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**BIOTIC INTERACTIONS BETWEEN SUBMERGED
AND EMERGENT AQUATIC MACROPHYTES**

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1. BACKGROUND AND OBJECTIVES

1.1 Interactions Among Aquatic Macrophytes

The EU Water Framework Directive (WFD) mandates that surface waters in EU countries must be of good quality based on specified physical, chemical, and biological indicators. The implementation of this poses serious challenges for hydrobiologists, as in our country, there are numerous standing waters whose quality does not meet the EU standards. Our surface waters provide numerous important services to society (drinking water, irrigation, swimming, water sports, fishing, etc.). These are collectively referred to as ecosystem services, which are fundamentally threatened by two factors: excessive nutrient supply (eutrophication) and global climate change. As a result of these environmental changes, the aquatic communities of Hungary's aquatic habitats are undergoing significant transformations: populations of some species are rapidly advancing, while others are suddenly disappearing. Climate change and eutrophication, amplifying each other's effects, increase the dominance of planktonic algae (SCHEFFER & VAN NES 2007) or floating plants (SCHEFFER et al. 2003, SMITH 2014). Furthermore, they contribute to the invasion of alien invasive plants (THUILLER et al. 2007). Anthropogenic activities (e.g., agriculture) leading to nutrient over-enrichment further exacerbate these processes (PORTIELJE & ROIJACKERS 1995, ROIJACKERS et al. 2004). Additionally, they cause the decline and destruction of native submerged plant populations, which positively influence water quality (PHILLIPS et al. 1978, 2016). As a result, significant ecological damages occur, which, on one hand, pose numerous harmful consequences for human health (e.g., cyanobacterial mass production invasion), and on the other hand, result in habitat degradation, loss of biodiversity, and deterioration of water quality (JAKLIČ et al. 2020). Due to this, the societal utility value of aquatic habitats ultimately decreases. However, to avoid

ecological damage, it is important to understand how abiotic environmental factors influence the biotic interactions among macrophytes in surface waters.

In our surface waters, groups of primary producer organisms (e.g., aquatic plants, algae) maintain numerous well-separated alternative stable states. These states transition to new states (regime shift) upon surpassing specific environmental thresholds, leading to significant changes in water quality (PINTO & O'FARRELL 2014). In recent decades, numerous studies have focused on uncovering the competitive dynamics between floating and submerged plants, taking into account the presence of algae as well. High concentrations of nutrients (nitrogen, phosphorus) in open water bodies exposed to waves result in algal dominance coupled with high turbidity (SCHEFFER et al. 1993), whereas the same factor in wave-free small waters may lead to the expansion of free-floating vegetation (SCHEFFER et al. 2003, PORTIELJE & ROIJACKERS 1995). The thick canopy of floating vegetation completely shades the water body, leading to oxygen depletion, and consequently, the extinction of submerged plants (MORRIS et al. 2003, PHILLIPS et al. 2016). Additionally, it causes the extinction of animals, smaller invertebrates, and planktonic algae (PINTO & O'FARRELL 2014). Global warming, supporting eutrophication, further increases the risk of invasion by floating aquatic plants (NETTEN et al. 2010). However, shallower water, coupled with lower nutrient concentrations (mesotrophic-eutrophic), may promote the establishment of stable dominance by rooted submerged plants (VAN ZUIDAM & PEETERS 2013, SMITH 2014), resulting in greater water transparency, increased habitat biodiversity, and consequently higher societal utility value. Under field conditions, several researchers have observed that floating plants are significantly less abundant above dense submerged vegetation (SCHEFFER et al. 2003, VAN ZUIDAM & PEETERS 2013). As a result, it has been hypothesized that the submerged plants exert inhibitory effects on the floating vegetation above them. It has been experimentally validated (SZABÓ et al. 2010, SZABÓ et al. 2022). Submerged

vegetation can maintain stable dominance over a wide range of nutrient concentrations. However, beyond a certain environmental threshold, their dominance may decline with either the expansion of planktonic algae or floating vegetation. The outcome of competition between submerged and floating vegetation can also be influenced by the algal covering (epiphyton) on the vegetation, as it significantly shades the submerged plants and reduces their nutrient uptake. Elevated nutrient concentrations, higher water temperatures and the presence of herbivorous macroinvertebrates can also alter the outcome of competition between algae and submerged vegetation, promoting the invasion of non-native aquatic plant species.

1.2 The problem of the spread of invasive aquatic plants and the impact of invasion on surface waters.

Today, besides climate change and eutrophication, another significant threat to biodiversity is the extensive expansion of non-native plants (DUDGEON et al. 2006, STRAYER 2010). In many surface waters, we encounter invasive aquatic plants, whose colonization and invasion success can be influenced by various factors. The appearance of non-native aquatic plants can endanger local plant communities in numerous ways. Non-native invasive aquatic plants, due to their rapid growth, widespread distribution, and high phenotypic plasticity can cause severe economic and ecological damage in the newly conquered areas (GETSINGER et al. 2014, BRUNDU 2015). Among the economic damages, we can mainly mention the obstruction of surface waters, which adversely affects not only shipping but also ecosystem services. Ecological damages include changes in abiotic environmental factors, including decreased light intensity in deeper layers of water (ROMMENS et al. 2003), drastic reduction in dissolved oxygen concentration (JAMES et al. 1999, VILAS et al. 2017) and decreased biodiversity due to anoxic conditions (MORRIS et al. 2003). Therefore, the ability of aquatic

plants to respond to the aforementioned changes could be crucial for the evolutionary success of aquatic vegetation. The biological mechanisms through which native and non-native vegetation maintain stable dominance are still largely unknown. Furthermore, the environmental and biological mechanisms that govern the establishment of non-native plant species in surface waters have not been fully explored yet.

Based on current data, it can be concluded that the invasion of non-native aquatic plants significantly influences the diversity of species and functional diversity characteristic of a given habitat (HEJDA & DE BELLO 2013). It is well-known that the spread of non-native species leads to a decrease in species diversity both in terrestrial (HEJDA & DE BELLO 2013) and aquatic environments (VOJTKÓ et al. 2017, HUSSNER et al. 2021). By replacing native species characteristic of the area, the various plant traits (such as relative growth rate, specific leaf area, leaf dry matter content) undergo significant changes, resulting in alterations to ecosystem functioning and stability (VILÀ et al. 2011).

1.3 The main objectives of the thesis

Each study presented in the thesis addresses global issues concerning surface waters, focusing on the interactions among aquatic macrophytes, the impact of global climate change, and the topic of plant invasion. Researching biotic interactions among aquatic plants creates the theoretical foundation for the sustainable use of ecosystem services. Through laboratory experiments and field data analysis, our aim was to uncover the interactions between floating and submerged aquatic plants that play a significant role in shaping the water quality and natural state of aquatic habitats.

The aim of the thesis is to explore:

- the role of epiphytic algae living on macrophytes and macroinvertebrates consuming them in the competition between submerged and emergent macrophytes,
- how native and non-native species already present in Hungarian waters react to changes in various environmental factors (light intensity, temperature, nutrient concentration),
- which functional traits make non-native species successful in competition against native species.

Armed with this knowledge, the water management sector can plan faster and more effective measures to better control the spread of invasive native and non-native species. Additionally, it can improve the societal utility value of our surface waters. We answer the research questions by analyzing data derived from laboratory (microcosm) experiments and field measurements (Hungarian Surface Water Database), comparing and contrasting their findings.

1.3.1 Concepts and objectives of the first study:

In surface waters, both floating and submerged vegetation are capable of maintaining alternative stable states (SCHEFFER et al. 2003, SZABÓ et al. 2010, SZABÓ et al. 2022). Under hypertrophic conditions, in channels and smaller lakes, the globally widespread hornwort (*Ceratophyllum demersum*) often forms dense stands below the water surface (LOMBARDO & COOKE 2003). However, in the same areas, we can often encounter common duckweed (*Lemna gibba*), which belongs to the group of floating macrophytes. However, the competitive relationship between the two groups of plants can be greatly influenced by epiphytic algae living on the surfaces of the plants. Epiphytic algae are important components of the littoral zone of water bodies, as they significantly determine the amount of nutrients available to plants and light conditions (TÓTH 2013, LEVI et al. 2015). The abundance of these algae is influenced by numerous factors, such as light conditions (CAO et al. 2017), nutrient concentration (YANG et al. 2020), or temperature changes (KAZANJIAN et al. 2018) as well as biotic factors including competition for resources (HANSSON 1988) and herbivores (CARPENTER & LODGE 1986). Snails are often present in aquatic ecosystems, and it is well-known that they preferentially consume epiphytic algae living on plant surfaces (PIP & STEWART 1976), which allows more light to reach the plants, thereby enhancing their growth (YE et al. 2019). The main objective of the study is to uncover the role of epiphytic algae living on macrophytes and the macroinvertebrates consuming them in the competition between submerged and floating plants.

1.3.2 Concepts and objectives of the second study:

Nowadays, the emergence of non-native species and global climate change are two factors that significantly threaten biodiversity. Climate change is one of the greatest challenges for environmental conservation, as it significantly promotes the process of eutrophication in freshwater ecosystems (JEPPESEN et al. 2010). Additionally, it renders native aquatic plants unable to compete with non-native species (REJMANEK & RICHARDSON 1996). Global warming intensifies the dominance of free-floating vegetation (PEETERS et al. 2013), a development further facilitated by high nutrient loading (SCHEFFER et al. 2003, SMITH 2014, SZABÓ et al. 2022), thereby reducing the amount of light available to submerged plants. The two submerged plants used in the study are fanwort (*Cabomba caroliniana*) and watermilfoil (*Myriophyllum spicatum*). *Cabomba* is a fast-growing submerged plant native to South America and the southeastern United States (ØRGAARD 1991). However, in recent years, it has been reported in large numbers in Europe due to its popularity and widespread use in aquascaping. *Myriophyllum* is a similar plant species, native to Europe, Asia, and North Africa (PATTEN 1954). These two plants are often found together in the same habitat, leading to competitive interactions between them. Therefore, our study aimed to explore the combined effects of various environmental factors (light intensity, temperature, nutrient concentration) on certain characteristics of these two plants. Another goal was to assess how competition between the two plants changes in response to varying environmental factors.

1.3.3 Concepts and objectives of the third study:

The reduction of functional diversity among aquatic plants due to biological invasion remains relatively understudied. Most newly established invasive non-native aquatic plants can spread rapidly, causing serious damage to the affected area (BRUNDU 2015, ZHAN et al. 2017). The spread of non-native plant species, both on terrestrial (HEJDA & DE BELLO 2013) and aquatic habitats (HUSSNER et al. 2021), adversely affects the biodiversity of the area. The spread of new invasive plant species is capable of fundamentally altering the functioning and stability of ecosystems (VILÀ et al. 2011). Characteristics such as higher growth rates, more efficient dispersal mechanisms (HUSSNER et al. 2021, TASKER et al. 2022), greater phenotypic plasticity (FLEMING & DIBBLE 2015, SZABÓ et al. 2019), shade tolerance (SZABÓ et al. 2020), and better resource utilization (LUKÁCS et al. 2017) contribute to the successful spread of invasive species over native ones. Due to these characteristics, these plants often create monospecific stands in the given habitat, altering the structure of the habitat. Therefore, the aim of this study is to explore how biological invasion changes the functional structure and diversity of native macrophyte communities.

2. MATERIALS AND METHODS

2.1 First study: The role of epiphytic algae and grazing snails in stable states of submerged and of free-floating plants

The duckweed (*Lemna gibba*) and coontail (*Ceratophyllum demersum*) and great pond snail (*Radix labiata*) were collected from the Igrice Canal near Nyíregyháza. The experiment was conducted under laboratory conditions, and the plants were incubated in a nutrient solution developed by BARKO & SMART (1985). We added 5 mg L⁻¹ of nitrogen (NaNO₃) and 1 mg L⁻¹ of phosphorus (K₂HPO₄) and the micronutrient content of the solution was ensured by adding 0.1 mL L⁻¹ of TROPICA Supplier micronutrient solution. The plants were cultivated for 14 days in 20 L containers under 220 μmol m⁻² s⁻¹ photon flux density, with a photoperiod of 16:8 (light:dark) hours, at 25°C. During the experiment, the incubation conditions remained unchanged; only the size of the containers varied. In this case, we used 2 L plastic aquariums, the sides of which were covered with black foil to eliminate any disturbing light effects. We added 10 mL L⁻¹ of algal suspension to the solution, which was rinsed from the surface of the coontail into the media. We placed 100 mg of wet weight duckweed into the PVC pipes located in the middle of the aquariums (SZABÓ et al. 2003). Overcrowding of the fronds and intraspecific competition was avoided in such a way that when *Lemna* fronds reached a 100% cover, a second series of enclosures, with a bigger diameter was placed around the previous one. Out of five treatment groups, we employed two different control cultures: free of algae and treated with algae. In the algae-treated control culture containers, the water surface was covered with a plastic sheet. In the mixed cultures of duckweed and coontail, we placed 0 g and 10 g of wet weight coontail shoots (KOLESZÁR et al. 2022, Figure 1). In addition to the algae-treated duckweed cultures and the mixed cultures of duckweed and coontail, we applied 3 pieces of large pond snails (1.5-3 g each) per aquarium to minimize algal growth. To prevent the snails from escaping and

to hinder duckweed consumption, adhesive tape was placed around the edges of the aquariums and the PVC pipes. The cultures were growing at low and high (0.5 and 5 mg N L⁻¹, NaNO₃) nitrogen concentrations with a constant phosphorus concentration (1 mg P L⁻¹, K₂HPO₄). Each treatment was conducted in triplicate. Water samples were collected from the culture media of the duckweed-watermilfoil (5 mg N L⁻¹) mixed cultures. The pH of the samples was measured and after filtration (0.45 µm pore size), the concentration of PO₄³⁻-P as well as the concentration of dissolved inorganic nitrogen (NO₃⁻-N, NH₄⁺-N) were determined (MSZ ISO 7150-1:1992, MSZ EN ISO 6878:2004, MSZ 1484-13:2009). The wet weight of the duckweed was measured on the 4th, 8th, and 12th days and then the growth rate (RGR) was calculated as follows: $RGR = (\ln W_t - \ln W_0) / t$, where W_0 is the initial wet mass, W_t is the wet mass measured on day "t" (LANDOLT & KANDELER 1987). On the 12th day, we measured the dry mass of the plants and the biomass of algae in the culture vessels. The algae were collected from the surfaces of the plants and the sides of the aquariums using a brush and transferred into the culture medium. Subsequently, the mixture was filtered through an algae filter (pore diameter: 5-8 µm). The filter paper was dried in a drying cabinet at 80 °C for 48 hours. The nitrogen content of the algae and macrophytes was determined using a Vario Max Cube analyzer. The nitrogen uptake of the plants (mg) was calculated from the difference in nitrogen content between the initial samples and the biomass measured on the last day. We compared the laboratory results with the data collected from the website of the National Water Authority (<https://www.ovf.hu/>), as well as with 349 measurements obtained from 17 different European countries between 1994 and 2011. These measurements were taken from areas where *Lemna gibba* and/or *Ceratophyllum demersum* are found.

We examined the interactions between independent and dependent variables using Generalized Linear Models (GLM). We checked the normal distribution and homogeneity of variances using Levene's test. Differences among treatments involving snails (*Lemna* biomass, *Lemna* and *Ceratophyllum* growth

rates, algal dry mass, pH, nitrogen uptake) were analyzed using pairwise comparisons (PC). The relationship between macrophytes (*Lemna*, *Ceratophyllum*) and phytoplankton chlorophyll-a, as well as the relationship between *Lemna* and *Ceratophyllum* coverage, was analyzed using Fisher's exact test. Statistical analyses were performed using SPSS 16.0 software.

2.2 Second study: Shade tolerance as a key trait in invasion success of submerged macrophyte *Cabomba caroliniana* over *Myriophyllum spicatum*

The *Cabomba caroliniana* used in the experiment was collected from Lake Hévíz, while the *Myriophyllum spicatum* was collected from the Eastern Main Channel. The plants were pre-incubated in containers before the experiment in a nutrient solution developed by BARKO & SMART (1985). The plants were cultivated in two different nutrient concentrations: eutrophic (0.5 mg N L⁻¹ and 0.05 mg P L⁻¹) and hypertrophic (2 mg N L⁻¹ and 0.2 mg P L⁻¹), achieved by adding NH₄NO₃ and K₂HPO₄. The supply of micronutrients was ensured by adding TROPICA Supplier micronutrient solution. We preincubated the selected apical shoots for 14 days under 230 μmol m⁻² s⁻¹ photosynthetically active radiation (PAR), 16:8 h L/D regime at 24.5 ± 0.5 °C. Before starting the experiment, we removed the water on the surface of the plants using centrifuge (Hajdu 407.6 centrifuge, 1400 RPM, 10 seconds), then we took samples from the shoots of both species and measured their wet and dry weights.

In the experiment, we placed 6 apical shoots (11-14 cm long) from each plant species, with approximately similar weights (7.4 ± 0.2 g wet weight), separately in 2 L aquariums. We covered the sides of the aquaria with black foil to avoid light penetration from the sides. The media for the aquariums was prepared as described above and the pH was adjusted to 7.3. We set two different

nutrient treatments (0.5 mg N L^{-1} , 0.05 mg P L^{-1} ; 2 mg N L^{-1} , 0.2 mg P L^{-1}) four different light intensities ($22\text{--}28$, $52\text{--}82$, $170\text{--}290$, and $260\text{--}330 \mu\text{mol m}^{-2} \text{ s}^{-1}$) and two different temperatures $21,5$ and $27,5 \pm 0,5 \text{ }^\circ\text{C}$). The experiment lasted for 8 days. Nutrient replenishment occurred every two days, specifically on the 2nd, 4th, and 6th days. Each treatment ($2 \times 2 \times 2 \times 4 = 32$) was replicated three times, meaning a total of 96 aquariums were used.

From each aquarium, three leaves were taken from the plants ($96 \times 3 = 288$) following the protocol of PÉREZ-HARGUINDEGUY et al. (2016), then we measured the leaf surface area using LI-3000 Leaf Area Meter + LI-3050C Transparent Belt Conveyor Accessory instruments. After that, we measured the total wet mass of the submerged plants and the wet mass of the three cut leaves and after drying them at 80°C for 48 hours, we measured their dry mass as well. Based on these values, we calculated the relative growth rate (RGR), specific leaf area (SLA), and leaf dry matter content (LDMC). The calculation of RGR was performed following the method detailed in the first study. Specific leaf area was calculated as $\text{SLA} = (\text{LA}/\text{W} \text{ mm}^2 \text{ mg}^{-1})$ where LA represents the leaf area and W the dry weight of the leaves (GARNIER et al. 2001). Leaf dry matter content was calculated as $\text{LDMC} = (\text{DW}/\text{WW} \text{ mg g}^{-1})$, where DW represents the dry weight and WW the wet weight of the leaves (GARNIER et al. 2001). The nitrogen and carbon content of the dried plants was determined using the Vario Max Cube elemental analyzer. We calculated the plasticity indices (PiL, PiT, PiN) of both species based on the changes in RGR, SLA and LDMC values due to light (T), temperature (T) and nutrient concentration (N) following the method outlined by VALLADARES et al. (2002, 2005). According to this method: $\text{PI} = (\text{maximum average} - \text{minimum average}) / \text{maximum average}$. The result is a number between 0 and 1, where "0" indicates no plasticity and "1" indicates maximum plasticity.

We checked the normal distribution of the variables using Kolmogorov-Smirnov test. We examined the interactions between the variables and their

significance level using a general linear model (GLM). We analysed the differences between species (*C. caroliniana*, *M. spicatum*) using pairwise comparisons (PC). The impact of independent variables on dependent variables was analysed using analysis of variance (ANOVA). Statistical analyses were conducted using the SPSS 16.0 software.

2.3 Third study: Intraspecific trait variability is relevant in assessing differences in functional composition between native and alien aquatic plant communities

The research was conducted at the Hévízi canal, a natural small river with a constant water level and an average annual temperature of approximately 20 °C. In the 1980s, aquarium plants were illegally cultivated in the upper section of the canal, leading to dense mats of invasive alien plants compared to the lower section of the canal where native aquatic vegetation predominates. In temperate regions, the ability of exotic tropical plants to survive the winter is a crucial factor for their overwintering. Freshwater habitats with higher water temperatures provide excellent conditions for cold-sensitive aquatic plants to overwinter. Such areas offer opportunities for tropical and subtropical species to overwinter in vegetative form or promote the survival of seeds and/or buds allowing them to form dense vegetation even before the spread of native aquatic plants in spring. In the European context, these areas are the main sites of aquatic plant invasion (Šajna et al., 2007; Hussner et al., 2014; Lukács et al., 2016) providing an ideal research area for studying functional diversity differences between native and invasive aquatic plants.

A total of 20 quadrats (2x2 meters each) were placed along the canal. 10 quadrats were located in the warm, upstream section of the Hévízi-canal, and the remaining 10 in the cooler, downstream section. This unequal distribution was

necessary due to the uneven distribution of native and invasive species. The quadrats were positioned along the centreline of the canal and the percentage cover of species was recorded between September 9-11, 2017. During the cover estimation, we considered that there could be significant overlap between different levels of vegetation, therefore, the total cover within the quadrats could exceed 100%. Following the estimation, we collected five leaf samples from each species within each quadrat to determine functional characteristics. Subsequently, we gathered the entire vegetation to determine the wet biomass. In each quadrat, we measured the water temperature, pH and conductivity using Hach Lange HQ40D multiparameter probes. We also took water samples for the determination of nitrogen and phosphorus content. Additionally, we measured the wet and dry weight of the leaves, as well as their leaf surface area. The dry weight values were measured after drying in a drying cabinet at 80°C for 48 hours. Leaf surface area was determined using LI-3000 Leaf Area Meter + LI-3050C Transparent Belt Conveyor Accessory instruments. The determination of specific leaf area (SLA) and leaf dry matter content (LDMC) was conducted as described in the second study. The dry weight values were measured after drying in a drying cabinet at 80°C for 48 hours. Leaf surface area was determined using LI-3000 Leaf Area Meter + LI-3050C Transparent Belt Conveyor Accessory instruments. The determination of specific leaf area (SLA) and leaf dry matter content (LDMC) was conducted as described in the second study.

We calculated the community-weighted mean trait values (GARNER et al. 2004) which are the mean values of the traits across species weighted by their abundance. Functional diversity values were calculated taking into account functional richness, functional evenness, and functional divergence (MASON et al. 2005, VILLÉGER et al. 2008). Functional richness represents the "trait space" occupied by species; functional evenness indicates the distribution of trait values within the community; functional divergence measures how well the distribution of abundances maximizes the dissimilarity of functional traits within the

community (MASON et al. 2005). Functional richness, functional evenness and functional divergence were calculated from species-level trait probability distributions (TPDs) following the method proposed by CARMONA et al. (2016, 2019). Species level TPDs were fitted by two ways. In global pooling, all measurements were used for fitting a single TPD for each species and these species-level TPDs were used for each plot. In optimal pooling, the approach proposed by Botta-Dukát & Lukács (2021) was applied. Functional diversity analyses made under R environment with the use of ks (DUONG et al. 2022), mclust (SCRUCCA et al. 2016) and TPD (CARMONA 2019) packages. Community-weighted mean trait values and functional diversity indices of invaded and uninvaded plots were compared by Wilcoxon tests. Figures and Wilcoxon test were made in Origin Pro 2023 software.

3. RESULTS

3.1 First study: The role of epiphytic algae and grazing snails in stable states of submerged and of free-floating plants

Both the presence of algae and coontail significantly reduced the biomass of duckweed. From the combined inhibitory effect of coontail and algae, 20% is attributable to algae. In mixed cultures of duckweed and coontail, at low nitrogen concentrations (0.5 mg N L^{-1}), there was no difference in duckweed growth rates between aquariums with and without snails. However, at high nitrogen concentrations (5 mg N L^{-1}), the presence of snails enhanced the growth of duckweed. We observed the same stimulatory effect in the case of coontail, as the biomass of coontail was significantly higher in the presence of snails compared to without snails. In mixed cultures of duckweed and coontail, snails reduced algae biomass by 67-86%. In the presence of snails, the pH of the nutrient solution decreased significantly (from $10.01 \pm \text{SE } 0.027$ to $9.63 \pm \text{SE } 0.036$). By the 6th day of the experiment, in the absence of snails, the concentration of $\text{NO}_3^- \text{-N}$ in the nutrient solution was 97% lower and the concentration of $\text{PO}_4^{3-} \text{-P}$ was 70% lower compared to when snails were present. In the presence of snails, the tissue nitrogen concentration of duckweed and coontail was higher (by 8% and 15%, respectively) and the nitrogen uptake of duckweed increased by 128% and that of coontail by 194%, while algae biomass showed a 96% decrease. Field measurements did not reveal a significant relationship between the coverage of pondweed or duckweed and the quantity of phytoplankton chlorophyll-a. Based on the analysis, the quantity of phytoplankton chlorophyll-a was highest in areas where the coverage of duckweed or coontail was low. Where the concentration of phytoplankton chlorophyll-a exceeded $30 \text{ } \mu\text{g L}^{-1}$ the coverage of duckweed and coontail was less than 3%. Analysing 715 European data points, the Fisher exact test showed a significant ($P < 0.001$) relationship between the coverage of duckweed and coontail, which was strongly negative. This means that the greater

the coverage of duckweed in a given area, the smaller the quantity of coontail. However, the results also indicated a positive correlation between the quantity of coontail and snails, as a higher density of coontail corresponded to a larger number of snails.

Based on the results of structural equation models, water nitrogen concentration stimulated both the biomass of duckweeds and epiphytic algae. However, increasing nitrogen concentration from 0.5 mg L⁻¹ to 5 mg L⁻¹ reduced the growth of coontail. Epiphytic algae raised the pH of the nutrient solution but reduced the concentration of inorganic nitrogen and phosphorus in the solution, as well as the biomass of duckweeds. The presence of snails decreased the biomass of algae and the pH of the media while strongly enhancing the growth of coontail and duckweeds.

3.2 Second study: Shade tolerance as a key trait in invasion success of submerged macrophyte *Cabomba caroliniana* over *Myriophyllum spicatum*

During the experiment, higher temperature (27.5 ± 0.5 °C) at low light intensity (22–28 and 52–82 $\mu\text{mol m}^{-2} \text{s}^{-1}$) significantly reduced the growth of both species. Overall, *Cabomba* had significantly higher growth rates compared to *Myriophyllum* throughout the experiment, however, this difference was even more pronounced under low light intensity conditions (22–28 and 52–82 $\mu\text{mol m}^{-2} \text{s}^{-1}$). However, under strongly illuminated conditions (170–290 and 260–330 $\mu\text{mol m}^{-2} \text{s}^{-1}$), there were no significant differences in growth rates between the species. *Cabomba* also had significantly higher specific leaf area values compared to *Myriophyllum*. Both light intensity and temperature influenced the specific leaf area values of *Cabomba*, while neither light intensity nor temperature, nor nutrient concentration affected *Myriophyllum*. In terms of leaf dry matter content,

Myriophyllum had higher values. Analysing the nitrogen to carbon ratio, it can be noted that *Myriophyllum*'s values were higher than *Cabomba*'s, and this difference was even more pronounced under lower light intensity conditions (22–28 and 52–82 $\mu\text{mol m}^{-2} \text{s}^{-1}$). Under low light intensity and high temperature, *Cabomba*'s nitrogen uptake was more than three times higher than *Myriophyllum*'s. Considering all variables, *Cabomba* showed significantly greater phenotypic plasticity compared to *Myriophyllum*.

3.3 Third study: Intraspecific trait variability is relevant in assessing differences in functional composition between native and alien aquatic plant communities

The lower, colder water temperature section of the Hévízi-canal was dominated by native aquatic vegetation (*Ceratophyllum demersum*, *Hydrocharis morsus-ranae*, *Lemna minor*, *Nuphar lutea*, *Spirodela polyrhiza*). No invasive species were present in this area. In contrast, the upper section, characterized by warmer water temperatures was dominated by invasive species (*Cabomba caroliniana*, *Hygrophila diformis*, *Nymphaea lotus*, *Nymphaea rubra*, *Rotala rotundifolia*, *Vallisneria americana*, *Vallisneria spiralis*) with no occurrence of native species in this region. In the upper section of the canal, the concentrations of all phosphorus and the water conductivity were significantly higher compared to the lower section, while the pH was lower. In areas dominated by native species, we observed a 64% lower wet biomass compared to the upper section of the canal. However, the leaf area (LA) of native species in these areas was larger, while their specific leaf area (SLA) was smaller compared to invasive species. Regarding leaf dry matter content (LDMC), no differences were found between invasive and native species. When interpreting the results, we observed significant differences between the global and optimal pooling methods. The global pooling method tended to overestimate functional richness regardless of

different traits (LA, SLA, LDMC) and community types. However, for invasive species, the global pooling method typically underestimated the functional divergence of SLA and LDMC. Regarding functional evenness, there was no significant difference between the two methods. According to the results of the global pooling method, functional richness and evenness of invasive species leaf area, as well as the functional evenness of leaf dry matter content and specific leaf area, were significantly higher. Conversely, the functional divergence of leaf area and the functional richness of specific leaf area were lower compared to native species. Applying the optimal pooling method, we found significant differences in only four out of these six factors. Accordingly, the higher functional richness and evenness of leaf area, as well as the higher functional evenness of leaf dry matter content and the lower functional divergence of leaf area in invasive communities matched the results of the global pooling method.

4. CONCLUSIONS AND RECOMMENDATIONS

The main objective of this thesis was to investigate and illustrate the biotic interactions between submerged and free-floating aquatic plants. These interactions were primarily examined within the framework of the first study, where several interactions were identified among floating and submerged plants, as well as epiphytic algae and snails, by monitoring changes in abiotic factors (pH value, nutrient concentration). In the experiment, the free-floating duckweed (*Lemna gibba*) and the submerged non-rooted coontail (*Ceratophyllum demersum*) represented the two different life forms of plant groups. In a previous study (SZABÓ et al. 2022), we investigated how these groups of plants are able to maintain their stable dominance over each other under different conditions. Based on the results of SZABÓ et al. (2022), we concluded that under lower nitrogen concentrations ($<3 \text{ mg N L}^{-1}$), coontail dominance develops, while under higher nitrogen concentrations ($>5 \text{ mg N L}^{-1}$), duckweed dominance becomes characteristic in a given water body. However, within the framework of the dissertation, the first study examined how the presence of large pond snails in the system affects algal community biomass, alters the nitrogen and phosphorus content of the media and what the role of algae in inhibiting duckweed growth. In the second and third studies, we placed greater emphasis on investigating the effects of abiotic environmental factors altered by climate change (light intensity, temperature, nutrient concentration) on native and invasive aquatic plant species, as well as on the problems and changes affecting the ecosystem caused by plant invasion.

Finally, I would like to summarize the interactions identified in the three studies presented within the dissertation framework, as well as draw conclusions and make recommendations based on their results.

According to the results presented in the dissertation, both the presence of epiphytic algae and coontail reduced the growth of duckweeds, mainly due to nutrient depletion. The coontail-algae complex reduced nitrogen and phosphorus concentrations in the media much faster in the absence of snails than in their presence. Moreover, both algae and coontail are capable of increasing the pH of the nutrient solution by releasing hydroxide ions (OH^-) during the uptake of bicarbonate ions (HCO_3^-) required for photosynthesis (PEDERSEN et al. 2013). The elevated pH of water reduces the uptake of anions (NO_3^- , PO_4^{3-}) (ULLRICH-EBERIUS 1981) and contributes to the precipitation of phosphate, iron, and manganese (OTSUKI & WETZEL 1972, STUMM & MORGAN 1995). The high pH (> 10) detected under laboratory conditions in the study is often found in field conditions as well, especially in areas where submerged plants (e.g., *Ceratophyllum*, *Elodea*) form dense stands (FRODGE et al. 1990). Snails were able to increase the growth of duckweeds, which can be attributed to an indirect effect because effective grazing reduces the photosynthetic activity and nutrient uptake of algae. As a result, the pH of the media decreases while the nutrient concentration (N, P) increases. Furthermore, snails also promoted the growth of submerged plants, as the algal covering on the plant surfaces forms a barrier (SAND-JENSEN 1977), preventing the plants from taking up the required nutrients. The inhibitory effect of epiphytic algae was stronger under high nutrient concentrations. At low nutrient concentrations, the inhibitory effect of algae on the growth of duckweeds was not significant because in this case, submerged aquatic plants are capable of sufficiently extracting nutrients from their surroundings, which inherently prevents the growth of epiphytic algae. Based on these findings, we can conclude that algae and snails can significantly influence the outcome of competition between submerged and free-floating plants, as well as the stable states of plant groups (floating and submerged). Despite promoting the growth of submerged plants, snails still destabilize the stable state of submerged plants because the consumption of algae reduces the negative impact

of submerged plants on floating plants. As a result, floating plants are able to establish dominance over submerged plants even at lower nutrient concentrations.

Nowadays, due to various effects of climate change, numerous factors are changing in the deeper layers of water, to which adaptation may prove to be a key factor for submerged plants. Our results indicate that the specific leaf area (SLA) of the alien species *Cabomba caroliniana* was significantly larger than the SLA values of *Myriophyllum spicatum*, while in terms of leaf dry matter content (LDMC) the *Cabomba* values were lower. The higher SLA and lower LDMC suggest that *Cabomba* can produce a significantly larger leaf area per unit dry biomass, resulting in more efficient light absorption and photosynthesis. Furthermore, several studies support (LAKE & LEISHMAN 2004, HAMILTON et al. 2005) that higher SLA can facilitate plant invasion. Moreover, another significant advantage of *Cabomba* could be its much higher relative growth rate (RGR) values in shaded areas. This could be crucial because, due to the anticipated effects of global climate change, water temperatures in our lakes are expected to rise by 2-4 °C (PACHAURI et al. 2014) and nutrient concentrations are also projected to increase (VELTHUIS et al. 2018, MEERHOFF et al. 2022). These factors amplify each other's effects and enhance the expansion of floating vegetation (NETTEN et al. 2010). In the first study, we showed that high nutrient concentrations result in either dominance of floating vegetation or dominance of planktonic and periphytic algae, leading to reduced underwater light intensity. Therefore, shade tolerance may prove to be a key factor in the invasive success of *Cabomba*. Another important factor that gives *Cabomba* an advantage over *Myriophyllum* is its more than three times higher nitrogen uptake capacity. However, it is important to consider that this study significantly differs from natural conditions and their complexity. The results come from laboratory experiments, so there may be numerous factors influencing the invasive success of different plant groups. Nevertheless, our findings support observations documented regarding *Cabomba* invasion up to the present day.

The invasion of aquatic plants in surface waters significantly threatens the biodiversity of aquatic habitats. Our results indicate that alien aquatic plants produce significantly greater biomass compared to native plants, which is consistent with the findings of DAWSON et al. (2010). We hypothesized that dense stands of alien species with higher growth rates would be highly exposed to self-shading effects. However, these species had lower leaf area (LA) compared to the native species. This suggests that they have either smaller leaves or more dissected leaves, thus ensuring a higher surface-to-volume ratio, which could be advantageous for light utilization. Moreover, a higher surface-to-volume ratio is favourable for mitigating self-shading effects because smaller or more dissected leaves are easier to position for optimal light capture (RITCHIE & OLFF, 1999; POORTER & ROZENDAAL, 2008). The higher functional richness characteristic of leaf area in alien communities indicate that these species cover a significantly broader range of leaf surface sizes, occupying a much larger portion of the trait space compared to native species, which may also contribute to more efficient light capture (NAEM, 1998). These findings are supported by the lower functional divergence of leaf area observed in alien plant communities. Regarding specific leaf area (SLA), we did not find significant differences between alien and native species, suggesting that SLA did not contribute to higher biomass production in this case. This finding is consistent with the results of GUSTAFSSON & NORKKO (2019), which suggest that SLA only indirectly influences the primary production of aquatic plants. When examining the leaf dry matter content (LDMC) of species, we did not find significant differences between native and alien species. The LDMC values of plants are consistent with palatability, both in terrestrial environments (PAKEMAN, 2014) and aquatic environments (ELGER & WILLBY 2003, ELGER & LEMOINE 2005, ZHANG et al. 2019) based on previous research. The difference between the results of the two different methods (global pooling, optimal pooling) used to compare functional diversity was more pronounced in the case of alien species. This

suggests that the trait distributions of alien species are more varied, likely due to their greater phenotypic plasticity and genetic diversity. In general, it can be said that the global pooling method overestimated the values of functional richness, which can be explained by the adaptation of traits to the environment. However, it underestimated the values of functional divergence, while there was no difference in examining functional evenness between the applied methods. Therefore, the differences between the results of the two methods greatly influence the comparison of alien and native species. Hence, studies based solely on the application of the global pooling method are strongly questionable based on these results.

5. NEW SCIENTIFIC RESULTS

- Based on the studies presented in the thesis, it has been showed that epiphytic algae significantly inhibit nitrogen and phosphorus uptake of both submerged and free-floating plants.
- We have shown that epiphytic algae were responsible for 20% of the inhibition of duckweed growth, while 80% was attributed to the chemical effects of coontail (*Ceratophyllum demersum*) on water parameters (increased pH, decreased nutrient concentration). Consequently, the consumption of algae by snails can destabilize the alternative stable states of free-floating and submerged plants.
- Using structural equation modelling, we successfully uncovered the strength of inhibitory and stimulating interactions among submerged and free-floating plants, as well as epiphytic algae and grazing snails, considering the nitrogen concentration and pH value of the media
- Evidence has been provided that the growth rate of the non-native *Cabomba caroliniana* surpassed that of the native *Myriophyllum spicatum* under low light intensity conditions.
- We have demonstrated that low light intensity and higher temperatures increased the specific leaf area of *Cabomba caroliniana*, which, along with lower leaf dry matter content and higher nitrogen uptake capacity, significantly contributes to the invasive success of the non-native species.
- For the first time, we have proven that the invasion of non-native aquatic plants not only negatively affects species diversity but also the functional diversity of the community.
- We have demonstrated that non-native plants produce significantly higher biomass, attributed partly to factors such as smaller and/or more dissected leaves, which enhance leaf positioning for optimal photosynthesis. Furthermore, various functional diversity indices (examining leaf surface

values showing higher functional richness and evenness, as well as lower functional divergence) also significantly contribute to the higher biomass yield of non-native plants.

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7. PUBLICATIONS RELATED TO THE TOPIC OF THE THESIS

7.1 Publications in scientific journals

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8. OTHER PUBLICATIONS

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