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Invasive shrub distribution varies with distance to roads and stand age in eastern deciduous forests in Indiana, USA

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Abstract

We documented the relationship between densities of invasive exotic shrubs, distance to road, and successional age of the forest in 14 forested sites throughout central and southern Indiana. Roadways are increasingly abundant, human-made features that can be conduits for the spread of invasive exotic plants in a number of ecosystems. Little is known, however, about the role of roads in eastern deciduous forest ecosystems where road density is high. Further, it is not known whether the distribution of exotic plants along roads depends on the successional age of the forest. In this study, densities of four of seven exotic shrub species declined with increasing distance to the nearest road across all successional ages. Greater densities of exotic shrubs were found in young and mid-successional forests than mature forests. However, there was no interaction between distance to road and forest age, suggesting that the role of roads in the invasion process does not change across forest successional ages. We outline several potential mechanisms that may drive patterns of shrub distribution along roadside edges as a guide for future research.

Introduction

Recent studies have shown that roads are contributing to the spread of invasive exotic plants in several ecosystems (Tyser and Worley 1992; Parendes and Jones 2000; Trombulak and Frissell 2000; Gelbard and Belnap 2003; Watkins et al. 2003). Roads facilitate the spread of exotic plants by providing corridors for invasion (Tyser and Worley 1992) and habitat suitable for exotic plants. Roadsides are characterized by frequent disturbance, nutrient rich soil (Trombulak and Frissell 2000), and exposure to sunlight (Parendes and Jones 2000; Watkins et al. 2003). Increased exposure, storm water runoff, and vehicle traffic along roads facilitate the easy movement of wind, water, and animals that transport seeds (Forman and Alexander 1998; Trombulak and Frissell 2000; Myers et al. 2004). The combination of high propagule pressure and favourable growing conditions has allowed exotic plants to establish along roadside edges in many ecosystems (Tyser and Worley 1992; Forman and Deblinger 2000; Parendes and Jones 2000; Gelbard and Belnap 2003; Watkins et al. 2003; Barton et al. 2004).

If roads are important corridors for exotic plants or if roadside edges provide good habitat for exotic plant growth, then one would predict decreased exotic plant density with increased distance to roads. In support, the prevalence and cover of exotic plants has been shown to decline with increasing distance to road in a number of ecosystems. Tyser and Worley (1992) reported that exotic species richness was nearly twice as great along roadside edges compared to 25 m from roads in grasslands in Glacier National

Park (USA). Further, the percent cover of exotic species was significantly greater at 10 m and 100 m from roads than at 1000 m from roads in central California (Gelbard and Harrison 2003). Other studies have shown similar results for the Chequamegon National Forest in northern Wisconsin (Watkins et al. 2003) and the Quail Ridge Reserve of the University of California Natural Reserve System in Napa County, California (Harrison et al. 2002).

Independent of distance to road, successional age might determine susceptibility of a community to exotic plant invasions. Young forests typically have higher light levels (Levine and Feller 2004), fewer competitors, and less litter than older forests (Leuschner 2002) while mature forest interiors are known to have lower light availability, cooler temperatures, and higher humidity than forest edges (Brothers and Spingarn 1992). We would therefore expect, based on levels of light penetration and microclimatic conditions, that older forests would have higher densities of invasive shrubs near the forest edge than in forest interiors and fewer invasive shrubs overall due to less recent disturbance events and less favourable environmental conditions. We would also expect that younger forests would show weaker correlations of densities of invasive shrubs with increasing distance to road since light levels are higher throughout young forests. This would result in an interaction between distance to road and forest age. To our knowledge, no prior studies have concurrently investigated the relationship between the invasion of exotic plants, distance to road, and the successional age of a community. While the effects of roads *per se* on exotic plants has been examined (Farnsworth 2004; Lundgren et al. 2004), no study has examined the correlation between distance to roads and invasions of exotic plants in eastern deciduous forest ecosystems.

The goal of this study was to quantify the density of invasive exotic shrubs along roads in eastern deciduous forests of varying successional ages in Indiana. Eastern deciduous forests cover much of the landscape east of the Mississippi River. Most of this region has been fragmented by urban and suburban development and roads such that ninety percent of all ecosystem areas in the eastern US are within 1061 m of a road (Riitters and Wickham 2003). We specifically addressed the following questions (1) Does the density of invasive exotic shrubs decline as the distance to a road increases? (2) Does the relationship between density and distance to road differ among exotic shrub species? and (3) Are invasive exotic shrubs less common in mature forests than in young successional forests? Answers to these questions will help develop a predictive framework for plant invasions and better inform management strategies.

Methods

Study sites

This study was conducted from June to September, 2003 at 14 forested sites in central and southern Indiana within 100 km of Bloomington, Indiana. Details of site location, age, and land – use history are provided in the Appendix. Sites were located on public and private land that bordered paved two-lane county and municipal roads with unimproved shoulders and mowed strips between the road and forest edge of less than 3 m. Sites were chosen that did not have ditches, ravines, cliffs, or embankments within 30 m of the road. Sites were located at least 1 km apart and all sites were located within 800 m of known exotic shrub invasions.

Sites were assumed to be succeeding to native forest following various anthropogenic practices including row-crop agriculture, grazing, and selective and clear-cut timber harvests. Forest age was calculated as the amount of time since anthropogenic disturbance ended. Forests were classified as “young” if they were less than 30 years old; “mid-successional” if they were between 30 and 60 years old and “mature” if the forest was older than 60 years. Forest age was determined by dated aerial photographs, personal communication with landowners, and measures of diameter at breast height (dbh) of the largest trees at the site. Young forest sites included a military installation and abandoned agricultural land. Mid-successional sites consisted of abandoned fields and land where clear-cuts for timber harvest were conducted between 30 and 60 years ago. Mature forest sites had not been used for agriculture or clear-cut for timber within the last 60 years and most of them were designated as forest preserves (see Appendix). Although land-use history is known to affect forest stand composition (Whitney and Foster 1988; Foster 1992) we did not have sufficient information to evaluate the effect of land-use history on stand composition or the presence of invasive exotic shrubs (see Appendix).

Central and southern Indiana forests are in the transitional zone where western mesophytic forest mixes with beech-maple forest (Braun 1950). The forest canopy typically included a variety of native tree species including *Acer* spp., *Carya* spp., *Fagus grandifolia*, *Liriodendron tulipifera*, *Fraxinus* spp. and *Quercus* spp. Common native understory trees and shrubs at the study sites typically included *Asimina triloba*, *Cercis canadensis*, *Cornus florida*, *Lindera benzoin*, *Ostrya virginiana*, *Rhus* spp., *Sassafras albidum*, and *Viburnum* spp.

Numerous exotic species of shrubs and small trees have been introduced to central and southern Indiana (Jacquart 2000). They were brought to the US from Europe and Asia for wildlife and horticultural purposes starting in the late 1800s (Miller 2003). All of the exotic shrubs we sampled have escaped cultivation and are invading natural areas in Indiana to varying degrees (Jacquart 2000). Many exotic shrubs have invaded natural areas because they produce large amounts of seed, are readily dispersed by birds, and germinate and grow well under a variety of conditions (Luken and Mattimiro 1991; Luken and Goessling 1995; Morris et al. 2002).

Study design

At each of the 14 sites, two transects were located perpendicular to the road. Transects were at least 20 m apart and at least 50 m from other forest openings such as creeks, fields, and other roads. Transects were located randomly by driving or walking along the road a distance determined using a random number table. Each transect started where the forest edge met the mowed strip along the road and extended 30 m into the forest. Rectangular quadrats, 1×10 m in size were arranged parallel to the road at 0, 10, 20, and 30 m from the road. The density of invasive exotic shrubs was quantified within each quadrat by counting the number of stems for each species. In total, invasive shrub density was determined for 28 transects across 14 sites of three successional ages and included 2674 stems in total.

Statistical analysis

We used a mixed general linear model to test the effects of forest age, distance to road, transect, and site on the number of shrub stems per square meter (Proc GLM, SAS Institute, Inc. 1999). Site was nested within age and transect was nested within age and site. Site, age, and distance were fixed effects while transect was a random effect. Site was treated as a fixed effect because the limited number of sites meeting our criteria were specifically selected for this study and not randomly chosen from a larger pool. Post-hoc Tukey tests were used to determine which levels of the independent variables were significantly different. The same general linear model was used to analyze the effects of age, distance to road, transect, and site on the density of individual species. The response variable, number of shrub stems/m^2, was marginally non-normal and so was rank transformed since the assumption of homogeneity of variance could not be met (Conover and Iman 1981). Tests on transformed data gave the same results so we only report results from untransformed data.

Results

We found seven exotic shrub species at the sample sites: *Berberis thunbergii* (Japanese Barberry), *Elaeagnus umbellata* (Autumn Olive), *Euonymus alata* (Winged Euonymus), *Ligustrum obtusifolium* (Privet), *Lonicera maackii* (Bush Honeysuckle), *Pyrus calleryana* (Pear), and *Rosa multiflora* (Multiflora Rose). At least 1 exotic shrub species was found at each site and no site contained all 7 species. On average, three exotic shrub species were found at each site. *Pyrus calleryana* was found at only one site near a nursery where it had been planted about 40 years prior to the sampling. *Rosa multiflora* and *Lonicera maackii* were the most common species being found at 13 and 8 sites respectively.

There was a negative correlation between distance to road and the density of exotic shrubs. Exotic shrubs were found at higher densities at 0 m than 10, 20, or 30 m from the road (Figure 1, Table 1). On average, there were 46% fewer stems per square meter at 10 m from the road than at 0 m from the road. Four of seven exotic shrub species were found in decreasing densities with increasing distance to roads (Figure 2, Table 1): *L.*

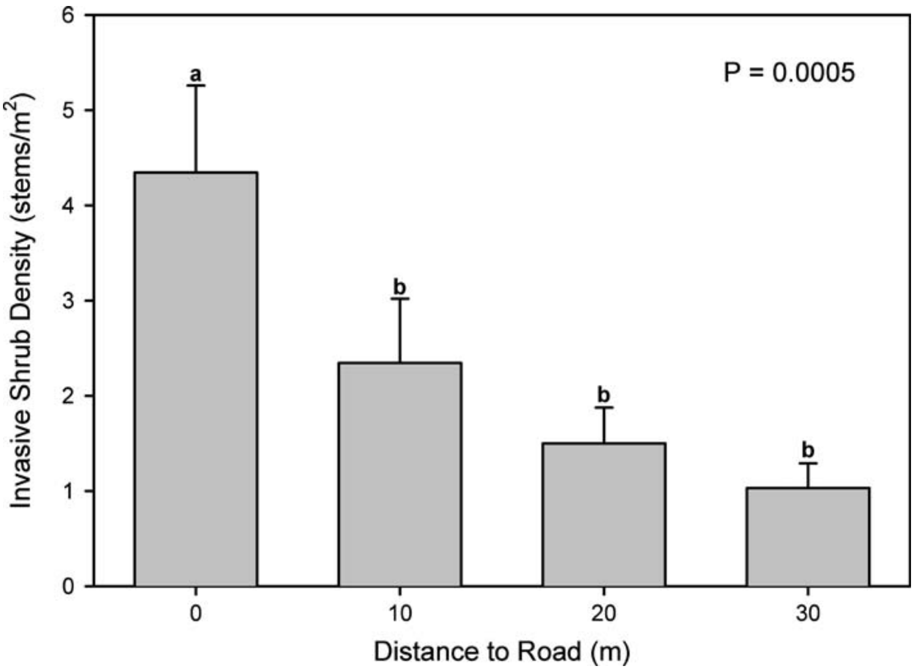

Figure 1. Mean (± 1 SE) invasive shrub stem density across all forest ages, sites, and transects at different distances to roads ($n = 28$). Different letters indicate a significant difference at the $\alpha = 0.05$ level as determined by a Tukey's *post-hoc* test. All results have been presented as untransformed raw means and standard errors to simplify interpretation of the results.

maackii, B. thunbergii, P. calleryana, and *E. alata*. *L. obtusifolium* and *E. umbellata* densities also decreased with increasing distance to the nearest road but the trend was not significant. The density of *R. multiflora* was not related to distance to road (Figure 2, Table 1). No species by distance interaction could be calculated because too few species co-occurred at individual research sites.

When the density of exotic shrub stems was compared across forest successional ages regardless of distance to road, we found that stem density was higher in young and mid-successional forest than mature forest (Figure 3, Table 1). There were approximately 70% fewer invasive shrub stems in mature forests than in young and mid-successional forests. Four of the individual species also showed significant differences in density with successional age.

There was no overall interaction between forest age and distance to road (Figure 4, Table 1), indicating that the relationship between invasive shrub stem density and distance to road did not vary with forest age. One species, *B. thunbergii*, did exhibit a significant interaction between distance and age but was the least abundant exotic shrub in this study.

Discussion

Does the density of invasive exotic shrubs decline as the distance to a road increases?

This study suggests that roads may contribute to the spread of invasive plants in eastern deciduous forests. We found a highly significant effect of distance to road over all species and for four of seven individual species. Deciphering the mechanisms by which these patterns of exotic shrub distribution have arisen will require further experimental study. We outline several possible mechanisms for the spatial distribution of exotic shrubs in roadside forests (Table 2). One possible mechanism for high densities of invasive shrubs along roads is that exotic shrub propagules are distributed evenly by birds with respect to distance to road and simply survived at a greater rate near the road due to better growth conditions. These conditions might include higher light conditions or increased nutrient or water availability (Brothers and Spingarn 1992; Parendes and Jones 2000; Watkins et al. 2003). Better survival and growth of exotic shrubs might also be due to decreased competition with native

Table 1. Results of the analysis on the effect of distance to road, age, site, transect, and interactions on the density of exotic shrubs. Results are also reported for individual species analysed using the same statistical model.

Effect	Invasive shrub density (stems/m^2)											
	All species			*Berberis thunbergii*			*Elaeagnus umbellata*			*Euonymous alata*		
	df	*F*	*p*	df	*F*	*p*	df	*F*	*p*	df	*F*	*p*
Distance	3,46	7.06	0.0005	3,6	20.47	0.0015	3,18	2.79	0.0703	3,12	5.50	0.0131
Age	2,15	30.61	< 0.0001	1,6	9.80	0.0203	2,6	0.12	0.8874	1,4	35.33	0.0040
Site (age)	11,14	8.10	0.0003	0,6	N/A	N/A	4,6	0.19	0.9328	5,4	41.87	0.0015
Transect (age × site)	14,46	0.66	0.8029	2,6	1.00	0.4219	6,18	5.72	0.0018	4,12	1.00	0.4449
Age × distance	6,46	0.44	0.8492	3,6	25.80	0.0008	6,18	1.68	0.1842	3,12	1.16	0.3657
Site × distance (age)	33,46	0.62	0.9203	0,6	N/A	N/A	12,18	1.06	0.4447	15,12	2.90	0.0348
	Ligustrum obtusifolium			*Lonicera maackii*			*Pyrus calleryana*			*Rosa multiflora*		
	df	*F*	*p*	df	*F*	*p*	df	*F*	*p*	df	*F*	*p*
Distance	3,18	1.02	0.4086	3,24	8.71	0.0004	3,3	18.55	0.0193	3,39	0.20	0.8967
Age	1,6	0.31	0.5978	2,8	33.42	0.0001	0,3	N/A	N/A	2,13	8.32	0.0047
Site (age)	4,6	1.05	0.4558	5,8	4.51	0.0298	0,3	N/A	N/A	10,13	1.61	0.2072
Transect (age × site)	6,18	3.44	0.0193	8,24	1.37	0.2610	1,3	5.49	0.1009	13,39	0.89	0.5666
Age × distance	3,18	0.87	0.4750	6,24	0.33	0.9134	0,3	N/A	N/A	6,39	0.85	0.5368
Site × distance (age)	12,18	1.04	0.4582	15,24	1.21	0.3276	0,3	N/A	N/A	30,39	1.21	0.2819

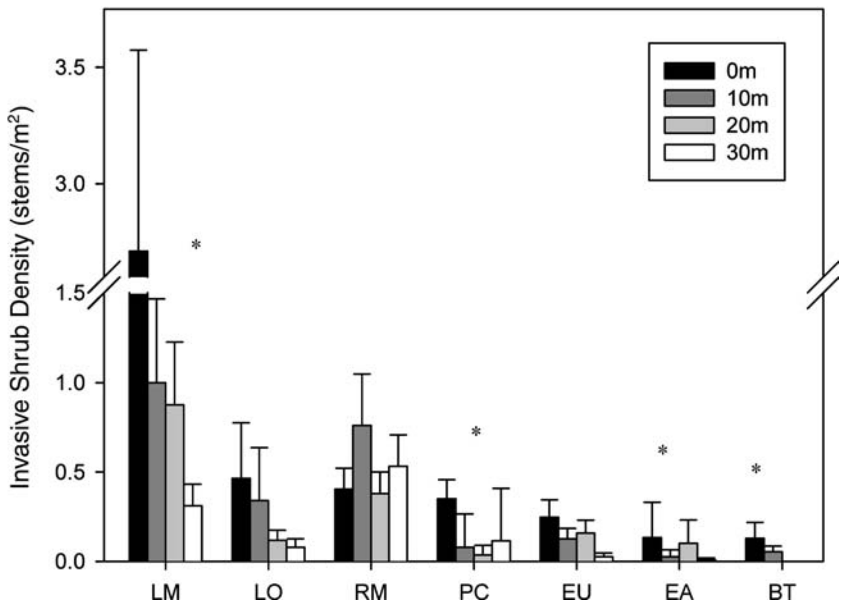

Figure 2. Mean (±1 SE) stem density of seven species of invasive shrubs at four distances to roads. LM = *Lonicera maackii*, LO = *Ligustrum obtusifolium*, RM = *Rosa multiflora*, PC = *Pyrus calleryana*, EA = *Euonymus alata*, EU = *Elaeagnus umbellata*, BT = *Berberis thunbergii*. Species marked with an asterisk differ in stem density with increasing distance to roads (see Table 1).

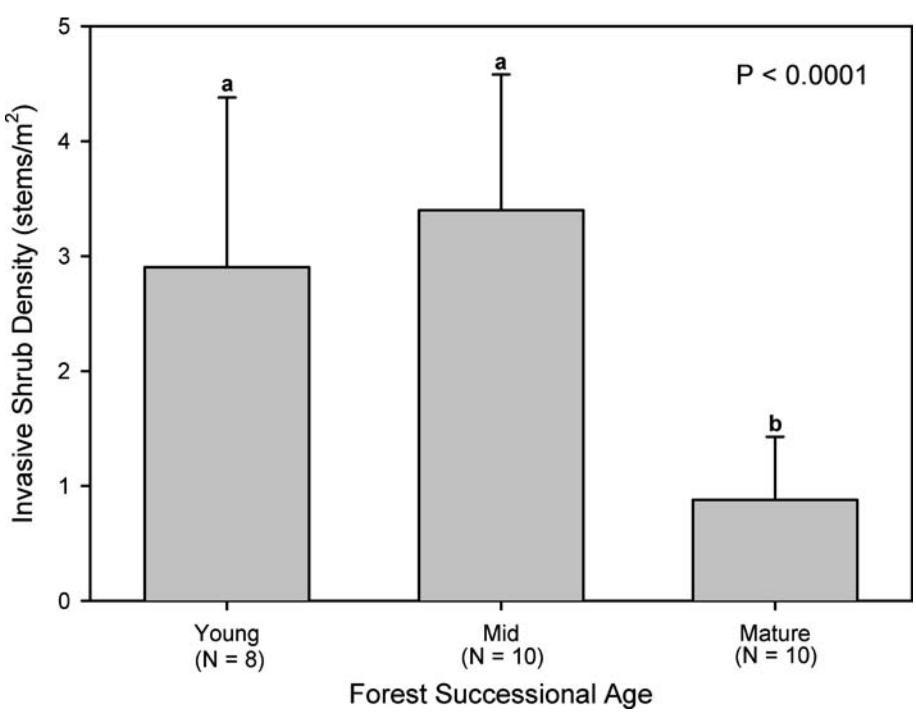

Figure 3. Mean (±1 SE) invasive shrub stem density for three forest successional ages without regard to distance to road. *N* indicates the number of transects.

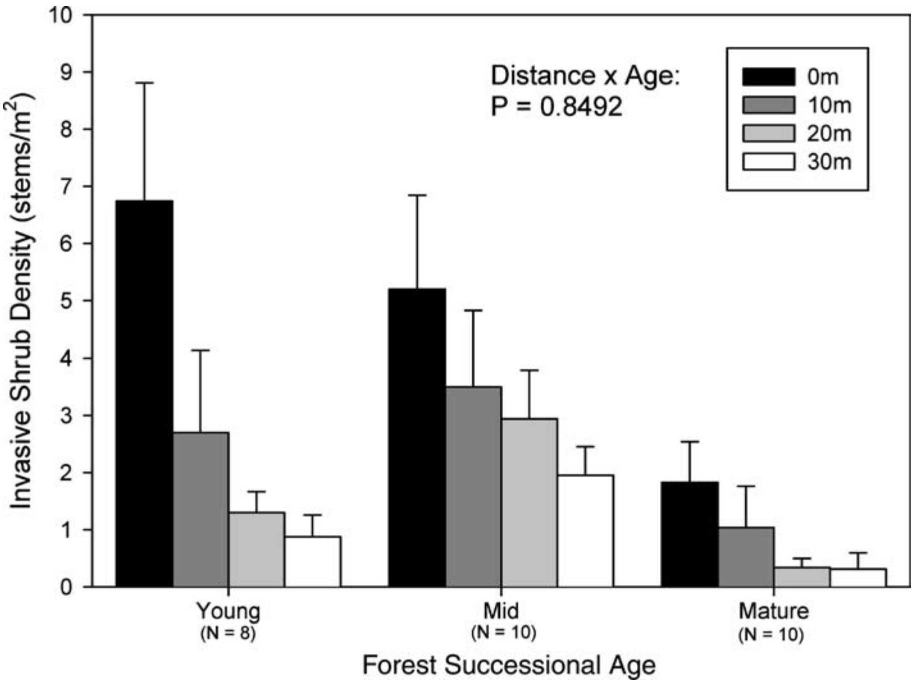

Figure 4. Mean (±1 SE) invasive shrub stem density at four distances to roads in three forest successional ages. *N* indicates the number of transects.

Table 2. Potential biotic and abiotic mechanisms that may encourage higher densities of invasive exotic plants near roads than in interior forests.

Mechanism	Potential life history stage affected	Supporting references
Biotic changes near roads		
↑ Dispersal of propagules	Seed	Tyser and Worley (1992); Parendes and Jones (2000); Gelbard and Belnap (2003)
↓ Native species	All	Gelbard and Harrison (2003); Watkins et al. (2003)
↑ Herbivory on native plant species	All	Flory (unpublished data)
↓ Litter	Seed	Haskell (2000); Gelbard and Harrison (2003); Watkins et al. (2003)
↑ Seed predation on native plants	All	Delgado et al. (2001)
Abiotic changes near roads		
↑ Light availability	All	Parendes and Jones (2000); Watkins et al. (2003)
↑ Soil moisture	All	Trombulak and Frissell (2000); Gelbard and Belnap (2003)
↑ Disturbance	Seed	Johnston and Johnston (2004); Gelbard and Belnap (2003); Truscott et al. (2005)
↑ Nutrient availability	All	Angold (1997); Trombulak and Frissell (2000); Truscott et al. (2005)

understory species. Native species may not survive as well along roadsides where runoff from pollutants and exposure to herbivores is greater (Forman and Alexander 1998; Cadenasso and Pickett 2000; Trombulak and Frissell 2000). A second possible mechanism is that exotic shrub seeds are distributed by birds and other animals in a pattern that parallels the distribution of shrubs that we found. This would mean that the density of dispersed seeds declines with increasing distance to the nearest road but that survival is unaffected by distance to road. A third possible mechanism is that exotic shrub propagules were initially distributed along roads by animals and vehicles and are invading the forest from the roadside edge. If this is the case, then we would expect shrubs at the roadside edge to be older than shrubs in the interior forest.

Does the relationship between density and distance to road differ among exotic shrub species?

Exotic shrub species have invaded eastern deciduous forest in Indiana to varying degrees with *L. maackii*, *R. multiflora*, and *L. obtusifolium* being found at the greatest densities in this study. The distribution of *L. maackii*, *L. obtusifolium*, *E. umbellata*, and *B. thunbergii* were each significantly affected by distance to the nearest road. All four of these species are fleshy-fruited and dispersed by animals. They are likely being transported predominantly by birds (Ingold and Craycraft 1983) and secondarily by deer, raccoons, and opossums (Myers et al. 2004). Many of these shrubs have been shown to negatively impact native plant communities. For example, *L. maackii* has been shown to reduce the growth and survival of native tree seedlings (Gorchov and Trisel 2003; Hartman and McCarthy 2004) and reduce native plant richness, growth, fecundity, and abundance (Gould and Gorchov 2000; Collier et al. 2002; Miller and Gorchov 2004). *L. obtusifolium* has been shown to reduce native plant diversity and forest regeneration (Merriam and Feil 2002).

Differences in patterns of invasion among shrub species is probably due to a combination of factors including life history traits (e.g. propagule production and distribution, germination success, and growth and survival requirements) and historical factors (e.g. time since introduction and geographic range of plantings). The limited abundance of some species across sites also constrained our statistical power to detect differences among species. *E. umbellata* and *L. maackii* have been widely planted in Indiana for wildlife food and cover since the early 1900s and many of the plantings occurred near roadsides. *R. multiflora* has been widely planted since the 1930s for wildlife cover, erosion control, and as ''living fences'' to confine livestock (National Park Service and U.S. Fish & Wildlife Service 2002). Its shade tolerance, broad growth and survival requirements, and dispersal by a variety of birds (National Park Service and U.S. Fish & Wildlife Service 2002) might explain the lack of a distance to road effect for this species.

Are invasive exotic shrubs less common in mature forests than in younger successional forests?

Successional age has been shown to affect exotic plant establishment in old fields in Minnesota with younger successional aged communities more susceptible to invasions and older communities more resistant (Inouye et al. 1987). Our results show that forest successional age plays a similar role in the distribution of invasive shrubs in eastern deciduous forests with invasive shrubs found in greater densities in young and mid-successional forests than mature forests. This is likely due to a combination of factors including differences in light regimes (Parendes and Jones 2000), dispersal of shrub seeds by birds (Ingold and Craycraft 1983), and land use history in forests of different successional ages (Whitney and Foster 1988).

Considering the temporal distribution of exotic shrubs over a successional gradient, we hypothesize that overall differences in shrub density can be explained by the age of the forest when exotic shrubs were first introduced and historical use of the land. Many exotic shrubs were not widely distributed until 40–60 years ago (The Nature Conservancy 2004) when mature forest stands were already well established. However, mid-successional forests were just beginning to form following abandonment of agricultural land or recovery from timber harvests and young forests did not yet exist. Exotic shrubs would have survived and grown much more successfully where they did not have to compete with existing trees or intact forests. This hypothesis could help to explain why we found fewer shrubs near the road in mature forests than young and mid-successional forests.

Light may be an important factor in the invasion of forest ecosystems since light availability is reported to vary with successional age (Levine and Feller 2004) and distance to road (Watkins et al. 2003). However, we found no interaction between forest age and distance to road (Figure 4). This indicates that roads similarly influence the distribution of invasive shrubs in young and mature forests. Light limitation may not affect exotic shrub distribution, or may be only one of many mechanisms. Propagule dispersal, disturbance, nutrient availability, herbivory, and litter depth might also be important mechanisms for determining the distribution of exotic shrubs in roadside forests (Table 2). These mechanisms have been discussed previously as possible factors determining invasive plant distribution at field – forest edges (Brothers and Spingarn 1992; Fraver 1994; Goldblum and Beatty 1999; Gehlhausen et al. 2000) and roadside edges (Gelbard and Belnap 2003; Watkins et al. 2003), but need to be evaluated experimentally to determine their relative importance. Our ongoing research seeks to clarify the mechanisms determining invasive exotic shrub distribution at roadside forest edges. Our present results suggest that conservation efforts should be focused on roadside edges in young and mid-successional forests to control the spread of invasive shrubs in eastern deciduous forests.

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Appendix

Table A. Research sites UTM Zone 16, NAD 83.

Site	Age	Location	Known land use history
1. Morgan-Monroe State Forest (Main Forest Road site)	Mature	550248 m E 4352786 m N	Agriculture until 1929
2. Eagle Creek State Park (62nd Street site)	Mature	561110 m E 4413198 m N	Selectively logged and grazed
3. Shakamak State Park (Lake Shakamak site)	Mature	479333 m E 4337259 m N	Unknown
4. Fort Harrison State Park (Office site)	Mature	583608 m E 4412963 m N	Unknown
5. Yellowwood State Forest	Mature	555536 m E 4343151 m N	Selectively logged and grazed
6. Indiana University – Griffy Woods Research and Teaching Preserve (Parking lot site)	Mid	542168 m E 4338236 m N	Agriculture until early 1970s
7. Morgan-Monroe State Forest (Beanblossom Road)	Mid	548725 m E 4349425 m N	Agriculture until 1929
8. Eagle Creek Park (Circle Drive site)	Mid	561129 m E 4413627 m N	Selectively logged and grazed
9. Betty Moore Property (private)	Mid	564395 m E 4346257 m N	Pasture until 1950s
10. Shakamak State Park (Lake Lenape site)	Mid	479371 m E 4335232 m N	Unknown
11. Indiana University – Griffy Woods Research and Teaching Preserve (Southern site)	Young	542058 m E 4338023 m N	Grazed until late 1950s
12. Crane Naval Weapons Support Center (CNWSC)	Young	510045 m E 4295610 m N	Cleared for right-of-way until mid 1970s
13. Fort Harrison State Park (Sledding Hill site)	Young	583485 m E 4413543 m N	Unknown
14. Sycamore Land Trust (Culver Property)	Young	520945 m E 4331790 m E	Abandoned agricultural land

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