

Environmental and community constraints on *Elodea nuttallii*: implications for early season control in an urban stretch of the Po River (NW Italy)

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Abstract

Invasive aquatic macrophytes represent an increasing concern for freshwater ecosystems, where they alter biodiversity, ecosystem functioning, and water-related services. Among them, the submerged species *Elodea nuttallii* has rapidly expanded across many European waterbodies, yet its ecology in regulated lowland rivers remains insufficiently explored, particularly compared to that in artificial canals, ponds, and lakes. This study investigates the environmental, hydrological, and biotic factors shaping the occurrence and distribution of *E. nuttallii* in an urban river system. Field surveys conducted in 2025 documented macrophyte assemblages and habitat conditions in the Po River, the longest Italian river, flowing through the city of Turin. A total of 150 presence-absence points for *E. nuttallii* were recorded, spaced at least 200 meters apart, along the urban stretch of the river, collecting information on temperature, dissolved oxygen, pH, conductivity, as well as the presence of other macrophytes and the extent of plant populations. The results show that most vegetated patches are dominated by *E. nuttallii*, which is associated with depositional areas characterised by soft sediments and significantly related to the presence of *Myriophyllum spicatum*, as demonstrated by Phi correlation analysis. Although interspecific competition appears to limit *E. nuttallii*'s relative abundance during the seasonal macrophyte community peak, when its mean relative cover drops from 89.2% to 60%, its extended vegetative season likely contributes to its persistence. Moreover, substrate type emerged as the primary abiotic factor shaping spatial distribution in a regulated lowland river, with sand and silt providing optimal conditions for its establishment. We further highlight the need for early season and site-specific management interventions. Given the ecological and recreational significance of the Po River and its role as a dispersal corridor, understanding the invasion dynamics of *E. nuttallii* is critical for informing management strategies, particularly in light of its designation as an EU-priority alien invasive species.

Key words: Invasive alien species; waterweed management; biotic interactions; physical and chemical variables; lotic regulated ecosystem.

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Introduction

The spread of invasive alien species (IAS) is a major threat to freshwater ecosystems worldwide, driving biodiversity loss, habitat alteration, and disruption of ecosystem structure and functioning (IPBES, 2023; IUCN, 2023). Aquatic environments are particularly vulnerable to plant invasions, which are often triggered by human introduction and facilitated by hydrological connectivity, thereby promoting the rapid dispersal of propagules (Bolpagni, 2021). Once established, alien macrophytes can alter sediment dynamics, nutrient cycling, and light availability, often displacing native communities (Bouma *et al.*, 2010; Emery-Butcher *et al.*, 2020; Tasker *et al.*, 2022).

In this context, the genus *Elodea* (Hydrocharitaceae) comprises some of the most widespread invasive submerged macrophytes in temperate regions. *Elodea nuttallii* (Planch.) H. St. John has shown remarkable invasive success across Europe, frequently replacing or co-occurring with the earlier established *Elodea canadensis* Michx. (Steen *et al.*, 2019; Buldrini *et al.*, 2023). *Elodea nuttallii* thrives in

a wide range of lentic and low-flow environments, exhibiting high phenotypic plasticity and tolerance to light, nutrient, and hydrodynamic conditions (Atapaththu and Asaeda, 2015; Szabó *et al.*, 2019). Its ability to form dense monospecific stands allows it to alter natural ecosystems and interfere with ecosystem services such as navigation, recreation, and water abstraction (Kelly *et al.*, 2015; Millane *et al.*, 2016). Due to its impacts, *E. nuttallii* is listed as an IAS of Union Concern under EU Regulation 1143/2014, requiring prevention, early detection, control and eradication measures. Previous studies show that *E. nuttallii* distribution and spread are regulated by abiotic gradients (nutrients, hydrodynamics), biotic interactions with other invasive species and native flora, and physiological plasticity that enables survival across diverse freshwater habitats, e.g., lakes and canals, as well as under laboratory conditions (Atapaththu and Asaeda, 2015; Crane *et al.*, 2022; Bučar *et al.*, 2024). Despite growing evidence that *E. nuttallii* thrives in regulated and artificial systems, where human pressures amplify ecological dynamics, and local communities directly perceive the impacts of invasive species, knowledge remains limited of long-term distribu-

tion dynamics in urban river systems (Grudnik and Germ, 2013).

In Italy, *E. nuttallii* has been recorded since the late 20th century (Desfayes, 1995; Selvaggi and Dellavedova, 2016) and has since spread across northern and central regions, especially in artificial canals, streams, and lakes (Bolpagni *et al.*, 2017). Buldrini *et al.* (2023) identified the Po River basin as a priority area for studying the invasion dynamics of *Elodea* species, due to its dual role as both a natural barrier and a dispersal corridor, facilitated by a dense network of artificial canals, connecting northern and central Italy. In this context, studies focusing on *E. nuttallii* populations within the Po River, particularly in its upper reaches, are crucial for understanding the species' ecological performance, as well as for supporting effective monitoring and management strategies aimed at limiting its spread and ecological impact, as required by the EU legislation.

The city of Turin (North-West Italy) is the biggest city crossed by the longest Italian river, the Po River. This river provides important ecosystem services, both through direct use for water-based activities (e.g., fishing, rowing) and through its high landscape value, supporting leisure and recreational opportunities in the surrounding riverside parks and walking areas. In 2022, this river stretch experienced a major invasion event by *E. nuttallii*, which thrived under conditions of extremely low water flow, stable sunny weather, and high nutrient concentrations (ENEA, 2022; Aree pro-

tette Po Piemontese, 2023). Management interventions, primarily manual harvesting, were implemented at the peak of the season (Regione Piemonte, 2023), reducing its biomass, although the species re-established in persistent patches over the following three years.

This study investigates the ecological factors influencing *E. nuttallii*'s occurrence and distribution in an urban section of the Po River. The specific objectives were to: i) assess its distribution during the growing season; ii) identify the environmental, hydrological, and biotic factors driving its spatial patterns; and iii) provide management recommendations tailored to the regulated lotic system. Overall, this study offers new insights into the invasion dynamics of *E. nuttallii* within an urban river ecosystem subject to substantial human pressures and contributes to improving management strategies for this EU-listed IAS.

METHODS

Study area

The study took place in an urban stretch of the Po River in Turin (NW Italy; Fig. 1). Turin is the first major city downstream of the river's source, located approximately 90 km away. Here, the

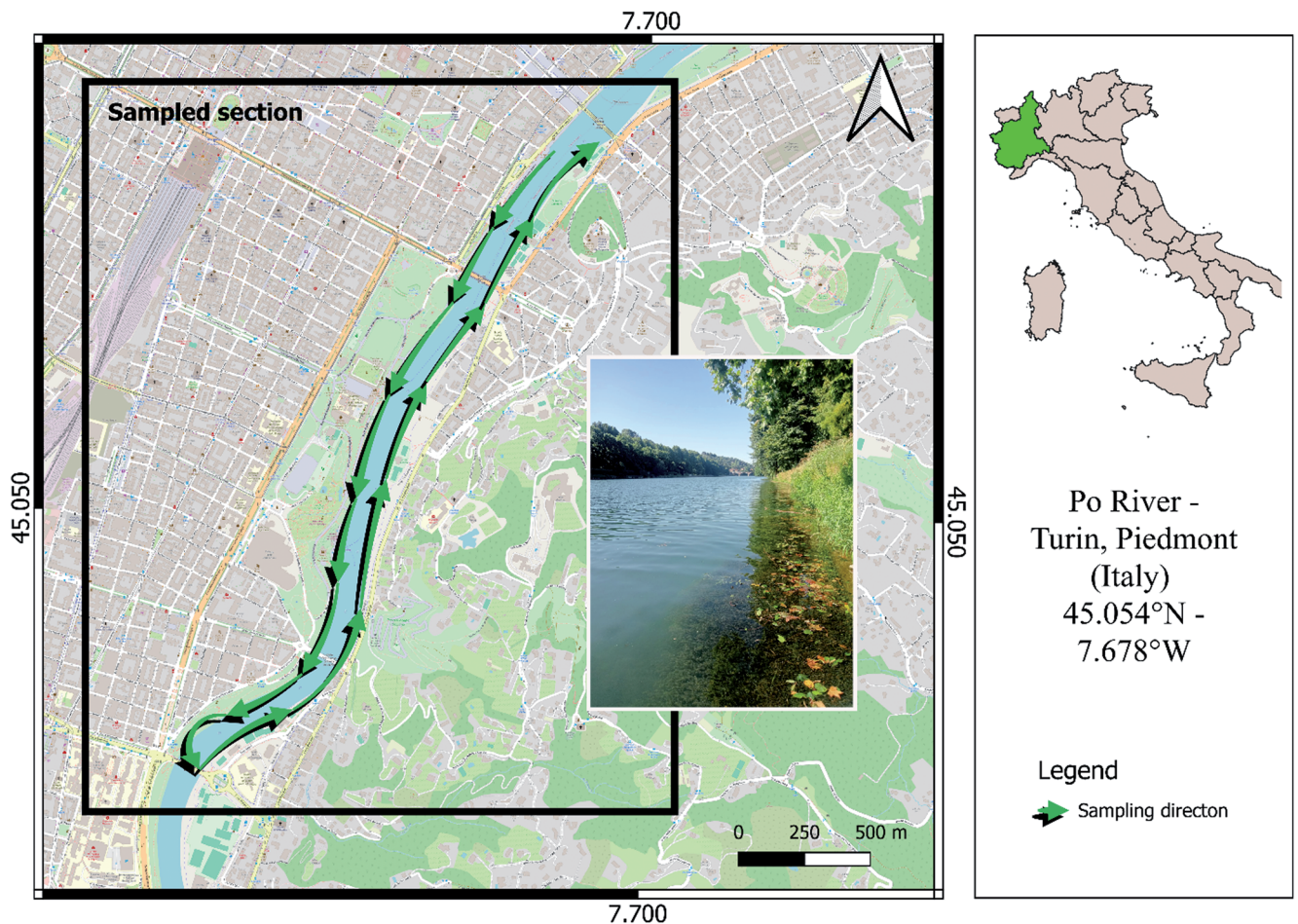


Fig. 1. Map of the sampling area and surveyed section of the Po River. (WGS84 - UTM Zone 32N– EPSG:32632; on QGIS 3.40.13 <http://tile.openstreetmap.org/{z}/{x}/{y}.png>).

river has the characteristics of a lowland river, approximately 100 m wide and up to 5 m deep. Riverbanks are largely artificial, and the flow is regulated by a downstream weir to maintain sufficient water depth for river navigation and to manage flood events. *Elodea nuttallii* was first documented in this area in 2022, during a major invasion event (Regione Piemonte, 2024). Possible introduction pathways include the discharge of water from aquariums, accidental transport, use of machinery for mowing aquatic vegetation, and transport by water birds.

Field surveys

Five surveys were carried out from June to September 2025, covering the entire vegetative season of *E. nuttallii*. Before June, intense rainfall and flood events prevented the establishment of a stable macrophyte community (see ARPA Piemonte (2024) hydrological portal for more details). A 3 km stretch of the river was surveyed by motorboat once a month (twice in August) at 30 random sites, each at least 200 metres apart and equally divided between locations with and without *E. nuttallii* (Fig. 1) At each site, presence/absence of *E. nuttallii* and co-occurring macrophytes, patch size, and proportional cover of *E. nuttallii* within each patch were recorded, along with substrate type and water depth (ISPRA, 2007). Macrophyte patches exhibited well-defined boundaries, permitting stand-level sampling and individual surface area measurements. Macrophyte identification and nomenclature followed the Portal to the Flora of Italy (<https://dryades.units.it/floritaly/>). The type of substrate was classified as artificial, depositional (sand and silt), transitional (gravel), or transport (cobble). Similarly, we classified the type of bank as natural, semi-natural, or artificial. Water temperature, dissolved oxygen (DO; % and mg L⁻¹), pH, and electrical conductivity (EC; $\mu\text{S cm}^{-1}$) were measured using a multiparametric probe (Manta+ 20, Solinst Eureka) at all sites. Two water samples were collected at the beginning and at the end of the river stretch on each sampling occasion to determine total suspended solids (TSS) (IRSA, 2004) and nutrient concentrations (N-NO₃⁻ and P-PO₄⁻; assay kits LCK 339 and LCK 349 - Hach, The Netherlands) in the laboratory. Further information on the sampling sites and protocol can be found in *Supplementary Material 1 (SM1)*.

The solar exposure of the banks was estimated retrospectively using the SunCalc web application (SunCalc, 2025). To estimate flow velocity, the channel width of each river section was first measured using standard OpenStreetMap (OSM; Fig. 1) in QGIS software (version 3.40.13, <https://qgis.org/download/>). The depth of the water in the middle of the Po River was obtained from the ARPA Piemonte (2024) hydrological portal, and these two parameters were used to calculate the cross-sectional area. Flow discharge for the corresponding sites was retrieved from ARPA Piemonte. Flow velocity was then computed for each sampling date as the ratio between discharge and cross-sectional area:

$$v = Q/A \quad (\text{Eq. 1})$$

v = flow velocity; Q = flow discharge; A = cross section area

Data analysis

Substrate preference was assessed by comparing the proportion of *E. nuttallii* occurrences across substrate categories (artificial, depositional, transport, and transitional). Patch extent of *E. nuttallii* was estimated using recorded size classes (e.g., < 3×3 m, > 3×3 m, > 6×6 m, > 10×10 m). For each patch, the minimum and maximum

area corresponding to the size class were calculated (0-9 m², 9-36 m², 36-100 m², > 100 m²), and the mean of these two values was used to estimate the average patch area. Data analysis and graphics were produced in R (R Core Team, 2022). To assess the influence of the measured environmental variables on the presence and absence of *E. nuttallii*, a Generalized Additive Model (GAM) with a binomial family and logit link was applied. Prior to model fitting, potential collinearity among environmental variables was evaluated using pairwise correlations and variance inflation factors (VIF), and highly collinear variables were removed (i.e., saturation percentage of dissolved oxygen). The remaining environmental parameters were included as smooth covariates in the model. Categories with a low number of observations were excluded to avoid biasing the results. This approach enabled us to highlight the limitations imposed by the environmental conditions at the site. Conversely, to assess the influence of environmental parameters on the extent of the target species, a Principal Component Analysis (PCA) was first conducted on the measured environmental variables. This approach allowed us to reduce collinearity and identify the key environmental factors shaping the patches of *E. nuttallii*. Subsequently, a GAM was performed between the scores of the first two principal components (PC1 and PC2) and the relative percentage cover of *E. nuttallii*. Lastly, to assess the correlation between the observed species, a Phi coefficient analysis was conducted, which is suitable for binary data (0 and 1). A schematic workflow of data analysis is reported in *Fig. S1*.

RESULTS

Overall water quality reflected a typical lowland river, sampled in a phase of moderate flow and low turbidity. There were no signs of serious eutrophication or anoxia, but moderate trophic enrichment was observed (2.40-2.61 mg N-NO₃⁻ L⁻¹). Moreover, peaks of pH >9 and DO% >90 suggest intense photosynthetic activity, typical of a slightly eutrophic system. In the area, fine substrate prevailed and shading from the terrestrial canopy was absent or partial. The weather and environmental conditions remained largely stable throughout the study period, with fluctuations mainly in conductivity and temperature, and particularly toward the end of the study period (*Tab. S1*). *Elodea nuttallii* mostly occurred within 10 m of the banks, at depths between 0.5 and 3 m. Larger stands were found along the left bank, where artificial sections are interspersed with natural and semi-natural sections. This bank is exposed to the southeast and is characterised by higher mean water temperatures in June and July, compared to the right bank. The main environmental parameters measured showed no evident difference between sites where *E. nuttallii* was present or absent, as indicated by the GAM (Fig. 2a). However, the PCA revealed that PC2 was strongly influenced by temperature (*Tab. 1*) and significantly positively associated with percentage cover of *E. nuttallii* ($p=0.005$; *Tab. 2*). Electrical conductivity at sites with *E. nuttallii* patches showed a narrower range compared to sites where the species was absent, while dissolved oxygen and pH were similarly distributed between the two groups. As indicated by the GAM analysis (*Tab. 3*), the relationship between *E. nuttallii* presence and substrate type, especially sand-silt substrate, was significant ($p=0.019$). The preference of *E. nuttallii* for different sediment types was further graphically analysed: sand accounted for ~38% of all sites but 47% of *E. nuttallii* occurrences, whereas gravel (27.5% of all sites) accounted for 23.5% of occurrences, and cobble presented fewer occurrences (Fig. 2b).

Aquatic vegetation occurred mainly in extensive patches concentrated along the right bank of the river, which is predominantly artificial and exposed to the northwest (*Supplementary Material 1*). Vegetation cover increased from approximately 10 m² in June to 100 m² by the end of August, then decreased in September (Fig. 3). The absolute cover of *E. nuttallii* showed a similar temporal pattern, reaching its maximum at the end of August. In contrast, the mean

relative cover of *E. nuttallii* (relative to the whole macrophyte cover) decreased over the season, from 89.2% in June to 60% at the end of August, indicating an increasing contribution of other macrophyte species during peak biomass. Overall, *E. nuttallii* was the dominant macrophyte in most patches, accounting for approximately 70% of the total vegetation cover, and reaching 100% cover in approximately 14% of patches. Nevertheless, Fig. 3 highlights a mid-summer

Tab. 1. Loadings of environmental variables on the first four principal components (PCs) from the PCA. Values in parentheses indicate the proportion of variance explained by each component. Loadings with higher absolute values indicate stronger contributions of the variable to the respective PC.

	PC1 (40%)	PC2 (32%)	PC3 (19%)	PC4 (6%)
Conductivity	-0.72	0.14	0.22	0.64
Dissolved oxygen	-0.40	0.04	-0.90	-0.15
Temperature	-0.22	0.80	0.21	-0.56
pH	0.52	0.57	-0.30	0.59

Tab. 2. Summary table of the GAM analysis of the ordinal extent class of *Elodea nuttallii* as a function of PC1 and PC2 of the environmental PCA. The ordinal response was modelled using quasibinomial(link = “log”).

	Estimate	Std. Error	t-value	Pr(> t)
PC1	0.207	0.151	1.369	0.175
PC2	0.505	0.176	2.873	0.005**

**Statistically significant at $p < 0.05$.

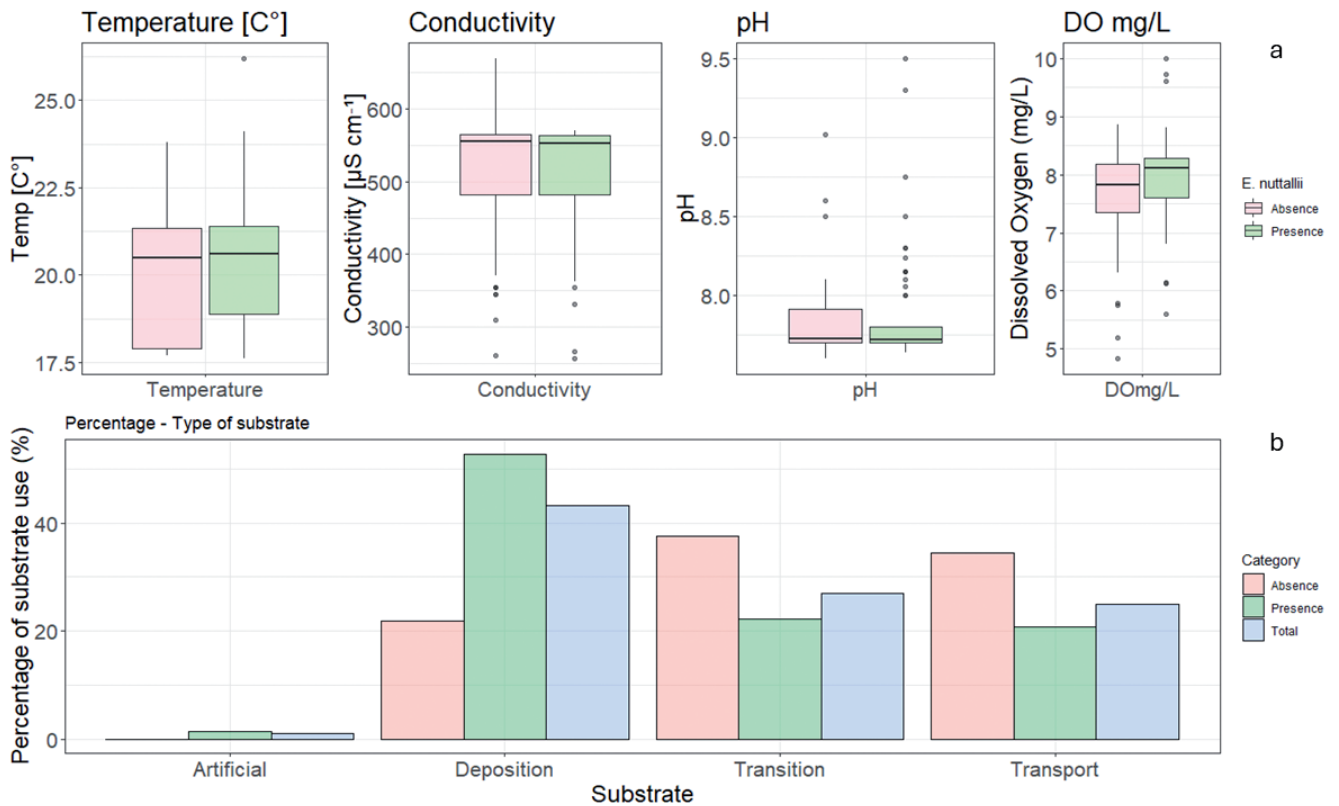


Fig. 2. Abiotic parameters in relation to the presence or absence of *Elodea nuttallii*. a) Boxplots summarising the physical parameters of water where *E. nuttallii* is present and where it is absent. b) Occurrence of *E. nuttallii* based on the type of substrate.

Tab. 3. Results of the GAM analysis between presence/absence of *Elodea nuttalli* and type of substrate, type of bank and environmental parameters. Binomial family with logit link; smooth terms included without modification of complexity (AIC values checked). Other macrophyte species were included in the GAM but are not displayed, since their results are indicated in the heatmap of the Phi correlation analysis.

	Estimate	Std. Error	Z value	Pr (> z)
Gravel	0.447	1.500	0.298	0.765
Sand with pebbles	1.601	1.495	1.071	0.284
Sandy-silt	3.697	1.581	2.338	0.019**
Semi-natural bank	1.328	1.244	1.077	0.286
	Eff	Ref. df	Chi.sq	p-value
Temperature	4.729	5.781	7.818	0.287
Conductivity	1.000	1.000	0.379	0.518
pH	2.647	3.243	2.306	0.699
Dissolved oxygen (mg L ⁻¹)	1.000	1.000	2.765	0.065

**Statistically significant at $p < 0.05$.

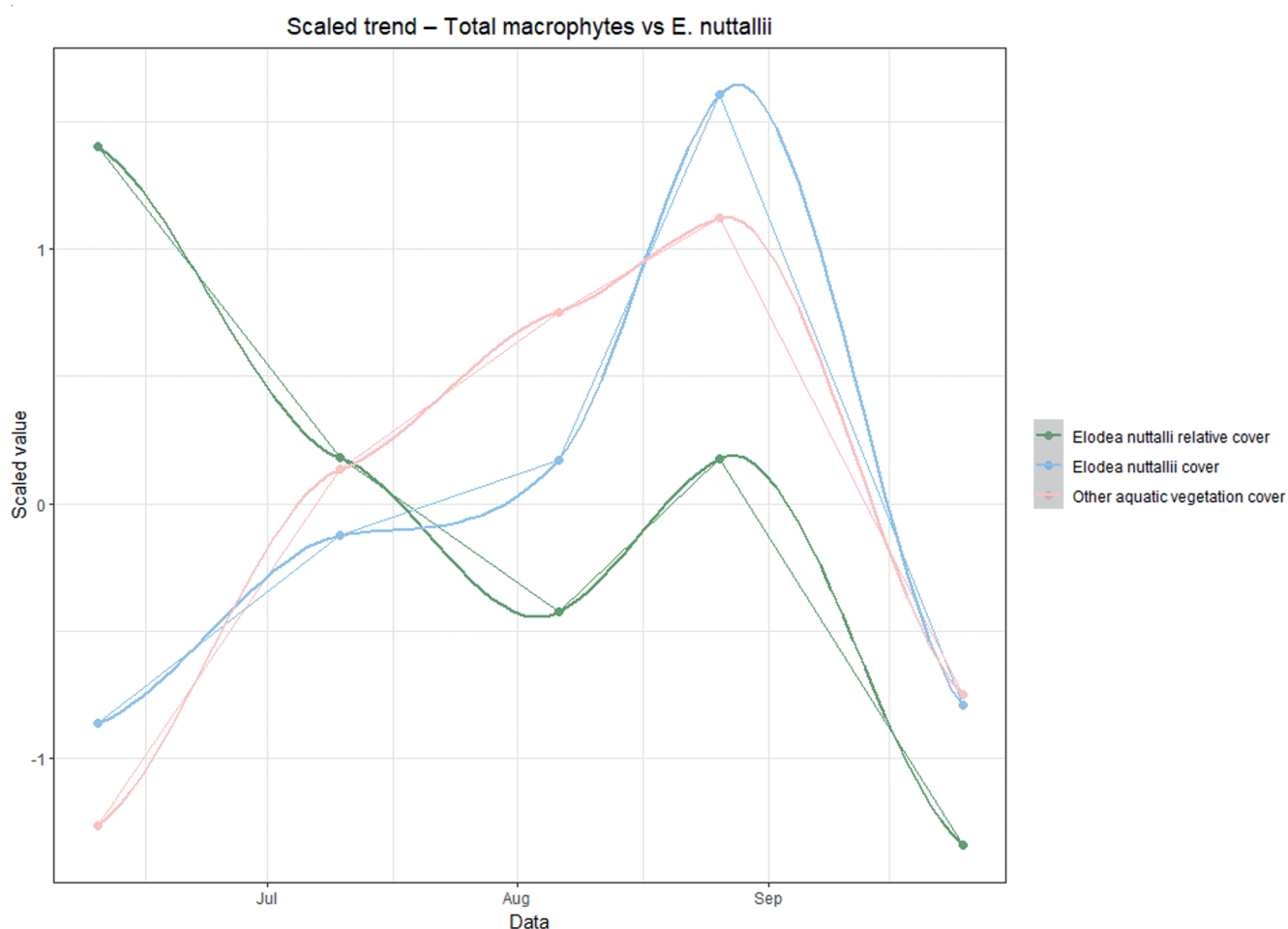


Fig. 3. Temporal trend of aquatic vegetation. The figure illustrates changes over time in *Elodea nuttallii* relative (%) and absolute (m²) cover, alongside the absolute cover (m²) of other macrophytes. Variables were scaled to enable comparison, and smoothed trends (geom_smooth, ggplot2) were used to emphasize overall temporal patterns.

decline in its relative dominance, despite sustained absolute cover. This pattern suggests that *E. nuttallii* has a longer period of high abundance compared to other macrophytes, being already well established and dominant early in the season, when other species are still present at low abundance, and maintaining high cover later into the summer.

In patches with multiple species, *E. nuttallii* co-occurred with *Stuckenia pectinata* (L.) Börner, *Potamogeton crispus* L., *Potamogeton natans* L., *Callitriche stagnalis* Scop., and *Lemna* spp., in order of abundance. Additionally, no significant association between *E. nuttallii* and *Myriophyllum spicatum* was observed based on Phi correlation analysis (including only co-occurring macrophyte species; Fig. S2). However, *M. spicatum* was present in approximately 70% of the cases where *E. nuttallii* occurred.

DISCUSSION

Hydrological and environmental drivers

Our study confirms the extensive presence of *E. nuttallii* in the examined stretch. We observed no clear relationships with DO, pH, or water depth, unlike previous studies that identified strong associations between *E. nuttallii* distribution and abiotic parameters, based on multi-year field surveys or controlled laboratory experiments (Grudnik and Germ, 2013; Atapaththu and Asaeda, 2015; Bučar *et al.*, 2024). However, PCA revealed that temperature has a strong influence, indicating that it is an important component of the environmental gradient associated with species extent. Nevertheless, this result is not entirely consistent with previous studies (Grudnik *et al.*, 2014; Qui *et al.*, 2025). These contrasting findings support evidence that the species exhibits broad ecological tolerance and high phenotypic plasticity (Kolada *et al.*, 2022). Even water depth was not a limiting factor for *E. nuttallii*, which was recorded here at depths ranging from 0.5 to 3 m, while previous studies reported it in narrower depth ranges (0.3–1 m; Bučar *et al.*, 2024) or over 1 m (Grudnik and Germ, 2013). In the present study, *E. nuttallii* was mostly present at conductivity values ranging from 256 to 570 $\mu\text{S cm}^{-1}$, while it was absent at higher conductivity levels. However, this pattern is not consistent across all sites. Specifically, *E. nuttallii* was not present in some locations within the same conductivity range. According to literature data, the species can tolerate and even thrive at conductivities exceeding 700 $\mu\text{S cm}^{-1}$ (Bučar *et al.*, 2024).

In contrast, substrate type emerged as a determinant of the presence of *E. nuttallii*, as suggested by the GAM and confirmed by the barplot. Soft sediments such as silt, sand, and fine gravel promote anchorage and nutrient uptake by macrophytes (Kuriata-Potasznik *et al.*, 2018; Gao and Hu, 2023). These substrates typically occur in depositional zones, where reduced flow energy allows fine sediments and organic matter to accumulate. Such environments favour macrophyte establishment and can create positive feedback loops in which dense stands further enhance sedimentation and habitat stability (Grudnik *et al.*, 2014; Buccheri *et al.*, 2019; Emery-Butcher *et al.*, 2020). Accordingly, along the Oglio River, Bolpagni *et al.* (2017) observed that the dammed stretches, characterised by fine sediments, are widely colonised by rooted macrophytes typical of slow-moving/lentic conditions (e.g. *Vallisneria spiralis* L., *Potamogeton* spp., and *M. spicatum*), which are characteristic plants of lacustrine systems rather than rivers.

Although *E. nuttallii* was found in depositional zones where

current velocity is reduced, all the stands were nonetheless exposed directly to the main river channel. This stretch of the Po River lacks secondary channels or refugia that typically protect submerged vegetation from flow stress. Under such conditions, *E. nuttallii* appears capable of maintaining growth and structural integrity even under lotic conditions. Nonetheless, flow velocities estimated during the vegetative period were relatively low (0.07–0.27 m s^{-1}), reflecting summer low-flow conditions. Notably, these values are substantially higher than the thresholds at which stress responses have been reported for *E. nuttallii* in the literature. Atapaththu and Asaeda (2015), for example, observed that flow velocities as low as 0.02–0.03 m s^{-1} can induce marked morphological and physiological stress responses in *E. nuttallii* (e.g., reduced shoot elongation, increased radial expansion, and altered cellulose, lignin, and chlorophyll content). These adaptive traits are interpreted as mechanisms to reduce drag and mechanical damage, enabling the species to persist in mildly turbulent environments. In contrast, in our study *E. nuttallii* was able to maintain growth and structural integrity at considerably higher velocities, suggesting a greater tolerance to moderate current stress than previously documented. This tolerance may enable the species to persist even in mildly turbulent environments, supporting its ability to colonize open-channel habitats such as those of the Po River, where summer hydrodynamic conditions are not extreme but still impose mechanical constraints on macrophyte establishment.

Overall, while *E. nuttallii* tolerates a wide range of environmental conditions, our data indicate that substrate type represents the primary determinant of its spatial distribution in lotic habitats at the local scale.

Interspecific competition

The relative homogeneity of water parameters across sites and the observed mid-season decline in *E. nuttallii* cover suggest that competition with other macrophytes can be a major factor shaping its distribution pattern. In the studied stretch of the Po River, *E. nuttallii* is the first macrophyte to establish extensively in spring, colonizing suitable substrates before other species begin their vegetative development. This early establishment is likely linked to its low temperature requirement for active growth, ranging between 8.2 and 12.0°C (Kunii, 1981), and it is supported by previous research in other European catchments (Wang *et al.*, 2019; Bučar *et al.*, 2024). This phenological advantage enables rapid colonization of suitable substrates before the emergence of other species. However, as temperature rises, co-occurring macrophytes, and particularly *M. spicatum*, which initiates growth above 15°C (Xiao *et al.*, 2010; Arts *et al.*, 2022), become more competitive. This leads to a reduction in *E. nuttallii* dominance during the peak of the growing season, although it remains abundant (above 50%) in most stands. Towards late summer, when many other species begin to senesce, *E. nuttallii* resumes growth, extending its vegetative period beyond that of native species. This pattern of early establishment, mid-season competitive limitation, and late-season resurgence reflects a temporal niche differentiation that promotes long-term persistence and dominance of *E. nuttallii* in mixed macrophyte assemblages. Such dynamics underline the importance of biotic interactions and seasonal timing in understanding and managing the spread of this invasive aquatic plant.

The specific mechanisms of competition remain uncertain. The reduction of invader success due to functional similarities with native species has been well documented in the scientific literature (Petruzzella *et al.*, 2018). In this study, *E. nuttallii* co-

occurred with other rooted submerged macrophytes exhibiting overlapping ecological niches and similar resource-use strategies. *Myriophyllum spicatum*, which co-occurred with *E. nuttallii* in ~70% of the stands, is known to produce allelochemicals that can inhibit the growth and photosynthetic performance of phytoplankton and herbivores (Gross *et al.*, 2012; Jeong *et al.*, 2021), but no allelopathic effects on plants are recorded in the literature. On the other hand, the association between the two species suggests that their coexistence may reflect an ecologically relevant relationship: *E. nuttallii* may tolerate competitive or inhibitory effects exerted by *M. spicatum*, and their frequent co-occurrence indicates that additional ecological factors may promote or facilitate their association. Further experimental work would be needed to disentangle the relative importance of allelopathy, functional overlap, and other biotic factors in shaping the distribution patterns of *E. nuttallii* within regulated lowland river ecosystems.

Management strategies and suggestions

Preventing the introduction and spread of *E. nuttallii* is a legal requirement across the EU, given its listing as an IAS of Union Concern (Regulation EU 1143/2014 and subsequent Commission Implementing Regulations). In Turin, a major invasion event occurred in 2022, when *E. nuttallii* rapidly outcompeted native macrophytes and occupied extensive areas of the Po River. The proliferation was likely favoured by reduced hydrological flow and stable sunny weather and elevated nutrient concentrations, which created suitable conditions for its establishment and expansion. To limit the infestation, a large-scale manual removal was carried out at the peak of the growing season, leading to substantial operational costs, high labour demand, and a considerable volume of biomass requiring disposal. Our findings underscore the importance of targeted, seasonally informed management, for which we propose the following measures:

- A. Early season removal.** This approach offers several advantages:
1. Selective removal: *E. nuttallii* accounted for ~90% of vegetation cover in June, allowing effective targeting with minimal disturbance to native plants;
 2. Lower biomass volume: early season harvesting reduces handling and disposal costs relative to peak biomass removal;
 3. Reduced regrowth: harvesting during the initial regeneration phase can substantially limit total seasonal biomass and regrowth capacity of *E. nuttallii* (Di Nino *et al.*, 2005);
 4. Cost efficiency: bioeconomic analyses (Marbuah *et al.*, 2019) demonstrate that early intervention minimizes management costs and ecological damages associated with invasive aquatic plants.
- B. Prioritization of removal areas.** Management efforts should focus on the areas experiencing high depositional processes, where *E. nuttallii* typically establishes, as well as on banks exposed to strong afternoon sunlight (Fig. S3).

CONCLUSIONS

This study characterizes the distribution and seasonal dynamics of *E. nuttallii* in a regulated urban stretch of the Po River. While it provides detailed insights at a local scale, it does not capture basin-wide invasion dynamics. Furthermore, the study was conducted over a single vegetative season, limiting its long-

term generalization, particularly given the potential climate dependence of *E. nuttallii* abundance and phenology. Despite these limitations, the results are robust for the year studied. Although *E. nuttallii* is the dominant species across much of the area, monospecific stands are less frequent than mixed assemblages with native macrophytes. Its temporal pattern -early colonization, mid-season limitation by competitors, and late-season recovery- suggests competitive interactions among macrophytes and a comparatively long vegetative season. Indeed, in the target site the species requires lower temperature for active growth compared to native macrophytes, yet it becomes limited by interspecific competition during the seasonal peak, highlighting the combined role of abiotic and biotic factors. On the other hand, substrate type emerged as the primary abiotic factor shaping spatial distribution, with sand and silt providing optimal conditions for its establishment. Water physicochemical parameters showed very limited influence, confirming the broad tolerance and adaptability of this IAS. Based on these findings, effective management strategies should focus on mechanical control early in the growing season, prioritizing depositional areas along the left riverbank to prevent large-scale proliferation and reduce intervention costs such as those incurred during the 2022 invasion event. By integrating ecological insight with practical management considerations, this study contributes to improving invasive macrophytes control within urban river restoration frameworks. In this regard, river management cannot ignore the ecological preferences of invasive macrophytes, given that the exploitation of water resources (such as river damming) may encourage their spread and affirmation. Future research should incorporate multi-year monitoring and expanded spatial coverage to better capture the responses of *E. nuttallii* to a wide range of environmental and climatic conditions and to more clearly identify the main drivers of its invasion dynamics. In addition, interactions with native macrophytes should be analysed in greater detail.

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Online supplementary material:

SM1 - Data collected during the five field surveys and protocols.

Fig. S1. Workflow of the statistical analyses for the presence/absence and coverage data of *Elodea nuttallii*.

Fig. S2. Graphical representation of the heatmap of the Phi correlation between macrophyte species including *Elodea nuttallii*.

Fig. S3. Graphical representation of the heatmap showing the priority areas for the management of *Elodea nuttallii*.

Tab. S1. Summary table of mean values for each sampling date.

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