Local disturbance by muskrat, an ecosystem engineer, enhances plant diversity in regionally-altered wetlands

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Abstract. Biotic ecosystem engineers are increasingly recognized as important drivers of biodiversity, structure, and function in many ecosystems. By regulating physical processes and creating local disturbances, ecosystem engineers can serve as important elements of passive habitat restoration, as they continuously alter and shape their environments. Native to North American temperate wetlands, the common muskrat (Ondatra zibethicus) is an ecosystem engineer that alters its environment through herbivory, house and structure building, and creation of activity networks. While the physical consequences of muskrat disturbances are well-known, few studies have quantified their impact on the wetland biotic community. We conducted a field study to investigate the effects of muskrat herbivory and structure building on plant biodiversity in wetlands along the upper St. Lawrence River (New York, USA) that have been extensively modified by long-term water regulation and non-native cattail invasion. Plant species richness and diversity were greater in muskrat-disturbed areas compared to at-large reference plots within the same wetlands. Soil saturation mediated the biodiversity impacts of muskrats, with intermediate moisture levels resulting in the highest species richness. These interacting drivers, muskrat activity and hydrology, had a compensatory effect on plant biodiversity loss associated with non-native cattail invasion. Multivariate analysis indicated a distinct plant community associated with muskrat disturbances. Analysis of spatiotemporal patterns of house locations suggests that some muskrats reuse house locations in sequential years, likely amplifying the intensity and duration of their impacts. This study demonstrates that muskrat disturbance influences wetland plant diversity at scales relevant to regional drivers of plant diversity.

Key words: biodiversity; disturbance ecology; ecology; ecosystem engineer; Ondatra zibethicus; restoration; Typha spp.

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INTRODUCTION

Ecosystem engineers are organisms that alter their surrounding environment to affect the quantity and quality of available resources (Jones et al. 1994, Gutierrez et al. 2003). By changing the amount and distribution of available resources in an area, ecosystem engineers often create unique habitats otherwise absent in the environment, thus opening up additional ecological niches that can support a more diverse species assemblage (Gutierrez et al. 2003, Law et al. 2017). In wetlands, the presence of ecosystem engineers can speed up, slow down, or reset ecological transitions, by creating disturbances of varying intensity and duration. In systems where physical
drivers have been strongly modified, ecosystem engineers may enhance restoration efforts and ecological recovery (Curran and Cannatelli 2014, Law et al. 2017). This can be especially important where altered physical conditions have decreased the competitive advantages of native species and facilitated biological invasions (Hecky et al. 2010, Kovach et al. 2015).

In the wetlands of North America, the North American beaver (Castor canadensis) and the common muskrat (Ondatra zibethicus) are two prominent mammalian ecosystem engineers (Higgins and Mitsch 2002, Mott et al. 2013, Curran and Cannatelli 2014, Rozhkova-Timina et al. 2018). A highly adaptable species, muskrats are relatively common throughout their native range in temperate North American wetlands, as well as in Europe and Asia where they are invasive and modify native ecosystems and human water control infrastructure (Cotner and Schooley 2011, Rozhkova-Timina et al. 2018).

Muskrats are medium-sized, semi-aquatic rodents, which primarily feed on robust emergent hydrophytes and occasionally on small animals such as freshwater mussels (Willner et al. 1980, Allen and Hoffman 1984, Ecke et al. 2014, Edelman et al. 2015). Like most rodents, muskrats can reproduce quickly and can have two to three litters per season with 4–8 kits each (Alexander 1956, Willner et al. 1980). They build a variety of structures using locally available plant material and substrate, including free-standing houses and bank burrows, which serve as refuge from predators and exposure to the elements (Dozier et al. 1948, Danell 1978).

Under optimal conditions, muskrat herbivory can remove large quantities of vegetation in a short period, creating extensive impact areas called “eat-outs” (Allen and Hoffman 1984, Higgins and Mitsch 2002). Muskrat herbivory can drastically reduce the biomass and cover of dominant emergent hydrophytes such as cattails (Typha spp.), because the animals remain active throughout the winter, continuously foraging for succulent roots and shoots of perennial plants (Alexander 1956, Willner et al. 1980, Toner et al. 2010). Ecological studies have documented the effects of muskrat activity on enhancing habitats for waterbirds (e.g., Chlidonias niger; Kiviat 1978), altering water chemistry (Connors et al. 2000), changing macroinvertebrate assemblages (De Szalay and Cassidy 2001, Nummi et al. 2006), and increasing biomass of non-dominant plants atop their houses (Kangas and Hannan 1985). However, few quantitative studies have investigated how muskrat disturbance interacts with other wetland ecosystem drivers to influence the biotic community as a whole (Danell 1978, Kadlec et al. 2007, Skyriené and Paulauskas 2013).

Muskrats’ capacity to remove large areas of robust emergent vegetation may create new ecological niches by changing the abiotic and biotic conditions in their habitats. Removal of large, canopy-forming, robust emergent hydrophytes would effectively reduce the interspecific competition among wetland plants in conjunction with increased availability of light and space. The construction of houses by muskrats creates topographic heterogeneity in the landscape, specifically locally elevated habitats that may allow less flood tolerant and more facultative wetland plants to occur. Aside from the direct impact on the wetland plant assemblage, these changes in environmental qualities could have emergent effects on the wetland community as a whole through the long-term and cumulative local disturbances present in wetlands with high muskrat densities.

Despite muskrats’ ubiquity and ecological importance, few studies have investigated and quantified their capacity as ecosystem engineers to influence the broader ecological community, including wetland plant assemblages. As such, muskrat-mediated changes in plant species composition and species diversity are poorly understood, particularly in respect to how muskrat disturbance interacts with other ecological drivers such as hydrology and biotic invasions. This question is particularly pressing with the introduction and spread of invasive cattails throughout large parts of the muskrats’ natural habitat in the North American Great Lakes region (Jansson et al. 2000, Wilcox et al. 2007, Tuchman et al. 2009, Freeland et al. 2013).

One area of concern in North America is the Thousand Islands (TI) archipelago of the St. Lawrence River (SLR), where decades of water level stabilization in conjunction with the expansion of the invasive cattails has led to degradation of wetland habitat throughout the region (Jansson et al. 2000, Wilcox et al. 2007, Farrell et al.
long-term modifications to assess the geographic scope and potential and temporal distribution of house locations of muskrat activity, wetland hydrology, and biotic competition via interaction effects between disturbance, resource supply, and biotic competition via interaction effects of muskrat activity, wetland hydrology, and cattail litter on biodiversity; and (3) analyze the spatial and temporal distribution of house locations to assess the geographic scope and potential long-term modifications to the ecosystem.

We hypothesized that muskrat disturbances would increase plant biodiversity by reducing the extent of the dominant canopy-forming species (in particular *Typha* spp.), thereby increasing habitat heterogeneity and available growing space for other species. A further question was whether muskrat disturbance would shift the plant community toward more wetland obligate or alternatively terrestrial species, and how local conditions of hydrology may mediate that shift (Reed Jr. 1988). Finally, we hypothesized that high densities of muskrat, whether due to natural site factors or due to wetland water level manipulation, should result in landscape-scale changes. We tested this idea by evaluating the spatiotemporal persistence of muskrat houses in a managed wetland with water levels manipulated to prevent artificial winter drawdown of the SLR hydrosystem.

**Materials and Methods**

**Study sites**

The TI region of the Upper SLR is a boundary water that separates northern New York State (NY) from Canada’s Ontario and Quebec provinces and spans approximately 78 km of the river’s length from the Lake Ontario outlet to Morrisstown, NY (Fig. 1). This reach of the SLR forms part of the St. Lawrence Seaway, which spans the waters between the Gulf of St. Lawrence and Lake Superior. The water levels of the TI region and the seaway are regulated by policies of the International Joint Commission (IJC) via the Moses-Saunders Power Dam at Massena (Roseman et al. 2014).

Currently, multiple anthropogenic stressors impact the TI region including agriculture runoff, human alterations to the SLR hydrologic regime, non-native species invasions, and pollution from industry and maritime trade (Roseman et al. 2014). River regulation following the 1958 completion of the Moses-Saunders Power Dam has dampened annual and interdecadal hydrologic fluctuations and lowered the river’s average winter water level (Farrell et al. 2010, Roseman et al. 2014). While a new IJC water regulation plan (International Joint Commission 2014) is intended to restore some of the region’s natural hydrologic variability, over five decades of water level stabilization in the SLR has facilitated the expansion of invasive cattails throughout the region’s coastal wetlands (Wilcox et al. 2008). The spread of hybrid *Typha × glauca* Godr., which is a cross of native broad-leaved cattail (*Typha latifolia*) with the non-native, invasive narrow-leaved cattail (*Typha angustifolia*), has led to a substantial decrease in ecologically important sedge meadow habitats (Galatowitsch et al. 1999, Jansson et al. 2000, Wilcox et al. 2008, Olson et al. 2009, Freeland et al. 2013, Szabo et al. 2018). *T. × glauca* exhibits hybrid vigor, which allows it to outcompete and displace *T. latifolia* throughout much of its native range (Pieper et al. 2018, Szabo et al. 2018).
Five sites were surveyed for this study, spanning two broad wetland systems, French Creek and Cranberry Creek (Fig. 1). Both wetlands have drowned river mouth geomorphology connected to the SLR and share a similar ecological community structure and invasive *Typha* dominance (Farrell et al. 2010). The ubiquitous effect of the IJC-managed regulation influences nearly 7000 ha of coastal wetlands and includes Cranberry Creek and other sites in French Creek (Farrell et al. 2010). Historically, Cranberry Creek and part of French Creek (Carpenters Branch) had local water control weirs as part of a field experiment by Farrell et al. (2010). While the water control structure at Cranberry Creek had been removed in 2003, the local water level at Carpenters Branch in French Creek is still experimentally managed via a passive weir to prevent artificial fall drawdowns and maintain higher winter water levels relative to the IJC-managed Moses-Saunders Dam-regulated water levels of the SLR and Lake Ontario. The locally water-controlled wetland has been shown to maintain a higher muskrat house density than the other sites (Farrell et al. 2010, Toner et al. 2010, Kua 2019) and allows assessment of disturbance effects relative to reference areas across a greater range of muskrat activity levels and hydrologic conditions.

**Field sampling**

To assess the local influence of muskrat activity on the wetland plant community, we conducted vegetation surveys in the TI region in
July and August 2018 during the peak growing season, comparing diversity and community composition in the vicinity of muskrat houses, which are disturbed areas, to relatively undisturbed reference areas (Table 1). To establish a baseline condition, a site-wide assessment of wetland plant diversity (“reference” plots) was conducted using variable length transects that spanned an elevation gradient from open water to the upslope wetland boundary. The sampling approach was designed to encompass the range of environmental heterogeneity within the wetlands. Plots were sampled with individual quadrats (1 m²) set along each transect at fixed elevation increments (0.5 m). Elevations as specified by the International Great Lakes Datum (1985) were determined from known-elevation benchmarks established using Trimble GeoXH 5800 at each plot location (Farrell et al. 2010). The percent cover of all plant species observed in the quadrats was estimated to the nearest percent by trained field technicians. Wetland plants were identified to the genus level at minimum, and species richness and Shannon’s diversity index were calculated for each quadrat. In addition, we characterized substrate moisture status as either “Dry,” “Saturated,” or “Flooded.” Plots dry to touch were considered “Dry,” plots wet to touch and/or with standing water <10 cm were categorized as “Saturated,” and plots inundated to >10 cm were classified as “Flooded.” Live Typha cover and dead litter cover were estimated (Kua 2019). Across both French Creek and Cranberry Creek systems, a total of 133 reference plots were surveyed along 26 transects (Table 1).

To assess muskrat impacts, the local area around selected houses (“muskrat” plots) was surveyed with quadrat sampling along 5-m length transects. Five meters corresponds with a radio-telemetry study on winter muskrat movement (MacArthur 1978). Twenty-eight muskrat houses were selected at random from a list of active houses detected during the prior winter house count survey (January–February 2018). The average area of the muskrat houses (as ellipses) was 1.9 m² ± 0.9 (±SD) with an average height of 61.8 cm ± 17.4. Using a square PVC frame, three 1 m² quadrats were sampled at 1 m spaced intervals along each transect with an additional quadrat centered on the muskrat house (Appendix S1: Fig. S1). Muskrat activity at each location was verified from field observations of well-maintained house structure, herbivory (i.e., signs of chewed plant material or cut plant stems) or cleared rivulets which signified muskrat runs. Data collection protocols were identical to those for the reference quadrats. Across both wetland systems, a total of 184 muskrat plots were surveyed at 28 separate house locations (Table 1).

### Statistical analyses

**Muskrat disturbance and habitat structure, plant diversity, and community composition.**—Typha spp. live cover between muskrat and reference plots were compared to test the difference in Typha live cover (abundance) between these two habitats. Species richness and Shannon’s diversity indices from vegetation plot data were compared to test for differences between muskrat and non-muskrat areas (i.e., a disturbance effect), and a multivariate community analysis was performed to explore the compositional dissimilarity between muskrat-disturbed and reference transects.

We used a mixed modeling approach to estimate the effects of active muskrat disturbance.

### Table 1. Vegetation plots surveyed at five sites within two wetlands complexes.

| Wetland         | Site                                | Reference Transect | Reference Plots | Muskrat Transect | Muskrat Plots |
|-----------------|-------------------------------------|--------------------|-----------------|------------------|--------------|
| Cranberry Creek | Cranberry Creek Downstream (CCD)    | 1.45               | 4               | 21               | 1            | 6            |
|                 | Cranberry Creek Upstream (CCU)      | 8.26               | 2               | 12               | 7            | 44           |
|                 | Cranberry Creek Extension (CCX)     | 3.66               | 3               | 16               | 0            | 0            |
| French Creek    | Carpenters Branch (CAR)             | 9.89               | 8               | 36               | 10           | 67           |
|                 | French Creek Main Channel (FCC)     | 7.29               | 9               | 48               | 10           | 67           |

*Note:* Reference sampling units were variable length transects with plots located at fixed elevation increments of 0.5 m from the mean water level datum (IGLD 85). Muskrat transects indicate number of house locations surveyed. For both muskrat and reference transects, plots consisted of 1 × 1 m square quadrats.
and two environmental covariates, quadrat moisture class (moisture), and *Typha* spp. litter cover (litter), on vascular plant species diversity and richness. Wetland site was nested within wetland system (French Creek or Cranberry Creek) as a random effect to account for potential spatial covariance across all of the surveyed sites. We fitted a generalized linear mixed model to the species richness data. The richness counts were right-skewed as demonstrated by a Kolmogorov-Smirnov test of normality (P < 0.001; KS test); therefore, a negative binomial model with log link function was applied to the data after comparison with other distributions (e.g., Poisson).

For the species diversity model, which also accounts for species evenness, we used a linear mixed model, as the KS test of the data distribution from year-to-year, as indications of the spatial scope and longer-term (i.e., interannual) impacts of muskrat disturbance on their local environment. These data were pooled with historical house count surveys conducted between 2001 and 2012 (Toner et al. 2010; J. M. Farrell, unpublished data). While the historical data had irregular lapses in annual surveys, they were useful to compare house density trends over time (Fig. 2).

We used these pooled data to analyze the spatial-temporal correlation of muskrat house distribution in Carpenters Branch, for eight survey years between 2001 and 2019. A Knox test was conducted on muskrat house locations with a critical spatial distance of 0.0001 decimal degrees (approximately 7.87 m at 45° N) and recurrence lag of one year to quantify and compare the observed spatiotemporally “close” house pairs with their expected value, under the null hypothesis of no space–time interactions (Knox and Bartlett 1964). The expected value was calculated through a Monte Carlo (MC) permutation approach that compared distances for all possible pairings of houses in the data set (Mantel–Anderson 1964). The expected value was calculated through a Monte Carlo (MC) permutation approach that compared distances for all possible pairings of houses in the data set (Mantel–Anderson 1964).
would indicate that a spatial-temporal correlation for muskrat houses exists, as would be expected if houses were reoccupied in sequential years.

An alpha value of 0.05 was used to determine significance in all tests apart from the Kruskal-Wallis test ($\alpha = 0.01$). All analyses were conducted using R 3.6.0 (R Core Team 2019) with packages car (Fox and Weisberg 2019), emmeans (Lenth 2019), fitdistrplus (Delignette-Muller and Dutang 2015), lme4 (Bates et al. 2015), MuMIn (Barton 2019), and vegan (Oksanen et al. 2019).

RESULTS

Muskrat disturbance and habitat structure

The best model selected to predict *Typha* spp. live cover included both muskrat disturbance and moisture as fixed effects without the interaction effect (Table 2). Results from the EM means comparison showed that *Typha* spp. live cover was primarily influenced by substrate moisture. In particular, *Typha* spp. cover in quadrats with “Saturated” moisture had significantly higher percent live cover (Fig. 3). While the absolute percent of live *Typha* spp. cover was lower in muskrat-disturbed quadrats compared to reference areas, the EM means comparison indicated that the differences were not statistically significant ($t = 1.899; P = 0.058$; Fig. 3).

Muskrat disturbance and plant diversity

Plant species richness and diversity were influenced by both muskrat disturbance and the environmental factors of substrate moisture and *Typha* litter cover. The best model predicting species richness included the three main effects for disturbance, litter, and moisture and the

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Fig. 2. Sequential maps of Carpenters Branch (NYSDEC French Creek Wildlife Management Area) showing the location of muskrat houses observed each surveyed year. Triangles represent house locations in years without the local water control structures in place (2001–2003). Circles represent house locations during the water control period, surveyed in 2004, 2012, and 2017–2019.
interactions of Typha spp. litter × disturbance and moisture × litter (Table 3). Comparison of the EM means showed that species richness was significantly higher in the habitat around muskrat houses than in reference sites for both “Saturated” and “Dry” quadrats but was similar in “Flooded” quadrats (Fig. 4). Typha spp. litter cover had a negative effect on species richness (Fig. 5). The disturbance × moisture interaction showed a significant difference in magnitude of the effect of disturbance under different moisture classes, whereas the disturbance × litter interaction showed a difference in the loss rate of species richness with increased litter under each disturbance (Fig. 5).

The best model predicting species diversity included disturbance, moisture, and their interaction with litter included as a covariate (Table 3). Estimated marginal means showed that within disturbances, there were no significant differences in Shannon’s diversity. However, Shannon’s diversity was higher around muskrat houses in both “Dry” and “Saturated” quadrats but was not significantly different in “Flooded” quadrats (Fig. 4). Similar to species richness, Shannon’s diversity decreased as Typha spp. litter cover increased (Fig. 5). The interaction between disturbance and moisture suggests a difference in the contrasts between disturbances in each moisture class (Fig. 5).

For all three models, there was no obvious deviation from normality and homoscedasticity based on visual inspection of the model residual plot.

Muskrat disturbance and wetland plant community composition

The PERMANOVA showed that community composition of wetland plants was significantly

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Table 2. Comparison of the all combinations of mixed models predicting cattail live cover differences between muskrat disturbance locations and reference areas.

| Rank | (Intercept) | Moisture | Dist | Moisture:Dist | df | logLik | AICc | ΔAICc | Weight |
|------|-------------|----------|------|--------------|----|--------|------|-------|--------|
| 1    | 6.77        | +        | +    | NA           | 7  | 301.78 | -589.20 | 0.00  | 0.63   |
| 2    | 8.09        | +        | NA   | NA           | 6  | 299.91 | -587.56 | 1.64  | 0.28   |
| 3    | 6.79        | +        | +    | +            | 9  | 301.85 | -585.11 | 4.09  | 0.08   |
| 4 (Null) | 4.89    | NA       | +    | NA           | 5  | 294.63 | -579.07 | 10.13 | 0.00   |
| 5 (Global) | 6.04    | NA       | NA   | NA           | 4  | 290.32 | -572.52 | 16.69 | 0.00   |

Note: Candidate models with different predictor combinations of disturbance (muskrat or reference), soil moisture class, and litter cover, plus their interactions, were compared using the Akaike information criterion corrected for small sample sizes (AICc). Coefficient values are shown for continuous variables; “+” indicates inclusion of categorical variables; and “NA” indicates omission. We considered values of ΔAICc > 2.0 to indicate substantially better models, as per Burnham and Anderson (2004). The selected model is highlighted in bold. "Dist" indicates disturbance. Global model = Typha Cover ~ Disturbance × Moisture.
Species richness

Anderson (2004). The selected model is highlighted in bold. Global model (Pseudo-

Table 3. Comparison of the top five mixed models and both the global and null model, predicting species richness (top) and Shannon diversity (bottom) differences between muskrat disturbance locations and reference areas.

| Rank | (Intercept) | L | M | D | LM | L:D | M:D | L:M:D | df | logLik | AICc | ΔAICc | Weight |
|------|-------------|---|---|---|----|-----|-----|-------|-----|---------|------|-------|--------|
| Species richness | 1 | 1.93 | −0.67 | + | + | NA | + | + | NA | 11 | −840.34 | 1703.55 | 0.00 | 0.47 |
| 2 | 1.92 | −0.54 | + | + | NA | NA | + | NA | 10 | −842.05 | 1704.82 | 1.27 | 0.25 |
| 3 | 1.90 | −0.38 | + | + | NA | NA | + | + | NA | 12 | −840.35 | 1705.73 | 2.18 | 0.16 |
| 4 | 1.92 | −0.54 | + | + | + | + | + | NA | 13 | −839.72 | 1706.64 | 3.09 | 0.10 |
| 5 (Global) | 1.93 | −0.65 | + | + | + | + | + | + | 15 | −838.80 | 1709.19 | 5.64 | 0.03 |
| Null | 2.14 | NA | NA | NA | NA | NA | NA | NA | 4 | −897.12 | 1802.37 | 98.82 | 0.00 |

Shannon's diversity

| Rank | (Intercept) | L | M | D | LM | L:D | M:D | L:M:D | df | logLik | AICc | ΔAICc | Weight |
|------|-------------|---|---|---|----|-----|-----|-------|-----|---------|------|-------|--------|
| 1 | 0.98 | −0.33 | + | + | NA | NA | + | NA | 10 | −244.74 | 510.20 | 0.00 | 0.34 |
| 2 | 0.89 | −0.34 | + | + | NA | NA | NA | NA | 8 | −247.00 | 510.47 | 0.26 | 0.30 |
| 3 | 0.92 | −0.49 | + | + | NA | NA | NA | NA | 9 | −246.38 | 511.34 | 1.14 | 0.19 |
| 4 | 0.99 | −0.43 | + | + | NA | + | + | NA | 11 | −244.93 | 512.73 | 2.53 | 0.10 |
| 5 | 0.84 | −0.19 | + | + | NA | NA | NA | NA | 10 | −246.44 | 513.60 | 3.40 | 0.06 |
| Null | 1.32 | −0.34 | NA | NA | NA | NA | NA | NA | 7 | −280.55 | 575.47 | 65.26 | 0.00 |
| Global | 1.17 | −0.36 | NA | NA | NA | NA | NA | NA | 6 | −253.75 | 519.77 | 9.57 | 0.00 |

Note: Candidate models with different predictor combinations of disturbance (D: muskrat or reference) soil moisture class (M), and litter cover (L), plus their interactions, were compared using the Akaike information criterion corrected for small sample sizes (AICc). Coefficient values are shown for continuous variables; “+” indicates inclusion of categorical variables; and “NA” indicates omission. We considered values of ΔAICc > 2.0 to indicate substantially better models, as per Burnham and Anderson (2004). The selected model is highlighted in bold. Global model = Response ~ Disturbance × Moisture × Typha litter.

different between muskrat and reference areas (Pseudo-$F = 4.7$; $R^2 = 0.08$; $P < 0.001$). Despite the reference group having a significantly larger dispersion ($F = 43.5$; $P < 0.05$), there was a clear separation of muskrat-disturbed and reference clusters along two of the three dimensions ($N = 54$; stress = 0.17; $k = 3$; Fig. 6; Appendix S1: Fig. S2).

The distribution of plant taxa that were more abundant around muskrat-disturbed areas, all are obligate wetland plants except for the facultative wetland species in the genus Galium. In reference transects, only Carex lacustris is an obligate wetland plant, whereas Phalaris arundinacea and Spirea alba are facultative wetland plants.

When quadrats over muskrat houses were removed, the PERMANOVA suggested that there were no significant differences between the wetland plant community assemblages (Pseudo-$F = 1.3$; $R^2 = 0.02$; $P > 0.1$). There were no significant differences in the dispersion between muskrat and reference groups as well ($F = 0.32$; $P > 0.5$). Consequently, there was no clear separation between the two clusters ($N = 54$; stress = 0.18; Fig. 6; Appendix S1: Fig. S3). Additionally, there were no significant differences in the distribution of plant taxa.

**Muskrat house distribution**

Muskrat house density at the Carpenters Branch site increased sixfold between 2001 and 2019, from an average of 8.33 houses (0.61 houses per hectare [ha]; $n = 3$ yr) prior to the installation of the water control weir, to an average of 50.8 houses (3.72 houses per ha; $n = 5$ yr) in the years afterward. The Knox test showed there was a significant spatiotemporal correlation ($P < 0.0001$) for muskrat houses in Carpenters Branch during the survey periods; the number of house pairs occurring within 0.0001 decimal degrees and 1 yr was significantly higher than expected (Appendix S1; Table S2). Based on the Monte Carlo permutations, the expected number of close pairs was 78, which was smaller than the observed 104 close pairs (Appendix S1; Fig. S4).
DISCUSSION

Our results suggest that muskrats act as ecosystem engineers in *Typha*-dominated wetlands of the Thousand Islands region and that they generate a disturbance regime with cascading effects on the biotic community, specifically on plants. Muskrat activities centered in these North American temperate wetlands create a more heterogeneous physical habitat and facilitate a more diverse and distinct local plant assemblage relative to areas with lower disturbance. We found lower (absolute) percent live cover of cattails in muskrat-disturbed areas; however, there were no statistical differences in overall *Typha* live cover in our surveyed locations. The wetland plant assemblage around muskrat houses had a greater biodiversity and a distinct community composition relative to the more homogeneous, adjacent wetland areas dominated by invasive *Typha*. Effects on biodiversity were influenced by abiotic factors (moisture) and biotic interactions (*Typha* litter), and these driver interactions were non-linear. Most of the impact of muskrat disturbance on the plant community centers on the house structure. Multiyear data on house distributions revealed that at high densities, muskrat houses are annually maintained or rebuilt in similar locations, which may amplify the intensity and scale of their impacts on the regional plant community and larger wetland ecosystem.

Muskrat disturbance increases wetland plant biodiversity

The higher levels of plant diversity and species richness observed around muskrat houses indicate that this local disturbance regime has a strong influence on the local wetland plant community. The distinct plant community composition around muskrat houses revealed in the multivariate analysis is consistent with the observed increased species richness and diversity relative to reference plots. We suggest that muskrat disturbance induces a type of patch dynamics, in which heterogeneity in microtopography and soil quality caused by house construction, in conjunction with herbivory on cattails, induced a competitive release for non-dominant plants in the wetland. Muskrat houses typically stand around 50 cm tall and create a distinct in situ elevation gradient within the surrounding habitat. The muskrat houses sampled in this study averaged approximately 61 cm tall, with most primarily constructed from cattails (in combination with some substrate and other plant materials). The difference in height between muskrat houses and the surrounding wetland creates a microtopography difference which may allow different species to establish and persist in the habitat. Moreover, Kangas and Hannan (1985) have shown that non-dominant plant species were more abundant on

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Fig. 4. Species richness (top) and Shannon’s diversity index (bottom) among quadrat moisture classes (Dry, Saturated, and Flooded) by disturbance (Muskrat and Reference). Points indicate the estimated marginal (EM) mean, and error bars indicate the 95% confidence interval of the mean. Means sharing a letter are not significantly different under Tukey-adjusted EM means comparisons (*P* < 0.05).
muskrat houses. Consequently, the observed community differences suggest that the area around active muskrat houses are distinct habitat patches in the wetlands.

The combination of muskrat structure building and foraging activities initiates a disturbance regime and diversity of habitat (i.e., removal of *Typha* spp., deeper water in rivulets, and drier habitats atop muskrat houses) that distinguishes the local environmental conditions from the surrounding wetland matrix (Fig. 8). As expected, the environmental factors of substrate moisture

![Graph showing species richness and Shannon's diversity index](image)

Fig. 5. Interaction plot of species richness (top) and Shannon's diversity index (bottom) showing decreasing richness and diversity with increasing litter cover and different responses by disturbance (Muskrat and Reference) and moisture classes (Dry, Moist, and Water). Lines indicate responses of each group to *Typha* litter percent cover based on the best generalized linear mixed model (top) and best linear mixed model (bottom).
and cattail litter cover had a significant effect on species richness and diversity. However, these contrasts were more pronounced under muskrat disturbance and the effect was most apparent in the quadrats of intermediate moisture levels (i.e., the “Saturated” group; Fig. 4). Our observations suggest that the maintenance of rivulets and herbivory around muskrat houses create an active transitional area between the most intensely disturbed areas and the surrounding wetland matrix. These activities create a higher level of spatial-environmental variation in the wetlands which would likely increase both microtopographic complexity and overall surface area available for plant colonization, similar to other ecological analogs such as tussock mounds in the Great Lakes wetlands (Peach and Zedler 2006). While this pattern seems consistent with predictions under the intermediate disturbance hypothesis (Connell 1978), where some studies validate the idea that levels of intermediate disturbance support the greatest species diversity in ecosystems with moderate levels of productivity (Petrakis et al. 1989, Kondoh 2001), many counter examples also exist and there is not general agreement on the mechanisms that underlie these patterns (Fox 2013).

In addition, disturbances caused by muskrats through the removal of the dominant emergent plant, *Typha* spp., likely contributed to the higher species richness and diversity in these wetlands. Removing cattails through herbivory and constructing structures benefit other plant species, not only by reducing interspecific competition of a dominant invasive, but also by recycling some of the nutrients and energy through decomposition of feces and processed plant material (Kangas and Hanan 1985, Berg 1987, Wainscott et al. 1990). Other studies have shown that muskrat activities can lead to changes in abiotic conditions beneficial to plants, including increases in net nitrogen mineralization and nitrification rates.

**Fig. 6.** Non-parametric multidimensional scaling (NMDS) plot mapping three dimensional ($k = 3$) axes (black lines) of wetland plant species community by transects including all sampled quadrats ($N = 54$; stress = 0.17; A) and excluding the muskrat house center quadrats ($N = 54$; stress = 0.18; B). Note the 95% confidence ellipses drawn to highlight the different clusters for muskrat transects (red points) vs. reference transects (blue points). The clusters were significantly different when all sampled quadrats were included (left; $P < 0.05$).
(Connors et al. 2000) as well as increases in temperature, pH, and dissolved oxygen (De Szalay and Cassidy 2001).

Although this study did not show significantly lower abundance of cattails in muskrat-disturbed areas, previous studies in the region demonstrate the capacity of muskrats to reduce Typha spp. biomass (Connors et al. 2000, Toner 2006). Reducing the abundance of the most dominant (invasive) species, specifically T. × glauca, would presumably allow other displaced native species to reestablish a foothold in the ecosystem. This idea is also supported within disturbance ecology where higher levels of disruption in the ecosystem handicap stronger competitors and give the advantage to better-adapted colonizers (Grime 1973, Kondoh 2001). While this study clearly shows the positive impact of muskrat activity on the wetland plant community, this effect is very likely dictated by greater seasonal hydrological patterns. This notion is supported by a study in the same region which showed that water levels were positively correlated with cattail stem density at half of the surveyed sites (Farrell et al. 2010). It is important to note that muskrats depend heavily on seasonal hydrological patterns and are likely to occupy optimal habitats in the wetland that allow them to overwinter. In this context, our results help shed some light on the complex interactions between muskrats, their surrounding wetland community, and the local and Great Lakes regional hydrology (Fig. 8).

Fig. 7. Boxplot of plant species relative abundance by transects between disturbances, that is, muskrat and reference. Pairs shown are significantly different under the Kruskal-Wallis test ($\alpha < 0.01$). Boxes indicate interquartile range with the center line indicating median. Whiskers indicate the minimum and maximum, while points indicate outliers (lesser or greater than Q1 or Q3 + 1.5 IQR). Asterisks (*) indicate introduced taxa. All taxa are emergent hydrophytes except Lemna minor which is a free-floating hydrophyte.
Supporting a distinct plant community with more wetland obligate species

The plant community in muskrat-disturbed areas was significantly different compared to the non-disturbed areas, with greater presence and coverage of some obligate wetland plants compared to the rest of the wetland. Muskrat house construction uses locally available material, typically a combination of soil, submerged aquatic hydrophytes, and robust emergent hydrophytes, which creates some degree of heterogeneity within the Typha-dominated wetland (Alexander 1956). This structure-building behavior creates microtopographic differences in the wetland and allows facultative wetland plants to occur and was shown to be the key driver in generating the community differences found in muskrat-disturbed sites.

Close to 70% of the taxa that were found in higher abundance around muskrat houses are classified as obligate wetland plants (Lichvar et al. 2016). Of the non-obligates, Galium spp. were typically found at the base of cattail stems or growing out from the house, while the wetland obligate, Bidens spp., was also largely found growing on cattail mats (Z. X. Kua, personal communication). Among the species identified to occur more in muskrat-disturbed transects, three taxa (i.e., Lysimachia spp., Scutellaria spp., and Cicuta bulbifera) were plants associated with sedge tussock mounds (Johnston and Zedler 2012). In this case, muskrat house structures may create similar physical structures which allow these tussock-associated plants to occur more frequently around muskrat houses. Moreover, the higher abundance of Lemma minor around muskrat-disturbed areas may be associated with the habitat type associated with muskrat activity. The lesser presence of C. lacustris around muskrat houses, alongside P. arundinacea, was also identified as wetland plants associated with tussock mounds (Johnston and Zedler 2012). However, inferences made based on these observed differences remain speculative and will require further studies and observations to help properly understand these phenomena.

Regional scale of muskrat disturbance

The results from the spatiotemporal analysis strongly suggest that muskrat house locations were not randomly distributed in space and time, but were more likely to occur in the same location from year-to-year. Although muskrat houses are typically transient in temperate zones, with spring floods flushing away the old houses, the results from this study suggest that under relatively stable hydrologic conditions, houses may be used for more than one year. Yearly winter surveys of muskrat house locations from Carpenters Branch suggested that houses, or at the very least house bases, were being reused interannually. Similarly, Alexander (1956) documented the reuse of house bases for several years in the marshes of central New York. Reusing whole or portions of houses whenever possible makes sense as muskrat density increases in a wetland.
and as prime space and limiting resources decrease. Due to the geography and water management in Carpenters Branch, spring melts are mitigated and dampened locally, which extends the lifespan of muskrat structures and allows reuse of houses interannually. Indeed, the structural permanence of houses in certain marshes has required researchers to develop alternative methods for estimating muskrat populations than simple house counts (Engeman and Whisson 2003). Thus, verifying the active status of muskrat structures is important for ensuring accurate population estimates.

A comparison of the muskrat house counts across all surveyed sites in the TI archipelago over the three periods spanning 17 yr (2001–2005, 2012–2013, and 2016–2018) yielded the highest densities in sites with local water control structures (Kua 2019). The highest absolute number of houses recorded was from Cranberry Creek in 2001 when it was under water level management, while the highest muskrat house density recorded was in Carpenters Branch in 2017 at 6.88 houses per ha (Kua 2019). Though the numbers fluctuate in relation to annual water levels throughout the region, there is a clear difference in house densities between sites with water control weirs (3.39 house per ha) and unmanaged wetlands (0.53 house per ha; Kua 2019). These results agree with Toner et al. (2010) where muskrat house density was highest in Carpenters Branch and had a strong relationship with winter water levels.

These spatiotemporal patterns in conjunction with high house densities suggest that the cumulative impacts of local muskrat disturbances at a landscape scale can be substantial. While published investigations of large-scale ecological changes caused by muskrat activity are rare, studies by Alexander and Radway (1951) in Montezuma Wildlife Refuge, New York, and Danell (1978) in northern Sweden documented extensive changes in wetland vegetation associated with high muskrat density. Therefore, it is likely that our findings of strong local effects of muskrat disturbance on wetland plant diversity and community composition were amplified at a landscape level in the wetlands with high muskrat densities and long-term longevity. Many wetland systems with regional hydrologic alteration such as the flow-regulated SLR have depressed muskrat populations, and thus, observations of potential landscape-scale muskrat impacts are largely confined to wetlands with locally managed water levels and corresponding high muskrat densities (e.g., Carpenters Branch and Montezuma Wildlife Refuge).

Visual comparisons of house distributions across our surveyed sites suggested that in wetlands without local water control structures (i.e., subject to the SLR system-wide flow regulation), muskrats tend to occupy areas adjacent to main channels. In wetlands where passive weirs were constructed to raise water levels, they colonize areas further into the wetlands, but only in years in which the weirs were operational. This observed expansion into the water-controlled wetland could be due to the deeper average winter water level, which effectively expanded the available habitat for overwintering animals. The increased area of high muskrat activity would likely amplify the effects of herbivory and house building on the ecological community throughout the wetland.

**Conclusions**

The high intensity of human development has led to a dramatic decline of wetlands in recent decades, with an estimated reduction in total area of 54–57% globally (Davidson 2014, Hu et al. 2017). Combined with climate change and other stressors such as systematic water regulation and species invasions, the decline of natural wetlands highlights the need to understand potentially mitigating effects of ecosystem engineers, including muskrats.

This study showed that muskrat disturbance has a positive effect on enhancing species richness and diversity in wetland ecosystems and supports a distinct plant assemblage. These effects are mediated through non-linear biophysical feedbacks with hydrology and with herbivory. Species richness peaked at intermediate moisture levels in muskrat-disturbed areas and biodiversity gains were greatest for wetland obligate plants.

These results improve our understanding of the ecosystem-level effects that muskrats create as an ecosystem engineer in temperate North American wetlands. Because they are sensitive to changes in water level, muskrats hold great importance as an integrative indicator of wetland health and, as such, have been used to inform...
international water regulatory policy (Tonner et al. 2010, International Joint Commission 2014). Results from the spatial-temporal case study in Carpenters Branch suggest that water level management in wetlands plays a role in amplifying the impacts of muskrat disturbance across a greater geographic scope within Typha-dominated wetlands. Restoring wetland hydrology by managing water levels to enhance muskrat activity may yield system-level benefits, especially in areas dominated by invasive plant.

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LITERATURE CITED

Alexander, M. M. 1951. The distribution and production of muskrats on the Montezuma National Wildlife Refuge. Journal of Wildlife Management 15:360–367.

Allen, A. W., and R. D. Hoffman. 1984. Habitat suitability index models: muskrats. Fish and Wildlife Service 10:39.

Anderson, M. J. 2006. Distance-based tests for homogeneity of multivariate dispersions. Biometrics 62:245–253.

Bakker, E. S., and J.-C. Svenning. 2018. Trophic rewinding: impact on ecosystems under global change. Philosophical Transactions of the Royal Society B: Biological Sciences 373:20170432.

Barton, K. 2019. MuMIn: multi-model inference. R Package Version 0.12.2/r18. http://R-Forge.R-project.org/projects/mumin/

Bates, D., M. Mächler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using [lme4]. Journal of Statistical Software 67:1–48.

Berg, K. M. 1987. Effects of muskrat mounds on decomposition in a southeastern Michigan wetland. Dissertation. Eastern Michigan University, Ypsilanti, Michigan, USA.

Bray, J. R., and J. T. Curtis. 1957. An ordination of the vegetation of the grassy ridgetop soils of the Allegheny Plateau. Industrial and Engineering Chemistry 49:65–70.

Brockman, J. H. 1990. Organisms as engineers: a useful framework for studying effects on ecosystems? Trends in Ecology and Evolution 10:51–52.

Burnham, K. P., and D. R. Anderson. 2004. Multimodel inference: understanding AIC and BIC in model selection. Sociological Methods & Research 33:261–304.

Coordinating Committee. Establishment of the International Great Lakes Datum. 1985. Coordinating Committee on Great Lakes Basic Hydraulic and Hydrologic Data. http://www.lre.usace.army.mil/Portals/69/docs/GreatLakesInfo/docs/CoordinatingCommitteePublications/EstablishmentOfInternationalGreatLakesDatum-1985.pdf

Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. Science 199:1302–1310.

Connor, L. M., E. Kiviäi, P. M. Groffman, and R. S. Ostfeld. 2000. Muskrat (Ondatra zibethicus) disturbance to vegetation and potential net nitrogen mineralization and nitrification rates in a freshwater tidal marsh. American Midland Naturalist 143:53–63.

Cotner, L. A., and R. L. Schooley. 2011. Habitat occupancy by riparian muskrats reveals tolerance to urbanization and invasive vegetation. Journal of Wildlife Management 75:1637–1645.

Curran, J. C., and K. M. Cannatelli. 2014. The impact of beaver dams on the morphology of a river in the eastern United States with implications for river restoration. Earth Surface Processes and Landforms 39:1236–1244.

Danell, K. 1978. Ecology of the muskrat in northern Sweden. Dissertation. University of Umeå, Umeå, Sweden.

Davidson, N. C. 2014. How much wetland has the world lost? Long-term and recent trends in global wetland area. Marine and Freshwater Research 65:934–941.

De Szalay, F. A., and W. Cassidy. 2001. Effects of muskrat (Ondatra zibethicus) lodge construction on invertebrate communities in a Great Lakes coastal wetland. American Midland Naturalist 146:300–310.

Delignette-Muller, M. L., C. Dutang, and S. Jabot. 2015. [tdisper]: An [R] package for fitting distributions. Journal of Statistical Software 64:1–34.

Déri, E., T. Magura, R. Horváth, M. Kisfali, G. Ruff, S. Lengyel, and B. Tóthmérész. 2011. Measuring the
short-term success of grassland restoration: the use of habitat affinity indices in ecological restoration. Restoration Ecology 19:520–528.

Dozier, H. L., M. H. Markley, and L. M. Llewellyn. 1948. Muskrat investigations on the Blackwater National Wildlife Refuge, Maryland. 1941–1945. Journal of Wildlife Management 12:177–190.

Ecke, F., A. Henry, and K. Danell. 2014. Landscape-based prediction of the occurrence of the invasive muskrat (Ondatra zibethicus). Annales Zoologici Fennici 51:325–334.

Edelman, A. J., J. Moran, T. J. Garrabrant, and K. C. Vorreiter. 2015. Muskrat predation of native freshwater mussels in Shoal Creek, Alabama. Southeastern Naturalist 14:473–483.

Engeman, R. M., and D. A. Whisson. 2003. A visual method for indexing muskrat populations. International Biodeterioration & Biodegradation 52:101–106.

Farrell, J. M., B. A. Murry, D. J. Leopold, A. Halpern, M. B. Rippke, K. S. Godwin, and S. D. Hafner. 2010. Water-level regulation and coastal wetland vegetation in the upper St. Lawrence River: inferences from historical aerial imagery, seed banks, and Typha dynamics. Hydrobiologia 647:127–144.

Fox, J. W. 2013. The intermediate disturbance hypothesis should be abandoned. Trends in Ecology and Evolution 28:86–92.

Fox, J., and S. Weisberg. 2019. An R companion to applied regression. Third edition. Sage, Thousand Oaks, California, USA.

Freeland, J., C. Ciotir, and H. Kirk. 2013. Regional differences in the abundance of native, introduced, and hybrid Typha spp. in northeastern North America influence wetland invasions. Biological Invasions 15:2651–2665.

Galatowitsch, S. M., N. O. Anderson, and P. D. Ascher. 1999. Invasiveness in wetland plants in temperate North America. Wetlands 19:733–755.

Grime, J. P. 1973. Competitive exclusion in herbaceous vegetation. Nature 242:344–347.

Gutiérrez, J. L., C. G. Jones, D. L. Strayer, and O. Iribarne. 2003. Mollusks as ecosystem engineers: the role of shell production in aquatic habitats. Oikos 101:79–90.

Hecky, R. E., R. Mugidde, P. S. Ramlal, M. R. Talbot, and G. W. Kling. 2010. Multiple stressors cause rapid ecosystem change in Lake Victoria. Freshwater Biology 55:19–42.

Higgins, C., and W. J. Mitsch. 2002. The role of muskrats (Ondatra zibethicus) as ecosystem engineers in created freshwater marshes. Pages 81–85. Olen-tangy River Wetland Research Park Annual Report. The Ohio State University, Columbus, OH. https://kb.osu.edu/handle/1811/358

Hu, S., Z. Niu, and Y. Chen. 2017. Global wetland datasets: a review. Wetlands 37:807–817.

International Joint Commission. 2014. Lake Ontario – St. Lawrence River Plan 2014: protecting against extreme water levels, restoring wetlands and preparing for climate change. Washington DC: International Joint Commission, 84. https://ijc.org/sites/default/files/IJC_LOSR_EN_Web.pdf

Jansson, R., C. Nilsson, M. Dynesius, and E. Andersson. 2000. Effects of river regulation on river-margin vegetation: a comparison of eight boreal rivers. Ecological Applications 10:203–224.

Johnston, C. A., and J. B. Zedler. 2012. Identifying preferential associates to initiate restoration plantings. Restoration Ecology 20:764–772.

Jones, C. G., J. H. Lawton, and M. Shachak. 1994. Organisms as ecosystem engineers. Oikos 69:373–386.

Kadlec, R. H., J. Pries, and H. Mustard. 2007. Muskrats (Ondatra zibethicus) in treatment wetlands. Ecological Engineering 29:143–153.

Kangas, P. C., and G. L. Hannan. 1985. Vegetation on muskrat mounds in a Michigan marsh. American Midland Naturalist 113:392–396.

Keddy, P. A. 2010. Wetland ecology: principles and conservation. Second edition. Cambridge University Press, New York, New York, USA.

Kiviat, E. 1978. Coastal and estuarine research federation vertebrate use of muskrat lodges and burrows. Coastal and Estuarine Research Federation 1:196–200.

Knox, E. G., and M. S. Bartlett. 1964. The detection of space-time interactions. Journal of the Royal Statistical Society, Series C (Applied Statistics) 13:25–30.

Kondoh, M. 2001. Unifying the relationships of species richness to productivity and disturbance. Proceedings of the Royal Society B: Biological Sciences 268:269–271.

Kovach, R. P., C. C. Muhlfeld, M. C. Boyer, W. H. Lowe, F. W. Allendorf, and G. Luikart. 2015. Dispersal and selection mediate hybridization between a native and invasive species. Proceedings of the Royal Society B: Biological Sciences 282. http://doi.org/10.1098/rspb.2014.2454

Kua, Z. X. 2019. Water regulation and muskrat (Ondatra zibethicus) effects on wetland plant assemblages. Thesis. College of Environmental Science and Forestry, State University of New York, Syracuse, New York, USA.

Larkin, D. J., G. L. Bruland, and J. B. Zedler. 2016. Heterogeneity theory and ecological restoration. Pages 142–164 in D. Falk, M. A. Palmer, and J. B. Zedler, editors. Foundations of restoration ecology. Second edition. Island Press, Washington, D.C., USA.

Law, A., M. J. Gaywood, K. C. Jones, P. Ramsay, and N. J. Willby. 2017. Using ecosystem engineers as tools in habitat restoration and rewilding: beaver
and wetlands. Science of the Total Environment 605–606:1021–1030.

Lenth, R. 2019. Emmeans: estimated marginal means, aka least-squares means. https://cran.r-project.org/web/packages/emmeans/index.html

Lichvar, R. W., D. L. Banks, W. N. Kirchner, and N. C. Melvin. 2016. Northcentral and Northeast 2016 regional wetland plant list. Pages 1–40. U.S. Army Corps of Engineers, Washington, D.C., USA.

MacArthur, R. A. 1978. Winter movements and home range of the muskrat. Canadian Field-Naturalist 92:345–349.

Mantel, N. 1967. The detection of disease clustering and a generalized regression approach. Cancer Research 27:209–220.

Mott, C. L., C. K. Bloomquist, and C. K. Nielsen. 2013. Within-lodge interactions between two ecosystem engineers, beavers (Castor canadensis) and muskrats (Ondatra zibethicus). Behaviour 150:1325–1344.

Nummi, P., V. M. Väänänen, and J. Malinen. 2006. Alien grazing: indirect effects of muskrats on invertebrates. Biological Invasions 8:993–999.

Oksanen, J., et al. 2019. vegan: community ecology package. https://cran.r-project.org/web/packages/vegan/index.html

Olson, A., J. Paul, and J. R. Freeland. 2009. Habitat preferences of cattail species and hybrids (Typha spp.) in eastern Canada. Aquatic Botany 91:67–70.

Peach, M., and J. B. Zedler. 2006. How tussocks structure sedge meadow vegetation. Wetlands 26:322–335.

Petraitis, P. S., R. E. Latham, and R. A. Niesenbaum. 1989. The maintenance of species diversity by disturbance. Quarterly Review of Biology 64:393–418.

Pieper, S. J., J. R. Freeland, and M. E. Dorken. 2018. Coexistence of Typha latifolia, T. angustifolia (Typhaceae) and their invasive hybrid is not explained by niche partitioning across water depths. Aquatic Botany 144:46–53.

R Core Team. 2019. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Reed Jr., P. B. 1988. National list of plant species that occur in wetlands: national summary. U.S. Fish and Wildlife Service 88:1–244.

Rippke, M. B., M. T. Distler, and J. M. Farrell. 2010. Holocene vegetation dynamics of an upper St. Lawrence River wetland: paleoecological evidence for a recent increase in cattail (Typha). Wetlands 30:805–816.

Roseman, E. F., P. A. Thompson, J. M. Farrell, N. E. Mandrak, and C. A. Stepien. 2014. Conservation and management of fisheries and aquatic communities in Great Lakes connecting channels. Journal of Great Lakes Research 40:1–6.

Rozhkova-Timina, I. O., V. K. Popkov, P. J. Mitchell, and S. N. Kirpotin. 2018. Beavers as ecosystem engineers – A review of their positive and negative effects. IOP Conference Series: Earth and Environmental Science 201:1–11.

Skyriéné, G., and A. Paulauskas. 2013. Distribution of invasive muskrats (Ondatra zibethicus) and impact on ecosystem. Ekologia 58:357–367.

Szabo, J., J. R. Freeland, and M. E. Dorken. 2018. The effects of leaf litter and competition from hybrid cattails (Typha x glauca) on the seed germination and seedling performance of its parental species. Aquatic Botany 145:29–36.

Toner, J. A. 2006. Muskrat house abundance and cattail use in Upper St. Lawrence River tributary wetlands: modeling the effects of water level regulation. Dissertation. College of Environmental Science and Forestry, State University of New York, Syracuse, New York, USA.

Toner, J., J. M. Farrell, and J. V. Mead. 2010. Muskrat abundance responses to water level regulation within freshwater coastal wetlands. Wetlands 30:211–219.

Tuchman, N. C., D. J. Larkin, P. Geddes, R. Wildova, K. Jankowski, and D. E. Goldberg. 2009. Patterns of environmental change associated with Typha x glauca invasion in a Great Lakes coastal wetland. Wetlands 29:964–975.

Wainscott, V. J., C. Bartley, and P. Kangas. 1990. Effect of muskrat mounds on microbial density on plant litter. American Midland Naturalist 123:399–401.

Wilcox, D. A., A. L. Hoare, K. P. Kowalski, M. L. Carlson, and H. N. Morgan. 2008. Cattail invasion of sedge/grass meadows in Lake Ontario: photointerpretation analysis of sixteen wetlands over five decades. Journal of Great Lakes Research 34:301–323.

Wilcox, D. A., T. A. Thompson, R. K. Booth, and J. R. Nicholas. 2007. Lake-level variability and water availability in the Great Lakes. Pages 1–29. U.S. Geological Survey, Reston, Virginia, USA.

Willner, G. R., G. A. Feldhamer, E. E. Zucker, and J. A. Chapman. 1980. Ondatra zibethicus. American Society of Mammalogists 141:1–8.

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