Mosaic Landscapes and Ecological Processes

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Landscape pattern and population conservation

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12.1 INTRODUCTION

Current estimates of species extinctions indicate a sharp increase in extinction rate over the past two decades due to human-caused changes in species' habitat (Groombridge, 1992). The most noticeable and probably most important change is the reduction of the amount of habitat available for many species due primarily to expansion of agriculture and increased deforestation. However, in addition to the amount of habitat available, the spatial and spatio-temporal pattern of the habitat can have important implications for population survival. In this chapter we first briefly review the theoretical literature exploring the relationships between landscape pattern and population survival. We then present several case studies from the empirical literature that illustrate these relationships. Finally we review areas that are unresolved and where future research should be directed.

12.2 REVIEW OF THEORY

Landscape pattern refers to the distribution of habitat and resources in the landscape. Although habitat types used by a species can be many and varied, the distribution and availability of breeding habitat is of primary importance for long-term population survival. In this chapter we restrict our definition of landscape pattern to the distribution of

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breeding habitat in the landscape; our use of the term 'habitat' refers to breeding habitat only. Landscape pattern can be divided into spatial pattern and spatio-temporal pattern (Fahrig and Merriam, 1994). In the former the landscape pattern is static, at least on a time-scale relevant to the dynamics of a species of interest. In the latter the landscape spatial pattern changes over time for one or both of two possible reasons: either the habitat itself is ephemeral (e.g. the habitat is patches of annual plants), or disturbances are common and widespread in the habitat.

In the context of single-species conservation, the spatial and temporal scales of landscape pattern are best viewed in relation to the inherent spatial and temporal scales of the species. For example, patch size and inter-patch distance are considered relative to the dispersal distance of the organism, and disturbance rate and patch lifespan are considered relative to the lifespan of the organism.

12.2.1 LANDSCAPE SPATIAL PATTERN

The main components of landscape spatial pattern are

- amount of habitat in the landscape
- mean size of habitat patches
- mean inter-patch distance
- variance in patch sizes
- variance in inter-patch distances
- landscape connectivity

Note that, since we are discussing breeding habitat, patch size refers to the number of breeding sites in the patch. If patches vary in quality, a high-quality patch of the same physical size as the lower-quality patches would be a 'larger' patch.

A non-resolvable difficulty in theory relating landscape pattern to population survival is that, within a given hypothetical landscape, habitat amount, mean patch size and mean inter-patch distance may not be varied independently (Fahrig, 1992). For example, for a given amount of habitat in an area, larger patches imply larger inter-patch distances. For a given patch size, larger inter-patch distances imply less habitat overall in the landscape (Figure 12.1). Alternatively, in order to maintain patch size and habitat amount constant while increasing inter-patch distance, the total landscape under consideration must increase. Therefore, when interpreting results from a theoretical study it is important to be aware of the components of habitat pattern that vary in addition to (or as a consequence of) the components that are the focus of the study.

The relationship between habitat amount and population survival is straightforward. As the amount of habitat decreases, the population size decreases. In a stochastic model this leads to an increasing probability

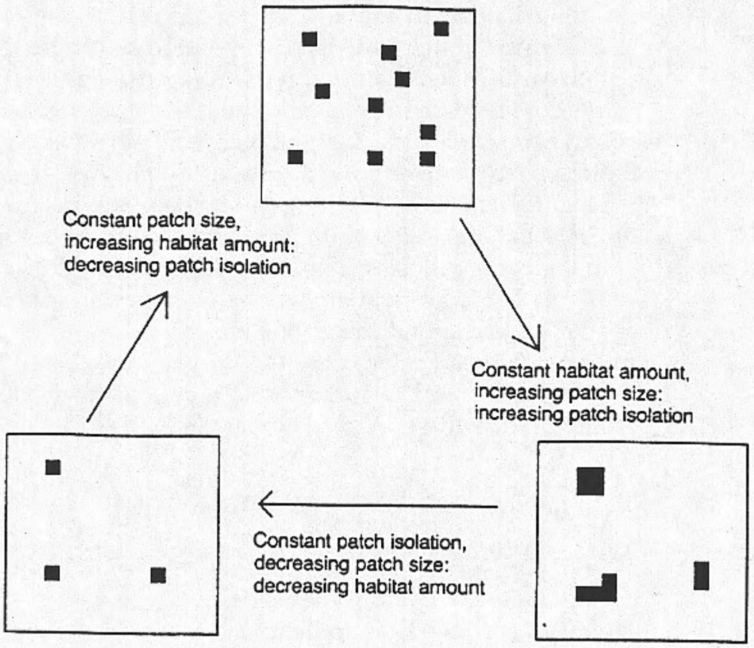

Figure 12.1 Relationship between habitat amount, mean patch size and mean patch isolation in a landscape of fixed size. If one of the three parameters is held constant and another changed, the third must change.

of regional population extinction (e.g. Stacey and Taper, 1992). Because of this clear and strong effect of habitat amount, many theoretical studies examining effects of habitat spatial pattern hold habitat amount constant and vary other aspects of landscape pattern.

Habitat clumping (i.e. increasing patch size) increases the probability of population survival (Herben, Rydin and Söderström, 1991; Adler and Nürnberger, 1994). In Adler and Nürnberger's study the size of the landscape decreases with increasing habitat clumping. However, Fahrig (in preparation) has found that this result holds even when the landscape size is constant and when the dispersal range of the organism is very limited. This suggests that, for a constant amount of habitat in a landscape of a certain size, the positive effects of increasing patch size outweigh the associated negative effects of increasing patch isolation (i.e. decreasing colonization probability).

The importance of high variance in patch sizes has been suggested in many theoretical studies. The early theory of island biogeography (MacArthur and Wilson, 1967) is an extreme example of this in which one 'patch', the mainland, is assumed to be infinitely large. This means that regional survival is ensured. The source–sink model (Pulliam, 1988; Danielson, 1992) is a less extreme version of inter-patch size variation, in which some patches (probably large, high-quality, stable ones) are sources of colonists for other patches (probably small, low-quality, frequently disturbed ones) which are sinks. The positive effect of increasing variance in patch size on regional survival is related to the result for habitat clumping above. In both cases the point is that whenever there is one or a few large patches in which population survival is virtually

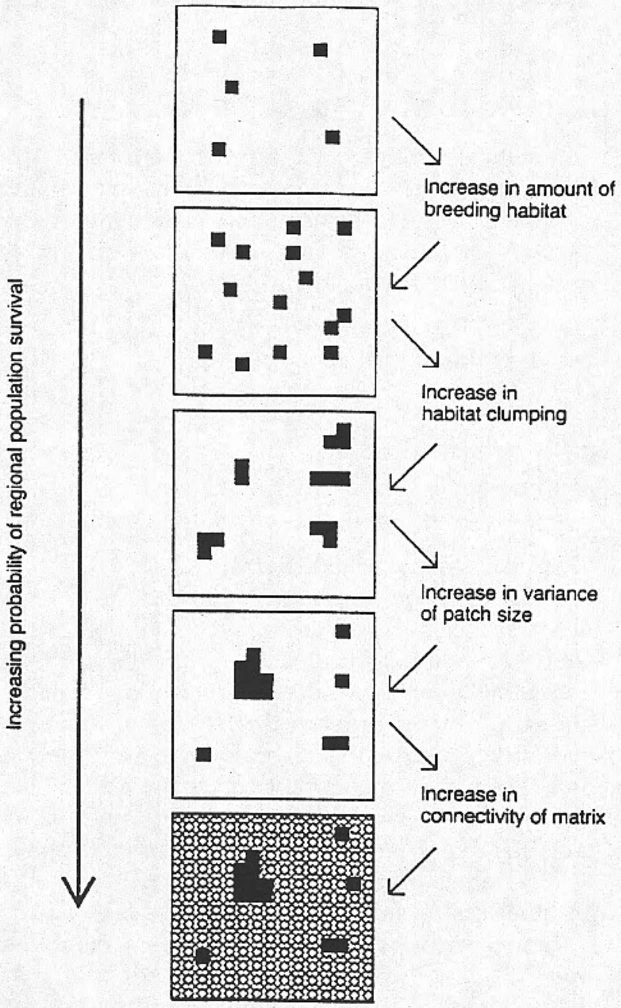

Figure 12.2 Effects of landscape spatial pattern on regional population survival, derived from general modeling studies.

ensured, these patch populations can act as colonists for other patches, and survival of the population on the landscape is ensured (Harrison, 1991; Wootton and Bell, 1992).

The final aspect of landscape spatial pattern that has a large effect on population survival is the nature of the inter-patch area or 'matrix'. The nature of the matrix determines the 'connectivity' of the landscape, or the ease with which individuals can move about within it (Taylor *et al.*, 1993). If the inter-patch area is inhospitable to moving individuals, rates of recolonization are reduced (Hansson, 1991). The effects of landscape spatial pattern on regional population survival are illustrated in Figure 12.2.

12.2.2 LANDSCAPE SPATIO-TEMPORAL PATTERN

Theoretical studies examining the effects of landscape spatial pattern, when that pattern changes over time, have generally found that the rate of change in landscape pattern is far more important than the spatial pattern itself in affecting population survival. Aspects of spatio-temporal pattern are, for disturbances,

- disturbance rate
- disturbance size
- temporal correlation in disturbances

and for ephemeral patches,

- rate of patch formation
- patch lifespan

(Herben, Rydin and Söderström, 1991).

Fahrig (1991) examined the importance of landscape spatial pattern in the presence of disturbance. Importance of spatial pattern was measured as the degree to which dispersal distance of the organism affects population survival. In an area of continuous habitat in which disturbances occur, when disturbance rate is low to moderate (less than half of the area in a disturbed state at any one time), spatial pattern of the habitat is not important for population survival. This is because disturbed areas are quickly recolonized from neighboring habitat. However, if disturbances are very large, the regional survival probability declines, since the central areas of the disturbances are not likely to be colonized before another disturbance occurs (Coffin and Lauenroth, 1989; Fahrig, 1991).

In an area of patchy non-ephemeral habitat, the higher the disturbance rate, the less important is the effect of habitat spatial pattern on population survival (Fahrig, in preparation). However, the effect of spatial pattern does remain detectable even at high disturbance rates. The effect of spatial pattern only disappears completely when the disturbance rate is so high that regional persistence is unlikely. In addition, the degree of synchrony of disturbances among habitat patches may affect survival rate (Harrison and Quinn, 1989; Gilpin, 1990). The more synchronous the disturbances, the less likely that there will be colonists available to recolonize disturbed sites during a time of low disturbance probability.

In ephemeral habitats, the 'birth' rate of new habitat patches is most important for population survival. There are two effects of patch birth rate. First, the lower the birth rate, the less habitat is available at any one time, therefore the smaller the regional population size and therefore the higher the extinction probability. Second, since habitat is ephemeral the residents of any patch must move to a newly formed patch before the one they are in 'dies'. The lower the patch birth rate, the less likely they are to successfully move to a new patch. Similarly, the shorter the lifespan of each patch, the greater is this imperative for individuals to move to other patches. Shorter patch lifespan therefore leads to lower population size even when patches are 'born' more often such that the overall amount of habitat at any one time is constant (Fahrig, 1992). This effect of patch lifespan far outweighs the effect of habitat spatial pattern on population survival. Notice that the case of extremely high disturbance rates in continuous habitat (above) is essentially the same as that of a landscape of ephemeral patches of short lifespan. The effects of landscape spatio-temporal pattern on regional population survival are illustrated in Figure 12.3.

12.3 CASE STUDIES

12.3.1 PATCHY NON-EPHEMERAL HABITATS

Interacting effects of habitat amount, patch size and patch isolation: forest birds

As temperate-zone forests become increasingly fragmented, the viability of remnant bird populations has become an increasing focus of concern. Habitat spatial pattern is clearly important; many studies have found that species composition and rates of local extinction are affected by patch size, isolation and the presence or absence of corridors (reviews in Opdam, 1990; Rolstad, 1991). The European nuthatch (*Sitta europaea*) is a typical example. Its local extinction rate on woodlots was negatively correlated with patch area, and colonization rate was negatively correlated with patch isolation (Verboom *et al.*, 1991). For species such as this, with relatively low rates of dispersal in comparison to inter-patch distance, there is a danger of population collapse if patches become fewer and more isolated. Note, however, that increasing patch isolation alone will not necessarily increase regional extinction probability. Theory predicts that increasing isolation will only have a negative effect on survival

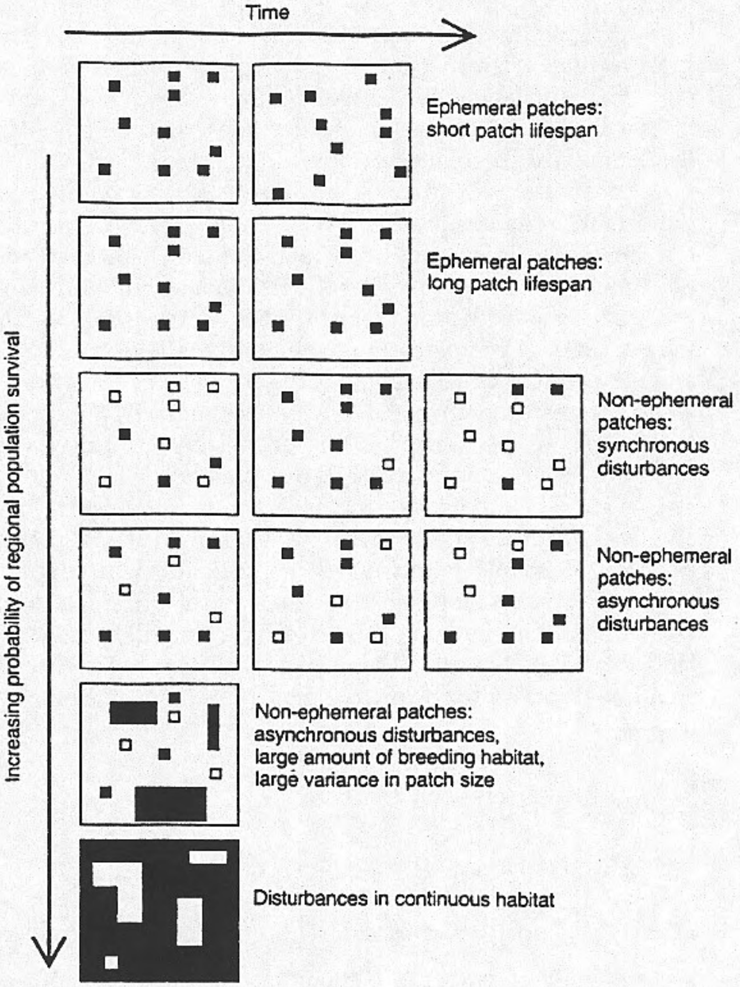

Figure 12.3 Effects of landscape spatio-temporal pattern on regional population survival, derived from general modeling studies.

if the overall amount of habitat in the landscape declines. If, instead, the amount of habitat remains constant but patch sizes increase, regional survival is predicted to be enhanced. Therefore, for making predictions about regional survival, habitat amount, patch size and patch isolation must be considered simultaneously.

One of the most ambitious attempts to deal with the spatial aspects of population viability concerns the northern spotted owl (*Strix occidentalis caurina*) in the north-western US. Less than 100 years ago, habitat of this species was an unbroken band of old-growth coniferous forest. Today less than 20% of its habitat remains, and it is highly fragmented by timber clear-cuts. The owl's philopatric behavior, and its requirement for pair territories of 1000–25 000 ha, makes it perhaps the most vulnerable of the species endemic to the north-west's old-growth forests. In addition to being a US endangered species, the owl is also a 'Management Indicator Species' for the US Forest Service, proprietor of 80% of the remaining old-growth forest in the owl's range.

With a few exceptions, such as the Olympic National Forest, few remaining fragments are large enough to support a viable population of the owl. Thus the focus has been on creating a network of forest fragments, close enough to one another to permit mutual exchange and recolonization. A team of agency scientists address this problem using a spatial simulation model of the owl population (Lamberson *et al.*, 1992; McKelvey, Noon and Lamberson, 1992). Like previous models of the owl and other spatially distributed populations (Lande, 1987, 1988; Doak, 1989), this model predicted the existence of thresholds for regional collapse. When forest fragments become too sparse and isolated, dispersing juvenile owls cannot find territories at a sufficient rate to balance the deaths of adult territory-holders, and the population quickly becomes extinct. Some evidence suggests the real owl population may already be at or near this threshold (Lande, 1988; Doak, 1989).

The owl population model used by the agency team predicted that a network of forest patches each large enough for > 20 owl pairs, and no more than 12 miles (19 km) from another patch, could maintain a viable owl population. This plan was adopted by the Forest Service. However, the plan was later blocked in court by environmentalist litigants who argued, among other things, that habitat dynamics had not been taken into account. The plan called for many small fragments to be cut, while other areas were to be allowed to regrow in order to produce the network of larger patches. Based on theoretical predictions, increasing the size of patches should be the most effective way of ensuring regional population survival. However, the plan involves a transition period of 50–150 years of net habitat loss followed by regrowth. The serious risk posed by this habitat loss to the regional survival of the owl was not addressed by the agency plan (Harrison, Stahl and Doak, 1993).

In some cases fragmentation has resulted in inter-patch distances much greater than a given species' dispersal ability. For example, populations of red-cockaded woodpeckers in remnant patches of pine forest in the US south-east (Walters, 1991) and amphibians in the same coniferous forest inhabited by the spotted owl (Welsh, 1990) may be so isolated from each other that there is essentially no interchange between patches. Therefore, patch spacing and corridors are probably not relevant to their survival. In this case the survival of each local population depends primarily on the patch size, and the survival of the regional population depends on the existence of one or more patches large enough to effectively ensure population survival there.

12.3.2 PATCHY, DISTURBED HABITATS

(a) Effect of variance in patch size: bay checkerspot butterfly

In central California, the bay checkerspot butterfly (*Euphydryas editha bayensis*) occupies patches of grassland on serpentine soil, which support its larval host plants. In dry years these plants senesce early, causing high larval mortality. Hence checkerspot populations appear to fluctuate and go extinct in response to yearly climatic patterns (Ehrlich *et al.*, 1980; Murphy and Erlich, 1980). At the same time, the butterfly's capacity to disperse to and colonize new patches is extremely limited (Harrison, Murphy and Ehrlich, 1988; Harrison, 1989). Regional persistence in this species appears to depend not on recolonization *per se*, but on the existence of a large mainland population. In 1987, one colony of about 10^6 adults was surrounded by nine much smaller (10^1–10^2) colonies, all within 4.5 km of the large colony. At distances of 5–20 km from the large colony there were 18 suitable patches of habitat, none of them occupied by the butterfly (Harrison, Murphy and Ehrlich, 1988).

The butterfly's regional distribution is thus highly sensitive to the spatial pattern of habitat, but its regional persistence is probably not. Schoener and Spiller (1987) found similar patterns in spider metapopulations on islands. Frequent population turnover occurred on small islands, but populations on large islands were highly persistent.

(b) Importance of habitat clumping: amphibians in freshwater ponds

At the northern limit of its range, the European pool frog (*Rana lessonae*) is found in shallow freshwater ponds at the edge of the Baltic Sea. Large ponds seldom contain frog populations, since they are inhabited by the predatory pike (*Esox lucius*). Within small ponds, frog populations may go extinct during cold winters that cause reproductive failure. Extinctions are also caused by the disappearance of ponds, due either to natural succession or to draining for forestry. Sjögren (1991) compared the distribution of frogs across 60 ponds to that recorded by another researcher in 1962, and found an average extinction rate of 2% per year. However, extinctions seldom occurred in ponds < 1 km from other occupied ponds, suggesting that the dispersal of frogs over such distances is sufficient to rescue declining populations. In this system, where all patches are small, theory predicts that regional survival is enhanced by close-spaced clumping of ponds. This effectively increases patch size.

Strikingly similar patterns are seen in other freshwater amphibians. Gill (1978) found that the newt (*Notopthalmus viridescens*) dispersed readily among neighboring ponds, and in each year a few ponds supplied the majority of recruits to all other ponds. Sinsch (1992) likewise found that natterjack toads (*Bufo calamita*) move frequently enough among ponds to compensate for local reproductive failures. Both *Bufo calamita* (Sinsch, 1992) and the wood frog *Rana sylvatica* (Berven and Grudzien, 1990) show patterns of genetic variation that indicate movement is frequent among nearby (< 1 km) ponds, but declines rapidly at greater distances. Because habitat (pond) quality is variable in space and time, movement among ponds is essential to the regional persistence of the species, and clusters of nearby ponds are necessary to support viable regional populations.

12.3.3. EPHEMERAL HABITATS

Importance of patch birth rate and patch lifespan: Butterflies and other insects

Many insects colonize patches of their food resource, and maintain local populations that last from one to several generations. These dynamics are exemplified by recent studies of milkweed beetles on patches of their host plant (McCauley, 1991) and forked fungus beetles on rotting logs (Whitlock, 1992). In both these cases, the founder effects associated with colonization created spatial genetic structure in the metapopulation (McCauley, 1991; Whitlock, 1992). However, insects immigrated to and emigrated from patches fairly frequently, suggesting that metapopulation persistence was not highly sensitive to habitat spatial pattern, as predicted by theory.

Several well-studied butterfly species in Great Britain occupy spatially and temporally variable habitats (e.g. Warren, Thomas and Thomas, 1984; Thomas and Harrison, 1992; Thomas, Thomas and Warren, 1992; Thomas and Jones, 1993). For example, in some regions the silver-studded blue butterfly (*Plebejus argus*) requires grassland 3–5 cm in height, and successional overgrowth may lead to the extinction of local populations. In other regions, *P. argus* is found in patches of heathland recently (< 10 years) affected by fire and other disturbance. The extinction and colonization rates of *P. argus* are higher in heathland than in grassland, because of more rapid disturbance and succession. But within either biotope, the butterfly is relatively good at tracking its shifting habitat mosaic. Only at distances of > 1 km from occupied patches are suitable patches likely to remain unoccupied for a significant period of time (Thomas and Harrison, 1992).

For *P. argus* and many similar species, regional population dynamics are essentially controlled by the rates and patterns of habitat processes, i.e. disturbance and succession (Thomas, 1994). The key to conservation of these species is the maintenance of a habitat mosaic in which the required successional stage(s) is always present. This may involve very active interventive management and/or the preservation of relatively large areas of biotope (patch plus matrix). Once the temporal continuity of the habitat mosaic is broken and the species becomes regionally extinct, natural long-distance recolonization may be extremely slow. For example, the skipper (*Hesperia comma*) may take decades to recolonize areas of chalk grassland from which it went extinct in the mid–1950s, when the destruction of rabbits by myxomatosis caused overgrowth of the habitat (Thomas and Jones, 1993).

In the US, the Karner blue butterfly (*Lycaeides melissa samuelis*) is an even more extreme example of an ephemeral habitat species. Its host plant, *Lupinus perennis*, flourishes in recently burned patches of pine barren habitat, found on sandy soils in the north-eastern US. The butterfly cannot tolerate fire in any of its life stages, and thus must continually track a shifting mosaic of burned and unburned patches. Habitat loss combined with fire suppression now threatens this species; Givnish, Menges and Schweitzer (1988) describe an attempt to devise an appropriate management regime for the butterfly on surviving fragments of pine barrens.

12.4 FUTURE DIRECTIONS

From a practical standpoint, the most pressing question remaining to be answered is: to what extent can alteration of landscape pattern compensate for loss of habitat? In other words, can we maintain high population survival probability while reducing the amount of habitat available, by carefully selecting the sizes and spatial locations of the remaining habitat fragments? Unfortunately it will be difficult or impossible to answer this question using the empirical data available. In most cases, habitat fragmentation involves simultaneously loss of habitat, reduction of patch sizes and increased patch isolation, which means that it is not possible to estimate the separate effects of these factors on population density and survival probability. Conservation programs will therefore depend to an increasing extent on spatially explicit population models which integrate local population dynamics and dispersal with landscape spatial and temporal pattern (e.g. Burgman, Ferson and Akçakaya, 1993). Although such detailed modeling is possible for some organisms (e.g. Fahrig and Merriam, 1985; Pulliam, Dunning and Liu, 1992), in most cases the information required is not available. Even for the well-studied spotted owl, the exemplary modeling effort by US Forest Service scientists (McKelvey, Noon and Lamberson, 1992; Lamberson *et al.*, 1992) was found to have significant shortcomings (Harrison, Stahl and Doak, 1993).

An additional important research question is therefore: under what circumstances (for what kinds of species in what kinds of landscapes) is spatially explicit modeling necessary for predicting the effects of habitat fragmentation on population survival?

Future research will also need to address the question: how can we predict the effects of alteration of habitat pattern on species diversity in the landscape? This is a difficult problem since the pattern of any one landscape is particular to each species living there. Species differ both in the kinds of habitat they use in the landscape and the spatial and temporal scales at which they interact with the landscape. For example, endangered amphibians of old-growth conifer forest in the north-western US occur as isolated independent remnant populations (Welsh, 1990) whereas birds using these same forest patches occur as more interconnected subpopulations. It appears unlikely that predictions of effects on diversity can be made using a composite of many spatially explicit population models. A more promising approach will be a statistical modeling approach in which the actual diversity in landscapes of differing spatial patterns are measured and compared to develop general relationships between species diversity and landscape pattern as viewed from the human perspective.

12.5 SUMMARY

Theory relating population survival to landscape spatial pattern is reviewed. Important generalizations are:

1. as the amount of habitat decreases the probability of regional population survival decreases;
2. for the same total amount of habitat, increased habitat clumping (i.e. increasing patch size) increases the probability of population survival, and this positive effect of increasing patch size outweighs the negative effect of increasing inter-patch distance;
3. increasing inter-patch variance in patch size increases the probability of regional survival;
4. when the landscape pattern is dynamic (patches are ephemeral or disturbance rate is high), landscape spatial pattern is relatively unimportant; and
5. when habitat is ephemeral, regional population survival increases with increasing patch lifespan.

Case studies illustrating these effects in real populations are given. However, we conclude that empirical studies cannot be used to rigorously test the theoretical predictions because human activities usually alter several aspects of landscape pattern simultaneously. Important questions for future research are

1. To what extent can careful planning of landscape pattern compensate for loss of habitat?
2. Under what circumstances (for what kinds of species in what kinds of landscapes) is spatially explicit modeling necessary for predicting the effects of habitat fragmentation on population survival?
3. How can we make predictions of effects of alteration of landscape pattern on species diversity?

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