



Perspective

Is habitat fragmentation good for biodiversity?



Robert J. Fletcher Jr^{a,*}, Raphael K. Didham^{b,c}, Cristina Banks-Leite^d, Jos Barlow^e, Robert M. Ewers^d, James Rosindell^d, Robert D. Holt^f, Andrew Gonzalez^g, Renata Pardini^h, Ellen I. Damschenⁱ, Felipe P.L. Melo^j, Leslie Ries^k, Jayme A. Prevedello^l, Teja Tscharntke^m, William F. Lauranceⁿ, Thomas Lovejoy^o, Nick M. Haddad^p

^a Department of Wildlife Ecology and Conservation, PO Box 110430, 110 Newins-Ziegler Hall, University of Florida, Gainesville, FL 32611-0430, USA

^b School of Biological Sciences, The University of Western Australia, 35 Stirling Highway, Crawley, WA 6009, Australia

^c CSIRO Land and Water, Centre for Environment and Life Sciences, 147 Underwood Ave, Floreat, WA 6014, Australia

^d Department of Life Sciences, Imperial College London, Silwood Park Campus, Buckhurst Road, Ascot, Berkshire SL5 7PY, UK

^e Lancaster Environment Centre, Lancaster University, LA1 4YQ, UK

^f Department of Biology, University of Florida, Gainesville, FL 32611-0430, USA

^g Department of Biology, McGill University, Montreal H3A 1B1, QC, Canada

^h Departamento de Zoologia, Instituto de Biociências, Universidade de São Paulo, Rua do Matão, travessa 14, 101, CEP 05508-090 São Paulo, SP, Brazil

ⁱ Department of Zoology, University of Wisconsin, Madison, WI, USA

^j Departamento do Botânica, Universidade Federal de Pernambuco, Rua Prof. Moraes Rego S/N, 50670-901, Recife, PE, Brazil

^k Department of Biology, Georgetown University, USA

^l Department of Ecology, Rio de Janeiro State University, 20550-013 Rio de Janeiro, Brazil

^m Agroecology, Department of Crop Sciences, University of Göttingen, Göttingen, Germany

ⁿ Centre for Tropical Environmental and Sustainability Science, and College of Science and Engineering, James Cook University, Cairns, Queensland 4878, Australia

^o Department of Environmental Science and Policy, George Mason University, USA

^p Kellogg Biological Station, Department of Integrative Biology, Michigan State University, 3700 E Gull Lake Dr, Hickory Corners, MI 49060, USA

ARTICLE INFO

ABSTRACT

Keywords:

Habitat amount
Habitat loss
Configuration
Biodiversity

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

* Corresponding author.

E-mail address: robert.fletcher@ufl.edu (R.J. Fletcher).

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 non-linear 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.

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, 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. Ramsey (1989) and Mac Nally and Lake (1999) argue that this type of analysis is flawed, yielding biased results (in the direction shown by Fahrig), and that it does not provide a means of assessing ‘significance’. Ries et al. (2004) , Fletcher Jr. 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.
Small number of large patches contain more species than large number of small patches	SLOSS ^a analysis on species richness: all 60 ‘significant’ responses were positive (higher richness in many small patches).	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). Pfeifer et al. (2017) meta-analysis shows that negative edge effects are typically observed for specialist species, positive for generalist species.
Edge effects are generally negative	No data. Authors of papers suggest that positive edge effects may drive positive responses to habitat fragmentation.	
Habitat fragmentation reduces connectivity	No data. Authors of papers suggest that greater functional connectivity may drive positive responses to habitat fragmentation.	
Habitat specialists show greater negative responses	No data. Pooled ‘endangered/threatened/specialist’: 29 of 30 significant responses to habitat fragmentation were positive.	
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 (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.

^a 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’.

3. Are these conclusions warranted?

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 the negative effects of fragmentation as 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 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 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 1926, 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 the generality of 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 experiment would have nearly doubled the number of negative responses reported ($n = 91$), potentially leading to different conclusions.

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 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 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 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 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 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 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 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 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 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 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 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). 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 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 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 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 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 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]-dominance probably is common and that it cannot be easily detected by using the simple graphical methods of Quinn and Harrison”.

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 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’ 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 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 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. (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% 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 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, 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 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 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 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 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 are highly variable and that species of greatest conservation concern tend to be negatively affected by habitat edge.

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 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 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 extinction debts (Hylander and Ehren, 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 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 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 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).

4. Origins of conflicting viewpoints

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 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 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 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 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 a greater spatial extent and environmental heterogeneity of the previously contiguous landscape (Chisholm et al., 2018; Lasky and Keitt, 2013; Rosch et al., 2015). Yet, even in such situations, models predict that this positive effect is 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 negative effects on biodiversity, over and above declining habitat amount.

A second point that Fahrig emphasizes is that there has been inappropriate extrapolation 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 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 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 of organisms, or local species interactions (Banks-Leite et al., 2010; Fletcher Jr., 2006; Hadley et al., 2014). Consequently, patch-scale studies can provide critical insight to the mechanisms by which habitat fragmentation influence biodiversity. Second, patch isolation metrics are frequently correlated with habitat amount in the surrounding landscape, so Fahrig argues that the habitat 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 have less habitat than larger patches” (p.3). These arguments imply that any spatial scale can be used to define a ‘landscape’, allowing the primacy of habitat amount in the ‘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 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 configuration (Cushman et al., 2008).

Arguably, since [Fahrig \(2013, 2017\)](#) argues ‘habitat amount’ is a primary predictor of 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 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 entirely on a neutral ‘sample area effect’ argument ([Haddad et al., 2017](#)). Yet at their core, isolation effects are relevant to habitat fragmentation through the disruption of successful dispersal. Both habitat 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 Jr. et al., 2014](#); [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 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 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 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 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 in increasingly small fragments ([Fletcher Jr., 2005](#)). There can also be complex and unpredictable ecological outcomes that emerge in small isolated fragments through random trajectories of 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 mechanisms suggested by [Fahrig \(2017\)](#), we argue that mechanistic understanding requires acknowledging that both habitat amount and configuration operate across spatial scales from local- to patch- to landscape-scales ([Didham et al., 2012](#); [Pardini et al., 2010](#)).

5. Implications for management and conservation in the real world

We believe that the overall goal for most science on habitat fragmentation is to gain a deeper 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 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 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 fragmentation should not be used to guide management.

First, [Fahrig](#) argues that conservation biologists have falsely emphasized habitat 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 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 collinear in real-world landscapes where conservation decision-makers are charged with making real-world choices ([Didham et al., 2012](#); [Villard and Metzger, 2014](#)).

Second, [Fahrig](#) emphasizes that more fragmented habitats have proportionally more edge, and that conclusions for these largely positive effects of habitat fragmentation were often 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 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., 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., [Echeverria et al., 2007](#); [Goswami et al., 2014](#)), and it can also facilitate further habitat loss ([Lawrance et al., 2009](#)).

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 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 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 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 [Alstad et al., 2016](#); [Banks-Leite et al., 2012](#)).

Fourth, [Fahrig](#) suggests that the review conclusions may contribute to the land sharing vs sparing debate in applied landscape management ([Fischer et al., 2014](#)), by supporting conservation of dispersed networks of several small fragments (assumed to reflect land-sharing) 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-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 alone.

Fifth, the review had a narrow focus on a habitat vs non-habitat dichotomy, assuming the functionally-relevant habitat was appropriately quantified and of comparatively similar quality across the landscape for the responses considered. For many species, the non-habitat matrix may 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 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 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 of conservation concern.

Sixth, and perhaps most importantly for decision-makers, [Fahrig \(2017\)](#) tends to 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 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 with habitat fragmentation, would be considered a ‘negative outcome’ for conservation. Given [Fahrig](#) does briefly acknowledge this issue (p.18), it is alarming that the review concludes that (p.19), “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”.

6. Conclusions and moving forward

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 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 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 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-species responses where different members of the community may be using different resources across heterogeneous landscapes, leading to greater beta-diversity in more fragmented 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, 2006; Tscharntke et al., 2012).

Fahrig's review provides insufficient evidence or context for the conclusion that habitat 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 polarized perspectives with invective can stymie research growth, and could have unintended and unjustified ramifications for conservation and management. The take-home message should 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 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, 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.

Acknowledgements

This research was supported by the National Science Foundation (DEB-1655555 to RF and RH). AG is supported by the Liber Ero chair in Biodiversity Conservation. RP is supported by a research fellowship from CNPQ (Conselho Nacional de Desenvolvimento Científico e Tecnológico) – 308205/2014-6.

Competing interests

The authors declare no competing interests.

References

Adler, F.R., Nuernberger, B., 1994. Persistence in patchy irregular landscapes. *Theor. Popul. Biol.* 45, 41–75.

Alstad, A.O., Damschen, E.I., Givnish, T.J., Harrington, J.A., Leach, M.K., Rogers, D.A., Waller, D.M., 2016. The pace of plant community change is accelerating in remnant prairies. *Sci. Adv.* 2.

Banks-Leite, C., Ewers, R.M., Metzger, J.P., 2010. Edge effects as the principal cause of area effects on birds in fragmented secondary forest. *Oikos* 119, 918–926.

Banks-Leite, C., Ewers, R.M., Metzger, J.P., 2012. Unraveling the drivers of community dissimilarity and species extinction in fragmented landscapes. *Ecology* 93, 2560–2569.

Barlow, J., Lennox, G.D., Ferreira, J., Berenguer, E., Lees, A.C., Mac Nally, R., Thomson, J.R., Ferraz, S.F.D., Louzada, J., Oliveira, V.H.F., Parry, L., Solar, R.R.D., Vieira, I.C.G., Aragao, L., Begotti, R.A., Braga, R.F., Cardoso, T.M., de Oliveira, R.C., Souza, C.M., Moura, N.G., Nunes, S.S., Siqueira, J.V., Pardini, R., Silveira, J.M., Vaz-de-Mello, F.Z., Veiga, R.C.S., Venturieri, A., Gardner, T.A., 2016. Anthropogenic disturbance in tropical forests can double biodiversity loss from deforestation. *Nature* 535 (144–+).

Betts, M.G., Fahrig, L., Hadley, A.S., Halstead, K.E., Bowman, J., Robinson, W.D., Wiens, J.A., Lindemayer, D.B., 2014. A species-centered approach for uncovering generalities in organism responses to habitat loss and fragmentation. *Ecography* 37, 517–527.

Blake, J.G., Karr, J.R., 1984. Species composition of bird communities and the conservation benefit of large versus small forests. *Biol. Conserv.* 30, 173–187.

Brooks, T.M., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B., Rylands, A.B., Konstant, W.R., Flick, P., Pilgrim, J., Oldfield, S., Magin, G., Hilton-Taylor, C., 2002. Habitat loss and extinction in the hotspots of biodiversity. *Conserv. Biol.* 16, 909–923.

Chisholm, R.A., Lim, F., Yeoh, Y.S., Seah, W.W., Condit, R., Rosindell, J., 2018. Species-area relationships and biodiversity loss in fragmented landscapes. *Ecol. Lett.* 21, 804–813.

Cote, I.M., Darling, E.S., Brown, C.J., 2016. Interactions among ecosystem stressors and their importance in conservation. *Proc. R. Soc. B Biol. Sci.* 283.

Cushman, S.A., McGarigal, K., Neel, M.C., 2008. Parsimony in landscape metrics: strength, universality, and consistency. *Ecol. Indic.* 8, 691–703.

Cushman, S.A., Shirk, A., Landguth, E.L., 2012. Separating the effects of habitat area, fragmentation and matrix resistance on genetic differentiation in complex landscapes. *Landscape Ecol.* 27, 369–380.

Debinski, D.M., Holt, R.D., 2000. A survey and overview of habitat fragmentation experiments. *Conserv. Biol.* 14, 342–355.

den Boer, P.J., 1968. Spreading of risk and stabilization of animal numbers. *Acta Biotheor.* 18, 165–194.

Didham, R.K., Kapos, V., Ewers, R.M., 2012. Rethinking the conceptual foundations of habitat fragmentation research. *Oikos* 121, 161–170.

Echeverria, C., Newton, A.C., Lara, A., Benayas, J.M.R., Coomes, D.A., 2007. Impacts of forest fragmentation on species composition and forest structure in the temperate landscape of southern Chile. *Glob. Ecol. Biogeogr.* 16, 426–439.

Ewers, R.M., Didham, R.K., 2006. Confounding factors in the detection of species responses to habitat fragmentation. *Biol. Rev.* 81, 117–142.

Ewers, R.M., Thorpe, S., Didham, R.K., 2007. Synergistic interactions between edge and area effects in a heavily fragmented landscape. *Ecology* 88, 96–106.

Fahrig, L., 2003. Effects of habitat fragmentation on biodiversity. *Annu. Rev. Ecol. Evol. Syst.* 34, 487–515.

Fahrig, L., 2013. Rethinking patch size and isolation effects: the habitat amount hypothesis. *J. Biogeogr.* 40, 1649–1663.

Fahrig, L., 2017. Ecological responses to habitat fragmentation *per se*. *Annu. Rev. Ecol. Evol. Syst.* 48, 1–23.

Fischer, J., Abson, D.J., Butsic, V., Chappell, M.J., Ekroos, J., Hanspach, J., Kuemmerle, T., Smith, H.G., von Wehrden, H., 2014. Land sparing versus land sharing: moving forward. *Conserv. Lett.* 7, 149–157.

Fletcher Jr., R.J., 2005. Multiple edge effects and their implications in fragmented landscapes. *J. Anim. Ecol.* 74, 342–352.

Fletcher Jr., R.J., 2006. Emergent properties of conspecific attraction in fragmented landscapes. *Am. Nat.* 168, 207–219.

Fletcher Jr., R.J., Ries, L., Battin, J., Chalfoun, A.D., 2007. The role of habitat area and edge in fragmented landscapes: definitely distinct or inevitably intertwined? *Can. J. Zool.* 85, 1017–1030.

Fletcher Jr., R.J., Acevedo, M.A., Robertson, E.P., 2014. The matrix alters the role of path redundancy on patch colonization rates. *Ecology* 95, 1444–1450.

Fletcher Jr., R.J., Burrell, N., Reichert, B.E., Vasudev, D., 2016. Divergent perspectives on landscape connectivity reveal consistent effects from genes to communities. *Curr. Landscape Ecol. Rep.* 1, 67–79.

Gilbert-Norton, L., Wilson, R., Stevens, J.R., Beard, K.H., 2010. A meta-analytic review of corridor effectiveness. *Conserv. Biol.* 24, 660–668.

Gonzalez, A., Lawton, J.H., Gilbert, F.S., Blackburn, T.M., Evans-Freke, I., 1998. Metapopulation dynamics, abundance, and distribution in a microecosystem. *Science* 281, 2045–2047.

Goswami, V.R., Vasudev, D., Oli, M.K., 2014. The importance of conflict-induced mortality for conservation planning in areas of human-elephant co-occurrence. *Biol. Conserv.* 176, 191–198.

Gurevitch, J., Koricheva, J., Nakagawa, S., Stewart, G., 2018. Meta-analysis and the science of research synthesis. *Nature* 555, 175–182.

Haddad, N.M., Brudvig, L.A., Clobert, J., Davies, K.F., Gonzalez, A., et al., 2015. Habitat fragmentation and its lasting impact on Earth. *Sci. Adv.* 1, e1500052.

Haddad, N.M., Gonzalez, A., Brudvig, L.A., Burt, M.A., Levey, D.J., Damschen, E.I., 2017. Experimental evidence does not support the habitat amount hypothesis. *Ecography* 40, 48–55.

Hadley, A.S., Betts, M.G., 2016. Refocusing habitat fragmentation research using lessons from the last decade. *Curr. Landscape Ecol. Rep.* 1, 55–66.

Hadley, A.S., Frey, S.J.K., Robinson, W.D., Kress, W.J., Betts, M.G., 2014. Tropical forest fragmentation limits pollination of a keystone under story herb. *Ecology* 95, 2202–2212.

Haila, Y., 2002. A conceptual genealogy of fragmentation research: from island biogeography to landscape ecology. *Ecol. Appl.* 12, 321–334.

Hanski, I., 2015. Habitat fragmentation and species richness. *J. Biogeogr.* 42, 989–993.

Hill, M.F., Caswell, H., 1999. Habitat fragmentation and extinction thresholds on fractal landscapes. *Ecol. Lett.* 2, 121–127.

Hylander, K., Ehrlen, J., 2013. The mechanisms causing extinction debts. *Trends Ecol. Evol.* 28, 341–346.

Jackson, S.T., Sax, D.F., 2010. Balancing biodiversity in a changing environment: extinction debt, immigration credit and species turnover. *Trends Ecol. Evol.* 25, 153–160.

Koper, N., Schmiegelow, F.K.A., Merrill, E.H., 2007. Residuals cannot distinguish between ecological effects of habitat amount and fragmentation: implications for the debate. *Landsc. Ecol.* 22, 811–820.

Koricheva, J., Gurevitch, J., Mengersen, K., 2013. *Handbook of Meta-analysis in Ecology and Evolution*. Princeton University Press.

Lasky, J.R., Keitt, T.H., 2013. Reserve size and fragmentation alter community assembly, diversity, and dynamics. *Am. Nat.* 182, E142–E160.

Laurance, W.F., Ueche, D.C., 2009. Environmental synergisms and extinctions of tropical species. *Conserv. Biol.* 23, 1427–1437.

Laurance, W.F., Nascimento, H.E.M., Laurance, S.G., Andrade, A., Ribeiro, J.E.L.S., Giraldo, J.P., Lovejoy, T.E., Condit, R., Chave, J., Harms, K.E., D'Angelo, S., 2006. Rapid decay of tree-community composition in Amazonian forest fragments. *Proc. Natl. Acad. Sci. U. S. A.* 103, 19010–19014.

Laurance, W.F., Goossem, M., Laurance, S.G.W., 2009. Impacts of roads and linear clearings on tropical forests. *Trends Ecol. Evol.* 24, 659–669.

Lindell, C.A., Riffell, S.K., Kaiser, S.A., Battin, A.L., Smith, M.L., Sisk, T.D., 2007. Edge responses of tropical and temperate birds. *Wilson J. Ornithol.* 119, 205–220.

Liu, Z.F., He, C.Y., Wu, J.G., 2016. The relationship between habitat loss and fragmentation during urbanization: an empirical evaluation from 16 world cities. *PLoS One* 11.

Mac Nally, R., Lake, P.S., 1999. On the generation of diversity in archipelagos: a re-evaluation of the Quinn-Harrison 'saturation index'. *J. Biogeogr.* 26, 285–295.

MacArthur, R.H., Wilson, E.O., 1967. The Theory of Island Biogeography. Princeton University Press, Princeton, NJ.

Mitchell, M.G.E., Bennett, E.M., Gonzalez, A., 2014. Forest fragments modulate the provision of multiple ecosystem services. *J. Appl. Ecol.* 51, 909–918.

Newbold, T., Hudson, L.N., Hill, S.L.L., Contu, S., Lysenko, I., Senior, R.A., Borger, L., Bennett, D.J., Choimes, A., Collen, B., Day, J., De Palma, A., Diaz, S., Echeverria-Londono, S., Edgar, M.J., Feldman, A., Garon, M., Harrison, M.L.K., Alhuseini, T., Ingram, D.J., Itescu, Y., Kattge, J., Kemp, V., Kirkpatrick, L., Kleyer, M., Correia, D.L.P., Martin, C.D., Meiri, S., Novosolov, M., Pan, Y., Phillips, H.R.P., Purves, D.W., Robinson, A., Simpson, J., Tuck, S.L., Weiher, E., White, H.J., Ewers, R.M., Mace, G.M., Scharlemann, J.P.W., Purvis, A., 2015. Global effects of land use on local terrestrial biodiversity. *Nature* 520 (45–+).

Pardini, R., Bueno, A.D., Gardner, T.A., Prado, P.I., Metzger, J.P., 2010. Beyond the fragmentation threshold hypothesis: regime shifts in biodiversity across fragmented landscapes. *PLoS One* 5.

Pfeifer, M., Lefebvre, V., Peres, C.A., Banks-Leite, C., Wearn, O.R., Marsh, C.J., Butchart, S.H.M., Arroyo-Rodríguez, V., Barlow, J., Cerezo, A., Cisneros, L., D'Cruze, N., Faria, D., Hadley, A., Harris, S.M., Klingbeil, B.T., Kormann, U., Lens, L., Medina-Rangel, G.F., Morante-Filho, J.C., Olivier, P., Peters, S.L., Pidgeon, A., Ribeiro, D.B., Scherber, C., Schneider-Maunoury, L., Struebig, M., Urbina-Cardona, N., Watling, J.I., Willig, M.R., Wood, E.M., Ewers, R.M., 2017. Creation of forest edges has a global impact on forest vertebrates. *Nature* 551, 187.

Quiggen, J., 2010. Zombie Economics: How Dead Ideas Still Walk Among Us. Princeton University Press.

Quinn, J.F., Harrison, S.P., 1988. Effects of habitat fragmentation and isolation on species richness: evidence from biogeographic patterns. *Oecologia* 75, 132–140.

Radford, J.Q., Bennett, A.F., 2007. The relative importance of landscape properties for woodland birds in agricultural environments. *J. Appl. Ecol.* 44, 737–747.

Ramsey, F.L., 1989. Comments on a saturation index. *Oecologia* 81, 569–570.

Ricketts, T.H., 2001. The matrix matters: effective isolation in fragmented landscapes. *Am. Nat.* 158, 87–99.

Ries, L., Fletcher, R.J., Battin, J., Sisk, T.D., 2004. Ecological responses to habitat edges: mechanisms, models, and variability explained. *Annu. Rev. Ecol. Evol. Syst.* 35, 491–522.

Ries, L., Murphy, S.M., Wimp, G.M., Fletcher Jr., R.J., 2017. Closing persistent gaps in knowledge about edge ecology. *Curr. Landscape Ecol. Rep.* 2, 30–41.

Rosch, V., Tscharntke, T., Scherber, C., Batary, P., 2015. Biodiversity conservation across taxa and landscapes requires many small as well as single large habitat fragments. *Oecologia* 179, 209–222.

Ruffell, J., Banks-Leite, C., Didham, R.K., 2016. Accounting for the causal basis of collinearity when measuring the effects of habitat loss versus habitat fragmentation. *Oikos* 125, 117–125.

Rybicki, J., Hanski, I., 2013. Species-area relationships and extinctions caused by habitat loss and fragmentation. *Ecol. Lett.* 16, 27–38.

Schipper, J., Chanson, J.S., Chiozza, F., Cox, N.A., Hoffmann, M., Katariya, V., Lamoreux, J., Rodrigues, A.S.L., Stuart, S.N., Temple, H.J., Baillie, J., Boitani, L., Lacher, T.E.,

Mittermeier, R.A., Smith, A.T., Absolon, D., Aguiar, J.M., Amori, G., Bakkour, N., Baldi, R., Berridge, R.J., Bielby, J., Black, P.A., Blanc, J.J., Brooks, T.M., Burton, J.A., Butynski, T.M., Catullo, G., Chapman, R., Cokeliss, Z., Collen, B., Conroy, J., Cooke, J.G., da Fonseca, G.A.B., Derocher, A.E., Dublin, H.T., Duckworth, J.W., Emmons, L., Emslie, R.H., Festa-Bianchet, M., Foster, M., Foster, S., Garshelis, D.L., Gates, C., Gimenez-Dixon, M., Gonzalez, S., Gonzalez-Maya, J.F., Good, T.C., Hammerson, G., Hammond, P.S., Happold, D., Happold, M., Hare, J., Harris, R.B., Hawkins, C.E., Haywood, M., Heaney, L.R., Hedges, S., Helgen, K.M., Hilton-Taylor, C., Hussain, S.A., Ishii, N., Jefferson, T.A., Jenkins, R.K.B., Johnston, C.H., Keith, M., Kingdon, J., Knox, D.H., Kovacs, K.M., Langhamer, P., Leus, K., Lewison, R., Lichtenstein, G., Lowry, L.F., Macavoy, Z., Mace, G.M., Mallon, D.P., Masi, M., McKnight, M.W., Medellin, R.A., Medici, P., Mills, G., Moehlman, P.D., Molur, S., Mora, A., Nowell, K., Oates, J.F., Olech, W., Oliver, W.R.L., Oprea, M., Patterson, B.D., Perrin, W.F., Polidoro, B.A., Pollock, C., Powel, A., Protas, Y., Racey, P., Ragle, J., Ramani, P., Rathbun, G., Reeves, R.R., Reilly, S.B., Reynolds, J.E., Rondinini, C., Rosell-Amabal, R.G., Rulli, M., Rylands, A.B., Savini, S., Schank, C.J., Sechrest, W., Self-Sullivan, C., Shoemaker, A., Sillero-Zubiri, C., De Silva, N., Smith, D.E., Srinivasulu, C., Stephenson, P.J., van Strien, N., Talukdar, B.K., Taylor, B.L., Timmins, R., Tirira, D.G., Tognelli, M.F., Tsytulina, K., Veiga, L.M., Vie, J.C., Williamson, E.A., Wyatt, S.A., Xie, Y., Young, B.E., 2008. The status of the world's land and marine mammals: diversity, threat, and knowledge. *Science* 322, 225–230.

Smith, A.C., Koper, N., Francis, C.M., Fahrig, L., 2009. Confronting collinearity: comparing methods for disentangling the effects of habitat loss and fragmentation. *Landscape Ecol.* 24, 1271–1285.

Smith, A.C., Koper, N., Francis, C.M., 2011. Landscape size affects the relative importance of habitat amount, habitat fragmentation, and matrix quality on forest birds. *Ecography* 34, 103–113.

Swift, T.L., Hannon, S.J., 2010. Critical thresholds associated with habitat loss: a review of the concepts, evidence, and applications. *Biol. Rev.* 85, 35–53.

Thompson, P.L., Rayfield, B., Gonzalez, A., 2017. Loss of habitat and connectivity erodes species diversity, ecosystem functioning, and stability in metacommunity networks. *Ecography* 40, 98–108.

Tilman, D., Lehman, C.L., 1997. Habitat destruction and species extinctions. In: Tilman, D., Kareiva, P. (Eds.), *Spatial Ecology: The Role of Space in Population Dynamics and Interspecific Interactions*. Princeton, Princeton University Press.

Tobler, W.R., 1970. Computer movie simulating urban growth in Detroit region. *Econ. Geogr.* 46, 234–240.

Tscharntke, T., Tylianakis, J.M., Rand, T.A., Didham, R.K., Fahrig, L., Batary, P., Bengtsson, J., Clough, Y., Crist, T.O., Dormann, C.F., Ewers, R.M., Frund, J., Holt, R.D., Holzschuh, A., Klein, A.M., Kleijn, D., Kremen, C., Landis, D.A., Laurance, W., Lindenmayer, D., Scherber, C., Sodhi, N., Steffan-Dewenter, I., Thies, C., van der Putten, W.H., Westphal, C., 2012. Landscape moderation of biodiversity patterns and processes - eight hypotheses. *Biol. Rev.* 87, 661–685.

Villard, M.A., Metzger, J.P., 2014. Beyond the fragmentation debate: a conceptual model to predict when habitat configuration really matters. *J. Appl. Ecol.* 51, 309–318.

With, K.A., King, A.W., 2001. Analysis of landscape sources and sinks: the effect of spatial pattern on avian demography. *Biol. Conserv.* 100, 75–88.