

Ecological Responses to Habitat Fragmentation Per Se

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Annu. Rev. Ecol. Evol. Syst. 2017. 48:1–23

First published online as a Review in Advance on
May 31, 2017

The *Annual Review of Ecology, Evolution, and
Systematics* is online at ecolsys.annualreviews.org

<https://doi.org/10.1146/annurev-ecolsys-110316-022612>

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Keywords

landscape pattern, landscape structure, landscape configuration, landscape complementation, landscape connectivity, landscape heterogeneity, patch area, patch isolation, edge effect, SLOSS

Abstract

For this article, I reviewed empirical studies finding significant ecological responses to habitat fragmentation per se—in other words, significant responses to fragmentation independent of the effects of habitat amount (hereafter referred to as habitat fragmentation). I asked these two questions: Are most significant responses to habitat fragmentation negative or positive? And do particular attributes of species or landscapes lead to a predominance of negative or positive significant responses? I found 118 studies reporting 381 significant responses to habitat fragmentation independent of habitat amount. Of these responses, 76% were positive. Most significant fragmentation effects were positive, irrespective of how the authors controlled for habitat amount, the measure of fragmentation, the taxonomic group, the type of response variable, or the degree of specialization or conservation status of the species or species group. No support was found for predictions that most significant responses to fragmentation should be negative in the tropics, for species with larger movement ranges, or when habitat amount is low; most significant fragmentation effects were positive in all of these cases. Thus, although 24% of significant responses to habitat fragmentation were negative, I found no conditions in which most responses were negative. Authors suggest a wide range of possible explanations for significant positive responses to habitat fragmentation: increased functional connectivity, habitat diversity, positive edge effects, stability of predator–prey/host–parasitoid systems, reduced competition, spreading of risk, and landscape complementation. A consistent preponderance of positive significant responses to fragmentation implies that there is no justification for assigning lower conservation value to a small patch than to an equivalent area within a large patch—instead, it implies just the opposite. This finding also suggests that land sharing will usually provide higher ecological value than land sparing.



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1. HABITAT PATCHINESS

Habitat patchiness has been an important concept in ecology for over 80 years, beginning with the observation by Gause (1934) that persistence of predator–prey systems depends on the availability of separate refuges for prey. Huffaker’s (1958) classic predator–prey experiment took this idea another step, showing that division of a food resource into a large number of patches allows a predator–prey system to persist by providing temporary prey refuge sites that move about in space and time, allowing the prey to stay one step ahead of the predators. Levins & Culver (1971) showed that habitat patchiness can also allow persistence of competing species through a similar dynamic, as long as the better competitor is the worse disperser. And den Boer (1968) showed more generally that habitat patchiness can increase species persistence by spreading the risk of local extinctions. Thus, from 1934 until approximately 1970, habitat patchiness was associated with the concept of habitat spatial heterogeneity and was generally considered to have a positive influence on population and community-level ecological responses.

This all changed with Levins’s (1970) extrapolation of the theory of island biogeography (MacArthur & Wilson 1967) to patches of habitat. From that point to the present, habitat patchiness has been associated with the concept of habitat fragmentation and is generally considered to have a negative influence on population and community-level responses (Villard & Metzger 2014, Hanski 2015).

Although these two major conceptualizations of habitat patchiness seem to make contradictory predictions, the contradiction is not real. In the earlier work, increasing habitat patchiness (or habitat spatial heterogeneity) generally implied an increase in the total amount of habitat available, or at least no decrease. In contrast, in the later work, increasing habitat patchiness (or habitat fragmentation) generally implied a decrease in the total amount of habitat (**Figure 1**). Therefore, in the former case the positive effect of patchiness is often associated with habitat gain, whereas in the latter case the negative effect of patchiness is associated with habitat loss. Thus, both views of habitat patchiness can represent a positive effect of increasing habitat amount on population and community responses.

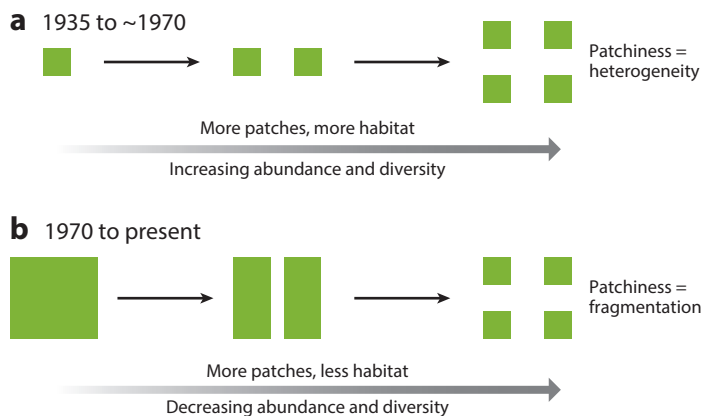


Figure 1

The concept of habitat patchiness in ecology. (a) From 1935 to approximately 1970, habitat patchiness was associated with the concept of habitat spatial heterogeneity and was assumed to have a positive effect on biodiversity. (b) From 1970 to the present, habitat patchiness has been associated with the concept of habitat fragmentation and is assumed to have a negative effect on biodiversity. This apparent contradiction is resolved by recognizing that the former is often associated with habitat gain, whereas the latter is associated with habitat loss.

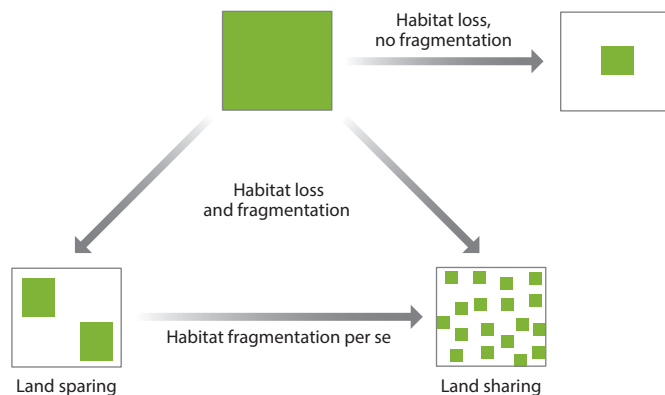


Figure 2

Habitat loss is a process whereby habitat is destroyed over time. In contrast, habitat fragmentation per se (hereafter referred to as habitat fragmentation) is a difference in spatial pattern. For a given amount of habitat, a more fragmented pattern has more, smaller patches, with more total edge in the landscape. The current dominant paradigm assumes that habitat fragmentation generally has negative effects on biodiversity. If this is true, then policies should favor land sparing over land sharing.

This then begs the question, what is the influence of patchiness itself on ecological responses, independent of its association with habitat amount? Some have argued that this question is a meaningless academic exercise: Habitat loss and fragmentation are so tightly linked that any effort to disentangle their effects is pointless (Didham et al. 2012). However, many examples of environmental policies assume large, negative effects of patchiness independent of habitat amount (i.e., negative effects of habitat fragmentation per se) (*sensu* Haila & Hanski 1984; **Figure 2**). For example, in Ontario, Canada, forestry policy specifies that large, contiguous clear-cuts can be justified if they “defragment a previous group of smaller cuts” (Ont. Min. Nat. Resour. 2002, p. 4). This policy is built on the assumption that large, contiguous blocks of forest have higher ecological value than the same total area of small, separated patches of forest (King et al. 1996, Hagan et al. 1997). In general, the assumption that fragmentation has large negative effects on biodiversity implies that policies should emphasize land sparing over land sharing (Green et al. 2005; **Figure 2**). Are such decisions grounded in fact?

2. STUDY DESIGNS FOR MEASURING EFFECTS OF HABITAT FRAGMENTATION INDEPENDENT OF HABITAT AMOUNT

Although habitat fragmentation is often thought of as a process involving both the loss and the breaking apart of habitat, habitat fragmentation independent of habitat loss constitutes a difference in pattern (or configuration) between landscapes (McGarigal & Cushman 2002). For a given amount of habitat, a more fragmented landscape has more, smaller habitat patches and contains a greater total length of habitat edge (**Figure 2**). For the remainder of this review, the term habitat fragmentation is used specifically to mean habitat fragmentation independent of habitat loss (i.e., habitat fragmentation per se).

Importantly, studies of patch size effects and patch isolation effects do not provide evidence for effects of habitat fragmentation, because both patch size effects and patch isolation effects are inherently confounded with effects of habitat amount (Fahrig 2003, 2013). Smaller patches have less habitat than larger patches, and more isolated patches are more isolated precisely because there is less habitat surrounding them than there is surrounding the less isolated patches (Moilanen

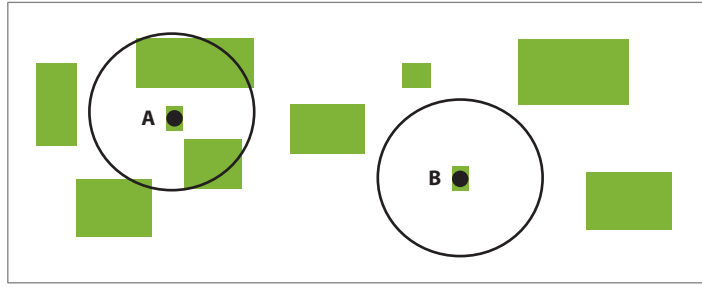


Figure 3

Patch isolation is an inverse measure of habitat amount. Patch A is less isolated than Patch B precisely because there is more habitat in the local landscape around Patch A than in the local landscape around Patch B.

& Nieminen 2002, Bender et al. 2003, Tischendorf et al. 2003, Prugh 2009, Ranius et al. 2010, Thornton et al. 2011, Martin & Fahrig 2012; **Figure 3**). Therefore, effects of habitat fragmentation must be measured at the landscape scale (McGarigal & Cushman 2002; **Figure 4**), that is, by comparing effects of habitat pattern across multiple landscapes while controlling for the total amount of habitat in them.

Researchers have used three different ways to estimate ecological responses to habitat fragmentation. In the first approach, a true landscape-scale experiment is conducted; in this experiment, one constructs multiple landscapes either across independent gradients of habitat amount and fragmentation (e.g., With et al. 2002; **Figure 5**) or across a gradient of fragmentation where all constructed landscapes have the same amount of habitat (e.g., Wolff et al. 1997, Goodwin & Fahrig 2002). In the second approach, a set of existing landscapes across gradients in habitat loss and fragmentation is selected. The landscapes may be selected either randomly (Smith

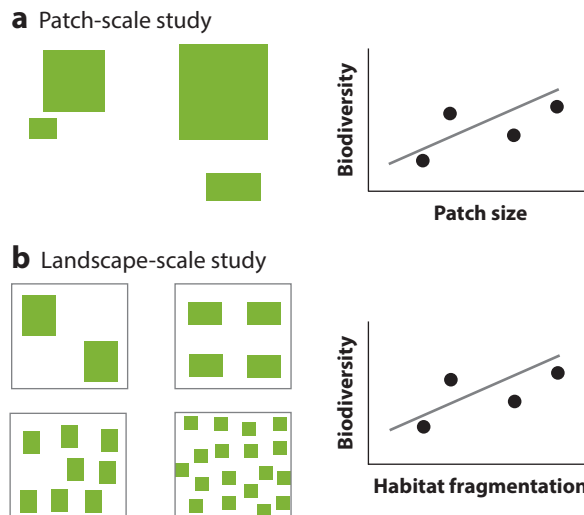


Figure 4

Illustration of the difference between a patch-scale study and a landscape-scale study. (a) In a patch-scale study, predictor variables are spatial attributes of individual patches (e.g., patch size, patch isolation). (b) In a landscape-scale study, predictor variables are spatial attributes of individual landscapes (e.g., percentage of the landscape in habitat, habitat fragmentation).

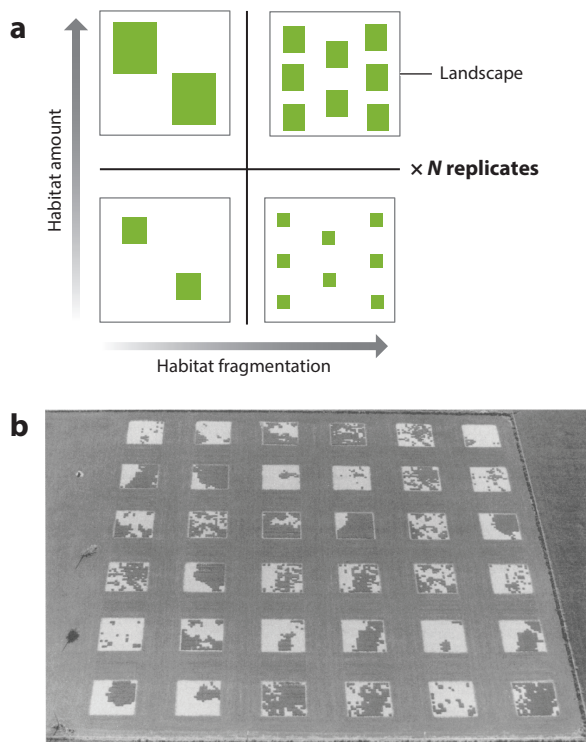


Figure 5

Multilandscape experimental approach for estimating fragmentation effects. (a) Experimental study design for evaluating the independent effects of habitat amount and habitat fragmentation. (b) Aerial photograph of an example of a multilandscape experiment where landscapes were constructed such that aphid habitat fragmentation was varied (two levels) independent of habitat amount (six levels), with three replicates of each combination of habitat fragmentation and habitat amount. The habitat is planted clover, and each landscape is 16 × 16 m. Panel b from With et al. (2002); used with permission.

et al. 2011) or purposefully in an attempt to minimize any correlation between habitat amount and fragmentation (e.g., Hovel & Lipcius 2001, Cushman & McGarigal 2003, Robertson et al. 2013, Plečaš et al. 2014). A variety of statistical methods are then used to estimate the effects of habitat fragmentation while statistically controlling for the effects of habitat amount. In the third approach, SLOSS (single large or several small) studies compare species richness across virtual landscapes—sets of patches that are subsets of a larger set, where all subsets contain the same total amount of habitat but vary in fragmentation (Figures 6 and 7).

3. REVIEW OBJECTIVES AND CRITERIA

In my previous review for the *Annual Review of Ecology, Evolution, and Systematics* (Fahrig 2003), I compared the effects of habitat fragmentation with the effects of habitat loss on a wide range of ecological responses and found that in general the effects of fragmentation are much weaker than the effects of habitat loss; usually no significant response to fragmentation is detected. In that review I also noted that, of the 31 cases in which studies detected a significant response to habitat fragmentation, only 10 of these responses were negative, whereas the remaining 21 were positive. Given the small sample size at that time (31 significant responses), it would have been premature to conclude that significant responses to habitat fragmentation are predominantly positive.

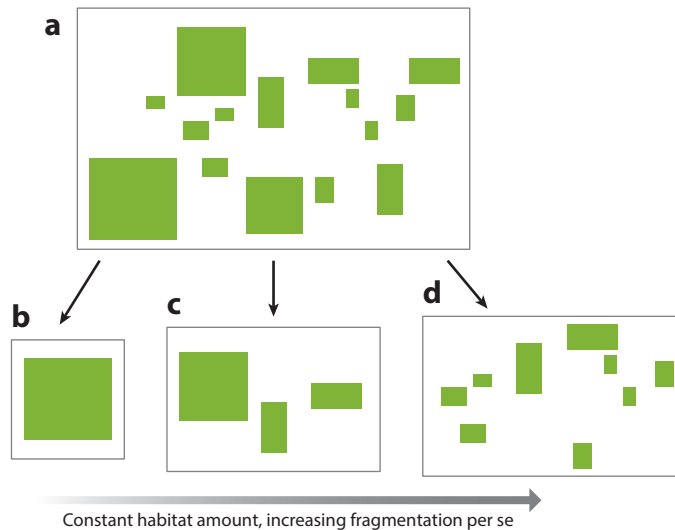


Figure 6

SLOSS (single large or several small)-type study. (a) Species are sampled in each patch within a global set of patches. (b–d) Subsets of the global set are shown, such that each subset has the same total habitat amount for all patches when combined but subsets vary in habitat fragmentation.

The current review addresses these two questions: Are most significant ecological responses to habitat fragmentation negative or positive? And do particular attributes of species or landscapes lead to a predominance of negative or positive significant responses to habitat fragmentation? I attempted a complete search for studies documenting significant responses to habitat fragmentation, whether positive or negative. Included studies used one of the three landscape-scale study designs described above to control for effects of habitat amount while estimating effects of habitat fragmentation: (a) multilandscape fragmentation experiment, (b) observational study of multiple landscapes with statistical control of habitat amount effects, and (c) SLOSS-type analysis.

I used the following criteria to screen articles for inclusion in this review.

1. The significant response to habitat fragmentation was based directly on an empirical test.
2. The ecological response variable was directly measured, not inferred (e.g., from a model).
3. The study included multiple landscapes, varying in degree of fragmentation.
4. The study evaluated responses to fragmentation of habitat or natural cover types such as forest, wetland, grassland, coral reef, etc. The response variable (species abundance, richness, etc.) was measured within the habitat or natural cover.
5. The study used landscape-scale (not patch-scale) measure(s) of habitat fragmentation; these could be either class-level or landscape-level measures (*sensu* McGarigal 2015).
6. The effect of habitat fragmentation was estimated independently of the effect of habitat amount, using one of the three study designs described above.
7. The response variable was one for which a direction of fragmentation effect (negative or positive) could be assigned (e.g., abundance, species richness, movement success, etc.). This excluded, for example, effects on community composition (e.g., Cisneros et al. 2015) or effects on community mean trait values (e.g., Perović et al. 2015).
8. The effect of fragmentation was statistically significant (negative or positive; $\alpha = 0.05$), fragmentation was in the top model set (in multimodel inference), or fragmentation had a high probability (≥ 0.7) of a nonzero coefficient; for simplicity, I refer to all of these as

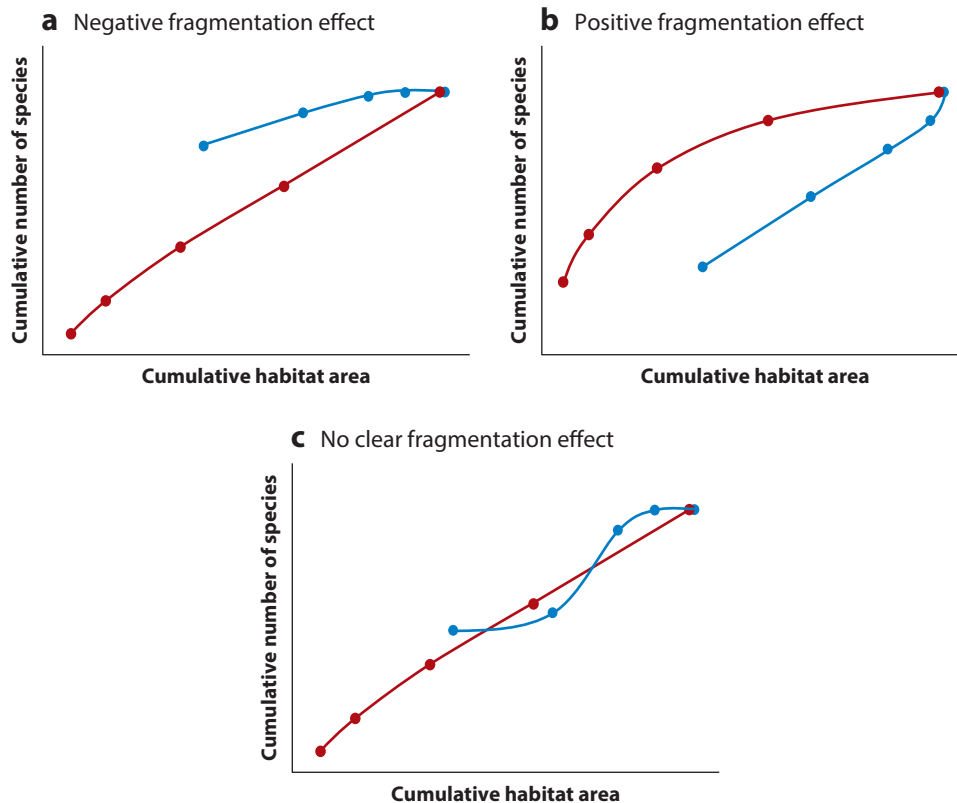


Figure 7

SLOSS (single large or several small)-type analysis. Species number is accumulated across patches, from the largest-to-smallest patch (*blue*) and from the smallest-to-largest patch (*red*). (*a*) When the largest-to-smallest curve is above the smallest-to-largest curve, fragmentation has a negative effect on species richness. (*b*) When the reverse is true, fragmentation has a positive effect on species richness. (*c*) When the lines are coincident or cross each other, no clear effect of fragmentation on species richness is seen.

“significant effects of fragmentation” below. For SLOSS-type studies, I defined a significant effect as one in which the largest-to-smallest and smallest-to-largest curves did not cross (Figure 7).

9. Finally, the direction of the significant fragmentation effect had to be nonambiguous. This criterion resulted in exclusion of a few cases in which the effect of fragmentation was significant but was nonmonotonic or the direction varied over time and/or spatial scales (e.g., Alofs et al. 2014, With 2016).

To find potential articles, I searched for all articles published up to the end of 2015, using the following search term sequence in Web of Science (<https://www.webofknowledge.com>): “fragmentation per se” or “SLOSS” or [(“edge density” or “edge length” or “number of patches” or “mean patch size” or “boundary length” or “patch density” or “median patch size” or “clumping index” or “splitting index” or “aggregation index” or “like adjacencies” or “fractal dimension” or “IJI” or “mean circumscribing circle” or “largest patch index” or “shape index” or “mean core area” or “proportion core area” or “mean nearest-neighbor” or “mean perimeter to area” or “mean edge to area”) and (“habitat” or “forest” or “grassland” or “wetland” or “coral” or “landscapes” or

“watersheds” or “catchments”)]. This procedure resulted in more than 5,000 hits. Most of these were eliminated on the basis of the titles, commonly because the study did not include an ecological response. On the basis of the abstracts, most of the remaining articles were eliminated for failure to meet one or more of the above criteria. In many cases, suitability could not be determined on the basis of the abstract, so some additional articles were eliminated after I read the methods and results sections. I also discovered additional articles in the literature cited sections of a few of the included articles.

I took the significant effects of fragmentation from the tables, figures, and appendices of the articles. I did not take significant effects from the text portions of the articles, in an effort to reduce bias caused by the tendency of authors to highlight results that support their preconceived notions (Fahrig 2017). This is a well-known phenomenon, termed theory tenacity or confirmation/expectation bias (Loehle 1987, Nickerson 1998, Jeng 2006). I did not calculate any effects, and I recorded only the sign—positive or negative—of only the significant effects. I did not attempt to estimate the overall effect size of habitat fragmentation because that would have required also extracting many hundreds of nonsignificant effects of fragmentation (see Section 6). In addition, by limiting the review to the significant effects, I included the studies with sufficient statistical power to detect a significant effect.

4. MOST SIGNIFICANT RESPONSES TO HABITAT FRAGMENTATION ARE POSITIVE

I found 381 significant responses to habitat fragmentation independent of habitat amount effects, drawn from 118 studies (see **Supplemental Appendix**). Of these significant responses to fragmentation, 290 (76%) were positive (**Figure 8**).

Most significant responses to fragmentation were positive, irrespective of the method used to control for habitat amount effects—true experimental, statistical, or SLOSS-type control (**Figure 9a**). All 60 significant SLOSS-type responses indicated species richness was higher in several small patches than in a single large patch (i.e., significant positive responses to fragmentation). This same result was found in early reviews of SLOSS-type studies by Simberloff & Abele (1982) and by Quinn & Harrison (1988). Despite this, authors of SLOSS-type studies published

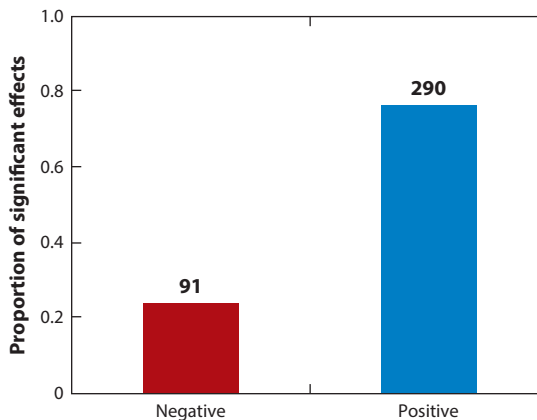


Figure 8

Proportion of significant fragmentation effects that are negative and positive, across all ecological responses. Numbers above the bars indicate the number of significant effects. Most significant fragmentation effects are positive.

after Quinn & Harrison (1988) are still surprised when they find positive effects of fragmentation. For example, Tscharrntke et al. (2002, p. 357) refer to their “surprising observation that patchy habitat supported more butterfly species than did the same area composed of only one or two fragments, even when only endangered species were considered.” The fact that authors continue to be surprised by significant positive effects of fragmentation indicates the level of entrenchment of the current paradigm that assumes negative effects of habitat fragmentation.

Most significant responses to fragmentation were positive, irrespective of the taxonomic group studied (**Figure 9b**). Birds showed a slightly higher proportion of significant negative responses (36%) than other taxa. I speculate that this is at least partly due to a bias in bird studies, as some authors specifically selected study species that were thought a priori to be sensitive to fragmentation (e.g., Smith et al. 2011).

Most significant responses to fragmentation were also positive irrespective of whether fragmentation was measured as number of patches, edge density, mean patch size, or as a whole-landscape (landscape-level sensu McGarigal 2015) metric (**Figure 9c**). In contrast, for studies using a clumping metric of fragmentation, 23 (56%) of the 41 significant responses to habitat fragmentation were negative (i.e., positive effects of clumping). However, I note that 11 of these 23 significant negative effects were taken from a single study (Radford & Bennett 2007), in which some individual species showed both significant negative responses to fragmentation measured as clumping and significant positive responses to fragmentation using other metrics of fragmentation. On closer inspection of that study, it appears that the application of the clumping metric in the data analysis introduced an unintended positive association between clumping and habitat amount (**Figure 10**). Therefore, in that study it is possible that the significant positive effects of clumping (negative effects of fragmentation) may be due to a positive effect of habitat amount.

Most significant responses to habitat fragmentation were also positive regardless of whether the ecological response was a single-species or a multispecies response (generally species richness) (**Figure 9d**). Of the 232 single-species significant effects, 13 were on movement success and 9 were on demographic responses such as survival rate or population growth rate. Most of these significant effects of habitat fragmentation were also positive (**Figure 9d**).

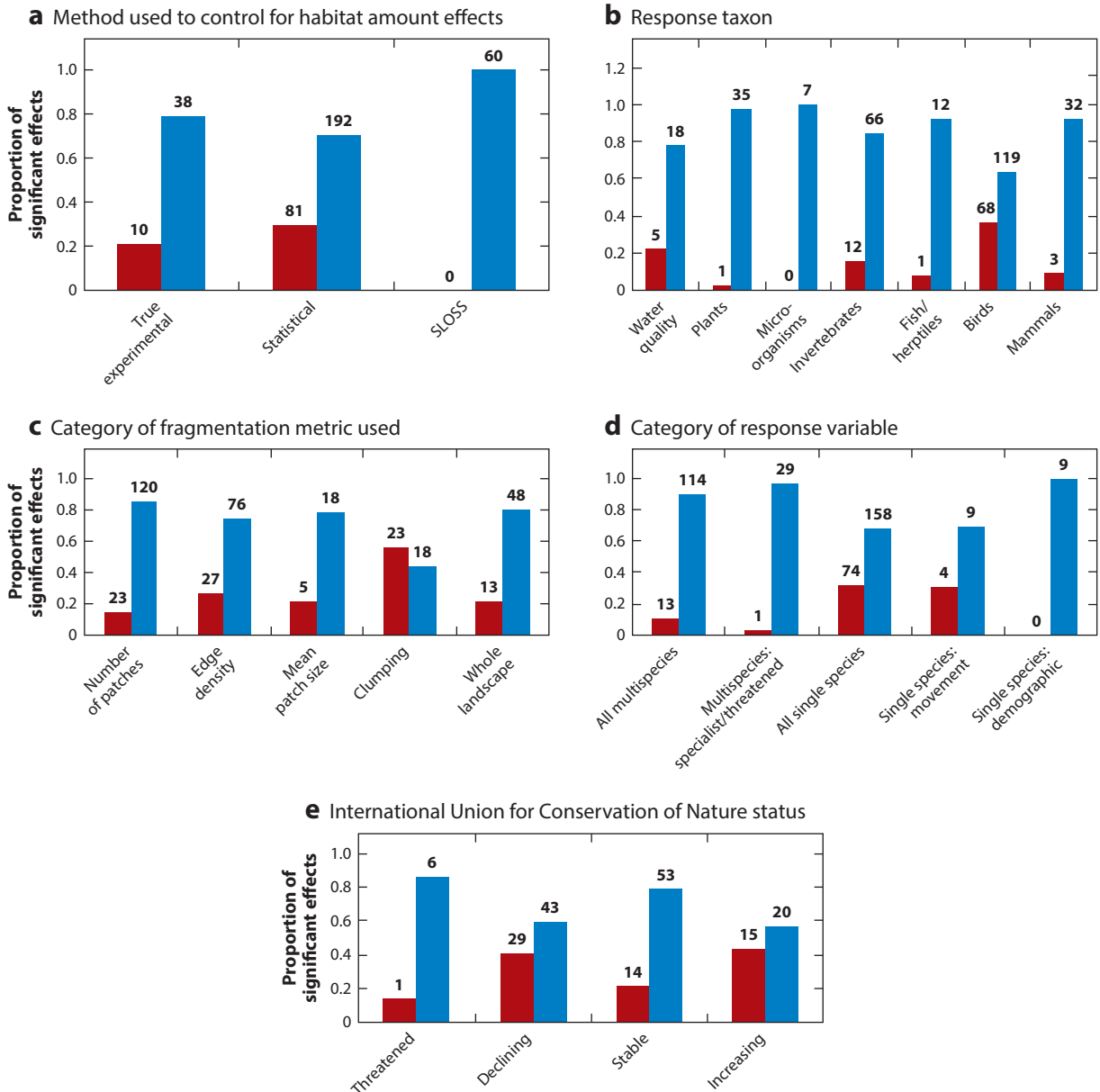
4.1. Responses of Habitat Specialists and Threatened or Declining Species

Within the significant species richness responses, several authors evaluated effects of fragmentation on species richness of habitat specialists and/or rare and/or threatened species (30 significant responses). Often this analysis was done in response to the author’s surprise at finding significant positive effects of habitat fragmentation on total species richness. Authors argued that perhaps in fragmented landscapes, habitat patches contain more generalist species or even matrix-preferring species. The higher habitat edge length in more fragmented landscapes would then result in more spillover of such species into habitat patches in more fragmented landscapes. This suggestion was not supported by the data. Twenty-nine (97%) of the 30 significant responses of species richness of specialist/rare/threatened species groups to fragmentation were positive (**Figure 9d**).

Similarly, for single-species responses, most significant effects of fragmentation were positive, irrespective of the International Union for Conservation of Nature (IUCN) status (IUCN 2015) of the species (**Figure 9e**). The majority of significant single-species responses were positive, irrespective of whether the species is listed as threatened or if its abundance is estimated to be increasing, stable, or declining. The “threatened” group in **Figure 9e** includes two species listed as endangered; one of these showed a negative response and the other a positive response to fragmentation. The other five species in this group are listed as near-threatened; all five showed significant positive responses to habitat fragmentation.

4.2. Tests of Hypotheses Predicting Negative Fragmentation Effects

In the current paradigm, which assumes that effects of fragmentation are generally negative, several hypotheses have been suggested to predict situations in which negative effects of fragmentation should be particularly likely. First, some authors have suggested that negative effects of forest fragmentation are more likely in tropical than in temperate regions, because forest animals in the tropics may be less likely to cross open areas than forest animals in temperate regions (Báldi 1996, Lindell et al. 2007, Cerezo et al. 2010). I found no support for this hypothesis. The majority of significant responses to fragmentation were positive, irrespective of biome (Figure 11a).



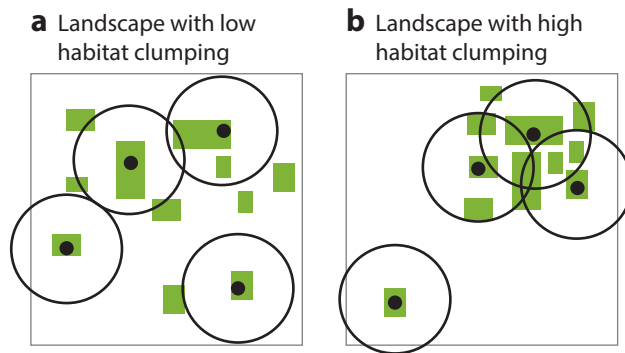


Figure 10

The effects of habitat clumping and habitat amount are confounded when the species response combines data from multiple sample sites (*black dots*) within the species' habitat in each landscape. In landscapes containing more clumped habitat (*b*), a larger proportion of sample sites are in parts of the landscape that contain more habitat in their local landscapes (*circles* surrounding sample sites) than in landscapes containing less clumped habitat (*a*).

Second, it has been suggested that species that interact with the landscape over larger areas are more likely to show negative effects of habitat fragmentation, as they are more likely to encounter nonhabitat (matrix) areas during their movements. I could not directly evaluate this idea because reliable movement range data are not available for the wide range of species and species groups covered in this review. However, I reasoned that the size of the replicate landscapes chosen for a study might be a rough indicator of the movement range of the species (Jackson & Fahrig 2012) and species groups studied, as authors should select the sizes of replicate landscapes to reflect

Figure 9

Proportion of significant fragmentation effects that are negative (*red*) and positive (*blue*). Numbers above the bars indicate the number of significant effects. Significant effects of habitat fragmentation are mostly positive, irrespective of (*a*) the method used to control for habitat amount effects, (*b*) the response taxon, (*c*) the fragmentation metric used, (*d*) the category of response variable, and (*e*) the International Union for Conservation of Nature (IUCN) status of the species. (*a*) In this panel, “true experimental” indicates multiple landscapes created to represent a gradient in fragmentation independent of habitat amount (Figure 5), “statistical” indicates statistical control of the effect of habitat amount while estimating the effect of habitat fragmentation across multiple landscapes, and SLOSS indicates single large or several small-type analysis (Figures 6 and 7). (*b*) Six significant responses to fragmentation combined two or more taxonomic categories; these were excluded here. “Water quality” includes variables such as abundances of water quality indicator taxa and water chemistry variables such as nutrient concentration in receiving waters; a significant negative effect of fragmentation on nutrient concentration was interpreted as a significant positive effect on water quality. (*c*) Infrequently used fragmentation metrics were relabeled according to the common metric to which they were most strongly related. For example, “splitting index” was relabeled as “number of patches,” “like adjacencies” as “clumping,” and “mean circumscribing circle” as “edge density.” When multivariate methods were used to create landscape measures, the composite variable (e.g., an axis from a principle components analysis) representing fragmentation was relabeled as the metric most strongly correlated to it. For SLOSS-type analyses, the metric was “number of patches.” “Whole-landscape metrics” were those measured across all cover classes (i.e., “landscape metrics” in McGarigal 2015). A significant positive response to a “clumping” metric was recorded as a significant negative fragmentation effect (and vice versa). (*d*) “Multispecies” includes mainly species richness but also species diversity measures and total cross-species abundance. “Multispecies: specialist/threatened” responses are a subset of “all multispecies” significant responses representing the cases in which the author limited the species group to the threatened and/or specialist species. “Single species: movement” and “single species: demographic” responses are subsets of “all single species” significant responses; most of the other single species responses were species abundance or occurrence. (*e*) IUCN (2015) status includes only single-species responses. “Threatened” includes two species listed as endangered, one showing a negative and one showing a positive significant fragmentation response, and five near-threatened species, all showing significant positive fragmentation responses. “Declining,” “stable,” and “increasing” are estimated species population trends.

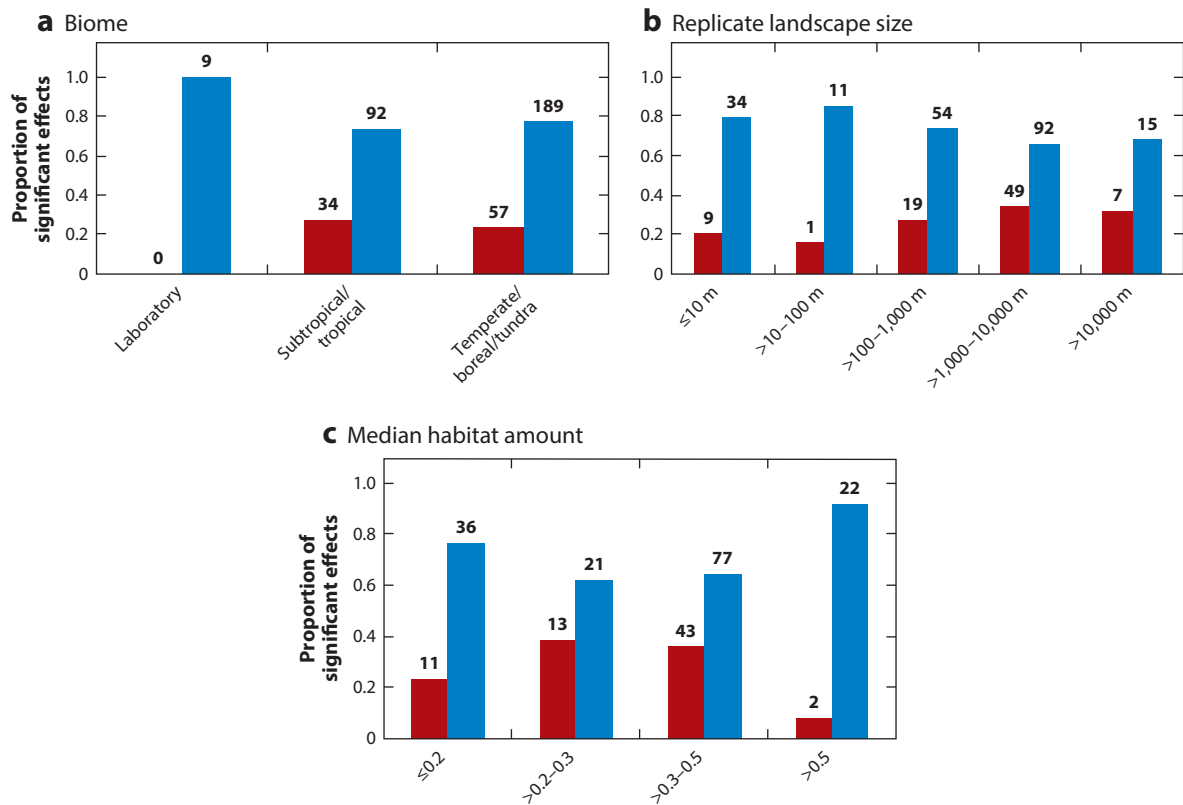


Figure 11

Proportion of significant fragmentation effects that are negative (*red*) and positive (*blue*). Numbers above the bars indicate the number of significant effects. No support was found for any of three hypotheses predicting situations in which the effects of habitat fragmentation should be strongly negative. (*a*) Significant responses were not more likely to be negative in tropical systems. (*b*) Species or species groups with larger movement ranges were not more likely to show significant negative than positive responses to fragmentation. Movement range was indexed as the maximum radius (in meters) of the individual replicate landscapes considered by the authors, on the assumption that authors chose to evaluate the effects of fragmentation over larger spatial extents for species with larger movement ranges. (*c*) Significant effects of habitat fragmentation were not more likely to be negative than positive at levels of habitat amount lower than 20–30% of the landscape. Habitat amount was indexed as the median habitat amount across landscapes in each study, where “median” was the actual median, the mean when the median was not given, or the midpoint in the range when neither the median nor the mean was given. Note, median habitat amount could not be determined in situations in which landscape area increased with fragmentation [e.g., SLOSS (single large or several small)–type analyses] or when fragmentation was a whole-landscape metric; these responses were excluded here.

movement range. Sizes of replicate landscapes varied across studies by four orders of magnitude. However, the majority of significant fragmentation effects were positive, irrespective of the sizes of replicate landscapes (**Figure 11b**). Therefore, the review did not support the movement range hypothesis. It seems likely that the expectation of negative effects of fragmentation on species with larger movement ranges is related more to effects of habitat loss than to effects of habitat fragmentation. Species with large movement ranges may have high habitat requirements, but that does not mean their habitat has to be contiguous.

Finally, several theoretical studies have suggested that negative responses to habitat fragmentation should be more likely when habitat amount is low, particularly when habitat covers less

than approximately 20–30% of the landscape, the so-called fragmentation threshold (Lande 1987, Bascompte & Solé 1996, Boswell et al. 1998, Fahrig 1998, Hill & Caswell 1999, With & King 1999; Flather & Bevers 2002). However, I found no evidence for the fragmentation threshold hypothesis in this review; the majority of significant responses to habitat fragmentation were positive, irrespective of the median level of habitat amount in the study (**Figure 11c**). Interestingly, With (2016) did find that fragmentation effects are more likely at low levels of habitat amount (10–20%) than at high levels (60–80%); however, the response to fragmentation at low levels of habitat amount was positive.

5. AUTHORS' EXPLANATIONS FOR SIGNIFICANT POSITIVE RESPONSES TO HABITAT FRAGMENTATION

According to the introductory sections of articles, most authors had an a priori expectation of negative responses to habitat fragmentation based on one (or more) of three assumptions: (a) negative edge effects, especially due to higher assumed predation or nest parasitism at habitat edges, (b) lower connectivity in landscapes with many small patches than in landscapes with a few large patches, and (c) minimum patch size effects. In the discussion sections of articles in which authors reported significant negative effects of habitat fragmentation, they generally referred to these effects as expected. Thus, the reigning paradigm assumes negative effects of habitat fragmentation.

The results of this review run counter to this paradigm, with 76% of significant responses to habitat fragmentation being positive. When authors obtained a significant positive response to fragmentation, they often expressed surprise in the discussion section, for example, “we obtained puzzling results . . . fragmented populations had larger abundances than nonfragmented populations” (Bancroft & Turchin 2003, p. 1763) or “our results do not support the underlying theoretical supposition that regional extinction should increase with increasing degrees of habitat subdivision” (Robinson & Quinn 1988, p. 79).

Given the unexpected preponderance of positive significant responses to fragmentation, I scoured the discussion sections of the studies containing these positive responses to extract the authors' explanations for them (**Figure 12**). Surprisingly, authors offered no explanations for 119 (41%) of the significant positive responses. Although I have no way of knowing the reason for this, I speculate that many authors are uncomfortable accepting the notion that their data indicate positive responses to fragmentation (see also Fahrig 2017). In addition to the 41% of cases in which no explanation was provided, in 10 cases the authors offered an explanation, but I was unable to understand it as an explanation for a positive response to fragmentation. The following discussion is therefore based on authors' explanations for the remaining 161 significant positive fragmentation effects.

5.1. Fragmentation Increases Functional Connectivity

The most common explanation offered by authors for significant positive responses to habitat fragmentation was that it increases functional connectivity of the landscape. That fragmentation can increase landscape functional connectivity is supported by the fact that 9 of the 13 significant effects of fragmentation on movement success were positive (**Figure 9d**).

Authors suggested two main mechanisms by which fragmentation can increase functional connectivity. First, higher fragmentation implies a larger number of smaller patches with smaller distances between them (**Figure 2**). Authors suggested that this topology can increase patch encounter rate, thus increasing patch immigration and reducing emigration from the system of patches. For example, “high faunal densities in patchy seagrass has [*sic*] been linked to high

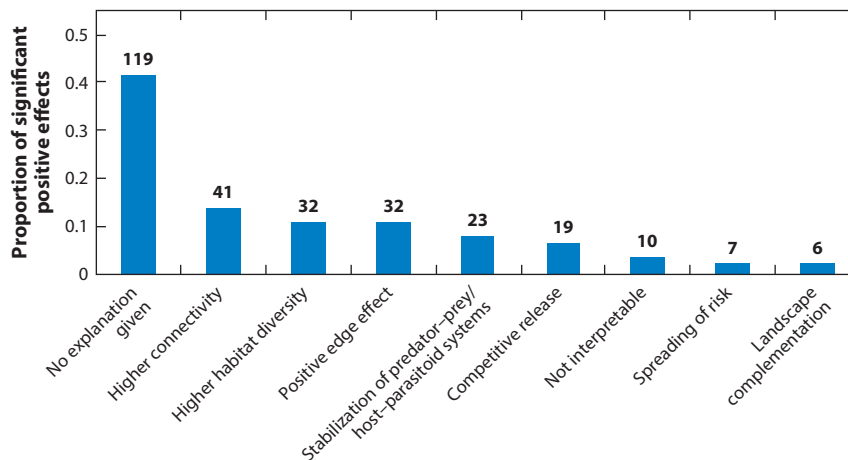


Figure 12

Explanations offered by the authors for their significant positive effects of fragmentation. Numbers above the bars indicate the number of significant effects. No explanation was suggested for 41% of significant positive fragmentation effects. Several authors suggested that landscapes with more small patches (i.e., more fragmented landscapes) had higher functional connectivity and/or higher habitat diversity than landscapes with fewer large patches. Some authors explained their positive fragmentation effects as resulting from positive edge effects such as higher survival and/or higher reproductive success at habitat edges. Other authors suggested that positive fragmentation effects are due to stabilization of predator-prey or host-parasitoid interactions or reduced intra- or interspecific competition in more fragmented landscapes. Some authors suggested that extinction risk is lower in more fragmented landscapes owing to the spreading of risk over multiple patches. Finally, a few authors suggested that habitat fragmentation increases landscape complementation by increasing accessibility among multiple required habitat types. For 10 responses the author offered an explanation for their significant positive fragmentation effect(s), but I was not able to interpret this explanation as a mechanism that could produce a positive fragmentation effect. Most of the explanations proposed by authors for their positive fragmentation effects have been present in the ecological literature for more than 40 years.

perimeter-to-area ratios of small patches, which may increase the probability that dispersing organisms will encounter the patch” (Healey & Hovel 2004, p. 167). This mechanism for a positive influence of habitat patchiness on movement success has also been shown in theoretical studies (Tischendorf & Fahrig 2000, Bowman et al. 2002, Saura et al. 2014).

Second, authors suggested that fragmentation increases functional connectivity because higher edge density in more fragmented landscapes facilitates movement for species that preferentially move along edges. For example, “the positive effect of edge density . . . suggests that field edges provided connectivity and facilitated wasp movements between trap nests and source habitats where dispersal started” (Holzschuh et al. 2010, p. 496) and “it may be that functional connectivity is higher in landscapes with a linear network of riparian and roadside vegetation” (Radford et al. 2005, p. 331).

5.2. More Fragmented Landscapes Contain a Higher Diversity of Habitats

Among articles measuring effects of habitat fragmentation on species richness (e.g., SLOSS-type analyses), habitat diversity was the most common explanation offered by authors for significant positive responses to fragmentation. For example, “a series of small- or medium-sized reserves capture a much greater habitat and habitat-environment heterogeneity than one large fragment”

(Tscharrntke et al. 2002, p. 358) or “a large number of patches can provide high habitat diversity for species with different environmental requirements and result in decreased regional extinction risks” (Hu et al. 2012, p. 8).

5.3. Positive Edge Effects

Authors attributed 32 of the significant positive responses to habitat fragmentation to positive edge effects. They argued that edges are more productive and more structurally diverse than habitat interiors, offering higher forage availability and refuge from predation (Klingbeil & Willig 2009, Walter et al. 2009, Henden et al. 2011, Moore et al. 2011). The idea that edges are high-quality habitats for many species goes back to the early 1900s (Leopold 1933).

The suggestion by some authors that habitat fragmentation reduces predation pressure at edges may seem surprising. Some studies have documented higher predation rates at forest edges than in forest interiors, particularly in agricultural regions where important predators are open-habitat generalist species (Robinson et al. 1995), although this is by no means a general pattern (Tewksbury et al. 1998, Carlson & Hartman 2001). Therefore, it seems likely that at least some of the 24% significant negative responses to habitat fragmentation are due to negative edge effects. Negative edge effects are, implicitly, the favored interpretation for significant negative effects of habitat fragmentation. Many authors made general references to interior specialist species, edge avoiders, and negative edge effects, particularly in the introduction sections of articles (e.g., McAlpine et al. 2006, Grossman et al. 2008, Cerezo et al. 2010). Oddly, however, I did not find any examples in discussion sections of authors linking their findings of significant negative effects of fragmentation to evidence of edge avoidance or negative edge effects for their study species, whether from their own work or from that of others.

5.4. Increased Persistence of Predator–Prey and Host–Parasitoid Systems

Authors attributed 23 of the significant positive effects of habitat fragmentation to the idea that habitat fragmentation stabilizes or increases persistence of predator–prey and host–parasitoid systems. As mentioned above in Section 1, this was the earliest explanation for positive effects of habitat patchiness. Fragmentation is thought to increase persistence of predator–prey and host–parasitoid systems either by offering refuges for the prey or host or by reducing the dispersal efficiency of the predator or parasitoid, allowing the prey to stay a step ahead of the predator in space and time; for example, “fragmented boreal forest may limit dispersal of parasitoids” (Roland 1993, p. 28).

5.5. Habitat Fragmentation Reduces Intraspecific and Interspecific Competition

Authors attributed 19 significant positive effects of fragmentation to negative effects of fragmentation on intraspecific or interspecific competition. For example, authors suggested that fragmentation allows more small mammal territories (Collins & Barrett 1997, Wolff et al. 1997) and more crab territories (Caley et al. 2001) to be defended, because the edges of individual patches are used as territory boundaries. In addition, theory suggests that fragmentation can increase coexistence of species if the stronger competitors are the weaker dispersers (Levins & Culver 1971), and some authors invoked this mechanism. For example, Dufour et al. (2006, pp. 580–81) argued that “spatial structure may indefinitely delay competitive exclusion” by allowing “repeated immigration” of poor competitors, and Hanski (1987) described decreasing covariance of competing species with increasing habitat fragmentation.

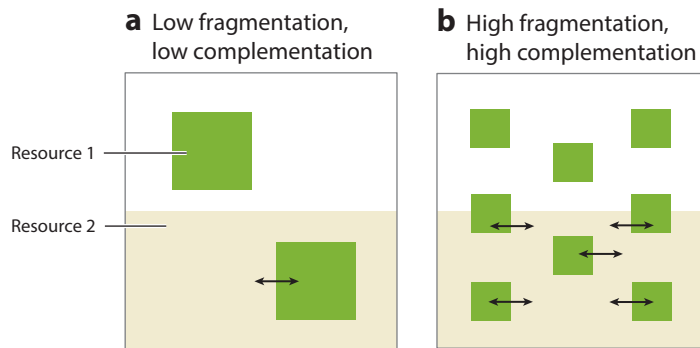


Figure 13

Illustration of how habitat fragmentation increases landscape complementation. Landscape complementation is higher when different required resources are more accessible to each other in the landscape (*black arrows*).

(a) When fragmentation is low, required resources are more likely to be inaccessible to each other.

(b) Higher habitat fragmentation increases interspersed of different resources in the landscape, which increases their accessibility to each other.

5.6. Habitat Fragmentation Spreads the Risk of Extinction

Seven significant positive responses to habitat fragmentation were attributed by authors to the idea that habitat fragmentation spreads the risk of extinction over a larger number of sites, thus reducing the risk of simultaneous extinction of all local populations (den Boer 1968). For example, Martínez-Sanz et al. (2012, p. 161) argued that “the presence of a number of ponds relatively close to each other and interconnected by dispersal can be particularly important for biodiversity.” Note that the spreading of risk explanation is a general form of the previous two explanations, as “risk” can be caused not only by disturbances but also by predation, parasitism, or competition.

5.7. Habitat Fragmentation Increases Landscape Complementation

Finally, a few authors argued that, for species that require two or more different kinds of habitat for persistence, habitat fragmentation increases accessibility of these different habitat types—in other words, it increases “landscape complementation” sensu Dunning et al. (1992). When a habitat type is more fragmented, it is more interspersed with other required habitat type(s), increasing access to them (Figure 13). As argued by Slancarova et al. (2014, p. 8), “A landscape with heterogeneous configuration contains multiple edges and notches, which both support species requiring diverse resources located in close proximity.”

5.8. Which Explanation Is Correct?

At this point, it is not possible to draw conclusions as to which of the mechanism(s) causing significant positive fragmentation effects are most important. In most cases, the explanation provided by the authors was post hoc speculation rather than an a priori prediction because authors often had assumed, before conducting the study, that any detected responses to habitat fragmentation would be negative. In addition, a given author was likely to invoke the same explanation for most or all significant positive fragmentation effects found in his or her study, which likely affected the distribution of explanations I found (Figure 12). Some authors suggested the combined actions of more than one mechanism. Overall, it seems likely that all of the mechanisms above, and possibly additional ones, operate in at least some situations.

5.9. Matrix Quality and Landscape Heterogeneity

An additional possible explanation for significant positive effects of habitat fragmentation is that the matrix or nonhabitat portion of the landscape may often be more wildlife friendly in landscapes containing many small habitat patches than in landscapes containing a few large habitat patches. This seems particularly likely for agricultural landscapes where crop fields form the matrix. In fact, several studies have found positive relationships between landscape configurational heterogeneity (*sensu* Fahrig & Nutton 2005, Fahrig et al. 2011) and biodiversity in agricultural landscapes (Concepción et al. 2012, Flick et al. 2012, Lindsay et al. 2013, Fahrig et al. 2015).

Of course, the opposite could be true in some cases, and this may explain some of the significant negative responses to habitat fragmentation. For example, in a particular region, if landscapes with many small patches contain more roads than landscapes with a smaller number of large patches, the matrix quality of the former will be lower than the matrix quality of the latter, which could lead to higher road mortality in the former and thus an apparent negative response to habitat fragmentation. Elucidation of the possible role of matrix quality in creating positive or negative significant responses to habitat fragmentation requires studies in which variables such as road density, cropping system, etc. are included along with the habitat amount and fragmentation variables.

The potential role of matrix quality in mediating significant positive or negative responses to habitat fragmentation suggests that a more holistic view of the landscape may be needed. The idea that patchiness or spatial heterogeneity of the whole landscape can benefit biodiversity was originally proposed by Duelli (1997) as the mosaic concept. Duelli argued that important positive correlates of biodiversity are the amount of natural and seminatural area, the number of patches, and the length of ecotones between patch types. Duelli explicitly recognized that significant positive effects of landscape spatial heterogeneity run counter to habitat patch size and isolation effects as inferred from the theory of island biogeography (see figure 6 in Duelli 1997). Although Duelli discussed his mosaic concept only in the context of agricultural landscapes, the results of this review suggest that positive effects of landscape spatial heterogeneity may be more general. For example, Sattler et al. (2010) found increasing arthropod diversity with increasing landscape spatial heterogeneity within cities in Switzerland, and Hovick et al. (2015) created replicate grassland landscapes on a gradient of increasing landscape spatial heterogeneity and found positive relationships between landscape heterogeneity and bird diversity and community stability.

6. LIMITATIONS AND CAVEATS

The overall conclusion of this review, that most significant responses to habitat fragmentation are positive, appears to be robust to a wide variety of conditions. I attempted to identify sets of conditions that differentiate between mostly positive and mostly negative significant fragmentation effects, but I did not find any situations in which most effects were negative. However, I note that this failure may be an artifact of the structure of the data. The conditions represented by the 381 significant responses—taxa, study types, response and predictor variables, spatial scales, etc.—are not mutually independent. For example, SLOSS-type studies all used the same response (species richness), and studies of birds almost exclusively used single-species responses. Thus, the fact that I did not find any conditions in which most significant responses were negative does not mean that such situations do not exist. I reiterate, though, that this review shows that across a very wide range of conditions the majority of significant responses to habitat fragmentation are positive.

It is also important to bear in mind that the first aim of this review was to answer the question, “Are most significant responses to habitat fragmentation negative or positive?” Therefore, I included only the significant effects of habitat fragmentation. This review does not answer the question, “What is the overall effect of habitat fragmentation?” As I have discussed elsewhere

(Fahrig 2003, 2013), the overall effect of habitat fragmentation appears to be very weak. As this review does not include articles that found no significant effects of habitat fragmentation, I do not know the number of such nonsignificant effects. However, I attempted a rough estimate using the mean proportion of effects of fragmentation that are significant across the studies in my review containing at least 10 responses (typically responses of different species). For this estimate, I excluded studies that tested effects of multiple fragmentation metrics on each response, as this would inflate Type I error. Fourteen of the studies in my review met these criteria. Across these 14 studies, the mean proportion of responses to habitat fragmentation that were significant was 0.29 (SD 0.22). Thus, a rough estimate of the number of nonsignificant effects of fragmentation in the literature is $381/0.29$ or approximately 1,300 nonsignificant effects. The true number is likely higher, as the 14 studies used to make this estimate are biased, in that each of them had at least one significant effect of habitat fragmentation, a criterion for inclusion in my review. Thus, with a predominance of nonsignificant effects, and the fact that significant effects are both negative and positive, there is likely very little overall effect of habitat fragmentation on ecological responses (see also Fahrig 2003, 2013).

It is also important to keep in mind that, in this review, when I refer to a significant positive relationship, I am referring to only the direction of the relationship. No value judgment is intended. In some cases, a positive relationship may be viewed as a negative effect, for example, in the case of invasive species, pest species, or overabundant species. Such value judgments can differ depending on the geographic location. Similarly, in some situations higher species diversity may be less desirable than a system state with lower species diversity. However, the majority of significant responses to habitat fragmentation were positive even for threatened/specialist species and irrespective of IUCN status. Therefore, applying value judgments to the definition of positive would not change the overall conclusion of this review.

7. FINAL CONSIDERATIONS

7.1. The Fragmentation Zombie

So-called zombie ideas are ideas that should be dead but are not (Fox 2011). The results of this review suggest that the idea that habitat fragmentation, independent of habitat loss, has widespread negative effects on ecological responses qualifies as a zombie idea. It arose from (a) confounding habitat patchiness with habitat loss (see Section 1) and (b) inappropriate extrapolation of patch-scale patterns to landscape-scale inferences. The fact that this zombie has persisted for more than 45 years is a testament to its intuitive appeal (Fahrig 2017).

This review also suggests that the fragmentation zombie actually encompasses a whole family of zombie ideas. For example, the general expectation that a small number of large patches should contain more species than a large number of small patches persists, despite consistent reviews showing the opposite (this review, in addition to Simberloff & Abele 1982, Quinn & Harrison 1988). Other members of the fragmentation zombie family include the ideas that edge effects are generally negative, fragmentation reduces connectivity, habitat specialists show particularly negative responses to fragmentation, and negative fragmentation effects are particularly strong at low levels of habitat amount and in the tropics. The results of this review challenge all of these long-standing, persistent ideas.

7.2. Reframing the Fragmentation Message

It is important to be very clear about the fragmentation message implied by the results of this review. If, as shown here, significant effects of habitat fragmentation are more often positive than

negative, this implies the need for a more cautious approach to habitat conservation. Significant positive responses to fragmentation mean 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. The results also suggest that, generally speaking, land-sharing policies will provide higher ecological value than land-sparing policies (**Figure 2**).

It is also important to keep in mind that approximately 24% of significant responses to habitat fragmentation are negative. Therefore, there are likely some situations for which minimizing habitat fragmentation is a reasonable conservation goal. This might occur when conservation action is aimed at a particular species that is known to show a negative response to habitat fragmentation. However, I emphasize that the results of this review do not suggest more significant negative effects of fragmentation for more threatened species; if anything, they suggest the opposite (**Figure 9d,e**). Thus, although fragmentation has significant negative effects in some particular situations, these effects cannot be generalized.

The results of this review also indicate that the language associated with much of the habitat loss and fragmentation literature is leading to erroneous conclusions. Prior to approximately 2005, it was common to see statements such as “habitat fragmentation is a major cause of biodiversity erosion” (Tabarelli et al. 1999, p. 119) or “habitat fragmentation is a leading cause of extinction” (Bruna & Oli 2005, p. 1816). These statements clearly confounded habitat fragmentation with habitat loss. They summarized the patch-scale findings on patch size and isolation effects which, as discussed above (Section 2), are strongly confounded with effects of habitat loss and do not provide information on independent effects of habitat fragmentation.

Since approximately 2005, many authors have acknowledged that habitat loss and fragmentation are separate, the former being a process and the latter being a pattern (**Figure 2**). However, most authors still assume that the effects of habitat fragmentation independent of the effects of habitat loss are generally negative, as evidenced by the following statements: “Habitat loss and fragmentation are major threats to terrestrial biodiversity” (Prugh et al. 2008, p. 20770), “habitat loss and fragmentation are the principal causes of the loss of biological diversity” (Mbora & McPeck 2009, p. 210), “habitat loss and fragmentation cause significant loss of species richness” (Barth et al. 2015, p. 122), and “habitat loss and fragmentation inevitably cause biodiversity decline” (Barelli et al. 2015, p. 23).

The results of this review indicate that such statements are in fact false. Although habitat loss is, without doubt, one of the most significant causes of biodiversity decline, the significant responses to habitat fragmentation independent of habitat amount are rare and mostly positive.

DISCLOSURE STATEMENT

The author is not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

ACKNOWLEDGMENTS

I am grateful for helpful comments on previous versions of the manuscript and related presentations from the following: Igor Coelho, Sara Collins, Susie Crowe, Michelle Fairbrother, Sandra Martins de Freitas, Jessica Gurevitch, Jochen Jaeger, Jean-Louis Martin, Andrew Moraga, Anne Munier, Genevieve Perkins, Margaret Sawatzky, Chris Souliere, Lutz Tischendorf, and members of the Geomatics and Landscape Ecology Friday Discussion Group. This work was supported by the Natural Sciences and Engineering Research Council of Canada.

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