PATTERNS OF ENVIRONMENTAL CHANGE ASSOCIATED WITH *TYPHA* X *GLAUCA* INVASION IN A GREAT LAKES COASTAL WETLAND

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Abstract: *Typha x glauca* (hybrid cattail) is an aggressive invader of wetlands in the upper Midwest, USA. There is widespread concern about declines in plant diversity following *Typha* invasion. However, relatively little is known about how *Typha* alters habitat characteristics, i.e., its potential to act as an "ecosystem engineer". Over five years, we measured physical, chemical, and plant community changes associated with *Typha* invasion in a Lake Huron wetland in northern lower Michigan. We compared uninvaded areas with patches varying in invasion intensity. Our study was observational, but we used statistical inference to try to separate effects of *Typha* and confounding variables, particularly water depth. We used space–for–time substitution to investigate whether *Typha*–associated changes increased over time, as predicted if *Typha* invasion was in part a cause (not only a consequence) of abiotic changes. Relative to uninvaded areas, *Typha*–invaded areas differed in plant–community composition and had lower species richness, higher litter mass, and higher soil organic matter and nutrient concentrations (all P < 0.001). Overall, *Typha* invasion appeared to displace native species and enrich wetland soils. These changes could benefit *Typha* at the expense of native species, potentially generating plant–soil feedbacks that pose special challenges for wetland management and restoration.

Key Words: cattail, invasive species, soil nitrogen, soil organic matter

INTRODUCTION

Invasive wetland plants are often associated with elevated nutrient inputs, functioning as "opportunists" better able to exploit surplus resources than the species they displace (Kercher and Zedler 2004, Zedler and Kercher 2004, Dethier and Hacker 2005). However, as with certain terrestrial invaders (e.g., Vitousek and Walker 1989), invasive wetland plants may also act as *drivers*, not just *passengers*, of change (MacDougall and Turkington 2005). In such cases, invasive species could lead to loss of native species and altered ecosystem functioning even in relatively undisturbed, nutrient–poor wetlands.

While disturbances such as nutrient enrichment commonly precede plant invasions, they are not a prerequisite. The presence of an invasive plant species can itself affect nutrient cycling, hydrology, and fire regimes (Vitousek and Walker 1989, Brooks et al. 2004, Callaway and Maron 2006). Ehrenfeld (2003) reviewed studies of 56 invasive plants and found that invaders frequently altered productivity, biomass, litter dynamics, and nitrogen (N) cycling. Problematic wetland invasive species like *Phragmites australis* (Cav.) Trin. ex Steud. and *Phalaris arundinacea* L. increase aboveground biomass and alter N fluxes (Windham and Meyerson 2003, Herr–Turoff and Zedler 2005). For effective management efforts, it is critical to know whether changes in nutrient dynamics are a *cause* or a *consequence* of invasion. This is especially true as invasive plants that alter soil N pools may be the most likely to act as long–term obstacles to restoration (Corbin and D'Antonio 2004).

Consistent with a passenger model of invasion (*sensu lato* MacDougall and Turkington 2005),

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invasive *Typha* spp. (cattails) are known to respond favorably to nutrient enrichment, forming dense stands with low plant diversity (Green and Galatowitsch 2001, Ehrenfeld 2003, Bowles and Jones 2006). For example, in the upper Midwest USA, the invasive *Typha x glauca* Godr. (a hybrid of *T. latifolia* L. and *T. angustifolia* L., Smith 1987) aggressively displaces native wetland flora under elevated nitrogen and phosphorus concentrations, expanding at rates as high as 5–m yr^{-1} (McDonald 1955, Woo and Zedler 2002, Craft et al. 2007). *Typha x glauca* poses a significant threat to wetland biodiversity where nutrients are abundant, even when managers try to counteract its dominance through control efforts and planting of native species (Bedford et al. 1999, Woo and Zedler 2002). However, dominant *Typha* stands have also been noted throughout the Great Lakes region in wetlands receiving relatively low nutrient inputs (Boers et al. 2007, Farrer and Goldberg 2009; D. Albert, Michigan Natural Features Inventory, personal communication).

The overall objective of our research was to determine the potential of invasive *Typha x glauca* (hereafter *Typha*) to act as a driver of ecosystem change in a low–nutrient, upper Great Lakes coastal wetland. We set out to determine whether abiotic and plant community characteristics differed between invaded and uninvaded areas. Having found strong correlations, especially between *Typha* and soil nutrient concentrations, we addressed the question of whether *Typha* was a cause or consequence of increased nutrients. Given that substantial exogenous nutrient inputs to the marsh were not found, we asked whether *Typha* could invade and survive in nutrient–poor areas. To this end, we compared recently invaded patches with uninvaded ones to assess if microsites where *Typha* established differed from the surrounding matrix of native vegetation.

METHODS

Study Site

Site Description. This study was conducted in Cheboygan Marsh, Cheboygan County, Michigan, USA (45°39′29″N, 84°28′47″E), a ~150–ha coastal wetland on the shores of Lake Huron in northern lower Michigan. Like other coastal wetlands in the region, Cheboygan Marsh has predominantly nutrient–poor sandy soils derived from lacustrine deposits (Soil Conservation Service 1991). The marsh is heterogeneous in its plant composition, with three distinct but contiguous vegetation zones: 1) a lakeside native plant community dominated by *Juncus*, *Schoenoplectus*, and *Eleocharis* species (hereafter "native"); 2) transitional bands of mixed vegetation as *Typha* invades the native community ("transition"); and 3) established, nearly monotypic stands of *Typha*, which occupy the majority of the marsh's area, especially on the upland side ("*Typha*"). The marsh is predominantly open to Lake Huron, with frequent seiche activity and about one–third of its area continuously inundated (Angeloni et al. 2006).

Typha *Invasion.* *Typha* now covers more than two–thirds of Cheboygan Marsh. Surveying the vegetation of Cheboygan Marsh in 1977, Henebry et al. (1981) found high frequency of the native cattail *T. latifolia* but did not report *T. angustifolia* or *T. x glauca*. However, herbarium specimens from the University of Michigan include *T. angustifolia* collected from Cheboygan County in 1953 and *T. x glauca* collected in 1966 (A.A. Reznicek, University of Michigan, unpublished data). Anecdotal reports suggest that substantial *Typha* invasion occurred in the marsh ~40 years ago (F. Cuthbert personal communication). To better approximate the site's invasion history, we examined nine aerial photos encompassing portions of Cheboygan Marsh that spanned from 1938–2006. Between 1953 and 1962, there was a two–fold increase (18 to 36% of area examined) of unknown vegetation in large, roughly circular patches. These patches spread rapidly, consistent with the clonal growth characteristic of *Typha*. The patches were also similar in appearance to known, ground–referenced *Typha* stands observed in the 2006 photo. Due to poor resolution of the 1938 photo (the only one that pre–dated 1953), we could not determine whether this suspected *Typha* was present at that time. Based on this evidence, it is likely that substantial *Typha* invasion occurred sometime between 1953 and 1962.

Exogenous Nutrient Inputs to Cheboygan Marsh. Lake Huron is oligotrophic (US EPA 2004) and its northern, non–urban coastal wetlands generally have sandy soils with low nitrogen and phosphorus concentrations (Soil Conservation Service 1991). Potential sources of exogenous nutrient inputs to Cheboygan Marsh include Lake Huron, surface flows from adjacent upland habitat, and atmospheric N deposition. No applicable nutrient data were available from the EPA STORET water quality database for sampling stations near Cheboygan Marsh (US EPA 2007). Therefore, we conducted our own sampling of surface waters flowing into the site, identifying Lake Huron and a persistent stream from a nearby residential area as the primary surface water sources (using satellite photography and

topographic maps). In July 2004, we sampled water at 18 locations along 1 km of the stream flowing into Cheboygan Marsh. To evaluate Lake Huron as a source of nutrients into the marsh, water samples were collected in August 2005 (three from open water at the lakeside margin and six from vegetation transect plots). All water samples were collected in acid–washed polyethylene bottles, placed on ice, and filtered through GF/F glass fiber filters to remove particulates. Water samples were analyzed for nitrate, ammonium, and phosphate using a Bran Luebbe Auto Analyzer 3 (Farmington, MI) at the University of Michigan Biological Station Analytical Chemistry Lab (Pellston, MI). Nitrate was determined using the cadmium reduction method, ammonium by the phenate method, and phosphate by the ascorbic acid reduction method (APHA 2005). Deposition data from the National Atmospheric Deposition Program were accessed online (NADP 2007). Data from the University of Michigan Biological Station's Douglas Lake monitoring station, the nearest location at ~20 km from Cheboygan Marsh, were used.

Sampling Design

To address our research questions, we established transects along gradients of increasing *Typha* density, spanning from native–dominated areas, through transition zones encompassing *Typha* invasion fronts, and into *Typha*–dominated zones. Transects were used as a spatial representation of vegetative and abiotic changes as *Typha* invades over time. Space–for–time substitution is often used to investigate ecological effects of invasive plant species. Invaded plots are compared against uninvaded plots, which are viewed as representing typical pre–invasion conditions (Pyšek and Pyšek 1995, Alvarez and Cushman 2002). A shortcoming of this approach is that invaded and uninvaded plots may have differed in important ways prior to invasion. To minimize biases, uninvaded and invaded stands should be close to each other and similar in physical habitat structure. Ideally, there should be ongoing spread of the invader, with heavily invaded areas transitioning into uninvaded patches (Hejda and Pyšek 2006). We believe that space–for–time substitution is justified in the present study because invaded and uninvaded areas were adjacent to and smoothly transitioned into each other with generally gradual changes in topography. However, water depth was a confounding variable that could not be fully disentangled from *Typha* density. While we conceptually use space as a substitute for time, we lack data to quantify time since invasion for most

parts of the marsh. However, *Typha* has been shown to increase in density with time since invasion (Boers et al. 2007), eventually forming nearly monotypic stands with high, relatively stable densities (Frieswyk et al. 2007). We used density of *Typha* as a rough, qualitative proxy for relative time since invasion but could not assign actual ages to invaded stands.

Throughout several years (2003–2007), we established transects that varied in length, resolution, and spatial scale to substitute space for time. We established two types of transects: 1) long, low–resolution transects over large spatial scales connecting uninvaded areas with areas deep within patches of dense, nearly monotypic *Typha*; and 2) short, high–resolution transects at smaller spatial scales connecting uninvaded areas with areas that, based on low *Typha* density, minimal litter depth, and prior observations, appeared to have been invaded more recently. We also assessed edaphic conditions under and adjacent to small clones of recently established *Typha* to see if establishment microsites differed from the surrounding matrix of native vegetation. Sample types, years, and variables measured are summarized in Table 1.

Long Transects. During the 2003–2007 growing seasons, we established long transects (~100 m) to assess broad patterns of change across zones of dominant vegetation.

2003. An initial survey of the site's plant community composition was conducted in 1 long (110–m) transect. We placed 12 1–m^2 plots at 10–m increments, identified species, and counted stems. This survey led to the identification of the 3 broad vegetation zones described above (native, transition, *Typha*).

2004. The vegetation survey was expanded to three parallel transects extending from nearly monotypic *Typha* through the transition zone and into the native vegetation zone. The ~90–120 m long transects each included 3 replicate 1–m^2 plots within each vegetation zone to account for spatial variability in physical, biological, and chemical variables. Thus, there were a total of 9 plots per zone and 27 total plots.

2005. Data from 2004 transects indicated that trends in physical, biological, and chemical parameters were spatially consistent within each vegetation zone; therefore, we only established one long transect in 2005. Four replicate 1–m^2 plots were placed in each of the 3 vegetation zones along the 100–m long transect for a total of 12 plots. In the *Typha* and native zones, plots were spaced at 8–m

Table 1.   Summary of measurements made.

Variables measured	Year(s)
Long transects	
Plant composition, *Typha* density, SOM, soil NO_3 and NH_4	2003, 2004, 2005, 2007
Water depth	2003, 2004, 2005
Soil PO_4	2003, 2004
Litter biomass	2004
Short transects	
Plant composition, *Typha* density, SOM, soil NH_4, water depth, litter depth	2005
Recently colonized *Typha* patches	
Plant composition, SOM, soil NH_4, water depth, litter depth	2005

increments. In the transition zone they were spaced closer together (every 4–m) because the spatial rate of change in vegetation and soil attributes was greater in this zone.

2007.   We established three > 100–m long transects across vegetation zones. In each transect, soil samples were collected from 3 plots within each zone for a total of 9 samples per zone, 27 total samples.

Short Transects.   Given that most changes in vegetation and soil parameters occurred within the transition zone (invasion front), in 2005 we placed 7 shorter transects across transition areas throughout the wetland for more intensive sampling, providing higher resolution data over smaller spatial scales. These transects were 10–30 m long (2 transects of 30–m, 4 of 20–m, and 1 of 10–m). Each consisted of contiguous 0.5–m long × 1–m wide plots (e.g., a 30–m long transect consisted of 60 plots).

Variables Measured in Transects

Plant Species Composition.   In the long and short transects, we collected data on number of stems of *Typha* and stem counts (long transects) or percent cover (short transects) for other plant species in 0.25 to 0.5–m^2 subplots. Data on frequency of taxa other than *Typha* spp. were collected in the short transects using a scale of 1–4, where 1) represented 1–5 stems, 2) 6–10 stems, 3) 11–50 stems, and 4) > 50 stems.

Quantity of Litter.   Litter biomass was sampled in 2004 in 2 replicate plots for each of the 3 long transects. Each plot was 0.25 m^2 in area and all dead leaf material was collected and separated from any green material, oven dried at 60°C, and weighed. We

also measured litter depth (cm) for all plots in the high–resolution short transects in 2005.

Water Depth.   For long transects, aboveground water depth was measured from the sediment to the water surface. In cases where no standing water was present, water depth was measured as the distance from the top of the soil to the water table below using piezometers placed along the 2005 long transect. For short transects, if no standing water was present but the soil surface was saturated, we assigned a water depth of 0 cm. In cases where the soil surface was not saturated, water depth was recorded as -5 cm.

Soil Nutrients.   Three to 4 replicate soil samples were collected from each transect plot (long transects) or every other plot (short transects) at depths of 0–10 cm. Replicate samples were composited and analyzed for soil organic matter (SOM) and ammonium (all transects) and nitrate and phosphate (long transects only). SOM was measured as mass loss on ignition in a muffle furnace (2 h at 550°C, APHA 2005). Soil inorganic nitrogen was extracted in 2 M KCl for 1 h on a shaker table. Nitrate and ammonium concentrations were determined using the cadmium reduction and automated phenate methods, respectively (APHA 2005). Total inorganic nitrogen (TIN) was calculated as the sum of nitrate and ammonium. Soil soluble reactive phosphorus was extracted with Troug's solution (Mehlich 1953) and determined by the automated ascorbic acid method (APHA 2005). All nutrients were analyzed using a Bran–Luebbe Auto–Analyzer 3 (Farmington, MI).

Correlations Between *Typha* and Environmental Variables

We assessed whether abiotic and plant community characteristics differed between invaded and uninvaded areas by determining the relationship between *Typha* density and environmental variables using linear and second–order polynomial regressions. For the long transects, the environmental variables included species richness of facultative and obligate wetland plants (as per Wetland Indicator Status, Reed and Porter 1988, Tiner 1991), SOM, litter biomass, water depth, NH_4, NO_3, TIN, and PO_4, and were measured in 2003, 2004, 2005, and 2007 (Table 1). All variables except for litter biomass were natural–log transformed. Data from all years were used in the analyses because transect plots were independently located between years. For the short transects, environmental variables included plant species richness, SOM, litter depth, water

depth, and NH$_4$, all measured in 2005 (Table 1). All variables except for species richness were natural–log transformed to better achieve normality and homogeneity of variance. Statistical analyses were performed in R 2.4.1 (R Development Core Team 2006).

Assessment of Recently Colonized *Typha* Patches

To address whether *Typha* could invade nutrient–poor areas, we compared recently invaded patches with uninvaded patches to assess if microsites where *Typha* established differed from the surrounding matrix of native vegetation. In 2005, we randomly selected 7 small ($\leq$ 3–m in diameter), newly established clones of *Typha* from areas of Cheboygan Marsh that are generally dominated by sedge–rush vegetation. We established a 1–m^2 plot in the center of each clone and a paired control plot with no *Typha* spp. located 1–2 m from the edge of each sampled clone. In each plot, we sampled *Typha* stem density, cover of all plant species (using cover classifications of < 1, 1–12.5, 13–25, 26–50, and 51–75%), and litter and water depth as the average of three separate measurements. We collected 3 soil cores of 0–10 cm depth in each plot, composited them, and measured NH$_4$ and SOM, following the methods described above.

We conducted 2–tailed paired t–tests using SPSS version 11.5.1 (SPSS Inc. 2001) to determine whether the areas in which *Typha* clones established differed from surrounding areas in terms of measured environmental variables.

Multivariate Analyses

To investigate whether increasing *Typha* density and other environmental variables are associated with changes in the native plant community, we tested the strength of environmental vectors (*Typha* density, water depth, [NH$_4$], and [SOM]) as explanatory variables for community composition in 3 different data sets approximating different stages of invasion: 1) long transects that extended well into heavily *Typha*–dominated patches, 2) short transects focused on areas of co–occurring *Typha* and native vegetation, and 3) recently colonized *Typha* patches.

For each of the data sets, we performed multivariate analyses of community data using non–metric multidimensional scaling (NMS), which effectively handles heterogeneously distributed data (McCune and Grace 2002). NMS analyses were performed using the vegan package in R 2.4.1 (Oksanen et al. 2006, R Development Core Team

2006). Dissimilarity matrices were calculated from log–transformed plant species data using Bray–Curtis distances. Scree–plots were constructed to select appropriate numbers of axes (dimensionality), determined to be 2 in all cases. NMS ordinations were performed using random starting configurations and iterated until solutions converged.

To enhance interpretation of community data, we fit vectors of measured environmental variables onto ordinations. Fitted vector arrows point in the direction of most rapid change (direction of the gradient) and their length is proportional to their explanatory strength. The significance of environmental vectors was tested using a permutation procedure (1000 permutations).

We explored species–specific effects of environmental variables using generalized additive models (GAMs). GAM uses a link function to establish a relationship between the mean of the response variable (species abundance) and a ''smoothed'' function of the explanatory variables. The response curve is hence more data– than model–driven; that is, the resulting fitted values do not come from an *a priori* model. As a result, GAM can detect features like asymmetry and bimodality, making it a useful tool for data exploration (Yee and Mitchell 1991). In these analyses, we used the 9 most frequent species (those present in > 20% of transect plots). Calculations were performed in CANOCO ver. 4.5 (ter Braak and Šmilauer 1998).

RESULTS

Exogenous Nutrient Inputs to Cheboygan Marsh

Surface water nutrient concentrations from both the upland and Lake Huron were low during our sampling. Inflowing stream water had mean NO$_3$–N of 5.2 $\pm$ 1.6 (SE) μg N L^{-1} and mean NH$_4$–N of 102.6 $\pm$ 15.6 μg N L^{-1}. Mean PO$_4$–P concentration was 27.9 $\pm$ 5.9 μg P L^{-1}. Mean concentrations of nutrients in lake water were 48.1 $\pm$ 7.0 (SE) μg N L^{-1} for NO$_3$–N, 45.6 $\pm$ 5.8 μg N L^{-1} for NH$_4$–N, and 2.2 $\pm$ 0.3 μg P L^{-1} for PO$_4$–P. Annual means for total inorganic N deposition (NH$_4$ + NO$_3$) ranged from 4.31–6.38 kg ha^{-1} (2000–2006; NADP 2007).

Correlations Between *Typha* and Environmental Variables

Long Transects. Increases in *Typha* density were significantly associated with environmental variables. Wetland plant species richness was negatively correlated with *Typha* stem density (Figure 1A). There were positive correlations between *Typha*
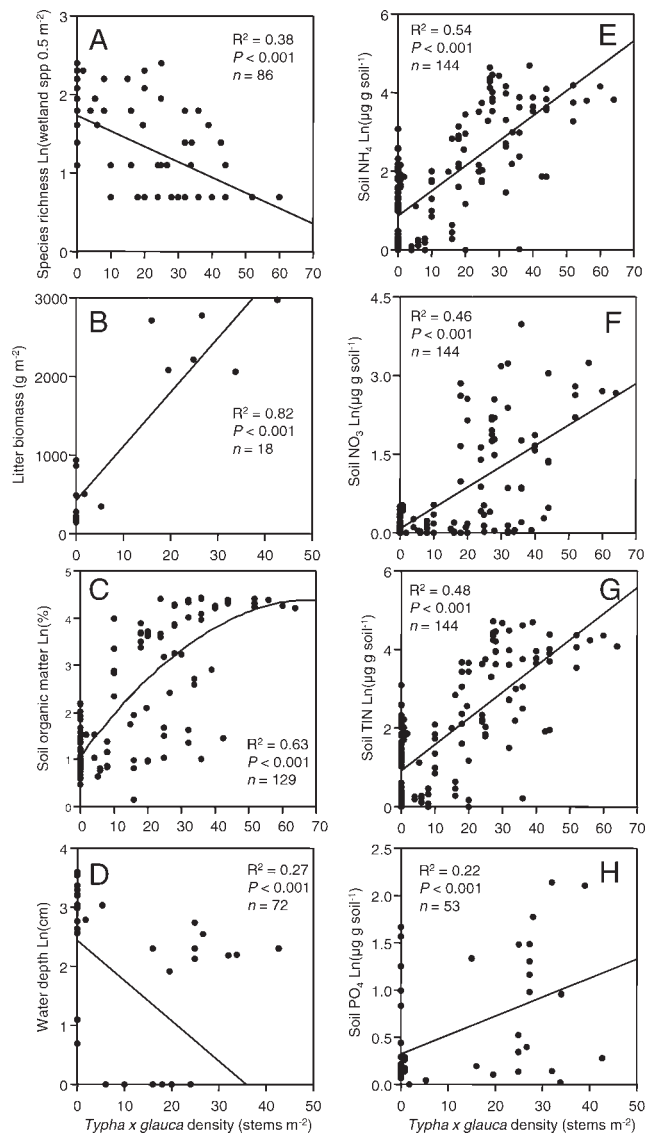
Figure 1. Correlations between *Typha x glauca* density and environmental variables for long transects.

density and litter biomass (Figure 1B), and SOM (Figure 1C). *Typha* density and water depth were significantly and negatively correlated (Figure 1D). Concentrations of soil–extractable N and P increased with increasing *Typha* density: TIN (NH$_4$ + NO$_3$, Figure 1G), NH$_4$ (Figure 1E), NO$_3$ (Figure 1F), and PO$_4$ (Figure 1H).

NMS ordination indicated significant variation in plant species composition associated with *Typha* density (Figure 2). SOM and NH$_4$ concentrations were also associated with changes in species composition, with SOM, but not NH$_4$, tightly and positively correlated with *Typha* density. Water depth was a significant variable (P = 0.015), showing a negative to orthogonal correlation with *Typha* density (Figure 2).
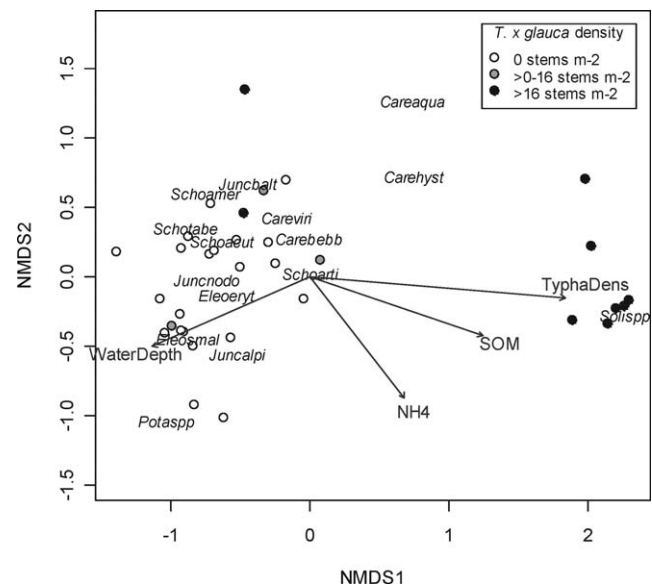

Figure 2. NMS analysis of species composition for long transects. Dissimilarity was based on Bray–Curtis distances and plot was constructed using two dimensions. Fitted vector arrows are significant (P < 0.05, by permutation procedure) and their length is proportional to their explanatory strength. Explanatory variables tested were NH$_4$ (P = 0.036), SOM (P = 0.005), *Typha* density (P < 0.001), and water depth (P = 0.015). Species codes (includes some that occur only in Figures 5 or 6): *Agalpurp = Agalinis purpurea, Agrostol = Agrostis stolonifera, Astelanc = Aster lanceolatus, Astepuni = A. puniceus, Careaqua = Carex aquatilis, Carehyst = C. hystericina, Careviri = C. viridula, Cicubulb = Cicuta bulbifera, Eleoeryt = Eleocharis erythropoda, Eleosmal = E. smallii, Euthgram = Euthamia graminifolia, Eupaperf = Eupatorium perfoliatum, Impacape = Impatiens capensis, Juncalpi = Juncus alpinoarticulatus, Juncarti = J. articulatus, Juncbalt = J. balticus, Juncdudl = J. dudleyi, Juncnodo = J. nodosus, Leeroryz = Leersia oryzoides, Lycoamer = Lycopus americanus, Mentaqua = Mentha aquatica, Phalarun = Phalaris arundinacea, Potaspp = Potamogeton spp., Sagispp = Sagittaria spp., Salispp = Salix spp., Schoacut = Schoenoplectus acutus, Schoamer = S. americanus, Schoarti = S. articulatus, Schotabe = S. tabernaemontani, Solispp = Solidago spp., Soliulig = Solidago uliginosa, Sparchlo = Sparganium chlorocarpum,* and *Utrivulg = Utricularia vulgaris.*

The relatively small number of long–transect plots (n = 34) made it possible to estimate significant GAM response curves for only a few species (Figure 3). However, within this subset of species, there were strong differences in responses to *Typha* density and water depth. *Eleocharis erythropoda* Steud. showed sharply decreasing abundance with increasing *Typha* density, but responded little to water depth. *Eleocharis smallii* Britton had peak abundance at intermediate water depth in the
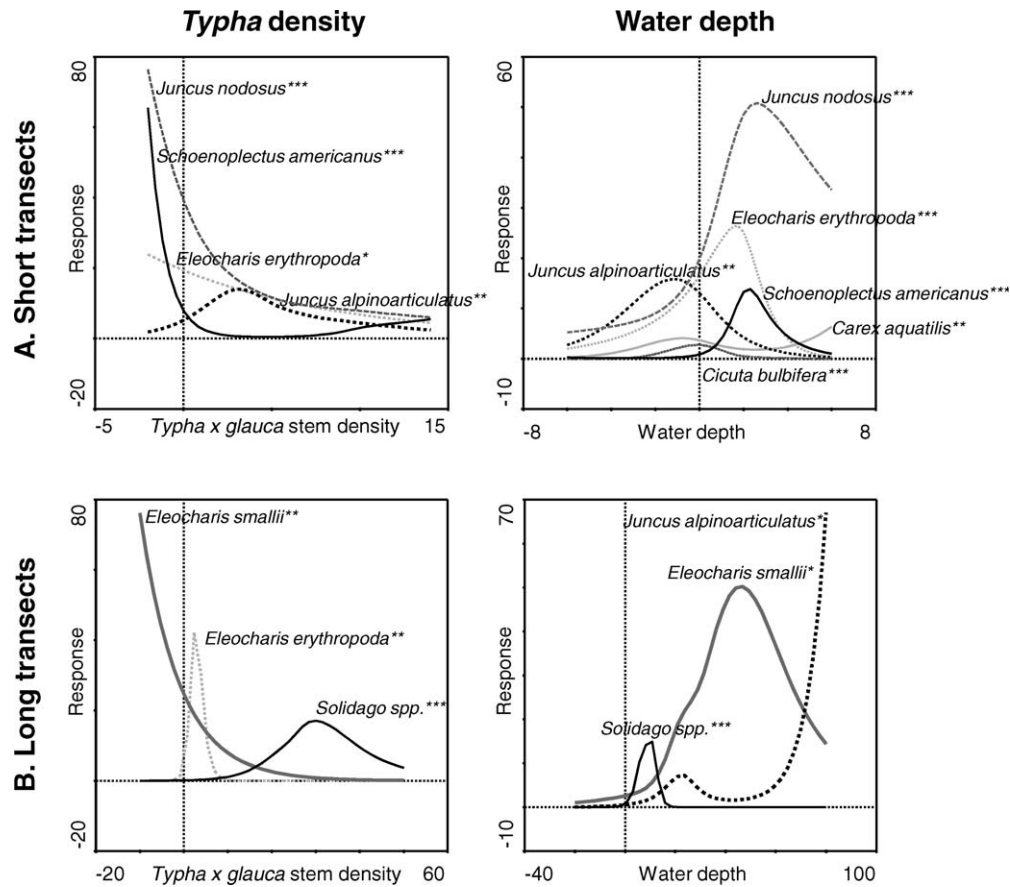
Figure 3.   Generalized Additive Model species response curves for A) short transects and B) long transects based on two gradients: density of *Typha* stems (left) and water depth (right). GAM species responses were calculated using CCA scores. Only species with significant response models (P < 0.05 using AIC criteria) are included. Significance for individual species is marked as: ***P < 0.001, **P < 0.01 and *P < 0.05.

absence of *Typha*, while *Juncus alpinoarticulatus* Chaix was strongly associated with deeper water. The more terrestrial *Solidago* spp. were associated with low water levels and higher *Typha* densities.

Short Transects.   In short transects, correlations between *Typha* density and environmental variables were weaker than for the long transects. *Typha* density did not significantly correlate with species richness (Figure 4A), SOM (Figure 4C), or soil NH_4 (Figure 4E). *Typha* density was positively associated with litter depth (Figure 4B) and negatively associated with water depth (Figure 4D). However, these 2 variables had low explanatory power despite large sample sizes (n = 340, litter depth: $R^2 = 0.091$, water depth: $R^2 = 0.056$).

   Typha density was a significant vector in NMS analysis (Figure 5). Concentrations of SOM and NH_4 were also significant and showed weak to orthogonal relationships with *Typha* density. As in the long transects, water depth was a significant

vector in NMS and was strongly negatively associated with *Typha* density.

   Species response curves generated using GAM indicated differential species responses to water depth and *Typha* density (Figure 3). Two of the most common native species of uninvaded areas, *Juncus nodosus* L. and *Schoenoplectus americanus* (Pers.) Volkart ex Schinz & R. Keller (both obligate wetland species), responded more to *Typha* density than water depth, with very strong decreases in abundance with small increases in *Typha* density. Note that water depth ranges differed substantially between long transects (from −2 to 70 cm) and short transects (from −5 to 5 cm).

Recently Colonized Typha *Patches.*   Soils associated with small, recently established patches of *Typha* did not differ from adjacent soils occupied by native species and lacking *Typha* in SOM, extractable NH_4, litter depth, or water depth (Table 2). Similarly, no environmental variables accounted for any signifi-
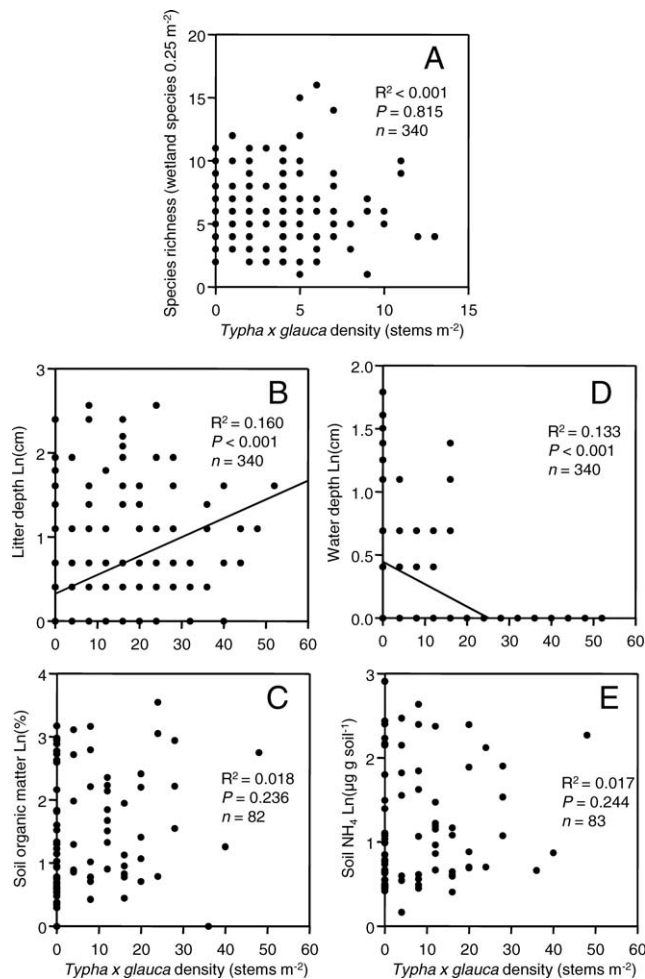
Figure 4. Correlations between *Typha x glauca* density and environmental variables for short transects.

cant variation in species composition in NMS analysis (Figure 6).

DISCUSSION

Invasive plant species are known to affect structure and functioning of wetlands (Ehrenfeld 2003, Zedler and Kercher 2004). However, the extent to which invasive species are causing *vs.* responding to changes in ecosystem structure and function is difficult to discern. We investigated environmental (biotic and abiotic) patterns associated with *Typha x glauca* invasion in Cheboygan Marsh, a Lake Huron coastal wetland in northern lower Michigan, USA. We found that *Typha* invasion was associated with decreased species richness, increased litter biomass and SOM, decreased water depth, and increased NH_4, NO_3, and PO_4.

One of the most widely recognized consequences of plant species invasions is a decline in native species diversity and our data support this pattern. Less understood are the effects of invasive species on ecosystem functions such as nutrient cycling (Ehrenfeld 2003). Having detected significant, positive relationships between *Typha* density and soil nutrient concentrations, we sought to determine if this pattern could be explained by pre–existing environmental conditions (i.e., *Typha* colonizing already–enriched areas). We found no evidence of high nutrient inputs to Cheboygan Marsh or evidence that nutrient inputs differed between invaded and uninvaded areas, with the caveat that our nutrient sampling was restricted in time and did not include groundwater sampling. However, because of the sandy soils of the study area, the water table roughly corresponds with the lake level and inputs from ground water are likely to be comparable in nutrient status to the predominantly oligotrophic waters of Lake Huron.

Furthermore, new, isolated patches of naturally colonizing *Typha* occurred in microsites that did not differ in nutrient status from uninvaded controls. Litter depth, SOM, and NH_4 were not higher in the presence of young *Typha* clones and multivariate analyses showed no significant *Typha* density, nutrient concentration, or water depth effects on the species composition of the native plant community. Concentrations of soil N under these small clones were very low relative to those found in high–density, well–established *Typha* clones (compare Table 2 and Figure 1). Consistent with the hypothesis that *Typha x glauca* can persist in oligotrophic conditions, experimentally transplanted *Typha* rhizomes survived and grew in previously uninvaded and nutrient–poor areas, indicating that *Typha* establishment is not restricted to areas with elevated nutrient concentrations (R. Wildova and D. Goldberg, unpublished data).

Do Patterns Associated with *Typha* Strengthen over Space/time?

We established transects that differed in length to substitute space for time (high–resolution, short transects extending from uninvaded portions of the marsh a short distance into *Typha*–dominated patches; low–resolution, long transects connecting uninvaded areas to locations deep within patches of nearly monotypic *Typha*). In long transects, we observed strong negative correlations between *Typha* density and species richness, a non–linear relationship between *Typha* density and water depth, and strong, positive correlations between *Typha* density and litter biomass, SOM, and nutrient
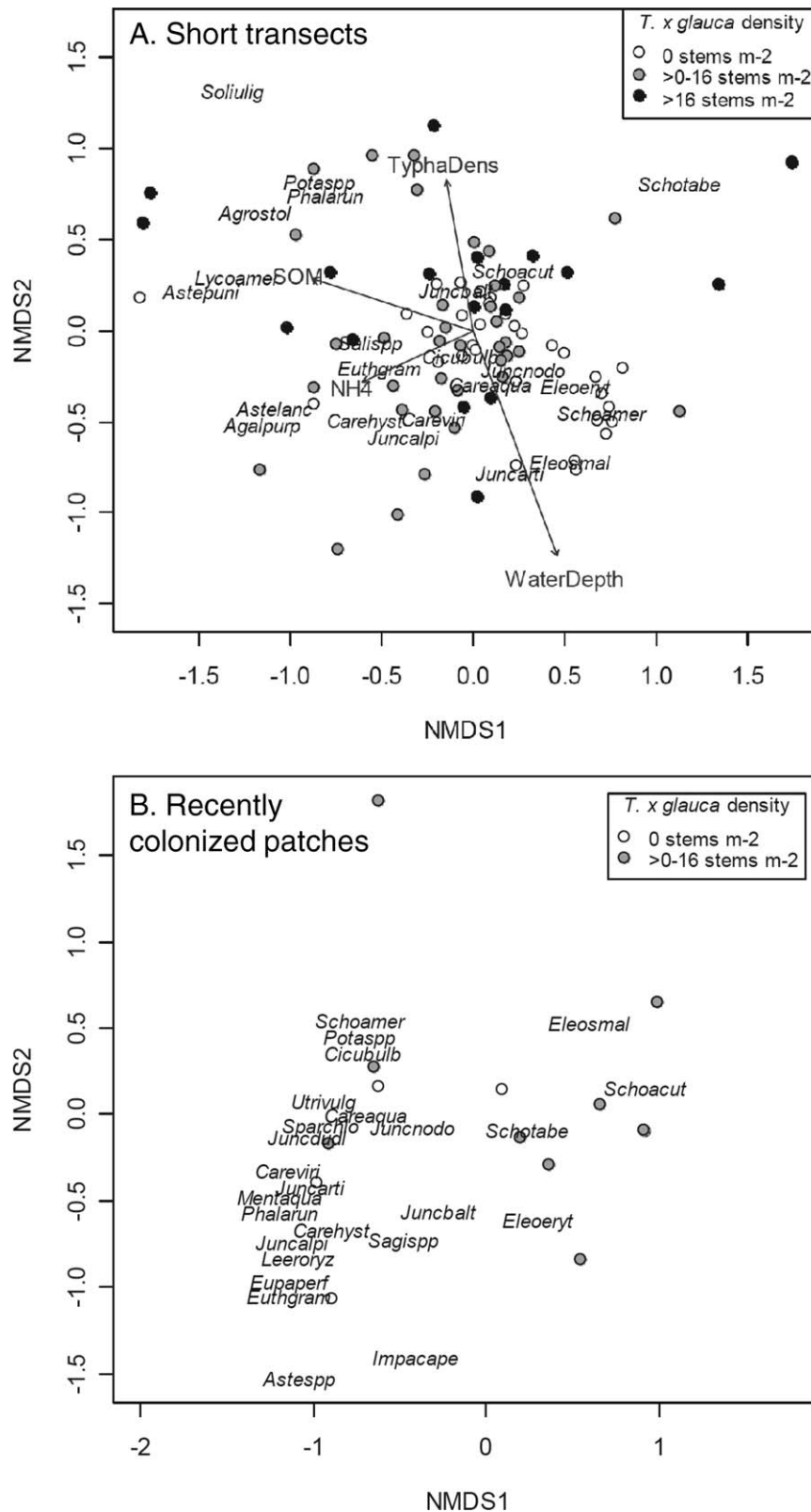
Figure 5. NMS analyses of species composition. See Figure 2 legend for ordination methods and species codes. A) Short transects. Explanatory variables tested were NH_4 (P = 0.042), SOM (P = 0.002), *Typha* density (P = 0.007), and water depth (P < 0.001). B) Recently colonized *Typha* patches and uninvaded control plots. Explanatory variables tested were NH_4 (P = 0.056), SOM (P = 0.808), *Typha* density (P = 0.555), and water depth (P = 0.645).

Table 2. Two–tailed paired t–test comparison of plots located in uninvaded sedge–rush dominated vegetation vs. those inside small, recently colonized *Typha* patches.

Variable	*Typha* absent		*Typha* present		
	Mean	S.D.	Mean	S.D.	P
SOM (%)	4.19	3.11	6.21	5.92	0.432
NH_4 ($\mu g\ g^{-1}$ soil)	1.72	0.46	3.39	4.72	0.309
Litter (cm)	1.21	0.99	1.86	1.86	0.263
Water depth (cm)	4.14	3.27	7.79	7.8	0.120

concentrations (Figure 1). Fewer significant correlations were observed among the same variables in the short transects and variance explained by *Typha* density was lower than in long transects, which presumably spanned more time since invasion. An increase in the strength of relationships between *Typha* and environmental correlates over time would be consistent with *Typha* being a driver of these patterns.

How Might *Typha* Influence Wetland Structure and Function?

The most likely mechanism by which *Typha* reduces species richness and changes composition of native vegetation is through its copious litter production. Light is strongly reduced under litter, and experimental addition of litter (but not of live stems without litter) significantly reduced native species richness (Freyman 2008, Farrer and Goldberg 2009). We suggest that the relatively small rhizomes of the mostly clonal native species do not provide sufficient resources to enable new ramets to grow through deep litter before reaching adequate light levels for photosynthesis.

We posit that *Typha* invasion drives increased soil nutrient concentrations through microbial mechanisms. *Typha* is a large, fast–growing plant with much higher biomass than the native species it displaces (Woo and Zedler 2002, Angeloni et al. 2006). This higher rate of carbon capture is expected to increase soil organic matter concentrations via decomposition of abundant litter, as well as elevated belowground root tissue and possibly root exudates (Alvarez and Becares 2006, Angeloni et al. 2006, Rothman and Bouchard 2007). Leachate from litter or increased concentrations of SOM provide carbon that can be used as a fuel source by heterotrophic microbes able to fix and mineralize nitrogen (Findlay et al. 2002, Ehrenfeld 2003, Farrer and Goldberg 2009; L. Barham, Loyola University Chicago, unpublished data).

If *Typha* is able to increase soil nutrient concentrations through carbon fixation that fuels microbial activity, this could lead to plant–soil positive feedbacks that favor *Typha* persistence and constrain restoration (Suding et al. 2004). Prior research indicates that *Typha* is better able to exploit increased nutrient availability than the native species it displaces (Woo and Zedler 2002). If *Typha* can "engineer" increased nutrient availability, it could drive its own invasion rather than being dependent on prior eutrophication.

Implications for Management

We believe that preventing nutrient inflows to wetlands is a critical but incomplete strategy for preventing spread of *Typha*. The patterns we observed suggest that *Typha* can have substantial effects on wetland structure and function and enrich previously nutrient–poor soils. Efforts to eradicate *Typha* at early stages of invasion are warranted for logistical reasons (higher probability of eradication at low abundance) and to avoid changes in soil properties. Restoration of sites where *Typha* has become established should address possible soil and functional legacies of invasion (Suding et al. 2004). This is especially true since *Typha* appears to alter nitrogen availability, which poses special challenges for restoration (Corbin and D'Antonio 2004).

While our data suggest that *Typha* may function as an ecosystem engineer, our analyses are correlative and do not allow for conclusions about causation. Ongoing work in Cheboygan Marsh, other Great Lakes coastal wetlands, and experimental mesocosms is being conducted to experimentally assess the mechanisms behind the patterns observed in this study.

Several traits of *Typha x glauca* (high biomass, fast–growing, quickly spreading via clonal growth) are shared with other problematic invaders of North American wetlands (e.g., *Phalaris arundinacea*, *Phragmites australis*, invasive *Spartina* spp.; Galatowitsch et al. 1999, Zedler and Kercher 2004). This suggests that changes in ecosystem function associated with *Typha* invasion may be general to other

wetland invasive plants. Observational studies of field patterns, controlled experiments, and meta–analyses are needed to investigate this possibility.

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