

Performance and reproduction of an exotic invader across temperate forest gradients

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Abstract. Widespread colonization by invasive species often obscures their underlying niche requirements. A robust inference into habitat requirements demands direct measures of invasive species performance linked with associated environmental conditions. In the context of general ecological theory, we investigated the niche requirements of *Microstegium vimineum*, an invasive grass in the U.S. that overruns native vegetation in forest understories. We examined *M. vimineum*'s performance and reproduction as a function of environmental drivers across forested and unforested habitats along a 100-km regional and climatic gradient in the southeastern U.S. from the southern Appalachian Mountains to the Georgia piedmont. We then measured *M. vimineum* performance and reproduction in response to direct environmental drivers (diffuse light, litter cover, soil moisture, herbaceous cover, soil pH, clay content and temperature) in paired invaded and uninvaded plots. Lastly, we experimentally investigated recruitment in the context of experimental and natural disturbances. We find that all habitats are not equally suitable for *M. vimineum*—even those within which it occurs—and that the environmental conditions associated with roadsides and waterways are most suitable for *M. vimineum* persistence and spread. *Microstegium vimineum*'s soil moisture, light and leaf litter requirements may delineate the boundaries of suitable habitat for the exotic invader. Significant decreases in *M. vimineum* recruitment, performance and reproduction along these environmental gradients suggest its potential niche limitations. Nevertheless, we also find significant dispersal limits on *M. vimineum* populations not subject to conspicuous overland water flow. We discuss our findings in the context of spread, impact and management of invasive species.

Key words: dispersal; edge habitat; exotic species; Japanese stiltgrass; *Microstegium vimineum*; Nepalese browntop; niche; plant invasion; understory.

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INTRODUCTION

Substantial colonization and spread by invasive species creates apparently homogenous monocultures that obscure underlying niche limitations. Forces such as land use history, disturbance regime and propagule pressure can distort the effects of environmental heterogeneity and permit populations to transcend assumed

habitat boundaries (Hutchinson 1957, Levins 1969, Pulliam 1988, Matlack 1994, Eriksson 1996, Clark et al. 1998, Pulliam 2000, MacDougall et al. 2009). These influences may be overlooked without considering invasive species within the context of ecological theory (Sax et al. 2005, Cadotte et al. 2006). Indeed, robust niche inference requires linking species performance directly with putative environmental drivers to

determine core requirements for persistence (Pulliam 2000), but a comprehensive delineation of the niche (sensu Hutchinson 1957) requires investment in resources and time that is often not viable (see Chase and Leibold 2003). Even if feasible, it likely would be untimely in terms of addressing the management of invasive species, and it would require experimental introductions that carry ethical concerns about the intentional introductions of exotics. So what is practical and required for invasive species research are case-studies that quantify potential environmental drivers, and associated species performance, to delineate potential suitable habitat. Such inferences will aid prediction of the spread and impact of invasive species.

Microstegium vimineum (Trin.) A. Camus is an annual grass native to southeastern Asia. Since arriving in the U.S. in the early 1900s (Fairbrothers and Gray 1972), it has spread throughout the eastern U.S. and midcontinental states. It invades roadsides, trails and waterways, along with associated forest understories and wetlands, displacing native vegetation (Cole and Weltzin 2004, Oswalt et al. 2007, Flory and Clay 2009a, b). Warren et al. (2011) synthesized published research on *M. vimineum* habitat distributions and hypothesized that the plant is limited by shade, drought and heavy aboveground leaf litter cover. This synthesis gave insights into the likely niche requirements of *M. vimineum*. Testing these predictions demands that *M. vimineum* performance and reproduction is measured concurrently with light, soil moisture, litter layer depth and other potential drivers, thereby accounting for the multiple interactions obscured within habitat designations (Hutchinson 1957, Pulliam 2000, Austin 2002, Kearney 2006). Moreover, the question remains as to whether discrete *M. vimineum* population boundaries—particularly across forest edges—indicate environmental niche and/or dispersal limitation (Cole and Weltzin 2004, 2005, Cheplick 2010, Miller and Matlack 2010). *Microstegium vimineum*'s ongoing colonization of multiple habitats throughout a large geographic area makes it an excellent choice to examine potential niche limitations in exotic species.

We investigate *M. vimineum* at 36 sites arrayed equally across three general locations positioned along a 100-km geographic gradient. The spatial

design captures a wide range of environmental gradients created by broad-scale shifts in elevation and latitude and fine-scale environmental heterogeneity. This investigation involves three steps that can be summarized as *M. vimineum*: (1) habitat observation, (2) niche observation and (3) niche experimentation. First, we verify *M. vimineum* habitat associations using kilometer transects to test whether *M. vimineum* exhibits the same landscape-level habitat patterns observed elsewhere (summarized in Warren et al. 2011). This approach not only provides a coarse approximation of *M. vimineum* niche requirements but also permits us to assess whether our results likely apply to *M. vimineum* in other parts of its invaded range, which currently spans approximately 25 U.S. states (USDA 2010). Second, we measure seven direct environmental drivers in adjacent invaded and uninvaded *M. vimineum* plots to disentangle potential niche requirements from parameters that co-vary with habitat (e.g., light and temperature both decrease as canopy closes). Third, we examine *M. vimineum* seedling recruitment and dispersal distance into previously uninvaded plots with experimental and natural disturbance as a function of environmental drivers. By examining *M. vimineum* performance and reproduction across divergent environmental conditions, our intention was to capture a broad range of its potential niche responses (Van Horne 2002).

If plots lacking *M. vimineum* represent dispersal limitation (Gibson et al. 2002, Oswalt and Oswalt 2007, Christen and Matlack 2009, Miller and Matlack 2010, Rauschert et al. 2010) and/or time since invasion (Richardson and Pysek 2006), (H_{1a}) we hypothesize that there will be little difference in environmental variables between invaded and uninvaded plots. However, if environmental variables limit or prevent *M. vimineum* establishment and persistence (H_{1b}), we expect significant differences in environmental variables between invaded and uninvaded habitats. Based on the conclusions presented by Warren et al. (2011), we expect *M. vimineum* performance and reproduction will correspond best with variation in soil moisture and light (H_{2a}); we include temperature, soil pH, leaf litter biomass, herbaceous biomass and soil clay content as alternate drivers (H_{2b}). Given that Warren et al. (2011) also suggested that *M.*

vimineum seedling recruitment may be limited by drought and leaf cover (H_{3a}), we expect colonization will correspond best with variation in soil moisture and litter; we include light, temperature, soil pH, herbaceous biomass and soil clay content as alternate drivers (H_{3b}). We also investigate the influence of overland water flow on *M. vimineum* spread into novel territory.

METHODS

Study design

Investigations were conducted at three locations spanning a 100-km gradient from the northern piedmont of Georgia to the southern Appalachian Mountains of North Carolina, USA (Fig. 1). The three locations were: (1) Whitehall Experimental Forest (WHF), Athens-Clarke County, GA (33°53' N, 83°21' W; 150–240 m elevation, 122 cm MAP, 17°C MAT), (2) Chattahoochee National Forest (CNF), Habersham County, GA (34°30' N, 83°29' W, 315–450 m elevation, 153 cm MAP, 14°C MAT) and Coweeta Hydrologic Laboratory (CWT), Macon County, NC, USA (35°03' N, 83°25' W; 750–1025 m elevation, 183 cm MAP, 13°C MAT). Four plots considered part of the CWT location were located nearby in the Little Tennessee Valley (35°04'03.57" N; 83°23'00.53" W, 612–622 m elevation) on land managed by the Land Trust for the Little Tennessee.

We first used transect-surveys (hereafter: 'habitat transects') to quantify *M. vimineum* presence (or absence) and cover across forested and unforested habitats at kilometer scales. This allowed us to compare the study populations with habitat distributions reported elsewhere for *M. vimineum*, but habitat type is a weak proxy for niche inference (Austin 2002, Kearney 2006). For example, we might assume that species associated with forest edges require higher light than those within the forest interior, but this habitat transition also includes shifts in temperature, soil moisture and leaf litter cover. We addressed the confounding effect of habitat and environmental gradients by employing direct measurement of environmental drivers and performance across invasion boundaries. We measured *M. vimineum* performance and reproduction in plot-surveys (hereafter: 'niche plots') as a function of diffuse light, litter cover, soil moisture, native herba-

ceous biomass, soil pH, clay content and temperature at meter-scales across defined invasion fronts. The first two parts of this investigation were observational and correlative, and we recognized that *M. vimineum* may influence, as well as be influenced by, its environment. We addressed this by examining subsequent *M. vimineum* seedling recruitment in uninvaded niche plots as a function of environmental drivers and experimental manipulations. We also examined putative dispersal mechanisms based on seedling recruitment across invasion fronts.

Habitat surveys

Approximately 22 km of GPS transects (0.5–2 km each, 150–990 m elev.) were established across forested and unforested habitats at the three locations. The initial transects were randomly stratified to follow roadways. Subsequent transects were established at random intervals perpendicular to the initial transects in a grid-like pattern (customized to the roadways and topography of each location) so that interior and exterior habitats were sampled with similar intensity. At 10 m intervals along each transect, 4 m² plots were investigated for the presence of *M. vimineum*. In total 221 plots and 884 m² were sampled during May–June 2009. *Microstegium vimineum* presence and cover, along with GPS position, elevation, aspect, slope percent, distance to nearest roadway, distance to nearest waterway, canopy cover and relative temperature were recorded for each plot. The relative temperature index was generated for each plot using latitude, slope angle and aspect (McCune and Keon 2002), and it was adjusted for elevation (Warren 2010).

Niche plots

Paired invaded and uninvaded plots were established at WHF, CNF and CWT in May 2009 (12 pairs at each location, $n = 72$ plots total). The plots intersected the edge of *M. vimineum* patches in a straight 6-m line so that three 0.25 × 0.25 m quadrats fell in adjacent invaded (1, 2 and 3 m from invasion edge) and uninvaded (–1, –2 and –3 m from invasion edge) patches (Fig. 1). The plot locations were selected for discrete invasion boundaries within apparently similar habitats (i.e., not crossing roads). Most of these occurred at or near, but did not span, forest

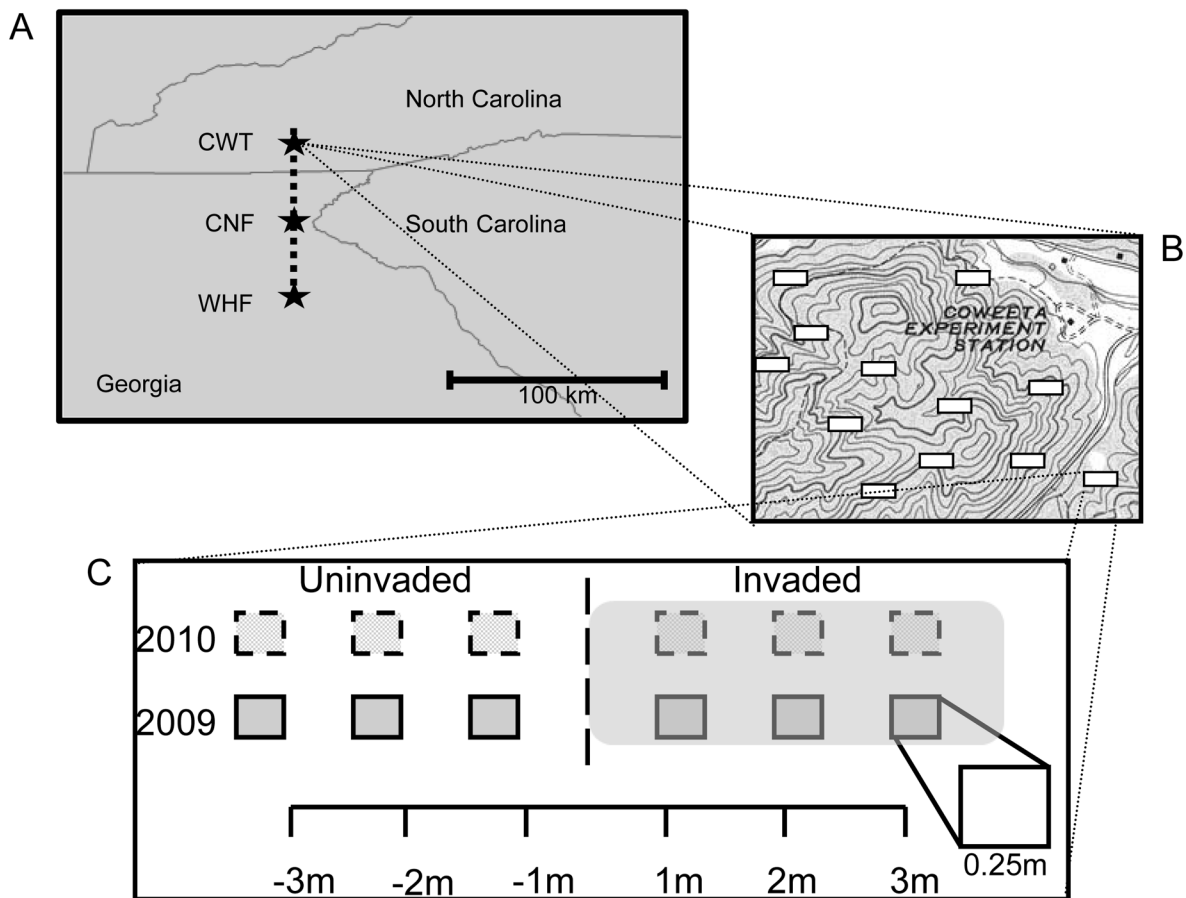


Fig. 1. Site and plot diagram for *Microstegium vimineum* observations. Study locations (a) were at Whitehall Experimental Forest (WHF, Athens-Clarke County, GA), Chattahoochee National Forest (CNF, Habersham County, GA) and Coweeta Hydrologic Laboratory (CWT, Macon County, NC), USA. In 2009, 12 plots (b) were established at each location ($n = 36$ total). *Microstegium vimineum* performance and reproduction was measured in three, pooled 0.25×0.25 quadrats within each plot (c), and these quadrats spanned adjacent invaded and uninvaded patches. All aboveground biomass was removed from these quadrats in 2009 and *M. vimineum* recruitment was measured in 2010. A second set of 0.25×0.25 quadrats were established in 2010 as undisturbed controls.

edges.

Microstegium vimineum cover (%), biomass (g) and reproductive output (mg) were measured in each plot (pooled per plot by invaded and uninvaded quadrats, giving 0.1875 m^2 areas). The *M. vimineum* vegetative biomass (g) was collected in June-July 2009, dried at 65°C and weighed. The biomass of all other herbaceous species, leaf litter and its coverage (%) were also measured. In October 2009, all reproducing plants were counted in temporary $0.25 \times 0.25 \text{ m}$ quadrats paired 25 cm below the permanent

quadrats. Seeds were collected from five randomly selected plants in the temporary quadrats and all seeds were pooled by plot. *Microstegium vimineum* produces both cleistogamous and chasmogamous seeds, but these were pooled because self-fertilization is common in annual plants and does not appear to adversely affect fitness, as it does in perennials (see Morgan 2001).

All abiotic measurements were taken in the three permanent quadrats per plot and averaged. Volumetric soil moisture (%) was measured

within each plot with a handheld Hydrosense Soil Water Content Measurement System (Campbell Scientific Inc., Logan, Utah, USA) in May, July and September 2009. Percent photosynthetically active radiation (PPFD, diffuse light) was calculated as the difference between plot-level PAR readings and a fully exposed PAR reference site. The understory measurements were taken in July 2009 with an LI-191 line quantum sensor and the open reference measurements were taken with an LI-200 spherical PAR sensor and logged with a LI-1400 datalogger (LiCor Inc., Lincoln, Nebraska, USA). Measurements were taken on cloudy days between 10 a.m. and 2 p.m. to minimize relative error in diffuse light. Ambient soil temperature was measured with a T-shaped digital thermometer inserted 8 cm into the soil in May and September 2009.

One soil core (8 cm dia., 0–10 cm depth) was taken from each of the three quadrats in each plot and pooled. They were then passed through a 4 mm sieve, homogenized, and stored at +5°C until pH determination. Soil pH (1:1, soil:H₂O by volume) was measured with a bench-top pH meter. A fraction of the sieved soil was air-dried to constant mass and texture was estimated using a simplified version of the hydrometer method as described by Gee and Or (2002). We use only percentage clay here as an estimate of texture, given the collinearity between sand, silt and clay and the effect this would have in our statistical models.

Recruitment

Living and detrital biomass were removed from each 0.25 × 0.25 m quadrat in July 2009 and again in February 2010. A second set of 0.25 × 0.25 m quadrats were paired 25 cm above the disturbed quadrats to measure recruitment without litter removal (Fig. 1). In addition, considerable overland sheet flow (hereafter: ‘flooding’) occurred between September 2009 and May 2010 in 14 plots. We observed flooding directly as temporary inundation and indirectly by evidence of previous overland flow such as asymmetrical litter accumulation on flagging and soil scouring. Because the degree and duration of these events was unknown, flooding was quantified as a factor (0 or 1) for statistical analysis. *Microstegium vimineum* seedlings were counted in May 2010, and diffuse light, soil moisture and temperature

were measured using the same protocols as previously described.

Data analysis

Habitat transects.—The conditional relationships between *M. vimineum* presence and coverage as a function of roadway distance, waterway distance, canopy cover and relative temperature were explored using classification tree (CART) models. Roadways were gravel forest roads at all locations, and waterways varied from drainage ditches to perennial streams. Canopy coverage was estimated as a discrete factor where >20% unblocked sky was considered “edge” canopy and <20% “interior.”

The CART models provide a robust alternative to multiple regression and analysis of variance, and they do not require data transformation or normalization, can handle continuous and discrete variables and are more straightforward in the interpretation of interactions and complex patterns (Breiman et al. 1984, De’ath and Fabricius 2000). The CART models were constructed using the RPART package (Therneau and Atkinson 1997) in the R statistical program (R Development Core Team 2009). To prevent overfitting (too many tree branches), trees were “pruned” using 10-fold cross-validation in the RPART package with the 1-SE rule established by Breiman et al. (1984) so that the final CART model was the smallest within 1 SE of the minimum error model. The control parameters for the model fitting were five minimum observations in a node before attempting a split and a minimum of two observations in a terminal node. The RPART summary information was used to evaluate surrogate splits and root node error. Surrogate splits are those that provide the most similar subsequent splits and trees as the variables chosen for a given node to create the best model (i.e., similar surrogates indicate collinearity between predictor variables but do not impact the entire CART tree as do competitor splits). Surrogate splits that were >75% in agreement with the fitted tree splits are reported.

Niche plots.—The three locations along the 100 km gradient were employed to increase the generalizability of results. The clustering of plots ($n = 12$ plots location⁻¹) at each location (WHF, CNF and CWT), although a standard approach in ecological research, introduces potential spa-

tial and temporal autocorrelation and unobserved error. For these reasons, we used mixed models with location as a random effect and diffuse light (%), litter cover (%), soil moisture (%), native herbaceous biomass (g), soil pH ($[H^+]$), clay content (%) and temperature ($^{\circ}C$) as fixed effects. The random effect itself is not strictly interpretable with three locations (Bolker et al. 2009); however, its inclusion in the models accounts for different means per location in the overall mean, and this allows inferences about environmental effects on the *M. vimineum* population as a whole.

We used generalized linear mixed models (GLMM) to evaluate the difference in fixed effects in invaded and uninvaded plots and the influence of the random and fixed effects on *M. vimineum* performance assuming a Poisson distribution (log function). Generalized linear models allow statistical regression analysis without the assumption of Gaussian error distribution. The Poisson distribution best approximates errors resulting from count data that cannot take on negative values, and we verified that the models were not overdispersed ($\phi < 2$). Performance was calculated as *M. vimineum* biomass \cdot percent coverage $^{-1} \cdot m^{-2}$. As *M. vimineum* is an annual species, and all individuals begin the season with no aboveground biomass, we estimated biomass per plant coverage to generate a per capita proxy for growth. We also used GLMMs assuming a Poisson distribution to evaluate the influence of the random and fixed effects on per capita *M. vimineum* reproduction (number: seeds \cdot percent coverage $^{-1} \cdot m^{-2}$; mass: mg \cdot seeds $^{-1} \cdot$ percent coverage $^{-1} \cdot m^{-2}$). The GLMM models were fit using the *Laplace approximation* in the “lme4” package (Bates and Maechler 2009) for the R statistical programming environment (R Development Team 2009). In evaluating the impact of the environmental variables on *M. vimineum*, the inclusion or exclusion of the fixed effects and their interactions was based on Akaike’s Information Criterion (AIC) values (Akaike 1973). AIC measures the distance of models to truth; that is, the information loss in the data given that the model is a simplification of reality and cannot explain full variance in the data (Burnham and Anderson 2002). Such a measure can only measure the relative information loss of each model because truth is not known. In effect

AIC is a measure of goodness-of-fit, as the more familiar R^2 measure, with an added penalty for model complexity as measured by the number of fit parameters in the model. The variance inflation factors for the fixed effects in all models were < 2 , indicating they independently explained variance. Given that biotic responses to abiotic variables often peak at intermediate levels, second-order polynomial terms were included but none were retained in any model. Litter cover (%) was a better predictor than litter biomass (g) of *M. vimineum* cover ($\Delta AIC = 24$) and biomass ($\Delta AIC = 4$), and so litter coverage was used in all models.

Recruitment.—We used a generalized linear mixed model (GLMM) assuming a binomial distribution in errors (logit function) and location as a random effect to evaluate mean difference in recruitment as a function of *M. vimineum* invasion and litter disturbance. The binomial distribution works best with data that only contains two possible values, such as “success” or “failure” in seed recruitment. Recruitment was calculated as 2010 seedlings \cdot 2009 seeds $^{-1} \cdot m^{-2}$. We calculated recruitment on a per capita basis to account for variation across plots in seed-producing plants. We assumed less propagule production in uninvaded than invaded plots, and we found that the best-fit model assumed propagule pressure in uninvaded plots at 20% of that in invaded plots ($\Delta AIC = 1411$). We also used a GLMM assuming a binomial distribution to evaluate recruitment as a function of diffuse light (%), soil moisture (%), temperature ($^{\circ}C$), soil pH and flooding, as well as recruitment distance in the disturbed quadrats 1, 2 and 3 m into uninvaded plots as a function of litter disturbance, flooding and slope degree. Location was included as a random effect.

RESULTS

Transect-surveys

The CART models diagrammed the hierarchical interactions between *M. vimineum* presence (classification model), coverage (regression model), roadway distance, waterway distance, canopy cover and relative temperature. The models provide information on the variance explained by each variable, and therefore their relative importance, as well as the threshold values of

independent variables at which they segregate between presence and absence and relatively high and low coverage. Distance to canopy cover and waterway were the most important variables explaining variance in *M. vimineum* presence. Canopy openness best explained presence, and 76% of edge habitat plots were occupied (Appendix A: Fig. A1a). A similar number of plots were occupied in the interior plots near waterways (75%), but only 7% of interior plots > 17.5 m from waterways were occupied. One surrogate split at the first node had a high degree of concordance with canopy that indicated that distance to roadway (96%) was somewhat interchangeable with canopy coverage.

As with presence, distance to canopy cover and waterway were the most important variables explaining variance in *M. vimineum* coverage except the CART model split distance to waterway at the first node and canopy cover at the second (Appendix A: Fig. A1b, Fig. 2a, b). *Microstegium vimineum* cover was greatest < 17.5 m from waterways (42%). Where it was > 17.5 m away, coverage was much greater in edge (29%) than interior (3%) habitats. As in the presence model, distance to roadway was a strong surrogate (98% of tree agreement) for canopy cover at the second node. Overall, *M. vimineum* cover (%) decreased with increasing distance to waterway (m), and this relationship was least pronounced at CWT (Fig. 2a). Within edge habitats, median *M. vimineum* cover was 38% and most plots fell within the 16–60% range, but it was extremely limited in interior habitats because median coverage was 0% and only scattered outliers occurred with higher coverage (Fig. 2b).

Plot-surveys

The ranges for environmental variables across plots and locations were: diffuse light (1 to 55%), litter cover (0 to 70%), soil moisture (11–78%), native herbaceous biomass (0 to 105 g m⁻²), soil pH (4–8), clay content (5–31%) and temperature (17–21°C). There was no difference between *M. vimineum* invaded and uninvaded plots in mean diffuse light (t -value = 0.29, p = 0.77), native herbaceous biomass (t -value = -0.74, p = 0.46), percent clay in the soil (t -value = 0.90, p = 0.38) or temperature (t -value = -0.22, p = 0.83) (Fig. 3). Litter cover was significantly lower in invaded

(16.8 ± 17%) than uninvaded (61.3 ± 38%) plots (t -value = -0.46, p < 0.0001), soil moisture significantly higher in invaded (24.7 ± 15%) than uninvaded (17.4 ± 9%) plots (t -value = 2.50, p < 0.02), and pH significantly less acidic in invaded (5.5 ± 0.1) than uninvaded (5.2 ± 0.3) plots (t -value = -2.14, p < 0.04).

The best-fit *M. vimineum* biomass (g•cover⁻¹•m⁻²) model included diffuse light, soil moisture and temperature, and dropped litter, native biomass, soil pH and clay content. *Microstegium vimineum* biomass increased significantly with diffuse light (coeff. = 0.02, SE = 0.01, z -val = 5.92, p < 0.001). *Microstegium vimineum* biomass also increased with soil moisture and temperature, and a significant soil moisture:temperature interaction (coeff. = 0.02, SE = 0.01, z -val = 4.82, p < 0.001) indicated that biomass was highest where both soil moisture and temperature were highest (Fig. 4). Light and temperature were the only parameters retained in the best-fit *M. vimineum* reproduction models for seed number (seeds•percent coverage⁻¹•m⁻²), which increased significantly with light (coeff. = 0.03, SE = 0.01, z -val = 11.70, p < 0.001) (Fig. 5a). Per capita seed mass (mg•seeds⁻¹•percent coverage⁻¹•m⁻²) also increased significantly with light (coeff. = 0.03, SE = 0.01, z -val = 8.00, p < 0.001) (Fig. 5b).

Recruitment

Seedling recruitment (2010 seedlings•2009 seeds⁻¹•m⁻²) differed across *M. vimineum* invasion fronts and with experimental disturbance of the litter layer. *Microstegium vimineum* recruitment increased in invaded plots and with disturbance, but a significant invaded:disturbance interaction (coeff. = -0.22, SE = 0.08, z -val = -2.59, p < 0.01) indicated that disturbance significantly increased recruitment in uninvaded plots but had no effect in invaded plots (Fig. 6). The best-fit *M. vimineum* model for recruitment in uninvaded plots included flooding, soil moisture, soil pH, diffuse light and temperature, and only dropped the interaction terms. *Microstegium vimineum* recruitment increased significantly with flooding (coeff. = 0.99, SE = 0.14, z -val = 7.42, p < 0.001) and soil moisture (coeff. = 0.05, SE = 0.01, z -val = 4.34, p < 0.001), and it decreased significantly with pH (coeff. = -4.33, SE = 4.03, z -val = -2.49, p < 0.05). The effects of diffuse light and temperature were not significant.

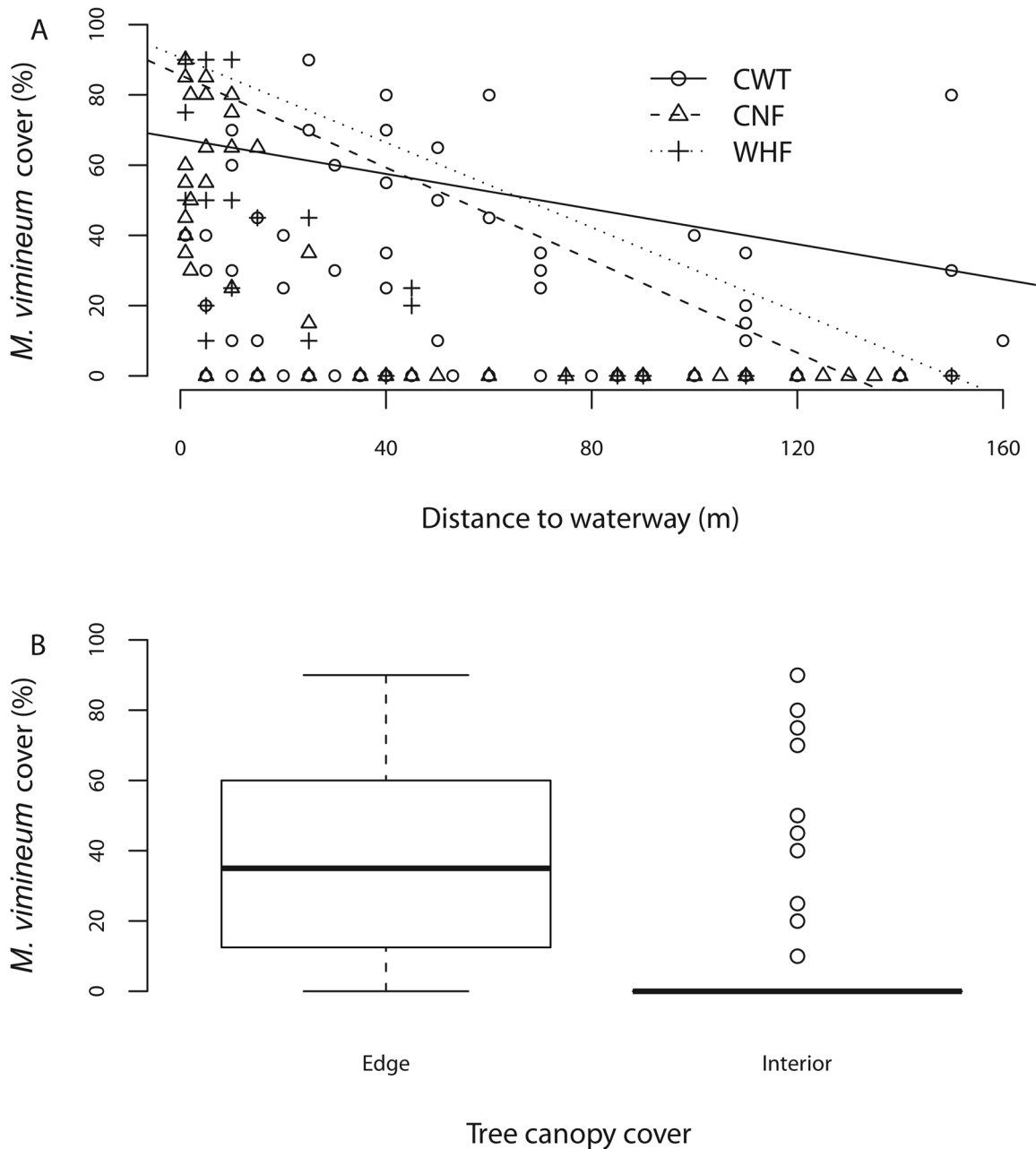


Fig. 2. Landscape-level patterns of *Microstegium vimineum* coverage as a function of distance to waterway (A) and canopy coverage (B). Maximum (90%) *M. vimineum* coverage (A) is represented using quantile regression so that the breakpoint (the environmental variable intensity where maximum recruitment success occurs) is represented by a fitted line at the 90th quantile (90% of the data points are below the line and 10% are above). *Microstegium vimineum* coverage in edge and interior forest canopy habitat (B) is represented using a box and whiskers plot where the solid line is median coverage, the box the 25th and 75th quartiles, the dotted lines the minimum and maximum observations and the circles indicate outliers.

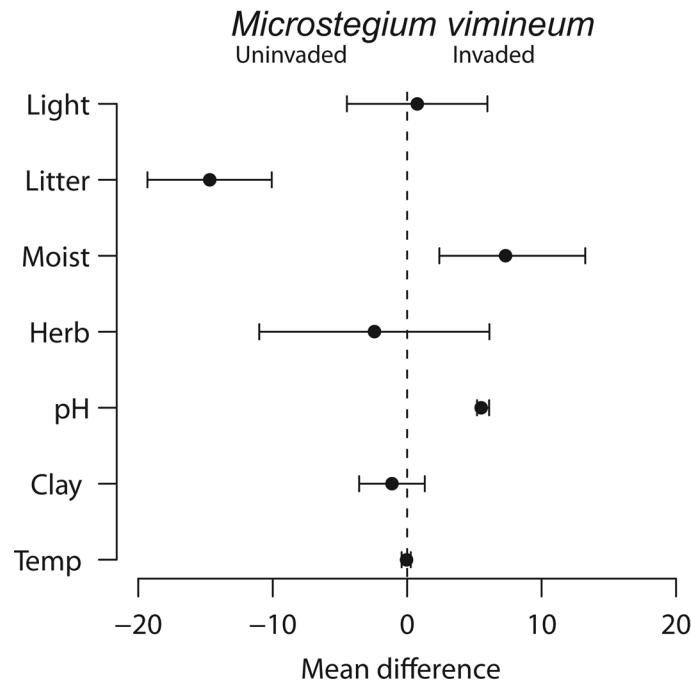


Fig. 3. Mean differences ($\pm 95\%$ CI) in soil moisture (% Moist), diffuse light (% Light), temperature ($^{\circ}\text{C}$, Temp), leaf litter (% Litter), herbaceous cover (Herb, g m^{-2}), soil clay content (Clay, %) and soil pH between plots invaded and uninvaded by *Microstegium vimineum*. Confidence intervals that do not cross zero (indicated by the dashed line) indicate statistically significant differences in means. The mean difference in leaf litter between plots was scaled down 1/3 for graphing with the other variables (the actual difference is $-56.3 \pm 27.2\%$).

Our placement of $0.25 \times 0.25\text{-m}$ quadrats 1, 2 and 3 m within invaded and uninvaded plots also allowed analysis of recruitment colonization distance into the uninvaded plots. Mean seedlings per quadrat decreased at distances of 1 m (27.6 ± 40 seedlings m^{-2}), 2 m (19.6 ± 40 seedlings m^{-2}) and 3 m (16.4 ± 36 seedlings m^{-2}) from the invasion edge. The statistical analysis of the maximum distance for seedling recruitment from invasion fronts as a function of litter-removal, flooding, slope degree and seed output from adjacent plots only retained flooding in the best-fit model. Specifically, seedling recruitment increased significantly from the invasion front ($\text{coeff.} = 0.406$, $z\text{-value} = 2.21$, $p < 0.027$) with flooding. Seedlings appeared 0.7 ± 1.0 m further into uninvaded habit where flooding occurred.

DISCUSSION

We investigated broad-scale habitat associa-

tions of *M. vimineum*, and its fine-scale niche requirements, at three locations along a 100-km climate and ecological gradient. Our results confirm roadsides and waterways as potential habitat for *M. vimineum* spread and persistence; and we establish that *M. vimineum*'s soil moisture, light and leaf litter requirements may delineate the boundaries of habitat suitability. Significant variability in *M. vimineum* performance, reproduction and recruitment along environmental gradients indicates potential niche limitations for the exotic invader. We also find significant dispersal limits on *M. vimineum* populations not subject to conspicuous overland water flow. What is clear is that the multi-scale, combined observational and experimental approach we employ permits us not only to quantify known habitat associations of a widespread invader but also identify the environmental drivers likely shaping these associations. These mechanistic insights can help inform prediction of *M. vimineum* spread and its

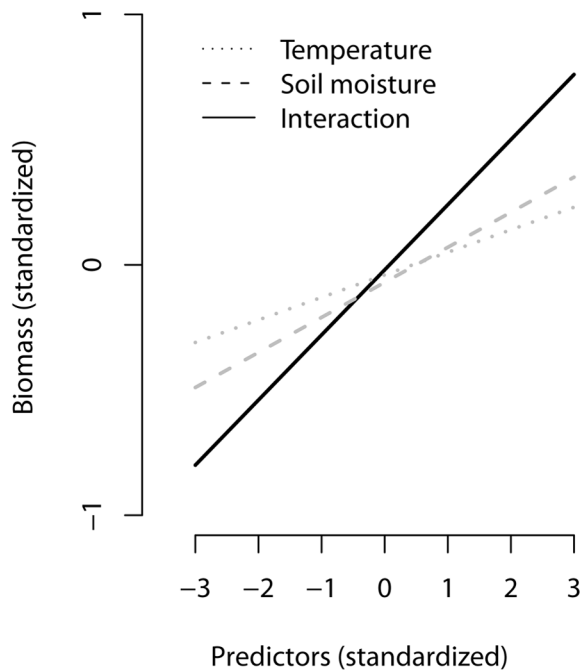


Fig. 4. Continuous interaction plot of the effects of temperature and soil moisture on *Microstegium vimineum* biomass ($\text{g} \cdot \text{cover}^{-1} \cdot \text{m}^{-2}$). The terms were re-centered for graphing. The significant non-additive effect of temperature and soil moisture on *M. vimineum* biomass indicates that the plant thrives considerably better where habitat is wet and warm.

management. For example, our analyses show that canopy disturbance (light) facilitates growth and reproduction, and if this disturbance also reduces the litter layer (as logging typically does) then recruitment also will be favored. Similar approaches to ours might help reveal niche limitations for other annuals (whether native or exotic), facilitating their management based on ecological information.

Habitat distribution and niche requirements

The strong association between *M. vimineum* and forest edges, particularly roadsides and waterways (Fig. 2), suggests these habitats are suitable for *M. vimineum* persistence, in addition to providing potential dispersal corridors (Mehrhoff 2000, Christen and Matlack 2009, Eschtruth and Battles 2009a). Yet, habitat associations cannot disentangle dispersal from niche limitations, and multiple environmental variables shift similarly along the transition from

forest interior to edge to exterior. For these reasons, we measured multiple environmental drivers across *M. vimineum* patch edges, and we find higher soil moisture and soil pH, and lower leaf litter, within invaded patches (Fig. 3), suggesting the absence of *M. vimineum* is not purely random or dispersal limited. It is plausible, however, that differences between invaded and uninvaded plots are an effect rather than cause of *M. vimineum* distributions. For example, *M. vimineum* invasion influences soil microbial communities and nitrogen cycling (e.g., nitrification) (Kourtev et al. 1998, Ehrenfeld et al. 2001, Kourtev et al. 2002a, Kourtev et al. 2002b, McGrath and Binkley 2009). These changes are associated with an increase in soil pH (Kourtev et al. 1998, Ehrenfeld et al. 2001, McGrath and Binkley 2009), suggesting that the less acidic pH in invaded areas (Strickland et al. 2010) may result from *M. vimineum* presence, as opposed to a specific niche requirement. *Microstegium vimineum* may also influence soil moisture via shading and accelerate leaf litter decomposition (Kourtev et al. 1998, Kourtev et al. 2002a, Cole and Weltzin 2004), but see (Ehrenfeld et al. 2001, DeMeester 2009). Although quantification of species performance per these variables does not establish whether they result from the plant's presence, it does permit inference into whether they influence its persistence, and we discuss below these limitations and how we strengthened the initial inferential approach.

We move beyond the simple presence or absence of *M. vimineum* by examining its per capita biomass and seed production. We find considerable variation in *M. vimineum* growth and reproduction per environmental drivers which indicates their importance in delineating a gradient in habitat suitability. *Microstegium vimineum* growth increases with increasing light, soil moisture and temperature—particularly where both soil moisture and temperature are highest (Fig. 4), whereas its reproduction increases only with increasing light and temperature (Fig. 5). These results are consistent with other researchers that report decreased *M. vimineum* growth and reproduction in drought and shade (Claridge and Franklin 2002, Cole and Weltzin 2004, 2005, Glasgow and Matlack 2007, Marshall and Buckley 2008a, Eschtruth and Battles 2009a, Flory and Clay 2009a, Cheplick

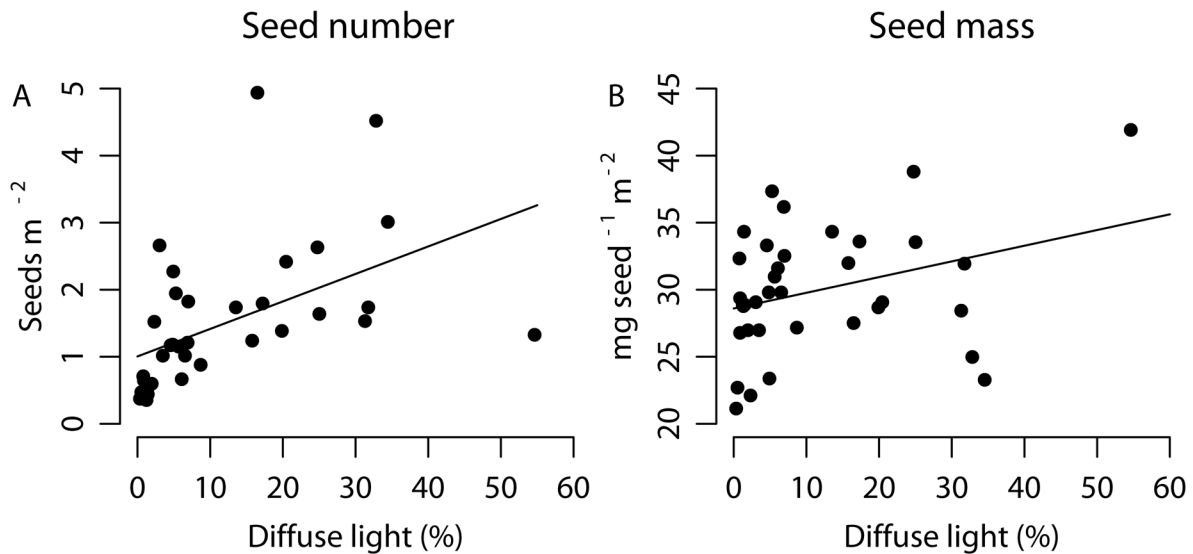


Fig. 5. Per capita reproduction as a function of diffuse light. Both the number of seeds per plant (a, seeds•percent coverage⁻¹•m⁻²) and the weight of each seed per plant (b, mg•seeds⁻¹•percent coverage⁻¹•m⁻²) only increase significantly ($p < 0.001$) with increased light in understory forest habitat.

2010, Droste et al. 2010, Flory 2010, Huebner 2010a, Schramm and Ehrenfeld 2010). Yet, as noted, these associations cannot fully decouple cause and effect in *M. vimineum* establishment. Admittedly, seed output is less likely an influence upon the abiotic environment than *M. vimineum* biomass; but there is an established correlation between *M. vimineum* vegetative biomass and seed output (Horton and Neufeld 1998, Claridge and Franklin 2002, Cheplick 2005), and we found a similar relationship ($coeff. = 4.8$, $f\text{-value} = 14.47$, $p < 0.0006$). For this reason, we test the importance of *M. vimineum*'s putative niche requirements by examining its per capita recruitment into novel habitat as a function of experimental and natural disturbances along the same environmental gradients.

Mechanically disturbing leaf litter cover on the forest floor significantly aids *M. vimineum* colonization of novel habitat whereas it has little effect in previously invaded plots (Fig. 6). The discrepancy between disturbance-induced recruitment in invaded and uninvaded habitat likely arises because there was less litter from the outset in the invaded than uninvaded plots (Fig. 3). The importance of disturbance for recruitment in the uninvaded habitat confirms the litter layer poses a substantial barrier for *M.*

vimineum invasion. In addition, we find that *M. vimineum* recruitment increases with wetter soil and decreases with more acid pH, results consistent with those of other researchers (Glasgow and Matlack 2007, Oswald and Oswald 2007, Nord et al. 2009, Touchette and Romanello 2010), suggesting these are essential niche requirements and not just effects of its invasion.

Microstegium vimineum recruitment also increases with the occurrence of flooding. The lack of significant interaction between flooding and soil moisture indicates that the hydrating effects of flooding have little to do with *M. vimineum* recruitment. Because we analyzed this dynamic in already disturbed plots, the structural changes induced by overland water flow (e.g., litter disturbance, scouring) also are minimized. This suggests that the key benefit of flooding for recruitment is seed transport. Indeed, we found that recruitment penetrated 32% further into previously uninvaded habitat with flooding. Our study design limited the assessment of maximal dispersal distances, and could include dormant seeds from previous years, so we conducted an additional experiment that tracked marked *M. vimineum* seeds (Appendix B). We found seeds transported up to 14.8 m from parental plants from roadside into forest interior via periodic

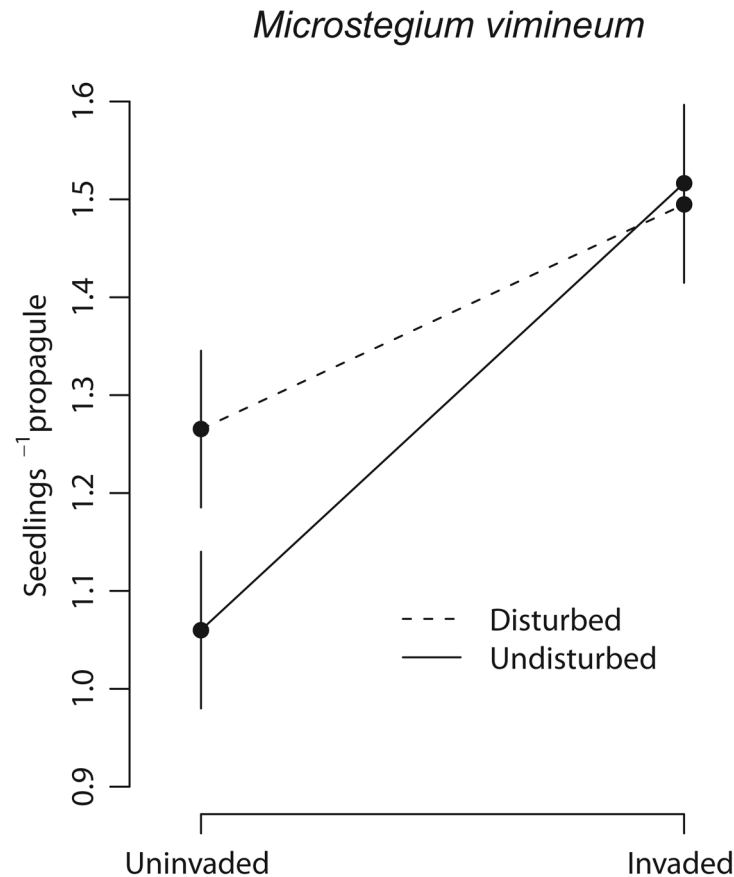


Fig. 6. Interaction plot of the effects of litter disturbance and invasion on *Microstegium vimineum* recruitment (2010 seedlings•2009 seeds⁻¹•m⁻²). The hatched and solid lines that connect the data-points are included to demonstrate that recruitment is a non-additive function of invasion status and leaf-litter disturbance (i.e., the lines are not parallel). Specifically, increased propagule pressure has no effect on subsequent seedling density in habitat already invaded by *M. vimineum*, but incurs a significant increase in seedling density when leaf litter is disturbed in uninvaded habitat.

stormwater run-off. In contrast, seeds from parental plants located in similarly sloped habitat without concentrated waterflow did not travel more than 1.5 m (Appendix B). This provides one of the few quantitative measures of natural *M. vimineum* dispersal distance (see Cheplick 2010). Additional vectors for *M. vimineum* dispersal (e.g., animal) have been proffered, but none confirmed, and anthropogenic transport may explain the plant's long-distance dispersal (see Warren et al. 2011 and references therein). However, long-distance dispersal likely is rare compared to local dispersal, and thus would be less influential at our scale of investigation.

Niche and dispersal limitation

Our results showing that passive *M. vimineum* seed dispersal is minimal (≤ 1.5 m) are consistent with the observations of others (Barden 1987, Gibson et al. 2002, Oswalt and Oswalt 2007, Christen and Matlack 2009, Huebner 2010b, Rauschert et al. 2010). Moreover, our results, along with additional recent work (Cheplick 2010, Miller and Matlack 2010), confirm earlier observations that dispersal distances increase considerably via floodwaters (Mehrhoff 2000, Eschtruth and Battles 2009a). As noted by Miller and Matlack (2010), however, much of the landscape is exempt from overland waterflow, including habitat occupied by *M. vimineum*.

Our results suggest that niche requirements, as well as dispersal limitation, influence the establishment and success of *M. vimineum* populations. For example, the habitat transects indicate that canopy openness best explains *M. vimineum* presence in forest edge habitats whereas distance to waterways best explains it in forest interior habitats. Habitat delineations are only suggestive, but this is consistent with higher *M. vimineum* reproduction with increased sunlight (forest edge) and higher recruitment with increased moisture (near waterways in forest interior). What is unknown based on the time period observed here is whether this represents a source-sink dynamic (see Pulliam 1988), in which forest interior populations depend on the edge populations for continued or periodic seed input, or a core-satellite dynamic (e.g., Auld and Coote 1980, Moody and Mack 1988), in which the forest interior populations persist through suboptimal periods and eventually spread to adjacent territory during favorable years. Such possibilities require further investigation if we are to inform predictions of this species' spread and impact, as well as management, because a source-sink scenario indicates that edge populations can be targeted for control whereas a core-satellite scenario indicates that interior populations also must be targeted.

Forest interiors contain far greater leaf litter cover than edge habitat (Lang and Orndorff 1982, Boerner 1984, Facelli and Pickett 1991), a recruitment barrier for many shade-adapted understory species (Xiong and Nilsson 1999) including *M. vimineum* (Glasgow and Matlack 2007, Oswalt and Oswalt 2007, Miller and Matlack 2010). Our results indicate a significant increase in *M. vimineum* recruitment with litter disturbance, but recruitment occurred, even if to a lesser extent, in undisturbed patches. Moreover, other workers have found mixed to marginal *M. vimineum* resistance to litter cover (Marshall and Buckley 2008b, Miller and Matlack 2010, Schramm and Ehrenfeld 2010). The efficacy for leaf litter to prevent *M. vimineum* invasion may depend on the level of seed input, and here again we find the need to know the plant's niche requirements. A key finding from our work is that seed output increases significantly with light and temperature, conditions found at forest edges where leaf litter is generally thinner. The

effect of diffuse light on reproduction was particularly marked where diffuse light was >20%, suggesting that the plant requires light levels greater than those typically found in forest understory habitats for vigorous seed production. Whereas *M. vimineum*'s potential for seed dormancy may overcome temporal variation in habitat suitability, ample evidence indicates that seed fitness, including dormancy potential, is strongly influenced by environmental conditions experienced by maternal plants during the reproductive phase (Evans and Etherington 1990, Gallagher and Fuerst 2006, Poorter et al. 2008). Individual seed mass is a strong proxy for seed fitness (Liu et al. 2000, Gallagher and Fuerst 2006, Padilla et al. 2007), and those data from our 36 plots show that in addition to seed number, a positive correlation exists between *M. vimineum* seed mass and diffuse light. This indicates that *M. vimineum* populations in shady conditions not only produce fewer seeds, but that those produced may be less viable.

Notably, the density of propagules and their interaction with local microsites greatly determines the success or failure of recruitment for most plants (Grubb 1977, Harper 1977, Eriksson and Ehrlén 1992, Crawley 1997, Clark et al. 2007, Moore 2009). In the case of exotic species, the interaction between propagule supply and establishment limitation likely acts as a crucial step in the invasion of novel habitat (Lockwood et al. 2005, Eschtruth and Battles 2009b, Tanentzap and Bazely 2009) and merits further study to understand better its role in making a system susceptible to invasion. Together, our data on establishment, reproductive output and seed quality suggest that competitive impacts of *M. vimineum* might be greatest in warm, moist, sunny sites given not only their presence, but also their potential for producing overwhelming seed output, a phenomenon often seen in invasive species (Von Holle and Simberloff 2005, Eschtruth and Battles 2009b, Tanentzap and Bazely 2009).

An emphasis on impact over impedance in invasive species research (Cadotte et al. 2006) can leave niche limitations overlooked. *Microstegium vimineum* is one of many exotic species currently invading deciduous forest, understory habitats (Horton and Neufeld 1998, Cole and Weltzin 2005, Martin et al. 2009). Whereas the impact of

these invasions is an important research target, it also is important to understand what niche parameters may enhance or limit such invasions. A comprehensive literature review (Warren et al. 2011) synthesized disparate research pertaining to potential niche limitations in *M. vimineum* and informed the structuring of our observational and experimental work. Most notably, the Warren et al. (2011) review suggested that as multiple environmental gradients shift concurrently across woodland boundaries, individual assessment of potential niche resources (e.g., light) fails to take interactions between abiotic drivers into consideration. We find such interactions in our multiple regression models (e.g., Fig. 4). This highlights the need for field observation and experimentation to measure multiple, potential niche resources.

What remains lacking from invasive species work, including that presented here, is long-term population demographic data. The discrepancies between reports favoring dispersal or niche limitation to explain species distributions may simply represent temporal stochasticity. In this context, demonstrated niche limitations would impose boundaries on *M. vimineum* populations, so that they shrink back to core populations during unfavorable periods. Whether this would curtail *M. vimineum*, which also may permanently expand its population distribution during favorable periods, is yet to be tested. A second limitation is the consideration of biotic interactions. The results presented here suggest an ecological niche, but do not account for variation in biotic interactions (e.g., Bradford et al. 2010, Kleczewski and Flory 2010) across environmental gradients which may well influence species' distributions. Further, *M. vimineum* patches in forest understory habitat may be established in locations where reproduction is insufficient to maintain a population and persist only through constant or periodic propagule immigration from proximate edge populations. Source or core populations for understory *M. vimineum* sinks likely occur along road, trail or water corridors (Gibson et al. 2002, Cole and Weltzin 2004, 2005, Christen and Matlack 2009, Huebner 2010a, b), but may only periodically interact with interior habitats because *M. vimineum* propagules do not typically travel >2 m from source plants (Barden 1987, Gibson et al. 2002, Oswalt and Oswalt 2007,

Christen and Matlack 2009, Huebner 2010b, Rauschert et al. 2010). However, flooding or other substantial waterflow can transport *M. vimineum* seeds from edge habitat at least 15 m into the forest interior (Appendix B). Experimental work is required to test whether source and/or core population dynamics contribute substantially to *M. vimineum* distribution and impact across the landscape.

Conclusions

Our results suggest that, instead of broad-scale herbicide application or other control efforts, eradication efforts might target putative core patches within what might otherwise appear homogenous monocultures. If effective, it would provide control with less resource outlay and fewer unintended consequences (e.g., non-target effects on native plants and amphibians). Our data suggest the conditions conducive to source populations would occur along forest edges and roadsides—these patches are far more accessible for management activities than the forest interior, and they are likely bereft of sensitive and relatively less common forest understory species. Such management efforts would be most effective just before fall seed set. A second and clear implication of our data for land managers is the importance of intact substrate, particularly leaf litter, as an impediment to *M. vimineum* recruitment. This insight may require the cessation of management activities such as prescribed burning and roadside scraping; however, as we show, litter disturbance most benefits the plant during its recruitment stage so necessary disturbances could be postponed until late summer or fall when the effective germination window has passed. Overall, our multi-scale, combined observational and experimental approach discerns what appears to be pronounced niche requirements of a widespread invader, and it indicates how these mechanistic insights might aid management.

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APPENDIX A

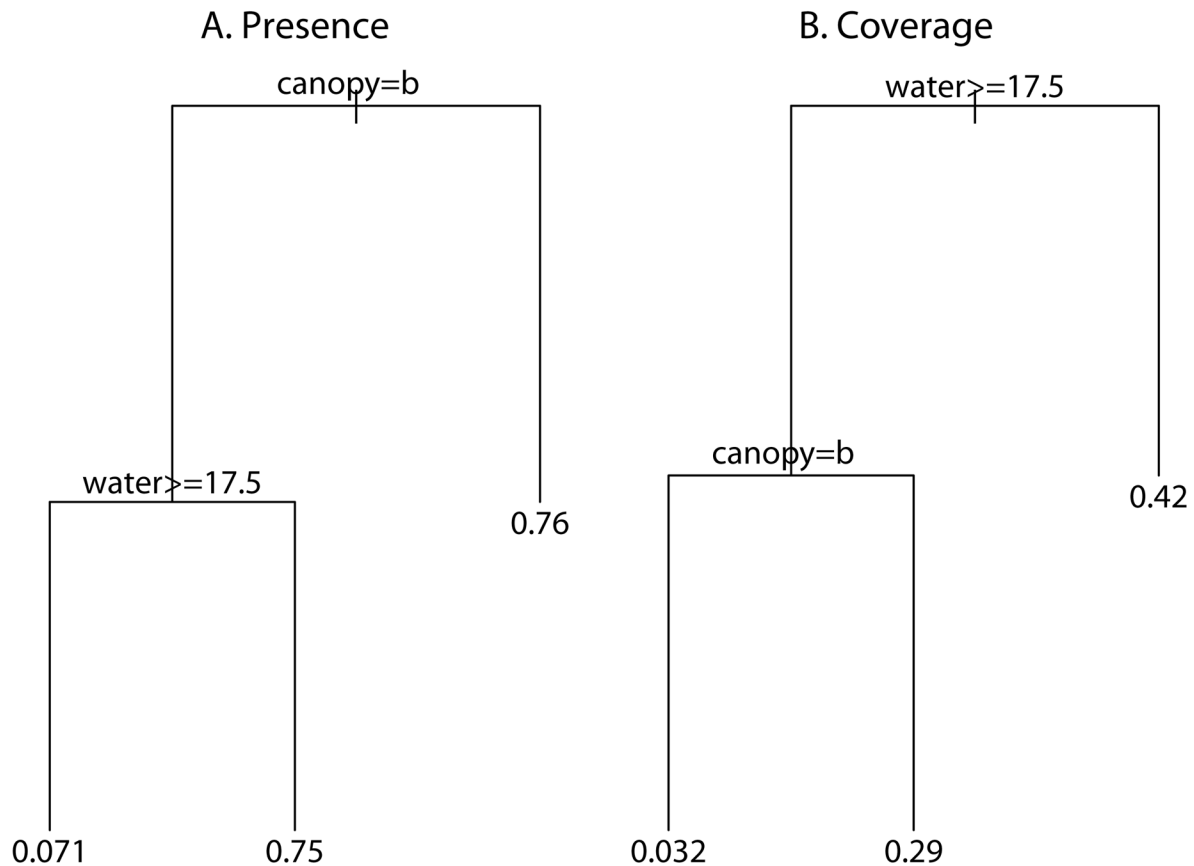


Fig. A1. Tree models between *Microstegium vimineum* presence (A, classification tree) or coverage (B, regression tree) and forest canopy cover (“canopy”, edge or interior) and distance to waterway (“water”, m). Canopy cover splits so that interior habitats follow the left branch and edge habitats follow the right (indicated by canopy = b). Waterway splits so that distances <17.5 m split the left and distances >17.5 m split to the right. The values for the percent of occupied plots (A) and percent plot coverage (B) are given at each terminal node.

APPENDIX B

MICROSTEGIUM VIMINEUM PASSIVE SEED DISPERSAL

Microstegium vimineum often is associated with edge habitats and waterways (Cole and Weltzin 2004, Christen and Matlack 2009), and this suggests that these habitats act as conduits for passive *M. vimineum* propagule dispersal (Mehrhoff 2000, Christen and Matlack 2009, Eschtruth and Battles 2009a). In September 2010, we located four *M. vimineum* patches in the southern Appalachian Mountains (North Carolina, USA). The percent slope for all patches was 23–29%, except patch 2 which was 5%. All patches were located in habitat not subject to flooding or substantial overland waterflow, except patch 4, which was located near a drainage channel where water periodically flowed from a roadway into forest interior. We used individual colors of fluorescent marking paint (Nelson Aero Spot, The Nelson Paint Company, Kingsford, MI, USA) to tag *M. vimineum* seeds before senescence from parent plants. This increased mean (\pm SD) seed weight ($n = 20$) from 1.2 ± 0.4 mg to 1.6 ± 0.4 mg.

In March 2010, we used a portable ultraviolet lamp (Raytech Industries, Middletown, CT, USA) after sundown to search 25 m² around each patch for the fluorescence of marked seeds. This initial search only resulted in the location of *M. vimineum* seeds downslope from the parental patches so subsequent searches concentrated on the areas 20 m below the parental patches. Discovered seeds were differentiated from accidentally marked vegetative material, and the location marked with flagging. The distance from the parental period to flags was measured the next day in daylight.

The most striking result is that seeds from patch 4, which is located near a periodic drainage channel, travelled significantly further (max. distance 8 m) than the other patches (max. 1.5

m) (Fig. 1). Conversely, seeds in from patch 2 (which has the lowest slope value) travelled significantly less (max. 0.2 m) than those with higher slope values. These results suggest that overland waterflow and gravity transports seeds up to 1.5 m, but stormwater flow can transport *M. vimineum* seeds much farther.

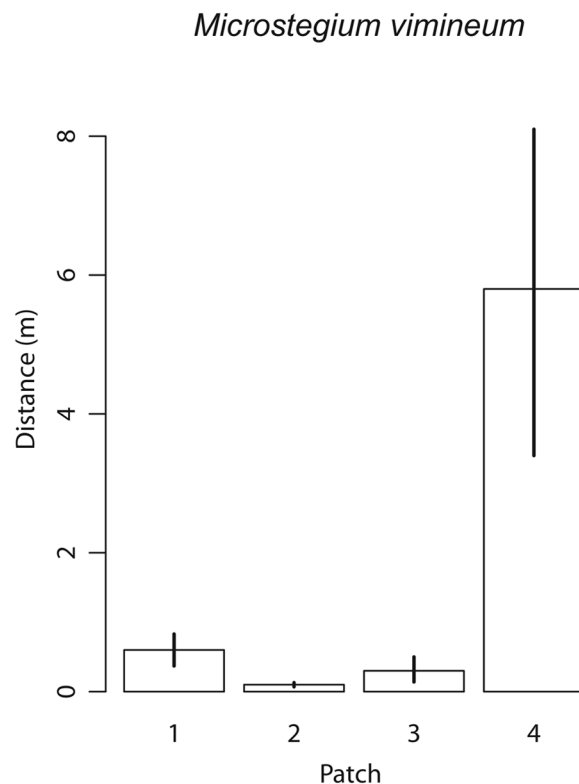


Fig. B1. Barplot for mean (\pm 95% CI) distance travelled by marked *Microstegium vimineum* seeds from parental source plants. All patches had similar ground slope (23–29%), except patch 2 (5%), and all patches were located away from substantial flooding or water flow, except for patch 4, which was next to a drainage channel.