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Drivers of Plant Invasion in Stream Restoration

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Abstract: This study characterized important environmental factors that contribute to plant invasion in the forested riparian zones surrounding stream restoration sites. We sampled vegetation and environmental variables (light availability, soil physiochemistry, and site age) across invasion gradients at multiple sites in Virginia, USA. Data analysis involved a multimetric statistical approach combining correlation and Canonical Correspondence Analysis (CCA) to arrive at a plausible model for invasion risk by species. We targeted three of the most problematic invaders in these systems: *Lespedeza cuneata* (sericea lespedeza), *Lonicera japonica* (Japanese honeysuckle), and *Microstegium vimineum* (Japanese stiltgrass). Our analysis revealed species-specific environmental drivers of invasion, with certain factors consistently important across all targeted invaders—notably, canopy cover, nitrogen availability, soil texture, and bioavailable phosphorus, as indicated by the importance of certain proxies (e.g., metal cations). The results of this research have been used to develop a suite of best practices that can be implemented at the outset of a stream restoration project to reduce the risk of invasion in the riparian forests surrounding these sites.

Keywords: stream restoration; stream mitigation; invasive plant species; invasive plant management; *Lespedeza cuneata*; *Lonicera japonica*; *Microstegium vimineum*

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1. Introduction

Biological invasion has become one of the most important contemporary issues in the field of restoration ecology, with invasive vegetation representing a significant consideration in terms of post-restoration invasion risk [1]. From the first principles in invasion ecology, we know that disturbance represents a mode of introduction for invasive plants, and ecological restoration sites can be particularly susceptible because the practices used to create, restore, or enhance ecological conditions are often the same types of disturbances that leave a site vulnerable to invasion [2]. This is especially true of stream restoration sites, which have open energy cycles and are exposed to multiple vectors of plant dispersal, such as flowing water and flooding of the riparian zone [3]. Invasive plant management on these sites has increased considerably in recent decades, and in most cases, it is compulsory, i.e., it is required as a condition of an environmental permit or a banking agreement for stream restoration after invasive plant species colonize [4]. This reactive posture to management typically results in the use of non-selective herbicides and significant collateral damage to native species [5], but what is needed is a proactive approach to stream restoration with best practices aimed at inhibiting invasion from the start.

To evaluate this problem, we began by studying the "invasion gradient"—by which we mean the transition from high to low abundance of a specific plant invader—within the forested riparian corridors surrounding existing stream restoration projects in Virginia, USA. Importantly, we focused on invasion gradients where the environmental conditions were apparently the same across the gradient (i.e., similar elevation, light availability, soil conditions, etc., from the invaded to the uninvaded end of the gradient). In this manner, we could more closely inspect the conditions that “tip the scale” in favor of invasion on sites that otherwise appear similar, ultimately developing an understanding of the environmental conditions that are most consistently correlated with a higher overall cover of invasive plant species on these sites.

For the purposes of this study, an “invasive plant species” is defined as one that colonizes a new habitat, rapidly expands in space once there, and has negative consequences for the species already in the space that it enters [6]. This definition is consistent with the criteria used to develop current regional lists of invasive plant species (e.g., [7]). We use “invader” and “invasive species” interchangeably throughout and refer to the condition of invasive species dominance on a site as “invasion” or “invaded”. Also, “stream restoration” means returning a degraded stream channel and its riparian corridor to a close approximation of its remaining ecological potential using the principles of natural channel design [8]. This definition accords with the one used by regulatory programs responsible for requiring stream restoration as compensatory mitigation for environmental impacts (e.g., Section 404 of the Clean Water Act and analogous state water protection laws), which is the administrative provenance for the sites in this study.

A comprehensive account of the theoretical ecology undergirding our expectations for outcomes was reviewed in a previous study by the authors (see [2]). The most important idea to highlight here is the role that the combination of stress and disturbance plays in structuring plant communities. From a plant ecology perspective, stress is defined as an abiotic or biotic factor that reduces fitness or growth (e.g., nutrient or light limitation), whereas a disturbance is a factor that results in the direct removal of biomass (e.g., flood scour, fire, or human land development; [9]). From our research, the model suggested by Alpert et al. [6] seems the most applicable to the forested ecosystems surrounding stream restoration sites. In that model, disturbance regimes of intermediate intensity and frequency combined with moderate stress regimes reduce the potential for plant invasion (Figure 1). Alternatively, sites that are recently disturbed and low in stress are prone to invasion.

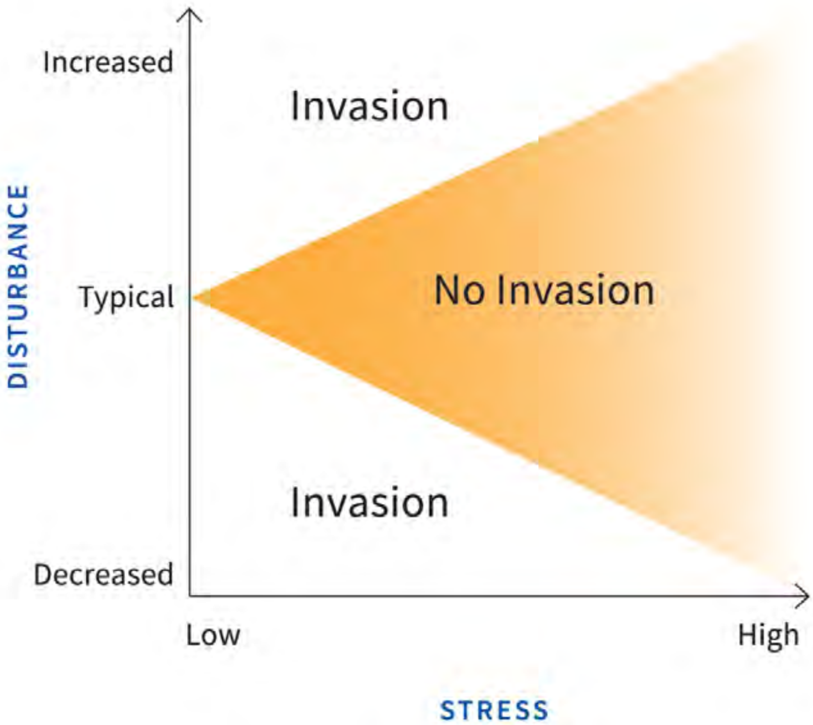


Figure 1. Conceptual model showing the relationship between stress, disturbance, and invasion (adapted from Alpert et al. [6]). Source: VHB, Inc., used with permission.

It is easy to see how a stream restoration project could result in the latter condition: the construction practices used to restore the channel and riparian corridor always involve disturbance [8], and the open nutrient and energy cycles within the floodplain of a stream system combined with potential increases in light availability from tree clearing lead to higher resource availability and, therefore, lower levels of stress [3,10]. From an invasion perspective, this condition is exacerbated by the reality that flood water is the main dispersal vector for many invasive plants [11], making stream restoration sites and their adjacent forested floodplains susceptible to recruitment by invaders originating from the upstream watershed [3].

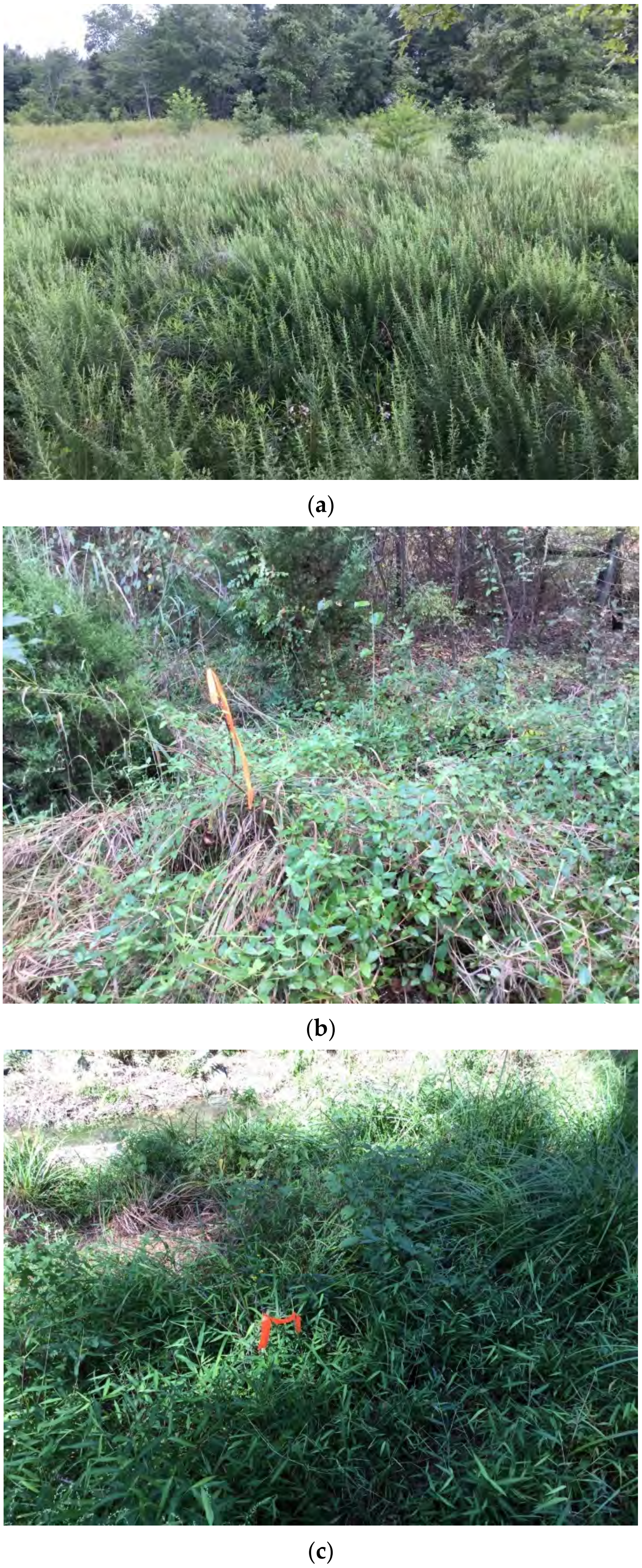
Recognizing that disturbance is a procedural reality of stream restoration, our question is whether or not the "stress side" of the stress–disturbance dynamic can actually be manipulated during the construction phase of a project to reduce the risk of plant invasion. The purpose of this study was to answer this question by first determining which environmental factors were correlated with higher percentages of our targeted invaders in the context of the overall plant community along the invasion gradient. We anticipated that both higher levels of light and soil nutrient availability would emerge as important factors.

1.1. Target Invaders

We met with several stream restoration practitioners (e.g., mitigation bankers, agency representatives, environmental consultants, etc.) to create a list of the most problematic invaders within the forested riparian zones surrounding stream restoration sites. From this list, we selected three target invaders based on site-level criteria: *Lespedeza cuneata*, *Lonicera japonica*, and *Microstegium vimineum*. These species are described below.

1.1.1. *Lespedeza cuneata* (Dum.-Cours.) G. Don (Family: Fabaceae)

Lespedeza cuneata (sericea lespedeza) is a warm season perennial legume from east Asia that grows to a height of 1–2 m and can form dense populations where established [12] (Figure 2a). It was introduced to the USA in the 1890s to be tested for agricultural production and erosion control and has escaped into many natural habitats since its introduction [13]. *Lespedeza cuneata* is classified as an invasive species in most states where it has naturalized, and in Virginia, it is listed among the species with the highest risk of invasion [7]. Like most legumes, *L. cuneata* benefits from symbiosis with nitrogen-fixing bacteria, enabling it to inhabit nutrient-poor conditions and eroded soils that are typically inhospitable to other plants; however, it is shade-intolerant and does not establish well under a dense canopy [14]. With an extensive taproot, *L. cuneata* can survive extended drought conditions in the well-drained soils that it frequents, and it can also survive in a wide range of soil pH conditions from strongly acid to slightly basic [12]. Modes of invasion in this species have been studied, with general consensus that *L. cuneata* is able to modify its environment and facilitate localized dominance [15,16]. The species has a high level of tannins in its tissues, making it unpalatable to wildlife and thus resistant to herbivory [17,18]. In addition, phenolic compounds emitted into the soil through root exudates or decomposing plant residues have been shown to have allelopathic properties, increasing its competitive ability by altering nutrient uptake efficiency and decreasing germination in other species [12,16]. *Lespedeza cuneata* can reduce nutrient availability for other species via the rapid acquisition of essential nutrients (e.g., phosphorus, potassium) and slow release back to the soil via lower rates of decomposition than other plants, a phenomenon mediated by secondary compounds [17]. All of these properties contribute to localized *L. cuneata* dominance, making the species a nuisance in ecosystem restoration and a particularly problematic invader of riparian restoration projects [16,19].



(**a**)

(**b**)

(**c**)

Figure 2. Representative photos of study species on stream restoration sites: (**a**) *L. cuneata*, (**b**) *L. japonica*, (**c**) *M. vimineum*.

1.1.2. *Lonicera japonica* Thunb. (Family: Caprifoliaceae)

Lonicera japonica (Japanese honeysuckle), a perennial vine that turns woody with age, is from eastern Asia and was introduced to the USA in the early 1800s as a garden plant [13]. Its ability to escape into natural habitats was first noticed along the Potomac River near Washington, DC, in 1882, and since that time, it has expanded and become invasive in nearly every USA state east of the Mississippi River [20]. In Virginia, it is listed among the species that pose the highest risk of invasion [7]. Like most successful invaders, *L. japonica* colonization is greatly enhanced by disturbance [21], with seeds being dispersed primarily by birds that forage on the fruits [13]. Although it is a prolific seeder, it does not form persistent seedbanks, and thus, populations typically expand vegetatively [22,23]. *L. japonica* inhabits a range of habitat types, soil moistures, and pH conditions but is generally found in the well-drained, circumneutral pH soils of forests, edges, and clearings. Due to high transpiration rates, it does not tolerate prolonged drought and therefore tends to prefer mesic habitats, making riparian zones, streambanks, and floodplains particularly susceptible to invasion [20,24]. Although it can live in shady habitats, partial or full shade has been shown to inhibit *L. japonica* growth, and studies consistently highlight its preference for open environments where it can aggressively exploit canopy gaps or clearings, grow in dense thickets, and effectively smother other species [20,25] (Figure 2b). Consensus on factors contributing to invasiveness in *L. japonica* has not been reached, but all of the following functional traits have been implicated in the literature: allelopathy [26]; no known enemies and a strong compensatory response to herbivory [20]; autogenic control via the modification of environmental conditions and community structure, including nitrogen and carbon pools and the relative availability of nutrients for other species [27]; and morphological plasticity of leaf area and growth habit, which has allowed for increased resilience and expansion under disturbed conditions [28]. All of these factors make *L. japonica* a considerable threat to restoration projects, particularly in streams and riparian zones [29].

1.1.3. *Microstegium vimineum* (Trin.) A. Camus (Family: Poaceae)

Microstegium vimineum is an annual grass originating from Asia that grows in a variety of habitats and field conditions. It has been described as shade- and flood-tolerant [30–32] (Figure 2c) and is adept at seed dispersal, making it a highly invasive plant species in the region [7]. *Microstegium vimineum* has been shown to reduce native plant richness [31,33] and negatively impact native insect communities [34]. Herbicides can be effective at managing the populations within a single year [35,36], but because *M. vimineum* forms persistent seed banks, it can develop resilience to chemical treatment due to residual seed bank germination in subsequent years [37,38]. Modes of invasion seem to be facilitated by increases in light availability and soil nutrient content [32]. Riparian zones can be particularly susceptible to invasion because flowing water is a primary dispersal mechanism for *M. vimineum* seeds, so floodwaters in unidirectional lotic systems contribute greatly to its expansion and distribution in watersheds. Much attention has been paid to studying *M. vimineum* in these types of habitats [30,32,36], and its invasion potential on stream restoration sites is of particular importance in the Mid-Atlantic Region [39].

2. Materials and Methods

2.1. Study Sites

Representative field sites were chosen from a pool of 30 available sites in Virginia, USA, based on the following selection criteria: (1) the sites had to be non-tidal stream restoration projects developed under the purview of federal and/or state environmental laws, and (2) the sites had to have populations from our target list of invaders dominating at least portions of the project area. Field sites were assigned to the following age classes so that age could be evaluated as a factor: 1–2 years, 3–5 years, 6–10 years, 11–15 years, and >15 years following restoration [40]. Some of the stream restoration sites had different sections of the site that were restored at different times, correlating to the above age classes.

These sections were treated as individual sites for sampling purposes if spatial or temporal separation was deemed sufficient, and the sections fell into different age classes.

Among the stream sites screened, 21 met the suitability criteria and were selected for the study, which was conducted during the 2018 and 2019 growing seasons. Site ages ranged from 1 to 19 years post-construction and were evenly distributed across the Piedmont (10 sites) and Coastal Plain (11 sites) physiographic provinces in Virginia (Figure 3).

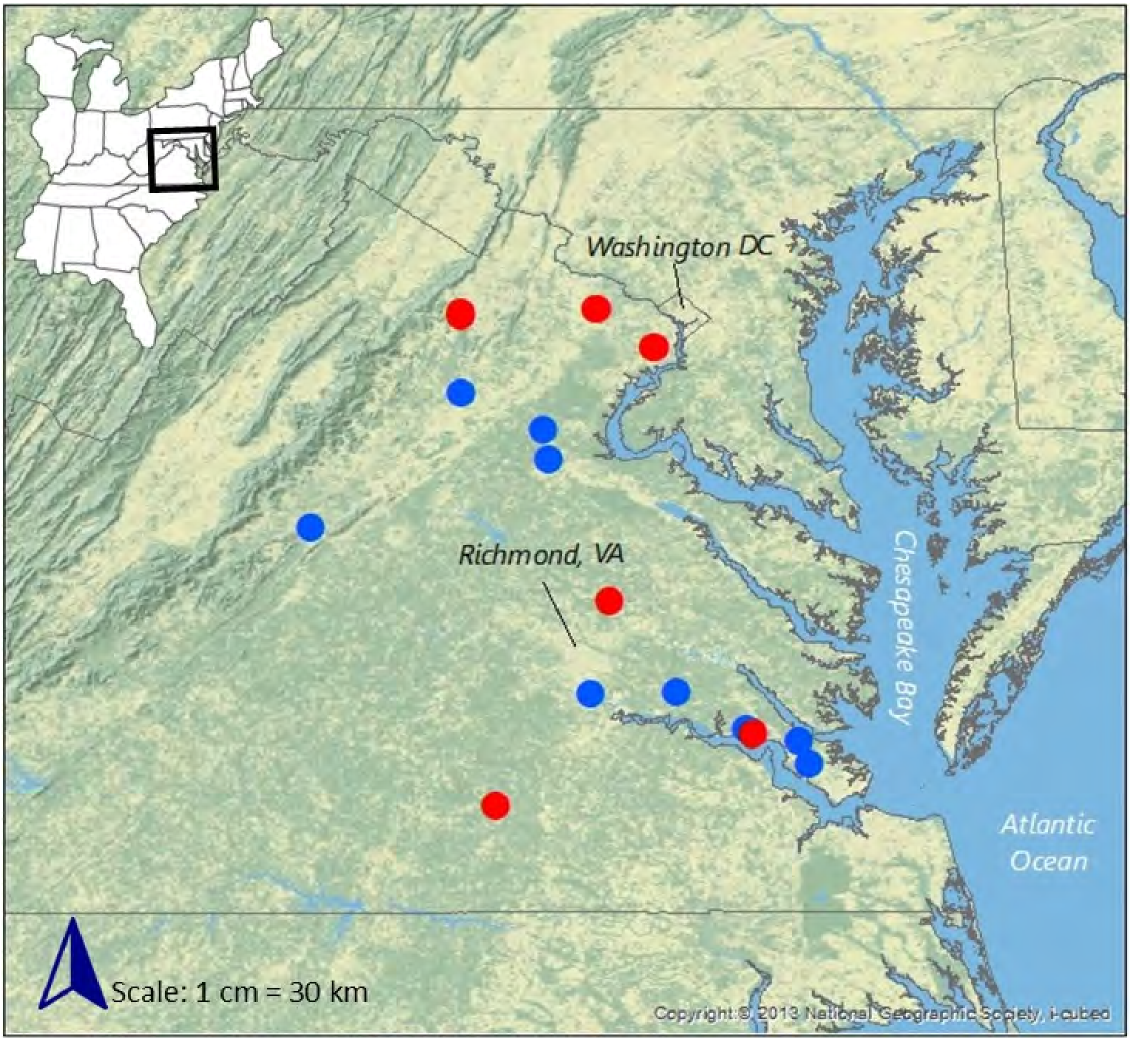


Figure 3. Stream restoration study site locations. Red symbols indicate sites in which more than one section of the site was sampled; blue symbols represent individual sites. (See text in Section 2.2 for explanation).

2.2. Sampling Methods

Hunter and DeBerry [2] described detailed methods for sampling across invasion gradients in wetland restoration sites, and these approaches were generally followed here with modifications as outlined below. The primary differences were in the transect orientation and randomization procedures used to determine plot locations.

Transect Configuration, Plot Locations, and Data Collection

Unlike wetland restoration sites, which are frequently constructed with gradual changes in relative elevation to target specific hydrologic regimes [41], stream restoration typically uses approaches that are designed to follow the geomorphology and natural contours of the surrounding landscape [8]. This means that relative elevations can change abruptly in the cross-sectional dimension of the stream valley from channel to floodplain and from floodplain to riparian buffer. To minimize the amount of apparent environmental variation across the invasion gradient, transects were aligned longitudinally with respect to the valley axis and positioned on one side of and parallel to the stream. Each of the five plots on a single transect was established at approximately the same distance away from the top-of-bank of the stream channel so that the elevation of each plot relative to the channel was approximately the same (Figure 4). The purpose of this modification was to ensure that the landscape position within the floodplain was similar for each plot along the invasion gradient. In other words, this configuration avoided the scenario of a randomly defined, straight-line transect with invaded plots down along the channel at one end of the gradient and uninvaded plots up on the ridgeline above the sidewalls of the valley (or vice versa)—an orientation that would have yielded easily detectable but unmeaningful environmental variation in the context of study objectives.

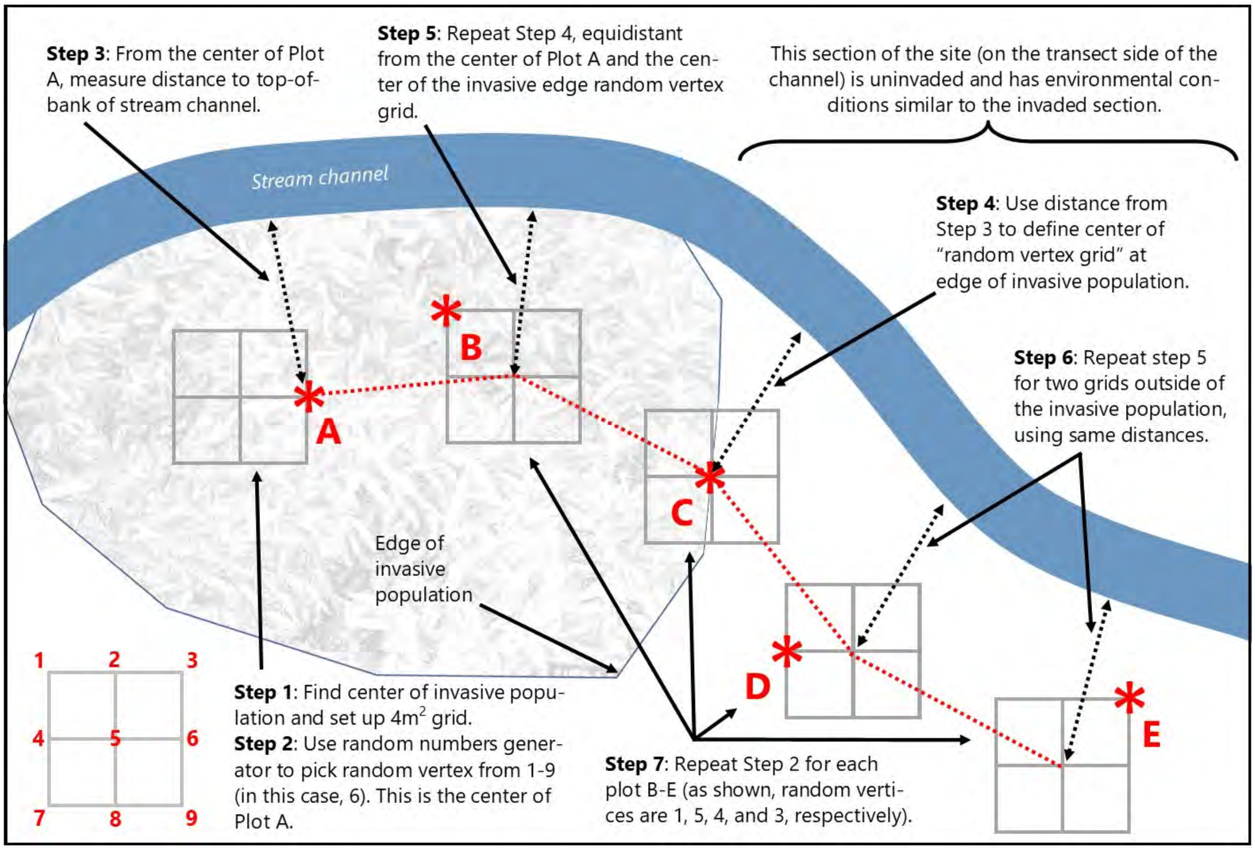


Figure 4. General layout of study design and transect configuration. Transect orientation, plot randomization, and final plot position (red asterisks) explained in text (Section 2.2).

The first plot location (Plot A, completely invaded) was determined using the 4 m^2 random vertex grid approach described by Hunter and DeBerry [2]. The distance from the center of Plot A to the top-of-bank of the stream channel was recorded, and this distance was used to define a new 4 m^2 grid centered at the edge of the invasive species population and offset the same distance from the channel bank. A third grid was established using the same offset distance from the stream bank, but this time within the invasive species population and equidistant from the center of Plot A and the center of the invasive edge grid. Using these same distances, the last two 4 m^2 grids were laid out at the uninvaded end of the transect. For each of the remaining plots (B, C, D, and E), random numbers between 1 and 9 were drawn to determine which vertex on each respective grid would be the center of each plot (Figure 4). This process ensured that all five plots along the invasion gradient were approximately the same distance from the channel (+/−1 m), with the exact location of each plot being randomized. The transects ranged in length from 30 to 100 m.

Soil sampling, canopy cover, and vegetation sampling methods all followed the same procedures described by Hunter and DeBerry [2]. There was one minor procedural difference: due to the prevalence of mature overstory canopies on the stream sites, cover estimates for tree species in plots were limited to a height of 3 m to avoid including abundance for taller trees growing outside of the transect study area. Canopy influence was assumed to be captured by canopy cover data. Also, wetland hydrology was not evaluated as an environmental factor because all stream sites were within upland portions of the forested floodplains adjacent to the restored stream channels.

2.3. Statistical Analysis

Data analysis was completed using R version 4.0.3 [42] including the packages vegan, Hmisc, and BiodiversityR [43–46]. The datasets for each invasive study species were analyzed separately due to expected variation in their relative tolerances for environmental stressors and discrepancies among growth requirements [11,13]. Correlations between environmental variables and relative invasion were calculated using the nonparametric Spearman rank-order correlation test, which is robust to deviations from normality and can detect both linear and monotonic relationships without appreciable loss of statistical power in comparison with parametric tests [47].

Canonical Correspondence Analysis (CCA) [48] was used to evaluate the overall community response to environmental variation along the invasion gradient. Rare species were removed from the abundance matrix of each dataset to neutralize their oversized effect on the X^2 distance used in CCA [49]. We used Borcard's stepwise approach based on the correspondence analysis (CA) component of CCA to evaluate the effect of progressive species removals and identify rare species accordingly [47]. Final CCA models were identified using the forward and backward model selection functionality in the ordistep() function of vegan, eventually eliminating model variables based on the significance of permutation tests in combination with the Akaike Information Criterion (AIC) [44]. We also identified and removed highly correlated variables by inspecting the variance inflation factor (VIF) [47]. The procedure described above produces a parsimonious model when all environmental variables are significant and the adjusted R^2 does not exceed that of the global model (i.e., the model with all environmental factors included) [44,50]. For CCA results, we report overall model inertia, which can be thought of as the total amount of variance in the model. In ordination approaches like CCA, "constrained" inertia represents the amount of variance explained by the environmental variables. For multivariate ecological data, values $+/-20\%$ are common [44,50]. All permutation tests were set at 1000 iterations, and all statistical analyses were evaluated at $\alpha = 0.05$.

3. Results

Two hundred eighty-six (286) species were documented in the overall stream restoration field study across 21 sites, 29 transects, and 145 plots sampled. Additional information on species composition and community properties may be found in [51]. Community modeling and environmental data are summarized below for each of the three target invasive species.

3.1. L. cuneata

Spearman results showed *L. cuneata* abundance significantly correlated with canopy cover ($r_s = -0.690$, $p << 0.001$). The relationship was negative, indicating that *L. cuneata* was more prevalent in areas with less canopy cover. No other environmental variables were significantly correlated with *L. cuneata* abundance in the Spearman analysis.

The CCA ordination was based on a community matrix with 11 dataset-rare species removed, leaving 148 species from the original matrix in the ordination. The final parsimonious CCA model for *L. cuneata* included five environmental variables—canopy cover, soil texture, nitrogen (N), potassium (K), and pH—which accounted for 25% of the total inertia in the ordination. All environmental factors were significant at $p \leq 0.01$ based on permutations. The ordination biplot (Figure 5) displays red arrows as vectors for environmental variables, with the vector length corresponding to the 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 were positively correlated with that environmental variable, and vice versa). Circles on the biplot represent plots, and circle size corresponds to the absolute abundance of *L. cuneata* within that plot (i.e., larger circles have higher abundance values). The first two ordination axes explained over 49% of the variation in the CCA model and thus were retained for the biplot. Figure 5 shows that, in general, canopy cover, pH, N, and K were negatively related to *L. cuneata* abundance in the context of the overall vegetative community. Soil texture appears positively correlated with *L. cuneata* abundance, suggesting that the invader tended to be on sites with coarser textures (i.e., texture values in the dataset were arranged on an ordinal scale from fine to coarse, so higher values corresponded to coarser-textured substrates).

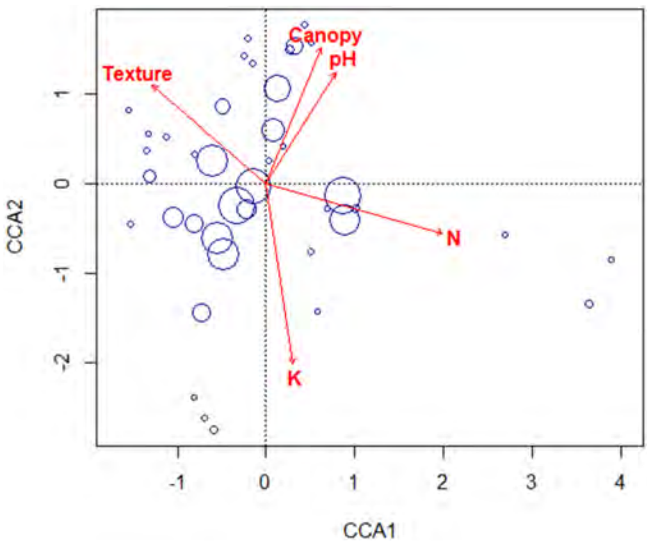


Figure 5. CCA biplot for *L. cuneata* dataset. Red arrows are vectors for environmental variables. Vector length indicates strength of correlation, and vector direction indicates a positive (pointing toward) or negative (pointing away) relationship to the plots, which are shown as circles with size corresponding to abundance of *L. cuneata* (i.e., larger circles = higher abundance). Plot relationships with environmental vectors are interpreted as perpendicular projections from blue circles to red arrows.

3.2. L. japonica

Spearman results indicated that *L. japonica* abundance was positively correlated with potassium (K) ($r_s = 0.298$, $p = 0.035$) and negatively correlated with canopy cover ($r_s = -0.749$, $p << 0.001$). For the CCA analysis, the *L. japonica* community matrix was reduced by 9 dataset-rare species, leaving 158 species from the original matrix in the ordination. The final parsimonious *L. japonica* CCA model included five environmental variables—canopy cover, texture, N, magnesium (Mg), and iron (Fe)—which accounted for over 20% of the total inertia in the ordination. All environmental factors were significant at $p < 0.01$ except texture ($p = 0.04$). The first two ordination axes displayed in Figure 6 explained 52% of the CCA variation. As with *L. cuneata*, canopy cover, and N showed a negative relationship with *L. japonica* abundance in the community, and texture showed a positive relationship with highly invaded sites. The other two important factors, Mg and Fe, both showed negative relationships with *L. japonica* abundance in the context of the plant community.

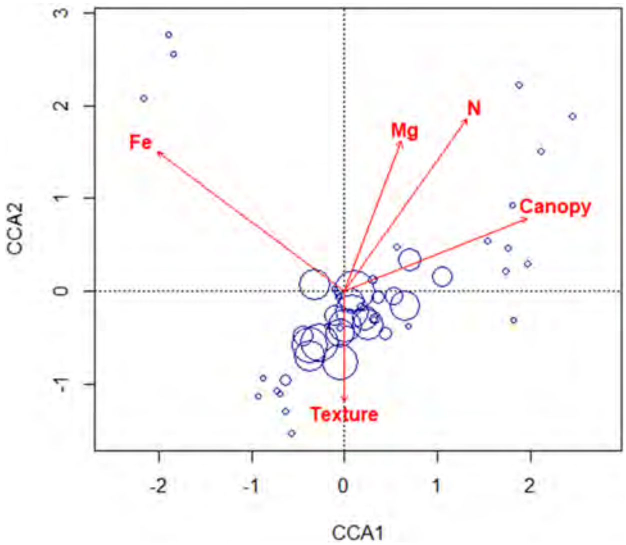


Figure 6. CCA biplot for *L. japonica* dataset. See *L. cuneata* text and Figure 5 caption for notes on interpretation.

3.3. *M. vimineum*

Spearman correlations showed that canopy cover was negatively correlated with *M. vimineum* abundance ($r_s = -0.467$, $p < 0.001$). No other environmental variables were significantly related to the *M. vimineum* invasion gradient in the correlation matrix. The CCA analysis for *M. vimineum* used a community matrix reduced by 24 dataset-rare species, leaving 167 species from the original matrix. The final parsimonious *M. vimineum* CCA model included four environmental variables—canopy cover, N, K, and manganese (Mn)—which accounted for 14% of the total inertia in the ordination. Canopy cover was significant in the model at $p < 0.001$; all other environmental factors were significant at $p < 0.05$. The first two ordination axes explained 57% of the CCA variation. As Figure 7 demonstrates, all four environmental variables showed a negative relationship with *M. vimineum* abundance in the vegetative community.

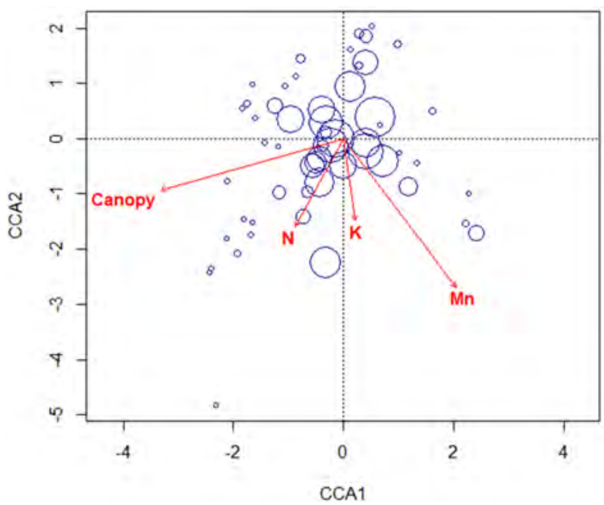


Figure 7. CCA biplot for *M. vimineum* dataset. See *L. cuneata* text and Figure 5 caption for notes on interpretation.

4. Discussion

Stream channels and their adjacent forested riparian zones are dynamic environments with open energy cycles [10]. The environmental drivers that structure plant communities in riparian zones—such as nutrient availability, sediment budgets, flood frequency and duration, and light availability—are all highly variable and subject to the pulsing forces that correspond to prevailing climate conditions and event-driven anomalies such as storms [52,53]. Floodplains are the "melting pots" of organic and inorganic matter that are shed from the upstream catchment, including the propagules of plants that use water or gravity as dispersal vectors in reproduction [54]. For stream restoration practitioners, this makes stream corridors some of the most challenging settings within which to develop planting plans and vegetation management strategies because the plant community is subject to continuous propagule pressure from upstream sources [55]. These factors are all the more challenging in view of biological invasion because, for many invasive plants, watersheds and drainage networks are the main conduits of dispersal [3].

Recognizing that most stream restoration projects will only be able to control environmental factors within project boundaries, the primary objectives of this study were directly related to the localized conditions within a stream restoration project that correlate with invasion gradients, i.e., the factors over which restoration designers and managers can have an influence. Ideally, stream restoration projects would be able to control entire watersheds, but that is neither practical due to costs nor achievable due to the intractability of acquiring land or gaining permission to access private property. Within the dynamic equilibrium (sensu [8]) ecosystem targets for a stream restoration project, there may be design and management considerations at localized scales that can help to build ecosystem resilience and resistance against future invasion [56]. With this in mind, the primary questions being addressed by this study were (1) What are the environmental drivers of plant invasion in stream restoration? (2) Based on the importance of stress and disturbance in structuring plant communities, are there best practices that can emerge from our understanding of these environmental drivers with the potential to reduce invasion risk at the outset of a restoration project?

The invasion gradients sampled in this study corresponded to light availability (canopy cover) and soil physiochemical variables, with canopy cover emerging as the most important factor across all datasets. Canopy cover was a significant variable in both the Spearman correlations and the CCA ordinations; thus, light availability exhibits a clear and distinct relationship with vegetation community development and invasive species impacts on these sites (see Figure 8). The influence of canopy cover and other environmental variables is discussed for each target invader below.

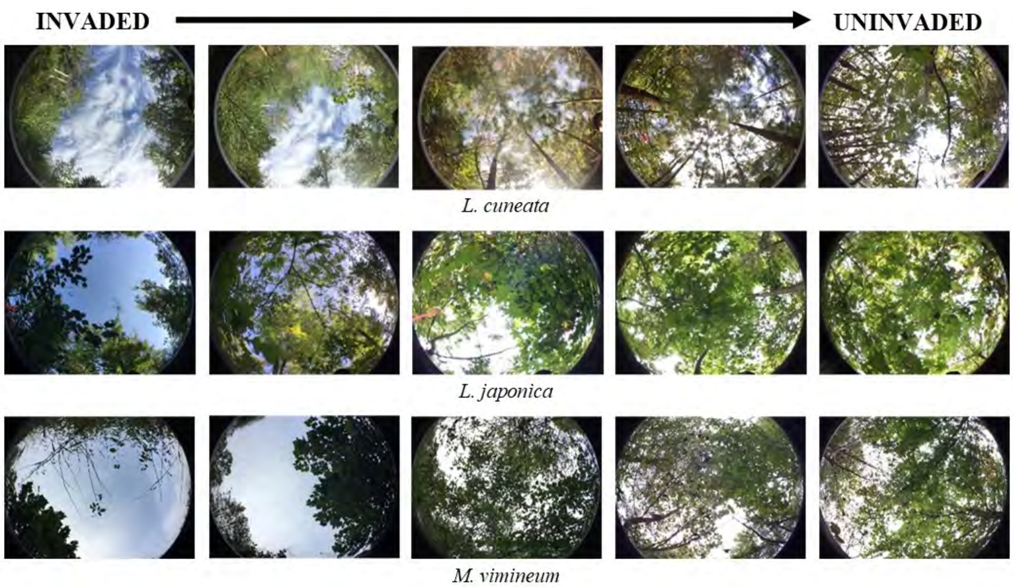


Figure 8. Representative hemispheric canopy photos taken above each plot from the invaded (**left** images) to the uninvaded (**right** images) ends of the invasion gradient. Per the methods described by Hunter and DeBerry [2], these images were analyzed to measure canopy cover. The left-to-right transition from partially open to closed canopy is apparent in all three series.

4.1. *L. cuneata*

Lespedeza cuneata is a shade-intolerant species [14], so the negative correlation between *L. cuneata* abundance and canopy cover in the stream study was not surprising. This result was also reflected in the CCA model (Figure 5), which accords with the notion that communities with *L. cuneata* as a dominant species would be more likely to have shade-intolerant associates like *Sorghastrum nutans*, *Panicum virgatum*, and *Solidago altissima*, all of which were co-dominants in the community matrix of this study. The negative relationships between *L. cuneata* abundance and soil N and K were unexpected but could have been predicted from the literature. As an "N-fixing" plant, *L. cuneata* benefits from N subsidies via a symbiotic relationship with *Rhizobium* bacteria in root nodules, which allows *L. cuneata* to inhabit nutrient-poor soils with low available N pools [16]. *Lespedeza cuneata* has been shown to reduce the availability of other macronutrients, including K, by rapid uptake and slow release back to the soil, a phenomenon that is apparently mediated by high levels of phenolic compounds (e.g., tannins) that reduce decomposition rates of its senescent tissues [17]. In dense *L. cuneata* populations on the stream sites in this study, autogenic control of nutrient availability could explain the K trends observed in the ordination.

The negative relationship between invasion and pH in the CCA model is also consistent with known ecological tolerances for *L. cuneata*, which has been documented in soils with pH as low as 4.0 [12]. On stream restoration sites, low pH could also be an indirect reflection of reduced soil nutrient status, as acidic substrates tend to be low in exchangeable bases, N, and P [57,58]. Finally, the positive relationship between *L. cuneata* dominance and coarse-textured substrates in the CCA model could signal localized disturbance in the riparian corridors of the study sites. Deposition of coarse-textured alluvium would be consistent with the type of flood-induced disturbance that could create habitat for a species like *L. cuneata* in a small stream floodplain. Anecdotally, evidence of fresh sediment accretion was noted on transects at several of the stream project sites, the consistency of which was predominantly sand and mostly occurred in close proximity to the portions of the site closest to the stream that had been more likely subjected to canopy thinning and, thus, higher light availability within the limits of disturbance during stream construction (D. DeBerry, pers. obs.). Soil like this with a low surface-to-volume particle ratio would likely also be low in ionic exchange sites for essential nutrients [58], a condition that would be consistent with the types of substrates that *L. cuneata* can exploit based on the above discussion.

All of this is consistent with *L. cuneata*'s relationship to the "high disturbance/high resource availability" model for invasion described in Section 1. With its ability to invade nutrient-poor soils, at face value, *L. cuneata* does not appear to use the "high resource" half of this strategy for dispersal and establishment. However, when the critical resource is light, *L. cuneata*'s mode of invasion does fit the paradigm because light-limited environments clearly reduce its abundance along the invasion gradient.

4.2. *L. japonica*

As with *L. cuneata*, the significant negative correlation between *L. japonica* abundance and canopy cover was anticipated and is consistent with its aggressive growth response to available light [25,27]. The positive correlation with K was not expected but is consistent with resource availability models for aggressive species [9]. Likewise, soil texture was positively related to *L. japonica* abundance in the CCA model (Figure 6), which, at the scale of the *L. japonica* transects in this study (30–80 m) most likely also signals some type of localized disturbance that is probably related to floodplain deposition.

The importance of soil N levels in the CCA model was expected, but the negative correlation between N and *L. japonica* abundance was not. Like *L. cuneata*, *L. japonica* has been shown to exhibit autogenic control over soil nutrient pools using different strategies. Morphological plasticity in *L. japonica* facilitates the opportunistic expansion of plant modules into favorable microhabitats [28], where fast-growing plants can exercise rapid uptake of mobile nutrients like N coupled to slow release back to the environment via the modification of labile carbon pools [27]. Additionally, studies have found allelopathic compounds in *L. japonica* tissues, with demonstrated effects on native species in eastern USA forests [26]. The "resource-hoarding" effects of rapid nutrient uptake and slow release could explain the lower ambient levels of soil N at the invaded end of the *L. japonica* gradient, and the "interference" effects of allelochemicals combined with morphological plasticity for micro-habitat exploitation would mean that lowering N pools would have minimal consequences for *L. japonica* itself. If this was occurring on stream sites, it would be consistent with the high disturbance/high resource concepts discussed above in that microsites exploited by *L. japonica* would have been characterized by both disturbance (habitat opening) and high resource availability (N, light), and only after *L. japonica* expansion and dominance would the relative availability of resources have been affected by autogenic controls.

The two remaining environmental variables that were important in the CCA model—soil Fe and Mg—are probably indirectly related to other factors influencing community structure along the invasion gradient. The most obvious one is the antagonistic relationship between Fe and bioavailable P, in which oxidized Fe immobilizes otherwise bioavailable P by chemical precipitation [59]. This would indirectly indicate a positive relationship between soil P and *L. japonica* abundance based on the reciprocal relationship with Fe in the model (Figure 6). The negative association between Mg and *L. japonica*-dominant sites in the CCA model could be indirectly related to soil texture. In the Mid-Atlantic Region, Mg deficiencies are often linked to coarse-textured soils from which cations are more easily leached [60]. On *L. japonica* sites, invasion was positively related to soil texture, so the Mg soil status could reflect this Mg-texture antagonism. If so, Mg would be viewed as less of a community driver and more of a secondary indicator in the *L. japonica* CCA analysis.

4.3. M. vimineum

As with the other two study species, the negative correlation between *M. vimineum* abundance and canopy cover is consistent with the literature. Although *M. vimineum* exhibits shade tolerance, it aggressively exploits available light and will correspond to relative light availability in forest understories [32,61,62]. The negative relationship between Mn and *M. vimineum* dominance in the CCA model (Figure 7) was unanticipated but is thought to reflect metal oxide/P dynamics. If so, the negative correlation would relate to greater P availability in *M. vimineum*-dominant sites in the same manner as described under *L. japonica* above for Fe-P complexes.

As with *L. japonica*, the influence of soil N on *M. vimineum* community dynamics was anticipated, but the direction of influence was not. Although functional traits are much different between the two species, there are similarities in their patterns of resource exploitation and habitat modification. Like *L. japonica*, *M. vimineum* rapidly acquires nutrients once it expands into a new area, can modify soil nutrient content [63], and has been shown to have allelopathic properties in competition experiments [64]. If this pattern of exploitation and resource depletion is characteristic of *M. vimineum* on stream restoration sites then it could explain the negative N relationship in the CCA model and possibly the negative K relationship as well, given the mobility of both of these elements in the soil and in plant tissues [60]. Admittedly, there is much variability in the overlap of the N and K vectors with *M. vimineum*-dominant plots in Figure 7, so it is probably prudent to view these relationships as less important than the other factors (particularly canopy cover, which was monotonically correlated with *M. vimineum* abundance).

5. Conclusions and Recommended Best Practices

By studying invasion gradients within the understory communities of forested riparian zones on stream restoration projects, we were able to identify environmental conditions that are correlated with increases in invasive plant species abundance on these sites. During the site screening phase, we chose to sample invasive populations where the apparent change in environmental conditions was negligible from the invaded end of the gradient to the uninvaded end (e.g., same relative elevations, same apparent native community structure, etc.). Through this, we were able to rephrase our environmental variation question in a more meaningful way: When there is no apparent difference in site conditions across an invasion gradient, what "tips the scale" in favor of invasion on stream restoration sites? The answer overwhelmingly pointed to canopy cover (light availability), which was directly correlated with the abundance of all three invaders. Further, based on CCA modeling, canopy cover was also important in structuring plant communities along the invasion gradients of all target species in this project. Other factors emerged in community modeling, the interpretation of which generally coincides with the literature on these species and on invasion ecology in general.

It is interesting to note that these findings were consistent with those of a related project on wetland restoration [2]. The fact that similar drivers of invasion were found in completely different ecological settings and among several different types of invaders (e.g., annual grasses, tall emergent perennials, semi-woody vines, and nitrogen-fixing forbs; [51]) suggests that there are unifying principles that can be used to assess potential risk of invasion on these types of projects. It should be noted that this study involved an extensive amount of fieldwork and analysis, and it would be neither practical nor cost-effective for stream restoration practitioners (e.g., mitigation bankers, consultants, managers, agency reviewers, etc.) to exert the same level of effort in diagnosing the relative risk of invasion and preemptively managing for it. However, our results do suggest a suite of proactive best practices that could be implemented during the construction phase of a stream restoration project to reduce or eliminate the amount of retroactive invasive species remediation required to meet performance standards in later years.

5.1. Best Practices

Recognizing that disturbance is a reality of the construction methods used to restore streams, we return to our question of whether the "stress side" of the stress-disturbance dynamic can be manipulated on stream restoration sites. We offer the following recommendations for planning and construction phase activities that could leverage the stress-disturbance relationship to preemptively inhibit plant invasions based on our research, organized by the most important environmental factors that emerged from this study.

5.1.1. Light Management

From our data, it is clear that light is the most important critical resource for plant invaders in the understories of these forested systems. This holds even for plants that are considered somewhat shade tolerant, like *M. vimineum* and *L. japonica*, two species for which any relative increase in light availability will stimulate rapid expansion [27,32]. Our thinking is that the quickest pathway to a closed forest canopy following construction is desirable, and this can be achieved in the following ways:

1. Limit tree clearing: The easiest and most effective way to promote canopy cover is to avoid removing it in the first place. Our study sites were located within riparian corridors that were already forested, so this would have been a viable alternative for the projects we studied and, based on the professional experience of both authors, most stream restoration projects within our region. Unfortunately, the techniques used to restore stream channels usually involve either relocating the channel or re-grading the existing channel to a new pattern and profile [8], all of which typically necessitate tree removal. However, with careful planning and proactive design specifications, many canopy trees can be saved, the value of which would be immeasurable in terms of proactive invasive plant management based on our results.
2. Plant larger trees: The planting plans that typically accompany stream restoration projects usually involve tree planting along with a performance standard for tree density. In Virginia, the density requirement has traditionally been 400 stems per acre (988 stems/hectare), which can be achieved by a "10-foot on-center" planting strategy [i.e., planting on a 10-foot (3.1-m) grid]. The problem with this standard is that it encourages practitioners to take the more economical route of planting

smaller, cheaper saplings to meet the density requirement. As might be expected, this will result in excess levels of sunlight within the riparian zone until the trees develop a closed canopy, which could take several years or even a few decades to evolve if the trees are grown from small saplings. One recent advancement in the area of ecological performance standards for wetland and stream mitigation is to measure "stem area at groundline" (SAG), which has a direct correlation with biomass accumulation and, therefore, ecosystem function in these systems [65]. Adopting a tree performance standard like SAG would be an important strategy to encourage restoration practitioners to plant larger trees and thereby hasten canopy closure with the disturbed portions of the stream restoration corridor.

3. Plant at a higher density: The logic behind this best practice follows from the concepts above. Although it comes at a higher cost, a high-density tree planting strategy would help to curtail understory invaders based on our research. In the cost–benefit analysis of this approach, projects would incur higher costs on the front end, but the benefits would most likely accrue over time as site managers would be spending much less money on invasive species removal over the life of a stream restoration project.
4. Plant early successional trees: Borrowed from the field of silviculture, this concept involves planting early successional trees in a "nurse crop" context, i.e., fast-growing trees with rapid canopy development that will ultimately facilitate the growth of other desirable, late-successional tree species [66]. In the eastern USA, examples of early successional trees include red maple (*Acer rubrum*), silver maple (*A. saccharinum*), river birch (*Betula nigra*), dogwood (*Cornus* spp.), sweetgum (*Liquidambar styraciflua*), sycamore (*Platanus occidentalis*), eastern cottonwood (*Populus deltoides*), and black willow (*Salix nigra*) [67–69].

5.1.2. Nutrient Management

As noted above, 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 over the course of this project have convinced us that the 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 [9,56]. Stress in stream restoration 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 via excavation, tilling, or the addition of soil amendments to improve conditions for target plant communities. Thus, the types of activities used in the construction sequence for a 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 the 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 [6,70], particularly in the establishment phase of a mitigation site [71]. For example, a potentially low-cost stress induction method would be to use soil amendments with a high carbon-to-nitrogen ratio (e.g., sawdust, wood chips, etc.). High carbon/nitrogen 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 [72,73]. Other examples include the 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) [74,75]. Industrially manufactured forms such as alum are reasonably affordable in bulk and have been used for this same purpose in freshwater lakes [76].

5.1.3. Diversity Management

Although not specifically addressed in this study, a related project identified the potential role that species richness might play in combating invasive plants on stream restoration sites [51]. In establishing herbaceous plants on these sites, one potentially effective strategy that could preemptively exclude invaders would be to introduce a species-rich native seed mix at a higher seeding rate than typically prescribed for restoration projects [77]. This strategy, combined with the concept of limiting similarity [78], could help practitioners design planting plans that effectively target invasive species exclusion from the outset of a stream restoration project. Pairing tall, fast-growing native herbs with comparatively large woody species (see above) could allow for canopy closure throughout the growing season and subsequent reduction in light availability near the soil surface, where invasive species would benefit most from light exposure at early growth stages.

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