Environmental Drivers of Plant Invasion in Wetland Mitigation

Dakota M. Hunter (dmhunter@email.wm.edu)
College of William & Mary: William & Mary https://orcid.org/0000-0002-2496-0538
Douglas A DeBerry
College of William & Mary: William & Mary

Research Article

Keywords: Invasive species, wetland mitigation, Microstegium vimineum, Arthraxon hispidus, Typha spp., environmental ecology

Posted Date: November 1st, 2022

DOI: https://doi.org/10.21203/rs.3.rs-2046029/v1

Version of Record: A version of this preprint was published at Wetlands on September 5th, 2023. See the published version at https://doi.org/10.1007/s13157-023-01718-y.

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 important environmental drivers of plant invasions on wetland mitigation sites. We sampled vegetation and environmental variables (site hydrology, light availability, soil physiochemistry, site age) across invasion gradients at multiple wetland mitigation sites in the Coastal Plain and Piedmont physiographic provinces of Virginia. Data analysis involved a multi-metric statistical approach combining correlation, AIC, and CCA to arrive at a plausible model for invasion risk by species based on environmental correlates. We targeted *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 analysis revealed species-specific environmental drivers of invasion with a few factors consistently important across all targeted invaders – notably, canopy cover (light availability), hydrology, and a handful of important 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 reduce the risk of invasion.

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 synergistically 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 disproportionally large presence in wetlands in comparison with other habitats (Zedler and Kercher 2004), and this is especially true for wetland mitigation sites (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 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* and *Typha* spp. (Galatowitsch et al. 1999; Zedler and Kercher 2004), but consensus remains unreached. On compensatory wetland mitigation sites (i.e., wetland sites created or restored to compensate for impacts to wetlands elsewhere), 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 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.

From the primary literature on invasion ecology, we believe that theoretical concepts developed around 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 strong evidence to support the notion that sites with high levels of disturbance – which is the case for most recently constructed wetland mitigation sites – combined with low levels of environmental stress (i.e., high resource availability) are the ones that are most susceptible to invasion (Alpert et al. 2000).

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 invasion (Alpert et al. 2000; Ehrenfeld 2010). However, in wetlands, hydrology 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 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, etc.), 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: *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. Although we expected wetland hydrology 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 wetland hydrology has 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 site hydrology. Conversely, *Typha* was reliably observed in lower, wetter areas, and was therefore expected to show a positive correlation with site hydrology. 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 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 association with changes in nutrient cycling and surface flow 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. On multi-user sites, distinct “phases” or areas constructed during separate time periods were treated independently so long as they fell into different age classes (this was a common condition on study sites operating as mitigation banks). The age classes were determined from site records on the number of complete growing seasons after site construction and included: 1-2 years old; 3-5 years old; 6-10 years old; 11-15 years old; and >15 years old.

Among the sites screened during site reconnaissance, 23 met suitability criteria and were selected for the study. 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 (Figure 2). Most sites were either mitigation banks or in-lieu fee sites (i.e., sites established under the Virginia Aquatic Resources Trust Fund).

Research Design and Data Collection

Sampling transects consisted of five identical $4m^2$ (2m x 2m) 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

The randomization procedure for transect/plot layout involved identifying the center of an invasive species population within a given site and establishing a $4m^2$ grid with 9 vertices (Figure 3). Using a random numbers 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 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 $4m^2$ 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) (Figure 3). Transect length varied among sites but typically ranged from 50 to 100 meters.

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 10cm using a 6cm-diameter soil corer. Soil samples were textured on-site using field methods (Ritchey et al. 2015), 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).

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 meter above the

ground in *Arthraxon* and *Microstegium* plots, and from 2 meters 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 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 $1m^2$ subplots nested in the $4m^2$ 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 $1m^2$ 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 (hydrology) between wetland sites (Atkinson et al. 1993; Tiner 2017). 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 Plantlist (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).

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).

Canonical Correspondence Analysis (CCA) (ter Braak 1986) was used to evaluate the overall community response to environmental variation along the invasion gradient. 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%), *Symphyotrichum 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 significantly correlated with canopy cover (r_s=-0.295, p=0.037) and hydrology (r_s= -0.363, p=0.010). In both cases, the relationship was negative, i.e., *Arthraxon* was more prevalent in areas with less canopy cover and relatively drier conditions. 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 five environmental variables – hydrology, canopy cover, texture, carbon:nitrogen ratio (C:N), and phosphorus (P) – which accounted for 23% of the total inertia in the ordination. All environmental factors (eigenvectors) were significant at p<0.001 with the exception of P (p=0.046).

The ordination biplot (Figure 4) displays red arrows as eigenvectors for environmental variables, with the vector length corresponding to strength of correlation and vector direction indicating either a positive or negative relationship (e.g., plots aligned in the direction of and projected perpendicularly to an arrow are positively correlated with that environmental variable, and vice-versa). Circles on the figure represent plots, and circle size corresponds to the absolute abundance of *Arthraxon* within that plot (i.e., larger circles have higher abundance values). The first two ordination axes explained over 53% of the variation in the CCA and thus were retained for the biplot. As Figure 4 shows, hydrology and C:N were strong environmental factors that appeared negatively correlated with higher *Arthraxon* abundance, while P appeared positively correlated. Texture was less important as an explanatory variable in the first two axes of the ordination but based on the eigenvector direction texture was negatively correlated with *Arthraxon* abundance (i.e., texture values in the dataset were arranged on an ordinal scale from fine to coarse, so plots with higher *Arthraxon* abundance tended to be associated with lower texture values and, therefore, finer textured soils). Finally, increasing canopy cover appeared to be more aligned with plots that had low abundance values for *Arthraxon*.

Microstegium

Spearman results indicated that *Microstegium* abundance was positively correlated with cation exchange capacity (CEC) (r_s=0.337, p=0.017) and negatively correlated with hydrology (r_s=-0.602, p<<0.001). 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 – hydrology, canopy cover, texture, nitrogen (N), and iron (Fe) – which accounted for 22% of the total inertia in the ordination. All environmental factors (eigenvectors) were significant at p<0.001 with the exception of Fe (p=0.005). The first two ordination axes displayed in Figure 5 explained over 51% of the CCA variation. As with *Arthraxon*, hydrology, canopy cover, and texture were negatively correlated with *Microstegium* abundance. The other two important factors, N and Fe, showed positive and negative relationships with *Microstegium* abundance, respectively.

Typha

Spearman correlations showed that hydrology was positively correlated with *Typha* abundance (r_s=0.374, p=0.001). No other environmental variables were significantly related to *Typha* in the correlation matrix. The CCA analysis used a *Typha* 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 – hydrology, canopy cover, site age, and manganese (Mn) – which accounted for 16% of the total inertia in the ordination. All environmental factors were significant in the model at p<0.001 except canopy cover (p=0.003). The first two ordination axes explained 65% of the CCA variation. As Figure 6 demonstrates, hydrology and canopy cover were important factors in the analysis, and canopy cover was negatively correlated with *Typha* abundance similarly to the other two wetland invaders. However, unlike *Arthraxon* and *Microstegium*, hydrology was *positively* associated with the invasion gradient, as indicated by the coalignment between the hydrology eigenvector and the plots where *Typha* was most dominant. 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 antagonistic.

Discussion

Along the invasion gradients sampled in this study, variables relating to soils, hydrology, and light availability (canopy cover) all emerged as drivers of plant community structure on wetland mitigation sites. Of these drivers, hydrology and canopy cover persistently showed a strong relationship with invasive species prevalence. As is common in analyses of complex ecological data, no single environmental variable materialized as the most important, although hydrology did show strong correlation with the abundance of all three invaders in both the Spearman analysis and the CCA ordinations (Figs. 4 through 6). This is not surprising given the importance of hydrology in structuring wetland plant communities (van der Valk 1981), and from our modeling it is evident that hydrology works synergistically 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 relationships between *Arthraxon* abundance and both hydrology and canopy cover were 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, 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 texture (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 antagonistic relationship between C:N and *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 significant negative correlation between *Microstegium* abundance and hydrology 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). 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 *Microstegium* abundance and canopy cover in the CCA analysis (Fig. 5), which seems counterintuitive given the documented shade-tolerance of this invader (Horton and Neufield 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 *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 variance 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 positive correlation between wetland hydrology and *Typha* abundance was expected based 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 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* 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 *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 Bécares 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). 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 sufficient to suppress competitors.

Summary And Recommendations

By studying environmental variability along invasion gradients in wetland mitigation settings, we have learned that a “high disturbance/low stress” model for plant invasion – which is one of the most important unifying principles in the foundational literature on plant invasions – accords with the ecological amplitudes and general resource acquisition strategies for all of our target invaders. It bears mentioning that this is the case 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).

Among environmental drivers, canopy cover (light availability) was conspicuous in that it was important across the invasion gradients 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 for 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 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) manipulating the stress-disturbance dynamic to establish environmental filters that will attenuate the risk of invasion during the establishment phase.

With respect to the latter, we believe that the most instructive model for understanding plant invasions on mitigation sites is one that combines environmental stress and disturbance to predict trends in resource acquisition and competition. Our observations suggest that risk of invasion increases with increased disturbance and decreased stress, which is consistent with 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, and soil conditions are often manipulated through excavation, tilling, or addition of soil amendments 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 typically “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 manipulate the “stress” half to reduce risk of invasion.

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, wood chips, etc.). 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). Our research team is currently engaged in field trials to evaluate the efficacy of these types of management strategies on wetland restoration sites.

Declarations

STATEMENT OF FUNDING

This research was supported by RFP #8 granted to D. A. DeBerry by the Resource Protection Group.

STATEMENT OF COMPETING INTERESTS

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

AUTHOR CONTRIBUTIONS

Both Douglas A. DeBerry and Dakota M. Hunter contributed to study conception and design, data analysis and material preparation. Data collection was performed entirely by Dakota M. Hunter and the first draft of this manuscript was written by Dakota M. Hunter. Both Douglas A. DeBerry and Dakota M. Hunter read and approved the final manuscript.

STATEMENT OF DATA AVAILABILITY

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

ACKNOWLEDGEMENTS

This research was funded by a grant from The Resource Protection Group, and we would like to thank Mike Rolband and Jennifer Van Houten from WSSI for their leadership roles in that organization and their support throughout the project. We also would like to express our gratitude to the many mitigation bankers and site managers who graciously provided access to field sites and project-specific data (e.g., maps, reports, monitoring data, etc.). That list includes Wetland Studies and Solutions, Falling Springs, Stantec, The Nature Conservancy, Liesfield Construction, Bunrootis LLC, Southampton County Administration, and Virginia Habitats. Thanks as well to the Virginia Tech Soil Testing Lab for analyzing soil samples taken during this project. Finally, we'd like to thank the following scientists for valuable input on the sampling approach in the early phases of this project: Jim Perry, Wes Hudson, Bob Peet, Mary Kentula, Teresa Magee, Randy Chambers, Matthias Leu, and Drew Lamar.

References

1. Adams SN, Engelhardt KAM (2009) Diversity declines in *Microstegium vimineum* (Japanese stiltgrass) patches. Biological Conservation 142:1003-1010. https://doi.org/10.1016/j.biocon.2009.01.009
2. Ahn C, Dee S (2011) Early development of plant community in a created mitigation wetland as affected by introduced hydrologic design elements. Ecological Engineering 37:1324-1333. https://doi.org/10.1016/j.ecoleng.2011.03.019
3. 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, Evolution and Systematics 3:52-66.
4. Álvarez JA, Bécares E (2006) Seasonal decomposition of *Typha latifolia* in a free-water surface constructed wetland. Ecological Engineering 28:99-105.
5. 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 Microbiology Letters 263:86-92. https://doi.org/10.1111/j.1574-6968.2006.00409.x

6. 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
7. Atkinson RB, Perry JE, Cairns J (2005) Vegetation communities of 20-year-old created depressional wetlands. Wetlands Ecology and Management 13:469-478.
8. 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.
9. Barden LS (1987) Invasion of *Microstegium vimineum* (Poaceae), an Exotic, Annual, Shade-Tolerant, C4 Grass, into a North Carolina Floodplain. The American Midland Naturalist 118:40-45. https://doi.org/10.2307/2425626
10. Bazzaz FA (1996) Plants in Changing Environments: Linking Physiological, Population, and Community Ecology. Cambridge University Press.
11. Beckschäfer P (2015) Hemispherical_2.0 – Batch processing hemispherical and canopy photographs with ImageJ – User Manual.
12. Bedford BL, Walbridge MR, Aldous A (1999) Patterns in nutrient availability and plant diversity of temperate North American wetlands. Ecology 80:2151-2169.
13. 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.
14. Borcard D, Gillet F, Legendre P (2018) Numerical Ecology with R. Springer, NY.
15. Brady NC, Weil RR. 2008. The Nature and Properties of Soils. Prentice Hall, NJ.
16. 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
17. 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.
18. Bryson CT, and Carter R (2004) Biology of pathways for invasive weeds. Weed Technology 18:1216-1220.
19. Callaway RM, Ridenour WM (2004) Novel weapons: invasive success and the evolution of increased competitive ability. Frontiers in Ecology and the Environment 2:436-443.
20. Chiang C, Craft CB, Rogers DW, Richardson CJ (2000) Effects of 4 years of nitrogen and phosphorus additions on Everglades plant communities. Aquatic Botany 68:61-78.
21. Craine JM (2009) Resource Strategies of Wild Plants. Princeton University Press.

22. DeBerry DA, Perry JE (2015) Using the floristic quality concept to assess created and natural wetlands: Ecological and management implications. Ecological Indicators 53:247-257. https://doi.org/10.1016/j.ecolind.2015.02.003
23. DeBerry DA, Perry J E (2012) Vegetation dynamics across a chronosequence of created wetland sites in Virginia, USA. Wetlands Ecology and Management 20:521-537. https://doi.org/10.1007/s11273-012-9273-3
24. DeBerry DA (2006) Floristic Quality Index: ecological and management implications in created and natural wetlands (PhD Dissertation). William and Mary, Williamsburg, VA.
25. DeMeester JE, Richter D (2010) Differences in wetland nitrogen cycling between the invasive grass Microstegium vimineum and a diverse plant community. Ecological Applications 20:609-619.
26. 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. Aquatic Ecology 50:385-405.
27. Ehrenfeld JG (2003) Effects of exotic plant invasions on soil nutrient cycling processes. Ecosystems 6:503-523.
28. Ehrenfeld JG (2010) Ecosystem consequences of biological invasions. Annual Review of Ecology, Evolution, and Systematics 41:59-80.
29. Flory SL (2010) Management of *Microstegium vimineum* invasions and recovery of resident plant communities. Restoration Ecology 18:103-112. https://doi.org/10.1111/j.1526-100X.2008.00425.x
30. 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
31. Gibson DJ, Spyreas G, Benedict J (2002) Life history of *Microstegium vimineum* (Poaceae), an invasive grass in southern Illinois. Journal of the Torrey Botanical Society 129:207-219.
32. Green EK, Galatowitsch SM (2001) Differences in wetland plant community establishment with additions of nitrate-N and invasive species (*Phalaris arundinacea* and *Typha* × *glauca*). Canadian Journal of Botany 79:170-178.
33. Grime JP (1977) Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. The American Naturalist 111:1169-1194.
34. Grime JP (1979) Plant Strategies and Vegetation Processes. John Wiley and Sons, London, UK.
35. Grime JP, Pierce S (2012) The Evolutionary Strategies that Shape Ecosystems. John Wiley & Sons.
36. Harrell FE, Dupont C (2020) Hmisc: Harrell Miscellaneous. R package version 4.4-2. https://CRAN.R-project.org/package=Hmisc
37. 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
38. Heffernan K, Engle E, Richardson C (2014) Virginia Invasive Plant Species List. Available via www.dcr.virginia.gov/natural_heritage/invspinfo.shtml

39. Hobbs R J, Huenneke LF (1992) Disturbance, diversity, and invasion: implications for conservation. Conservation Biology 6:324-337.
40. Hogan DM, Jordan TE, Walbridge MR (2004) Phosphorus retention and soil organic carbon in restored and natural freshwater wetlands. Wetlands 24:573-585.
41. 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.
42. Iannone III BV, Galatowitsch SM (2008) Altering light and soil N to limit *Phalaris arundinacea* reinvasion in sedge meadow restorations. Restoration Ecology 16:689-701.
43. 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.
44. Judge CA, Neal JC, Derr JF (2005). Response of Japanese stiltgrass (*Microstegium vimineum*) to application timing, rate, and frequency of postemergence herbicides. Weed Technology 19:912-917. https://doi.org/10.1614/WT-04-272R.1
45. Keane RM, Crawley MJ (2002) Exotic plant invasions and the enemy release hypothesis. Trends in Ecology & Evolution 17:164-170.
46. Kindt R, Coe R (2005) Tree Diversity Analysis: A Manual and Software for Common Statistical Methods for Ecological and Biodiversity Studies. World Agroforestry Centre.
47. Larkin DJ, Freyman MJ, Lishawa SC, Geddes P, Tuchman NC (2012) Mechanisms of dominance by the invasive hybrid cattail *Typha* X *glauca*. Biological Invasions 14:65-77. http://dx.doi.org/10.1007/s10530-011-0059-y
48. Lawrence BA, Lishawa SC, Rodriguez Y, Tuchman NC (2016) Herbicide management of invasive cattail (*Typha* × *glauca*) increases porewater nutrient concentrations. Wetlands Ecology and Management 24:457-467. https://doi.org/10.1007/s11273-015-9471-x
49. Legendre P, Gallagher ED (2001) Ecologically meaningful transformations for ordination of species data. Oecologia 129:271-280.
50. Legendre P, Legendre L (2012) Numerical Ecology. Elsevier, Amsterdam, The Netherlands.
51. Lichtenthaler HK (1996) Vegetation stress: an introduction to the stress concept in plants. Journal of Plant Physiology 148:4-14.
52. Lichvar RW, Banks DL, Kirchner DL, Melvin NC (2016) The National Wetland Plant List: 2016 wetland ratings. Phytoneuron 2016:1-17.
53. Lockwood JL, Hoopes MF, Marchetti MP (2013) Invasion Ecology. John Wiley & Sons, UK.
54. Maguire RO, Heckendorn S E (2019) Laboratory procedures: Virginia Tech Soil Testing Laboratory. Publication 452-881, SPES-91P, Virginia Polytechnic Institute and State University, Blacksburg, Virginia
55. Marshall JM, Buckley DS (2009) Influence of *Microstegium vimineum* presence on insect abundance in hardwood forests. Southeastern Naturalist 8:515-526.

56. Matthews JW, Endress AG (2008) Performance criteria, compliance success, and vegetation development in compensatory mitigation wetlands. Environmental Management 41:130-141.
57. 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.
58. Matthews JW, Spyreas G (2010) Convergence and divergence in plant community trajectories as a framework for monitoring wetland restoration progress. Journal of Applied Ecology 47:1128-1136.
59. McCune B, Grace JB (2002) Analysis of Ecological Communities. MjM Software Design.
60. McLeod KW, Reed MR, Nelson EA (2001) Influence of a willow canopy on tree seedling establishment for wetland restoration. Wetlands 21:395-402.
61. Miller NP, Matlack GR (2010) Population expansion in an invasive grass, *Microstegium vimineum*: a test of the channelled diffusion model. Diversity & Distributions 16:816-826. https://doi.org/10.1111/j.1472-4642.2010.00690.x
62. Mitsch WJ, Gosselink JG (2015) Wetlands. 5th Ed. Wiley, NJ.
63. 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.
64. Mueller-Dombois D, Ellenberg H (1974) Aims and Methods of Vegetation Ecology. Wiley and Sons.
65. Noon KF (1996) A model of created wetland primary succession. Landscape and Urban Planning 34:97-123.
66. 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.
67. Oksanen J, Guillaume Blanchet F, Friendly M, Kindt R, Legendre P, McGlinn D, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Henry M, Stevens H, Szoecs E, Wagner H (2020) vegan: Community Ecology Package. R package version 2.5-7. https://CRAN.R-project.org/package=vegan
68. 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.
69. 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. Forest Ecology and Management 242:727-732. https://doi.org/10.1016/j.foreco.2007.02.008
70. Peck J (2016) Multivariate Analysis for Ecologists: Step by step (2nd ed.). Gleneden Beach, OR: MjM Software Design.
71. Perry LG, Galatowitsch SM, Rosen CJ (2004) Competitive control of invasive vegetation: a native wetland sedge suppresses Phalaris arundinacea in carbon-enriched soil. Journal of Applied Ecology 41:151-162.
72. 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.

73. Petru BJ, Ahn C, Chescheir G (2013) Alteration of soil hydraulic properties during the construction of mitigation wetlands in the Virginia Piedmont. Ecological Engineering 51:140-150.
74. Ponnamperuma FN (1972) The chemistry of submerged soils. In: Advances in Agronomy. Academic Press, New York, New York pp 29-96.
75. R Core Team (2014) R: A Language and Environment for Statistical Computing. Available via. https://www.r-project.org/
76. Reddy KR, Wetzel RG, Kadlec RH (2005) Biogeochemistry of phosphorus in wetlands. Agronomy Monographs 46:263-316.
77. Reinartz JA, Warne EL (1993) Development of vegetation in small created wetlands in southeastern Wisconsin. Wetlands 13:153-164.
78. 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
79. Robertson DJ, Robertson MC, Tague T (1994) Colonization dynamics of four exotic plants in a northern Piedmont natural area. Bulletin of the Torrey Botanical Club 121:107-118.
80. Rueden CT, Schindelin J, Hiner MC et al. (2017), ImageJ2: ImageJ for the next generation of scientific image data, BMC Bioinformatics 18:529
81. Schramm JW, Ehrenfeld JG (2010) Leaf litter and understory canopy shade limit the establishment, growth and reproduction of Microstegium vimineum. Biological Invasions 12:3195-3204.
82. Sullivan L, Wildova R, Goldberg D, Vogel C (2010) Growth of three cattail (*Typha*) taxa in response to elevated CO. Plant Ecology 207:121-129. https://doi.org/10.1007/s11258-009-9658-4
83. 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.
84. Swearingen J, Slattery B, Reshetiloff K, Zwicker S. (2010) Plant Invaders of Mid-Atlantic Natural Areas, 4th ed. National Park Service and U.S. Fish and Wildlife Service. Washington, DC.
85. ter Braak CJ (1986) Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. Ecology 67:1167-1179.
86. Tiner RW (2017) Wetland Indicators: A Guide to Wetland Formation, Identification, Delineation, Classification, and Mapping. CRC press
87. 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. Aquatic Botany 49:91-105.
88. Touchette BW, Romanello GA (2010) Growth and water relations in a central North Carolina population of Microstegium vimineum (Trin.) A. Camus. Biological Invasions 12:893-903.
89. 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.

90. 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
91. van der Valk, A.G. (1981) Succession in wetlands: a Gleasonian approach. Ecology 62:688-696.
92. Warren RJ, Wright JP, Bradford MA (2011) The putative niche requirements and landscape dynamics of *Microstegium vimineum*: an invasive Asian grass. Biological Invasions 13:471-483. https://doi.org/10.1007/s10530-010-9842-4
93. Weakley AS, Ludwig JC, Townsend JT, Fleming GP (2020) Flora of Virginia. With significant additions and updates. Mobile app. Crowder, B (ed.). Foundation of the Flora of Virginia Project Inc., Richmond, VA. High Country Apps, Bozeman, MT.
94. 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. Pacific Conservation Biology 26:45-56.
95. Wiltermuth MT, Anteau MJ (2016) Is consolidation drainage an indirect mechanism for increased abundance of cattail in northern prairie wetlands? Wetlands Ecology and Management 24:533-544. https://doi.org/10.1007/s11273-016-9485-z
96. Woo I, Zedler JB (2002). Can nutrients alone shift a sedge meadow towards dominance by the invasive *Typha* × *glauca*. Wetlands 22:509-521. https://doi.org/10.1672/0277-5212(2002)022[0509:CNASAS]2.0.CO;2
97. Zedler JB, Kercher S (2004) Causes and consequences of invasive plants in wetlands: opportunities, opportunists, and outcomes. Critical Reviews in Plant Sciences 23:431-452.
98. Ziska LH., Tomecek MB, Valerio M, Thompson JP (2015). Evidence for recent evolution in an invasive species, *Microstegium vimineum*, Japanese stiltgrass. Weed Research 55:260-267. https://doi.org/10.1111/wre.12138

Figures

Figure 1a.

Figure 1b.

Figure 1c.

Figure 1

a. Arthraxon dominant on one of our wetland mitigation study sites.

b. Microstegium demonstrating tolerance to shade in a disturbed forest understory.

c. Typical habitat condition for Typha on study sites (lead author pictured).

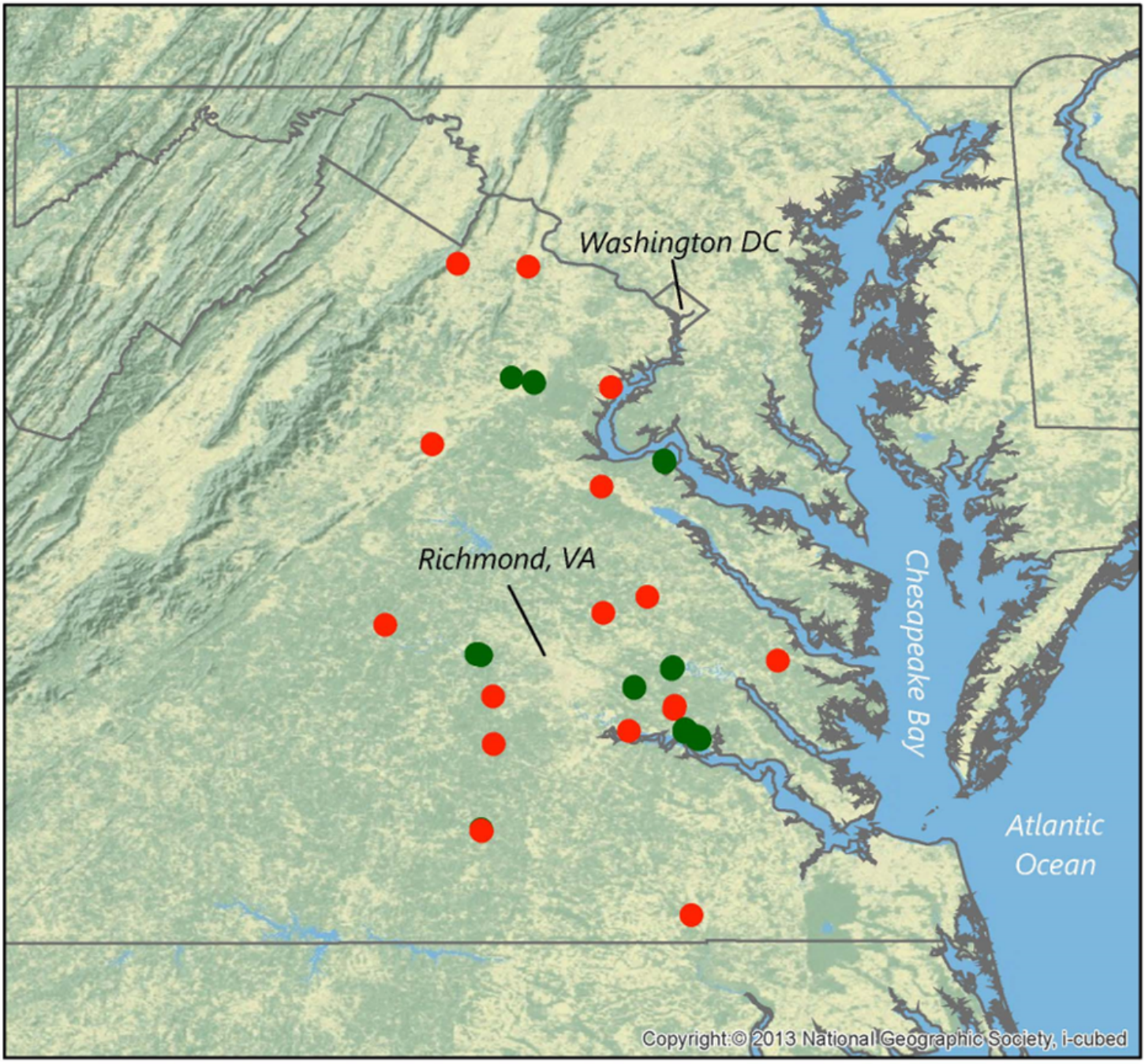

Figure 2

Wetland mitigation study site locations. Red symbols indicate sites in which more than one phase was sampled; green symbols represent single-phase sample sites.

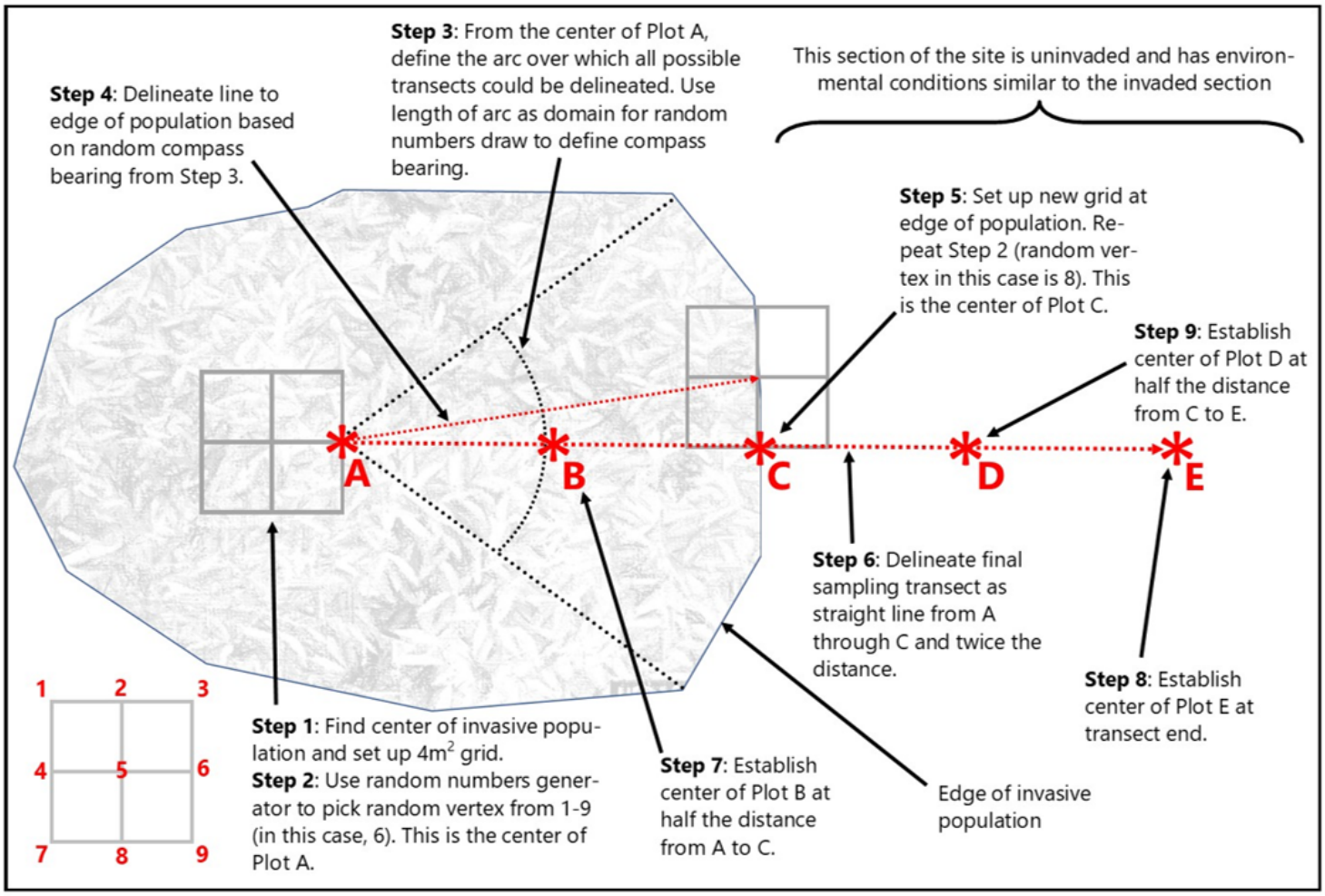

Figure 3

General layout of study design and transect configuration.

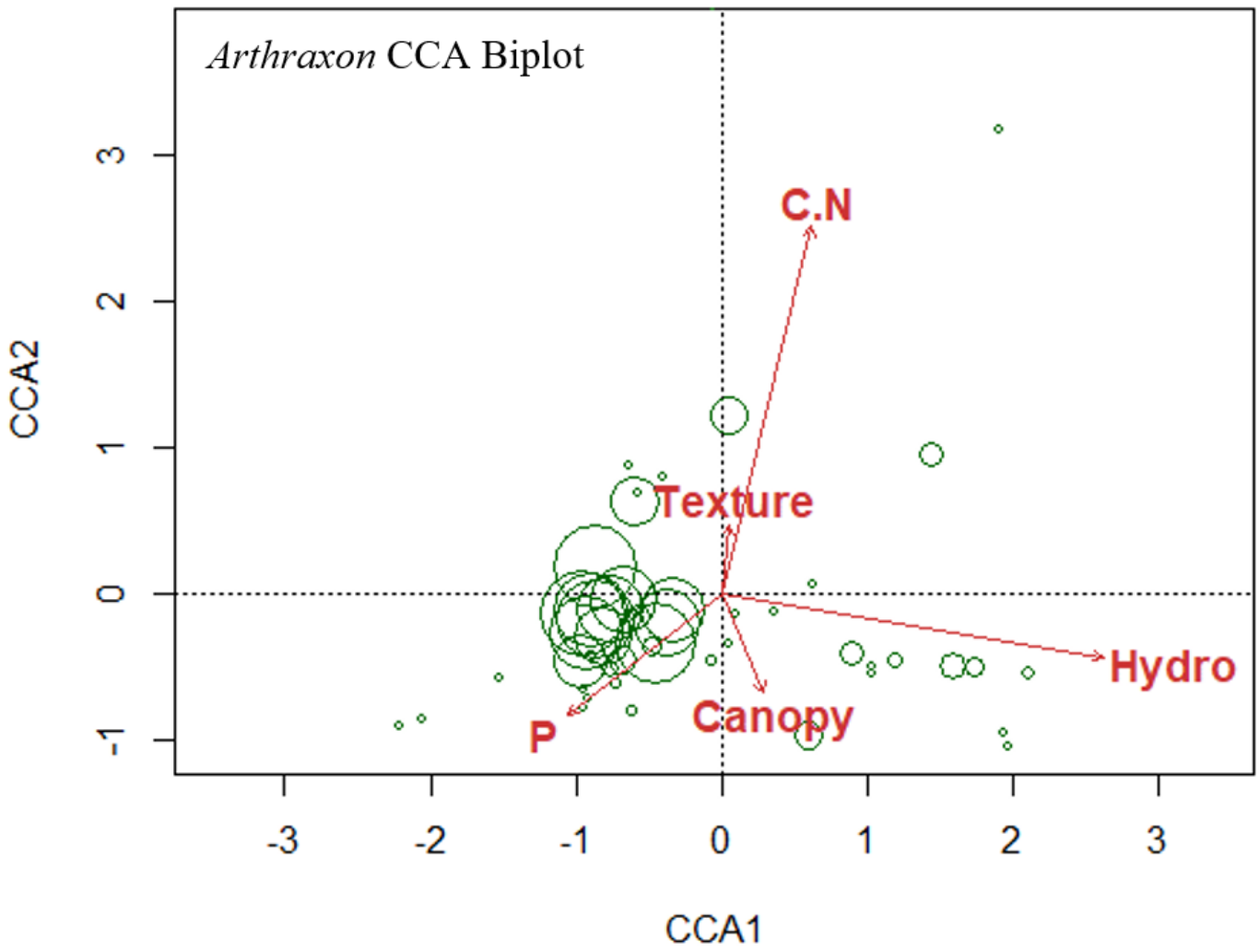

Figure 4

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 vectors are interpreted as perpendicular projections from green circles to red arrows.

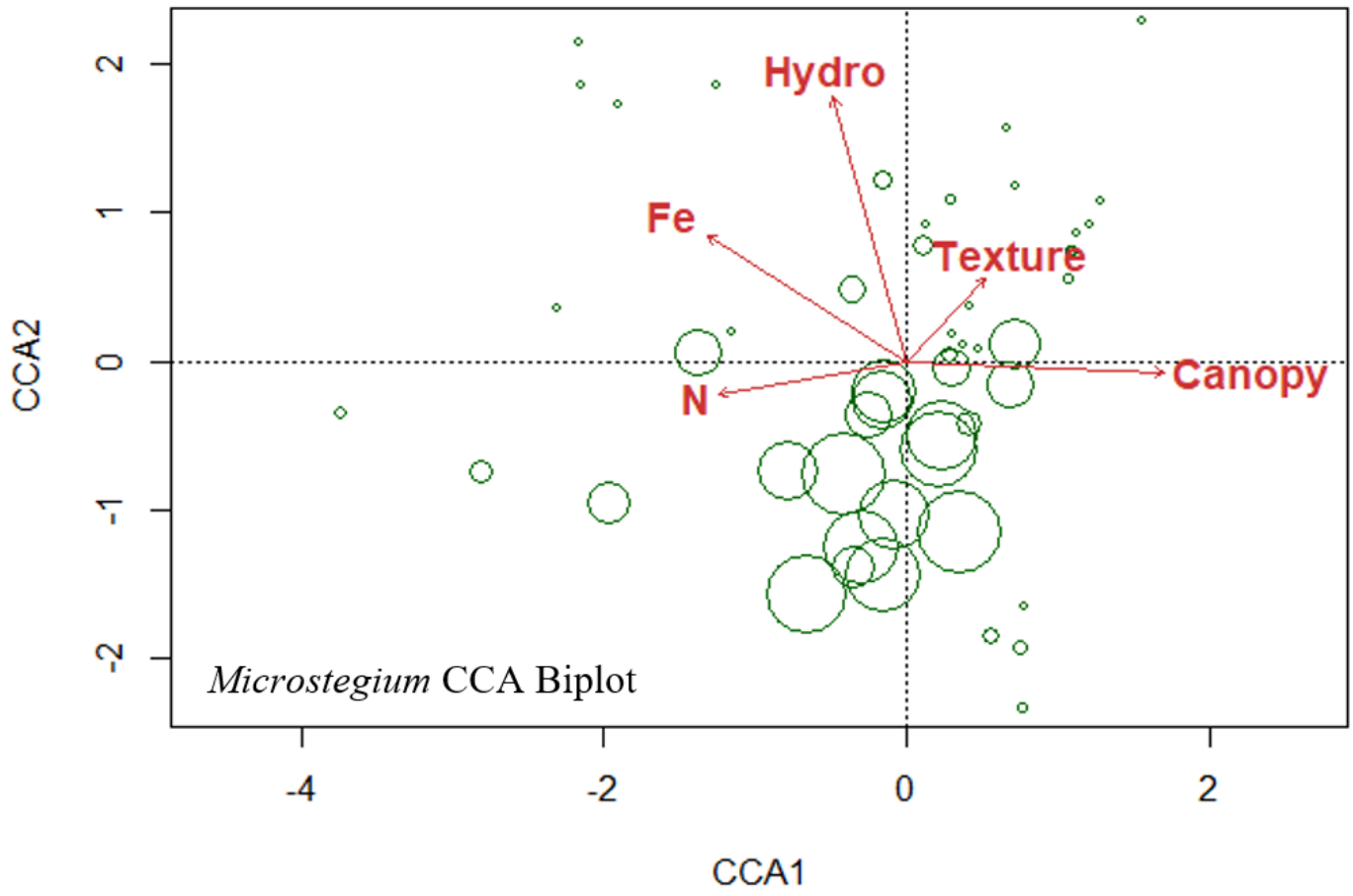

Figure 5

CCA biplot for *Microstegium*dataset. See *Arthraxon* text and Figure 4 caption for notes on interpretation.

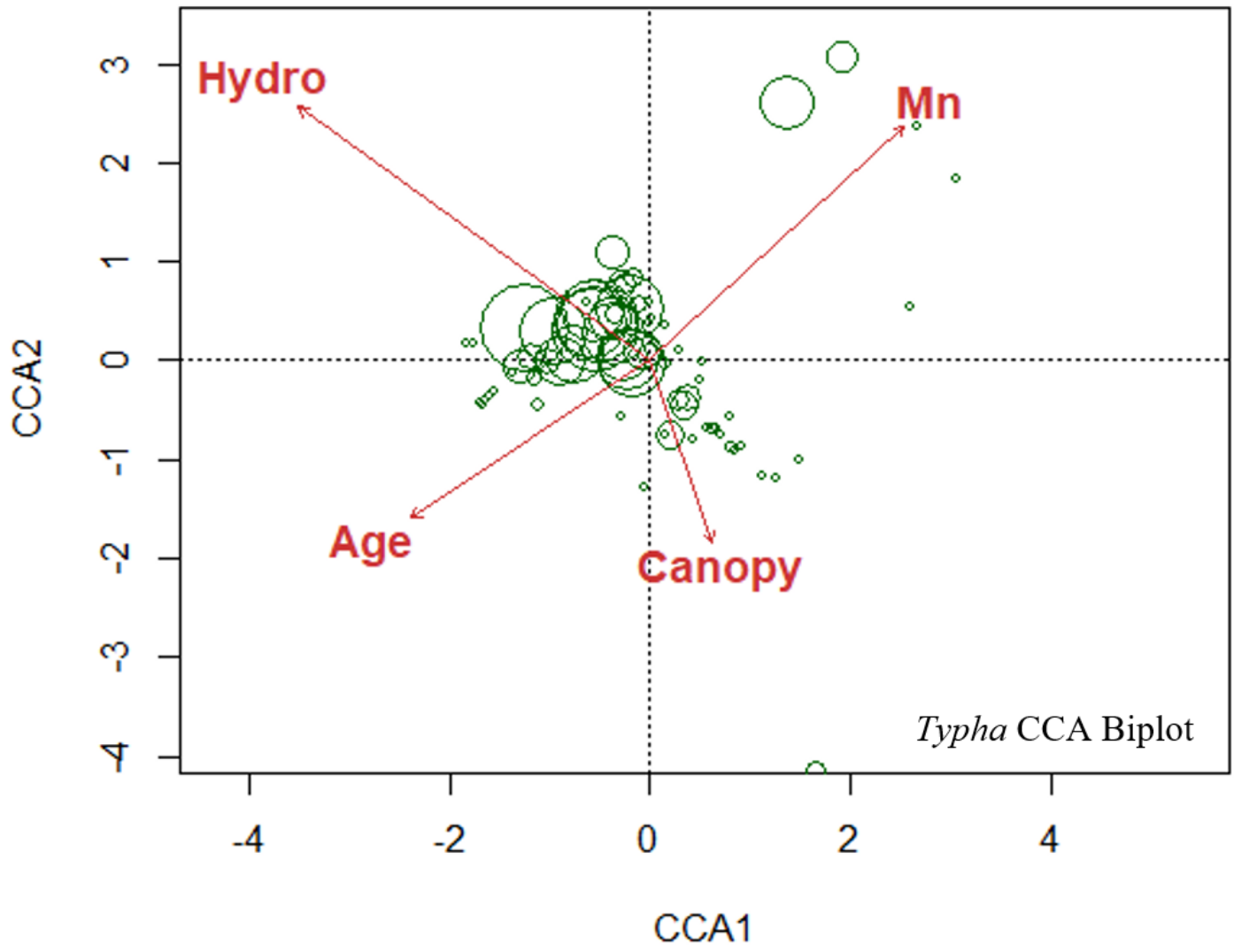

Figure 6

CCA biplot for *Typha* dataset. See *Arthraxon* text and Figure 4 caption for notes on interpretation.