
Conservation of Fragmented Populations

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Abstract: *In this paper we argue that landscape spatial structure is of central importance in understanding the effects of fragmentation on population survival. Landscape spatial structure is the spatial relationships among habitat patches and the matrix in which they are embedded. Many general models of subdivided populations make the assumptions that (1) all habitat patches are equivalent in size and quality and (2) all local populations (in the patches) are equally accessible by dispersers. Models that gloss over spatial details of landscape structure can be useful for theoretical developments but will almost always be misleading when applied to real-world conservation problems. We show that local extinctions of fragmented populations are common. From this it follows that recolonization of local extinctions is critical for regional survival of fragmented populations. The probability of recolonization depends on (1) spatial relationships among landscape elements used by the population, including habitat patches for breeding and elements of the inter-patch matrix through which dispersers move, (2) dispersal characteristics of the organism of interest, and (3) temporal changes in the landscape structure. For endangered species, which are typically restricted in their dispersal range and in the kinds of habitat through which they can disperse, these factors are of primary importance and must be explicitly considered in management decisions.*

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Conservación de poblaciones fragmentadas

Resumen: *En este trabajo nosotros argumentamos que la estructura espacial del paisaje es de central importancia para la comprensión de los efectos de la fragmentación sobre la supervivencia de las poblaciones. La estructura espacial del paisaje consiste en la relación espacial entre parches de hábitas y la matriz en la cual están incluidos. Muchos modelos de poblaciones subdivididas asumen que (1) todos los parches de hábitat son equivalentes en tamaño y calidad y (2) todas las poblaciones locales (en los parches) son igualmente accesibles a los dispersores. Modelos que trivializan los detalles espaciales de la estructura del paisaje pueden ser útiles par desarrollos teóricos pero casi siempre serán engañosos cuando se los aplique a problemas reales de conservación. Nosotros demostramos que las extinciones locales de poblaciones fragmentadas son comunes. De esto se deduce que la recolonización de extinciones locales es crítica para la supervivencia regional de las poblaciones fragmentadas. La probabilidad de recolonización depende de (1) relaciones espaciales entre los elementos del paisaje usados por las poblaciones, incluyendo parches de hábitats para cría y elementos de la matriz inter-parches a través de los cuales los dispersores se movilizan, (2) características de dispersión del organismo en cuestión y (3) cambios temporales en la estructura del paisaje. Estos factores son de primordial importancia y deben ser considerados explícitamente en las decisiones de manejo para especies en peligro de extinción, las cuales están típicamente restringidas en su rango de dispersión y en los tipos de hábitats a través de los cuales se dispesan.*

Introduction

The habitat of all species is heterogeneous on many scales due to both natural processes and human activities (Lord & Norton 1990). This results in heterogeneous distributions of populations at different spatial scales (Wiens 1989). Andrewartha and Birch (1984) simplify this spatial structuring to two relevant scales for understanding the population dynamics of any species: the "local population" scale (small scale) and the "natural population" scale (large or regional scale). The local population is the unit within which the classical assumption of random mating holds (see Wright 1977). Because of disturbances and demographic variability, the local population is often prone to extinction. For many populations, survival at the larger regional scale depends on recolonization of these local extinctions from other areas through dispersal (Addicott 1978; Henderson et al. 1985; Harrison et al. 1988; Paine 1988; Wegner & Merriam 1990; Merriam & Wegner 1992; Villard et al. 1992). The natural or regional population is "the sum of a large number of interacting local populations." The regional population is persistent even though the local populations are ephemeral. Andrewartha and Birch (1984:184) assert the general importance of this spatial structuring of populations in their statement that "No general theory about the distribution and abundance of animals should have a chance of being accepted as realistic unless it takes full cognizance of the patchy dispersion of animals in natural populations." Note that the scales of local and regional populations depend on the size and dispersal capability of the organism. The regional population of a small immobile organism may cover a smaller area than the local population of a large mobile organism (Kotliar & Wiens 1990).

Several general theoretical constructs have been proposed for subdivided populations. Den Boer (1977, 1979) envisioned the local population or "interaction group" from which offspring are spread to other asynchronously fluctuating interaction groups, forming a "multipartite population." Levins (1970) coined the term "metapopulation" for such a "population of populations." Wilson (1980) proposed the "winking patches" model for the extinction and recolonization dynamic of local populations. Hastings and Wolin (1989) and Hastings (1991) developed a model in which patches are grouped in "classes" defined by their population sizes. Pulliam (1988) developed the "source-sink" model of interaction among local populations, in which some patch populations act as sources of colonists for other patches that depend on these sources for persistence.

In "core-satellite" or "island-mainland" models (Boorman & Levitt 1973), precipitated by the work of MacArthur and Wilson (1967), one patch, the mainland, acts as the ultimate source of immigrants for the local island

populations. Although the spatial structure of some patchy populations conforms to the island-mainland analogue, we focus here on the increasingly common spatial structure in which there is no mainland equivalent. Because any patch can experience an extinction, and because recolonization is not assured by the presence of a large mainland source (see Karr 1990), spatial configuration of the habitat patches is particularly important in this situation.

Models of subdivided populations have been useful for development of theoretical insights, but their application to real problems of conservation biology is dangerous for the following reasons: (1) many of the models, especially the metapopulation and winking patches models assume that all patches are equivalent in size and quality; and (2) the models frequently assume that all local populations are equally accessible by dispersers—in other words, the models are not spatially explicit. There are some exceptions (for example, Harrison & Quinn 1989), which are reviewed in Kareiva (1990). In a recent paper, Adler and Nürnbergger (in press) conducted a spatially explicit simulation of patchy populations and compared the regional population size to that predicted by an approximation that ignores spatial structure. They concluded that the approximation failed to predict the spatially explicit simulation results.

In this paper we present arguments and evidence for the view that, if the goal is species conservation, the spatial structure of the landscape in which the species is found must be explicitly considered. The following factors must be examined: (1) differences among the patch populations in terms of habitat area and quality; (2) spatial relationships among landscape elements; (3) dispersal characteristics of the organism of interest, and (4) temporal changes in the landscape structure. Parallel issues arise when one investigates genetic questions, but in this paper ecological concerns will be the focus.

Static Landscape Structure

Persistent Populations Extend across Several Habitat Patches

A habitat patch is defined as any discrete area that is used by a species for breeding or for obtaining other resources. Note that continuous habitat, such as forest, is internally heterogeneous (Freemark & Merriam 1986). For a particular species, extensive habitat may actually contain several habitat patches with functionally separate, local populations (Krohne et al. 1984; Tomialojc et al. 1984; Wilcove 1988; Krohne & Burgin 1990).

Fluctuations in local abundance mean that there is always some possibility that the local population in a habitat patch will become extinct. For regional survival, it is important that the fluctuations of the local populations are not synchronous, since this would result in a

high chance of simultaneous extinction of all local populations (Gilpin 1990; Hanski 1991). The number of habitat patches and the spatial scale over which they are distributed must be large enough for recolonizations to balance local extinctions.

In Figure 1 we present recorded annual extinction rates of local populations for a variety of organisms in habitat patches. Since scales of observation vary from study to study, the extinction and recolonization rates in these studies should not be directly compared. They do serve to demonstrate, however, that local extinctions and recolonizations are common, often in the range of 10–20% of local populations becoming extinct per year. Other authors have reported frequent local extinctions without presenting annual rates. For example, in a study of four species of aphids on fireweeds, Addicott (1978) found that local populations became extinct and colonizations occurred throughout the summer. Henderson et al. (1985) found that local extinctions of chipmunks (*Tamias striatus*) were recolonized within three to nine weeks. Many measures of turnover rates also imply high rates of local extinctions and colonizations (see Williamson 1983; Schoener & Spiller 1987).

Landscape Spatial Structure Constrains Regional Survival

Because local extinctions occur, population survival (both locally and over the landscape) depends on re-

colonization of habitat patches that have experienced extinctions. Whether or not patches can be recolonized depends on the availability of dispersing individuals and the ease with which these individuals can move about within the landscape. Both of these depend on landscape spatial structure. If the landscape spatial structure restricts movement between patches, the area (number of habitat patches) required for population survival is large. For example, Duelli (1990) studied movements of 97 species of arthropods across the edges of agricultural fields. Depending on the species, the edge could restrict movement, enhance movement, or have no effect on movement. Also, Mader et al. (1990) found that movements of arthropods are restricted by some kinds of linear barriers (tracks and roads) but not by others. If movement is enhanced by landscape spatial structure, only a small number of patches is needed for regional survival.

Landscape spatial structure is defined as the spatial relationships among the landscape components. Landscape components include both habitat patches and components of the matrix in which the patches are imbedded. They are areas in the landscape that are defined functionally for a particular species by the way in which they are used by that organism. Examples are patches of breeding habitat or feeding habitat, areas of inhospitable habitat, and areas that can be used as part or all of a dispersal route. The characteristics of landscape spatial structure are:

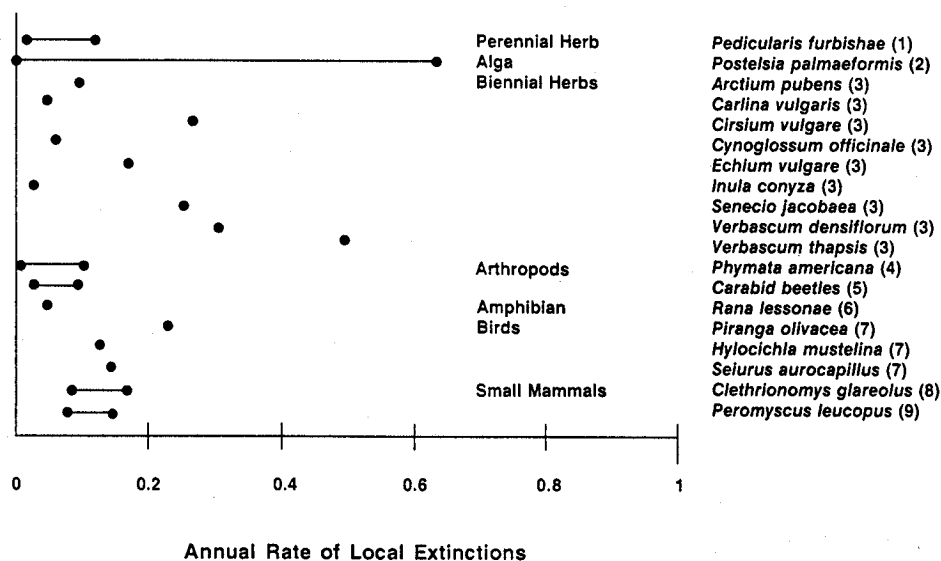


Figure 1. Rate of local extinctions per year (the fraction of local populations becoming extinct per year) for different organisms. Data from true islands are not included. Numbers to the right of the organism correspond to the following habitats and sources: (1) river bank (Menges 1990), (2) rocky intertidal (Paine 1988), (3) coastal sand-dunes (van der Meijden et al. 1985), (4) goldenrod patches (Mason 1977), (5) grassy sites (den Boer 1985), (6) ponds (Sjögren 1991), (7) forest fragments (Villard et al. 1992), (8) forest fragments (R. van Apeldoorn, Research Institute Nature Management, The Netherlands [personal communication]), and (9) forest fragments (Merriam & Wegner 1992).

(1) SIZE, SHAPE, AND QUALITY OF PATCHES

The size of a patch has been shown to influence local population persistence. Verboom et al. (1991) have shown a relationship between habitat patch size and persistence of local populations of the European nuthatch (*Sitta europea*). Also, the positive relationships found between patch size and local population size (see Lynch & Whigham 1984) and between local population size and population persistence (see Paine 1988; Berger 1990) imply a positive relationship between patch size and population persistence.

One way that patch shape can influence population survival is if the population dynamics change in relation to the distance from the edge of the patch. For example, Gates and Gysel (1978) found that the number of passerine birds increased at the field-forest edge, but this was accompanied by increased rates of predation and nest parasitism. Ambuel and Temple (1983) suggest that forest-edge and farmland bird species exclude certain forest-dwelling species, and that this exclusion has a greater impact than changes in patch area or isolation. Two patches of the same area but with different amounts of edge may therefore have different population dynamics.

Patch quality can also influence the survival and abundance of populations. For example, Saunders et al. (1985) and Saunders and Ingram (1987) have shown that the availability of trees with nesting holes within range of food resources can influence the population survival of cockatoos. Dingle (1991) showed that 36% of the variability among patch populations of the large milkweed bug was due to patch quality.

(2) THE PRESENCE OF DISPERSAL ROUTES THROUGH THE LANDSCAPE

Dispersal routes are comprised of components of the matrix through which the organism can move. A habitat patch can also form part of a dispersal route between two other patches. White-footed mice in a landscape of woodlots and farmland move mainly through fencerows, as shown in a radiotagging study of Merriam and Lanoue (1990). Fahrig and Merriam (1985) showed that the function of these fencerows as dispersal routes is important for regional population abundance of white-footed mice in this landscape. A shrub strip between a forest and a littoral zone was shown to act as a dispersal route for birds (Dmowski & Kozakiewicz 1990). Bennett (1990) studied small mammal populations in a fragmented landscape in Australia. Survival of regional populations was found to be facilitated by movements between remnant forest patches along vegetated dispersal routes. The presence of red squirrel (*Sciurus vulgaris*) in wooded fragments was shown to be positively related to the amount of hedgerow surrounding the fragments (Verboom & van Apeldoorn

1990). Note that "corridors" connecting habitat patches can either enhance or reduce regional population survival (Hobbs 1992; Simberloff et al. 1992).

(3) THE QUALITY OF DISPERSAL ROUTES

Quality can affect the likelihood of dispersers using the route and/or the probability that dispersers using the route will survive. Henein and Merriam (1990) showed in a simulation study that the quality of dispersal routes can be important for the abundance of the regional population. If an additional habitat patch is added to a region but is connected to other patches by a dispersal route of low quality (in terms of the survival probability of dispersers), then adding the patch will create a sink and lower the regional population abundance. Quality of dispersal routes can refer to more than just quality for movement. Availability of dispersal routes with qualities permitting both breeding and movement between patches is also important to population survival (Bennett 1987).

At the extreme of low quality, an element of the matrix having zero quality for movement is a movement barrier. For example, Duelli (1990) showed that edges of agricultural fields can be barriers to movement through the landscape by some farmland arthropods. Mader et al. (1990) showed that minor roads stopped some forest arthropods. Merriam et al. (1989) demonstrated the differential effects of roads and cropland as barriers to *Peromyscus leucopus*.

(4) THE SPATIAL CONFIGURATION OF THE COMPONENTS OF THE LANDSCAPE

Landscape components include both habitat patches and the matrix in which the patches are imbedded. Lefkovich and Fahrig (1985) showed in a simulation study that, for population survival and abundance, the total number of dispersal routes in the landscape may be less important than their configuration relative to the habitat patches. In particular, they found that it is the overall shape and size of the geometric figure formed by interconnected patches that is most important; large, closed figures produce the highest probability of regional persistence. In a model of a one-dimensional patchy population in which one patch was different from the others in terms of population demography and/or dispersal, Seno (1988) showed that the spatial location of this patch affected the regional population dynamics: the more central the patch, the greater its impact. The degree of clumping of substrate patches was shown in a modeling study to affect persistence of moss populations (Herben et al. 1991). The positive effect of clumping on population persistence has been shown in a general model by Adler and Nürnberger (in press). The effect of spatial configuration on regional population

survival also depends on the spatial configuration of the high- versus the low-quality patches and connections.

Many field studies have demonstrated the importance of the spatial configuration of the landscape, particularly the importance of patch isolation on local population abundance and persistence. Carnaby's Cockatoo is more likely to persist in agricultural landscapes that have nest sites linked to feeding areas by well-vegetated strips (Saunders & Ingram 1987). Lawton and Woodroffe (1991) showed that breeding water voles were less likely to be present in isolated sites. The large milkweed bug is less likely to be found in host patches that are far from major rivers, possibly due to the fact that the bugs follow water courses during migration (Dingle 1991). Potter (1990) found that degree of isolation of forest remnants affected the probability of use by the Brown Kiwi in New Zealand. If large remnants are interspersed with small ones, the kiwis can move between the large remnants by using the small ones as "stepping stones." Similar use of stepping stones by forest carabid beetles in Brittany farmland was reported by Burel (1989).

Effect of Landscape Spatial Structure on Regional Survival is Determined by Dispersal and Its Underlying Behaviour

Even if the spatial structure of the landscape is static, local population abundance fluctuates, which can lead to local extinctions. Recolonization of locally extinct patch populations depends on dispersal. If the landscape structure restricts dispersal, extinctions will cover larger areas and these areas will remain extinct for longer. Therefore, the population must cover a larger area, including more patches, to ensure regional survival (Merriam 1984; Hansson 1991). Our use of the term dispersal refers to a change in location of organisms, accompanied by reproduction. Reproduction can occur after the move to the new area, or the organisms may reproduce in the original area and their offspring disperse to a new one (Lidicker 1975).

Fahrig (1990) conducted a simulation study in which local populations in patches could become extinct with a given probability. The dispersal rate resulting in the highest probability of regional survival depends on the probability of local extinction. Populations that typically experience high rates of local extinction are expected to have relatively high dispersal rates, while those that typically experience low rates of local extinction are expected to have low dispersal rates. In the former case, the positive effect of recolonization on regional survival outweighs the negative effect of dispersal mortality. In the latter case, where recolonization is less critical for regional survival, the negative effect of dispersal mortality outweighs the positive effect of recolonization. It must be noted, however, that this result depends on the assumption that dispersers experience higher mortality

rates than nondispersers; evidence for this is equivocal at best (see, for example, Dhont 1979; Greenwood et al. 1979; Johnson & Gaines 1987; Merriam & Lanoue 1990).

The components of dispersal that are important for population response to the constraint of landscape structure are as follows:

- (1) Dispersal probability, or the probability of individuals leaving patches per unit time.
- (2) Dispersal distance, or the probability of individuals successfully reaching a range of distances or landscape components. If the dispersers do not travel far enough to move between habitat patches, they will not be able to recolonize local extinctions.
- (3) Temporal pattern of dispersal. For example, dispersal may be seasonal. If local extinctions are more likely to occur at some times of the year than others, then the timing of movement that results in recolonization will affect its demographic impact.
- (4) Dispersal behavior that improves the probability of dispersers finding habitat patches and/or that decreases the risk of disperser mortality. For example, some herbivorous insects, including bark beetles (McMullen & Atkins 1962), desert locusts (Wallace 1958), and cabbage root fly (Prokopy et al. 1983), locate and orient toward host-plant patches from a distance.

Fahrig and Paloheimo (1988a) conducted a simulation experiment in which they examined the relative importance of various components of demography and dispersal on regional abundance in patchy environments. In general, dispersal was shown to be more important than demographics (such as birth rate) in determining regional population abundance. This result is supported by a study of small rodent populations in which immigration was found to be more important than local demographics in affecting local population persistence (Blaustein 1981). Fahrig and Paloheimo (1988a) also found that the most important determinant of regional population abundance was the probability that dispersers successfully locate new patches. The exact spatial pattern of habitat patches was found to be most important when dispersal distances are small relative to the distance between patches.

It is important to note that the spatial pattern of interconnectance among habitat patches can not be described in isolation from the nature of the landscape matrix or the dispersal behavior of the particular species under study. For example, Fahrig and Paloheimo (1987, 1988b) studied the effect of the spatial pattern of habitat patches (patches of cabbages) on the local abundance of

the cabbage butterfly. In this case, patches that are very close together (less than about 100 m) are in fact more isolated from each other for cabbage butterfly dispersal than are patches somewhat farther apart (about 200–400 m) because of the dispersal behavior of the butterflies.

Dynamic Landscape Structure

Landscape spatial structure is not constant but changes over time. The higher the rate of landscape change, the lower the probability of regional population survival.

Habitats are clearly variable over time on the scale of the local population (seasonal changes, for example). However, changes also occur at larger (regional or landscape) scales. These we refer to as changes in landscape spatial structure; they normally occur on longer time scales than changes at the local scale (Urban et al. 1987). Examples of changes in landscape spatial structure include (1) fragmentation and/or habitat removal, (2) increase or decrease in the number and/or quality of dispersal routes, and (3) spatial reorganization in which the proportions of various patch types remain constant but the patches change location. These changes can be gradual or abrupt, natural or anthropogenic. If the landscape structure changes, the constraint imposed by the landscape structure on regional survival also changes.

For example, Chew (1981) attributes local extinction of the butterfly *Pieris oleracea* near Boston to changes in landscape structure resulting in reduction of the host-plant distribution. Saunders and Ingram (1987) and Saunders (1990) found that in southwest Western Australia the rate of change of the landscape due to clearing of natural vegetation was so high that local extinctions of Carnaby's Cockatoo (*Calyptorhynchus funereus latirostris*) accumulated into regional extinctions. Decreasing population survival was associated with decreased landscape connectivity. Den Boer (1990) showed that habitat change due to cultivation in the Netherlands has meant that carabid beetle species with low powers of dispersal can no longer compensate for local population extinctions by recolonization.

Fahrig (1992) showed in a simulation study that in a dynamic landscape the rate of change in landscape structure is more important than the degree of patch isolation in determining population survival and abundance. If the changes in landscape structure occur at an "unnaturally" high rate (as in some anthropogenic changes), dispersal may not be able to keep up with the high rates of local extinction. In this case the regional population will become extinct. Figure 2 shows simulation results from Fahrig's (1992) model for the regional sustainable (long-term average) population size of a hypothetical forest-floor plant having a generation time of

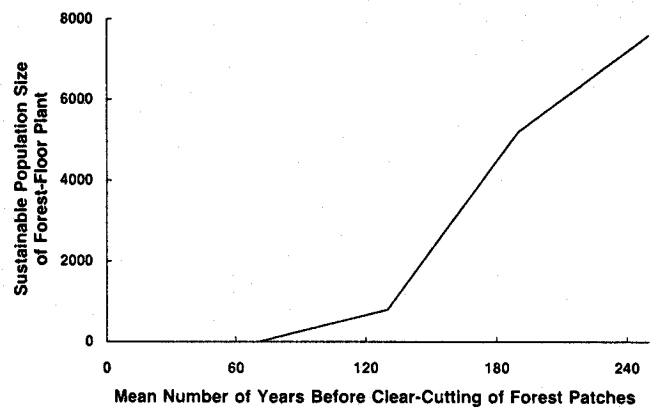


Figure 2. Simulation results from the model described in Fahrig (1992) for the regional sustainable (long-term average) population size of a hypothetical forest-floor plant species in a fragmented landscape with 10% cover by forest patches, versus mean number of years before clear-cutting of patches. Note that new patches of forest grow in so that the landscape is always comprised of 10% forest; the amount of habitat available to the forest-floor plant is therefore constant among and within simulations over time.

10 years. Ten percent of the landscape is assumed to be comprised of forest fragments; these fragments are the habitat patches for the forest-floor plant. When a forest fragment is clear-cut, the local population of the forest-floor plant dies out. Cutting of different fragments is not synchronous but is spread out approximately evenly over some time period, so that all of the forest present at the beginning of the period has been cut by the end. New patches of forest grow in over the same period, so that the landscape is always comprised of 10% forest. The simulations show that there is a lower limit of approximately 80 years for the mean number of years before clear-cutting, below which the regional population of the forest-floor plant cannot persist. Above this limit, population size increases with increasing time before clear-cutting. This result is due completely to the rate of change in landscape structure, since the amount of habitat available to the forest-floor plant (10% of the landscape) is constant among and within simulations over time.

Rapidly changing landscape structure can result in increased distance and rate of dispersal. If the rate of change in dispersal is not as fast as the rate of change in the landscape, the regional population will not survive.

If the regional population does survive in the face of a rapidly changing landscape structure, it is due to changes in dispersal behaviour (Merriam 1991). The changes can be either learned or genetically based, resulting from strong selection pressure (Pease et al.

1989; Olivieri et al. 1990). This pressure favors increasingly flexible and exploratory dispersal behavior. Exploratory behavior is favored in the short term because individuals need access to resources over larger areas; the animal is not able to count on certain locations for certain resources. An increase in exploratory behavior leads to an increased probability of dispersers finding new habitat patches (see Wegner & Merriam 1990). This leads to an increase in dispersal scale (Hansson 1991). For example, in its original habitat of woods or brush, *Peromyscus leucopus* used home ranges on the scale of less than 0.5 ha. Where agricultural clearing has fragmented wooded habitat, this mouse uses up to tens of hectares and may move hundreds of meters in a night's activity (Merriam & Lanoue 1990; Wegner & Merriam 1990). Also, Capman et al. (1990) found that different spacings of host-plant patches can alter the dispersal behavior of the Common Sooty-Wing Skipper. Finally, dispersal distances of the red fox (*Vulpes vulpes*) are greater in urban environments than in boreal forest habitats (Lindström 1989; Hansson 1991).

The interaction between the rate of change of landscape spatial structure and the rate of change in dispersal behavior determines the probability of a species' regional survival. As long as the rate of change in dispersal behavior is greater than the rate of change in landscape spatial structure, it is possible for the organism to survive in the changing landscape by moving around in it and integrating the resources over space. However, there will be a maximum possible rate of change in dispersal behavior. If the landscape structure is changing at a rate higher than this, the organism will be unable to recolonize local extinctions at a sufficient rate and the regional population will become extinct.

Discussion

The aim of this paper is to argue that landscape structure is of central importance in understanding the effects of population subdivision on population survival for conservation. Models that gloss over spatial details of landscape structure can be useful for theoretical developments (Hastings 1991) but will almost always be misleading when applied to real-world conservation problems. This is particularly important for endangered species and populations. For example, the inaccuracies due to the assumption of equal accessibility are largest when the proportion of occupied patches is small (Gurney & Nisbet 1978; Hanski 1991), which is often the case for endangered species. Endangered species are also often poor dispersers (see Cappucino & Kareiva 1985), and these are the conditions under which the landscape spatial structure has the greatest effect (Fahrig & Paloheimo 1988a). As stated by Hanski (1991), "When quantitative predictions are needed it may be

necessary to assume the more realistic stepping-stone dispersal and to resort to simulation studies. . . . There is an urgent need to develop metapopulation models that include variation in habitat patch size and quality."

A related point concerns the definition of the "metapopulation." Some authors focus on the dynamic of extinction and recolonization (such as Hanski & Gilpin 1991), while others focus on the relative rates of movement within versus between local populations (such as Harrison 1991). The fact that populations are subdivided on many scales means that the delimitation of the local population is often subjective (Hanski & Gilpin 1991). We believe that, for application of the metapopulation concept to real problems of conservation, it is most profitable to recognize that all populations are spatially structured, and to focus on the spatial structuring and dynamics of the population at hand.

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