European frogbit (Hydrocharis morsus-ranae) invasion facilitated by non-native cattails (Typha) in the Laurentian Great Lakes

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A B S T R A C T

Plant-to-plant facilitation is important in structuring communities, particularly in ecosystems with high levels of natural disturbance, where a species may ameliorate an environmental stressor, allowing colonization by another species. Increasingly, facilitation is recognized as an important factor in invasion biology. In coastal wetlands, non-native emergent macrophytes reduce wind and wave action, potentially facilitating invasion by floating plants. We tested this hypothesis with the aquatic invasive species European frogbit (Hydrocharis morsus-ranae; EFB), a small floating plant, and invasive cattail (Typha spp.), a dominant emergent, by comparing logistic models of Great Lakes-wide plant community data to determine which plant and environmental variables exerted the greatest influence on EFB distribution at multiple scales. Second, we conducted a large-scale field experiment to evaluate the effects of invasive Typha removal treatments on an extant EFB population. Invasive Typha was a significant predictor variable in all AIC-selected models, with wetland zone as the other most common predictive factor of EFB occurrence. In the field experiment, we found a significant reduction of EFB in plots where invasive Typha was removed. Our results support the hypothesis that invasive Typha facilitates EFB persistence in Great Lakes coastal wetlands, likely by ameliorating wave action and wind energy. The potential future distribution of EFB in North America is vast due in part to the widespread and expanding distribution of invasive Typha and other invading macrophytes, and their capacity to facilitate EFB’s expansion, posing significant risk to native species diversity in Great Lakes coastal wetlands.

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Introduction

Invasion biology has tended to focus on competitive interactions between introduced and native species with the diversity resistance hypothesis, suggesting that more diverse community assemblages are less prone to invasive species due to increased numbers of competitive and predatory interactions with native species (Kennedy et al., 2002). Alternatively, numerous examples exist of synergistic effects among invaders leading to the dominance of an invader, codominance of multiple invaders, or cascading ecological disruptions across trophic levels (O’Dowd et al., 2003; Ricciardi, 2001; Simberloff and Von Holle, 1999). Facilitative relationships between species, where one or multiple species moderate or buffer against stressful physical conditions and allow other species to establish or persist, are well-documented (Bertness and Callaway, 1994; Bruno et al., 2003; Stachowicz, 2013; Von Holle, 2013). Facilitation plays a role in terrestrial environments prone to climatic extremes (Franco and Nobel, 1989; Freestone, 2006; Lawrence and Barradough, 2016; Ryser, 1993), as well as coastal environments that face disturbance through wave and tidal action (Altieri et al., 2007; Bertness and Leonard, 1997; Bruno, 2000; Wright et al., 2014).

The Laurentian Great Lakes have been a hotspot for biological invasions, because of a history of commerce, industry, anthropogenic development, and international shipping through the St. Lawrence Seaway (Ricciardi, 2006; Ricciardi and Madsen, 2000). The presence of numerous concurrent invasions has created unique community assemblages and species interactions among invasive and native species. Repeated introductions to the Great Lakes have led to large shifts in ecosystem structure and function (Ricciardi, 2001), which has been cited as an example of an invasional meltdown (sensu, Simberloff and Von Holle, 1999). Here, we focus on the interaction and apparent facilitative relationship between two invasive taxa, Typha spp. and European frogbit (Hydrocharis morsus-ranae L.; EFB).

In the Laurentian Great Lakes, both narrow leaf and hybrid cattail (Typha angustifolia L.; T. × glauca Godr.; hereafter invasive Typha) are...
invasive aquatic macrophytes that began spreading in the early 1900s along with expanding human populations and agricultural activity in the region (Shih and Finkelstein, 2008). In the intervening century, invasive Typha has become a common plant of coastal wetlands throughout all five Great Lakes and major connecting rivers, dominating 13.5% of total Great Lakes wetland area through 2013 (Carson et al., 2018). Invasive Typha dominance is associated with well-documented reductions of plant diversity (Lishawa et al., 2010; Martina et al., 2014; Tuchman et al., 2009; Wilcox et al., 2008), reduced abundance of invertebrates (Lawrence et al., 2016) and fish (A. Schrank, University of Minnesota, personal communication, 2018), reduced habitat complexity (Kranzd, 1986; Lawrence et al., 2016), and altered biogeochemical cycling regimes (Larkin et al., 2012; Lawrence et al., 2017; Lishawa et al., 2014).

EFB, a small free-floating perennial aquatic plant native to Europe (Catling et al., 2003; Zhu et al., 2018), is a relatively recent invader to the Great Lakes. The North American population has been traced back to the Dominion Arboretum in Ottawa, Canada in 1932 where it had been introduced from the Zurich Botanical Garden, in Zurich, Switzerland (Catling et al., 2003). EFB subsequently spread up the St. Lawrence River to Lake Ontario, where it was observed in 1991 (D. Wilcox, personal observation, 1991). By 2004 it was found in 75% of wetlands sampled (Trebitz and Taylor, 2007; Zhu et al., 2018) to the west and north to Lakes Erie and Huron. EFB now extends as far north as the St. Marys River, the connecting channel between Lakes Huron and Superior, where it was first documented in 2010 (D. Albert, personal observation, 2010). With its dense, intertwine growth habit, EFB can effectively outcompete native wetland taxa, especially floating plants, leading to a marked reduction in plant diversity (Catling et al., 1988). EFB can also be a nuisance to recreational and commercial boating (Catling et al., 2003). Seasonal die-offs of EFB in the fall and subsequent decomposition have caused reductions in dissolved oxygen (Zhu et al., 2008), which can have detrimental impacts on invertebrate and fish communities dependent on Great Lakes coastal wetlands (GLCW) (Jude et al., 2005). EFB’s reproductive strategy, including production of easily-dispersed vegetative propagules (turons) that can remain dormant for at least two years (Catling et al., 2003), make eradication of EFB populations especially challenging. As a watch-listed invasive species in U.S. states (Nault and Mikulyuk, 2009; Weibert, 2015) and Canadian provinces surrounding the Great Lakes, understanding its ecological associations is critical to predicting its spread and managing invaded wetlands.

In GLCWs, EFB commonly co-occurs with invasive Typha (Johnston and Brown, 2013; Lemein et al., 2017; Trebitz and Taylor, 2007), a co-occurrence also documented in their home ranges in Europe (Sager and Clerc, 2006). GLCWs are highly dynamic ecosystems that are exposed to physical stress from wind, wave action, and seiche activity (Trebitz, 2006). To evaluate whether invasive Typha was facilitating EFB in GLCWs, we tested their co-occurrence at two scales. At the regional Great Lakes scale, we used plant data from a Great Lakes-wide coastal wetland monitoring study. At the local scale, we analyzed associations between the two species using intensively collected data within Munuscong Bay, a Great Lakes coastal wetland that harbors both species. Secondly, at Munuscong Bay, we tested the ability for invasive Typha to facilitate EFB directly by conducting a large-scale (60 × 15 m plots), multi-year invasive Typha-removal study. We hypothesize that existing populations of invasive Typha facilitate and allow the emerging invader EFB to persist and spread throughout Great lakes coastal wetlands.

Methods

Regional co-occurrence analyses

To evaluate regional occurrences, we used data from the Great Lakes Coastal Wetland Monitoring Program (GLCWMP) (Uzarski et al., 2017) collected in 2011–2012 and 2014–2015. The GLCWMP sampled >500 GLCWs using a standardized methodology (Uzarski et al., 2017). In each wetland, three transects were located parallel to the water-depth gradient, thereby bisecting the three typically occurring vegetation zones: wet meadow, emergent marsh, and submergent marsh. Along each transect, five evenly spaced 1-m² sampling plots were located within each vegetation zone (Uzarski et al., 2017). Transect lengths varied depending on the width of vegetation zones. At each plot, vegetation sampling crews determined plant community composition by assigning areal cover values (~1–100%) for each plant species, total vegetation, and standing dead vegetation. Additional environmental data were collected from each vegetation plot including wetland zone (meadow, emergent, submergent), water depth, and soil organic layer depth. Soil organic layer depth was measured by gently pushing a graduated pole through the easily penetrable organic layer to the mineral sediment margin. Additionally, for each individual wetland site, we calculated the fetch by measuring the distance from the upland edge of the wetland (at the center of the linear extent of the wetland’s shoreline) to the longest distance across open water to the lake’s opposite shore. We modeled data at the plot-level, treating all vegetation plots independently, and at the site-level, by calculating the average for all numerical values within each site.

Munuscong Bay invasive Typha-removal study

We conducted our invasive Typha-removal experiment at the Munuscong Bay in Chippewa County, Michigan (46.20 N, 84.25 W, Fig. 1). Munuscong Bay is a connecting channel river delta marsh (Albert et al., 2005) positioned at the outlet of the Munuscong River to the St. Marys River, which connects Lake Superior to Lake Huron. Munuscong Bay harbors an extensive population of invasive Typha, the dominant emergent macrophyte, which has been abundant in the site for >30 years (Albert et al., 1987). EFB was first found at Munuscong Bay in 2010 (D. Albert, personal observation, 2010), but the EFB population has since expanded, reaching areal cover values of over 50% in some parts of the marsh and becoming a dominant species in the Typha understory.

To test facilitation of EFB by invasive Typha, we set up an invasive Typha-removal experiment during July 2016 in Munuscong Bay. Using a low ground pressure amphibious, tracked vehicle (Softtrak Cut and Collect, Logologic, Devon, UK), we implemented two treatments: 1) One-time above water harvest (TyHarvAW), where all invasive Typha biomass >20 cm above the water line was cut and removed from the marsh by the Softtrak harvester’s flail-style chopping mechanism, and 2) One-time below water harvest (TyHarvBW), which involved harvesting above water biomass, then subsequently cutting all remaining severed invasive Typha stems ~20 cm below the water surface using a specialized sickle-bar mower attachment (Logologic, Devon England). Each management plot was 15 × 60 m in size, with the narrow part of the plot oriented towards the open-water edge of the marsh to maximize water-depth variability within plots. The experiment consisted of three replicate blocks within which we randomly assigned each of our two treatments and an unmanipulated control. All blocks contained invasive Typha as the dominant emergent species, with EFB growing at the water’s surface. Pre-treatment percent cover data on invasive Typha and EFB revealed some variability between blocks in Typha and EFB cover (ranging from 11.0 to 13.5% and 4.1–11.6%, respectively), but differences were not statistically significant as determined by ANOVA (p > 0.05).

To monitor the vegetative response to our invasive Typha removal experiment, we established four 1-m² subplots in each treatment plot within each of our three blocks (4 subplots × 3 treatments × 3 blocks for n = 36 subplots). Subplots were evenly spaced along the central axis of each treatment plot. In each subplot, we collected data mirroring the methods of the Great Lakes Coastal Wetland Monitoring Program: water depth, depth of the organic soil layer, and aerial percent cover.
values (<1–100%) for each of the following: total vegetative cover, standing dead vegetation, detritus below the water surface, and cover for each vascular plant species (Uzarski et al., 2017). Percent cover was determined via visual inspection from multiple samplers standing above each plot. We sampled each subplot once per year in late July or early August in 2017 and 2018 to coincide with peak plant coverage and precede EFB’s propagule production (Catling et al., 2003).

Analyses: regional co-occurrence

We analyzed the regional co-occurrence between EFB and environmental variables, plant community assemblage, and dominant invasive plant presence using logistic regression and stepwise Akaike Information Criteria (AIC) model selection to identify the model with the highest parsimony (Burnham and Anderson, 2004). Models with ΔAIC values < 2 were considered to be significant when assessing EFB presence/absence (Burnham and Anderson, 2004). We created models of EFB occurrence in established populations (Lake Ontario) and invading populations (all other Great Lakes and Great Lake connecting channels), at the plot and site levels, with data from all four sampling years (2011–2012, 2014–2015). Continuous predictor variables in full models included: fetch, water depth, standing dead cover, and organic depth. Discrete predictor variables included: wetland zone (meadow, emergent, or submergent), invasive Typha presence, Phragmites australis presence, and Phalaris arundinacea presence. We aggregated data to the site level by calculating the mean value of continuous numerical variables across all plots within each wetland.

Analysis: Munuscong Bay invasive Typha-removal study

For our field experiment, we analyzed the effects of treatment and year on plant and environmental data using linear mixed-effects modeling (LME; Bates et al., 2015). We accounted for the non-independence of measures collected over two separate years by including treatment and year as factors. Because the treatment for each plot was randomly assigned and subplot locations were approximated within each plot by GPS, each subplot was treated as a nested random effect within plot and block in the LME model. To minimize type I errors, we fit models using restricted maximum likelihood method and generated type-III ANOVAs using approximated degrees of freedom with Satterthwaite’s method (Kuznetsova et al., 2017; Luke, 2017). The assumption of normality of residuals was checked visually with QQ plots, and log+1 transformation was used on all response variables to meet assumptions of normality and homogeneity of variance. When overall models were significant (p ≤ 0.05), multiple contrasts were
assessed among controls and treatment levels and were calculated using Tukey's Honest Squared Differences method.

Treatment effects on species assemblages were averaged at the plot level to avoid absences in the species cover matrix and were analyzed using permutation multivariate analysis of variance (PERMANOVA; Anderson, 2001). PERMANOVA is a nonparametric multivariate statistical tool that can be used to examine differences between treatments while simultaneously considering multiple factors, in this case assemblages of many different plant species, which is robust to heterogeneity in data (Anderson and Walsh, 2013) and instances with repeated measures (Anderson, 2001). Communities were visualized in 2-dimensional space using nonmetric multi-dimensional scaling (NMDS; McCune et al., 2002) of species percent cover data aggregated at the plot-level, with dissimilarity based on Bray-Curtis distances. Fitted vectors of environmental variables: organic matter depth (cm), unvegetated cover (%), total vegetation cover (%), standing dead vegetation cover (%), belowwater detritus cover (%), water depth (cm), invasive Typha cover (%), and EFB cover (%), were displayed over NMDS plots at a significance level of $p \leq 0.05$, as determined by permutation procedure (with 10,000 replicate permutations). We performed all analyses in R 3.4.2 (R Core Team, 2017) with the 'vegan' package (Oksanen et al., 2018) for diversity metrics and NMDS, the 'adonis' function for PERMANOVA analysis (Anderson, 2001; Anderson and Walsh, 2013), the 'lme4' package for LME models (Bates et al., 2015), and the 'lmerTest' package to generate $p$-values from LME models (Kuznetsova et al., 2017).

Results

Regional co-occurrence

Across all AIC-selected models of EFB occurrence in the Great Lakes (at the site-level, plot-level, established, and invading populations) invasive Typha presence was the first or second most important predictor variable (Table 1), and was significantly ($p < 0.05$) positively correlated with EFB presence (Table 2). Within the range of well-established EFB populations (Fig. 2; i.e., Lake Ontario EFB first detected in 1991 and frequent since 2002; D. Wilcox, personal observation, 2002; Trebitz and Taylor, 2007), invasive Typha was positively related and Phragmites australis was negatively related to EFB presence at the site-level (Table 1). Both relationships were significant ($p < 0.05$; Table 2). In a second substantially supported model ($\Delta$AIC = 1.28; Burnham and Anderson, 2004), standing dead was also included as a positive predictor of EFB presence (Table 1). At the plot-level in the established population, meadow zone and standing dead were negatively related, while invasive Typha, emergent zone, and Phragmites australis were positively related to EFB presence (Table 1). All positive and negative correlations were highly significant ($p < 0.001$) except for Phragmites australis presence (Table 2).

Within the EFB invading range (i.e. all other Great Lakes and connecting channels) at the site-level, invasive Typha, standing dead, organic depth, and Phalaris arundinacea were all positive predictors (Table 1) that significantly ($p < 0.05$) correlated with EFB presence (Table 2). The second supported model ($\Delta$AIC = 0.12; Burnham and Anderson, 2004) also included Phragmites australis as a positive predictor of EFB presence (Table 1). At the plot-level, the AIC-selected model included invasive Typha, Phragmites australis, and standing dead as positive predictor variables and meadow zone, fetch, and organic depth as negative predictor variables (Table 1). All positive and negative correlations were significant ($p < 0.01$; Table 2).

Munuscong Bay Typha removal study

In our linear mixed effects model across 2017 and 2018 for our harvest experiment we found significant effects of invasive Typha removal treatment but not year or the interaction of treatment and year on invasive Typha cover, EFB cover, standing dead vegetation, and total vegetation cover (Fig. 3; $p = 0.005$, $p = 0.041$, $p = 0.030$, $p = 0.014$, respectively). In pairwise comparisons, invasive Typha cover was significantly reduced in TyHarvBW treatments compared to controls in both 2017 and 2018 (Fig. 3b; $p = 0.001; p = 0.003$, respectively), as was EFB cover (Fig. 3a; $p = 0.050; p = 0.036$, respectively), standing dead vegetation (Fig. 3c; $p = 0.041$; $p = 0.008$, respectively), and total vegetation cover (Fig. 3d; $p = 0.007; p = 0.015$, respectively).


| Table 2 |
| Summary of the strength and direction of the relationships between predictor variables, identified through logistic regression and AIC model selection, and Hydrocharis morsus-ranae (EFB) presence in Great Lakes coastal wetlands. Predictor variables listed in order of reducing predictive power. Significance ($p$): $P < 0.05$; $** P < 0.005$; $*** P < 0.001$. |

<table>
<thead>
<tr>
<th>Variable</th>
<th>Estimate</th>
<th>Std. Error</th>
<th>Z value</th>
<th>P</th>
<th>Odds Ratio</th>
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<tr>
<td>Site-level Established population</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Invasive Typha</td>
<td>3.06</td>
<td>1.20</td>
<td>2.55</td>
<td>*</td>
<td>21.27</td>
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<tr>
<td>Phragmites</td>
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<td>0.74</td>
<td>-2.33</td>
<td>*</td>
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<tr>
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<td>0.68</td>
<td>5.25</td>
<td>**</td>
<td>35.60</td>
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<tr>
<td>Standing dead</td>
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<td>**</td>
<td>1.07</td>
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<td>0.001</td>
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<tr>
<td>Plot-level Established population</td>
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<td></td>
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<tr>
<td>Meadow zone</td>
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<td>0.21</td>
<td>-7.10</td>
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<td>0.22</td>
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<td>0.14</td>
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<td>2.47</td>
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<td>Emergent zone</td>
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<tr>
<td>Standing dead</td>
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<td>0.001</td>
<td>-5.27</td>
<td>**</td>
<td>0.99</td>
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<tr>
<td>Phragmites</td>
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<td>0.40</td>
<td>-0.29</td>
<td>NS</td>
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<td>Invading population</td>
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</tr>
<tr>
<td>Invasive Typha</td>
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<td>0.16</td>
<td>13.07</td>
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<td>7.54</td>
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<tr>
<td>Meadow zone</td>
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<td>Fitch</td>
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<tr>
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<td>0.01</td>
<td>0.004</td>
<td>2.61</td>
<td>**</td>
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| Table 1 |
| Logistic regression models of Hydrocharis morsus-ranae (EFB) presence in Great Lakes coastal wetlands across four years (2011–2012, 2014–2015) in the established population (Lake Ontario) and invading population (other lakes and connecting channels) at the site and plot level. Substantially supported models, with $\Delta$AIC < 2.0, as determined by stepwise AIC model selection (Burnham and Anderson, 2004), are displayed in decreasing order of support. Sign in parentheses following each variable indicates a negative influence on EFB presence. |

<table>
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<tr>
<th>Site level</th>
<th>AIC</th>
<th>$\Delta$AIC</th>
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<tr>
<td>Established population (n = 102)</td>
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<tr>
<td>EFB presence -</td>
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<tr>
<td>Invasive Typha + Phragmites (-)</td>
<td>89.44</td>
<td>0.00</td>
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<tr>
<td>Invasive Typha + Phragmites (-) + standing dead</td>
<td>90.72</td>
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</tr>
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<td>97.06</td>
<td>7.62</td>
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<tr>
<td>Invading population (n = 419)</td>
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<tr>
<td>EFB presence -</td>
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<td></td>
</tr>
<tr>
<td>Invasive Typha + standing dead + organic depth + Phalaris</td>
<td>329.90</td>
<td>0.00</td>
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<tr>
<td>Invasive Typha + standing dead + organic depth + Phragmites</td>
<td>330.02</td>
<td>0.12</td>
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<td>Phalaris + Phragmites</td>
<td>482.35</td>
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<td>Plot level</td>
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<td>Established population (n = 3746)</td>
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<tr>
<td>EFB presence -</td>
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<td></td>
</tr>
<tr>
<td>Meadow zone (-) + invasive Typha + Emergent zone + standing dead (-) + Phragmites</td>
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<td>4276.50</td>
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<tr>
<td>Invading population (n = 12,901)</td>
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<tr>
<td>EFB presence -</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Invasive Typha + Meadow zone (-) + fetch (-) + Phragmites + organic depth (-) + standing dead</td>
<td>1659.30</td>
<td>0.00</td>
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<tr>
<td>NULL (intercept only)</td>
<td>2049.00</td>
<td>379.70</td>
</tr>
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</table>
Multivariate analyses of plant communities one and two years after treatments showed a significant shift in vegetation. When considering both years' species community data in a PERMANOVA, treatment effects led to a significant shift in vegetation community ($F = 4.093, p = 0.01$), while year and the interaction of treatment and year did not, so we analyzed plant community data together for both 2017 and 2018 datasets. In pairwise PERMANOVA analyses, plant communities varied significantly between TyHarvBW and control treatments ($F = 6.853, p = 0.01$), and TyHarvAW and TyHarvBW treatments ($F = 4.777, p = 0.02$).

NMDS plots visually illustrate differences in plant community assemblages between treatments in two-dimensional space across both years (Fig. 4). Our NMDS showed a good fit to the data, with a stress of 0.059 (Clarke, 1993). Across both years, TyHarvBW treatments tended to diverge from control and TyHarvAW treatments, while TyHarvAW treatments and controls tended to overlap. Fitted vectors to the NMDS showed the significant vector for % cover unvegetated correlated positively with TyHarvBW treatments, while control and TyHarvAW treatments were correlated positively with % cover EFB and % cover total vegetation. Percent cover invasive Typha and % cover standing dead also varied together in the direction of TyHarvAW and control plots.

Discussion

This study sought to clarify the relationship of an emergent invasive, *Typha*, and a floating invader, EFB, across multiple scales in GLCWs. We found evidence that not only are the two species associated, but that invasive *Typha* may provide structural facilitation for EFB, most likely by ameliorating common stressors in GL coastal wetlands, including waves, wind, and seiches (Keough et al., 1999; Trebitz, 2006).

Our Great Lakes-wide analysis revealed that invasive *Typha* is an important predictor of the presence of EFB across multiple spatial scales. In both established (Lake Ontario) and invading (all other Great Lakes and Great Lake connecting channels) populations at the site and plot level, invasive *Typha* presence was the first or second factor in all AIC-selected models (Table 1).

Environmental variables in this study’s models provide insights into EFB’s niche in GLCWs. EFB requires standing water to persist, is naturally associated with emergent and submergent plant communities (Catling et al., 2003), and would be unlikely to occur in meadow zones with little to no standing water or in shallow water zones that are often dewatered. As such, wetland zonation appeared in both plot-level models with emergent zone positively predictive of EFB presence in the established population and meadow zone negatively associated with EFB in the invading and established populations (Table 1). Further,
wind and wave exposure, as quantified by fetch (the farthest distance from the center of a wetland across open water, and a useful proxy for exposure to wind, waves, and seiche activity [Burton et al., 2004]) was a negative predictor of EFB presence in the invading population. Because EFB is a free floating species, vulnerable to disturbances from wave and wind activity (Catling et al., 2003), it follows that more exposed wetlands, with greater fetch, would be less suitable habitat for EFB, and it adds additional support for the proposed mechanism of invasive Typha facilitating EFB by providing physical shelter in high energy GLCWs.

Over time, Typha invasion is associated with organic sediment deposition and increased detritus and standing dead cover (Lishawa et al., 2013; Lishawa et al., 2014; Mitchell et al., 2011), which confers competitive dominance over native plants (Larkin et al., 2012; Vaccaro et al., 2009). Our Great Lakes-wide models identify some interesting and contrasting relationships between EFB, standing dead vegetation, and organic matter that may point to thresholds of EFB tolerance associated with old and highly established invasive Typha. Standing dead cover had contrasting relationships with EFB; it was negatively associated with EFB at the plot-level in established populations (Lake Ontario) and positively associated in established populations at the site-level and invading populations in all cases (Table 1). Standing dead litter can provide important structure for EFB, protecting it from wind, wave, and seiche activity. However, beyond a certain cover threshold, dense standing dead material may exclude EFB by preventing adequate light penetration to the water surface; EFB is vulnerable to shading levels above 70% (Zhu et al., 2014), which are common in the understory of established invasive Typha stands (Lishawa et al., 2015). In the well-established population of EFB (Lake Ontario) the negative relationship between standing dead cover and EFB may be indicative of this

![Fig. 3. Results from facilitation experiment in Munuscong Bay showing mean percent areal coverage by year and treatment for: live Hydrocharis morsus-ranae (EFB; a), live invasive Typha (b), standing dead vegetation (c), and total of all live vegetation (d). Error bars represent standard error. Control = unmanipulated plots; TyHarvAW = above water Typha harvest only; TyHarvBW = above water Typha harvest with subsequent below water cutting. Indicators of a statistically significant result in within-year pairwise comparisons between controls and treatments as determined by linear mixed effects models: * p < 0.05, ** p < 0.01, *** p < 0.001.](https://doi.org/10.1016/j.jglr.2019.07.005)
threshold at the plot-level. At the site-level, however, wetlands containing standing dead were positively associated with EFB presence, possibly due to the increased prevalence of standing dead material in sites invaded by *Typha* (Mitchell et al., 2011), where less dense *Typha* stands in the emergent zone may provide structural support for EFB (Table 1).

Organic soil depth had contrasting relationships with EFB in the invading population, with a negative effect at the plot-level. In part, this may be explained by the preference of EFB for the emergent and submergent marsh zones, which tend to have shallower organic soils than the meadow zone (Albert et al., 2005). In contrast, at the site-level, organic soil depth was positively correlated with EFB, which may be due to the association of structure-providing invasive *Typha* with rapid accumulation of organic matter (Lishawa et al., 2013; Mitchell et al., 2011).

Interestingly, both *Phragmites australis* and *Phalaris arundinacea*, two common invasive grasses in the Great Lakes, were also positively associated with EFB in some cases of Great Lakes-wide modeling, although in fewer models and with lesser predictive strength than invasive *Typha* (Table 1). Both species share physical and ecological similarities with invasive *Typha*: they are tall, perennial, rhizomatous graminoids that form dense, low-diversity clones (Zedler and Kercher, 2004) that can provide structural support for EFB. However, *Phragmites australis* also appeared as a negative predictor of EFB presence in the established population (Lake Ontario) at the site-level, which may be indicative of competitive exclusion or the tendency of *Phragmites* to grow in drier and shallower conditions than *Typha* (Asaeda et al., 2005) which are unsuitable for EFB. It is also important to note that native emergent species in GLCWs have the potential to facilitate EFB populations by providing structural support and shelter from wind, wave, and seiche activity in GLCWs. This study focused on the most abundant and dominant plants in the region, and thus did not directly test facilitative relationships between EFB and native species, which merits further investigation.

While results of Great Lakes-wide models reveal a close association between invasive *Typha* and EFB, the facilitative relationship between the two plants is further illuminated in the invasive *Typha*-removal experiment. Invasive *Typha* was effectively removed and killed in the TyHarvBW treatments, where both *Typha* and EFB cover dropped precipitously (Fig. 3). The TyHarvAW treatments, however, did not reduce invasive *Typha* or EFB cover. This is due to the fact that *Typha*, a perennial plant, has a robust system of underground rhizomes that can allow the plant to rebound quickly from cutting (Keyport et al., 2018; Lishawa et al., 2015). Cutting below the water surface with sustained flooding, however, severs the atmospheric connection between *Typha* stems and their underground rhizomes. *Typha*, like all plants, requires oxygen to metabolize sugars, and relies on a system of hollow plant tissue, called aerenchyma, to conduct oxygen down to rhizomes. TyHarvBW cutting severed this connection and effectively killed plants,
leading to a more open vegetation structure than the pre-treatment emergent marsh (Lishawa et al., 2017). Creation of these openings was accompanied by a drastic (five-fold) decrease in EFB coverage (Fig. 3a), as the plant was now exposed to wind and seiche activity in the treatment plots. This reduction was also accompanied by a reduction in standing dead material, which otherwise provides structural shelter for EFB plants and reproductive turions. The appearance of standing dead as a positive indicator in regression models mirrors the effects seen in the removal experiment, where EFB cover is higher in treatments containing higher standing dead cover, except for the TyHarvAW treatment in 2017 (Fig. 3). The negative impacts of standing dead cover via shading or competitive exclusion were not tested in this experiment due to EFB’s co-dominance with invasive Typha at this site. NMDS results further emphasize the shift in vegetative community from control to TyHarvBW, where the environmental vector “unvegetated” correlates with the TyHarvBW treatment, while EFB cover, invasive Typha cover, and standing dead cover correlated with the plots containing EFB after treatment (Fig. 4: Control and TyHarvAW). NMDS vectors reflect important factors in the regression models, with invasive Typha and EFB tending to vary together along with standing dead cover. The fact that EFB cover was lower over two years in TyHarvBW treatment where invasive Typha had been removed suggests a facilitative relationship not unlike that of the root-stabilized invasive plant, alligator weed (Alternanthera philoxeroides), and a secondary invader, the floating plant, water hyacinth (Eichhornia crassipes). Like invasive Typha and EFB, both species occupy the same habitat while the root-stabilized species’ presence leads to increased growth of the floating species by providing structure and protection (Wundrow et al., 2012). Although alligator weed improved growth of water hyacinth, it also limited establishment of the plant through direct competition, a commonly observed phenomenon in instances of facilitation (Flory and Bauer, 2014). Furthermore, dominant plants that facilitate other species may also competitively exclude species in instances of dense growth or reduced disturbance (Van De Koppel et al., 2006). Data from the Great Lakes-wide models suggesting the presence of standing dead cover as a negative predictor of EFB point to the need for future research on the relationship between invasive Typha, its detritus, and EFB to determine thresholds of EFB establishment and persistence.

This study has implications not only for facilitation biology, but also for invasive species management. EFB is an emerging invader to the Laurentian Great Lakes, where invasive Typha is already an established dominant. While invasive Typha stands appear to be the most suitable habitat for EFB in the Great Lakes, our modeling reveals that stands of Phalaris arundinacea and Phragmites australis also harbor EFB. The tolerance of EFB for stands of these three common invaders indicates that vast potential exists for expansion of EFB’s current range through future invasions; as of 2013, over 36% of total GLCW area was dominated by these three invasive plants (Carson et al., 2018). Therefore, proper management of EFB is not likely to be successful unless the other emerging invasive plants that harbor it are also controlled.

Conclusion

Here, we offer a unique analysis of two invasive plant populations, a well-established invasive macrophyte, Typha and an emerging floating invader, EFB over multiple spatial scales. An analysis of Great Lakes-wide survey data reveals a close association between these two plants, along with a clear illustration of EFB’s habitat preferences. Combined with an experimental removal study, this paper elucidates the facilitative relationship between invasive Typha and EFB, whereby Typha provides structural protection from EFB against wind, wave, and seiche activity. These results show that we expect new EFB populations to colonize Great Lakes coastal wetlands that already contain established invasive Typha populations. Furthermore, EFB control is contingent upon control of co-occurring invasive Typha. Taken together, this paper has implications for the early detection and rapid response to EFB in the Great Lakes.

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