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Effects of Habitat Fragmentation on Birds and Mammals in Landscapes with Different Proportions of Suitable Habitat: A Review

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## MINI- REVIEW

**Minireviews** provides an opportunity to summarize existing knowledge of selected ecological areas, with special emphasis on current topics where rapid and significant advances are occurring. Reviews should be concise and not too wide-ranging. All key references should be cited. A summary is required.

# Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review

Henrik Andrén

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Habitat fragmentation implies a loss of habitat, reduced patch size and an increasing distance between patches, but also an increase of new habitat. Simulations of patterns and geometry of landscapes with decreasing proportion of the suitable habitat give rise to the prediction that the effect of habitat fragmentation on e.g. population size of a species would be primarily through habitat loss in landscape with a high proportion of suitable habitat. However, as the proportion of suitable habitat decreases in the landscape, area and isolation effects start influencing the population size of the species. Hence, the relative importance of pure habitat loss, patch size and isolation are expected to differ at different degrees of habitat fragmentation.

This conclusion was supported by a review of studies on birds and mammals in habitat patches in landscapes with different proportions of suitable habitat: the random sample hypothesis was a good predictor of the effects of habitat fragmentation in landscapes with more than 30% of suitable habitat. In these landscapes, habitat fragmentation is primarily habitat loss. However, in landscapes with highly fragmented habitat, patch size and isolation will complement the effect of habitat loss and the loss of species or decline in population size will be greater than expected from habitat loss alone.

Habitat patches are parts of the landscape mosaic and the presence of a species in a patch may be a function not only of patch size and isolation, but also of the neighbouring habitat. Habitat generalists may survive in very small patches because they can also utilize resources in the surroundings. Furthermore, the total species diversity across habitats in a given landscape may increase when new patches of habitat are created within the continuous habitat, since new species may be found in these new habitats, even if they are human-made.

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Habitat fragmentation, the process of subdividing a continuous habitat into smaller pieces, occurs in natural systems, e.g. through fire (Wright 1974, Pickett and Thompson 1978) and windfall (Foster 1980). However, the most important and large-scale cause of habitat fragmentation

is the expansion and intensification of human land use (Burgess and Sharpe 1981). Habitat fragmentation has three major components, namely loss of the original habitat, reduction in habitat patch size, and increasing isolation of habitat patches, all of which contribute to a de-

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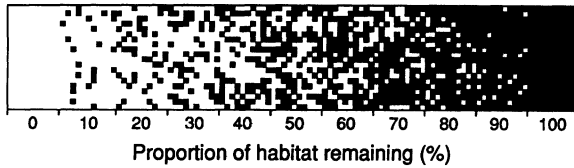


Fig. 1. Composite example of artificial maps generated by a random process, showing habitat fragmentation in a landscape of different proportion of two habitats. The shaded area represents the original habitat and the unshaded areas the extent of habitat loss.

cline in biological diversity within the original habitat (Wilcox 1980, Wilcox and Murphy 1985).

The recent development of landscape ecology has yielded many models describing changing landscape patterns (Franklin and Forman 1987, Gardner et al. 1987, Krummel et al. 1987, Baker 1989, Turner et al. 1989a, b, Gardner and O'Neill 1991, Gustavson and Parker 1992). These studies have usually compared patterns of real landscape with landscape patterns generated using neutral models (Gardner and O'Neill 1991). No attempts have been made to compare data on abundance and distribution of organisms in landscapes with different patterns and proportions of habitats.

Effects of habitat fragmentation on species richness have usually been studied using the theory of island biogeography (MacArthur and Wilson 1967, Brown 1971, Diamond and May 1981, Harris 1984). However, the simplest explanation for the decline in species richness with decreasing island size is that islands can be considered as random samples from source areas, i.e. the random sample hypothesis (Connor and McCoy 1979, Haila 1983a). These two hypotheses have been proposed to explain the species richness on islands, but they have also been used to describe the effect of habitat fragmentation in continental areas.

The metapopulation concept, the idea that the persistence of a species regionally depends on the colonization and extinction of subpopulations (Levins 1969, 1970), has usually been applied in studies of single species living in a landscape with fragmented habitat (Hanski and Gilpin 1991). Metapopulation dynamics have very much in common with the theory of island biogeography, as they both work with the same fundamental population ecological processes, i.e. extinction and colonization of islands/habitat patches. The random sample hypothesis can also be applied to individual species and one prediction is that the change in population size in relation to habitat fragmentation will be linearly related to the change in proportion of suitable habitat in the landscape.

Both the theory of island biogeography and metapopulation dynamics assume that the suitable habitat patches are isolated from one another by hostile habitat, i.e. a divided landscape (Addicott et al. 1987). Other important assumptions are that individuals of each species only use

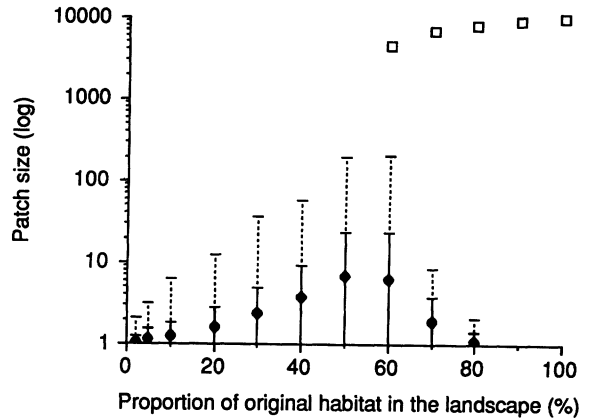


Fig. 2. Patch size in relation to the proportion of that habitat in the landscape. The maps were randomly generated and had a size of  $100 \times 100$  units. Mean, one standard deviation and the maximum size are given. Open squares indicate size of continuous patches.

one habitat patch and that each patch has a local population, i.e. a coarse-grained landscape (Levins 1968).

The aim of this paper is to combine ideas from landscape ecology with classical aspects of communities in habitat islands to try to identify the factors influencing the abundance and distribution of species in landscapes with different degrees of habitat fragmentation. The paper consists of three parts. First, I will describe the relationships between patch size, isolation between patches and the proportion of original habitat remaining in the landscape by generating artificial maps and summarizing the attributes. Secondly, the effect of habitat fragmentation on species living in the original habitat will be examined

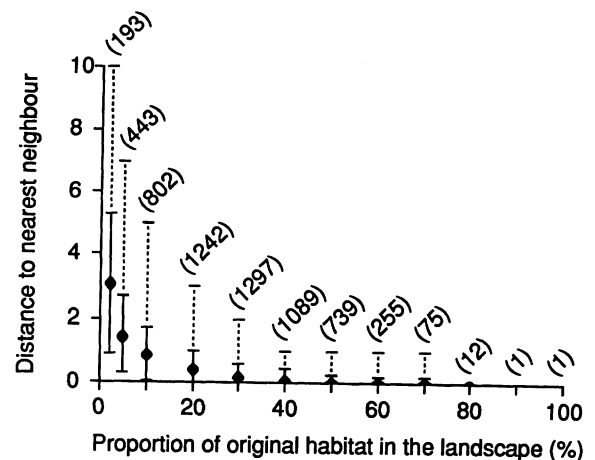


Fig. 3. Distance between patches in relation to the proportion of that habitat in the landscape. The maps were randomly generated and had a size of  $100 \times 100$  units. Mean, one standard deviation and the maximum nearest neighbour distance are given. Number of habitat patches in each landscape are given within parentheses.

by reviewing studies on birds and mammals from landscapes with different proportion of original habitat. In this part I focus on the effect of pure habitat loss and the effects of patch size and isolation. Finally, I will examine the effect of habitat fragmentation on the total species diversity in a landscape mosaic.

## Nonlinearity in landscape patterns

The relationships between the proportion of habitat in the landscape and patch size and isolation has been estimated by simulating landscapes with varying degrees of habitat loss (e.g. Franklin and Forman 1987, Gardner et al. 1987, Krummel et al. 1987, Turner et al. 1989a, b, Gardner and O'Neill 1991, Gustavson and Parker 1992). I created artificial maps with only two habitat types. I chose to generate these maps by randomly removing grains of habitat with a size of 1 unit (Fig. 1). The artificial maps had an extent of 10 000 units (100 × 100 units). I made 10 maps for each proportion of habitat loss. For each map I counted the number of patches and calculated the mean, standard deviation and maximum for both patch size and distance to nearest neighbour (Figs 2 and 3).

The generated maps indicate that the original habitat broke down from one continuous patch to several patches when around 60% of the original habitat still remained. The rapid change in landscape pattern is illustrated by the very strong decline in maximum patch size between 60 and 50% of original habitat in the landscape, from about 4400 units (74% of all original habitat in that landscape) to about 200 units (4% of all the original habitat in that landscape; Fig. 2). The decline in mean patch size above 60% of original habitat in the landscape shows that there are fewer and smaller patches, i.e. almost all original habitat is found within the continuous habitat patch (indicated by open squares in Fig. 2). Percolation theory predicts a value of 59.28% for site percolation for randomly dispersed patches, i.e. connections between spatially distributed systems that share common edges (Gardner and O'Neill 1991). Below this threshold there was a continuous decline in patch size with decreasing proportion of original habitat in the landscape (Fig. 2). However, no patches were actually isolated in landscapes with more than 40% of the original habitat remaining, because the maximum distance between patches of original habitat was only 1 unit, i.e. the side of a grain (Fig. 3). However, in landscapes with a low proportion of original habitat (<20%), a further reduction in this habitat will result in an exponential increase in the distance between patches of original habitat (Fig. 3).

Other patterns of grain dispersal (aggregated or over-dispersed) will influence patch size and distances between patches. Gardner et al. (1987) found that forest patches in three real landscapes (40, 60 and 80% of forest in the landscape) were more aggregated than expected from random processes. The patches were larger and

further apart than for random dispersion in these landscapes. The other extreme, landscapes with completely regular grain dispersion was created by Franklin and Forman (1987). The result was smaller patches that were closer to one another than for random dispersion. Moreover, the probability of having a percolating landscape, i.e. connections between patches, decreased with more clumped dispersion of grains (Gardner and O'Neill 1991).

The main conclusion from all models based on percolation theory is that there are rapid changes in the size and isolation of patches at critical proportions of habitat in the landscape (Turner 1989, Gardner and O'Neill 1991, Gustavson and Parker 1992). Thus, patch size and isolation of patches are not linearly related to proportion of original habitat. There are certain important thresholds in the process of habitat fragmentation. This may result in radical changes in the patterns of movement of animals or in the spread of disturbance, such as forest fire, at critical proportions of habitat in the landscape (Turner et al. 1989a). An important issue is how these differences in landscape geometry at different proportions of habitat will influence the abundance and distribution of organisms in the landscape. The radical changes in landscape patterns suggest that the relative importance of pure habitat loss, patch size and isolation between patches to species living in the original habitat will be different in landscapes with different proportions of this habitat.

## Population responses to habitat fragmentation

An expectation based on the nonlinear relationships in the landscape patterns (describe above) is that the effect of habitat fragmentation on population size would be pure habitat loss in landscapes with a high proportion of suitable habitat, i.e. the random sample hypothesis will predict the effect of habitat fragmentation. In these landscapes there are simply no small and isolated habitat patches. As the proportion of suitable habitat decreases in the landscape, small and isolated habitat patches will appear. Therefore, patch size and degree of isolation of patches might influence the population size of individual species, i.e. the population size is smaller than predicted from the random sample hypothesis. To examine the relative importance of pure habitat loss, patch size and isolation on the distribution of species in habitat patches in landscapes with different proportions of suitable habitat, I reviewed such studies on the effect of habitat fragmentation on birds and mammals that have tested the random sample hypothesis (see Appendix). Moreover, it was necessary to get the proportion of suitable habitat in the landscape, which sometimes could be measured from maps. Only studies from real islands that were from archipelagoes were included, because these may correspond more closely to habitat fragmentation than a single

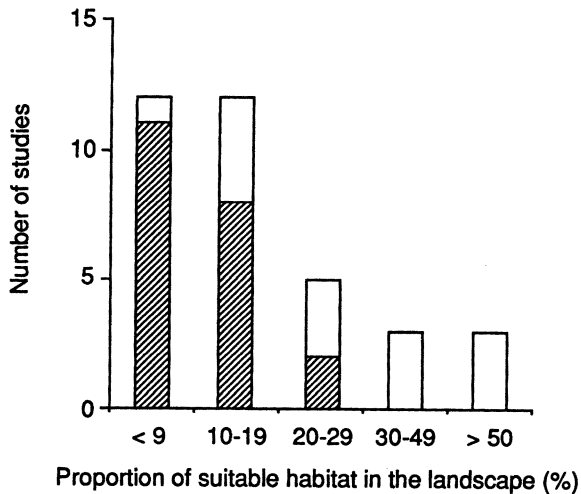


Fig. 4. Number of studies of birds and mammals that were not significantly different from the random sample hypothesis (open parts of the bars) and those that found an effect of area and/or isolation on species number or density (shaded parts of the bars) in relation to proportion of suitable habitat in the landscape (from Appendix).

isolated oceanic island. However, real islands are different from habitat islands in that they are surrounded by a habitat hostile to most terrestrial species, whereas habitat patches are parts of a landscape mosaic, i.e. the matrix may be habitable to some extent.

There are several different possible methods to test the random sample hypothesis. Some studies have adopted random placement models, i.e. comparing species richness in artificially drawn samples from a source area with species richness in real patches (e.g. Coleman et al. 1982, Haila 1983a). Another possibility is to compare patches with similar-sized subplots in large areas (e.g. Martin 1983, Bolger et al. 1991). The most common test, I found, was to test for a relationship between density and patch size (e.g. Nilsson 1978, Ambuel and Temple 1983). In some cases it was not possible to test the random sample hypothesis based only on patch size, but if there was a significant effect on the occurrence or abundance

of species due to isolation in a multiple regression with both patch size and isolation, then the effect of habitat fragmentation was different from the prediction of random sampling (e.g. Lomolino et al. 1989, Verboom and Apeldoorn 1990). However, a rejection of the random sample hypothesis is not necessarily a support for the theory of island biogeography or metapopulation dynamics. Firstly, it depends on the scale of habitat fragmentation. If habitat fragmentation occurs on the scale of individuals, then habitat fragmentation will not result in the subdivision of the population (see below). Secondly, the hypotheses make similar predictions about density in relation to patch size. Random samples of a large area would yield the same density irrespective of patch size. The survival model in MacArthur and Wilson (1967) states that the population on an island would reach the carrying capacity if natality exceeds mortality. Everything else being equal, an island being twice as big as another one should have a population of twice the size, i.e. the population density should be the same. However, the population density on very small islands might be lower than on big islands, because the population on small islands might not be able to reach carrying capacity, as the extinction probability might be high. Therefore, there could be a positive relationship between population density and patch size within a certain range of patch size, but no relationship within other parts of the range. However, a rejection of the random sample hypothesis means that the effect of habitat fragmentation on species richness or population size is larger than expected from pure habitat loss and that configuration of habitat patches influence the species richness or population size.

Many studies have found that communities or populations of single species in small patches were not random samples from large patches (see Appendix). The proportion of suitable habitat in the landscape had a significant effect whether the random sample hypothesis was rejected or not (logistic regression; likelihood ratio test,  $G = 17.7$ ,  $df = 1$ ,  $p < 0.001$ ,  $R^2 = 38\%$ , Hosmer and Lemeshow 1989). Thus, studies that found an effect of area and/or isolation on species number or density were from landscapes with highly fragmented habitat, whereas those yielding results that were not different from those

Table 1. The effect of different variables on the probability that a study has rejected the random sample hypothesis, using logistic regressions (Hosmer and Lemeshow 1989). Data from the Appendix.

Variable	G	df	p	Increase in $R^2$
Step 1				
% suitable habitat in the landscape	17.7	1	<0.001	38%
Step 2				
One variable at the time with % suitable habitat in the landscape included.				
Mammals vs birds	0.38	1	0.54	1%
Resident vs migratory birds	0.32	1	0.60	1%
Mean fragment size	1.34	1	0.18	3%
Mean nearest neighbour distance	0.76	1	0.31	2%



predicted by the random sample hypothesis were mainly from landscapes with a larger proportion of suitable habitat (Fig. 4). Depending on the differences in the abilities of flying birds, especially migratory birds, and nonvolant mammals to disperse across hostile habitat one may expect that the probability to reject the random sample hypothesis would differ between the groups. However, neither the difference between mammals and birds nor the difference between resident birds and migratory birds were significant in a multiple logistic regression, where proportion of suitable habitat was included (Table 1).

The decline in population size of a species living in the original habitat seems to be linearly related to the proportion of original habitat lost, at the initial stages of habitat fragmentation. At some threshold, area and isolation of patches of original habitat will also begin to influence the population size in the original habitat patches. Hence, after this threshold, i.e. in landscapes with highly fragmented habitat, patch size and isolation will strengthen the effect of habitat loss and the decline in population size will be faster than predicted from the random sample hypothesis. Therefore, the effects of area and isolation in these landscapes with highly fragmented habitat will be different from landscapes with higher proportions of original habitat. By comparing studies that only differ in the proportion of suitable habitat in the landscape, one could get evidence for the change in the relative importance of pure habitat loss and area and isolation on species richness and population size. Two studies performed in the Finnish archipelagoes, performed about 250 km apart, differ in this respect. The islands in the Åland Archipelago covered 29% of the area and the land bird communities on islands were not significantly different from predictions from the random sample hypothesis (Haila 1981, 1983a, Haila and Järvinen 1983). On the other hand, the bird communities on islands in the Sipoö Archipelago, where islands covered 12% of the area, were significantly different from the random sample hypothesis (Martin 1983, Martin and Lepart 1989). The decrease in species richness with decreasing area was greater on islands than in similarly sized plots on the mainland. Similarly, Dorp and Opdam (1987) and Askins et al. (1987) found that the proportion of forest in the landscape influenced the probability of occurrence some forest birds in small forest patches.

My review indicated that there might be a threshold in proportion of suitable habitat in the landscape, above which habitat fragmentation is pure habitat loss, i.e. the random sample hypothesis gives a good prediction of the effects of habitat fragmentation on species richness or population size. The threshold might be between 10 and 30% of the suitable habitat remaining in the landscape for birds and mammals (see Appendix and Fig. 4). This threshold value is probably related to changes in landscape geometry. The artificial maps indicated that at around 20% of original habitat in the landscape, small and isolated patches of original habitat started arising and a further reduction in habitat will result in an exponential

increase in the nearest neighbour distances (Fig. 3). In landscapes with a higher proportion of original habitat, small patches will have larger patches very close and hence will not suffer severe species loss.

Another threshold in the proportion of suitable habitat in the landscape is related to population persistence, i.e. extinction threshold (sensu Lande 1987). Metapopulation models predict a threshold in the proportion of suitable habitat below which the metapopulation cannot persist, if extinction rates increase with decline in patch size and colonization rates decrease with increasing patch isolation (Gilpin 1987). The same was predicted by Lande (1987), in a metapopulation model modified to be applied on a set of individual territories instead of a set of local population. Lande's (1987) model was also applied to predict the effect of future habitat fragmentation on a population of northern spotted owl (*Strix occidentalis caurina*) and suggested that the population would go extinct if the proportion of old forest was reduced to less than 20% over a large region (Lande 1988, Lamberson et al. 1992).

One problem with almost all the studies in my review (see Appendix), is that they were performed during one or two seasons. Thus, most studies are snap-shots and one does not know the spatio-temporal dynamics. Another problem is that human-caused habitat fragmentation is sometimes very recent. Thus, the habitat patches might be overcrowded and the decline in population size has not yet occurred (Lovejoy et al. 1986). Interestingly, Soulé et al. (1988) found that the time since a habitat patch was isolated influenced negatively the survival probabilities of species in the patch. There is certainly a need for more long-term studies on the effects of habitat fragmentation.

## The scale of habitat fragmentation

Habitat fragmentation might occur on different scales, e.g. the scale of individuals or populations (Haila 1990). The theory of island biogeography and metapopulation dynamics assume that subpopulations living in habitat patches are relatively isolated from each other (MacArthur and Wilson 1967, Levins 1969, 1970). However, these models have often been applied to describe the effects of habitat fragmentation, even if it is doubtful whether the population is divided into subpopulations, e.g. to single pairs of birds breeding in different patches. However, several models, that studied the effect on single individuals instead of on local populations, have reached similar results as the original metapopulation model (Lande 1987, 1988, Verboom et al. 1991, Lamberson et al. 1992). For example, the equilibrium occupancy of territories declined with decreasing proportion of suitable territories in a region. The probability that an individual will find an empty territory declined, while the survival rate within occupied territories was constant. This corresponded to a lower colonization rate, while keeping the

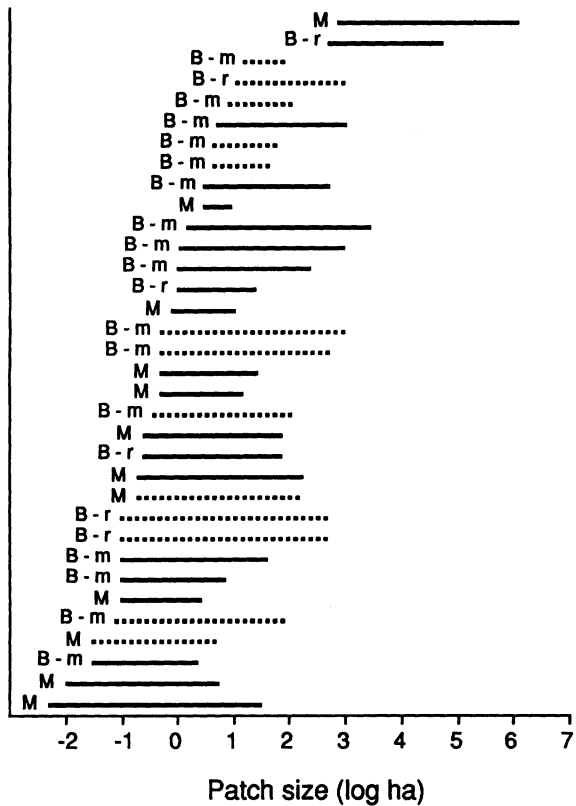


Fig. 5. The range in patch size of the studies in the Appendix. Dotted lines indicate studies that were not significantly different from the random sample hypothesis and thick lines those that found an effect of area and/or isolation on species number or density. M; indicates studies on mammals, B - r; resident birds and B - m; migratory birds.

extinction rate constant in Levins's metapopulation model, and the result would be a lower proportion of suitable habitat patches occupied (Levins 1969, 1970). Therefore, it seems that models based on the metapopulation concept could be used to describe the effects of habitat fragmentation on a species, as long as one fulfils the assumption that the occupation of a patch is related to its size and that the probability of reoccupation of an empty patch is related to the distance to occupied patches. However, to understand the effects of habitat fragmentation it is essential to specify the scale of habitat fragmentation. Habitat fragmentation on the individual scale is related to area requirements of individuals, home-range boundaries and movement patterns of individuals (Haila 1990, Haila et al. 1993). The individuals living in the patches are a part of the same regional population in the surrounding areas. On the other hand, habitat fragmentation on the population scale means isolation of local populations, exchange of individuals between generations and the survival probabilities of local populations (Haila 1990, Haila et al. 1993). The theory of island biogeography and metapopulation dynamics are most rel-

evant on the population scale. Species turnover in patches will occur on both scales, but the reasons will be different (Haila et al. 1993). Local turnover on the individual scale might be due to individuals changing their territories or to death of an individual occupying a territory. On the population scale, local turnover means extinction and colonization of local populations, i.e. real metapopulation dynamics (sensu Levins 1969, 1970). The random sample hypothesis can be rejected on both the scale of individuals and populations, but the mechanisms causing the rejection might be different. On the individual scale, the random sample hypothesis might be rejected because the patch is smaller than the area requirement of an individual, patches are isolated, conspecific attraction (Smith and Peacock 1990) or avoidance of habitat edge (Wilcove 1985). On the other hand, one may reject the random sample hypothesis on the population scale by showing that the population really is divided into local, relatively independent, subpopulations and that the survival of these local populations are related to patch size and that recolonization is related to distance to other occupied patches. However, a rejection of the random sample hypothesis means that the effect of habitat fragmentation on species richness or population size is larger than expected from pure habitat loss and that configuration of habitat patches influence the species richness or population size.

Surprisingly, many studies referred to in the Appendix have applied the theory of island biogeography or metapopulation dynamics, although the effect of habitat fragmentation seems to be on the scale of individuals. Out of 35 studies, 57% had a maximum patch size < 100 ha,

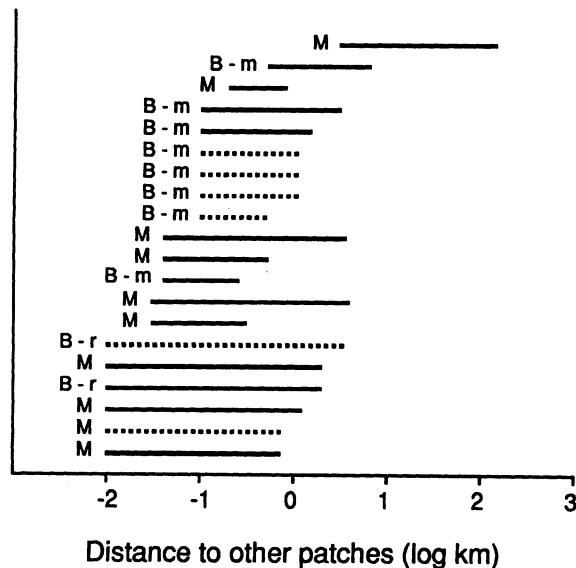


Fig. 6. The range in nearest neighbour distances of the studies in the Appendix. Dotted lines indicate studies that were not significantly different from the random sample hypothesis and thick lines those that found an effect of area and/or isolation on species number or density. M; indicates studies on mammals, B - r; resident birds and B - m; migratory birds.

another 31% had a maximum between 100 and 1000 ha. Very small patches (< 1 ha) were included in 61% of the studies (Fig. 5). It is unlikely that patches of a few ha could hold a local population of birds or mammals. The range of distance to nearest neighbour was given in 20 studies. The maximum distance was < 500 m in 20% of these studies, another 30% had a maximum nearest neighbour distance < 1000 m (Fig. 6). Furthermore, migratory birds were involved in 47% of the studies. Defining colonization and extinction of local population might not be ecological meaningful for birds which leave the breeding grounds in autumn and "recolonize" in spring (Haila 1983a). Two studies were performed in a range of patch sizes where it might be relevant to talk about a set of local populations (raptors in national parks on Java, 5–500 km<sup>2</sup>, Thiollay and Meyburg 1988; small mammals in montane forests, 7–11 000 km<sup>2</sup>, Lomolino et al. 1991). The scale of habitat fragmentation might influence the probability to reject the random sample hypothesis. However, neither the mean patch size nor the mean nearest neighbour distance were significant in a multiple logistic regression, where proportion of suitable habitat was included (Table 1).

## Landscape effects

Habitat patches are parts of a landscape mosaic, and the presence of a given species in a patch may be a function not only of patch size and isolation, but also of the kind of neighbouring habitat. The main hypothesis advanced in order to explain the number of species in a habitat patch (theory of island biogeography, MacArthur and Wilson 1967) might be violated in many cases, because it assumes that suitable habitat patches are isolated from one another by hostile habitat, i.e. a divided landscape (Addicott et al. 1987), and that individuals of each species only use one habitat patch, which is bigger than the area requirement of that particular species, i.e. a coarse-grained landscape (Levins 1968).

The first assumption, namely that the landscape is divided, might be violated by species which are habitat generalists, i.e. species which use several habitats in the landscape although they may differ in suitability. They inhabit what has been called a heterogeneous undivided landscape (Addicott et al. 1987). The population density of habitat generalists will be a function of the whole landscape composition. For example, Andrén (1992) found that the density of hooded crows (*Corvus corone*) was higher in landscapes with a mixture of farmland and forest than in landscapes dominated by either farmland or forest. Another effect is that the species number will be over-estimated in small patches compared to large ones if habitat generalists are included. Habitat generalists may use very small patches because they also use the surroundings. Therefore, it is not surprising that Loman and

von Schantz (1991) found that the number of species was higher in several small forest patches than in a few large ones, because they included all species found in the forest patches, also such that were dependent on the surrounding farmland. They have actually studied the species richness in different landscapes, not species richness in habitat patches as they claim.

Another consequence of habitat patches being part of a landscape mosaic is that species with large home ranges may use several habitat patches, i.e. inhabit a fine-grained landscape (Levins 1968, Rolstad 1991). This may explain how some species can survive in landscapes with habitat patches smaller than their home ranges. For example, pairs of the spotted owl (*Strix occidentalis*) preferring old-growth forest, remained in their territories with as little as 20–30% of this habitat. This was possible because the old-growth forest was fragmented in a fine-grained pattern. The home range of spotted owl ranged from 550 to 3400 ha, while the clear-cuts were 10–20 ha (Forsman et al. 1984). Similarly, capercaillie (*Tetrao urogallus*) cocks, having territories of about 50 ha and preferring old forest, accepted a fine-grained cutting procedure yielding small clear-cuts (0.3 ha) within their territories (Rolstad 1989). But the capercaillies compensated for the reduction in amount of preferred habitat by having larger territories (Wegge and Rolstad 1986). Similarly, patches of preferred old forest are fragmented in a fine-grained pattern for the goshawk (*Accipiter gentilis*), which has a home range of 3400–8000 ha, while most patches of old forest were smaller than 30 ha (Widén 1989). The density per forest area of black woodpecker (*Dryocopus martius*) was not different between a forest landscape (80% forest) and a forest-farmland landscape (26% forest), but in the forest-farmland area a territory included many patches of forest (mean number per territory was 76), i.e. a fine-grained landscape (Tjernberg et al. 1993). Furthermore, neither the reproduction nor the survival were different between the two study area. Thus, the effect of forest fragmentation on black woodpecker could be described as pure habitat loss.

Instead of looking simply at the species diversity within a habitat, one may also be interested in measuring species diversity across all habitats in the landscape mosaic, i.e. the so-called beta diversity (Whittaker 1960) or between-habitat diversity (MacArthur 1965). Beta diversity will increase when new patches of habitat are created within a continuous habitat, as new species will be found in these new patches. This increase will probably also occur when the new habitat is human-made. Franklin and Forman (1987) suggested that the beta diversity in a landscape with two habitats should be highest when they occurred in about equal proportions. This suggestion was confirmed for corvids in forest-farmland landscape by Andrén (1992). Although patterns in alpha diversity, such as the species-area relationship are major themes in ecological studies, far less attention has been paid to beta diversity (Harrison et al. 1992). However, to understand the effect of habitat fragmentation on biological diversity



one will have to measure both alpha and beta diversity in the landscape.

## Conclusions

In most landscapes the total area of suitable habitat will be of greater importance than its spatial arrangements for species living in this particular habitat. This is especially true for landscapes with a high proportion (more than 30%) of the suitable habitat left. In such landscapes the random sample hypothesis probably will be a good predictor of the effects of habitat fragmentation on the abundance and distribution of organisms living in the suitable habitat, i.e. the only consequence of habitat fragmentation is loss of habitat. Still some patches may be smaller than the area requirements for certain species even at 60–70% of the suitable habitat in the landscape. However, provided these patches are fairly close to other patches they may be included within the home range of some individuals. Thus, in landscapes with a high proportion of suitable habitat, the configuration of the habitat is less important.

The negative effects of patch size and isolation on the original sets of species may not occur until the landscape consists of only 10–30% of the original habitat. For mobile organisms, the effects of isolation may appear only in landscapes with very fragmented habitat. In landscapes with highly fragmented habitat, a further reduction in habitat results in an exponential increase in distances between patches. Thus, in landscapes with highly fragmented habitat, the spatial arrangement of habitat patches is very important. Moreover, the effect of patch size and isolation will not only depend on the proportion of original habitat in the landscape, but also on the suitability of the surrounding habitats.

Finally, the total diversity in the landscape, beta diversity, may increase when new patches of habitat are created within a continuous habitat, because new species may be found in these, even if the new patches are human-made. The beta diversity in the landscape will probably be highest when two habitats occur in about equal proportions.

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## Appendix

Studies of birds and mammals in landscapes with different proportion of suitable habitat. Effect of area and/or isolation means that the number of species or density of certain species was different from expected from the random sample hypothesis.

Landscape type and species or group of species	% of the area covered by the habitat	Effect of area (range)	Effect of isolation (range)	Method for testing the random sample hypothesis	Source (Habitat and landscape type)
<b>Archipelagoes:</b>					
Land bird community	8 <sup>1</sup>	Yes (0.03–2.2 ha)	No (0.04–0.25 km)	Significant relationship between density and island size	Nilsson 1978, 1986
Land bird community	29 <sup>1</sup>	No (0.5–582 ha)	No (<0.1–1 km)	Number of species on islands in agreement with a random placement model	Haila 1981, 1983a Haila and Järvinen 1983
Field vole ( <i>Microtus agrestis</i> )	11 <sup>1</sup>	Yes (0.5–26 ha)	No (0.01–1.2 km)	Lower density on small islands than on large ones	Pokki 1981
Land bird community	3 <sup>1</sup>	No (0.09–70 ha)	No (<0.1–0.5 km)	Number of species on islands in agreement with a random placement model	Coleman et al. 1982
Land bird community	27 <sup>2</sup>	No (0.5–885 ha)	No (<0.1–1 km)	Number of species on islands in agreement with a random placement model	Haila 1983b
Land bird community	12 <sup>1</sup>	Yes (1–233 ha)	Yes (<0.1–1.5 km)	The decrease in species richness with decreasing area was greater on islands than in similarly sized plots from the mainland	Martin 1983 Martin and Lepart 1989
<b>Forest patches in farmland:</b>					
Bird community	22 <sup>2</sup>	Yes (1.1–905 ha)	Yes (index)	Significant relationship between density and patch size and isolation	Whitcomb et al. 1981
Bird community	<5 <sup>3</sup>	Yes (3–500 ha)	–	Significant relationship between density and patch size	Ambuel and Temple 1983
Bird community	10–20 <sup>4</sup>	No (3.6–40.1 ha)	No	Number of species in forest patches in agreement with a random placement model	Woolhouse 1983, 1987
Bird community	<5 <sup>3</sup>	Yes (0.1–7 ha)	Yes	Bird communities in forest patches different from control plots in continuous forest	Howe 1984
Bird community	20 <sup>5</sup>	Yes (5–1000 ha)	Yes (0.1–3 km)	Significant relationship between density and patch size and isolation	Lynch and Whigham 1984
Bird community	2–10 <sup>6</sup>	Yes (0.1–39 ha)	Yes (0.5–6.2 km)	The incidence functions for a few bird species depended on the proportion of forest in the landscape	Opdam et al. 1984, 1985 Dorp and Opdam 1987
Bank vole ( <i>Clethrionomys glareolus</i> )	15 <sup>1</sup>	Yes (0.2–160 ha)	Yes (0–0.7 km)	Significant relationship between density and patch size and isolation	Geuse et al. 1985
Wood mouse ( <i>Apodemus sylvaticus</i> )	15 <sup>1</sup>	No (0.2–160 ha)	No (0–0.7 km)	No significant relationship between density and patch size and isolation	Geuse et al. 1985
Chipmunk ( <i>Tamias striatus</i> )	6 <sup>1</sup>	Yes (2.9–8.9 ha)	Yes (0.2–0.8 km)	Significant relationship between density and patch size and isolation	Henderson et al. 1985
Bird community	15 <sup>1</sup>	Yes (1.5–2600 ha)	Yes (index)	Significant relationship between density and patch size and isolation	Askins et al. 1987
Raptors	8–12 <sup>2</sup>	Yes (5–500 km <sup>2</sup> )	–	Significant relationship between density and patch size	Thiollay and Meyburg 1988
Red squirrel ( <i>Sciurus vulgaris</i> )	8 <sup>7</sup>	? (0.5–14 ha)	Yes (0.04–3.5 km)	Significant effect of patch size and isolation on presence/absence	Verboom and Apeldoorn 1990
Small mammals	10 <sup>1</sup>	No (0.03–4 ha)	No	No significant relationship between density and patch size and isolation	Loman 1991a, b



Landscape type and species or group of species	% of the area covered by the habitat	Effect of area (range)	Effect of isolation (range)	Method for testing the random sample hypothesis	Source (Habitat and landscape type)
Nuthatch ( <i>Sitta europaea</i> )	5 <sup>2</sup>	Yes (1–24 ha)	Yes (0–>2 km)	Occupation of larger and less isolated patches higher than expected from random occupation	Verboom et al. 1991
Bank vole ( <i>Clethrionomys glareolus</i> )	8 <sup>1</sup>	? (0.1–2.6 ha)	Yes (0.03–3.8 km)	Significant relationship between abundance and patch size and isolation	Apeldoorn et al. 1992
Red squirrel	18 <sup>2</sup>	Yes (0.8–10 ha)	No (0.03–0.3 km)	Lower density in small patches than in a large nearby patch	Wauters et al. 1994
<b>Forest landscapes:</b>					
Black grouse ( <i>Tetrao tetrix</i> )	42 <sup>2</sup>	No/yes <sup>8</sup> (0.1–500 ha)	No	No significant relationship between density and patch size and isolation	Angelstam 1983 (Young forest)
Capercaillie ( <i>Tetrao urogallus</i> )	31 <sup>2</sup>	No/yes <sup>8</sup> (0.1–500 ha)	No	No significant relationship between density and patch size and isolation	Angelstam 1983 (Old forest)
Bird community	12 <sup>2</sup>	No (8–100 ha)	No	No significant relationship between density and patch size and isolation	Helle 1984, 1985 (Young forest)
Bird community	27 <sup>2</sup>	No (4–50 ha)	No	No significant relationship between density and patch size and isolation	Helle 1984, 1985 (Middle aged forest)
Bird community	54 <sup>2</sup>	No (18–70 ha)	No	No significant relationship between density and patch size and isolation	Helle 1984, 1985 (Old forest)
Bird community	50 <sup>2</sup>	No (0.4–101 ha)	No (0.1–1 km)	Species occurrence and species number in agreement with a random placement model	Haila et al. 1987, 1993 (Old forest)
Capercaillie	30–60 <sup>2</sup>	No/yes <sup>8</sup> (10–850 ha)	No (<3 km)	No significant relationship between density and patch size and isolation	Rolstad and Wegge 1987 (Old forest)
Bird community	70 <sup>2</sup>	No	–	No loss of species with a reduction in forest area in the region	Daniels et al. 1990 (Old forest)
<b>Other landscapes:</b>					
Pikas ( <i>Ochotona princeps</i> )	6 <sup>1</sup>	? (0.01–5 ha)	Yes (0.04–0.5 km)	Significant relationship between abundance and patch size and isolation	Smith 1974, 1980 (Tailings in sagebrush)
Bird community	<10 <sup>2</sup>	Yes (0.25–68 ha)	No	The decrease in species richness with decreasing area was greater for patches than for similarly sized plots in a large patch	Soulé et al. 1988 Bolger et al. 1991 (Chaparral in suburban areas)
Small mammals	15 <sup>1</sup>	? (7–11,000 km <sup>2</sup> )	Yes (3–140 km)	Significant effect of patch size and isolation on presence/absence	Lomolino et al. 1989 (Montane forest in desert scrub)
Mammals	<10 <sup>2</sup>	Yes (0.25–68 ha)	Yes	The decrease in species richness with decreasing area was greater for patches than for similarly sized plots in a large patch	Soulé et al. 1992 (Chaparral in suburban areas)
Columbian ground squirrel ( <i>Spermophilus columbianus</i> )	10 <sup>1</sup>	? (0.005–30 ha)	Yes (0.01–2 km)	Significant effect of patch size and isolation on presence/absence	Weddell 1991 (Uncultivated grasslands in an agricultural landscape)

1. Measured on map.
2. Given in the cited paper.
3. According to Curtis 1956.
4. According to Marchant et al. 1990.
5. According to Whitcomb et al. 1981.
6. Pers. comm.
7. According to Apeldoorn et al. 1992
8. No effect of density in patches larger than the home range of the species.