Gypsy moth response to landscape structure differs from neutral model predictions: implications for invasion monitoring

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Abstract Simulations of dispersal across computer-generated neutral landscapes have generated testable predictions about the relationship between dispersal success and landscape structure. Models predict a threshold response in dispersal success with increasing habitat fragmentation. A threshold is defined as an abrupt, disproportionate decline in dispersal success at a certain proportion of habitat in the landscape. To identify potential empirical threshold responses in invasion success to landscape structure, we quantified the relationship between progression of the gypsy moth (*Lymantria dispar*) invasion wave-front across Michigan (1985–1996) and the structure of the Michigan landscape using two indices of invasion success and six landscape metrics. We also examined the effect of scale of analysis and choice of land cover characterization on our results by repeating our analysis at three scales using two different land cover maps. Contrary to simulation model predictions, thresholds in invasion success did not correspond closely with thresholds in landscape structure metrics. Increased variation in invasion success indices at smaller scales of analysis also suggested that invasion success should be studied at larger spatial extents (≥ 75 km^2) than would be appropriate for characterizing individual dispersal events. The predictions of individual dispersal models across neutral landscapes may have limited applications for the monitoring and management of vagile species with excellent dispersal capabilities such as the gypsy moth.

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Abbreviations

p_{crit}	Percolation critical threshold, or proportion of habitat at which a disproportionate decline in dispersal success is observed
p	Proportion of habitat

Introduction

The relationship between rate of invasive species movement and landscape structure remains poorly understood (Hunter 2002; King and With 2002) in part because empirical studies of the topic would require invasion monitoring data collected over large spatial extents and long time periods. In the absence of such monitoring data, many invasion ecologists have simulated the invasion process across computer-generated landscapes to generate testable predictions about the relationship between invasion (or dispersal) success and landscape structure (Schwartz 1992; Collingham et al. 1996; Malanson and Cairns 1997; With and King 1999; Collingham and Huntley 2000). These simulation models predict a threshold response in dispersal success with increasing habitat fragmentation. A threshold is defined as a sudden, disproportionate decline in dispersal success at a certain proportion of habitat called the percolation critical threshold, or p_{crit} (With and Crist 1995; Newcomb Homan et al. 2004). A threshold response is thought to indicate that habitat fragmentation has begun to impede dispersal (O'Neill et al. 1988). Below p_{crit}, the negative effects of habitat fragmentation compound that of decreasing habitat, leading to a sudden, dramatic decline in successful dispersal events.

Analysis of neutral landscapes (computer generated random or fractal landscapes) has shown that several measures of landscape structure also exhibit critical thresholds as the proportion of habitat (p) decreases in a given landscape (With and King 1999). For example, connectivity of habitat patches in a landscape may decline suddenly once a certain amount of habitat loss has occurred (With and King 1999) because large habitat patches that span most of the landscape and aid dispersal begin to break down into many small habitat patches (O'Neill et al. 1988; Andren 1994; With and Crist 1995). To identify the aspect or aspects of a heterogeneous landscape that are most important in determining dispersal success, values of p_{crit} in dispersal success are compared with those of landscape structure metrics (e.g. connectivity). With and King (1999) compared thresholds in simulated dispersal across neutral landscapes with thresholds in six measures of

heterogeneity for those landscapes (connectivity, average distance between patches, size of largest patch, total number of patches, total length of edges, and lacunarity). Only lacunarity, a measure of landscape "gappiness", exhibited a critical threshold similar to that of dispersal success; lacunarity increased abruptly when dispersal success declined abruptly at $p = ~0.05–0.1$.

Neutral landscape models may provide valuable guidelines for predicting and controlling the spread of invasive species (King and With 2002). However, simulation model results must first be compared with empirical dispersal data. In order to test the predictions of neutral landscape models, measurements of invasion success must be collected systematically across the entire landscape throughout the course of an invasion. One such monitoring program tracked the invasion of gypsy moths (*Lymantria dispar*) across Michigan (Gage et al. 1990; Yang et al. 1998). The gypsy moth is an exotic insect native to Europe that has caused extensive defoliation across much of the eastern United States since its introduction to Massachusetts in 1868 (Elkinton and Liebhold 1990). The first breeding population of gypsy moths in Michigan was the result of an independent introduction in 1954 and a second possible reintroduction occurred near Midland in the 1980s (O'Dell 1955; Hanna 1981). Gypsy moths quickly spread across the state, reaching most areas of the Lower Peninsula by the early 1990s and the western Upper Peninsula by the late 1990s (Lele et al. 1998; Yang et al. 1998).

Sharov et al. (1999) used this Michigan gypsy moth dataset to examine the effect of landscape composition on rate of invasive spread and found that rate of spread was positively correlated with forest susceptibility (percentage of land area with >50% tree basal area in preferred host tree species). However, their study did not explore the relationship between landscape structure (e.g. habitat patch size and spacing) and rate of spread because adequate statewide land cover maps were not available at the time (Sharov et al. 1999). The goal of this study was to use recent statewide landcover maps to quantify the relationship between progression of the gypsy moth invasion wavefront and the structure of Michigan's landscape. Our objectives were to (1) identify critical

thresholds in invasion success and landscape structure with decreasing proportion of habitat, (2) compare empirical critical threshold with those predicted by dispersal models, (3) explore the effect of scale on our results by repeating all analyses at three spatial scales, and (4) explore the effect of habitat characterization on our results by using two different classified land cover maps of Michigan to calculate landscape structure metrics.

Methods

Invasion data

Pheromone-baited traps were placed in sections 8 and 26 of every township in Michigan over 12 years from 1985 to 1996 (Gage et al. 1990; Yang et al. 1998). At each trap, the total annual male moth catch and the trap location in UTM coordinates were recorded. Traps were monitored between 1985 and 1996 in Michigan's Lower Peninsula and between 1986 and 1996 in Michigan's Upper Peninsula. A subset of 1,090 traps was selected for this analysis from over 3,000 placed in a regular grid across the state. Only traps operated all 12 years at the same location were selected to avoid change of support in the analysis (Isaaks and Srivastava 1989). Traps located in the Upper Peninsula were excluded because the invasion was still in the early stages by 1996.

Land cover data

Analyses of landscape structure were repeated using two 30 m resolution raster images representing the land cover of Michigan. The first map (Map 1) was the Michigan Resource Information System statewide land cover classification (Michigan Department of Natural Resources 1999). Map 1 was derived from 1978 color-infrared aerial photographs and depicts 52 categories of urban, agricultural, wooded, wetland, and other land cover types. The second map (Map 2), the 2001 Michigan Gap Analysis Project land cover image created for the Michigan Department of Natural Resources (Donovan et al. 2004), was derived from the classification of Landsat Thematic

Mapper 5 and 7 imagery collected during spring, summer, and fall from 1999 to 2001. This map depicts 32 categories of urban, agricultural, wooded, wetland, and other land cover types.

Gypsy moths are polyphagous herbivores that prefer oaks (*Quercus* spp.) and aspens (*Populus* spp.) but will eat a wide variety of other deciduous tree species as well (Elkinton and Liebhold 1990). Therefore, each land cover map was reclassified so that all deciduous forest cover classes were combined to represent gypsy moth habitat. All remaining types of land cover were considered unsuitable for gypsy moths. This simple reclassification allowed us to explore broad patterns of structure in gypsy moth habitat across the landscape without complicating the analysis with more detailed (and often less accurately classified, Donovan et al. 2004) distinctions among deciduous tree communities or species (Li and Wu 2004).

Scale of analysis

We repeated analyses of landscape structure and invasion success at three different spatial extents to assess the effect of scale (Garnder et al. 1989; Doak et al. 1992; Li and Wu 2004). Because female gypsy moths are incapable of flight, it was assumed that the invasion wavefront was driven largely by wind-dispersed larvae that are passively transported up to ~40 km away from their hatching site (Elkinton and Liebhold 1990). Although a small percentage of larvae may actually survive such a long trip, occasional long-distance dispersal events (in combination with human-aided dispersal of egg masses) likely explain the high observed expansion rates of >20 km/year (Taylor and Reling 1986; Liebhold et al. 1992). In Michigan, average rates of spread were reported to be 15.8 km/year (SD = 25.4 km/year) and those estimates ranged between –30 and 85 km/year (Sharov et al. 1999). Therefore, we chose analysis windows of 75, 45 and 15 km on each side to represent spatial extents that were (respectively) slightly smaller than the reported maximum estimated dispersal distance, approximately half the maximum dispersal distance reported, and approximately equal to the average dispersal distance reported.

At each scale of analysis, the Lower Peninsula of Michigan was clipped into multiple subsections using square-shaped analysis windows (the shape required for lacunarity calculations). At each scale of analysis, the maximum number of windows that could fit inside the Lower Peninsula of Michigan were created and aligned so as to maximize the number of traps included in the analysis. Altogether, 12 boxes 75 km on each side, 37 boxes 45 km on each side, and 207 boxes 15 km on each side were created and used to clip each land cover map.

Characterizing invasion success and landscape structure

Sharov et al. (1999) previously reported that rate of spread was positively correlated with forest susceptibility (a measure of landscape composition). However, their scale of analysis did not match the scale of landscape structure analysis chosen for this study. Therefore, we recalculated measures of invasion success at the three scales of analysis mentioned above so that a valid comparison with our measures of landscape structure could be made.

Time series in total annual catch at each trap revealed a dramatic increase (from tens to hundreds or thousands) in the number of moths caught at most traps once about 25 individuals had been caught in a given year. Also, Sharov et al. (1999) found that estimated rates of spread were highly variable when thresholds of 30 or more individuals were used to define the location of the invasion wavefront. Therefore, year of colonization was defined as the year in which total trap catch reached 25 or greater individuals. To obtain a rough estimate of how far away each trap was located from the initial introduction site in Michigan, the distance from each trap to a trap located near the Midland and Bay County border was calculated. At each scale of analysis, traps were grouped by analysis window and two indices of invasion success were calculated. The first index was a measure of invasion rate and was defined as the distance of a trap from the original introduction site divided by years to colonization. These values were then averaged across all traps

in an analysis window. The second index was a measure of invasion variability across a landscape defined as the range in years to colonization among all traps in an analysis window.

Analysis windows were used to clip out subsections of both land cover maps for landscape metric calculations. Each clipped land cover raster file was converted to an ascii text file and imported into the software package APACK Version 2.22 (Mladenoff and DeZonia 2002). Within APACK, proportion of gypsy moth habitat (p) and six landscape structure metrics similar to those used by With and King (1999) were calculated for each subsection of the landscape: lacunarity, total number of habitat patches, size of largest habitat patch, total length of edges, average area per patch, and centroid connectivity. Lacunarity was calculated using moving window sizes of 1, 5, 10, 50, 100, 150, 200, and 250 cells.

Detecting critical thresholds in invasion success and landscape structure

Once all indices of invasion success and landscape structure were calculated for each analysis window, index values were plotted individually against p to identify potential threshold responses to decreasing proportion of habitat in the landscape. To identify critical threshold values, we searched for large, sudden declines or increases in the slope of each plot. Two methods typically used to identify ecological thresholds include piecewise regression (Neter et al. 1985; Newcomb Homan et al. 2004) and reduction of deviance (Qian et al. 2003). However, we did not want to identify thresholds visually, so we chose not to use piecewise regression. We did not use the reduction of deviance method because our sample size for the 75 km scale of analysis (12 analysis windows) was too small. Instead, we employed a spline-like method that estimated the slope of a regression line fit to a series of subsetted points in each plot. We began in a manner similar to reduction of deviance by creating all possible subsets of 5, 11, or 31 (at the 75, 45, and 15 km scales of analysis, respectively) successive points for each plot; for example, the first few subsets

for a 75 km scale plot would include points 1–5, 2–6, and 3–7. We then obtained a rough estimate of the derivative at the midpoint of each subset by estimating the slope of a simple linear regression line through the subset of points. Once slopes had been estimated for all subsets of points in a given plot, we selected the first subset (if any) for which slope values fell consistently below (if dependent values were decreasing) or rose above (if dependent values were increasing) 10% of the maximum slope for the plot. Ten percent of the maximum slope was chosen as a threshold cutoff value after inspecting other studies of ecological threshold responses to changes in proportion of habitat (With and King 1999; Newcomb Homan et al. 2004). We identified p_{crit} as the proportion of habitat associated with the midpoint of the selected subset. Some landscape metrics displayed a peaked response to changes in proportion of habitat in the landscape. For such peaked plots, p_{crit} was defined as the value of p corresponding with the subset midpoint at which the sign of the regression slope switched consistently from positive to negative (With and King 1999). For all plots, inverse predictions were made to calculate standard errors and 95% confidence intervals for each threshold (Neter et al. 1985).

Results

Proportion of gypsy moth habitat in an analysis window ranged from: 0.13–0.54 and 0.15–0.50 for Maps 1 and 2 in 75 km landscapes; 0.09–0.55 and 0.11–0.58 for Maps 1 and 2 in 45 km landscapes; 0.004–0.71 and 0.02–0.70 for Maps 1 and 2 in 15 km landscapes. In concurrence with Sharov et al. (1999), we found that invasion rate increased with increasing p at the 75 and 45 km scale of analysis (Fig. 1a, b). At the 15 km scale of analysis, invasion rate increased with increasing p, but with much more variability (Fig. 1c). Because invasion success patterns were largely similar between land cover maps, only Map 1 results are presented. Invasion variability within an analysis window decreased with increasing p across all scales of analysis (Fig. 1d–e).

The gypsy moth invasion wavefront typically exhibited either a linear response to decreasing proportion of habitat across the Michigan landscape or a threshold response at a higher proportion of habitat that predicted by simulation models (Table 1, Fig. 1). No critical thresholds in invasion rate were detected at the 75 km scale of analysis (Table 1). A threshold was detected at $p_{\text{crit}} = {\sim}0.2$ for both maps at the 45 km scale of analysis (Table 1, Fig. 1). A threshold was detected at $p_{\text{crit}} = 0.1$ for Map 2 data (Table 1). In general, invasion success thresholds ($p_{\text{crit}} = {\sim}0.1\text{–}0.23$) occurred at a slightly higher proportion of habitat than thresholds predicted by With and King's (1999) neutral landscape models ($p_{\text{crit}} = {\sim}0.05\text{–}0.1$). All thresholds in invasion rate detected were subtle and certainly not as abrupt as critical thresholds in simulated invasions; in addition, confidence intervals were wide ($\pm0.47\text{–}0.9$).

Most thresholds in invasion variability were detected at $p_{\text{crit}} = 0.42\text{–}0.5$ (Table 1). At the 45 km scale of analysis, a threshold was detected using Map 2 at $p_{\text{crit}} = 0.24$. All invasion variability thresholds ($p_{\text{crit}} = {\sim}0.24\text{–}0.5$) occurred at a much higher proportion of habitat than thresholds predicted by With and King's (1999) neutral landscape models ($p_{\text{crit}} = {\sim}0.05\text{–}0.1$). Similar to invasion rate thresholds, invasion variability thresholds were not as sudden as critical thresholds in simulated invasions and confidence intervals were quite large ($\pm0.87\text{–}4.7$).

Lacunarity decreased with increasing p in the landscape (Figs. 2–4). Total number of patches exhibited a peaked response to changing proportion of habitat. Total length of edges increased with increasing proportion of habitat and then leveled off. Size of largest patch, average area per patch, and connectivity increased with increasing p. Most landscape metrics exhibited a threshold response to changing p with both land cover maps and at all three scales of analysis (Table 1 and Figs. 2–4). Overall behavior of landscape metrics in response to increasing p was similar between land cover maps; therefore, only Map 1 results are presented.

Values of p_{crit} for several landscape metrics were similar to values of p_{crit} for invasion rate, including lacunarity (at 15 km), total number of patches (at 45 km), size of largest patch (at
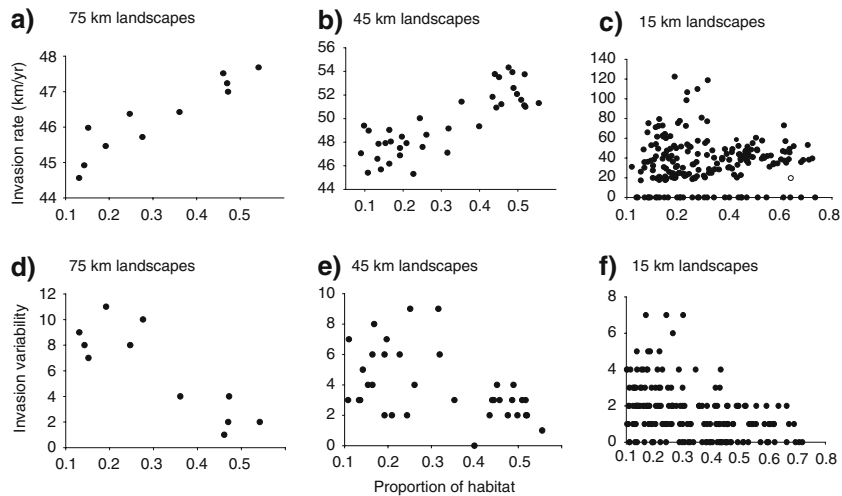
Fig. 1 Gypsy moth invasion rate (distance of trap from site of introduction/years to colonization) largely increased with increasing proportion of habitat. Map 1 results are reported for each scale of analysis: (**a**) 75 km, (**b**) 45 km, and (**c**) 15 km. Invasion variability (range in years to colonization among traps located in the same analysis window) declined with increasing proportion of habitat. Map 1 results are reported for each scale of analysis: (**d**) 75 km, (**e**) 45 km, and (**f**) 15 km

Table 1 Summary of critical thresholds in two invasion success indices and six landscape metrics with habitat loss at three scales of analysis (analysis window sizes of 75, 45, and 15 km on a side) using two land cover maps

	75 km		45 km		15 km	
	Map 1	Map2	Map 1	Map 2	Map 1	Map 2
Invasion rate	–	–	0.23 ± 0.61	0.20 ± 0.90	–	0.1 ± 0.47
Invasion variability	–	0.42 ± 2.20	–	0.24 ± 4.70	0.50 ± 2.03	0.45 ± 0.87
Lacunarity	–	–	0.44 ± 0.02	–	0.10 ± 0.001	0.15 ± 0.08
Total number of patches	0.28 ± 0.36	0.27 ± 0.63	0.23 ± 0.76	0.27 ± 0.53	0.22 ± 15.12	–
Size of largest patch	0.15 ± 0.10	0.27 ± 0.08	0.14 ± 0.11	0.24 ± 0.13	0.12 ± 0.002	0.18 ± 0.98
Total length of edges	0.28 ± 1.4	0.27 ± 2.20	0.32 ± 1.84	0.28 ± 1.68	0.315 ± 0.36	0.26 ± 5.12
Average area per patch	0.15 ± 0.11	0.22 ± 0.11	0.14 ± 0.09	0.16 ± 0.16	0.22 ± 0.004	0.09 ± 0.08
Connectivity	0.25 ± 0.09	0.51 ± 1.20	0.42 ± 1.10	0.42 ± 0.18	0.31 ± 0.005	0.09 ± 0.11

Dashes indicate no threshold response was detected

Fig. 2 Thresholds in landscape metrics with increasing proportion of habitat calculated using land cover Map 1 and a 75 km analysis window
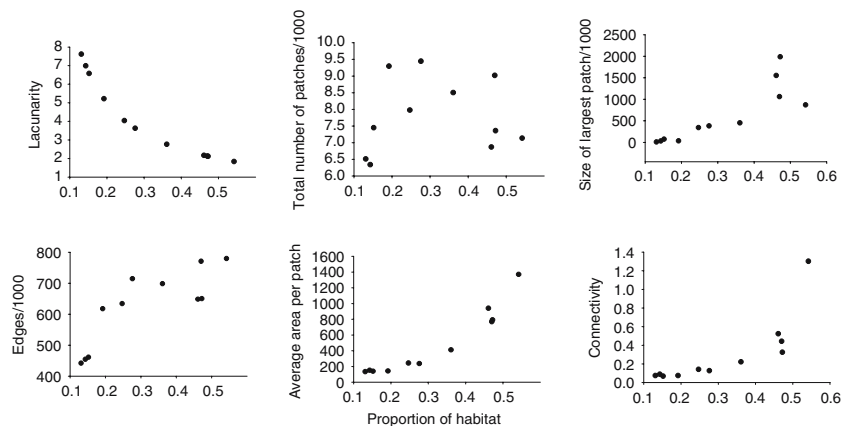
Fig. 3 Thresholds in landscape metrics with increasing proportion of habitat calculated using land cover Map 1 and a 45 km analysis window
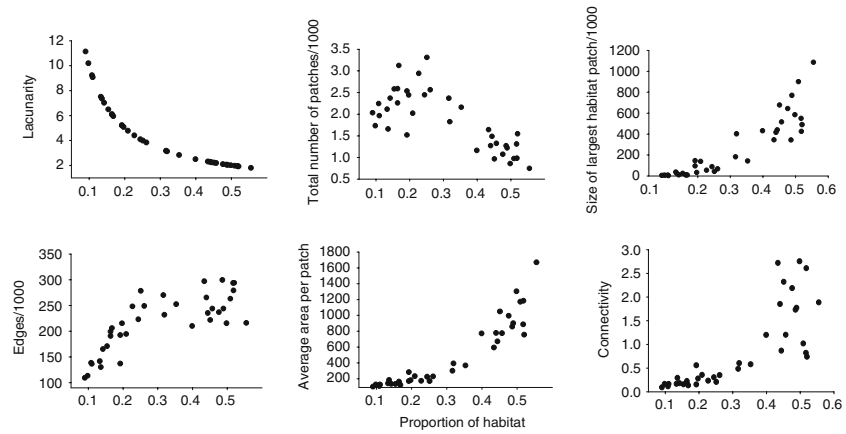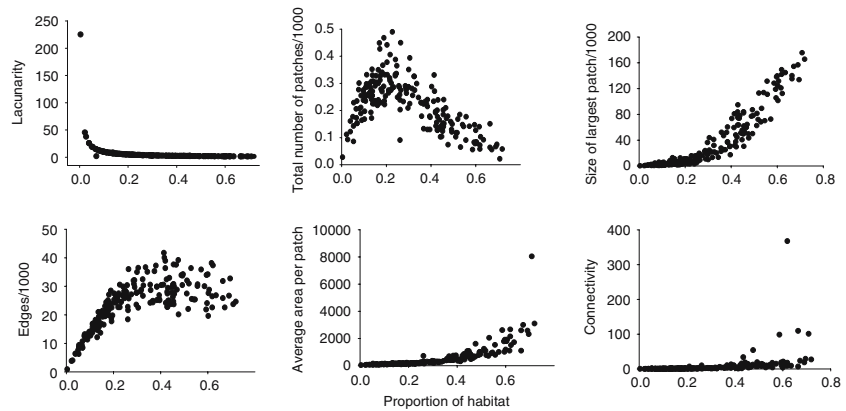

Fig. 4 Thresholds in landscape metrics with increasing proportion of habitat calculated using land cover Map 1 and a 15 km analysis window

15 km), connectivity (at 15 km), and average area per patch (15 km). Values of p_{crit} for several landscape metrics were similar to most values of p_{crit} for invasion variability, including total number of patches (at 45 km) and size of largest patch (at 45 km). Several landscape metrics exhibited threshold responses that were less abrupt but similar in location to dispersal success thresholds predicted by With and King's (1999) neutral landscape models (p_{crit} = ~0.05–0.1), including lacunarity (at 15 km), and average area per patch and connectivity (for Map 2 at 15 km).

Discussion

In general, gypsy moths did not appear to exhibit a strong threshold response to changes in landscape structure, meaning that habitat fragmentation did not greatly compound the negative effects of habitat loss for this species. The thresholds we detected in invasion success indices were more gradual than other ecological thresholds reported for amphibian distributions (Newcomb Homan et al. 2004) or various environmental gradients (Qian et al. 2003). Also, confidence intervals around our estimates of invasion success thresholds were quite wide (Table 1) compared to confidence intervals for more abrupt threshold behavior such as that exhibited by lacunarity at the 15 km scale of analysis (Fig. 4).

Contrary to the predictions of neutral landscape models (With and King 1999; King and With 2002), thresholds in invasion success indices did not correspond well with any measures of landscape structure. Similarities in critical threshold values were primarily observed at smaller scales of

analysis, especially at the 15 km scale. Although the threshold in invasion rate for Map 2 at the 15 km scale of analysis was quite similar to that of lacunarity (Table 1), the threshold increase in invasion rate (Fig. 1c) was certainly not as clear and abrupt as the decline in lacunarity (Fig. 4).

One potential reason for the apparent discrepancy between our results and that of published dispersal simulations may be that this study measured large-scale movement of the invasion wavefront instead of relatively smaller movements of individual dispersers. Most research conducted on the relationship between dispersal and landscape structure has involved either individual-based simulation models (Schwartz 1992; With and Crist 1995; Pitelka 1997; With and King 1999; Matlack and Monde 2004) or experiments documenting short distance, terrestrial movements of beetles (Wiens and Milne 1989; Wiens et al. 1997). In our study, abrupt increases in gypsy moth trap catch data indicate that the invasion wavefront (including larvae and non-vagile adult females) recently arrived in the area near that trap, not that a number of individual male moths have recently flown into the region. Therefore, the index of invasion success used in this study may be displaying a macroecological phenomenon, an emergent property of the combined individual dispersal movements of all individuals in the population (Brown 1995; Maurer 1999). Emergent properties are common features of large, complex systems, but they are not observable in data collected at smaller scales. Therefore, data collected at the scale of individual dispersal movements may not be sufficient to predict the relationship between overall invasion success and landscape heterogeneity.

Alternatively, invasion success may exhibit a more linear response to landscape structure because it is strongly affected by non-random movement and environmental factors not accounted for in most simulation models. Many dispersal models assume organisms move randomly across the landscape (Wiens et al. 1997). However, gypsy moths are carried passively by directed winds that do not allow for purely random dispersal (Elkinton and Liebhold 1990). Decreasing proportion of habitat will, of course, have the effect of increasing the probability that gypsy moth

larvae will be deposited by atmospheric motion systems or rainfall events into unsuitable areas and fail to survive (Isard and Gage 2001). However, anemochorous species like the gypsy moth (and, perhaps, species that actively fly) may not be as negatively affected by the same loss of habitat and patch connectivity as active terrestrial dispersers. In addition, most neutral landscapes do not represent the true complexity of real landscapes. Models of dispersal across neutral landscapes do not consider the effects of environmental conditions such as topography, disturbance history, climate, or ecological processes such as competition and predation (Gardner et al. 1987; With and King 1999; King and With 2002). Therefore, real invasion data may not exhibit typical threshold responses because environmental factors may mediate the effects of changing habitat structure. The exact response of a species to the landscape likely depends on a number of additional factors such as dispersal strategy and ability, degree of habitat specialization, and rate of habitat turnover in dynamic landscapes (With and Crist 1995; King and With 2002; Matlack and Monde 2004).

Although thresholds in invasion success were more gradual than might be expected, the amount of time necessary to complete the invasion of a given area did increase with habitat loss (Fig. 1). For example, landscapes with $p > 0.3$ represent landscapes in the northern Lower Peninsula where the number of years to colonization were all small even though these traps were located relatively far away from the site of the original gypsy moth introduction. Landscapes with $p < 0.3$ represent areas from across the peninsula that were not invaded as quickly or as uniformly; in other words, some traps in a given analysis window were invaded early in the monitoring period while others were not colonized for up to 11 years later. Thus, for excellent dispersers like the gypsy moth, habitat loss and fragmentation may slow the invasion wavefront but not cause a sudden, non-linear decline below a critical level of habitat loss.

Scale of analysis and land cover characterization

Our results contrasted with simulation results in that lacunarity thresholds did not uniquely

correspond with most thresholds in invasion success. In addition, lacunarity proved to be quite variable in threshold location at different scales of analysis. Invasion success only exhibited threshold behavior similar to that of lacunarity at the 15 km scale of analysis, suggesting that invasion success is not affected by habitat loss in the same fashion as lacunarity at larger scales. Given that lacunarity did not display unique critical threshold values at larger spatial scales, we suggest that lacunarity not be used as the primary predictor of an invasion wavefront's response to landscape structure. The close correspondence between dispersal success and lacunarity thresholds observed by With and King (1999) may only be generated by processes occurring at spatial extents similar to individual movements; this relationship may not ''scale up'' (Li and Wu 2004) to the movement of an invasion wavefront.

We observed increased variation in invasion success indices at smaller scales of analysis (45 and 15 km), suggesting that our ability to characterize invasion success began to break down when analysis windows of <75 km on a side were used. Our findings are supported by Yang et al.'s (1998) observation that the annual average increase in area infested in Michigan between 1992 and 1994 was 6,053 km². This area of expansion is equivalent to a square that is 78 km on a side, and is roughly the same as our largest analysis window (75 km on a side). Such areal expansion may seem remarkably large, but a small number of larvae may survive long distance dispersal events. Those individuals may then begin forming their own new colonies, or ''nascent foci'' (Moody and Mack 1988), ahead of the invasion wavefront that eventually merge with the wavefront. The formation of nascent foci typically results in much higher rates of expansion than would be expected given the average individual dispersal distance because the invasion wavefront speeds up rapidly as it begins to engulf newly formed colonies (Moody and Mack 1988; Shigesada et al. 1995). If the effects of landscape heterogeneity on invasion progress are to be quantified, invasions may need to be monitored, and landscape metrics calculated, at the spatial extent of long-distance dispersal events.

Observed thresholds in landscape metrics were remarkably similar between the two land cover maps of Michigan for several landscape metrics despite the fact that these maps were generated almost 20 years apart using different types of imagery and classification methodology. Although overall behavior of landscape metrics in response to changing proportion of habitat was similar, three patch-based metrics (size of largest patch, average area per patch, and connectivity) exhibited large differences in the location of critical thresholds. One reason these metrics are sensitive to choice of land cover maps is that they all measure the size of patches in the landscape and the two maps used in this study differed in their characterization of patch size. In general, Map 2 paints a much patchier picture of the Michigan landscape than Map 1. For example, the total number of patches/1,000 ranged from 6.34–9.45 for Map 1 and 33.8–102.2 for Map 2 in 75 km landscapes. This is likely due to the fact that Map 2 was generated from satellite imagery using a complex classification methodology and because habitat fragmentation likely increased in Michigan between the year Map 1 was created (1978) and the year Map 2 was created (2001).

Implications for monitoring and management

Our results indicate that gypsy moths may be more resilient to habitat fragmentation than previously thought. Therefore, the concept of creating areas of fragmented habitat to be used as a ''fire-break'' to slow the invasion wavefront (Sharov and Leibhold 1998; With 2004) may be limited for good dispersers like the gypsy moth. We observed that invasion success of gypsy moths in Michigan did not exhibit a typical threshold response to declining proportion of habitat and that habitat fragmentation did not compound the negative effects of habitat loss for this species. Although habitat fragmentation likely contributed to a slowing of the invasion, it did not prevent the invasion from reaching all areas of the Lower Peninsula in a relatively short period of time (<10 years in most cases). Therefore, creating firebreaks of fragmented habitat will probably not be a successful long-term strategy

for generalists like the gypsy moth that show great dispersal capacity.

This study also suggests that the scale of data collection and analysis must be carefully matched to the scale of the process of interest if invasion management is to be effective. Although studies of individual dispersal movements advance our understanding of dispersal ecology, such data are not easy to obtain across a large spatial extent or over long time periods and, thus, may not be practical enough for use in invasion management. Studies conducted on individual dispersal movements may not be applicable to processes occurring at much larger spatial extents and should be used with caution when planning management actions. We encourage the collection and analysis of more long-term, large-scale data aimed at characterizing movement of invasion wavefronts. Such data are time-consuming and expensive to collect, but they may be crucial to advancing our understanding of how to predict and manage the spread of invasive species at statewide, national, or international levels.

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