Fahrig L. In press. Forty years of bias in habitat fragmentation research. In: Kareiva P, Silliman B, Marvier M. *Effective conservation science: Data not dogma*. Oxford University Press, Oxford, UK.

Chapter 5. Forty years of bias in habitat fragmentation research

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Abstract

The idea that habitat fragmentation seriously threatens biodiversity is so widespread that it might be considered a "conservation biology principle". However, effects attributed to habitat fragmentation are usually confounded with effects of habitat loss. Recently, I reviewed the effects of habitat fragmentation *per se* (effects independent of habitat loss). 76% of significant effects of fragmentation *per se* were positive, and I found no situations where most effects were negative. Here I evaluate biases that may contribute to the common misrepresentation of fragmentation as a major threat to biodiversity. Most strikingly, I find that only 40% of authors who found *only* positive fragmentation effects actually discuss these in their abstracts. Thus, authors themselves reinforce the misrepresentation of the fragmentation literature. I speculate that this derives from authors' fears that their results could be incorrectly used to justify habitat destruction.

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Conservation biology textbooks discuss habitat fragmentation as a factor contributing to declining biodiversity and species extinction. Conservation organizations, government agencies, and popular writings commonly draw attention to the threat of habitat fragmentation. Commonly used conservation planning tools such as Marxan have options that allow planners to optimize conservation by minimizing fragmentation. Indices or metrics that quantify fragmentation at the landscape scale, such as those in FRAGSTATS, are commonly used to compare conservation plans, with the idea that lower fragmentation is always desirable, even when the financial costs may be high. In short, the idea that fragmentation is bad is deeply entrenched in conservation, and might even be considered a "conservation biology principle." Here I briefly trace the history of our thinking about fragmentation, and then consider the weight of evidence for fragmentation as a negative factor for biodiversity.

5.1 Origins and confounding of "habitat fragmentation" with "habitat loss"

The earliest references to habitat fragmentation identify it as a landscape-scale process associated with, but distinct from, habitat loss (Figure 5.1). Landscape ecologists generally attribute the concept of fragmentation to Curtis (1956), who mapped and measured the loss of forest cover from 1831 to 1950 in Cadiz Township, Wisconsin. Curtis (1956) was mainly concerned about the overall loss of forest in the township, but he also observed that, as forest loss proceeded, the remaining forest was distributed in a larger number of "fragments." The first use of the term "fragmentation" is in Moore's (1962) study of heathlands. Moore (1962) clearly differentiated between the concepts of habitat loss and habitat fragmentation, measuring them separately, as total heath area and number of heath patches, respectively (Moore 1962).

<insert Figure 5.1 here>

Curtis (1956) and Moore (1962) were able to think about habitat loss and fragmentation as independent processes only because they measured habitat amount and pattern over whole landscapes. But, with the advent of the theory of island biogeography (MacArthur and Wilson 1967) and its application to habitat patches (Levins 1970), the focus of "fragmentation" research shifted from effects of landscape-scale habitat loss and fragmentation to effects of the size and isolation of individual habitat patches on biodiversity (Haila 2002). Unfortunately, this shift caused a complete confounding of the consequences of habitat fragmentation with the consequences of habitat loss (Fahrig 2003). Patch isolation as a measure of fragmentation is particularly problematic because a patch becomes isolated precisely *because* the habitat around it is lost (Figure 7 in Fahrig 2003; Figure 6 in Fahrig 2013). Therefore, studies of patch size and isolation cannot distinguish between effects of habitat loss and habitat fragmentation. Although some have suggested that this distinction is unnecessary (Didham, Kapos, and Ewers 2012), decisions about how to remove habitat (or how to add it) are at the core of landscape management. Should land management policies and regulations aim to minimize the breaking apart (fragmentation) of habitat? This question can be answered only through studies that isolate the effects of habitat fragmentation from the effects of habitat loss (Figure 5.2).

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5.2 Positive and negative effects of fragmentation

Both Curtis (1956) and Moore (1962) appreciated that there could be both negative and positive effects of habitat fragmentation. For example, they noted that fragmentation reduced the spread of fire through the landscape, from which they inferred a positive effect on native biota. However, the possible positive effects of habitat fragmentation on biodiversity became

consistently overlooked when fragmentation became confounded with habitat loss (Lindenmayer and Fischer 2007). When habitat fragmentation is confounded with habitat loss, it is almost inevitable that studies will conclude that fragmentation has dire consequences for biodiversity. And indeed conservation ecologists commonly make this claim, e.g.: "Habitat fragmentation is a major cause of biodiversity erosion" (Tabarelli, Mantovani, and Peres 1999); "Habitat fragmentation is a leading cause of extinction" (Bruna and Oli 2005).

In contrast, landscape-scale studies that estimate the effects of habitat fragmentation independent of habitat amount effects (Figure 5.2) generally find that fragmentation effects are weak and positive, not strong and negative. In an earlier review (Fahrig 2003) I found 17 studies that estimated the effects of fragmentation independent of habitat amount. These contained 31 significant effects of fragmentation, 10 of which were negative and 21 positive, showing increasing abundance, occurrence, or species richness with increasing fragmentation *per se*. Although Fahrig (2003) has been highly cited, most authors continue to confound habitat loss and fragmentation (Hadley and Betts 2016). While there has been a notable shift in language such that many authors now refer to "habitat loss and fragmentation" rather than simply to "habitat fragmentation", most authors continue to assume large, negative fragmentation effects, e.g.: "Habitat loss and fragmentation are among the major drivers of population declines and extinction" (Cushman et al. 2016); " Habitat loss and fragmentation are major drivers of biodiversity loss" (Fleschutz et al. 2016).

There are now many more studies than there were in 2003, and an update of the evidence base is possible (Fahrig In press). As of 2015, I found 118 studies reporting 381 significant effects of habitat fragmentation independent of habitat amount; of these, 76% of fragmentation effects were positive. This trend towards positive effects was robust: irrespective of the

taxonomic group, the type of response variable, the conservation status of the species or species group, the study biome, the species movement range, or the median habitat cover. Note that a "positive" effect of fragmentation does not imply a value judgement. A particular positive effect can have a negative connotation if, for example, the study species is a pest or a non-native species. However, most significant effects of fragmentation *per se* were positive for specialist species and for threatened species (Fahrig In press). Therefore, the predominance of positive fragmentation effects cannot be written off as simply positive responses of weedy or common species.

5.3 Publication bias in fragmentation research

Clearly there is a large disconnect between the dominant view that habitat fragmentation has large negative effects on biodiversity and the actual literature, which shows that, when present, most significant effects of fragmentation independent of habitat loss are positive. One has to wonder whether there is also a publication bias, further distorting the evidence. To address this, I conducted additional comparisons using the set of 118 studies reviewed in Fahrig (In press) to ask if the actual proportion of positive fragmentation effects might be even higher than the 76% found in Fahrig (In press).

First, I asked whether there exists a publication bias in favour of negative over positive fragmentation effects. To evaluate this, I began by comparing effect-level fragmentation effects to study-level fragmentation effects. At the effect level, 76% of the 381 significant fragmentation effects were positive. In comparison, at the study level, 90% of the 93 single-direction studies found positive fragmentation effect(s). Note that single-direction studies are those studies that found either only positive or only negative effects of fragmentation *per se*. This difference

between 76% positive effects at the effect level and 90% positive effects at the study level might have occurred by chance. Or, it might have occurred because authors who find both negative and positive effects of fragmentation may have a tendency to omit or ignore some positive effects, on the assumption that positive effects are likely spurious. There would be no such omission for studies finding only positive effects, because without those effects the authors would have no significant effects to report!

A second way of examining bias is to consider how the framing of the studies might impact the frequency with which positive effects were reported. I hypothesized that studies described as investigations of "fragmentation" might be less likely to report positive fragmentation effects than studies described as investigations of habitat patchiness, landscape configuration, habitat heterogeneity, or SLOSS (Single Large Or Several Small). The reason for this is that the word "fragmentation" is often used to indicate a "threat" in conservation, whereas the other framings derive more from ecological theory. I identified author-defined fragmentation studies as those with "fragmentation" in the title, abstract, or author's key words. Of the 118 studies, 54 were labelled by authors as fragmentation studies. Within the 64 studies that were not defined as fragmentation studies, 86% of the 158 significant fragmentation effects were positive. However, within the studies defined as fragmentation investigations, only 70% of the 223 significant fragmentation effects were positive.

In summary, these two comparisons point to an under-reporting of positive effects of fragmentation *per se*, especially if the study is explicitly identified as a "fragmentation study" by the authors.

5.5 Confirmation bias: How has the misrepresentation of the fragmentation literature persisted for so long?

Even with a publication bias in favour of negative fragmentation effects, over three-quarters of the significant reported effects of fragmentation are positive. Nevertheless, the received wisdom within the conservation community remains that habitat fragmentation has negative effects on biodiversity. How has this misrepresentation of the literature persisted for over 40 years?

I evaluated two possible explanations. First, I asked whether readers are more likely to encounter papers showing negative results. In other words, are papers showing negative fragmentation results more likely to be published in more widely-read journals? To answer this I compared the impact factors of journals publishing positive and negative fragmentation effects. I made this comparison at the study level rather than the effect level, as publication decisions are, at least in theory, made on whole papers, not on individual effects within papers. The median and mean impact factors of the journals were similar among papers finding only positive significant fragmentation effects, papers finding only negative effects and papers finding both positive and negative effects (means: 5.4, 4.2, 4.7, and medians: 4.0, 4.2, 4.7, respectively). Thus, there does not seem to be an important association between journal quality and the direction of fragmentation effects.

Second I evaluated the possibility of confirmation bias (Loehle 1987; Nickerson 1998; Jeng 2006) in the fragmentation literature. I reasoned that many readers rely on the abstracts of papers for information about the main results of the papers. If abstracts portray a biased view of the direction of fragmentation effects found in papers, this could reinforce the incorrect assumption of predominant negative fragmentation effects.

To evaluate whether abstracts of fragmentation papers may be creating a biased view of the fragmentation literature, I compared the actual findings of the papers to the manner in which the authors portrayed those findings in the abstracts. Using information presented in the tables and figures of the papers (as in Fahrig In press), I categorized the 118 papers as finding only positive effects of fragmentation *per se*, finding only negative effects, and finding both directions of effect. Then I categorized the 118 Abstracts as: (i) authors present fragmentation effects as positive, (ii) authors present fragmentation effects as negative, (iii) authors present fragmentation effects as neutral or mixed, or (iv) authors ignore their findings of significant fragmentation effects. If there were no confirmation bias the Abstracts should reflect the results found in the tables and figures. That was not the case.

<insert Figure 5.3 here>

The confirmation bias revealed by contrasting the language of abstracts with the actual data was striking. Authors finding only negative effects of fragmentation *per se* were highly likely (7 of 9) to emphasize these negative effects in the abstract (Figure 5.3). In contrast, only 40% of studies finding *only* positive effects of fragmentation actually discussed these as positive effects in the abstracts. Instead they largely ignored the positive effects or gave neutral or mixed messages. And even when the authors did admit to finding positive fragmentation effects, they often used language aimed at down-playing their results. For example, eight authors warned against extrapolation of their positive fragmentation effects, while no authors warned against extrapolation of negative effects. In addition, positive fragmentation effects were often described in the abstracts as positive heterogeneity effects rather than positive fragmentation effects.

5.5 Fear of misinterpretation can hinder effective conservation

It is clear that significant effects of fragmentation independent of habitat loss are usually positive. It is also clear that there may be a bias against reporting these positive effects, and there is clearly a bias against discussing these results transparently. I can only guess at the reason for this neglect and denial of evidence, but I believe it derives from a conviction that positive fragmentation effects will be misunderstood and used as justification for habitat destruction. My evidence for this is admittedly anecdotal, based on my experiences with reviewers and seminar audiences over the past two decades. The fear that positive fragmentation effects will be used to justify habitat destruction is perverse and may even cause us to overlook occasional conservation opportunities. For example, the preponderance of positive significant fragmentation effects implies that small patches of habitat are often more important than the *same area* of habitat within a large patch. Patch-scale studies that confound habitat loss and fragmentation lead to the conclusion that small patches have low value. Landscape-scale studies showing neutral or positive effects of habitat fragmentation independent of habitat amount imply that all bits of habitat are valuable for conservation.

Although most *significant* effects of habitat fragmentation *per se* are positive, most tests of habitat fragmentation effects independent of habitat amount reveal weak, non-significant fragmentation effects (Fahrig 2003; Fahrig 2013; Fahrig In press). Therefore, the results here and in Fahrig (In press) do not imply that landscape management aimed at increasing habitat fragmentation *per se* should be a priority. However, they do imply that landscape management aimed at minimizing fragmentation *per se* is generally misguided. Landscape management for conservation should aim to increase the amount of habitat available to species of concern, irrespective of the spatial pattern of the habitat.

While the majority of documented effects of fragmentation *per se* are positive, there are some negative effects. This means that there are likely some particular situations where management aimed at reducing fragmentation is important. In Fahrig (In press) I attempted to find such situations by looking for categories of responses where the majority of significant effects are negative. I did not find any. However, I was limited by the studies available. For example, one might speculate that animals subject to poaching should show negative responses to fragmentation because habitat divided into many small pieces would provide easier access for poachers than the same area of habitat in larger blocks. This situation could apply to some iconic species of conservation concern such as white rhinos and African elephants, both of which suffer from poaching and human-wildlife conflicts. Thus, my findings do not imply that protecting large intact habitat is a foolish conservation goal. Rather, they suggest that, unless one has evidence to the contrary, the default assumption should not be that fragmentation *per se* is bad. Rather, the default assumption should be that loss of habitat, including the loss of small patches of habitat, is bad for biodiversity.

Finally, I note that in addition to habitat loss many other human alterations to landscapes, such as insertion of roads, are inappropriately equated to habitat fragmentation. In fact, Lindenmayer and Fisher (2007) point out that "habitat fragmentation" is often used to encompass all forms of human-caused landscape change, rendering it a "panchreston" or a term so general it becomes meaningless. I suggest that "habitat fragmentation" should be used exclusively to mean the breaking apart of habitat. This is necessary to avoid misdiagnosing the causes of biodiversity loss. If, as my review suggests, the significant effects of habitat fragmentation *per se* are generally positive then the negative impacts of various landscape alterations are likely not due to any association with fragmentation *per se*. For example, the negative effects of roads on wildlife

populations are almost certainly caused mainly by direct mortality and reduced habitat quality rather than by habitat fragmentation (Fahrig et al. 1995; Rytwinski and Fahrig 2012). It is time to think more clearly about fragmentation if we wish to manage landscapes to benefit biodiversity.

Forty years of authors' reluctance to acknowledge their findings of positive fragmentation effects has led to 40 years of misguided conservation advice and misinformed researchers and teachers. My current graduate students tell me that their undergraduate professors taught them that habitat fragmentation has strong negative effects on biodiversity. This idea permeates text books, government documents, and web sites including Wikipedia. As such it qualifies as a "zombie idea" (Fox 2011), an idea that should be dead but still roams the earth striking fear in the hearts of conservation ecologists and practitioners.

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Figure 5.1. Illustration of the difference between habitat loss and habitat fragmentation. Large squares delineate landscapes, and dark areas within landscapes represent habitat. Arrow from A to B: habitat loss can occur without habitat fragmentation. Arrows from A to C and from A to D: habitat loss and fragmentation can occur simultaneously. Arrow from B to C to D: The same loss of habitat can result in different levels of fragmentation. The effects of habitat fragmentation independent of habitat loss (fragmentation *per se* (Haila and Hanski 1984): B vs. C vs. D) are

relevant in the context of land management decisions for conservation. Different management decisions can lead to the same loss of habitat but very different levels of habitat fragmentation.

Figure 5.2. Illustration of a study design for estimating the independent effects of habitat fragmentation and habitat amount. The observational unit is the landscape (square outlines). Dark rectangles represent habitat within landscapes. Study landscapes are selected to minimize the correlation between habitat amount and habitat fragmentation. For a given level of habitat amount, habitat fragmentation is measured as, for example, the number of patches or the edge density in the landscape (see also Fahrig In press).

Figure 5.3. Authors of studies finding only positive significant effects of fragmentation *per se* are biased against reporting those effects as positive in the Abstract. X-axis: 'negative-only studies' = studies finding only negative significant fragmentation effects; 'positive-only studies' = studies finding only positive significant fragmentation effects; 'both-direction studies' = studies finding both positive and negative significant fragmentation effects. Y-axis: proportion of studies where the Abstract referred to the significant fragmentation effects as positive, negative, or neutral/both-direction, or where there was no mention of the significant fragmentation effect(s) ('ignore') in the Abstract. Numbers above the bars are the number of studies (N=118 studies).

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Figure 5.1

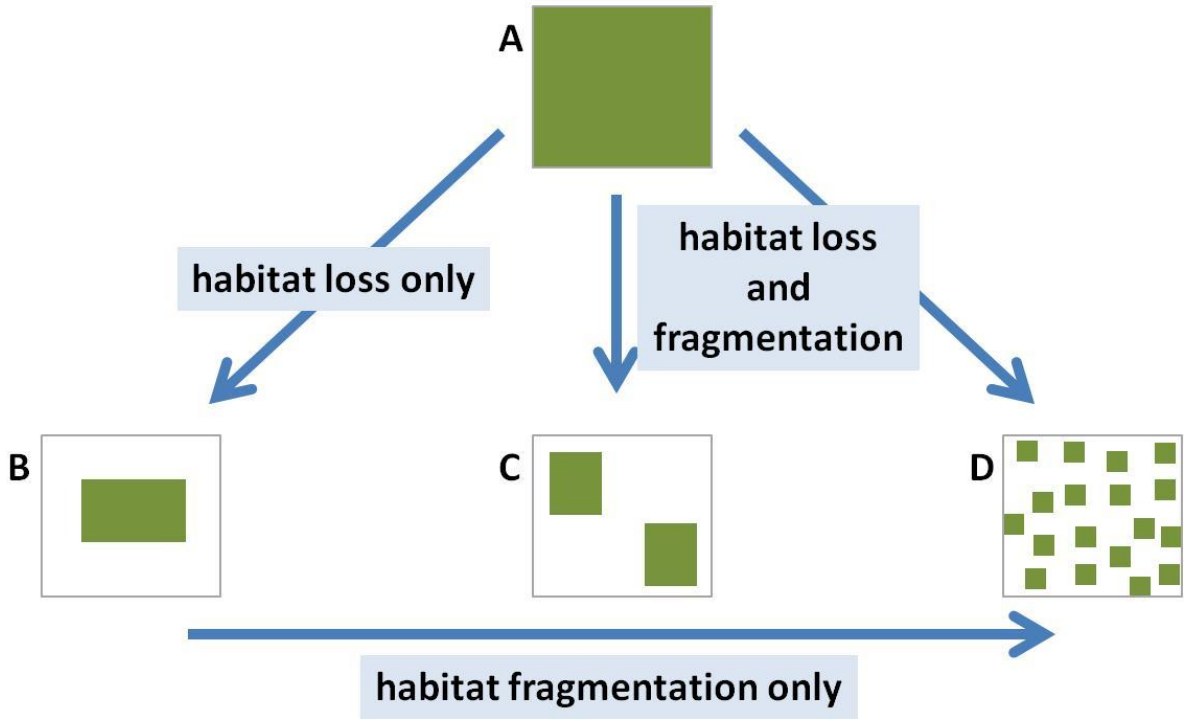

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Figure 5.2

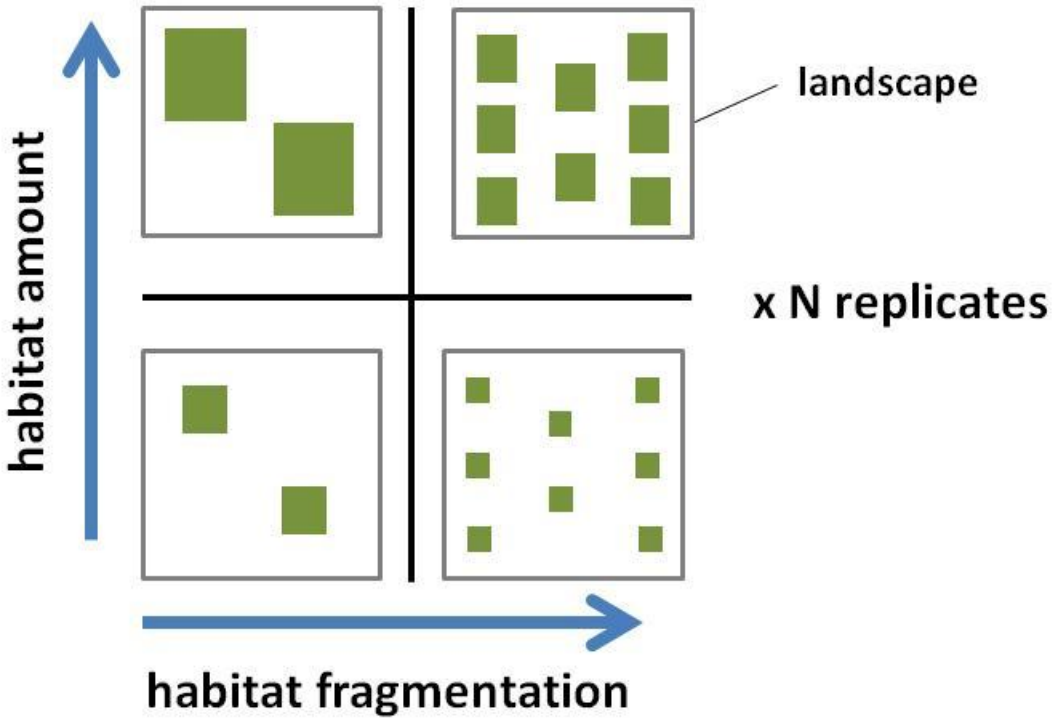

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Figure 5.3