

The habitat and conduit functions of roads in the spread of three invasive plant species

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Abstract Nonnative plant species commonly occur along roadsides, and populations are often assumed to invade by spread along the road axis. To distinguish between the function of roadsides as movement corridors and as habitat, nonnative plant species were surveyed along roads in deciduous forest sites in southeastern Ohio, USA. The importance of road proximity was tested by comparing nonnative species abundance in 100 m transects along roads with transects in undisturbed forest. Nonnative species were most abundant and most frequently observed in roadside sites in valleys. Three common species were chosen for closer scrutiny. In a seed sowing experiment roads and open sites proved to be better locations for the germination and growth of *Microstegium vimineum* than non-roadside and closed-canopy sites. *Tussilago farfara* and *Rosa multiflora* occurred in a small number of disjunct patches suggesting infrequent arrival in the sampled transects. Both species were strongly clustered at scales consistent with diffusive spread by vegetative growth and short-range seed dispersal. Comparisons of distributions parallel and perpendicular to roads showed no evidence for enhanced dispersal along the road axis. *Microstegium* distributions were correlated with local light availability implying site saturation. *Microstegium*

micro-distributions suggested that spread along the road axis was facilitated by movement of dormant seeds in road maintenance. Thus, roadsides appear to function as both habitat and a conduit for population expansion, with the rate of spread dependent on the life history of the individual species. These results suggest a hierarchical process of regional invasion, with different dispersal mechanisms functioning at different spatial scales.

Keywords Diffusive spread · Dispersal · Forest · Hierarchical model · Invasion · *Microstegium* · Roadside · *Rosa* · *Tussilago*

Introduction

Rapid spread is one of the defining features of invasive nonnative species, with humans often contributing to the rate and range of their dispersal (Everett 2000; Mack and Lonsdale 2001). Because nonnative plant species commonly occur in roadsides, propagation along road corridors is widely assumed to be an important mode of invasion. If this is true, the extent of human-created road networks and their proximity to natural communities potentially make roads an important element of regional invasion (Forman et al. 2003). Spread along roads has not actually been demonstrated at a demographic level, however, and its true importance is unknown (Christen and Matlack 2006). In this paper, we test

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the function of roads in the spread of invasive plant species by examining individual species' distributions in light of a theoretical model. We suggest that it is more practical to control nonnative species early in the invasion process than to try to eradicate them later, when they have become abundant and widely established. From this perspective, understanding the function of roads in plant invasions is an issue of central importance in managing nonnative species (D'Antonio et al. 2004).

Roads as paths of invasion

Roadsides are human-created sites differing from surrounding communities in drainage, availability of light, stem density, and substrate character (Greenberg et al. 1997; Gordon et al. 2005). They provide a distinctive habitat often supporting weedy and invasive plant species which are absent from natural communities (Gelbard and Belnap 2003; Pauchard and Alaback 2004; Lu and Ma 2006; Flory and Clay 2006). It is also possible that roadsides function as movement corridors, acting through either of two mechanisms. First, populations may expand by a simple diffusive process resulting from random dispersal in all directions (Andow et al. 1990). Expansion is channeled along the road axis by the linear structure of the congenial roadside habitat. Indirect evidence suggests that native plant populations sometimes expand along linear features such as hedgerows or connected habitat patches (Corbit et al. 1999; Verheyen et al. 2003; Kirchner et al. 2003; Matlack 2005) implying that such expansion is also possible in nonnative species. Second, expansion may be facilitated along the road axis by nonrandom dispersal. Seeds may be dispersed by animals or vehicles moving along the road (Schmidt 1989; Tewksbury et al. 2002; Haddad et al. 2003), or carried by wind funneled along a road lined with trees (Liu et al. 1996). Wind dispersed seeds may be pulled along in eddies behind cars, as observed with trains (Kent 1960; Mack 1986). At a coarse scale, there are many qualitative reports of species' distributions expanding along roadsides, and the assumption that roadsides serve as dispersal corridors in regional invasions is widely accepted (e.g. Brothers 1992; Matlack 2002; Dark 2004; Essl 2005).

We question the function of roadsides as corridors for several reasons. It is often not clear that nonnative species are limited to roadsides—the appearance of

roadside distributions may simply be an artifact of observation from the road (Christen and Matlack 2006). Further, assumptions of selective movement along the road axis may be inaccurate. It is possible that long-distance dispersal allows transmission of propagules across the inter-road gap, colonizing points on a roadside without requiring transmission along the road axis (Pysek and Hulme 2005; Garnier and Lecomte 2006). If long-range dispersal events are relatively frequent ("fat tails" of the dispersal kernels; Kot et al. 1996), long-range dispersal may control the rate of range expansion making road networks irrelevant (Pearson and Dawson 2005; Christen and Matlack 2006). Dispersal may also be occurring within a site, but regional invasion is not necessarily an extension of local dispersal processes (Shigasada et al. 1995; Clark et al. 2001).

The character of a regional plant invasion will depend on the relative strengths of within-site and between-site colonization. In practice, models based on local dispersal data have been found to match distributions of invading species reasonably well at fine scales, but underestimate range expansion at coarse scales, perhaps because they fail to account for infrequent colonizations at long distances (Clark and Fastie 1998; Cain et al. 1998; Pysek and Hulme 2005; Matlack 2005). Conversely, arrival of a nonnative species in a region may be less important to invasion of natural communities than the local rate of spread within the landscape. Kudzu (*Pueraria lobata*), for example, spread rapidly by intentional human planting in the early twentieth century. Natural dispersal is weak, however, and individual kudzu patches expand slowly posing only a modest threat to nearby natural areas (Matlack 2002).

Interpreting snapshot data

Ideally invasions should be documented by direct observation of dispersal, establishment, and population expansion. Such monitoring, while desirable, is often impractical because invasions typically occur on a long time scale. Invasions may not be noticed until after they have occurred, and they may involve dispersal of propagules over areas too large for effective monitoring. An alternative approach, used in this study, is to infer the mode, range, and frequency of dispersal from a species' distribution at a single point in time. Such an approach requires a demographic model of invasion which makes testable predictions. We use a simple diffusion model in

which a species' distribution is assumed to expand in space by the cumulative effect of many random dispersal and establishment events (Skellam 1951; Andow et al. 1990). The advancing edge of a random distribution approximates a normal (Gaussian) distribution, and spreads at a constant rate from the initial point of colonization (Andow et al. 1990; Turchin 1998). In a real population deviation from a Gaussian distribution would imply non-random dispersal and/or establishment (Christen and Matlack 2006).

In the case of an uncolonized road segment, the progress of invasion would be determined by the relative strengths of dispersal at local and regional scales. If long-range dispersal was strong relative to local dispersal (the "fat tails" scenario) the diffusion model predicts propagules would arrive frequently and independently of one another, leading to low spatial autocorrelation of individual plants. Conversely, if long-range dispersal is weak relative to local dispersal, propagules would arrive infrequently reflecting a thin tail of the distribution. The roadside would be colonized largely by within-site dispersal, which would lead to strong spatial autocorrelation around the point of arrival in the manner of a microbial colony spreading on a petri dish.

In this study we examine distributions of three invasive nonnative species to test the widely held assumption of road-conduit function. This approach subsumes all population processes and ecological factors into the spatial distribution of stems, a necessary simplification in studies of range expansion. First we seek to understand the contribution of roadside-as-habitat and roadside-as-conduit in species' distributions. Within-site environmental limitation is examined by comparison of small-plot stem density with gradients of light and litter cover. We then use spatial distribution to estimate the frequency of dispersal within and between roadside sites. Inferences about habitat and dispersal were made on the basis of different forms of data from each species as appropriate to their life histories and local distributions.

Methods

Study sites

Populations were examined along forest roads in the Wayne National Forest (39°29'N, 82°14'W), Zaleski

State Forest (39°22'N, 82°18'W) and Vinton Furnace Experimental Forest (39°11'N, 82°23'W) in southeastern Ohio, USA. The area has a humid-continental climate with an average annual temperature of 11.3°C and annual precipitation of 1024 mm (NOAA 2005). The dominant landform is an eroded plateau, highly dissected into small valleys and narrow ridges with elevations ranging from 200 to 300 m a.s.l. Soils are moderately to well-drained silty loams derived from siltstone, shale, and sandstone (ODNR 2005). Natural vegetation is an oak-dominated, mixed mesophytic forest typical of the Low Hills section of the Unglaciaded Allegheny Plateau (Braun 1950).

Sites were selected beside woodland roads and in undisturbed forest nearby. "Roads" were unpaved forest access roads with a surface maintained by periodic grading. At the road edge a 1–2 m wide strip dominated by grasses and weedy forb species was maintained by infrequent mowing. Roads typically had a narrow canopy opening and received more light than undisturbed forest sites, although the degree of openness varied considerably within a site. To simplify habitat structure and standardize study sites, road sections were selected for study at least 50 m from other forms of anthropogenic disturbance (parking areas, power lines, intersections, etc.). Study sections were selected in level, well-drained sites without streams or ditches adjacent to the road. All roads were at least 46 years old at the date of measurement (except one recently constructed section, which was 4 years old), as judged from historical aerial photos. Study sections were >50 m from forest edges to avoid edge-related physical gradients (Matlack 1993, 1994).

Nonnative species

Distributions were described in three regionally common nonnative plant species. *Microstegium vimineum* (Trin.) A. Camus (Poaceae) is an annual grass in the tribe Andropogonae originating in SE Asia. It first appeared in Tennessee ca. 1919 and spread throughout the eastern United States, with particularly rapid expansion in the last 10 years (Hunt and Zaremba 1992; Southeast EPPC 2006). In southeastern Ohio it occurs in moist forest sites with exposed soil and an open canopy (Glasgow and Matlack 2007). It particularly favors exposed sediment along small streams. Seeds have no obvious means of

dispersal, but may remain dormant in the soil for several years (Gibson et al. 2002).

Rosa multiflora Thunb. (Rosaceae) is a large shrub usually found in open habitats (Drake et al. 2003; Southeast EPPC 2006). Seed is dispersed by birds attracted to its fleshy fruits. Long, drooping stems may root in contact with the ground, allowing vegetative propagation. *Rosa* was originally introduced from Asia in the late 1700s as an ornamental shrub. In the early twentieth century it was actively promoted by the US Department of Agriculture for hedgerows and wildlife habitat. *Rosa* is common in forest edges and old fields in southeast Ohio, but isolated individuals can also be found in undisturbed forest. *Tussilago farfara* L. (Asteraceae) is a rosette perennial which presumably arrived from northern Europe with the earliest colonists (Southeast EPPC 2006). *Tussilago* produces achenes with a small pappus, but little is known about its dispersal. It can also spread by vegetative propagation on a scale of cm (Bakker 1960). The species is generally intolerant of shade, but is common along woodland roadsides in southeast Ohio.

Species distributions

All nonnative species were recorded in belt transects (2×100 m) established parallel to the road sections. Transect width was measured from the edge of the graded road surface. To test the initial impression that nonnative species are more common along roadsides than in undisturbed forest, similar transects were established in undisturbed forest sites ≥ 50 m from the nearest road. Transects in both habitat types were replicated ten times. To consider interactions with landscape position, five transects of each habitat type were situated on ridges and five in valleys. Each transect was partitioned into fifty 2×2 m plots in which the stem number and percent coverage of all nonnative species were recorded. Canopy cover was measured with a hemispherical densiometer (Lemmon 1957) over the center of each plot, and percent bare soil was estimated visually.

Roadside patches of *Tussilago farfara* were described to compare population spread along the road with spread into the adjacent forest. Five patches were selected for their apparent vigor and clear separation from adjacent plots. In each patch, one 2×10 m transect started at the patch center and ran

parallel to the road; a second transect started at the same point but was oriented perpendicular to the road and extended into the forest. Each transect was divided into twenty 2×0.5 m plots in which stem number was recorded, documenting the gradual decline in stem density with distance from the patch center.

Habitat quality was examined in a seed-sowing experiment with *Microstegium* (*Tussilago* and *Rosa* were not included due to insufficient wild seed). One hundred wild-collected *Microstegium* seeds were planted in a 25×40 cm plot (i.e. 1 seed 10 cm^{-2}) at each of ten sites in each of four different habitat types: roadsides with open canopy, roadsides with closed canopy, open-canopy forest, and closed-canopy forest. Closed-canopy sites had $<5\%$ canopy openness, whereas open-canopy sites had $>25\%$ openness due to road width or treefall gaps. All plots were contained in shallow plastic tubs to prevent possible site contamination, and allow easy removal at the end of the experiment. Tubs were perforated to allow drainage, filled with locally collected soil, and dug in so the lip was even with the natural soil surface. Seedling establishment and growth were monitored at monthly intervals. No *Microstegium* were ever observed outside the experimental plots, providing a no-seed control.

Data analysis

Abundance of *Rosa multiflora* in road and interior habitats was compared between ridge and valley landscape positions using a two-factor ANOVA. To test the effect of microhabitat quality on *Rosa*, *Tussilago*, and *Microstegium* distributions, stem number and percent cover were regressed on canopy openness and percent bare soil in a forward step-wise manner.

Transect data were used to determine the spatial scale of clustering of all species. Moran's I was calculated as a measure of spatial autocorrelation at scales of 2–30 m and plotted against lag distance in each transect. Ninety-five percent confidence intervals were calculated using Rookcase (Sawada 1999), an add-in to the Excel spreadsheet (Microsoft, Redmond, Washington). Only transects in which the species occupied five or more plots were used, to avoid stochastic effects.

The perpendicular and parallel transects were compared to distinguish dispersal facilitated along

the road axis from merely random dispersal. Stem densities of *Tussilago* were log transformed and plotted against distance from the patch center. Equivalent slopes of density on distance would imply equal dispersal effectiveness parallel and perpendicular to the road axis, whereas a shallower slope along the road would imply superior dispersal in that direction (Christen and Matlack 2006). To test for presence of an advancing wave front at the edge of a patch, Gaussian, exponential, and power functions were fit to stem distributions at patch edges and compared on the basis of R^2 values.

In the seed-sowing experiment, establishment and growth of *Microstegium* were compared between road and interior sites and open and closed canopy conditions with a two-factor ANOVA, applied on each of three sampling dates.

Results

Seven non-native species were encountered: *Rosa multiflora*, *Lonicera japonica*, *Tussilago farfara*, *Elaeagnus umbellata*, *Berberis thunbergii*, *Alliaria petiolata*, and *Glechoma hederacea*. All species were more frequently encountered along roads than in undisturbed forest. All species occurred more frequently in valleys than on ridges (except *Elaeagnus*, which was equally frequent in both landscape positions). *Rosa* was most common, occurring in all habitat types; *Lonicera* was common along roadsides in valleys but rare or absent elsewhere. The other species were encountered in only a few sites, and appeared in only 1–3 plots where present. *Rosa multiflora* was the only nonnative species found in undisturbed forest sites.

Roadside as habitat

Canopy openness was significantly greater in road sites than in undisturbed forest (mean cover_{road} = 85.7%; cover_{forest} = 96.3%; $F = 21.16$, 1 df, $P = 0.0003$). Valley and ridge sites were not significantly different in canopy openness ($P > 0.05$).

In road sites, more *Rosa multiflora* stems were encountered in valleys than on ridges (valley road = 35.6 stems transect⁻¹ ± 9.2 se; ridge road = 12.8 ± 3.6; $F_{\text{landscape position}} = 5.53$, 1 df, $P = 0.0320$) because more occupied plots occurred in

valleys (density per plot was ca. 1.3 stems m⁻² in both landscape positions). Far fewer stems were recorded in undisturbed forest than along roads (valley forest = 2.0 stems transect⁻¹ ± 1.2; ridge forest = 1.2 ± 1.0; $F_{\text{road proximity}} = 20.28$, 1 df, $P = 0.0004$). Occupied forest plots showed means of 0.8 and 0.6 stems m⁻² in valleys and ridges, respectively. Multiple regression recognized a negative relationship of *Rosa* stem number and/or cover to canopy cover in four out of ten transects, suggesting that canopy openness promotes establishment of this species (Table 1). The regression was repeated excluding zero values to examine growth of established patches. Significant and strong (large R^2) negative relationships were observed between canopy cover and *Rosa* cover in three of ten transects implying that canopy openness also promotes patch expansion (Table 2). Only one of ten transects showed a significant regression on bare soil.

Tussilago farfara occurred at densities of 400–1700 stems transect⁻¹ with means of 6–20 stems m⁻² in occupied plots. Stem number showed significant regressions on canopy cover in three of five transects (Table 1). In two cases the coefficient was negative, consistent with stronger recruitment under an open canopy. *Microstegium vimineum* was represented by much higher stem densities (est. 2000–30000 stems transect⁻¹; means of 30–300 stems m⁻² in occupied plots) than *Rosa* or *Tussilago*. Stem density of *Microstegium* was negatively related to canopy cover in three transects (Table 1).

In the *Microstegium* sowing experiment, germination occurred in the last two weeks of June with numbers in roadside sites stabilizing thereafter (Fig. 1a). Significantly more *Microstegium vimineum* seedlings established in roadsides than undisturbed forest sites (Table 3). Initially canopy openness did not appear to influence establishment, but open-canopy plots had significantly more stems by September, reflecting the decline in numbers in closed-canopy forest sites from July to September. As with establishment, plant growth showed clear separation of plots on the basis of road proximity and canopy openness (Fig. 1b). By August significantly more leaves per plant were recorded in road sites and in open habitats (Table 3). This trend continued into September with a significant road × canopy interaction.

Among closed-canopy sites, the contrast of roadside and forest locations (Fig. 1) implies that some feature of the roadsides in addition to canopy cover

Table 1 Distribution of *Rosa multiflora*, *Tussilago farfara*, and *Microstegium vimineum* along roadsides

Species	Transect	Response variable	Independent variable	R ²	Pr > F	
<i>Rosa multiflora</i>	Valley 1	Stem no.	Canopy	0.137	0.0083	
		% cover	Canopy	0.125	0.0118	
	Valley 2	% cover	Canopy	0.234	0.0004	
	Valley 3	% cover	Soil	0.081	0.0451	
	Valley 5	% cover	Canopy	0.186	0.0018	
	Ridge 2	Stem no.	Canopy	0.312	<0.0001	
		% cover	Canopy	0.384	<0.0001	
	<i>Tussilago farfara</i>	Tf 2	Stem no.	Canopy	0.949	<0.0001
			% cover	Canopy	0.896	<0.0001
		Tf 3	Stem no.	Canopy	0.124	0.021
% cover			Canopy	0.117	0.025	
Tf 4		Stem no.	Canopy	0.177	0.003	
		% cover	Canopy	0.127	0.012	
<i>Microstegium vimineum</i>	Mv 1	Stem no.	Canopy	0.163	0.0036	
	Mv 3	Stem no.	Canopy	0.205	0.0010	
	Mv 4	Stem no.	Canopy	0.141	0.0073	

Stem number and % cover were regressed on canopy cover and % bare soil in a forward-stepwise manner. Transects showing no significant are not included

Table 2 Distribution of *Rosa multiflora* cover in plots where stems are present

Transect	Variable	Parameter estimate	R ²	F value	Pr > F
Valley 2	Overall	165.94	0.307	6.65	0.0210
	Intercept	-2.01			
	Canopy				
Valley 5	Overall	218.91	0.713	29.85	0.0001
	Intercept	-2.48			
	Canopy				
Ridge 4	Overall	163.79	0.769	16.66	0.0095
	Intercept	-1.64			
	Canopy				

Regressions of *Rosa* % cover on canopy cover and % bare soil in road valley and ridge transects using only plots with stems present

must also be important to the establishment of *Microstegium*. Qualitative observations suggest the importance of poor drainage: *Microstegium* was particularly dense and vigorous in swales with moist soil. Within plots stems were concentrated in micro-sites with bare soil, and they rarely appeared in deep litter or where larger herb species imposed shade. Clusters of stems often occurred on low (<10 cm) gravel mounds created by a road grading machine.

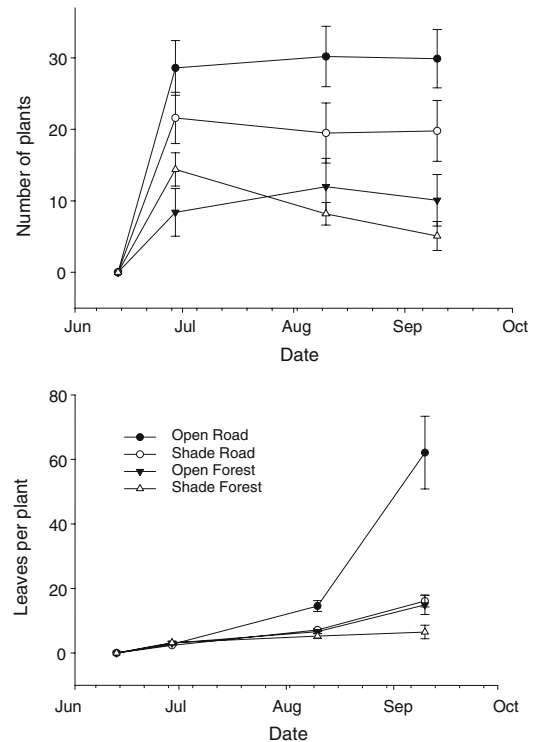


Fig. 1 Germination and growth of *Microstegium vimineum* in road and interior habitats, in open and shaded environments. (a) Mean number of plants per plot, from June to September. (b) Mean leaves per plant. Bars indicate standard errors. Seeds were sown in mid-June

Table 3 Establishment of *Microstegium vimineum* in experimental plots

Variable	Month	Overall	Road proximity	Canopy openness	Position × openness
Stem number	July	6.97	17.04	ns	ns
		0.0008	0.0002		
	Aug	7.00	16.20	ns	ns
Leaves plant ⁻¹	July	9.28	22.95	4.40	ns
		0.0001	<0.0001	0.0431	
	Aug	18.15	25.12	19.82	9.51
	Sept	<0.0001	<0.0001	<0.0001	0.0039
		17.63	22.45	20.61	9.83
		<0.0001	<0.0001	<0.0001	0.0034

Analysis of variance of road proximity (adjacent to road, forest interior) and canopy openness (open, shade). Numbers listed are *F* value (above) and *P* (below). “ns”, not significant at the 0.05 level

Spatial autocorrelation

Rosa multiflora showed strong positive autocorrelation at a lag distance of 2 m (Fig. 2). Positive autocorrelation was also observed at distances of 8–12 m (significant in four of eight transects). At other scales, *Rosa* showed nonsignificant (slightly negative) autocorrelation in both ridge and valley transects. *Tussilago farfara* was positively autocorrelated at distances of 2 and 4 m in four of five transects, and up to 14 m in two transects (Fig. 3a). *Microstegium vimineum* was strongly clustered at distances of 2 and 4 m in all transects but most transects were not significantly clustered at coarser scales (Fig. 3b). Stems on transect three, which was dominated by a single large patch, remained significantly autocorrelated up to 18 m.

Expansion along the road

Patches of all three species extended farther parallel to the road than perpendicular to it, indicating greater patch expansion along the road axis. *Microstegium vimineum* was only observed >2 m from the road when water diversion channels extended the zone of disturbed soil into the adjacent forest.

Distributions of *Tussilago farfara* suggested contrasting patterns of establishment parallel and perpendicular to the road (Fig. 4). Perpendicular

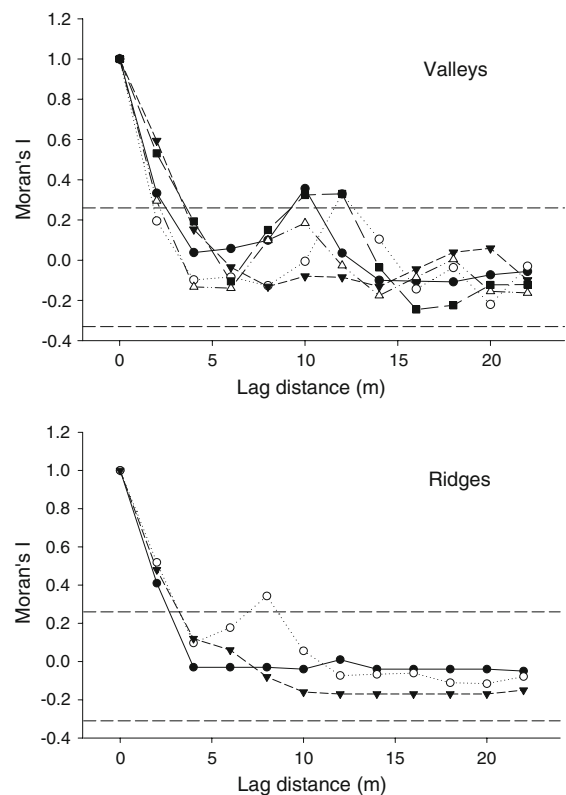


Fig. 2 Spatial distribution of *Rosa multiflora* in roadside habitats. Moran's I index of spatial autocorrelation is presented for (a) five transects in valleys and (b) three on ridges. Significant values ($Z > 1.96$, $P < 0.05$) lie outside the 95% confidence interval, indicated by the horizontal dashed lines

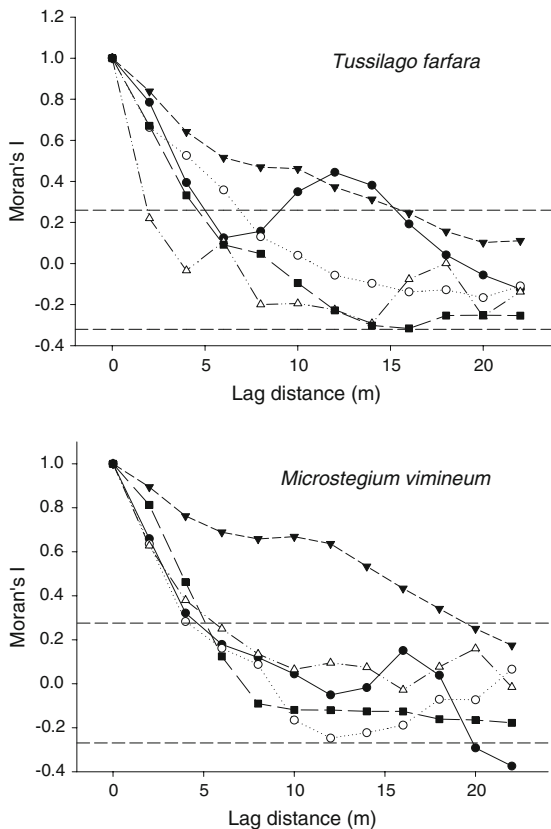


Fig. 3 Spatial distributions of *Tussilago farfara* (a) and *Microstegium vimineum* (b) in roadside habitats. Moran's I index of spatial autocorrelation is presented for five transects for each species. Significant values ($Z > 1.96$, $P < 0.05$) lie outside the 95% confidence interval, indicated by the horizontal dashed lines

spread ended ca. 2 m from the patch center in all cases, whereas parallel spread extended 4–6 m. A shallower slope in regressions of stem number on distance suggests farther dispersal along the road axis in all patches. In the parallel transects, in patches *a* and *c*, stem number varied little within 2–3 m of the patch center, suggesting a high and stable density after passage of the wave front. If these distances are omitted from the regression, slopes of the road-parallel transects are similar to the perpendicular transects in both cases, demonstrating greater expansion distance along the road axis but implying no difference in dispersal range. Stem distributions in patches *d* and *e* were quite irregular, perhaps because physical heterogeneity has also shaped roadside distributions.

Gaussian curves have the highest R^2 values in three of the five patches (Fig. 4) suggesting diffusive spread. Although exponential curves provided best fits in the two irregular patches, they were only slightly better than Gaussian curves in either case.

Discussion

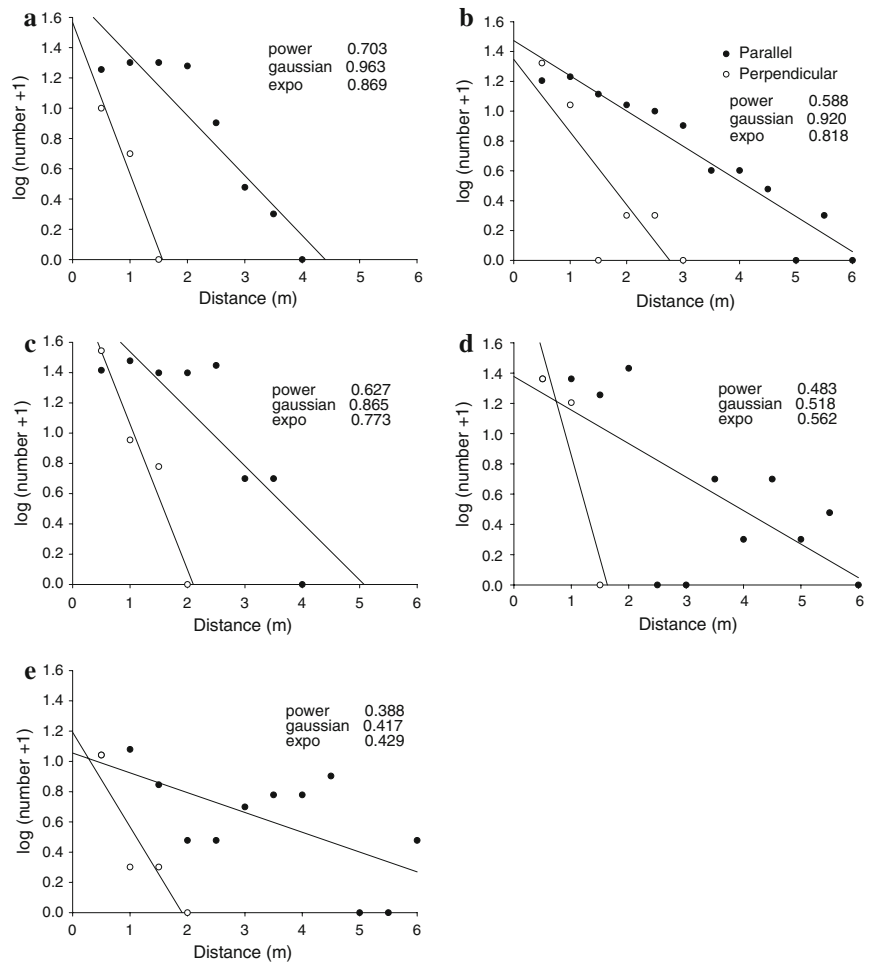
The roadsides we surveyed had more nonnative plant species and higher stem densities than forest sites, in agreement with the large literature on nonnative distributions. Abundance along roadsides was apparently linked to habitat quality. Elevated light distinguished roadside from forest sites, and corresponded to micro-distributions of *Rosa*, *Microstegium*, and *Tussilago* within road sites. Habitat quality created by road proximity interacted with natural gradients of canopy openness and landscape position. Roadsides in valleys, for example, were favored over ridges, reflecting the greater soil moisture found in valley sites (Olivero and Hix 1998; Hutchinson et al. 1999) and the common observation that nonnative species are more abundant in moist sites (Knops et al. 1995; Merriam 2003). In addition to providing habitat, road corridors appear to be channeling population expansion. At the regional scale, however, many apparently suitable roadside sites are still unoccupied. Beyond these generalizations, each species showed a distinctive pattern of invasion.

Rosa multiflora

Roadsides provided high quality habitat for establishment of *Rosa multiflora*, probably due to available light. Light also appeared to influence *Rosa* cover (a measure of growth), and to a lesser extent distribution, at the scale of plots within sites. These observations are consistent with previous work showing higher frequencies and local densities of *Rosa* in successional habitats, open areas and forest edges (Robertson et al. 1994; Lundgren et al. 2004; Yates et al. 2004). The contrast between ridges and valley sites suggests soil moisture as a secondary controlling gradient (Glasgow and Matlack 2007).

The mechanism of *Rosa* spread within sites can be inferred from its spatial distribution along the roadside. Spatial autocorrelation defined patches less than 4 m long, i.e. the scale of an individual mature plant. Clustering at this scale is consistent with the

Fig. 4 Shape of roadside patches of *Tussilago farfara*. Numbers of individuals are plotted against distance from the patch center in parallel and perpendicular transects in five patches (a–e). Least squares regression lines are shown for each transect. R^2 values are reported for power, Gaussian, and exponential curves fitted to the data from parallel transects. Symbols: ○, transects perpendicular to the road; ●, transects parallel to the road



observation that most reproduction in these sites occurred by vegetative propagation. Drooping stems root on contact with the ground, and rhizomes may produce aboveground shoots up to 1.8 m from the parent plant (D.C. Christen, pers. obs.). By contrast, very few seedlings were observed. We infer that within-site spread of *Rosa* is driven by vegetative propagation in close proximity to parent plants. Patch expansion will be diffusive assuming that vegetative growth is initiated in random directions. Expansion will progress at a rate determined by vegetative growth, presumably much slower than possible by vertebrate dispersal of seeds. Expansion will be channeled along roads if roadsides allow better ramet survival, as habitat observations suggest. Autocorrelation was also observed at the 10–12 m scale (clearly beyond the range of vegetative propagation), which may reflect occasional within-site propagation by seedling establishment.

Dispersal between sites appears to be quite rare. One-hundred meter transects typically showed 2–5 distinct *Rosa* patches, each presumably arising from a single seed germinating in a period >46 years, implying a frequency of site colonization much lower than the rate of establishment within sites. Rare seedling establishment may be expected in the tail of a strongly skewed seed distribution (Kot et al. 1996), but it is surprising that seedlings were also uncommon within meters of potential parent plants. Seed dispersal has not saturated the roadsides we examined despite apparent habitat suitability, proximity of potential parent plants, and passage of several decades. Thus *Rosa*'s roadside distribution appears to be due to a combination of moderate habitat specificity (particularly a requirement for light), vigorous vegetative propagation, and broad but infrequent seed dispersal, a finding which is counterintuitive considering the apparent potential for vertebrate dispersal.

Tussilago farfara

Roadsides created opportunities for *Tussilago farfara* colonization which apparently did not exist away from roads. Seedlings have been observed to establish most readily on moist, exposed soil with minimal shade (Bakker 1960), conditions rarely found in the study area except in roadsides (banks in road cuts seem particularly suitable). *Tussilago* appears to expand along the road axis by simple diffusive spread channeled along the corridor of roadside habitat.

Distributions observed here suggest that propagation occurs through both extension of rhizomes and germination of wind dispersed seeds. In a recently drained Dutch polder, *Tussilago* patches expanded by 2.5–3.5 m in 2 years (Bakker 1960). Such rates were clearly not attained in our populations, but the slopes of frequency parallel to the road, and the occurrence of isolated shoots outside of patches, suggest that patches were expanding when measured. The scale of clustering reported here (4–6 m) is well beyond the range of vegetative propagation, implying either long site occupation or effective short-range seed dispersal. Because one of the *Tussilago* road sites was only ~4 years old at the time of measurement, and already supported a patch 5–6 m long, effective seed dispersal is the likely explanation. Skarpaas and Stabbertorp (2003) report a modal dispersal distance of 0.2–2 m, extending up to 6 m depending on wind direction. On the scale of a 100 m transect such distances suggest incremental patch expansion by short-range seed dispersal. Most transects had 2–4 distinct patches suggesting ca. three colonization events since the roads were constructed—far fewer than the implied within-site colonization rate. Although patch frequency suggests that *Tussilago* is able to reach roadside sites as often as *Rosa*, *Tussilago* appears to colonize more rapidly within sites by virtue of longer dispersal and more frequent seedling establishment. Expansion is narrowly channeled along roadsides by a high degree of habitat specificity.

Microstegium vimineum

Microstegium appeared to be habitat limited at several scales. A light requirement is suggested by the vigorous germination and growth of seeds in open-canopy sites, and the correlation of stem number with light in roadside transects.

Microdistributions corresponding to small mounds of roadside gravel suggested a response to soil disturbance. These observations are consistent with previous work identifying light and bare soil as requirements for establishment (Cole and Weltzin 2004, 2005; Glasgow and Matlack 2007). Understory openness may also be a limiting factor at the local scale (Cole and Weltzin 2005; the present study). High stem densities and close conformity to microsite boundaries were apparent in several sites, leading to significant autocorrelation at fine scales. It's possible that close correspondence to environmental gradients indicates site saturation, and within-site expansion is no longer occurring (Redman 1995; Cole and Weltzin 2004). The possibility that habitat limitation, rather than dispersal limitation, is defining patches makes it difficult to estimate inter-site movement from patch frequency, as was done for *Rosa* and *Tussilago* (above). Inter-site movement is implied by rapid regional spread and occurrence in widely separated sites, but such dispersal is limited; seed-sowing experiments demonstrate that there were many suitable sites in the study area which *Microstegium* had not reached at the time of this study (Glasgow and Matlack 2007; the present study).

Within sites, local abundance in small piles of gravel created by the road grader implicates road maintenance in population expansion. Movement of seeds by water is suggested by patches of *Microstegium* in water diversion channels leading off the road, and along streams below these anthropogenic features. In the presence of soil-moving processes, within-site dispersal seems to be assured by seed dormancy. Within the 2-year span of this study, occasional roadside patches expanded into dense road- and streamside populations >100 m long, presumably spread by these mechanisms. Despite having no obvious dispersal mechanism *Microstegium* has been able to move quickly along roadsides and spread into the adjacent forest. Soil movement appears to be a more efficient mechanism than the wind dispersal of seeds in *Tussilago* or vertebrate dispersal in *Rosa*. In the absence of soil movement, however, strong habitat limitation makes it difficult for *Microstegium* to spread.

Invasion in a heterogeneous landscape

Interpreting invasion from static pattern is an imperfect art. Much uncertainty remains about the age of sites, location of source populations, the range of seed

dispersal, and the extent of habitat limitation in each species. Nevertheless, these observations allow us to make useful inferences about the role of roads in plant invasions. Roadsides evidently function as conduits by both of the mechanisms postulated above: In *Tussilago farfara* and *Rosa multiflora*, roadsides provide continuous strips of congenial habitat that channel natural population expansion, while in *Microstegium vimineum* dispersal along the road is facilitated by road maintenance. The resulting distributions are individualistic to each species, a product of specific habitat requirements, dispersal capacity, and seed dormancy.

All three species are also capable of long-range colonization, but on a scale of 100 m transects and >46 years of colonization opportunity, between-site colonization events appear to be rare. All three species appear to propagate more vigorously within sites than between them. It is possible that both within- and between-site propagation of each species are controlled by a single form of seed dispersal which produces a severely skewed dispersal kernel (Kot et al. 1996). The wide separation and infrequent occurrence of populations would be caused by stochastic variation at great distances from the parent. Alternatively, the contrast between intra- and inter-site colonization can be explained by a hierarchical model of invasion in which fundamentally different mechanisms are acting at different scales (Shigasada et al. 1995). *Microstegium*, for example, spreads by road grading within sites—a mechanism which cannot plausibly be extended to inter-site colonization. *Rosa*'s within-site spread by vegetative propagation clearly does not apply to inter-site colonization. The hierarchical model seems more appropriate in these two species, although the character of long-range dispersal is still unclear.

We suggest that regional range extension of these species is occurring through a nucleation process (Moody and Mack 1988) in which roadsides function as areas of congenial habitat independently of their linear structure. Local patches support establishment of a few founder individuals arriving from a great distance. Founders reproduce to densely colonize the immediate area, and a small number of propagules disperse to distant sites. Although roadsides may function as conduits in local patch expansion, they do not appear to be serving as avenues of range extension at the regional scale. Extension of ranges

by the cumulative effect of many short-range dispersal events (i.e. a traveling wave; Turchin 1998) has been reported in vertebrate species along interstate highways (Getz et al. 1978; Forman et al. 2003) and inferred from casual observation in many plant species. However, wave behavior does not seem to be occurring over long distances in the species examined here.

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