The Landscape Ecology of Invasive Spread

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Abstract: *Although habitat loss, fragmentation, and invasive species collectively pose the greatest threats to biodiversity, little theoretical or empirical research has addressed the effects of landscape structure—or spatial pattern more generally—on the spread of invasive species. Landscape ecology is the study of how spatial pattern affects ecological process. Thus, a landscape ecology of invasive spread involves understanding how spatial pattern, such as habitat fragmentation or resource distributions, affects the various stages of the invasion process. Landscape structure may affect the spread of invasive species and the invasibility of communities by (1) enhancing spread above some threshold level of landscape disturbance directly, or indirectly through landscape effects on dispersal vectors; (2) affecting the various stages of the invasion process (e.g., dispersal vs. population growth) in different, potentially contrasting, ways; (3) interacting with the distribution of invasive species to facilitate spread (e.g., nascent foci); (4) promoting or altering species interactions in ways that enhance the invasibility of communities (e.g., edge effects); (5) compromising the adaptive potential of native species to resist invasion, or—alternatively—enhancing the adaptive response of invasive species, in fragmented landscapes; and (6) interacting with the dynamics of the disturbance architecture to create spatiotemporal fluctuations in resource availability, which enhance system invasibility. Understanding the landscape ecology of invasive spread may thus afford new insights and opportunities for managing and restoring landscapes so as to control the spread of invasive species and minimize the invasibility of communities.*

La Ecología de Paisaje de Extensiones Invasoras

Resumen: *Aunque la pérdida de hábitat, la fragmentación y las especies invasoras colectivamente son las mayores amenazas para la biodiversidad, poco trabajo teórico o empírico se ha dirigido a los efectos de la estructura del paisaje (o, más generalmente, el patrón espacial) sobre extensiones invasoras. La ecología de paisaje se dedica al estudio de cómo el patrón espacial afecta al proceso ecológico. Así, la ecología de paisaje de extensiones invasoras involucra comprender cómo el patrón espacial (e.g., fragmentación de hábitat o distribución de recursos) afecta las diversas etapas del proceso de invasión. La estructura del paisaje puede afectar la propagación de especies invasoras y la susceptibilidad a la invasión de una comunidad 1) al incrementar la extensión por encima de algún umbral de perturbación del paisaje, de forma directa o indirecta, afectando los vectores de dispersión a nivel de paisaje; 2) al afectar las diferentes etapas del proceso de invasión (por ejemplo, dispersión frente a crecimiento poblacional) de maneras diferentes y potencialmente contrastantes; 3) al interactuar con la distribución de especies invasoras para facilitar su propagación (por ejemplo, focos nacientes); 4) al promover o alterar interacciones de especies de manera tal que aumente la susceptibilidad a la invasión de comunidades (por ejemplo, efectos de borde); 5) al comprometer el potencial adaptivo de especies nativas de resistir a la invasión, o como alternativa, al incrementar la respuesta adaptiva de especies invasoras en paisajes fragmentados; y 6) al interactuar con la dinámica de la arquitectura de perturbación para crear fluctuaciones espacio-temporales en la disponibilidad de recursos, que incrementan la susceptibilidad del sistema. Por lo tanto, entender la ecología de paisaje de extensiones invasoras puede proporcionar nuevos puntos de vista y oportunidades para manejar y restaurar paisajes para controlar extensiones invasoras y minimizar la susceptibilidad de comunidades a la invasión.*

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Introduction

The impact of invasive species on human economic systems has been estimated at millions to billions of dollars annually (Pimentel et al. 2000), but the magnitude of the biotic costs to ecological systems is just now being assessed (e.g., Vitousek et al. 1996; Mooney & Hobbs 2000). The title of a report published recently by the U.S. Federal Interagency Committee for the Management of Noxious and Exotic Weeds, "Invasive Plants: Changing the Landscape of America" (Westbrooks 1998), highlights one of the most dramatic outcomes of biological invasions: when a non-native species takes over a community and completely alters landscape structure and ecosystem function. Landscape transformation can thus be viewed as the final stage of a terminal invasion.

Given the profound effect that exotic species have on the structure and dynamics of landscapes, landscape ecology can provide a much-needed perspective on the study and management of invasive species. In turn, human land-use patterns may enhance the invasibility of landscapes (Hobbs 2000). Landscape transformation by humans has been rapid, widespread, and extraordinarily thorough in many cases (Whitney 1994). It is no coincidence, therefore, that anthropogenic disturbances resulting in habitat destruction and fragmentation are viewed as the leading threats to biodiversity, followed by the threat posed by invasive species (Wilcove et al. 1998). Fragmentation is characterized as a "landscape-level" disturbance (Hobbs & Huenneke 1992), and disturbance is almost unanimously acknowledged to influence invasive spread (Fox & Fox 1986). Thus, habitat loss and fragmentation may facilitate the spread of invasive species. It is therefore surprising that little theoretical or experimental work has addressed the effects of habitat fragmentation on invasive spread. We do not know at what critical level of habitat loss and fragmentation invasive spread is most likely to occur, which stages of the invasion process might be enhanced by fragmentation, how the spatiotemporal dynamics of disturbances affect the invasibility of communities, or to what extent landscapes can be managed or restored to control invasive spread. The consequences of human land-use and global climate change on invasive spread have recently been addressed elsewhere (Mooney & Hobbs 2000). My purpose here is to explore what landscape ecology can contribute to the study and management of invasive species by addressing specifically how landscape structure (and spatial pattern more generally) is expected to affect invasive spread (Fig. 1).

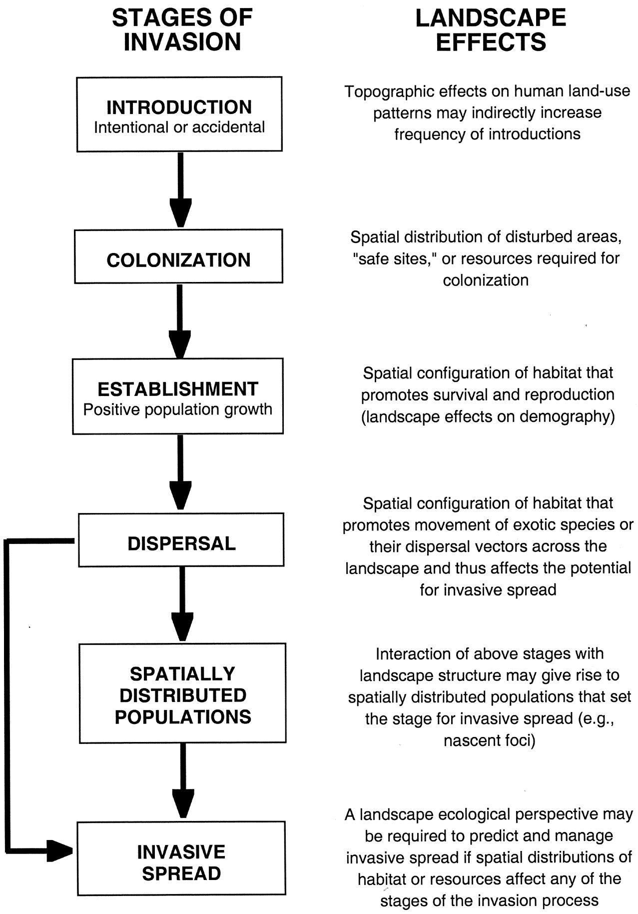

Figure 1. How landscape structure may affect the process of invasive spread.

Landscape Ecology: the Effect of Spatial Pattern on Ecological Process

Landscape ecology has been variously defined as (1) "the study of the structure, function and change in a heterogeneous land area composed of interacting ecosystems" (Forman & Godron 1986); (2) "the investigation of ecosystem structure and function at the landscape scale" (Urban et al. 1987); and (3) the study of the "effect of pattern on process" (Turner 1989). The first two definitions imply that a landscape is an area of broad spatial extent that occurs at a level of organization above ecosystems and communities (but below the biome) in the traditional ecological hierarchy. If this is the case, then landscape ecology is little more than "big-scale" or regional ecology, in which the questions being asked are the same as those in other areas of ecology, but at much broader scales. This approach is not a trivial undertaking, even with the advent of remote sensing and geographical information systems (e.g., Mack 2000). The invasive species problem can benefit from a macroscopic approach, especially in terms of documenting general patterns of invasibility and monitoring regional patterns of spread, because more-robust relationships are likely to emerge at broader scales (e.g., Lonsdale 1999). Such a definition of landscape ecology does not by itself represent a particularly unique contribution to the study of invasive species, however. Furthermore, equating landscape with broad spatial scales is anthropocentric because it is based on the spatial scales at which humans operate rather than the scale of the ecological phenomena being studied within a landscape context. It also imposes a level of organization on ecological investigations that is inappropriate if landscapes do not represent a true level of ecological organization (i.e., above ecosystems; King 1997; Allen 1998).

Adopting a broader view of a landscape as a "spatially heterogeneous area" (Turner & Gardner 1991) allows for a much richer definition and scope for the discipline of landscape ecology. *Landscapes* are defined at any scale relative to the ecological process or organism under investigation (Wiens 1989). *Landscape ecology* is then uniquely defined as the study of the ecological consequences of spatial pattern (Turner 1989). This is the perspective I adopt throughout this essay. A landscape ecological perspective on invasive spread thus involves understanding how the spatial distribution of resources, populations, or habitat at any scale affects various stages of the invasion process. I begin by reviewing the classes of spatial models that have been applied to predict invasive spread. This provides a point of departure for exploring what spatially structured models—those that explicitly incorporate the effects of landscape structure—can contribute to the problem of the spread of invasive species.

Spatial Models of Invasive Spread

Spatial models of invasive spread have a long tradition in ecology, beginning with the work of Skellam (1951), who used simple reaction-diffusion (RD) models to describe the spread of muskrats (*Ondatra zibethicus*) in central Europe. Reaction-diffusion models are still the most common models of invasive spread (Andow et al. 1990; Higgins & Richardson 1996; Higgins et al. 1996) and are based on partial differential equations of the general form

$$\frac{\partial N}{\partial t} = rN + D\left[\frac{\partial^2 N}{\partial x^2} + \frac{\partial^2 N}{\partial y^2}\right], \tag{1}$$

where $N(x,y,t)$ is the population density at time t at point x,y on the landscape, r is the per capita population growth rate, and D is the diffusion coefficient (the rate of random movement across the landscape). Thus, although RD models are spatial in that population density varies across the landscape, the landscape is spatially homogeneous and the redistribution of individuals is assumed to occur as a random-dispersal process.

Empirical dispersal data for a wide range of organisms, however, typically show leptokurtic or "fat-tailed" distributions in which rare long-distance dispersal events occur. Such dispersal functions can be incorporated within integrodifference equation (IDE) models, which also have a long history, although their appearance in the ecological literature has been relatively recent (e.g., Kot et al. 1996). Unlike RD models, which assume that dispersal and reproduction occur simultaneously and continuously, IDE models break dispersal and population growth into separate stages, as is typical of many organisms. The model is composed of two parts: a difference equation that describes population growth at each point on the landscape (here a one-dimensional transect) and an integral operator that accounts for the dispersal of organisms in space (i.e., the dispersal kernel). Integrodifference equation models thus have the general form

$$N_{t+1}(x) = \int_{-\infty}^{\infty} k(x,y) f[N_t(y)]dy, \tag{2}$$

where $N_{t+1}(x)$ is the population density at some destination point x, which is a function of the population growth at each source point y ($f[N_t(y)]$) and the movement of individuals from y to x according to the shape of the dispersal kernel, k.

Integrodifference equation models reveal that it is the long-distance component of dispersal that ultimately governs invasion speed, even when long-distance dispersal is rare (Kot et al. 1996; Lewis 1997; Neubert & Caswell 2000). Although the shape of the dispersal distribution has been assumed to be more important than demographic parameters in influencing invasions (van den Bosch et al. 1992), models that lack stage-structured dispersal will always overestimate invasion speed because not all life stages disperse (Neubert & Caswell 2000). Furthermore, demography may be just as important as dispersal in determining the rate of invasive spread. Invasion speed is highly correlated with population growth rate (λ) in teasel (*Dipsacus sylvestris*), which invades fields in the northeastern United States, to which it was introduced from Europe in the late nineteenth century (Neubert & Caswell 2000). Similarly, the spread of House Finches (*Carpodacus mexicanus*) throughout the eastern United States, following their release from Long Island in 1940, was strongly correlated with the rate of population growth near the center of their range (Veit & Lewis 1996). The inclusion of a mild Allee effect at the front of the invasion wave (where a small proportion of long-distance migrants are unsuccessful in finding mates) was responsible for significantly slowing the rate of invasion, especially during the period of initial spread (Veit & Lewis 1996; Lewis 1997). These studies highlight the importance of demography by demonstrating that the rate of invasive spread cannot be predicted from the shape of the dispersal kernel alone.

Although RD and IDE models are spatial models, they generally have not considered how spatial pattern influences invasive spread, assuming instead that the landscape is homogeneous in order to simplify the mathematical expression of this process. If individual dispersal or demography are affected by landscape structure (e.g., With 1994; With & King 1999*a*, 2001), however, it may be inappropriate to treat these as fixed rates independent of spatial pattern. Thus, RD and IDE models may not predict invasive spread adequately when spatial pattern significantly influences dispersal or demography, although to what extent spatial pattern might "significantly influence" invasive spread is currently unknown. Spatially structured models of invasive spread are needed to determine the degree to which spatial structure influences the process of invasion and thus when the addition of spatial structure is required to predict rates of invasive spread. I next examine how adopting a landscape ecological perspective can contribute to an understanding of how spatial pattern affects invasive spread.

Toward a Landscape Ecology of Invasive Spread

Effect of Landscape Structure on the Potential for Invasive Spread

Although habitat loss and fragmentation are expected to enhance invasive spread, it is unknown at what level of landscape disturbance this might occur. To address this problem, it is necessary to define when landscapes become critically disturbed or fragmented. Neutral landscape models (NLMs) have been used to predict when landscapes become fragmented, which is defined in terms of overall landscape connectivity (Gardner et al. 1987; With 1997; With & King 1997). Landscape connectivity is determined by the ability of organisms (or their propagules or dispersal vectors) to move among habitat patches, which in turn is affected by the spatial arrangement of habitat. The disruption of landscape connectivity is predicted to occur abruptly, at a threshold level of habitat loss and fragmentation called the percolation threshold (With 1997).

The significance of percolation thresholds for invasion biology is that invasive spread may occur most rapidly and extensively above a threshold level of disturbance (i.e., amount of habitat destruction). The specific threshold at which that occurs, however, depends on the pattern of disturbance (i.e., the degree of fragmentation). To illustrate, consider an invasive plant that can spread only to neighboring cells (dispersal neighborhood, $n = 4$ cells), provided that disturbed habitat suitable for colonization is available (e.g., presence of bare-ground sites). Thus, the species has limited dispersal ability (local dispersal), but then not all invasive species are good dispersers (e.g., agricultural weeds). If disturbances are small and localized, so as to create a more fragmented pattern of disturbed habitat, the spread of this species will be confined to a small portion of the landscape until about 70% of the landscape is disturbed, at which point it is able to percolate across the entire map (Fig. 2a; Fig. 3a, random curve). If disturbances are large and concentrated, however, this species would be able to percolate across a landscape in which as little as 30% of the habitat had been disturbed (Fig. 2c; Fig. 3a, clumped fractal curve).

From this it follows that fragmentation of the habitat through which the species is able to disperse might provide a means for controlling invasive spread (e.g., Turner et al. 1989). This may involve reducing the ex-

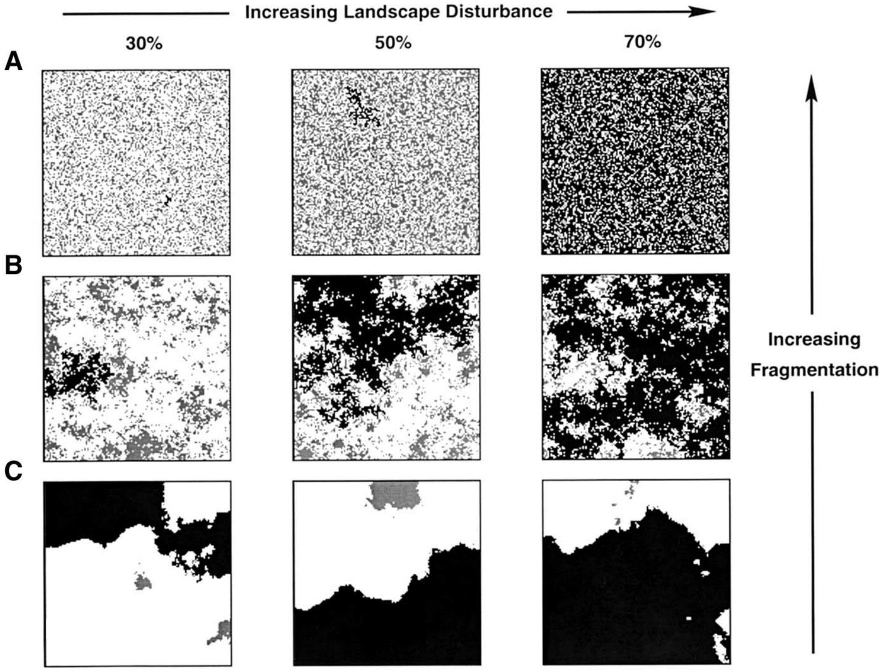

Figure 2. Effect of landscape structure on the potential for invasive spread (black). The invasive species shown here has poor dispersal ability and is constrained to move only through adjacent cells of suitable habitat (neighborhood size, n *= 4). (a) Spread in a random landscape (maximum fragmentation) at different levels of habitat disturbance. (b) Spread across a fragmented fractal landscape in which disturbances are spatially uncorrelated (*H *= 0.0). (c) Spread in a clumped fractal landscape where disturbances are spatially autocorrelated (*H *= 1.0).*

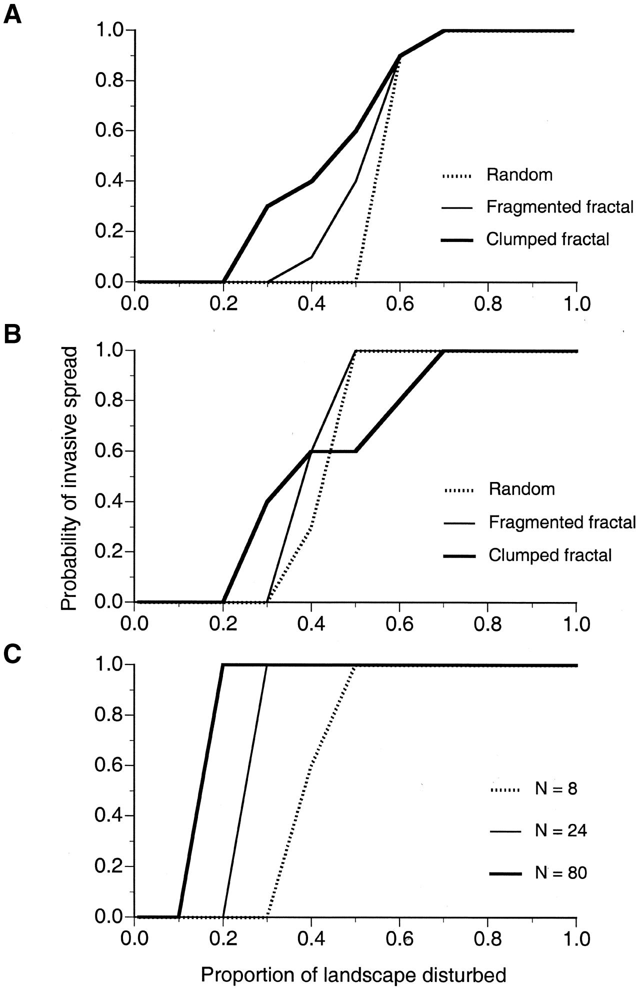

Figure 3. Probability of invasive spread as a function of landscape disturbance. (a) An invasive species with poor dispersal ability constrained to move only through adjacent cells of suitable habitat (neighborhood size, $n = 4$*) in different landscapes (cf. Fig. 2a). (b) Probability of invasive spread for a species with better dispersal ability (*$n = 8$*) in different landscapes. (c) Invasive species in fragmented fractal landscapes (e.g., Fig. 2b) that vary in dispersal ability. Figures modified from those of With (1999).*

tent and connectivity of disturbed habitats that promote the spread of exotic species. Not all exotic species spread through disturbed areas, however. Some species may spread through native habitats, in which case intentional fragmentation in strategic sections of the landscape may help slow the rate of spread. Such a proposal may at first seem antithetical to conservation, because habitat fragmentation may have adverse effects on indigenous species, especially those with poor dispersal abilities and low reproductive output (low demographic potential) that are particularly sensitive to habitat loss and fragmentation (e.g., With & King 1999*b*). Fragmentation may also facilitate the spread of other exotic species across the landscape. Where appropriate, however, deliberate habitat fragmentation may act as a "fire break" to minimize or control the spread of invasive species with limited dispersal abilities. This is consistent with the management practice of creating "barrier zones" at invasion fronts where eradication or suppression activities are employed to prevent or slow the rate of expansion, as the U.S. Forest Service has done to control the spread of gypsy moths (*Lymantria dispar*) (Sharov & Liebhold 1998). In this case, the barrier zone would be a physical one that disrupts the movement of organisms across the landscape.

Deliberate habitat fragmentation is not appropriate for the management of all invasive species, however. Consider another invasive species with better dispersal abilities (spread to adjacent and diagonal cells; dispersal neighborhood, $n = 8$ cells). As before, fragmentation minimizes invasive spread at low levels of disturbance (20–40%, random or fragmented fractal landscape; Fig. 3b). At intermediate levels of disturbance (40–60%), however, this species may be able to spread farther across a fragmented landscape by using fragments as stepping stones to dispersal (Fig. 3b). In general, good dispersers are expected to be less affected by fragmentation and are capable of percolating at lower levels of disturbance (Fig. 3c).

Another concern is that habitat fragmentation creates more edge, which may facilitate invasion into habitat remnants by species that move primarily between habitat types. For example, the occurrence of non-native plants is greater along edges of forest fragments (woodlots) in agriculturally dominated landscapes in the midwestern United States (Brothers & Spingam 1992). In eastern Australia, the invasion of dry sclerophyll bushland by *Pittosporum undulatum* is enhanced along urban edges in fragmented landscapes (Rose 1997). These types of invasive species might therefore benefit from a moderately fragmented landscape where edge is maximized.

Thus, fragmentation per se cannot be embraced as a general management guideline for controlling invasive spread, although landscape management to minimize spread should be possible in theory. To my knowledge, no study has yet explored the feasibility of landscape manipulation (or the manipulation of the spatial distribution of resources at any scale) to control invasive spread, probably because efforts are generally targeted at the eradication or suppression of specific populations as a means of controlling spread.

Although these percolation-based landscape models are based on assumptions about dispersal, such as the gap-crossing abilities of species, they do not incorporate specific processes that contribute to invasive spread, such as demographic factors leading to successful colonization and establishment. Their main contribution is thus to enhance our understanding of how landscape structure might affect the potential for invasive spread in fragmented landscapes. To make this approach more process-based, the next step in developing a landscape ecology of invasive spread involves understanding how spatial pattern—resource distributions or habitat fragmentation—affects various stages of the invasion process.

Effect of Landscape Structure on the Invasion Process

The invasion process involves several stages, which include (1) introduction, (2) colonization (e.g., germination), (3) successful establishment (i.e., survival and successful reproduction in new location), (4) dispersal to new sites, which may lead to (5) spatially distributed populations, which may set the stage for (6) invasive spread (Fig. 1). Given that many invasions are initiated by the intentional or accidental introduction of a nonindigenous species by humans, it is unlikely that landscape structure plays a role in the initial arrival of such species, which involves transport across some geographic barrier (e.g., Richardson et al. 2000*a*). The exception is when topography and other features of the landscape also shape human land-use patterns and thus indirectly facilitate the introduction of exotic species (landscape effects on introduction, Fig. 1). Similarly, landscape position may also influence whether invasions become initiated. For example, the proximity of pine-tree (*Pinus*) plantations to native habitat types affected the likelihood that pines escaped cultivation and spread into the adjacent forests, shrublands, and grasslands of South Africa (Higgins & Richardson 1998).

Successful colonization requires high propagule pressure (number of propagules arriving at a site), repeated introductions into the appropriate habitat, or overcoming environmental barriers that affect survival (Richardson et al. 2000*a*). The ability of a species to colonize successfully may nevertheless depend on the availability of suitable sites, which may occur ephemerally as a spatiotemporal mosaic of disturbance (i.e., an interaction between species' dispersal abilities and landscape dynamics; Fig. 1, landscape effects on colonization), and will be discussed later in the section on how landscape dynamics affect the invasibility of communities.

Effect of Landscape Structure on Dispersal Success of Invasive Species

Predicting the effects of habitat fragmentation on invasive spread will require, at a minimum, an understanding of the scale at which species interact with the scale of landscape structure. The observation that the dispersal distances of many species (or their propagules) exhibit a leptokurtic distribution indicates that rare long-distance movements across unsuitable habitat are to be expected. If these rare long-distance movements ultimately govern invasion speed (Lewis 1997; Higgins & Richardson 1999; Neubert & Caswell 2000), it might be argued that landscape structure—the spatial arrangement of habitat or resources—should have little or no effect on invasive spread. Indeed, this was demonstrated for wind-dispersed pine trees (*Pinus pinaster*) invading the fynbos of South Africa, in which a small percentage of seeds (0.1%) moved long distances (1–10 km; Higgins & Richardson 1999). Good dispersers are not necessarily good colonizers, however. Long-range dispersal is unnecessarily risky when suitable habitat is patchily distributed (i.e., clumped or aggregated in space; Lavorel et al. 1994, 1995) or when Allee effects occur (Veit & Lewis 1996, Lewis 1997). In landscapes where colonization sites are clumped, short-range dispersal ensures that most propagules will fall within the same local neighborhood where other suitable habitat sites (or mates) are likely to be found, which eventually leads to full landscape occupation (i.e., spread; Lavorel et al. 1995). Where two species might be competing for space (e.g., an invasive vs. a native plant species), the species with the shorter dispersal distance will inevitably displace the other, all else being equal (Lavorel et al. 1994).

Some research related to how landscape structure affects dispersal and invasive spread involves the recent modeling efforts directed at simulating tree migration within fragmented landscapes in response to climate change (e.g., Schwartz 1992; Dyer 1995; Malanson & Cairns 1997; Pitelka et al. 1997; Higgins & Richardson 1999; Collingham & Huntley 2000). Schwartz (1992) found that fragmentation at moderate levels affected migration rate when dispersal was mostly local (i.e., a negative exponential dispersal function) but affected it less so when a leptokurtic distribution was used, which allowed for the occasional long-distance dispersal event. This is consistent with the expectation that fragmentation is unlikely to affect species that are capable of long-distance movements, even though these events are rare. In contrast, Dyer (1995) suggested that continuous tracts of favorable habitat might be required to facilitate migration of wind-dispersed species (e.g., *Pinus*), in spite of their occasional feats of long-distance dispersal (modeled as one 2.5-km dispersal event per generation), because wind dispersal is inherently random (or at least was modeled as such), making establishment tricky if the species drifted too far beyond the source patch. This is consistent with the tradeoff between dispersal distance and colonization success in fragmented landscapes discussed by Lavorel et al. (1995). Habitat fragmentation reduced the migration rate of wind-dispersed species in Dyer's (1995) model because typical dispersal distances tended to be shorter than those of bird-dispersed species such as *Quercus* (e.g., 200 m vs. 1.1 km, respectively). In fact, migration of bird-dispersed species might actually be enhanced in fragmented landscapes, because habitat fragments create stepping stones along which jays deposit acorns (forest edges), resulting in a more directed dispersal across the landscape than achieved by wind. This is also suggested by percolation models of invasive spread (see "Effect of Landscape Structure on the Potential for Invasive Spread"), in which good dispersers were more likely to spread across fragmented than clumped landscapes at intermediate levels of disturbance (Fig. 3b).

Many of these researchers found that migration rates are critically reduced below a certain threshold of habitat availability. Schwartz (1992) found an order-of-magnitude reduction in migration rate when suitable habitat for colonization occupies only 20% of the landscape. Malanson and Cairns (1997) found that a threshold in migration rate occurs when suitable habitat is reduced to <33% of the landscape. Collingham et al. (1996) found that migration rates are little affected by fragmentation until <10% of a landscape represents habitat suitable for colonization. Landscape structure affects migration rates only when suitable habitat falls below 10–25%, depending on the pattern of fragmentation (Collingham & Huntley 2000). In that study, migration rates were slowest in clumped landscapes that had large gaps between habitat patches (suitable sites for colonization).

The recurring threshold in dispersal or migration rates at low levels of suitable habitat—or at high levels of fragmentation or disturbance—is probably related to lacunarity thresholds, rather than percolation thresholds of landscape connectivity (With & King 1999*a*). Lacunarity measures the distribution of gap sizes (interpatch distances) on the landscape (Plotnick et al. 1993). The lacunarity index (Λ) increases nonlinearly on landscapes with <10–20% suitable habitat, meaning that the distance between patches increases suddenly below this threshold (Fig. 4). Consequently, dispersal success declines precipitously in the same domain as lacunarity thresholds, particularly on clumped landscapes where the interpatch distances (gap sizes) are greatest (With & King 1999*a*; Fig. 4). Thus, manipulating such thresholds in landscape structure may offer a means of controlling invasive spread.

Thresholds in dispersal or migration rates might not always occur, however. A linear decline in migration rate as a function of habitat loss was observed in the simulated migration of a wind-dispersed tree (*Pinus pinaster*; Higgins & Richardson 1999). This study also failed to document an effect of fragmentation on tree-migration rates, in contrast to Dyer's (1995) model, which was parameterized for a generic wind-dispersed pine. In Dyer's study, dispersal was modeled to include both short and long distances, but these are basically independent events, and most dispersal occurs to neighboring cells. The dispersal function in Higgins's and Richardson's (1999) model simultaneously includes the short- and long-distance components of dispersal (by fitting a mixture of Weibull distributions to the frequency distribution of seed-dispersal data). This dispersal function thus integrates across the various scales at which different dispersal processes operate, which may mitigate any effect of habitat fragmentation on dispersal or migration rate. Again, the scale(s) at which dispersal interacts with the scaling of habitat or resource distributions determines whether or to what extent landscape structure will affect dispersal success and, ultimately, invasive spread.

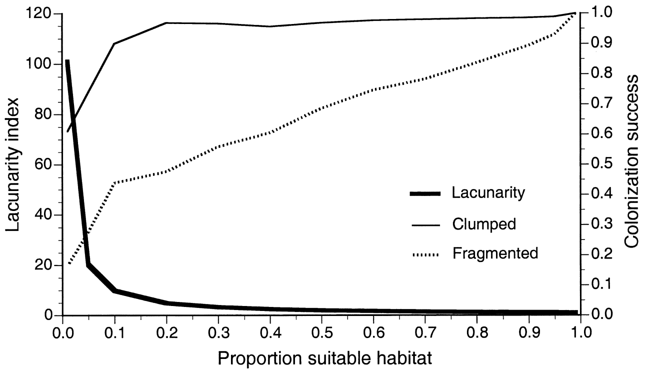

*Figure 4. Effect of landscape structure on colonization success for an invasive species with local dispersal (*n = 8*) on clumped and fragmented fractal landscapes (cf. Fig. 2b & 2c). Thresholds in dispersal (colonization success) coincide with thresholds in lacunarity, a measure of interpatch distances (assessed here at the finest scale of a 1 × 1 box size; With & King 1999*a*).*

Although landscape structure may affect the dispersal of exotic species or their propagules, it may also have an effect on the movement or activities of dispersal vectors, which has obvious implications for invasive spread. For example, pied curragwongs (*Strepera graculina*) have been implicated in the spread of the forest-dwelling *P. undulatum* into bushland habitats that adjoin residential developments (Rose 1997). Pied currawongs are the primary dispersal vectors for fruits of *P. undulatum*, and are one of the few native species that have been successful in exploiting suburban areas. Their increased abundance and concentrated activity along these suburban-bushland edges have facilitated the spread of *P. undulatum* beyond its native range. Fragmentation may also promote the spread of exotic species across landscapes if habitat remnants attract or concentrate vertebrate seed dispersers, such as when birds perch and defecate on trees within woodlots scattered throughout an agricultural landscape. The planting of windbreaks has been advocated as a means of accelerating natural succession in degraded or agricultural areas, because trees attract seed dispersers and thus increase the seed rain of forest plants into these areas (Harvey 2000). It is thus possible that in the same manner such forest fragments could also serve to accelerate invasion by exotic species into these landscapes.

Effect of Landscape Structure on Demography of Invasive Species

Successful dispersal is only part of the equation. Many of the previously discussed landscape models do not incorporate demographic processes or examine fragmentation effects on demographic rates. Recent theoretical work has demonstrated that demographic rates might ultimately be more important than dispersal ability for predicting the ability of populations to persist in fragmented landscapes (South 1999; With & King 1999*b*). Fragmentation may affect tree migration rates more through a reduction in source strength (the number of propagules produced) than through the creation of dispersal barriers, once some threshold is exceeded (Malanson & Cairns 1997). Thus, landscape effects on demography involve factors that affect fecundity or survivorship of exotic species (population vital rates), which may affect establishment and thus govern the rate of invasive spread (Fig. 1).

As an example, consider how landscape structure might affect population vital rates in plants. Habitat destruction and fragmentation may increase resource availability (such as light) that can be exploited by invasive species directly (Luken et al. 1997) or indirectly by mediating competition with native plants, which may increase the performance of exotic species in disturbed areas by increasing germination, growth, or seed set. Using a combination of simulation models and field experiments, Bergelson et al. (1993) demonstrated that the size and distribution of disturbed areas influence the probability that seeds of the weed *Senecio vulgaris* will survive to maturity. This effect of landscape structure (distribution of bare-ground areas) on survivorship ultimately affects the population growth rate and determines the rate at which *Senecio* can spread across the landscape.

Demographic rates of exotic species may be different in novel environments than in their native habitats, which may fundamentally alter their response to landscape alteration. For example, the Australian shrub *Acacia cyclops* exhibits higher fecundity in the fynbos of South Africa than in its native land (Richardson et al. 2000*b*). This is typical of many exotic plants and is generally attributed to a release from seed predators in the new environment. High fecundity interacts strongly with rare, long-distance dispersal events, such that more seeds are dispersed farther on the landscape (Higgins & Richardson 1999). Subsequently, the invasive spread of *A. cyclops* was predicted to be little affected by landscape structure in the South African fynbos, although lower levels of fecundity would have reduced its rate of spread when habitat was limiting in its native Australia (Richardson et al. 2000*b*). To control the spread of this species, management efforts might first be directed at reducing its fecundity, which would then increase its sensitivity to fragmentation or other land-management practices.

Invasive spread requires successful dispersal and positive population growth rates. Assessing the relative contributions of dispersal and 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. (1993) demonstrated that *Senecio* is able to disperse farther when bare-ground areas are distributed uniformly across the landscape (i.e., landscape is fragmented). In contrast, the population growth rates of *Senecio* are enhanced when disturbed areas are aggregated in space (i.e., not fragmented). More plants are able to establish successfully when suitable sites for colonization are clumped, because a greater concentration of seeds can build up in these sites (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 it and the species can move farther or “percolate” across the entire landscape. In contrast, population persistence and growth rates are enhanced in landscapes with more-aggregated habitat. Even for an aggressive weed like *Senecio*, such trade-offs might make it difficult for a species to persist on the landscape simply by outdispersing superior competitors. An inferior, but established, competitor can slow the advance of an invading species (Hart & Gardner 1997). Successful invasion requires a species to maintain positive growth rates ($\lambda > 0$) on the landscape, but the demographic aspects of the invasion process, particularly in terms of how landscape structure affects population vital rates, have received less attention than dispersal and are in need of further study.

Spatially Distributed Populations and Invasive Spread

Most invasions do not occur along a single wave front or as a single expanding focus, as depicted in most spatial models of invasive spread (see “Spatial Models of Invasive Spread”). The interaction of landscape structure with dispersal and demography may produce a spatially distributed population that sets the stage for further invasion (Fig. 1). Such spatially distributed populations are characterized by multiple foci resulting from repeated introductions or ongoing dispersal from an initial point of introduction that create satellite populations, or “nascent foci” (Moody & Mack 1988). Invasion occurs through continued establishment of nascent foci in outlying areas, which then grow and coalesce. These spatially distributed populations vary tremendously in size owing to different dates of establishment, constraints of landscape structure (size and geometry of habitat), and the inherent stochasticity of small populations (Moody & Mack 1988). The importance of controlling the invasive spread of exotic plants by eradicating these small, nascent foci on the periphery of the main area of infestation has been demonstrated by Moody and Mack (1988).

Landscape Effects on Invasibility

The invasibility of a system is determined by several factors, including climate, disturbance regime, and the competitive abilities of native species (Lonsdale 1999). In particular, landscape structure might affect species interactions, such as competition, in ways that favor invasion or reduce the resistance of communities to invasion. Habitat fragmentation produces edge effects, in which the direction or magnitude of species interactions may be enhanced or even altered (e.g., Fagan et al. 1999). For example, enhanced competition with, or intense predation or parasitism by, an invasive species may negatively effect the survivorship and reproductive success of native species, increasing their susceptibility to extinction and thus the vulnerability of the community to invasion. Not all ecological interactions that promote invasion are negative, however. The presence and spatial distribution of mutualists on the landscape, such as dispersal vectors, pollinators, or mycorrhizal fungi, may be critically important for the success and spread of an invasive species (Richardson et al. 2000*c*). These mutualistic interactions may occur between native species that perform these services for exotic species or may result from a synergy that develops between two or more introduced species.

Evolutionary Constraints on Invasion Resistance in Fragmented Landscapes

Negative ecological interactions between exotic and native species may also create landscape sinks in which native populations are unable to persist ($\lambda < 0$) without continual immigration from outside sources (e.g., Pulliam 1988). Such source-sink dynamics in fragmented populations may then compromise the ability of native species to mount an evolutionary defense to invasion. Habitat loss and fragmentation may decrease population sizes and the genetic diversity of native populations, compromising the potential for adaptive responses to invasive species. At the same time, such disturbances may facilitate the spread of invasive species (e.g., Bergelson et al. 1993), thus increasing gene flow and contributing to the high genetic variability of invasive species. This further promotes the adaptability of invasive species in response to disturbance (Dietz et al. 1999).

For example, the invasion of the eastern United States by Brown-headed Cowbirds (*Molothrus ater*), an avian brood parasite, was apparently facilitated by widespread deforestation following European settlement in the nineteenth century (Mayfield 1965). Given that cowbirds were not native to this region historically, native forest-breeding songbirds generally lacked defenses for dealing with brood parasitism, such as egg-rejection strategies that have developed in regions where cowbirds and their hosts have coevolved. Cowbird parasitism has significantly curtailed reproduction in at least some species, which should generate strong selective pressure (Robinson et al. 1995). Rapid evolutionary changes can emerge in populations subjected to strong selective pressures (Thompson 1998, 1999). Why, then, have avian hosts failed to evolve adaptive strategies for dealing with brood parasitism in the 200 or so years since cowbirds have invaded the eastern United States?

An intriguing hypothesis (R. Holt, personal communication) posits that adaptive constraints in host-parasite interactions are expected in fragmented landscapes as the result of source-sink dynamics that arise in the host population (Holt & Gaines 1992; Holt & Gomulkiewicz 1997). The midwestern and eastern United States consist of a mosaic of fragmented and continuously forested landscapes (e.g., Donovan et al. 1997). Because fragmented landscapes are population sinks for some forest-interior birds (Donovan et al. 1995; With & King 2001), these populations are sustained by immigration from landscape sources. Consequently, selection for behaviors, such as egg rejection, in sink landscapes would be constantly diluted by immigrants from source landscapes where selection is less stringent. Landscape structure (habitat fragmentation) may thus impose a constraint on the ability of native species to adapt to invasive species.

The spatial configuration of patches within a landscape can also promote the adaptive response of exotic species to new environments. The invasion of serpentine grasslands in California by Mediterranean grasses such as *Avena fatua* and *Bromus hordeaceus* is greatly enhanced within small patches (<5 ha) of serpentine grasslands because of the high influx of seeds from the surrounding landscape matrix (i.e., edge effects are greater in small patches than large ones; Harrison et al. 2001). An adaptive response leading to the differentiation of a "serpentine ecotype," in which these exotic grasses perform better on serpentine than nonserpentine soils, occurs within small patches and is likely facilitated by the grasses' high dispersal rate, which provides the necessary genetic variation upon which selection can operate.

Influence of Landscape Dynamics on Invasibility

Landscape dynamics refer to changes in the patch structure of habitat, resources, or land use, which usually may occur in response to disturbance. Disturbances may be natural or anthropogenic and occur across a wide range of temporal and spatial scales (Pickett et al. 1989). Different types of disturbance are likely to affect system invasibility in different ways and at different scales, and a given disturbance may have contrasting effects on different stages of the invasion process (e.g., colonization vs. invasive spread; Bergelson et al. 1993). Untangling the complexity of interactions between disturbances and species' life-history attributes to determine invasion success is a research challenge. Disturbance alters the availability of resources, which may be a key factor controlling ecosystem invasibility (Davis et al. 2000). Resource availability may increase due to a decline in resource use by the community, as might occur after a disturbance, or because of increased resource supply to the system (e.g., increased precipitation, nutrient enrichment, elevated light levels). The increase in resource availability is often transient (e.g., Seastedt & Knapp 1993), but the ecosystem is particularly vulnerable to invasion during these relatively brief windows of opportunity (Davis et al. 2000). If a general theory of invasion biology is to emerge, it must incorporate the effect of the spatiotemporal dynamics of interacting disturbances on the invasion process.

Summary

Although habitat loss, fragmentation, and invasive species pose the greatest threats to biodiversity, there has been little research that integrates these areas of study into a comprehensive framework for understanding and predicting the effects of landscape structure (or spatial pattern more generally) on invasive spread. The need for a landscape ecology of invasive spread was recognized by Mooney and Drake (1989) over a decade ago: "Spread through a patchy environment is likely to depend on the degree of habitat heterogeneity, size and distribution of patches, distance between suitable patches, and population characteristics such as growth rate . . . and dispersal ability." Yet the question remains: how does landscape pattern affect the invasion process and the rate of invasive spread? I have outlined six ways in which landscape structure can affect invasive spread and the invasibility of communities.

(1) Thresholds in landscape structure occur and may affect invasive spread. Landscape models predict that the potential for invasive spread may be greatly enhanced past some threshold level of disturbance, which is determined by the spatial pattern of disturbance, the mode of dispersal, and the shape of the dispersal-distance function. Such thresholds in landscape structure might be manipulated to control the spread of invasive species through habitat management or restoration efforts.

(2) Landscape structure may affect different stages of the invasion process in different and possibly contrasting ways. Land management to minimize invasive spread may be complicated if landscape structure affects the dispersal and demography of an invasive species in contrasting ways. For example, fragmentation may reduce establishment and source strength but enhance dispersal success. Deciding which land-management scenario will best control invasive species will depend on whether dispersal or demography contributes more to invasive spread.

(3) Landscape structure may alter species interactions in ways that enhance the invasibility of communities. Habitat fragmentation may directly affect the population viability of native species, thereby enhancing extinction risk and rendering such communities more vulnerable to invasion. In addition, ecological interactions may be altered at habitat edges in ways that give invasive species an advantage over native species. The occurrence and spatial distribution of mutualists (e.g., seed dispersers) on the landscape may also facilitate invasive spread.

(4) Landscape structure may affect the distribution of exotic species in fragmented landscapes, resulting in satellite populations (nascent foci) beyond the population core, which may greatly accelerate invasive spread.

(5) The adaptive potential of native species to resist invasion may be compromised in fragmented landscapes. Fragmented landscapes may function as overall population sinks, which are maintained by immigration from source populations in more intact landscapes. Native species may thus fail to evolve adaptative strategies for dealing with invasive species, because selection is continually diluted by immigrants from source landscapes where selective pressures are less stringent. Alternatively, fragmented landscapes may enhance the adaptive response of exotic species to novel environments, particularly if continual dispersal or introduction enhances genetic variation within these populations.

(6) The disturbance architecture of landscapes likely affects the invasibility of communities. The spatiotemporal dynamics of landscapes may create windows of opportunity (or vulnerability), such as transient increases in resource availability, that may facilitate invasion.

Understanding the effect of landscape structure on invasion biology may thus be important for predicting and halting the spread of invasive species. Spatially structured models of invasive spread are required to determine the degree to which landscape structure influences invasive spread and the stages of invasion most affected by landscape structure. Empirical or experimental investigations into the effect of spatial pattern on invasion are also required, not only for model calibration and verification but also for documenting the effect exotic species have in fragmented landscapes and how fragmentation facilitates invasive spread, and for evaluating the potential of land-management strategies for controlling the spread of invasive species. A landscape ecology of invasive spread may thus afford new insights into and opportunities for the study and management of invasive species.

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