Effects of Habitat Fragmentation on Biodiversity
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EFFECTS OF HABITAT FRAGMENTATION ON BIODIVERSITY

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Key Words habitat loss, landscape scale, habitat configuration, patch size, patch isolation, extinction threshold, landscape complementation

■ **Abstract** The literature on effects of habitat fragmentation on biodiversity is huge. It is also very diverse, with different authors measuring fragmentation in different ways and, as a consequence, drawing different conclusions regarding both the magnitude and direction of its effects. Habitat fragmentation is usually defined as a landscape-scale process involving both habitat loss and the breaking apart of habitat. Results of empirical studies of habitat fragmentation are often difficult to interpret because (*a*) many researchers measure fragmentation at the patch scale, not the landscape scale and (*b*) most researchers measure fragmentation in ways that do not distinguish between habitat loss and habitat fragmentation per se, i.e., the breaking apart of habitat after controlling for habitat loss. Empirical studies to date suggest that habitat loss has large, consistently negative effects on biodiversity. Habitat fragmentation per se has much weaker effects on biodiversity that are at least as likely to be positive as negative. Therefore, to correctly interpret the influence of habitat fragmentation on biodiversity, the effects of these two components of fragmentation must be measured independently. More studies of the independent effects of habitat loss and fragmentation per se are needed to determine the factors that lead to positive versus negative effects of fragmentation per se. I suggest that the term "fragmentation" should be reserved for the breaking apart of habitat, independent of habitat loss.

INTRODUCTION

A recent search of the Cambridge Scientific Abstracts database revealed over 1600 articles containing the phrase "habitat fragmentation." The task of reviewing this literature is daunting not only because of its size but also because different authors use different definitions of habitat fragmentation, and they measure fragmentation in different ways and at different spatial scales.

This diversity of definitions of habitat fragmentation can be readily seen in the titles of some articles. For example, "Impacts of habitat fragmentation and

patch size..." (Collingham & Huntly 2000) suggests that habitat fragmentation and patch size are two different things. However, other authors actually use patch size to measure habitat fragmentation (e.g., Golden & Crist 2000, Hovel & Lipicus 2001). "The effects of forest fragmentation and isolation..." (Goodman & Rakotodravony 2000) suggests that forest fragmentation and isolation are different, in contrast to authors who use forest isolation as a measure of forest fragmentation (e.g., Mossman & Waser 2001, Rukke 2000). "Effect of land cover, habitat fragmentation, and..." (Laakkonen et al. 2001) contrasts with many authors who equate landscape fragmentation with land cover (e.g., Carlson & Hartman 2001; Fuller 2001; Gibbs 1998, 2001; Golden & Crist 2000; Hargis et al. 1999; Robinson et al. 1995; Summerville & Crist 2001; Virgós 2001). "The influence of forest fragmentation and landscape pattern..." (Hargis et al. 1999) contrasts with researchers who define fragmentation as an aspect of landscape pattern (e.g., Wolff et al. 1997, Trzcinski et al. 1999). As a final example, "Effects of experimental habitat fragmentation and connectivity..." (Ims & Andreassen 1999) suggests that habitat fragmentation and connectivity can be examined independently, whereas some researchers actually define fragmentation as "a disruption in landscape connectivity" (With et al. 1997; see also Young & Jarvis 2001).

My goal in this review is to discuss the information available on the effects of habitat fragmentation on biodiversity. To meet this objective I first need to examine the different ways in which habitat fragmentation is conceptualized and measured. Of course, the concept of biodiversity is probably at least as wide-ranging as the concept of habitat fragmentation. However, I do not deal with the issues surrounding the concept of biodiversity. Instead, I include any ecological response variable that is or can be related to biological diversity (see Table 1).

To determine current usage of the term habitat fragmentation, I conducted a search of the Cambridge Scientific Abstracts (Biological Sciences) database on 11 April 2002 for papers containing either "habitat fragmentation," "forest fragmentation," or "landscape fragmentation" in the title of the paper. I reviewed in detail the most recent 100 resulting papers, irrespective of the journal in which they appeared. I limited this search to papers containing "fragmentation" in the title to ensure that my sample included only papers that are directly on the subject of habitat fragmentation. The results are summarized in Table 1.

I then surveyed the broader ecological literature to ask the following: How strong are the effects of habitat fragmentation on biodiversity, and are the effects negative or positive? Habitat fragmentation is generally thought to have a large, negative effect on biodiversity and is therefore widely viewed as an aspect of habitat degradation (Haila 2002). However, as I show, this conclusion is generally valid only for conceptualizations of fragmentation that are inseparable from habitat loss. Other ways of conceptualizing habitat fragmentation lead to other conclusions. I end the paper with recommendations.

TABLE 1 Summary of 100 recent fragmentation studies*

	Biodiversity (response) variables									
Fragmentation (predictor) variables	**Abundance/ density (35)**	**Richness/ diversity (28)**	**Presence/ absence (26)**	**Fitness measures (15)**	**Genetic variability (12)**	**Species interactions (10)**	**Extinction/ turnover (8)**	**Individual habitat use (5)**	**Movement/ dispersal (4)**	**Population growth (3)**
Patch size[a] (63)	26	21	20	11	3	7	3	3	3	3
Habitat loss/amount (60)	21	17	13	9	8	5	5	3	2	1
Patch isolation[a] (35)	14	7	11	2	6	3	0	0	1	0
Edge[a] (22)	11	5	3	2	0	4	1	2	0	1
Number of patches (10)	2	1	0	2	0	2	3	1	0	1
Structural connectivity[b] (8)	3	1	1	2	0	2	1	0	1	1
Matrix quality (7)	3	2	1	1	2	0	0	2	0	0
Patch shape[a] (4)	0	1	2	0	0	1	0	0	0	0
Qualitative only (28)	13	9	7	10	4	0	1	3	0	1
Patch scale[c] (42)	17	14	16	6	7	4	0	2	1	1
Landscape scale[d] (37)	7	7	4	4	3	3	8	2	3	1
Patch and landscape scales (21)	10	6	6	5	2	3	0	1	0	1

[a]Predictor variables that can be measured at either the patch scale (individually for each patch) or at the landscape scale (averaged or summed across all patches in the landscape).

[b]Includes both connectivity studies and corridor studies.

[c]Each data point in the analysis represents information from a single patch.

[d]Each data point in the analysis represents information from a single landscape.

*Table entries are the numbers of papers that studied the given combination of predictor (fragmentation) variable or scale and response (biodiversity) variable. Numbers in parentheses after variable names are the total number of papers (of 100) using that variable. Columns and rows do not add to 100 because each study may contain more than one fragmentation variable and more than one biodiversity variable.

CONCEPTUALIZATION AND MEASUREMENT OF HABITAT FRAGMENTATION

Fragmentation as Process

Habitat fragmentation is often defined as a process during which "a large expanse of habitat is transformed into a number of smaller patches of smaller total area, isolated from each other by a matrix of habitats unlike the original" (Wilcove et al. 1986) (Figure 1). By this definition, a landscape can be qualitatively categorized as either continuous (containing continuous habitat) or fragmented, where the fragmented landscape represents the endpoint of the process of fragmentation.

Many studies of the effect of habitat fragmentation on biodiversity conform to this definition by comparing some aspect(s) of biodiversity at "reference" sites within a continuous landscape to the same aspect(s) of biodiversity at sites within a fragmented landscape (e.g., Bowers & Dooley 1999, Cascante et al. 2002, Diaz et al. 2000, Groppe et al. 2001, Laurance et al. 2001, Mac Nally & Brown 2001, Mahan & Yahner 1999, Morato 2001, Mossman & Waser 2001, Renjifo 1999, Walters et al. 1999). From my sample of 100 recent studies, 28% conducted such comparisons of continuous versus fragmented landscapes (Table 1). In these studies, the continuous landscape represents a landscape before fragmentation (time 1 in Figure 1) and the fragmented landscape represents a landscape following fragmentation (time 2 or time 3 in Figure 1).

Although this approach conforms to the definition of fragmentation as a process, it has two inherent weaknesses. First, because habitat fragmentation is a landscape-scale process (McGarigal & Cushman 2002), the sample size in such studies, for questions about the effects of habitat fragmentation on biodiversity, is typically

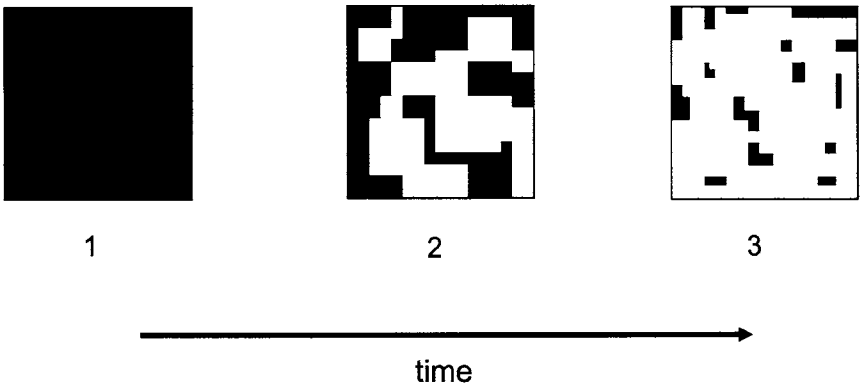

Figure 1 The process of habitat fragmentation, where "a large expanse of habitat is transformed into a number of smaller patches of smaller total area, isolated from each other by a matrix of habitats unlike the original" (Wilcove et al. 1986). Black areas represent habitat and white areas represent matrix.

only two, i.e., one continuous landscape and one fragmented landscape. With such a design, inferences about the effects of fragmentation are weak. Apparent effects of fragmentation could easily be due to other differences between the landscapes. For example, Mac Nally et al. (2000) found consistent vegetation differences between fragments and reference sites and concluded that apparent effects of fragmentation on birds could be due to preexisting habitat differences between the two landscapes.

Second, this characterization of habitat fragmentation is strictly qualitative, i.e., each landscape can be in only one of two states, continuous or fragmented. This design does not permit one to study the relationship between the degree of habitat fragmentation and the magnitude of the biodiversity response. Quantifying the degree of fragmentation requires measuring the pattern of habitat on the landscape. The diversity of approaches in the fragmentation literature arises mainly from differences among researchers in how they quantify habitat fragmentation. These differences have significant implications for conclusions about the effects of fragmentation on biodiversity.

Fragmentation as Pattern: Quantitative Conceptualizations

The definition of habitat fragmentation above implies four effects of the process of fragmentation on habitat pattern: (*a*) reduction in habitat amount, (*b*) increase in number of habitat patches, (*c*) decrease in sizes of habitat patches, and (*d*) increase in isolation of patches. These four effects form the basis of most quantitative measures of habitat fragmentation. However, fragmentation measures vary widely; some include only one effect (e.g., reduced habitat amount or reduced patch sizes), whereas others include two or three effects but not all four.

Does it matter which fragmentation measure a researcher uses? The answer depends on whether the different effects of the process of fragmentation on habitat pattern have the same effects on biodiversity. If they do, we can draw general conclusions about the effects of fragmentation on biodiversity even though the different studies making up the fragmentation literature measure fragmentation in different ways. As I show in Effects of Habitat Fragmentation on Biodiversity, the different effects of the process of fragmentation on habitat pattern do not affect biodiversity in the same way. This has led to apparently contradictory conclusions about the effects of fragmentation on biodiversity. In this section, I review quantitative conceptualizations of habitat fragmentation. This is an important step toward reconciling these apparently contradictory results.

FRAGMENTATION AS HABITAT LOSS The most obvious effect of the process of fragmentation is the removal of habitat (Figure 1). This has led many researchers to measure the degree of habitat fragmentation as simply the amount of habitat remaining on the landscape (e.g., Carlson & Hartman 2001, Fuller 2001, Golden & Crist 2000, Hargis et al. 1999, Robinson et al. 1995, Summerville & Crist 2001, Virgós 2001). If we can measure the level of fragmentation as the amount of habitat, why do we call it "fragmentation"? Why not simply call it habitat loss? The

reason is that when ecologists think of fragmentation, the word invokes more than habitat removal: "fragmentation ... not only causes loss of the amount of habitat, but by creating small, isolated patches it also changes the properties of the remaining habitat" (van den Berg et al. 2001).

Habitat can be removed from a landscape in many different ways, resulting in many different spatial patterns (Figure 2). Do some patterns represent a higher degree of fragmentation than others, and does this have implications for biodiversity? If the answer to either of these questions is "no," then the concept of fragmentation is redundant with habitat loss. The assertion that habitat fragmentation means something more than habitat loss depends on the existence of effects of fragmentation on biodiversity that can be attributed to changes in the pattern of habitat that are independent of habitat loss. Therefore, many researchers define habitat fragmentation as an aspect of habitat configuration.

FRAGMENTATION AS A CHANGE IN HABITAT CONFIGURATION In addition to loss of habitat, the process of habitat fragmentation results in three other effects: increase in number of patches, decrease in patch sizes, and increase in isolation of patches. Measures of fragmentation that go beyond simply habitat amount are generally derived from these or other strongly related measures (e.g., amount of edge). There are at least 40 such measures of fragmentation (McGarigal et al. 2002), many of which typically have strong relationships with the amount of habitat as well as with each other (Bélisle et al. 2001, Boulinier et al. 2001, Drolet et al. 1999, Gustafson 1998, Haines-Young & Chopping 1996, Hargis et al. 1998, Robinson et al. 1995, Schumaker 1996, Trzcinski et al. 1999, Wickham et al. 1999) (Figure 3).

The interrelationships among measures of fragmentation are not widely recognized in the current fragmentation literature. Most researchers do not separate the effects of habitat loss from the configurational effects of fragmentation. This leads to ambiguous conclusions regarding the effects of habitat configuration on biodiversity (e.g., Summerville & Crist 2001, Swenson & Franklin 2000). It is also common for fragmentation studies to report individual effects of fragmentation measures without reporting the relationships among them, which again makes the results difficult to interpret.

THE PATCH-SCALE PROBLEM Similar problems arise when fragmentation is measured at the patch scale rather than the landscape scale. Because fragmentation is a landscape-scale process (Figure 1), fragmentation measurements are correctly made at the landscape scale (McGarigal & Cushman 2002). As pointed out by Delin & Andrén (1999), when a study is at the patch scale, the sample size at the landscape scale is only one, which means that landscape-scale inference is not possible (Figure 4; see Brennan et al. 2002, Tischendorf & Fahrig 2000). However, in approximately 42% of recent fragmentation studies, individual data points represent measurements on individual patches, not landscapes (Table 1). Similarly, using a different sample of the literature, McGarigal & Cushman (2002)

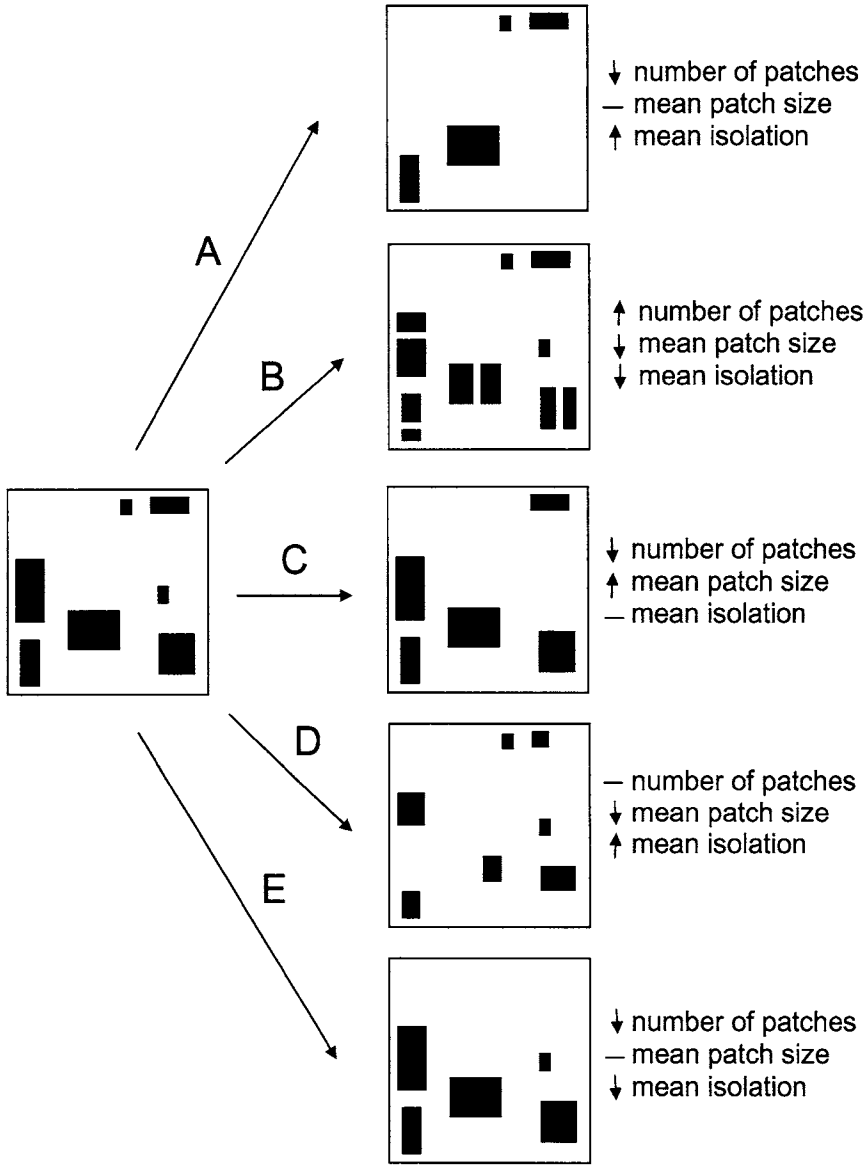

Figure 2 Illustration of habitat loss resulting in some, but not all, of the other three expected effects of habitat fragmentation on landscape pattern. Expected effects are (*a*) an increase in the number of patches, (*b*) a decrease in mean patch size, and (*c*) an increase in mean patch isolation (nearest neighbor distance). Actual changes are indicated by arrows.

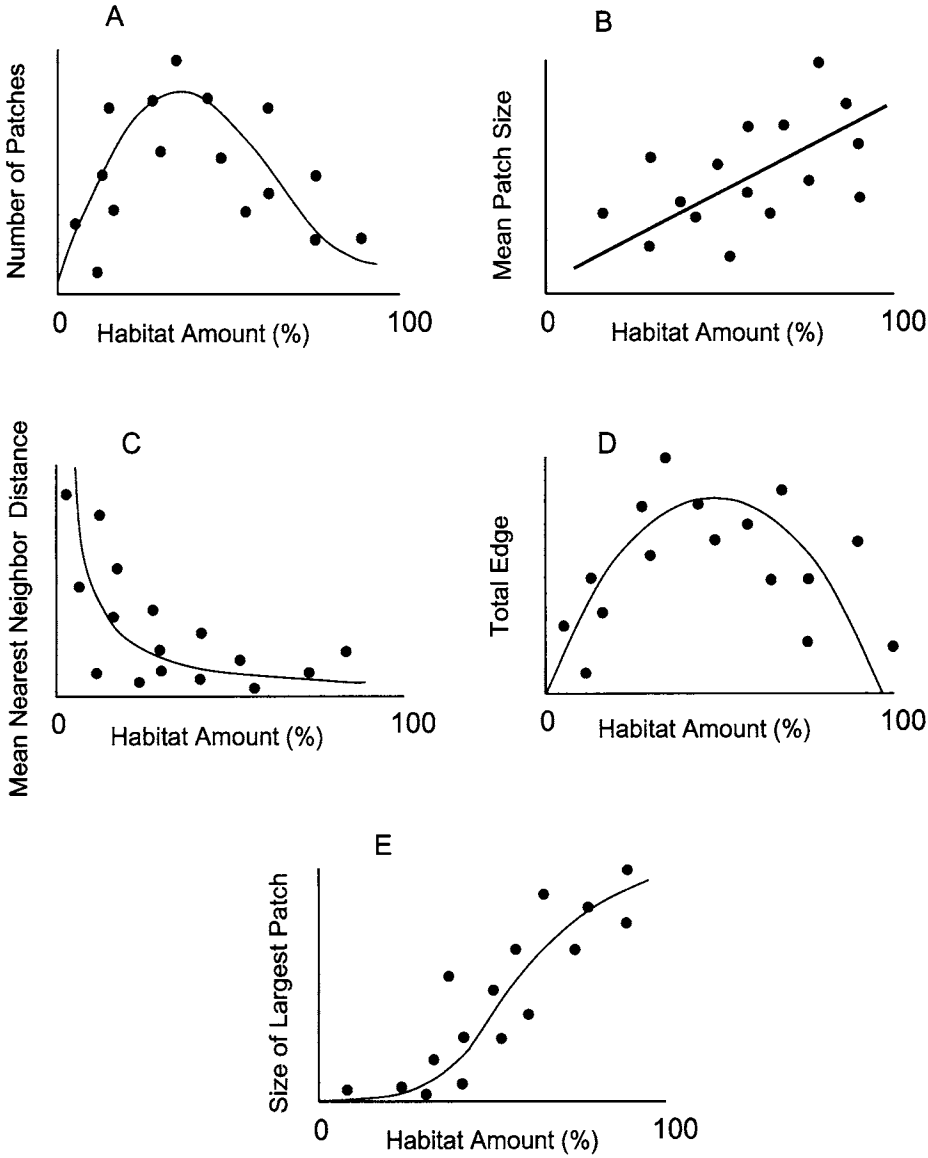

Figure 3 Illustration of the typical relationships between habitat amount and various measures of fragmentation. Individual data points correspond to individual landscapes. Based on relationships in Bélisle et al. (2001), Boulinier et al. (2001), Drolet et al. (1999), Gustafson (1998), Haines-Young & Chopping (1996), Hargis et al. (1998), Robinson et al. (1995), Schumaker (1996), Trzcinski et al. (1999), and Wickham et al. (1999).

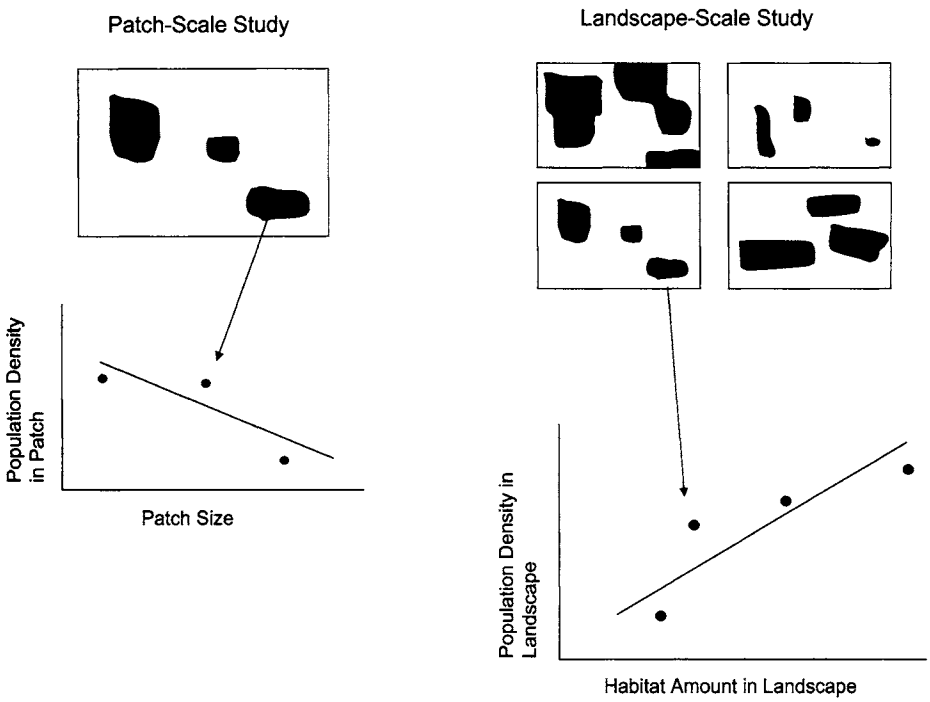

Figure 4 (*A*) Patch-scale study. Each observation represents the information from a single patch. Only one landscape is studied, so sample size for landscape-scale inferences is one. (*B*) Landscape-scale study. Each observation represents the information from a single landscape. Multiple landscapes, with different structures, are studied. Here, sample size for landscape-scale inferences is four.

estimated that more than 57% of all fragmentation studies are at the patch scale. Some researchers even refer to patch-scale measures as landscape features (e.g., Fernandez-Juricic 2000, Schweiger et al. 2000).

Patch size: an ambiguous measure of fragmentation The relationship between patch size and fragmentation is ambiguous because both habitat loss and habitat fragmentation per se (i.e., the breaking apart of habitat, controlling for changes in habitat amount) result in smaller patches (Figure 5). Using patch size as a measure of habitat fragmentation per se implicitly assumes that patch size is independent of habitat amount at the landscape scale (e.g., Niemelä 2001). However, regions where patches are large often correspond to regions where there is more habitat (Fernandez-Juricic 2000, McCoy & Mushinsky 1999) (Figure 6). Ignoring potential relationships between a patch-scale measure (e.g., patch size) and landscape-scale habitat amount does not control for this relationship; it can lead to misinterpretation of results.

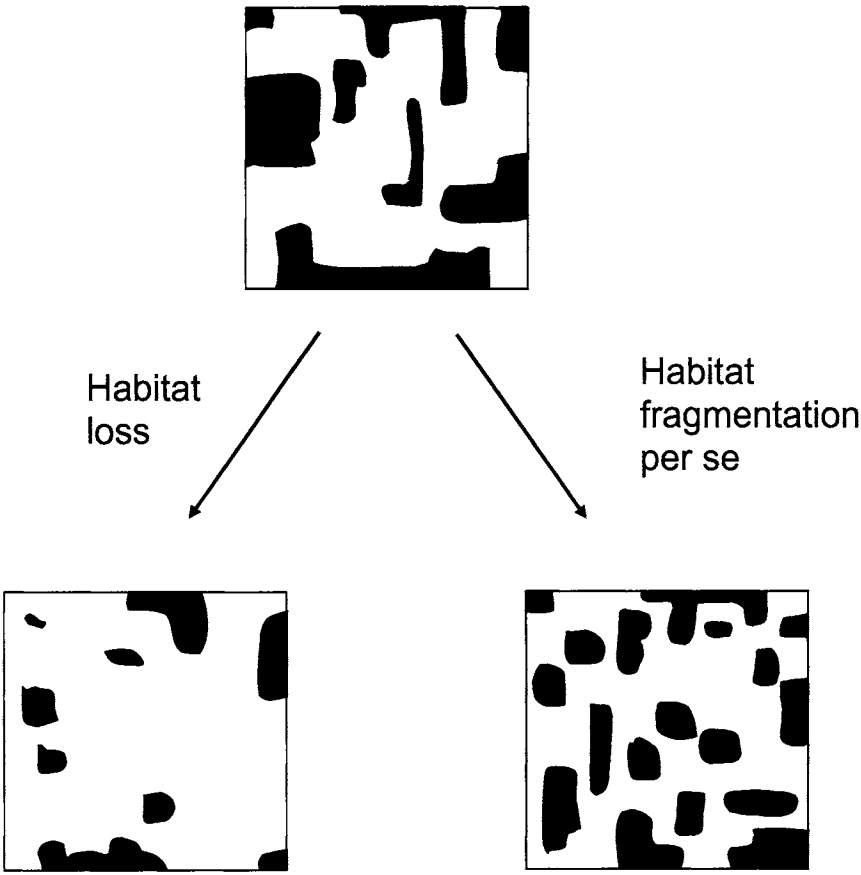

Figure 5 Both habitat loss and habitat fragmentation per se (independent of habitat loss) result in smaller patches. Therefore, patch size itself is ambiguous as a measure of either habitat amount or habitat fragmentation per se. Note also that habitat fragmentation per se leads to reduced patch isolation.

Patch isolation: a measure of habitat amount In the fragmentation literature, patch isolation is almost universally interpreted as a measure of habitat configuration. However, patch isolation is more accurately viewed as a measure of the lack of habitat in the landscape surrounding the patch. The more isolated a patch is, generally speaking, the less habitat there is in the landscape that surrounds it (Figure 7). Therefore, when translated to the landscape scale, isolation of a patch is a measure of habitat amount in the landscape, not configuration of the landscape.

Bender et al. (2003) reviewed measures of patch isolation. All measures are strongly negatively related to habitat amount in the surrounding landscape. The most common measure of patch isolation is the distance to the next-nearest patch,

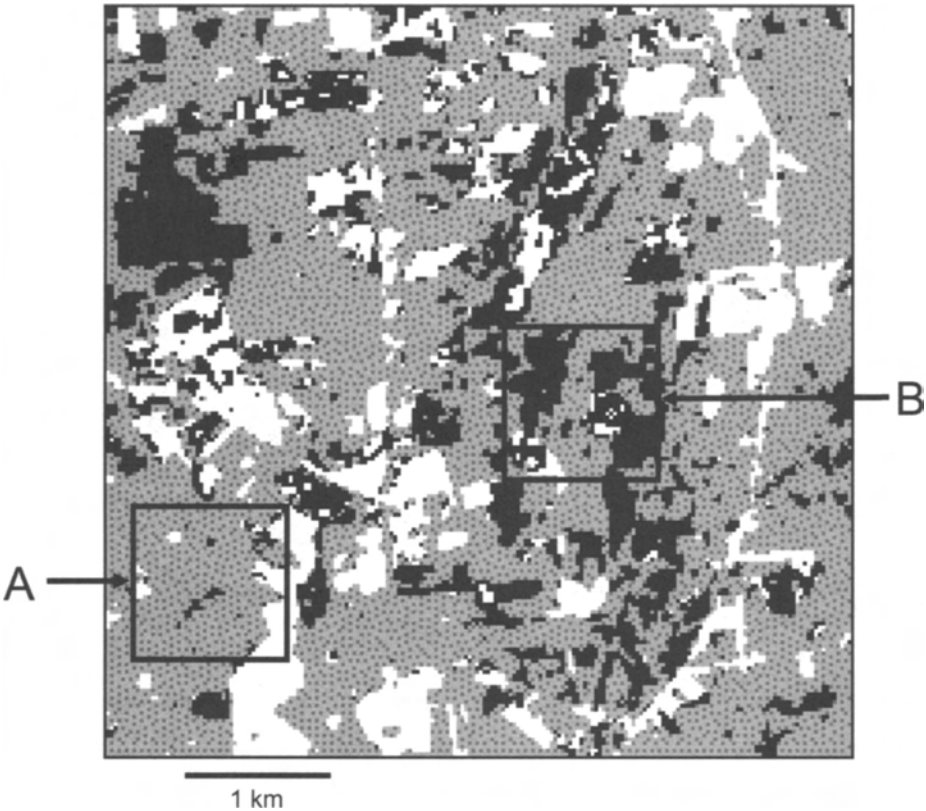

Figure 6 Landscape in southern Ontario (from Tischendorf 2001) showing that regions where forest patches (black areas) are small typically correspond to regions where there is little forest. Compare (*A*) and (*B*), where (*A*) has small patches and less than 5% forest and (*B*) has larger patches and approximately 50% forest.

or "nearest-neighbor distance" (e.g., Delin & Andrén 1999, Haig et al. 2000, Hargis et al. 1999). Patches with small nearest-neighbor distances are typically situated in landscapes containing more habitat than are patches with large nearest-neighbor distances (Figure 7), so in most situations this measure of isolation is related to habitat amount in the landscape. Another common measure of patch isolation is the inverse of the amount of habitat within some distance of the patch in question (e.g., Kinnunen et al. 1996, Magura et al. 2001, Miyashita et al. 1998). In other words, patch isolation is measured as habitat amount at the landscape scale. All other measures of patch isolation are a combination of distances to other patches and sizes of those patches (or the populations they contain) in the surrounding landscape (reviewed in Bender et al. 2003). As such they are all measures of the amount of habitat in the surrounding landscape.

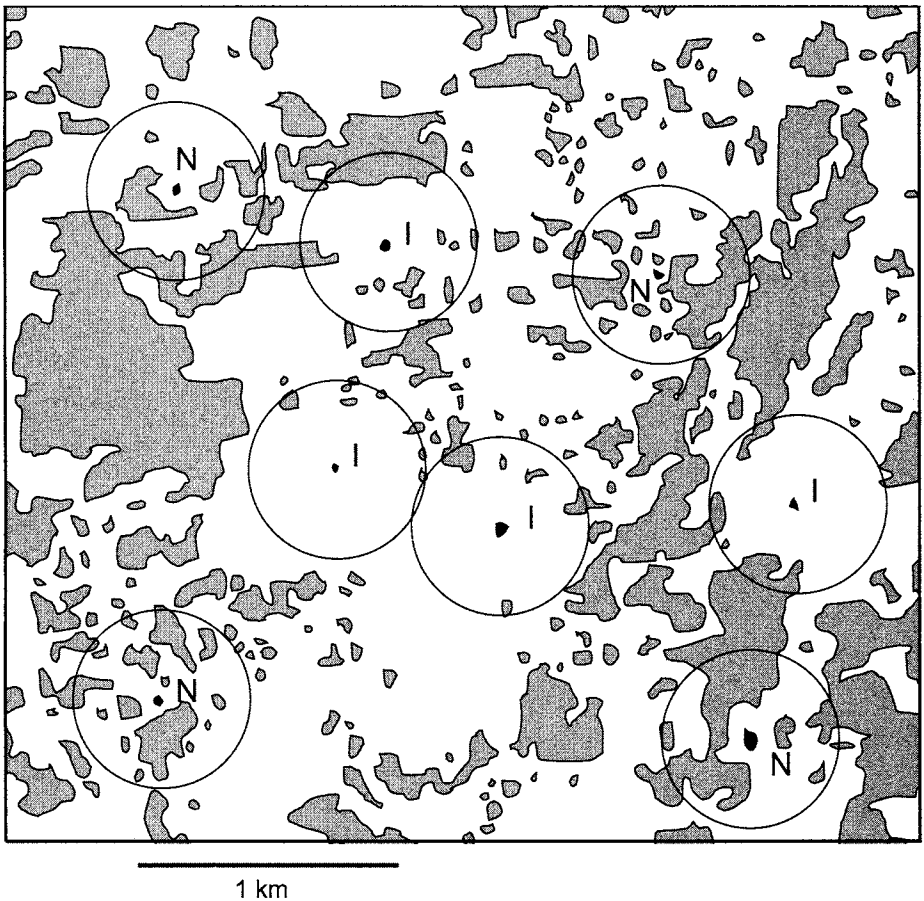

Figure 7 Illustration of the relationship between patch isolation and amount of habitat in the landscape immediately surrounding the patch. Gray areas are forest. Isolated patches (*black patches labeled "I"*) are situated in landscapes (*circles*) containing less forest than are less isolated patches (*black patches labeled "N"*).

MEASURING HABITAT FRAGMENTATION PER SE How can we measure habitat fragmentation independent of habitat amount? Some researchers have constructed landscapes in which they experimentally controlled habitat amount while varying habitat fragmentation per se (e.g., Caley et al. 2001, Collins & Barrett 1997). Researchers studying real landscapes have used statistical methods to control for habitat amount. For example, McGarigal and McComb (1995) measured 25 landscape indices for each of 30 landscapes. They statistically corrected each index for its relationship to habitat amount and then entered the corrected variables into a PCA. Each axis of the resulting PCA represented a different component of

landscape configuration. In a similar approach, Villard et al. (1999) measured the number of forest patches, total length of edge, mean nearest-neighbor distance, and percent of forest cover on each of 33 landscapes. They used the residuals of the statistical models relating each of the first three variables to forest amount as measures of fragmentation that have been controlled for their relationships to habitat amount.

EFFECTS OF HABITAT FRAGMENTATION ON BIODIVERSITY

In this section I review the empirical evidence for effects of habitat fragmentation on biodiversity. This review is not limited to the 100 papers summarized in Table 1. The fragmentation literature can be distilled into two major effects: the generally strong negative effect of habitat loss on biodiversity, and the much weaker, positive or negative effect of fragmentation per se on biodiversity. Because the effect of fragmentation per se is weaker than the effect of habitat loss, to detect the effect of fragmentation per se, the effect of habitat loss must be experimentally or statistically controlled.

Effects of Habitat Loss on Biodiversity

Habitat loss has large, consistently negative effects on biodiversity, so researchers who conceptualize and measure fragmentation as equivalent to habitat loss typically conclude that fragmentation has large negative effects. The negative effects of habitat loss apply not only to direct measures of biodiversity such as species richness (Findlay & Houlahan 1997, Gurd et al. 2001, Schmiegelow & Mönkkönen 2002, Steffan-Dewenter et al. 2002, Wettstein & Schmid 1999), population abundance and distribution (Best et al. 2001, Gibbs 1998, Guthery et al. 2001, Hanski et al. 1996, Hargis et al. 1999, Hinsley et al. 1995, Lande 1987, Sánchez-Zapata & Calvo 1999, Venier & Fahrig 1996) and genetic diversity (Gibbs 2001), but also to indirect measures of biodiversity and factors affecting biodiversity. A model by Bascompte et al. (2002) predicts a negative effect of habitat loss on population growth rate. This is supported by Donovan & Flather (2002), who found that species showing declining trends in global abundance are more likely to occur in areas with high habitat loss than are species with increasing or stable trends. Habitat loss has been shown to reduce trophic chain length (Komonen et al. 2000), to alter species interactions (Taylor & Merriam 1995), and to reduce the number of specialist, large-bodied species (Gibbs & Stanton 2001). Habitat loss also negatively affects breeding success (Kurki et al. 2000), dispersal success (Bélisle et al. 2001, Pither & Taylor 1998, With & Crist 1995, With & King 1999), predation rate (Bergin et al. 2000, Hartley & Hunter 1998), and aspects of animal behavior that affect foraging success rate (Mahan & Yahner 1999).

INDIRECT EVIDENCE OF EFFECTS OF HABITAT LOSS Negative effects of habitat loss on biodiversity are also evident from studies that measure habitat amount indirectly, using measures that are highly correlated with habitat amount. For example, Robinson et al. (1995) found that reproductive success of forest nesting bird species was positively correlated with percentage of forest cover, percentage of forest interior, and average patch size in a landscape. Because the latter two variables were highly correlated with percentage of forest cover, these all represent positive effects of habitat amount on reproductive success. Boulinier et al. (2001) found effects of mean patch size on species richness, local extinction rate, and turnover rate of forest birds in 214 landscapes. Because mean patch size had a 0.94 correlation with forest amount in their study, this result most likely represents an effect of habitat amount.

Patch isolation effects Patch isolation is a measure of the lack of habitat in the landscape surrounding the patch (Figure 7). Therefore, the many studies that have shown negative effects of patch isolation on species richness or presence/absence represent further evidence for the strong negative effect of landscape-scale habitat loss on biodiversity (e.g., McCoy & Mushinsky 1999, Rukke 2000, Virgós 2001).

Bender et al. (2003) and Tischendorf et al. (2003) conducted simulation analyses to determine which patch isolation measures are most strongly related to movement of animals between patches. They found that the "buffer" measures, i.e., amount of habitat within a given buffer around the patch, were best. This suggests a strong effect of habitat amount on interpatch movement. It also suggests, again, that effects of patch isolation and landscape-scale habitat amount are equivalent.

Patch size effects Individual species have minimum patch size requirements (e.g., Diaz et al. 2000). Therefore, smaller patches generally contain fewer species than larger patches (Debinski & Holt 2000), and the set of species on smaller patches is often a more-or-less predictable subset of the species on larger patches (e.g., Ganzhorn & Eisenbeiß 2001, Kolozsvary & Swihart 1999, Vallan 2000). Similarly, the amount of habitat on a landscape required for species occurrence there differs among species (Gibbs 1998, Vance et al. 2003), so landscapes with less habitat should contain a subset of the species found in landscapes with more habitat.

Despite this apparent correspondence between patch- and landscape-scale effects, the landscape-scale interpretation of patch size effects depends on the landscape context of the patch. For example, Donovan et al. (1995) found that forest birds had lower reproductive rates in small patches than in large patches. If small patches occur in areas with less forest, the reduced reproductive rate may not be the result of patch size, but may result from larger populations of nest predators and brood parasites that occur in landscapes with more open habitat (Hartley & Hunter 1998, Robinson et al. 1995, Schmiegelow & Mönkkönen 2002).

EXTINCTION THRESHOLD The number of individuals of any species that a landscape can support should be a positive function of the amount of habitat available to

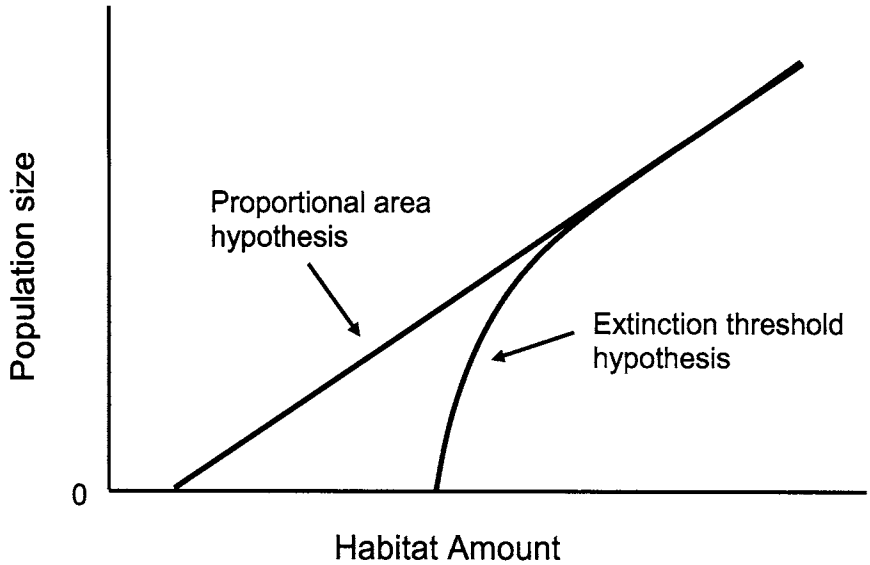

Figure 8 Illustration of the extinction threshold hypothesis in comparison to the proportional area hypothesis.

that species in the landscape. However, several theoretical studies suggest that the relationship is not proportional; they predict a threshold habitat level below which the population cannot sustain itself, termed the extinction threshold (Bascompte & Solé 1996, Boswell et al. 1998, Fahrig 2001, Flather & Bevers 2002, Hill & Caswell 1999, Lande 1987, With & King 1999; Figure 8). There have been very few direct empirical tests of the extinction threshold hypothesis (but see Jansson & Angelstam 1999).

Note that the predicted occurrence of the extinction threshold results from habitat loss, not habitat fragmentation per se. Theoretical studies suggest that habitat fragmentation per se can affect where the extinction threshold occurs on the habitat amount axis. Also, the effects of habitat fragmentation per se are predicted to increase below some level of habitat loss (see The 20–30% Threshold, below). However, the occurrence of the extinction threshold is a response to habitat loss, not fragmentation per se. This has led to some ambiguity in interpretation of empirical literature. For example, Virgós (2001) found that patch isolation affects badger density only for patches in landscapes with <20% forest cover. As explained above, patch isolation is typically an index of habitat amount at the landscape scale. Therefore, this result probably suggests a threshold effect of forest loss on badger density. This conclusion is different from that of the author, who interpreted the isolation effect as an effect of habitat configuration. The interpretation is ambiguous because the relationship between habitat amount and patch isolation was not statistically controlled in this study. Similarly, Andrén (1994) reviewed patch size and patch isolation effects on population density and concluded that these effects

increase below a threshold amount of habitat in the landscape. Because patch size and isolation can be indicators of habitat amount at a landscape scale (see Patch size: An Ambiguous Measure of Fragmentation and Patch Isolation: A Measure of Habitat Amount, above), this result could be interpreted as an intensification of the effects of habitat loss at low habitat levels, i.e., it supports the extinction threshold hypothesis (Figure 8). This result has also been viewed as evidence for configuration effects below a threshold habitat level (e.g., Flather & Bevers 2002, Villard et al. 1999). Again, the interpretation is ambiguous because the relationships between patch size and isolation and amount of habitat surrounding each patch were not controlled for.

Effects of Habitat Fragmentation per se on Biodiversity

In this section I review the empirical evidence for fragmentation effects per se, i.e., for effects of "breaking apart" of habitat on biodiversity, that are independent of or in addition to the effects of habitat loss. The 17 studies in Table 2 represent all of the empirical studies of fragmentation per se of which I am aware. Some theoretical studies suggest that the effect of habitat fragmentation per se is weak relative to the effect of habitat loss (Collingham & Huntley 2000, Fahrig 1997, Flather & Bevers 2002, Henein et al. 1998), although other modeling studies predict much larger effects of fragmentation per se (Boswell et al. 1998, Burkey 1999, Hill & Caswell 1999, Urban & Keitt 2001, With & King 1999; reviewed in Fahrig 2002). All these recent models predict negative effects of habitat fragmentation per se, in contrast with some earlier theoretical work (see Reasons for Positive Effects of Fragmentation, below). The empirical evidence to date suggests that the effects of fragmentation per se are generally much weaker than the effects of habitat loss. Unlike the effects of habitat loss, and in contrast to current theory, empirical studies suggest that the effects of fragmentation per se are at least as likely to be positive as negative.

The 17 empirical studies on the effects of habitat fragmentation per se (Table 2) range from small-scale experimental studies to continental-scale analyses. They cover a range of response variables, including abundance, density, distribution, reproduction, movement, and species richness. About half of the studies are on forest birds; other taxa include insects, small mammals, plants, aquatic invertebrates, and a virus, and other habitats include grasslands, cropland, a coral reef, and an estuary.

The 17 studies used a variety of approaches for estimating the effect of fragmentation per se. In five of them, experimental landscapes were constructed to independently control the levels of habitat amount and fragmentation per se. Four of these varied both habitat amount and fragmentation per se, and one varied only fragmentation, holding the amount of habitat constant. Three of the 12 studies in real landscapes compared the response variable in one large patch versus several small patches (i.e., holding habitat amount constant). In the remaining nine studies in real landscapes, the effect of fragmentation per se was estimated by statistically controlling for the effect of habitat amount.

TABLE 2 Summary of empirical studies that examined the effects of habitat fragmentation per se, i.e., controlling for effects of habitat amount on biodiversity

Study	Taxa and response variable(s)	Relative effects of habitat loss versus habitat fragmentation per se	Direction of effect(s) of fragmentation per se on biodiversity
Studies in real landscapes			
Middleton & Merriam 1983	111 forest taxa (various): distribution	n.a.[a]	No effect
McGarigal & McComb 1995	15 late-seral forest bird species: abundance	Amount ≫ fragmentation	6 positive, 1 negative
Meyer et al. 1998	Northern spotted owl: presence/absence, persistence, reproduction	Amount ≫ fragmentation	No effect
Rosenberg et al. 1999	6 Tanager species and populations: presence/absence	Amount ≫ fragmentation	2 negative
Trzcinski et al. 1999	31 forest bird species: presence/absence	Amount ≫ fragmentation	2 positive, 4 negative
Drolet et al. 1999	14 forest bird species: presence/absence	Amount ≫ fragmentation	No effect
Villard et al. 1999	15 forest bird species: presence/absence	Amount ≅ fragmentation	4 positive, 2 negative
Bélisle et al. 2001	3 forest bird species: homing time and homing success	Amount ≫ fragmentation	Positive
Langlois et al. 2001	Hanta virus: incidence	Amount ≫ fragmentation	Positive

(*Continued*)

TABLE 2 *(Continued)*

Study	Taxa and response variable(s)	Relative effects of habitat loss versus habitat fragmentation per se	Direction of effect(s) of fragmentation per se on biodiversity
Hovel & Lipcius 2001	Blue crab: juvenile survival, adult (predator) density	n.a.[a]	1 positive (juvenile survival), 1 negative (adult density)
Tscharntke et al. 2002	Butterflies: species richness, endangered species richness	n.a.[a]	2 positive (total and endangered species richness)
Flather et al. 1999	Forest birds: abundance	Amount ≫ fragmentation	No effect
Studies in experimental landscapes:			
Collins & Barrett 1997	Meadow vole: density	n.a.[a]	Positive
Wolff et al. 1997	Gray-tailed vole: abundance, density, reproductive rate, recruitment	Fragmentation > amount	Positive
Collinge & Forman 1998	Grassland insects: abundance, species richness	Not stated	Positive
Caley et al. 2001	8 coral commensals: species richness and abundance	Amount ≫ fragmentation	1 positive
With et al. 2002	Clover insects: spatial aggregation	Amount ≫ fragmentation	n.a.[b]

[a]Habitat amount was held constant; only fragmentation was varied.

[b]Response variable was spatial distribution of the insects.

The overall result from these studies is that habitat loss has a much larger effect than habitat fragmentation per se on biodiversity measures (Table 2). When fragmentation per se did have an effect, it was at least as likely to be positive as negative (Table 2). Given the relatively small number of studies and the large variation in conditions among studies, it is not possible to tease apart the factors that lead to positive versus negative effects of fragmentation per se. However, the positive effects of fragmentation can not be explained as merely responses by "weedy," habitat generalist species. For example, the results reported from McGarigal & McComb (1995) are specifically limited to late-seral forest species, and Tscharntke et al. (2002) found a positive effect of fragmentation per se on butterfly species richness, even when they only included endangered butterfly species.

THE 20–30% THRESHOLD Some theoretical studies suggest that the effects of fragmentation per se should become apparent only at low levels of habitat amount, below approximately 20–30% habitat on the landscape (Fahrig 1998, Flather & Bevers 2002). To date, there is no convincing empirical evidence for this prediction. If the threshold does occur, it should result in a statistical interaction effect between habitat amount and habitat fragmentation per se; such an interaction would indicate that the effect of fragmentation per se depends on the amount of habitat in the landscape. Trzcinski et al. (1999) tested for this interaction effect but found no evidence for it. The hypothesis that fragmentation effects increase below a threshold of habitat amount has not yet been adequately tested.

REASONS FOR NEGATIVE EFFECTS OF FRAGMENTATION PER SE Negative effects of fragmentation are likely due to two main causes. First, fragmentation per se implies a larger number of smaller patches. At some point, each patch of habitat will be too small to sustain a local population or perhaps even an individual territory. Species that are unable to cross the nonhabitat portion of the landscape (the "matrix") will be confined to a large number of too-small patches, ultimately reducing the overall population size and probability of persistence.

The second main cause of negative effects of fragmentation per se is negative edge effects; more fragmented landscapes contain more edge for a given amount of habitat. This can increase the probability of individuals leaving the habitat and entering the matrix. Overall the amount of time spent in the matrix will be larger in a more fragmented landscape, which may increase overall mortality rate and reduce overall reproductive rate of the population (Fahrig 2002). In addition, there are negative edge effects due to species interactions. Probably the most extensively studied of these is increased predation on forest birds at forest edges (Chalfoun et al. 2002).

REASONS FOR POSITIVE EFFECTS OF FRAGMENTATION PER SE More than half of the effects of fragmentation per se that have been documented are positive (Table 2). Some readers will find this surprising, probably because habitat loss is inextricably

included within their conceptualization of habitat fragmentation. In this case even if fragmentation per se has a positive effect on biodiversity, this effect will be masked by the large negative effect of habitat loss.

Haila (2002) describes how the current concept of habitat fragmentation emerged from the theory of island biogeography (MacArthur & Wilson 1967). The two predictor variables in this theory are island size and island isolation, or distance of the island from the mainland. When this theory was conceptually extended from island archipelagos to terrestrial systems of habitat patches, the concept of isolation changed; isolation was now the result of habitat loss, and it represented the distance from a patch to its neighbor(s), not the distance to a mainland. Because of its roots in island biogeography, isolation was viewed as representing habitat subdivision even though it was inextricably linked to habitat loss.

However, a parallel research stream, which arose independently of the theory of island biogeography, suggested that habitat fragmentation could have positive effects on biodiversity. Huffaker's (1958) experiment suggested that subdivision of the same amount of habitat into many smaller pieces can enhance the persistence of a predator-prey system. He hypothesized that habitat subdivision provides temporary refugia for the prey species, where they can increase in numbers and disperse elsewhere before the predator or parasite finds them. The plausibility of this mechanism was supported by early theoretical studies (Hastings 1977, Vandermeer 1973). Early theoretical studies also suggested that habitat fragmentation enhances the stability of two-species competition (Levin 1974, Shmida & Ellner 1984, Slatkin 1974), and in an empirical study, Atkinson & Shorrocks (1981) found that coexistence of two competing species could be extended by dividing the habitat into more, smaller patches. Enhanced coexistence resulted from a trade-off between dispersal rate and competitive ability. This trade-off, along with asynchronous disturbances that locally removed the superior competitor, allowed the inferior competitor (but superior disperser) to colonize the empty patches first, before being later displaced by the superior competitor (Chesson 1985). Other researchers suggested that habitat subdivision could even stabilize single-species population dynamics when local disturbances are asynchronous by reducing the probability of simultaneous extinction of the whole population (den Boer 1981; Reddingius & den Boer 1970; Roff 1974a,b).

Why has this early work, suggesting positive effects of habitat fragmentation per se, been largely ignored in the more recent habitat fragmentation literature? One reason is that later theoretical and empirical studies (reviewed in Kareiva 1990) demonstrated that the predicted positive effects of fragmentation per se depend strongly on particular assumptions about the relative movement rates of predator versus prey (or host versus parasite), the trade-off between competitive ability and movement rate, and the asynchrony of disturbances. It seems that the sensitivity to these assumptions, along with the misrepresentation of patch isolation as a measure of habitat subdivision, led researchers to ignore the possibility that fragmentation per se could have a positive effect on biodiversity.

There are at least four additional possible reasons for positive effects of habitat fragmentation per se on biodiversity. First, Bowman et al. (2002) argued that, for many species, immigration rate is a function of the linear dimension of a habitat patch rather than the area of the patch. For these species, overall immigration rate should be higher when the landscape is comprised of a larger number of smaller patches (higher fragmentation per se) than when it is comprised of a smaller number of larger patches. In situations where immigration is an important determinant of population density, this could result in a positive effect of fragmentation per se on density.

Second, if habitat amount is held constant, increasing fragmentation per se actually implies smaller distances between patches (Figure 5). Therefore, a positive effect of fragmentation per se could be due to a reduction in patch isolation.

Third, many species require more than one kind of habitat (Law & Dickman 1998). For example, immature insects and amphibians often use different habitats than those they use as adults. A successful life cycle requires that the adults can move away from the habitat where they were reared to their adult habitats and then back to the immature habitat to lay eggs. The proximity of different required habitat types will determine the ease with which individuals can move among them. For example, Pope et al. (2000) showed that the proximity of feeding habitat to breeding ponds affected the abundance of leopard frog populations. Pedlar et al. (1997) found that raccoon abundance was highest in landscapes with intermediate amounts of forest. They suggested that this level of forest maximized the accessibility to the raccoons of both feeding areas (grain fields) and denning sites in forest.

The degree to which landscape structure facilitates movement among different required habitat types was labeled "landscape complementation" by Dunning et al. (1992). For the same amount of habitat, a more fragmented landscape (more, smaller patches, and more edge) will have a higher level of interdigitation of different habitat types. This should increase landscape complementation, which has a positive effect on biodiversity (Law & Dickman 1998, Tscharntke et al. 2002).

Finally, it seems likely that positive edge effects are a factor. Some species do show positive edge effects (Carlson & Hartman 2001, Kremsater & Bunnell 1999, Laurance et al. 2001). For a given amount of habitat, more fragmented landscapes contain more edge. Therefore, positive edge effects could be responsible for positive effects of fragmentation per se on abundance or distribution of some species.

CONCLUSIONS AND FUTURE DIRECTIONS

Habitat Loss Versus Fragmentation

Most researchers view habitat fragmentation as a process involving both the loss of habitat and the breaking apart of habitat. The fact that most fragmentation research does not differentiate between these two effects has led to several problems. First,

the apparent inconsistency in the effects of a single process (fragmentation) gives the impression that fragmentation effects are difficult to generalize. In fact, generalization is possible, but only for the separate components of fragmentation, not for the combined concept of loss and breaking apart of habitat. Empirical evidence to date suggests that the loss of habitat has large negative effects on biodiversity. On the other hand, the breaking apart of habitat, independent of habitat loss, has rather weak effects on biodiversity, which are as likely to be positive as negative.

Second, the merging of these two aspects of fragmentation has obscured the fact that the effects of habitat loss outweigh the effects of habitat fragmentation per se. In fact, the effects of fragmentation per se are absent or too small to be detected in most empirical tests to date. This is in contrast to several theoretical predictions (Burkey 1999, Hill & Caswell 1999, Urban & Keitt 2001, With & King 1999) and has important implications for conservation. It suggests that conservation efforts should focus on habitat preservation and restoration. It also suggests that research in support of particular conservation problems should focus on determining the amount of habitat required for conservation of the species of concern. The fact that effects of fragmentation per se are usually small and at least as likely to be positive as negative suggests that conservation actions that attempt to minimize fragmentation (for a given habitat amount) may often be ineffectual.

Note, however, that this conclusion is preliminary because there are still only a small number of relevant empirical studies. To my knowledge there are, to date, no studies in tropical regions of the effects of forest fragmentation per se (controlling for habitat loss). Laurance et al. (2002) concluded that in Brazilian tropical forest there are strong negative effects of forest edge on several taxa. These effects are apparently much stronger than negative edge effects in temperate systems (Kremsater & Bunnell 1999). Negative edge effects could translate into a negative effect of fragmentation per se at the landscape scale because fragmentation per se increases the amount of edge on the landscape. This suggests that effects of fragmentation per se may be greater in tropical systems than in temperate systems. This prediction remains to be tested.

Third, ambiguous empirical results could lead to errors in modeling studies. For example, Donovan & Lamberson (2001) constructed a model to look at the effects of habitat fragmentation on population growth rate. They held amount of habitat constant and varied mean patch size. For input parameters they used empirical work suggesting that reproductive success increases with increasing patch size. However, as they point out, in these empirical studies patch size was highly correlated with habitat amount in the surrounding landscape. It is not known whether reproductive success increases with increasing patch size when habitat amount in the landscape is held constant. It could be that reproductive success increases with amount of habitat on the landscape, independent of habitat fragmentation per se. If this is true, the results of the simulation may be misleading.

These conclusions are based on the relatively small, but growing, number of empirical studies that separate the effects of habitat loss and fragmentation per se. So far these studies have been conducted on a limited set of taxa primarily within

North America. More research is needed to determine how general the conclusions are (Harrison & Bruna 1999).

IS "FRAGMENTATION" A USEFUL TERM? The term "fragmentation" is quickly losing its usefulness as more and more effects of human activities are incorporated into this single term. Some authors have even suggested that some species are "indicators of fragmentation" (e.g., Hager 1998, Niemelä 2001). The implication that fragmentation can be indicated by the decline of some species or species group suggests that the term is becoming a catchall for human-caused habitat changes that have negative effects on biodiversity. As questioned by Haila (2002), "Is a conceptually ambiguous and empirically multifaceted term fruitful as a generic description of human effects on landscapes?"

I suggest that the term "fragmentation" should be limited to the breaking apart of habitat. Habitat loss should be called habitat loss; it has important effects on biodiversity that are independent of any effects of habitat fragmentation per se. Habitat fragmentation should be reserved for changes in habitat configuration that result from the breaking apart of habitat, independent of habitat loss.

Implications for Biodiversity Conservation

Does our knowledge about fragmentation effects have general implications for conservation of biodiversity, particularly simultaneous conservation of multiple species? The fragmentation literature provides strong evidence that habitat loss has large, consistently negative effects on biodiversity. This implies that the most important question for biodiversity conservation is probably "How much habitat is enough?" Different species use different kinds of habitat, and different species require different amounts of habitat for persistence. Therefore, conservation of all species in a given region requires identifying which species in that region are most vulnerable to habitat loss (Fahrig 2001, With & King 1999) and estimating the minimum habitat required for persistence of each of these most vulnerable species. This determines the minimum habitat amounts for each kind of habitat in the region. In addition, many species require more than one kind of habitat within a life cycle. Therefore, landscape patterns that maintain the required habitat amounts, but intersperse the different habitat types as much as possible, should produce the largest positive biodiversity response (Law & Dickman 1998).

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