



# Environmental Drivers of Plant Invasion in Wetland Mitigation

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## Abstract

Invasive plant species can alter natural communities and degrade ecosystem function, yet the factors influencing species invasion are poorly understood. The purpose of this study was to characterize environmental drivers of plant community structure and invasive plant prevalence within invaded portions of wetland mitigation sites. We sampled vegetation and environmental variables (prevalence index, light availability, soil physiochemistry, site age) across invasion gradients within and adjacent to invasive plant populations at multiple wetland mitigation sites in the Coastal Plain and Piedmont physiographic provinces of Virginia (USA). Data analyses involved a multi-metric statistical approach combining correlation and CCA to arrive at a plausible model for drivers of plant community structure in the context of invasive species prevalence based on environmental correlates. We targeted populations of *Arthraxon hispidus* (joint-head grass), *Microstegium vimineum* (Japanese stiltgrass), and *Typha* spp. (cattail), three invasive species that are known to be problematic on wetland mitigation sites in the region. Our analyses revealed specific environmental drivers of plant community structure and invasive species prevalence associated with populations of each invader, and a few factors consistently emerged as important drivers across populations of all targeted invaders – notably, canopy cover (light availability), prevalence index (representing frequency and duration of inundation and shallow soil saturation), and a handful of physiochemical variables. The results of this research have been used to develop a suite of recommended best practices that can be implemented at the outset of a wetland mitigation project to encourage desirable wetland plant communities and reduce the risk of invasion.

**Keywords** Invasive species · Wetland mitigation · *Microstegium vimineum* · *Arthraxon hispidus* · *Typha* spp. · Environmental ecology

## Introduction

Environmental conditions are key drivers of plant community dynamics, and environment/community interactions are important for assessing the relative distribution and abundance of species in vegetation assemblages (van der

Valk 1981; Bazzaz 1996). Temperature, light availability, nutrient availability, and moisture regime often influence the geographic areas that represent available niche space for plant species and community types (Craine 2009). Additionally, plants often exhibit various life-history strategies that determine the habitats in which they can become established and, in some cases, dominate the vegetative community (Grime 1977; Grime and Pierce 2012). Invasive species have a disproportionately large presence in wetlands in comparison with other habitats (Zedler and Kercher 2004), and this is especially true for compensatory wetland mitigation sites (i.e., wetland sites created or restored to compensate for impacts to wetlands elsewhere) (Matthews and Spyreas 2010).

Despite the foundational understanding that ecological tolerance and life-history strategy combine to shape the distribution of plant species, the specific conditions under which invasive plants dominate communities and impact

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ecosystem function have yet to be resolved. Studies have attempted to determine which environmental correlates are important to the dominance of problematic invasive species such as *Microstegium vimineum* (Schramm and Ehrenfeld 2010) and *Typha* spp. (Galatowitsch et al. 1999; Zedler and Kercher 2004), but consensus remains unreached. On wetland mitigation sites, invasive plant species present one of the greatest challenges to mitigation managers, designers, and natural resource agency reviewers (Brooks and Gebo 2013). The capital outlay for invasive species management in compensatory wetland mitigation has increased considerably over the past couple of decades, and in some cases it can represent the largest investment of money and resources in terms of post-construction maintenance (Bergdolt et al. 2005). Despite these issues, there has been relatively little applied research on plant invasions in wetland mitigation (but see Matthews and Endress 2008; Matthews et al. 2009). Understanding the specific relationships between invasive plants, native plant communities, and environmental conditions on wetland mitigation sites could provide managers with options for disrupting the life-history strategies of invaders and preventing the ecological damage commonly caused by invasive plants and encouraging the development of more desirable native plant communities.

From the primary literature on invasion ecology, we believe that theoretical concepts developed based on the resource strategies of plants have the most explanatory value in wetland mitigation contexts (Craine 2009). Although many theories about novel phenotypes and lack of natural enemies have been advanced to explain how non-native species become invasive [e.g., novel weapons (Callaway and Ridenour 2004), introgression (Galatowitsch et al. 1999), enemy release (Keane and Crawley 2002), etc.], those invoking environmental factors and the relationship between stress and disturbance on sites are the most compelling. As these terms are typically applied in plant ecology, *stress* refers to an environmental or biological factor that causes a negative physiological response resulting in a reduction in fitness or growth (e.g., nutrient limitation or drought), whereas *disturbance* refers to a change in the environment that results in a removal of biomass (e.g., mowing or bulldozing a site) (Grime 1979; Hobbs and Huenneke 1992; Bazzaz 1996; Lichtenthaler 1996). Levels of stress and disturbance vary in space and time, and the interactions between the two can often be used to predict plant responses to environmental conditions (Craine 2009). In evaluating this “stress-disturbance dynamic” on wetland mitigation sites, we find evidence that the plant community with populations of each study species responds to certain environmental stressors differently. Disturbance varied across sites, with all sites experiencing denudation and earthworks prior to construction and recurrent removal of invasive species

once construction activities concluded. These disturbances combined with low levels of environmental stress (i.e., high resource availability) appear to facilitate growth and dominance of study species depending on the environmental variables at play.

In the case of most plant invaders, low stress (high resource availability) typically refers to soil nutrient status and, in particular, levels of bioavailable nitrogen and phosphorus (Chiang et al. 2000; Woo and Zedler 2002; Tuchman et al. 2009). Disturbed sites that are high in these essential nutrients have been shown to be prone to plant community alteration and biological invasion (Alpert et al. 2000; Ehrenfeld 2010). However, in wetlands, saturation and inundation can represent an important source of stress for plants because microbially-mediated chemical reduction renders saturated soils anaerobic and therefore depleted of molecular oxygen required for respiration (Mitsch and Gosselink 2015). For some species, the limiting resource in forested ecosystems is light availability, and a disturbance event that opens the canopy and allows light to enter the understory will effectively remove stress, encourage growth of highly competitive species within the plant community, and facilitate invasion (Robertson et al. 1994; Woo and Zedler 2002; Warren et al. 2011). In each of these scenarios, disturbance is the mode of entry, and high resource availability ensures success for the invader. Once established in a new habitat, the mechanisms used to outcompete native species are unique to each invader (e.g., allelopathy, autogenic control, rapid nutrient acquisition, and slow decomposition), but it is typically the case that the competitive ability of invaders will be reduced in stressful environments (Lockwood et al. 2013). In restoration ecology, if the important factors that control invasion are known, the interplay of stress and disturbance can potentially be controlled to minimize risk of invasion (Perry et al. 2004), and on mitigation sites this would be most critical during the first several years of vegetation development (Noon 1996; DeBerry and Perry 2015).

We evaluated these concepts by establishing transects across invasion gradients of three known wetland mitigation invaders in Virginia (USA): *Arthraxon hispidus* (Thunb.) Makino [Poaceae] (hereafter “*Arthraxon*”), *Microstegium vimineum* (Trin.) A. Camus [Poaceae] (hereafter “*Microstegium*”), and *Typha* L. spp. [Typhaceae] (hereafter “*Typha*”). These taxa were selected as representative organisms due to their abundance on available field sites and the varying degrees to which they express tolerance for soil saturation and light availability. As used in this study, the term “invasion gradient” signifies the transition from high to low abundance of a target invader, which was evaluated using plots arrayed on transects across the gradient. Within plots, we documented relative abundance of species within the plant community and collected data on environmental variables.



**Fig. 1** **Top:** *Arthraxon hispidus* dominant on one of our northern Virginia (USA) wetland mitigation study sites. **Middle:** *Microstegium vimineum* demonstrating tolerance to shade in a disturbed forest understory at an eastern mountains and piedmont (EMP) site near Richmond, Virginia (USA). **Bottom:** Typical habitat condition for *Typha sp.* on study sites. Photograph taken in at a coastal plain (AGCP) site near Charles City, Virginia (USA) (lead author pictured)

Although we expected prevalence index and available light to be important factors, evidence suggests that phosphorus is a limiting nutrient for plants on wetland mitigation sites, and that areas with higher than average levels of phosphorus would therefore allow invasive plants to proliferate (DeBerry and Perry 2015).

Because variability in hydrologic conditions relating to the frequency and duration of inundation and soil saturation have been shown to influence vegetation dynamics and patterns on wetland mitigation sites (Ahn and Dee 2011), we also hypothesized that our study species would respond differently to variation in hydrologic conditions. During site reconnaissance, *Arthraxon* and *Microstegium* were observed at higher elevations within wetland mitigation sites, indicating that there may be a negative correlation with these species and anoxic conditions resulting from persistent high water tables and/or frequent flooding. Conversely, *Typha* was reliably observed in lower, wetter areas, and was therefore expected to show a positive correlation with those hydrologic conditions. Finally, we anticipated that *Microstegium* would be capable of tolerating stressful, low light conditions, while *Arthraxon* and *Typha* would not.

### Species Descriptions

*Arthraxon* is an annual grass from east Asia that has received little attention in the literature but is listed as moderately invasive in Virginia and throughout the U.S. Mid-Atlantic Region (Swearingen et al. 2010; Heffernan et al. 2014). Reports from mitigation practitioners across Virginia suggest that the species merits greater concern and further scientific examination (Fig. 1a). Although infestations on study sites were observed more commonly in the Piedmont physiographic province, *Arthraxon* was present on Coastal Plain sites as well. Most mitigation sites colonized by this species were adjacent to active farmland or within the floodplains of major rivers, and invasion was commonly observed on wetland “edges” where localized disturbance was more prevalent. These observations are consistent with the limited information on *Arthraxon* available from research on other continents (e.g., White et al. 2020).

*Microstegium* is an annual grass native to Asia that grows in a variety of wetland and upland habitats. *Microstegium* has a known tolerance for shading (Barden 1987; Oswalt et al. 2007; Fig. 1b) and flooding (Warren et al. 2011). Because of its environmental tolerances and prolific seeding capabilities, *Microstegium* has been identified as a highly invasive plant species in Virginia (Heffernan et al. 2014). It has been documented to reduce native plant diversity (Oswalt et al. 2007; Adams and Engelhardt 2009) and alter insect community structure (Marshall and Buckley 2009). Its ability to disperse high numbers of viable seeds into a persistent seed

bank makes it difficult for land managers to treat (Miller and Matlack 2010; Ziska et al. 2015), but post-emergence herbicide application can be effective within a single year (Judge et al. 2005; Flory 2010). Despite the abundance of research on this species, consensus on the specific environmental conditions that stimulate invasion by *Microstegium* has not been reached; however, high nutrient loads and light availability have both been identified as likely candidates (Warren et al. 2011).

*Typha* represents a group of two cattail species (*Typha latifolia* L. and *Typha angustifolia* L.) and a hybrid of those species (*Typha x glauca* Godron) that are native to the U.S. but regulated as invasive species on wetland mitigation sites (Perry et al. 2009). *Typha* typically inhabits lower, wetter areas (Fig. 1c), and increases in nutrient availability have also been documented where *Typha* is present (Woo and Zedler 2002; Zedler and Kercher 2004; Angeloni et al. 2006; Wiltermuth and Anteau 2016). Recent studies suggest that species in the genus may be increasing in prevalence due to anthropogenic activities related to runoff and sedimentation in wetlands (Angeloni et al. 2006; Sullivan et al. 2010). However, little evidence exists that *Typha* directly inhibits native plant diversity, and potential for positive species responses to the presence of *Typha* have been demonstrated (Green and Galatowitsch 2001; Perry et al. 2009). Nonetheless, herbicide application is regularly used to combat *Typha* growth, often with only temporary results (Brandon et al. 2004; Lawrence et al. 2016).

## Methods

### Site Selection and Study Area

Representative field sites were chosen from a pool of over 30 available sites based on location and size of invasive species populations, common native plant assemblages, site layout, and accessibility. Only non-tidal wetland mitigation sites displaying dominant patches of target organisms were used. Field sites were assigned age classes consistent with DeBerry and Perry (2012) due to the documented importance of age for plant community structure on wetland mitigation sites. Within mitigation areas with multiple users, populations of target species occurring within distinct “phases” or sections of a single mitigation area constructed during separate time periods were treated as independent sites so long as they fell into different age classes (this was a common condition on study areas operating as mitigation banks). The age classes were determined from records on the number of complete growing seasons after construction of the mitigation area and included: A - -2 years old (2 sites);

B - 3–5 years old (3 sites); C - 6–10 years old (6 sites); D - 11–15 (7 sites) years old; and E - >15 years old (5 sites).

Among the sites screened during site reconnaissance, 23 met suitability criteria and were selected for the study. Two sites fell within age class A, three sites fell within age class B, six sites fell within age class C, seven sites fell within age class D, and five sites fell within age class E. Sites were drawn from a total of 18 mitigation areas. Of the available areas, 14 had a single phase that was suitable for sampling, three areas had two phases that were suitable for sampling, and 1 area had three distinct phases that were suitable for sampling. Of the phases sampled, 14 contained a transect for only a single study species that was suitable for sampling, seven contained transects for two study species that were suitable for sampling, and two contained transects for all three study species that were suitable for sampling. The project therefore encompassed 170 2 m x 2 m plots across 34 transects within 23 sites and 18 mitigation areas. Site ages ranged from 1 to 23 years post-construction and were evenly distributed across the Piedmont (11 sites) and Coastal Plain (12 sites) in Virginia, USA (Fig. 2). Most sites fell within mitigation banks or in-lieu fee sites (i.e., sites established under the Virginia Aquatic Resources Trust Fund).

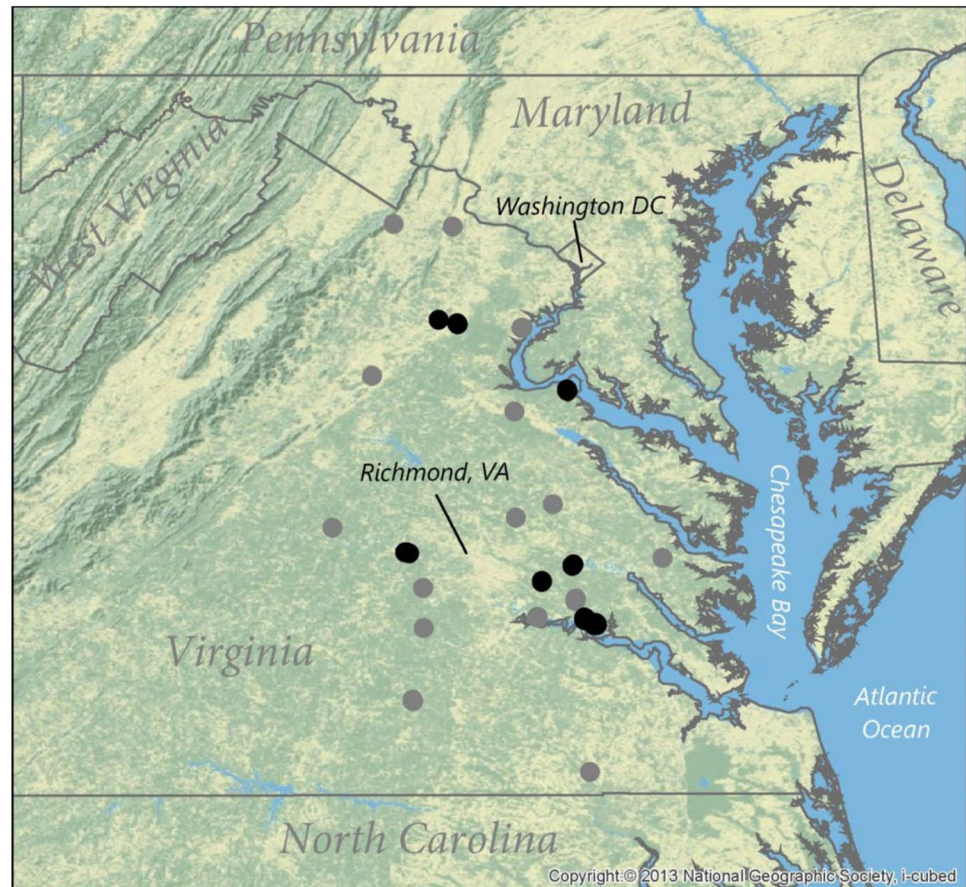
### Research Design and Data Collection

A single transect was constructed for each study species present on each field site using five identical 4m<sup>2</sup> (2 m x 2 m) vegetation plots, randomly assigned to an area that captured the gradient from completely invaded (i.e., the invasive species was considered dominant, or comprising at least 20% of the overall relative dominance of the community) to uninvaded (i.e., the invasive species was absent or not comprising more than 5% relative dominance).

### Transect Configuration and Plot Locations

Both transect and plot locations were randomized to minimize bias toward sampling visually similar vegetation communities along the invasion gradient. The randomization procedure for transect/plot layout involved identifying the center of an invasive species population within a given site and establishing a 4m<sup>2</sup> grid with 9 vertices (Fig. 3). Using a random number generator, a random number between 1 and 9 was selected, and its location on the grid was defined as the center of the vegetation plot for the most invaded site (Plot A). From that point, the direction of the transect was initially determined by defining an arc through which all possible transects could be delineated that would lead toward an uninvaded section of the site with similar environmental conditions. The length of this arc was taken as the domain for another random numbers draw, this time with

**Fig. 2** Wetland mitigation study site locations. Grey symbols indicate sites in which more than one phase, or section of a single mitigation area constructed at a different time, was sampled; black symbols represent single-phase sample sites



the value representing the compass bearing from the center of Plot A to the edge of the invasive species population. At the edge of the population, another 4m<sup>2</sup> grid was established and another random vertex was drawn, this one representing the center of Plot C. From this point, a straight line was defined from the center of Plot A to the center of Plot C and then an equivalent distance beyond the edge of the invasive population to delineate the remainder of the sampling transect. The center of Plot B (“second most invaded”) was then defined at half the distance between Plots A and C. The center of Plot E (uninvaded) was established at the far end of the transect, and the center of Plot D (“second least invaded”) was established at half the distance between C and E. This procedure resulted in five plots along the invasion gradient from most invaded (Plot A) to edge of invasion (Plot C) to uninvaded (Plot E) (Fig. 3). Transect length varied among sites but typically ranged from 50 to 100 m.

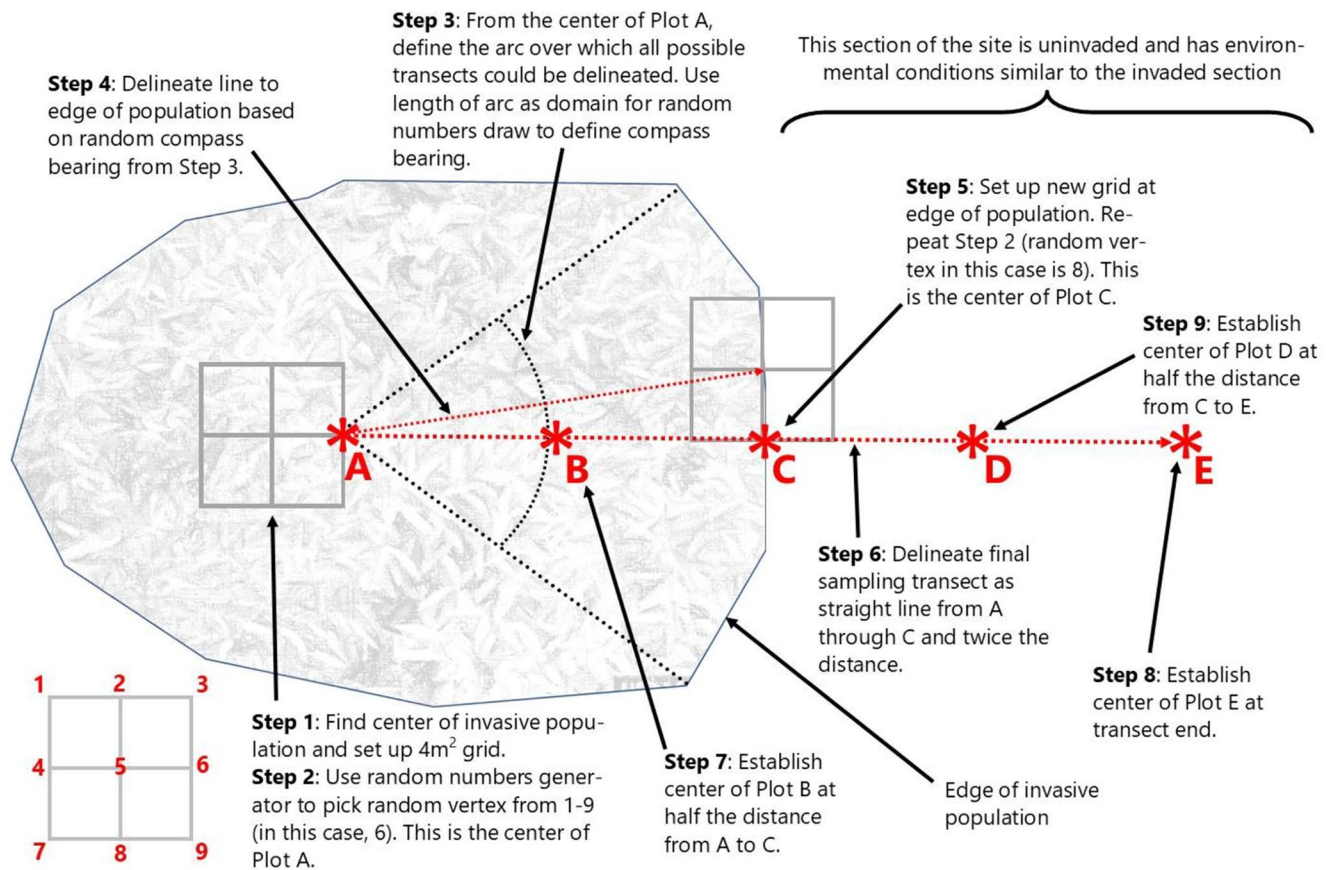
### Soil Sampling

The center of each plot was GPS-located in the ESRI-based Collector application for iPad, then a soil sample was taken to a depth of 10 cm using a 6 cm-diameter soil corer. Soil samples were textured on-site using field methods (Ritchey

et al. 2015) to estimate texture at each sampling plot. For data analysis, texture was transformed into an ordinal scale from fine to coarse (i.e., lower numbers represented finer textures soils and larger numbers represented coarser soils). Samples were then shipped to the Virginia Tech Soil Testing Lab where soil chemical variables were measured with Mehlich extractions for P, K, Ca, Mg, CEC, Zn, Mn, Cu, Fe, and B, and Elementar high-temperature combustion for total values of C and N. Finally, an automated pH analyzer was used to measure pH values of wet samples at a 1:1 soil:water ratio (Maguire and Heckendorn 2019). Cation exchange capacity (CEC) was derived from the results of Mehlich extractions and included in the list of soil variables.

### Canopy Cover

Canopy cover was measured by taking a skyward, hand-leveled photograph from the center of each plot using a 180-degree hemispheric lens adapter for iPad. Photographs were taken from 1 m above the ground in *Arthraxon* and *Microstegium* plots, and from 2 m above the ground in *Typha* plots. These photograph heights allowed us to capture canopy cover skyward of the target organisms while avoiding any potential effects of self-shading. Photographs



**Fig. 3** General layout of study design and transect configuration

were analyzed using ImageJ (Rueden et al. 2017) and the package Hemispherical 2.0 (Beckschäfer 2015) to obtain a ratio of open sky to canopy cover.

### Vegetation Sampling

We quantified vegetation abundance using cover estimates for all species within each of four 1m<sup>2</sup> subplots nested in the 4m<sup>2</sup> plots. Cover estimates were based on a modified Daubenmire cover class scale with midpoints used for analysis (Mueller-Dombois and Ellenberg 1974). The cover classes, with midpoints in parentheses (rounded to the nearest whole integer), included: 0–1% (1%); 1–5% (3%); 5–25% (15%); 25–50% (38%); 50–75% (63%); 75–95% (85%); and 95–100% (98%). Cover classes were recorded for each species and then averaged across the four 1m<sup>2</sup> subplots. Identifications of all vascular plants were either obtained onsite or samples were gathered and preserved for later verification. Intact collections were deposited at the William & Mary Herbarium (WILLI) following confirmation of identity by a senior botanist. Nomenclature follows Weakley et al. (2020).

### Hydrology

Following transcription of the vegetation data, prevalence index (PI) values were calculated for use as a proxy of relative wetness between wetland sites (Tiner 2017). Given the point-in-time sampling approach and the large number of sites/observations, traditional methods for wetland hydrology monitoring such as groundwater wells were not feasible or practical for this study. PI is a viable tool for this type of study because the vegetation entrains short- and long-term variability in site hydrology over time, providing a more reliable representation of hydrology regime than surface or groundwater observations that would respond to episodic events such as storms or dry periods (Atkinson et al. 1993). PI values are calculated from the wetland indicator status values for all species recorded within a plot. Wetland indicator status values are numbers assigned to wetland indicator status codes in accordance with the National Wetland Plant List (Lichvar et al. 2016). The values include: 1 = obligate wetland species (OBL); 2 = facultative wetland species (FACW); 3 = facultative species (FAC); 4 = facultative upland species (FACU); and, 5 = obligate upland species (UPL). Each species' indicator status value is multiplied by

the relative abundance of that species within the plot then summed to produce a weighted average index between 1 and 5. Plots closer to 1 are considered to have wetter conditions and plots closer to 5 are drier (Tiner 2017). To remove the potential for circularity of evaluating invasive species abundance relative to PI, an adjusted PI (PIadj) was calculated by omitting the invader from the abundance matrix.

## Statistical Analysis

Data analysis was completed using R version 4.0.3 (R Core Team 2020) including the packages *vegan*, *Hmisc*, and *BiodiversityR* (Kindt and Coe 2005; Borcard et al. 2018; Harrell et al. 2020; Oksanen et al. 2020). The datasets for each invader were analyzed separately due to expected variation in their relative tolerances for environmental stressors and discrepancies among growth requirements (Zedler and Kercher 2004; Swearingen et al. 2010). The correlation between relative abundance of each invader and variables in the environmental matrix was calculated using the nonparametric Spearman rank-order correlation test. The Spearman test was chosen due to its robustness to deviations from normality, as well as its ability to detect both linear and monotonic relationships, without appreciable loss of statistical power in comparison with parametric tests (Legendre and Legendre 2012). When plotted against environmental variables, study species abundance possessed an obvious leftward skew, likely due to the study design and collection of 2 points with few if any study species individuals present at each transect.

Canonical Correspondence Analysis (CCA) (ter Braak 1986) was used to evaluate the overall community response to environmental variation along the invasion gradient. We chose this approach over alternatives such as linear mixed modeling because it allowed us to evaluate invasive species' responses to environmental variation in the context of the overall vegetation community. Relationships between individual species and environmental variables are often skewed or masked by interspecific interactions that are unavoidable during in-situ experiments. Therefore, we elected to use CCA to determine the drivers of plant community structure in invaded wetland communities and impose the overlay of invasive species prevalence to determine whether associations with key environmental variables and invasive species prevalence were positive or negative.

Prior to CCA analysis, rare species were removed from the abundance matrix of each dataset due to the outsized influence that rare species have on the  $X^2$  distance used in CCA (Legendre and Gallagher 2001; Peck 2016). Rare species reduction followed the Borcard method, which uses a stepwise approach based on the correspondence analysis (CA) component of CCA to evaluate the effect of progressive

species removals (Legendre and Legendre 2012). Final CCA models were chosen with a combination of forward and backward model selection using the *ordistep()* function of *vegan*, which eliminates environmental variables based on significance of permutation tests in combination with the Akaike Information Criterion (AIC) (Borcard et al. 2018), in addition to variance inflation factor (VIF) to identify and remove highly correlated variables (Legendre and Legendre 2012). This procedure results in a parsimonious model when all environmental variables retained in the model are statistically significant and the adjusted  $R^2$  for the final model doesn't exceed the adjusted  $R^2$  for the global model (global model = all environmental parameters included) (McCune and Grace 2002; Borcard et al. 2018). All permutation tests of significance were set at 1000 iterations, and statistical analyses were evaluated at  $\alpha = 0.05$ .

## Results

One hundred ninety-four (194) species were documented in the overall field study across 23 sites, 34 transects, and 170 plots sampled. In the *Arthraxon* community dataset, 124 species were sampled from 50 plots along 10 transects. *Arthraxon* comprised 19.5% of the overall relative abundance within the community matrix. Co-dominants included *Leersia oryzoides* (8.2%), *Symphytotrichum racemosum* var. *racemosum* (6.1%), *Juncus effusus* (5.2%), *Salix nigra* (3.8%), *Fraxinus pennsylvanica* (3.6%), *Platanus occidentalis* (2.7%), and *Eleocharis tenuis* var. *tenuis* (2.6%). The *Microstegium* community dataset included 116 species sampled from 50 plots across 10 transects. *Microstegium* comprised 20.6% of the overall relative abundance within the community matrix. Co-dominants included *Acer saccharinum* (7.7%), *Scirpus cyperinus* (5.9%), *Fraxinus pennsylvanica* (5.7%), *Pinus taeda* (5.4%), *Betula nigra* (4.4%), and *Juncus effusus* (3.7%). The *Typha* community matrix included 106 species sampled from 70 plots across 14 transects. *Typha* accounted for 19.5% of the overall relative abundance, with co-dominants *Persicaria hydropiperoides* (11.6%), *Juncus effusus* (10.8%), *Leersia oryzoides* (7.7%), and *Scirpus cyperinus* (4.9%).

## Environmental Variation and Community Modeling

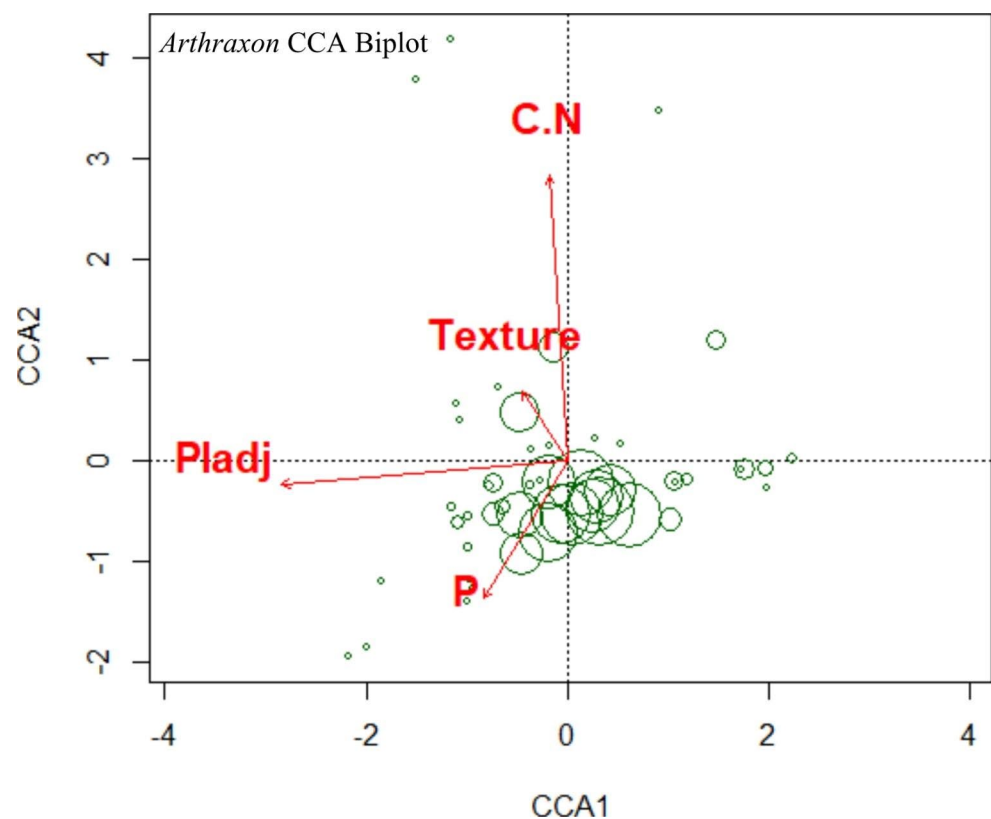
### Arthraxon

Spearman results showed *Arthraxon* abundance negatively correlated with canopy cover ( $r_s = -0.295$ ,  $p = 0.037$ ). No other environmental variables were significantly correlated with *Arthraxon* abundance in the Spearman test. The CCA model for *Arthraxon* was based on a community matrix with

46 dataset-rare species removed, leaving 78 species from the original dataset in the ordination. The final parsimonious CCA model included four environmental variables – Pladj, texture, carbon:nitrogen ratio (C:N), and phosphorus (P) – which accounted for 19% of the total inertia in the ordination. All environmental factors (eigenvectors) were significant at  $p < 0.001$  with the exception of texture ( $p = 0.002$ ).

The first two ordination axes explained over 62% of the variation in the CCA and thus were retained for the biplot. As Fig. 4 shows, Pladj was a strong environmental factor that appeared positively correlated with plant communities characterized by high *Arthraxon* abundance, indicating that *Arthraxon* was more commonly found at higher densities on drier sites. C:N was also a strong environmental factor that appeared negatively correlated with higher *Arthraxon* abundance. Both P and texture were less important as an explanatory variable in the first two axes of the ordination, but based on the eigenvector direction, P was positively correlated and texture was negatively correlated with *Arthraxon* abundance (i.e., regarding the latter, plots with higher *Arthraxon* abundance tended to be associated with smaller texture values, and therefore, finer textured soils).

**Fig. 4** CCA biplot for *Arthraxon* dataset. Red arrows are eigenvectors for environmental variables. Vector length indicates strength of correlation and vector direction indicates positive (pointing toward) or negative (pointing away) relationship to the plots, which are shown as circles with size corresponding to abundance of *Arthraxon* (i.e., larger circles = higher abundance). Plot relationships with environmental variables are interpreted as perpendicular projections from green circles to red arrows. Environmental variables determined to be significant within the model include carbon: nitrogen ratio (C:N), soil particle size, with larger particles such as sands and gravels representing higher values within the environmental matrix (Texture), prevalence index, a measure of the affinity for the plant community toward drier environments, adjusted to exclude the target species from the calculation (Pladj), and phosphorus (P)



## Microstegium

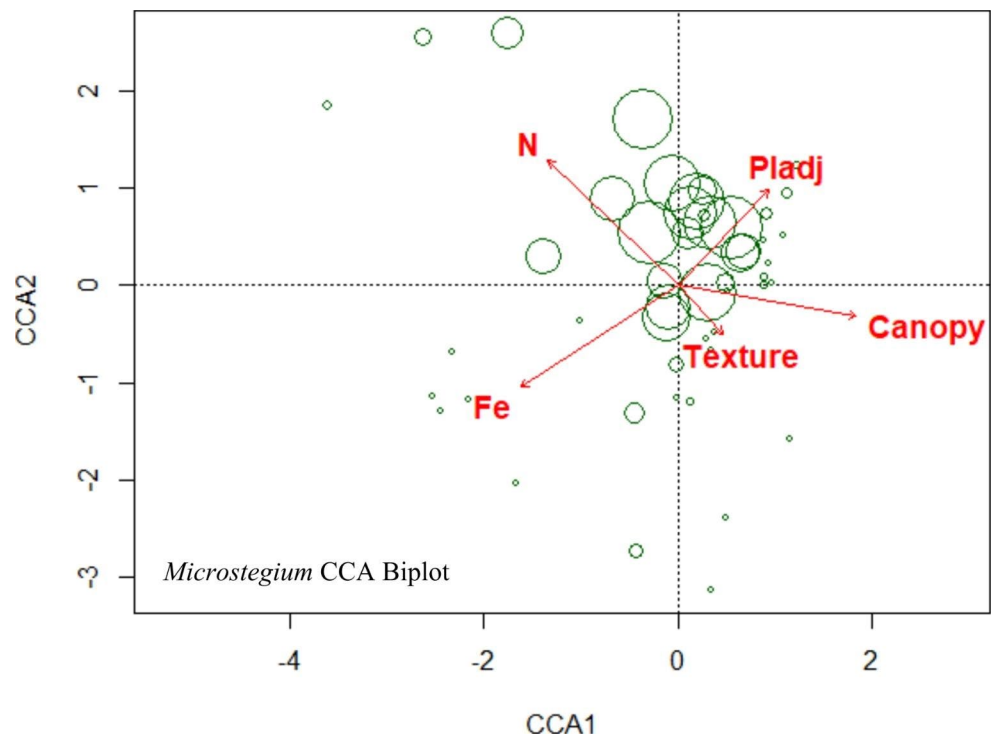
Spearman results indicated that *Microstegium* abundance was positively correlated with cation exchange capacity (CEC) ( $r_s = 0.337$ ,  $p = 0.017$ ). For the CCA analysis, the *Microstegium* community matrix was reduced by 41 dataset-rare species, leaving 75 species from the original dataset in the ordination. The final parsimonious *Microstegium* CCA model included five environmental variables – Pladj, canopy cover, texture, nitrogen (N), and iron (Fe) – which accounted for 20% of the total inertia in the ordination. All environmental factors (eigenvectors) were significant at  $p < 0.001$  with the exception of Fe ( $p < 0.01$ ) and texture ( $p = 0.023$ ). The first two ordination axes displayed in Fig. 5 explained over 51% of the CCA variation. As with *Arthraxon*, canopy cover and texture were negatively correlated with plant communities characterized by high *Microstegium* abundance and Pladj was positively correlated. The other two important factors, N and Fe, showed positive and negative relationships with *Microstegium* abundance, respectively.

## Typha

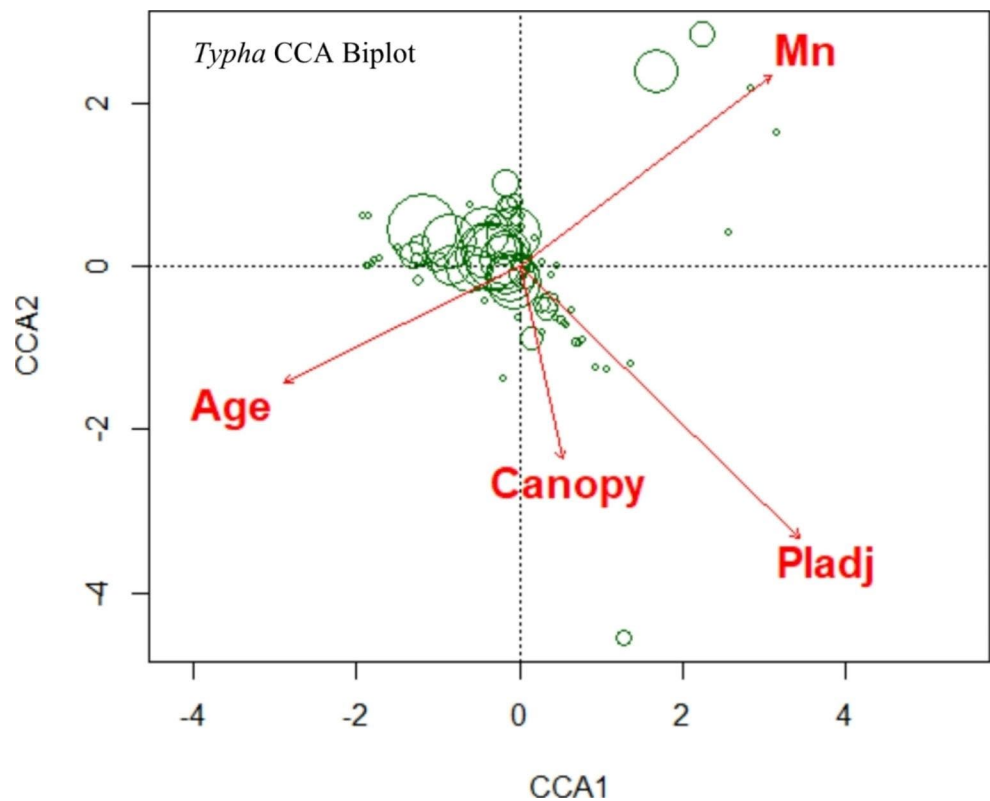
Spearman correlations showed that no environmental variables were significantly related to *Typha* abundance in the correlation matrix. The CCA analysis used a *Typha*



**Fig. 5** CCA biplot for *Microstegium* dataset. See *Arthraxon* text and Fig. 4 caption for notes on interpretation. Environmental variables determined to be significant include iron (Fe), nitrogen (N), prevalence index adjusted to exclude the target species from the calculation (Pladj), canopy cover (Canopy), and soil particle size, with larger particles such as sands and gravels representing higher values within the environmental matrix (Texture)



**Fig. 6** CCA biplot for *Typha* dataset. See *Arthraxon* text and Fig. 4 caption for notes on interpretation. Environmental variables determined to be significant within the model include the number of years following construction of the site that had passed prior to the sampling of each plot (Age), manganese (Mn), prevalence index adjusted to exclude the target species from the calculation (Pladj), and canopy cover (Canopy)



community matrix reduced by 27 dataset-rare species, leaving 79 species from the original dataset. The final parsimonious *Typha* CCA model included four environmental variables – Pladj, canopy cover, site age, and manganese (Mn) – which accounted for 15% of the total inertia in the

ordination. All environmental factors were significant in the model at  $p < 0.001$  except Mn ( $p = 0.002$ ) and site age ( $p = 0.005$ ). The first two ordination axes explained 65% of the CCA variation. As Fig. 6 demonstrates, Pladj and canopy cover were important factors in the analysis, and

canopy cover was negatively correlated with plant communities characterized by high *Typha* abundance similarly to the other two wetland invaders. However, unlike *Arthraxon* and *Microstegium*, Pladj was negatively associated with the invasion gradient. Finally, site age and Mn were identified as important factors in the parsimonious model, with the former being positively associated with the invasion gradient and the latter negatively associated.

## Discussion

Along the invasion gradients sampled in this study, variables relating to soils, prevalence index, and light availability (canopy cover) all emerged as correlates to plant community structure on wetland mitigation sites. Of these factors, prevalence index and canopy cover persistently showed a strong relationship with plant communities characterized by high invasive species prevalence. As is common in analyses of complex ecological data, no single environmental variable materialized as the most important, although prevalence index did show strong correlation with the communities possessing a high abundance value for each of the three invaders in the CCA ordinations (Figs. 4, 5 and 6). Each invaded community's relationship with prevalence index indicates that study species possess a greater chance of dominating specific niches, likely related to the frequency, timing, and duration of soil saturation, and flooding. This is not surprising given the importance of hydrologic factors in structuring wetland plant communities (van der Valk 1981), and from our modeling it is evident that soil saturation and flooding work in aggregate with other environmental factors to influence community dynamics along the invasion gradients on our wetland sites. These factors are discussed for each invader below.

### Arthraxon

The monotonic relationship between *Arthraxon* abundance and canopy cover was expected. *Arthraxon* is not a shade-tolerant grass (White et al. 2020), so the significant negative correlation with canopy cover was consistent with other studies. Likewise, the importance of hydrology as represented by Pladj in the CCA results is consistent with our site-level observations: although *Arthraxon* occurs across a broad range of moisture conditions, we consistently observed its distribution along the edges of wetlands where microtopography raised the relative elevation of the invaded area and created drier microhabitats. Dense populations of *Arthraxon* on our sites may also have been associated with localized disturbance conditions, which could have been secondarily associated with soil texture. Soil mixing and removal can

modify particle size distribution (Petru et al. 2013), and we believe that there is evidence for an effect on our sites based on the negative relationship between texture and *Arthraxon* abundance in the CCA model (e.g., *Arthraxon* was associated with finer textured soils; Fig. 4). CCA modeling also showed that bioavailable P was positively correlated with *Arthraxon* abundance (Fig. 4), and this result is consistent with the other wetland studies that have found P availability important in regulating invasive populations (Chiang et al. 2000; Woo and Zedler 2002), as well as the potential for a P-limiting condition to be attenuated by the chemical reduction sequence in developing wetland soils (see discussion under *Microstegium* below).

Finally, the negative relationship between C:N and plant communities characterized by high *Arthraxon* abundance was not expected but is consistent with recent research on plant invasion. Conceptually, a high C:N condition would stimulate increased microbial activity, and as microbes oxidize low-nitrogen organic substrates for energy additional nitrogen sources will be required for protein synthesis, thus depleting nitrogen from the soil and causing an N-limitation (Iannone et al. 2008). Most invaders do not compete well under nutrient limitation (Bedford et al. 1999; Olde Venterink et al. 2003; Perry et al. 2004), so the negative correlation here is plausible. High C:N soil amendments have recently been reviewed as a potential invasive species control mechanism on some wetland invaders (Iannone et al. 2008; Hazelton et al. 2014).

### Microstegium

As with *Arthraxon*, the positive relationship between plant communities characterized by high *Microstegium* abundance and Pladj in the CCA model was anticipated. Although *Microstegium* tolerates periodic flooding (Touchette and Romanello 2010), in wetland environments it tends to inhabit moist, well-drained soils of floodplains and wetland edges (Warren et al. 2011) and does not appear to survive under long-term inundation (Nord et al. 2010). Plant species with higher (and therefore drier) wetland indicator values scores often inhabit wetland edges where soil saturation and flooding would occur less frequently and for shorter durations, making their association with *Microstegium* abundance understandable. The significant positive relationship between CEC and *Microstegium* abundance in the Spearman correlation analysis was not expected; however, it is supported by results of other studies in wetland habitats (Barden 1987; but see Gibson et al. 2002 for results in uplands) and coincides with a high disturbance/high resource availability model for *Microstegium* invasion (Nord et al. 2010; Warren et al. 2011) in that CEC tends to be positively related to soil fertility (Brady and Weil 2008). We suspect that the

negative relationship between soil texture and *Microstegium* abundance in the CCA model (Fig. 5) could be related to the CEC gradient as finer-textured soils would support an increase in cation adsorption sites, although it is also possible that texture could be related to localized disturbance gradients as discussed for *Arthraxon* above. The positive relationship between soil N and *Microstegium* abundance shown in the CCA analysis (Fig. 5) is consistent with the findings of other wetland studies (DeMeester and Richter 2010; Warren et al. 2011) and may reflect the positive feedback between enhanced N-uptake rates and increased nitrification rates under influence of a dominant *Microstegium* population (Ehrenfeld 2003).

Of interest is the negative relationship between plant communities characterized by high *Microstegium* abundance and canopy cover in the CCA analysis (Fig. 5), which seems counterintuitive given the documented shade-tolerance of this invader (Horton and Neufeld 1998). However, in most studies *Microstegium* has been shown to have a positive relationship with available light (Gibson et al. 2002; Nord et al. 2010; Schramm and Ehrenfeld 2010; Warren et al. 2011), so it ends up being the relative amount of light across the invasion gradient that is most important. *Microstegium* is competitive in lower light conditions due in part to the reduction of other herbaceous competitors imposed by shade (Oswalt et al. 2007), but also to superior photosynthetic efficiency when light becomes available (Horton and Neufeld 1998). On forested mitigation sites, increasing canopy closure results in a reduction in shade-intolerant herbaceous species (DeBerry and Perry 2012), and this can create a more suitable competitive environment for *Microstegium* as long as light levels are high enough to promote expansion (Gibson et al. 2002; Warren et al. 2011).

We believe that the negative relationship between Fe and plant communities characterized by high *Microstegium* abundance in the CCA model is an indirect indication of bioavailable P, which could be explained by the soil reduction sequence on developing wetland sites (DeBerry and Perry 2015). Although soil redox potential does not directly affect P transformations, an indirect effect may occur in the presence of metal oxides such as iron, manganese, and aluminum oxide, which immobilize otherwise bioavailable P by chemical precipitation (Ponnamperuma 1972; Mohanty and Dash 1982). As anoxia proceeds in saturated soils, metal oxide-bound P may be released as bioavailable phosphate during the chemical reduction sequence mediated by anaerobic microbial respiration on wetland mitigation sites (Stauffer and Brooks 1997; Hogan et al. 2004), in which case lower levels of Fe would indicate higher levels of P and support the high disturbance/high resource availability discussion above. Conversely, Fe-rich soils have been shown to increase the presence of P-sorption sites in

restored wetlands even under reducing conditions (Hogan et al. 2004), suggesting that areas that are high in Fe are likely to be low in bioavailable P. Although we measured soil P directly on our sites, there was a large degree variability in the P levels – over two orders of magnitude difference – and neither data transformations nor outlier analysis were able to rectify the large degree of variability in the correlations or the CCA analysis. Although the source of P variability was not clear, it seemed to be related to a few sites in the dataset and therefore could have been the result of the different management techniques used on those sites.

## Typha

The negative relationship between PIadj and plant communities characterized by high *Typha* abundance in the CCA model, which indicates that *Typha* inhabits wetter sites, was expected based on the extensive body of literature on this taxon (see Bansal et al. 2019 for a comprehensive review). *Typha* uses pressurized ventilation to induce convective throughflow of gases through its extensive rhizome network, thereby delivering oxygen to the roots and allowing *Typha* to persist in deeper water alongside other obligate hydrophytes for prolonged periods of time (Tornbjerg et al. 1994). Further, species in the genus are generally considered shade-intolerant (Bansal et al. 2019), so the negative relationship between canopy cover and *Typha* abundance in our CCA model was not surprising (Fig. 6).

We did not expect the negative relationship between soil Mn and *Typha* communities that emerged from the CCA analysis; however, we attribute this to the metal oxide/P-sorption dynamics described under *Microstegium* above. Oxidized Mn functions in much the same way as other metal cations to immobilize bioavailable P (Reddy et al. 2005), so we suspect that the Mn eigenvector in Fig. 6 is an indirect reflection of P dynamics across the invasion gradient (with the same caveat regarding variability in P measurements noted under the *Microstegium* discussion above).

Finally, that site age was positively related to plant communities characterized by high *Typha* abundance was also unexpected (Fig. 6). *Typha* has been shown to exhibit autogenic control over its own habitat through detritus accumulation (Vaccaro et al. 2009; Larkin et al. 2012), owing mostly to the refractory nature of *Typha* litter (Álvarez and Bécarea 2006). Under this scenario, we expected accumulated litter to increase substrate elevations, create a localized drying effect, and encourage recruitment of other species that could more successfully compete with and eventually eliminate *Typha* over time (Perry et al. 2009; DeBerry and Perry 2012). However, studies on *Typha* invasion have suggested that litter production serves to suppress competition and promote invasion (Vaccaro et al. 2009; Tuchman

et al. 2009; Larkin et al. 2012), and on wetland mitigation sites this has been referred as a “autogenic dominance” in reference to plant community development (Noon 1996; DeBerry and Perry 2012). Shading by both living and dead *Typha* tissue has been demonstrated to incur a similar autogenic result (Elgersma et al. 2017; Woo and Zedler 2002) and may have played a role in the resulting age-dependent relationship with *Typha* communities on mitigation sites. Although several of our *Typha* sites were 15+ years old, autogenic dominance has been noted by others on created wetland sites as old as 20 years in Virginia (Atkinson et al. 2005). If this is happening on our sites, it would explain the positive relationship between *Typha* dominance and age, and presumably indicate that *Typha* populations on younger sites had not yet developed a litter layer or low-light condition sufficient to suppress competitors.

## Summary and Recommendations

By studying environmental variability along invasion gradients in wetland mitigation settings, we have learned that environmental variables serving as potential stressors also function as potential drivers for plant community composition and invasive species prevalence on compensatory wetland mitigation sites. We anticipate that a “high disturbance/low stress” model for plant invasion could explain the general resource acquisition strategies for all of our target invaders, but further study specifically examining the disturbance component of this hypothesis would be required to adequately substantiate the model’s bearing on our findings. The specified result holds true even though our target invaders exhibit different life history strategies (e.g., annual grasses vs. tall emergent perennials) and span a wide range of tolerance for environmental gradients (e.g., *Typha* vs. *Microstegium* with respect to site hydrology), suggesting that these concepts could be generalizable to other invasive species.

Among environmental drivers, canopy cover (light availability) was conspicuous in that it was an important driver of plant community structure within populations of all three target organisms. This is noteworthy because it indicates a potential confluence between theory and practice that could be actionable on mitigation sites during the construction phase (see below). This is also the case for wetland hydrology, which was a significant factor influencing community structure within populations of all study species in the datasets. Although our evaluation of soil chemistry produced results that varied by species, our interpretation is that the usual suspects from the literature (N and P) underlie the gradients we observed in our community models. Where soil texture was important, it seemed to signal localized

disturbance, and this was judged to be a very probable consequence of legacy effects from construction-phase activities, and active site management.

All of the above environmental drivers give us a clearer picture of the causes and consequences of invasion on mitigation sites and suggest some potential proactive measures that could be implemented to reduce risk of invasion and encourage desirable native plant communities at the outset of a mitigation project: (1) planting trees from larger stock types, at higher densities, and/or with a composition that favors early successional species (e.g., *Salix nigra*; McLeod et al. 2001; DeBerry and Perry 2012) to promote canopy development and hasten canopy cover; (2) planting a seed mix with a high percentage of fast-growing annual species supplemented with high richness of perennials and early successional tree seeds to maximize potential for rapid germination and ecosystem resiliency, thereby advantaging the native species via the competitive edge promoted by early establishment (Reinartz and Warne 1993; Stauffer and Brooks 1997); (3) proactively managing hydrology during the establishment phase (1–5 years post construction) to reduce risk of invasion by targeting ecological tolerances of invaders (DeBerry and Perry 2015); and, (4) managing the number and severity of stressors within a site to establish environmental filters that will attenuate the risk of invasion during the establishment phase.

With respect to the latter, we believe that environmental stressors play a role in resource acquisition and competition by both native and invasive vegetation on wetland mitigation sites. Our observations suggest that risk of invasion increases under decreased stress, especially when baseline levels of environmental disturbance are high. These results receive some support in the literature on biological invasion and resource strategies of wild plants (Craine 2009; Lockwood et al. 2013). Stress in wetland mitigation is experienced by plants in various ways, but disturbance is more or less the same: sites are cleared and graded as necessary to establish appropriate elevations and desired landforms, soil conditions are often manipulated through excavation, tilling, or addition of soil amendments, and vegetation is selectively removed by herbicide application, mowing, or hand-pulling to improve conditions for target plant communities. Thus, the types of activities used in the construction sequence for a wetland mitigation site are also the types of activities that could “open the door” for biological invasion. If the “disturbance” half of the stress-disturbance dynamic is an unavoidable consequence of the construction sequence, there may be alternative approaches that would allow mitigation designers and managers to introduce stressful conditions to limit the opportunities for specific invaders to colonize and dominate a site.

Imposing stress on a mitigation site seems like a counterintuitive management strategy, but our research suggests that it could be used to increase native species richness and reduce the risk of invasion (Alpert et al. 2000; Bryson and Carter 2004), particularly in the establishment phase of a mitigation site (DeBerry and Perry 2015). Factors that could be controlled to induce environmental stress include shade (#1 and #2 above), hydrology (#3), and nutrient availability and/or limitation. One example of a potentially low-cost stress induction method would be to use soil amendments with a high carbon:nitrogen ratio (e.g., sawdust, or wood chips). High carbon:nitrogen ratio materials have been shown to stimulate microbially-mediated removal of nitrogen from the soil, thereby inducing a nitrogen limitation (stress) that could potentially favor native species over invaders (Perry et al. 2004; Iannone and Galatowitsch 2008). Other examples include addition of metal oxides such as aluminum and iron oxide to the soil. Metal oxides and other cationic forms with strong anion exchange capacities are known to complex with and immobilize phosphate, thus reducing its bioavailability and potentially inducing a phosphorus limitation (stress) (Stauffer and Brooks 1997; Hogan et al. 2004). Industrially manufactured forms such as alum are reasonably affordable in bulk and have been used for this same purpose in freshwater lakes (Douglas et al. 2016). Field trials to evaluate the efficacy of these types of management strategies on wetland restoration sites would enhance habitat manager's ability to implement ecology-based management strategies and limit invasive plant prevalence in created and restored wetlands.

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**Data Availability** The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

## Declarations

**Competing Interests** The authors have no relevant financial or non-financial interests to disclose.

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## References

- Adams SN, Engelhardt KAM (2009) Diversity declines in *Microstegium vimineum* (japanese stiltgrass) patches. *Biol Conserv* 142:1003–1010. <https://doi.org/10.1016/j.biocon.2009.01.009>
- Ahn C, Dee S (2011) Early development of plant community in a created mitigation wetland as affected by introduced hydrologic design elements. *Ecol Eng* 37:1324–1333. <https://doi.org/10.1016/j.ecoleng.2011.03.019>
- Alpert P, Bone E, Holzapfel C (2000) Invasiveness, invasibility and the role of environmental stress in the spread of non-native plants. *Perspectives in Plant Ecology. Evol Syst* 3:52–66
- Álvarez JA, Bécares E (2006) Seasonal decomposition of *Typha latifolia* in a free-water surface constructed wetland. *Ecol Eng* 28:99–105
- Angeloni NL, Jankowski KJ, Tuchman NC, Kelly JJ (2006) Effects of an invasive cattail species (*Typha × glauca*) on sediment nitrogen and microbial community composition in a freshwater wetland. *FEMS Microbiol Lett* 263:86–92. <https://doi.org/10.1111/j.1574-6968.2006.00409.x>
- Atkinson RB, Perry JE, Smith E, Cairns J (1993) Use of created wetland delineation and weighted averages as a component of assessment. *Wetlands* 13:185–193. <https://doi.org/10.1007/BF03160879>
- Atkinson RB, Perry JE, Cairns J (2005) Vegetation communities of 20-year-old created depressional wetlands. *Wetlands Ecol Manage* 13:469–478
- Bansal S, Lishawa SC, Newman S, Tangen BA, Wilcox D, Albert D, Anteau MJ, Chimney MJ, Cressey RL, DeKeyser E, Elgersma KJ (2019) *Typha* (cattail) invasion in north american wetlands: biology, regional problems, impacts, ecosystem services, and management. *Wetlands* 39:645–684
- Barden LS (1987) Invasion of *Microstegium vimineum* (Poaceae), an exotic, Annual, Shade-Tolerant, C4 grass, into a North Carolina Floodplain. *Am Midl Nat* 118:40–45. <https://doi.org/10.2307/2425626>

- Bazzaz FA (1996) Plants in changing environments: linking physiological, Population, and Community Ecology. Cambridge University Press
- Beckschäfer P (2015) Hemispherical\_2.0 – Batch processing hemispherical and canopy photographs with ImageJ – User Manual
- Bedford BL, Walbridge MR, Aldous A (1999) Patterns in nutrient availability and plant diversity of temperate north american wetlands. *Ecology* 80:2151–2169
- Bergdolt FS, Prehmus CA, Barham JB (2005) An evaluation of Wetland Mitigation Site Compliance at the Washington State Department of Transportation. Washington State Department of Transportation. Olympia, WA
- Borcard D, Gillet F, Legendre P (2018) Numerical Ecology with R. Springer, NY
- Brady NC, Weil RR (2008) The Nature and Properties of Soils. Prentice Hall, NJ
- Brandon AL, Gibson DJ, Middleton BA (2004) Mechanisms for dominance in an early successional old field by the invasive non-native *Lespedeza cuneata* (dum. Cours. ) G Don Biological Invasions 6:483–493. <https://doi.org/10.1023/B:BINV.0000041561.71407.f5>
- Brooks RP, Gebo NA (2013) Wetlands Restoration and Mitigation. In: Brooks RP, Heller DW (eds.) Mid-Atlantic Freshwater Wetlands: Advances in Wetlands Science, Management, Policy, and Practice. Springer New York, pp 421–440
- Bryson CT, Carter R (2004) Biology of pathways for invasive weeds. *Weed Technol* 18:1216–1220
- Callaway RM, Ridenour WM (2004) Novel weapons: invasive success and the evolution of increased competitive ability. *Front Ecol Environ* 2:436–443
- Chiang C, Craft CB, Rogers DW, Richardson CJ (2000) Effects of 4 years of nitrogen and phosphorus additions on everglades plant communities. *Aquat Bot* 68:61–78
- R Core Team (2014) R: A Language and Environment for Statistical Computing. Available via. <https://www.r-project.org/>
- Craine JM (2009) Resource strategies of wild plants. Princeton University Press
- DeBerry DA, Perry JE (2012) Vegetation dynamics across a chronosequence of created wetland sites in Virginia, USA. *Wetlands Ecol Manage* 20:521–537. <https://doi.org/10.1007/s11273-012-9273-3>
- DeBerry DA, Perry JE (2015) Using the floristic quality concept to assess created and natural wetlands: ecological and management implications. *Ecol Ind* 53:247–257. <https://doi.org/10.1016/j.ecolind.2015.02.003>
- DeMeester JE, Richter D (2010) Differences in wetland nitrogen cycling between the invasive grass *Microstegium vimineum* and a diverse plant community. *Ecol Appl* 20:609–619
- Douglas GB, Hamilton DP, Robb MS, Pan G, Spears BM, Lurling M (2016) Guiding principles for the development and application of solid-phase phosphorus adsorbents for freshwater ecosystems. *Aquat Ecol* 50:385–405
- Ehrenfeld JG (2003) Effects of exotic plant invasions on soil nutrient cycling processes. *Ecosystems* 6:503–523
- Ehrenfeld JG (2010) Ecosystem consequences of biological invasions. *Annu Rev Ecol Syst* 41:59–80
- Elgersma KJ, Martina JP, Goldberg DE, Currie WS (2017) Effectiveness of cattail (*Typha* spp.) management techniques depends on exogenous nitrogen inputs. *Elem Sci Anth* 5:19. <https://doi.org/10.1525/elementa.147>
- Flory SL (2010) Management of *Microstegium vimineum* invasions and recovery of resident plant communities. *Restor Ecol* 18:103–112. <https://doi.org/10.1111/j.1526-100X.2008.00425.x>
- Galatowitsch SM, Anderson NO, Ascher PD (1999) Invasiveness in wetland plants in temperate North America. *Wetlands* 19:733–755. <https://doi.org/10.1007/BF03161781>
- Gibson DJ, Spyreas G, Benedict J (2002) Life history of *Microstegium vimineum* (Poaceae), an invasive grass in southern Illinois. *J Torrey Bot Soc* 129:207–219
- Green EK, Galatowitsch SM (2001) Differences in wetland plant community establishment with additions of nitrate-N and invasive species (*Phalaris arundinacea* and *Typha × glauca*). *Can J Bot* 79:170–178
- Grime JP (1977) Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *Am Nat* 111:1169–1194
- Grime JP (1979) Plant strategies and vegetation processes. John Wiley and Sons, London, UK
- Grime JP, Pierce S (2012) The evolutionary strategies that shape ecosystems. John Wiley & Sons
- Harrell FE, Dupont C (2020) Hmisc: Harrell Miscellaneous. R package version 4.4-2. <https://CRAN.R-project.org/package=Hmisc>
- Hazelton EL, Mozdzer TJ, Burdick DM, Kettenring KM, Whigham DF (2014) Phragmites australis management in the United States: 40 years of methods and outcomes. *AoB Plants* 6:plu001
- Heffernan K, Engle E, Richardson C (2014) Virginia Invasive Plant Species List. Available via [www.dcr.virginia.gov/natural\\_heritage/invspinfo.shtml](http://www.dcr.virginia.gov/natural_heritage/invspinfo.shtml)
- Hobbs RJ, Huenneke LF (1992) Disturbance, diversity, and invasion: implications for conservation. *Conserv Biol* 6:324–337
- Hogan DM, Jordan TE, Walbridge MR (2004) Phosphorus retention and soil organic carbon in restored and natural freshwater wetlands. *Wetlands* 24:573–585
- Horton JL, Neufeld HS (1998) Photosynthetic responses of *Microstegium vimineum* (trin.) A. Camus, a shade-tolerant, C4 grass, to variable light environments. *Oecologia* 114:11–19
- Iannone BV III, Galatowitsch SM (2008) Altering light and soil N to limit *Phalaris arundinacea* reinvasion in sedge meadow restorations. *Restor Ecol* 16:689–701
- Iannone III BV, Galatowitsch SM, Rosen CJ (2008) Evaluation of resource-limiting strategies intended to prevent *Phalaris arundinacea* (reed canarygrass) invasions in restored sedge meadows. *Ecoscience* 15:508–518
- Judge CA, Neal JC, Derr JF (2005) Response of Japanese stiltgrass (*Microstegium vimineum*) to application timing, rate, and frequency of postemergence herbicides. *Weed Technol* 19:912–917. <https://doi.org/10.1614/WT-04-272R.1>
- Keane RM, Crawley MJ (2002) Exotic plant invasions and the enemy release hypothesis. *Trends Ecol Evol* 17:164–170
- Kindt R, Coe R (2005) Tree diversity analysis: a Manual and Software for Common Statistical Methods for Ecological and Biodiversity Studies. World Agroforestry Centre
- Larkin DJ, Freyman MJ, Lishawa SC, Geddes P, Tuchman NC (2012) Mechanisms of dominance by the invasive hybrid cattail *Typha × glauca*. *Biol Invasions* 14:65–77. <https://doi.org/10.1007/s10530-011-0059-y>
- Lawrence BA, Lishawa SC, Rodriguez Y, Tuchman NC (2016) Herbicide management of invasive cattail (*Typha × glauca*) increases porewater nutrient concentrations. *Wetlands Ecol Manage* 24:457–467. <https://doi.org/10.1007/s11273-015-9471-x>
- Legendre P, Gallagher ED (2001) Ecologically meaningful transformations for ordination of species data. *Oecologia* 129:271–280
- Legendre P, Legendre L (2012) Numerical Ecology. Elsevier, Amsterdam, The Netherlands
- Lichtenthaler HK (1996) Vegetation stress: an introduction to the stress concept in plants. *J Plant Physiol* 148:4–14
- Lichvar RW, Banks DL, Kirchner DL, Melvin NC (2016) The National Wetland Plant List: 2016 wetland ratings. *Phytoneuron* 2016:1–17
- Lockwood JL, Hoopes MF, Marchetti MP (2013) Invasion Ecology. John Wiley & Sons, UK
- Maguire RO, Heckendorn SE (2019) Laboratory procedures: Virginia Tech Soil Testing Laboratory. Publication 452–881, SPES-91P.

- Virginia Polytechnic Institute and State University, Blacksburg, Virginia
- Marshall JM, Buckley DS (2009) Influence of *Microstegium vimineum* presence on insect abundance in hardwood forests. *Southeast Nat* 8:515–526
- Matthews JW, Endress AG (2008) Performance criteria, compliance success, and vegetation development in compensatory mitigation wetlands. *Environ Manage* 41:130–141
- Matthews JW, Spyreas G (2010) Convergence and divergence in plant community trajectories as a framework for monitoring wetland restoration progress. *J Appl Ecol* 47:1128–1136
- Matthews JW, Peralta AL, Soni A, Baldwin P, Kent AD, Endress AG (2009) Local and landscape correlates of non-native species invasion in restored wetlands. *Ecography* 32:1031–1039
- McCune B, Grace JB (2002) Analysis of Ecological Communities. MjM Software Design
- McLeod KW, Reed MR, Nelson EA (2001) Influence of a willow canopy on tree seedling establishment for wetland restoration. *Wetlands* 21:395–402
- Miller NP, Matlack GR (2010) Population expansion in an invasive grass, *Microstegium vimineum*: a test of the channelled diffusion model. *Divers Distrib* 16:816–826. <https://doi.org/10.1111/j.1472-4642.2010.00690.x>
- Mitsch WJ, Gosselink JG (2015) *Wetlands*, 5th edn. Wiley, NJ
- Mohanty SK, Dash RN (1982) The Chemistry of Waterlogged Soils. In: Gopal B, Turner RE, Wetzel RG, Whigham DF (eds) *Wetlands – Ecology and Management*. Natural Institute of Ecology and International Scientific Publications, Jaipur, India, pp 389–396
- Mueller-Dombois D, Ellenberg H (1974) *Aims and methods of Vegetation Ecology*. Wiley and Sons
- Noon KF (1996) A model of created wetland primary succession. *Landsc Urban Plann* 34:97–123
- Nord AN, Mortensen DA, Rauschert ES (2010) Environmental factors influence early population growth of Japanese stiltgrass (*Microstegium vimineum*). *Invasive Plant Science and Management* 3:17–25
- Oksanen J, Guillaume Blanchet F, Friendly M, Kindt R, Legendre P, McGlenn D, Minchin PR, O'Hara RB, Simpson GL, Solyomos P, Henry M, Stevens H, Szocs E, Wagner H (2020) *vegan*: Community Ecology Package. R package version 2.5-7. <https://CRAN.R-project.org/package=vegan>
- Olde Venterink H, Wassen MJ, Verkroost AW, De Ruiter PC (2003) Species richness–productivity patterns differ between N-, P-, and K-limited wetlands. *Ecology* 84:2191–2199
- Oswalt CM, Oswalt SN, Clatterbuck WK (2007) Effects of *Microstegium vimineum* (trin.) A. Camus on native woody species density and diversity in a productive mixed-hardwood forest in Tennessee. *For Ecol Manag* 242:727–732. <https://doi.org/10.1016/j.foreco.2007.02.008>
- Peck J (2016) *Multivariate Analysis for Ecologists: step by step*, 2nd edn. MjM Software Design, Gleneden Beach, OR
- Perry LG, Galatowitsch SM, Rosen CJ (2004) Competitive control of invasive vegetation: a native wetland sedge suppresses *Phalaris arundinacea* in carbon-enriched soil. *J Appl Ecol* 41:151–162
- Perry JE, Morgan EE, Bevington AE, DeBerry DA (2009) Understanding cattail (*Typha* spp.) invasion and persistence in forested wetlands created by the Virginia Department of Transportation. Technical Report FHWA/VTRC 09-CR10. Virginia Transportation Research Council, Charlottesville, VA
- Petru BJ, Ahn C, Chescheir G (2013) Alteration of soil hydraulic properties during the construction of mitigation wetlands in the Virginia Piedmont. *Ecol Eng* 51:140–150
- Ponnamperuma FN (1972) The chemistry of submerged soils. *Advances in Agronomy*. Academic Press, New York, New York, pp 29–96
- Reddy KR, Wetzel RG, Kadlec RH (2005) Biogeochemistry of phosphorus in wetlands. *Agron Monogr* 46:263–316
- Reinartz JA, Warne EL (1993) Development of vegetation in small created wetlands in southeastern Wisconsin. *Wetlands* 13:153–164
- Ritchey EL, McGrath JM, Gehring D (2015) *Determining Soil Texture by Feel*. Agriculture and Natural Resources Publications, Cooperative Extension Service, University of Kentucky. AGR-217. [https://uknowledge.uky.edu/anr\\_reports/139](https://uknowledge.uky.edu/anr_reports/139)
- Robertson DJ, Robertson MC, Tague T (1994) Colonization dynamics of four exotic plants in a northern Piedmont natural area. *Bull Torrey Bot Club* 121:107–118
- Rueden CT, Schindelin J, Hiner MC et al (2017) ImageJ2: ImageJ for the next generation of scientific image data. *BMC Bioinformatics* 18:529
- Schramm JW, Ehrenfeld JG (2010) Leaf litter and understory canopy shade limit the establishment, growth and reproduction of *Microstegium vimineum*. *Biol Invasions* 12:3195–3204
- Stauffer AL, Brooks RP (1997) Plant and soil responses to salvaged marsh surface and organic matter amendments at a created wetland in central Pennsylvania. *Wetlands* 17:90–105
- Sullivan L, Wildova R, Goldberg D, Vogel C (2010) Growth of three cattail (*Typha*) taxa in response to elevated CO<sub>2</sub>. *Plant Ecol* 207:121–129. <https://doi.org/10.1007/s11258-009-9658-4>
- Swearingen J, Slattery B, Reshetiloff K, Zwicker S (2010) *Plant Invaders of Mid-Atlantic Natural Areas*, 4th edn. National Park Service and U.S. Fish and Wildlife Service. Washington, DC
- ter Braak CJ (1986) Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. *Ecology* 67:1167–1179
- Tiner RW (2017) *Wetland Indicators: a guide to Wetland formation, identification, Delineation, classification, and Mapping*. CRC press
- Tornbjerg T, Bendix M, Brix H (1994) Internal gas transport in *Typha latifolia* L. and *Typha angustifolia* L. 2. Convective throughflow pathways and ecological significance. *Aquat Bot* 49:91–105
- Touchette BW, Romanello GA (2010) Growth and water relations in a central North Carolina population of *Microstegium vimineum* (trin.) A. Camus. *Biol Invasions* 12:893–903
- Tuchman NC, Larkin DJ, Geddes P, Wildova R, Jankowski K, Goldberg DE (2009) Patterns of environmental change associated with *Typha x glauca* invasion in a great lakes coastal wetland. *Wetlands* 29:964–975
- Vaccaro LE, Bedford BL, Johnston CA (2009) Litter Accumulation promotes dominance of Invasive Species of cattails (*Typha* spp.) in Lake Ontario Wetlands. *Wetlands* 29:1036–1048. <https://doi.org/10.1672/08-28.1>
- van der Valk AG (1981) Succession in wetlands: a Gleasonian approach. *Ecology* 62:688–696
- Warren RJ, Wright JP, Bradford MA (2011) The putative niche requirements and landscape dynamics of *Microstegium vimineum*: an invasive Asian grass. *Biol Invasions* 13:471–483. <https://doi.org/10.1007/s10530-010-9842-4>
- Weakley AS, Ludwig JC, Townsend JT, Fleming GP (2020) *Flora of Virginia*. With significant additions and updates. Mobile app. In: Crowder B (ed) *Foundation of the Flora of Virginia Project Inc. High Country Apps*, Bozeman, MT, Richmond, VA
- White L, Catterall C, Taffs K (2020) The habitat and management of hairy jointgrass (*Arthraxon hispidus*, Poaceae) on the north coast of New South Wales, Australia. *Pac Conserv Biology* 26:45–56
- Wiltermuth MT, Anteau MJ (2016) Is consolidation drainage an indirect mechanism for increased abundance of cattail in northern prairie wetlands? *Wetlands Ecol Manage* 24:533–544. <https://doi.org/10.1007/s11273-016-9485-z>
- Wool I, Zedler JB (2002) Can nutrients alone shift a sedge meadow towards dominance by the invasive *Typha x glauca*. *Wetlands* 22:509–521.

[https://doi.org/10.1672/0277-5212\(2002\)022\[0509:CNASAS\]2.0.CO;2](https://doi.org/10.1672/0277-5212(2002)022[0509:CNASAS]2.0.CO;2)

Zedler JB, Kercher S (2004) Causes and consequences of invasive plants in wetlands: opportunities, opportunists, and outcomes. *CRC Crit Rev Plant Sci* 23:431–452

Ziska LH, Tomecek MB, Valerio M, Thompson JP (2015) Evidence for recent evolution in an invasive species, *Microstegium*

*vimineum*, japanese stiltgrass. *Weed Res* 55:260–267. <https://doi.org/10.1111/wre.12138>

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