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RESEARCH ARTICLE

Effectiveness of cattail (*Typha* spp.) management techniques depends on exogenous nitrogen inputs

Kenneth J. Elgersma*, Jason P. Martina[†,‡,§], Deborah E. Goldberg[‡] and William S. Currie[§]

Wetlands occupy a position in the landscape that makes them vulnerable to the effects of current land use and the legacies of past land use. Many wetlands in agricultural regions like the North American Midwest are strongly affected by elevated nutrient inputs as well as high rates of invasion by the hybrid cattail *Typha × glauca*. These two stressors also exacerbate each other: increased nutrients increase invasion success, and invasions increase nutrient retention and nutrient loads in the wetland. This interaction could create a positive feedback that would inhibit efforts to manage and control invasions, but little is known about the effects of past or present nutrient inputs on wetland invasive plant management. We augmented a previously-published community-ecosystem model (MONDRIAN) to simulate the most common invasive plant management tools: burning, mowing, and herbicide application. We then simulated different management strategies and 3 different durations in low and high nutrient input conditions, and found that the most effective management strategy and duration depends strongly on the amount of nutrients entering the wetland. In high-nutrient wetlands where invasions were most successful, a combination of herbicide and fire was most effective at reducing invasion. However, in low-nutrient wetlands this approach did little to reduce invasion. A longer treatment duration (6 years) was generally better than a 1-year treatment in high-nutrient wetlands, but was generally worse than the 1-year treatment in low-nutrient wetlands. At the ecosystem level, we found that management effects were relatively modest: there was little effect of management on ecosystem C storage, and while some management strategies decreased wetland nitrogen retention, this effect was transient and disappeared shortly after management ceased. Our results suggest that considering nutrient inputs in invaded wetlands can inform and improve management, and reducing nutrient inputs is an important component of an effective management strategy.

Introduction

Wetlands in human-dominated landscapes are increasingly impacted by multiple stressors. Understanding how the interactions between stressors affects community- and ecosystem-level attributes of impacted wetlands is a major challenge, due in part to potentially nonlinear responses and thresholds that can arise when stressors interact (Davis et al. 2010). Because of their connection to and position within the surrounding landscape, wetlands in particular are disproportionately affected by multiple stressors from the surrounding landscape, such

as the combination of eutrophication and plant invasion. Because wetlands are often tightly connected to the surrounding landscape, invasive plant propagule pressure is high, resulting in higher invasion rates in wetlands and riparian areas than neighboring uplands (Brown & Peet 2003). Invasion reduces native plant diversity and some wetland ecosystem functions (Moreno-Mateos et al. 2012), although community and ecosystem responses to invasion are not necessarily linear (Elgersma & Ehrenfeld 2011, Eviner et al. 2012, Currie et al. 2014, Martina et al. 2016).

The landscape position of wetlands as a sink makes them prone to eutrophication (Junk et al. 2013, and references therein). Wetlands in human-dominated landscapes receiving nutrient-rich surface water and groundwater flows also tend to be more heavily invaded (Tsai et al 2012, Matthews et al 2009) in part because nutrient addition promotes the growth and dominance of important invasive species over natives (Woo & Zedler 2002, Tyler et al 2007, Holdredge et al. 2010). This interaction between eutrophication and invasion could accentuate the non-linearity of invasion impacts. Because eutrophication influences invasion rates, it is also reasonable to expect that eutrophication

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influences the effectiveness of invasive plant management techniques. However, since restorations are influenced by hydrology, landscape position, nutrient inputs, climate, substrate, and a myriad of other context-dependent factors that vary uniquely from site to site, it is challenging to discern general patterns about the underlying causes of successful invasive species control efforts (Higgs et al 2014, Palmer et al 2014, Lamers et al 2015).

In the Laurentian Great Lakes region of North America, *Typha × glauca* (hereafter *Typha*) is one of the most common invasive plants in emergent wetlands. *Typha* spreads rapidly via underground rhizomes and can heavily dominate sites with up to 90% cover (Lishawa et al 2015). Efforts at controlling and reducing the dominance and spread of *Typha* and similar invaders (e.g., *Phragmites australis, Phalaris arundinacea*) are common and typically involve herbicide, fire, mowing, or some combination of these three practices (NROC 2016, Hazelton *et al.* 2014, MDEQ 2014). However, treatments are often done sporadically with little follow-up, making broad patterns on the effectiveness of different management techniques difficult to discern (Martin & Blossey 2013, Hazelton *et al.* 2014). In addition, restoration assessments focus heavily on plant community composition and only rarely assess the restoration of wetland ecosystem functions (Matthews & Endress 2008). This is especially problematic in managing *Typha*, which alters wetland functions in ways that promotes its own invasion (Farrer & Goldberg 2009, 2014, Larkin et al 2012a, 2012b). Once established, *Typha* creates a thick accumulation of litter that reduces light at the soil surface and ramps up internal nitrogen cycling (Currie et al. 2014). *Typha* also increases carbon storage and nutrient retention in eutrophic wetlands (Martina et al. 2014, Martina *et al.* 2016). These changes in wetland ecosystem function promote the growth of *Typha*, making the restoration of ecosystem function vital to the long-term success of a *Typha* management program.

While significant resources are invested into managing *Typha* invasions, little is known about the effectiveness of the different management options (but see Lawrence et al. 2016). Best practices are largely based on personal experience and informal knowledge, mostly from the highly impacted, eutrophic wetlands where *Typha* tends to dominate (NROC 2016, MDEQ 2014). Given the strong potential for non-linear responses across a nutrient gradient, it is unclear how the effectiveness of management options or ecosystem-level responses of a wetland will change across a nutrient gradient, and best practices developed in eutrophic wetlands may not be the best approach in lower-nutrient wetlands.

To determine how the effectiveness of management techniques varies across a broad range of nutrient conditions and how these practices affect ecosystem function, we augmented a previously-published model (MONDRIAN; Currie et al. 2014) with modules to simulate burning, mowing, and herbicide application. We used a modeling approach because restoration success could be based on many potentially-interacting factors including nutrient inputs, technique and duration of management, hydrology, and propagule pressure, making it

untenable to fully test management effectiveness in the field experimentally. Our modeling framework facilitates testing non-linear responses to multiple interacting factors under one unified framework. Additionally, it is rare to test the consequences of management on ecosystem function, and using MONDRIAN allows us to investigate consequences of management on C and N cycling.

Our goal was to determine the most effective management approach for controlling *Typha* in different nutrient conditions, and to determine how each approach influenced the ecosystem-level responses of nutrient retention and carbon storage. We focus here on *Typha* because relatively little formal study has been done to determine the effectiveness of different treatment options for this invader. We hypothesized that the effectiveness of different management approaches would vary across a nutrient gradient, with the most successful being a combination of approaches. We also hypothesized that in highly eutrophic systems, *Typha* invasion would increase nutrient retention and carbon storage. Therefore management that effectively reduced *Typha* would also reduce nutrient and carbon storage.

Methods

MONDRIAN is an individual-based model that spans several major levels of ecological organization, from individual plant physiology to ecosystem function, and is formulated through a set of algorithms in an object-oriented programming language (Visual Basic.Net). MONDRIAN was fully described by Currie *et al.* (2014), with additional code development described in Martina et al. (2016). Here we briefly describe the previously published model followed by more detail on additions made for the research described here.

MONDRIAN models the ecology of wetlands at the individual, population, community and ecosystem level. By simulating up to thousands of ramets per square meter, including both internal source-sink C and N translocation within each plant and size-symmetric competition for available N, N availability becomes heterogeneous. This leads to competition among individual ramets for limited N, which takes place in spatially explicit, discrete grid cells. Plants can scavenge for N by growing clonally across grid cells. Additionally, light competition occurs from shading from neighboring plants and species-specific light extinction curves that reduces the growth rate of each ramet using a Michaelis-Menten equation of relative growth rate as a function of light availability (Martina et al. 2016). C and N demand to create a daughter ramet from rhizomes during clonal reproduction connects resource competition among individuals to population dynamics in a heterogeneous environment. Mortality due to age or inability to acquire sufficient resources can lead to the loss (and conversion to litter) of individual ramets or whole genets. Species coexistence and competitive exclusion, biodiversity changes over time, and biotic resistance to invasion are all emergent community dynamics caused by competition for resources and mortality among modeled species (up to five). Plant growth, population fluctuations, and community composition shifts, along with

externally driven hydrology, N inputs, and light limitation cause ecosystem level processes. For a further description of C and N cycling in Mondrian, including controls on decomposition, decomposition feedbacks on N mineralization, and plant growth and uptake of N see Currie *et al.* (2014). For a description of hydrology and anaerobic zonation and their effects on C and N cycling, see Martina et al. (2016).

For this study, we further augmented Mondrian to model the commonly used management practices of mowing, burning, and herbiciding. Mowing was added by allowing the user to simulate cutting the stems of all individuals in all grid cells at a user-defined height above the soil surface on user-defined days during the year. The user also controls whether the cut stem biomass becomes litter (mulching) or is removed from the modeling area to simulate harvesting of cut biomass. Mowing is not species-specific; all individuals are cut to the height indicated by the user and removed or mulched.

Herbicide effectiveness is mainly controlled by the depth of herbicide penetration, a user-controlled parameter defined as the zone of herbicide influence from the top of the canopy. We therefore assume herbicide is applied by aerial spray rather than hand-wiping or other more labor-intensive methods. Mondrian locates the tallest individual in each grid cell and then calculates the depth of herbicide penetration based on that height. All individuals in all grid cells within this height range are affected by the herbicide. For those individuals, each of their aboveground and belowground biomass pools are converted to litter to indicate individual death. Death due to herbicide application is on the ramet (individual) basis. We modeled the effects of a generic broad-spectrum herbicide and did not include characteristics or side-effects unique to specific herbicides such as imazapyr or glyphosate. Aboveground biomass converted to litter remains standing and influences the local light environment until transferred to the ground litter pool by either natural decomposition, mowing, or burning.

The use of fire for management is controlled in Mondrian by three parameters. First, a fire severity parameter controls the proportion of litter layer C that is volatilized by the fire. This is used to calculate a burn depth in the ground litter layer, above which all ground litter, standing litter, and live biomass is subject to burning. Litter C is completely removed from the modeling area to simulate combustion, but because few fires consume 100% of live biomass (Tian et al. 2010), an additional parameter (live tissue burn efficiency) controls the proportion of the aboveground live biomass consumed in the fire. Live tissue not removed from the modeling area becomes litter/char post-fire. Of the living and dead biomass that burns, fire N volatilization is a parameter that controls the proportion of N lost from the ecosystem via volatilization. The remaining N is mineralized and added to the soil inorganic N pool, where it continues to be part of the ecosystem N cycle including immobilization in remaining litter or availability for plant uptake. When fire is introduced to the modeling area, the entire area is burned at the same severity; fire is not patchy in Mondrian. Water depth influences the depth of burn as well. Regardless of fire severity, no C or N below the current water depth is able to burn.

For all management treatments, the year in which management begins and ends is controlled by the user. Additionally, the day of the year for each treatment is also controlled by the user to allow different management strategies (e.g. early versus late season burn) to be simulated. Any combination of management practices within a year can also be modeled.

Simulation design and setup

We used Mondrian to model a 52.5 × 52.5 cm area consisting of 49 grid cells, each 7.5 × 7.5 cm in area. Each simulation run lasted 45 years, with native species introduced in year one. Natives were randomly distributed into the modeling area in four cohorts of 65 genets in years 1, 3, 5, and 7 and had largely stable NPP and density by year 15. Two cohorts of 15 invader (*Typha*) genets each were introduced at random locations in years 15 and 20, after natives had become well established. After initial introduction of a species, one individual genet was randomly added to the modeling area per year to represent natural colonization. The simulation ran for 10 more years after invasion to allow successful *Typha* establishment before management began in year 30 (except in the no-management simulations). For all data analysis, total NPP of natives and invasives, C stocks, and N retention were recorded the year directly after the last year of treatment (or year 31 for the no-management simulations). This enabled comparison among treatment levels to determine the effectiveness and consequences of different management practices, even when treatment durations differed.

Experimental design

Management treatments simulated were as follows: no management, burning (B) alone, herbicide (H) alone, mowing (M) alone, and all combinations (BH, BM, HM, BHM). Additionally, we used two versions of mowing where biomass was either removed from the modeling area or left as mulch, and two burn dates (DOY 135 and 235). However, because there was little difference due to timing of fire or removal of biomass, we omit results from the less commonly used approaches of biomass removal and early-season fire, and present only results of late-season burning and mulching. This results in a total of 7 management treatment options. Mowing was carried out on DOY 200 (approximate peak biomass) at a mowing height of 0.1 m. Herbiciding was carried out on DOY 213 (approximate peak biomass, but after mowing if both were simulated during the same run) and canopy penetration was 1 m. Fire severity was set at 0.4 (Certini 2005, White et al. 2008), fire N volatilization at 0.55 (Tian et al. 2010) and live tissue burn efficiency at 0.7 (Tian et al. 2010). Each treatment only occurred once a year.

To simulate variation in management duration, each management treatment lasted one, three, or six years. In management treatments lasting multiple years, treatments occurred at the same time using the same treatment parameters each year.

The four levels of N input ranged from 4 to 30 g N m⁻² y⁻¹ and were constant throughout each model run. The lowest N input represents a level slightly higher than present-day rain-fed N deposition in northern Michigan (wet + dry inorganic N deposition plus atmospheric organic N deposition) (NADP 2009, Neff *et al.*, 2002). The highest N input represents eutrophic wetlands influenced by agricultural runoff (Davis *et al.*, 1981; Neely and Baker 1989, Kovacic *et al* 2000, Jordan et al. 2011). Earlier modeling results (Martina et al. 2016) showed that invasions fail at N loading < 4 g N m⁻² y⁻¹ and a threshold for highly successful invasion usually occurs between 12–18 g N m⁻² y⁻¹, so we included two N input levels around this range (12.5 and 20 g N m⁻² y⁻¹).

The factorial design of 7 management scenarios with 3 management durations at 4 levels of N loading, along with a control (no management) treatment at each of the 4 N loading levels, resulted in 88 management scenarios. Each scenario was replicated 4 times in Mondrian with stochastic differences both in initial plant distributions and spatial movements during clonal reproduction.

We parameterized Mondrian using realistic species parameters as in Martina *et al.* (2016). Three native species (*Eleocharis palustris* (L.), *Juncus balticus* (Willd.), and *Schoenoplectus acutus* (Bigelow) A. Love & D. Love) and the invasive species *Typha × glauca* were parameterized and used in the *in silico* experiments we report here. These native and invasive species commonly occur in Great Lakes coastal wetlands. All plant species were parameterized using multiple values found in both the literature and our own unpublished data collected from the Great Lakes region (see Martina et al. 2016 for details).

Statistics
Analysis of variance was used to measure the effectiveness of management scenarios in controlling both the net primary productivity (NPP) of *Typha* and *Typha* dominance (measured as the proportion of total community NPP attributed to *Typha*) in the year after management treatments ended. We also used analysis of variance to determine whether total ecosystem carbon and nitrogen retention (the proportion of annual N inputs remaining in the ecosystem) differed significantly among management scenarios in the year after management ended. Inspection of model residuals confirmed that the assumptions of normality and homoscedasticity were appropriate. All statistical analyses were conducted using R version 3.2 (R Core Team 2015).

Results
Overall management effects on Typha
Across all simulations, the overwhelmingly most important single factor affecting the productivity and dominance of *Typha* was the amount of nutrients entering the system (**Table 1**). This was partially expected based on Martina et al. (2016), though the results from those simulation runs did not include management scenarios. In addition

to its strong effect on total productivity in the wetland, nutrients also had a strong effect on *Typha* dominance (measured as the proportion of the wetland productivity due to *Typha*). In fact, nutrients alone explained approximately 65% of the variation in *Typha* dominance (partial R² = 0.652), whereas all types of management combined explained only about 20% of the variability and the strongest individual management effects explained only around 3 – 5%. While these proportions are largely determined by the range of conditions used in our simulations, it is important to note that we used the full range of conditions present in the Great Lakes region, making these proportions representative of conditions in the landscape.

Most importantly, nutrient inputs interacted strongly with management treatments (**Table 1**), suggesting that the most effective treatments depended on the amount of nutrients entering the wetland.

Because management practices had vastly different effects in low-N wetlands compared to high-N wetlands, we analyzed the effects of management duration and combining management options separately in the lowest-N and highest-N wetlands. This approach allows us to elucidate the role of management decisions under these very different wetland conditions. In most cases, results in the medium-N (12.5 or 20 g N · m⁻² · y⁻¹) wetlands were intermediate between the high-N and low-N wetlands (Figure S1).

#### Effects of single management treatments on Typha
In the most eutrophic wetlands, management treatments applied singly for only one year were relatively ineffective in reducing *Typha* productivity in the following year (**Figure 2**). Repeating the applications of herbicide, mowing, or burning for 3 or 6 years increased efficacy (p < 0.0001, **Table 2**), and herbicide was the most effective of these three singly-applied treatments (**Figure 1a–c**). Three years of herbicide application in these high-N wetlands reduced invader productivity by 59% between the year prior to treatments and the year after treatments, and slightly increased productivity of native species. Three years of fall burning did not strongly affect the absolute or relative productivity of invasive *Typha*, and, surprisingly, mowing stimulated *Typha* productivity during the 3-year management period (likely due to increased light levels associated with mowing), though post-management *Typha* productivity quickly returned to pre-management levels (**Figure 1a–c**).

In contrast, in low-nutrient wetlands management had little effect on *Typha* productivity and *Typha* was relatively unproductive with or without management, even sustained management for 6 years (**Figure 1d–f**). Herbicide application in these wetlands actually caused a substantial *increase* in invader productivity in the 5 to 10 years following treatments. This was likely due to the nearly 20% decrease in native species' productivity post-management compared to pre-management (**Figure 1f**). The duration of treatment (1, 3, or 6 years) also had surprisingly little overall influence on the effectiveness of the treatments in low-N wetlands. Additional

Table 1: Effects of nitrogen and management activities on *Typha* dominance in the year following the end of management.[a] DOI: https://doi.org/10.1525/elementa.147.t1

Source	SS	Df	F	p	Partial R²
N	19.0384	1	1373.25	< 0.0001	0.652
Herbicide	0.8598	1	62.02	< 0.0001	0.029
Burn	0.0658	1	4.74	0.0301	0.002
Mow	0.844	1	60.88	< 0.0001	0.029
Duration	0.3843	1	27.72	< 0.0001	0.013
N:Herbicide	1.5138	1	109.19	< 0.0001	0.052
N:Mow	0.3464	1	24.99	< 0.0001	0.012
Herbicide:Mow	1.2694	1	91.56	< 0.0001	0.043
Burn:Mow	0.092	1	6.64	0.0104	0.003
N:Herbicide:Mow	0.113	1	8.15	0.0046	0.004
Herbicide:Mow:Duration	0.0734	1	5.30	0.0220	0.003
Residuals	4.4641	322			
Total	**29.21971**	**351**			

[a] Dominance is measured as *Typha*'s proportion of the total community NPP. Note that only significant interactions are shown for brevity, though all interactions were included in the model.
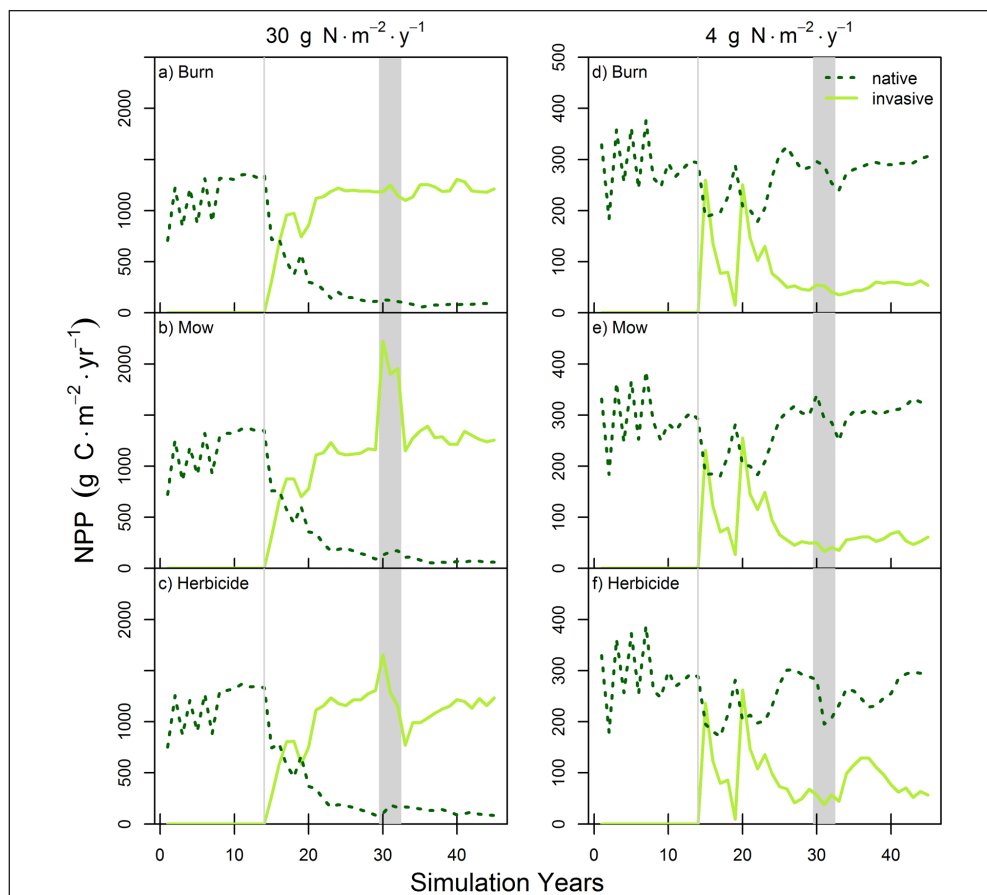
Figure 1: Annual net primary productivity (NPP) of native plants and invasive *Typha* simulated over 45 years. Gray shading indicates the 3-year time period during which burning **(a, d)**, mowing **(b, e)**, or herbicide treatments **(c, f)** were applied. Wetlands received either 30 g N · m⁻² · y⁻¹ (panels a–c) or 4 g N · m⁻² · y⁻¹ (panels d–f). Note the difference in y-axis scales between left and right columns. DOI: https://doi.org/10.1525/elementa.147.f1

Table 2: Analysis of variance for the effect of management activities on *Typha* dominance in the lowest-nutrient
(4 g N · m^{-2} · y^{-1}) and highest-nutrient (30 g N · m^{-2} · y^{-1}) wetland simulations.[a] DOI: https://doi.org/10.1525/ele-menta.147.t2

Source	Df	4 g N · m^{-2} · y^{-1}			30 g N · m^{-2} · y^{-1}		
		F	p	Partial R^2	F	p	Partial R^2
Herbicide	1	**67.41**	**< 0.001**	**0.289**	**187.563**	**< 0.001**	**0.490**
Burn	1	**5.006**	**0.028**	**0.021**	**6.466**	**0.013**	**0.017**
Mow	1	**40.174**	**< 0.001**	**0.172**	**37.957**	**< 0.001**	**0.099**
Duration	1	**5.513**	**0.022**	**0.024**	**42.867**	**< 0.001**	**0.112**
Herbicide:Burn	1	0.060	0.808	< 0.001	0.002	0.965	< 0.001
Herbicide:Mow	1	**25.643**	**< 0.001**	**0.110**	2.553	0.114	0.007
Burn:Mow	1	**4.653**	**0.034**	**0.020**	3.489	0.066	0.009
Herbicide:Duration	1	**6.568**	**0.013**	**0.028**	0.164	0.686	< 0.001
Burn:Duration	1	0.822	0.368	0.004	0.112	0.739	< 0.001
Mow:Duration	1	2.097	0.152	0.009	**19.669**	**< 0.001**	**0.051**
Herbicide:Burn:mow	1	0.932	0.338	0.004	0.434	0.512	0.001
Herbicide:Burn:Duration	1	0.497	0.483	0.002	0.045	0.832	0.0001
Herbicide:Mow:Duration	1	0.762	0.385	0.003	**8.457**	**0.005**	**0.022**
Burn:Mow:Duration	1	0.071	0.790	< 0.001	0.387	0.536	0.001
Residuals	73			0.313			0.191
Total	**87**						

[a]Dominance is measured as *Typha*'s proportion of the total community NPP.

years of treatment application did significantly reduce invader biomass (**Table 2**), but the difference was nearly imperceptible (**Figure 3**).

Effects of combined management treatments on *Typha*

Under high-nutrient conditions, combinations of treatments were generally more effective than treatments applied singly (**Figure 2**). Repeated applications of herbicide combined with either burning or mowing was particularly effective in reducing *Typha* biomass and dominance. In addition, the herbicide + burning combination was most effective in increasing native biomass in the year after treatments ended.

Combinations were *not* more effective than singly-applied treatments in the low-N wetlands (**Figure 3**, 4 g N m^{-2} y^{-1}) and in fact, while combining treatments increased efficacy in high-N wetlands, some of these same combined treatments promoted invasion in low-N wetlands. For example, under low nutrient conditions the herbicide-mowing and burning-herbicide-mowing combinations were significantly worse than the unmanaged control, resulting in approximately twice as much invader biomass and only 40% as much native biomass as the unmanaged control. In the highly eutrophic wetlands, these treatment combinations were some of the most effective at reducing invader biomass and increasing native biomass.

Management effects on C and N flux

Nitrogen retention (the proportion of N input that remains in the wetland) was highly variable over time, but decreased during management periods regardless of the management method (**Figure 4a–c**). Of the management treatments applied singly, herbicide caused the largest reduction in N retention, and this reduction was most severe in low-N wetlands where herbicide application resulted in the wetland becoming a net N exporter. After a 3-year treatment period ended, N retention returned in most cases to pre-treatment levels within 5 years (**Figure 4**). Management duration had little effect on the degree of decline in N retention or in the rate of post-treatment recovery (data not shown).

Management efforts had minor effects on carbon accumulation. Fire predictably resulted in a decrease in C stored in the ecosystem, especially in high-productivity eutrophic wetlands (**Figure 4d**). This decrease was modest however; even in the most eutrophic wetlands where burning had the greatest effect, fire reduced the total amount of C stored by 5% in the first year. The accumulation of C in the ecosystem did not resume until after fire treatments stopped, but rebounded within only a few years post management. Mowing had little effect at all on C accumulation (**Figure 4e**), while herbicide caused the accumulation of C to stagnate during the treatment period (**Figure 4f**). For all types of management, the effect of management treatments dissipated rapidly after the
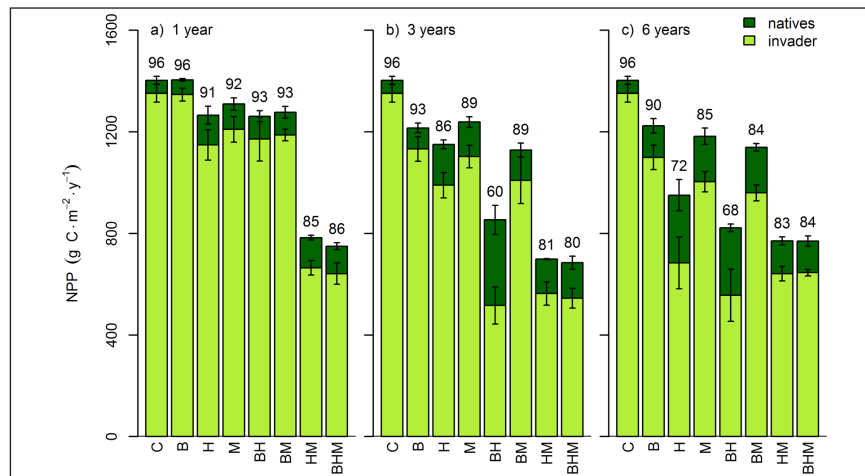
Figure 2: Annual net primary productivity of native plants and invasive *Typha* in the year following management in high-N wetlands. Treatments include one **(a)**, three **(b)**, or six **(c)** years of simulated burning (B), herbicide (H), mowing (M), no management (control; C), or combinations of these management techniques. Numbers above each bar represent the percentage of total NPP that comes from the invasive *Typha*. Simulated wetlands received inputs of 30 g N · m^{-2} · y^{-1}. DOI: https://doi.org/10.1525/elementa.147.f2
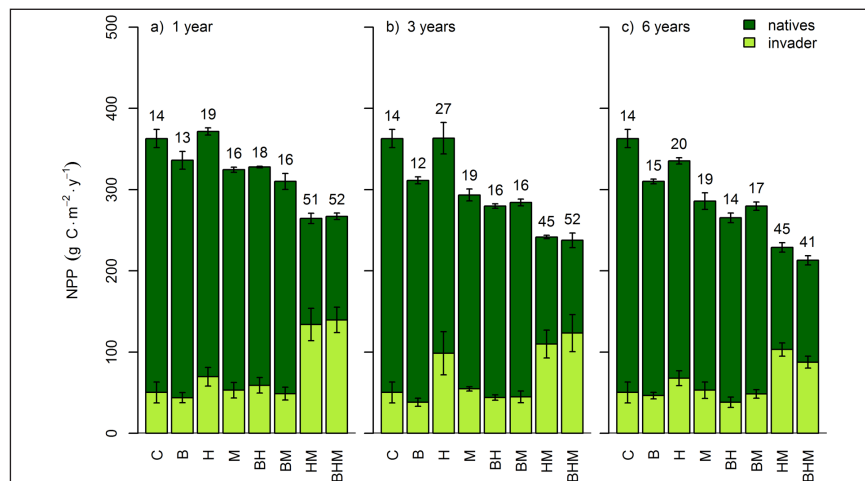
Figure 3: Annual net primary productivity of native plants and invasive *Typha* in the year following management in low-N wetlands. Treatments include one **(a)**, three **(b)**, or six **(c)** years of simulated burning (B), herbicide (H), mowing (M), no management (control; C), or combinations of these management techniques. Numbers above each bar represent the percentage of total NPP that comes from the invasive *Typha*. Simulated wetlands received inputs of 4 g N · m^{-2} · y^{-1}. DOI: https://doi.org/10.1525/elementa.147.f3

treatment period ended and C accumulation rebounded quickly to the levels found in untreated wetlands.

Discussion

As expected, low-N wetlands had much lower overall community biomass than nutrient-rich wetlands, and had proportionately lower invader biomass even in the unmanaged controls. This indicates that *Typha* was a less successful invader in the lowest-nutrient wetlands, where it comprised less than 15% of the community NPP on average. As a result, the amount of nitrogen entering the wetland had a far greater effect on the amount and dominance of the invader than any of the management treatments did. This result is largely driven by the very wide range of nutrient conditions that we simulated in our study, but because the range we simulated reflects

the range of conditions seen in the Great Lakes region, this result demonstrates that eutrophication is strongly antagonistic toward efforts to control *Typha* in the landscape. This conclusion is consistent with the findings of Currie *et al.* (2014) and Martina et al. (2016), who found using MONDRIAN that large-sized clonal invaders (such as *Typha*) invade established plant communities best at high N inputs but are much less successful at low N inputs. Goldberg *et al.* (unpublished MS) further found this to be true even in the absence of competition from an established plant community, and demonstrated the importance of a potential trade-off in clonal plants between the competitive benefits of large size and the increased reproductive costs for larger clonal plants. Thus, though it is not surprising that we found higher invasion success of a relatively large species at high N, what is striking in
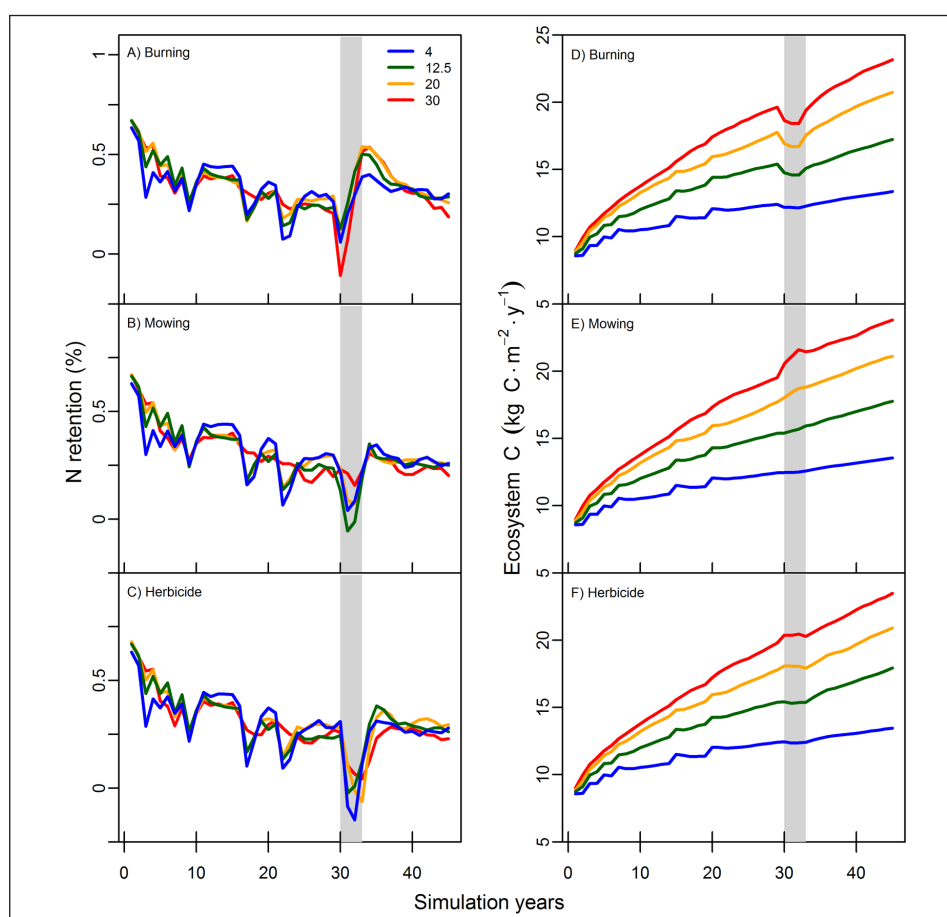
Figure 4: N retention and C accumulation in managed wetland simulations. The percent of incoming N retained **(a–c)** and amount of C accumulated **(d–f)** in the wetland over 45 simulation years. Wetlands received 4 (blue), 12.5 (green), 20 (yellow) or 30 (red) g N · m^{-2} · y^{-1}. Gray shading indicates the 3-year time period during which burning (a, d), mowing (b, e), or herbicide treatments (c, f) were applied. DOI: https://doi.org/10.1525/elementa.147.f4

these results is how strongly nitrogen regulates invader dominance compared to non-selective burning, mowing, or herbicide treatments. This suggests that to control wetland invasions, practices to reduce N loading should be implemented together with traditional approaches for removing, eradicating, or treating the invasives.

Wetlands are usually positioned as sinks in the landscape, so the amount of nitrogen entering a wetland is often outside of the control of wetland land managers. Thus, plant invasions are seldom managed by efforts to reduce eutrophication, even though excess nutrients are often acknowledged as a driver of invasion in wetlands (Woo & Zedler 2002, Zedler & Kercher 2004, Ehrenfeld 2008). A recent literature survey of *Phragmites australis* management practices showed 88% of studies investigated herbicide, mowing, and/or fire as management tools; none investigated nutrient reduction strategies (Hazelton *et al.* 2014). Similarly, a survey of state, federal, municipal, and private managers found that nearly all managers utilized herbicide to control *Phragmites*; less than 10% used "other" methods that may have included nutrient reduction (Martin & Blossey 2013). While there has been less systematic review of the most common management strategies for *Typha* (Lawrence et al. 2016), management techniques are presumably similar to

Phragmites given these species are commonly found in close proximity and often co-occur (pers. obs.).

In the management literature, nutrient reduction strategies within a wetland generally fall into one of two categories: sequestering nutrients in the soil, or removing nutrients through biomass or (rarely) soil removal. *Typha* biomass has long been used to effectively remediate wastewater based on high nutrient uptake rates (Coleman *et al.* 2001, Ciria *et al.* 2005, Calheiros *et al.* 2009), and the biomass that results from wastewater treatment has even been suggested as an efficient feedstock for cellulosic biofuel production (Liu *et al.* 2012). *Typha* biomass is usually removed to directly reduce *Typha* dominance, but burning or repeated cutting and removal of nutrient-rich *Typha* biomass also has the effect of removing nutrients from a wetland (Lishawa et al 2015). This approach would furthermore prevent the large accumulation of litter that alters wetland ecosystem function and negatively affects native plants (Larkin et al 2012, Farrer & Goldberg 2014), thereby breaking the cycle of positive feedbacks between increasing *Typha* dominance, larger amounts of litter production, and increased nutrient cycling (Currie *et al.* 2014).

Despite the potential theoretical benefits of removing N in biomass, our results show little restoration benefit of biomass removal, suggesting limited effectiveness of this

approach. Burning alone caused only a slight and transient reduction in *Typha* dominance, which is likely due to the fact that fall burning of senescent tissues does little to remove N; much of the plant's nutrients are retranslocated to belowground rhizomes as tissues senesce in the field (Sharma *et al* 2006, Asaeda *et al.* 2008) and in Mᴏɴᴅʀɪᴀɴ. Mowing in our simulations was not effective at removing N because the cut vegetation was not removed. We simulated mowing without biomass removal because removal is rarely done in the field due to the added labor and cost. We also ran additional simulations (not presented here) that included biomass removal, and while this more effectively removed N, it did not greatly improve control of *Typha* (data not shown). Mowing for 1, 3, or 6 years did little to affect *Typha* dominance in the year directly after treatments ended. This may be because non-selective mowing removes N and biomass from native plants as well, and the benefit to native plants of short-term N reduction may not outweigh the cost of their own biomass loss. In a recent field experiment, Lishawa *et al.* (2015) also found that two years of harvesting aboveground biomass in *Typha* stands left stands dominated by *Typha* (> 60% *Typha*), though notably the aboveground harvest also doubled native plant species diversity, especially in younger stands with healthier seedbanks. In a mesocosm study comparing the effects of herbicide to mowing with or without biomass removal, Lawrence et al. (2016) also observed no significant effect of biomass removal on post-management *Typha* biomass or density. In the high-N scenarios in our study, mowing actually stimulated *Typha* productivity during the management period (likely due to a reduction in canopy shading), and other field studies have shown that mowing alone can stimulate wetland invader density as it did in our simulations (Asaeda *et al.* 2006, Warren *et al.* 2001). Thus, removing N by burning or mowing biomass alone is not likely to effectively control *Typha*, especially in wetlands with chronically high N inputs where inputs exceed the amount of N removed by burning or mowing.

A second strategy for reducing nutrient availability, which our simulations did not address, would be to sequester nutrients in soil and soil microbial biomass. This approach has been successfully used to control invasive plants on a small scale in a variety of upland systems using carbon-rich amendments such as sawdust or wood chips (Blumenthal *et al.* 2003, Prober *et al.* 2005, Kulmatiski & Beard 2006, Burke *et al* 2013). Amendments of C-rich, N-poor detritus create a N sink by shifting the C:N ratio of organic matter available for microbial breakdown, increasing microbial demand for N resulting in N immobilization. This strategy has rarely been tested in wetlands, though Perry *et al* (2004) found C additions effective for reducing the competitive dominance of invasive *Phalaris arundinacea* in an experimental greenhouse study. While this suggests C additions could be used to limit *Typha* growth, there are major logistical constraints to this approach. Large quantities of C would be needed for a site-scale restoration, and in many wetlands with highly dynamic hydrology or high physical disturbance regimes, sawdust or wood chips would likely be washed away relatively rapidly, especially in coastal wetlands affected by wave action and storms. Even if C amendments were retained in the managed wetland, continual addition of C would be needed due to the microbial breakdown of the added organic matter.

The focus for most restoration projects is not a reduction in N loading, but eradication by herbicide application (Hazelton *et al.* 2014). Herbicide is the most commonly-used method for controlling invasive plants (Hazelton *et al.* 2014, Kettenring & Adams 2011), but our results showed that its effectiveness was strongly context-dependent. In high-N wetlands, the most effective single treatment for reducing the biomass and dominance of *Typha* was herbicide, and it was even more effective when combined with mowing or burning. These results agree with Lawrence et al (2016), who found significantly lower *Typha* biomass and density in herbicide-treated mesocosms compared to mowed or untreated mesocosms. In less eutrophic wetlands, our results showed herbicide was the worst single treatment and actually caused a notable *increase* in *Typha* biomass and dominance. It is important to note that we simulated blanket-spraying herbicide over the entire modeling area, which concurrently reduced native vegetation and increased available N for *Typha* growth. Large-scale disturbances like this could promote invasion by reducing biotic resistance of the native community. We did not simulate spot-application of herbicide, which would not affect a community's biotic resistance and may still be quite effective in low-nutrient conditions.

Because we simulated applying herbicide from above the canopy, taller ramets experience disproportionately more mortality compared to short ramets. In high-N environments where *Typha* is dominant and tall relative to natives, most of the herbicide is intercepted by a dense canopy of *Typha*, while at least some of the smaller native plants are protected from herbicide by the *Typha* canopy. In low-nutrient environments, however, herbicide can more easily penetrate the sparse and patchy *Typha* canopy and cause mortality of native plants. High levels of mortality in these low-nutrient conditions create a large disturbance that allows *Typha* to re-invade and rapidly increase. In the field, *Typha* often rapidly colonizes disturbed areas (Tulbure *et al.* 2007) and may even require such disturbances for establishment since it competes poorly with well-established stands of native vegetation in (DGE, unpublished data). In high N environments with a dense canopy, herbicide does not create a completely open canopy, which may limit the ability of *Typha* to reinvade and make herbicide more effective.

Furthermore, in high-nutrient simulations, much of the *Typha* biomass is converted to standing dead litter, and over time, to a litter layer on the ground. Standing dead litter continues to inhibit native plants through shading both in our model and in the field (Farrer & Goldberg 2009), and as litter decomposes it releases N and augments the internal N cycle, which feeds back to promote *Typha* invasion (Currie *et al.* 2014, Lawrence et al. 2016). Combining herbicide with late-season fire removes standing dead litter, benefitting resprouting native plants by

removing shading and internal N feedbacks. Similarly, combining mowing with the herbicide treatment reduces the amount of standing dead litter by reducing the amount of standing biomass at the time of the herbicide application. Combining all three treatments does not cause increased control mainly because both fire and mowing augment the herbicide treatment's effects through litter reduction, and are thus redundant.

The most common approach used by managers in the field to control *Phragmites* (herbicide and fall burning, Hazelton *et al.* 2014) and presumably also *Typha* is the optimal approach for high-nutrient conditions based on our results. This is concordant with our findings since many severe invasions that are being actively managed occur in highly eutrophic conditions. However, our results also show that managers should not assume that the methods that have been effective in high-nutrient conditions will also be effective in lower-nutrient wetlands.

Ecosystem level effects of the different management strategies on wetland C and N retention were surprisingly modest and short-lived in our simulations, despite the large changes in NPP. While some treatments (notably herbicide) caused significant reductions in wetland N retention (**Figure 4**), these effects dissipated very quickly (~1 year) after treatments ended and once *Typha* resumed high growth rates. Lawrence et al (2016) also observed a large pulse of porewater N and P following treatment, but it is unclear how long these effects would last. Our work suggests that changes in nutrient retention are likely to be ephemeral, but future long-term studies would be useful to resolve the duration of effects on nutrient retention.

High nutrient levels resulted in *Typha* rapidly re-invading after management treatments were applied. This rapid re-invasion could be driven either by continued high N inflows, or by an invasion legacy effect in which preceding periods of high N inflow had caused muck and sediment organic matter to build up large accumulations of N, thereby favoring invaders (Currie et al 2014). Many other studies have also demonstrated significant legacy effects of invasion on nutrient cycling even after successful removal of the invasive (Rodríguez-Echeverría et al 2013, Elgersma et al 2011, Corbin & D'Antonio 2004). Since either one or both of these explanations may explain the short duration of invader suppression, manipulative experiments in wetlands or more long-term post-restoration field monitoring of ecosystem functions would be helpful to tease apart the effects of legacy nutrient accumulations in muck and sediments versus continuing exogenous N inflows in allowing recovery of invader populations.

In summary, our results show that *Typha* invasion success is strongly influenced by the availability of nutrients in the wetland, and controlling nutrients is potentially more effective than control efforts that employ burning, mowing, and / or herbicide. Furthermore, the effectiveness of these different control efforts is context-dependent and strongly modified by nutrient availability. We found the most effective practice in high-nutrient wetlands where *Typha* is most dominant was a combination of herbicide and fire. This is the most commonly-used approach used by managers in practice, but our results suggest this same practice would be detrimental if implemented in lower-nutrient wetlands. Very few empirical data exist on how these control efforts influence wetland C and N cycling, but our model results suggest control efforts do not strongly influence these ecosystem-level wetland functions, and more field-based research is needed to fill this vital knowledge gap.

Data Accessibility Statement
All data generated for this publication are publicly available from the University of Northern Iowa ScholarWorks repository.

Supplemental File
The supplemental file for this article can be found as follows:

· **Figure S1.** Net primary productivity of invading *Typha* and native wetland plants in the year following management treatments. DOI: https://doi.org/10.1525/elementa.147.s1

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Competing interests
The authors have no competing interests to declare.

Author contributions
KJE, JPM, DEG, and WSC conceived and designed the study; KJE, JPM, and WSC acquired the data; KJE analyzed the data; KJE and JPM drafted the manuscript; KJE, JPM, DEG, and WSC revised and approved the manuscript.

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