Acta Limnologica Brasiliensia

Publication of the Brazilian Association of Limnology

Original Article
*Acta Limnologica Brasiliensia,* 2026, vol. 38, e14
https://doi.org/10.1590/S2179-975X4725
ISSN 2179-975X on-line version

# Shifting shapes, shifting risks: density-driven leaf plasticity in *Salvinia auriculata* (Salviniaceae) and its effects on herbivory by *Samea multiplicalis* (Lepidoptera, Pyralidae)

Se a forma muda, os riscos mudam: plasticidade foliar influenciada pela densidade em *Salvinia auriculata* (Salviniaceae) e seus efeitos na herbivoria por *Samea multiplicalis* (Lepidoptera, Pyralidae)

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**Cite as:** Oliveira, G.C.S., Demetrio, G.R. and Coelho, F.F. Shifting shapes, shifting risks: density-driven leaf plasticity in *Salvinia auriculata* (Salviniaceae) and its effects on herbivory by *Samea multiplicalis* (Lepidoptera, Pyralidae). *Acta Limnologica Brasiliensia*, 2026, vol. 38, e14. https://doi.org/10.1590/S2179-975X4725

**Abstract: Aim:** This study investigated whether phenotypic plasticity induced by different plant density conditions in *Salvinia auriculata* affects herbivory and the abundance of *Samea multiplicalis* larvae. **Methods:** The study consisted of two stages: (i) In October 2022, four weekly samplings were conducted, during which ~30 clonal structures of *S. auriculata* were collected from two ponds differing in plant density. From each pond, 30 ramets were randomly selected to measure floating leaf width and length. Larval presence and the frequency of herbivory on floating leaves were also recorded; (ii) An experiment was conducted using 30 ramets from each density condition, placed individually in 500 mL containers. Five larvae were introduced per container, and after seven days, the number of partially and fully consumed leaves was recorded. **Results:** *S. auriculata* displayed density-dependent plasticity: plants from high-density conditions developed longer, wider, and more vertically oriented leaves. Despite this, leaf consumption did not differ between density conditions, although both larval abundance and herbivory marks were higher under high-density conditions. **Conclusions:** Our findings suggest that the high-density phenotype of *S. auriculata* may facilitate the establishment and herbivory of *S. multiplicalis*, potentially by offering structural refuge against predators and environmental stressors.

**Keywords:** aquatic macrophyte; freshwater ecosystems; macrophyte–insect interactions; pond; southeast Brazil.

**Resumo: Objetivo:** Este estudo investigou se a plasticidade fenotípica induzida por diferentes condições de densidade de plantas em *Salvinia auriculata* afeta a herbivoria e a abundância de larvas de *Samea multiplicalis*. **Métodos:** O estudo consistiu em duas etapas: (i) Em outubro de 2022, foram realizadas quatro amostragens semanais, durante as quais, aproximadamente 30 estruturas clonais de *S. auriculata* foram coletadas de duas lagoas com densidade de plantas diferentes. Em cada lagoa, 30 rametes foram selecionados aleatoriamente para medir a largura e o comprimento de suas folhas flutuantes. A presença de larvas e a frequência de herbivoria em folhas flutuantes também foram registradas; (ii) Um experimento foi conduzido utilizando 30 rametes de cada condição de densidade, armazenados em recipientes de 500 mL. Cinco larvas foram introduzidas em cada recipiente e, após sete dias, o número de folhas parcial e totalmente consumidas foi registrado. **Resultados:** *S. auriculata* apresentou plasticidade dependente da densidade: plantas de condições de alta densidade desenvolveram folhas mais longas, mais largas e orientadas verticalmente. Apesar disso, o consumo de folhas não diferiu entre as diferentes condições de densidade, embora tanto a abundância larval quanto as marcas de herbivoria tenham sido maiores em condições de alta densidade. **Conclusões:** Nossas descobertas sugerem que o fenótipo de alta densidade de *S. auriculata* pode facilitar o estabelecimento e a herbivoria de *S. multiplicalis*, potencialmente oferecendo refúgio estrutural contra predadores e estressores ambientais.

**Palavras-chave:** ecossistemas de água doce; lago; interações inseto-macrófitas, macrófitas aquáticas; sudeste do Brasil.

## 1. Introduction

Phenotypic plasticity, defined as the ability of a genotype to express different phenotypes in response to varying biotic and abiotic conditions (Sultan, 2000), is a characteristic frequently observed in aquatic plants (Santamaría, 2002; Puijalon & Bornette, 2006; Eckert et al., 2016). This ability has been associated with adaptive traits to environmental changes in heterogeneous aquatic environments, e.g., variations in water level, shading, and water current (Medeiros et al., 2017; Carvalho et al., 2018). Morphological and histological changes in leaves are one of the most common examples of phenotypic plasticity in these plants in response to environmental heterogeneity (Wells & Pigliucci, 2000; Li et al., 2019). Although studies have shown that structural differences resulting from phenotypic plasticity in terrestrial plants can lead to significant bottom-up (i.e., effects of plant traits on higher trophic levels, such as herbivores and their natural enemies - Hunter & Price, 1992) impacts on associated insect communities (Bukovinszky et al., 2008; Demetrio et al., 2016; Ohgushi, 2016), there is limited information on how this occurs in aquatic plants (see Fares et al., 2022). In this context, species of the aquatic fern genus *Salvinia* provide an excellent model system due to their strong density-dependent morphological plasticity (Coelho et al., 2000; Boschilia et al., 2006), clonal growth forming dense mats (Room, 1983; Coelho et al., 2000), and well-documented interactions with herbivorous insects (Oliveira et al., 2025).

Plants of the genus *Salvinia* are modular organisms composed of iterative units known as ramets (Room, 1983). These structures consist of two photosynthetic floating leaves and one desiccated filamentous submerged leaf (Miranda & Schwartsburd, 2019). Due to efficient clonal reproduction, *Salvinia* species can form extensive mats on the water surface (Nagalingum et al., 2006; Gałka & Szmeja, 2013), a condition that can lead to population densification, which in turn induces morphological changes in their leaves (Coelho et al., 2000). Under high-density conditions, *Salvinia auriculata* Aubl. exhibits phenotypic plasticity, and its ramets develop significantly larger, folded, and vertically oriented floating leaves (Coelho et al., 2000), whereas under low-density conditions, *S. auriculata* produces smaller ramets with circular and flat leaves (Room, 1990; Gopal & Goel, 1993). These contrasting architectures may influence herbivory through multiple mechanisms (Hanley et al., 2007), including changes in leaf accessibility and apparency (Bröcher et al., 2023), and potential differences in mechanical resistance and tissue quality (Awmack & Leather, 2002), which may ultimately influence leaf palatability to herbivorous insects.

Floating leaves of *Salvinia* are susceptible to herbivory by various invertebrates, with larvae of the moth *Samea multiplicalis* (Guenée, 1854) (Lepidoptera, Pyralidae) being among the most common herbivores of these plants (Knopf & Habeck, 1976; Pelli et al., 2008). *Samea multiplicalis* is a lepidopteran species associated with aquatic environments found from North America to Argentina, which larvae feed on different species of floating aquatic plants (Knopf & Habeck, 1976). The larvae can consume up to 12% of the annual

biomass production of *Salvinia* spp. (Pelli et al., 2008). Caterpillars are one of the main groups of herbivorous insects and are typically found feeding on the abaxial side of leaves, a behavior considered a strategy to avoid predators, parasitoids, and adverse abiotic conditions such as wind and sunlight (Heinrich, 1979). However, it remains unclear whether phenotypic plasticity in aquatic plants can influence larval consumption and abundance.

Given this context, the aim of this study was to investigate whether phenotypic plasticity in *S. auriculata* induced by different density conditions influences the consumption and abundance of *S. multiplicalis* larvae. Our hypothesis is that high-density conditions induce morphological changes in *S. auriculata* that increase leaf size and structural complexity, and that these phenotypic differences promote higher larval abundance and herbivory by *S. multiplicalis*, potentially by providing greater refuge and more favorable microhabitats.

## 2. Material and Methods

The study was conducted in two stages. First, four weekly samplings (on October 1, 8, 15, and 22, 2022) were carried out, collecting approximately 30 clonal structures of *S. auriculata* from two ponds with high (>90% of the water surface covered by plants, 21°07'37.20"S / 44°13'37.67"W) and low (<20% of the water surface covered by plants, 21°07'28.73"S / 44°13'26.64"W) plant density conditions. Density categories were based on other studies that also evaluated this condition effect on aquatic macrophytes (e.g. Andrade et al., 2013; Coelho et al., 2000, 2005). These ponds are part of a floodplain system of the Rio das Mortes, located in the municipality of Santa Cruz de Minas, Minas Gerais. The two ponds are not directly connected and are approximately 135 meters apart. Plants were randomly collected from various points within each pond.

The presence of *S. multiplicalis* larvae was recorded, and the frequency of herbivory on the floating leaves of each *S. auriculata* ramet was quantified. All herbivory marks on *S. auriculata* leaves were attributed to *S. multiplicalis*, as it was the only herbivore observed on the plants during repeated surveys throughout the study period. Nevertheless, we acknowledge that this attribution is based on field observations and that undetected herbivores may have contributed to the observed damage. Subsequently, 30 ramets were randomly selected from the clonal structures, and the length and width of their floating leaves were measured, totaling 120 ramets and 240 leaves measured in each pond. In the second stage, we set an experiment in which two types of treatments were applied. Thirty *S. auriculata* intact ramets, showing no signs of herbivory, from each density condition (high and low) were placed in 500 ml polypropylene containers, and five *S. multiplicalis* larvae of similar lengths were released into each container. After seven days from the start of the experiment, the number of partially and fully consumed leaves was assessed. This stage aimed to identify whether *S. multiplicalis* larvae would exhibit differences in consumption between the two phenotypes.

### *2.1. Data analysis*

To test the effect of density on the morphological measurements of *S. auriculata* ramets, we used generalized linear mixed models with a Gaussian distribution, in which each morphological variable was used as the response variable and density condition as the predictor. In these models, ramet side (right or left) nested within ramet identity was included as a random effect. The models were built using the glmmTMB function from the glmmTMB package (Brooks et al., 2017).

To test whether there was a difference in the intensity of consumption by *S. multiplicalis* larvae on leaflets from high or low density conditions, we applied a chi-square test comparing the frequencies of unconsumed, partially consumed, and fully consumed leaves by density condition. We used a significance level of 5% ($\alpha = 0.05$), and all analyses were conducted in the R environment (R Core Team, 2023). Graphs were generated using the ggplot2 package (Wickham, 2016).

In addition to the inferential analyses described above, larval abundance and the proportion of ramets showing herbivory in each density condition were calculated for each sampling event and subsequently summarized across the study period to characterize field patterns. Herbivory frequency was assessed as the presence or absence of visible feeding damage on the floating leaves of each ramet. A ramet was considered herbivorized when at least one of its floating leaves showed signs of damage, and the proportion of herbivorized ramets was then calculated for each sampling event. The proportion of herbivory was obtained by dividing the number of ramets with visible damage by the total number of sampled ramets per sampling event.

## 3. Results

The morphological measurements of the floating leaves of *S. auriculata* were influenced by density, with leaves from the high-density condition exhibiting greater values for both length (Table 1, Figure 1, Figure 2A) and width (Table 1, Figure 1, Figure 2B).

The chi-square test result indicated no difference in the consumption intensity of *S. auriculata leaves* by *S. multiplicalis* larvae on ramets from different density conditions ($\chi^2$ = 3.0299, p = 0.3178). In plants from the high-density pond, a total of 38 *S. multiplicalis* larvae were found at different


**Figure 1.** High-density (A) and low-density (B) phenotypes of *S. auriculata*; C – Adult individual of *Samea multiplicalis*; D-F – *Samea multiplicalis* larvae; D – larvae on the abaxial surface and leaf damage caused by herbivory of *S. multiplicalis* larvae; E – *Samea multiplicalis* larva in a tunnel between *S. auriculata* ramets; F – *Samea multiplicalis* larva in its pupation cocoon feeding on *S. auriculata*.

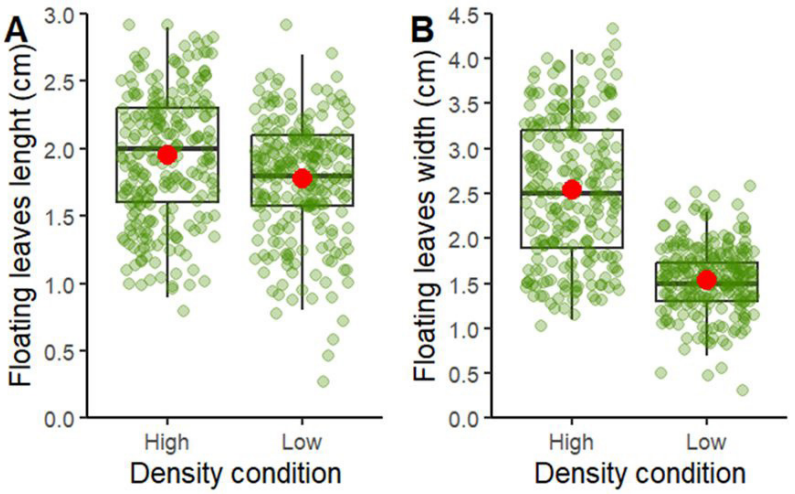


**Figure 2.** Leaf morphological variation of *Salvinia auriculata* ramets under different density conditions. A – Leaf length of floating leaves; B – Leaf width of floating leaves. The boxes represent the interquartile distance, and contain 50% of the data. The black lines are the median, and the red dot represents the mean. The whiskers represent the standard error. Each green point represents a measured leaf.

**Table 1.** Results of generalized linear mixed models for the effect of density on the morphological measurements of floating leaves of *Salvinia auriculata* exposed to different density conditions.

| Response variable | Source of variation | Estimate | Std. Error | z-value | p-value |
|---|---|---|---|---|---|
| Leaf length (cm) | Intercept | 1.95 | 0.03 | 61.28 | **<0.001** |
| | Low density | -0.17 | 0.03 | 5.73 | **<0.001** |
| Leaf width (cm) | Intercept | 2.53 | 0.04 | 55.87 | **<0.001** |
| | Low density | -0.99 | 0.04 | 22.57 | **<0.001** |

**Table 2.** Number of *Samea multiplicalis* larvae and *Salvinia auriculata* ramets showing signs of *S. multiplicalis* larval herbivory on floating leaves of ramets in the field along the sampling period.

| Sampling event | High density | | Low density | |
|---|---|---|---|---|
| | Larvae number | Number of consumed ramets | Larvae number | Number of consumed ramets |
| 01/oct | 7 | 25 | 1 | 2 |
| 08/oct | 12 | 30 | 0 | 2 |
| 15/oct | 8 | 26 | 0 | 0 |
| 22/oct | 11 | 28 | 0 | 1 |
| Total | 38 | 109 (90.83%) | 1 | 5 (4.16%) |

**Table 3.** Number and percentage of fully and partially consumed leaves during the consumption experiment of floating leaves from high- and low-density phenotypes of *Salvinia auriculata* by *Samea multiplicalis* larvae.

| High density ramets | | Low density ramets | |
|---|---|---|---|
| Fully consumed leaves | Partially consumed leaves | Fully consumed leaves | partially consumed leaves |
| 11 (18.33%) | 47 (78.33%) | 19 (31.66%) | 40 (66.66%) |

developmental stages. The larvae were located on the abaxial surface of the floating leaves, which in *Salvinia* plants face upward, or inside tunnels constructed by the larvae to move between ramets (Figure 1E). Regarding the damage caused by caterpillar herbivory, 90.83% (n = 120) of the analyzed clonal structures showed signs of *S. multiplicalis* herbivory. In contrast, in the low-density pond, only one *S. multiplicalis* larva was found, and only 4.16% of the analyzed clonal structures exhibited apparent herbivory damage by *S. multiplicalis* (Table 2)

In the experiment, the high-density treatment showed 78.33% of ramet leaves partially consumed, 18.33% fully consumed, and only 3.34% without any signs of herbivory. In the low-density treatment, 66.66% of the leaves were partially consumed, 31.66% fully consumed, and only 1.68% showed no herbivory damage (Table 3).

## 4. Discussion

We corroborated our hypothesis that different density conditions affect the leaf traits of *S. auriculata*. As observed by Coelho et al. (2000), our sampled *S. auriculata* ramets also exhibited density-dependent leaf phenotypic plasticity. The fact that ramets under high-density conditions showed larger, folded, and vertically oriented leaves is likely an adaptive morphological plastic response to intraspecific competition for sunlight, as this phenotype allows the plant to maximize leaf photosynthetic area, promoting growth under high competition (Coelho et al., 2000). Similar patterns have been observed in other floating aquatic plants, such as *Pontederia crassipes* (Pontederiaceae), which also exhibits vertical growth with petiole elongation under high-density conditions (Center & Spencer, 1981; Agami & Reddy, 1990; Andrade et al., 2013), *Pistia stratiotes* (Araceae), where density promoted increased leaf and rosette length (Coelho et al., 2005), and *Lemna minor* (Araceae), which showed larger leaves under high-density conditions (Kufel et al., 2018). Phenotypic plasticity in plants can be driven by herbivory (Karban & Baldwin, 1997; Ohgushi, 2016), which promotes the development of anti-herbivory strategies, typically physical and/or chemical, in plant tissues (Ohgushi, 2016). However, in the case of *S. auriculata*, leaf morphological variation appears to be driven primarily by density conditions (Coelho et al., 2000).

The results suggest that *S. multiplicalis* does not exhibit differences in consumption intensity of ramets according to phenotypic plasticity, as observed in the experimental condition. In contrast to the findings of Pelli et al. (2008), who under experimental conditions observed that *S. multiplicalis* larvae exhibit a preference for young over mature leaves of *Salvinia molesta* DS Mitchell. Other studies have shown that aquatic macrophytes escape herbivory by developing morphological and chemical defense strategies in response to herbivory (Lemoine et al., 2009; Fornoff & Gross, 2014; Thiébaut et al., 2017). In the Neotropical region, Fares et al. (2022) found that herbivory on *Montrichardia* spp. (Araceae), a common species of macrophyte, is influenced by abiotic factors (patch isolation and water depth) as well as plant traits (leaf characteristics and defense compounds).

One possible explanation for the lack of difference in consumption between phenotypes is that the morphological changes induced by density, although affecting leaf size and orientation, may not substantially alter leaf palatability or chemical defenses, resulting in similar acceptability for larvae (Awmack & Leather, 2002). In addition, structural differences between phenotypes may primarily influence habitat architecture rather than tissue quality, affecting herbivore distribution and establishment in the field but not feeding rates once larvae are in direct contact with the leaves (Ohgushi, 2005). It is also possible that the experimental conditions, which excluded predation and limited environmental variability, reduced the influence of plant structural traits on feeding behavior, leading larvae to consume available resources more uniformly (Hunter & Price, 1992). Our data show that *S. multiplicalis* larvae apparently consume leaves of both *S. auriculata* phenotypes, which may indicate that the anatomical and morphological modifications occurring in the transition from the low-density to high-density phenotype do not alter leaf palatability. This would be reasonable, as variation in leaf morphology does not necessarily imply differences in mechanical resistance or nutritional traits, which are key determinants of herbivore performance and consumption (Hanley et al., 2007). Even under high plant density conditions, few *S. multiplicalis* larvae were found, contrasting with the large number of ramets damaged by herbivory. A possible explanation for this pattern is the presence of predators in the sampled area. *Samea multiplicalis* larvae are preyed upon by various social wasps (Oliveira et al., 2023; Oliveira & Souza, 2023), Furnariid birds (Oliveira, 2024), and likely spiders (Oliveira & Brescovit, 2024). Additionally, Parys & Johnson (2012) observed that fire ants, *Solenopsis invicta* (Hymenoptera: Formicidae), prey on *S. multiplicalis* larvae and eggs, while Knopf & Habeck (1976) demonstrated that 52% of observed *S. multiplicalis* larvae were parasitized by dipteran and parasitoid wasps. This could also explain the higher density of *S. multiplicalis* larvae on *Salvinia* plants with the high-density phenotype, as larger, folded, and vertically oriented leaves may provide shelter to larvae, reducing predation pressure. Conversely, low-density phenotype ramets, with smaller and flat leaves, likely expose larvae more to predators. A similar situation has been observed in terrestrial plants, in which Watanabe et al. (2018) found in experimental conditions that lepidopteran larvae on the adaxial leaf surface were more parasitized than those on the abaxial surface, thus being more susceptible to natural predators.

The greater abundance of *S. multiplicalis* larvae in the high-density phenotype of *S. auriculata* may also be explained by the fact that *Salvinia* spp. form extensive mats through vegetative growth (Julien et al., 2002; Coelho et al., 2005), a condition that can provide greater substrate stability where *S. multiplicalis* larvae reside. According to Knopf & Habeck (1976) and personal observations, *S. multiplicalis* larvae exhibit high motility and construct tunnels at the base of floating leaves to move between ramets. During this movement, there is likely an increased risk of accidental death by drowning, similar to what has been observed in the migration of semi-aquatic beetle larvae among floating leaves of yellow water-lily, *Nuphar lutea* (Nymphaeaceae) (Kouki, 1991). These authors further suggest that beetles achieve greater success in establishing large populations where dense water-lily populations occur with shorter distances between leaves, thereby reducing the risk of drowning from accidental falls. Additionally, aspects of the biology of *S. multiplicalis* may have contributed to the greater abundance of larvae in the high-density phenotype, as larvae approaching the pupation stage cease movement and fix themselves by constructing a cocoon-like structure made of silk, binding the faces of the ramet leaves (Figure 1F), and continue feeding near this site until pupation begins. Therefore, the high-density phenotype, characterized by larger, folded, and upward-facing leaves, apparently facilitates the construction of the pupation cocoon.

On the other hand, under low-density conditions, since most of the water surface is free of *S. auriculata*, the water surface becomes more susceptible to wind action, which causes small waves and unpredictable movements of *S. auriculata* plants. This also causes ruptures in the rhizomes, fragmenting their ramets and favoring clonal dispersal (Li et al., 2018). During different times of the day, the plants are displaced in various directions within the pond according to wind direction. These conditions promote instability of *S. auriculata* plants, which can hinder the establishment and herbivory by *S. multiplicalis* larvae. In terrestrial plants, aphid herbivory was negatively affected in plant parts exposed to wind (Devegili et al., 2019). Similarly, under experimental conditions, Chen et al. (2018) showed that wind can negatively affect the survival and development of some moth larvae species. Therefore, environmental factors such as wind can negatively influence insect herbivory by directly affecting these herbivores (i.e., bottom-up factors) (Maguire et al., 2016).

## 5. Conclusion

Our results showed that *S. auriculata* exhibits leaf phenotypic plasticity dependent on density, and this condition appears to favor the establishment and herbivory by *S. multiplicalis*, as this phenotype may provide refuges against predation and abiotic factors. Therefore, despite differences caused by leaf phenotypic plasticity apparently not altering the intensity of ramet consumption, *S. multiplicalis* larvae are less abundant on low-density ramets because they provide a less stable substrate and make the larvae more visible and susceptible to predators. These findings highlight the importance of phenotypic plasticity as a driver of plant–herbivore interactions in aquatic systems, suggesting that structural changes in plant architecture can influence herbivore distribution and abundance even when leaf-level consumption remains unchanged. More broadly, our study contributes to understanding how density-dependent plant traits can mediate ecological interactions by shaping habitat structure and refuge availability. Future studies should investigate the role of chemical and mechanical leaf traits, as well as the influence of predators, to better disentangle the mechanisms linking plant plasticity and herbivory in aquatic environments. In addition, evaluating how environmental variability (e.g., wind disturbance or habitat connectivity) and predator pressure interact with plant density to shape herbivore dynamics would provide a more comprehensive understanding of these interactions.

## Data availability

The entire dataset supporting the results of this study has been published in the article itself.

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Received: 11 June 2025
Accepted: 06 May 2026

**Associate Editor:** Thaisa Sala Michelan.