Forest Loss and Fragmentation: Which has the Greater Effect on Persistence of Forest-dwelling Animals?

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Because habitat loss and fragmentation typically co-occur, the term “fragmentation” is often used as a short-hand for both processes. However, the loss of habitat has a far greater effect than the fragmentation, or “breaking apart”, of habitat on population survival, and many or most species may exhibit a threshold response to habitat loss. Use of the word “fragmentation” as a short-form for loss and fragmentation or, in some cases, for loss only, shifts research focus away from habitat loss and toward habitat pattern. This has the unfortunate consequence of shifting conservation focus away from habitat conservation and restoration. Since “forest” and “habitat” are not synonymous for forest-interior species, the breaking apart of forest habitat entails additional loss of habitat (i.e., interior forest) for these species. I suggest that there is currently an over-emphasis on habitat configuration and an under-emphasis on habitat amount. Since habitat loss is the main factor causing species extinctions, this shift in focus is detrimental to species conservation.

Key words: habitat loss, habitat destruction, habitat fragmentation, habitat configuration, landscape scale, forest-interior, forest-edge, threshold, conservation, habitat restoration

1. DEFINITION OF HABITAT FRAGMENTATION: JUST SEMANTICS?

Habitat loss is the most important factor causing the current species extinction event (Groombridge 1992, Bibby 1995, Ehrlich 1995, Thomas and Morris 1995). This fact was, however, not reflected in a speech by Dr. Robert Watson of the World Bank at the 1996 annual meeting of the Ecological Society of America. Dr. Watson, head of environmental policy for the Bank, did not even include habitat loss on his list of factors causing species extinctions. His list did, however, include “habitat fragmentation”.

Just what did Dr. Watson mean by “habitat fragmentation”? More importantly, what do the directors of the World Bank think Dr. Watson means when he tells them that “habitat fragmentation” is an important threat to biodiversity?

According to the dictionary, “fragmentation” means “the breaking apart or up into pieces” (Merriam-Webster Inc. 1987). Presumably, then, “habitat fragmentation” means the breaking apart of habitat. Unfortunately, the dictionary definition of fragmentation does not apply perfectly to habitat fragmentation. When a porcelain vase is “fragmented”, the amount of porcelain remains constant. Habitat fragmentation, on the other hand, generally occurs through habitat removal. Therefore, habitat loss and habitat fragmentation are inextricably linked.

Because of the co-occurrence of habitat loss and fragmentation, the term “fragmentation” is often used as a short-hand for the
combined processes of habitat loss and fragmentation (e.g., Diffendorfer et al. 1995, Schumaker 1996). However, replacing the words “habitat loss” with “habitat fragmentation” has negative consequences for species conservation. If species go extinct mainly because of habitat loss, the solution is straightforward: habitat conservation and restoration. On the other hand, if species go extinct mainly because of the fragmentation or “breaking apart” of habitat, the problem may appear less severe and at the same time more complex, and the solution seems less obvious. One might even conclude that: (i) loss of habitat is not a serious threat to species survival, as long as the remaining habitat is not broken apart; and (ii) to restore endangered populations we need not restore large tracts of habitat, but just enough to connect up the “broken apart” pieces of remaining habitat.

Such conclusions would be erroneous. Available evidence (reviewed below) suggests that the effect of habitat loss on population persistence is much greater than the effect of “breaking apart” habitat.

The definition of “habitat fragmentation” is therefore not simply an issue of semantics. Use of the word “fragmentation” as a short form for habitat loss and fragmentation or, in some cases, for loss only (Andrén 1996, Taylor and Merriam 1996), shifts research focus away from habitat loss and toward habitat pattern. This has the unfortunate consequence of shifting conservation focus away from habitat conservation and restoration.

2. FRAGMENTATION EFFECTS MUST BE STUDIED AT A LANDSCAPE SCALE

One of the reasons that habitat loss and fragmentation have been used synonymously is that “fragmentation” studies are typically conducted at a scale too small to differentiate between the effects of loss and breaking apart of habitat. Almost all studies that report effects of “habitat fragmentation” on population density or distribution use the patch as the unit of observation. Evidence of patch size effects or patch isolation effects are cited as “fragmentation effects” (e.g., Dodd 1990, Robinson et al. 1992, van Apeldoorn et al. 1992, Celada et al. 1994, Hunter et al. 1995, Andrén 1994, Hinsley et al. 1996, Schniegelow et al. 1997, Vos and Chardon 1998). As stated by McGarigal and McComb (1995), “nearly all of the studies on fragmentation have employed a patch-centered sampling scheme in which independent forest patches, not landscapes, were sampled. Based on a variety of “patch” characteristics, such as patch size and isolation, inferences often have been made about how “landscape” structure affects wildlife populations. Yet it is unclear whether relationships derived at the patch level can be extrapolated to the landscape level.”

In fact, relationships derived at the patch scale can not be extrapolated to infer effects of habitat fragmentation. Decreases in patch size and increases in patch isolation do not necessarily imply that the habitat has become more broken apart (fragmented). Habitat loss alone at the landscape scale can account for these changes (Figure 1).

Documentation of the effects of habitat fragmentation therefore requires a truly landscape-scale study. In such a study the landscape is the unit of observation (e.g., McGarigal and McComb 1995, Miller et al. 1997, Trzcinski et al., in press). The structures of many independent landscapes are quantified and then the measures of landscape structure are related to density, diversity, or distribution of the focal organism(s). In such studies, each data point is an individual landscape (not a patch).

3. RELATIVE IMPORTANCE OF HABITAT LOSS AND FRAGMENTATION: SIMULATIONS AND DATA

Several studies have documented the effects of habitat fragmentation while holding habitat amount constant (e.g., Andreassen et al. 1998). In such studies, different treatments contain the same amount of habitat broken up into different numbers of pieces. These studies have revealed negative (Burkey 1989, 1995, Atmar and Patterson 1993, Adler and Nuernberger 1994, Irlandi
Habitat Loss

Figure 1. Definition of habitat loss and fragmentation. Decreasing patch size (A) and patch isolation (B) can result from habitat loss alone. From Fahrig (1997).


To date, 1 simulation study (Fahrig 1997) and 3 empirical studies (McGarigal and McComb 1995, Miller et al. 1997, Trzcinski et al., in press) have documented the relative effects of habitat amount and fragmentation. In all cases, the effects of habitat amount were found to greatly outweigh the independent effects of breaking apart or fragmentation of the habitat. For example, Trzcinski et al. (in press) determined the independent effects of forest cover and forest fragmentation (i.e., configuration after controlling for cover), on the probability of presence of forest-breeding birds in 94 10 km x 10 km landscapes in southern and eastern Ontario, Canada. Of the 31 species studied, 25 showed statistically significant positive effects of forest cover (i.e., negative effects of forest loss). Only 6 species showed significant effects of forest fragmentation; 4 of these fragmentation effects were negative and 2 were positive.

While both McGarigal and McComb (1995) and Trzcinski et al. (in press) looked at responses of birds to landscape structure, McGarigal and McComb worked in mainly forested landscapes of the Oregon Coast Range, while Trzcinski et al. used data from agricultural landscapes in southern Ontario. The similar conclusion produced by these studies, that effects of forest loss far outweigh effects of forest fragmentation, in very different regions, suggests that the conclusion may be quite general.

These results suggest that conservation emphasis should be placed primarily on conservation and restoration of habitat. While there are certainly some circumstances in which habitat configuration affects species (McGarigal and McComb 1995, Fahrig 1998),
very little benefit will accrue to most species of concern through manipulations or judicious planning of habitat configuration alone. Emphasis on habitat configuration appears largely misguided if the objective is species conservation.

Why then has there been so much emphasis on habitat configuration relative to habitat loss? First, as argued above, the use of the term “habitat fragmentation” in place of habitat loss has led to an over-estimate of the importance of habitat configuration, because the term “fragmentation” itself implies configuration (not loss).

Second, while many researchers have investigated the potential effects of habitat spatial pattern, very few have actually compared the relative effects of habitat pattern and habitat amount. In a conservation context, it is not enough to know that a certain factor (e.g., fragmentation) can have an effect on population survival. We must also know how large this effect is in comparison with other factors. In the absence of such comparison, and in light of the large number of studies of the effects of spatial pattern, it has been tempting to conclude that habitat configuration is at least as important as habitat amount (e.g., Kareiva and Wennergren 1995). This conclusion is unfounded.

A final reason for the misplaced emphasis on pattern over amount of habitat is that habitat loss appears to be inevitable. One could argue that, if habitat loss cannot be stopped, then we must make the best of a bad situation and at least ensure that the remaining habitat is not too fragmented. This would be a reasonable stance if habitat configuration could in fact mitigate habitat loss to some extent. However, the studies to date indicate that this is highly unlikely. In fact, if insufficient habitat remains for a population’s survival, that population will not persist, no matter how that habitat is arranged. Focussing on habitat arrangement in this case creates a false hope. Efforts would be much better spent on determining how much habitat is necessary to ensure population survival and working toward restoring habitat to that level.

4. HOW MUCH IS ENOUGH?: THRESHOLD RESPONSE OF POPULATION EXTINCTION TO HABITAT LOSS

If the effects of habitat loss cannot be mitigated by alterations in habitat configuration, the most important question conservation biologists must answer is: how much habitat is enough? For example, how much mature forest of various types must be maintained on the landscape to ensure persistence of species that depend on these forest types? Several studies (Lande 1987, Bascompte and Solé 1996, Fahrig, unpublished data) suggest that the answer to this depends mainly on 2 factors: (i) the demographic potential of the organism; and (ii) the survival rate of the organism while travelling through non-habitat or “matrix” areas. The greater the demographic potential and the less hostile the matrix habitat, the less habitat the organism needs to ensure its survival on the landscape.

It also seems likely that the relationship between habitat loss and population survival is a threshold phenomenon (Bascompte and Solé 1996). Figure 2 illustrates the relationship between habitat amount and regional population survival probability, from simulations using the model described in Fahrig (1997, 1998). These simulations indicate a very sharp threshold in the relationship. The occurrence of such a threshold suggests, again, that it would be catastrophic for conservation efforts to ignore habitat amount while emphasizing pattern. It would be easy to inadvertently cross the threshold in habitat amount, thus ensuring population extinction, no matter what the configuration of the remaining habitat.

5. FOREST FRAGMENTATION VS. HABITAT FRAGMENTATION: INTERIOR SPECIES AND EDGE EFFECTS

While this discussion has been framed in terms of habitat loss and fragmentation, the focus of the conference on which this book is based was forest fragmentation. The difference between habitat and forest depends on the focal organism. For species for which
forest and habitat are synonymous, I conclude that forest amount is the main issue. However, for forest-edge species and forest-interior species, the mere breaking apart of forest (with no forest loss) changes the amount of habitat. The more broken apart the forest, the less habitat there is available to forest-interior species, and the more habitat there is available to forest-edge species (Figure 3).

Bender et al. (1998) conducted a meta-analysis of all patch size-density studies and found that population density was positively related to forest patch size for forest-interior species and negatively related to forest patch size for edge species. In such studies, density is computed as number of individuals divided by forest patch area. Since interior species do not use the edge (by definition), as the patch size decreases the population density decreases, since it is calculated over the whole patch. The reverse is true for edge species. Note that this is true even if the density of each species in its actual habitat (edge or interior) remains constant with forest patch size.

Therefore, forest fragmentation can be expected to have a negative effect on forest-interior species because it represents an additional loss of forest interior habitat. The predictions for forest-edge species, at the landscape scale, however, will depend on the total amount of edge in the landscape as forest is removed. Forest removal can reduce the total amount of edge at the landscape scale (e.g., Trzcinski et al., in press) which should have an overall negative effect on edge species. However, if the remaining forest is very broken apart, forest removal may increase the total amount of edge, which would have a positive effect on edge species.

6. MORE ON THE DEFINITION OF FRAGMENTATION

To understand the relationship between alterations of forest structure and population responses of focal species it is therefore critical to: (i) view the problem from a landscape (not a patch) scale; (ii) differentiate between “forest” and “habitat”; and (iii) differentiate between “loss” and “fragmentation” of forest or habitat. To illustrate the confusion over the use of the term “fragmentation”, I end with some examples from the literature. These fall into 3 categories: (i) fragmentation = loss; (ii) fragmentation = loss and breaking...
apart; and (iii) fragmentation = breaking apart only.

6.1 Examples of Studies that Use Fragmentation Synonymously with Loss

The oft-cited paper by Andrén (1994) is the most important example of inconsistency in use of the term “fragmentation”. Andrén defines habitat fragmentation as “the process of subdividing a continuous habitat into smaller pieces...” While this definition does imply “breaking apart” of habitat, Andrén goes on to state, “Habitat fragmentation has three major components, namely loss of the original habitat, reduction in habitat patch size, and increasing isolation of habitat patches...” Clearly, however, habitat loss alone leads to a reduction in habitat patch size, and increasing isolation of habitat patches (Figure 1). Therefore, Andrén’s use of the term fragmentation is inconsistent. While the definition itself implies breaking apart, the proposed components of fragmentation do not.

Taylor and Merriam (1996) state: “Habitat fragmentation occurs when parts of a continuously distributed habitat are replaced by new habitat that differs from the original... An example is forest fragmentation - a landscape where parts of a continuous forest have been replaced by non-forest.” This definition does not involve breaking apart of habitat. In fact, a few clear-cuts in a continuous forest would meet this definition of fragmentation, i.e., replacement of part of a continuous habitat with a new habitat. Since the forest remains contiguous, this use of fragmentation clearly involves only loss of habitat.

6.2 Examples of Studies that Use Fragmentation Synonymously with Loss and Breaking Apart

In his memo to the conference speakers, Jim Rochelle defined forest fragmentation as “the process of reducing size and connectivity of stands that compose a forest.” This is similar to Andrén’s definition above, in that it focuses at the patch scale (forest stands). At the landscape scale, the main process of reducing size of stands is removal of forest (Figure 1). However, by including connectivity in the definition, Rochelle goes further than loss alone to include breaking apart of forest. This definition of fragmentation is identical to that used by Dooley and Bowers (1998): “Habitat fragmentation, the process by which relatively continuous areas of habitat are broken into smaller parcels or fragments...”

Similarly, With and Crist (1995) state that through “habitat fragmentation...the landscape becomes dissected into smaller and smaller parcels.” Again, reduction of the size of individual parcels can occur through habitat loss alone. However, the word “dissected” implies that the habitat also becomes broken apart. In a later paper, With et al. (1997) define habitat fragmentation as “a disruption in landscape connectivity”, where landscape connectivity is “the functional linkage among habitat patches, either because habitat is physically adjacent or because the dispersal abilities of the organisms effectively connect patches across the landscape.” This definition focuses more on “breaking apart” and less on loss of habitat, although the disruption of connectivity presumably occurs mainly through habitat loss.

As a final example, Diffendorfer et al. (1995) refer to “habitat fragmentation, an anthropogenic process that increases heterogeneity across space by degrading one-continuous natural habitats into remnant pieces.” Again, this definition implies both loss and breaking apart of habitat.

6.3 Examples of Studies that Use Fragmentation Synonymously with Breaking Apart

The final set of examples illustrates the use of habitat fragmentation to refer only to the breaking apart of habitat. As stated above, the dictionary definition of fragmentation refers only to “breaking apart”. McGarigal and McComb (1995) state: “Habitat fragmentation alters the spatial configuration of habitats, leading to population subdivision.” This definition focuses solely on subdivision or breaking apart, and their distinction between breaking apart and loss of habitat is
reflected in the methods they used to analyze their data.

Several authors imply that habitat loss and fragmentation are separate factors through their explicit use of both terms. For example, Nève et al. (1996) state: “Habitat loss and fragmentation are the main threats to biodiversity...”, and Lindenmayer and Possingham (1996) state: “The destruction of temperate and tropical forests and the fragmentation of the remaining forested areas is a major problem...” Finally, Bascompte and Solé (1996) express the difference very explicitly: “...we can define habitat destruction..., a reduction of the fraction of available sites. Habitat fragmentation, on the other hand, is a consequence of such destruction.”

7. CONCLUSIONS

(i) Habitat loss has a much greater effect on population persistence than changes in habitat configuration.

(ii) Population survival may show a threshold response to habitat loss.

(iii) Conservation efforts should focus primarily on habitat conservation and restoration. Alteration of habitat configuration cannot compensate for habitat loss.

(iv) Patch-scale data such as patch size or patch isolation cannot provide evidence for landscape-scale fragmentation effects. Such effects can only be observed through landscape-scale studies.

(v) The term “fragmentation” should not be used if habitat loss is the main factor being considered. Focus on “fragmentation effects” leads to the erroneous conclusion that negative effects of habitat loss can be
compensated by alteration of habitat configuration.

LITERATURE CITED


Trzcinski, M.K., L. Fahrig and G. Merriam. Independent effects of forest cover and fragmentation on the distribution of forest breeding birds. Ecological Applications, in press.


