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Review

Forest Roads Facilitate the Spread of Invasive Plants

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The distribution and abundance of invasive species can be strongly influenced by habitat suitability and by corridors that facilitate dispersal. We synthesize results from a large-scale invasive plant survey with a patch-scale expansion experiment. The large-scale survey involved transects up to 250 m away from of all roads in a 32,000 ha forest. The patch experiment involved initiating invasions in different habitat types (roadside, wetland, disturbed, and intact forests), and then fitting statistical models to patch spread rates. The large-scale survey highlighted the importance of roads in predicting the presence of invasive plants, also revealing that one invasive plant, *Microstegium vimineum*, has spread rapidly since its purported introduction in 1994. The patch-scale experiments focused on *Microstegium* and demonstrated that spread rates are higher in roadsides than in forested and wetland patches, even in the absence of major disturbances. These results highlight the importance of landscape features when designing prevention and management practices aimed at limiting invasive plant abundance and spread.

Nomenclature: Japanese stiltgrass, *Microstegium vimineum* (Trin.) A. Camus.

Key words: Invasive plant management, weed mapping, weed population dynamics, invasive plant survey, spatial analysis.

Landscape-scale surveys of natural systems can be useful for documenting the extent of a plant invasion and predicting areas where invasions are likely to occur (Stohlgren et al. 2001). Surveys also provide ecological insights about invasive plant populations that inform development, implementation, and evaluation of weed management strategies (Rew and Pokorny 2006).

Collecting meaningful survey data in large, previously unsurveyed sites is a formidable challenge. A number of researchers have explored methods to adequately sample such areas. Prather (2006) used adaptive sampling to identify species new to an area and rare species, where invasive plant presence was known to be associated with areas of disturbance or human activity. Here, the sampling intensity was guided by the distance from the source feature where no invasive plant was observed. Rew and Maxwell (2006) argue that stratified random sampling is the method of choice for establishing an unbiased survey of invasive plant populations. Applied in the Northern Range of the Yellowstone National Park, roads were used to stratify the sample and invasive plant abundance was estimated continuously along 2,000-m (6562 ft) transects perpendicular to roads. Using site characteristic data, they mapped the probability of finding invasives along roads. For one species, *Linaria dalmatica* (L.) P. Mill. (Dalmatian toadflax), they found a three-fold higher probability of occurrence within 100 m of a road than at distances greater than 100 m. This finding made it possible to derive probability of occurrence maps for several important invasive plants (Rew et al. 2005).

Logistic regression (Higgins et al. 1999; Rew et al. 2005; Rouget et al. 2001) has been used to quantify the strength of association between invasive plant presence and environmental factors. The presence and abundance of invasive plant populations has been widely reported to be associated with the attributes of the site (Brooks 1999; Marco et al. 2002; Sher and Hyatt 1999; Stohlgren et al. 2001). Site features that have been associated with invasibility include both environmental and anthropogenic factors such as disturbance (Almasi 2000; Silveri et al. 2001), proximity to roads (Harrison et al. 2002), soil

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Interpretive Summary

Roads can play a profound role in the spread and growth of invasive species by serving as corridors for movement as well as providing prime habitat for establishment. For example, forest managers have reported that tens of kilometers of forest roads have been invaded by *Microstegium* in a period of less than 10 yr. A large-scale survey of the presence and abundance of 13 invasive plants found that the most abundant species, *Microstegium*, was strongly associated with proximity to roads. In order to better understand these high rates of spread and the role that site condition plays, we deliberately introduced *Microstegium* patches in a forested site similar to the one in which the survey was conducted, and allowed patches to naturally expand over 4 yr before controlling all patches. Through this multiyear study, we found the natural spread rate was surprisingly slow, several orders of magnitude slower than that observed by the forest managers we work with. We also found that spread was greatest in habitats adjacent to forest roads. It is clear that the rates of spread occurring in forests throughout the study region are aided by management practices such as road grading, employed frequently to maintain the dirt and gravel roads. Management of this troublesome invasive can be enhanced with a multifaceted integrated management approach. Particular attention should be paid to infestations that serve as sources for seed dispersal into uninvaded or environmentally sensitive areas. The primary vectors of long-distance dispersal, such as road maintenance activities or vehicle traffic, should be identified and mitigating steps taken. Finally, it is important to minimize road edge disturbance to the extent possible as such disturbance provides an ideal seedbed for the newly dispersed *Microstegium* seed.

nutrients, topographic position, and forest fragmentation (Brothers and Spingarn 1992; Cadanasso and Pickett 2001).

Recently, Schramm (2008) underscored the importance of legacies of past land use. Land uses that dated 80 to 100 yr prior to an invasive plant survey strongly influenced the probability of invasion. Sites that had been in continuous forest cover had a very low probability of invasive plant presence, while in transitioned sites (forest to agriculture back to forest), the probability of occurrence was as high as 80%. This underscores the importance of having the right site data to construct meaningful predictive maps.

In order to understand how individual populations of invasives grow and spread, it is necessary to understand the patch-scale dynamics of a species. Such finer-scale studies can allow quantitative predictions of population growth and spread in order to appropriately target management efforts. Invasion speed can differ greatly in different habitats (Urban et al. 2008), necessitating detailed studies about the local dynamics of species in different habitats. The importance of interactions such as interspecific competition may vary at different scales. For example, Menke et al. (2007) demonstrate that invasive ants did not respond to the same abiotic factors as native ants at a fine scale, an effect that was different than the large-scale effects observed. One way to deal with issues of scale is to include multiple scales of study (Wiens 1989).

This paper summarizes work initiated to survey invasive plants in a 32,000 ha tract of deciduous forest managed by The Nature Conservancy. The goal of this survey was to identify the invasives that were most abundant and the factors that were associated with invasive plant presence. That survey revealed that *Microstegium vimineum* (Trin.) A. Camus (Japanese stiltgrass: Poaceae; hereafter referred to as *Microstegium*) was the most abundant and widely distributed invasive plant, and that it was actively invading deciduous forests in the study region. In order to predict where this species is likely to invade and to understand its spread and population dynamics, a long-term experiment was initiated in a range of sites, and the resulting small-scale invasions were followed for a period of 4 yr. This synthesis was prepared to explore ways in which spatially explicit approaches to the study of invasive plant populations can reveal important insights into their invasion dynamics and management.

Materials and Methods

Large-Scale Forest Survey. The large-scale survey was conducted in a 32,000-ha (79,000 ac) parcel located within the Green Ridge State Forest in western Maryland along the Potomac River. The site, dissected by a network of paved and unpaved roads and trails, is located in the ridge-valley physiographic province, and is comprised of a mix of protected natural areas administered by The Nature Conservancy, and areas designated for recreational use. The survey was stratified along forest roads with transects placed at 0.8-km (2,640-ft) intervals (Figure 1a). Each transect was positioned perpendicular to the road and extended 150 m into the forest on each side, with five sampling points on each side of the road. Each transect was geo-referenced with a differentially corrected global positioning system.

At each of the 10 sampling points, a circle with a radius of 5 m (78.5-m^2 area) was centered on the transect. A suite of habitat variables were measured (Table 1), including information about the road and the surrounding landscape. We also recorded presence and percent cover of the following invasive plants: *Ailanthus altissima* (Mill.) Swingle (tree of heaven), *Alliaria petiolata* (M.Bieb.) Cavara & Grande (garlic mustard), *Berberis thunbergii* DC (Japanese barberry), *Centaurea maculosa* Lam. (spotted knapweed), *Coronilla varia* L. (trailing crownvetch), *Elaeagnus umbellata* Thunb. (autumn olive), *Linaria vulgaris* Mill. (yellow toadflax), *Lonicera japonica* Thunb. (Japanese honeysuckle), *Lonicera spp.* L. (exotic bush honeysuckles), *Microstegium*, *Polygonum cuspidatum* Siebold & Zucc. (Japanese knotweed), *Polygonum perfoliatum* L. (mile-a-minute), and *Rosa multiflora* Thunb. (multiflora

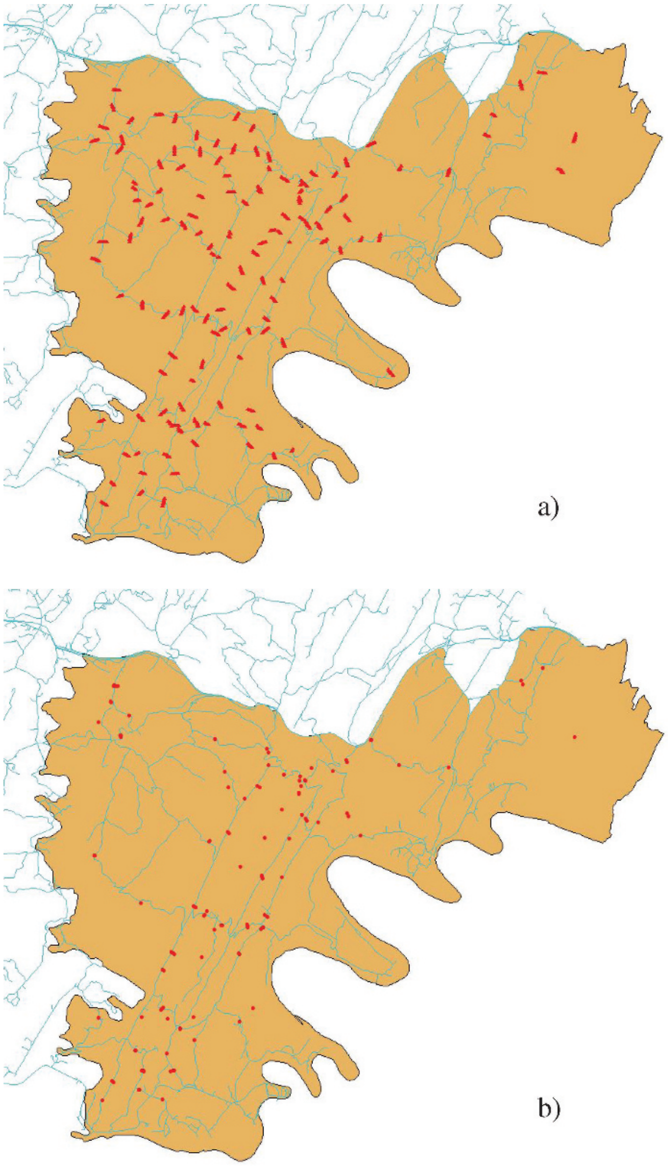

Figure 1. Green Ridge survey sampling design and plots containing more than one invasive. Survey transects were conducted approximately every half-mile along traversable roads (a). Each transect was parallel to the road and consisted of a series of plots: the first was located 10 m off the road, and each subsequent subplot was located 50 m further until 150 m was reached in each direction. At each subplot, a circle with a radius of 5 m was studied. A total of 254 transect pairs were surveyed. Most subplots with more than one invasive present (b) were close to roads.

rose). These species were known or suspected to occur in the 32,000-ha forest and were therefore considered threats to several cove forest streams and shale barrens, rare sites which were important conservation targets for The Nature Conservancy. Due to changes in the survey protocol, the full set of habitat variables was recorded for 629 of the total of 1,113 sampling points taken; we focus all analyses on these plots.

Distribution maps were constructed using ARCVIEW 8.1 (ESRI, Inc.) to visualize the distribution of invasive species. To assess the relationship of site characteristics and invasive plant presence, logistic regression was applied (Collett 1991). Logistic models were derived from the full model by using stepwise regression with AIC (Akaike Information Criterion) for model selection and by applying the step function in R (R Development Core Team 2008), using both forward and backward selection. Due to nonlinear differences observed between site occupancy and distance from the road, we used distance as a categorical rather than a numerical variable. Cross-validation (Stone 1974) was performed because one of the goals of the study was to predict invasive species presence in unsurveyed sites based on environmental variables; cross-validation allows an estimate of the ability to predict with future data. We used leave-one-out–cross-validation, which uses a single observation from the original data for validation, while the rest of the data is used to develop the model; this procedure is repeated until each observation has served as the validation data. This approach allows the estimate of a prediction error for this response variable of the dataset. All analyses were performed in R (R Development Core Team 2008), with the function glm for logistic regression and cv.glm (Canty and Ripley 2008; Davison and Hinkley 1997) for cross-validation. To graphically illustrate the most important variables for the *Microstegium* model, a simpler logistic model was run using three of the most influential predictor variables.

Small-Scale Patch Study. Having identified roadsides as important predictors of the presence of *Microstegium*, experiments were begun in 2003 to quantify the success of invasions in different habitats. The full details of this experiment are described elsewhere (Peskin 2005; Rauschert et al. 2009). Thirty invasions were created in six different habitat types in 2003 (disturbed/undisturbed forest with and without understory, wet meadow, and roadside); the habitats were chosen with the intent of later parameterizing larger-scale models of invasion risk with different types of habitats. There were five replicates of each habitat; however, the distribution of the habitats in the landscape did not permit blocking. The roadside plots were located along a little-used, unpaved road that receives little maintenance. The area was free of *Microstegium* invasion; the nearest known infestation was 5 km away.

The patches were created in the spring of 2003 by scattering *Microstegium* seeds in two adjacent 1-m^2 areas, one of which was disturbed by lightly raking the litter while the other was left undisturbed. The number of seedlings that emerged in each 1 m^2 was counted in the spring. Starting in 2004, data was collected about the populations

Table 1. Habitat variables measured in the Green Ridge survey that were used in the logistic regression modeling.

Attribute	Number of levels	Description of levels
Road surface	2	Paved or dirt/gravel
Ditched	2	Does the roadside have a ditch (Y/N)
Bermed	2	Is the roadside bermed (Y/N)
Position in the landscape	5	Bench, drainage way, foot of slope, ridge top, side of slope
Aspect	4	Northeast, northwest, southeast, southwest
Slope class	5	0–5 degrees, 6–10 degrees, 11–25 degrees, 26–45 degrees, 45+ degrees
Canopy class	3	Closed (51–100%), moderate (26–50%), open (0–25%)
Forest type	3	Deciduous, evergreen or mixed
Understory class	3	Open-, over-, well-developed
Land type	3	Floodplain, upland, wetland
Spring present	2	Present, absent
Soil disturbance	2	Was the soil disturbed or undisturbed
Trash	2	Present, absent
Cuts present	3	None, many, isolated
Trails present	2	Present, absent
Campsite	2	Present, absent
Pushout	2	Present, absent

in a spatially explicit manner. A grid of 20 by 20-cm (7.87-in) cells was laid out, and the number of seedlings in each cell was counted each spring. In 2006, all populations were sprayed with sethoxydim herbicide to begin the multiyear process of eradication.

The spatially explicit population data allowed the development of population growth and spread models. Maximum likelihood techniques were used to develop spatially explicit models of population growth and spread following Ribbens et al. (1994) and Humston et al. (2005), using the data to parameterize the models. Using the spatially-explicit seedling count in 1 yr, the spatial distribution of the next year's population was predicted assuming a Gaussian dispersal function, where seeds were most likely to land in nearby cells. This prediction was then compared to actual observations in the next year, and the likelihood of observing this data given the model predictions was calculated. Two population parameters were estimated: the dispersal parameter D and reproductive ratios R. Starting at estimated initial values for these parameters, optimization algorithms (Nelder-Mead and simulated annealing) were used to find the parameter values that maximized the likelihood of observing the data for each transition, using the optim function in R (R Development Core Team 2008). Reproductive ratios were calculated for each year transition of the experiment (i.e., 2003 to 2004, 2004 to 2005, and 2005 to 2006), and one dispersal parameter was estimated for the whole experiment. See Rauschert et al. (2009) for a full description of the model. In this paper we focus on the insights from these models for roadside populations. To address the question of whether patch expansion was more rapid on the roadside than in the forest, we use Poisson regression, which is more suitable for count data not expected to be extremely high (Bolker 2008), to compare the number of cells occupied in roadside vs. nonroadside habitat.

Results and Discussion

Roads appear to be playing an important role in facilitating the movement of invasive plants through forests. *Microstegium* was not present in the Green Ridge area in large numbers before 1994 (D. Keech, personal communication), but in less than 10 yr, it had become the most common invasive in the survey area. While not the focus of this study, an almost identical account of rapid invasion was reported by foresters in a state forest in Pennsylvania (Peskin 2005). An important insight from the patch-scale study is that natural dispersal of this troublesome invader is actually quite localized. The largest dispersal kernels were found to be in roadside habitats, but even these are not capable of explaining the large-scale spread. It seems most probable that human facilitated dispersal, the likely result of maintenance and water movement associated with forest roads, is largely responsible for the spread of this species.

The forest road network in Green Ridge Forest is typical of those found in state forests in the region, providing access for logging equipment, recreational use, and hunting. Twenty percent of the roads are paved; the remainder are dirt and gravel. Paved sections were most heavily trafficked, were more likely to have private residences located along them, and were the most heavily

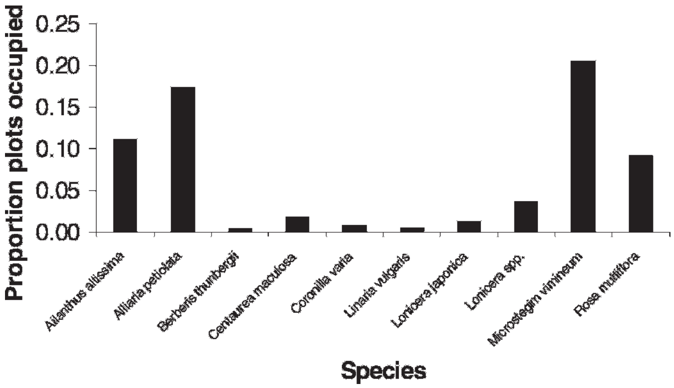

Figure 2. Proportion of subplots in the Green Ridge survey containing nonindigenous species. *Microstegium* and *Alliaria petiolata* were the most commonly observed species, followed by *Ailanthus altissima* and *Rosa multiflora*. *Elaeagnus umbellata*, *Polygonum cuspidatum*, and *Polygonum perfoliatum* were not observed in the survey.

invaded. For example, almost all of the *A. altissima* observed in the survey occurred along paved roads. Most sites containing more than one invasive plant species were along roads (Figure 1b), and sites containing three or more invasive species were only observed along paved roads. From the survey, plants were grouped in one of the following three categories: relatively common (found in 9 to 18% of sampling points), rare ($< 2\%$) and not observed. The most common species in the survey was *M. vimineum* which occurred in 24% of sampling points, followed by *A. altissima* (15%), *A. petiolata* (14%), and *R. multiflora* (9%). *B. thunbergii*, *C. maculosa*, *L. vulgaris*, *L. japonica*, and *C. varia* were rare in the sample, and *E. umbellata*, *P. perfoliatum*, and *P. cuspidatum* were not observed (Figure 2).

For the survey data, model fitting to elucidate site associations revealed several patterns. *Microstegium* was strongly associated with roads (Table 2, Figure 3). *Ailanthus altissima* and *A. petiolata* were most commonly found along highly traveled roads (the road surface was an important part of the best model) while *Microstegium* was found throughout the road network. The probability of observing *Microstegium* along forest roads was as high as 83% on east-facing aspects, while the probability of occurrence fell to 15 to 40% deeper in the forest. Soil disturbance was an important predictor of *Microstegium* abundance, with more disturbed sites having more *Microstegium* present. The cross-validation estimate of prediction error was low (0.14), likely partially due to the large sample size, indicating a relatively good ability to predict sites with *Microstegium* present. The sample size for the rare species was not large enough to perform the model fitting, although it was clear from inspection of the data that the less common invasives were more likely to be found along the more heavily trafficked roads.

Table 2. Logistic regression results for *Microstegium* presence. Distance, landscape position, aspect, and canopy cover, each of which had three or more levels, were all modeled as categorical variables; the level used in the base model is listed. The cross-validation prediction error of this model is 0.14.

Parameter	Estimate	Standard error	P-value[a]
Intercept	−0.82899	0.81634	0.309866
Distance from road (base value is 0 m)			
10	−1.76427	0.32633	6.43e-08 ***
50	−2.14019	0.36204	3.39e-09 ***
100	−2.76692	0.44192	3.82e-10 ***
150	−2.29547	0.43341	1.18e-07 ***
Landscape position (base value is bench)			
Drainage way	0.87634	0.63095	0.164859
Foot of slope	−0.12628	0.62056	0.838744
Top of ridge	−0.93121	0.50307	0.064162·
Side of slope	−0.01223	0.37987	0.974310
Aspect (base value is Northeast)			
Northwest	−0.93802	0.32485	0.003882 **
Southeast	−0.12913	0.32307	0.689372
Southwest	−1.76395	0.44306	6.85e-05 ***
Canopy cover (base value is closed)			
Moderate	−0.93062	0.31949	0.003582 **
Open	−0.15338	0.30595	0.616141
Spring present	0.71829	0.48956	0.142313
Soil disturbance	1.03411	0.28994	0.000362 ***

[a] The stars indicate significance of < 0.001 for ***, < 0.01 for **, < 0.05 for *, and · for < 0.1.

The forest roads through the Green Ridge study site appear to serve as a network of corridors for movement and establishment of important invasive plants. There are two major reasons for this: road building and frequent, intensive maintenance have the potential to spread propagules over long distances and can deposit propagules in disturbed areas, which are very conducive to the establishment of such species (Gordon et al. 2005).

Roadsides generally provide excellent opportunities for the establishment of invasive species (Rentch et al. 2005), often because frequent disturbances make resources available. Besides the disturbance associated with creating new roads, most roads constantly undergo ''pulse'' type disturbance (sensu Bender et al. 1984) in the form of road maintenance. For example, mowing and thinning, performed to enhance visibility and drainage, create a continuous light gap along roadsides. In central Pennsylvania, limestone gravel is typically applied to rural road surfaces; the dust and runoff associated with this practice raise the pH of the surrounding

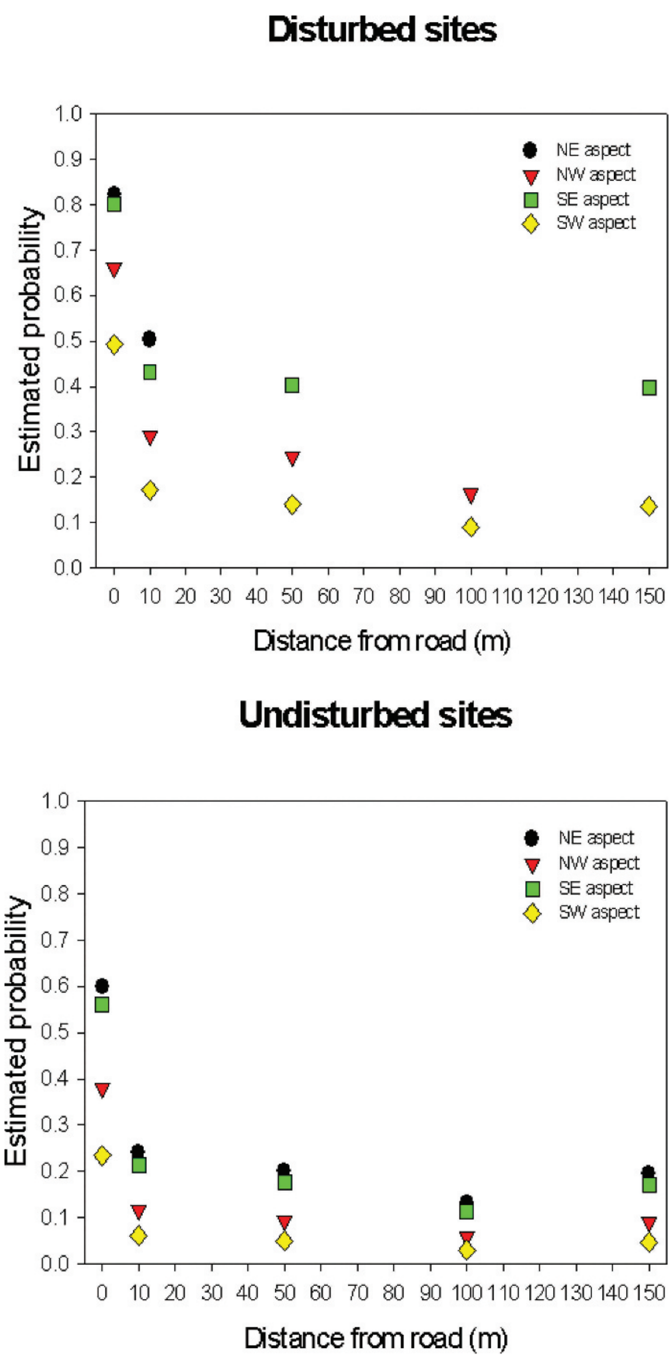

Figure 3. Relationship of *Microstegium* occurrence probability to distance off-road from the Green Ridge survey. *Microstegium* was most likely to occur immediately at the roadside, whether in disturbed sites (upper panel) or undisturbed sites (lower panel). Overall, occurrence probabilities were higher in disturbed sites, as well as higher in sites with northeast aspect. The results shown are from the logistic model of *Microstegium* occurrence with distance from the road, with aspect and soil disturbance as predictors. Certain aspect-distance combinations did not occur in the dataset; thus, we do not include predictions for these.

soils (Nord, unpublished data), enhancing the success of species like *Microstegium* relative to the ericaceous native understory, which prefers lower pH. Nonnative species are more likely to occur along roadsides; the probability of their establishment in the interior of the forest is generally lower (Hansen and Clevenger 2005).

In the patch-scale experiment, the results were consistent with the larger-scale observations that *Microstegium* does well in roadside sites. The roadside habitats had on average the largest populations in 2005 and 2006, although there was considerable variation in population sizes within the four habitat types. For comparison, the disturbed forest patches, which might have been expected to be most similar to roadside patches, had generally much smaller patches in extent and population size (Figure 4). The dispersal parameter was highest on average in roadside patches (0.95 m for roadside habitat vs. 0.50 m for nonroadside habitat), indicating greater dispersal in roadside habitats. The physical meaning of these parameters is that approximately 67% of seeds will land within one dispersal parameter, and 95% will land within two times the dispersal parameter. This implies that most seeds will remain within 2 m in a roadside habitat, and 1 m in a nonroadside habitat. A unique outcome in the roadside habitats was the formation of satellite populations in several patches that were separate (more than 1 m away) from the initial patch where seeds were sown. Half of the patches showing population increases in every year were in the roadside habitat. The Poisson regression of cells occupied by the end of the experiment clearly showed that roadside populations occupied a larger spatial extent than patches in other habitats ($P < 0.001$, Figure 5). The variance in cells occupied in roadside habitats is smaller than nonroadsides, but this is most likely due to the difference in sample size for this comparison (5 roadside vs. 20 nonroadside patches).

It is also widely known that roads can serve as corridors for the movement of invasive species (Christen and Matlack 2006), but not enough research has actually quantified the movement of propagules along roads (but see Hodkinson and Thompson 1997). A well-established patch along a roadside is likely to have its seeds dispersed long distances, and many potential vectors such as vehicles, pedestrians, and maintenance equipment are transported great distances along roads. Following dispersal, propagules are likely to be deposited in roadside environments, which are generally favorable for establishment. It is likely that road maintenance equipment can transport seeds even further than recreational vehicles (Ferguson et al. 2003). The movement of propagules off of roads may be facilitated by features of the road, such as culvert outwashes.

Microstegium is not the only species whose presence and movement has been linked to roadways. In the Green

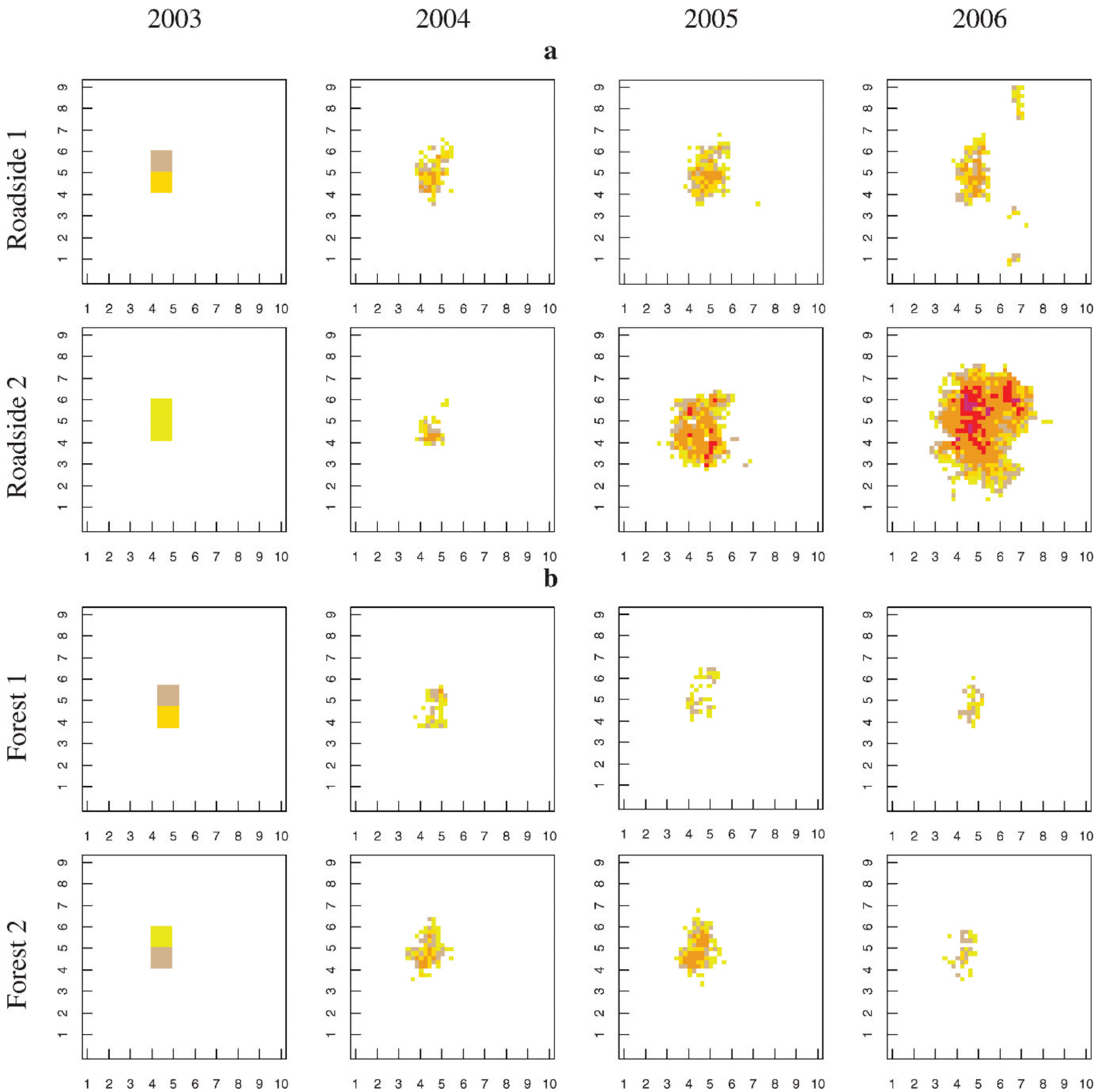

Figure 4. Patch trajectories from the *Microstegium* experiment over a 4-yr period. Roadside (a) and disturbed forest (b) sample trajectories (distances in m) demonstrate typical patch expansion patterns. Roadside patches often led to the formation of satellite patches and often became quite large. Disturbed forest patches did not generally expand as rapidly in size and spatial extent as roadside populations. Note that the 2003 data was collected as a total count for each subplot; more detailed spatial data was collected starting in 2004.

Ridge data set, the presence of *A. altissima* was also correlated with roads. Other troublesome invasives reported to benefit from dispersal opportunities provided by roadways include *Imperata cylindrica* (L.) P. Beauv. (cogongrass) (Jose et al. 2002) and *Phragmites australis* (Cav.) Trin. Ex Steud. (common reed) (Jodoin et al. 2008).

Almost certainly, the management of forest roads is playing a critical role in driving invasion success. Left to its own dispersal ability, *Microstegium* is a surprisingly weak invader (Rauschert et al. 2009). The spatially explicit patch study yielded dispersal rates of approximately 1 to 2 m a year in the habitats studied. Clearly, such slow rates of

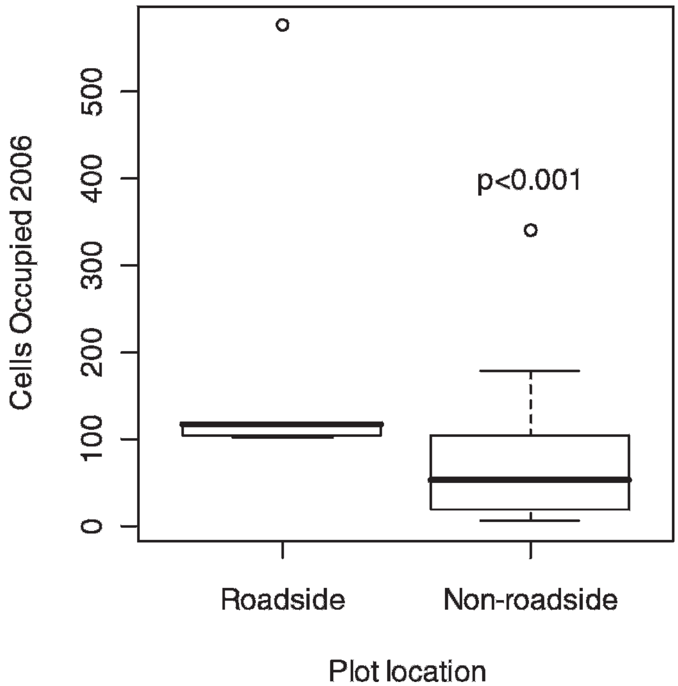

Figure 5. Spatial extent in roadside vs. nonroadside populations. Using data from the patch experiment of *Microstegium*, we compared the spatial extent by the end of the experiment (total cells occupied in 2006) in roadside vs. nonroadside populations. Roadside populations have a larger spatial extent than nonroadside populations.

patch expansion cannot account for the rapid invasion of tens of kilometers of forest roads in less than 10 yr (Pennsylvania Bureau of Forestry, personal communication). Work is currently underway to assess the role that management along roads is playing in facilitating propagule movement. Preliminary studies reveal dispersal distances some 100 to 200 times greater than the natural dispersal kernel when road maintenance equipment passes over an established seedbank (Rauschert, unpublished data). Frequent disturbance coupled with dispersal vectors that include water movement along roads and road maintenance operations almost certainly play an important role in this plant's ability to invade large areas of forest.

These results have important implications for management. An emphasis on containing local patches will not prevent the spread of *Microstegium*. In order to contain the spread of this invasive species, it is necessary to identify the human-mediated means of spread and target management at reducing them. Further detailed knowledge of local and regional dispersal can be combined with information about demography in different habitats to allow more realistic modeling of the spread of this species.

Given that plant invasions can be structured by landscape features such as roads, it is essential to incorporate this knowledge into predictions of invasive spread. This spatially-explicit approach is needed to accurately assess the risk of spread into new areas. Understanding the critical factors that govern the success of this troublesome invader is particularly helpful when tractable management options are available; this is the case for *Microstegium*. *Microstegium* is easily suppressed with a range of commonly used selective postemergence grass-killing herbicides (Peskin et al. 2005), and a well-timed mowing can significantly limit seed production. Altering management of roads to limit establishment success and propagule dispersal represents an important element in an integrated invasive plant management strategy. Supplemental site-specific management of populations along forest roads would complement such practices. For example, in addition to changes in road maintenance practices, emerged populations that threaten sensitive environmental areas or that serve as source populations for recently disturbed sites (e.g., by logging) could be targeted with mowing or application of selective herbicides. Increasingly, budgets for invasive plant management are strained, and a priority is placed on tractable, cost-effective approaches. Coupling knowledge of key drivers of the distribution and abundance of the invasive with site-specific management will provide forest managers with manageable solutions to invasive plant problems.

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