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The importance of heterogeneity over dominant species in associations between wetland epiphytic invertebrate assemblages and hydrophytes

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Abstract

Macroinvertebrate and hydrophyte interactions influence wetland ecosystem structure and function. Submerged hydrophytes with dissected leaves are predicted to enhance macroinvertebrate diversity and abundance while nonnative hydrophytes often suppress metrics. However, such patterns are not universal among ecosystems. We collected macroinvertebrates from a North American temperate wetland dominated by one of four hydrophyte species with disparate growth forms, including one invasive species (*Hydrachoris morsus-ranae*). When macroinvertebrates were compared using the dominant hydrophyte as a categorical designation, results countered expectations. The sole hydrophyte with a submerged growth form (*Ceratophyllum demersum*) harbored significantly lower arthropod diversity and fewer mollusks than *H. morsus-ranae*. *Nuphar lutea*, with floating leaves, supported intermediate macroinvertebrate diversity and abundance due to favorable oxygen conditions and association with emergent hydrophytes. Despite results, a multivariate approach that included structural attributes of all encountered hydrophytes affirmed a positive relationship between submerged hydrophyte cover and arthropod abundance and diversity. Our results demonstrate the capacity of hydrophytes to harbor distinct macroinvertebrate assemblages among species but also reinforce the need to consider all hydrophytes and not just the dominant species. Patches of invasive wetland hydrophytes may also be capable of supporting greater biodiversity and abundance relative to native species. Finally, our findings affirm the importance of sub-dominant hydrophytes and assemblage-scale heterogeneity when assessing the capacity to support macroinvertebrates.

Introduction

Aquatic macroinvertebrates substantially contribute to the structural and functional attributes of wetland ecosystems. For instance, shredding macroinvertebrates such as caddisfly (Limnephilidae) and cranefly (Tipulidae) larvae can provide the first level of detritus processing in wetlands, with greater diversity yielding greater rates of litter conversion (Huryn et al. 2002; Wissinger et al. 2021). Mollusk grazing often serves as the primary biological mechanism limiting periphyton populations and promoting denitrification in many aquatic systems (Atkinson et al. 2023). Many wetland benthic macroinvertebrates also create habitat (e.g. empty shells, cases, nettings, and burrows) and aerate sediments through bioturbation (Chakraborty et al. 2022). Additionally, macroinvertebrates serve as indicators to assess wetland ecological integrity, as key common taxonomic groups like some Plecoptera in the Nemouridae family, the bivalve family Sphaeriidae, and the Ephemeroptera genus *Caenis* are acutely sensitive to impacted water quality or habitat degradation (Feio et al. 2007; Liston et al. 2008; Menetrey et al. 2008; Nguyen et al. 2017; Edwards 2021). Consequently, understanding the physical and chemical attributes that significantly structure macroinvertebrate wetland assemblages can advance an understanding of ecological structure and functions.

Concurrently, vascular plants fulfill critical ecological roles that directly shape wetland ecosystems, including macroinvertebrate assemblages. Aquatic hydrophytes engineer wetlands through nutrient cycling, water purification, and habitat creation (Li et al. 2013; Thomaz 2023; Srivastava et al. 2008). Such hydrophytes can effectively reduce the concentrations of key elements such as P, Na, and Ca as well as total suspended solids

and some heavy metals that some invertebrates are sensitive to (Makumbe et al. 2022; Banda et al. 2023). Hydrophytes also provide grazing habitat by forming structure for epiphytic algae; thus, hydrophyte diversity and biomass often promote macroinvertebrate diversity and richness (Nascimento-Filho et al. 2021). Additionally, hydrophytes support microbial communities via nutritional root exudation that are distinctly unique to the plant species (Crump & Koch 2008). Such microbial diversity and richness help to sustain biogeochemical processes in wetlands like nitrification, humification, and absorption of nutrients into the sediment (Chandra et al. 2020).

Yet invasive wetland plants specifically may form nuanced relationships with macroinvertebrate assemblages. For example, Verdonschot & Verdonschut (2013) found that macroinvertebrate assemblages in the Netherlands were not immediately impacted by the low light and hypoxic conditions caused by invading hydrophytes like *Elodea nuttallii* and *Phragmites australis*. However, assemblages eventually did change with long term conditions: macroinvertebrates with low mobility eventually decreased while swimming taxa increased in abundance. Some common invasive hydrophytes in the eastern United States, such as *Trapa natans* and *Hydrilla verticillata,* harbor highly biodiverse assemblages (Theel et al. 2008; Kornijów et al. 2010). However, in other settings invasive wetland plant species can induce the opposite effect. Stiers et al. (2011) in Belgium observed more negative invertebrate compositional changes in ponds with invasive *Hydrocotyle ranunculoides*, *Ludwigia grandiflora*, and *Myriophyllum aquaticum* growing in high densities, including the complete loss of sensitive macroinvertebrates like Ephemeroptera.

Wetland hydrophytes create physical habitat for invertebrates; therefore, plant structure can determine the nature of such interactions. Macroinvertebrates may directly rely on leaves, stems, roots, and flower/fruits as a food source or for a physical template for foraging. A foundational hypothesis proposed by Krecker (1939) posited that hydrophyte structural complexity promotes invertebrate diversity and abundance. Krecker tested this hypothesis among species of submerged, leafy hydrophytes in Lake Erie and found that the most structurally complex species (*Myriophyllum spicatum*) supported significantly more invertebrates. In a later effort that focused on mollusks, Lodge (1985), found submerged hydrophyte species supported more diverse and abundance mollusks, likely because periphyton are more diverse and abundant in submerged, complex hydrophytes (Warfe & Barmuta 2006; Hao et al. 2017). However, support for the theory may vary among aquatic ecosystems. Although Ferreiro et al. (2011) detected greater invertebrate abundance associated with hydrophyte complexity, the biomass, richness, and diversity of invertebrates. Support for the Krecker hypothesis has been generally confirmed in lentic habitats, with submerged hydrophytes and especially species that promote diverse periphyton assemblages capable of supporting abundant and diverse macroinvertebrates (Humphries 1996; Xie et al. 2005; Cremona et al. 2008; Fontanarrosa et al. 2012; Ferreiro 2013; Pettit et al. 2015; Wang et al. 2025).

Given the ecological importance of hydrophyte and invertebrate interactions, we aimed to determine how arthropod and mollusk assemblage structure varied among dominant hydrophyte species in a temperate wetland. Metrics of diversity, abundance, and assemblage composition for arthropods and mollusks separately were compared among

three native and one invasive hydrophyte species. We hypothesized that we would detect distinct patterns of assemblage structure among our four target hydrophyte species given their distinct growth patterns and anatomical structures. The single submerged hydrophyte that we considered, *Cerotophyllum demersum*, was expected to harbor the most abundant and diverse assemblages as posited by the Krecker hypothesis. Furthermore, we predicted that the invasive hydrophyte (*Hydrocharis morsus-ranae*) would support fewer invertebrates and harbor assemblages with lower diversities given the invasive status of this plant. Finally, we compared arthropod assemblages in the context of plant structural attributes beyond our four species categorical designation to determine if hydrophyte growth forms offered additional explanatory power. Our findings are meant to advance an understanding of how hydrophytes shape invertebrate communities in botanically diverse wetland complexes.

Methods

Study site

The 2.4 km^2 Jamestown Audubon Community Nature Center (ACNC) is a wetland reserve maintained by a chapter of the Audubon Society in Chautauqua County, New York state in the United States of America (42.024554°, -79.1708858°). Most land within the reserve is a mixture of emergent herbaceous wetlands and mixed hardwood/deciduous forests with a canopy dominated by *Quercus*, *Acer*, and *Tsuga* species. Our study was conducted in two wetland pond complexes locally termed the Big Pond and Turtle Pond East. The pond wetlands are separated by approximately ~200 m of relatively high terrain but are

connected through culverts and groundwater. The ACNC is located within the warm-summer humid continental (D6b) climate zone, with a mean annual precipitation of ~1167 mm (NOAA 2026).

Study areas within the wetland were broadly categorized into microhabitats representing the dominant wetland plant among four common hydrophyte species: *Nuphar lutea* (Yellow Pond Lily), *Brasenia schreberi* (Watershield), *Hydrocharis morsus-ranae L.* (European Frogbit), and *Cerotophyllum demersum* (Coontail). *N. lutea* and *B. schreberi* (both in the order Nymphaeales) have simple broad leaves although *N. lutea* grows much larger leaves, ranging around 40 cm long and 30 cm wide (Nash & Stroupe 1998). *H. morsus-ranae*, the sole invasive species investigated, grows simple, rounded leaves while *C. demersum* produces short, whorled leaves. Only *N. lutea* and *B. schreberi* have true rhizomes that are directly connected to the substrate, while *H. morsus-ranae* and *C. demersum* have stolons and rhizoids, respectively. Growth density was also included in our analysis, as the structural complexity of both *C. demersum* and *B. schreberi* creates enhanced horizontal (on the water surface) and vertical (amongst the water column to the sediment) plant biomass density. *N. lutea* and *H. morsus-ranae* do not form such growth patterns under the surface.

Field and laboratory methods

Sections of the ACNC wetlands dominated by one of the four species were selected for organism sampling. Our criteria for categorizing an area as dominated by one of the four species included the following criteria: 1) coverage of the target species ≥50% that 2)

consisted of an area ≥25 m^2. Additionally, designated study areas 3) possessed a depth that was accessible for technicians using chest waders but was also 4) ≥5 m away from banks, large tree or log snags, or inflows.

For each target hydrophyte, four plots were selected in wetland areas with a dominant hydrophyte species. Within each plot we randomly selected 5, 1-m^2 subplots to sample from, giving a sample size of 80, which allows for statistical sound analysis (Cheruvelil et al. 2000). A single PME miniDOT ® logger 7450 dissolved oxygen automated sensor (Precision Measurement Engineering Inc. (PME), Vista, CA, United States) was placed in the center subplot of one randomly selected plot of each hydrophyte species at a depth of 0.3 meters that recorded dissolved oxygen and temperature data every 15 minutes.

Sampling was conducted using an adjusted sweeping protocol from the United States Geological Survey (Keith et al. 2022) that included both benthic and water column sweeps with dip nets at each subplot. Subplots closest to the edges of the plot were sampled first to minimize disturbance in adjacent subplots. A 1-m^2 PVC quadrant was placed over the selected subplot and staked down facing the technician. We completed a standard estimate of plant coverage (%) of all hydrophyte species encountered in the subplot and collected a depth reading at the time of sampling prior to entering the sampling zone. Subsequently, a modified dip net with 0.5 mm mesh (angled to 90 degrees facing upwards) was used three times on the closest side of the quadrat, going left to right for a water column sweep, careful not to go low enough to disturb sediment. Invertebrate collection was completed between July 21st and August 2nd, 2025, which likely had less overall

diversity than autumn months, but allowed for the highest diversity available for the peak growth periods and maturity of our target plant species (Hill et al. 2016).

Any plant material on top of the net was gently pushed over the rim. Due to occasional large patches of deep, fine sediment, gentle net shaking by the technician was used to reduce captured sediment. Bycatch organisms such as fish or amphibians were released back into the wetland. All plant material, sediment, and macroinvertebrates were preserved in 70% ethanol.

Samples were stored in a temperature-controlled area with limited exposure to light. Macroinvertebrates were extracted from plant material and sediments within three weeks of sampling to limit degradation. Sediment and large pieces of vegetation were filtered out of the samples via a five mm sieve and gently shaken with water and hands for around 20 minutes. Each subplot sample was processed for thirty minutes and placed into a singular vial of 70% ethanol solution. Macroinvertebrates were identified to the lowest feasible taxa, with a goal of genus for arthropods and species for mollusks. The primary taxonomic references used were Merritt et al. (2019), Arnett & Thomas (2000), Burch (1975), and Burch (1982).

Statistical Analysis

Our primary objective was to compare abundance, diversity metrics, and community composition of mollusk and arthropod assemblages among the four dominant hydrophyte species in the wetland. We employed a mix of parametric models, generalized linear models, and multivariate statistics to assess such differences.

We first aimed to characterize physical characteristics and plant community attributes of sampling locations in each of the four dominant hydrophyte categories. Depth was recorded in each subsample, and the mean depths were compared among the four hydrophytes with an analysis of variance (ANOVA) model. We also calculated the proportion of time dissolved oxygen was recorded above the thresholds of 1 and 2 mg/L, the points just above hypoxic and anoxic conditions, in each of the four hydrophyte stations and in open water. Hydrophyte assemblages of all plant species among the four dominant hydrophyte categories were compared using non-metric multidimensional scaling (NMDS) ordination with the total cover of each species as the input variable.

Diversity metrics for mollusks were not calculated due to a high frequency of samples that lacked individuals (30 out of 80 sites). However, we compared mean mollusk abundance among the four dominant hydrophytes using a generalized linear model (GLM). Although we first considered a Poisson distribution, the model was overdispersed. We therefore assessed mean abundance using a negative binomial distribution. Pairwise comparisons among hydrophyte categories were conducted using estimated marginal means (Tukey-adjusted) on the response scale. Mollusk assemblages with one or more specimens were compared among hydrophyte categories using an NMDS ordination. This was complemented by a permutational analysis of variance (PERMANOVA) analysis with 999 permutations to assess if community-scale differences were statistically significant. Potential quantitative relationships between individual species and the ordination were assessed using vector fitting by regressing each species count onto the ordination axes.

Statistically significant taxa were those associated with the axes at the $\alpha<0.05$ threshold via permutation testing with 999 permutations.

Arthropods were more abundant than mollusks, which allowed us to calculate several diversity metrics. Mean arthropod richness, evenness, Shannon-Weiner biodiversity, and abundance were compared among dominant hydrophyte species. Diversity metrics were statistically compared with ANOVA models, and the abundance (counts) were compared using a GLM model with a negative binomial distribution. Community composition was compared in an NMDS ordination on Hellinger-transformed count data followed by a PERMANOVA analysis. As with mollusks, we assessed taxonomic relationships with ordination axes via vector fitting and permutational analyses. Taxa were considered significantly associated with the axes at $\alpha<0.05$ following 999 permutations.

We also explored relationship between arthropod diversity and hydrophyte structural attributes. Each of the fifteen encountered hydrophyte species was categorized by growth form (emergent, submerged, floating leaf, or free-floating), whether the species was rooted to the substrate, and by the presence or absence of finely dissected leaves. For each sample, we summed percent cover across all recorded species within each trait category (rooted, finely dissected, and each growth form) to generate sample-level structural cover total. A principal components analysis (PCA) was performed on these sample-level structural cover totals. Axes with eigenvalues greater than 1.0 were retained for further analyses. Subsequently, we performed a likelihood ratio test (for abundance) and F-tests (for Shannon diversity) to determine if principal component axes explained significantly more variance for arthropod diversity and abundance than the models with dominant

hydrophyte category alone. Resulting p-values were corrected for multiple comparisons across response variables using the Holm method. For response variables with a significant improvement in fit, we examined individual PCA coefficients to identify the direction and magnitude of structural associations and assessed correlations between species-level cover with PCA scores to confirm that axis associations were not attributable to a single hydrophyte species.

All statistical models and ordination systems were developed using R version 4.5.3 (R Core Team 2026). Models with negative binomial distributions were assessed with package MASS (Ripley & Venables 2002) and overdispersion analyses with package performance (Lüdecke et al. 2021). Diversity metrics, NMDS ordinations, and permutational vector analyses of taxa associations with ordination axes were calculated using package *vegan* (Oksanen et al. 2026). PERMANOVA models were developed with package *adonis* (Stevens 2019) and post-hoc comparisons were made using *pairwiseAdonis* (Martinez Arbizu 2020).

Results

Physical conditions varied among patches dominated by target hydrophytes. Dissolved oxygen (DO) concentrations at 0.3 m depth throughout the wetland complex were highly heterogeneous and subject to strong diel signals (Fig. 1). In open water, the highest recorded values reached >6 mg/L during the day and occasionally near zero overnight. Levels recorded by sensors deployed in the four dominant hydrophytes were uniformly lower, with anoxic conditions dominating in *H. morsus-ranae* and *B. schreberi*. Values within the *N. lutea* patch were the highest among the four hydrophytes followed by *C.*

dermersum. The mean proportion of time that each DO sensor deployed within a hydrophyte patch recorded values above 1 mg/L among deployment dates was under 50% in all four sites and near zero for *H. morsus-ranae* and *B. schreberi*. Mean sample point depths varied among dominant hydrophyte categories ($F_{3,72}$=3.2, p=0.0285) and ranged from 71.8 cm in *C. demersum* to 85.0 cm to *H. morsus-ranae* locations. However, post-hoc Tukey comparisons noted only one significant difference between hydrophyte categories, that of *C. demersum* and *H. morsus-ranae* (p=0.021).

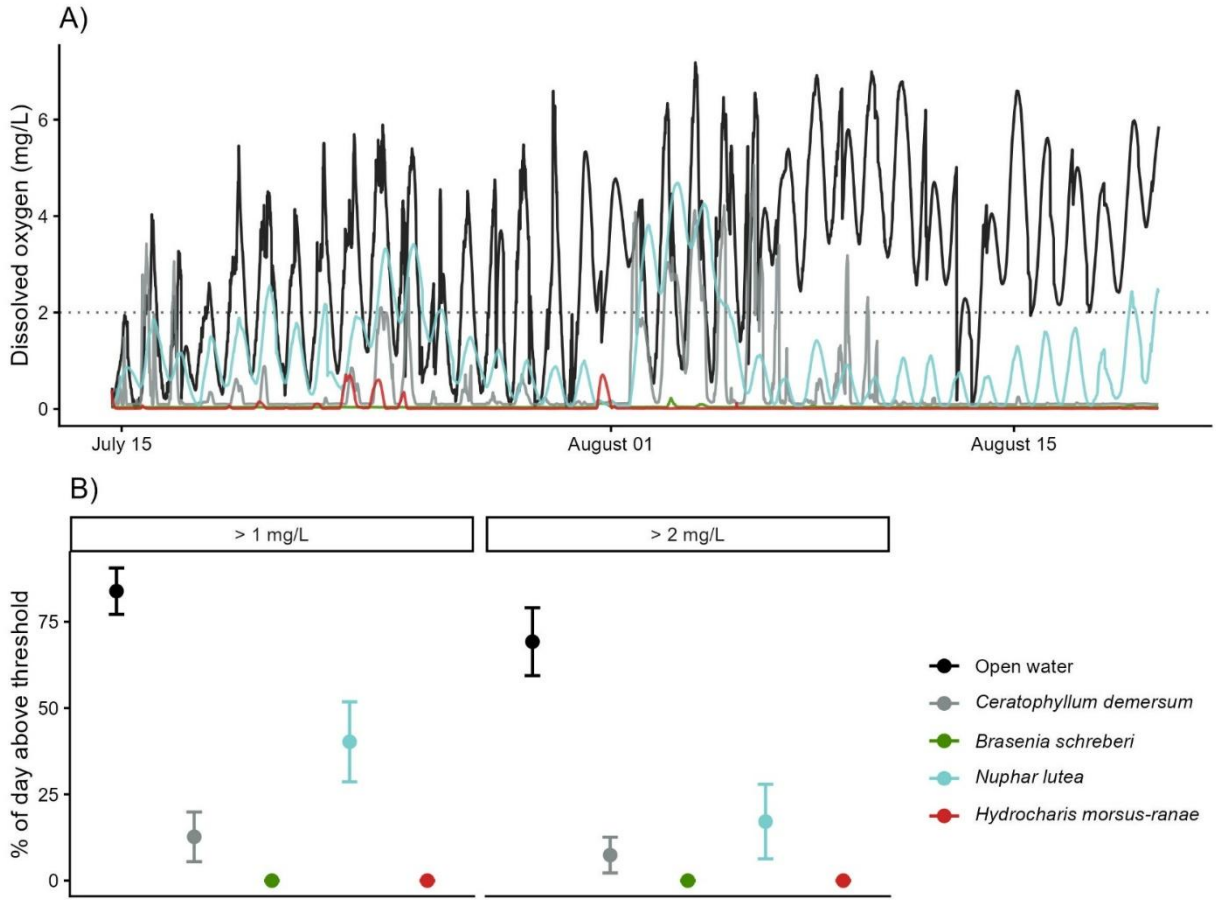
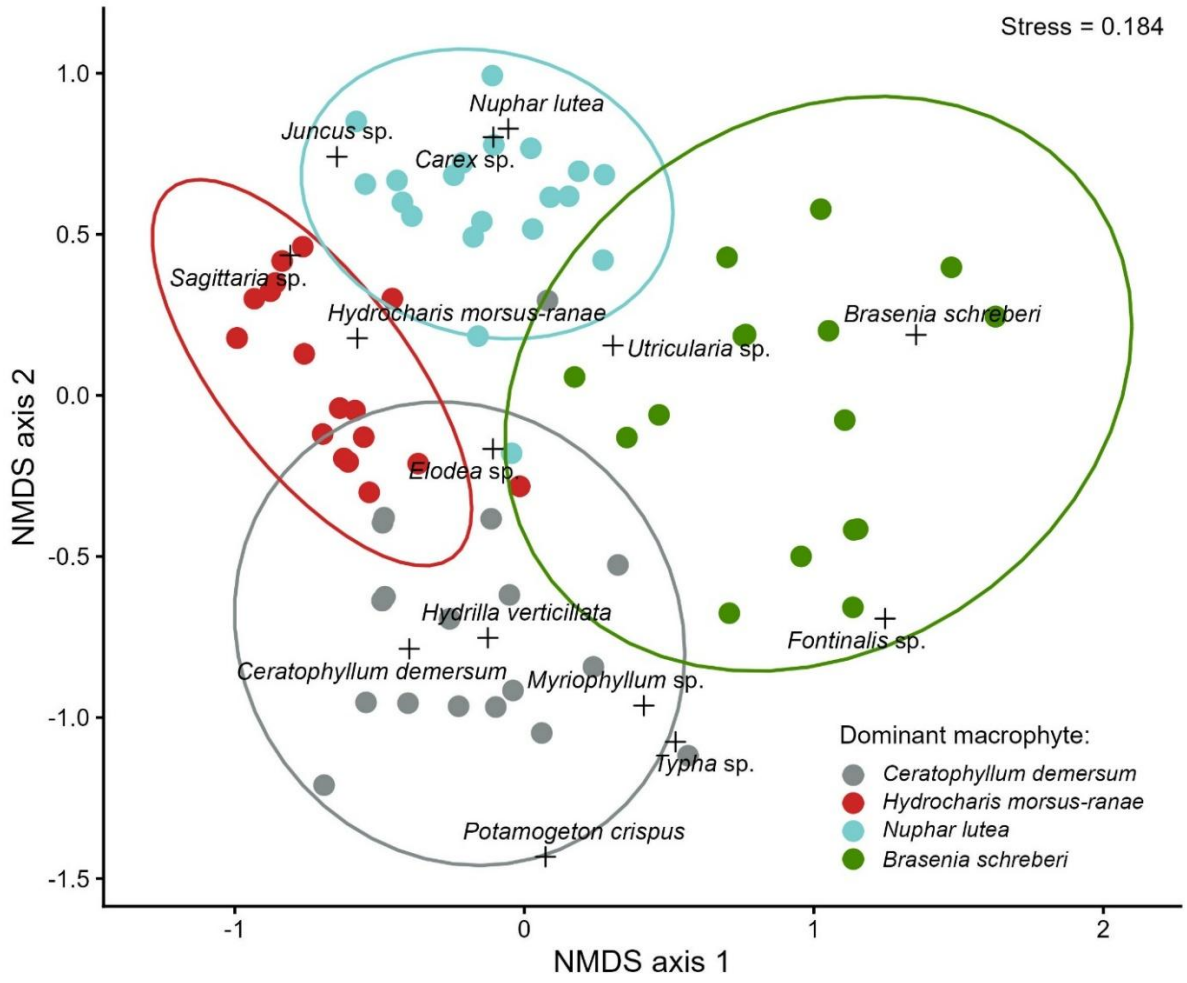


Fig.1 (a) Dissolved oxygen profiles recorded at sensors deployed in 0.3 m of water within each dominant hydrophyte and an open water reference site. (b) Mean daily proportions of readings above 1 and 2 mg/L at each station among dominant hydrophyte categories.

Plant assemblages were largely coherent within wetland areas dominated by the study target hydrophytes. An NMDS ordination (stress=0.184) revealed clear separation of hydrophyte assemblages as designated by our four dominant target species and non-target species that consistently associate with them (Fig. 2). For example, wetland areas with abundant *N. lutea* were commonly encountered with rushes (*Juncus* sp.) and sedges (*Carex* sp.) while *C. demersum* was commonly associated with *Hydrilla verticillata*, *Myriophylllum* sp., and *Typha* sp. One hydrophyte, *Elodea* sp., was found to be relatively cosmopolitan within the wetland.



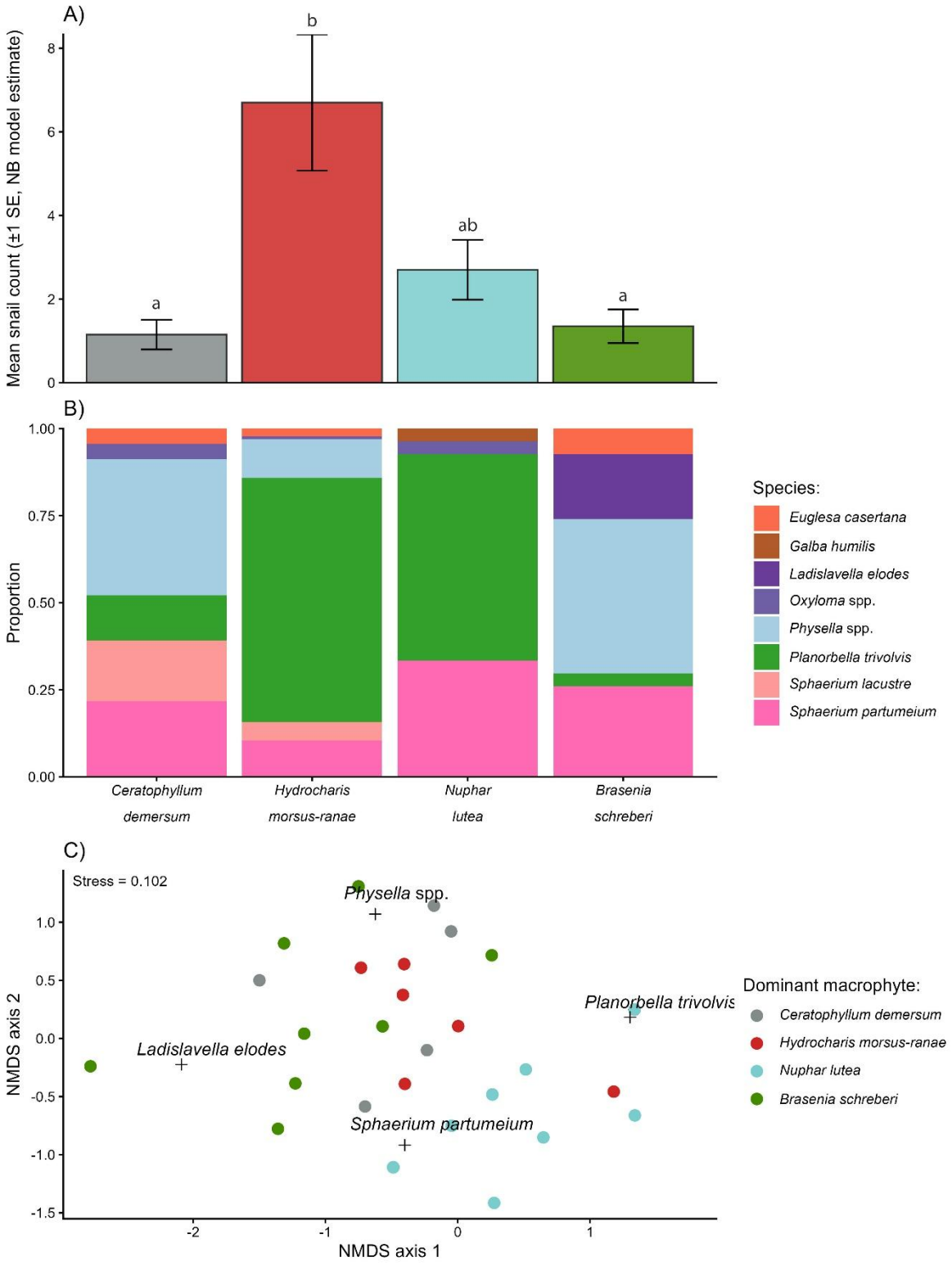
264

265 **Fig. 2** A non-metric multidimensional scaling ordination system of hydrophyte cover at
266 each sampling location. Ellipses represent 95% confidence intervals for each dominant
267 hydrophyte category. Coordinates for all encountered hydrophyte taxa are shown.

268

269 Mollusk assemblages appeared to be distinct among our target hydrophyte species. We
270 recovered a total of 238 mollusks from our collections from 7 genera and 6 species. Among
271 all individuals, 198 were identified to species and 40 to genus. Samples lacking mollusks
272 were common, with 30 out of 80 total (37.5%) containing no mollusks. A generalized linear

model with a negative bimodal distribution revealed significant (χ^2=28.1, df=3, p<0.0001) differences in mollusk abundance among target hydrophytes, with the most collected from *H. morsus-ranae* and the least from *C. demersum* (Fig. 3A). Post-hoc comparisons indicated that the only significant difference in mollusk means among hydrophytes were between *H. morsus-ranae* and both *B. schreberi* (Z=4.1, p=0.0002) and *C. demersum* (Z=4.4, p<0.0001). The difference between *H. morsus-ranae* and *N. lutea* was marginally significant (Z=2.5, p=0.0591).


A)
Mean snail count (±1 SE, NB model estimate)
a
b
ab
a
B)
Proportion
Ceratophyllum demersum
Hydrocharis morsus-ranae
Nuphar lutea
Brasenia schreberi
Species:
Euglesa casertana
Galba humilis
Ladislavella elodes
Oxyloma spp.
Physella spp.
Planorbella trivolvis
Sphaerium lacustre
Sphaerium partumeium
C)
Stress = 0.102
Physella spp.
Planorbella trivolvis
Ladislavella elodes
Sphaerium partumeium
NMDS axis 1
NMDS axis 2
Dominant macrophyte:
Ceratophyllum demersum
Hydrocharis morsus-ranae
Nuphar lutea
Brasenia schreberi

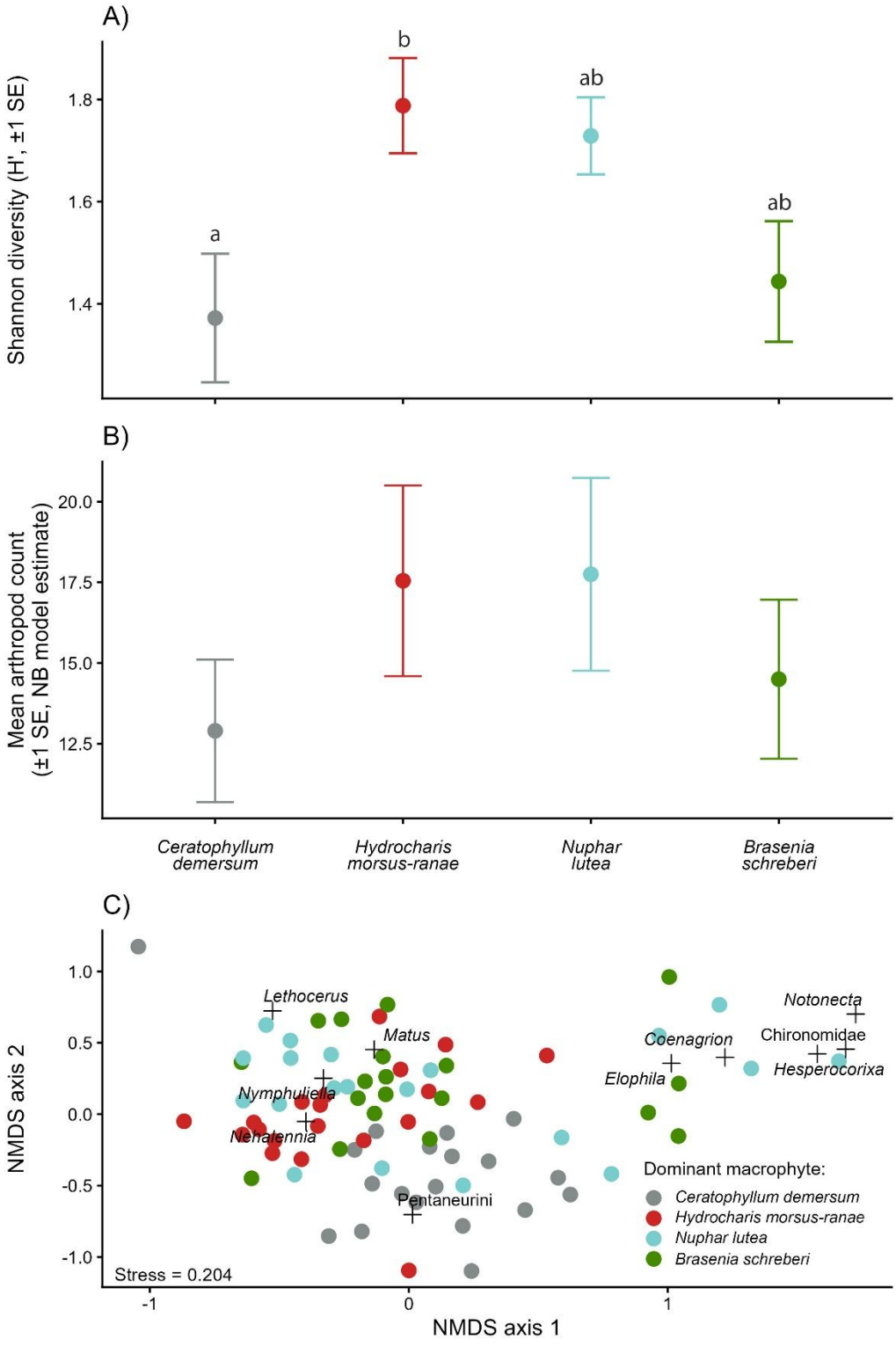
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Fig. 3 Snail assemblage attributes among dominant hydrophyte categories. (a) Mean abundance (±1 standard error derived from the GLM model) among hydrophytes. Letters denote significant differences between means at α=0.05. (b) The proportion of each mollusk taxon totaled among hydrophyte categories. (c) An NMDS ordination of mollusk assemblages. Taxa shown represent only those with coordinates significantly associated with the ordination axes using vector fitting. Taxonomic proportions and NMDS scores were calculated only from samples where mollusks were present.

The structure of mollusk assemblages also differed among hydrophytes. Samples collected from *H. morsus-ranae* and *N. lutea* were dominated by *Planorbella trivolvis*, while *Physella* spp. dominated in *B. schreberi* and *C. demersum* (Fig. 3B). An NMDS ordination (stress=0.102) revealed distinct clustering in mollusk assemblages among some hydrophyte species, especially *N. lutea* and to a lesser degree *C. demersum* (Fig. 3C). A PERMANOVA model confirmed that snail assemblages were significantly different among hydrophyte categories ($F=4.5$, $R^2=0.22$, $p<0.001$). Post-hoc comparisons suggested that all pairwise differences in mollusk assemblages among target hydrophytes were significantly different ($p\leq0.004$) except between *C. demersum* and *B. schreberi* ($p=0.251$) and between *N. lutea* and *H. morsus-ranae* ($p=0.054$).

Arthropods were relatively more abundant with assemblages that varied among target hydrophytes. The number of arthropods retrieved from samples ranged from 1 to 46, with a total of 1254 individuals summed from all samples. Among arthropods, 87% were

identifiable to genus. A GLM with a negative binomial distribution suggested that mean arthropod abundance did not significantly vary among hydrophyte categories (χ^2=2.5, df=3, p=0.4813). Similarly, an ANOVA model comparing mean evenness values among samples revealed no meaningful differences ($F_{3,75}$=4.8, p=0.7000). But an ANOVA model comparing the means of Shannon-Weiner biodiversity among samples showed significant differences ($F_{3,75}$=3.9, p=0.0127, Fig. 4A). Post-hoc comparisons indicated significant pairwise differences in Shannon-Weiner diversity only between *H. morsus-ranae* and *C. demersum* (p=0.0328).


A)
Shannon diversity (H', ±1 SE)
1.8
1.6
1.4
a
b
ab
ab
B)
Mean arthropod count
(±1 SE, NB model estimate)
20.0
17.5
15.0
12.5
Ceratophyllum demersum
Hydrocharis morsus-ranae
Nuphar lutea
Brasenia schreberi
C)
NMDS axis 2
1.0
0.5
0.0
-0.5
-1.0
Lethocerus
Matus
Nymphuliella
Nehalennia
Pentaneurini
Notonecta
Coenagrion
Chironomidae
Elophila
Hesperocorixa
Dominant macrophyte:
Ceratophyllum demersum
Hydrocharis morsus-ranae
Nuphar lutea
Brasenia schreberi
Stress = 0.204
-1
0
1
NMDS axis 1

310

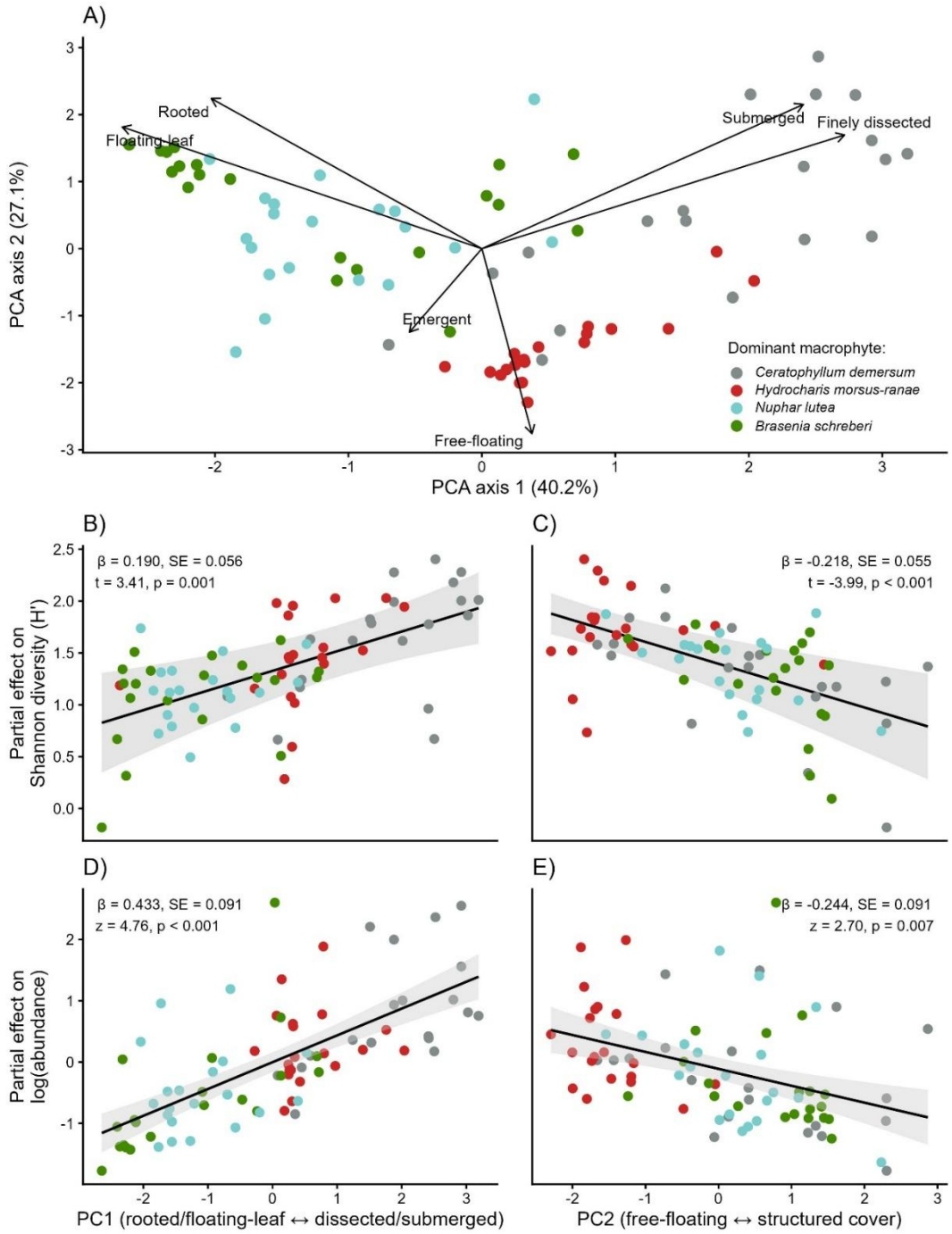
311 **Fig. 4** Mean (±1 SE) Shannon diversity (a) and abundance (b) of arthropods retrieved from
312 samples among the four target hydrophyte categories. Letters denote significant
313 differences between means at α=0.05. (b) An NMDS ordination of arthropod assemblages
314 with coordinates of species found to be significantly associated with the ordination axes
315 shown.

316

317 Arthropod assemblage structure varied among the four hydrophyte categories, albeit to a
318 lesser degree than mollusks. An NMDS ordination (stress=0.204) revealed both separation
319 and overlap of arthropod assemblages among target hydrophyte species (Fig 4C).
320 Assemblages collected from *C. demersum* were relatively consistently distinct from those
321 collected in *H. morsus-ranae* patches. In contrast, assemblages from *N. lutea* and *B.*
322 *schreberi* patches overlapped broadly with the other two categories in ordination space. A
323 PERMANOVA model indicated significant differences in assemblage composition among
324 hydrophyte categories ($F=3.3$, $R^2=0.12$, $p=0.0010$). Post-hoc comparisons indicated
325 significant differences in all pairwise comparisons ($p \leq 0.026$) except for between *N. lutea*
326 and *B. schreberi* ($p=0.22$). The coordinates of ten taxa were significantly aligned with the
327 ordination axes, including three heteropterans, three zygopterans, chironomids, and two
328 lepidopterans.

329 The abundance and diversity of arthropods appear to be significantly associated with plant
330 structural attributes. A principal components analysis (PCA) of structural attributes for all
331 encountered hydrophyte species indicated distinct clustering among our four categories

(Fig 5A). The first two axes accounted for 67.1% of structural attributes, with the first axis (40.2% variance) aligned with a gradient of roots and floating leaves to submerged and finely dissected leaf structures. The second axis (27.1% variance) primarily separated samples with free-floating vegetation from others. Several non-target hydrophyte species were correlated with PCA axes. For instance, *Myriophyllum* sp. (r=0.58, n=13) and *Juncus* sp. (r=-0.636, n=14) were positively and negatively correlated with PCA axis 1, respectively. *Elodea* sp. (r=0.46, n=10) and *Myriophyllum* sp. (r=0.46, n=13) were positively correlated with PCA axis 2 while *Sagittaria* sp. was negatively correlated (r=-0.41, n=9). Nested model comparisons indicated that including PCA axes significantly improved predictive power over models with only the dominant hydrophyte category for both arthropod abundance (likelihood-ratio χ^2=19.4, p=0.0002) and diversity ($F_{3,72}$=7.2, p=0.0003). In the full model with PC axes and the original hydrophyte category, PC axes 1 and 2 were positively and negatively associated with Shannon diversity, respectively (Figs 5B and 5C). The same directional pattern was observed for the abundance model (Figs 5D and 5E).



346

347 **Fig. 5** (a) A principal components analysis (PCA) biplot of hydrophyte assemblages among

348 sample locations based on percent cover of structural attributes. After accounting for the

effects of hydrophyte category, both PC axes significantly predicted additional variance in arthropod Shannon diversity (B-C) and abundance (D-E).

One notable aspect of this model was that arthropods within *C. demersum* sites had the lowest Shannon diversity (significantly lower than *H. morsus-ranae*) and were numerically least abundant. Yet *C. demersum* possesses structural attributes that are positively associated with both metrics on PC axis 1 (i.e., dissected and submerged leaves). This suggests that while hydrophyte structural attributes do independently predict arthropod assemblage metrics, identity effects remain important and some aspects of *C. demersum*-dominated habitat may suppress arthropod diversity and abundance.

Discussion

Our results demonstrate that arthropod and mollusk assemblages exhibit distinct patterns among dominant hydrophyte species in a northeastern North American wetland. Similarly heterogeneous patterns among hydrophyte species have been observed in ponds (Lodge 1985; Declerck et al. 2011; Walker et al. 2013), reservoirs (Son et al. 2021), river habitat complexes (Humphries 1996; Wolters et al. 2017; Ambrožič et al. 2018), and other wetlands (Olson et al. 1995; Huikkonen et al. 2020; da Silva & Henry 2019; Wang et al. 2025). However, the degree to which patterns varied among hydrophyte species differed among metrics and between invertebrate assemblages. Arthropod abundance and evenness were not statistically significantly different among dominant hydrophytes while Shannon-Weiner diversity did vary, but significantly so only between *H. morsus-ranae* and

C. demersum. In contrast, Cyr & Downing (1988) and Walker et al. (2013) detected differences in abundance metrics among lake hydrophytes while the latter study did not detect differences in diversity metrics within a pond. Such discrepancies could be partially attributable to differences in aquatic ecosystem structure. For example, ponds are smaller and have less vegetation, especially emergent species, with growth more likely confined to banks which could result in more homogenous hydrophyte assemblages compared to those of wetlands (Richardson et al. 2022).

The invasive target species in our study, *H. morsus-ranae*, did not harbor reduced diversity or abundance of arthropods or mollusks. In fact, both mollusks and arthropods were most diverse and dense within *H. morsus-ranae*, albeit not always statistically significantly higher compared to other dominant hydrophytes. Such findings directly contrast with our hypothesis that *H. morus-ranae* would harbor fewer macroinvertebrates, yet other studies have reported similar findings with the same species and other invasive hydrophytes. For example, Zhu et al. (2015) detected increased biodiversity of macroinvertebrates in habitat invaded by *H. morsus-ranae* compared to habitat with little to none of the plant within a lake bay in New York, although some taxa were negatively impacted by the invasion. Kornijów et al. (2010) and Theel et al. (2007) found that macroinvertebrate assemblages collected from other invasive hydrophytes of the eastern U.S., such as *Trapa natans* and *Hydrilla verticillata*, were equal or more taxonomically rich than those collected from patches of native hydrophytes. If an invasive hydrophyte elevates habitat complexity, macroinvertebrate abundance and diversity can be sustained or even higher than in habitat with native hydrophytes only (Schultz & Dibble 2011).

In contrast, the least diverse and abundant invertebrate assemblages were collected from patches of the native *C. demersum*, a species with a growth form that should promote the opposite pattern. Among our four target species, *C. demersum* is the only one with whorled, finely dissected leaves that are sporadically toothed and an entirely submerged growth pattern that enhances both vertical and horizontal biomass density. Such a growth form typically creates more surface area for biofilm, arguably the most important trophic resource for wetland invertebrates (Nascimento-Filho et al. 2021). Perhaps due to such structural complexity, some related efforts report patterns that contrast our findings. For example, Bhat et al. (2012) found that *C. demersum* tended to harbor greater abundances (but not diversity) of macroinvertebrates compared to two other submerged hydrophytes in a Himalayan lake. Bogut et al. (2007) and Cattaneo et al. (1998) also observed greater abundances of invertebrates in *C. demersum* compared to emergent and floating hydrophytes. Yet other efforts report patterns among hydrophytes that concur with our findings. Cyr & Downing (1988) recorded lower densities of invertebrates in *C. demersum* compared to other hydrophyte species in a Canadian lake. Similarly, Schramm et al. (1987) retrieved relatively higher densities of invertebrates from floating (*Eichhornia*) and emergent (*Utricularia*) hydrophytes in a Florida lake. Chilton (1990) concluded that although *C. demersum* sometimes harbored elevated macroinvertebrate densities relative to other hydrophytes in a Wisconsin lake, the pattern was often reversed among sites or across time.

Consequently, although *C. demersum* possesses a growth form that should promote macroinvertebrate abundance, other attributes of this plant may dampen the positive

414 effects of structural complexity. One potentially influential factor unique to this species is
415 allelopathy that could reduce forage abundance. *C. demersum* releases allelopathic
416 chemicals that suppress growth rates of epiphyton, phytoplankton, and cyanobacteria to
417 but to varying degrees among taxa. For example, Amorim et al. (2019) found that
418 allelopathy by *C. demersum* reduced cyanobacteria biomass by 85-99% but analogous
419 effects on chlorophytes were weak (50% reduction) for one taxon and altogether absent for
420 another. In a mesocosm experiment, Amorim et al. (2024) found that *C. demersum*
421 allelopathy reduced cyanobacteria, diatom, and green algae abundance by 78-85%.
422 Grazing gastropods may also actively avoid feeding on *C. demersum* and often prefer other
423 submerged hydrophytes such as *Elodea* spp. (Sheldon 1987; Pinowska 2002). Another
424 potential source of variability in how invertebrates interact with *C. demersum* is
425 intraspecific morphological heterogeneity. Németh and Engloner (2025) reported
426 intraspecific differences in orders of magnitude among *C. demersum* traits that are
427 potentially important for invertebrates, such as internode density and shoot surface area.

428 Yet our results nevertheless offer support for the Krecker hypothesis predicting elevated
429 invertebrate diversity and abundance in submerged hydrophytes with dissected leaves. As
430 the sole hydrophyte species with an entirely submerged growth form, we expected to
431 observe the highest density of macroinvertebrates on this species yet found the opposite.
432 However, the residual influence of submerged hydrophytes with dissected leaves on
433 macroinvertebrate biodiversity and abundance in aggregate were clearly positive after
434 accounting for differences among assigned dominant categories. Such findings suggest
435 that integrating all present hydrophyte species concurrently is important when exploring

436 relationships with macroinvertebrate assemblages, even if one species appears to
437 dominate. Indeed, recent works point to hydrophyte diversity rather than abundance as a
438 key driver for promoting macroinvertebrate abundance and diversity (Yofukuji et al. 2021),
439 especially when such diversity elevates functional heterogeneity (Huikkonen et al. 2020;
440 Aleixo et al. 2024).

441 Macroinvertebrates found within patches of the species with the largest floating leaves
442 among the dominant hydrophytes we considered, *N. lutea*, potentially benefitted from
443 relatively high dissolved oxygen concentrations. Our sensors recorded dissolved oxygen
444 concentrations that were the most like the profile observed in open water among all four of
445 the dominant hydrophytes we studied, albeit overall concentrations were lower relative to
446 open water. The growth form of *N. lutea*, which includes limited underwater structures and
447 large leaves that possibly limit submerged hydrophyte growth, may promote water
448 exchange and consequently higher dissolved oxygen (Holmroos et al. 2015; Żbikowski et al.
449 2010). A relatively oxygenated environment may promote greater macroinvertebrate
450 densities within *N. lutea* patches (Żbikowski et al. 2010), although submerged or emergent
451 species in the same system typically harbor greater diversity (Van de Meutter et al. 2008). In
452 our system, *N. lutea* was strongly associated with *Juncus* spp. and *Carex* spp., emergent
453 taxa that can support disproportionately high macroinvertebrate densities (Bazzanti et al.
454 2010). Therefore, the intermediate diversity and abundance of macroinvertebrates found
455 within *N. lutea* patches may also reflect the habitat heterogeneity.

456 One important limitation of our results is the temporal scale, as our collections reflect a
457 single-instance observation in a system where plant biomass and invertebrate abundance

458 is likely temporally variable. In temperate lentic systems, hydrophyte biomass tends to
459 peak in mid to late summer (Fernández-Aláez et al. 2002), which corresponds to our
460 sampling window. Yet peak biomass dates can sometimes vary among hydrophyte species
461 (Torso et al. 2020) and maximum values for some are observed in spring (Camacho et al.
462 2016; Yang et al. 2020). Macroinvertebrate abundance and diversity in temperate wetlands
463 also seasonally varies due to heterogeneous patterns of emergence and development
464 (Chilton 1990; Miller et al. 2008). Our results may therefore overlook important seasonal
465 dynamics in how macroinvertebrate assemblages associate with hydrophytes. However,
466 macroinvertebrates are mobile and therefore able to migrate within wetlands in search of
467 optimal structural complexity. At least one effort (Gallardo et al. 2017) detected seasonally
468 consistent relationships between hydrophytes and macroinvertebrates among seasonal
469 disparities in plant biomass and invertebrate abundance.

470 In conclusion, our results contribute to the literature that demonstrates distinct
471 macroinvertebrate assembly among hydrophytes species but with a key analytical caveat.
472 Like many preceding efforts (Cattaneo 1998; Bhat et al. 2012; Ambrožič et al. 2018; Son et
473 al. 2021), we ascribed categorical zones within our focal wetland by dominant hydrophyte
474 and detected distinct patterns of macroinvertebrate abundance and diversity among plant
475 species. In contrast to expectations and most related works (although see Cyr & Downing,
476 1988), the sole submerged hydrophyte species with dissected leaves supported fewer
477 mollusks and lower arthropod diversity relative to the invasive hydrophyte with floating
478 leaves. Yet after accounting for the variance in arthropod diversity explained by dominant
479 hydrophyte category, the cover of submerged hydrophytes with dissected leaves

aggregated across all plant species was positively related to arthropod diversity and abundance. Therefore, our results contribute to the idea that hydrophyte heterogeneity promotes aquatic invertebrate abundance and diversity (Huikkonen et al. 2020; Yofukuji et al. 2021; Aleixo et al. 2024).

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Abigail Barton designed the study with input from Ryan M. Utz, Ph.D. Field sampling was done primarily by Abigail G. Barton. Identification of specimens was done by Abigail G. Barton, Alani Taylor, Ph.D., and Mollusca by Timothy Pearce, Ph.D. Analysis was done by Ryan M. Utz, Ph.D. and Abigail G. Barton with input from all authors. Manuscript was edited and reviewed by all authors prior to submission.

Data Availability Statement: All data collected, generated, and analyzed during and for this study can be accessed via the supplementary file attached with the digital study.

Ethical Approval: Not applicable due to study not including humans, vertebrates, or protected invertebrate species.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- DOdata.csv
- NYmacrosData.xlsx