

COMENTARIO

Population spatial structure, human-caused landscape changes and species survival

Estructura espacial de las poblaciones, cambios antropogénicos del paisaje y sobrevivencia de especies

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ABSTRACT

Population survival depends on the spatial structure of the population, which is defined as the set of local populations that make up the population and the probability of exchange of individuals among them. Therefore, population spatial structure depends on the interaction between the landscape spatial pattern and the dispersal characteristics of the organisms. Human activities have profound effects on population spatial structure. Habitat loss decreases the number of local populations and therefore decreases overall population size. This results in a decrease in the number of dispersers available for recolonization and rescue of local populations, which further reduces overall population size. Eventually local extinctions can accumulate to regional extinctions. Habitat fragmentation per se exacerbates this problem by increasing the probability of local extinction. However, the effects of habitat loss far outweigh the effects of fragmentation per se. Species interactions are a critical component of ecosystem function, and alterations of population structure by human activity have significant effects on them. Mutualisms may be disrupted, coexistence may be either increased or decreased, predator-prey interactions may be destabilized, and new predator-prey interactions may be introduced. Realistic predictions of the effects of changes in landscape pattern on population survival and population interactions depend on an accurate understanding of their effects on population spatial structure.

Key words: habitat fragmentation, habitat loss, population spatial structure, species interactions, metapopulations.

RESUMEN

La sobrevivencia de las poblaciones depende de la estructura espacial de éstas, la que se define como el conjunto de poblaciones locales que conforman una población y la probabilidad de intercambio de individuos entre ellas. Así, la estructura espacial de una población depende de la interacción entre el patrón espacial del paisaje y las características de dispersión del organismo. Las actividades humanas tienen efectos profundos en la estructura espacial de las poblaciones. La pérdida de hábitat disminuye el número de poblaciones locales y con ello el tamaño total de una población. Esto resulta en un decremento en el número de dispersores disponibles para la recolonización y rescate de poblaciones locales, lo que reduce aún más el tamaño poblacional. Eventualmente, las extinciones locales pueden causar extinciones regionales. La fragmentación del hábitat per se exagera este problema al incrementar la probabilidad de extinciones locales. Sin embargo, los efectos de la pérdida de hábitat son más fuertes que los efectos de la fragmentación del hábitat per se. Las interacciones entre especies pueden verse afectadas por alteraciones en la estructura poblacional debido a la actividad humana. Los mutualismos pueden ser alterados negativamente, la coexistencia de especies puede incrementar o decrecer según la magnitud de la perturbación antrópica, las interacciones depredador-presa pueden desestabilizarse y nuevas interacciones depredador-presa pueden incorporarse al ecosistema. Predicciones más reales sobre los efectos de los cambios en el paisaje sobre la sobrevivencia de las poblaciones y las interacciones entre especies dependen de un entendimiento preciso de sus efectos en la estructura espacial de las poblaciones.

Palabras clave: estructura espacial poblacional, fragmentación del hábitat, pérdida de hábitat, interacciones entre especies, metapoblaciones.

INTRODUCTION

Human-caused alterations of habitat are recognized as the primary cause of the

current species extinction event (WCMC 1992). However, predicting the effects of habitat alteration on species survival depends on a mechanistic understanding of the

extinction process. In this paper we argue that extinction probability depends on population spatial structure. Human activities alter this spatial structure, thus altering (typically increasing) extinction probability, and also modifying species interactions.

HOW ARE POPULATIONS STRUCTURED?

Most populations are comprised of more or less distinct local populations (Andrewartha & Birch 1984, Hanski 1989). Local populations typically inhabit discrete areas of habitat, or "habitat patches". Individuals within local populations have high probabilities of interaction, whereas movements between local populations (termed "dispersal") are relatively rare. Extinction of a population occurs through the accumulation of extinctions of its local populations. To avoid population extinction we must therefore understand the process by which smaller scale (i.e., local) extinctions accumulate to larger scale extinctions.

Local populations do not have independent probabilities of extinction because they interact with each other through the exchange of dispersing individuals. This exchange reduces population extinction probability by recolonization of locally extinct areas and by "rescue" of local populations from low numbers (Levins 1969, Brown & Kodric-Brown 1977, Hanski 1982, Harrison 1991). Population spatial structure determines the rate and pattern of dispersal among local populations, and hence affects local population extinction probability which in turn affects the probability of population extinction.

Population spatial structure is the combination of the spatial pattern of a population, and the dispersal scale and ability of the organism. For example, a population of birds inhabiting 10 small forest patches could have a similar spatial structure to a population of dung beetles inhabiting 10 dung pats. Also, a population of frogs inhabiting 10 ponds separated by 1 km within a large forested area could have a spatial structure similar to a population of the same species inhabiting 10 ponds separated by 100 m but isolated from each other by roads or other barriers to dispersal.

Functionally, population spatial structure is the spatial arrangement of the local populations combined with the set of probabilities of dispersal between all pairs of local populations. Note that local demographic processes affect these movement probabilities. Population spatial structure affects both local extinction and (re)colonization rates. If dispersal between local populations is restricted, the population must cover a larger area including more patches, to ensure regional survival (Merriam 1984, Hansson 1991). On the other hand, if dispersal rate between local populations is high, a smaller number of patches is needed for regional survival.

Dispersal between any two local populations depends on four factors: (i) the size and quality of the habitat of each local population (also called a "habitat patch"), (ii) the distance between the local populations, (iii) the dispersal attributes of the organism, and (iv) the degree to which the area separating the local populations (the "landscape matrix") is conducive to movement by the organism.

EFFECT OF POPULATION SPATIAL STRUCTURE ON POPULATION SURVIVAL

Size and quality of patches of habitat

Small, low quality habitat patches contain small local populations (e.g., Lynch & Whigham 1984). Local extinction probability is negatively correlated with local population size (Paine 1988, Berger 1990). Therefore, as patch size and quality decrease the local population size decreases, which increases the probability of local population extinction (Stacey & Taper 1992, Verboom et al. 1991).

Since large, high quality habitat patches are more likely to sustain large, permanent local populations, these patches are also more likely to contribute dispersers to other habitat patches. Patch size and quality therefore affect the probability of dispersal between local populations and therefore the spatial structure of the population.

Distance between local populations

Population survival probability increases with increasing spatial contagion of local

populations (Herben et al. 1991, Adler & Nurnberger 1994, Fahrig unpublished data). The closer together local populations occur in space the more likely they are to exchange individuals. This increases the overall survival probability of the whole population by increasing the rates of recolonization and rescue. For example, it has been reported that distance between breeding ponds affects the success rate of between-pond dispersal which affects survival rate of local populations of a newt, a frog, and a toad (Gill 1978, Sjögren 1991, Sinsch 1992, respectively). Also, water voles are less likely to be present in isolated sites (Lawton & Woodroffe 1991) and recolonization of local populations of the European nuthatch is negatively correlated with patch isolation (Verboom et al. 1991). Note however, that if local extinctions are caused by large-scale disturbance events, habitat contagion may increase the probability of simultaneous extinction of all local populations in a region.

Dispersal attributes of the organism

Dispersal attributes of organisms determine population spatial structure, since the probability of dispersal among local populations depends on the relative scales of the landscape spatial pattern and the dispersal. Dispersal attributes have been found to be more important than demography in determining local population abundance and persistence in patchy environments (Blaustein 1981, Fahrig & Paloheimo 1988a). The components of dispersal that affect population spatial structure and population survival are: (i) dispersal probability, or the probability of individuals leaving habitat patches, (ii) dispersal distance, or the probability of individuals successfully reaching a range of distances. If the dispersers do not travel far enough to move between habitat patches, they will not be able to recolonize after local extinctions, (iii) timing 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 dispersal between patches will affect its demographic impact, (iv) dispersal behaviour that improves the probability of dispersers finding habitat

patches and/or decreases the risk of disperser mortality.

An important determinant of local population abundance is the probability that dispersers successfully locate patches, which will depend on the components of dispersal mentioned above (Fahrig & Paloheimo 1988a). For example, although Bay checkerspot butterflies are able to travel long distances in search of habitat, the combination of hilly terrain which impedes their movement, with their limited ability to orient towards habitat from short distances, results in low colonization probability (Harrison 1989). On the other hand, although cabbage butterflies cannot orient toward their host patches (Fahrig & Paloheimo 1987), the large dispersal probability, large dispersal distance, and high survival rate of dispersers results in high probability of movement between habitat patches (Root & Kareiva 1984, Fahrig & Paloheimo 1988b). Therefore, the spatial pattern of habitat patches should not be described in isolation from the dispersal behaviour of the particular species under study.

Quality of the landscape matrix

Often conservation studies and programs focus only on habitat patches such as reserve areas. However, survival rate of organisms in transit between local populations has a large effect on population spatial structure and therefore on population survival (Fahrig & Merriam 1994). Survival rate between habitat patches depends on the spatial pattern and qualities of the habitat types that occur in the area between patches (the landscape matrix), which are potential dispersal routes through which the organism can move. Several studies have demonstrated the importance of dispersal routes for regional population abundance and persistence of small mammals (Fahrig & Merriam 1985, Bennett 1990, Merriam & Lanoue 1990), birds (Saunders & Ingram 1987, Dmowski & Kozakiewicz 1990) and insects (Dingle 1991).

A habitat patch can also form part of a dispersal route between two other patches, acting as a stepping stone. For example, when large forest remnants are interspersed

with small ones, kiwis can move between the large remnants by “hopping” between the small patches (Potter 1990). A similar use of stepping stones by forest carabid beetles in Brittany farmland has been reported by Burel (1989).

It is important to note that the total number of dispersal routes in the landscape may be less important than their configuration relative to the habitat patches. In particular, the overall shape and size of the geometric figure formed by interconnected patches has a large effect on population survival. Large, closed figures produce the highest probability of population persistence (Lefkovich & Fahrig 1985).

EFFECTS OF HUMAN-CAUSED LANDSCAPE
CHANGE ON POPULATION SPATIAL STRUCTURE
AND POPULATION SURVIVAL

Human-caused landscape change includes (i) changes in amount and/or quality of habitat, (ii) fragmentation of habitat, (iii) changes in the landscape matrix (non-habitat area) that affect dispersal between local populations, and (iv) alterations in the “natural” rate of landscape change. All of these changes affect population spatial structure and population survival.

Note that “habitat fragmentation” is often used broadly to include both fragmentation and loss of habitat; in fact “fragmentation” and “deforestation” are often used synonymously (e.g., de Vries & den Boer 1990, Andren & Delin 1994). However, habitat fragmentation and habitat loss have independent effects on population spatial structure and therefore on population survival. Therefore we use “fragmentation” in its literal sense only, i.e., the breaking apart of habitat.

It can be argued that, since the two processes typically occur simultaneously, it is pointless or even misleading to consider them separately. However, in conservation research the goal is not just to understand the effects of past changes but also to predict effects of future changes. When considering alternative land management schemes (e.g., forest harvesting schemes) it is useful to understand the separate effects of habitat loss and fragmentation.

*Changes in amount and/or quality
of habitat*

Habitat loss is the most important factor in population and species extinction (WCMC 1992). However, the effect of habitat loss on survival is not proportional to the loss of habitat. Depending on the spatial structure of the population, the effect of small losses of habitat can often be minor while the effect of large amounts of habitat loss can be greater than predicted based just on the area lost (Andren 1994, Fahrig unpublished data).

In general the less habitat and/or the lower the quality of habitat within an area, the smaller the local populations will be and this will lower the probability of local population survival. Small local population sizes have the additional effect of reducing dispersal rates among local populations thereby altering population spatial structure and increasing the probability of population extinction (Lamberson et al. 1992, McKelvey et al. 1992, Lande 1987, 1988, Doak 1989).

Many population extinctions have been attributed to habitat loss. Local extinction of the butterfly *Pieris oleracea* near Boston is attributed to changes in landscape structure resulting in reduction of its host plant distribution (Chew 1981). The large amount of clearing of natural vegetation in southwest Western Australia resulted in local extinctions of Carnaby’s cockatoo accumulating into regional extinctions (Saunders & Ingram 1987, Saunders 1990). Habitat loss due to cultivation in the Netherlands has resulted in local population extinctions of carabid beetle species (den Boer 1990).

Fragmentation of habitat

Fragmentation of habitat also leads to reduced population survival even in the absence of habitat loss. Simulation studies have shown that a given amount of habitat fragmented into many small units results in greater probability of extinction than the same amount of habitat distributed as a few large units (Herben et al. 1991, Adler & Nurnberger 1994, Fahrig unpublished data). There are practical implications of this finding. For example it suggests that, given a certain amount of habitat loss due to

deforestation, the harvest should be conducted in such a way that the largest possible blocks of unharvested area are left, rather than leaving a larger number of smaller blocks, in order to enhance population survival.

Changes in the landscape matrix

Human-caused alterations in the landscape matrix that result in reduced success rate of dispersal can also have large effects on population spatial structure and population survival. An important example is the effect of roads on disperser mortality rate. Increased road traffic increases the mortality rate of amphibians, decreasing population densities (Fahrig et al. 1995). Road mortality has also been shown to be significant for many other species including amphibians, reptiles, small and large mammals, birds, and some invertebrates (e.g., Mader 1984, Siegel 1986, Merriam et al. 1989, Baur & Baur 1990, Rosen & Lowe 1994). The effect of road mortality is increasingly significant, since traffic volume and total road length worldwide have doubled in the past 20 years (United Nations 1992, Glover & Simon 1992).

Removal of vegetation cover due to agriculture or other development greatly alters the population spatial structure of organisms that will only travel under cover. At the extreme this alteration results in complete isolation of habitat patches. For example, local populations of red-cockaded woodpeckers in remnant patches of pine forest in the US southeast (Walters 1991) and local populations of amphibians in remnant coniferous forests in the US southwest (Welsh 1990) may be so isolated from each other that there is essentially no interchange between patches. In this case the survival of each local population depends primarily on patch size, and the survival of the population depends on the existence of some patch(es) that are large enough to effectively ensure population survival there (Harrison & Fahrig 1995).

Changes in the "natural" rate of landscape change

Landscapes are naturally variable over time at both large and small scales. However,

alterations in the rate of change of landscapes can have profound effects on population spatial structure and population survival. Fahrig & Merriam (1994) present results from a simulation model (Fahrig 1992) for the regional sustainable (long-term average) population size of a hypothetical forest floor plant having a generation time of 10 years. When the rate of change of the landscape spatial pattern is too high (i.e., forestry rotation period shorter than 80 years), local populations cannot build up to high enough levels to provide colonists for other habitat patches, and the entire population dies out.

If the regional population does survive in the face of rapidly changing landscape pattern, it is often 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 favours exploratory dispersal behaviour in the short term because individuals need to access resources over larger areas. An increase in exploratory behaviour leads to an increased probability of dispersers finding new habitat patches (e.g., 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 reduced and fragmented wooded habitat this mouse uses up to tens of hectares and may move hundreds of metres in a night's activity (Merriam & Lanoue 1990, Wegner & Merriam 1990). Also, different spacings of host plant patches can alter the dispersal behaviour of the common sooty wing skipper (Capman et al. 1990).

The interaction between the rate of change of landscape spatial pattern and the rate of change in dispersal behaviour determines the probability of regional survival. As long as the rate of change in dispersal behaviour is greater than the rate of change in landscape spatial pattern, 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 behaviour. If the landscape pattern

is changing at faster than this, the organism will be unable to recolonize local extinctions at a sufficient rate and the regional population will become extinct.

Relative importance of habitat loss, habitat fragmentation, and rate of landscape change

Fahrig (1992) conducted simulations assessing the relative importance of the rate of landscape change and habitat fragmentation. The total amount of habitat was held constant but the degree of habitat contagion and the "lifespan" of patches were altered. In simulations with short patch lifespans, the habitat becomes a moving target for the organism. Results suggested that the rate of change of the landscape was much more important than fragmentation in determining survival time of the population. Similarly, recent simulation studies (Fahrig unpublished data) compared the relative importance of habitat fragmentation and habitat loss. Again, results suggest that the effects of habitat loss on survival probability far outweigh the effects of habitat fragmentation *per se*. These results suggest that conservation efforts are most effectively directed at reducing habitat loss and reducing the rate of landscape change. Minimizing habitat fragmentation will not compensate for increased loss of habitat or increased rate of landscape change in any significant way.

EFFECTS OF HUMAN-CAUSED LANDSCAPE
CHANGE ON POPULATION SPATIAL STRUCTURE
AND SPECIES INTERACTIONS

Species interactions are fundamental for the maintenance of ecosystem function and biodiversity (Meffe & Carroll 1994). These interactions occur heterogeneously in space, depending on the spatial pattern of the landscape and the dispersal behaviour of the species. Consequently, changes in landscape spatial pattern and therefore the spatial structure of the interacting populations may have crucial effects on the outcome of a species interaction.

Habitat loss and fragmentation may have significant effects on species interactions. These effects may be the result of local

changes in species composition (species loss or species addition), or simply the result of changes in local population abundances. The effect of habitat loss and fragmentation on species interactions depends on their effects on the survival of each of the interacting populations which, as already discussed, will ultimately depend on the combined effects of the dispersal attributes of the species and the spatial pattern of the remaining habitat.

Competitive interactions and species coexistence

Several models describe how habitat destruction may favour the establishment of inferior competitors. These models are based on the assumption that competitive ability and dispersal ability are negatively correlated. If the superior competitor is a poor disperser, even moderate habitat destruction may cause its extinction in remnant patches, and may result in an increase in the total number of patches occupied by the inferior, but more dispersive competitor. Therefore, multi-species coexistence may occur in the whole area (Nee & May 1992, Dytham 1994, Tilman et al. 1994). However, as habitat destruction increases further species are predicted to become extinct, from the best to the poorest competitors (Tilman et al. 1994). The selective extinction of the best competitors may have further consequences since these species are often advanced as the major regulators of ecosystem functions (Tilman et al. 1994).

Predator-prey interactions

Habitat fragmentation and loss may have profound effects on predator-prey interactions. For example, they may increase the probability that an intruder predator invades habitat patches. This has been observed in agroecosystems, where ladybird beetles immigrate faster to fragmented habitat (Grez unpublished data). Also, higher predation rates by birds and mammals on bird nests have been reported in small as compared to large forest fragments, usually due to a higher edge effect in small fragments. Predators coming from the landscape matrix

are more likely to penetrate these smaller patches (Wilcove 1985, Wilcove et al. 1986, Andren & Angelstam 1988, Small & Hunter 1988, Paton 1994).

The above are examples of the consequences of predator species addition after habitat loss and fragmentation. But habitat loss and fragmentation may also jeopardize pre-existing predator-prey interactions. Isolation of patches may decrease the probability that a local predator moves between patches. This may lead first to locally and ultimately to regionally unstable predator-prey relationships. Therefore, the effect of habitat loss and fragmentation will depend on the specific behaviour of the organisms using the habitat (Kareiva 1987). A stable predator-prey relationship may be achieved in remnant habitats as long as spatio-temporal prey refuges have not been removed (Kareiva 1990). This may be attained if: (i) population densities fluctuate asynchronously in different patches, (ii) predator and prey dispersal rates are above some minimal rate to assure recolonization of patches, and (iii) predators do not disperse so effectively as to find prey patches as soon as prey colonize vacant patches (Kareiva 1990, Crowley 1981, Reeve 1988, Taylor 1988).

Mutualism

Disruption of mutualisms such as pollination and seed dispersal is one of the most threatening consequences of habitat loss and fragmentation (Bawa 1990). For example, loss and fragmentation of the Chaco Serrano negatively affects native flower visitors and facilitates the access of the exotic honey bee *Apis mellifera* (Aizen & Feinsinger 1994a). This change in pollinator fauna results in an overall decline in pollination effectiveness, measured by the number of pollen tubes in floral styles, and seed output (Aizen & Feinsinger 1994b). This disruption in pollination service may have consequences for the demography of plants. For instance, the lower seed set of the caryophyllaceous herb, *Dianthus deltoides*, in remnant habitats of Sweden, has been explained by the reduction of pollinator service by butterflies as compared with large unfragmented sites (Jennersten 1988).

FINAL REMARKS

We have shown evidences supporting that population survival depends on the spatial structure of the populations, which in turn depends on the interaction between the landscape spatial pattern and the dispersal characteristics of the organism. As a consequence of human activities, habitat loss and habitat fragmentation may reduce local and overall population size, increasing the probability of local and regional extinctions. Further, alterations of population structure by human activities may have also significant effects on species interactions. Mutualisms may be disrupted, species coexistence may increase or decrease, predator-prey interactions may be destabilized, and new predator-prey interactions may be introduced. An accurate understanding of the mechanisms involved in the extinction of spatially structured populations, such as the ones discussed here, will provide more realistic predictions of the effect of human induced changes in landscape pattern on population survival and species interactions.

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