

The role of landscape connectivity in assembling exotic plant communities: a network analysis

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Abstract. Landscape fragmentation and exotic species invasions are two modern-day forces that have strong and largely irreversible effects on native diversity worldwide. The spatial arrangement of habitat fragments is critical in affecting movement of individuals through a landscape, but little is known about how invasive species respond to landscape configuration relative to native species. This information is crucial for managing the global threat of invasive species spread. Using network analysis and partial Mantel tests to control for covarying environmental conditions, we show that forest plant communities in a fragmented landscape have spatial structure that is best captured by a network representation of landscape connectivity. This spatial structure is less pronounced in invasive species and exotic species dispersed by animals. Our research suggests that invasive species can spread more easily in fragmented landscapes than native species, which may make communities more homogeneous over time.

Key words: beta diversity; graph theory; habitat fragmentation; invasion; seed dispersal; spatial pattern.

INTRODUCTION

Habitat destruction is the number one threat to biodiversity worldwide (Wilcove et al. 1998), as it not only eliminates local communities but also reduces the exchange of propagules among remnant habitat patches within a landscape. Invasive plants can exacerbate the effects of habitat destruction by displacing native species through mass effects (Rouget and Richardson 2003) and competition for resources (Levine et al. 2003). The combined effects of habitat destruction and invasive species on biodiversity can be easily seen in forested landscapes of the eastern United States, where human development has created a mosaic of forested, cultivated, and urban land. These landscapes are likely to experience a large proportional change in diversity should present trends in human activity and the movement of introduced organisms continue (Sala et al. 2000).

Ecologists have long known that the size of and distance between habitat patches constrain species richness and influence the distribution of species (MacArthur and Wilson 1967). Recently, the spatial arrangement of these patches and their connectivity have also been suggested to play an important role in the assembly of communities at local and landscape scales (Gray et al. 2004, Uezu et al. 2005). Higher connectivity among habitat patches allows immigration to offset extinction events, leading to higher local species richness

but lower variability in community composition across the landscape (i.e., beta diversity; Whittaker 1972). In contrast, lower connectivity can isolate patches, leading to lower local species richness but higher species turnover across the landscape (Economio and Keitt 2008). Within this theoretical framework, it is uncertain how exotic species should respond to landscape connectivity compared to native species. Seed dispersal can have a strong influence on the assembly of exotic plant communities (Levine 2001, DiVittorio et al. 2007), but it is not clear how seed exchange among patches is affected by landscape connectivity. Most studies to address the effects of landscape connectivity on plant communities have used experimental corridors (Tewksbury et al. 2002, Haddad et al. 2003, Damschen et al. 2006). While these studies illuminate how species move through linear strips of habitat, they do not address the issue of dispersal through nonhabitat (e.g., seeds blown across a parking lot). Corridors may be the exception rather than the rule in fragmented landscapes, so it is important to understand how dispersal connections through the matrix affect community composition across the landscape. Furthermore, understanding how landscape connectivity affects spread of exotic species is essential for predicting and managing their spread.

Quantifying landscape connectivity can be problematic (Calabrese and Fagan 2004). Direct observation of movement, ideally in a designed experiment (Belisle and St. Clair 2002), is preferable but impractical over broad spatial or long temporal extents or for a large number of species. Connectivity analysis through movement simulations provides an alternative evaluation of connectivity (Vogt et al. 2008), though development and calibration of simulation algorithms can be prohibitively demand-

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ing. Network analysis, which uses graph theory, offers an approach to assessing connectivity at relatively large scales for a range of species with minimal data requirements (Calabrese and Fagan 2004).

Here, we employ network analysis to investigate how landscape connectivity affects communities of native and exotic plants with different invasiveness and dispersal modes in a patchy landscape of the eastern United States. We show that native and exotic plant communities are affected similarly by landscape connectivity, but that the spatial structure of invasive exotic species is less constrained by landscape configuration than noninvasive exotic species. We also show that seed dispersal mode (abiotic vs. biotic; gravity, wind, adhesion, or ingestion) is related to the spatial structure of forest plant communities. Our approach considers the spatial arrangement of landscape elements explicitly to elucidate patterns and thereby provide important insights into the processes that drive plant invasions in fragmented landscapes.

METHODS

Study site.—The location for this study was Antietam National Battlefield, a 1300-ha park managed by the National Park Service (Fig. 1). Antietam is located in the Appalachian Ridge and Valley province in Washington County, Maryland, USA and was probably mostly forested prior to European settlement. A central goal of park management is to maintain the landscape at it was during the famous Civil War battle of 1862. As a result, the park preserves a mixture of farmland, pastures, and woodlands, and is an ideal environment for studying connectivity within a fragmented landscape.

Plant data.—Most of the plant data were originally collected as part of a vascular plant inventory for parks in the National Capital Region (Engelhardt 2005). Forty-six 0.04-ha plots from the vascular plant inventory were randomly assigned to patches of upland hardwood forests across the park. We supplemented the inventory data with an additional 12 plots that were strategically located in smaller forest patches to achieve a wider range of patch size and connectivity. Presence of every species was recorded in each plot and species that were present in more than one plot were retained for analysis. We grouped plants by their nativeness and further grouped exotic species by their invasiveness according to the WeedUS database (Swearingen 2007). Exotic species are classified as invasive species if they grow and spread quickly and cause environmental or economic harm. Because a species' invasiveness differs geographically, we only included plants that were defined as invasive in the State of Maryland (Swearingen 2007). Finally, we placed species into one of four dispersal groups: wind, ingestion, adhesion, and unassisted dispersal. Dispersal mode of each species was classified using the primary literature, or, if necessary, deduced from congeneric dispersal mode or seed or fruit morphology. A few species had other dispersal modes (e.g., hoarded nuts) or remained

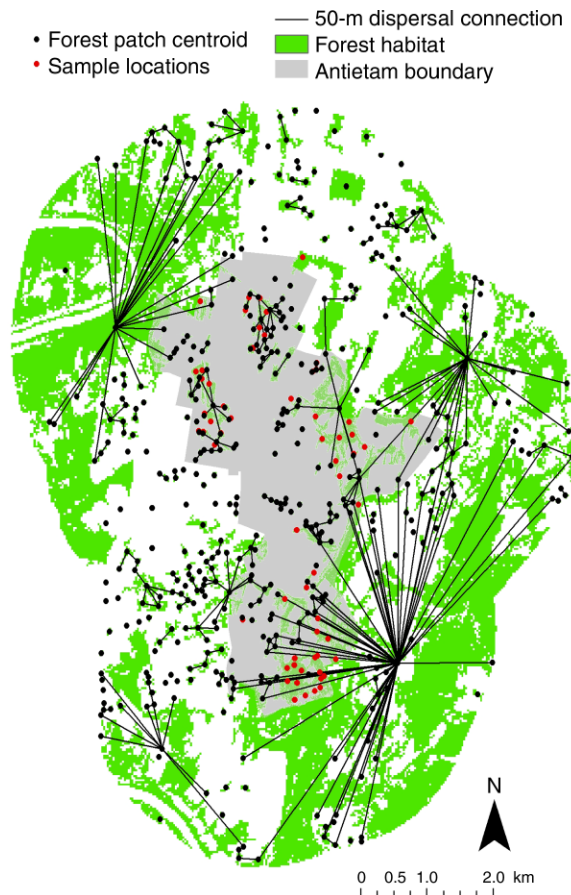


FIG. 1. Forest map and network representation of Antietam National Battlefield, Maryland, USA, and 2-km surrounding buffer. Forest patches connected by black lines are assumed to be connected via seed dispersal based on a 50-m maximum dispersal distance.

unclassified and these were excluded from the analysis. We used a chi-square test to test for differences in dispersal mechanisms between native, invasive exotic, and noninvasive exotic plant groups.

Network analysis.—We calculated network distance between every pair of sample locations to assess connectivity and potential seed dispersal between plots. Network distance is based on graph theory, a branch of mathematics that deals with connectivity and flow in networks (Harary 1969). Recently, graph theory has been used to measure landscape connectivity in a variety of ecological systems (Urban and Keitt 2001, Rhodes et al. 2006, Minor and Urban 2007). In a landscape network, habitat patches are said to be connected to each other if dispersal is possible between them. This dispersal may occur in a stepping-stone fashion over multiple generations, but the implication is that gene flow and colonization are possible between connected patches. Groups of interconnected patches form components; by definition, dispersal is possible within a component but not between components. Visually,

habitat patches are represented by dots at their centroids and dispersal connections are represented by lines between pairs of patches (Fig. 1). Drawing lines between connected habitat patches offers a quick visual assessment of the landscape and makes it easy to determine whether the focal species could move from one side of the landscape to the other.

If available, empirically derived dispersal data can be used to assign connectivity between pairs of patches. More often, however, connections are assigned based on limited knowledge of a species' dispersal ability (Minor and Urban 2008). We tested a range of connection distances and found that, in general, each test demonstrated maximum explanatory power with a connection distance of 50 m. Similarly, published data suggest that forest patches within 50 m of each other may be considered connected for plants (Geertsema 2005, Soons et al. 2005). Therefore, we created our habitat network by connecting every pair of habitat patches within 50 m of each other (Fig. 1). Each pair of plots was assigned a network distance of 0, 1, or 2, based on network topology. If two plots were located in the same forest patch, they were assigned a distance of 0. If two plots were located in different forest patches but in the same network component, they were assigned a distance of 1. Finally, if two plots were located in different components, they were assigned a distance of 2. This allowed us to contrast plots that were not separated by the matrix (i.e., in the same forest patch) with plots that were separated by the matrix but within dispersal distance (same component) to plots that were not connected by dispersal at all (different components). By using network distance in a Mantel's test (described in *Methods: Mantel tests*), we were able to ask whether plots that were in the same habitat patch were more similar to each other in species composition than plots in different habitat patches, and whether plots that were in the same component were more similar to each other than plots in different components. In other words, a significant Mantel correlation between species turnover and network distance would indicate that the community is structured, at least partially, by landscape connectivity.

Environmental variables.—We gathered a set of environmental variables for each plot, including hill slope, solar radiation, normalized difference vegetation index (NDVI), soil pH, and forest patch size. Hill slope and solar radiation were calculated from a 30-m digital elevation model. Solar radiation included an estimate of direct and diffuse radiation over the entire year based on topographic shading (Pierce et al. 2005). Normalized difference vegetation index (NDVI) was developed from Landsat imagery (30-m resolution) and used as an indicator of biomass and greenness of the forest canopy (Carlson and Ripley 1997). Soil pH was obtained from digital soil maps of Washington County developed by the National Cooperative Soil Survey. Finally, forest patch size was measured from a land cover map created using Ikonos satellite imagery (4-m resolution). The

Ikonos imagery (and subsequent connectivity analysis) was clipped to a 2-km buffer around the park boundary to better characterize connectivity for the park within its broader context.

Mantel tests.—We used Mantel tests (Smouse et al. 1986) to examine changes in plant community composition relative to spatial location and environmental variables. A simple Mantel test computes a correlation between two distance matrices. For example, one matrix might represent spatial distances between pairs of plots while the other represents differences in species composition. These tests can be used to determine whether plots that are close together in space are also similar in species composition, or whether plots that are similar environmentally are also similar in species composition. A partial Mantel test can be used to examine the effects of one matrix (e.g., spatial distance) on another (e.g., difference in species composition) while controlling for the variation in a third matrix (e.g., environmental variables) (Goslee and Urban 2007).

We used four distance or dissimilarity matrices in the Mantel tests: Euclidean distance, network distance, species dissimilarity, and environmental dissimilarity. Euclidean and network distances represent alternate views of spatial distance between pairs of plots. Euclidean distance is simply straight-line distance between each pair of plots, while network distance considers whether each pair of plots is potentially connected via seed dispersal. Species dissimilarity was calculated using the Bray-Curtis dissimilarity index. The environmental dissimilarity matrix was computed as Mahalanobis distance between environmental variables on each pair of plots (Orloci 1978). To assess the relative importance of the two distance measures in structuring the plant communities, we calculated a Mantel ratio for each plant group: the fragmentation sensitivity index. This ratio was simply the Mantel correlation for network distance divided by the Mantel correlation for Euclidean distance. High values represent cases where spatial proximity alone is inadequate to explain community structure, indicating that fragmentation and connectivity may be altering the spatial structure of plant communities.

Simple Mantel tests were used to identify the important environmental variables for each plant group; variables with a P value ≤ 0.10 were retained for inclusion in the environmental dissimilarity matrix. Partial Mantel tests allowed us to ask whether plots that were close together in space or connectivity were also similar in species composition after controlling for the effects of environmental variables. We also asked the inverse: whether plots that were similar environmentally were also similar in species composition after controlling for spatial autocorrelation.

RESULTS

Of the 208 plant species included in the analysis (Appendix), 61 were exotic species (Table 1). Factors

TABLE 1. Fragmentation sensitivity index for plant groups categorized by nativeness, invasiveness, and dispersal mechanism.

Plant group	Number of species	Environmental variables†	Fragmentation sensitivity index‡
Native species			
All native species	147	NDVI, pH, patch size	1.45
Exotic species			
All exotic species	61	slope, NDVI, patch size	1.75
Noninvasive exotics	16	NDVI	3.36
Invasive exotics	45	slope, radiation, NDVI, patch size	1.54
Unassisted dispersal	22	NDVI	5.00
Wind dispersal	10	NDVI, pH	1.47
Ingestion dispersal	14	slope, radiation, patch size	0.93
Adhesion dispersal	8	slope, radiation, pH, patch size	0.04

Note: NDVI stands for the normalized difference vegetation index.

† Variables with $P \leq 0.10$ in simple Mantel tests were included in the environmental dissimilarity matrix.

‡ Fragmentation sensitivity index is the partial Mantel correlation for network distance divided by the partial Mantel correlation for Euclidean distance. Larger values indicate greater sensitivity to landscape fragmentation.

governing exotic plant community assembly as a whole appeared to be very similar to the factors governing native plant communities (Fig. 2). Neither group showed a significant relationship between environmental turnover and species turnover ($P > 0.05$; Fig. 2), while both groups showed a spatial pattern after removing the effects of environmental variability (exotic species, $P < 0.001$; native species, $P < 0.001$; Fig. 2). Species turnover of both groups was more strongly correlated with network distance than with Euclidean distance as indicated by non-overlapping 95% confidence limits (Fig. 2).

When exotic plants were split into invasive and noninvasive species, two different patterns emerged (Fig. 3). Turnover of both invasive and noninvasive exotics was related to environmental turnover (invasive species, $P = 0.05$; noninvasive species, $P = 0.001$; Fig. 3) and network distance (invasive species, $P < 0.001$; noninvasive species, $P < 0.001$; Fig. 3). However, turnover of noninvasive species was more strongly related to environmental turnover and network distance than was turnover of invasive species as indicated by nonoverlapping 95% confidence limits (Fig. 3). Overall, noninvasive plant communities appeared to be more highly structured—both environmentally and spatially—than were invasive plant communities.

Exotic species responded differently to landscape connectivity dependent on their dispersal mode (Fig. 4). Network distance was most strongly correlated with changes in community composition for abiotic dispersers (unassisted, Mantel $r = 0.30$, $P < 0.001$; wind, Mantel $r = 0.22$, $P < 0.001$) and less correlated with turnover of communities with animal-assisted dispersal (ingested, Mantel $r = 0.13$, $P = 0.02$; adhesive, Mantel $r = 0.007$, $P > 0.05$; Fig. 4). Turnover of adhesive dispersers was not correlated with network distance at all. Conversely, Euclidean distance was least correlated with turnover for the unassisted dispersal group (Mantel $r =$

0.06, $P = 0.04$) and more strongly correlated with the other three dispersal groups (wind, Mantel $r = 0.15$, $P < 0.001$; ingested, Mantel $r = 0.14$, $P < 0.001$; adhesive, Mantel $r = 0.14$, $P = 0.008$; Fig. 4).

The fragmentation sensitivity index indicates the importance of habitat connectivity for each plant group. The exotic plants with unassisted dispersal had the highest fragmentation sensitivity index followed by the noninvasive exotic plants, while the two plant groups that are dispersed by animals had the lowest fragmentation sensitivity index (Table 1).

The proportion of species that disperse primarily by abiotic (e.g., wind, gravity) rather than biotic (e.g.,

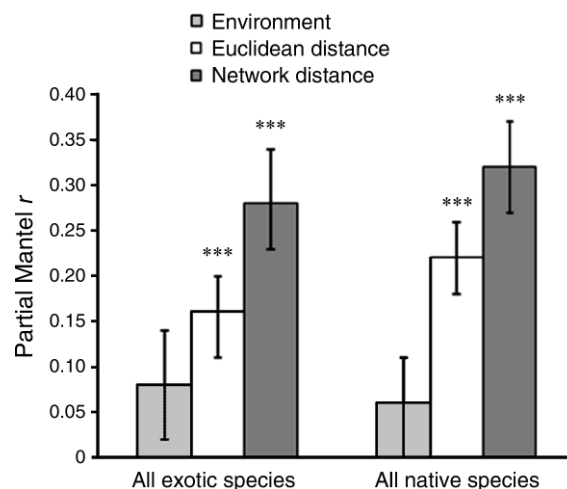


FIG. 2. Partial Mantel correlations for exotic species and native species. Network distance (i.e., landscape connectivity) is the most important factor in assembling both exotic and native species, Euclidean distance between samples is less important, and differences in environmental variables (e.g., soil pH) between samples show no significant effect on plant communities. Error bars represent 95% confidence intervals for correlation coefficients.

* $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$.

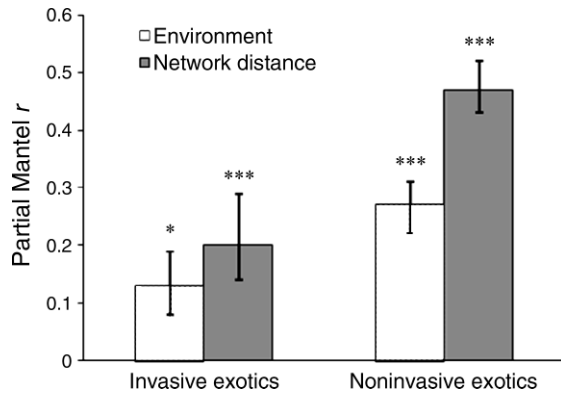


FIG. 3. Partial Mantel correlations for invasive and noninvasive exotic species; error bars represent 95% confidence intervals for correlation coefficients. Noninvasive exotics are more structured than invasive exotics, both by environmental factors and by landscape connectivity.

* $P < 0.05$; *** $P < 0.001$.

ingestion, adhesion) mechanisms was not different between noninvasive exotic and native species ($\chi^2 = 0.13$, $P = 0.72$), but was different between invasive exotic and native species ($\chi^2 = 3.86$, $P = 0.05$). A greater proportion of invasive species dispersed through biotic means (Fig. 5).

DISCUSSION

We quantified spatial turnover among forest plant communities with two different measures of distance: Euclidean distance vs. network distance. By contrasting these two distance measures, we can infer whether dispersal limitations play a role in structuring exotic plant communities (correlation with Euclidean distance) and whether community composition is related to the spatial configuration of habitat (correlation with network distance). Partial Mantel tests allowed us to

account for variability in environmental conditions across the landscape so that pure distance effects could be separated from environmental effects. Every plant group in this analysis showed a significant spatial pattern after environmental variability was removed, suggesting a dispersal limitation for all groups. Furthermore, community turnover was related more to network distance than Euclidean distance, which is compelling evidence that the network is an accurate representation of plant movement across the landscape, and that landscape connectivity is an important factor in assembling native and exotic plant communities in fragmented landscapes.

Dispersal limitation is often thought to constrain and structure ecological communities (Ehrlén and Eriksson 2000, Hubbell 2001), particularly in fragmented landscapes or island communities (MacArthur and Wilson 1967, McEuen and Curran 2006, Pharo and Zartman 2007). It is unclear whether exotic plants suffer this effect, since it is commonly believed that habitat fragmentation encourages the spread of exotic species (Pyle 1995, With 2004, Yates et al. 2004). While many exotic plants thrive on the forest edges that are prevalent in fragmented landscapes (McDonald and Urban 2006), and some disperse better than average (Vila and D'Antonio 1998, Truscott et al. 2006), our results suggest that exotic species as a group face the same dispersal limitations and environmental constraints as do native species (Fig. 2). However, our results indicate that all exotic species are not equal. The partial Mantel tests suggest that invasive species are less limited by both dispersal and their environment than are other exotic species (Fig. 3). In other words, they are invasive because they disperse more successfully in fragmented landscapes and are not constrained by specific habitat conditions.

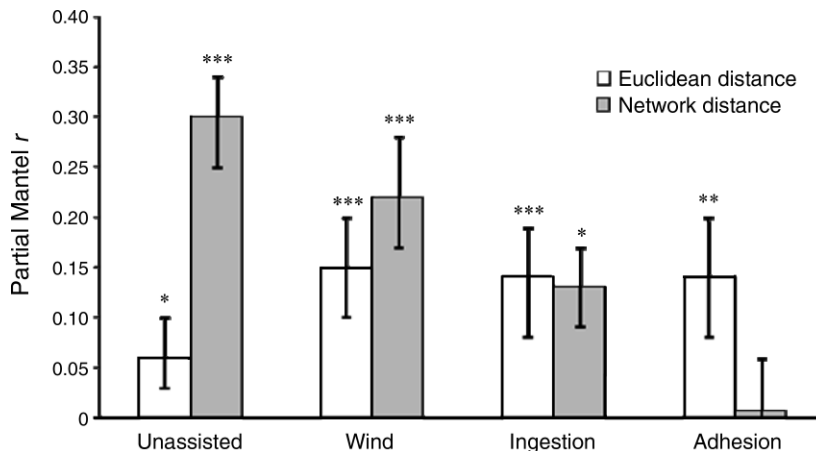


FIG. 4. Separating spatial patterning of exotic species by dispersal mode reveals that landscape connectivity (i.e., network distance) is more important for structuring species dispersed by abiotic means (unassisted and wind) than species dispersed by biotic means (ingestion or adhesion); error bars represent 95% confidence intervals for correlation coefficients.

* $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$.

We examined the prevalent dispersal modes for each plant group to explore why the spatial structure of invasive exotic species was weaker than the spatial structure of both noninvasive exotic species and native species and found that a greater proportion of invasive species dispersed through biotic means (Fig. 5). Furthermore, dispersal mode appeared to be related to fragmentation sensitivity of exotic plants. Exotic species with unassisted and wind-dispersed seeds had a relatively high fragmentation sensitivity index, indicating a stronger relationship with network distance and a greater sensitivity to fragmentation. Conversely, exotic species with animal-dispersed seeds (by ingestion or adhesion) had a low fragmentation sensitivity index. Incidentally, native species in our plots also showed a higher fragmentation sensitivity index for abiotic dispersers than for animal-assisted dispersers (data not shown).

These results suggest that landscape connectivity may be more important to the spread of species with abiotic dispersal than for animal-dispersed species, which concurs with previous studies indicating that animal-dispersed plants are less likely to be dispersal limited in fragmented landscapes (Buckley et al. 2006, Aronson et al. 2007). However, the literature on dispersal ability of different plant groups is limited and conclusions are mixed. Some studies suggest greater movement for animal-dispersed species (Matlack 1994, Honnay et al. 2002, Takahashi and Kamitani 2004), others suggest that animal-dispersed species may suffer dispersal limitation in fragmented habitats (Grashof-Bokdam 1997), and still others indicate that dispersal mode does not affect a species' sensitivity to habitat isolation (Dupre and Ehrlen 2002). In Antietam National Battlefield, exotic species with adhesive dispersal mechanisms seemed especially unaffected by the configuration of the forest habitat. The distribution of this group in our study system is likely to result in part from deer populations moving easily between forest and field, but also from increased probability of survival in nonforest matrix. Many of the exotic adhesive plants in this study (e.g., *Arctium minus*, *Bromus sterilis*) are species often found in fields and open areas. It would be illuminating to repeat our analyses without these species, but we do not currently have enough information about the environmental constraints of each species to distinguish between generalist and specialist exotic plants. Such information, which is clearly needed for invasive exotic species (Evangelista et al. 2008), would allow us to remove those generalist invasives that do not have a fragmented distribution through the study area.

Most studies that seek to explain community turnover in space indicate that variability in environmental conditions drives community assembly (Tuomisto et al. 2003). Our data on plant communities, however, show that distance among habitat patches, rather than environmental variables, explained more of the variation in species turnover. We offer two possible explanations

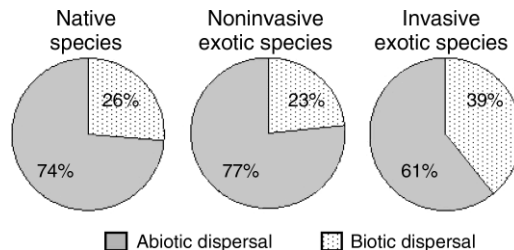


FIG. 5. Relative to native and noninvasive exotic species observed at the site, biotic dispersal is more common for invasive exotic species. This suggests a mechanism by which invasive species may be less constrained by habitat fragmentation.

for this pattern. First, the range of variability in sampled environmental conditions was relatively small since the sampling locations were selected in a way to ensure their similarity (i.e., all were in upland forests). Still, the topography of the study areas was variable and environmental conditions were not uniform. A second more plausible reason for the strong spatial pattern in community composition is that our study took place in a fragmented landscape rather than the intact landscape setting of most previous studies. Habitat fragmentation is likely to lead to isolation of habitat patches and therefore dispersal limitation of species in those habitats. Dispersal limitations, by default, lead to spatial patterns in community composition (Hubbell 2001).

It has been argued that spatial pattern alone is insufficient to explain ecological process (Cale et al. 1989). This may be true with traditional spatial analysis, as many environmental phenomena display a predictable pattern with Euclidean distance (e.g., forest fire, harvest history) and it can be difficult to tease apart confounding factors. However, none of the environmental variables showed even a weak relationship with network distance (data not shown), refuting the idea that the observed spatial patterns reflect environmental effects that covary with distance.

Ecological studies such as ours that attempt to understand species' distributions may suffer from sampling biases. Species detection is imperfect, particularly for rare and inconspicuous species, and every location on the landscape cannot be sampled. However, we sought to minimize these potential problems in two ways. First, we followed the sampling method proposed by Peet et al. (1998), which uses nested plots and species-area curves to ensure that plots are large enough to detect 90% of species in an area. Second, we sampled our study area as thoroughly as possible. Our sample plots covered about 10% of the forested area in Antietam National Battlefield, and an even greater percentage of the upland forests which were the focus of this study. In addition, while roughly three quarters of our sample locations were randomly chosen, we placed the remaining sample plots in a way to maximize our coverage of the area and to ensure adequate sampling of

smaller and more isolated habitat patches. Finally, although some statistical methods interpret unsampled locations as absences, Mantel tests focus only on the spatial pattern of sampled locations and therefore may help to minimize those biases.

Our study used network analysis to assess landscape connectivity within a fragmented forested landscape and to evaluate how that connectivity may affect turnover of invasive exotic species relative to noninvasive exotic and native species. Our data suggest that forest connectivity is less of a constraint for invasive species than for exotic noninvasive species and native species, which implies that exotic invasive species have a greater ability to disperse in a patchy environment or to survive in the agricultural matrix between forested patches. As a consequence, differences in species dispersal mechanisms and habitat preferences may favor the spread of invasive species relative to native species in a fragmented landscape. Therefore, if we are to predict the ecological impacts of invasive species and if we hope to protect native biodiversity in forested landscapes, we will need to better understand species traits that relate to dispersal ability and species response to fragmentation.

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APPENDIX

Dispersal mode of plants found in Antietam National Battlefield (*Ecological Archives* E090-126-A1).