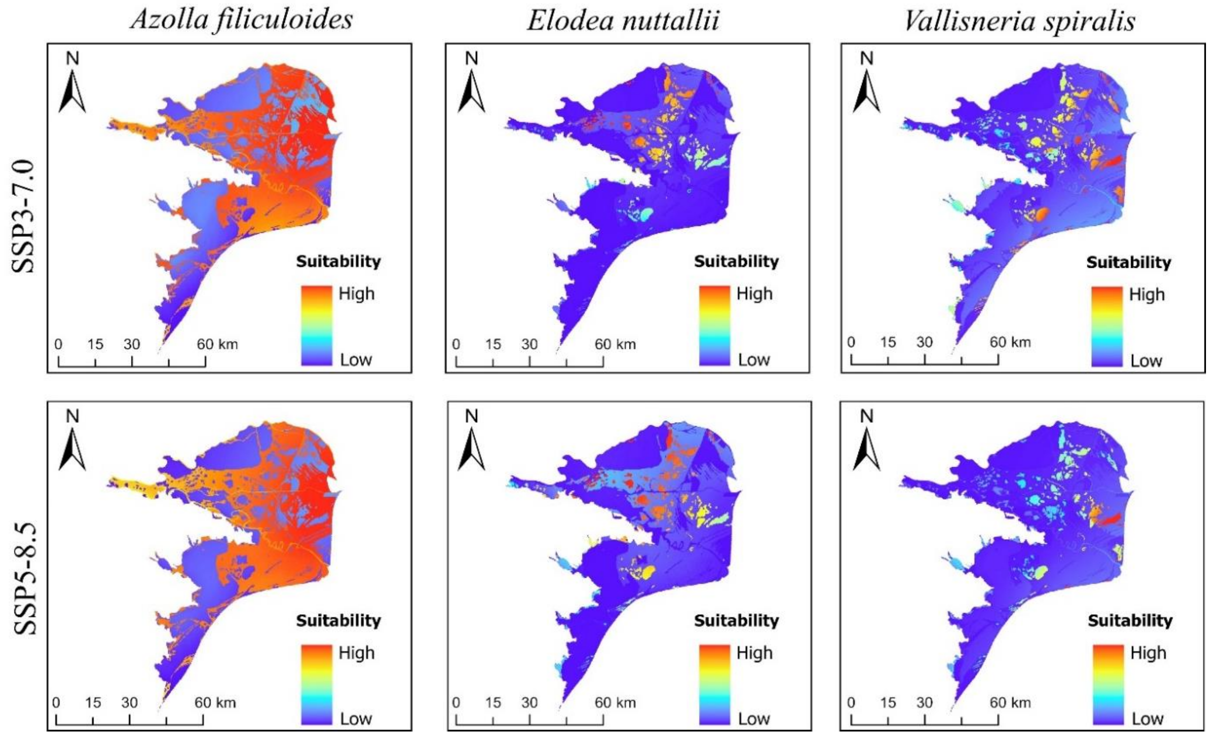

Figure 12. Future distribution of species in the Danube Delta Biosphere Reserve. Period 2071-2100

Changes in the distribution of the three target aquatic macrophytes

The results showed different changes in the potential distribution for the three species analysed (Figs. 13-15). For *A. filiculoides*, the distribution remains almost completely stable in the period 2040–2070, as the stable area is very large, about 2395.9 km², and losses are absent. More obvious changes occur in the period 2071–2100: in the SSP3-7.0 scenario, the gain of suitable habitat (478.1 km²) slightly exceeds the loss (424.1 km²), indicating a small net expansion. In contrast, in SSP5-8.5, the losses (276.2 km²) are higher than the gains (120.1 km²). For *E. nuttallii*, in the period 2040–2070, the losses are higher than the gains in both scenarios, indicating a reduction in the suitable area. In 2071–2100, the SSP3-7.0 scenario maintains the same trend of reduction, but in SSP5-8.5, a net expansion occurs, as the area gained (272.6 km²) clearly exceeds the area lost (126.5 km²). For *V. spiralis*, suitable habitat expands in 2040–2070 in both scenarios, as the gains are much greater than the losses. The same trend is maintained in 2071–2100 for SSP3-7.0, but not for SSP5-8.5, where habitat loss (196.8 km²) exceeds the gain (82.6 km²). Gain, loss and stable areas for each species, scenario and period are detailed in Supplementary Table S3.

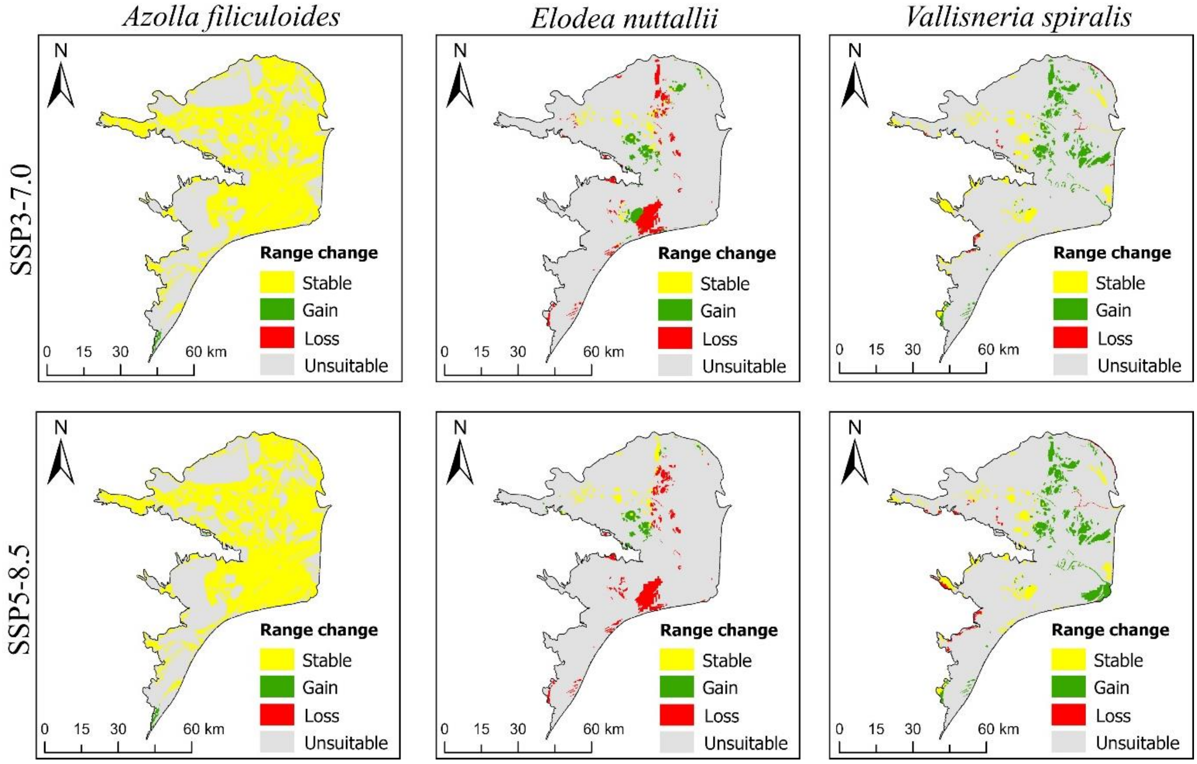

Figure 13. Map showing changes in species distribution for the period 2040-2070 under the SSP3-7.0 and SSP5-8.5 climate scenarios

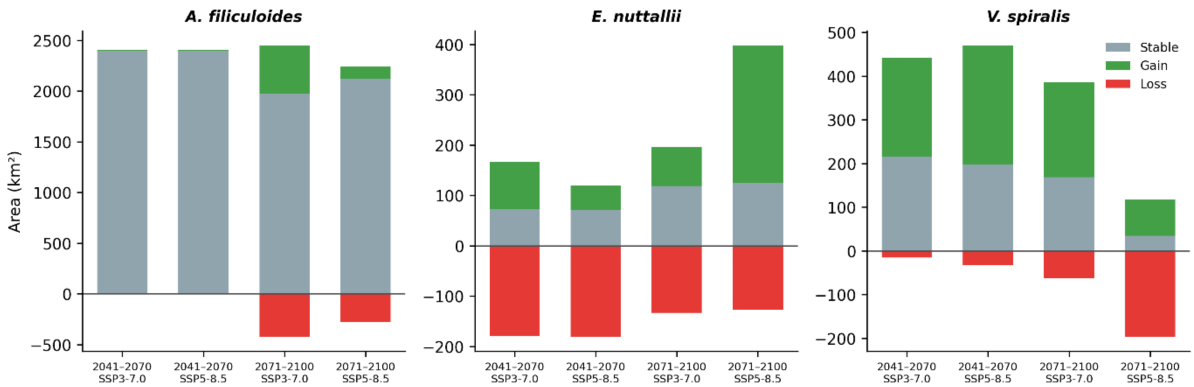

Figure 14. Spatial dynamics of suitable habitat (stable, gain and loss areas, km²) for *A. filiculoides*, *E. nuttallii* and *V. spiralis* under the future climate scenarios

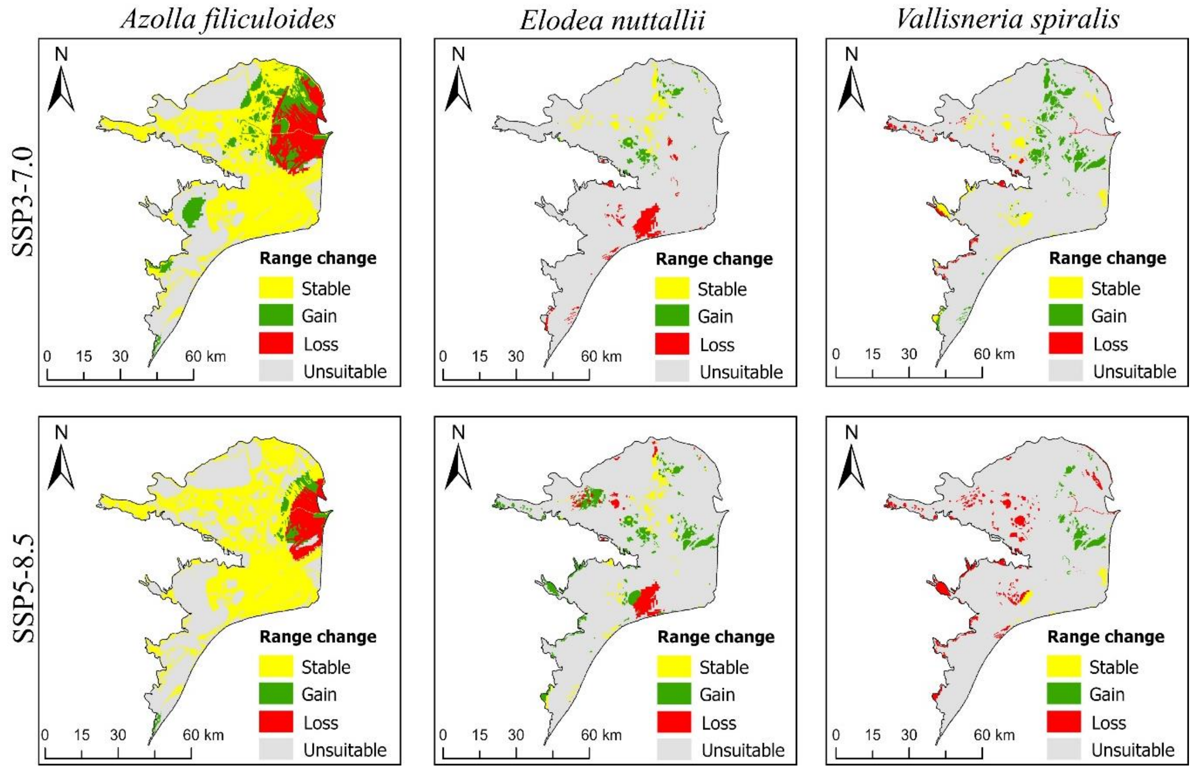

Figure 15. Map showing changes in species distribution for the period 2071-2100 under the SSP3-7.0 and SSP5-8.5 climate scenarios

Discussions

Spatial modelling of aquatic macrophytes in the context of climate change

One of the standard tools for assessing the risk of invasive species expansion is species distribution modelling (SDM), especially for aquatic macrophytes. In aquatic environments, absence data are often incomplete, and species occurrence is closely linked to climatic conditions and land use. Accordingly, approaches combining SDM methods such as MaxEnt with CMIP6 climate projections (SSP3-7.0 and SSP5-8.5) are useful for estimating future climatic suitability. However, model outputs should be interpreted as estimates of potential suitability rather than as direct estimates of realised occurrence, because environmentally suitable areas may remain unoccupied due to dispersal limitations or biotic interactions (Elith and Leathwick 2009).

For the Danube Delta, the favourable climatic conditions estimated by SDM must be interpreted in relation to the hydrological regime characteristic of the deltaic system. The correspondence between climatic favourability and the effective presence of the species can be facilitated or limited by the connectivity between lakes, channels and the main branches of the Danube. Reduced hydrological connectivity and weak hydrodynamics can therefore create source areas for invasive processes. Conversely, areas characterised by active water circulation can reduce the impact of climate warming on aquatic macrophytes.

Azolla filiculoides: expanding climate favourability

The results of our study indicated an expansion of favourable habitats for *A. filiculoides* in all climate scenarios analysed. This agrees with Rodríguez-Merino et al. (2019), who reported an increase in climatic favourability for this species in Europe using SDM, correlated with increasing temperature and stable water regime. However, Rodríguez-Merino et al. (2019) indicated that this expansion should not be interpreted as a uniform global increase in habitat suitability. This expansion reflects a spatial redistribution of suitable climatic areas, which may involve losses in some parts of the native range and gains in newly vulnerable regions, especially at higher latitudes. The role of land use (LULC) in our models matches the ecology of the species, where *A. filiculoides* prefers stagnant or poorly circulating water bodies, characteristic of anthropized or eutrophicated habitats. Also, *A. filiculoides* may occupy climatic conditions in the invaded range that are not fully equivalent to those in its native range. This suggests some degree of niche shift and ecological flexibility during the invasion process. These processes may be amplified by climate warming, by extending growing periods and intensifying vegetative reproduction (Pinero-Rodríguez et al. 2021). Furthermore, Rodríguez-Merino et al. (2019) showed that A. filiculoides could expand towards northern and eastern Europe under future climate scenarios, which is particularly relevant for transitional wetlands and floodplain habitats that may become increasingly susceptible to colonization.

The modelled potential expansion for *A. filiculoides* in the Danube Delta indicates a high ecological risk. This can be observed in lakes with reduced hydrodynamics, where the development of floating formations could affect water oxygenation and the structure of submerged communities. *Azolla filiculoides* forms dense surface mats that can contribute to light limitation, habitat simplification, and the decline of submerged macrophytes and associated aquatic communities, thereby amplifying ecosystem-level impacts in shallow freshwater habitats.

***Elodea nuttallii*: shrinkage and fragmentation of favourable habitats**

For *E. nuttallii*, SDM results indicated a reduction and fragmentation of suitable habitats under future climate scenarios in the Danube Delta. This echoes the findings of Steen et al. (2019), who identified a spatially heterogeneous distribution of climatic suitability for the species across the European Union, with distinct hot spots rather than a continuous suitable range. A recent global modelling study (Qi et al. 2025) suggests that *E. nuttallii* may expand its potential range to wider spatial scales under future climate scenarios. As such, the contraction observed here should be interpreted as a regional response rather than a contradiction to the global trend. The importance of precipitation and temperature predictors in published SDM studies parallels the strong contribution of BIO12 and temperature seasonality in our models. This may indicate that *E. nuttallii* is sensitive to hydroclimatic structure and seasonal thermal regimes.

Ecological studies (CIRCABC 2014; Bučar et al. 2024) show that *E. nuttallii* is associated with nutrient-enriched and low-flow or stagnant waters. Accordingly, future occurrence may remain restricted to areas that retain favourable local conditions, and the persistence of only limited favourable areas in our projections indicates a likely local survival in some lake sectors, but reduced regional connectivity and a more limited expansion potential in the medium and long term.

Vallisneria spiralis: relative stability under future climate scenarios

For *V. spiralis*, the models indicated an initial expansion of favourable habitats in the period 2040–2070, followed by a decline towards the end of the century, particularly under SSP5-8.5. This pattern fits previous observations of a broad ecological amplitude in the species (Rimac et al. 2021). The contribution of annual precipitation and temperature seasonality further reflects the species' dependence on the hydrological regime. Compared to *E. nuttallii*, *V. spiralis* exhibits a reduced vulnerability to climate warming scenarios. This explains the maintenance of extensive areas of favourable habitat in the modelled projections. Under conditions of moderate climate warming, our results also indicate that *V. spiralis* may remain an important component of submerged vegetation, especially in lakes with active hydrological circulation and fine substrate. Comparatively analysed, the analysed species (*A. filiculoides*, *E. nuttallii*, and *V. spiralis*) show separate ecological strategies in the context of climate change. *Azolla filiculoides* exhibits opportunistic behaviour, associated with a positive response to increasing temperatures and anthropized habitats, which explains the increase in favourable climatic conditions. *Elodea nuttallii* seems to be more sensitive to increasing climate variability and thermal extremes, even if it is effective as an invasive species in temperate conditions. In contrast, *V. spiralis* showed relative distributional stability across climate scenarios, which may support the maintenance of suitable habitats under moderate warming scenarios.

Implications and limitations of modelling

The data obtained have direct implications for defining monitoring and management priorities in the Danube Delta. The extension of favourable climatic conditions for *A. filiculoides* may indicate an increase in risks in lakes with reduced hydrodynamics, where early interventions may be important. For *E. nuttallii*, the maintenance of fragmented favourable habitats indicates the importance of focusing efforts on refuge areas. For *V. spiralis*, the tendency for the dominance of submerged vegetation makes it necessary to assess the impact on native communities, even without a pronounced expansion. Moreover, the models used indicate potentially favourable climatic conditions, without including physicochemical variables determined in situ.

Using only climatic variables may overestimate favourable conditions for submerged species, especially in eutrophicated or intensively managed ecosystems (Lind et al., 2022). However, our results align with other SDM studies that reported broadly stable model behaviour, which strengthens their value for identifying areas of high ecological risk and for guiding monitoring and adaptive management in the Danube Delta.

MaxEnt-based SDM models are subject to inherent uncertainties, mainly due to the low number of occurrence points for some species. Even so, the spatial patterns obtained agree with the literature, and the consistency of the results across climate scenarios supports a regional approach. SDM therefore provides a useful preliminary basis for identifying areas where monitoring should be prioritized.

Conclusions

The three aquatic species analysed differed clearly in their current climatic conditions, in the environmental predictors of their distribution and in their responses to future climate scenarios. Although the studied species differ in their biogeographical status, with *Azolla filiculoides* and *Elodea nuttallii* being alien invasive species and *Vallisneria spiralis* representing a non-native range-expanding macrophyte, the results indicated distinct distribution patterns and different degrees of sensitivity to climate change. *Azolla filiculoides* presented the highest expansion capacity under future climate scenarios. The expansion of favourable habitats correlated with the dominant influence of land use and the secondary role of climate variables. This indicates that the species could be favoured by climate warming and the maintenance or amplification of anthropogenic pressures. In the Danube Delta, these projections suggest an increase in ecological risk, especially in lakes characterised by reduced hydrodynamics, where *A. filiculoides* can quickly develop high densities and modify the functioning of aquatic ecosystems.

In contrast, *E. nuttallii* experienced a reduction and fragmentation of suitable habitats under most climate scenarios analysed. The strong contribution of annual precipitation and temperature seasonality indicated increased vulnerability to climate variability and thermal extremes. Although models indicate a partial improvement in suitable climate conditions in the period 2071–2100 under SSP5-8.5, potential distribution remains limited, suggesting that *E. nuttallii* may be more climatically constrained under future conditions.

Compared with *E. nuttallii*, *V. spiralis* showed greater stability across the analysed climate scenarios. Despite an initial expansion of suitable habitats in the period 2040–2070 and a subsequent decline towards the end of the century, particularly under SSP5-8.5, the species retained relatively extensive favourable areas overall, suggesting that it may remain an important component of aquatic plant communities under moderate climate change.

Cluster analysis revealed that all three species analysed are mainly associated with their own vegetation types, but can also occur in other associations, where their participation is generally reduced.

The DCA ordination confirmed the existence of floristic gradients. The gradient length values on the first axis were 3.2 SD for *A. filiculoides*, 3.7 SD for *E. nuttallii* and 3.8 SD for *V. spiralis*, indicating a moderate floristic variation in the case of *A. filiculoides* and stronger in *E. nuttallii* and *V. spiralis*.

Hydromorphological conditions in the studied lakes varied considerably and are likely to influence their ecological functioning. Differences in connectivity, water exchange and turbidity therefore appear important in shaping habitat suitability for macrophytes.

Author contributions

Simona Dumitrița Chirilă: Conceptualization, Methodology, Investigation, Software, Data curation, Writing-Original draft preparation;

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Nicu Alexandru Gîlea: Conceptualization, Methodology, Software, Data curation, Writing-Original draft preparation, Supervision;

Nikolay Velev: Methodology, Software, Data curation, Writing—review and editing, Supervision;
Florentina Tudose: Visualization, Investigation, Writing—review and editing, Supervision;
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