



Secondary invasion by the floating aquatic plant *Hydrocharis morsus-ranae* increases macroinvertebrate biomass and diversity in a Great Lakes coastal wetland

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Abstract Invasive wetland plants reduce structural complexity and plant functional group diversity leading to concomitant reductions in macroinvertebrates and the potential for cascading food web effects. In Laurentian Great Lakes coastal wetlands (GLCW), hybrid cattail (*Typha* × *glaucia*) is a widespread invader that reduces submerged and floating vegetation. European Frogbit (*Hydrocharis morsus-ranae*; EFB) is a floating macrophyte and a secondary invader in *T. × glaucia* stands, where it thrives in

the understory. EFB invasion of *T. × glaucia* stands increases structural complexity, with unknown effects on faunal diversity. In this study, we assessed the influence of a primary (*T. × glaucia*) and secondary (EFB) plant invasion on aquatic macroinvertebrate diversity and productivity in a GLCW (Munuscong Bay, Michigan, USA). We quantified plant community composition and macroinvertebrate metrics (biomass, abundance, diversity, and community composition) in four wetland vegetation types: uninvaded wet meadow, uninvaded submergent marsh, *Typha*-dominant, and *Typha*+EFB co-dominant. We compared macroinvertebrate metrics among these vegetation types with multivariate ordinations, indicator species analyses, and Bayesian multinomial mixed-effects regression models. We found that *Typha*+EFB co-dominant stands had greater aquatic macroinvertebrate richness and biomass than *Typha*-dominant stands, but macroinvertebrate metrics did not differ between *Typha*+EFB and uninvaded submergent marsh. Thus, a secondary plant invasion by EFB increased the diversity and biomass of aquatic macroinvertebrates relative to the primary *Typha*-dominant stands. Consideration of a secondary invader's physical and functional traits is therefore critical to predict its ecological impacts.

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Introduction

Plant invasions tend to reduce biodiversity (Vilà et al. 2011; Xu et al. 2022) particularly when measured at smaller spatial scales (Powell et al. 2011, 2013). The loss of biodiversity is associated with a reduction in the functional diversity of ecosystems (Hejda and de Bello 2013; Castro-Díez et al. 2016). Furthermore, biodiversity loss reduces the efficiency and stability of ecosystem functioning over time (Cardinale et al. 2012). However, not all measures of diversity are equivalent; plant functional group diversity may be more important than plant species diversity for the maintenance of ecological processes (Tilman et al. 1997; Díaz and Cabido 2001). In wetland ecosystems, submerged aquatic vegetation is at particular risk of loss with plant invasions (Stiers et al. 2011). Because aquatic macroinvertebrates largely rely on submerged and floating vegetation for forage and are key components of aquatic food webs (Cyr and Downing 1988; Schultz and Dibble 2012), the loss of these plant physiognomic groups poses an indirect but particularly acute threat to biodiversity. In other words, dominant invasive emergent wetland plant invasion is anticipated to reduce aquatic macroinvertebrate abundance by locally extirpating submergent and floating plant species, and the loss of macroinvertebrates can have cascading impacts on higher trophic levels.

Great Lakes coastal wetlands (GLCWs) provide critical wildlife habitat for bird and fish populations and ecosystem services such as nutrient retention, sediment retention, and carbon sequestration (Jude and Pappas 1992; Howe et al. 2007; Sierszen et al. 2012). However, over 50 invasive wetland plants are now established within GLCWs (Ricciardi and MacIsaac 2000; Ricciardi 2006). New species interactions and ecosystem dynamics resulting from multiple concurrent invasions are expected to shift GLCWs into alternative stable states (sensu Beisner et al. 2003) with new community assemblages, reduced biodiversity, and modified food webs (Hobbs and Norton 1996; Stewart et al. 1998; Ricciardi 2001). Further, facilitation amongst invaders may result in an invasional meltdown in the Great Lakes (Simberloff and Von Holle 1999; Ricciardi 2001) whereby the cooccurrence of non-native species leads to greater invasive species survival, increased susceptibility to additional species invasions, and ultimately increased ecological impacts.

Narrow leaf and hybrid cattail (*Typha angustifolia* L., *T. × glauca* Godr.; hereafter invasive *Typha*) are among the most common invasive emergent macrophytes in GLCWs (Carson et al. 2018). Invasive *Typha* possesses numerous qualities typical of aggressive invaders, such as high phenotypic plasticity, a wide range of environmental tolerances, the ability to form clonal monotypic stands, high litter production, and greater biomass production and average height (> 2 m) compared to native plant communities (Woo and Zedler 2002; Tuchman et al. 2009; Larkin et al. 2012). These characteristics have enabled invasive *Typha* to outcompete native vegetation across the region; *Typha* was the dominant vegetation type across 13% of GLCW total area as of 2013 (Carson et al. 2018). The presence of invasive *Typha* is associated with altered plant community composition and reduced diversity (Farrer and Goldberg 2009; Larkin et al. 2012; Bansal et al. 2019). Additionally, *Typha* alters the physical structure of wetlands by reducing the abundance of submerged and floating species and replacing heterogeneous vegetation with homogeneous and monotypic stands (Lishawa et al. 2010; Schultz and Dibble 2012). These structural changes result in reduced abundance of macroinvertebrates (Lawrence et al. 2016) and associated fish communities (Schrunk and Lishawa 2019).

In the Great Lakes, *Typha* facilitates the invasion and persistence of a secondary floating-leaved macrophyte invader, European frogbit (*Hydrocharis morsus-ranae* L., hereafter EFB) (Monks et al. 2019). EFB is a relatively recent invader (< 20 years) to the Upper Great Lakes that spreads and reproduces quickly by producing 100–150 small, asexual vegetative propagules (i.e., turions) per plant per season (Zhu et al. 2018). Flowing waters, boats, and migratory birds easily disperse turions to new locations where they can remain dormant for at least two years (Catling et al. 2003). EFB leaves and roots form intertwining bundles, creating dense floating mats that prevent light penetration and shade or displace native submergent plants (Catling et al. 2003; Zhu et al. 2014). Reduced dissolved oxygen concentrations have been reported under EFB mats resulting from a lack of atmospheric gas exchange, seasonal die-offs, and increased decomposition rates (Zhu et al. 2008, 2018). EFB co-occurs and is facilitated by invasive *Typha*, an emergent plant which provides structural support and protection from wind and wave action

(Monks et al. 2019). EFB is also associated with *Phragmites australis*, an invasive emergent plant that is structurally-similar to *Typha* (Bonello and Judd 2020). *Typha* invasions tend to reduce submergent and floating macrophyte abundance, but the secondary invader EFB, which is able to coexist with *Typha*, could replace some of the lost submerged vegetation structure and habitat complexity that is critical to macroinvertebrates (Grabas et al. 2012).

To assess the influence of primary and secondary plant invasions on macroinvertebrates, we asked the following question: How do *Typha* (primary invasion) and EFB (secondary invasion) influence macroinvertebrate composition, structure, and productivity compared to common native wetland plant assemblages? To address this, we collected field samples within four wetland vegetation types in Munuscong Bay, Michigan: uninvaded wet meadow (dominated by native sedges and rushes), uninvaded submergent marsh (dominated by native floating and submerged species), *Typha*-dominant, and *Typha*+EFB co-dominant. Within each vegetation type, we quantified vegetative plant cover and macroinvertebrate metrics (biomass, diversity, and community composition) across two sampling periods (July 2020; September 2020). We hypothesized that a) plant composition would be distinct among the four vegetation types, b) native vegetation types would have greater macroinvertebrate diversity, abundance, and biomass compared to either invaded vegetation type, and c) *Typha*+EFB co-dominant stands would have greater macroinvertebrate diversity, abundance, and biomass compared to *Typha*-dominated vegetation type as a result of increased habitat complexity found in secondary invasion plant assemblages.

Methods

Field site description

We conducted our research in 2020 at Munuscong Marsh in Chippewa County, Michigan (46.20 N, 84.25 W). Munuscong Marsh is a river delta marsh (Albert et al. 2005) located at the confluence of the Munuscong River and St. Marys River, the connecting channel between Lake Superior and Lake Huron. Munuscong Marsh has been dominated by the primary invasion of *Typha* for over 30 years (Albert

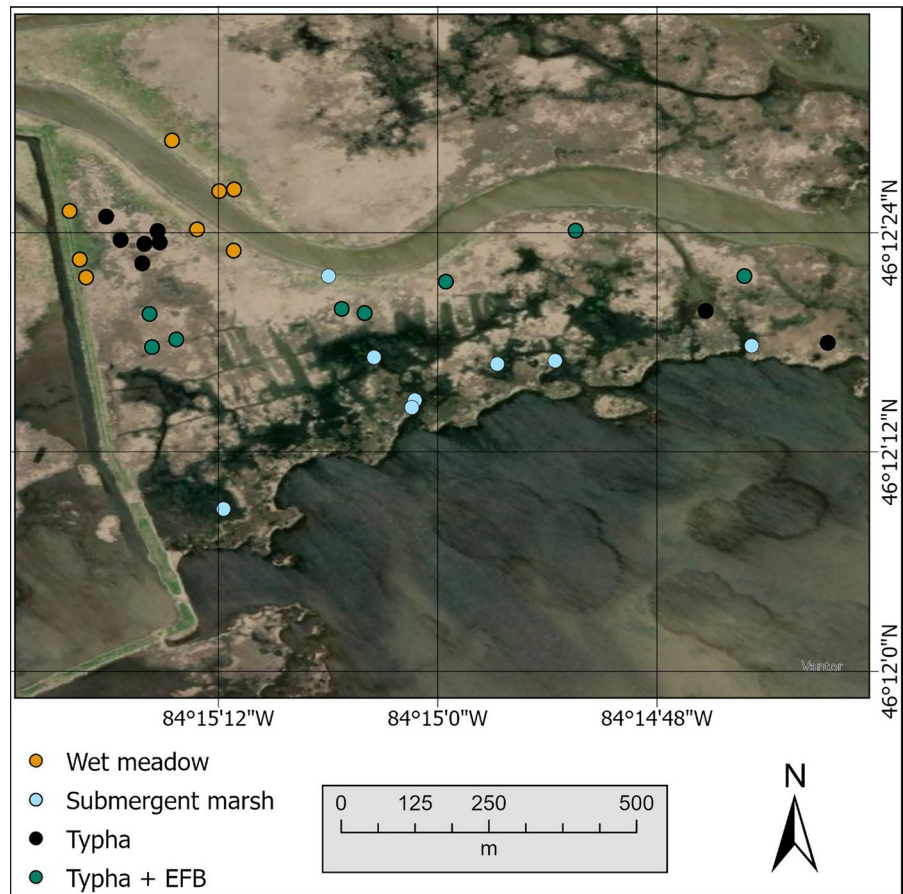
et al. 1987; Lishawa et al. 2019) and the secondary invader, EFB, was first detected at Munuscong Marsh in 2010. As of 2020, EFB had continued to spread throughout the wetland and was co-dominant across approximately 50% of the area of the primary *Typha* invasion (Monks et al. 2019).

In 2020, we classified four distinct vegetation types at Munuscong Marsh: wet meadow (native; *Calamagrostis canadensis* and *Carex stricta* co-dominant), submergent marsh (native; *Nymphaea odorata* and *Ceratophyllum demersum* co-dominant), *Typha*-dominant (primary invasion), and *Typha*+EFB co-dominant (secondary invasion). We delineated polygons demarcating the extent of each vegetation type using Geographic Information Systems (GIS; ArcMap, Environmental Systems Research Institute, Redlands, CA, USA), aerial photography, and field ground-truthing prior to our experimental deployment in July 2020. In each classification polygon, we generated eight random points using the Generate Random Points tool in ArcMap to establish sampling plot location in Munuscong Marsh (Total Plots = 32) (Fig. 1).

Vegetation and environmental data collection

We conducted vegetation and environmental sampling twice in 2020 during peak growing season of *Typha* and EFB populations (July 27–30) and prior to fall senescence (September 8–11). During each sampling period, we collected vegetation cover and environmental data from one, 1 m² quadrat established at each randomly selected sampling plot location. At each quadrat, two observers estimated areal percent cover for: total vegetation, each individual vascular plant species (taxonomic authority Voss and Reznicek 2012), above water detritus, and below water detritus. Using a graduated pole, we measured water depth (water surface to sediment surface) and organic sediment depth (sediment surface to mineral sediment layer). In invaded plots, all *Typha* stem heights were measured in each 1 m² quadrat from sediment surface to tallest leaf. We estimated total *Typha* biomass using an allometric equation (biomass (kg) = 0.0005265 e^{1.751*height (m)}, r² = 0.81) developed to convert *Typha* stem heights to biomass (Lishawa et al. 2015). Following vegetation data collection, we calculated plant diversity metrics (Shannon's H', species richness) and categorized plant cover into plant growth forms (floating, submerged, emergent, and

Fig. 1 Location of study plots in Munuscong Marsh on the St. Marys River in the eastern Upper Peninsula of Michigan, USA



sedge/grass) for statistical analyses. Vegetative sampling protocols were identical during both sampling events, except the exclusion of organic depth and *Typha* stem heights for predicting *Typha* biomass in September 2020. At each sampling period, we also employed a calibrated multiparameter probe (Yellow Springs Instruments Yellow Springs, OH, model Professional Plus 2019) to collect water physicochemical data (temperature, dissolved oxygen (DO), pH, and oxidation–reduction potential (ORP)) from approximately 5–10 cm below the water surface in each plot.

Macroinvertebrate collection

We collected macroinvertebrates twice (July 30–31; September 8–11) within each plot using dipnet sampling following a modified version of the macroinvertebrate sampling and laboratory processing standard operating procedure from the Great Lakes Coastal Wetland Monitoring Program (GLCWMP; Uzarski

et al. 2017). We collected samples from the water column below the quadrat following vegetation and water chemistry data collections to minimize disturbance. At each plot, dipnets were swept through the entire water column, substrate, and plant stems with a 0.5 mm-mesh D-shaped dipnet. We performed three 1 m sweeps within each plot to cover the entire 1 m² area and attempted to conduct an equivalent effort across all plots and vegetation types. All collected materials were transferred into 1-L jars in the field and processed within 24 h at the lab by picking all visible macroinvertebrates from the sediment and vegetation. Collected macroinvertebrates were stored in small collection bottles filled with 80% EtOH to preserve the organisms until identification. After preservation, we identified all macroinvertebrates to the lowest taxonomic unit possible using Merritt et al. (2019) and Thorp and Covich (2009). Most taxa were identified to genus, except for Araneae, Chironomidae, Hydrachnidia, and Lumbriculidae which

were identified to family and Hirudinea, which were identified to subclass. Macroinvertebrates were classified into functional feeding groups (collector, shredder, piercer, scraper, and predator) using Merritt et al. (2019).

To calculate macroinvertebrate biomass, we used length-mass regressions with a power function $M = aL^b$ where M is organism mass (mg), L is body length (mm), and a and b are taxa specific constants (Benke et al. 1999; Mährlein et al. 2016). To accomplish this, we measured each macroinvertebrate body length from the anterior tip of the head to the posterior tip of the abdomen. We converted body lengths into biomass using established length-mass regressions at the lowest available taxonomic unit (Johnston and Cunjak 1999; Benke et al. 1999; Miserendino 2001; Baumgärtner and Rothhaupt 2003; Gruner 2003; Edwards et al. 2009; Rosati et al. 2012; Mährlein et al. 2016). For genera that did not have published length-mass regressions (*Cordulia*, *Eloeophila*, *Neocloeon*, *Neoplea*, *Neoscuropterus*, and *Ranatra*), we used regressions from species with comparable morphology (Reese and Batzer 2007; Lawrence et al. 2016).

Statistical analysis

We analyzed the effects of vegetation type on macroinvertebrate species assemblages using permutational multivariate analysis of variance (PERMANOVA; 999 permutations; Bray-Curtis dissimilarity index) with the ‘adonis’ function in R. We visualized macroinvertebrate and plant communities in a 2-dimensional space (2-dimensions used by default) using non-metric multidimensional scaling (NMDS) of Wisconsin double transformed species abundance (macroinvertebrates) or percent cover (plants) at the plot level, with dissimilarity based on Bray–Curtis distances (McCune and Grace 2002), and 10 random starting configurations. We fitted vectors of environmental variables over NMDS plots at a significance level of $p \leq 0.05$ as determined by permutation procedure with the length of fitted vectors proportional to their explanatory strength. We performed all multivariate analyses using the ‘vegan’ package (Oksanen et al. 2018) in R. Additionally, to identify macroinvertebrate and plant taxa that corresponded with the different vegetation types, we used indicator species analysis with the ‘indicspecies’

package (Dufrene and Legendre 1997) in R. Indicator species analysis calculates indicator values that range from 0 (no indication) to 1.0 (perfect indication) for each species in a vegetation type.

We evaluated the effects of the four vegetation types on several macroinvertebrates metrics: (1) the relative proportions of macroinvertebrates within functional group categories; (2) macroinvertebrate biomass; (3) macroinvertebrate richness; and (4) macroinvertebrate abundance (i.e., total number of individuals of all species). To evaluate differences between vegetation types, we created four Bayesian multinomial mixed effects models with the vectors of macroinvertebrate functional group count, total biomass, total richness, and total abundance as the response variables. For interpretability, the response variables were modeled as log-odds relative to a baseline (predators for functional group analysis, submergent community for vegetation type analysis). Fixed effects included in the model were indicators for vegetation type, water temperature, vegetation diversity (H'), and sampling week (week 1 chosen as baseline). We included plot as a random intercept due to repeated measures at plots several weeks apart. Priors for the fixed effects parameters were normal with mean 0 and variance 1000 and the prior for the variance of the random intercepts was chosen to be truncated normal (i.e., the positive part of a normal with mean 0 and variance 1000). Two measurements were dropped due to inaccurate dissolved oxygen level readings (DO 22.7 and 22.3 mg/L; greater than saturation levels for freshwater; Lind 1979). As a result, 62 total observations were included in this analysis, with two wet meadow observations from the second date removed due to incompleteness of data. We log-transformed biomass to meet model assumptions, while richness and abundance were untransformed. All Bayesian models were implemented using the R package rjags (Plummer 2023). All statistical tests were conducted using R (Version 4.0.3, R Core Development Team 2020).

Results

Multivariate community analyses

Multivariate analysis of plant species revealed significant differences in composition between vegetation

types. NMDS plots illustrated clear separation in plant species composition between each vegetation type (Fig. 2), with the wet meadow and submerged communities diverging from all other vegetation types, and *Typha*-dominant and *Typha*+EFB co-dominant stands showing less separation. Fitted vectors showed litter, macroinvertebrate H', *Typha* cover, water depth, and ORP were significant factors that covaried with vegetation type (Fig. 2). The plant litter and macroinvertebrate H' vectors were negatively correlated, with the litter vector most strongly associated with the *Typha*-dominant stands and the invertebrate H' strongly related to the submergent marsh vegetation type. PERMANOVA analysis confirmed statistical differences between vegetation types ($F=41.82$, $p<0.01$) and pairwise comparisons revealed that each type differed from the other (*Typha*-dominant vs wet meadow: $F=38.98$, $p<0.01$; *Typha*-dominant vs submergent: $F=78.46$, $p<0.01$; *Typha*-dominant vs *Typha*+EFB co-dominant: $F=22.76$, $p<0.01$; *Typha*+EFB co-dominant vs wet meadow: $F=34.48$, $p<0.01$; *Typha*+EFB co-dominant vs submergent: $F=65.02$, $p<0.01$; submerged vs wet meadow: $F=26.09$, $p<0.01$).

Multivariate analysis of macroinvertebrate data illustrated differences between vegetation types. NMDS plots illustrate some separation in

macroinvertebrate assemblage by vegetation type; the wet meadow macroinvertebrate communities diverged from those in all other vegetation types while the submergent, *Typha*-dominant stands, and *Typha*+EFB co-dominant stands had more overlap (Fig. 2). Fitted vectors for the NMDS revealed that ORP, water depth, plant diversity (H'), and pH significantly covaried with macroinvertebrate communities (Fig. 2). PERMANOVA results confirm statistical differences in macroinvertebrate community composition between vegetation types ($F=5.87$, $p<0.01$) and pairwise PERMANOVA comparisons revealed that macroinvertebrate community compositions differed between all vegetation types ($p<0.05$) except between the *Typha*-dominant and *Typha*+EFB co-dominant stands ($p=0.17$).

Indicator species analyses

Indicator species analysis revealed that several macroinvertebrate taxa were significantly associated with the wet meadow and submergent vegetation types. Three types of snails (spiral, cone, and other morphology) and *Bezzia* spp. were indicative of the wet meadow vegetation type, *Holocentropus* spp. and *Fabria* spp. were indicators of the submerged vegetation type, while no taxa were significant indicators

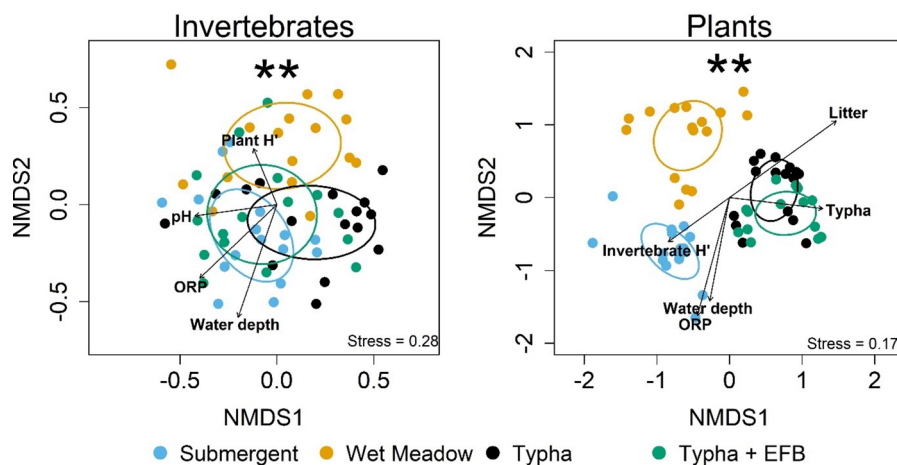


Fig. 2 Non-metric multidimensional scaling ordinations of aquatic macroinvertebrate and plant species assemblages by vegetation type (submergent marsh, wet meadow, *Typha*-dominant, *Typha*+EFB co-dominant) at Munuscong Bay, Michigan. Macroinvertebrate data represent total abundance and plant data represent percent cover of all taxa present in plot; ovals represent one standard deviation around the mean

location of each group; fitted vectors are significant ($p<0.05$) post-hoc correlations between environmental variables or diversity metrics and plots and their length is proportional to their explanatory strength; ** indicates significant ($p<0.01$) differences between vegetation types, determined with Permutational Analysis of Variance (PERMANOVA)

of the *Typha*-dominant stands and *Typha* + EFB co-dominant stands (Table 1). We found that several plant taxa were significant indicators of each vegetation type: *Calamagrostis canadensis*, *Carex stricta*, *Phalaris arundinacea*, *Cx. lacustris*, and *Persicaria amphibia* were indicative of the wet meadow vegetation type; *Nymphaea odorata*, *Ceratophyllum demersum*, *Myriophyllum sibiricum*, *Potamogeton gramineus* and *Potamogeton* spp. were indicators of the submerged vegetation type; *Hydrocharis morsus-ranae* was indicative of the *Typha* + EFB co-dominant

stands; and *Equisetum fluviatile* was an indicator of the *Typha*-dominant stands (Table 1). Additionally, two taxa, *Epitheca* (dragonflies) and *Crangonyx* (a freshwater amphipod), were entirely absent from the *Typha*-dominant stands, but were found in the *Typha* + EFB co-dominant stands.

Functional groups

The proportions of macroinvertebrate functional groups varied across the four different vegetation types (Fig. 3; Table 2). In particular, the relative proportion distribution within the wet meadow differed from the three other vegetation types with larger proportions of collectors and scrapers and a smaller proportion of shredders (Fig. 3). A chi-squared test of independence between vegetation type and macroinvertebrate functional groups yields a *p*-value of < 0.0001 for both sampling periods allowing us to reject the null hypothesis of independence between vegetation type and macroinvertebrate type.

Kernal density estimates of the posterior distributions of regression coefficients for each vegetation type with a vertical reference line at 0 illustrate the differences in macroinvertebrate functional group distribution by vegetation type (Supplementary Fig. 1). For interpretability, the proportions of functional groups were modeled in terms of the log-odds of a particular macroinvertebrate functional group type for the given settings relative to predators. Distributions with density to the right of the reference line (i.e., positive estimates) indicate that the proportion of that specific macroinvertebrate functional feeding group (relative to predators) is larger for a given vegetation type relative to the submergent marsh. Likewise, distributions with density to the left of the reference line (i.e., negative estimates) indicate smaller proportions relative to the submergent marsh. For example, the proportion of scrapers in the wet meadow (i.e., Supplementary Fig. 1, first row, third column) is substantially larger than the proportion in the submergent marsh, consistent with the visual representation of abundances (Fig. 3). Relative to the submergent marsh, the wet meadow had a lower proportion of shredders and higher proportions of collectors and piercers; *Typha*-dominant stands had higher proportions of shredders and scrapers and a lower proportion of collectors; and *Typha* + EFB co-dominant stands

Table 1 Indicator species analysis results for plant and macroinvertebrate data from Munuscong Bay, Michigan by vegetation type (meadow, submergent marsh, *Typha* + EFB co-dominant stands, *Typha*-dominant stands; *n* = 8). All taxa shown are significant (*p* < 0.05). Indicator values range from 0 (no indication) to 1.0 (perfect indication)

Taxa	Indicator value	<i>p</i>
Wet meadow		
Macroinvertebrate		
Snail spiral	0.865	0.005
Snail cone	0.679	0.015
<i>Bezzia</i> spp.	0.500	0.015
Snail other	0.433	0.050
Plant		
<i>Calamagrostis canadensis</i>	0.968	0.005
<i>Carex stricta</i>	0.931	0.005
<i>Phalaris arundinacea</i>	0.707	0.015
<i>Carex lacustris</i>	0.661	0.005
<i>Persicaria amphibia</i>	0.612	0.005
Submergent marsh		
Macroinvertebrate		
<i>Holocentropus</i> spp.	0.787	0.010
<i>Fabria</i> spp.	0.493	0.025
Plant		
<i>Nymphaea odorata</i>	0.935	0.005
<i>Ceratophyllum demersum</i>	0.909	0.005
<i>Myriophyllum sibiricum</i>	0.829	0.005
<i>Potamogeton gramineus</i>	0.737	0.005
<i>Potamogeton</i> spp.	0.697	0.005
<i>Nuphar variegata</i>	0.559	0.005
<i>Typha</i> + EFB co-dominant		
Plant		
<i>Hydrocharis morsus-ranae</i>	0.975	0.005
<i>Typha</i>-dominant		
Plant		
<i>Equisetum fluviatile</i>	0.537	0.005

Fig. 3 Distribution of macroinvertebrate functional groups across the four vegetation types where numbers of macroinvertebrates per functional group were summed across both sampling periods

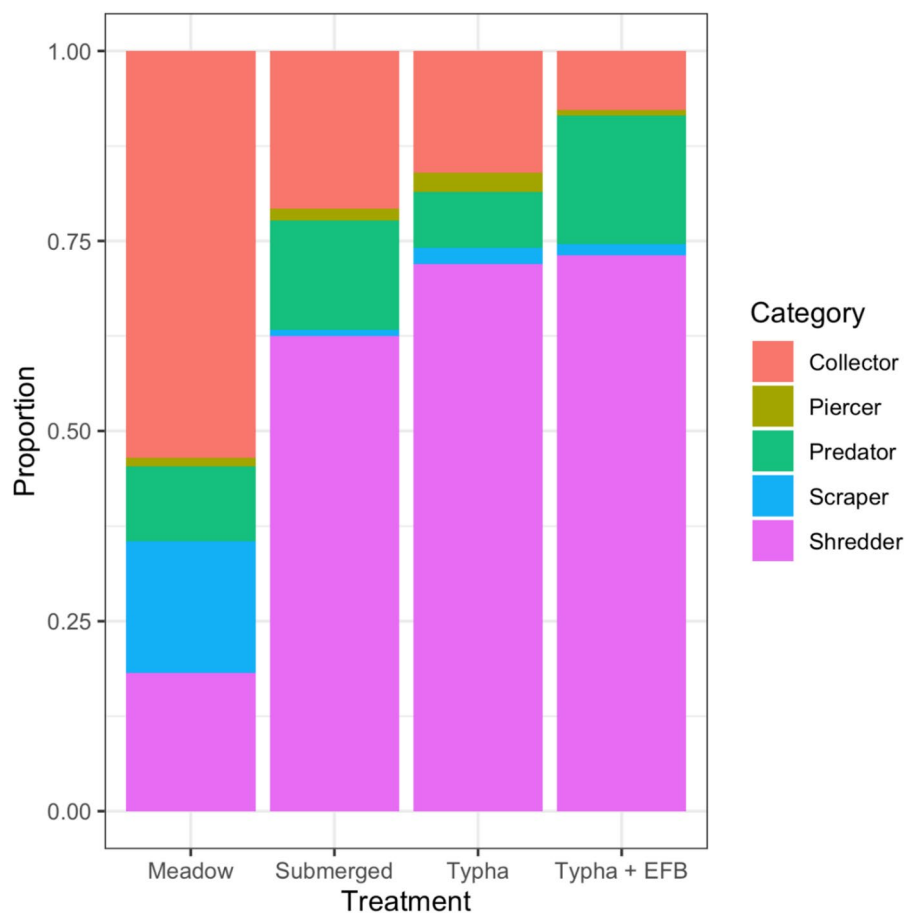


Table 2 Abundance of macroinvertebrates by functional feeding group and vegetation types

	Collectors	Shredders	Piercers	Scrapers	Predators	Total
Vegetation type	Week 1 (July 30–31)					
Wet meadow	556	102	11	217	34	920
Submergent marsh	97	176	8	4	33	318
<i>Typha</i> + EFB co-dominant	44	260	4	13	56	377
<i>Typha</i> -dominant	55	388	5	21	32	501
	Week 2 (September 8–11)					
Wet meadow	141	135	3	8	94	381
Submergent marsh	78	350	5	3	88	524
<i>Typha</i> + EFB co-dominant	26	396	2	0	96	520
<i>Typha</i> -dominant	124	415	23	3	50	615

had a smaller proportion of collectors and piercers and a similar proportion of shredders and scrapers.

Additional patterns were revealed when we evaluated the posterior distributions of the proportions of each macroinvertebrate functional group type by vegetation type while fixing the levels of the other

covariates, rather than looking at the individual regression coefficients. Specifically, we fixed water temperature, vegetation H' , and dissolved oxygen at their mean levels, and fixed week to week 1 (Fig. 4; Table 3). Across all vegetation types, piercers, predators, and scrapers were relatively rare (all posterior

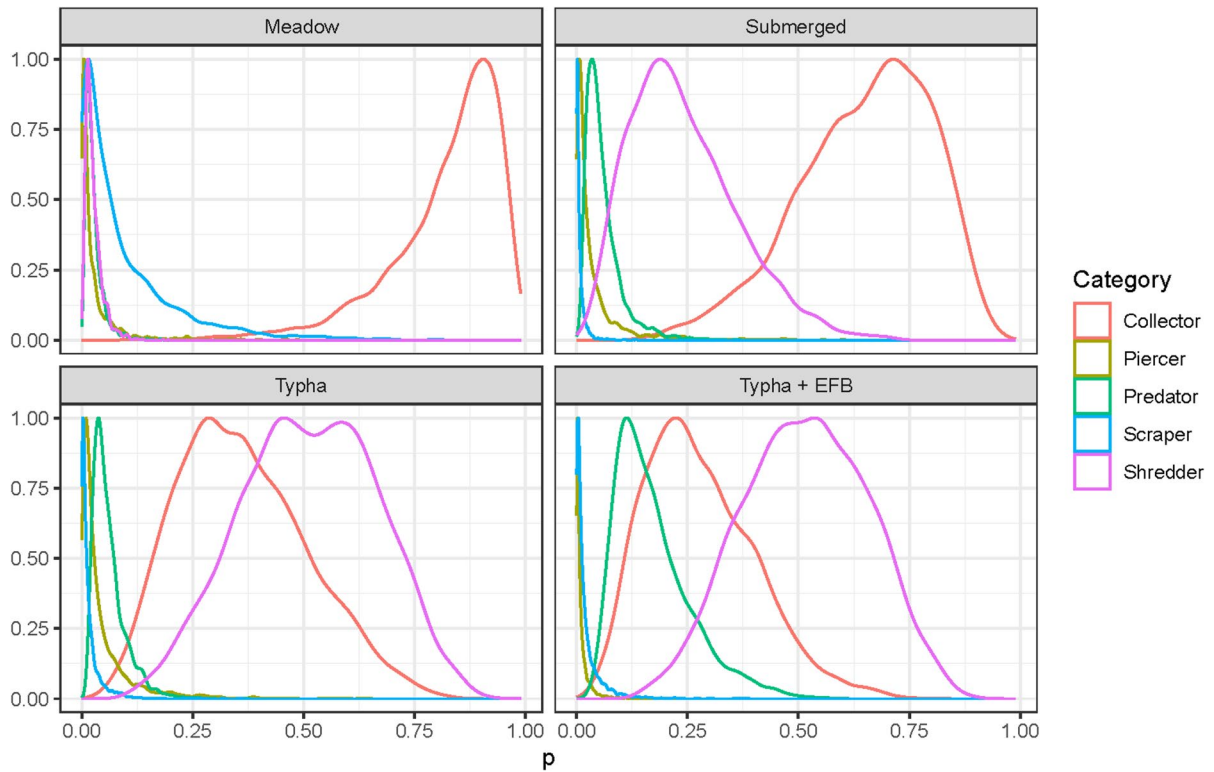


Fig. 4 Posterior estimates for proportions of macroinvertebrates in different vegetation types with covariates fixed at mean water temperature, mean vegetation H', week 1, and mean dissolved oxygen (2.69 mg/L)

Table 3 Posterior mean proportions (with 95% credible intervals) in different vegetation types with covariates fixed at mean water temperature, mean vegetation H', week 1, and mean dissolved oxygen (2.69 mg/L)

	Collector	Piercer	Predator	Scraper	Shredder
Wet Meadow	0.822 (0.483, 0.968)	0.032 (0.001, 0.213)	0.026 (0.006, 0.084)	0.095 (0.002, 0.426)	0.026 (0.000, 0.079)
Submergent Marsh	0.651 (0.319, 0.881)	0.042 (0.001, 0.246)	0.059 (0.015, 0.175)	0.008 (0.000, 0.039)	0.241 (0.062, 0.523)
<i>Typha</i> -dominant	0.362 (0.125, 0.670)	0.047 (0.002, 0.252)	0.061 (0.019, 0.156)	0.018 (0.000, 0.090)	0.512 (0.219, 0.788)
<i>Typha</i> + EFB co-dominant	0.279 (0.086, 0.562)	0.012 (0.000, 0.069)	0.172 (0.061, 0.394)	0.021 (0.000, 0.110)	0.516 (0.246, 0.779)

means below 10%) with the exception of scrapers in the wet meadow (posterior mean 10.4% (0.28%, 44.8%)) and predators in *Typha* + EFB co-dominant stands (posterior mean 13.4% (4.75%, 31.3%)). In all four vegetation types, shredders and collectors dominated the observed proportions of macroinvertebrates. In *Typha*-dominant and *Typha* + EFB co-dominant stands, the proportions of shredders and collectors made up the majority of the observed macroinvertebrates with both groups having posterior

means near 50% for shredders and posterior means of 40.4% (15.6%, 70.7%) and 32.0% (11.1%, 60.3%) for *Typha*-dominant and *Typha* + EFB co-dominant stands, respectively. Both submergent marsh and wet meadow were dominated by collectors with wet meadow being nearly completely dominated by collectors (posterior mean of 83.4% (49.6%, 97.1%)) and submergent marsh having a posterior mean around 70% for collectors with shredders making up most of the rest of the macroinvertebrates observed in

this vegetation type (posterior mean 22.1% (5.4%, 49.1%)).

Macroinvertebrate Biomass, Richness, and Abundance

We assessed the differences in macroinvertebrate biomass, richness, and abundance by vegetation type using Bayesian mixed-effects regression models. For ease of interpretation, we included indicators for vegetation type (with submergent marsh chosen as the baseline level), and fixed mean water temperature, mean vegetation H' , week 1 in the models. A random intercept for plot was included due to the repeated measures at plots. We determined the kernel density estimates of the differences in posterior distributions of regression coefficients for each vegetation type with a vertical reference line at 0; distributions with larger density to the right of the reference line (i.e., positive estimates) indicate that the average response is greater for the vegetation type in the given row compared to the coefficient for the vegetation type in the given column (Supplementary Fig. 2, 3, 4). Likewise,

distributions with density to the left of the reference line (i.e., negative estimates) indicate that the average response is less for the vegetation type in the given row compared to the coefficient for the vegetation type in the given column.

Macroinvertebrate biomass was relatively lower in *Typha*-dominant stands than in *Typha* + EFB co-dominant stands, submergent marsh, or wet meadow (Supplementary Fig. 2; Table 4). Similarly, macroinvertebrate taxonomic richness was lower in the *Typha* vegetation type than in the other three communities sampled; wet meadow had greater macroinvertebrate biomass than submergent marsh or *Typha* + EFB co-dominant stands; and *Typha* + EFB co-dominant stands did not differ from the submergent marsh (Supplementary Fig. 3; Table 4). The wet meadow also had greater average macroinvertebrate abundance compared to *Typha* + EFB co-dominant stands, *Typha*-dominant stands, and submergent marsh (Supplementary Fig. 4; Table 4); all other coefficients for biomass, richness, and abundance were relatively symmetric around 0, suggesting no statistical difference in their averages.

Table 4 Posterior probability of the difference in the vegetation type and baseline coefficients being greater than 0 along with posterior means and 95% credible intervals for macroinvertebrate biomass, richness, and abundance regressions

Vegetation type	Baseline	P ($\beta_{diff} > 0$)	Mean (95% CI)
Biomass			
Wet meadow	<i>Typha</i> + EFB co-dominant	0.615	0.119 (−0.723, 0.942)
Wet meadow	<i>Typha</i> -dominant	0.873	0.557 (−0.398, 1.532)
Wet meadow	Submergent marsh	0.619	0.129 (−0.642, 0.945)
<i>Typha</i> + EFB co-dominant	<i>Typha</i> -dominant	0.871	0.438 (−0.367, 1.222)
<i>Typha</i> + EFB co-dominant	Submergent marsh	0.514	0.010 (−0.732, 0.750)
<i>Typha</i> -dominant	Submergent marsh	0.156	−0.427 (−1.267, 0.411)
Richness			
Wet meadow	<i>Typha</i> + EFB co-dominant	0.794	0.823 (−1.134, 2.770)
Wet meadow	<i>Typha</i> -dominant	0.964	2.081 (−0.226, 4.345)
Wet meadow	Submergent marsh	0.818	0.845 (−0.945, 2.620)
<i>Typha</i> + EFB co-dominant	<i>Typha</i> -dominant	0.918	1.258 (−0.579, 3.086)
<i>Typha</i> + EFB co-dominant	Submergent marsh	0.517	0.024 (−1.731, 1.701)
<i>Typha</i> -dominant	Submergent marsh	0.104	−1.236 (−3.188, 0.686)
Abundance			
Wet meadow	<i>Typha</i> + EFB co-dominant	0.984	45.89 (3.562, 86.33)
Wet meadow	<i>Typha</i> -dominant	0.952	39.74 (−6.163, 83.11)
Wet meadow	Submergent marsh	0.983	39.18 (4.142, 73.22)
<i>Typha</i> + EFB co-dominant	<i>Typha</i> -dominant	0.388	−6.145 (−46.77, 33.96)
<i>Typha</i> + EFB co-dominant	Submergent marsh	0.344	−6.704 (−41.31, 27.12)
<i>Typha</i> -dominant	Submergent marsh	0.486	−0.559 (−35.92, 34.91)

Discussion

Invasive plants can cause dramatic losses of biodiversity in wetland ecosystems (Zedler and Kercher 2004). Secondary invaders, which are facilitated by primary invaders (O'Loughlin and Green 2017), are largely thought to exacerbate ecological impacts caused by primary invasion (Simberloff and Von Holle 1999; Ricciardi 2001). However, macroinvertebrate diversity has been positively correlated with increased submergent plant biomass and associated habitat complexity regardless of “invasive” or “native” plant designation (Cyr and Downing 1988). This relationship suggests that in certain circumstances invasive macrophyte establishment could enhance the diversity and complexity of macroinvertebrate communities. In this study, we sought to determine what affect wetland plant invasions have on macroinvertebrate community composition, structure, and productivity and we questioned the presumption of secondary invasion compounding impacts to biodiversity by evaluating a secondary invader's potential to increase the aquatic macroinvertebrate diversity in a wetland that had been heavily impacted by primary plant invasion.

Plant and macroinvertebrate communities

Multivariate analyses of plant and macroinvertebrate communities revealed biological patterns and identified several likely environmental drivers of variations in macroinvertebrate community composition. We found greater overlap in total plant community composition between the *Typha*-dominant and *Typha* + EFB co-dominant stands compared to native submergent marsh and wet meadow vegetation types. Additionally, a suite of common native floating and submergent species were significantly associated with the submergent marsh but were nearly absent from the *Typha*-dominant and *Typha* + EFB co-dominant stands. These patterns illustrate a substantial shift in plant community composition associated with *Typha* invasion, a pattern well documented in GLCWs (Tuchman et al. 2009; Bansal et al. 2019). This study adds further evidence for negative effects of EFB on native plants, particularly submerged aquatic species (Catling et al. 1988, 2003; Zhu et al. 2018). In our study, litter cover was also negatively correlated with macroinvertebrate H', indicating a possible driver for

diversity loss. While plant litter from emergent vegetation provides a substrate for algae, a primary food source for macroinvertebrates (Campeau et al. 1994), litter quality and diversity are important factors determining macroinvertebrate community composition and diversity (Leroy and Marks 2006). *Typha* produces abundant standing dead litter, its persistence excludes native plants, and litter has been identified as a mechanistic driver for *Typha*'s establishment and dominance (Farrer and Goldberg 2009; Tuchman et al. 2009; Larkin et al. 2012).

Macroinvertebrate functional groups

Macroinvertebrate functional feeding group composition reflects the relative availability of different food sources within a habitat (Cummins and Klug 1979). Our study found a marked shift in the functional group distributions between wetland vegetation type (Fig. 4). The wet meadow and submergent marsh vegetation types were highly dominated by collectors, whereas the *Typha*-dominant and *Typha* + EFB co-dominant stands had relatively even mixes of shredders and collectors. Differences between the quality of litter from sedges (in the wet meadow) and *Typha* leaf litter (in *Typha*-dominant and *Typha* + EFB co-dominant stands) likely explain observed differences in functional feeding group composition. Leroy and Marks (2006) found that leaf litter quality and diversity affect litter decomposition rates, with high quality and diverse litter mixtures decomposing faster than low quality single species litter. As such, our wet meadow plots had the highest plant diversity with high quality litter, thus supported a greater abundance of collectors that feed on fine particulate organic matter from more rapidly decomposing sedges and forbs. In contrast, low diversity and quality *Typha* litter in *Typha*-dominant and *Typha* + EFB co-dominant stands provided a more abundant food source for shredders. Additionally, the *Typha* + EFB co-dominant stands had an anomalously high relative proportion of predators indicating abundance of prey species within this vegetation type.

Macroinvertebrate Biomass, Richness, and Abundance

The *Typha*-dominant stands clearly had the lowest macroinvertebrate biomass and richness of the four

vegetation types, including the submergent marsh type. In particular, the native wet meadow vegetation type had greater measures of macroinvertebrate abundance, richness, and biomass compared to the *Typha*-dominant stands, and greater abundance and richness compared to the native submergent marsh or the *Typha* + EFB co-dominant vegetation type. These findings were not surprising, given that *Typha* invasion has been associated with reduced macroinvertebrate density and biomass in GLCWs likely owing to reductions in structural complexity of habitat (Lawrence et al. 2016), and lack of heterogeneity of food sources. The loss of highly dissected submerged vegetation with low lignin content, such as *Utricularia vulgaris*, within *Typha* stands may also reduce macroinvertebrate abundance (Schultz and Dibble 2012), particularly for taxa such as *Holocentropus*, *Acentria*, and *Parapoynx* that shelter in submerged plants. This finding in part supports our second hypothesis, namely that the uninvaded vegetation types would harbor more diverse macroinvertebrate communities.

Interestingly, *Typha* + EFB co-dominant stands had greater aquatic macroinvertebrate richness and biomass compared to *Typha*-dominant stands. Further, macroinvertebrate biomass, richness, and abundance did not differ between the secondary invasion vegetation type and the submergent marsh vegetation type, whereas the *Typha*-dominant stands had lower biomass and richness than the submergent marsh reference. Additionally, the *Typha* + EFB co-dominant stands had quantities of macroinvertebrates that were statistically equivalent to the submergent marsh vegetation type. Taxonomic group recovery within the secondary invasion was observed but limited. For instance, two taxa, *Epitheca* (dragonflies) and *Cranogonyx* (a freshwater amphipod), were entirely absent from the *Typha*-dominant stands, but were found in the *Typha* + EFB co-dominant stands. These findings, taken together with our multivariate community analysis, provide partial support for our third hypothesis: a secondary invasion resulted in a recovery in the productivity of macroinvertebrates, but did not result in a clear community shift toward the reference submergent marsh vegetation type. Thus, EFB appears to be providing an incomplete replacement for native submergent biodiversity lost through the primary invasion by *Typha* (Lawrence et al. 2016) and through competitive exclusion by the secondary invader EFB (Catling et al. 1988). Interestingly, EFB

does not appear to be exacerbating biodiversity loss or macroinvertebrate declines. These findings are not altogether unexpected given that macroinvertebrate diversity tends to increase with increasing habitat heterogeneity and vegetation cover (Cyr and Downing 1988; Schultz and Dibble 2012). We posit that the submergent structural complexity provided by EFB increases habitat complexity in *Typha* stands with some benefit to macroinvertebrate communities and their productivity.

Study limitations

We acknowledge several limitations to our study. First, due to the widespread distribution of *Typha* and EFB at the study site, native wet meadow and *Typha*-dominant (without EFB) vegetation types were limited in their extent and distribution across the wetland. As a result, we sampled the *Typha*-dominant and wet meadow vegetation types at a higher intensity (plots per area) than the submergent marsh and *Typha* + EFB vegetation types. We contend that plot replication ($n=8$) and randomization across each vegetation type allowed for a thorough and representative spatial sampling of the large wetland. Second, sampling aquatic macroinvertebrates within the dense submergent vegetation was difficult to perform consistently across vegetation types. Though we attempted to sample with equal effort at all plots, it is likely that variable density of aquatic vegetation between vegetation types introduced some error into our data.

Conclusions

The response of macroinvertebrate communities to plant invasions varies depending on the invader and its traits, such as biomass production and leaf dissection (Schultz and Dibble 2012). For instance, submergent and floating invaders such as *Myriophyllum* spp. and *Trapa natans* can increase vegetation surface area and biomass, increasing macroinvertebrate habitat complexity, providing refuge from predators, and increasing macroinvertebrate abundance and diversity (Strayer et al. 2003; Valinoti et al. 2011). However, when invaders displace native plants and reduce vegetation surface area and biomass, a lack of suitable habitat can reduce macroinvertebrate biomass and abundance (Houston and

Duivenvoorden 2002; Lawrence et al. 2016). Thus, the native or non-native status of a species may be less important than its functional role in providing macroinvertebrate habitat, particularly in sites experiencing secondary invasions. Further, habitat complexity and structural heterogeneity are likely better predictors of macroinvertebrate diversity than plant species identity.

The implications of our findings are important to consider in the context of continued global biodiversity loss (Cardinale et al. 2012), the increasing prevalence of secondary invasions (O'Loughlin and Green 2017), and the critical role that macroinvertebrates play in supporting aquatic food webs and aquatic ecosystem functions (Wallace and Webster 1996). If, as in our study system, a secondary plant invader increases structural complexity and food availability (i.e., greater macroinvertebrate density and richness) compared to the primary invasion, then we should not assume a simple model of additive invader impacts on higher trophic levels. Therefore, consideration of a secondary invader's physical and functional traits is critical to predict its ecological impacts.

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Data availability Data will be made publicly available upon publication of the article.

Declarations

Conflict of interest The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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