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Habitat fragmentation: A long and tangled tale

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Abstract

In this essay: I provide a brief history of habitat fragmentation research; I describe why its "non-questions" ('Is habitat fragmentation a big problem for wildlife species?" and, "Are the effects of habitat fragmentation generally negative or positive?") are important to conservation; I outline my role in tackling these questions; I discuss reasons why the culture of habitat fragmentation research is largely incapable of accepting the answers; and I speculate on the future of habitat fragmentation research.

KEYWORDS
habitat fragmentation, habitat loss, landscape complementation, landscape heterogeneity, number of patches, patch size, SLOSS, spatial scale, species conservation, Ursula Franklin

1 | INTRODUCTION: URSULA FRANKLIN

In 2002, I attended a lecture by Ursula Franklin (Figure 1), a physicist, pacifist, Holocaust survivor and the recipient of nearly every honor that Canada has to offer. Franklin was 81 years old at the time. She began her lecture with a story about her early research career. In the 1960s, Franklin had been hired by a mining company to develop a new alloy of stainless copper. Her new alloy held up well in field exposure trials in Montreal, but after a year in Birmingham it "looked like it had chicken pox". When the mining company offered Franklin more money to develop a better alloy, she replied, "No way. You don't need better alloys; what you need is better air". Franklin's exhortation to the audience was to "treasure different eyes and different questions" (Franklin, 2014a). That lecture has stuck with me over the years. Each time I find an unexpected result, which happens quite often, I try to see things with different eyes.

Franklin also said that sometimes a field of research gets so stuck in one line of thought that it becomes almost impossible to ask certain questions. She called these "non-questions": "those things that seem so self-evident, so secure, so unchallenged as not to need to be coped with. When such issues are raised, those encapsulated in the establishment of a particular culture and thought process find it difficult even to acknowledge a question has been asked" (Franklin, 2014b).

For researchers encapsulated in the culture of conservation biology, the assertion that habitat fragmentation is bad for wildlife species seems self-evident and secure. Thus, questions such as, "Is habitat fragmentation a big problem for wildlife species?" or, "Are the effects of habitat fragmentation generally negative or positive?" seem frankly absurd. They are non-questions.

In this essay, I provide a history of habitat fragmentation research, I describe why these non-questions are important, I outline my role in tackling them, I discuss reasons why the fragmentation research culture remains largely incapable of changing, and I speculate on the future of habitat fragmentation research.

FIGURE 1 Ursula Franklin, 1920–2016: 'treasure different eyes and different questions'

2 | THE ORIGINS OF HABITAT FRAGMENTATION AND WHAT WENT WRONG

Most ecologists and conservation biologists believe the concept of habitat fragmentation started with MacArthur and Wilson's (1967) theory of island biogeography. But in fact the idea was introduced by Curtis (1956) and Moore (1962), independently. For Curtis and Moore, habitat fragmentation was exactly what it sounds like: the breaking apart of habitat. Habitat fragmentation increases the number of habitat patches, through the removal of habitat (Figure 2). Thus, both Curtis and Moore conceptualized habitat fragmentation as something apart from, although caused by, habitat loss. For example, in describing changes in heathland from 1811 to 1960 in Dorset, England, Moore observed that "the reduction of heath continued at approximately the same rate…; [its] fragmentation progressed much faster".

Importantly, in Curtis and Moore's concept of habitat fragmentation, habitat removal does not necessarily entail habitat fragmentation. For example, if a single large area of habitat is made smaller, this is not habitat fragmentation because the number of patches has not increased. Likewise, habitat fragmentation does not occur when a whole habitat patch is removed from an area, because the number of patches has not increased but rather decreased. Given that we humans are currently the main cause of habitat loss and that the same level of habitat loss can result in no fragmentation, extensive fragmentation or anything in between, it is important that we know whether removal of habitat in ways that increase its fragmentation actually matters to species.

Habitat fragmentation research began to go off the rails when Levins (1970) extrapolated the theory of island biogeography (MacArthur & Wilson, 1967) to habitat patches. From that time onwards, the measurement of habitat fragmentation shifted in scale from the landscape down to the patch. In the landscape view, a fragmentation effect is measured as a change in an ecological response across landscapes having different numbers of patches. In contrast, in the patch view, a fragmentation effect is measured as a change in the ecological response across patches differing in their size and/or isolation (Figure 3). Both approaches relate ecological responses across space to differences in the pattern of habitat. But the shift from landscape-based measures to patch-based measures created an inherent confounding of habitat fragmentation with habitat amount; a larger patch has more habitat, and a more isolated patch is more isolated exactly because there is less habitat nearby. It is therefore not logically possible to make inferences about the effects of habitat fragmentation, independent of habitat amount, by documenting effects of patch size and patch isolation (Fahrig, 2003). However, this is exactly what has been going on for the past 30+ years.

To give them credit, MacArthur and Wilson (1967) and Levins (1970) did not extrapolate from patch effects to fragmentation effects. Rather, this is attributed to Diamond (1975), who published a figure illustrating a series of "geometric principles" for the design of nature reserves. The figure shows two columns, with the "better" designs on the left side of the figure and the "worse" designs on the right side. Principle A shows a single large patch on the left side and a single small patch on the right side. So far, so good. But then Principle B shows a single patch on the left side and four smaller patches on the right side, where each of the four small patches is one-quarter the size of the patch on the left side. Principle B says that habitat fragmentation is bad for species conservation. Diamond (1975) provided no empirical evidence for Principle B; he deemed it correct "for essentially the reasons underlying Principle A." In other words, he justified Principle B based on an extrapolation from patch size effects to fragmentation (number of patches) effects, without any direct empirical support.

In fact, early empirical evidence suggested that this extrapolation was flawed. One of the first study types to evaluate fragmentation effects independent of habitat amount was the classic SLOSS (single large or several small) study. Here one has a list of species found in each of several different-sized habitat patches. The data are then analysed by combining the patches into subsets containing different numbers of patches, where each subset has the same total area. This creates a gradient in fragmentation while controlling for the amount of habitat. Reviews of SLOSS studies (Quinn & Harrison, 1988; Simberloff & Abele, 1982) showed no empirical support for the expected negative effect of fragmentation on species richness. In fact, habitat fragmentation had either no effect or a positive effect on species richness, exactly the opposite conclusion from that drawn by Diamond in his extrapolation from patches to landscapes. Accordingly, Simberloff and Abele (1982) concluded that

FIGURE 2 The loss and fragmentation of heath in Dorset, UK, from 1811 to 1960, as documented by Moore (1962). Habitat fragmentation was initially conceptualized as an increase in the number of patches as an outcome of habitat loss. However, habitat fragmentation is not equivalent to habitat loss, and the two can be measured independently. In the case of the Dorset County heaths, 'the reduction of heath continued at approximately the same rate…; [its] fragmentation progressed much faster' (Moore, 1962) [Colour figure can be viewed at wileyonlinelibrary.com]

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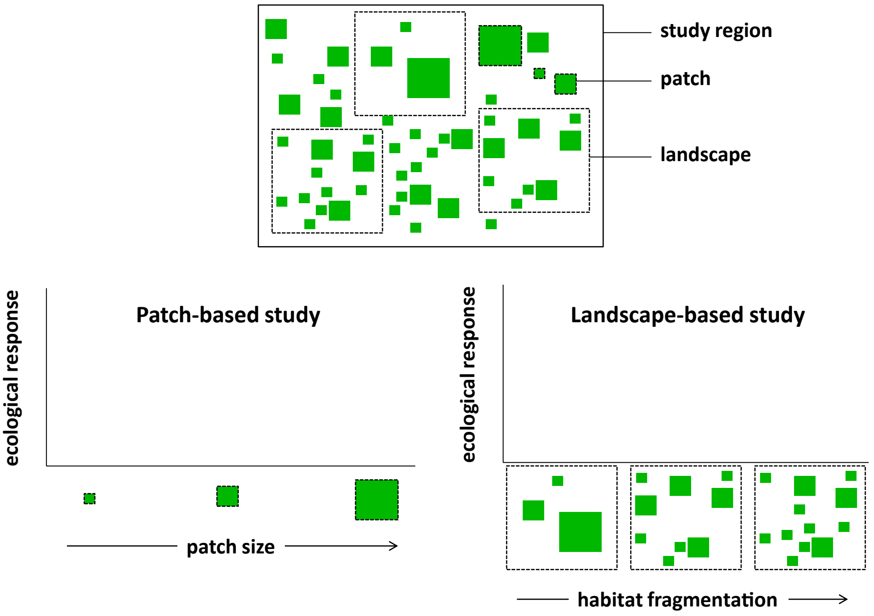

FIGURE 3 Illustration of patch-based and landscape-based studies. In both cases, an ecological response is measured across multiple sample locations. In a patch-based study, sample locations are patches, selected along gradients of patch size (shown here) and/or isolation. These gradients are not measures of habitat fragmentation per se because they are confounded with habitat amount; a larger patch has more habitat, and a more isolated patch is more isolated because there is less habitat surrounding it. In a landscape-based study, multiple landscapes are selected along a gradient of fragmentation (number of patches). These can be selected to avoid a correlation with the amount of habitat, allowing estimation of the effects of habitat fragmentation independent of the effects of habitat amount [Colour figure can be viewed at wileyonlinelibrary.com]

"[t]he application of island biogeography theory to conservation was a worthwhile experiment, but experience and further deliberation have shown that it is not very helpful". But hardly anyone listened to them.

The shift from landscape-based to patch-based evaluation of fragmentation effects washed over the field of habitat fragmentation research like a huge tidal wave. Only a small proportion of studies labelled "fragmentation" estimated fragmentation effects by comparing ecological responses across landscapes containing different numbers of patches, while controlling for habitat amount (reviewed by Fahrig, 2003, 2017a). The vast majority of studies continued and still continue to make the impossible extrapolation from patch size or isolation effects to fragmentation effects.

3 | WHY IT MATTERS: DISEMPOWERMENT OF SMALL-SCALE CONSERVATION EFFORTS

The mis-labelling of patch size effects as fragmentation effects has caused a critical error in the transfer of science to policy. This is because words have meanings. "To fragment" means "to break apart"; it does not mean "to shrink". When a researcher shows that species abundance or richness is lower in a small patch than in a large patch and then refers to that finding as a fragmentation effect, conservation agencies interpret the result to mean that a set of small, broken apart (fragmented) bits of habitat has much lower conservation value than a large, contiguous area, even though the researcher did not, in fact, show this.

This incorrect inference has driven conservation efforts worldwide. In 1980, the IUCN produced its World Conservation Strategy (IUCN, 1980), a very influential document used by countries around the world to guide their conservation efforts. The Strategy contains a reproduction of Diamond's (1975) figure described above, with the simple description: "preferable size and distribution patterns are shown in the left-hand column." In other words, the IUCN stated that habitat fragmentation is bad for conservation, based on a hypothetical and unsupported principle. Thus began, and continues, four decades of conservation policies around the world that favour contiguous habitat and assume that small bits of habitat are not worth conserving. For example, most small wetlands around the world have little or no protection (reviewed by Hill et al., 2018). The same is true for small forest patches: forestry policy in Ontario, Canada, recommends cutting patterns that "defragment" the remaining forest by removing small patches (OMNR, 2002); and in Mexico, landowners and communities can be paid to preserve forest, but only patches larger than 25 ha (Hernández-Ruedas et al., 2014).

The assumption that small bits of habitat have little value for conservation does a disservice to conservation, especially in the places where natural habitats are already scarce. These are exactly the places where the remaining habitat most needs protection (Bennett & Arcese, 2013). They are also often places that are close to people, and some of those people care deeply about them. A small wetland, stream or wood can be precious to a local community. Often, people are more willing to work for the conservation of such places than for more distant, larger ones. However, lack of support from conservation scientists can pull the rug out from under such local efforts.

As an early case in point, Willis (1984) commented: "one wonders sometimes if people protecting trees on their street or dozens of little city parks are not wasting efforts that could go to protect single large parks". As it turns out (see the following section), this and other such speculations are not based on data and are therefore detrimental to effective species conservation.

4 | UNEXPECTED AND UNWELCOME RESULTS: FRAGMENTATION EFFECTS ARE GENERALLY WEAK AND POSITIVE

Over the past 27 years, my understanding of fragmentation effects has changed completely. Initially, like nearly everyone else, I assumed that fragmentation has large negative effects on species abundance and distribution (Fahrig & Merriam, 1994). This was based on arguments such as those used by Diamond (1975), incorrectly extrapolating from patch size and isolation effects to fragmentation effects. Gradually, however, I came to realize that observed fragmentation effects on individual species and groups of species are very weak and, in fact, generally positive if present. Here, I describe how that transition took place.

Immediately after taking up my present faculty position in 1991, I bought a brand new Sparc II, an expensive and powerful computer for the time. My plan was to use a simulation model to ask, "Are there any situations where habitat fragmentation does *not* reduce population persistence?" I was steeped in the dogma that fragmentation is generally bad, but I reasoned that if I could find conditions in which fragmentation does not matter much, this would simplify conservation in those particular situations. So, I built the simulation model and began looking for combinations of life history, dispersal and landscape attributes where varying habitat fragmentation from low to high did not influence population persistence (Figure 4). Six months later, I still had not found a single situation where fragmentation *did* matter. I did not expect this at all. Eventually, I found a very small set of conditions (less than half of 1% of the entire parameter space) where fragmentation reduced population persistence. It took me 5 years and I had to try five journals to publish that result (Fahrig, 1998); nobody wanted to hear that habitat fragmentation might not matter much at all.

It was during those 5 years struggling to publish an unwelcome result that I came to realize that virtually all conservation biologists were confounding habitat fragmentation with habitat amount, by extrapolating patch size and isolation effects to habitat fragmentation effects. I realized this partly because, although my simulations showed almost no fragmentation effects, they did show large positive effects of habitat amount (Fahrig, 1997). And this was empirically supported in our study of forest birds (Trzcinski, Fahrig, & Merriam, 1999); all species showed positive responses to the amount of forest, most of them significant. In contrast, very few species showed significant responses to fragmentation.

I then began to search for other empirical studies that estimated the effects of habitat fragmentation independent of habitat amount

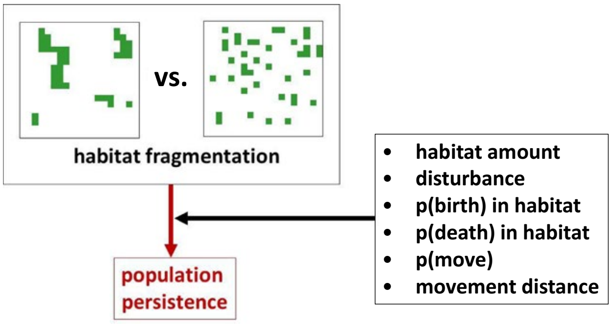

FIGURE 4 Simulation study design used by Fahrig (1998) to ask, 'Are there any situations where habitat fragmentation does *not* reduce population persistence?' Thousands of simulation runs using different levels of fragmentation, for each of thousands of combinations of other model parameters, revealed no detectable effects of habitat fragmentation on population persistence in 99.6% of the parameter space [Colour figure can be viewed at wileyonlinelibrary.com]

(fragmentation per se). This turned out to be a search for the proverbial needle in a haystack. Over 1,600 studies had used the term "habitat fragmentation" or "forest fragmentation", but by 2002 I had found only 12 studies that estimated effects of fragmentation independently of habitat amount. These confirmed that the effects of habitat fragmentation are generally weak to non-existent (Fahrig, 2003).

That paper (Fahrig, 2003) is very highly cited, and at the time I believed it to be a game changer. I had become convinced that habitat fragmentation per se is generally unimportant to species conservation, and so I shifted my research focus to other human impacts: habitat loss, roads and traffic, agricultural intensification and urbanization (e.g., Fahrig et al., 2015; Patenaude, Smith, & Fahrig, 2015; Rytwinski & Fahrig, 2011; Vance, Fahrig, & Flather, 2003). However, a decade or so later I realized that, despite its high citation rate, Fahrig (2003) was having no real impact (Hadley & Betts, 2016), in part owing to inappropriate citation practices (see Section 5.4). Nearly everyone was still inferring fragmentation effects from patch size and isolation effects. The habitat fragmentation literature had grown over the intervening years, but the tiny proportion of studies that estimated effects of fragmentation per se had remained nearly constant.

Nevertheless, in 2014 I began another search, but this time focused on the direction of fragmentation effects, when present. In Fahrig (2003) I had found 31 significant effects of fragmentation per se, from the 12 studies. About two-thirds of these effects were positive, with fragmentation increasing species occurrence, abundance or richness. Very few people had noticed this finding, even though it was stated in the abstract of Fahrig (2003). Therefore, I carried out a new search. The overall fragmentation literature had grown 10-fold in a dozen years. The bulk of fragmentation effects remained weak and non-significant. However, with the increase in the size of the literature, this time I found 381 significant effects of fragmentation per se, from 118 studies. Seventy-six per cent of these effects were positive (Fahrig, 2017a). Importantly, the majority of significant fragmentation effects were positive even for threatened or declining species and for rare or specialist groups of species.

5 | IF FRAGMENTATION EFFECTS ARE GENERALLY WEAK AND POSITIVE, WHY DOES EVERYONE THINK THEY'RE STRONG AND NEGATIVE?

Over the past nearly three decades, I have discussed these findings on habitat fragmentation with a lot of people: individuals, discussion groups, audiences, manuscript reviewers and journal editors. One thing that remains clear is that most people still do not want to believe that small patches of habitat have as much value for conservation as the same-sized area contained in large, contiguous habitat. This observation was recently confirmed in an informal poll by Fox (2018), who asked readers to rate, on a scale of one (definitely false) to five (definitely true), the statement: "Habitat fragmentation per se (as distinct from habitat loss) typically reduces biodiversity". About 60% of respondents chose four or five (true), 21% chose one or two (false), and 19% had a mixed opinion, choosing three. Here, I suggest probable reasons why the idea that habitat fragmentation is generally bad for conservation remains so persistent.

5.1 | Process versus pattern

First, it is not easy to think about habitat fragmentation as something separate from habitat loss. This is because we usually think about fragmentation as a process rather than as a pattern. When we think about how a given landscape changes over time, the processes of habitat loss and fragmentation are inextricably linked, leading to the intuitive conclusion that habitat fragmentation cannot have ecological effects that are independent of the effects of habitat loss (Didham, Kapos, & Ewers, 2012). Thus, if habitat loss reduces population abundance and species richness, we infer that habitat fragmentation must also reduce these ecological responses.

How then is it possible that many researchers have, in fact, measured the effects of fragmentation independently of the effects of habitat loss (reviewed by Fahrig, 2017a)? To understand this, we must consider that the processes of habitat loss and fragmentation can take different trajectories in different landscapes, resulting in different patterns in different landscapes (Figure 3). In some landscapes, the remaining habitat is fragmented into more bits than in other landscapes, even for the same amount of habitat removed. Likewise, in some landscapes more habitat is lost than in other landscapes, even for the same level of fragmentation. Therefore, when comparing over multiple landscapes, habitat loss and fragmentation are decoupled and can be studied as independent gradients.

5.2 | Emotion

Possibly the most important reason why ecologists believe that a large, contiguous habitat area is better than a number of small ones that sum to the same total area is simply that ecologists like large, contiguous natural areas. As my colleague Joe Bennett points out, many ecologists like to take long hikes or canoe trips. These experiences are not nearly so enjoyable or even possible if natural habitats occur in little bits rather than in large contiguous areas. I think Joe is onto something. Humans (and scientists are human) often give greater weight to personal experiences than to objective data. If our experience tells us that large, contiguous natural areas are important for us, then as ecologists we are likely to infer that they are also important for the rest of nature.

The emotional element underlying ecologists' conviction that fragmentation is bad is reflected in some researchers' responses to results that show the opposite. For example, Willis (1984) used violent imagery to refute Simberloff and Abele's SLOSS review, stating, "Simberloff [has] announced that *dismemberment* is good for animals" (my italics). The image of dismemberment was meant to evoke an emotional response in readers, and it revealed Willis's emotional attachment to the concept that habitat fragmentation is bad. It also revealed his inability to conceive of habitat fragmentation as something other than habitat loss.

5.3 | Imitation and caution

A more proximate reason that researchers continue to believe that fragmentation is bad for conservation is the tendency of many researchers uncritically to repeat the methods and especially the interpretations of previous researchers. This has reinforced the inappropriate measurement of fragmentation effects as patch size and isolation effects. Now that thousands of researchers have done so, it has become a sort of standard. It is tempting to think that this is only a problem of semantics, and to fix it we simply need to redefine fragmentation as patch size. But as mentioned above, this is not possible, because words have meanings. "Habitat fragmentation" evokes an image of habitat broken into pieces and leads to the unsupported conclusion that a group of small patches has lower value for conservation than a large patch of the same total area.

As discussed above, this conclusion does a disservice to conservation, although ironically, the opposite is often assumed. Several people have cautioned me that it is "dangerous" to state that habitat fragmentation is not harmful; they feel it gives carte blanche for habitat destruction. This assumption illustrates the ongoing confounding of habitat fragmentation and habitat amount effects. Habitat destruction has clear negative effects on species. But the data so far suggest that it does not matter much whether habitat destruction creates multiple small patches or few large patches. But some ecologists believe that we should propagate a myth rather than admit the data, in case the message is misinterpreted.

5.4 | Unsubstantiated hyperbolae and inappropriate citations

Another reason for widespread ignorance of the general lack of fragmentation effects is the use of unsubstantiated hyperbolae in the fragmentation literature. For example, many papers open with statements such as "Habitat fragmentation is a major driver of biodiversity loss" or, "Habitat fragmentation is a fundamental cause of population decline." Such statements are then echoed by conservation groups, for example, "Habitat fragmentation is a major problem across the earth" (https://treesforlife.org.uk/forest/human-impacts/habitat-fragmentation/), and this ultimately leads to conservation policies that aim to reduce habitat fragmentation and that ignore the conservation value of small patches.

Often, such statements are made without any supporting references, and when references are provided these do not, in fact, demonstrate the claim made. For example, MacArthur and Wilson's (1967) monograph is often cited as support, despite the fact that the theory of island biogeography is about individual islands and not about habitat fragmentation. Theoretical papers are often cited even though theory alone cannot provide evidence that fragmentation effects are widespread in nature; this requires empirical evidence. Some authors do cite relevant empirical evidence, but often incorrectly. For example, many authors cite Fahrig (2003) as providing evidence of widespread negative fragmentation effects, exactly the opposite of the findings of that paper. Worst, many authors simply cite a previous author who made the same unsubstantiated claim, and so on, effectively turning rumour into dogma. The damage to science caused by such inappropriate citation practices cannot be overstated.

5.5 | Valuing ideas over data, and a problem of pride

An additional reason that the fragmentation dogma persists is that many ecologists appear to give primacy to ideas over data. Two such ideas are: negative edge effects should produce negative fragmentation effects; and large area requirements should produce negative fragmentation effects. But there are also many longstanding ideas in ecology that predict positive effects of habitat fragmentation on species, including but not limited to the spreading of risk (den Boer, 1968), reduced competition (Levins & Culver, 1971) and stabilization of predator–prey interactions (Huffaker, 1958). In science, when different, reasonable-seeming ideas predict different patterns, the arbiter is the data. The data show that effects of fragmentation per se are generally weak and positive (Fahrig, 2017a). Thus, although both sets of ideas may be valid, the set that leads to positive fragmentation effects apparently has more influence on real ecological responses. Next steps in fragmentation research could be to understand why that is the case and to determine what situations lead to positive or negative fragmentation effects. This cannot happen as long as researchers continue to place their confidence in particular ideas rather than in the data.

Related to this is another reason for continued propagation of the fragmentation dogma: human pride. Once a researcher has claimed something repeatedly over several years, it can be difficult to admit to him/herself that something else is, instead, true (Kahneman, 2011). In fact, some researchers view such an about-face as a type of failure. For example, Hanski (2015) implied failure on my part when he pointed out that early on I had argued that habitat fragmentation has strong negative effects on species, whereas more recently I have been saying the opposite. But in my view, this is exactly how science is supposed to work. When the data do not support the prediction, we need to revise our thinking and change the hypothesis. This means we need to be willing to say that our old idea was wrong, irrespective of whether our career has been built on claiming it. As an aside, apparently Steven Hawking did this on a regular basis, and his career did not suffer for it (Minter, 2018).

5.6 | Publication biases

The misconception that habitat fragmentation effects are generally bad for conservation is reinforced through biases in the publication process. Elsewhere, I have documented a bias of *ca*. 15% against publishing findings of positive effects of fragmentation per se on ecological responses (Fahrig, 2017b). I also found a very strong confirmation bias. Authors finding positive responses to fragmentation per se are far less likely to include these findings in the abstracts of their papers than are authors who find negative responses to fragmentation (Fahrig, 2017b). And authors who do report their positive fragmentation effects in the abstract often include a caveat warning against extrapolation of their results. Such caveats do not accompany findings of negative fragmentation effects. Thus, there is a persistent confirmation bias in favour of negative fragmentation effects, not only among researchers who unconsciously measure fragmentation in ways that confound it with habitat amount, but also among researchers who understand the importance of estimating their independent effects. This bias, undetected by readers, reinforces the perception that habitat fragmentation is generally bad for species.

6 | THE WAY FORWARD

To begin, I note that even though the empirical results so far strongly suggest that the effects of habitat fragmentation per se are generally weak and positive, many taxa and regions are under-represented in studies to date. More empirical studies are needed that clearly separate the effects of habitat fragmentation from habitat loss and that evaluate interaction effects of habitat fragmentation with other landscape attributes. It is possible that the accumulation of such work might even change the overall picture.

In the meantime, the finding that habitat fragmentation effects are generally weak and positive (Fahrig, 2017a) opens new avenues for research and conservation. One avenue for research that I suspect will be particularly fruitful is the linkage between habitat fragmentation and landscape heterogeneity (Fahrig & Nuttle, 2005). This is because a more fragmented pattern of a given habitat type implies more intermingling of that habitat type with other habitat types. Such intermingling can increase accessibility among different resources that are needed by an organism over the course of its life. In other words, habitat fragmentation increases landscape complementation (Dunning, Danielson, & Pulliam, 1992), and landscape complementation increases the

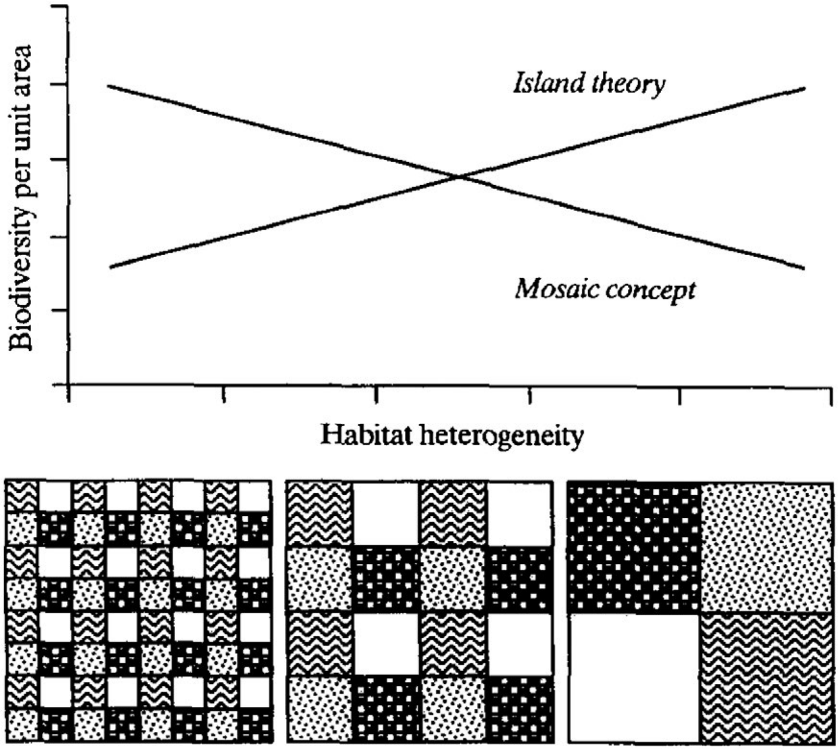

FIGURE 5 Reproduction of fig. 6 from Duelli (1997). Duelli argued that interspersion of small patches of different cover types in an agricultural landscape (the 'mosaic concept') leads to higher biodiversity than amalgamating each cover type into a single contiguous area (the 'island theory')

abundance and occurrence of species that use multiple resource types (e.g., Ethier & Fahrig, 2011; Pope, Fahrig, & Merriam, 2000). These include, for example, any species whose immature stage uses a different habitat type from that used by its adult stage (e.g., many amphibians and insects) and any species whose breeding and feeding habitats are different (e.g., many bats and birds).

The benefits of intermingling different habitat types to increase landscape complementation have been discussed and explored extensively in the context of agricultural systems (Fahrig et al., 2011). For example, Duelli (1997) introduced the "mosaic concept", arguing that farmlands with smaller patches have higher biodiversity (Figure 5). Daily, Ehrlich, and Sánchez-Azofeifa (2001) proposed a similar idea using the term "countryside biogeography." We have found strong empirical support for these ideas across a range of agricultural regions and taxa, finding higher wildlife abundance and diversity in farmlands with smaller crop fields, even after controlling for total crop cover (Collins & Fahrig, 2017; Fahrig et al., 2015; Hass et al., 2018; Monck-Whipp, Martin, Francis, & Fahrig, 2018).

Finally, the finding that habitat fragmentation effects are generally weak and positive (Fahrig, 2017a) also opens avenues for species conservation. In particular, local conservation efforts will obtain a good boost if researchers acknowledge the conservation value of all bits of habitat, not only the large, contiguous ones. This gives an individual or community the scientific underpinning for efforts to protect a small pond or woodlot or even a single tree. I have come to believe that the combination of such small-scale acts can benefit many species, as they accumulate over large areas. They can also be a vehicle for spreading societal support for conservation efforts from the green fringe to the mainstream. I think Ursula Franklin would agree. She called it the "earthworm theory," the idea that small acts prepare the ground for the emergence of a common good.

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BIOSKETCH

Lenore Fahrig studies how landscape structure affects species abundance, distribution and diversity.

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