Biological Conservation 232 (2019) 271–273

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Editorial

How does habitat fragmentation affect biodiversity? A controversial question at the core of conservation biology

Does habitat fragmentation harm biodiversity? For many years, most conservation biologists would say "yes." It seems intuitive that fragmentation divides habitats into smaller patches, which support fewer species (Haddad et al., 2015). Edge effects further erode the ability of small patches to support some species. This reasoning has been invoked, for example, when interpreting the results of iconic conservation experiments and studies, such as the large forest fragments experiment in the Brazilian Amazon (Laurance et al., 2011), and has been supported by meta-analyses of the findings of fragmentation experiments (Haddad et al., 2015). The negative effects of fragmentation are taught to students in introductory biology, ecology, and conservation courses and featured in textbooks.

A recent review by Fahrig (2017), however, reveals weaknesses in how we understand the relationship between habitat fragmentation and biodiversity, and the evidence on which we base our understanding. This review has sparked a lively exchange in the literature (e.g. Fletcher Jr et al., 2018; Fahrig et al., 2019), which we think is healthy and which we hope spurs more targeted research into this important question. This intense discussion is reminiscent of earlier controversies on whether biodiversity is declining, stable, or increasing at local scales (Vellend et al., 2013; Cardinale et al., 2018; Primack et al., 2018), and the values associated with the "new conservation science" (Kareiva and Marvier, 2012; Doak et al., 2013; Tallis and Lubchenco, 2014). The discussion also has similarities with the earlier "single large or several small" (SLOSS) debate, regarding the relative value of large reserves versus collections of small reserves that protect the same total area (Simberloff and Abele, 1976, 1982; Wilcox and Murphy, 1985). In all of these debates, many leading conservation biologists with considerable experience differed sharply on fundamental concepts and the interpretation of data in conservation biology.

Getting the answer right in this latest debate—whether fragmentation, independent of other drivers of environmental change, actually harms biodiversity—is important for many reasons, but especially because it will help us to prioritize the protection and management of lands in cases when there are choices to protect large intact habitats or fragmented habitats (with the same total amount of habitat). It will also help us better understand the effects of roads, urban development, and other fragmentation-inducing human actions on biodiversity, and assess how much of their effects are due to habitat fragmentation *per se*, or are caused by habitat loss and other factors, such as hunting and car strikes. Based on the prevailing view that fragmentation is bad for biodiversity, most conservation organizations advocate that people avoid actions that fragment habitats and prioritize the protection of large intact tracts over fragmented habitat. In some cases, policies allow managers to remove small forest fragments from landscapes managed for timber production based in part on concerns about the negative effects of fragmentation (OMNR, 2002; Fahrig, 2017).

Fahrig (2017) recently argued that the evidence base for these beliefs, recommendations, and actions is not as strong as many think, largely due to the confounding effects of scale, habitat amount, and fragmentation. In a separate essay, Fahrig (2018) described the history of research that led to the current understanding (or misunderstanding) regarding the effects of fragmentation on biodiversity. Processes that occur at local patch scales—the scale of the vast majority of fragmentation studies—may not be the dominant processes that affect biodiversity at larger landscape scales. Moreover, in practice, landscapes with more fragmentation tend to also have less habitat, making it difficult to separate the effects of fragmentation and habitat loss.

Landscape-scale studies that compare landscapes with large patches of habitat with landscapes with smaller patches of equal total area are rare, as are studies that use other methods to isolate the effects of fragmentation from habitat amount and other confounding factors. In two review articles, Fahrig (2003, 2017) reported that the majority of studies that examined the effects of fragmentation on biodiversity, separate from the effects of habitat loss, found no statistically significant effect of fragmentation. In the more recent of these reviews, Fahrig (2017) found that 70% of the responses to fragmentation documented in the literature were not statistically significant. Of the statistically significant responses, 76% were positive. That is, studies tended to find that increases in fragmentation resulted in increases in the values of the response variables. These response variables included measures such as the occurrence of target species, species richness, inter-patch movement, reproduction, and measures of water quality (Fahrig, 2017). Her findings were based on 118 studies that found 381 significant effects of fragmentation on biodiversity—the only ones that met her criteria (i.e. studies that empirically estimated fragmentation effects independent of habitat amount effects at landscape scales) out of the vast fragmentation literature (Fahrig, 2017). A practical implication of this study is that protecting many small to medium-sized habitat fragments within managed landscapes might be a more effective strategy for biodiversity conservation than protecting a few large protected areas (Wintle et al., 2018). The article dramatically drove home its main thesis by labeling the idea that habitat fragmentation is generally bad for biodiversity as a "zombie idea"—an idea that should be dead, but somehow remains alive.

According to Google Scholar, Fahrig (2017) has already been cited over 80 times, reflecting the very active research on fragmentation and the relevance of the paper to ecology and conservation biology. Some of the citing papers have been critical of the paper's conclusions. Fletcher Jr et al. (2018), in particular, published a sharp critique of the methods

https://doi.org/10.1016/j.biocon.2018.12.029
Received 14 December 2018; Accepted 21 December 2018
Available online 17 January 2019
0006-3207/ Published by Elsevier Ltd.

and conclusions of Fahrig (2017) in *Biological Conservation*. They pointed to the lack of other research making similar claims of positive effects of fragmentation on biodiversity and argued that the criteria for selecting literature and the vote-counting analytical method that Fahrig (2017) used may have biased the results. Fletcher Jr et al. (2018) also pointed out several recent meta-analysis papers, including Haddad et al. (2015) and Pfeifer et al. (2017), that document the negative effects of fragmentation, but were not mentioned in Fahrig (2017), presumably because they included studies that did not meet the criteria of her review. Fletcher Jr et al. (2018) also argue that our understanding that fragmentation harms biodiversity has withstood a long history of extensive study. More persuasively, they argue that in practice, it is useful to avoid fragmentation because fragmentation is almost always linked with habitat loss and some of the "positive" effects for biodiversity described by Fahrig (2017) may include increases in the abundance of disturbance-adapted and invasive species that can pose problems for species of conservation concern.

In response to Fletcher Jr et al. (2018), Fahrig et al. (2019) argue that too little research has considered the effects of fragmentation at broader spatial scales. We know a lot about processes at patch scales and how they can harm biodiversity, but have not adequately tested whether these processes are as important at broader scales, or whether they might be outweighed by other broad-scale effects, such as positive edge effects, reduced competition, increased habitat diversity, spreading of risk, or higher success at moving between patches (Fahrig et al., 2019). The ability of both Fletcher Jr et al. (2018) and Fahrig et al. (2019) to assemble large international teams of coauthors is a testament to the relevance of this debate for conservation biology, and to the quality and importance of the arguments being discussed.

We think this is a productive debate that will have positive outcomes for conservation science and practice. Science advances through periodic questioning of the evidence supporting core tenets. For example, conservation biologists have recently debated why we value biodiversity (e.g. Kareiva and Marvier, 2012; Doak et al., 2013), and whether biodiversity is declining at local scales (e.g. Vellend et al., 2013; Cardinale et al., 2018). Questioning such core beliefs can help us refine our understanding and improve approaches to answering questions. As we debate these questions, it is important that we consider the implications for the practice of conservation (Fletcher Jr et al., 2018). Some people might use findings of positive effects of fragmentation to justify development, logging, or road building in areas or in ways that really would reduce habitat quantity and quality and harm native biodiversity. Alternatively, if the effects of fragmentation are positive, or even negligible, we should not discount the conservation value of fragmented habitats. We believe that concern for how scientific debates might influence conservation practice is not reason to hamper the scientific discourse, but rather it is a reason that we should take care to communicate findings clearly and be transparent about the implications of those findings. Here we, as editors of *Biological Conservation*, want to highlight a few key points in the debate about the effects of fragmentation on biodiversity.

First, we emphasize that none of these findings question the species-area relationship—that the loss of habitat harms biodiversity. Habitat loss is the leading cause of species extinctions and the global loss of biodiversity. There is good evidence from empirical data and simulation studies that habitat amount influences biodiversity at all scales (e.g. Bender et al., 1998; Flather and Bevers, 2002; Fahrig, 2013). Fragmentation is often accompanied by loss of habitat, so in practice it is usually good to avoid actions that fragment landscapes, if only to avoid the loss of habitat that is associated with those actions.

Second, it is clear that we have too few studies of fragmentation at landscape scales. We need to know more about the processes taking place in landscapes with fragmented habitats, how the effects of fragmentation interact with other effects across scales (e.g. habitat loss, edge effects, and other stressors), and which species benefit and which are harmed by fragmentation at landscape scales (Didham et al., 2012). The responses of biodiversity to changes in habitat configuration are seldom linear (Ewers and Didham, 2006), and the definitions of thresholds and tipping points in population and community dynamics are scale-dependent (both grain and extent) and related to the dispersal capabilities of the study organisms.

Third, we need to better understand the role of the matrix as an influence on species persistence, (e.g. Fahrig, 2001; Kennedy et al., 2013), on dispersal (Prugh et al., 2008), and on the effects of fragmentation. For example, conversion of rainforest to pasture makes fire more likely on the edges of forest patches, creating a fire-fragmentation tipping point that is strongest when the proportion of edge in the landscape is highest (Cumming et al., 2012). Also, the effects of forest fragmentation might be greater if the matrix is soybean fields instead of secondary forests.

Fourth, some of the disagreement regarding the effects of fragmentation could be due to the confounding effects of temporal scale (Krauss et al., 2010), which Fahrig (2017) could not evaluate in her review (Fahrig et al., 2019). More habitat fragmentation might result in greater initial changes in some populations and later changes in others. We cannot assume that the initial rates of biodiversity change observed at different levels of fragmentation will remain over longer time periods. In theory, one might expect extinction debts to accumulate following fragmentation, creating a delay between observed habitat changes and biodiversity responses (Tilman et al., 1994; Kuussaari et al., 2009). Evidence from fragmentation experiments suggests that the impacts of configuration may become more, rather than less, important over time (Cook et al., 2005; Haddad et al., 2015); and over longer time periods, interaction effects between spatial and temporal processes can create outcomes ("ecological surprises") that existing theory does not predict (Debinski and Holt, 2000).

Fifth, terminology can add to the confusion in conservation discussions. For example, the terms "positive" and "negative" are frequently used to both describe statistical relationships between variables and whether effects benefit or harm particular species or meet conservation goals. Positive statistical relationships do not necessarily imply positive conservation outcomes, but when reading about the positive effects of fragmentation for biodiversity they can be easy to confuse. Fahrig (2017) uses "positive" to refer to statistical relationships between fragmentation and a variety of response variables. However, it is not always clear whether that positive relationship is "good" for conservation goals. For example, positive relationships between fragmentation and species richness may reflect increasing occurrences of species that are undesirable from a conservation perspective (e.g. nonnative or invasive species) and mask declines in species of conservation concern. Fahrig (2017) found positive relationships between fragmentation and biodiversity even when considering only rare and threatened species; but because Fahrig (2017) considered such a wide range of responses to fragmentation, ranging from species richness to movement to various measures of water quality to coexistence, it is not always obvious what a positive relationship means. This confusion could be potentially harmful in a discussion leading to real-world effects on the practice of conservation if it encourages managers to take actions based on misunderstandings of terminology.

In summary, understanding the effects of habitat fragmentation on biodiversity is of core importance for the science and practice of nature conservation. The conclusions of Fahrig (2017) may appear surprising to many of us, but they highlight the need to ensure we continue to investigate central questions in conservation biology and check the evidence supporting our understanding and decisions. Conservation biology is currently re-examining many of its central tenets (e.g. Kareiva and Marvier, 2012; Vellend et al., 2013; Dornelas et al., 2014; Primack et al., 2018). These provocative papers have contributed to much discussion and new research (e.g. Doak et al., 2013; Tallis and Lubchenco, 2014; Cardinale et al., 2018; Godet and Devictor, 2018; Hillebrand et al., 2018). We think this process is healthy for the field, especially if we can keep dialogues productive and respectful, and can communicate the implications clearly to managers and policy makers. This is an exciting time for conservation, and we appreciate the contributions of Fahrig (2017), Fletcher Jr et al. (2018), and Fahrig et al. (2019) to moving the field forward.

Acknowledgements

The findings and conclusions in this paper are those of the authors and do not necessarily represent the views of the US Department of the Interior or the US Government. We thank Lenore Fahrig, Nick Fisichelli, Rob Fletcher, and Kathryn Miller for comments on earlier versions of this paper.

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