

Assessing the Risk of Invasive Spread in Fragmented Landscapes

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Little theoretical work has investigated how landscape structure affects invasive spread, even though broad-scale disturbances caused by habitat loss and fragmentation are believed to facilitate the spread of exotic species. Neutral landscape models (NLMs), derived from percolation theory in the field of landscape ecology, provide a tool for assessing the risk of invasive spread in fragmented landscapes. A percolation-based analysis of the potential for invasive spread in fragmented landscapes predicts that invasive spread may be enormously enhanced beyond some threshold level of habitat loss, which depends upon the species' dispersal abilities and the degree of habitat fragmentation. Assuming that invasive species spread primarily through disturbed areas of the landscape, poor dispersers may spread better in landscapes in which disturbances are concentrated in space, whereas good dispersers are predicted to spread better in landscapes where disturbances are small and dispersed (i.e., fragmented landscape). Assessing the risk of invasive spread in fragmented landscapes ultimately requires understanding the relative effects of landscape structure on processes that contribute to invasive spread—dispersal (successful colonization) and demography (successful establishment). Colonization success is predicted to be highest when >20% of the landscape has been disturbed, particularly if disturbances are large or aggregated in space, because propagules are more likely to encounter sites suitable for colonization and establishment. However, landscape pattern becomes less important for predicting colonization success if species are capable of occasional long-distance dispersal events. Invasive species are also more likely to persist and achieve positive population growth rates (successful establishment) in landscapes with clumped disturbance patterns, which can then function as population sources that produce immigrants that invade other landscapes. Finally, the invasibility of communities may be greatest in landscapes with a concentrated pattern of disturbance, especially below some critical threshold of biodiversity. Below the critical biodiversity threshold, the introduction of a single species can trigger a cascade of extinctions among indigenous species. The application of NLMs may thus offer new insights and opportunities for the management and restoration of landscapes so as to slow the spread of invasive species.

KEY WORDS: Community invasibility; complex systems theory; critical biodiversity; demography; dispersal; landscape connectivity; landscape ecology; neutral landscape models; percolation theory; thresholds

1. INTRODUCTION

Although habitat loss, fragmentation, and invasive species collectively pose the greatest threats

to biodiversity,⁽¹⁾ there has been little theoretical or empirical research that has addressed how the alteration of landscape structure might promote invasive spread.⁽²⁾ There are several reasons why habitat loss and fragmentation might be expected to enhance the spread of invasive species. Humans are

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the primary drivers of land-use change and have also been directly or indirectly responsible for transporting species beyond their native range. Human land-use activities may thus enhance the invasibility of ecological communities,⁽³⁾ particularly through landscape transformation that results in the destruction and fragmentation of native habitats. Fragmentation is characterized as a “landscape-level” disturbance,⁽⁴⁾ and disturbance is almost unanimously acknowledged to influence invasive spread.⁽⁵⁾ Thus, fragmentation ought to enhance the spread of invasive species, and if so, it might be possible to manage landscapes so as to minimize the risk of invasive spread.

Landscape structure may affect any or all of the stages of the invasion process that include (1) introduction, (2) colonization, (3) establishment, (4) dispersal, which interacts with landscape structure to create, (5) spatially distributed populations, which may set the stage for invasive spread.⁽²⁾ Although the arrival of an exotic species to a landscape generally results from the intentional or accidental introduction by humans, which involves overcoming a geographic barrier, landscape structure may still affect introduction if it governs human land-use activities and enhances the probability of introduction. Establishment depends upon successful colonization, which may be a function of propagule pressure or number of introductions to a locale. Establishment requires attaining positive population growth rates, which may be affected by landscape structure if population vital rates are affected by fragmentation (e.g., increased competition, predation, or parasitism at habitat edges may negatively impact birth rates, b).⁽⁶⁾ The movement of organisms or their dispersal vectors can be affected by the spatial arrangement of habitat or resources,^(7–10) and in combination with the above processes, can lead to spatially structured populations that may set the stage for invasion (e.g., nascent foci, Reference 11).

My objective in this article was to explore how alteration of landscape structure in the form of habitat loss and fragmentation contributes to the risk of invasive spread. Little theoretical or empirical work has directly investigated the effects of landscape structure—or spatial pattern more generally—on invasive spread.⁽²⁾ Therefore, much of the research I highlight in this article was actually developed to investigate other questions related to fragmentation effects on dispersal, population persistence, and community dynamics. Invasive spread is a result of successful dispersal and positive population growth rates within landscapes, and a general under-

standing of how landscape structure affects these processes in other species should give us some insight into how fragmentation might promote invasive spread. The key is to redefine the landscape context of these other studies in terms of the availability of habitat that is suitable for invasive spread. Thus, applications that investigated the effect of habitat abundance on population persistence to demonstrate that extinction risk was reduced beyond some threshold level of available habitat, can also be interpreted in the context of identifying the threshold level of habitat required for population establishment of invasive species (e.g., disturbed areas of landscapes) that may promote invasive spread.

2. EVALUATING THE POTENTIAL RISK FOR INVASIVE SPREAD

As a first approximation, the risk of invasive spread in different landscapes can be modeled as a percolation process using neutral landscape models (NLMs). NLMs were developed in landscape ecology as an extension of percolation theory, which studies flows through spatially heterogeneous media.⁽¹²⁾ Neutral landscapes were first presented as a null model of what landscape patterns are expected in the absence of any organizing or formative process that typically gives rise to landscape pattern, by assuming a random distribution of land cover or land use.^(13–14) Since their introduction, NLMs have evolved greater spatial complexity^(15–18) and have been used to develop spatially explicit theory of how landscape structure (and spatial pattern more generally) affects a wide range of ecological phenomena,⁽¹⁹⁾ including the spread of disturbances,⁽²⁰⁾ the dispersal of organisms,^(7,9,10,21) extinction risk for species in fragmented landscapes,⁽²²⁾ and coexistence of species in space.^(23–25)

Complex landscape patterns can be generated across a gradient of habitat availability and fragmentation severity (Fig. 1). Because many invasive species, such as exotic plants, spread through disturbed areas where native habitat has been cleared, the available habitat for these species is represented by the distribution of disturbances in space (gray cells in Fig. 1). Disturbances can be simulated as a random process, or as a fractal distribution in which the degree of spatial contagion (H) can be adjusted to produce disturbances that are either aggregated ($H = 1.0$) or dispersed across the landscape ($H = 0.0$). For example, disturbances may occur at a local scale and

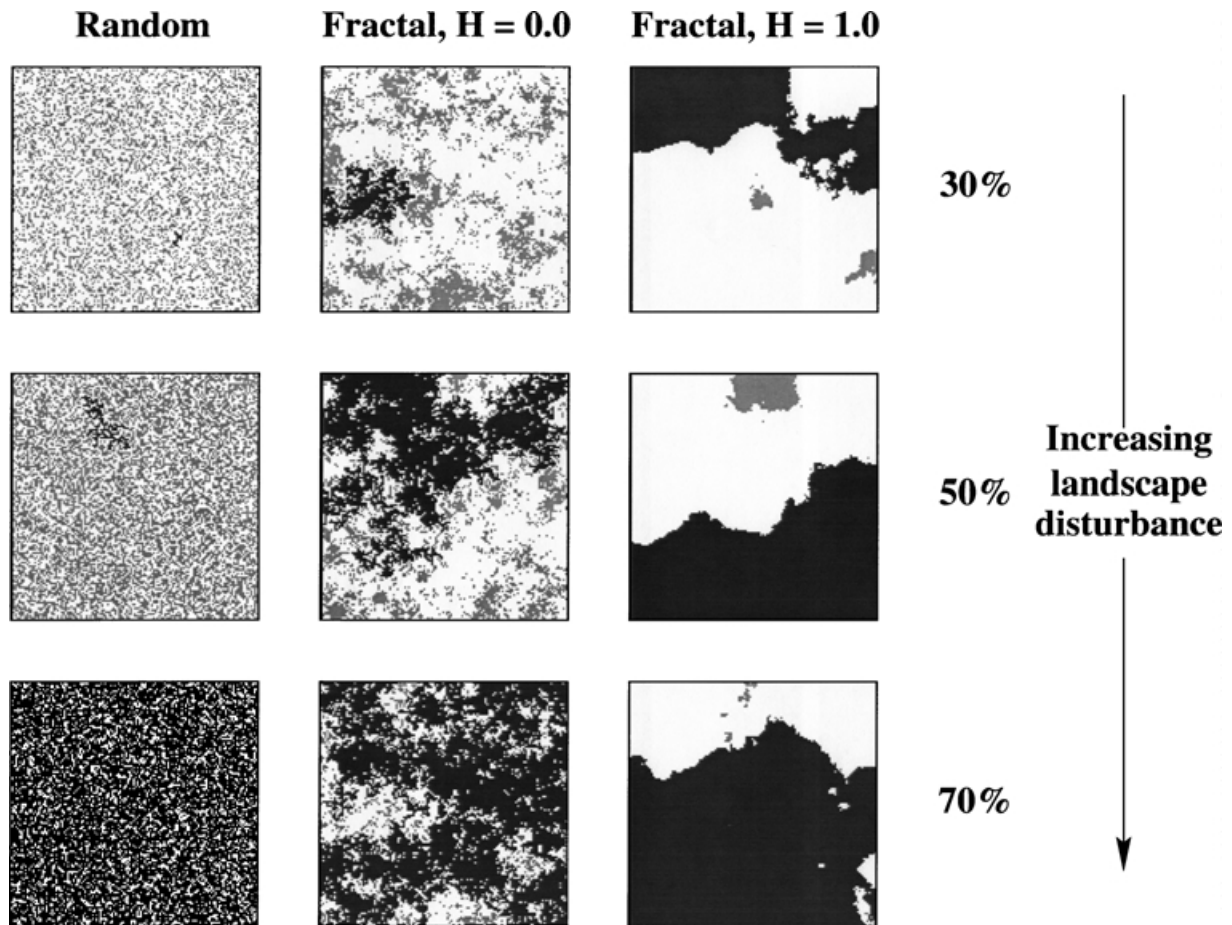


Fig. 1. Effect of landscape structure on the potential for invasive spread. Neutral landscape models, derived from percolation theory, are used to generate complex spatial patterns representing a gradient of landscape disturbance and fragmentation (random is the most fragmented; H refers to the degree of spatial autocorrelation of the fractal landscape patterns with $H = 1.0$ representing the highest degree of spatial contagion). The spread of a hypothetical species constrained to disperse through adjacent cells of disturbed habitat (gray) is highlighted in black. The species is said to “percolate” if it is capable of spreading across the entire landscape (black cluster spans the landscape).

be distributed as many small clearings throughout the landscape (e.g., random landscapes, Fig. 1). Alternatively, disturbances may be concentrated in space and occur as a few large clearings on the landscape (e.g., fractal, $H = 1.0$ landscapes, Fig. 1).

2.1. Identifying Critical Thresholds in Invasive Spread

The probability of invasive spread is determined by the presence of a spanning cluster of available habitat (disturbed areas in this case), which would permit the species to spread (or percolate) across the entire landscape. The critical level of disturbance at which this occurs depends upon the spatial pattern of the disturbance and the dispersal abilities of the species. For example, consider a species that has localized dis-

persal and is constrained to spread through adjacent cells of disturbed habitat (i.e., cells that are connected along an edge). If disturbances are small and localized (random), such a species would not be able to spread across the landscape until $>50\%$ of the landscape had been disturbed (invasive spread through disturbed habitat depicted in black in Fig. 1). Alternatively, if disturbances are large and concentrated in space (fractal, $H = 1.0$), invasive spread can occur when as little as 30% of the landscape has been disturbed, owing to the greater connectivity of habitat (Fig. 1).

Invasive spread is predicted to occur as a threshold response to habitat destruction (Fig. 2A). By convention, the critical level of disturbance at which invasive spread occurs is taken as a $\geq 50\%$ probability of percolation across the landscape. Thus, the critical

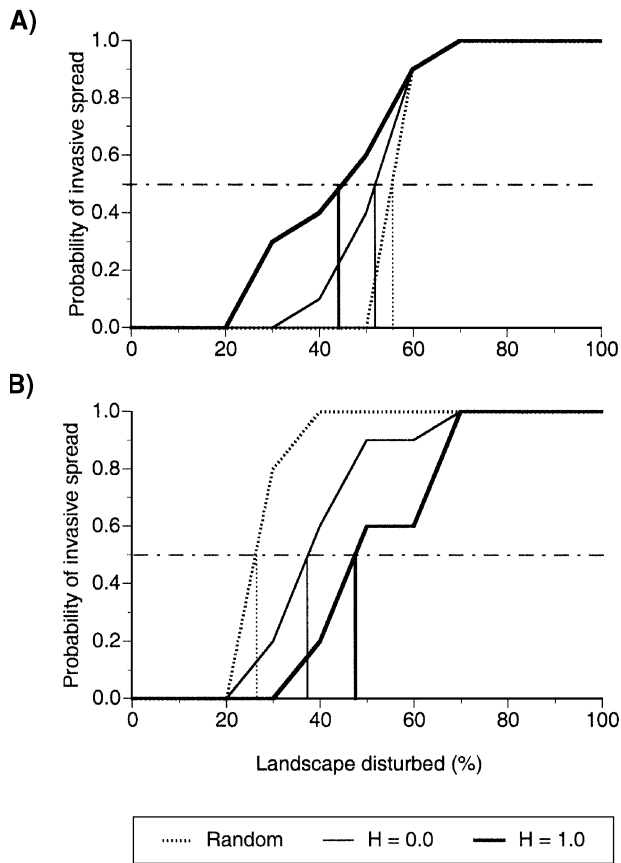


Fig. 2. The probability of invasive spread as a function of disturbance in different landscapes (cf. Fig. 1) for species constrained to disperse through adjacent cells of disturbed habitat (A) and those capable of crossing a single cell of unsuitable habitat (i.e., species has gap-crossing abilities, B). Invasive spread is defined here in a percolation context, as the probability that a species can percolate across the landscape (cf. Fig. 1).

threshold of invasive spread occurs when 57% of the landscape has been disturbed if disturbances are small and localized (random curve), but at only 43% when disturbances are large or concentrated in space ($H = 1.0$ curve, Fig. 2A). In other words, invasive spread occurs at a lower level of disturbance when disturbances are large or clumped in distribution on the landscape.

If the species has better dispersal abilities and is able to cross gaps of unsuitable habitat (single cells of nondisturbed habitat in this case), then critical thresholds of invasive spread are shifted (Fig. 2B). Now, invasive spread is more likely to occur on landscapes in which disturbances are small and localized (a reversal in the ordering of random and $H = 1.0$ response curves) when only 26% of the landscape has been disturbed (random curve, Fig. 2B). This is be-

cause the more dispersed pattern of disturbance facilitates invasive spread by providing “stepping stones” to dispersal for species capable of crossing gaps (Fig. 3). In contrast, invasive spread on landscapes in which disturbances are concentrated in space would not occur until nearly half (48%) of the landscape had been disturbed (Fig. 2B). The threshold for invasive spread thus changes little in landscapes with a concentrated pattern of disturbance (at least for these two types of species), but is reduced significantly for better dispersers in landscapes with small, localized disturbances. Increasing the dispersal neighborhood of the species would result in further shifts in the critical threshold of invasion, such that spread occurs at increasingly lower levels of habitat disturbance.⁽²⁾

Thus, based on this application of percolation theory, land management to reduce the risk of invasive spread for species with limited gap-crossing abilities should strive to concentrate disturbances within a particular region of the landscape (i.e., restrict habitat clearing to one or a few regions of the landscape). Land management to reduce invasive spread for species with localized dispersal should instead create a dispersed or fragmented pattern of disturbance across the landscape. Because these species cannot cross gaps of unsuitable habitat (nondisturbed sites), fragmentation would serve as a barrier to control their spread. A similar recommendation has been made previously to control the spread of disturbances such as fire across landscapes.⁽²⁰⁾ The notion of creating “fire-breaks” to control invasive spread is also behind the practice by the U.S. Forest Service of creating “barrier zones” at invasion fronts to slow the spread of gypsy moths (*Lymantria disparare*) through forested landscapes of the eastern United States.⁽²⁶⁾ Activities targeting the eradication or at least suppression of gypsy moths are concentrated along these invasion fronts, thus creating a barrier (absence of mates) that slows their rate of spread. The efficacy of managing landscapes to control invasive spread has not yet been demonstrated to my knowledge, but the results of these percolation-based studies suggest that different land-management strategies may be required to control the invasive spread of species that differ in dispersal ability.

2.2. When is Landscape Pattern Important for Predicting Invasive Spread?

The importance of landscape structure for invasive spread is expected to diminish as the dispersal range of the species increases. Although a species

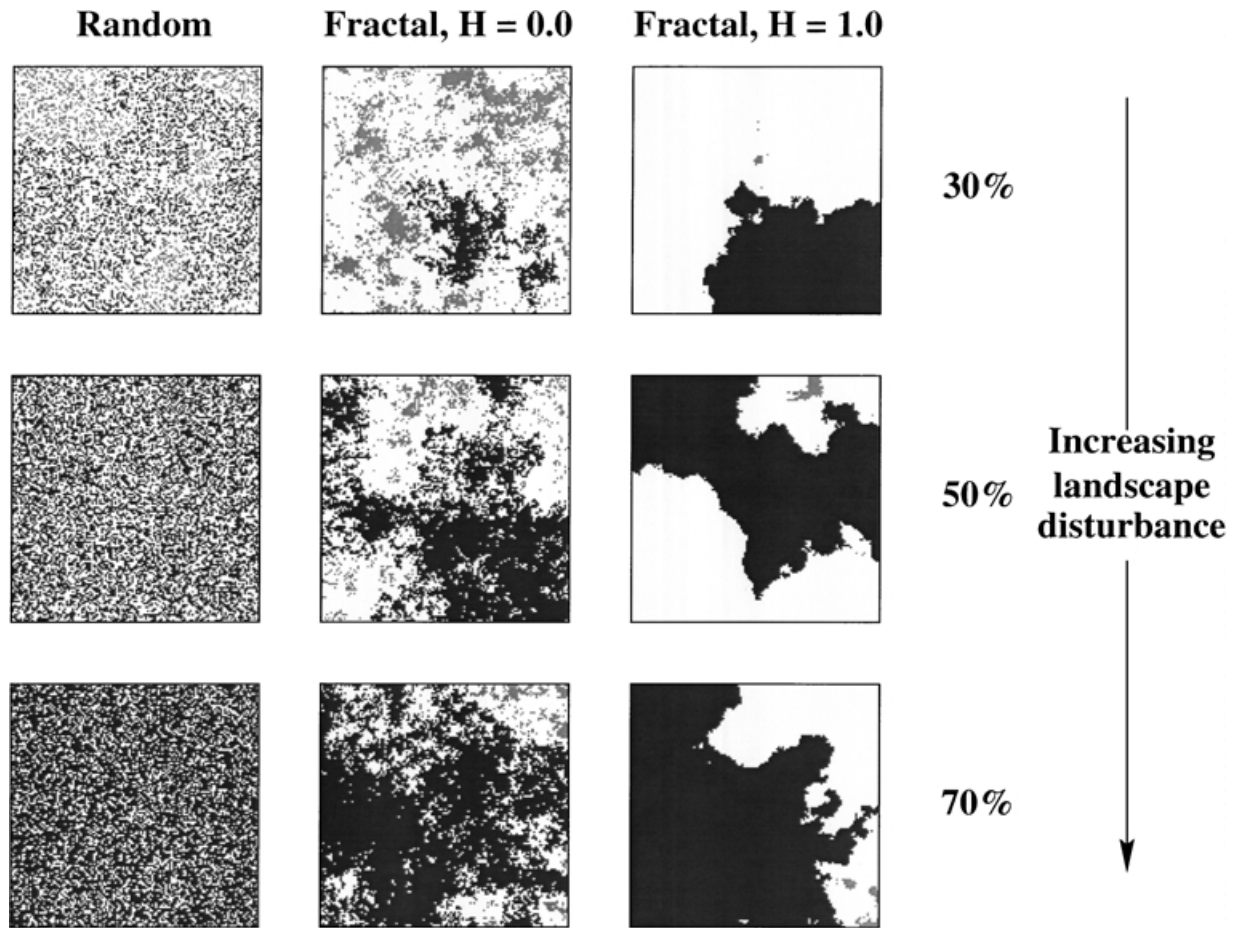


Fig. 3. Effect of landscape structure on the potential for invasive spread in a species that has gap-crossing abilities (i.e., can cross a single cell of unsuitable habitat). Note that invasive spread is possible in fragmented (random) landscapes when as little as 30% of the landscape is disturbed (cf. Fig. 2B) because the more dispersed pattern of disturbance acts as “stepping stones” to dispersal.

may generally exhibit local dispersal, it is the infrequent long-distance dispersal events that ultimately govern the rate of invasive spread.^(27,28) For example, landscape pattern was unimportant for predicting the spread of pine trees (*Pinus pinaster*) invading the fynbos of South Africa in a simulation model where a small percentage of seeds (0.1%) were capable of dispersing long distances (1–10 km) by the wind.⁽²⁹⁾ Landscape pattern—the specific arrangement of disturbances in space—may in fact be important for predicting the rate of invasive spread only when some threshold of disturbance has been crossed.

Tree migration rates reflect the potential for range expansion, and thus represent a form of invasion on a regional or continental scale. In one simulation study, landscape structure affected tree migration rates only when suitable habitat (forest) fell below 10–25% (i.e., 75–90% of the landscape had been deforested), de-

pending upon the specific pattern of disturbance.⁽³⁰⁾ Tree migration rates were slowest in landscapes in which disturbances were aggregated in space, thus creating large gaps between forest patches.⁽³⁰⁾ Landscape pattern may not always be important for predicting the risk of invasive spread, but identifying when it is and thus the extent to which landscapes can be managed to minimize invasive spread is an important research question that needs to be addressed.

2.3. Edge Effects on the Potential for Invasive Spread

Assessing the risk of invasive spread in landscapes also depends on whether species are moving primarily within or between habitat types.⁽²⁰⁾ Thus far, it has been assumed that the invasive species are moving primarily through disturbed areas, but some species

are then able to infiltrate native habitats (moving between habitat types), especially along habitat edges. For example, the invasion of dry sclerophyll bushland in Australia by *Pittosporum undulatum* has been enhanced along suburban edges because these areas attract birds such as pied currawongs (*Strepera graculina*), which eat the fruits of *P. undulatum* and are the primary dispersal agent for this plant.⁽³¹⁾ Land-management activities that minimize habitat fragmentation of native habitats would reduce such edge effects and decrease the potential for biotic exchanges between different habitats or land uses.

3. EFFECT OF LANDSCAPE STRUCTURE ON THE INVASION PROCESS

Although percolation models are process based in that they incorporate local dispersal neighborhoods in assessing the risk of spread across spatially structured landscapes, they do not explicitly incorporate the effects of landscape structure on the specific processes that contribute to invasive spread, such as dispersal (successful colonization) and demography (successful population establishment). Their main contribution has thus been to provide an assessment of the *potential* for invasive spread in different landscapes. Although the effect of landscape structure on the process of invasive spread has not yet been addressed formally,⁽²⁾ results from other theoretical investigations into how landscape structure affects dispersal and demography at least provide some insights into how the invasion process may be affected by habitat fragmentation.

3.1. Assessing the Risk of Fragmentation on the Dispersal Phase of Invasive Spread

Consider a species that colonizes disturbed areas but is capable of moving through other habitats. What is the probability that individuals will be successful in locating habitat suitable for colonization in landscapes that differ in the amount and distribution of disturbances? If dispersal occurs as a random search (random direction and distance moved with each step), then landscape pattern is not important and only the amount of habitat and the dispersal ability (m , the number of steps or dispersal attempts) of the organism affect colonization success. The probability of colonization success can be defined as

$$\text{Pr}(\text{success}) = 1 - (1 - \varepsilon)(u + ph)^m, \quad (1)$$

where γ is the probability the individual does not disperse; $u = 1 - h$, where h is the amount of habitat on the landscape; and p is the proportion of suitable sites already colonized.⁽³²⁾ If ε is set to 0 to force dispersal and $p = 0$ (all suitable sites are available for colonization), then this expression simplifies to

$$\text{Pr}(\text{success}) = 1 - (u)^m. \quad (2)$$

Landscape structure is important for predicting colonization success when individuals are constrained to move through the adjacent cells and must interact with the spatial patterning of habitat (i.e., search occurs at a local scale relative to landscape pattern). The probability of dispersal success on fractal landscapes cannot be derived analytically from first principles and may lack a closed-form solution; thus, it was necessary to obtain the probability of dispersal success as an empirical fit to simulation results.^(9,33) Dispersal was simulated as a modified-percolation process on fractal landscapes, in which individuals initiate dispersal from a habitat cell (e.g., a natal territory or propagules produced by a plant on a disturbed site) and move with random directionality through the adjacent cells up to m -steps in search of a suitable site for colonization. Colonization success on fractal landscapes is assessed as the proportion of individuals that locate suitable habitat, and can be approximated by the equation

$$\text{Pr}(\text{success}) = 1 - (1 - \varepsilon)[(1 - h')^{m\beta_1} + (ph')^{m\beta_2}], \quad (3)$$

where γ , p , and m are as in Equation (1); $h' = a + bh$, where h is the abundance of habitat and a and b are fitted parameters that vary with the spatial contagion H of the landscape. The parameters β_1 and β_2 are also fitted; β_1 varies with H , and β_2 varies with both H and h . The mathematical form of this function was selected for its relative simplicity and consistency with the analytical form of Equation (1); this equation provided the best fit among several other functions generated.⁽²²⁾

Colonization success declined precipitously below a threshold level of disturbance (Fig. 4).⁽⁹⁾ In other words, as the availability of habitat suitable for colonization (disturbed areas) falls below a threshold of about 10%, the probability that individuals will encounter such habitat declines rapidly (Fig. 4A). In this scenario, colonization success is expected to be higher in landscapes in which disturbances are large or concentrated in space ($H = 1.0$) because dispersers originate from disturbed areas and are thus more likely to land or encounter suitable habitat when dispersal is

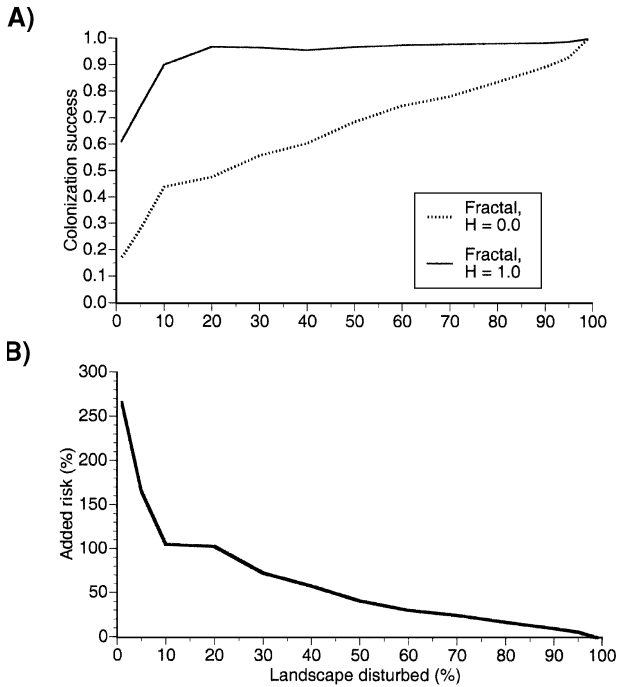


Fig. 4. (A) The effect of habitat fragmentation on colonization success—the probability that a species will locate suitable habitat—as a function of landscape disturbance. The hypothetical species depicted here is able to move through unsuitable habitat in its search for a suitable colonization site (i.e., disturbed areas), but is constrained to move through the adjacent cells up to the dispersal range of the species (m). Landscapes are as in Figs. 1 and 3 (after Reference 9). (B) Added risk of fragmentation on the dispersal phase of invasive spread. Added risk is assessed as the percent difference in colonization success between landscapes (fractal, $H = 0.0$ and fractal, $H = 1.0$ depicted in A).

localized, especially if the species is capable of moving through the areas of unsuitable habitat. Spread is thus more likely in these landscapes than in ones in which disturbances are small and localized ($H = 0.0$) owing to higher colonization success (Fig. 4A). Again, species with long-distance dispersal may not exhibit such dispersal thresholds and may be more affected by the amount of suitable habitat available for colonization, than the spatial arrangement of that habitat on the landscape (Equation (1)). The importance of landscape pattern for colonization success (and thus invasive spread) ultimately depends on how the scale of dispersal interacts with the scale of landscape disturbances.

Added risk is the increase in risk that results from some impact on a population.⁽³⁴⁾ The added risk of fragmentation on the dispersal aspects of invasive spread can be calculated as the percent difference in colonization success between two landscapes

(Fig. 4B). In this scenario, it is at low levels of disturbance that landscape pattern—the distribution of disturbances in space—is expected to have the greatest effect on colonization success, and by inference, on invasive spread. Beyond this, the added risk of fragmentation on invasive spread declines linearly, such that the extent of disturbance (percent of landscape disturbed) becomes more important than the pattern of disturbance.

Many models that simulate tree migration in fragmented landscapes also found thresholds in migration rate at low levels of available habitat (e.g., References 30, 35–37). With and King⁽⁹⁾ suggested that such thresholds in dispersal or colonization success might be more related to lacunarity thresholds than percolation thresholds. Lacunarity is derived from fractal geometry and is a measure of the variability in gap-size distributions (interpatch distances) on the landscape.⁽³⁸⁾ At low levels of available habitat on the landscape (<10%), there is a dramatic increase in the lacunarity index (i.e., a lacunarity threshold) that corresponds with the threshold in dispersal or colonization success (Fig. 4A).⁽⁹⁾ Thus, invasive spread might be limited more by the size and distribution of gaps among patches of suitable habitat than by the connectivity of suitable habitat patches (as measured by percolation thresholds). However, this remains a hypothesis to be tested. Empirical evidence for movement thresholds at low levels of habitat (<20%) has been found for some terrestrial insects within experimental landscapes inspired by NLMs (tenebrionid beetles on random landscapes, Reference 8; early instar crickets, *Acheta domestica*, on fractal landscapes, Reference 10).

3.2. Assessing the Risk of Fragmentation on the Demographic Phase of Invasive Spread

Invasive spread involves more than dispersal to and successful colonization of new sites; the species must also be able to persist and achieve positive population growth ($\lambda > 1$) in the new habitat. Most population models ignore the effect of landscape structure on demography, despite the fact that edge effects (a consequence of landscape fragmentation) may alter species interactions in ways that negatively (or sometimes positively) affect demographic rates (reproductive output, survivorship). For example, With and King⁽⁶⁾ devised a functional relationship between patch structure and reproductive success for various neotropical migratory songbirds as part of a spatially structured demographic model developed to

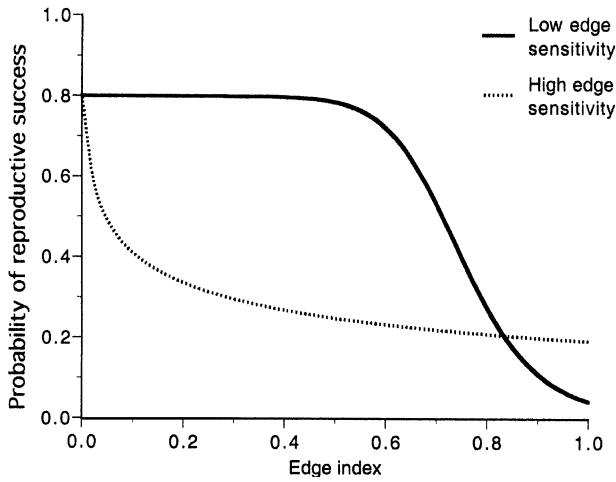


Fig. 5. Functional relationship between avian reproductive success and patch geometry (assessed by an edge index derived as the normalized perimeter-to-area ratio of the patch) for two hypothetical species that vary in edge-sensitivity. Patch geometry is influenced by landscape structure (the amount and spatial arrangement of habitat). This function thus provides an explicit link between spatial pattern and demography (after Reference 6).

assess population viability in fragmented landscapes (Fig. 5). Reproductive success in a given patch, S_i , can be obtained as

$$S_i = S_{\max} \frac{1}{1 + (e_i/k^\theta)}, \quad (4)$$

where S_{\max} is the maximum probability of reproductive success in the absence of edge effects (normalized patch edge-to-area ratio $\rightarrow 0.0$). This was set at $S_{\max} = 0.8$ in this analysis (i.e., not all eggs hatch, even in the absence of predation or brood parasitism). The parameter e_i is the normalized edge-to-area ratio of patch i and k is the value of e_i where $S_i = 0.5S_{\max}$. The parameter θ determines the rate at which reproductive success declines as a function of increasing edge (i.e., edge effects). Some species were “edge-sensitive” and exhibited a steep decline in reproductive output in small or irregularly shaped patches that were dominated by edge (high edge index), which is consistent with the results of field studies documenting a decline in nesting success in such patches owing to increased nest predation or brood parasitism by brown-headed cowbirds, *Moluthrus ater* (e.g., Reference 39). Although the focus here is on bird species that exhibit negative edge effects, some birds are actually “edge species,” which exhibit a nesting preference for, and thus have higher reproductive success along, habitat edges. It is not clear whether exotic bird species would necessarily exhibit such positive

edge effects, given that their breeding habitat is likely to be disturbed areas and thus they should still perform better in large disturbance patches (low edge index) producing some degree of (negative) edge sensitivity. Nevertheless, such positive edge responses can be easily incorporated as another type of functional response to patch geometry (landscape structure) in the model. The unique aspect of this model is that it explicitly incorporates the effects of spatial pattern on demography.

The demographic consequences of landscape structure were assessed as the expected number of female offspring produced per female, b , for the population across the entire landscape as

$$b = \frac{\sum_{i=1}^n \sum_{j=1}^{N_i} F_{ji}}{\sum_{i=1}^n N_i}, \quad (5)$$

where F_{ji} is the number of female offspring produced in territory j of patch i , N_i is the number of territorial females in patch i , and n is the total number of patches. The number of female fledglings (F_{ji}) is the product of the number of territories in patch i (T_i), species-specific clutch size (here a uniform distribution of 4–5 eggs), the probability of reproductive success for patch i (S_i , Equation (4)), and the fledgling sex ratio (1:1). A simple two-stage life-table combining fecundity (b) and survivorship (juvenile, s_0 , and adult, s) was then constructed for each species (e.g., Fig. 5) in a given landscape (e.g., Fig. 1). From the life table, we calculated the finite rate of population increase (λ) given by the solution to the characteristic equation:⁽⁴⁰⁾

$$\lambda^\alpha - s\lambda^{\alpha-1} - b l_\alpha = 0, \quad (6)$$

for $\alpha \geq 1$ and $0 < s < 1$, where l_α is survivorship at the age of first breeding, s is the annual probability of survivorship for breeding adults (>1 year), and b is derived from the population across the entire landscape (Equation (5)). The population is stable when $\lambda = 1.0$, declining when $\lambda < 1.0$, and increasing when $\lambda > 1$.

Although the goal of this analysis was to determine the potential of different landscapes to support persistent and increasing populations (i.e., population sources) for birds of conservation concern, the model structure is general enough that the results could also be interpreted from the opposite perspective of identifying landscape configurations that would support increasing populations of potentially invasive species, which would increase the risk of their spread. Negative ecological interactions at edges, such as

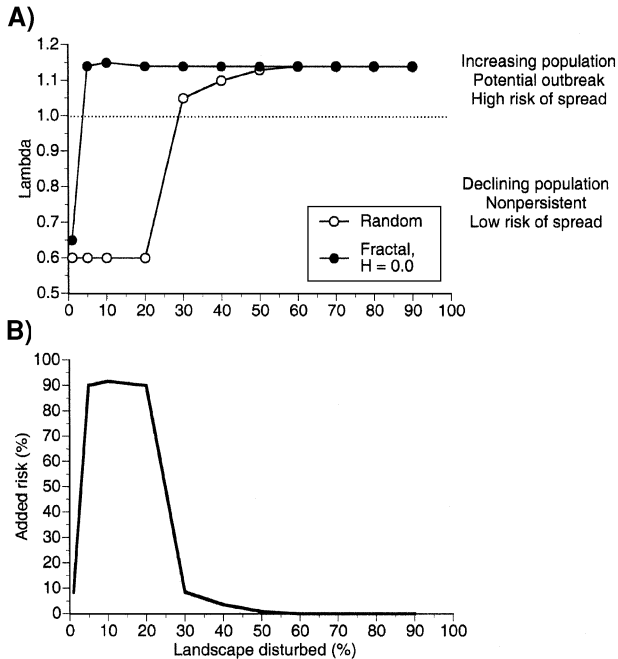


Fig. 6. (A) Effect of habitat fragmentation on population growth rates (λ) as a function of landscape disturbance. The hypothetical species depicted here has low edge sensitivity, in which reproductive success is reduced only in patches dominated by edge effects (e.g., small areas of disturbed habitat). The horizontal line is a threshold of population establishment ($\lambda = 1.0$). Below this threshold, populations are declining ($\lambda < 1.0$), populations are unlikely to become established, and the risk of spread is low. Above this threshold, populations are increasing ($\lambda > 1.0$), which increases the risk of invasive spread. Landscapes are as depicted in Figs. 1 and 3 (after Reference 6). (B) Added risk of fragmentation on the demographic phase of invasive spread. Added risk was assessed as the difference in population growth rates (λ) between landscapes for the species depicted in (A).

increased competition, predation, or parasitism, may affect reproductive success even in invasive species. As an example, consider a species with low edge sensitivity, in which reproductive success is not reduced except in fragments dominated by edge effects (e.g., small disturbed areas surrounded by habitat unsuitable for colonization). Landscapes in which disturbances were small and localized (random) would not be able to support persistent populations of this species as long as <30% of the landscape was disturbed (Fig. 6A). Conversely, if disturbances are even slightly clustered in space (fractal, $H = 0.0$), the landscape could support persistent and increasing populations when as little as 5% of the landscape had been disturbed (Fig. 6A). These results are not general and are specific to this particular scenario (i.e., a species with low edge sensitivity), but demonstrate

how such spatially structured demographic models might be used to assess the effect of landscape structure on demography and thus on the potential for invasive spread.

The added risk of fragmentation on the demographic aspects of invasive spread can again be assessed as the difference between population growth rates (λ) in different landscape scenarios (random and fractal, $H = 0.0$). The added risk of fragmentation on invasive spread is greatest at low levels of disturbance (5–20%; Fig. 6B). It is in this range that the specific pattern of disturbance has the greatest effect on the ability of the population to achieve positive population growth rates, and thus where there is the greatest potential risk of spread. Once 30% of the landscape has been disturbed, however, this species is able to achieve positive population growth regardless of the pattern of disturbance (i.e., landscape configuration). Again, this should not be viewed as a general result, as it is specific to the particulars of how the model is parameterized for this species (e.g., edge sensitivity; Equation (4), Fig. 5). Landscape structure may affect the demographic aspects of invasive spread even at high levels of disturbance for species with greater edge sensitivity (i.e., habitat fragmentation affects population growth rates of edge-sensitive species even when the landscape is mostly suitable for colonization; Reference 6).

3.3. Assessing the Relative Effects of Dispersal and Demography on Invasive Spread

Invasive spread requires both successful dispersal (colonization) and positive population growth rates (establishment) in new habitats. Assessing the relative contributions of dispersal versus demography to invasive spread is complicated by the fact that landscape structure may affect different stages of the invasion process in contrasting ways. For example, Bergelson *et al.*⁽⁴¹⁾ demonstrated that the weed *Senecio vulgaris* was able to disperse farther when bare-ground areas were uniformly distributed across the landscape (i.e., landscape is fragmented). In contrast, population growth rates of *S. vulgaris* were enhanced when disturbed areas were aggregated in space (i.e., not fragmented). More seedlings were able to establish successfully when suitable sites for colonization were clumped because a greater concentration of seeds was able to accumulate in these sites (i.e., higher propagule pressure). This illustrates a trade-off that may exist for many species in fragmented landscapes. Dispersal may be facilitated in a

fragmented landscape because colonization sites are well distributed across the landscape and the species can move farther or “percolate” across the entire landscape (e.g., random landscapes in Fig. 3). In contrast, the population persistence and growth rates are enhanced in landscapes with more aggregated habitat (e.g., fractal, $H = 0.0$ landscapes in Fig. 6A). The demographic aspects of the invasion process, particularly in terms of how landscape structure affects population vital rates, have generally received less attention than dispersal and are in need of further study. Land management to control invasive spread may be complicated if landscape structure affects the dispersal and demography of an invasive species in contrasting ways. Deciding which land-management scenario will best control the invasive species in this situation will depend on whether dispersal or demography contributes more to invasive spread.

4. THE EFFECT OF LANDSCAPE STRUCTURE ON THE INVASIBILITY OF COMMUNITIES

The attributes of communities may influence their susceptibility to invasion.⁽⁵⁾ The invasibility of communities thus needs to be considered when assessing the risk of invasive spread. Although there has been considerable debate as to whether species-rich communities are more resistant to invasion than species-poor communities (e.g., References 5, 42–46), there may nevertheless exist a critical level of biodiversity⁽⁴⁷⁾ that contributes to system resilience and makes communities less susceptible to local perturbations, such as species introductions. For example, critical biodiversity may be evident in studies that have documented a threshold effect of species richness on system stability or resilience. Productivity in a grassland system declined precipitously below a threshold number of species ($S = 9$; Reference 48). Species-rich communities maintained productivity in the face of a severe drought, and were able to recover more fully after this type of disturbance than species-poor communities.

Recently, With and King⁽⁴⁹⁾ adopted a complex systems approach⁽⁵⁰⁾ to assess how landscape structure affected community organization and critical biodiversity thresholds. Briefly, this approach involves generating simple rules governing how species evolve (mutation events that lead to increased competitiveness for a particular niche or a shift to a new niche), interact (competition for existing niche space), and spread across landscapes (see Reference 47 for a full description of the model). These local rules of inter-

action give rise to global system properties such as community structure and resilience. Although not specifically designed to assess the invasibility of communities, this research may nevertheless have implications for understanding the resilience of communities to perturbations, such as the introduction of an exotic species.

The critical biodiversity threshold is the level of species richness at which the system is most susceptible to small perturbations, such as the introduction or extinction of a single species, whose effects are then able to propagate throughout the entire system and trigger a mass extinction event.⁽⁴⁷⁾ Beyond this threshold, species spontaneously form ordered communities with well-defined spatial structure such that local perturbations are no longer able to trigger system-wide catastrophes such as mass extinctions. The susceptibility to extinction, $\chi(S)$, is the average extinction size as a function of diversity (S) and is defined as

$$\chi(S) \equiv \frac{1}{S} \int_{t_0}^{\infty} E(t, S'(t)) \theta(S', S) dt$$

$$\begin{cases} \theta = 0 & : S' \geq S \\ \theta = 1 & : S' < S \end{cases} \quad s'(t_0) > s, \quad (7)$$

where E is the sum total of extinctions integrated over a range of species S' .⁽⁴⁷⁾ The level of species richness (S) at which the susceptibility to extinction, $\chi(S)$, is greatest defines the critical biodiversity threshold (S_c , Fig. 7). Spatial contagion was found to enhance the susceptibility of communities to extinction, and thus the critical biodiversity threshold increased in landscapes with high spatial contagion (random: $S_c = 15$; fractal, $H = 1.0$: $S_c = 20$; Reference 49). Landscapes with clumped habitat or resource distributions might initially be more susceptible to invasion until this threshold is reached, because extinctions resulting from the introduction of a novel species can propagate more readily owing to the greater spatial contagion of habitat. A greater level of species richness might therefore be required before the system is able to resist invasion.

Thus, the landscape conditions that generally favor invasive spread (clumped distribution of habitat suitable for colonization and population establishment) appear to enhance the invasibility of communities to invasion. Although landscapes with high spatial contagion may initially be more sensitive to local perturbations (invasion, extinction) than random landscapes, they nevertheless were more likely to evolve beyond the critical biodiversity threshold and

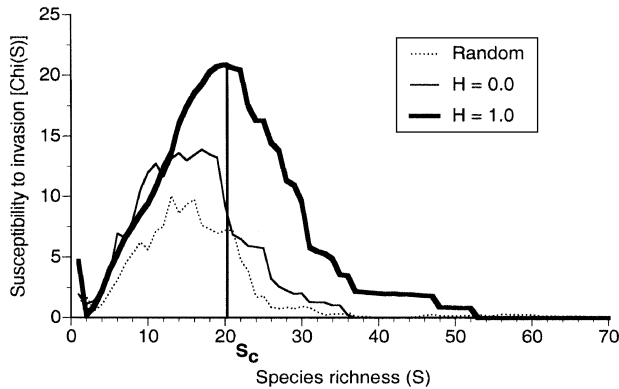


Fig. 7. Susceptibility of communities to invasion as a function of species richness that evolves on heterogeneous landscapes (comprised of six habitat types) that differ in spatial contagion (cf. Figs. 1 and 3). The critical biodiversity threshold is the level of species richness at which communities are most susceptible to disturbance, such as species introductions (i.e., invasion). The critical biodiversity threshold (S_c) is depicted in the figure for clumped fractal landscapes ($H = 1.0$) (after Reference 49).

form ordered, highly structured communities that are resilient to such disturbances.⁽⁴⁹⁾ Thus, communities that have originated in landscapes with patchy habitat or resource distributions may be more resilient to invasion, as opposed to communities that have not or where broad-scale disturbances have pushed these systems below the critical biodiversity threshold. This needs to be tested empirically.

5. SUMMARY

Because human land-use activities create a dynamic disturbance mosaic that may facilitate invasive spread across landscapes, theoretical approaches are needed to assess at what level of disturbance invasive spread is likely to occur and how landscape structure may influence the various stages of the invasion process. NLMs, derived from percolation theory in the field of landscape ecology, provide a first approximation for assessing the risk of invasive spread in landscapes subjected to different levels and patterns of disturbance. These percolation-based models predict that invasive spread may be enormously enhanced beyond a threshold level of disturbance, which depends upon the dispersal abilities of the species and the specific pattern of disturbance. Invasive spread of poor dispersers is enhanced in landscapes in which disturbances are large or concentrated in space. Conversely, the invasive spread of good dispersers is enhanced in landscapes in which disturbances are small and local-

ized, because the resulting pattern of fragmentation creates “stepping stones” to dispersal. Species with very good dispersal abilities are expected to be relatively unaffected by landscape structure, but good dispersers are not necessarily good colonizers (i.e., able to locate suitable habitat) because long-distance dispersal may be unnecessarily risky when habitat is clumped in space. In such landscapes, short-range dispersal would ensure that most propagules land in the same local neighborhood where other suitable habitat can be found.^(7,24)

However, invasive spread ultimately requires both successful colonization and positive population growth rates ($\lambda > 1.0$). Colonization success is expected to decline precipitously when the amount of suitable habitat falls below a threshold of about 20%.⁽⁹⁾ Thresholds in population establishment ($\lambda = 1.0$) are more variable, however, and depend upon how landscape structure affects demographic rates (reproductive success, survivorship). The ability of landscapes to support persistent and increasing populations ($\lambda \geq 1.0$) may be affected by the species’ “edge sensitivity,” the degree to which reproductive success declines (or mortality increases) in small patches of suitable habitat that tend to be dominated by edge effects (negative ecological interactions with other species, such as increased predation, parasitism, or competition, although species facilitation—such as the presence of dispersal vectors or mutualists—may also result in positive edge responses for invasive species). However, landscape structure may affect the different stages of the invasion process in contrasting ways.⁽⁴¹⁾ Devising land-management strategies for controlling the spread of invasive species will thus depend upon whether dispersal or demography contributes more to invasive spread.

Finally, the invasibility of communities may also depend upon the spatial patterning of habitats or resources. Communities that form on landscapes with clumped habitat or resource distributions may initially be more sensitive to local perturbations resulting from the introduction or extinction of a single species, because even these small disturbances can propagate readily throughout the system to trigger catastrophic mass extinction owing to the greater spatial contagion of the landscape. The critical biodiversity threshold for such landscapes is thus higher, meaning that a higher level of species richness is required for system resilience. Communities on such landscapes are nevertheless more likely to evolve beyond the critical biodiversity threshold and thus

should be able to resist invasions unless disturbances are widespread (rather than local) and species richness is seriously eroded. Unfortunately, the nature of human disturbances on landscapes has been both widespread and has seriously eroded biodiversity. Theory suggests that not only should communities in such landscapes be more susceptible to invasion, but also that the alteration of landscape structure by human land-use activities may well be facilitating the spread of invasive species. Future research should assess the feasibility of managing or restoring landscapes to control the spread of invasive species and to enhance the ability of communities to resist invasion.

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