

# 2. METAPOPOPULATION DYNAMICS: PERSPECTIVES FROM LANDSCAPE ECOLOGY

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## 2.1 INTRODUCTION

It is no coincidence that the current biodiversity crisis occurs at a time when landscapes are being transformed faster than ever before in human history (With, 2004). Many conservation issues are ultimately human land-use issues (Wiens, 2002), which is why the discipline of landscape ecology has become increasingly relevant for the management and conservation of biological diversity (e.g., Gutzwiller, 2002). Processes that operate at broader spatial scales likely influence the occurrence and persistence of an organism at a local scale, and thus a landscape perspective is ultimately required for assessing species' extinction risk.

Such acknowledgment of the importance of landscape ecology for conservation reinforces the common misconception that landscape ecology is concerned solely with broad spatial scales, however. In the present context, this would entail understanding metapopulation dynamics at a "landscape scale" (e.g., Rushton et al., 1997). Apart from the usual broad-scale anthropocentric definition of landscape, a landscape is defined more appropriately as a "spatially heterogeneous area" (Turner and Gardner, 1991) that is scaled relative

to the process or organism of interest (Wiens, 1989). By this rendering, metapopulation dynamics can then be studied in fragmented landscapes that range in scale from that encompassing bacteria and protozoan communities (Burkey, 1997) to spotted owls (*Strix occidentalis*; Gutiérrez and Harrison, 1996). The landscape thus provides a spatial context for understanding processes contributing to metapopulation dynamics and persistence in fragmented landscapes.

Although metapopulation theory is the current paradigm for the conservation of spatially structured populations in fragmented landscapes (Hanski and Simberloff, 1997), landscape ecology provides an additional perspective and suite of approaches that can complement metapopulation theory, particularly in applications that are not handled well by existing theory, such as those involving continuous habitat distributions or recently fragmented landscapes. Metapopulation theory is not applicable to species in landscapes in which the habitat is not distinctly patchy or already fragmented extensively (Moilanen and Hanski, 2001). Nor is the application of metapopulation theory necessarily appropriate for species in recently fragmented systems, given the assumption of equilibrium colonization–extinction dynamics that underlies much of the theory [but see Ovaskainen and Hanski (2002) and Chapter 4 for advances in metapopulation theory involving transient dynamics]. In particular, landscapes fragmented by human land-use activities may represent transient nonequilibrium dynamics in which a formerly continuous population has become subdivided into smaller, more isolated populations. Dispersal among populations is disrupted such that a functional metapopulation is not created; local extinctions are not balanced by recolonization, and consequently, all populations slowly decline to extinction (Hanski and Simberloff, 1997). Thus, a declining population may superficially resemble a metapopulation in structure, but not function like one. Spatial subdivision is a necessary, but not sufficient, condition for metapopulation dynamics.

Metapopulation theory has nevertheless drawn attention to the importance of landscape structure and dispersal for maintaining population persistence (Wiens, 1996). Indeed, the effect of patch structure on dispersal and colonization success is a unifying theme in both metapopulation theory and landscape ecology (Wiens, 1997). Colonization success is not simply a function of the distance between patches, but also depends on the nature of the intervening habitat or land-use matrix through which organisms disperse, which determines the “effective isolation” of patches (Ricketts, 2001). Incorporation of the more complex mosaic structure of real landscapes into metapopulation models has been viewed as the main promise of landscape ecology for metapopulation theory (e.g., Hanski and Simberloff, 1997; Wiens, 1997).

In a couple of earlier reviews, Wiens (1996, 1997) identified several landscape ecological concepts that are relevant to metapopulation ecology and which emphasize the dual importance of dispersal and heterogeneous landscape mosaics for understanding metapopulation dynamics: (1) landscape connectivity, which emerges as the interaction of individual movement with landscape pattern, is important for metapopulation persistence; (2) the landscape matrix matters for metapopulation dynamics because it affects dispersal and thus colonization success; (3) landscapes are heterogeneous mosaics of habitats and land uses, such that habitat quality varies across the landscape,

setting the stage for source–sink population dynamics (Chapter 16); and (4) landscape dynamics may affect, or even generate, metapopulation dynamics. The latter represents landscape heterogeneity in time as well as space.

In addition to these potential contributions of landscape ecology to metapopulation ecology, a more fundamental principle emerges from the definition of landscape ecology itself. Landscape ecology is the study of the effect of spatial pattern on ecological process (Turner, 1989). From this it follows that adopting a landscape ecological perspective to metapopulation dynamics entails understanding how spatial pattern, such as habitat fragmentation or heterogeneity, affects processes that contribute to the dynamics of spatially structured populations. This might involve, for example, understanding the relative effects of habitat fragmentation on dispersal (colonization) and demography on metapopulation persistence. This expanded perspective of landscape ecology is adopted in this chapter.

The objectives in this chapter are thus to (1) demonstrate what a landscape ecological perspective can contribute toward understanding metapopulation dynamics, beyond the usual suggestions that landscape ecology offers a broader scale perspective or more spatially complex rendering of landscape structure; (2) discuss how landscape structure is expected, or has been demonstrated, to affect various processes (dispersal, demography) that affect metapopulation persistence and thus extinction risk; (3) assess the implications of adopting a landscape ecological perspective for management and conservation; and (4) identify theoretical and empirical research needs that would help contribute to the further development of this “exciting scientific synthesis” between metapopulation biology and landscape ecology (see Hanski and Gilpin, 1991).

## 2.2 CONTRIBUTIONS OF LANDSCAPE ECOLOGY TO UNDERSTANDING METAPOPOPULATION DYNAMICS

This section addresses how landscape structure affects, or is expected to affect, the dynamics of metapopulations. This includes a discussion on issues pertaining to landscape connectivity, landscape connectivity and dispersal thresholds, the relative importance of dispersal for metapopulation persistence, landscape effects on demography and extinction risk, the source–sink potential of landscapes, extinction risk in dynamic landscapes, and the relative effects of habitat loss and fragmentation on metapopulation persistence.

### Landscape Connectivity Issues: Patch-Based vs Landscape-Based Measures

Habitat connectivity is a central theme in both landscape ecology and metapopulation ecology (Hanski, 1999a; Tischendorf and Fahrig, 2000a). Connectivity refers to the ability of organisms to access habitat, which affects colonization rates and thus metapopulation persistence on the landscape (e.g., Gonzalez et al., 1998; Kindvall, 1999). The emphasis in metapopulation ecology, however, has been on deriving *patch-based measures* related to the proximity and area of neighboring patches, which quantify the accessibility of

habitat patches to an individual on the landscape (Hanski, 1999a; Moilanen and Hanski, 2001). An overall measure of patch connectivity for the landscape can be obtained as a weighted average of patch isolation, which then gives the amount of habitat accessible to a random individual on the landscape (Hanski, 1999a). Overall patch connectivity may give an indication of landscape connectivity, but the latter is not formally derived mathematically from such patch-based measures (Tischendorf and Fahrig, 2001). Patch-based connectivity measures are best applied to extensively fragmented or distinctly patchy landscapes and are less applicable to more continuous habitat distributions (Moilanen and Hanski, 2001).

In contrast, landscape ecologists have focused on deriving measures of overall *landscape connectivity*. Habitat connectivity is thus being assessed at different scales — patch based vs landscape based — in these two disciplines. Landscape connectivity is defined as the degree to which various habitat types facilitate movement across the landscape (Taylor et al., 1993; With et al., 1997; Tischendorf and Fahrig, 2000a) and can thus be assessed for continuous habitat distributions and heterogeneous landscapes (Schippers et al., 1996; With et al., 1997). Landscape connectivity can be quantified in a number of ways, such as by the use of percolation theory and its neutral landscape derivatives (Gardner et al., 1987; With, 1997, 2002; With and King, 1997), graph theory (Urban and Keitt, 2001), and various other approaches (e.g., Schumaker, 1996; Tischendorf and Fahrig, 2000a,b). Although a full rendering of how landscape connectivity can be quantified lies beyond the scope of this chapter, the common theme underlying all of these approaches is how the movement behavior of organisms interacts with the patch structure of landscapes. Landscape connectivity thus emerges as a species-specific response to landscape structure based on factors such as the species' habitat affinities, gap-crossing abilities, movement rates, response to patch boundaries, and differential mortality through elements of the landscape (Wiens et al., 1993; Dale et al., 1994; With, 1997; With et al., 1997; Tischendorf and Fahrig, 2001; Vos et al., 2001).

Landscape connectivity is important for understanding the emergence of spatial structure in populations, which in turn is expected to have implications for the persistence and dynamics of metapopulations. As an example of how species-specific responses to heterogeneity affect landscape connectivity and population distributions, With and Crist (1995) used habitat-specific rates of movement in an individual-based simulation model inspired by percolation theory to predict the distributional patterns of two acridid grasshopper species in a heterogeneous landscape within the shortgrass steppe of the North American Great Plains. The largest species (*Xanthippus corallipes*) moved rapidly through the grass matrix (65% of the landscape), suggesting that the overall landscape was highly connected from the standpoint of this species. Its reduced rate of movement in the remaining third of the landscape resulted in the observed patchy population distribution, consistent with model expectations that good dispersers should exhibit patchy distributions when the landscape contained  $\leq 35\%$  preferred habitat because their high mobility allows individuals to locate and aggregate within the preferred habitat (assuming that individuals reduce their rates of movement and exhibit greater residence times in preferred habitats). In contrast, the lower mobility of the

smaller species (*Psoloessa delicatula*) prevented large numbers of individuals from locating and aggregating within its preferred habitat, which constituted a minor (8%) component of the landscape. Because of its relatively greater rates of movement through other grassland habitats, this species was expected to be distributed randomly across the landscape, which was consistent with its observed distribution in the field.

## Landscape Connectivity Issues: Data Requirements

Patch-based connectivity measures that form the basis of metapopulation theory have the distinct advantage of ease of model parameterization (Hanski, 1999b; Hanski et al., 2000; Chapter 5). Consistent with metapopulation theory's abstraction of landscape structure as discrete patches embedded in an ecologically neutral matrix, patchwise measures of connectivity have often been based on simplistic measures such as nearest-neighbor distances (Moilanen and Nieminen, 2002). More sophisticated measures of patch connectivity have been developed, however, which incorporate patch-area effects on emigration and immigration rates and species-specific dispersal distances (Moilanen and Hanski, 2001; Vos et al., 2001; Chapter 4). As the aforementioned grasshopper example illustrates, however, the connectivity of habitat patches is not just a simple function of the distance between patches. Because the intervening matrix may determine the effective isolation of patches (Ricketts, 2001), and thus overall landscape connectivity (With et al., 1997), explicit consideration of how the complex mosaic structure of heterogeneous landscapes affects colonization success and population extinction risk has typically been viewed as one of the most important contributions that landscape ecology has to offer metapopulation ecology (Hanski and Simberloff, 1997; Wiens, 1997).

The connectivity of heterogeneous landscapes is not easily captured by a simple index or landscape metric unfortunately, but is commonly tackled with an individual-based simulation modeling approach. Empirical data on habitat-specific movement parameters or residence times within different elements of the landscape are used to parameterize a rule- or vector-based movement model to simulate dispersal across a heterogeneous landscape map. Landscape connectivity is then inferred by extrapolating habitat-specific rates of movement, and perhaps other information (if available) about behavior at habitat edges (Lidicker and Koenig, 1996) or mortality risk while dispersing through the different elements of the landscape, to determine whether individuals are able to colonize a suitable habitat successfully. Some presumed correlate of a connected landscape, such as dispersal success, degree of population aggregation (With and Crist, 1995; With et al., 1997), or population connectivity (Schippers et al., 1996), is then used as an indirect measure of landscape connectivity.

Admittedly, quantifying the resistance of different habitat types to movement is a challenge in practice. Direct observation of individual movement responses to landscape structure is time intensive and is necessarily limited in temporal (and therefore spatial) extent, although this is bound to change with the increasing availability of satellite-tracking devices that permit the near-continuous monitoring of individuals. As an alternative, investigators

typically rely upon mark–recapture techniques to derive estimates of inter-patch movements in different matrix types (e.g., Pither and Taylor, 1998; Ricketts, 2001) or make inferences about matrix resistance based on observed patterns of patch occupancy in different landscape contexts (e.g., Moilanen and Hanski, 1998). For example, mark–recapture data were used to quantify the resistance of different matrix types to butterfly movement within a naturally heterogeneous landscape located in an alpine valley of the Colorado Rocky Mountains (Ricketts, 2001). Movement through coniferous forests was 3–12 times less likely than movement through willow thickets for the majority of these meadow butterfly species. Meadows separated by coniferous forest are thus effectively more isolated than meadows separated by a similar distance, but embedded in a willow matrix. Because of the difficulty and cost of attempting to reconnect habitat fragments with corridors or stepping stones to enhance dispersal and thus colonization success, it might be more practical to reduce the effective isolation of patches by altering management practices in the surrounding matrix (Ricketts, 2001). Corridors need not be linear features of the landscape, but can occur or be created through the juxtaposition of certain matrix types, such as different habitats or land uses, which serve to funnel individuals among habitat patches (Gustafson and Gardner, 1996; Vos et al., 2002).

### **Landscape Connectivity Issues: Asymmetrical Connectivity Among Populations**

Connectivity in heterogeneous landscapes may thus be difficult to identify from a simple analysis of landscape structure. Nor is the transfer of individuals among patches necessarily symmetrical in a heterogeneous landscape matrix. Gustafson and Gardner (1996) developed an individual-based simulation model to explore how altering landscape heterogeneity affected dispersal success for a generic organism among fragments of deciduous forest in several agricultural landscapes located in the midwestern United States. Emigration and immigration rates among forest fragments often were not symmetrical, leading Gustafson and Gardner (1996) to speculate that such asymmetrical transfers may be the rule rather than the exception in heterogeneous landscapes. If true, this presents a problem for patchwise connectivity measures in which colonization probabilities are based on interpatch distances that ignore matrix effects. To overcome this problem, distances between patches would need to be specified by direction and weighted by the resistance of the intervening matrix habitat to movement (i.e.,  $d_{ij} \neq d_{ji}$ ; see Urban and Keitt, 2001).

The potential for asymmetrical connectivity among populations of European badgers (*Meles meles*) was indicated by a GIS-based random walk model applied to a landscape in the central part of The Netherlands (Schippers et al., 1996). Urban areas, canals, and motorways either created barriers to movement or increased mortality such that asymmetries in the connectivity of populations emerged. Asymmetrical connectivity has also been found among populations of the critically endangered Iberian lynx (*Lynx pardinus*) in a human-dominated and therefore extensively fragmented region in southwestern Spain (Ferrerias, 2001). Although two source populations had similar emigration rates, they differed in their connectivity to outlying populations

because of differences in the matrix type surrounding each source. One of the sources was embedded in an agricultural matrix, which lynx avoided, and were instead funneled along a narrow corridor of a more suitable habitat to populations in the south and west. The other source population was located in the southwestern region, which consisted mainly of Mediterranean scrubland and tree plantations, and most dispersing individuals from this population settled in this region instead of dispersing toward the northeast. Thus, there is an asymmetrical transfer of individuals that occurs among populations: individuals tend to disperse from the northeast to the southwest, but not in the opposite direction. Such asymmetries could lead to a reduction in the effective connectivity, and thus metapopulation capacity (see Hanski and Ovaskainen, 2000), of the landscape for the species.

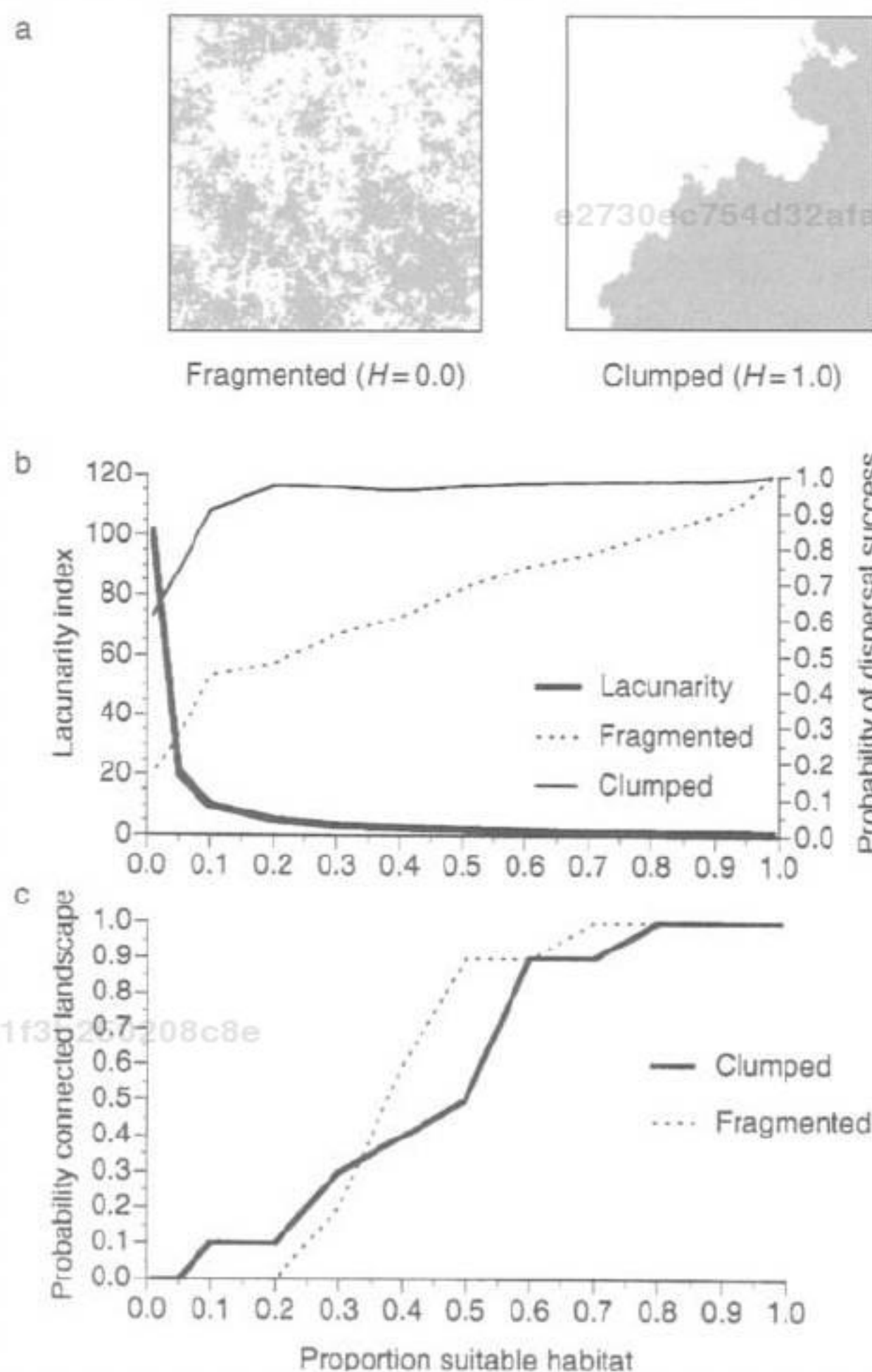
### Landscape Connectivity Issues: Thresholds in Connectivity

Because of the importance of landscape connectivity for evaluating the structure and dynamics of metapopulations, it would be advantageous to identify when landscapes become disconnected and thus when metapopulation processes such as colonization rates are likely to be disrupted. Both patch connectivity measures (Hanski, 1999a) and measures of landscape connectivity (With, 2002) predict critical thresholds in habitat connectivity, where the habitat network becomes abruptly disconnected at a critical level of remaining habitat. In percolation-based approaches, for example, landscape connectivity is assessed by whether a single habitat cluster (the *percolating cluster*) spans the landscape. Landscape connectivity is disrupted when the critical habitat nodes forming the “backbone” of the percolating cluster are destroyed, which abruptly breaks the percolating cluster into two or more fragments. The critical level of habitat at which landscape connectivity becomes disrupted (*percolation threshold*) depends on a number of assumptions regarding species-specific movement attributes (gap-crossing abilities, movement rates through different habitat types, matrix mortality) and the representation and configuration of the landscape itself (grid geometry, degree of habitat fragmentation) (for a review, see With, 2002). The issue, however, is whether thresholds in landscape connectivity, or measures of landscape connectivity more generally, relate to processes such as colonization success and local extinction rates, which are important for predicting metapopulation persistence on landscapes. In other words, is landscape connectivity both a necessary and a sufficient condition for metapopulation persistence (e.g., With, 1999)?

### Landscape Connectivity Thresholds and Dispersal Success

Dispersal is the “glue” that keeps metapopulations together (Hansson, 1991), and thus colonization success is deemed crucial to metapopulation persistence. Clearly there should be some relationship between landscape connectivity and dispersal (colonization) success: dispersal success is expected to be higher in landscapes with a high degree of connectivity. What is less clear, however, is whether thresholds in landscape connectivity should necessarily coincide with thresholds in dispersal or colonization success.

To address this, With and King (1999a) quantified dispersal success on a series of landscapes with complex (fractal) habitat distributions that represented a gradient of fragmentation severity (Fig. 2.1a). Dispersal success was defined as the proportion of independent dispersers that successfully located a suitable habitat patch (cell). Consider that if dispersal is truly random, such that dispersal occurs to a random point on the landscape, then the underlying spatial pattern of the landscape is unimportant for predicting dispersal success



**Fig. 2.1** (a) Examples of fractal landscape patterns illustrating extremes in fragmentation severity ( $H$ , spatial autocorrelation of habitat). (b) Dispersal success declines precipitously below 20% habitat (dispersal threshold), coinciding with the lacunarity threshold of landscape structure, which is a landscape-wide measure of interpatch distances. The lacunarity index is not affected by the landscape pattern for analyses conducted at the finest scale ( $1 \times 1$  grid cell), shown here for clarity of presentation. The lacunarity curve at other scales is qualitatively similar, but lacunarity indices tend to be higher in clumped fractal landscapes than in fragmented ones due to the greater variability in gap sizes. (c) Percolation thresholds, a patch-based assessment of landscape connectivity, do not coincide with dispersal thresholds (assuming a 12-cell dispersal neighborhood). Modified from With and King (1999a).



and only the fraction of habitat ( $h$ ) and number of dispersal steps ( $m$ ; equivalently the “dispersal neighborhood” or “dispersal ability” of the species) affect dispersal success as

$$\Pr(\text{success}) = 1 - (1 - h)^m. \quad (2.1)$$

Equation (2.1) represents the mean-field approximation. If dispersal is instead constrained to movement through adjacent cells (but still random in direction) to force individuals to interact with the patch structure of the landscape, then dispersal success on fractal landscapes can no longer be derived from first principles and may lack a closed-form solution. Thus, dispersal success on fractal landscapes had to be obtained through numerical simulations (With and King, 1999a).

As expected, dispersal success declined with decreasing habitat and increasing fragmentation of the landscape, but the rate of this decline accelerated once the amount of habitat fell below 10–20% (Fig. 2.1b). In other words, dispersal success exhibited a threshold response to habitat amount. This dispersal threshold did not coincide with percolation thresholds used to quantify landscape connectivity, even after allowing for a larger dispersal neighborhood to define habitat connectivity, in which individuals could move through cells of nonhabitat in their search for a suitable habitat site (as in the simulation; Fig. 2.1c). Intuitively, dispersal success is expected to decline as patches become smaller and more isolated because the disperser ends up spending much of its time in the matrix where mortality may be greater. Lacunarity analysis quantifies the “gap structure” of landscapes and is related to the variance-to-mean ratio of the distances among patches on the landscape (Plotnick et al., 1993). The higher the lacunarity index, the greater the variability in distances among patches. Lacunarity is not merely the inverse of some measure of patch structure, such as the fractal dimension of the landscape, however; it can resolve differences in landscape pattern that may be obscured by patch-based measures (Plotnick et al., 1993). Landscape lacunarity exhibited a strong threshold effect around 20% habitat; interpatch distances became greater and more variable when habitat fell below this critical level (With and King, 1999a; Fig. 2.1b). Thresholds in dispersal success thus coincide with lacunarity thresholds rather than percolation thresholds of landscape connectivity.

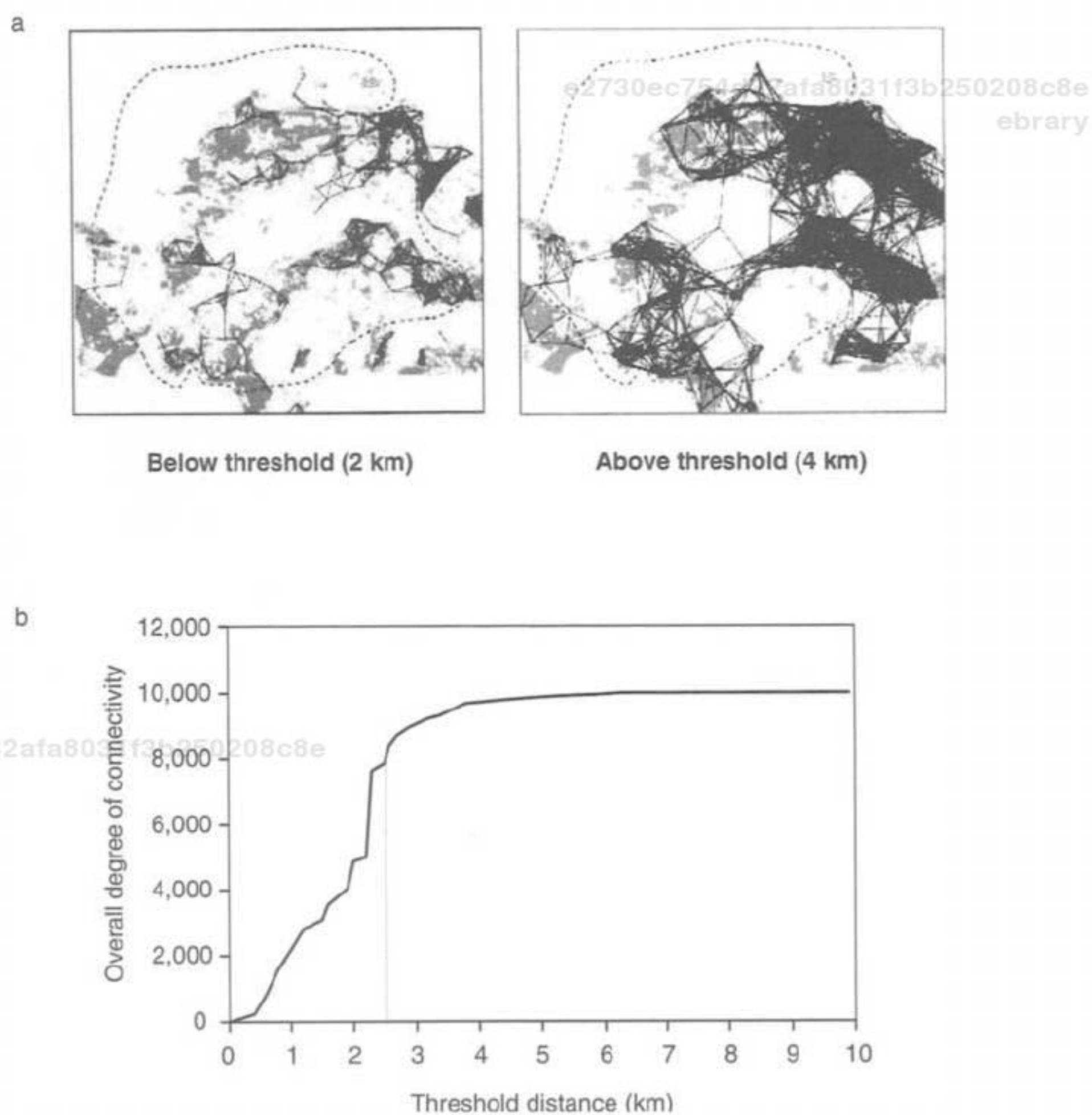
Empirical tests of percolation theory have been performed in the field with insects moving across experimental “microlandscapes” in which habitat (grass sod) was arrayed as either a random or a fractal distribution (Wiens et al., 1997; McIntyre and Wiens, 1999; With et al., 1999). Although it is not clear whether parameters that describe movement pathways should exhibit threshold behavior, let alone coincide with percolation thresholds in landscape connectivity (With et al., 1999), tenebrionid beetles (*Eleodes obsoleta*) nevertheless exhibited threshold behavior in several movement parameters when grass cover fell below 20% (Wiens et al., 1997). This is in the domain of lacunarity thresholds (With and King, 1999), suggesting that landscape measures of gap structure may ultimately be better predictors of dispersal success than landscape measures of patch structure. This reiterates one of the main tenets of metapopulation theory, that patch isolation measures (and therefore patch-based connectivity measures

that incorporate interpatch distances) are a strong correlate of colonization success, at least in extensively fragmented landscapes that meet the metapopulation ideal of habitat patches embedded in an ecologically neutral matrix. As discussed previously, the relationship between landscape structure and colonization success is more complicated in heterogeneous landscapes, where patch isolation may be less important than the quality of the matrix habitat through which the organism disperses. For example, large-scale forestry in Sweden resulted in extensive ditching to drain clear-cut areas, which created an inhospitable matrix that prevented pool frogs (*Rana lessonae*) from colonizing breeding ponds, irrespective of their proximity to an occupied pond (Sjögren-Gulve and Ray, 1996).

The lack of concordance between percolation thresholds and dispersal success has led investigators to invent other, seemingly more-relevant measures of landscape structure for predicting dispersal or colonization success (e.g., Schumaker, 1996; Tischendorf and Fahrig, 2000a). The problem is not the measure used to quantify landscape connectivity, however, but with the scale at which habitat connectivity is assessed relative to the scale of dispersal. Landscape connectivity relates to the potential of organisms to traverse the entire landscape, whereas dispersal or colonization success pertains only to the likelihood that a dispersing organism will successfully find a suitable habitat patch (or cell in a grid-based landscape). Although the two are related, assessments of landscape connectivity and dispersal success are ultimately performed at different scales. Individual movement is constrained in the latter assessment (success is scored for individuals that locate suitable habitat within a dispersal neighborhood, at which point colonization occurs and individuals are assumed to stop moving), but not in the former where the emphasis is on the ability of individuals to move across the entire landscape (whether the organism actually does or not). Thus, the grain of movement may be the same — how individuals move within or between habitat types or cells — but the spatial extent of movement is different.

Habitat connectivity is obviously important for colonization success at some scale. The challenge is to identify what scale is appropriate for predicting colonization success in a given species, however. This involves adopting a species' perspective of habitat connectivity (Wiens and Milne, 1989; With, 1994; Pearson et al., 1996; Vos et al., 2001). Although this has been done using percolation-based neutral landscape models (see With, 2002), a related approach involves the use of graph theory. In graph theory, the grid structure of the landscape is represented as a graph in which habitat patches (vertices or nodes) are connected across varying distances (lines or edges) (Urban and Keitt, 2001). The graph representation permits a process-based measure of connectivity for individual patches as well as the entire landscape. Overall connectivity of the graph (i.e., landscape) is simply assessed in terms of whether each node is connected to some other node. Although there might be several ways to connect the various nodes of the graph to form a *spanning tree*, the one with the shortest length is termed the *minimum spanning tree*. There is a critical threshold distance at which the graph becomes disconnected, reminiscent of the percolation threshold of landscape connectivity for grid-based landscapes (Urban and Keitt, 2001). Using a graph-theoretic approach, van Langevelde (2000) identified different scales of connectivity and related this to colonization patterns of the European nuthatch (*Sitta europaea*) occupying woodlots within fragmented

landscapes of The Netherlands (Fig. 2.2a). Patch occupancy patterns of nuthatches were correlated with a critical threshold distance of 2.4–3 km (Fig. 2.2b), such that woodlots located  $>3$  km from a neighboring forest patch were unlikely to be colonized by dispersing nuthatches (van Langevelde, 2000). The extinction of local nuthatch populations is related to both the connectivity and the size of forested patches (Verboom et al., 1991) and underscores again the importance of habitat connectivity — at some scale — for population persistence (e.g., Fahrig and Merriam, 1985). The metapopulation dynamics of nuthatches within this fragmented landscape have also been assessed using an incidence function model (Ter Braak et al., 1998).



**Fig. 2.2** (a) A graph theoretic analysis of habitat connectivity for European nuthatches (*Sitta europaea*) in an agricultural landscape based on an analysis assuming a dispersal distance of 2 km (just below the landscape connectivity threshold; b) and a dispersal distance of 4 km (above the landscape connectivity threshold; b). Gray areas are habitat fragments, and black lines indicate connections among patches based on the indicated dispersal distance. (b) Landscape connectivity exhibits a threshold in this landscape at about 2.5 km. Patches farther than 3 km apart were unlikely to be colonized by nuthatches. Modified from van Langevelde (2000).

## Relative Importance of Dispersal for Metapopulation Persistence

Studies on how landscape structure and matrix heterogeneity affect dispersal (colonization) assume that the fine-scale movements of individuals translate into broader patterns of population distribution (e.g., Turchin, 1991; With and Crist, 1996; With et al., 1997), which in turn may have consequences for metapopulation persistence on the landscape. How important is dispersal for predicting metapopulation persistence? Dispersal is a key component of most spatially explicit population models, which serve as the main arsenal in the landscape ecological approach to predicting metapopulation persistence in fragmented landscapes, particularly in evaluating the consequences of different scenarios of land-use change on extinction risk for species of conservation concern (Dunning et al., 1995). As mentioned previously, it is difficult to obtain species- and habitat-specific information on dispersal, which may result in errors in the estimation of dispersal success. Such estimation errors may propagate in spatially explicit models and affect estimates of species' extinction risk (Ruckelshaus et al., 1997), although the magnitude of these errors may initially have been overestimated (Mooij and DeAngelis, 1999).

Landscape structure is not always important for predicting dispersal success, however. Using an individual-based model of dispersal on neutral landscape models, King and With (2002) found that the mean-field approximation [Eq. (2.1)] was sufficient for predicting dispersal success when >40% of the landscape was suitable; below this level, specifics related to dispersal behavior and landscape pattern became more important. Given that many species of conservation concern occur in landscapes with substantially <40% suitable habitat, however, it is likely that landscape structure — the configuration and heterogeneity of land-cover types — will generally be important for predicting dispersal success.

Although dispersal (colonization) success is considered an important process necessary for metapopulation persistence, demographic factors that affect extinction risk may actually be more important for some species (South, 1999; With and King, 1999b). This is especially true for good dispersers, such as birds, where landscape structure has a greater effect on reproductive output through edge effects than on immigration rates (e.g., Donovan et al., 1995b; Dooley and Bowers, 1998). The effect of landscape structure on demography and extinction risk on metapopulation persistence is explored in the next section.

## Landscape Effects on Demography and Extinction Risk

Habitat loss and fragmentation pose the greatest threats to biodiversity (Wilcove et al., 1998) and are the inevitable consequence of the transformation of landscapes by humans (With, 2004). Beyond the sheer magnitude and rate of this transformation lies a more insidious problem: the effects of habitat loss and fragmentation on population viability are not linear. Habitat loss may precipitate a sudden and rapid decline in the probability of metapopulation persistence (i.e., a threshold). Using a demographic model founded on Levins' (1969) classic metapopulation model, Lande (1987) first defined *extinction thresholds* for territorial vertebrates as a function of their demographic potentials ( $k$ , a composite parameter derived algebraically from

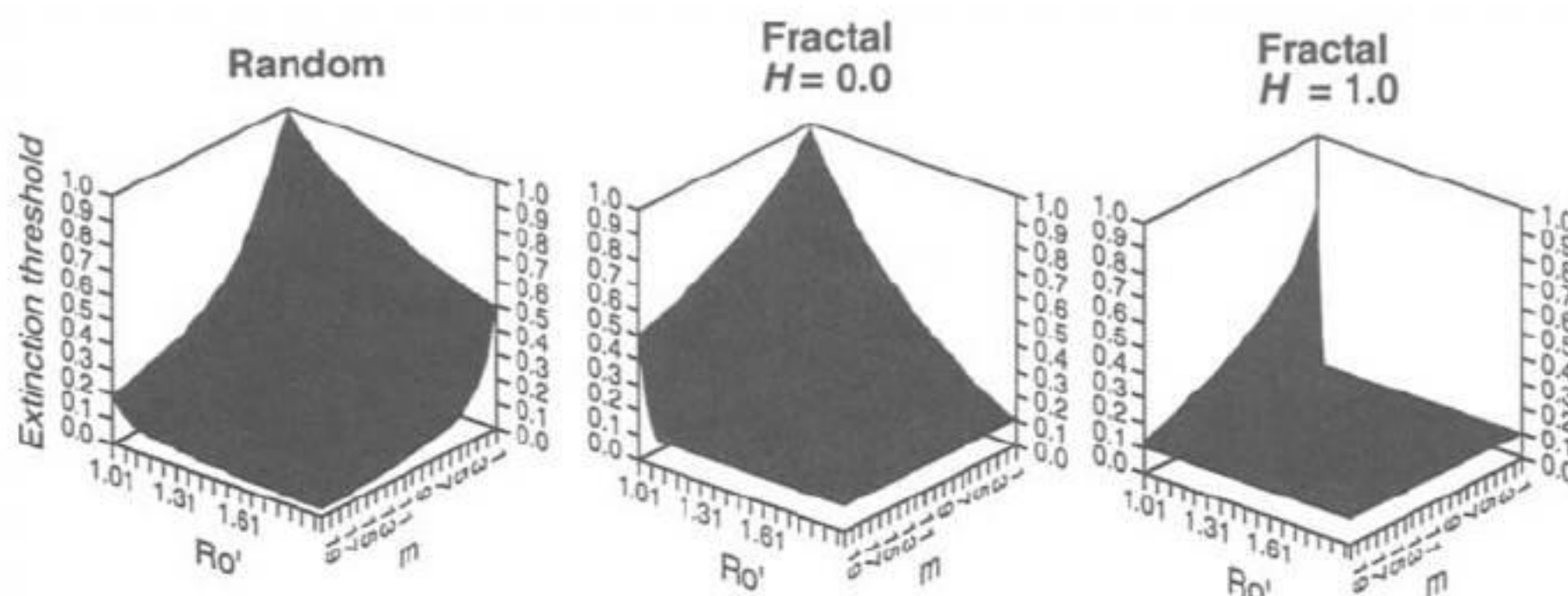
life-history parameters such as net lifetime reproductive output,  $R'_o$ , and dispersal ability,  $m$ ). The extinction threshold is the critical level of habitat ( $h_c$ ) at which the population no longer occurs on the landscape (patch occupancy,  $p^* = 0$ ) and is defined mathematically as  $h_c = 1 - k$ . The decline in patch occupancy accelerates past a certain reduction in habitat, such that the approach to the extinction threshold ( $h_c$ ) is usually nonlinear.

Lande's (1987) model was in the tradition of the classical metapopulation model, which only assumes the existence of habitat patch structure (i.e., it is spatially implicit). Habitat is assumed to be distributed randomly across the landscape or, alternatively, is randomly accessible by dispersing individuals. Bascompte and Solé (1996) developed a spatially explicit realization of this model using grid-based landscapes with random habitat distributions and found that extinction thresholds generally occurred at about the same level ( $h_c$ ) as in Lande's (1987) spatially implicit model, but the decline in patch occupancy occurred faster, resulting in steeper thresholds.

The effect of habitat fragmentation on extinction thresholds has been explored using fractal landscapes, which generate complex landscape patterns across a gradient of fragmentation severity (e.g., Fig. 2.1a; With and King, 1999b; Hill and Caswell, 1999). Because of the complexities of how species interact with fractal landscape patterns, it was necessary to parse the demographic potential ( $k$ ) into its constituent parameters ( $R'_o$  and  $m$ ) to evaluate the relative effects of these life-history parameters on extinction. Different combinations of  $R'_o$  and  $m$  may give rise to the same demographic potential ( $k$ ), but have very different consequences for metapopulation persistence on the landscape in terms of their extinction thresholds. On fractal landscapes, reproductive output ( $R'_o$ ) had a much greater effect on population persistence ( $h_c$ ) than dispersal ability ( $m$ ), which is the opposite of what was found in Lande's (1987) model, which assumes (in essence) a random landscape (i.e., compare the rate at which  $h_c$  declines as a function of increasing  $R'_o$  as opposed to increasing  $m$  in fractal landscapes, relative to the rate at which those same parameters decline in the random landscape, Fig. 2.3). Enhancing reproductive output, such as through the conservation of high-quality habitats or supplementation of nesting habitat, may thus have a greater effect than enhancing dispersal success, by the maintenance or restoration of habitat connectivity, on mitigating extinction risk.

This is not to say that landscape structure had no effect on population persistence, however. Populations in landscapes that were not fragmented ( $H = 1.0$ ) were generally able to persist throughout almost the entire range of habitat availability (i.e.,  $h_c \leq 0.1$ ;  $H = 1.0$ , Fig. 2.3). Reducing fragmentation and maintaining habitat connectivity thus mitigate extinction risk, as expected. In fact, species with low demographic potentials, due to a combination of low reproductive output ( $R'_o$ ) and poor dispersal ability ( $m$ ), generally went extinct sooner on fragmented landscapes ( $H = 0.0$ ) than predicted by Lande's (1987) model. Because many species of conservation concern have these combined traits of low fecundity and poor dispersal ability, such species may be at a greater risk of extinction from habitat loss and fragmentation than previously suspected.

The problem of how habitat fragmentation affects extinction thresholds has also been tackled by evaluating the *metapopulation capacity* of the landscape. The metapopulation capacity is basically the sum of the relative contribution of



**Fig. 2.3** Fragmentation effects on extinction thresholds for species with different demographic potentials (the combined effects of reproductive output,  $R'$ , and dispersal ability,  $m$ ). Random landscapes are the most extensively fragmented; fractal landscapes,  $H = 1.0$  are the least fragmented (i.e., clumped; Fig. 2.1a). Data from With and King (1999b).

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individual patches (their “value”) to metapopulation persistence based on their size and degree of connectivity to other habitat fragments in the landscape (Hanski and Ovaskainen, 2000; Chapter 4). This is a spatially realistic extension of Levin’s (1969) model in which landscape structure (patch area and isolation) is allowed to affect the metapopulation processes of colonization and extinction. For example, the probability of extinction is calculated as a function of the inverse of patch area because extinction is more likely in small patches than in large ones (see Chapter 4 for the mathematical details of this model). For a given landscape, the metapopulation capacity increases with the dispersal range of the species because dispersal enhances connectivity and thus patch colonization rates. For a given species, landscapes can be ranked according to their capacity to support viable metapopulations. A landscape is capable of supporting a viable metapopulation if its metapopulation capacity (analogous to the fraction of habitat in Lande’s model) exceeds a threshold determined by the “metapopulation potential” of the species (the ratio of the species’ extinction to colonization rates, analogous to the demographic potential in Lande’s model). Landscape fragmentation, created by the random destruction of habitat, resulted in a decline in the metapopulation capacity of the landscape that was roughly proportional to the amount of habitat lost. Destruction of habitat in large blocks caused the metapopulation capacity to decline slower than the loss of habitat, and therefore was less detrimental to metapopulation persistence. Landscape structure thus affects extinction thresholds and metapopulation persistence, which is consistent with the findings of other spatially realistic metapopulation models (Hill and Caswell, 1999; With and King, 1999b).

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Although these theoretical investigations demonstrate that some critical level of habitat is required for metapopulation persistence, what empirical evidence is there to support the existence of extinction thresholds? Although extinction thresholds have been quantified mathematically for various species based on available demographic information and estimates of the fraction of suitable habitat in the landscape (e.g., Lande, 1988; Carlson, 2000), extinction thresholds have been identified empirically as an abrupt decline in the occupancy of habitat patches across a series of landscapes that vary in the amount of habitat. For example, the endangered Glanville fritillary butterfly (*Melitaea cinxia*) exhibited

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a threshold response to declines in the metapopulation capacity of patch networks distributed among the Åland Islands in southwest Finland (Hanski and Ovaskainen, 2000; Chapter 4). Many birds may not exhibit a threshold response to the amount of habitat, however, particularly if they are migratory and exist regionally due to coupled source and sink landscape dynamics (With and King, 2001). Such species may be able to occupy all remaining habitat fragments even in extensively fragmented landscapes, as was found for most neotropical migratory songbirds across a landscape gradient of increasing agricultural dominance in southern Ontario, Canada (Villard et al., 1999). Threshold responses to a reduction in forest cover were generally absent for most species, except for two species (ovenbird, *Seiurus aurocapillus*; black-and-white warbler, *Mniotilta varia*) that were not found in landscapes with <10% mature forest.

For many species, such as neotropical migrants, the efficiency of patch occupancy does not decline with habitat loss and fragmentation. Many plant species may also maintain constant patch occupancy despite a reduction in suitable habitat, due to life-history strategies such as seed dormancy (i.e., species escape in time as well as space; Chapter 18). Although the extinction threshold is defined as the fraction of all sites that are suitable but not occupied on a landscape, Eriksson and Kiviniemi (1999) performed a modified calculation in which the “quasi-equilibrium” threshold was obtained as only the fraction of suitable sites that were not occupied ( $b'_c$ ). By this measure, 44% (8/18) of the grassland plants they evaluated in southeastern Sweden were existing below the extinction threshold, which means that although such species were currently found in these landscapes, the amount of suitable habitat was not sufficient to permit the long-term persistence of these species; species exhibited a lagged response to habitat loss. Thus, the identification of extinction thresholds, based on site occupancy and availability of suitable habitat, may not always be sufficient for evaluating population persistence and extinction risk. In such cases, an analysis of lagged population responses to landscape change is required (see *Extinction Risk in Dynamic Landscapes*).

### The Source–Sink Potential of Landscapes

Spatial heterogeneity, resulting from differences in the size, shape, and quality of habitats comprising the landscape, affects species' demographic rates. Reproductive success may be maximized, or survivorship may be minimized, in a particular habitat. Habitat-specific survivorship and reproductive success set the stage for source–sink dynamics (Pulliam, 1988) in which population growth rates are positive (birth rates exceed death rates) in some patches (sources) but are negative in others (sinks). The relative amount of source and sink habitat on a landscape may thus affect persistence of the metapopulation at the landscape scale (Pulliam and Danielson, 1991; Donovan et al., 1995b; Chapter 16).

A landscape perspective is ultimately required to assess source–sink dynamics and to evaluate how changes in landscape structure, such as from habitat fragmentation or land-use change, may affect these dynamics and thus metapopulation persistence. Unfortunately, most of the previous efforts to model source–sink dynamics have been spatially implicit (e.g., Pulliam and Danielson, 1991), including those that have attempted to determine the effects of habitat fragmentation on the source–sink status of populations

(e.g., Donovan et al., 1995a; but see Ritchie, 1997). Although demographic rates vary spatially in such models, they are usually fixed input parameters that are independent of landscape structure. In birds, for example, landscape structure is known to affect reproductive output in many species due to higher *edge effects* in fragmented landscapes in which nesting success is lower in habitat fragments because of greater nest predation or brood parasitism (such as by the brown-headed cowbird, *Moluthrus ater*, in North America) along fragment edges (Donovan et al., 1995b, 1997). Thus, reproductive output (a demographic rate) is spatially dependent and varies as a function of patch size and shape, being reduced in fragments dominated by edge and maximized in large patches of contiguous habitat.

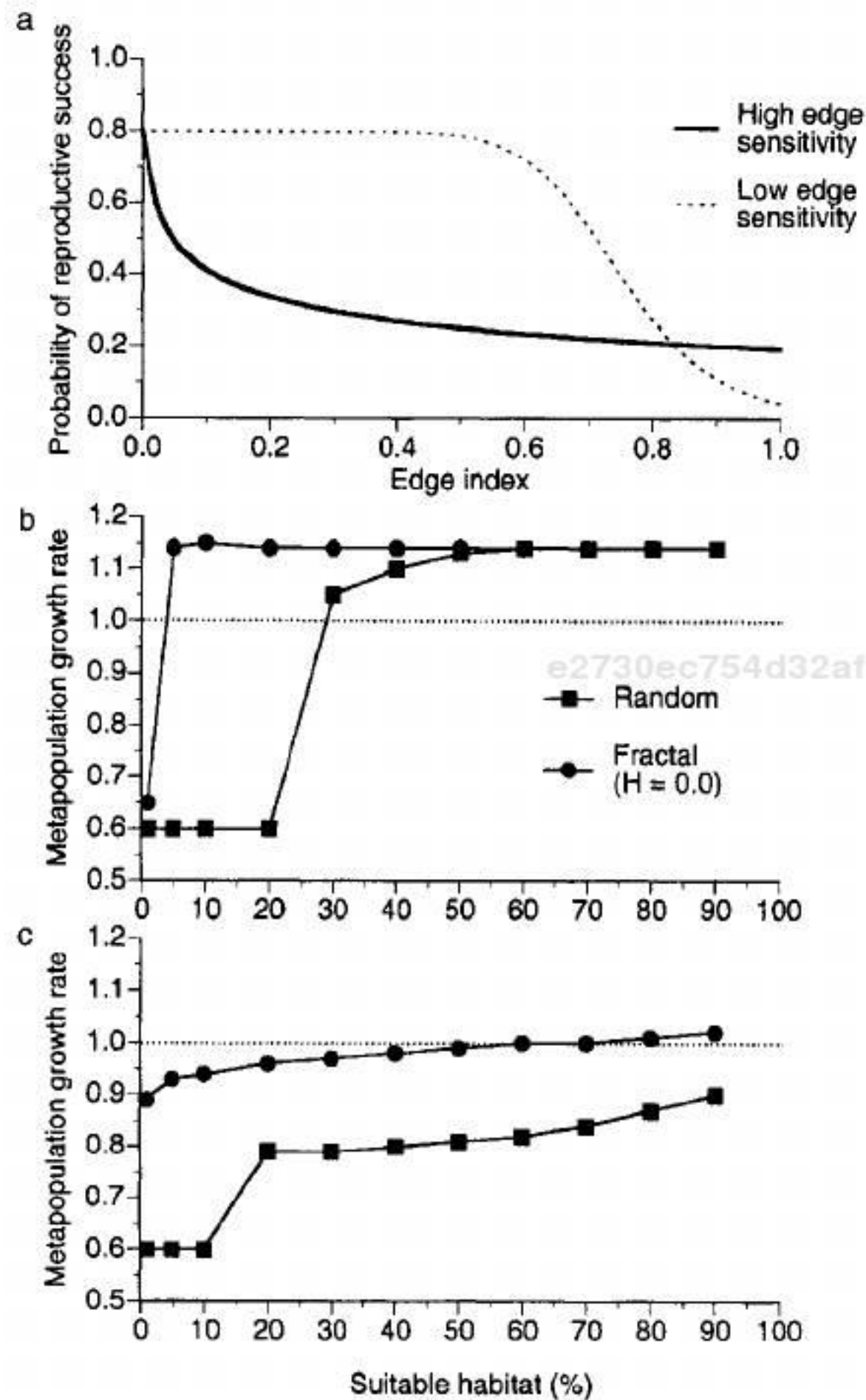
With and King (2001) devised a functional relationship between patch structure and reproductive success for neotropical migratory songbirds as part of a spatially structured demographic model developed to assess the source–sink potential of fragmented landscapes. Reproductive success declines as a function of increasing edge (i.e., negative edge effects). For example, some species were “edge sensitive” and exhibited a steep decline in reproductive output in small or irregularly shaped patches that were dominated by edge (edge index  $\rightarrow 1.0$ ; Fig. 2.4a). The demographic consequences of landscape structure were assessed as the expected number of female offspring produced per female, per patch, for all individuals across the entire landscape ( $b_L$ ). A simple two-stage life table combining fecundity ( $b_L$ ) and survivorship (juvenile,  $s_o$  and adult,  $s$ ) was then constructed for each species (Fig. 2.4a) in a given landscape (e.g., Fig. 2.1a). From the life table, we calculated the finite rate of increase for the entire landscape population ( $\lambda_L$ ) as the solution to the characteristic equation (Lande, 1988):

$$\lambda_L^\alpha - s\lambda_L^{\alpha-1} - b_L l_\alpha = 0 \quad (2.2)$$

for  $\lambda \geq 1$  and  $0 < s < 1$ , where  $l_\alpha$  is survivorship at the age of first breeding,  $s$  is the annual probability of survivorship for breeding adults ( $>1$  yr), and  $b_L$  is derived from the population across the entire landscape. The landscape population was stable when  $\lambda_L = 1.0$ , declining when  $\lambda_L < 1$  and increasing when  $\lambda_L > 1$ . The annual rate of change in the size of the metapopulation (%/yr) is  $(\lambda_L - 1.0) * 100$ . Thus, this modeling approach treats a demographic rate ( $b$ ) as a spatially dependent variable; it is a model output rather than a fixed model parameter as in traditional demographic models. Furthermore, this approach extends the concept of source–sink populations from the scale of patches to the entire landscape, such that the potential of a given landscape to function as a population source or sink is ultimately assessed.

For species with low edge-sensitivity (Fig. 2.4a), landscapes supported viable metapopulations and had the potential to function as sources across a wide range of available habitat (Fig. 2.4b; With and King, 2001). Fragmented landscapes (random) could not support viable metapopulations of this species, however, and functioned as sinks ( $\lambda_L < 1.0$ ) when habitat fell below 30% (Fig. 2.4b). The situation was bleaker for species with high edge-sensitivity, which had a difficult time persisting in landscapes with  $<50\%$  habitat even when the landscape was managed to preserve large tracts of contiguous habitat ( $H = 1.0$ , Fig. 2.4c).





**Fig. 2.4** (a) Degree of edge sensitivity — the decline in reproductive success as a function of increasing edge — for a couple of generic migratory songbirds. (b) Effect of fragmentation (random = maximum fragmentation) on a species with low edge-sensitivity. (c) Effect of fragmentation on a species with high edge-sensitivity. Modified from With and King (2001).

This spatially structured avian demographic model was parameterized for the Henslow's sparrow (*Ammodramus henslowii*) in a heavily managed landscape of north-central Kentucky in the eastern United States (King et al., 2000). Henslow's sparrow is an area-sensitive species that requires large tracts of dense tallgrass prairie for nesting (patch sizes  $\geq 30$  ha; Herkert, 1994) and is thus a species of conservation concern given that  $<1\%$  of the historical tallgrass prairie remains throughout the Great Plains of North America (Knopf and Sampson, 1994). Only 0.6% of the managed landscape was suitable breeding habitat, which was fragmented and consisted of many small patches barely large enough to support a breeding pair, let alone meet the area requirements of this species (the largest patch was 51 ha). The finite rate of increase for the Henslow's sparrow metapopulation in this landscape was  $\lambda_L = 0.86$ . Thus, the Henslow's sparrow was declining at an annual rate of 14%/yr such that the

landscape was a sink for this species. Reproductive output,  $b$ , must be increased by about 1.5 times its current level to restore the Henslow's sparrow to a stable or increasing metapopulation, which would require an increase in the landscape-wide nesting success from 39 to 58%. To reverse the current decline in this metapopulation, a land manager should thus minimize disturbances that contribute to habitat fragmentation of grassland habitat, thereby increasing patch sizes and minimizing edge effects that decrease reproductive output.

Although this spatially structured demographic model focuses on how patch geometry for a single habitat type affects reproductive success, this approach can be extended easily to heterogeneous landscapes in which reproductive success or survivorship additionally varies as a function of habitat quality.

## Extinction Risk in Dynamic Landscapes

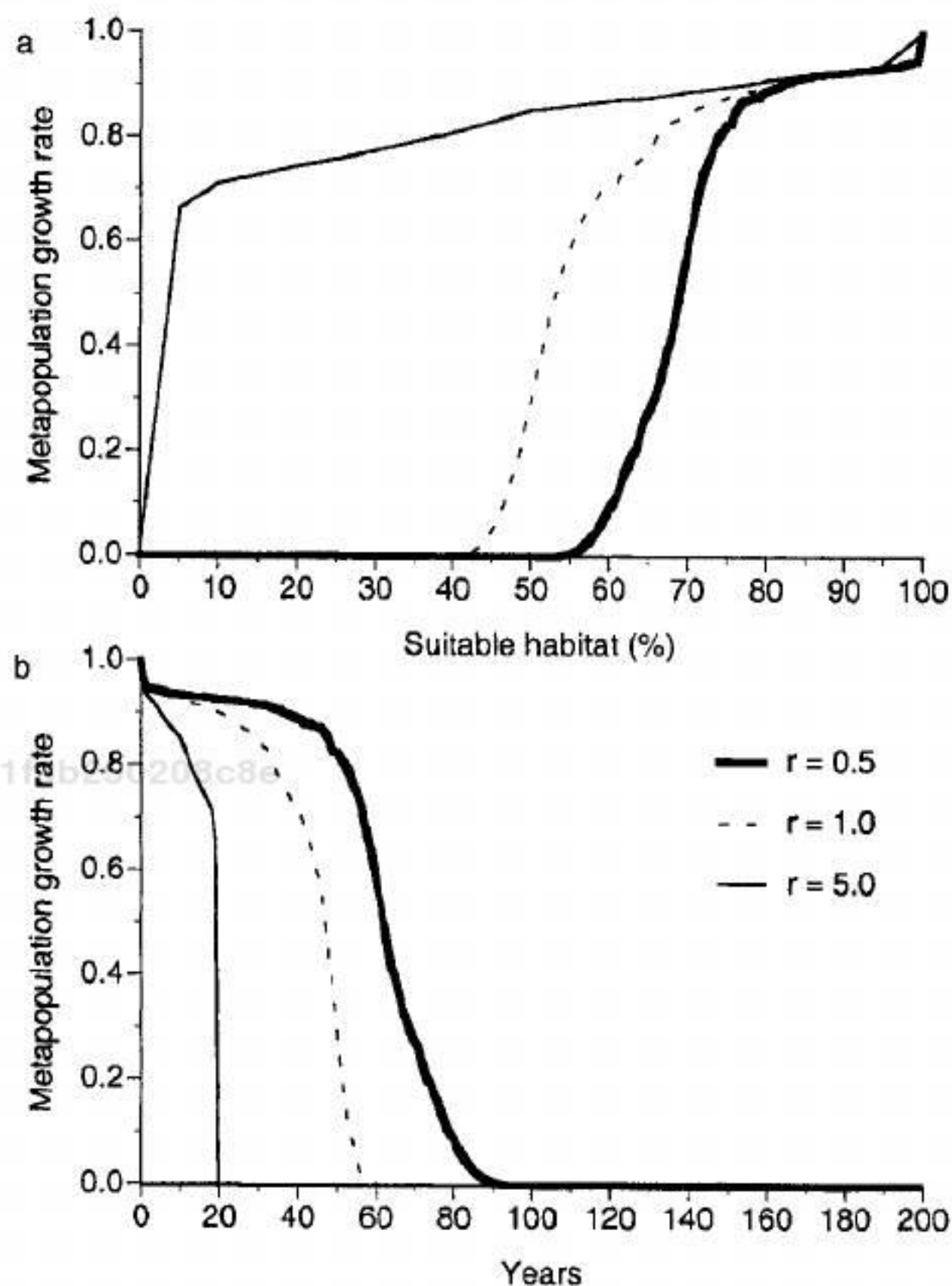
The effects of landscape structure on the metapopulation processes discussed thus far have assumed a static landscape in which the amount, suitability, and configuration of habitat patches remain unchanged on the landscape. Even studies that have explored the effects of habitat loss and fragmentation on metapopulation persistence have been conducted on a series of static landscapes representing a gradient of habitat availability and fragmentation severity (e.g., Bascompte and Solé, 1996; Hill and Caswell, 1999; With and King, 1999b, 2001), which assumes that these landscapes all lie on a particular trajectory of landscape change. Real landscapes are not static, however, especially given the current rate at which most landscapes are being transformed by human land-use activities. Different trajectories of land-use change could generate similar landscape patterns, but have very different consequences for the dynamics and persistence of metapopulations on these landscapes.

The rate of landscape change is an important component of landscape structure that affects extinction risk (e.g., Fahrig, 1992; Keymer et al., 2000) and which may be responsible for generating metapopulation dynamics, particularly in ephemeral or successional habitat (Hanski, 1999a; Johnson, 2000). Patch demographics, such as the life span of a patch, drive the dynamics of the metapopulation in these systems. For a given species, there is a critical rate of patch turnover in which the landscape changes too fast relative to the scale of the extinction–colonization process to permit metapopulation persistence (Keymer et al., 2000). Metapopulation extinction is thus predicted to occur more frequently in dynamic than in static landscape scenarios.

These recent theoretical treatments of metapopulations on dynamic landscapes have been concerned primarily with systems in which there is a constant rate of habitat turnover (but see Hanski and Ovaskainen, 2002; Ovaskainen and Hanski, 2002; Chapter 4). Many landscapes are subjected to chronic habitat loss and fragmentation, however, in which habitat that has been destroyed is not restored. To address this latter scenario, Schrott, With and King (unpublished) extended the spatially structured avian demographic model of With and King (2001) to a dynamic landscape context in which habitat was destroyed at various rates (0.5, 1 and 5%/yr) until the landscape was entirely denuded. The most surprising result of this analysis was that the metapopulation appeared to persist across a greater range of habitat destruction when habitat was lost rapidly (5%/yr) than when it was destroyed slowly (0.5%/yr); in other words,

extinction appeared to occur sooner in landscapes subjected to lower rates of disturbance (Fig. 2.5a). This paradox is resolved by considering the decline in metapopulation growth rates as a function of time (Fig. 2.5b), which demonstrates that populations on landscapes subjected to rapid rates of habitat loss (5%/yr) will go extinct within 20 yr (the time to total landscape denudation), whereas populations in landscapes subjected to lower rates of habitat loss can persist for up to three times as long. The apparent prolonged persistence of metapopulations in landscapes undergoing rapid change results from a lagged response by the species. The generic migratory songbird being modeled in this study had a life span of 8 yr, such that at a habitat loss rate of 5%/yr, total denudation of the landscape would occur in a little over two generations. The landscape is changing more rapidly than the demographic potential of the species, and thus declines in the metapopulation growth rate ( $\lambda_L$ ) lag behind the rate of habitat loss. This “extinction debt” has been demonstrated to be

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**Fig. 2.5** (a) Effect of the rate of habitat destruction ( $r$ , % habitat destroyed/yr) on metapopulation persistence for a species with intermediate edge sensitivity in moderately fragmented ( $H = 0.5$ ) dynamic landscapes. Because of the initial conditions of the model, in which the metapopulation growth rates are stabilized ( $\lambda_L = 1.0$ ), the landscape population can only decline as habitat is lost. (b) Time to extinction for the same species in dynamic landscapes undergoing moderate fragmentation ( $H = 0.5$ ) at different rates. From Schrott, With and King (unpublished).

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especially great for metapopulations that are close to their extinction thresholds following habitat loss and fragmentation (Hanski and Ovaskainen, 2002).

These results emphasize the importance of understanding the historical forces shaping landscape patterns, such as the rate of land-use change or habitat destruction, for assessing species' extinction risk. Two landscapes with identical metrics could have achieved their present state via vastly different trajectories of landscape change, with different consequences for metapopulation persistence (Fig. 2.5a). Conventional landscape metrics thus cannot be used to evaluate extinction risk for metapopulations in dynamic landscapes. Time lags in species' responses to landscape change may also create relict distributions in which the species' occurrence is better explained by a historical landscape configuration than the current one ("ghosts of landscape past"; Nagelkerke et al., 2002). For example, the distribution of carabid beetles (*Abax parallelepipedus*) in a hedgerow network within an agriculturally dominated landscape of France was better explained by the well-connected hedgerow distribution from 40 yr ago than the current network (Petit and Burel, 1998). From a conservation and land-management standpoint, the potential for lagged population responses is especially disquieting because the effects of landscape change may go unnoticed for long periods of time, such that the window of opportunity for affecting a recovery may close before the problem is realized and action is taken. Alternatively, such lagged effects may buy the necessary time in which to implement conservation and restoration measures before the species goes extinct. This assumes that the problem can be recognized in time, which argues for the importance of performing theoretical and empirical analyses of the effect of dynamic landscape change on extinction risk.

### Relative Effects of Habitat Loss and Fragmentation on Metapopulation Persistence

A number of empirical and theoretical investigations have attempted to assess the relative importance of the amount of habitat versus the degree of habitat fragmentation on species occurrence and extinction thresholds (e.g., McGarigal and McComb, 1995; Trzcinski et al., 1999; Villard et al., 1999; Fahrig, 1997, 2002; Flather and Bevers, 2002). Part of the difficulty in evaluating the relative effects of these two components of landscape structure, however, has been differences in how extinction thresholds are defined, which is a consequence of the specific modeling approach or measure of population viability used to assess extinction risk. Depending on the modeling construct, extinction thresholds have been defined variously as the critical level of habitat at which the population (1) is unlikely to persist for (or after) some specified amount of time (e.g., duration of run in individual-based simulation models; Fahrig, 1997; Flather and Bevers, 2001), (2) no longer occupies any of the available habitat (metapopulation models, where  $p^* = 0$ ; Lande, 1987; Bascompte and Solé, 1996; With and King, 1999b), or (3) is no longer stable, as assessed by some demographic index, such as net reproductive rate ( $R_0$ ) or the finite rate of population growth ( $\lambda$ ) (spatially structured demographic models, where  $R_0$  or  $\lambda < 1.0$ ; With and King, 2001). Some measures of population viability may be more sensitive to fragmentation effects, however (Flather and Bevers, 2002); for example, patch-based measures of population

viability (patch occupancy,  $p^*$ , of metapopulation models) may be more sensitive to fragmentation effects than probabilities of population persistence derived from individual-based simulation models. Thus, the debate over the relative effects of habitat loss and fragmentation on metapopulation persistence is muddled by the specific modeling approach employed in theoretical studies (Flather and Bevers, 2002), the corresponding measure of population viability used, and the taxonomic group being assessed in the case of empirical studies. For example, birds may not be the best test of the relative importance of fragmentation effects, as many species are efficient at occupying available habitat even when habitat is rare (e.g., Villard et al., 1999).

Nevertheless, habitat amount is generally the best predictor of metapopulation persistence, although fragmentation — the explicit arrangement of patches in space — becomes increasingly important below the extinction threshold (Fahrig, 1997; Flather and Bevers, 2002). As pointed out in the previous section, however, the discussion of the relative effects of habitat loss and fragmentation on metapopulation persistence is moot in the absence of information on landscape dynamics. The rate of patch turnover or habitat destruction has been shown to have a more profound effect on extinction thresholds than either the amount or the fragmentation of habitat (Keymer et al., 2000; Schrott, With and King (unpublished)).

### 2.3 SUMMARY

Although landscape ecology and metapopulation ecology share a common goal in predicting the persistence of spatially structured populations in fragmented landscapes, they differ in scope and academic tradition, which is reflected in the different approaches typically employed by ecologists from the two disciplines. Landscape ecology is an interdisciplinary field that arose from European traditions of regional geography and vegetation science, and which combined the spatial approach of the geographer with the functional approach of the ecologist (Turner et al., 2001). As a consequence, there has been greater emphasis placed on remotely sensed data, geographical information systems, and spatial statistics to generate, display, and analyze complex landscape patterns within landscape ecology, as opposed to the more abstract representation of landscapes inspired by the patch-based ecological theory adopted by metapopulation ecology. In North America, the systems ecology background of many “first-generation” landscape ecologists contributed to the widespread use of computer simulation models to tackle problems related to the effect of land-use change on resource management, an application that additionally could take advantage of GIS. Subsequently, this led to the development of spatially explicit population models, the main tool of the landscape ecologist for assessing population viability in fragmented landscapes. In contrast, metapopulation ecologists hail from a background in population ecology that is rich in mathematical theory and thus tend to approach the problem of population persistence in fragmented landscapes analytically rather than numerically.

Despite its diverse disciplinary breadth, landscape ecology is fundamentally concerned with the effects of spatial pattern on ecological processes (Turner, 1989), at whatever scale spatial heterogeneity emerges. In the context of metapopulation dynamics, any study that incorporates the effect of spatial

pattern, such as habitat fragmentation or matrix heterogeneity, on processes contributing to metapopulation persistence is, by definition, adopting a landscape ecological perspective. Thus, it could be argued that the “exciting scientific synthesis” between landscape ecology and metapopulation theory that was envisioned by Hanski and Gilpin (1991) a decade ago is well underway. This is evident in current metapopulation theory that utilizes spatially explicit (or realistic) models (e.g., Hanski, 1999b) and by the use of analytical approaches from metapopulation theory in landscape ecology (e.g., With and King, 1999b).

The goal of this chapter has been to demonstrate that landscape ecology has more to offer metapopulation ecology than just the incorporation of a broader spatial scale or landscape heterogeneity to existing metapopulation theory by providing a spatial context for understanding processes contributing to the dynamics and persistence of metapopulations. Nevertheless, there are still several areas at this nexus of landscape ecology and metapopulation biology that are in need of further research: First, spatially structured demographic models require further development and testing. Demographic factors, such as reproductive output and survivorship, may be spatially dependent. Estimates of metapopulation viability that ignore this spatial dependency may give erroneous and overly optimistic assessments of a species’ status on a landscape (With and King, 2001). Second, matrix effects on dispersal success and extinction risk need to be evaluated further. Research has demonstrated the potential importance of managing the matrix for enhancing colonization success and reducing extinction risk, and thus we need to move beyond assessment of mere patch size and isolation effects on metapopulation persistence (e.g., Fleishman et al., 2002), particularly in understanding asymmetrical flows among populations and evaluating the source–sink potential of landscapes for species of conservation concern. Third, the effect of landscape dynamics on extinction thresholds deserves greater attention (e.g., Keymer et al., 2000; Schrott, With and King (unpublished)). Chronic habitat loss and fragmentation increase the potential for lagged responses to landscape change, which may produce an extinction debt (Hanski and Ovaskainen, 2002), such that the status and future viability of metapopulations may not be well predicted by current landscape patterns. Fourth, metapopulation viability analysis needs to be extended to a broader, regional scale. A “metalandscapes modeling approach” is particularly important for assessing dynamics among source–sink landscape populations (e.g., Donovan et al., 1995a). Finally, empirical work to address these issues, analogous to how metapopulation theory has been applied to real metapopulations in metapopulation ecology (Chapters 4 and 5), should be a research priority in landscape ecology. Otherwise, continued progress toward this developing synthesis between landscape ecology and metapopulation ecology will slow.