SYNTHESIS

The Habitat Amount Hypothesis implies negative effects of habitat fragmentation on species richness

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Abstract
The habitat amount hypothesis (HAH) predicts that species richness in a habitat site increases with the amount of habitat in the 'local landscape' defined by an appropriate distance around the site, with no distinct effects of the size of the habitat patch in which the site is located. It has been stated that a consequence of the HAH, if supported, would be that it is unnecessary to consider habitat configuration to predict or manage biodiversity patterns, and that conservation strategies should focus on habitat amount regardless of fragmentation. Here, I assume that the HAH holds and apply the HAH predictions to all habitat sites over entire landscapes that have the same amount of habitat but differ in habitat configuration. By doing so, I show that the HAH actually implies clearly negative effects of habitat fragmentation, and of other spatial configuration changes, on species richness in all or many of the habitat sites in the landscape, and that these habitat configuration effects are distinct from those of habitat amount in the landscape. I further show that, contrary to current interpretations, the HAH is compatible with a steeper slope of the species–area relationship for fragmented than for continuous habitat, and with higher species richness for a single large patch than for several small patches with the same total area (SLOSS). This suggests the need to revise the ways in which the HAH has been interpreted and can be actually tested. The misinterpretation of the HAH has arisen from confounding and overlooking the differences in the spatial scales involved: the individual habitat site at which the HAH gives predictions, the local landscape around an individual site and the landscapes or regions (with multiple habitat sites and different local landscapes) that need to be analysed and managed. The HAH has been erroneously viewed as negating or diminishing the relevance of fragmentation effects, while it actually supports the importance of habitat configuration for biodiversity. I conclude that, even in the cases where the HAH holds, habitat fragmentation and configuration are important for understanding and managing species distributions in the landscape.

KEYWORDS
habitat amount hypothesis, habitat fragmentation, habitat spatial configuration, landscape management, SLOSS, spatial scales, species richness, Species–Area Relationships
1 | THE HABITAT AMOUNT HYPOTHESIS (HAH)

Understanding how habitat amount and configuration affect species richness, occurrence or abundance has been one of the major focuses of research in ecology and biogeography, given its central importance for conservation planning and for landscape (or seascape) management. In particular, there is a vigorous debate on the relative importance of habitat amount (total area of habitat) and habitat spatial configuration (the spatial arrangement of the habitat) for biodiversity patterns and persistence (Fahrig, 2013, 2015; Haddad et al., 2015; Hanski, 2015; Martin, 2018; Wilcox & Murphy, 1985). The most widely accepted conceptual model, and the predominant consensus among ecologists, has been that both habitat amount and configuration (e.g. fragmentation) matter and need to be considered in conservation management (e.g. Haddad et al., 2015; Hanski, 2015).

Fahrig (2013) challenged this conceptual model by proposing the habitat amount hypothesis (HAH). The HAH states that species richness in a given habitat site should increase with the amount of habitat in the circular ‘local landscape’ defined by a certain distance D surrounding that site (scale of effect), with no additional (distinct) effects of the area of the habitat patch in which the habitat site is located.

The implications of the HAH are important, and the interpretations that have been made of this hypothesis since it was proposed are strong, both from a conceptual and conservation point of view. Fahrig (2013) stated that if the HAH was supported, considering habitat configuration independent of habitat amount would be unnecessary; there would be no distinct effects of habitat patch size and isolation on species richness. Torrenta and Villard (2017) stated that the HAH challenges the contention that fragmentation effects in the strict sense actually exist, which has important implications, both from a theoretical and a conservation perspective. Bueno and Peres (2019) stated that support for the HAH would imply that biodiversity conservation strategies should focus on retaining the maximum overall amount of habitat regardless of its configuration. MacDonald, Anderson, Acorn, and Nielsen (2018) stated that the HAH ‘negates fragmentation effects and predicts that only total habitat area determines the diversity of species persisting on fragmented landscapes’. Haddad et al. (2017) stated that ‘if supported, the Habitat Amount Hypothesis would fundamentally transform how landscapes are conserved by shifting focus away from considerations of habitat configuration and connectivity, toward total habitat area alone’. Melo, Sponchiado, Cáceres, and Fahrig (2017) concluded, after finding support for the HAH, that their results ‘support the notion that biodiversity protection policies should focus on habitat amount, irrespective of its spatial configuration’. Since it was proposed, the HAH has been supported by some studies (e.g. Melo et al., 2017; Rabelo, Bicca-Marques, Aragón, & Nelson, 2017; Seibold et al., 2017) but rejected by others (e.g. Evju & Sverdrup-Thygeson, 2016; Haddad et al., 2017; Lindgren & Cousins, 2017); see Martin (2018) for a meta-analysis.

I here challenge the interpretation that the HAH implies that habitat fragmentation or configuration is not important for species richness. I argue that even if the HAH holds, conservation strategies cannot focus only on the amount of habitat in the landscape, and should also consider the spatial arrangement of habitat in the landscape. I do not provide any arguments or empirical results supporting or rejecting the HAH. I assume that the HAH actually holds. I elaborate on the implications that the HAH actually has for the distribution of species richness in a landscape or region, contrary to the prevailing understanding on the implications of the HAH. I explain that the misinterpretation of the implications of the HAH in previous studies has been due to the confusion of different spatial scales: the individual habitat site, the local landscape around that site and the scale of an entire landscape or region comprising multiple habitat sites and local landscapes around them. Not clearly differentiating these spatial scales has led to misunderstandings on what the HAH really implies and how it can be actually tested.

2 | EVALUATING THE PREDICTIONS OF THE HABITAT AMOUNT HYPOTHESIS IN THE LANDSCAPE

2.1 | The local landscape and the habitat sites in the HAH

A key specification of the HAH is the distance D that defines the circular ‘local landscape’ (scale of effect) over which the amount of habitat determines species richness in a site (Fahrig, 2013). The distance D has no universal value, but has to be determined empirically in each case as the distance at which the habitat amount shows the strongest correlation with species richness. The studies that have evaluated the HAH have found D to range from 40 m to 5,500 m (Bueno & Peres, 2019; Evju & Sverdrup-Thygeson, 2016; Gardiner, Bain, Hamer, Jones, & Johnson, 2018; Lindgren & Cousins, 2017; Melo et al., 2017; Rabelo et al., 2017; Seibold et al., 2017; Thiele, Kellner, Buchholz, & Schirmel, 2018; Torrenta & Villard, 2017; Vieira, Almeida-Gomes, Delciellos, Cerqueira, & Crouzeilles, 2018), with an average D value of about 1,000 m. I make no assumption on the particular value of D, but just assume that the HAH holds, and therefore, that such scale of effect exists and has been determined in each particular case.

Here, I just assume that the habitat sites are equally sized and much smaller than the local landscape, as in all studies on the HAH. The particular relative size of the two (site versus local landscape) is not important for the illustrative cases shown and the arguments...
made hereafter. See Appendix S1 in Supporting Information for further details.

I will here use, for brevity, the term 'landscape' to refer to an area of any extent in which habitat is distributed. It may or may not be larger than the extent of a 'local landscape' (circle with radius $D$) as defined in the HAH; this will be specified in each particular case only when necessary. There is a key distinction between these two terms ('landscape' and 'local landscape'). When I refer to a 'landscape', I am concerned with the distribution of species richness in all the habitat sites found within the landscape; see for example any of the eight rectangular landscapes in Figure 1. When I refer to a 'local landscape', I take the HAH perspective and focus on an individual habitat site located in the centre of that local landscape; see any of the examples of individual habitat sites and their local landscapes highlighted in green within the landscapes of Figure 1. In this latter case, the concern is species richness only in a focal individual habitat site; this is the one for which the HAH gives the predictions based on the habitat amount in the local landscape around that site. Other habitat sites different from the focal habitat site may sum to the total amount of habitat in the local landscape (if the sites are close enough to the focal one) but the HAH does not predict species richness in the rest of the habitat sites from the information of that local landscape. In the HAH, the local landscape is determined specifically for a single focal site, and the HAH uses the information in that local landscape to give predictions for that focal habitat site only.

I will here consider that the habitat patches, and the landscapes that contain the habitat patches, may or may not be smaller than the scale of effect (extent of the local landscape, given by $D$), which is consistent with the studies on the HAH (Appendix S2). In any case, I

**FIGURE 1** Eight landscapes with the same habitat amount but different habitat spatial configuration. All these landscapes are larger than the extent of a local landscape (circle with radius $D$) of the habitat amount hypothesis. The three first landscapes (a-c) correspond to an increase in habitat fragmentation, with patch size larger than (a), equal to (b) or smaller than (c) the size of a local landscape in the habitat amount hypothesis, which is given by the distance $D$ (scale of effect). Landscapes d, e, f and h have a single habitat patch (as in a) but with different degrees of perforation or elongation. Landscape g is as b but with the habitat patches much closer to each other. The crosses ($\times$) and circles in green colour indicate some examples of habitat sites and their local landscapes (circles of radius $D$ around the sites), respectively, that differ in their location within landscapes a-h and in the amount of habitat in the local landscape.
will show that the conclusions below hold equally for patches larger or smaller than \( D \).

2.2 | Illustrative landscapes with the same habitat amount but different habitat spatial configuration: evaluating the implications of the HAH

I here consider two illustrative sets of landscapes that have the same amount of habitat but differ in the spatial configuration of it (Figures 1 and 2). The landscapes in Figure 1 are larger than a local landscape in the HAH (they are larger than a circle with radius \( D \)), and the individual habitat patches are larger or smaller than the extent of a local landscape depending on the cases (Figure 1). The landscapes in Figure 2 have the same extent as a local landscape (they are circles with radius \( D \)), and hence all the individual patches contained within these landscapes are smaller than the extent of a local landscape. The habitat in each of these landscapes in Figures 1 and 2 is distributed in equally sized habitat sites that are much smaller than \( D \); being so numerous and small, they are not shown, for the sake of clarity, in Figures 1 and 2. The particular size of the habitat sites is in any case inconsequential for the purposes here (see Appendix S1 for details).

I assume that the HAH for the distance \( D \) holds and I calculate, as described in the next section, species richness in each habitat location (site) in these landscapes using solely the HAH predictions, that is, as a function of the amount of habitat in the local landscape for each site. Some illustrative examples of habitat sites and their local landscapes are highlighted in green in Figure 1. These examples range from the full local landscape for a site covered by habitat, as in the green colour example to the left in Figure 1a, to considerably smaller percentages of habitat in the local landscape (<50%), as in the green colour examples in landscapes c and h in Figure 1.

2.3 | Calculating species richness in each habitat site in the landscape through the HAH

The formulation of the HAH does not explicitly specify or demonstrate which should be the functional form (e.g. linear or nonlinear) that best relates species richness in the habitat site with the amount of habitat in the local landscape. In the calculations presented below, I assume a linear relationship between habitat amount and species richness, as the simplest and most parsimonious function for the illustrative cases here considered. A linear relationship is also suggested from the results of the studies on the species-area relationship that have focused on ranges of habitat areas close to those typically considered in the HAH (see section S3.1 in Appendix S3). I also assume that species richness is zero in the site when there is no habitat in the local landscape. The linear relationship is hence given by:

\[
S_i = k \times A_i
\]

where \( S_i \) is species richness in the habitat site \( i \), \( A_i \) is the amount (area) of habitat in the local landscape of the site \( i \) (circle of radius \( D \) around the centre of \( i \)) and \( k \) is a constant relating both variables.

I apply this linear relationship, individually, to each of the locations (habitat sites) in the landscapes in Figures 1 and 2, and hence obtain the HAH-predicted value of \( S_i \) in each habitat site.

I then normalize the species richness values as \( S_{\text{norm},i} = S_i / S_{\text{max}} \), where \( S_{\text{max}} \) is the maximum value of \( S_i \) found in any of the landscapes in each of the figures in this study (a different \( S_{\text{max}} \) value for each figure is considered). The maximum \( S_{\text{max}} \) is found in the habitat site that, in each of these figures, has the largest habitat area in the local landscape. In Figure 1 there are some habitat patches that are larger than the extent of the local landscape (larger than a circle with radius \( D \)); hence some of the habitat sites have their local landscapes fully covered with habitat, and \( S_{\text{max}} \) is equal to \( k \) times the size of the

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**FIGURE 2** Five landscapes with the same habitat amount but different habitat spatial configuration in which the habitat is all distributed within the extent of a single local landscape (circle with radius \( D \)) of the habitat amount hypothesis. All habitat in landscapes a and e is found in a single habitat patch, which is more elongated in e. The habitat in landscapes b, c and d is fragmented in five equally sized habitat patches, but the distance between them differs in each of these landscapes. In these examples, it is assumed that no additional habitat is found beyond the boundaries shown for each of the landscapes.
local landscape. In the landscapes in Figure 2 this is not however the case, and the habitat site with the maximum values of $A_i$ and $S_i$ has about one fifth of the local landscape covered by habitat; hence, for Figure 2, $S_{max}$ is about 0.2k times the size of the local landscape. The $S_{norm,i}$ values are independent from $k$ and easier to interpret, and are hence those shown in Figures 3 and 4: $S_{norm,i} = 100\%$ corresponds to the maximum $S_i$ value found in the considered landscapes and 0% to the case of no habitat in the local landscape.

Finally, I calculate the following summary statistics of species richness over the entire habitat area in each landscape (aggregated values for all the habitat sites in each landscape): mean (Mean) and maximum (Max) value of $S_{norm,i}$ and percentage of habitat area in each landscape that has a $S_{norm,i}$ value within the top quartile (Q1: within the 75%-100% range). The results are shown in Figures 3 and 4.

In summary, I calculate species richness in each location (site) in these landscapes using solely the HAH predictions (Figures 3 and 4). That is, I calculate species richness in each location exclusively as an increasing function of the amount of habitat in the local landscape around each site.

By doing so, I obtain distributions of the species richness variable that are necessarily in full accordance with the HAH. In my elaborations

**FIGURE 3** Species richness ($S_{norm,i}$) predicted by the habitat amount hypothesis (HAH) in each of the landscapes in Figure 1, that is, calculated for each location (habitat site) $i$ as a linear function of the amount of habitat in the local landscape (distance $D$) around the site, as described in section 2.3. The figure indicates, for each landscape, the mean (Mean) and maximum (Max) value of $S_{norm,i}$ in the landscape as predicted by the HAH, as well as the percentage of habitat area in each landscape that has a value of $S_{norm,i}$ within the top quartile (Q1: within the 75%-100% range). The results show that an increased habitat fragmentation (breaking apart of habitat), elongation or perforation, while holding constant the amount of habitat, has negative effects on species richness in the landscape according to the HAH predictions. The species richness values are normalized ($S_{norm,i}$) so that 100% corresponds to the maximum value found in these landscapes (which happens when the entire local landscape is covered by habitat) and 0% to the case of no habitat in the local landscape. All habitat sites in these examples have however some amount of habitat in their surrounding local landscapes, so that $S_{norm,i}$ never goes below 15% in these examples. See Appendix S3 for a similar figure but calculating species richness as a power function of the habitat amount in the local landscape; the numbers of Mean, Max and Q1 vary, but they lead to the same trends and conclusions [Colour figure can be viewed at wileyonlinelibrary.com]
and discussion below, however, I will examine the broader results for the entire landscape (considering all habitat sites together) rather than narrowly focusing on an individual habitat site only.

All the conclusions obtained below hold for other plausible non-linear relationships, such as a power law giving a convex shape of the function between habitat amount in the local landscape and species richness in the site (linear relationship when both variables are log-transformed), as shown in sections S3.2 and S3.3 in Appendix S3.

3 | THE HABITAT AMOUNT HYPOTHESIS IMPLIES THE IMPORTANCE OF HABITAT FRAGMENTATION AND CONFIGURATION FOR BIODIVERSITY

3.1 | The HAH actually implies negative effects of habitat fragmentation on species richness

The predictions of the HAH in these illustrative landscapes (Figures 3 and 4) show clear effects of habitat configuration on species richness. The distribution of species richness, as predicted by the HAH, differs considerably across landscapes with the same total amount of habitat depending on habitat configuration (Figures 3 and 4).

Habitat fragmentation (breaking apart of the habitat into a larger number of smaller patches) in the landscape, while holding constant the amount of habitat, negatively affects, according to the HAH predictions, species richness in all or many of the habitat sites in the landscape. Compare, for example, Figure 3a with Figure 3c. All habitat sites in Figure 3a have a higher species richness than any of the habitat sites in Figure 3c. See Figures S4.1 and S4.2 in Appendix S4 for additional examples with even higher habitat fragmentation.

A more elongated shape of the habitat patches (narrower patches), or larger perforations within the patches, while holding constant the number of patches and the total habitat amount, also imply, according to the HAH predictions, a decline in species richness in all or many of the habitat sites in the landscape. This is apparent by comparing for instance Figure 3h with Figure 3a for the effect of patch elongation, or by comparing Figure 3f or 3d with 3a for the effect of patch perforation. All habitat sites in Figure 3a have
a higher species richness than any of the habitat sites in Figure 3h or 3f.

An increase in the distance between the habitat patches, while holding constant the total habitat amount and the number, size and shape of the patches, can also lead to declines in species richness in the landscape, depending on the cases. Compare for example Figure 3b with Figure 3g, or Figure 4b with Figure 4d.

A more detailed discussion on specific examples of the effect of habitat fragmentation, patch elongation, patch perforation or inter-patch distance on species richness, based on the cases in Figures 3, S4.2 and 4, is provided in section S4.1 in Appendix S4.

3.2 Habitat configuration in the landscape affects the amount of habitat around different habitat sites

I have shown that the values and distribution of species richness over the landscape are influenced by the spatial configuration of the habitat over the landscape when the HAH is assumed to hold. This is because the amount of habitat in the local landscapes surrounding each habitat site does depend on the spatial configuration of the habitat, and not just on its amount, at the landscape scale (Figures 1-4). In smaller, more elongated or perforated patches, and in some cases also in more distant patches, there will be less habitat sites with a high amount of habitat in their surrounding local landscapes. This makes species richness in the sites decline with habitat fragmentation or with other habitat spatial configuration changes in the landscape, even when the total amount of habitat in the landscape does not vary (Figures 3 and 4). See sections S4.2 and S4.3 in Appendix S4 for further details and discussion.

3.3 The scale of effect in the HAH is an explicit recognition of the negative effect of habitat isolation on species richness

It is also relevant to note that the distance D (scale of effect) in the HAH can be seen as an explicit recognition of the importance, and of the negative effect, of habitat isolation for species richness. According to the HAH, the distance between habitat sites matters, so that when the habitat sites, or the habitat patches (which contain sites), are located at large distances (compared to D) from each other, biodiversity is affected negatively. This is captured in the HAH through the amount of habitat in a local landscape; if sites are farther from each other, there will be less habitat locally, within the extent of the local landscape of each site. In the extreme, if all habitat sites are separated by distances larger than D, all the habitat found in the local landscape of any of the sites will be just that contained within the individual site. It also follows that if habitat sites or habitat patches are located at any distance larger than D, any additional increase in their distance will not translate in any further decline in species richness as predicted by the HAH. Beyond D, the characteristics (area of habitat) of a given habitat site or patch will have no influence on the species richness of the other habitat site or patch. It is therefore possible to view the distance D in the HAH basically as an isolation distance or as a maximum dispersal distance that is conceptually similar to that considered in many connectivity metrics and analyses.

4 WHY HAVE THE IMPLICATIONS OF THE HABITAT AMOUNT HYPOTHESIS BEEN MISINTERPRETED? THE CONFUSION OF DIFFERENT SPATIAL SCALES

4.1 The HAH predicts species richness at the scale of individual habitat sites, which is not the landscape scale

The HAH means that:

(i) species richness in an individual habitat site is only determined by the amount of habitat in the local landscape surrounding the site (distance D around the site), regardless of the configuration of habitat in the local landscape.

This statement cannot be however generalized or extrapolated further.

In particular, the HAH does not imply that:

(ii) species richness in an entire landscape, composed of multiple habitat sites with their different local landscapes distributed throughout the entire landscape, is only determined by the amount of habitat in the entire landscape regardless of habitat configuration.

There is a big difference between statements (i) and (ii). Statement (i) is correct as it refers only to the scales that are directly involved in the HAH as originally proposed, that is, an individual habitat site and the local landscape around it. Statement (ii) is incorrect because it involves and refers to spatial scales that are outside of the domain of the HAH as originally proposed; that is, it makes a statement about habitat amount and configuration over an entire landscape, rather than over the extent of an individual local landscape defined specifically for an individual habitat site. The HAH does not make any direct statement on the effects of habitat amount or configuration over an entire landscape; it is constrained to separately consider individual local landscapes around individual habitat sites. It is, therefore, not correct to state that, if the HAH holds, species richness in all of the habitat sites in the landscape is affected only by the amount of habitat in the entire landscape and not by the spatial configuration of habitat in the entire landscape.
Confounding these different scales, and wrongly considering these two different statements as equivalent, is the main reason why the HAH has been significantly misinterpreted to date. One of these misinterpretations is, for example, stating that, because the HAH holds, biodiversity protection policies should focus on habitat amount, irrespective of its spatial configuration (Melo et al., 2017). Other similar misinterpretations can be found in the statements on the HAH implications that are summarized in the third paragraph of the Introduction. As I have shown above, the HAH does in fact predict, when applied over entire landscapes made up of multiple habitat sites, negative effects of habitat fragmentation, elongation or inter-patch distance on species richness in all or many of the habitat sites in the landscape. This holds both when considering landscapes with the same extent as a local landscape (Figure 4) and when considering larger landscapes (Figures 3 and S4.2), as well as when considering patches either smaller or larger than the extent of a local landscape (Figures 3, S4.2 and 4).

4.2 | The HAH predicts species richness at the site scale, which is not the scale at which habitat amount is quantified

Regarding the two scales that are actually considered in the formulation of the HAH, it is important to remark that the HAH predicts species richness at a different scale from that at which habitat amount is quantified. The HAH only deals with, and only gives direct predictions on, species richness at the scale of the habitat site. The predictions of species richness in a habitat site are obtained from a single explanatory variable, the habitat amount in the local landscape. The extent or scale of effect involved in the explanatory variable (local landscape for the distance $D$) is different and much larger than the extent of the habitat site involved in the response variable (species richness). This difference in the extent of the site (scale of the response variable) and of the local landscape (scale of the explanatory variable) is clear and explicit in the description of the HAH (Fahrig, 2013). However, the meaning and implications of this scale difference for the interpretation and use of the HAH have not been sufficiently emphasized, and in some case have been overlooked, in the literature on the HAH. Fundamentally, this difference in the scale of the species richness and habitat amount variables in the HAH means that the HAH cannot be used to make any direct statement on species richness at any scale different from (larger than) the site scale, including the scale of the local landscape. This condition has been often not kept in mind in the uses, applications and tests of the HAH.

All in all, the confusion of the spatial scales and of the actual reach of the HAH has led to other significant and unreported misinterpretations of the HAH and its implications, as described next in Sections 5 and 6.

5 | The habitat amount hypothesis is compatible with higher species richness for a single large patch than for several small habitat patches (SLOSS)

One of the long-standing debates in ecology is the single large or several small (SLOSS) debate (e.g. Wilcox & Murphy, 1985). To maximize species richness, is it better to have a single large habitat patch or several small habitat patches with the same total habitat area?

Fahrig (2013) stated, in the legend of figure 5 on the empirical evaluation of SLOSS in her paper, that the HAH predicts that species number should increase with total area, irrespective of the number of patches making up that total, that is, that, according to the HAH, the same number of species should be found in a large patch as in several small patches with the same total area. Therefore, Fahrig (2013) considered the HAH to be ‘SLOSS neutral’, which is the term I will use here to refer to the case in which a large patch has the same species richness as several small patches with the same total area.

The statement of Fahrig (2013) on the HAH implying SLOSS neutrality does not necessarily hold however. Consider for instance the single large patch in Figure 3a and compare it with the 18 smaller patches with the same total area in Figure 3c. According to the HAH predictions applied to all sites in these landscapes, Figure 3c has a much lower mean and maximum species richness than Figure 3a. Figure 3c has no habitat site with a species richness in the top quartile (75%-100%), compared to about two-thirds of the habitat area in the top quartile of species richness in the large patch in Figure 3a. All habitat sites in Figure 3a have higher species richness than any of the habitat sites in Figure 3c. Because the HAH provides species richness predictions only at the scale of individual habitat sites, and not at the scale of an entire patch or landscape, it is not possible to determine, using the HAH, the total species richness in the landscape, which will depend on species turnover not predicted by the HAH. However, it is perfectly possible, and the most plausible result, that the total species richness in the landscape would be lower in Figure 3c compared to Figure 3a and other similar cases, as discussed in more detail in Appendix S5.

Therefore, I conclude that the HAH does not imply, in general, that several small patches will have the same species richness as a large patch with the same total area. It is perfectly compatible with the site-scale predictions of the HAH that total species richness is higher in a single large habitat patch than in several small ones with the same total area. Fahrig (2013) considered that having more species in a single large patch than in several small patches of the same total area would be indicative of an island effect consistent with the island biogeography theory (IBT). I here have argued, however, that the HAH is compatible with that same result and, therefore, whether the HAH or the IBT hold cannot be judged simply based on this SLOSS comparison without any additional, more detailed consideration. If, in general, the same number of species is found in a set of fragmented patches than in a single large patch of the same total area.
area, the explanation has to be found in a theory or hypothesis different from, or additional to, the HAH.

6 | A STEEPER SLOPE OF THE SPECIES–AREA RELATIONSHIP FOR MORE FRAGMENTED HABITAT IS COMPATIBLE WITH THE HABITAT AMOUNT HYPOTHESIS

Species–Area Relationships (SARs), which describe how the number of species recorded increases with the sampled area, are one of the most important laws in ecology (Scheiner, 2003; Triantis, Guilhaumon, & Whittaker, 2012).

Fahrig (2013) stated that the HAH can be tested by comparing the slope of the SAR across a set of different-sized patches with the slope of the SAR across a set of sample areas equal in size to these patches but contained within a region of continuous habitat. A steeper slope for the fragmented patches would be, according to Fahrig (2013), consistent with the island effect of the island biogeography theory (IBT) and inconsistent with the HAH. Other studies have followed this way of testing the HAH proposed by Fahrig. These studies either concluded support for the HAH because of no difference in the SAR slope in that comparison (Rabelo et al., 2017) or rejected the HAH because they found a steeper slope of the SAR for the non-continuous patches (Bueno & Peres, 2019; Haddad et al., 2017).

However, the HAH predictions lead to species richness patterns that differ considerably between habitat patches and sample areas with the same size in continuous habitat. This is clearly illustrated in the landscapes in Figure 5 and in the results of Figure 6, which I obtained using the same calculation procedure as described in section 2.3 (i.e. the same procedure applied above to produce Figures 3, 4 and S4.2). This difference in the predictions can be such that both mean and maximum species richness decrease in the fragmented habitat patches compared to the equivalent sample areas in continuous habitat (compare Figure 6Bf and 6Bc). Alternatively, it can be such that mean species richness decreases but there are some (even if much less) habitat sites with the same maximum value of species richness as in the non-fragmented case (compare Figure 6Af and 6Ac).

The HAH does not predict species richness at any scale larger than the habitat site, nor the species turnover between habitat sites. Therefore, it is not possible to use the HAH predictions to determine the slope of the SAR, which requires estimating species richness at scales (sampled areas) larger than the scale of a habitat site. However, given the difference in species richness in the habitat sites in the different-sized patches in Figure 6Af and 6Bf, and the lack of any difference in species richness in the sites in comparable sample areas in continuous habitat (Figure 6Ac and 6Bc), all of which result from the HAH predictions, it is perfectly possible that the SAR slope for the fragmented patches is steeper than for the continuous habitat. This steeper slope for fragmented habitat would be possible for a SAR of Type IV (Scheiner, 2003), in which each data point is from a sample corresponding to a unique area (patch), but also for other SAR types, such as those constructed by estimating the mean diversity for a given area from multiple combinations of habitat sites (Scheiner, 2003). This is further discussed in Appendix S5.

Therefore, the HAH is compatible with, and can imply in cases such as those illustrated in Figure 6, different SAR slopes

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**FIGURE 5** Two sets of different-sized non-continuous patches in fragmented landscapes (Af and Bf) compared to a set of sample areas (dashed lines) equal in size to these patches but contained within a landscape with continuous habitat (Ac and Bc). In case A, some of the habitat patches (Af) and sample areas (Ac) are larger than the size of a local landscape of the habitat amount hypothesis (HAH), as given by the distance $D$ (scale of effect). In case B, however, all habitat patches (Bf) and sample areas (Bc) are smaller than the size of a local landscape of the HAH.
depending on the degree of habitat fragmentation, and steeper SAR slopes for different-sized patches than for sample areas equal in size to these patches but contained within continuous habitat. It is not possible to support or reject the HAH based on the SAR slope. This highlights the need to revisit the ways in which the HAH can be tested, as well as the support, or the lack of support, to the HAH that has been concluded in previous studies based on the slope of the SAR (Bueno & Peres, 2019; Haddad et al., 2017; Rabelo et al., 2017).

The other ways to test the HAH proposed by Fahrig (2013) different from the SAR slope, which are summarized in figures 7 and 11 in her paper, remain appropriate for testing the HAH. This is so because, unlike for the SAR slope, these other ways of testing the HAH refer exclusively to predictions at the habitat site level that are made from the amount of habitat in the local landscape surrounding the site, which are respectively the response and explanatory scales involved directly in the HAH predictions.

7 | HANSKI’S RESPONSE TO FAHRIG

Hanski (2015) elaborated, in his reply to Fahrig (2013), on four objections to the HAH, the first of which was: ’My first concern is that the spatial scale of the habitat amount hypothesis is the local landscape around an individual study plot. This is a narrow perspective, which does not allow one to address fundamental questions about the occurrence of species within large landscapes with more or less habitat that is more or less fragmented’. This is indeed an important point, to which I would only add two notes. First, that there are two spatial scales, and not just one, in the HAH: the scale of the local landscape, where the habitat amount

**FIGURE 6** Species richness ($S_{norm,i}$) predicted by the habitat amount hypothesis (HAH) in each of the landscapes in Figure 5, that is, calculated for each location (habitat site) $i$ as a linear function of the amount of habitat in the local landscape (distance $D$) around the site, as described in section 2.3. The figure indicates, for each landscape, the mean (Mean) and maximum (Max) value of $S_{norm,i}$ in the landscape as predicted by the HAH, as well as the percentage of habitat area in each landscape that has a $S_{norm,i}$ value within the top quartile (Q1; within the 75%–100% range). In the landscapes with continuous habitat (Ac and Bc), the habitat is assumed to extend beyond the boundaries of the shown rectangles, and hence species richness remains high even close to the rectangle border. The species richness values are normalized ($S_{norm,i}$) so that 100% corresponds to the maximum value found in these landscapes (which happens when the entire local landscape is covered by habitat) and 0% to the case of no habitat in the local landscape. All habitat sites in these examples have however some amount of habitat in their surrounding local landscapes, so that $S_{norm,i}$ never goes below 12% in these examples. See Appendix S3 for a similar figure but calculating species richness as a power function of the habitat amount in the local landscape; the numbers of Mean, Max and Q1 vary, but they lead to the same trends and conclusions [Colour figure can be viewed at wileyonlinelibrary.com]
is measured, and the scale of the habitat site (study plot as named by Hanski) in which species occurrence or richness is predicted. Second, that even when the HAH only predicts the species richness in individual (small) habitat sites, it is possible to use the HAH, if one assumes that it holds, to predict species richness in each of the sites over large landscapes, providing the HAH-based pattern of species richness within large landscapes with more or less fragmented habitat, as done here in Figures 3, 4 and 6.

Hanski (2015) continued, stating that the conclusion on the unimportance of habitat configuration related to the HAH ‘may be valid for small spatial scales and when the total amount of habitat is large, but modelling and empirical studies demonstrate adverse demographic consequences of fragmentation when there is little habitat across large areas’. He continued with the following example: ‘to see the significance of this distinction, consider a focal site with its local landscape, which in one case is completely isolated from the rest of the habitat in the landscape, in another case completely surrounded by other habitat. It would be most surprising if the landscape context was not to make a difference to the occurrence of the species’. Hanski (2015) did not elaborate further on this issue. Particularly he did not notice, and this has not been noted either in any other article on the HAH so far, that the HAH itself, regardless of any other modelling approaches or empirical studies, does predict the importance of habitat configuration (or landscape context) in cases such as the one described by Hanski (2015). In fact, the example given by Hanski (2015) is demonstrated as true even if assuming that the HAH holds, and using the predictions from the HAH: compare the patches in Figure 6Af and 6Bf, which are ‘isolated’ from (not adjacent to) the rest of the habitat in the landscape, with the sample areas of the same size in Figure 6Ac and 6Bc respectively. The habitat sites in the isolated patches show lower species richness than the habitat sites in equivalent sample areas surrounded by habitat (Figure 6). Landscape context and habitat spatial configuration do make a difference, and have effects that are distinct from and go beyond those of habitat amount in a landscape. This conclusion is reached without needing an alternative hypothesis to the HAH or other mechanisms or theories such as island biogeography or metapopulation theory; this is the prediction that arises from the HAH itself.

8 | CONCLUSIONS

The HAH has triggered an intense debate, and a considerable number of empirical studies, on the relative importance of habitat amount and habitat fragmentation for biodiversity patterns and persistence. The prevailing view and interpretation of the HAH has been that, if or where it holds, it negates the existence of fragmentation effects and implies that conservation strategies should focus on retaining the maximum overall amount of habitat regardless of its configuration (Bueno & Peres, 2019; Fahrig, 2013; Haddad et al., 2017; MacDonald et al., 2018; Melo et al., 2017; Torrenta & Villard, 2017), as summarized in the Introduction.

I have here shown that, contrary to the current interpretations of the HAH, the predictions of the HAH actually imply clearly negative effects of habitat fragmentation on species richness in the habitat sites of a landscape or region, and that these fragmentation effects are distinct from those of habitat amount in the landscape or region. Therefore, even if the HAH holds, conservation strategies cannot focus only on the amount of habitat in a landscape or region, and should also consider its spatial configuration.

Many of the misunderstandings of the HAH arise from the omission of the key difference between the spatial scales involved in the HAH and the landscape or regional scales at which conservation management actions are to be applied. The HAH is based on measuring the amount of habitat in the local landscape (scale of effect) around a given habitat site, but only provides direct predictions on species richness at the scale of the individual habitat sites, which are much smaller than the landscape scale, the local landscape scale or the patch scale. When the site-scale HAH predictions are applied over entire landscapes, rather than to individual habitat sites considered separately, the important and distinct effects of habitat configuration in the landscape clearly show up. The difference in the scale of the species richness and habitat amount variables in the HAH means that the HAH cannot be used to make any direct statement on species richness at any scale different from (larger than) the site scale, including the scale of the local landscape. This condition has often not been kept in mind in the use, application and conceptualization of the HAH, which has led to significant and previously unreported misinterpretations of the implications of this hypothesis and of the ways it can be actually tested.

I reiterate that I have here not provided any argument in favour or against the validity of the HAH. My arguments only refute some of the interpretations that have been made regarding the meaning or implications of this hypothesis, but not the HAH itself, which I have assumed to hold in all my arguments. My conclusions do not mean that concepts behind the HAH logic, such as considering equally sized habitat sites instead of habitat patches as the natural spatial units for measuring and analysing species richness (Fahrig, 2013), are not of value for landscape ecology and biogeography. Even some empirical studies that have not found support for the HAH have agreed with the interest of shifting from habitat patches to equally sized units of analysis (Torrenta & Villard, 2017).

Hanski (2015) concluded, in his response to Fahrig (2013) objecting the validity of the HAH, that ‘habitat fragmentation poses a threat to biodiversity, in addition to the threat posed by the loss of the total amount of habitat. Fragmentation effects should not be overlooked in ecology or in conservation’. Haddad et al. (2017) concluded, in their study rejecting the HAH, that ‘in conservation, only considering one attribute of landscapes (i.e. habitat amount) … could misguide protected area management’. I support these conclusions, and show that they are, in fact, a prediction of the HAH. Reaffirming the importance of habitat fragmentation and configuration for biodiversity does not depend on rejecting the HAH and using other explanatory framework, hypothesis or theory; on the contrary, the actual implications and predictions of the
HAH support the importance of habitat fragmentation and configuration for biodiversity.

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DATA AVAILABILITY STATEMENT
There are no data associated with this article.

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REFERENCES
Bueno, A. S., & Peres, C. A. (2019). Patch-scale biodiversity retention in fragmented landscapes: Reconciling the habitat amount hypothesis with the island biogeography theory. Journal of Biogeography, 46(3), 621–632. https://doi.org/10.1111/jbi.13499
Evju, M., & Sverdrup-Thygeson, A. (2016). Spatial configuration matters: A test of the habitat amount hypothesis for plants in calcareous grasslands. Landscape Ecology, 31, 1891–1902. https://doi.org/10.1007/s10980-016-0405-7
Fahrig, L. (2013). Rethinking patch size and isolation effects: The habitat amount hypothesis. Journal of Biogeography, 40, 1649–1663. https://doi.org/10.1111/jbi.12130
Fahrig, L. (2015). Just a hypothesis: A reply to Hanski. Journal of Biogeography, 42, 993–994. https://doi.org/10.1111/jbi.12504
Gardiner, R., Bain, G., Hamer, R., Jones, M. E., & Johnson, C. N. (2018). Habitat amount and quality, not patch size, determine persistence of a woodland-dependent mammal in an agricultural landscape. Landscape Ecology, 33, 1837–1849. https://doi.org/10.1007/s10980-018-0722-0
Haddad, N. M., Brudvig, L. A., Clobert, J., Davies, K. F., Gonzalez, A., Holt, R. D., ... Townshend, J. R. (2015). Habitat fragmentation and its lasting impact on Earth’s ecosystems. Science Advances, 1, e1500052. https://doi.org/10.1126/sciadv.1500052
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. https://doi.org/10.1111/ecog.02535
Hanski, I. (2015). Habitat fragmentation and species richness. Journal of Biogeography, 42, 989–993. https://doi.org/10.1111/jbi.12478
Lindgren, J. P., & Cousins, S. A. (2017). Island biogeography theory outweighs habitat amount hypothesis in predicting plant species richness in small grassland remnants. Landscape Ecology, 32, 1895–1906. https://doi.org/10.1007/s10980-017-0544-5
MacDonald, Z. G., Anderson, I. D., Acorn, J. H., & Nielsen, S. E. (2018). Decoupling habitat fragmentation from habitat loss: Butterfly species mobility obscures fragmentation effects in a naturally fragmented landscape of lake islands. Oecologia, 186, 11–27. https://doi.org/10.1007/s00442-017-4005-2
Martin, C. A. (2018). An early synthesis of the habitat amount hypothesis. Landscape Ecology, 33, 1831–1835. https://doi.org/10.1007/s10980-018-0716-y
Melo, G. L., Sponchiado, J., Cáceres, N. C., & Fahrig, L. (2017). Testing the habitat amount hypothesis for South American small mammals. Biological Conservation, 209, 304–314. https://doi.org/10.1016/j.biocon.201702.031
Rabelo, R. M., Bicca-Marques, J. C., Aragón, S., & Nelson, B. W. (2017). Are fluvial islands “real” islands for arboreal mammals? Uncovering the effect of patch size under the species–area relationship. Journal of Biogeography, 44, 1802–1812. https://doi.org/10.1111/jbi.13034
Scheiner, S. M. (2003). Six types of species–area curves. Global Ecology and Biogeography, 12, 441–447. https://doi.org/10.1046/j.1466-822X.2003.00061.x
Seibold, S., Bässler, C., Brandl, R., Fahrig, L., Förster, H., Heurich, M., ... Müller, J. (2017). An experimental test of the habitat-amount hypothesis for saproxylic beetles in a forested region. Ecology, 98, 1613–1622. https://doi.org/10.1002/ecy.1819
Thiele, J., Kellner, S., Buchholz, S., & Schirmel, J. (2018). Connectivity or area: What drives plant species richness in habitat corridors? Landscape Ecology, 33, 173–181. https://doi.org/10.1007/s10980-017-0606-8
Torrenta, R., & Villard, M. A. (2017). A test of the habitat amount hypothesis as an explanation for the species richness of forest bird assemblages. Journal of Biogeography, 44, 1791–1801. https://doi.org/10.1111/jbi.13022
Triantis, K. A., Guilhaumon, F., & Whittaker, R. J. (2012). The island species–area relationship: Biology and statistics. Journal of Biogeography, 39, 215–231. https://doi.org/10.1111/j.1365-2699.2011.02652.x
Vieira, M. V., Almeida-Gomes, M., Delciellos, A. C., Cerqueira, R., & Crouzeilles, R. (2018). Fair tests of the habitat amount hypothesis require appropriate metrics of patch isolation: An example with small mammals in the Brazilian Atlantic forest. Biological Conservation, 226, 264–270. https://doi.org/10.1016/j.biocon.2018.08.008
Wilcox, B. A., & Murphy, D. D. (1985). Conservation strategy: The effects of fragmentation on extinction. The American Naturalist, 125, 879–887. https://doi.org/10.1086/284386

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SUPPORTING INFORMATION
Additional supporting information may be found online in the Supporting Information section.

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