



PHENOTYPIC PLASTICITY AND COMPETITIVE INTERACTIONS IN AQUATIC PLANT SPECIES UNDER CONTROLLED ENVIRONMENTAL CONDITIONS

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ABSTRACT

The aim of this study was to explore the effects of phenotypic plasticity and competition between the floating aquatics *Lemna minor* and *Spirodela polyrhiza* in a controlled competitive setting. Two datasets were used: a competition dataset (535 observations) and a trait dataset (37 observations) that included species identity, treatment, numbers of conspecifics and heterospecifics, focal growth, specific leaf area (SLA), and root and shoot traits. Analysis of variance was used to determine phenotypic variation and multiple regression models and interaction models were used to determine the effects of species, treatment, and abundance of competitors on focal growth. SLA exhibited high species-specific plasticity and a high Species $\times$ Treatment interaction, as compared with the root–shoot responses. Focal growth was significantly reduced by both conspecific and heterospecific abundance, but in different proportions in each species. *S. polyrhiza* was more sensitive to intraspecific competition, while *L. minor* was more sensitive to the negative effect of heterospecific abundance. The integrated model of competition accounted for 40.2% of the variance in focal growth and demonstrated that there was a significant interspecific competition response within species. In conclusion, the data show that the combined effects of species identity, competitor density, and phenotypic plasticity all affect the performance of aquatic plants and help to drive coexistence between species under different biotic environments.

Keyword: Phenotypic plasticity; aquatic plants; *Lemna minor*; *Spirodela polyrhiza*; competitive interactions

1. Introduction

Aquatic plants play a crucial role in freshwater ecosystems due to their role in primary production, nutrient cycling, habitat creation, and ecological diversity. They are strongly influenced by environmental conditions and interactions with other organisms in growth and spatial distribution. The species also modify the habitat around them, which produces spatial structure that affects the diversity of the community and species coexistence (Cornacchia et al., 2018). Biological interactions, like herbivory and competition, are also shown to have a significant effect on the structure of aquatic vegetation and the entire lake ecosystem through experimental studies (Vejříková et al., 2018). So environmental factors play a role in the performance of aquatic plants, especially if altering the light environment, nutrient levels, water level and/or resource supply alters the growth strategy and competitive outcome.

The rapid vegetative growth and sensitivity to environmental variation of duckweeds like *Lemna minor* and *Spirodela polyrhiza* make them useful model systems for the investigation of such responses. Growth responses of *L. minor* can differ significantly as a function of environmental factors and the importance of controlled environment to assess aquatic plant performance is highlighted (Van Dyck et al., 2021). Likewise, the manipulation of light intensity results in unique growth strategies for *L. minor* and *S. polyrhiza* and the manipulation of nutrient availability and spectral composition has a significant impact on productivity of *S. polyrhiza* (Strzałek & Kufel, 2021; Xu et al., 2019).

Phenotypic plasticity: the ability of an organism to adjust its shape, physiological function and/or functional traits in response to environmental variation. Plasticity can be a key adaptive mechanism for aquatic plants where environmental conditions change quickly. Phenotypic plasticity has been linked to ecological success in submerged aquatic plants and *Elodea nuttallii* is one of those aquatic plants that is invasive. The functional traits and plastic responses also affect species coexistence under different environmental conditions (Pérez-Ramos et al., 2019).

It is also established from the duckweed studies that sensitivity and performance of plants can be altered by environmentally induced plasticity. The responses of *L. minor* to stress are subject to environmental variation by means of phenotypic plasticity (Roubeau Dumont et al., 2019). Similarly, submerged macrophytes have the ability to alter morphology in response to multiple changes in light and water depth (Chou et al., 2022). In a more general way, plastic traits increase the range of environmental conditions for which competing species coexist and evidence for phenotypic plasticity per se promoting stable coexistence of species exists (Hess et al., 2022; Muthukrishnan et al., 2020).

Competition is a major factor in regulating the abundance, growth and community structure of plants. Intraspecific competition is between members of the same species and interspecific competition is between different species. Thus, even if interspecific competition is strong, intraspecific competition may often be even stronger and contribute to the mechanisms of coexistence across plant communities (Adler

et al., 2018). Density is a key factor for fast-growing aquatic plants, where *L. minor* growth and morphology can be affected by overcrowding (Kufel et al., 2018).

Environmental conditions and functional characteristics further influence competitive results. Water exchange may alter interspecific competition of submerged macrophytes, with trait hierarchies being a factor in obtaining competitive dominance (Pan et al., 2021). Furthermore, the submerged/free-floating macrophyte interaction is important in shaping alternative states of aquatic vegetation and ecosystem stability (Szabó et al., 2022).

While phenotypic plasticity and interactions between plants of different species have received extensive study, the combination of functional trait variation, conspecific density, heterospecific density, species identity, and environmental treatment has been studied less. The present study aims to investigate phenotypic plasticity and competitive interactions of aquatic plant species under controlled environmental conditions. It analyses the phenotypic response to variation in traits between species and treatments, the effects of conspecific and heterospecific abundance on focal plant growth, the competitive response of species and how functional traits relate to competitive performance.

2. Materials and Methods

2.1 Study Design

Two floating aquatic plants, *Lemna minor* and *Spirodela polyrhiza*, were selected for the study of phenotypic plasticity and competitive interactions between them in a controlled experiment. During the induction of the plants plasticity, they were exposed to two competitive environments, `high_freq` and `low_freq`, that correspond to the different relative frequencies of the focal species. The design enabled an analysis of the effects of previous competitive conditions on the plant characteristics and growth responses that followed.

2.2 Data Source

Two open-access datasets were employed, from the experimental study of phenotypic plasticity and species coexistence (Hart, 2021). The competition dataset consisted of 535 observations and 11 variables: focal species, treatment, initial abundance of conspecifics, initial abundance of heterospecifics, final abundance of focal species, focal growth. A total of 37 observations and 7 traits describing species identity, treatment, frond sampling, specific leaf area, and root–shoot traits were included in the trait dataset. The data were collected in both cases under controlled experimental conditions.

2.3 Study Species

Lemna minor and *Spirodela polyrhiza* are known as the focal species and were represented in the datasets by `minor` and `spiro` codes, respectively. Both are fast-growing free-floating aquatic plants that would be good for experimental study of competition and phenotypic response. Comparisons between species were

nearly even in the competition dataset with 268 observations for *L. minor* and 267 observations for *S. polyrhiza*.

2.4 Experimental Treatments

The treatment factor consisted of `high_freq` and `low_freq` conditions. High-frequency treatments were those in which the focal species was relatively common, and thus had more conspecific interaction, while low-frequency treatments were those in which the focal species was relatively rare and had more heterospecific interaction. The treatments were conducted in a controlled laboratory environment, and, therefore, the differences that were observed were due mainly to differences in competitive environment and/or phenotypic plasticity.

2.5 Competition Variables

Focal species, `conspecific_initial`, `heterospecific_initial`, `focal_final`, and `focal_growth` were used to assess competitive effects. Initial conspecific abundance was defined as the number of individuals of the same species as the focal plant while initial heterospecific abundance was the number of individuals of the competing species. Final abundance and focal growth were used as measures of plant performance. These variables allowed for direct comparison of intraspecific and interspecific competitive effects for each species and within each treatment.

2.6 Phenotypic Trait Variables

Phenotypic plasticity was calculated in terms of `SLA_cm2_per_g`, `root_shoot_cm_per_g`, `root_shoot_scaled` and `nr_fron_d_sampled`. Specific leaf area (SLA) was indicative of variation in morphological and resource-acquisition strategy, root:shoot ratios were indicative of variation in biomass allocation and plant structure. These traits were tested to see if they were different between *L. minor* and *S. polyrhiza* in two contrasting competitive environments, using species and treatment variables.

2.7 Statistical Analysis

Continuous variables were described by mean, standard deviation, minimum and maximum values. Analysis of variance or equivalent linear models, with Species $\times$ Treatment interaction, were used to compare phenotypic traits among species and treatments. The competitive effects on focal growth were assessed by multiple regression or mixed-effects models with species, treatment, conspecific abundance, and heterospecific abundance as predictors. Species $\times$ Treatment, Species $\times$ Conspecific Abundance, Species $\times$ Heterospecific Abundance, and Treatment $\times$ Competition were the species interactions included. Associations among continuous trait variables were examined by correlation tests and the relationships between traits and performance were only examined where appropriate for experimental linkage. A *p*-value of less than 0.05 was statistically significant and model assumptions were checked via residual diagnostics.

3. Results

3.1 Descriptive Characteristics

The experimental data exhibited a relatively equal number of observations of both focal species but more competition observations were made in the high-frequency treatment than in the low-frequency treatment. The mean focal growth for *Lemna minor* was 1.507 and 1.672 for the high-frequency and low-frequency treatments, respectively, while for *Spirodela polyrhiza*, it was 1.969 and 2.413, respectively. The competitive environment present at the beginning of the experiment varied greatly between treatments. Specifically, a greater mean conspecific abundance was observed in the high-frequency *L. minor* treatments and a greater heterospecific abundance in the low-frequency treatments. Table 1 indicates that *S. polyrhiza* mostly had higher focal growth than *L. minor*.

Table 1. Descriptive characteristics of competition observations by species and treatment

Species	Treatment	n	Focal growth, Mean $\pm$ SD	Mean conspecific abundance	Mean initial heterospecific abundance	Mean initial focal abundance	Mean final focal abundance
<i>L. minor</i>	High frequency	178	1.507 $\pm$ 0.453	81.99	34.61		113.08
<i>L. minor</i>	Low frequency	90	1.672 $\pm$ 0.692	3.93	68.86		6.58
<i>S. polyrhiza</i>	High frequency	180	1.969 $\pm$ 0.669	36.02	85.33		51.07
<i>S. polyrhiza</i>	Low frequency	86	2.413 $\pm$ 0.809	2.00	162.66		4.83

The descriptive pattern therefore suggested both species-specific differences in growth and substantial contrasts in the competitive environments represented by the two treatments.

3.2 Phenotypic Trait Variation

The SLA was found to be treatment-dependent and yielded clear treatment variation. The mean SLA in *L. minor* increased from 604.67 cm² g⁻¹ in the high-frequency condition to 734.87 cm² g⁻¹ in the low-frequency condition. A reverse trend was seen in *S. polyrhiza* with a reduction in mean SLA from 805.42

to $653.93 \text{ cm}^2 \text{ g}^{-1}$. Two-way ANOVA confirmed a significant species effect on SLA, $F(1,33) = 5.00$, $p = .032$, and, more importantly, a strong Species $\times$ Treatment interaction, $F(1,33) = 24.58$, $p < .001$. The overall treatment main effect was not significant ($p = .806$), meaning that the direction of the phenotypic response was related to species identity.

Scaled root–shoot was also found to be different between species, $F(1,33) = 4.33$, $p = .045$, although neither the treatment effect ($p = .119$) nor the Species $\times$ Treatment interaction ($p = .330$) was statistically significant. Therefore, there was the most explicit evidence of phenotypic plasticity in response to treatment in the case of SLA. The contrasting SLA response of the two species (shown in Figure 1) illustrates the non-uniform nature of phenotypic plasticity, which is species-dependent.

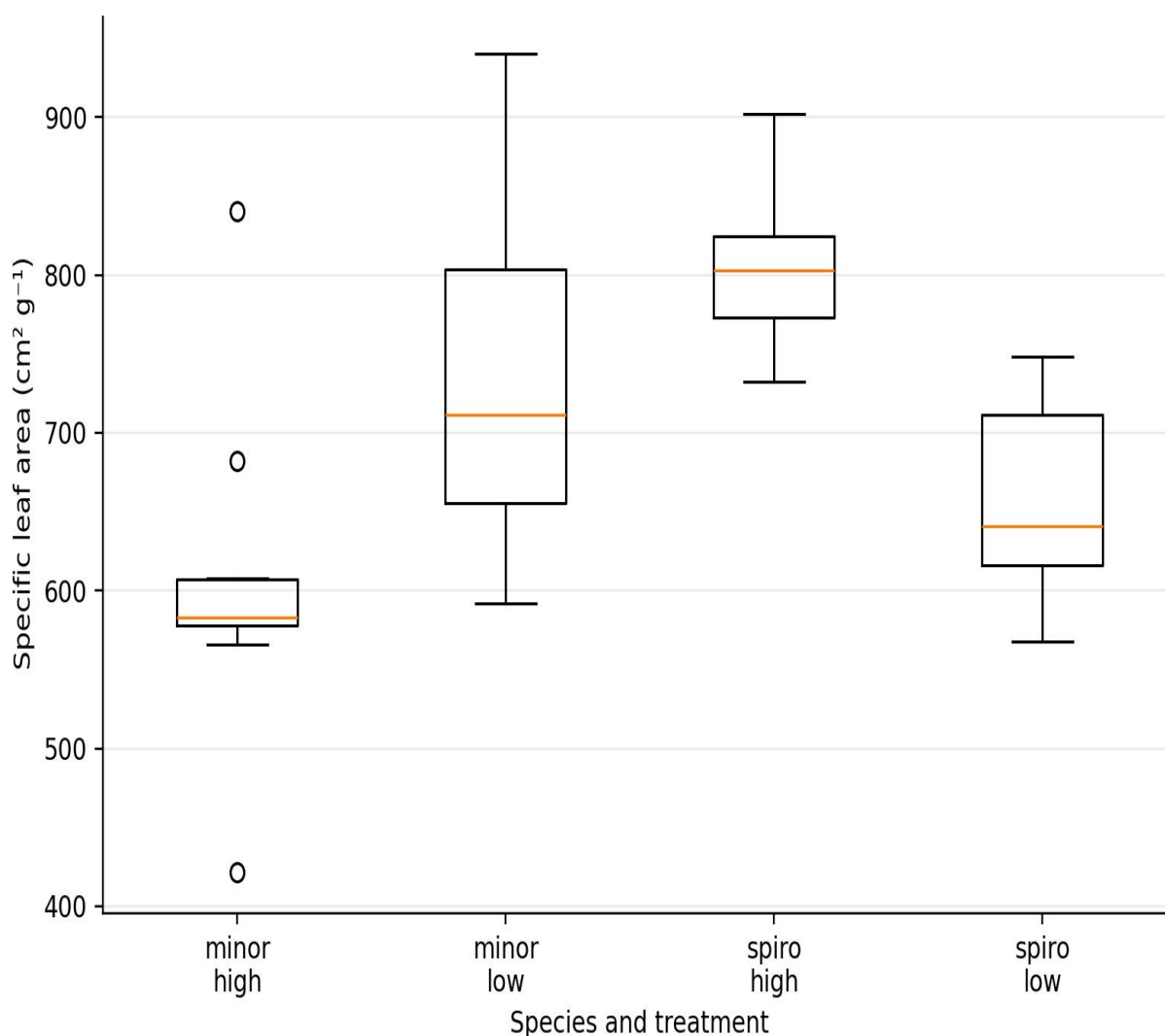


Figure 1. Specific leaf area across species and competitive treatments

3.3 Effects of Intraspecific Competition

After controlling for heterospecific abundance and treatment, initial abundance of conspecifics was negatively related to focal growth for both species. The degree of this association, however, varied significantly for each species. For *L. minor*, there was a reduction in focal growth of about 0.00085 units per additional conspecific individual. For *S. polyrhiza*, the reduction was of the order of 0.00604 units, which is considerably more density-dependent.

Both coefficients were statistically significant at $p < .001$ as reported in Table 2. The model accounted for about 19.8% and 34.9% of the variance in *L. minor* growth and *S. polyrhiza* growth, respectively. These results suggest that the focal performance was reduced by an increase in conspecific density for both species, and that *S. polyrhiza* was the species more sensitive to an increase in intraspecific crowding.

Table 2. Adjusted effects of initial conspecific abundance on focal growth

Species	Regression coefficient (B)	SE	95% CI	p-value	R ²
<i>L. minor</i>	-0.00085	0.00011	-0.00107 to -0.00064	<.001	0.198
<i>S. polyrhiza</i>	-0.00604	0.00064	-0.00728 to -0.00479	<.001	0.349

The higher coefficient of *S. polyrhiza* thus means that intraspecific competition had a stronger negative growth pressure on this species in the observed density range.

3.4 Effects of Interspecific Competition

Heterospecific abundance was also negatively related to focal growth in both aquatic plant species. After controlling treatment and conspecific density, the heterospecific coefficient was -0.00321 for *L. minor* (95% CI: -0.00374 to -0.00268, $p < .001$) and -0.00180 for *S. polyrhiza* (95% CI: -0.00245 to -0.00116, $p < .001$). Therefore, the extensive presence of the competing species had a great impact on reducing growth in the two focal species.

The slope of *L. minor* was larger, which implies that the focal growth of *L. minor* decreased faster with the increase in the abundance of heterospecifics in contrast to that of *S. polyrhiza*. This is in contrast with the intraspecific pattern, where *S. polyrhiza* exhibited the greater response. Focal growth tended to decline with increasing heterospecific competitor abundance as shown in Figure 2, which demonstrates a significant competitive effect between species that is measurable.

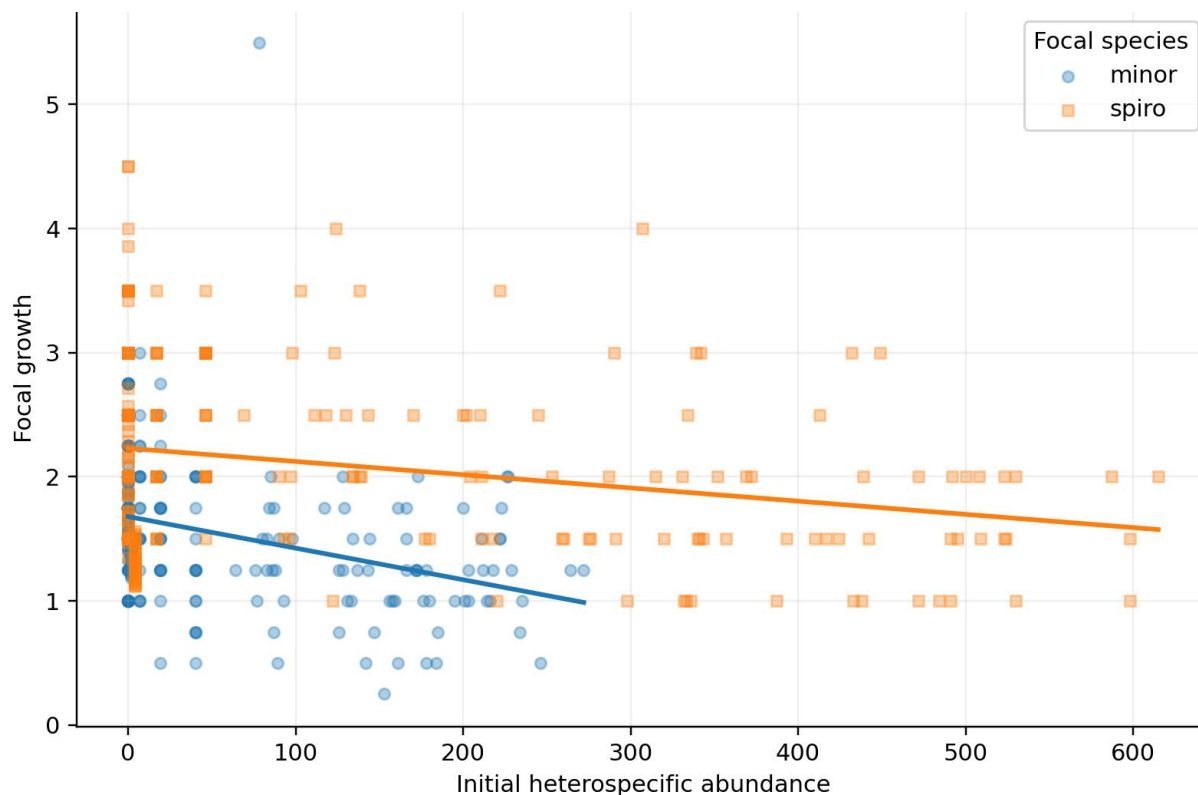


Figure 2. Relationship between heterospecific abundance and focal plant growth

3.5 Treatment Effects on Plant Growth

Both species had higher mean focal growth at the higher level when they received low-frequency treatment. In *L. minor*, the mean growth was raised to 1.672 with a difference of 0.166 with no adjustment. This however, was not significant at the conventional level of significance by use of cluster-robust inference ($p = .067$). Contrary to this, *S. polyrhiza* recorded a significantly larger increase between 1.969 and 2.413 with a difference of 0.444, which was statistically significant ($p = .007$). These findings indicate that, as indicated in Table 3, previous competitive frequency had a greater impact on future growth performance in *S. polyrhiza* compared to *L. minor*.

Table 3. Focal growth under high- and low-frequency treatments

Species	High-frequency mean	Low-frequency mean	Difference (Low – High)	95% CI	p-value
<i>L. minor</i>	1.507	1.672	0.166	-0.012 to 0.343	.067
<i>S. polyrhiza</i>	1.969	2.413	0.444	0.119 to 0.769	.007

These results indicate that the low-frequency competitive environment was associated with greater subsequent growth, particularly for *S. polyrhiza*.

3.6 Species × Competitive-Treatment Interaction

The interaction of species with treatment went further to investigate species-specific growth responses. *S. polyrhiza* had a higher mean focal growth than *L. minor* in all treatment groups. The species main effect was significant ($B = 0.462$, $p < .001$), while the low frequency treatment effect for the reference species was less pronounced ($B = 0.166$, $p = .067$).

The unadjusted Species × Treatment interaction was positive, but insignificant ($B = 0.278$, 95% CI: -0.090 to 0.647, $p = .139$). Thus, while the overall growth response to treatment was larger for *S. polyrhiza* under low frequency, the evidence did not warrant the conclusion that the growth response for the two species differed. *S. polyrhiza* showed the largest treatment difference in focal growth while *L. minor* showed a smaller treatment difference as seen in Figure 3.

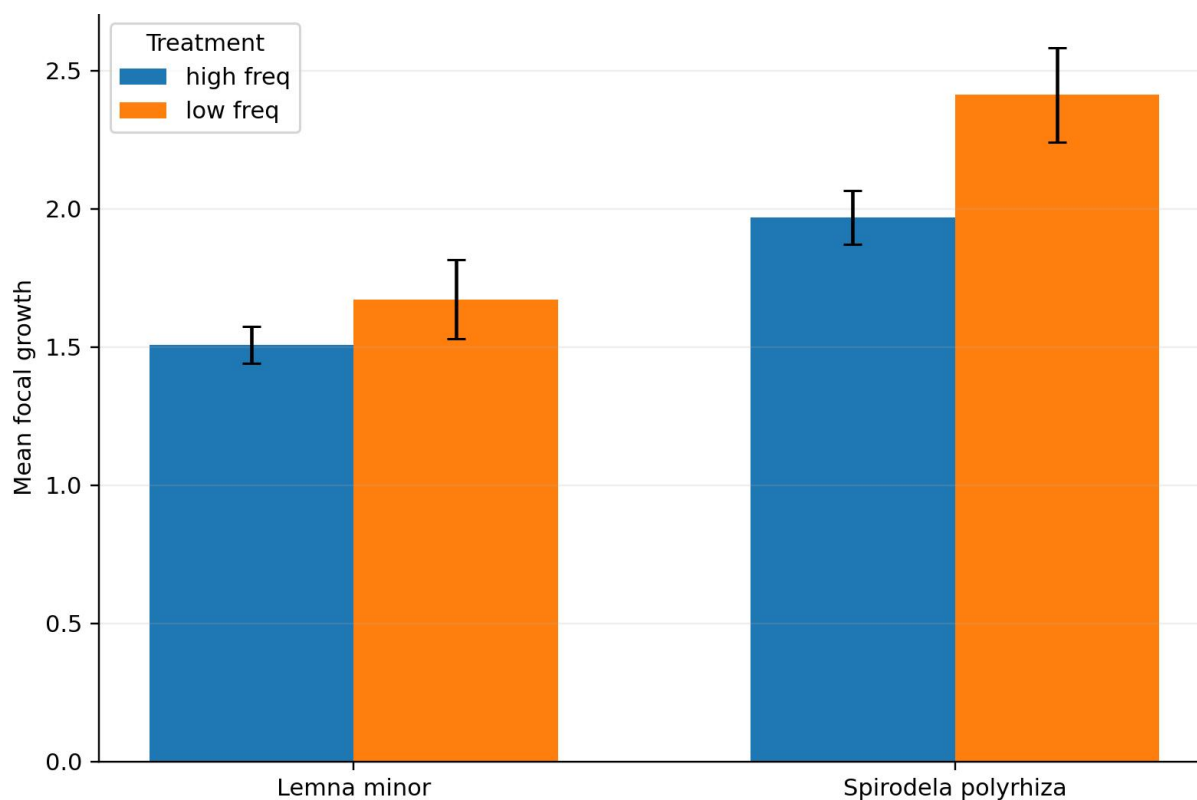


Figure 3. Species-specific focal growth under high- and low-frequency competitive treatments

3.7 Integrated Competition Model

Both species identity and treatment, conspecific abundance, heterospecific abundance, and their specified interactions were evaluated simultaneously in the integrated regression model. The model explained 40.2% of the observed variation in focal growth ($R^2 = 0.402$; adjusted $R^2 = 0.392$; $n = 534$).

Competitor abundance was expressed per 100 initial individuals to facilitate interpretation, and both an increase in conspecific abundance ($B = -0.086$, $p < .001$) and an increase in heterospecific abundance ($B = -0.326$, $p < .001$) had a significant effect on a decrease in focal growth. As predicted, the Species $\times$ Conspecific interaction was highly negative ($B = -0.520$, and $p < .001$), implying a substantially stronger negative effect that conspecific competition had on *S. polyrhiza*. In contrast, the Species $\times$ Heterospecific interaction effect was positive and significant ($B = 0.143$, $p < .001$), which suggests that the negative heterospecific effect was weaker for *S. polyrhiza* than for *L. minor* shown in Table 4.

Table 4. Integrated regression model predicting focal growth

Predictor	B	SE	95% CI	p-value
Intercept	1.690	0.041	1.609 to 1.771	<.001
<i>S. polyrhiza</i> vs. <i>L. minor</i>	0.654	0.078	0.502 to 0.806	<.001
Low vs. high frequency	0.489	0.254	-0.008 to 0.986	.054
Species $\times$ Treatment	0.023	0.148	-0.267 to 0.313	.878
Conspecific abundance, per 100	-0.086	0.012	-0.109 to -0.063	<.001
Species $\times$ Conspecific abundance	-0.520	0.061	-0.638 to -0.401	<.001
Treatment $\times$ Conspecific abundance	-7.229	7.958	-22.826 to 8.368	.364
Heterospecific abundance, per 100	-0.326	0.023	-0.371 to -0.281	<.001
Species $\times$ Heterospecific abundance	0.143	0.034	0.076 to 0.210	<.001
Treatment $\times$ Heterospecific abundance	0.008	0.044	-0.078 to 0.093	.863

Overall, the integrated model demonstrates that species identity and competitor density were stronger determinants of focal growth than the treatment main effect itself.

3.8 Association Between Traits and Competitive Performance

To prevent artificial individual-level matching between both data sets, phenotype characteristics were only associated with competitive performance at matched replicate, species and treatment levels. This resulted in 35 matched observations. In all matched observations, SLA was not significantly correlated with mean focal growth ($r = 0.052$, $p = .765$). A weak negative overall relationship was also seen between root shoot allocation and growth ($r = -0.242$, $p = .161$).

However, in contrast to this there were contrasting patterns within species. SLA was slightly positively correlated with competitive performance for *L. minor* ($r = 0.169$, $p = .516$). SLA was moderately negatively associated with mean focal growth in *S. polyrhiza* ($r = -0.523$, $p = .026$). There were no significant species-specific relationships with root–shoot allocation. No common trait–performance relationship was observed between both species, but the negative SLA–growth association in *S. polyrhiza* implies that phenotypic responses affect competitive performance in a species-specific manner (Figure 4).

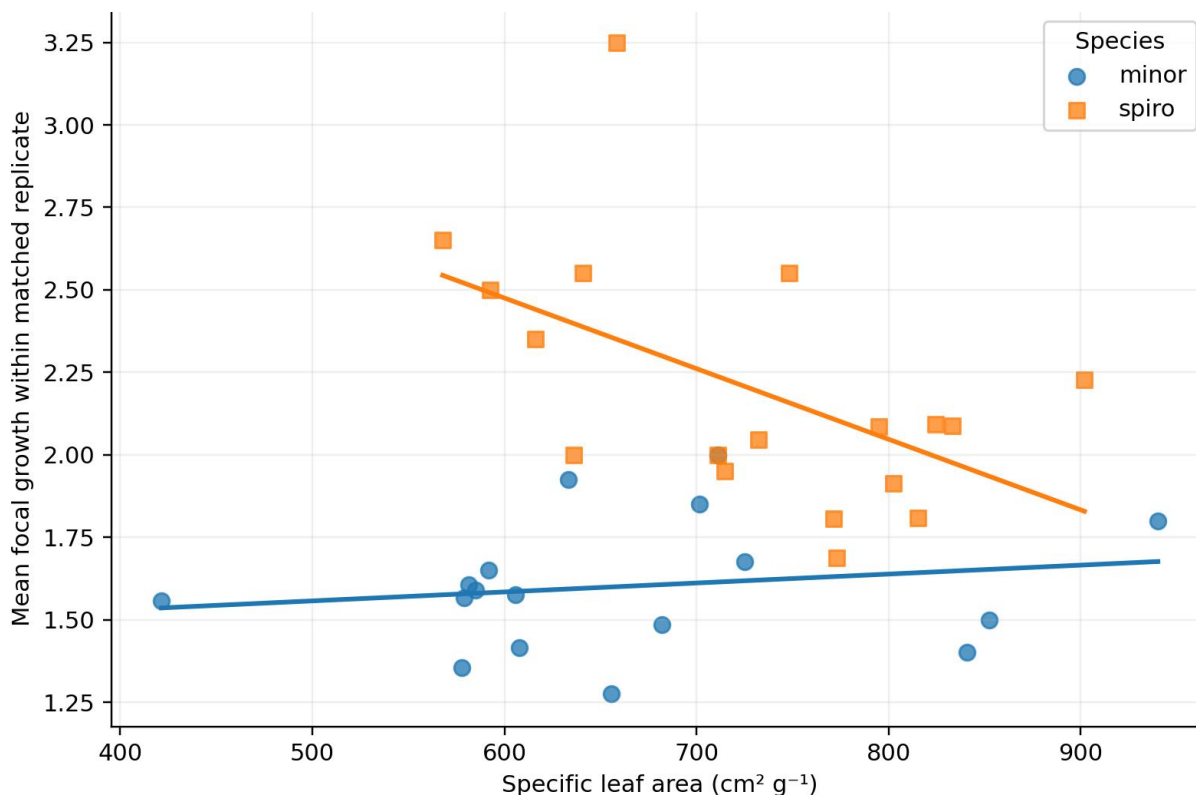


Figure 4. Association between specific leaf area and matched competitive performance

The findings overall are generally in line with the methodology and support three main findings: phenotypic plasticity was clearly seen in SLA, intra- and inter-specific competitor abundance negatively affected the focal growth, and the importance of these competitor effects appeared to be species-specific.

4. Discussion

In the present study, the interaction between phenotypic plasticity and competitive interactions was found to affect both species of Lemnaceae during experimental growth. SLA exhibited an apparent Species $\times$ Treatment response, while there was a stronger species than treatment response for root–shoot traits. The abundance of conspecifics and heterospecifics each inhibited focal growth, but to varying degrees for the two species. This result is corroborative of the general picture where plasticity and competition influence co-existence and plant performance under environmental variation (Fontanari et al., 2023; Govaert et al., 2021).

The response that was observed between the two species in SLA was contrasting and gives evidence of the species' phenotypic plasticity. *L. minor* had the highest SLA at low frequencies while *S. polyrhiza* had the lowest. This change of traits represents variation in resource-acquisition strategies and/or patterns of resource allocation. Macrophyte traits are well established as indicators of macrophyte response to environmental variations (Dalla Vecchia et al., 2020). In fish, the same kind of plastic changes are linked to variations in nutrients, light, and other aspects of growth (Skovsholt et al., 2024). Nutrient availability significantly affects growth and biochemical composition in *L. minor* and cultivation conditions (nutrients, light and carbon dioxide) have a significant influence on biomass production (Schmidt & Goldbach, 2022; Ullah et al., 2022).

Intraspecific and interspecific competition were important factors in limiting the growth of the focal plants, as the density of competitors was important for aquatic plant performance. Interspecific competition was especially intense for *S. polyrhiza*, while interspecific density had a relatively greater effect on *L. minor*. These differences suggest that there is no general rule of competitive effect between species. Interspecific competition among aquatic plants has also been demonstrated to be not only a function of density, but also of species identity and ecological situation (Nunes & Camargo, 2020). Parental and clonal effects in duckweed competitive interactions also highlight the complexity of species interactions (He et al., 2025).

Both species had a distinctive pattern of growth and competitive sensitivity. *S. polyrhiza* was found to have higher focal growth, especially at low frequency, and was negatively affected by conspecific crowding to a greater extent. These species-specific responses can be due to different traits of morphology, growth and resource use. Plant species traits can be a greater driver of aquatic plant productivity and competition than external shading effects (Austin et al., 2023). Aquatic plants (especially those that are clonal or asexual) may also vary in their performance due to environmental or genetic variation (Jewell & Bell, 2023).

The effect of the controlled treatment structure was that the growth response to the treatments was affected by the growth environment that the plants had been subjected to before the treatments, but that the effect was more pronounced for *S. polyrhiza*. Aquatic plant competition can be significantly affected by environmental conditions, especially when light and nutrient availability interact with each other (Yu et al., 2025). These results indicate that species may react differently to adjacent plants depending on their competitive past and controlled environmental setting.

The significance of the results is for aquatic community structure and coexistence. Variations in the amounts of plasticity and competitive sensitivity may make it possible for species to occupy different ecological niches, or for a species to react differently to changes in resources. Trait-mediated responses have an impact on productivity, competitive dominance, and persistence in aquatic plant communities.

Also, simulation models suggest that floating and submerged plants interact and influence community changes and changes in ecosystem stability (Ali, 2025).

Limiting factors of the study were the relatively small number of phenotypic trait data sets compared to the competition data sets. Further, environmental factors were mostly recorded in the form of experimental treatments instead of measurements of several abiotic factors like temperature, nutrient concentration, water chemistry and light intensity.

More aquatic species, more traits, and extended experimental times should be incorporated into future studies. The direct manipulation of nutrients, temperature, light and water chemistry would give a more detailed understanding of the effects of the environment on competition. Incorporating morphological, physiological, biochemical and reproductive attributes also illuminates the mechanisms that relate phenotypic plasticity to competitive performance and coexistence.

5. Conclusion

In the present study, it was found that the growth responses of *Lemna minor* and *Spirodela polyrhiza* are influenced by phenotypic plasticity and interactions between the two species under the controlled experimental conditions. Specific leaf area showed significant species-specific plasticity and opposite responses to high and low frequencies, while root-shoot traits were more affected by species than by treatment. Conspecific abundance adversely influenced focal plant growth, as did heterospecific abundance, demonstrating the importance of density-dependent competition in structuring aquatic plant performance. The extent of these effects however varied by species. *Spirodela polyrhiza* was more sensitive to intraspecific crowding and *Lemna minor* was relatively more sensitive to heterospecific abundance. Growth was also affected by the treatment conditions, with *S. polyrhiza* performing better at the low-frequency conditions. The integrated analysis also showed that species identity and competitor density, were more important variables for growth than treatment alone. The results suggest that phenotypic plasticity is strongly related to competitive responses and can help to explain species coexistence through functional trait shifts in response to different biotic environments in aquatic plants. The findings highlight the ecological significance of considering trait variation and species identity, in addition to competitive context, in assessing plant performance and dynamics in freshwater environments.

References

1. Adler, P. B., Smull, D., Beard, K. H., Choi, R. T., Furniss, T., Kulmatiski, A., Meiners, J. M., Tredennick, A. T., & Veblen, K. E. (2018). Competition and coexistence in plant communities: Intraspecific competition is stronger than interspecific competition. *Ecology Letters*, 21(9), 1319–1329. <https://doi.org/10.1111/ele.13098>
2. Ali, A. A. (2025). Modeling competitive interactions between floating and submerged macrophytes in shallow lakes using field data. *Theoretical Ecology*, 18(1), 28. <https://doi.org/10.1007/s12080-025-00622-x>
3. Austin, Å. N., Hansen, J. P., Donadi, S., Kautsky, L., & Eklöf, J. S. (2023). Stronger effect of individual species' traits than shading on aquatic plant community productivity and interspecific

- competition. *Aquatic Botany*, 187, 103647.
4. Chou, Q., Zhang, W., Chen, J., Ren, W., Yuan, C., Wen, Z., Zhang, X., Cao, T., Ni, L., & Jeppesen, E. (2022). Phenotypic responses of a submerged macrophyte (*Vallisneria spiralis*) to low light combined with water depth. *Aquatic Botany*, 176, 103462.
 5. Cornacchia, L., Van De Koppel, J., Van Der Wal, D., Wharton, G., Puijalon, S., & Bouma, T. J. (2018). Landscapes of facilitation: How self-organized patchiness of aquatic macrophytes promotes diversity in streams. *Ecology*, 99(4), 832–847. <https://doi.org/10.1002/ecy.2177>
 6. Dalla Vecchia, A., Villa, P., & Bolpagni, R. (2020). Functional traits in macrophyte studies: Current trends and future research agenda. *Aquatic Botany*, 167, 103290.
 7. Fontanari, J. F., Matos, M., & Santos, M. (2023). Local adaptation, phenotypic plasticity, and species coexistence. *Frontiers in Ecology and Evolution*, 11, 1077374.
 8. Govaert, L., Gilarranz, L. J., & Altermatt, F. (2021). Competition alters species' plastic and genetic response to environmental change. *Scientific Reports*, 11(1), 23518.
 9. Hart, S. (2021). Effects of phenotypic plasticity on species coexistence. <https://doi.org/10.5281/zenodo.5726005>
 10. He, L.-X., Jin, Y., Zhang, X.-M., Luo, F.-L., Xue, W., Lei, J.-P., Liu, H., & Yu, F.-H. (2025). Clonal parental effects on competitive interactions between two duckweeds. *Frontiers in Plant Science*, 16, 1587907.
 11. Hess, C., Levine, J. M., Turcotte, M. M., & Hart, S. P. (2022). Phenotypic plasticity promotes species coexistence. *Nature Ecology & Evolution*, 6(9), 1256–1261.
 12. Jewell, M. D., & Bell, G. (2023). Environmental and genetic variation in an asexual plant. *Aquatic Botany*, 188, 103675.
 13. Kufel, L., Strzałek, M., & Przetakiewicz, A. (2018). Plant response to overcrowding—*Lemna minor* example. *Acta Oecologica*, 91, 73–80.
 14. Muthukrishnan, R., Sullivan, L. L., Shaw, A. K., & Forester, J. D. (2020). Trait plasticity alters the range of possible coexistence conditions in a competition–colonisation trade-off. *Ecology Letters*, 23(5), 791–799. <https://doi.org/10.1111/ele.13477>
 15. Nunes, L. S. C., & Camargo, A. F. M. (2020). The interspecific competition of tropical estuarine macrophytes is not density-dependent. *Aquatic Botany*, 164, 103233.
 16. Pan, Y., Yuan, D., Wu, Q., Jin, L., Xie, M., Gu, Y., & Duan, C. (2021). Effect of water exchange rate on interspecies competition between submerged macrophytes: Functional trait hierarchy drives competition. *Plant and Soil*, 466(1–2), 631–647. <https://doi.org/10.1007/s11104-021-05081-x>
 17. Pérez-Ramos, I. M., Matías, L., Gómez-Aparicio, L., & Godoy, Ó. (2019). Functional traits and phenotypic plasticity modulate species coexistence across contrasting climatic conditions. *Nature Communications*, 10(1), 2555.
 18. Roubeau Dumont, E., Larue, C., Pujol, B., Lamaze, T., & Elger, A. (2019). Environmental variations mediate duckweed (*Lemna minor* L.) sensitivity to copper exposure through phenotypic plasticity. *Environmental Science and Pollution Research*, 26(14), 14106–14115. <https://doi.org/10.1007/s11356-019-04630-3>
 19. Schmidt, K.-M., & Goldbach, H. E. (2022). Modelling of *Lemna minor* L. growth as influenced by nutrient supply, supplemental light, CO₂ and harvest intervals for a continuous indoor cultivation. *Heliyon*, 8(12). [https://www.cell.com/heliyon/fulltext/S2405-8440\(22\)03482-X](https://www.cell.com/heliyon/fulltext/S2405-8440(22)03482-X)
 20. Skovsholt, L. J., Matheson, F., Riis, T., & Hawes, I. (2024). Trait-specific groups of aquatic macrophytes respond differently to eutrophication of unshaded lowland streams. *Science of the Total Environment*, 954, 176724.
 21. Strzałek, M., & Kufel, L. (2021). Light intensity drives different growth strategies in two duckweed species: *Lemna minor* L. and *Spirodela polyrrhiza* (L.) Schleiden. *PeerJ*, 9, e12698.
 22. Szabó, S., Koleszár, G., Zavanyi, G., Nagy, P. T., Braun, M., & Hilt, S. (2022). Disentangling the mechanisms sustaining a stable state of submerged macrophyte dominance against free-floating competitors. *Frontiers in Plant Science*, 13, 963579.
 23. Ullah, H., Gul, B., Khan, H., Akhtar, N., Rehman, K. U., & Zeb, U. (2022). Effect of growth medium nitrogen and phosphorus on nutritional composition of *Lemna minor* (an alternative fish and poultry feed). *BMC Plant Biology*, 22(1), 214. <https://doi.org/10.1186/s12870-022-03600-1>
 24. Van Dyck, I., Vanhoudt, N., & Battle, J. V., Horemans, N., Nauts, R., Van Gompel, A., Claesen, J., & Vangronsveld, J. (2021). Effects of environmental parameters on *Lemna minor* growth: An integrated

- experimental and modelling approach. *Journal of Environmental Management*, 300, 113705.
25. Vejříková, I., Vejřík, L., Lepš, J., Kočvara, L., Sajdlová, Z., Čtvrtlíková, M., & Peterka, J. (2018). Impact of herbivory and competition on lake ecosystem structure: Underwater experimental manipulation. *Scientific Reports*, 8(1), 12130.
26. Xu, Y.-L., Tan, L. I., Guo, L., Yang, G.-L., Li, Q. I., Lai, F., He, K.-Z., Jin, Y., Du, A., & Fang, Y. (2019). Increasing starch productivity of *Spirodela polyrhiza* by precisely control the spectral composition and nutrients status. *Industrial Crops and Products*, 134, 284–291.
27. Yu, W., Dong, L., Li, Z., Huang, R., Chao, C., Xia, L., & Li, F. (2025). Nutrient and Light Interactions Shape Competitive Dynamics Between Two Co-Occurring Submerged Macrophytes. *Freshwater Biology*, 70(12), e70147. <https://doi.org/10.1111/fwb.70147>

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