# Habitat, dispersal and propagule pressure control exotic plant infilling within an invaded range

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**Abstract.**    Deep in the heart of a longstanding invasion, an exotic grass is still invading. Range infilling potentially has the greatest impact on native communities and ecosystem processes, but receives much less attention than range expansion. 'Snapshot' studies of invasive plant dispersal, habitat and propagule limitations cannot determine whether a landscape is saturated or whether a species is actively infilling empty patches. We investigate the mechanisms underlying invasive plant infilling by tracking the localized movement and expansion of *Microstegium vimineum* populations from 2009 to 2011 at sites along a 100-km regional gradient in eastern U.S. deciduous forests. We find that infilling proceeds most rapidly where the invasive plants occur in warm, moist habitats adjacent to roads: under these conditions they produce copious seed, the dispersal distances of which increase exponentially with proximity to roadway. Invasion then appears limited where conditions are generally dry and cool as propagule pressure tapers off. Invasion also is limited in habitats >1 m from road corridors, where dispersal distances decline precipitously. In contrast to propagule and dispersal limitations, we find little evidence that infilling is habitat limited, meaning that as long as *M. vimineum* seeds are available and transported, the plant generally invades quite vigorously. Our results suggest an invasive species continues to spread, in a stratified manner, within the invaded landscape long after first arriving. These dynamics conflict with traditional invasion models that emphasize an invasive edge with distinct boundaries. We find that propagule pressure and dispersal regulate infilling, providing the basis for projecting spread and landscape coverage, ecological effects and the efficacy of containment strategies.

**Key words:**   Japanese stiltgrass; *Microstegium vimineum*; migration; patch; road corridor.

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## INTRODUCTION

Invasive species disperse at a wide range of spatial scales when spreading across the landscape. The greatest dispersal distances are associated with initial establishment as many exotic species undergo transcontinental dispersal *en route* to colonizing novel landscapes (Mooney and Hobbs 2000, Ruiz et al. 2000, Normile 2004, Diez et al. 2008). Invasive species traverse the next greatest dispersal distances after establishment through intracontinental dispersal, facilitating geographic expansion. Dispersal at intercontinental and intracontinental scales is long-distance and generally human-mediated, proceeding via mechanisms that likely differ from those for the local dispersal that occurs after range establishment (Pysek and Hulme 2005).

Historically, species migration consid-

ered invasion a diffuse spread of random propagules resulting in a relatively homogenous range with distinct boundaries (e.g., Skellam 1951). However, mechanisms of large-scale species dispersal may differ from those that promote infilling within an invaded range (Shigesada et al. 1995, Muirhead et al. 2006, Miller and Matlack 2010, Rauschert et al. 2010). It is common to find isolated satellite population patches outside the core large-scale invasion fronts (Hanski 1982, LeBrun et al. 2008), but isolated, patchy populations also remain behind leading edge invasions (Hanski 1982, Shigesada et al. 1995, Zhu et al. 2007). Patchiness within invaded ranges can occur when disparate mechanisms control long-distance and local dispersal so that invasion occurs in "jumps" (Zhu et al. 2007). Local dispersal (infilling) reaches the gaps left by patchy advancing invasion fronts and, notably, is the least-studied dispersal scale for invasive species (Johnson et al. 2012). Yet, post-invasion infilling likely results in the highest landscape coverage by invasive species, as well as the greatest impacts on communities and ecosystems (Wangen and Webster 2006, Zhu et al. 2007, Miller and Matlack 2010).

A snapshot picture of patchy invasions does not give the full picture of the ecological processes and limitations that explain an invasive species distribution. For example, an invasive population in the process of infilling may form an aggregated distribution pattern. Aggregated patterning due to dispersal limitation may be indistinguishable from habitat limitation in which an invading species disperses throughout the landscape, but only persists where conditions are suitable (Eriksson and Ehrlen 1992, Moore and Elmendorf 2006, Warren et al. 2011a). If habitat limited, the local invasion is saturated and the potential for further impacts, such as the displacement of native species, is low. The potential for further impacts is much higher, however, if rather than unsuitable habitat, marginal habitat limits the invasion. The invading species may establish in habitat conducive to persistence but subpar for reproduction so that it does not generate enough propagule pressure to invade adjacent, potentially suitable habitat (Lockwood et al. 2005, Colautti et al. 2006, Tanentzap and Bazely 2009, Warren et al. 2012). The similarity in these patterns obscures under-

lying mechanisms so that a snapshot picture of an exotic species distribution within an invaded range may not distinguish pattern from process (With 2002, Pysek and Hulme 2005, Vaclavik and Meentemeyer 2012).

*Microstegium vimineum* (Trin) A. Camus (Japanese Stiltgrass, Nepalese Browntop) arrived in the U.S. from China sometime in the early 1900s (Fairbrothers and Gray 1972), and it has since spread throughout the eastern and midcontinental U.S. (USDA, NRCS 2012). Its invasion is associated with losses of soil organic carbon (Kramer et al. 2012), decreases in native plant cover (Flory and Clay 2009c) and changes in arthropod diversity (Tang et al. 2012). Despite its rapid spread, *M. vimineum* populations within its range are patchy, often aggregated along roadsides and waterways (Warren et al. 2011a, Warren et al. 2011b). The aggregated *M. vimineum* populations suggest habitat limitations, particularly in low light and thick leaf litter (Oswalt and Oswalt 2007, Flory et al. 2011a, Warren et al. 2011a, Warren et al. 2011b), but *M. vimineum* also appears dispersal limited (Miller and Matlack 2010, Rauschert et al. 2010, Warren et al. 2011a), except along roadsides and waterways (Christen and Matlack 2009, Eschtruth and Battles 2009). Despite these limitations, *M. vimineum* compensates with copious seed production that may overcome establishment barriers (Eschtruth and Battles 2009, Warren et al. 2012).

Because snapshot studies (e.g., Warren et al. 2011a) of *M. vimineum* dispersal, habitat and propagule limitations cannot determine whether the landscape is saturated or whether active infilling is occurring, we track the localized movement and expansion of patchy *M. vimineum* populations from 2009 to 2011 at sites along a 100-km regional gradient. We examine invasion as an interaction between critical life stages and environment (see With 2002 and references therein) to determine *M. vimineum* propagule, dispersal and habitat limitations. As these life stages and their environmental constraints are not necessarily independent and may interact, we examine them as multiple competing hypotheses to determine which best explain infilling. We examine seed output (propagule pressure) in invaded 2009 patches by moisture, temperature and light. We examine the movement of patch boundaries from 2009 to 2011 (dispersal distance)

by landscape structure (distance to road, distance to waterway and slope angle), habitat structure (native herbaceous cover, leaf litter thickness, local flooding) and habitat quality (moisture, temperature, light). Finally, we examine the establishment of 2011 *M. vimineum* plants outside 2009 patch boundaries as a product of seed production in 2009 patches, dispersal distance and habitat quality (moisture, temperature and light) in 2011 patches.

## METHODS

### Study species

*Microstegium vimineum* is an invasive species of concern in the eastern U.S. (see Warren et al. 2011*b* for full review). It is an annual, $C_4$ grass (Poaceae) native to southeastern Asia that can invade shady forest understories and crowd out native vegetation (Oswalt et al. 2007, Flory and Clay 2009*b*, Marshall et al. 2009). It is commonly found in moist habitats, both in riparian zones under canopies and in open areas (Fairbrothers and Gray 1972, Barden 1987, Warren et al. 2011*a*). In the eastern U.S., *M. vimineum* germinates in early-to-mid spring (depending on latitude) but does not reach full growth potential until mid-summer when it can reach 2 m in length and eventually produce copious seeds in autumn (Barden 1987, Hunt and Zaremba 1992, Redman 1995, Warren et al. 2012). However, *M. vimineum* is sometimes habitat-limited by shade, soil moisture and leaf-litter, and it appears dispersal-limited without anthropogenic activities (Flory et al. 2007, Flory and Clay 2009*a*, Warren et al. 2011*a*, Warren et al. 2011*b*).

### Study sites

In 2009, we established three *M. vimineum* study locations along a 100-km transect oriented north-south from the northern Piedmont of Georgia to southern Appalachian Mountains of North Carolina, U.S. (Warren et al. 2011*a*). 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′ N; 83°23′ W, 612–622 m elevation) on land managed by the Land Trust for the Little Tennessee. Individual sites were located using location-scale transect surveys.

### Study design

In 2009, we conducted exhaustive surveys of WHF, CNF and CWT to locate *M. vimineum* invasion patches (Warren et al. 2011*a*). The *M. vimineum* patches typically occurred along road-sides, waterways and along forest edges. We selected a subset of invaded patches with discrete invasion boundaries ($n = 12$ per WHF, CNF and CWT, $n = 36$ total) to investigate whether the patch boundaries reflected habitat limitation (Warren et al. 2011*a*). We placed paired invaded (INV) and uninvaded (UNI) plots (3 m$^2$) across the edges of the *M. vimineum* patches (Fig. 1). Plant sampling and environmental monitoring occurred in three $0.25 \times 0.25$ m quadrats located 1, 2 and 3 m within invasion edges (INV) and 1, 2 and 3 m outside invasion edges (UNI) (Fig. 1).

In July 2011, we re-sampled all plots except for two plots at CNF and one plot at WHF that were destroyed between 2009 and 2011. The 2009 plots were re-surveyed in 2011 to assess the extent of new invasion (in UNI) as indicated by shifts in the invasion edge. In many instances, the new invasion front exceeded the bounds of the UNI plots, and so the distance to the new invasion front was marked and measured. In these re-surveys, we only scored edges of continuous *M. vimineum* patches leading from the 2009 invasion edge, and we omitted isolated, satellite populations, which might arise from seeds dispersing from unmeasured populations. This approach made our dispersal distances conservative estimates of infilling.

Native herbaceous and *M. vimineum* cover (%) and biomass (g) were measured separately in each plot (data pooled by INV and UNI classification) in 2009 and 2011. Vegetative biomass (g) was collected in late-June through July 2009 and July 2011, dried at 65°C and weighed. Quadrat cover (%) by shrubs, litter, coarse woody material and exposed soil also was estimated. The distance (m) of *M. vimineum* invasion patches from roadways and waterways
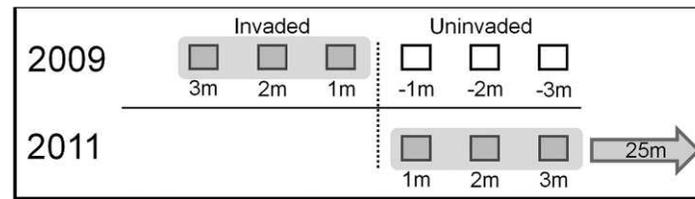
Fig. 1. Plots were established at the edge of *Microstegium vimineum* patches in 2009 that bisected invasion boundaries so that 0.25 × 0.25 sampling quadrats fell 1, 2 and 3 m within and outside invaded habitat. In 2011, invasion into the previously uninvaded plots was measured, as well as the distance of invasion fronts that moved beyond the plots (as far as 25 m).

(e.g., streams and active drainage) was estimated in the field and verified using digitized maps. Slope angle degree and slope aspect were also measured in the field.

Abiotic environmental conditions were measured in each plot and pooled by INV and UNI. Soil moisture and temperature were measured in May, July and September 2009 and 2011. Volumetric soil moisture (%) was measured within each plot with a handheld Hydrosense Soil Water Content Measurement System (Campbell Scientific Inc., Logan, Utah, USA). Ambient soil temperature was measured with a T-shaped digital thermometer inserted 8 cm into the soil. Percent photosynthetically active radiation (PPFD, diffuse light) was calculated as the difference between plot-level PAR readings and a fully exposed PAR reference site in July 2009 and 2011. The understory measurements were taken 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 (LI-COR Inc., Lincoln, Nebraska, USA). Measures were taken between 10 am and 2 pm on cloudy days, and a single, annual estimate of diffuse light taken in this manner is robust for making comparisons of understory light across space (Warren and Bradford 2011).

### Data analysis

We examined *M. vimineum* invasion from a demographic perspective so that we could elucidate the factors governing each stage in the process: propagule pressure (seed production) in INV plots, propagule dispersal from INV to UNI patches and habitat limitations in UNI plots. We converted INV plant biomass to seed number

using the intercept and slope value (162.3 + 142.1 × biomass) from field plots used in the same study sites (Warren et al. 2011a). The resulting estimate (mean ± SD) for *M. vimineum* seed production (2508 ± 1683 seeds m$^{-2}$) was similar, though a little higher and more variable, to that reported for other natural *M. vimineum* populations (1963 ± 652 m$^{-2}$) by Cheplick (2005). Note that *M. vimineum* vegetative biomass and seed output are highly correlated across habitats (Cheplick 2005, Warren et al. 2011a, Warren et al. 2012), meaning that vegetative biomass is a robust predictor of seed output. Although *M. vimineum* does produce selfed and outcrossed seeds, there is little fitness consequence to selfed seeds for annuals (see Morgan 2001) and, even if there was lower fitness for selfed seeds, Warren et al. (2012) found no difference in the proportion of selfed to outcrossed seeds across experimentally modified habitats. Furthermore, although habitat-mediated differences in the proportion of selfed : outcrossed *M. vimineum* seeds have been observed (Cheplick 2005, 2007, Huebner 2011), the ratio of seed types likely is inconsequential because the species consistently produces hundreds of seeds per m$^2$ (Warren et al. 2011a, Warren et al. 2012) and yet it only takes 2–3 seeds to establish a reproducing population (Warren et al. 2012).

We used mixed models to evaluate how landscape structure (distance to road, distance to waterway, slope and aspect), biotic interactions (herbaceous cover, litter cover) and habitat quality (flooding, soil moisture, temperature and light) impacted *M. vimineum* dispersal distance, propagule production and population establishment. Along with the fixed effects, we included site as a random effect in the mixed models,

which do not assume independent variance among units (Bolker et al. 2009). The random effect accounts for unmeasured site-specific influences on *M. vimineum* dynamics and autocorrelation from the clustering of plots. We use a continuous rather than discrete approach in assessing the correspondence between *M. vimineum* dynamics and environmental conditions given the power of regression approaches to reveal ecological relationships (Cottingham et al. 2005) and because setting up strict control groups in observational invasive species research is difficult for ethical reasons (e.g., introducing new populations to uninvaded habitat).

We used a generalized linear mixed model assuming a Poisson error distribution for dispersal distance as a function of the fixed effects. We included an individual-level random effect in the generalized mixed model due to a moderate amount of overdispersion (<5) (e.g., Elston et al. 2001). Graphical analysis of dispersal as a function of distance to road indicated the invasion response might be nonlinear so we fit a negative exponential model ($y = e^{(a+bx)}$) using the nls() package (Bates and Watts 1988) in the R statistical package (R Development Core Team 2012). We used linearized mixed models assuming Gaussian error distributions for *M. vimineum* propagule production and population establishment in UNI plots.

The mixed models were fit using the Laplace approximation in the "lme4" package (Bates and Maechler 2009) for the R statistical programming environment (R Development Core Team 2012). The inclusion or exclusion of random effects was based on Akaike's Information Criterion (AIC) values (Akaike 1973) calculated using maximum likelihood. 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 (Burnham and Anderson 2002). There was little collinearity between explanatory variables in any models (variance inflation < 6). We evaluated the slope value of the fixed effects and considered coefficients with $p$-value < 0.05 significant and coefficients with $p$-value < 0.10 marginally significant (sensu Hurlbert and Lombardi 2009). Because the F-statistic is not considered accurate in mixed models, making $p$-values anticonservative, we used Markov Chain Monte Carlo

(MCMC) sampling in the "language" package (Baayen 2007) for the R statistical programming environment (R Development Core Team 2012) to estimate the coefficients and $p$-values for retained parameters in LMMs. We also examined potential interactions between the retained parameters (lowest AIC model).

Graphic analysis indicated a residual pattern consistent with propagule pressure as imposing a maximum limit (a "wedge-shaped" regression) on *M. vimineum* invasion so we used the "quantreg" package (Koenker 2008) for R to further analyze these data using quantile regression. The variance in ecological data often result from complex, unequal influences, but quantile regression can be used to assess a potential limiting factor that constrains all responses (Cade and Noon 2003). The advantage of quantile vs. traditional least-squares regression is that it accommodates the fact that most variables are influenced by multiple limiting factors (see Cade and Noon 2003), creating a "wedge-shaped" regression pattern and a significant relationship only at the 90th quantile (not the 50th as in least-squares regression). We estimated the 90th quantile, propagule pressure, slope coefficient and significance using Markov chain marginal bootstrapping.

## RESULTS

The percentage of native herbaceous cover dropped approximately 12% in UNI plots between 2009 and 2011, whereas native herbaceous cover remained the same in the INV plots. Concurrently, *M. vimineum* coverage went from 0 to 16% between 2009 and 2011 in the UNI plots but dropped 24% in the INV plots. The establishment of *M. vimineum* in the plots that were uninvaded in 2009 (UNI) was associated with an increase in *M. vimineum* biomass (from 0 to 10 g m$^{-2}$) by 2011 (Fig. 2). The decrease in *M. vimineum* cover in the INV plots between 2009 and 2011 coincided with a 27 g m$^{-2}$ increase in *M. vimineum* biomass in the INV plots.

We found that the best fitting seed production model (based on AIC selection) included all three environmental predictors (temperature, moisture. light), but the relationship between reproduction and light did not differ significantly from zero (coeff. = −0.203, pMCMC = 0.656), and there
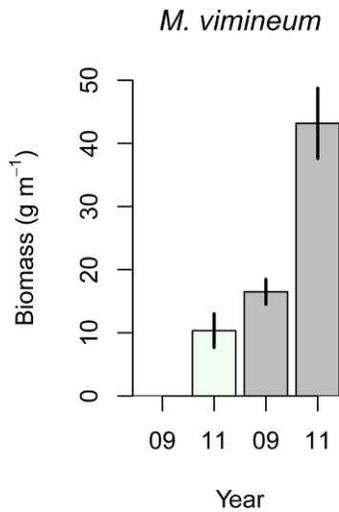
## M. vimineum



Fig. 2. *Microstegium vimineum* biomass (g m$^{-2}$; mean ± 95% CI) in the years 2009 (09) and 2011 (11). Light bars indicate plots that were uninvaded in 2009; dark bars indicate plots that were invaded in 2009.

## Interaction plot



Fig. 3. Continuous interaction plot of the effects of temperature and soil moisture on *Microstegium vimineum* biomass (g 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 grows better with soil moisture and temperature but thrives considerably better where habitat is both wet and warm.

was a significant soil moisture x temperature interaction (coeff. = 0.641, pMCMC = 0.035). This interaction indicated that *M. vimineum* reproduction increased with both soil moisture and temperature, but increased most where both were highest (Fig. 3).

The best fitting model (AIC) for dispersal distance included distance to road and flooding. Dispersal distance decreased exponentially (coeff. = −0.0145, SE = 0.007, $z$-value = −2.318, $p$ = 0.021) with increasing distance to road (Fig. 4) but the relationship with flooding did not differ from zero (coeff. = −0.256, SE = 0.489, $z$-value = −0.523, $p$ = 0.601). Dispersal was as far as 25 m for populations along roads whereas it generally dropped to <5 m when road was >1 m from a population. A significant fit was generated for the $a$ (coeff. = 1.817, SE = 0.255, $t$-value = 7.125, $p$ < 0.001) but not $b$ (coeff. = −0.0678, SE = 0.046, $t$-value = −1.471, $p$ = 0.158) coefficient in the nonlinear regression, indicating a strong initial decline (in dispersal distance) that levels off (with distance to road; Fig. 4).

We investigated the 2011 abundance (as biomass) of *M. vimineum* plants in UNI plots using parameters representing propagule pressure (2009 seed production in INV plots), dispersal distance and habitat quality (litter coverage, soil moisture, temperature and diffuse
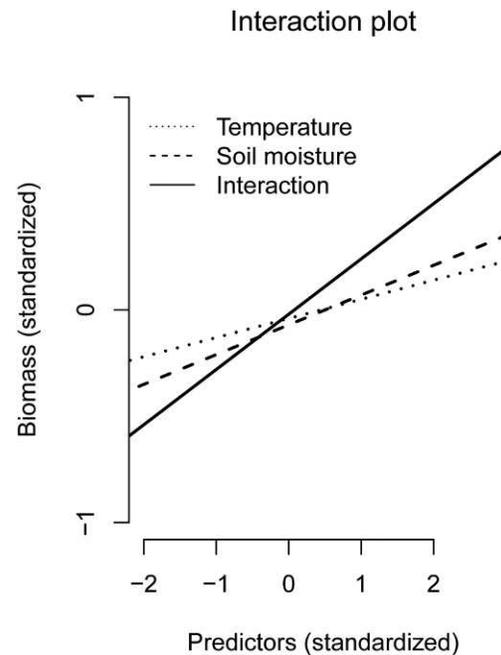
light in UNI plots). The best fitting model included propagule pressure and dispersal distance, with no interaction between the two. *Microstegium vimineum* abundance in the UNI plots increased significantly (coeff. = 0.320, pMCMC = 0.031) with propagule pressure in adjacent INV plots (Fig. 5A) and with dispersal distance (coeff. = 2.428, pMCMC < 0.001) from the INV plots (Fig. 5B).

## DISCUSSION

*Microstegium vimineum* has spread throughout the eastern U.S., and established in the 1930s about 100–150 km from our study sites (Knoxville, TN; Fairbrothers and Gray 1972). Since then, it has expanded its range across 25 states in the eastern U.S. and we find that continued infilling within its current invasive range proceeds most rapidly when local populations in
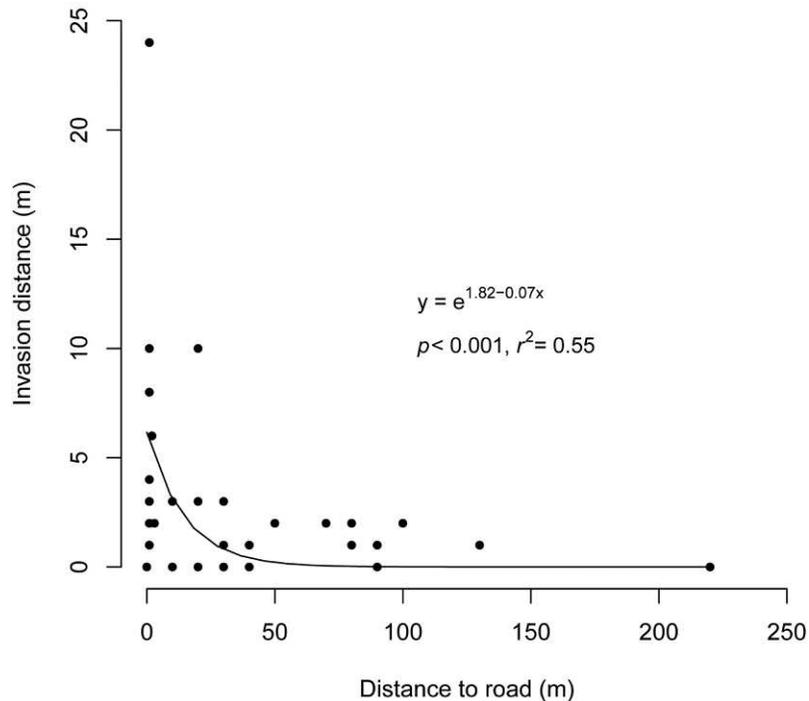
## Microstegium vimineum dispersal



$$y = e^{1.82-0.07x}$$

$$p < 0.001, \; r^2 = 0.55$$

Fig. 4. *Microstegium vimineum* dispersal distance is best explained as a function of invaded patch proximity to roadway. The relationship is a negative exponential, with *M. vimineum* dispersal distance decreasing precipitously just meters from roadway.

warm, moist habitats produce copious seeds (Fig. 3) near to roads, because with increasing proximity to roadways dispersal distances increase exponentially (Fig. 4). We find little habitat limitation in uninvaded patches. As long as *M. vimineum* seeds are available and transported, the plant generally invades quite vigorously (Fig. 5) across the forest edge and understory habitats where we originally located invasions in 2009.

Between 2009 and 2011, *M. vimineum* coverage of previously uninvaded plots (adjacent to invaded plots) increased from 0 to 16% and the patch boundaries expanded on average by almost 3 m (max. = 24 m). Concurrently, native herbaceous coverage dropped 34%, mirroring findings in other studies that *M. vimineum* negatively affects native plant communities (Flory and Clay 2009b, c, Flory 2010). As *M. vimineum* spread outward into uninvaded habitat between 2009 and 2011, its coverage within the 2009 invaded plots declined 32% but its biomass

more than doubled. *Microstegium vimineum* growth and reproduction are density dependent (Warren et al. 2012), and native herbaceous cover did not change in invaded plots (INV) between 2009 and 2011, suggesting self-thinning among the *M. vimineum* populations. Notably, *M. vimineum* reproduction is biomass- not cover-driven, so that its reproductive output likely increased by 160%.

Many researchers report that light limits *M. vimineum* seed production (Barden 1987, Cole and Weltzin 2005, Droste et al. 2010, Schramm and Ehrenfeld 2010, Flory et al. 2011a, b), but we find temperature and soil moisture mainly limiting and this may be because we had lower light availabilities across our plots than are commonly investigated. The interaction between temperature and soil moisture indicates that *M. vimineum* growth (and hence reproduction) responded positively to increased temperature and soil moisture, and it increased dramatically
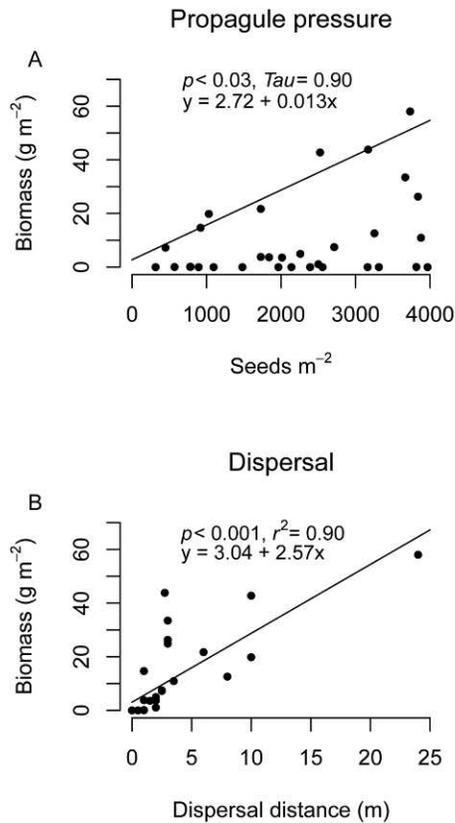
## Propagule pressure



A

$p < 0.03$, Tau = 0.90
$y = 2.72 + 0.013x$

## Dispersal

B

$p < 0.001$, $r^2 = 0.90$
$y = 3.04 + 2.57x$

Fig. 5. Positive associations with *Microstegium vimineum* biomass (g m$^{-2}$) in UNI plots (see methods) and propagule (A) and dispersal (B) pressures from adjacent populations. In A, maximum (90%) biomass is represented using bootstrapped quantile regression (see *Methods*) so that the breakpoint (propagule pressure intensity where maximum new invasion occurs) is represented by a fitted line at the 90th quantile (90% of the data points are below the line and 10% are above). The quantile regression indicates that propagule pressure limited invasion potential even when multiple additional factors (creating the residual 'wedge') influenced seed production. The linear regression between dispersal distance and *M. vimineum* invasion (B) indicates significantly higher plant biomass where *M. vimineum* dispersal distances were greatest.

where both environmental drivers were high. This pattern is not surprising considering that *M. vimineum* does not tolerate drought well (Warren et al. 2011*b*), so that its best opportunity to exploit hot environments occurs where high soil moisture prevents desiccation. Warren et al.

(2011*a*) observed similar 2009 reproduction patterns in these plots, highlighting that microhabitat-scale environmental variation likely is strongly linked with *M. vimineum* performance and consequently its potential to invade adjacent habitat.

The key to *M. vimineum* infilling is not only propagule production but also the ability to disperse to adjacent habitat. The only robust predictor of *M. vimineum* movement, including habitat structure and quality, was patch proximity to roads, though localized flooding may have some impact. The association between roads and invasive species is well studied (Cole and Weltzin 2004, Ulyshen et al. 2004, Christen and Matlack 2009, Flory and Clay 2009*a*, Mortensen et al. 2009, Cheplick 2010, Huebner 2010*a*, *b*), but the dispersal mechanism(s) is unknown. Human agents—such as mowing, vehicle movement and fill soil—may facilitate spread along roads (Lonsdale and Lane 1994, Von der Lippe and Kowarik 2007, Christen and Matlack 2009, King et al. 2009, Mortensen et al. 2009). Because *M. vimineum* produces copious seeds that can remain dormant for several years, the appearance of new 2011 *M. vimineum* plants in plots uninvaded in 2009 could be explained by: emigration (dispersal from already invaded plots) or habitat change that prompts germination from an established seed bank. Given that we find proximate propagule pressure and dispersal distance, rather than habitat quality, as the strongest limits on the establishment of new *M. vimineum* patches, the first possibility (i.e., emigration) seems most likely. Further, that 2/3 of our monitored patches expanded by at least 1 m (and on average almost 3 m) between 2009 and 2011 suggests that a great deal of suitable *M. vimineum* habitat remains uninvaded within the landscape.

Whereas seeds dispersing from non-target populations could cause overestimation of dispersal distances, we only counted edges of continuous patches, which omits isolated satellite colonization from our estimates and so makes our dispersal distances conservative. Additional investigation into the interaction between satellite populations and invasion edges in infilling is needed. Moreover, longer-term assessment and demographic analysis would determine whether the observed patch shifts represent continuous

infilling or temporary source-sink dynamics. *Microstegium vimineum* patches may have migrated (shifting lead and trailing edges) rather than expanded across 2009–2011, or they may have moved laterally from our edge plots; however, the plots were established at the edge of *M. vimineum* patches with no bias toward direction or landscape structure (e.g., downhill). That 2/3 of the edges advanced 2009 to 2011 suggests that the *M. vimineum* patches are expanding rather than shifting. Still, we acknowledge that our field study targeted the mechanics of infilling and is inadequate to address the regional extent of infilling. Necessary follow up projects are needed to determine the extent of *M. vimineum* infilling in the study area (but see Anderson et al. 2012).

Distinguishing between propagule, dispersal and habitat limitations, or at least the relative importance of each for invasive infilling, is essential for determining the potential impact of exotic species on native ecosystems and management of invasive spread (Glasgow and Matlack 2007). For example, *M. vimineum* suppresses forest understory communities (Flory and Clay 2009*b*, *c*) and leads to losses of soil carbon (Kramer et al. 2012), but if it is habitat limited, most damage to communities and ecosystem properties is already done within the invaded range as its suitable habitat is saturated. However, if an invasive species is dispersal limited, or dependent on specific dispersal corridors, it should eventually infill uninvaded gaps and substantial ecological impacts remain to be realized. Our data suggest that the impacts of *M. vimineum* in the southeastern U.S. will continue as the species infills uninvaded patches. We find that the potential for continued *M. vimineum* infilling within its invaded range remains high, and that investigating roadside dispersal vectors may provide the best solution for containment. The ecological effects of infilling may be more important away from roads, and in subsequent stages of infilling, more populations may establish further from roads. However, approximately 1/3 of our study plots occur >100 m from roads so that our results give an indication of overall infilling dynamics; that is, infilling occurs most rapidly near roads. Our results suggest that, once roadside habitats are *M. vimineum* saturated, habitats away from roads may infill, but at a much slower rate.

## Conclusions

Localized dispersal infills uninvaded patches behind advancing invasion fronts, but it is the least-studied dispersal scale for invasive species (Johnson et al. 2012). Infilling likely results in the highest landscape coverage by invasive species, and hence the greatest impact on communities and ecosystems (e.g., Zhu et al. 2007). Moreover, the same general limitations that regulate infilling by invasive species, namely propagule, dispersal and habitat limitations, also should regulate the migration of natives species in a rapidly changing climate. Understanding how these three limitations interact to determine rates of infilling will be necessary for mitigation of invasive species spread and conservation of migrating natives. Rather than a diffuse spread of random propagules that create a relatively homogenous range with distinct boundaries (e.g., Skellam 1951), our data suggest more stratified dispersal processes and a lag between initial invasion and infilling. Our data also suggest that propagule and dispersal limitations regulate infilling, providing necessary empirical data for developing models of spread to project landscape coverage and management impact.

## Acknowledgments

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