

ARTICLE

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Landscape and site factors drive invasive *Phragmites* management and native plant recovery across Chesapeake Bay wetlands

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Abstract

Successful invasive plant management—where invaders are sufficiently reduced and diverse native plant communities recover—remains an elusive goal for land managers. The site- and landscape-scale drivers of variable management outcomes and vegetation recovery are poorly understood due to a lack of rigorous experiments that characterize longer term vegetation trends across contexts. We present the results of a five-year experiment across eight subestuaries of Chesapeake Bay, representing a gradient of watersheds with differing dominant land-use types and anthropogenic impacts, to evaluate invasive and native plant response to herbicide management. The focal invader, *Phragmites australis* (common reed), is one of the most aggressive and pervasive invasive plants in North American wetlands. We found that with multiyear herbicide treatments, it was possible to greatly reduce *Phragmites* across an array of subestuaries while increasing the cover and quality of native plant communities. Yet, by the end of the study, plant community composition in all *Phragmites*-managed sites remained distinct from, even if composition was shifting toward, reference sites. There was also large inter-site variation in the vegetation responses related to site environmental conditions and subestuary vegetation conditions. We uncovered specific aspects of the surrounding landscape that were linked to improved vegetation recovery—the species richness and conservation value of nearby wetlands. Results from this five-year experiment conducted at multiple sites in Chesapeake Bay inform what is possible for management, particularly in more degraded landscapes and sites where setting realistic expectations and pragmatic goals will be essential. Assessing environmental and vegetation conditions of the site and surrounding landscape prior to commencing invasive species management is critical to predict the time and effort required to achieve restoration goals.

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KEYWORDS

common reed, ecosystem restoration, estuary, herbicide, invasive plant, natural recolonization, revegetation, wetland restoration

INTRODUCTION

A primary goal of ecosystem restoration following invasive plant management is to rapidly recover native plant communities (Kettenring & Adams, 2011; Matthews, Spyreas, et al., 2009). However, attaining this goal can be elusive due to factors beyond just ineffective management treatments, particularly related to context dependency (Catford et al., 2022). The application of one management treatment may be successful in one site (defined here as a large reduction in an invader and recovery of high-quality native plant communities) but may lead to undesirable outcomes in another area (defined here as when an invader rebounds, a secondary invader emerges, or natives do not readily return; Hacker & Dethier, 2009; Kettenring & Adams, 2011; Pearson et al., 2016). Processes operating across spatial scales, particularly site and landscape factors, can influence restoration outcomes and even overwhelm management treatments (Brudvig, 2011; Matthews, Peralta, et al., 2009; Palmer, 2009; Reid et al., 2009). Yet, without an understanding of how specific site and landscape factors drive context-dependent management outcomes, restoration practitioners have limited insight into how to select sites and anticipate the resources required to reach restoration success across variable landscapes (Catford et al., 2022). There is a need, then, to quantify how context dependency (here landscape and site factors) might drive restoration outcomes in support of the ultimate goal of improving predictions in restoration to guide decision-making and overall success (Brudvig, 2017; Brudvig et al., 2017; Catford et al., 2022; Holl et al., 2003).

Landscape factors operating at multiple spatial scales—geomorphic processes, nutrient cycling, and plant community dynamics—drive both the process of invasion and recovery after invader management (Galatowitsch, 2006; Holl et al., 2003; Matthews, Peralta, et al., 2009). Wetlands in particular are highly prone to invasions because of their downstream locations and as integrators of watershed-scale anthropogenic disturbances (Zedler & Kercher, 2004). Anthropogenic land-use changes and associated increases in nutrients, sedimentation, and physical disturbances directly and indirectly damage native vegetation and contribute to invasions (Holl et al., 2003; King et al., 2007; Palmer, 2009; Zedler & Kercher, 2004). Many invaders, including those found in wetlands, opportunistically respond to pulses of nutrients and light that result from

disturbances (Davis et al., 2000; Zedler & Kercher, 2004). In addition, how a plant community recovers after restoration is influenced by the characteristics of the local plant species pool and the degree of connectivity of the managed site to nearby sites dominated by native species (Galatowitsch, 2006; Suding, 2011; Zobel et al., 1998). Experimental approaches that evaluate restoration outcomes across sites with differing landscape and local scale contexts are critical to inform site selection for restoration (Long et al., 2017; Suding, 2011; Zedler & Kercher, 2004).

One of the most problematic wetland invaders in North America is the Eurasian lineage of *Phragmites australis* (Chambers et al., 1999; Saltonstall, 2002). Even though *Phragmites*-dominated wetlands in some parts of the world support a diversity of organisms (Kiviat, 2019), in North America its removal is a wetland management priority (Hazelton et al., 2014). Due to high primary production and clonal propagation in North America, *Phragmites* often forms tall, dense, impenetrable stands (Amsberry et al., 2000; Holdredge & Bertness, 2011; Price et al., 2014), transforming native-dominated wetland plant communities to invasive monocultures (Chambers et al., 1999; Price et al., 2014; Tulbure et al., 2007). This conversion of native vegetation to *Phragmites* domination leads to cascading alterations in animal communities like arthropods, birds, and fish (Balouskus & Targett, 2018; Gratton & Denno, 2005; Prosser et al., 2018; Whyte et al., 2015). Furthermore, *Phragmites*-dominated wetlands often have negative social consequences such as diminished waterfowl hunting opportunities and degraded visionscapes (Chambers et al., 1999; Holdredge & Bertness, 2011; Rohal et al., 2018).

The undesirable ecological, cultural, and social impacts of non-native *Phragmites* have motivated intense evaluation of potential management techniques (Hazelton et al., 2014; Martin & Blossey, 2013; Rohal et al., 2018). Unfortunately, incomplete eradication and reinvasion are common outcomes of *Phragmites* management efforts (Elsley-Quirk & Leck, 2021; Hazelton et al., 2014; Quirion et al., 2018). Furthermore, the ultimate restoration goal—recovery of diverse native plant communities following invader management—has been elusive with inconsistent recovery rates (Ailstock et al., 2001; Breen et al., 2014; Carlson et al., 2009; Farnsworth & Meyerson, 1999; Rohal, Cranney, Hazelton, et al., 2019; Rohal, Cranney, & Kettenring, 2019; Whyte et al., 2009; Zimmerman et al., 2018).

Mixed success in *Phragmites* management is likely due to factors that operate at a variety of scales, but the specific factors that account for this variability have only been evaluated in limited cases (e.g., Rohal, Cranney, Hazelton, et al., 2019; Rohal, Cranney, & Kettenring, 2019). At the landscape scale, the conversion of native plant-dominated natural habitats to agriculture and urbanization land uses results in *Phragmites* invasion and proliferation in estuarine wetlands (Bertness et al., 2002; King et al., 2007; Maheu-Giroux & de Blois, 2007; Sciance et al., 2016). Once *Phragmites* has established, eradication or long-term management is difficult, especially in estuarine landscapes where hydrologically connected wetlands/embayments facilitate *Phragmites* reinvasion from wind- and water-dispersed seeds (Hazelton et al., 2014; Quirion et al., 2018; Rohal, Cranney, & Kettenring, 2019). Management of *Phragmites* followed by restoration of native vegetation is most likely to be successful in landscapes where *Phragmites* patches are embedded in a landscape matrix with largely intact native plant-dominated wetlands (Rohal, Cranney, & Kettenring, 2019).

Site-specific conditions like the availability of native seed banks and environmental factors (e.g., salinity, moisture) are also potential drivers of restoration outcomes. Interestingly, many tidal wetlands in Chesapeake Bay—even those dominated by *Phragmites*—have a diverse, abundant native seed bank (Baldwin et al., 2010; Hazelton et al., 2018). However, it is unclear whether the presence of these seed banks is sufficient to facilitate rapid native plant recovery post-*Phragmites* management or whether other factors are also important drivers. Determining the relative importance of site and landscape factors to *Phragmites* management can improve predictions of restoration outcomes and facilitate prioritization of restoration sites (Long et al., 2017).

The goal of this research was to assess the context dependencies of *Phragmites* management and native plant recovery to improve restoration efforts in estuarine wetlands. We evaluated management outcomes across an array of subestuaries that covered a spectrum of anthropogenic degradation, building on prior research that found nutrient enrichment and *Phragmites* abundance were higher where watersheds were dominated by agriculture or development (King et al., 2007). We addressed three questions: (1) To what extent can *Phragmites* performance (cover, stem density, and inflorescence density) be reduced with herbicide treatments? (2) Do native plant communities recover following *Phragmites* management to resemble the cover, quality, and composition of native reference sites? (3) What site environmental and subestuary vegetation conditions explain *Phragmites* reduction and native plant recovery? We conducted a multiyear experiment in eight subestuaries of the Chesapeake Bay chosen

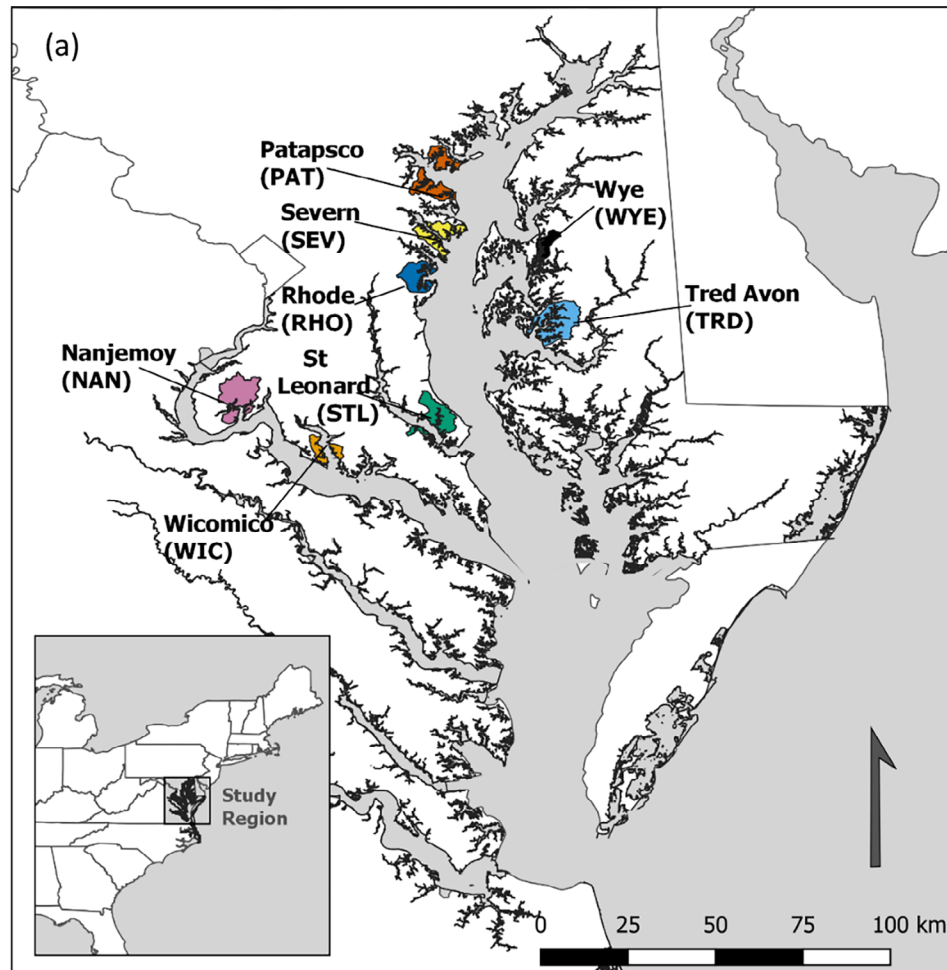
to represent a range of site environmental conditions (nutrients, salinity, and tidal height), subestuary vegetation conditions (i.e., extent of *Phragmites* and native vegetation in the subestuary), and watershed land-use compositions (forested, agricultural, and developed). In a *Phragmites*-dominated site in each subestuary, we applied herbicide for 3 years and quantified changes in *Phragmites* and native plant communities for an additional 2 years. Vegetation changes were compared with an adjacent *Phragmites*-dominated site left untreated and a nearby, native-dominated reference site. The overarching assumption was that there would be differences in *Phragmites* and native plant responses related to site environmental conditions as well as the broader vegetation conditions in the subestuaries in which sites were located.

METHODS

Subestuaries and site-level treatments

The Chesapeake Bay's complex shoreline encloses over 100 tributary embayments ("subestuaries"), each of which has its own local watershed (Li et al., 2007). We selected eight subestuaries (Figure 1) where there were patches of *Phragmites* that were large enough (0.5 to >1 ha) to warrant management and watershed land-use compositions that were within the framework of the study: forests, agriculture, and (sub)urban development (King et al., 2007; Sciance et al., 2016; Table 1). Accordingly, we expected that these subestuaries would experience differing levels of anthropogenic degradation (e.g., nutrient inputs and disturbances to vegetation) that would impact *Phragmites* management and native plant community restoration (Kettenring et al., 2011, 2015; King et al., 2007; McCormick et al., 2020).

Within each subestuary, we selected tidal wetland sites dominated by *Phragmites* and nearby sites with native wetland vegetation (see Figure 1 for a depiction of site layout). As much as possible, we selected sites that were in close proximity to each other within the same part of the subestuary. All selected sites had shoreline distances between 50 and 200 m. The two sites dominated by *Phragmites* were randomly assigned to be treated with herbicide (described below; hereafter "*Phragmites*-managed site") or left as an untreated *Phragmites* experimental control (hereafter "*untreated Phragmites* site"). The *Phragmites* sites had to be near-monocultures of *Phragmites* in a single patch large enough to fit the three monitoring transects (see below). We chose herbicides for management because they are the most frequently used method to control *Phragmites* and two products (glyphosate, the focus of the present



(b) Example site layout in a subestuary

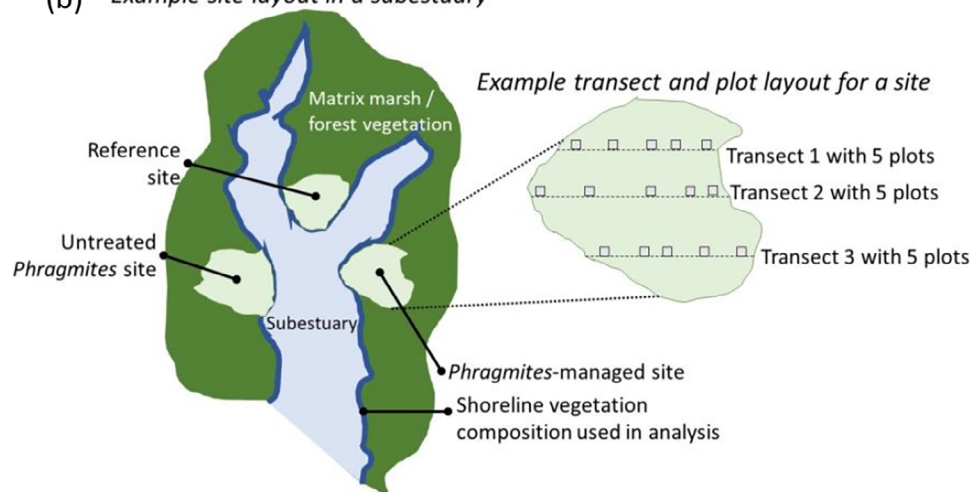


FIGURE 1 Map of Chesapeake Bay (a) depicting locations of the subestuaries in the eastern United States. In subsequent figures and tables, codes for subestuaries are: NAN, Nanjemoy; PAT, Patapsco; RHO, Rhode; SEV, Severn; STL, St Leonard; TRD, Tred Avon; WIC, Wicomico; WYE, Wye. Conceptual figure (b) depicting an example of the site layout within a subestuary and the transect and plot layout within each site.

study, and imazapyr) are widely employed (Bonello & Judd, 2020; Cheshier et al., 2012; Hazelton et al., 2014; Rapp et al., 2012; Rohal et al., 2018; Whyte et al., 2009;

Zimmerman et al., 2018). A single area without *Phragmites* served as a native reference site, which represented the target wetland plant community for

TABLE 1 (a) Site environmental conditions in 2011 prior to treatment initiation in *Phragmites*-managed sites in each subestuary. (b) Shoreline vegetation conditions and watershed land-use composition are also presented and were derived from <https://www.vims.edu/ccrm/research/inventory/maryland/index.php> and Sciance et al. (2016).

(a) Site environmental conditions					(b) Shoreline vegetation conditions and watershed land-use composition (%)				
Site	Phosphate ($\mu\text{g PO}_4^-$ g dry resin ⁻¹)	Ammonium (ppm ^a)	Salinity (ppt)	Tidal maximum (cm)	Shoreline		Watershed		
					<i>Phragmites</i>	Native marsh	Agricultural land	Developed land	Forested land
NAN	0.24 ± 0.12	69.34 ± 9.73	3.9 ± 0.9	19.0 ± 4.2	0.5	35.4	11.8	5.7	57.0
PAT	2.51 ± 0.51	56.76 ± 23.76	4.5 ± 0.4	12.7 ± 3.9	13.9	7.7	0.5	75.4	12.5
RHO	1.01 ± 0.32	40.17 ± 8.97	6.2 ± 0.4	5.7 ± 1.5	15.3	16.4	17.2	13.0	43.7
SEV	0.62 ± 0.32	152.35 ± 18.16	3.7 ± 0.4	10.9 ± 1.7	10.4	13.5	3.8	37.9	31.3
STL	1.04 ± 0.47	89.12 ± 21.72	7.0 ± 0.7	19.9 ± 1.7	0.4	51.1	9.3	13.0	60.2
TRD	1.39 ± 0.35	49.91 ± 9.83	9.7 ± 0.2	10.4 ± 2.2	14.8	40.1	33.4	21.5	10.2
WIC	1.90 ± 0.51	42.82 ± 14.15	8.1 ± 0.4	18.2 ± 2.7	2.2	30.3	23.0	12.3	42.1
WYE	0.67 ± 0.15	59.41 ± 10.33	9.1 ± 0.3	6.2 ± 2.3	16.6	27.6	58.3	7.5	11.0

Abbreviations: NAN, Nanjemoy; PAT, Patapsco; RHO, Rhode; SEV, Severn; STL, St Leonard; TRD, Tred Avon; WIC, Wicomico; WYE, Wye.

^aUnits are ppm per resin mass eluted.

recovery following herbicide treatment (hereafter “reference site”).

In autumn 2011, a helicopter was used to spray the *Phragmites* removal areas with a 3% glyphosate solution (Aqua Neat). In October 2012 and 2013, herbicide spraying was repeated by using backpack sprayers at a rate of approximately 20–24 L per 0.4 ha. A surfactant (Cide-Kick) and a marking dye (Hi-Light) were used with the herbicide. The herbicide was applied in the autumn to minimize impacts on nontarget native species that go dormant before *Phragmites* (Mozdzer et al., 2008).

Monitoring of *Phragmites* and native plant responses

To establish transects for monitoring, we measured the shoreline length of each site and divided each into three segments of equal length. Within each segment, we randomly selected the location of a starting point along the shoreline for the establishment of a transect that was perpendicular to the shoreline. We measured the distance between the shoreline starting point for each transect and the upland boundary, or in instances where the *Phragmites* patch ended before the upland boundary was reached, to the end of the *Phragmites* patch. The length of each transect was divided into five segments and along each segment the location of a 1 × 1 m plot was randomly determined for monitoring vegetation (5 plots per transect; 15 per site; see Figure 1 for example plot layout).

In each 1 × 1 m plot, the percent cover of all species including *Phragmites* was estimated using a Braun-Blanquet scale (cover classes: <5, 5–25%, 25–50%, 50–75%, and 75–100%; Furman et al., 2018) in September/October 2011–2015. The first sampling was completed before aerial application of the herbicide. Sampling in the autumn of 2012 and 2013 represented 2 years in which herbicide was applied using backpack sprayers. Sampling in 2014 and 2015 represented 2 years of recovery following cessation of herbicide application. We used absolute cover in all subsequent analyses; cover could be >100% due to the multiple layers of vegetation that often occurred in these wetlands. We also quantified the number of *Phragmites* shoots (stem density) and the number of shoots with inflorescences (inflorescence density) in a 50 × 50 cm subplot within each 1 × 1 m plot. We compared plot-level species composition using a Floristic Quality Assessment (FQA) approach (Lopez & Fennessey, 2002; Matthews et al., 2015; Miller & Wardrop, 2006). FQA is a method for calculating a numerical index that reflects the species composition of a plant community and indicates the relative balance between species that are tolerant to disturbance, like invasive species, and species that are only found in undisturbed locations. For each plot, we calculated the mean coefficient of conservatism (mean C) for all species present (Matthews et al., 2005). Coefficient of conservatism values (i.e., CC value) for each species were drawn from a regional database for the Mid-Atlantic region (Chamberlain & Ingram, 2012). CC values range from 0 to 10; disturbance-tolerant, often invasive, species typically found in highly degraded habitats have a low CC value

(e.g., *Phragmites* is 0), whereas disturbance-intolerant, obligate native species have a high CC value (e.g., *Spartina alterniflora* is 7).

Site environmental conditions

We measured three interstitial soil water variables—phosphate, ammonium, and salinity—at each site from 2011 to 2014 at the same time vegetation data were being collected (nutrient data were not collected in 2015 due to budget limitations). The nutrients were measured as indicators of the extent of anthropogenic impacts to different subestuaries with varying watershed land-use compositions. Soil water NH_4^+ and PO_4^{4-} were measured using mixed anion and cation exchange resins (Binkley & Matson, 1983; Hazelton et al., 2010; Theodore & Roths, 1999). Resin bags were placed in the top 10 cm of the wetland soil in June and were retrieved in August each year. In the laboratory the resins were dried at 60°C, sieved to remove any nonresin materials, and stored until analysis. The samples were eluted with 1 M KCl prior to analysis. Phosphate concentrations were determined calorimetrically (APHA, 2005). Ammonium concentrations were measured on an API Autoanalyzer. Salinity (in parts per thousand [ppt]) of interstitial water (i.e., porewater) was extracted from within the top 10 cm of soil with a soil sipper and read with a handheld refractometer. Resin bag placement and porewater sampling were done immediately adjacent to the 1 × 1 m vegetation plots. Porewater samples were collected at the same time vegetation cover was measured and resin bags were collected when the sites were not tidally flooded.

In fall 2015, we measured the maximum tidal height, as a proxy for marsh inundation, at each vegetation plot. We used wooden dowels coated in a combination of a water-soluble dye and water-soluble glue. Dowels were left in place for a complete tide cycle, and inundation was determined as the distance from the wetland surface to the line where the tides removed the dye solution.

Watershed land-use composition and subestuary shoreline vegetation conditions

In addition to incorporating vegetation conditions in the untreated *Phragmites* and reference sites into our analyses (described below), we also included data on the percent of shoreline in each subestuary that was occupied by *Phragmites* or by native vegetation. We used these data as another indicator of the varying extent of anthropogenic

impacts and accompanying degradation to the eight subestuaries that we expected might drive *Phragmites* management and native plant community restoration. Shoreline data were obtained from the Virginia Institute of Marine Sciences Maryland Shoreline Inventory (<https://www.vims.edu/ccrm/research/inventory/maryland/index.php>). In addition, watershed land-use composition (agriculture, developed, and forested) was derived from Sciance et al. (2016). Agricultural land included pasture and cultivated crops in the watershed. Developed land included low-intensity to high-density developed areas and developed open space. Forested land included deciduous, evergreen, and mixed forest types in the watershed.

Data analysis

Broad patterns in *Phragmites* and native plant responses to management

To address questions 1 and 2, we first evaluated plant community and *Phragmites*-specific responses in *Phragmites*-managed sites relative to untreated *Phragmites* and reference sites over time (2011–2015). We summarized findings across the eight subestuaries using effect sizes for three *Phragmites* response metrics (*Phragmites* cover, stem density, and inflorescence density) and two plant community response metrics (native cover and mean *C* scores). Specifically, we calculated the Hedges' *g* effect size ($(\bar{y}_1 - \bar{y}_2)/\text{pooled standard deviation}$) of a *Phragmites* or plant community response metric in a *Phragmites*-managed site relative to an untreated *Phragmites* or reference site. Effect sizes and bootstrap confidence intervals (CIs) were calculated using the R package BootES using vegetation metrics averaged across all plots and transects within a site for each year. When the community metrics in *Phragmites*-managed sites were relativized to untreated *Phragmites* sites in the effect size calculations, we were able to track shifts in the native plant communities in *Phragmites*-managed sites potentially diverging from untreated *Phragmites*. When they were relativized to the reference site, we were able to track potential shifts in the plant communities toward the reference site vegetation.

Phragmites and native plant responses to management by subestuary

To further address questions 1 and 2, we were interested in *Phragmites* and native plant responses in individual subestuaries based on our assumption that the different

site environmental and subestuary vegetation conditions in which sites were located might result in variable responses. We graphically compared changes in *Phragmites* cover, native cover, and mean *C* scores between 2011 and 2015 for *Phragmites*-managed sites in each subestuary. For the native cover and mean *C* score graphs, we also present the 2015 values for those response metrics for the reference sites to visually evaluate if *Phragmites*-managed site plant communities in each subestuary were moving toward reference site plant communities.

To bolster these graphical evaluations, we used ANOVA to look at the effects of subestuary and time on the three vegetation response variables. We used contrasts for three comparisons: differences (1) between subestuaries in 2011, (2) between subestuaries in 2015, and (3) between 2011 and 2015 for each individual subestuary.

Relativized *Phragmites* and native plant responses to management in each subestuary

To delve further into plant response to management for individual subestuaries (questions 1 and 2), we used effect sizes to relativize *Phragmites* and plant community response in *Phragmites*-managed sites to untreated *Phragmites*-managed and reference sites. Effect sizes were calculated as above for the three main response variables (*Phragmites* cover, native cover, and mean *C*) for 2011 and 2015. We were particularly interested in large shifts in the effect sizes between the start and end of the study, and when the effect size CIs transitioned from overlapping with zero to not (or vice versa), indicating statistical significance (Nakagawa & Cuthill, 2007). Effect sizes for *Phragmites*-managed versus untreated *Phragmites* sites that overlapped with zero indicated that the vegetation in the managed site did not differ significantly from the untreated sites. This comparison was important because if there was no difference between 2011 and 2015 the conclusion would be that multiyear *Phragmites* management was not effective. Effect sizes for the *Phragmites*-managed versus reference sites that overlap with zero indicate that the managed site has native vegetation that is similar to the reference site (and is a potential benchmark of restoration success).

Linking 2011 vegetation metrics in managed and reference sites with 2015 management outcomes

To address question 3, we used separate stepwise linear regressions (using JMP Pro 15, Version 15, 1989–2021,

SAS Institute Inc., Cary, NC) to assess the relationships between response variables in the last year of the field study (2015) and the pretreatment year (2011) in either *Phragmites*-managed or the nearby native reference sites. The vegetation metrics used in the regressions were *Phragmites* cover, native plant cover, mean *C* score, species richness, and non-native plant cover (excluding *Phragmites*). We did not include interactions in the stepwise regression due to limited degrees of freedom. For variable selection, we used *k*-fold cross validation using forward selection, as this method is appropriate for small sample sizes since it makes efficient use of limited amounts of data (Martens & Dardenne, 1998). We transformed independent and dependent variables as needed to meet model assumptions of normality and homoscedasticity (Appendix S1: Table S1). We assessed each selected model for multicollinearity by evaluating the variance inflation factor (VIF) and removed the less important (as determined by a smaller R^2 in simple linear regressions) variable if the VIF was over two.

Plant community shifts in *Phragmites*-managed, untreated *Phragmites*, and reference sites

In addressing question 3, we were interested in evaluating multivariate plant community shifts in response to *Phragmites* management. We used nonmetric multidimensional scaling (NMDS) ordination to visualize how plant communities changed from 2011 to 2015 in all subestuaries across the three site types (*Phragmites*-managed, untreated *Phragmites*, and reference) using the R package *vegan* (Oksanen et al., 2015; R Development Core Team, 2013). To choose the model, we evaluated a scree plot, selecting the model with the fewest dimensions that resulted in a stress value under 0.20 (McCune et al., 2002). We graphed the centroids of each plant community to visually evaluate how each site type and subestuary overlapped and shifted between 2011 and 2015. Centroids that cluster together in the graph space indicate similar plant community compositions, thus we were particularly interested in whether *Phragmites*-managed sites shifted toward reference sites (and away from untreated *Phragmites* sites) by 2015 and whether those patterns varied by subestuary. We paired this NMDS approach with permutational multivariate analysis of variance (PERMANOVA; Anderson, 2001), which was conducted using the *adonis* function (Bray–Curtis distances, 999 permutations) to evaluate differences between plant communities in 2011 and 2015 from the different site types (Oksanen et al., 2015). Factors in this PERMANOVA included subestuary, site type, year (2011, 2015), and the interaction between site type and year.

Factors correlating with plant communities in *Phragmites*-managed sites in 2015

To further address question 3, we used NMDS analysis to visualize differences in the 2015 plant communities in *Phragmites*-managed sites in the eight subestuaries. We overlaid vectors for site environmental conditions (phosphate, ammonium, maximum tidal height, and salinity) and subestuary vegetation conditions (percent of watershed land use as forested, agriculture, and developed land; percent native marsh and *Phragmites* along the shoreline), retaining significant variables as potential drivers of recovery. We also calculated Pearson's correlations between the NMDS axis scores and these factors to assess the strength of the correlative relationship between the plant community with the site environmental and subestuary vegetation conditions.

RESULTS

Broad patterns in *Phragmites* and native plant responses to management (questions 1 and 2)

We found that *Phragmites* cover in *Phragmites*-managed sites decreased substantially relative to untreated *Phragmites* sites and remained below the pretreatment levels for the duration of the study (Figure 2a). The cover of native species in *Phragmites*-managed sites was not appreciably different from untreated *Phragmites* sites in 2012 after the initial 2011 herbicide application (Figure 2b). However, native cover increased in subsequent years such that by 2015 it was significantly higher than untreated *Phragmites* sites. The cover of native species in *Phragmites*-managed sites was, however, still significantly lower than native cover in reference sites (i.e., effect size values did not overlap with the zero line; Figure 2c) even after the 3 years of herbicide application (2011–2013) and 2 years of recovery (2014, 2015). The floristic quality of native vegetation in *Phragmites*-managed sites, as represented by the mean *C* score, increased gradually over time (Figure 2d,e). Compared with untreated *Phragmites* sites, the mean *C* in *Phragmites*-managed sites was significantly higher by 2014 and 2015 (Figure 2d). The mean *C* in *Phragmites*-managed sites approached those of reference sites such that by 2015 the effect size values nearly overlapped with the zero line (Figure 2e). *Phragmites* stem density decreased significantly by 2013 and remained reduced relative to untreated sites for the remainder of the study (Appendix S1: Figure S1). *Phragmites* inflorescence density was reduced relative to untreated sites starting 1 year after the initial treatment (2012–2014; Appendix S1: Figure S1).

Phragmites and native plant responses to management by subestuary (questions 1 and 2)

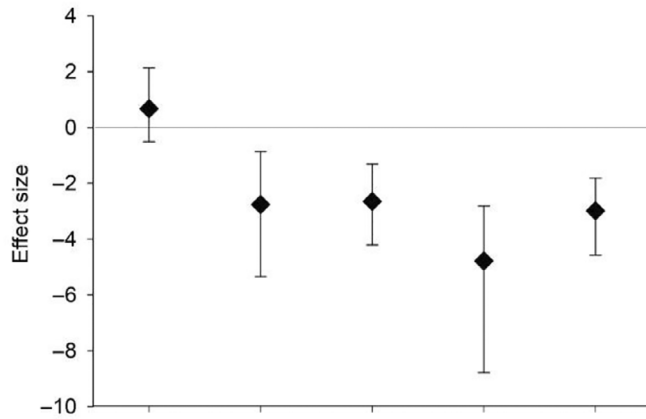
We found a significant subestuary \times monitoring year interaction for *Phragmites*' response to management ($F_{28,557} = 4.2$; $p < 0.01$). Between 2011 and 2012, there was a sharp decline in *Phragmites* cover in *Phragmites*-managed sites in all subestuaries except the Tred Avon (TRD) (Figure 3a). However, by 2015, *Phragmites* cover increased from the lowest *Phragmites* cover values achieved in 2012–2014 in each *Phragmites*-managed site.

We found a significant subestuary \times monitoring year interaction for native cover response to *Phragmites* management ($F_{28,557} = 3.9$; $p < 0.01$). Native cover changes in *Phragmites*-managed sites varied across subestuaries 2011–2015 (Figure 3b; Appendix S1: Tables S2–S4). Native cover was low in *Phragmites*-managed sites at the start of the study in the Wicomico (WIC), Patapsco (PAT), St Leonard (STL), Nanjemoy (NAN), and Severn (SEV) subestuaries, whereas the TRD, Wye (WYE), and Rhode (RHO) had somewhat higher native cover at the start of the experiment. Native cover was higher (sometimes substantially) in all *Phragmites*-managed sites by 2015. Nonetheless, native cover in *Phragmites*-managed sites was still lower than reference sites in 2015 (gray box at right in Figure 3b), particularly for the NAN.

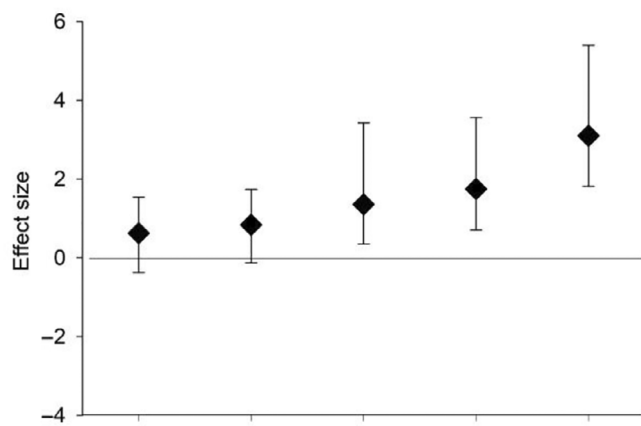
We found a significant subestuary \times monitoring year interaction for mean *C* response to *Phragmites* management ($F_{28,557} = 2.7$; $p < 0.01$). For *Phragmites*-managed sites that had relatively high mean *C* scores at the start of the experiment (i.e., TRD, WYE, RHO, WIC), the mean *C* changed little over time (Figure 3c; Appendix S1: Tables S2–S4). In contrast, there was a large increase in the mean *C* from 2011 or 2012 to 2015 for *Phragmites*-managed sites in the NAN, PAT, SEV, and STL. Mean *C* scores in some *Phragmites*-managed sites in some subestuaries were quite similar by 2015 to reference sites (shown in gray box, e.g., PAT), whereas others still differed greatly from reference sites (e.g., STL, SEV).

Relativized *Phragmites* and native plant responses to management in each subestuary (questions 1 and 2)

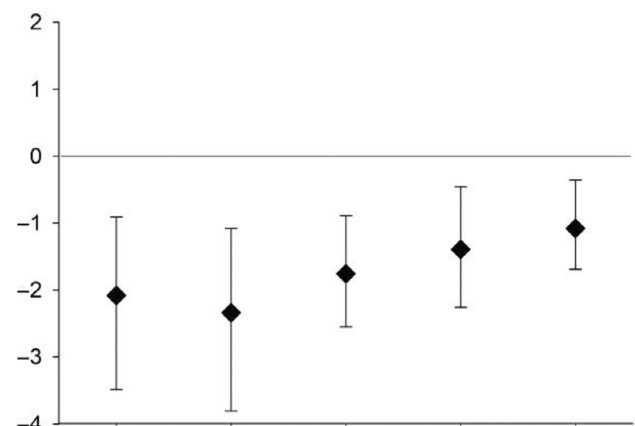
Phragmites-managed sites in the PAT, STL, and WIC had slightly higher *Phragmites* cover relative to untreated *Phragmites* sites at the start of the experiment (2011; Figure 4a). *Phragmites* cover was reduced between 2011 and 2015 in *Phragmites*-managed sites relative to untreated *Phragmites* sites in each subestuary (Figure 4a). However, the degree of change varied substantially

(a) *Phragmites* cover in managed versus untreated sites

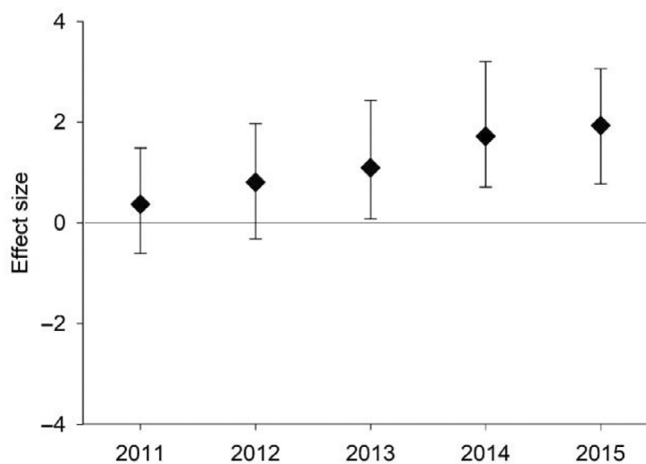
(b) Native cover in managed versus untreated sites



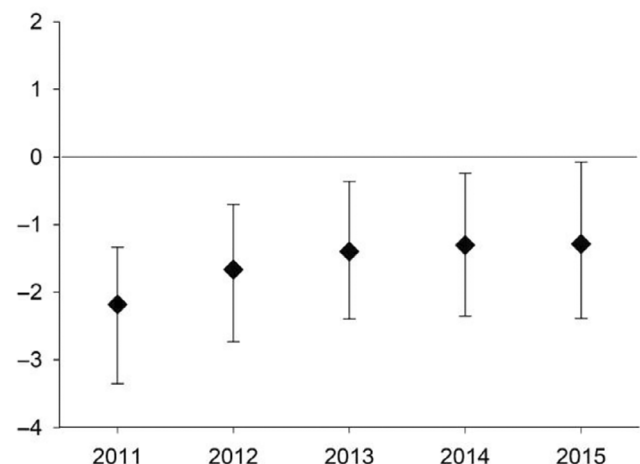
(c) Native cover in managed versus reference sites



(d) Mean C scores in managed versus untreated sites



(e) Mean C scores in managed versus reference sites



Year

FIGURE 2 Changes in (a) *Phragmites* cover, (b, c) native plant cover, and (d, e) mean C scores in *Phragmites*-managed sites relative to untreated *Phragmites* sites and reference sites. Symbols represent Hedges' g effect sizes and error bars are bootstrap confidence intervals (CIs). CIs that overlap with zero indicate no significant differences between contrasts.

among subestuaries, with large reductions in *Phragmites* in the NAN and WIC and small changes in the RHO and TRD subestuaries.

Native cover increased between 2011 and 2015 in *Phragmites*-managed sites relative to untreated *Phragmites* sites in all subestuaries except the TRD (Figure 4b).

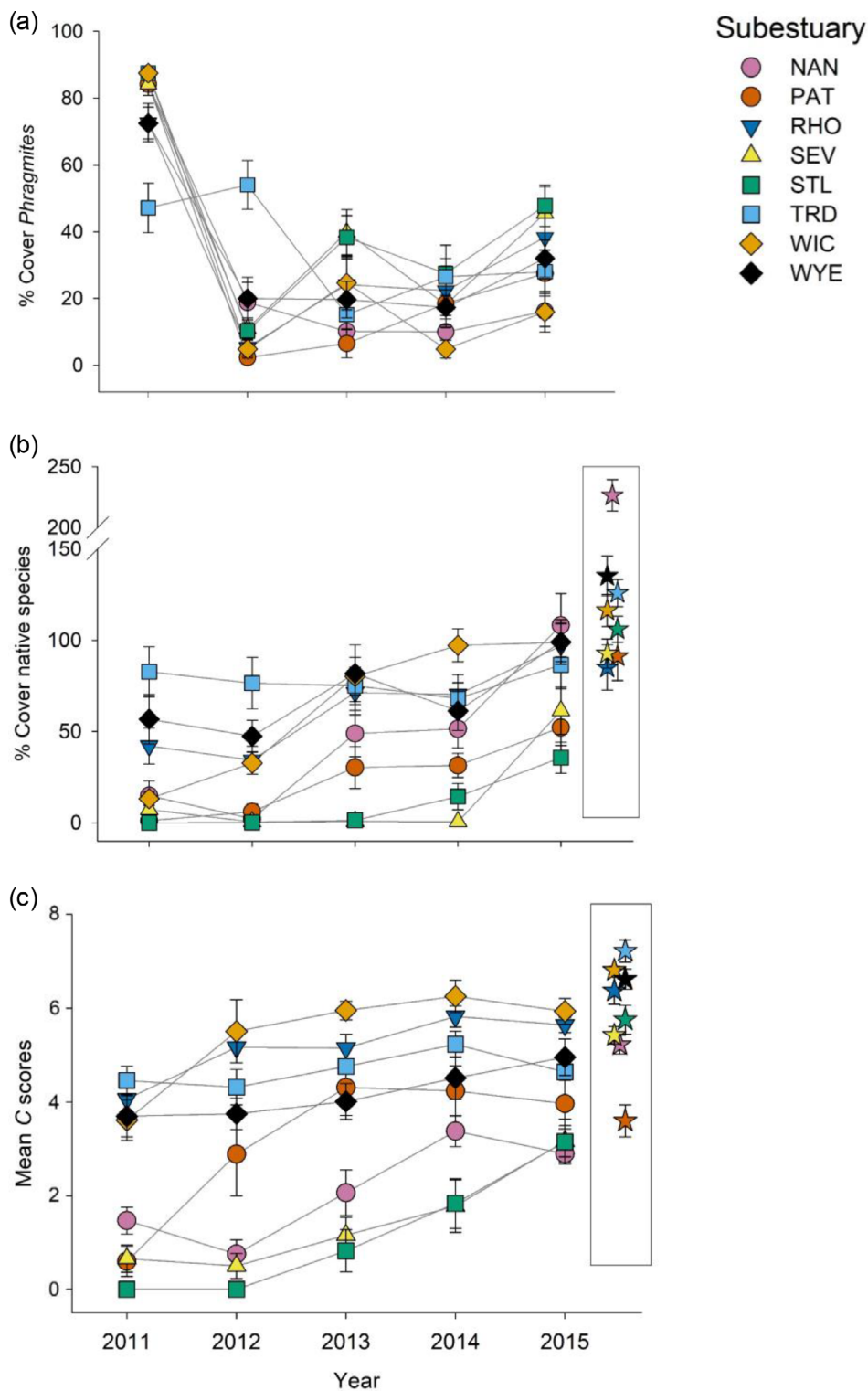
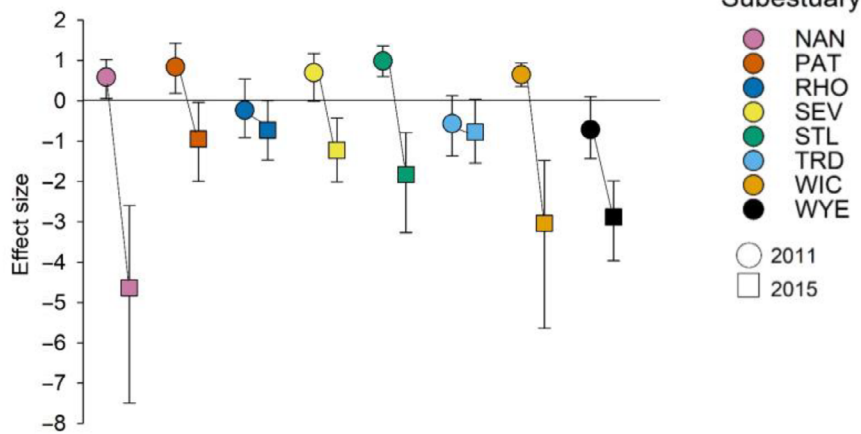


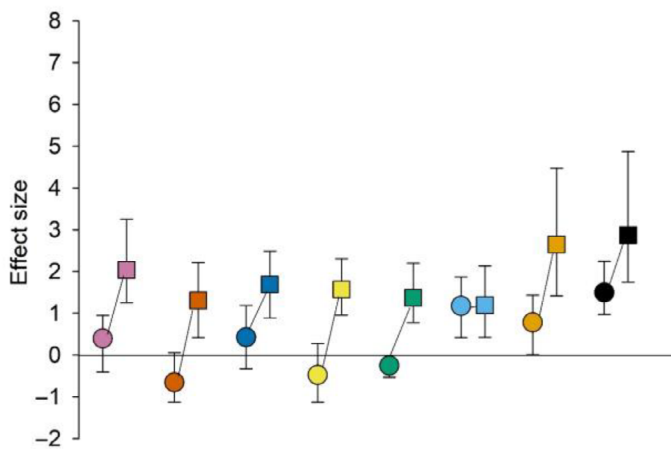
FIGURE 3 Change in (a) *Phragmites* cover, (b) native plant cover, and (c) mean *C* scores in *Phragmites*-managed sites over 5 years in the eight subestuaries (see legend to Figure 1 for an explanation of subestuary abbreviations). Herbicide treatments were conducted in 2011–2013. Stars in the gray box at right represent (b) native cover and (c) mean *C* scores in reference sites in 2015.

The increase between 2011 and 2015 in native cover varied among subestuaries, with more moderate increases in the RHO and WYE and larger increases in the NAN, PAT, and SEV. Even though some *Phragmites*-managed sites in some

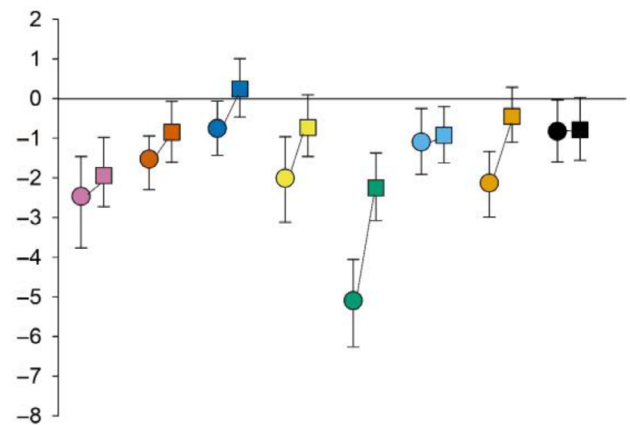
subestuaries did not experience large changes in native cover (e.g., WYE), all *Phragmites*-managed sites in all subestuaries had high native cover by 2015 relative to untreated *Phragmites* sites. While native cover increased in

(a) *Phragmites* cover in managed versus untreated sites

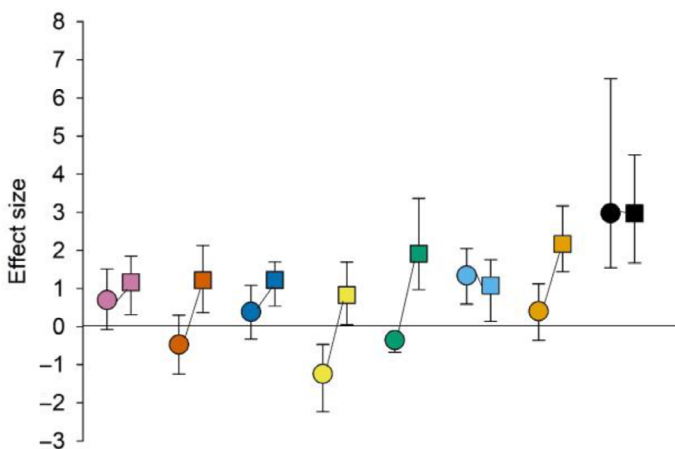
(b) Native cover in managed versus untreated sites



(c) Native cover in managed versus reference sites



(d) Mean C scores in managed versus untreated sites



(e) Mean C scores in managed versus reference sites

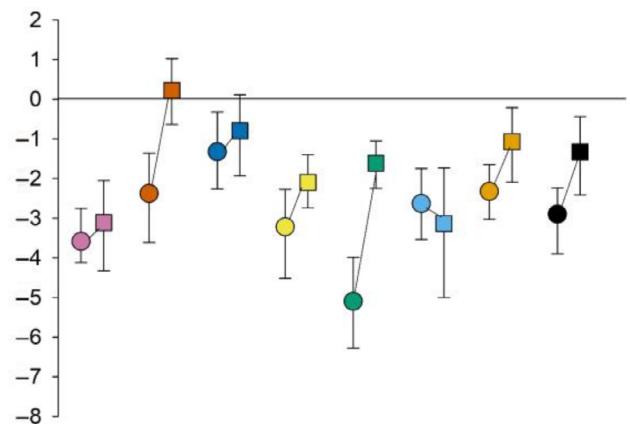


FIGURE 4 Differences between 2011 and 2015 in (a) *Phragmites* cover, (b, c) native plant cover, and (d, e) mean *C* scores in the *Phragmites*-managed sites in eight subestuaries (see legend to Figure 1 for an explanation of subestuary abbreviations). Values are standardized using Hedges' *g* effect sizes by comparing managed versus untreated sites in (a), (b), and (d) and managed versus native reference sites in (c) and (e). Error bars are bootstrapped confidence intervals.

Phragmites-managed sites across subestuaries, the changes were small relative to native cover in the reference sites and only STL changed dramatically (Figure 4c). None of

the shifts in native cover between 2011 and 2015 were greater than zero (which would indicate a higher native cover in *Phragmites*-managed vs. reference sites) but by

2015 *Phragmites*-managed sites in the RHO, SEV, WIC, and WYE subestuaries had native cover similar to that of reference sites (Figure 4c).

Mean *C* scores increased to varying degrees between 2011 and 2015 in *Phragmites*-managed sites relative to untreated *Phragmites* sites in all subestuaries except the TRD and WYE (Figure 4d). The *Phragmites*-managed site in the WIC was the only instance where there was a significant increase in mean *C* scores between 2011 and 2015 such that by 2015 the mean *C* in *Phragmites*-managed sites was substantially higher than that of untreated *Phragmites* sites. The increase in mean *C* scores in *Phragmites*-managed versus reference sites between 2011 and 2015 varied from large (PAT, STL), to small (NAN, RHO), to no change (TRD). By 2015, the mean *C* scores in *Phragmites*-managed sites were similar to reference sites only in the PAT and RHO subestuaries.

Linking 2011 vegetation metrics in managed and reference sites with 2015 management outcomes (question 3)

According to the stepwise regression results, there was a relationship between the 2015 plant community (*Phragmites* and native plant cover) in *Phragmites*-managed sites and the plant community of *Phragmites*-managed sites

prior to treatment (2011) as well as the composition of nearby reference sites (Table 2). The strongest relationship was a negative association between the 2015 *Phragmites* cover in *Phragmites*-managed sites and the 2011 mean *C* in those same sites as well as with species richness in reference sites.

Compared with 2015 *Phragmites* cover, there was a stronger relationship (as indicated by the *p* values and R^2 values; Table 2) between 2015 native plant cover in *Phragmites*-managed sites and 2011 plant metrics. Specifically, there was a large, positive relationship between 2011 pretreatment mean *C* scores in *Phragmites*-managed sites and 2015 native plant cover. Likewise, there was a strong, positive relationship between mean *C* and species richness in reference sites in 2011 and the 2015 native plant cover in *Phragmites*-managed sites.

Plant community shifts in *Phragmites*-managed, untreated *Phragmites*, and reference sites (question 3)

The first NMDS analysis depicted how each site type within each subestuary overlapped and shifted between 2011 and 2015 (Figure 5). The companion PERMANOVA results revealed that plant communities differed significantly by subestuary ($F_{7,47} = 4.38$; $p < 0.01$) and there was a

TABLE 2 Results of stepwise multiple regression analyses examining the relationship between dependent variables (2015 *Phragmites* cover and native plant cover in *Phragmites*-managed sites) and independent variables (2011 pretreatment plant community metrics: *Phragmites* cover, native plant cover, mean *C* score, species richness, and non-native [excluding *Phragmites*] plant cover) in *Phragmites*-managed and reference sites.

2011 pretreatment metrics	2015 <i>Phragmites</i> cover				2015 native plant cover			
	Coeff	<i>F</i>	<i>p</i>	R^2 adj.	Coeff	<i>F</i>	<i>p</i>	R^2 adj.
2011 <i>Phragmites</i> -managed sites								
<i>Phragmites</i> cover	-7.45e ⁻⁹				X			
Native plant cover	X				X			
Mean <i>C</i> scores	-4.59				1990.29			
Species richness	N/A				X			
Non-native plant cover	X				X			
Model summary statistics		2.29	0.19	0.27		9.75	0.02	0.56
2011 native reference sites								
Native plant cover	X				X			
Mean <i>C</i> scores	X				5908.77			
Species richness	-17.76				4930.99			
Non-native plant cover	X				X			
Model summary statistics		2.88	0.14	0.31		13.56	0.01	0.78

Note: When a variable was retained, we reported the coefficient (coeff), or if it was excluded we denoted it with an X. Species richness was excluded from the 2011 *Phragmites*-managed site model because it was collinear with the mean *C* variable (and denoted with an N/A = not applicable).

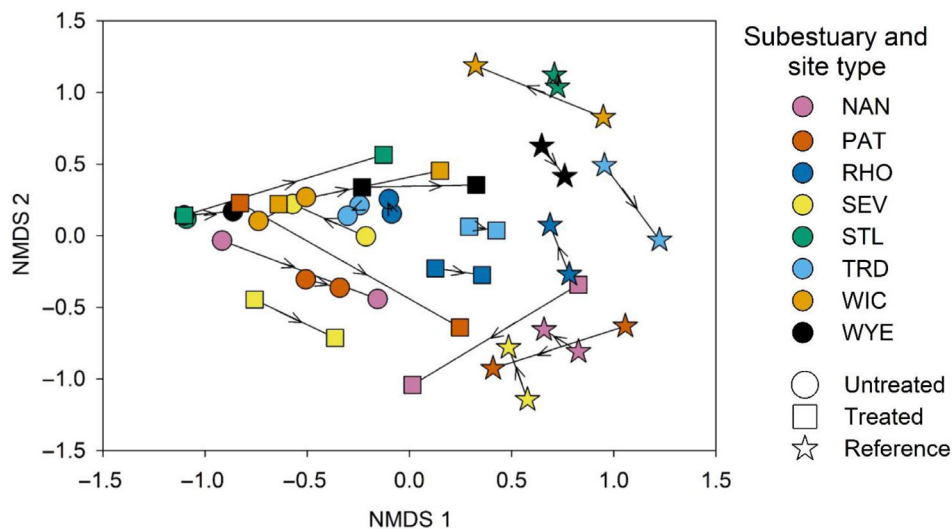


FIGURE 5 Plant community composition in untreated *Phragmites*, *Phragmites*-managed, and reference sites between 2011 and 2015 in the eight subestuaries (depicted by the eight distinct colors; see legend to Figure 1 for an explanation of subestuary abbreviations). Symbols represent the centroid for each plant community (site type \times subestuary for each year) with lines connecting the 2011 and 2015 timestamps and an arrow pointing toward the 2015 centroids. Stress = 0.18. NMDS, nonmetric multidimensional scaling.

significant site type \times year interaction ($F_{2,47} = 2.83$; $p = 0.01$). Post hoc evaluation of this interaction showed that, while plant communities in *Phragmites*-managed sites shifted toward reference sites between 2011 and 2015 (and became significantly different from untreated *Phragmites* sites), these assembling communities remained significantly different from the reference plant communities (Appendix S1: Table S5).

Factors correlating with plant communities in *Phragmites*-managed sites in 2015 (question 3)

NMDS analyses were also used to determine whether site differences were related to site environmental and subestuary vegetation conditions, and watershed land use (Figure 6; Table 3). The separation of sites on the first axis of the ordination was strongly related to the amount of shoreline *Phragmites* in the subestuary, the soil water ammonium concentrations in the upper 10 cm of the soil, porewater salinity, and mean tidal height. Watershed land-use composition variables were not significant vectors in the NMDS analysis; however, sites were organized moderately by land-use category (Pearson's correlations showed moderate significance at $\alpha \leq 0.10$), with the first axis representing a gradient from forest-dominated watersheds on the left to agriculture-dominated watersheds on the right. The agriculture-dominated watershed WYE on the Eastern Shore of Chesapeake Bay was the

rightmost subestuary on the first ordination axis and it had the highest percentage of shoreline *Phragmites* (16.6%; Figure 6; Table 1). In contrast, the forest-dominated watersheds NAN and STL had 0.5% and 0.4% shoreline *Phragmites*, respectively, and were located to the left in the ordination. The ammonium concentrations in the upper 10 cm of the soil were highest at 152.4 ppm in the SEV, which was to the left in the ordination. The three subestuaries (NAN, PAT, and SEV) with the lowest mean salinities (<6.0 ppt) were clustered to the left and center of the ordination. The three subestuaries with the highest tidal maximum heights (NAN, STL, and WIC at 18–20 cm) were clustered to the upper left in the ordination. The amount of native marsh in the subestuary was highly correlated with axis 2, indicating it is the primary driver of site separation along this axis (Figure 6; Table 3). The forest-dominated STL had a high percentage of native marsh (51.1%) relative to the more developed watersheds of SEV (13.5%) and PAT (7.7%; Table 1), which clustered lower on the y-axis gradient.

DISCUSSION

Reaching the goal of restoring a diverse native plant community following invasive plant management is often elusive due to unaccounted-for factors operating at both site and landscape scales. To better predict the context dependency of invasive species management and native plant restoration for *Phragmites* and most other

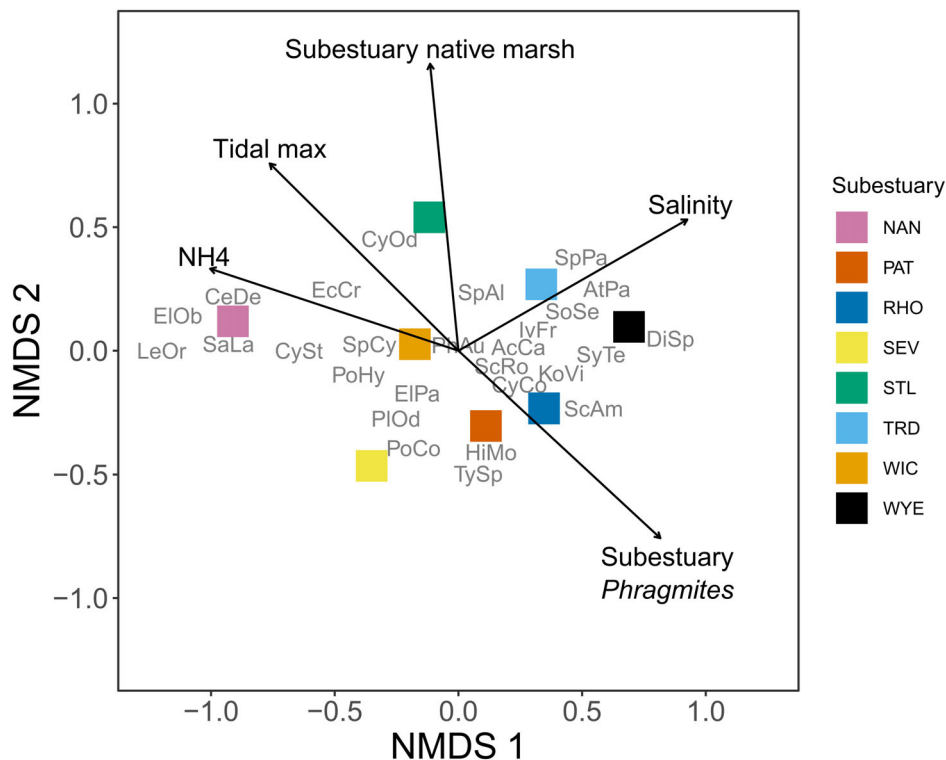


FIGURE 6 Plant communities in 2015 in *Phragmites*-managed sites in the eight subestuaries with 2011 site environmental conditions and the subestuary shoreline vegetation conditions (see Table 3) vectors overlaid (see legend to Figure 1 for an explanation of subestuary abbreviations). Native species (with CC score in parentheses) are: CeDe, *Ceratophyllum demersum* (4); CyCo, *Cyperus compressus* (2); CyOd, *Cyperus odoratus* (2); CySt, *Cyperus strigosus* (2); DiSp, *Distichlis spicata* (8); ElOb, *Eleocharis obtusa*; ElPa, *Eleocharis parvula* (6); HiMo, *Hibiscus moscheutos* (5); IvFr, *Iva frutescens* (6); KoVi, *Kosteletzkya virginica* (8); LeOr, *Leersia oryzoides* (2); PlOd, *Pluchea odorata* (6); PoCo, *Pontederia cordata* (6); SaLa, *Sagittaria latifolia* (4); ScAm, *Schoenoplectus americanus* (9); ScRo, *Schoenoplectus robustus* (9); SoSe, *Solidago sempervirens* (2); SpAl, *Spartina alterniflora* (7); SpCy, *Spartina cynosuroides* (7); SpPa, *Spartina patens* (7); SyTe, *Symphytotrichum tenuifolium* (8); TySp, *Typha* spp. (2). Introduced species are AcCa, *Acorus calamus* (0); AtPa, *Atriplex patula* (0); EcCr, *Echinochloa crus-galli* (0); PhAu, *Phragmites australis* (0); PoHy, *Polygonum hydropiper* (0). Stress = 0.08. NMDS, nonmetric multidimensional scaling.

invaders, large-scale, multisite, and multiyear empirical studies are needed (Kettenring & Adams, 2011). As one of the most aggressive and pervasive invasive plants in North American wetlands, *Phragmites* presents a formidable challenge to land managers. There has been keen interest by researchers and managers alike that has resulted in a robust literature on *Phragmites* management (e.g., Ailstock et al., 2001; Breen et al., 2014; Farnsworth & Meyerson, 1999; Karberg et al., 2018; Lombard et al., 2012; Mozdzer et al., 2008; Whyte et al., 2009) and emerging biocontrol tools (Blossey et al., 2018; Kowalski et al., 2015). However, most research has been short-term, small-scale, and with minimal native plant recovery monitoring (Hazelton et al., 2014).

We evaluated the context dependency of *Phragmites* management outcomes by conducting a five-year experiment across eight subestuaries of Chesapeake Bay to evaluate invasive *Phragmites* and plant community response to herbicide management. We found that with multiyear herbicide treatments, it was possible to greatly

reduce *Phragmites* across an array of subestuaries while increasing the cover and quality of native plant communities. Yet, by the end of the study, plant community composition in all *Phragmites*-managed sites remained distinct from, even if composition was shifting toward, reference sites. There was also large intersite variation in the *Phragmites* and native plant response. The plant community composition of the *Phragmites*-managed sites following herbicide treatment was more strongly associated with site environmental conditions and shoreline subestuary vegetation conditions than watershed land use, indicating that site and adjacent landscape conditions are the most important drivers of vegetation recovery. We uncovered specific aspects of the surrounding landscape that are linked to improved vegetation recovery—the species richness and conservation value of nearby wetlands. Greatly reducing *Phragmites* with multiyear herbicide treatments is possible but restoration of native plant communities comparable to reference sites remains elusive, particularly in subestuaries

TABLE 3 Pearson's correlations between nonmetric multidimensional scaling (NMDS) axis scores and site environmental and subestuary vectors from the ordination of 2015 plant communities in *Phragmites*-managed sites in the eight subestuaries (see Figure 6).

Site environmental and subestuary vegetation conditions	NMDS 1	NMDS 2
Ammonium	-0.86	0.18
Salinity	0.83	0.31
Tidal maximum	-0.76	0.48
Shoreline native marsh	-0.15	0.96
Shoreline <i>Phragmites</i>	0.80	-0.47
Watershed forested land	-0.68	0.33
Watershed agricultural land	0.64	0.33
Watershed developed land	0.06	-0.57

Note: Site environmental conditions used were ammonium, salinity, and tidal maximum while subestuary vegetation conditions used were the percent of native marsh and *Phragmites* along shorelines and watershed land-use composition. Phosphorus was omitted from this analysis because it was not a significant variable in the original NMDS analysis. Variables that were significantly ($\alpha \leq 0.05$) related to the first two NMDS axes appear in boldface ($\alpha \leq 0.05$), while moderately significant variables appear in italics ($\alpha \leq 0.10$).

with extensive degradation and anthropogenic impacts; such sites will require substantially more effort to restore. Assessing environmental and vegetation conditions at the site and in the surrounding landscape prior to making a management decision to remove *Phragmites* is essential to predict the time and effort required to achieve restoration goals (Galatowitsch & Bohnen, 2020; Matthews, Peralta, et al., 2009; Reid et al., 2009).

Managing *Phragmites* and restoring native plant communities: What matters?

The reasons for divergent management and restoration results are often difficult for managers to discern, as they can be tied to management decisions, but also the site or landscape context. To highlight the factors that matter most for vegetation outcomes, we evaluated our results in light of six broad themes from the invasive plant management literature. We bring particular focus to previous *Phragmites* research studies that have evaluated the context dependency of *Phragmites* management with large-scale, multisite, and multiyear empirical research, especially the studies since the Hazelton et al. (2014) review.

First, and not surprisingly, the type of treatment used drives both invasive plant removal and native plant recovery (Abella et al., 2013; Flory & Clay, 2009). For *Phragmites*, herbicide-based treatments (especially glyphosate) lead to more complete *Phragmites*

management and corresponding increases in native plant cover (Breen et al., 2014; Cheshier et al., 2012; Derr, 2008a, 2008b; Farnsworth & Meyerson, 1999; Mozdzer et al., 2008; Rohal, Cranney, & Kettenring, 2019). Herbicide has the benefit of controlling existing stands by killing rhizomes if the herbicide is effectively translocated belowground (most effective with a later growing season herbicide application; Rohal, Cranney, Hazelton, et al., 2019). For these reasons, we solely pursued fall (October in Maryland, USA) glyphosate-herbicide applications in this study.

Second, the initial size of the invader patch is important for management, with effective removal and robust native plant recruitment more likely at smaller scales (Eppinga et al., 2021; Erskine Ogden & Rejmánek, 2005). For *Phragmites*, treatment of smaller patches (especially those that are extremely small like $<5 \text{ m}^2$) resulted in more complete *Phragmites* reductions and native plant restoration (Quirion et al., 2018; Rohal, Cranney, & Kettenring, 2019; Zimmerman et al., 2018). Rohal, Cranney, and Kettenring (2019) found that even moderately sized *Phragmites* patches (1000 m^2) should be expected to have substantial restoration success relative to large infestations ($12,000 \text{ m}^2$). In the present study, all *Phragmites* patches were similarly moderately sized, thus patch size was not a confounding factor in this experiment even if it is an important factor for guiding management decision-making.

Third, the number of years of treatment is a critical determinant in the success of management efforts and the likelihood for reinvasion (Alday et al., 2013; Reid et al., 2009; Wilson et al., 2004). The greatest reductions in *Phragmites* generally occur in the first year of treatment but follow-up, targeted treatments are essential for long-term reductions (Lombard et al., 2012; Rohal, Cranney, Hazelton, et al., 2019; Rohal, Cranney, & Kettenring, 2019; this study). Indeed, we initially found large reductions (year 2, 1 year after herbicide application) and then more muted reductions (years 3–4) in *Phragmites* cover, stem density, and inflorescence density although there were exceptions when sites were viewed individually. Prior studies that herbicide-treated *Phragmites* only 1 year in the field (e.g., Farnsworth & Meyerson, 1999; Mozdzer et al., 2008; Whyte et al., 2009) or under controlled greenhouse and mesocosm conditions (e.g., Cheshier et al., 2012; Derr, 2008a, 2008b) must be interpreted in this context since a highly effective one-time treatment may provide a false sense of management success.

On the other hand, (near-)continuous treatments over many years can yield success. In the Great Lakes region, Bonello and Judd (2020) assessed *Phragmites*-treated wetlands 6–10 years after an initial herbicide treatment in

2007 or 2011 (and with a variable number of years of follow-up spot treatments). When all sites were monitored in 2018, they found substantial reductions in *Phragmites* cover and significant increases in native species diversity relative to untreated wetlands. Lombard et al. (2012) found similar success with repeated *Phragmites* treatments during 2002–2008 in 99 interdunal wetland swales in Cape Cod, Massachusetts, USA. Their repeated management efforts resulted in substantial reductions in *Phragmites* stem densities and, as importantly, significant declines in herbicide use and personnel time as the invasion was brought under control. Complete control of *Phragmites* requires addressing its abundant seed production (Kettenring et al., 2011), its large reservoir of stored seeds in seed banks (Hazelton et al., 2018; Rohal et al., 2021), and its extensive belowground rhizome network that may be only partially killed with a single or poorly timed herbicide application (Rohal, Cranney, Hazelton, et al., 2019). Therefore, it should not be surprising that lasting control of *Phragmites* will take many years of diligent management and long-term monitoring (sensu La Peyre et al., 2001).

Fourth, the time since last treatment is important for assessing management success and predicting long-term recovery trajectories (Kettenring & Adams, 2011). Following management, *Phragmites* cover, density, and reproduction are almost always universally low for at least a few months. But once treatments cease, there can be slow or rapid return of *Phragmites* depending on the effectiveness of initial and follow-up management (e.g., if rhizomes were killed along with aboveground vegetation in addition to depleting the invader seed bank) and the extent of landscape degradation that drives the potential for native recovery (Bonello & Judd, 2020; Rohal, Cranney, Hazelton, et al., 2019; Rohal, Cranney, & Kettenring, 2019; this study). In the present study, our timeframe for assessing *Phragmites* performance once herbicide application ceased was relatively short, a common methodological limitation of invasive plant control experiments (Kettenring & Adams, 2011). Like Rohal, Cranney, Hazelton et al. (2019) and Rohal, Cranney, and Kettenring (2019), we saw *Phragmites* starting to rebound once herbicide treatments ceased, underscoring the need for longer term follow-up treatments (Lombard et al., 2012). One of the authors (DW) has been able to continue monitoring most of the subestuaries used in this study and by 2020, 7 years after herbicide application ended, *Phragmites* completely dominated the RHO, STL, and WYE *Phragmites*-managed sites.

Fifth, the reference site type used offers different perspectives on whether restoration success occurred and what additional steps (e.g., active revegetation) must be taken to achieve desired restoration outcomes

(Guido & Pillar, 2017). In past *Phragmites* studies, some have used an untreated *Phragmites*-dominated site for reference (Rohal, Cranney, Hazelton, et al., 2019; Rohal, Cranney, & Kettenring, 2019; this study) while others chose a native-dominated reference site (Robichaud & Rooney, 2021; Rohal, Cranney, Hazelton, et al., 2019; Zimmerman et al., 2018; this study). Comparisons made to untreated *Phragmites* stands indicate that management actions have been highly effective because often substantial reductions in *Phragmites* occurred. In fact, we documented large declines in *Phragmites* performance following herbicide application in managed relative to untreated sites. Studies that compare results to native, high-quality reference sites reveal that complete restoration with return of desired native plant communities of sufficient cover and diversity is rarely achieved. In our study, native cover in *Phragmites*-managed sites remained distinct from reference sites as did mean *C* scores, indicating that multiple aspects of native plant communities failed to recover sufficiently. A common limitation of invasive species management research and practice is that the vital step of reintroducing native vegetation is neglected (Kettenring & Adams, 2011). Seeding or planting wetlands is essential to preempt invaders and more rapidly recover lost ecosystem functions and services (Galatowitsch & Van der Valk, 1996; Kettenring & Tarsa, 2020).

Finally, site and landscape conditions strongly drive invasive plant management outcomes (Diez et al., 2009; Matthews et al., 2017; Matthews, Peralta, et al., 2009; Prasad et al., 2018). Given the broad regions in North America where *Phragmites* has invaded and where restoration has been pursued, it is not surprising that there are myriad site and landscape drivers at least in the few studies that have evaluated these linkages. Rohal, Cranney, Hazelton et al. (2019) found that site hydrology was the strongest driver of plant responses to different *Phragmites* management treatments in six Great Salt Lake wetlands, Utah, USA. Drier sites exhibited greater *Phragmites* rebound likely due to ineffective herbicide uptake when plants were drought-stressed. In a companion study, Rohal, Cranney, and Kettenring (2019) found that site inundation and landscape conditions (i.e., the extent of intact healthy wetlands in the vicinity of the treatment area) were strong drivers of *Phragmites* reductions and native plant recovery. The presence of nearby seed sources for desirable species was hypothesized to be important and the slow recovery of native vegetation in some sites was thought to be due to the lack of seed input from historically abundant perennial, habitat-forming graminoids (Rohal, Cranney, & Kettenring, 2019). Similarly, in the present study, site hydrology (tidal maximum) was a strong driver of plant community responses; however, nutrients and

salinity conditions also related to vegetation responses in the present study but were not significant drivers in either Rohal, Cranney, Hazelton et al. (2019) and Rohal, Cranney, and Kettenring (2019).

Similar to what Rohal, Cranney, and Kettenring (2019) found in the West, USA, in Chesapeake Bay the landscape vegetation conditions were important drivers of *Phragmites* reductions and native recovery. We extend these assessments by highlighting specific aspects of the surrounding landscape that are linked to improved vegetation recovery—the species richness and conservation value of nearby uninvaded sites. In other words, it is not just proximity to intact native stands that drives recovery (as found by Rohal, Cranney, & Kettenring, 2019), but also the quality and diversity of the surrounding areas that are important. Given the importance of restoring diverse native vegetation for future invasion resistance to *Phragmites* (Byun et al., 2013; Byun, de Blois, et al., 2020), it is essential to restore wetlands in watersheds where the vegetation in the larger landscape is of sufficient quality and diversity to facilitate rapid recovery. Where this approach is infeasible, it is important to recognize that landscape conditions will constrain what is possible in a restoration site (Matthews, Peralta, et al., 2009) and that greater financial investment is required including to augment recovery by reintroducing appropriate native species.

Conclusion and management implications

Invasive plant managers need guidance to inform site selection and plan realistically for the long-term resources required to achieve restoration success. While site-specific outcomes have long been observed following invasive plant management, this study highlights how an experimental approach across variable site and landscape conditions can bring to light some of the specific factors that account for the divergent outcomes. Because it is very difficult to completely remove *Phragmites* and success requires multiple years of management with a focus on small infestations (Quirion et al., 2018; Rohal, Cranney, & Kettenring, 2019), managers will need to commit extensive resources to curbing the invasion as well as plan for the long-term effort required to ensure it does not rebound. If eradication is not achieved (as found in our study and many others), *Phragmites* will certainly return following the cessation of management, even if the floristic quality of the recovering vegetation may have an upward trajectory.

However, our research demonstrates that with ongoing management, native vegetation will begin to recover although the recovery is unlikely to be linear, rapid, or

complete (Bonello & Judd, 2020; Hacker & Dethier, 2009; Rohal, Cranney, Hazelton, et al., 2019; Suding, 2011; Zedler, 2000) and the eventual trajectory may be site specific. Choosing restoration sites closer to intact, high-quality wetlands is likely to yield greater success (Galatowitsch, 2006); we demonstrated that the quality and diversity of plant communities in the landscape around the restoration are critical. Degraded sites embedded within highly impacted landscapes will require more effort (e.g., multiple years of revegetation) and longer time frames for sufficient native recovery. Extensive seeding and planting can alter the recovery pathway and more rapidly reestablish diverse native plant communities (Byun, Oh, et al., 2020; Kettenring & Adams, 2011; Kettenring & Tarsa, 2020; Matthews & Spyreas, 2010; Schuster et al., 2018), particularly in less degraded sites and watersheds where it is likely to be most effective and less costly (Zedler, 2000). We are currently conducting a follow-up experiment to determine whether planting native species at sites where *Phragmites* has been removed will expedite vegetation recovery. Initial results indicate that plantings can be effective in obtaining rapid development of native species but site characteristics (e.g., substrate type, salinity) will impact the outcome (D. Whigham, personal communication, 2022). It may not be possible to achieve the exact composition of nearby native reference wetlands. Nonetheless given how few successes there are for invasive plant management and native plant recovery even with active revegetation (Kettenring & Adams, 2011; Kettenring & Tarsa, 2020; Matthews & Spyreas, 2010), it is still imperative to enhance learning (Young & Schwartz, 2019) and improve prediction in restoration (Brudvig, 2017; Brudvig et al., 2017; Holl et al., 2003).

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CONFLICT OF INTEREST


Authors have no conflicts of interest to disclose.

DATA AVAILABILITY STATEMENT

Data (Rohal et al., 2022) are available from Figshare: <https://doi.org/10.6084/m9.figshare.19643265.v1>.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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