For: Perspective

Is habitat fragmentation good for biodiversity?

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Running header: Responses to habitat fragmentation

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.

Highlights

- Habitat loss and fragmentation have long been considered to have negative effects on biodiversity, yet recent review by Fahrig (2017) argues that in fact habitat fragmentation has largely positive effects on biodiversity.

- We highlight several key short-comings to the approach taken in Fahrig (2017) that limits conclusions regarding habitat fragmentation effects.

- Several sources of counter evidence not considered in Fahrig (2017) illustrate that negative effects of habitat fragmentation are common and that positive effects can be misleading or not of conservation importance.

- We provide six key reasons why the conclusions in Fahrig (2017) should not be used in conservation decision-making.

Keywords: Habitat amount, habitat loss, configuration, biodiversity

1. Introduction

36 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

38 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.

40 2017). Conservation threat assessments in fragmented landscapes repeatedly emphasize that there are multiple causal agents of biodiversity decline that operate in complex and often

42 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

44 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

46 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

48 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

50 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

52 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

54 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

56 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).

58   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

60   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

62   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

64   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

66   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,

68   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

70   by which habitat loss influences ecological responses via the mediating effects of altered habitat

configuration.

72   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

74   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

76   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

78   Metzger 2014). The 'loss versus fragmentation' question has consequently become a major focus

of research within landscape ecology and conservation (Hadley and Betts 2016).

80   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

82   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

84   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

86   several small patches of similar combined area, edge effects are typically negative, habitat

fragmentation reduces connectivity, habitat specialists have stronger negative responses to

88   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).

90   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

92   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

94   habitat fragmentation. Second, they have major implications for the management of the world's

fragmented ecosystems.

96   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

98   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

100   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

102   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

104   fragmentation effects.

106   **2. The review and conclusions on fragmentation effects**

Over the past two decades, several reviews and meta-analyses have suggested that the effects of

108   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

110   Didham 2006; Fletcher et al. 2016; Fletcher 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

112   have not been attempts to discriminate the relative effects of altered spatial configuration

(Fahrig's 'habitat fragmentation per se') from habitat loss.

114   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

116   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

118   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

120   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

122   (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

124   Harrison 1988). Fahrig also included only those studies that could be summarized as habitat

fragmentation having simple positive or negative effects, while non-linear effects (e.g., hump-

126   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

128   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

130   individual study was the independent sampling unit). Results were only taken from tables and

figures; the main text was ignored.

132   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.,

134   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)

136   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

138   the conservation value of small patches should not be lower than for an equivalent area within a

large patch.

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3. Are these conclusions warranted?

142   The results in Fahrig (2017) were surprising, yet the review's main conclusions come from a

narrow subset of literature and do not provide reliable evidence or sufficient context to dismiss

144   the negative effects of fragmentationas a 'zombie' idea. We focus on three key reasons why this

is the case: 1) the search terms and review criteria led to the omission of key literature; 2) the use

146   of a vote-counting approach likely biased the relative weighting of findings; and 3) there has

been no evidence of repeated, widespread refutation of negative habitat fragmentation effects in

148   the literature prior to Fahrig's review.

First, the search terms and review criteria used by Fahrig (2017) led to the omission of a

large body of relevant literature on habitat fragmentation effects. The only search term used to

explicitly capture habitat fragmentation was "fragmentation per se", rather than a more general

term such as "fragmentation" or a wild-card search on "fragment*". Based on a Web of Science

search on 18 April 2018, the number of hits using Fahrig's search phrase was 1,926, whereas the

same search with "fragmentation" yielded 141,148 hits, and "fragment*" yielded 525,066 hits.

Clearly, not all of these latter hits reflect investigations on habitat fragmentation, but focusing

just on "fragmentation per se", a phrase popularized by Fahrig (2003), greatly narrowed the

scope of articles considered and likely led to a biased selection of articles on fragmentation and

its effects. As a consequence, some rigorous, landscape-scale experiments that show striking

negative effects of fragmentation were missed (e.g., Gonzalez et al. 1998). Moreover, Fahrig

only considered landscape-scale investigations. Such investigations are useful but not sufficient

for interpreting habitat fragmentation effects, because there are many rigorous patch-scale

investigations that are highly relevant to the questions addressed. For instance, the Savannah

River Corridor Experiment provides a large-scale, long-term, patch-focused experiment in which

patches are either connected with corridors (less fragmented) or not (more fragmented), while

overall habitat amount is controlled (Haddad et al. 2017). Based on an analysis of 171 response

variables (from 41 articles) using the same vote counting approach as described in Fahrig (2017;

note this approach has limitations–see below), corridors had 4.7 times more positive effects than

negative effects, providing strong experimental evidence for negative effects of at least one

component of habitat fragmentation (Haddad et al. 2015). A meta-analysis of larger-scale

observational studies on corridors found very similar effects (Gilbert-Norton et al. 2010). None

of this work was included in the review (see Appendix in Fahrig 2017). The inclusion of this one

172   experiment would have nearly doubled the number of negative responses reported ($n = 91$),

potentially leading to different conclusions.

174   The criteria also favored particular study designs that provide relatively weak inference in

their ability to detect habitat fragmentation effects. Most of the investigations (72%; 273 of 381

176   responses) come from observational studies that used statistical techniques that first partition out

all variance associated with habitat loss, and then interpret habitat fragmentation as the residual

178   variance left in the model. However, the more fragmented the landscape, the larger the spatial

extent that is sampled from a previously contiguous landscape in observational studies (e.g., see

180   Figures 1, 2, 4 and 5 in Fahrig 2017), such that trends for a greater number of species with

increasing habitat fragmentation may be inherently confounded with the greater spatial extent of

182   the area sampled. Increasing spatial extent is problematic for comparisons because of Tobler's

First Law of Geography (Tobler 1970), which emphasizes that environmental conditions at close

184   locations are more similar than conditions farther away such that an increasing extent will no

doubt capture greater environmental heterogeneity irrespective of habitat loss and fragmentation

186   effects. Furthermore, these statistical techniques have been repeatedly shown to be limited in

their ability to discriminate habitat fragmentation effects and implicitly attribute most of the

188   intercorrelated variance to effects of habitat loss (Koper et al. 2007; Ruffell et al. 2016; Smith et

al. 2009). Such a bias in the statistical methods being used to test for 'independent' effects may

190   reflect the starting assumptions of the authors rather than processes impacting biodiversity.

A related limitation regarding the criteria for analysis and interpretation of data was the

192   use of SLOSS analyses, where species accumulation curves are compared when ranking patches

from small-to-large and from large-to-small patches. These curves are then typically summarized

194   with a 'saturation index' that reflects whether species number tends to be greater with habitat

subdivision for a given amount of habitat (Quinn and Harrison 1988). With this approach, Fahrig

196   found all 60 investigations had more rapid species accumulation when ranking from small-to-

large, a rather striking pattern that suggests a positive effect of fragmentation (Table 1).

198   However, this approach has been criticized for several fundamental reasons. First, it does not

provide a measure of 'significance' (Mac Nally and Lake 1999), despite Fahrig stating that the

200   review only included 'significant' responses. Second, and more importantly, this general

approach has been shown to lead to bias in favor of several small reserves in a variety of

202   situations (Ramsey 1989). For example, Mac Nally and Lake (1999) used mechanistic models

for species occurrence under scenarios of greater species accumulation in several small versus

204   single large patches. They illustrate how conclusions based on species accumulation curves, like

that used by Fahrig, tend to conclude positive effects of fragmentation even when mechanistic

206   models simulating preference of the community for larger patches fit empirical data better than

assuming preference for small patches. Mac Nally and Lake (1999) conclude, "it [small-to-large

208   vs large-to-small ranking] is a deeply flawed technique that provides spurious implications about

the nature of diversity generation in archipelagos and systems of patches…SL [Single-large]-

210   dominance probably is common and that it cannot be easily detected by using the simple

graphical methods of Quinn and Harrison".

212   Second, vote counting approaches have well-known limitations in drawing inference

across studies due to bias generation, low statistical power, and inability to provide relevant

214   information to appropriately summarize results from a set of studies (Gurevitch et al. 2018;

Koricheva et al. 2013). Fahrig's results were based on simple counts of 'statistically significant'

216   responses, rather than estimated effect sizes that acknowledge effect magnitude and sample size,

such that variation in study design is ignored. As a consequence, a study including few

218   landscapes but many measured response variables had more weight in the review than a study

with a more robust sampling design that included many landscapes but that focused on few

220   response variables. For example, two articles highlighted in Fahrig (2017) include Radford and

Bennett (2007), who reported 19 significant responses using 24 landscapes, and Smith et al.

222   (2011), who reported 3 significant responses with 2951 landscapes. In this case, Radford and

Bennett (2007) had the potential to provide 6× more weight in conclusions, despite having <1%

224   of the sample size of Smith et al. (2011).

Third, even if the search terms and inclusion criteria were valid, the finding of a mix of

226   positive and negative responses to habitat fragmentation does not satisfy the criterion for a

'zombie' idea – that the concept has been repeatedly refuted over time and yet lives on (Quiggen

228   2010). The conclusion drawn by Fahrig (2017) that positive fragmentation effects are more

common than negative effects represents a new claim; there have not been repeated prior

230   syntheses making similar claims sufficient to suggest that this is a 'zombie' idea. Even Fahrig's

compilation suggests 24% of responses are negative, illustrating that negative effects based on

232   the review criteria are not uncommon. Importantly, Fahrig does not provide any explicit data or

evidence to support several other related 'zombie' ideas (Table 1), such as those on edge effects

234   or connectivity, and these assertions are in stark contrast to the decades of empirical evidence on

these topics (Haddad et al. 2015; Ries et al. 2004). For example, Fahrig argues that the idea that

236   edge effects are typically negative is false, without providing any data to support this argument,

while Pfeifer et al. (2017) clearly illustrate from data collected across the planet that edge effects

238   are highly variable and that species of greatest conservation concern tend to be negatively

affected by habitat edge.

240   Finally, we emphasize that key responses to fragmentation can be missed in studies of

short duration, such as many of those reviewed in Fahrig (2017). Unlike habitat amount, habitat

242 loss and fragmentation explicitly capture temporal processes—habitat is lost and fragmented

over time. Yet, investigators often use space-for-time substitution, focusing on the pattern of

244 habitat to infer how loss and fragmentation impact biodiversity. Temporal effects from

environmental change can arise for a variety of reasons, such as time lags in impacts and

246 extinction debts (Hylander and Ehrlen 2013; Jackson and Sax 2010). For example, many of the

effects that arise from the creation of habitat edges require time to manifest, such as changes in

248 vegetation structure arising from tree mortality that frequently occurs near edges (Laurance et al.

2006). Long-term experiments and observational studies have shown delayed effects of

250 fragmentation on biodiversity over time (e.g., Haddad et al. 2015). Consequently, current habitat

amount and configuration, as emphasized in Fahrig (2017), may not be a good predictor of

252 ongoing effects of habitat loss and fragmentation. Temporal effects of fragmentation have a

strong theoretical and empirical basis and should be assessed when possible (Haila 2002).

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4. Origins of conflicting viewpoints

256 Fahrig (2017) argues several reasons why most other researchers erroneously believe that habitat

fragmentation has negative effects. One point Fahrig raises (p.2, 18) is that early conceptual

258 work relevant to habitat fragmentation confounded habitat patchiness with habitat amount (e.g.,

den Boer 1968; MacArthur and Wilson 1967). Decades of advances in metapopulation and

260 metacommunity theory show clearly that effects of habitat fragmentation can increase extinction

rates and decrease colonization rates, leading to reduced likelihood of population persistence and

262 lower diversity (e.g., Adler and Nuernberger 1994; Hill and Caswell 1999; Thompson et al.

2017; Tilman and Lehman 1997). In some cases, positive effects of habitat fragmentation at the

264   community level are predicted to arise from increases in beta-diversity driven by different

resource requirements of species and the fact that more fragmented habitats typically encompass

266   a greater spatial extent and environmental heterogeneity (Chisholm et al. 2018; Lasky and Keitt

2013; Rosch et al. 2015). Yet, even in such situations, models predict that this positive effect is

268   expected to reverse when habitat amount reaches low levels (Rybicki and Hanski 2013). Much of

this large body of theory emphasizes that habitat fragmentation is often predicted to have

270   negative effects on biodiversity, over and above declining habitat amount.

        A second point that Fahrig emphasizes is that there has been inappropriate extrapolation

272   of patch-scale patterns to landscape-scale inferences. Fahrig argues that fragmentation effects

must be tested at the landscape-scale. The rationale for dismissing patch-scale effects appears to

274   be three-fold. First, Fahrig (Fahrig 2003, 2017) argues that habitat fragmentation is a landscape-

scale phenomenon, and therefore patch-scale studies are not relevant. While habitat

276   fragmentation often (but not always) occurs at landscape scales, the mechanisms of biodiversity

responses can in fact occur from patch-scale changes, such as edge effects, changes in behavior

278   of organisms, or local species interactions (Banks-Leite et al. 2010; Fletcher 2006; Hadley et al.

2014). Consequently, patch-scale studies can provide critical insight to the mechanisms by which

280   habitat fragmentation influence biodiversity. Second, patch isolation metrics are frequently

correlated with habitat amount in the surrounding landscape, so Fahrig argues that the habitat

282   amount explanation takes primacy and therefore isolation effects are actually habitat amount

effects. Third, patch size effects are dismissed as habitat amount effects because "smaller patches

284   have less habitat than larger patches" (p.3). These arguments imply that any arbitrary spatial

scale can be used to define a 'landscape', allowing the primacy of habitat amount in the

286 'landscape' to be invoked over patch-scale effects. Both of these lines of reasoning are

problematic for paring down either the effects of habitat loss or spatial configuration to their root

288 mechanistic causes (Didham et al. 2012), and ignore the fact that patch metrics are not only

correlated with habitat amount but are also highly cross-correlated with aspects of habitat spatial

290 configuration (Cushman et al. 2008).

Arguably, since Fahrig (2013, 2017) argues 'habitat amount' is a primary predictor of

292 biodiversity change in response to land clearing and habitat fragmentation effects are rare, then it

should be possible to infer that the underlying mechanism(s) relate directly to habitat availability

294 in the landscape, and not to potential dispersal limitation of organisms, or their ability to survive

in a local patch once they arrive. To explain the habitat amount effect, Fahrig (2013) focuses

296 entirely on a neutral 'sample area effect' (Haddad et al. 2017). Yet at their core, isolation effects

are relevant to habitat fragmentation through the disruption of successful dispersal. Both habitat

298 configuration and spatial characteristics of the matrix have been shown repeatedly to be critical

for movement, dispersal, and gene flow (e.g., Cushman et al. 2012; Fletcher et al. 2014;

300 Gonzalez et al. 1998; Ricketts 2001), such that empirical research on movement does not

mechanistically support the idea that isolation effects are solely habitat amount effects. Even if

302 habitat amount can statistically explain responses without explicit inclusion of measures of

fragmentation, such conclusions are misleading if a key part of the true underlying mechanistic

304 pathway for their effects is via augmenting connectivity and dispersal. In addition, simply

reducing patch-size effects to habitat amount effects is inconsistent with decades of research on

306 edge and patch-size effects, where there is incontestable evidence that habitat suitability can vary

spatially within patches in relation to configuration variables, such as distance from edge. Edge

308 effects can be positive or negative (Pfeifer et al. 2017), and can drive emergent patch-level

outcomes (Banks-Leite et al. 2010; Ewers et al. 2007), particularly where multiple edges interact

310   in increasingly small fragments (Fletcher 2005). There can also be complex and unpredictable

ecological outcomes that emerge in small isolated fragments through random trajectories of

312   change in species interaction networks, and it is challenging to see how 'habitat amount in the

landscape' could be mechanistically linked to these kinds of effects. In the absence of alternative

314   mechanisms suggested by Fahrig (2017), we argue that mechanistic understanding requires

acknowledging that both habitat amount and configuration operate across spatial scales from

316   local- to patch- to landscape-scales (Didham et al. 2012; Pardini et al. 2010).

5. Implications for management and conservation in the real world

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We believe that the overall goal for most science on habitat fragmentation is to gain a deeper

320   mechanistic understanding of why habitat configuration effects occur, how they might mediate

the relationship between habitat loss and biodiversity decline, and ways to mitigate the impacts

322   of habitat loss and related land-use change (e.g., via conservation corridors). Ignoring or

diminishing the importance of spatial configuration effects as a core part of that mechanistic

324   understanding comes with significant risks for landscape management and conservation. Here we

briefly outline six reasons why Fahrig's (2017) conclusions on the effects of habitat

326   fragmentation should not be used to guide management.

First, Fahrig argues that conservation biologists have falsely emphasized habitat

328   fragmentation over habitat loss as the most significant cause of biodiversity decline, when in fact

only habitat loss has substantive effects. However, this conclusion only arises because of the

330   implicit assumption that multiple predictors can be treated as 'independent' for conservation,

when in fact changes in habitat amount and configuration through time are almost always

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332   collinear in real-world landscapes where conservation decision-makers are charged with making

real-world choices (Didham et al. 2012; Villard and Metzger 2014).

334   Second, Fahrig emphasizes that more fragmented habitats have proportionally more edge,

and that conclusions for these largely positive effects of habitat fragmentation were often

336   attributed to edge effects. Edges can indeed have positive or negative effects on species (Pfeifer

et al. 2017; Ries et al. 2004); however, positive edge effects most commonly have several

338   practical (and frequently negative) consequences for conservation and management. Species

associated with edges are often generalists or invasive (Banks-Leite et al. 2010; Pfeifer et al.

340   2017). Increased edge in fragmented landscapes can also increase risk from a suite of negative

pressures, such as livestock incursion, wildfire, logging, and human-wildlife conflict (e.g.,

342   Echeverria et al. 2007; Goswami et al. 2014), and it can also facilitate further habitat loss

(Laurance et al. 2009).

344   Third, approximately one quarter (24.4%) of Fahrig's results focused on species richness,

with little consideration of species identity. Species richness is useful for summarizing ecological

346   patterns but can mask compositional changes that are highly relevant to conservation. For

example, Fahrig (2017) included results from Blake and Karr (1984) as a positive response to

348   fragmentation, where more bird species were found in several small relative to single large

fragments. However, Blake and Karr (1984) emphasized that richness of two groups of major

350   conservation concern (long-distance migrants and forest interior species) decreased with

fragmentation, two negative responses that were not included in Fahrig's summary (see also

352   Alstad et al. 2016; Banks-Leite et al. 2012).

Fourth, Fahrig suggests that the review conclusions may contribute to the land sharing vs

354   sparing debate in applied landscape management (Fischer et al. 2014), by supporting

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conservation of dispersed networks of several small fragments (assumed to reflect land-sharing)

356   over a single large block of forest (assumed to reflect land-sparing). This conclusion is

unwarranted, given that the land sharing/sparing debate emphasizes production yields and socio-

358   ecological interactions as integral components to these issues in the real world (Fischer et al.

2014), neither of which are included when considering habitat loss and fragmentation effects

360   alone.

        Fifth, the review had a narrow focus on a habitat vs non-habitat dichotomy, assuming the

362   functionally-relevant habitat was appropriately measured and of comparatively similar quality

across the landscape for the responses considered. For many species, the non-habitat matrix may

364   also provide resources and generic habitat delineation can obscure variation in habitat

fragmentation effects (Betts et al. 2014). Landscapes can thus be classified as more fragmented

366   even though they may actually be less fragmented from a species' perspective. For instance,

many positive edge responses can be explained by putative 'non-habitat' actually providing

368   resources to species (Ries et al. 2004). As such, positive effects of habitat fragmentation are

expected for species that are not specialized in the given habitat type—species that are often not

370   of conservation concern.

        Sixth, and perhaps most importantly for decision-makers, Fahrig (2017) tends to

372   erroneously conflate statistical and ecological conclusions. Throughout most of the review,

Fahrig focuses on the statistical direction of response being either positive or negative. This

374   should not be confused with a 'positive outcome' in a qualitative sense from a conservation

perspective, where some positive effects, such as an increase in the number of exotic species

376   with habitat fragmentation, would be considered a 'negative outcome' for conservation. Given

Fahrig does briefly acknowledge this issue, it is alarming that the review concludes that (p.19),

378 "there is no justification for assigning lower conservation value to small patches than to an

equivalent area within a large patch—instead, it implies just the opposite".

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6. Conclusions and moving forward

382 We agree with Fahrig that habitat loss is well known to have large negative effects on

biodiversity, and that small fragments can have conservation value for biodiversity and

384 ecosystem services (e.g., Mitchell et al. 2014). We also agree that the term 'habitat

fragmentation' is often used interchangeably as both a loose catch-phrase to refer to the overall

386 process of changing amount and configuration of habitat through time, and as a more refined

characterization of altered spatial configuration in the landscape (as we have attempted to do

388 here). Semantic issues aside, we agree that habitat fragmentation (in the broad or strict sense) can

sometimes lead to statistical increases in ecological response variables, particularly in multi-

390 species responses where different members of the community may be using different resources

across heterogeneous landscapes, leading to greater beta-diversity in more fragmented

392 landscapes. None of these factors are in dispute, nor have they been in dispute for many years

prior to Fahrig's review (e.g., see syntheses by Debinski and Holt 2000; Ewers and Didham

394 2006; Tscharntke et al. 2012).

Fahrig's review provides insufficient evidence for the conclusion that habitat

396 fragmentation effects are largely positive. Such a conclusion is only possible with an

unreasonable set of assumptions that narrows the evidence base. We caution that fueling

398 polarized perspectives with invective can stymie research growth, and could have unintended

and unjustified ramifications for conservation and management. The take-home message should

400 be a call to all scientists working at the forefront of issues on habitat loss and fragmentation to

more clearly discriminate the mechanisms via which they impact biodiversity and to consider

402   mechanistic modeling in addition to the statistical and correlative approaches that have fueled the

present disagreements. Understanding why and when these habitat fragmentation effects occur,

404   how they interact with other human-induced changes, and under what situations fragmentation

effects will be positive or negative will be essential for conserving biodiversity.

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Competing Interests

414   The authors declare no competing interests.

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Table 1. Major conclusions regarding 'zombie ideas' in Fahrig (2017), the evidence provided, and a non-exhaustive summary of counter evidence not considered in the review (focusing on meta-analyses, systematic reviews, and prior rebuttals).

Fahrig's 'zombie ideas'	Fahrig's evidence	Counter evidence not considered
Habitat fragmentation has widespread negative effects	76% of 'significant' responses to habitat fragmentation from landscape studies were positive.	Haddad et al. (2015) provide a meta-analysis on long-term, patch-focused experiments for area, edge, and isolation, with edge and isolation effects controlling for habitat area and habitat heterogeneity. Effects are consistently negative (80% isolation; 82% edge) and increasingly so over time, emphasizing limitations of space-for-time substitution.
Small number of large patches contain more species than large number of small patches	SLOSS* analysis on species richness: all 60 'significant' responses were positive (higher richness in many small patches).	Ramsey (1989) and Mac Nally and Lake (1999) argue that this type of SLOSS analysis is flawed, yielding biased results (in the direction shown by Fahrig), and that it does not provide a means of assessing 'significance'.
Edge effects are generally negative	**No data.** Authors of papers suggest that positive edge effects may drive positive responses to habitat fragmentation.	Ries et al. (2004), Fletcher et al. (2007), and Pfeifer et al. (2017) show variable edge effects. Pfeifer et al. (2017) meta-analysis shows that species with negative edge effects are 3.7 times more likely to be of conservation concern (IUCN threatened), while positive responses include pest/invasive species.
Habitat fragmentation reduces connectivity	**No data.** Authors of papers suggest that greater functional connectivity may drive positive responses to habitat fragmentation.	Meta-analysis on corridor effects shows positive effect of corridors (less fragmented), with 50% increase in movement ($n = 28$ studies) along corridors when controlling for habitat area (Gilbert-Norton et al. 2010).
Habitat specialists show greater negative responses	**No data.** Pooled 'endangered/threatened/specialist': 29 of 30 significant responses to habitat fragmentation were positive.	Pfeifer et al. (2017) meta-analysis shows that negative edge effects are typically observed for specialist species, positive for generalist species.
Negative habitat fragmentation responses are stronger at low levels of habitat amount	Proportion of negative responses to habitat fragmentation were similar when comparing <0.2 (31%) habitat to >0.2 (33%).	Theory emphasizes that specific thresholds are contingent on assumptions regarding movement (e.g., patch-delineation rules; Swift and Hannon 2010)(Hanski 2015; With and King 2001). Fahrig's results do not support this claim when considered a larger threshold : < 0.5 (33.3% negative) versus > 0.5 (8% negative).

| Negative fragmentation responses are stronger in the tropics | Proportion positive responses similar for 'subtropical/tropical' versus other. | Lindell et al. (2007) meta-analysis shows that tropical birds are more likely to avoid edges than temperate birds. |

SLOSS analyses based on species accumulation curves. Only the lack of crossing accumulation curves was taken as 'significant', although Mac Nally and Lake (1999) show this conclusion provides no statistical inference on 'significance'.