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Perspective

# Is habitat fragmentation good for biodiversity?

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ABSTRACT

Habitat loss is a primary threat to biodiversity across the planet, yet contentious debate has ensued on the importance of habitat fragmentation 'per se' (i.e., altered spatial configuration of habitat for a given amount of habitat loss). Based on a review of landscape-scale investigations, Fahrig (2017; Ecological responses to habitat fragmentation per se. Annual Review of Ecology, Evolution, and Systematics 48:1-23) reports that biodiversity responses to habitat fragmentation 'per se' are more often positive rather than negative and concludes that the widespread belief in negative fragmentation effects is a 'zombie idea'. We show that Fahrig's conclusions are drawn from a narrow and potentially biased subset of available evidence, which ignore much of the observational, experimental and theoretical evidence for negative effects of altered habitat configuration. We therefore argue that Fahrig's conclusions should be interpreted cautiously as they could be misconstrued by policy makers and managers, and we provide six arguments why they should not be applied in conservation decision-making. Reconciling the scientific disagreement, and informing conservation more effectively, will require research that goes beyond statistical and correlative approaches. This includes a more prudent use of data and conceptual models that appropriately partition direct vs indirect influences of habitat loss and altered spatial configuration, and more clearly discriminate the mechanisms underpinning any changes. Incorporating these issues will deliver greater mechanistic understanding and more predictive power to address the conservation issues arising from habitat loss and fragmentation.

## 1. Introduction

Land-use change is impacting biodiversity across the planet (Newbold et al., 2015). There is no question that the extent and condition of native vegetation has declined precipitously in recent decades, such that most species now live in fragmented patches of degraded habitat, subject to rising threats from the surrounding anthropogenic matrix (Haddad et al., 2015; Pfeifer et al., 2017). Conservation threat assessments in fragmented landscapes repeatedly emphasize that there are multiple causal agents of biodiversity decline that operate in

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complex and often synergistic ways (e.g., Cote et al., 2016; Laurance and Useche, 2009).

It is surprising, then, that claims have been made that habitat loss, and not the configuration of remaining habitat, is sufficient to explain effects of land clearing on biodiversity loss, whereas the effects of habitat fragmentation (i.e., altered spatial configuration of habitat for a given amount of habitat loss) are often 'weak' or 'absent' (Fahrig, 2003, p. 508). The argument is that the effects of habitat loss are overwhelming and that the complexity of effects due to habitat fragmentation, such as declining patch areas, reductions in connectivity, or increasing edge effects, are not needed to explain patterns of biodiversity change in most landscapes. These claims have had a major impact in focusing efforts on understanding the effects of habitat loss relative to habitat fragmentation (see summary in Hadley and Betts, 2016), and it is clear that habitat loss has severe effects on biodiversity (e.g., Brooks et al., 2002; Schipper et al., 2008), as emphasized in Fahrig (2003). However, a large body of evidence runs counter to claims that habitat fragmentation effects are weak or absent. Not only have the pattern and process of habitat fragmentation been shown to have substantial and lasting effects on biodiversity (e.g., Haddad et al., 2015), but also the spatial configuration of habitat loss has been shown to influence how habitat loss effects extend into remaining habitat (Barlow et al., 2016; Pfeifer et al., 2017).

The viewpoint that fragmentation is not important has arisen primarily because statistical models that attempt to partition 'independent' effects of habitat loss from habitat fragmentation tend to show greater effects of habitat loss (Fahrig, 2003). These models would be valid if the processes of habitat loss and fragmentation were conceptually and empirically independent, and the resulting spatial patterns of habitat amount and configuration could be treated as statistically independent (Koper et al., 2007; Smith et al., 2009). However, others have argued that habitat loss and fragmentation are frequently linked, such that statistical independence of the resulting patterns must be explicitly tested rather than assumed (Didham et al., 2012). In fact, landscapes across most regions of the world exhibit very high collinearity between habitat amount and configuration (e.g., Cushman et al., 2008; Liu et al., 2016). Because of these real-world patterns, Ruffell et al. (2016) argue that the causal basis of this collinearity should be incorporated explicitly into statistical models, most logically by partitioning the direct vs indirect mechanisms by which habitat loss influences ecological responses via the mediating effects of altered habitat configuration.

Even though there is apparent disparity in philosophical and analytical perspectives, it is important to point out that both perspectives share a fundamental motivation for discriminating the effects of habitat amount and configuration: to allow more targeted and cost-effective use of scarce conservation resources on the factor(s) of greatest importance for biodiversity loss (Fahrig, 2003; Ruffell et al., 2016). After all, conservation strategies may well differ in their effectiveness when focusing on mitigating habitat loss versus changes in habitat configuration (Villard and Metzger, 2014). The 'loss versus fragmentation' question has consequently become a major focus of research within landscape ecology and conservation (Hadley and Betts, 2016).

Now, however, Fahrig (2017) has made a new claim in a review of studies that attempt to separate the effects of habitat fragmentation 'per se' from habitat loss. Fahrig concludes that the weight of evidence supports largely positive effects of habitat fragmentation 'per se' on biodiversity, and that the negative effect of habitat fragmentation on biodiversity is a "zombie idea" – a concept that is repeatedly refuted but yet somehow survives (Quiggen, 2010). Fahrig then casts a wide net for other so-called 'zombie' ideas: large patches contain more species than several small patches of similar combined area, edge effects are typically negative, habitat fragmentation reduces connectivity, habitat specialists have stronger negative responses to habitat fragmentation relative to generalists, and negative effects of habitat fragmentation are stronger in the tropics and at low levels of habitat amount (Table 1).

These assertions, if supported, would be remarkable for two reasons. First, they run counter to mainstream empirical and theoretical research on diverse components of habitat configuration effects (e.g., Haddad et al., 2015; Tilman and Lehman, 1997), suggesting the ecological research community has been mired in consensus and blind to the positive effects of habitat fragmentation. Second, they have major implications for the management of the world's fragmented ecosystems.

Given the importance of these issues, we re-evaluate Fahrig's assessment. First, we discuss why the review process utilized by Fahrig likely biased the findings and led to unwarranted conclusions. Second, we address the origins of the conflicting viewpoints, illustrating that there is ample empirical evidence and theory that laid the foundation for the idea of negative effects of habitat fragmentation that were not acknowledged in Fahrig (2017) (see Table 1 for a non-exhaustive list of summaries). Third, we discuss why these conclusions should not be applied to conservation in fragmented landscapes. We conclude by highlighting areas of consensus to help advance the conceptual understanding and applied relevance of habitat fragmentation effects.

## 2. The review and conclusions on fragmentation effects

Over the past two decades, several reviews and meta-analyses have suggested that the effects of different spatial components of habitat fragmentation, such as habitat edge or isolation, have undesirable or variable effects on ecological responses (Debinski and Holt, 2000; Ewers and Didham, 2006; Fletcher Jr. et al., 2016; Fletcher Jr. et al., 2007; Gilbert-Norton et al., 2010; Haddad et al., 2015; Pfeifer et al., 2017; Ries et al., 2004; Ries et al., 2017). Yet in some of these reviews there have not been attempts to discriminate the relative effects of altered spatial configuration (Fahrig's 'habitat fragmentation per se') from habitat loss.

Fahrig (2017) attempted to fill this important gap by conducting "a complete search for studies documenting statistically significant responses to habitat fragmentation" (p.6). Fahrig screened over 5000 articles, but just 118 of these (381 significant responses) met nine criteria used for inclusion. Notable criteria included the sole use of landscape-scale studies (where the landscape location and size were defined by the investigator), such that patch-scale studies were ignored. Habitat fragmentation was separated from habitat loss in one of three ways: through experimental manipulations of landscapes, through statistical analysis aimed at partialling out variation due to habitat amount, and through the use of what Fahrig refers to as 'SLOSS' designs (where variation in species richness between Single Large or Several Small patches is compared using species accumulation curves as a function of habitat amount in the landscape; Quinn and Harrison, 1988). Fahrig also included only those studies that could be summarized as habitat fragmentation having simple positive or negative effects, while nonlinear effects (e.g., hump-shaped relationships) and other complex effects (e.g., changes in community composition, scale-dependent effects) were not included. Inference was taken from what the authors of the original studies reported as 'significant' rather than using a formal meta-analysis, and all conclusions were based on responses reported rather than summaries of studies (i.e., the response variable in an individual study was the independent sampling unit). Results were only taken from tables and figures; the main text was ignored.

Fahrig found that 76% of the significant fragmentation effects used in the review were positive. In this context, 'positive effects' refer to situations where response variables (e.g., abundance, richness, movement success) increase with increasing values of habitat fragmentation metrics (e.g., number of patches, mean patch size, edge density and so on). Fahrig (2017, p. 18) then concluded that the widespread notion that habitat fragmentation generally has negative effects is a 'zombie idea' and several other conservation-focused conclusions (Table 1), such as the conservation value of small patches should not be lower than for an equivalent area within a large patch.