CORRESPONDENCE

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What the habitat amount hypothesis does and does not predict: A reply to Saura

Abstract

Saura (2020) used the habitat amount hypothesis (HAH) to predict negative effects of fragmentation per se on mean species density per site over a region. This prediction is valid but incomplete; the HAH can also predict positive effects of fragmentation on mean species density per site over a region. Saura also stated, "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)." Importantly, the HAH does not predict species-area relationship (SAR) slopes or SLOSS. These require information about how species composition changes over space, while the HAH only predicts species density per site. The HAH is therefore equally compatible with a steeper or shallower SAR slope for fragmented than continuous habitat, and the HAH is equally compatible with either outcome of SLOSS.

Saura (2020) used the habitat amount hypothesis (HAH) to predict negative effects of habitat fragmentation per se of a region, on mean and maximum species density (number of species at a site) across sites over the region. He also stated that "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)." As pointed out by Saura, some predictions that have been attributed to the HAH do not logically derive from it. Saura's predictions regarding effects of habitat fragmentation per se on mean and maximum species density across sites in a region are valid, but they are incomplete; the HAH can also predict positive effects of fragmentation per se on mean and maximum species density across sites in a region. In addition, it is important to clarify that the HAH makes no predictions about species-area relationship (SAR) slopes or SLOSS. Such predictions require information about how species composition changes over space, while the HAH only

makes predictions about species density at individual sites. The HAH is therefore equally compatible with either a steeper or shallower slope of the species–area relationship for fragmented than for continuous habitat, and the HAH is equally compatible with either higher or lower species richness for a single large patch (or few large patches) than for several small patches with the same total area (SLOSS).

1 | CORE PREDICTIONS OF THE HAH

The HAH (Fahrig, 2013) predicts that species richness at a sample site (species density) is positively related to the amount of habitat within a biologically meaningful distance of that sample site (its "local landscape"; Figure 1). The habitat within the local landscape determines the species pool available to colonize the site. The HAH further predicts that this effect of habitat amount encompasses the combined effects on species density of the size and isolation of the patch containing the sample site. Put another way, the HAH argues that the size and isolation of the patch containing a sample site only influence species richness at that site through their relationships to the amount of habitat in the site's local landscape. Habitat amount in the local landscape generally increases with the size of the local patch and decreases with its isolation. The HAH thus argues that the effects of local patch size and isolation on species density at a site are both contained within the effect of habitat amount, and therefore the effect of habitat amount on species density at a site is as strong as or stronger than the effect of local patch size, local patch isolation or their combination. Furthermore, once habitat amount is accounted for, there should be no residual effects of local patch size or isolation on species density at a sample site.

Note that the size of the local landscape must be empirically estimated (e.g., Watling et al., 2020; see Figure 1). Measuring habitat amount over an area that is too small (or too large) will underestimate (or overestimate) the habitat contributing the species pool for the sample site. Thus, while the size and isolation of the patch containing the sample site can be measured directly, measuring the amount of habitat requires first estimating the size of the local landscape. Guesstimating the size of the local landscape a priori is generally not successful (Jackson & Fahrig, 2015), likely because it depends on a large number of interacting factors (Miguet et al., 2016). Rather, it should be estimated in a multi-scale empirical analysis (see Figure 1).
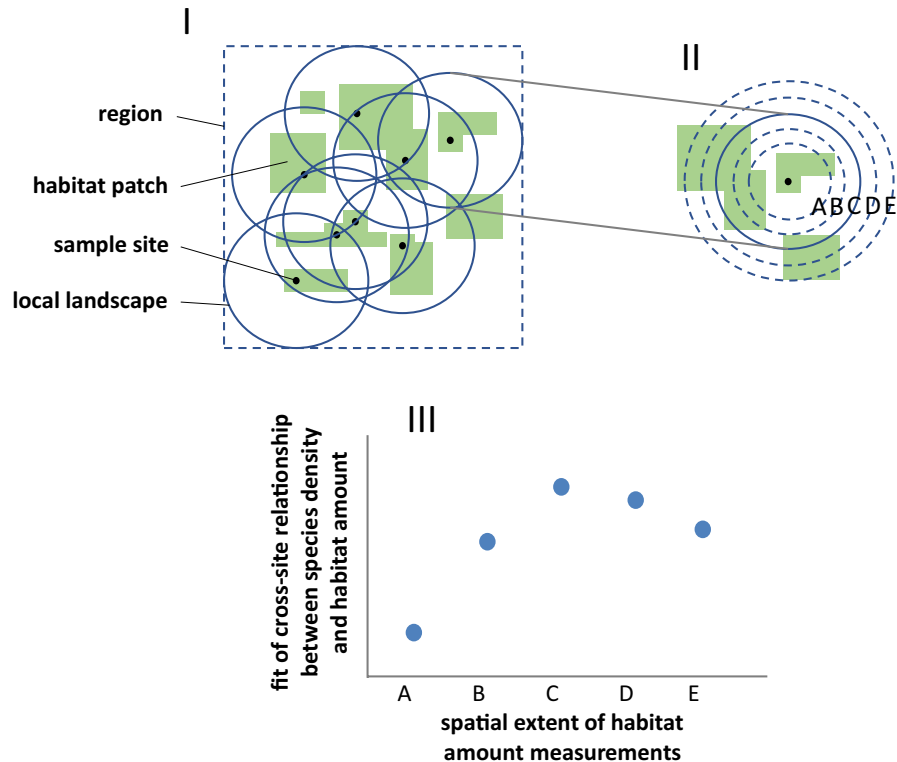
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FIGURE 1 I: Illustration of a region containing habitat patches (green shapes), sample sites within habitat patches (black dots), and the local landscape surrounding each sample site (circles centred on black dots). The habitat amount hypothesis (HAH) predicts that the number of species at a sample site (species density) increases with the amount of habitat in its local landscape, and that this relationship is as strong as or stronger than the combined effects of the size and isolation of the patch containing the sample site on species density at the site. II and III: While the size and isolation of a habitat patch can be measured directly, measuring the amount of habitat in the local landscape first requires estimating the size of the local landscape (C). This can be done by estimating the relationship between species density and habitat amount measured at each of multiple nested spatial extents. Measuring habitat amount over an extent that is too small (A and B) will underestimate the habitat contributing the species pool for the sample site. Measuring habitat amount over an extent that is too large (D and E) will overestimate the habitat contributing the species pool for the sample site [Colour figure can be viewed at wileyonlinelibrary.com]

Note also that the arguments leading to the HAH do not specify a particular size for sample sites. However, all sample sites in a given study should be the same size and completely contained within habitat. It is not yet known whether or how the size of the local landscape depends on the size of the sample sites.

I emphasize that the HAH does not argue that habitat amount is the only determinant of species density. For example, habitat quality and matrix quality also affect species density (Fahrig, 2013). The HAH only argues that the effects of local patch size and isolation on species density at a sample site are contained in, and therefore can be replaced by, the effect of habitat amount in the local landscape.

Testing the core predictions of the HAH requires estimates of species density at sample sites across multiple patches that vary in size and/or isolation (see figures 7 and 11 in Fahrig, 2013). The strongest tests of the HAH have low correlations between habitat amount in the local landscapes and both local patch size and isolation, allowing detection of effects of local patch size and isolation independent of habitat amount effects, if they exist (which would counter the HAH). Watling et al. (2020) conducted the most comprehensive test to date of the core predictions of the HAH, using species density data from 32 studies of 5,675 forest-associated

species from eight major taxa in 554 forest patches on six continents. I recommend that future tests of the HAH follow the methods in Watling et al. (2020).

2 | WHAT THE HAH DOES AND DOES NOT PREDICT ABOUT EFFECTS OF HABITAT CONFIGURATION

2.1 | Habitat configuration in the local landscape

In addition to these core predictions, if the HAH is correct then we can infer that the spatial configuration of habitat within the local landscape has little or no effect on species density at the sample site. This is because, for a given total amount of habitat within the local landscape, altering the size and isolation of the local patch alters the configuration of habitat in the sample site's local landscape. If two sample sites have the same amount of habitat in their respective local landscapes, but differ in the size and/or isolation of their respective local patches, the HAH predicts no difference in species density at the two sites. Therefore, to the extent that differences in local patch

size and isolation indicate differences in habitat configuration in the local landscape, the HAH predicts no effect of habitat configuration within the local landscape on species density at the sample site, beyond the effect of habitat amount. As habitat fragmentation per se is an aspect of habitat configuration, i.e. the number of patches for a given amount of habitat, this leads to the prediction that habitat fragmentation per se within the local landscape has no effect on species density at a sample site.

Watling et al. (2020) tested and found support for this prediction in a global analysis of forest taxa. Fragmentation per se of habitat within the local landscape, measured as the number of forest patches, was not included in the most plausible model of species density in over 85% of studies examined (28 of 32 studies). Interestingly, in all four studies with a detectable effect of fragmentation per se, species density increased with fragmentation per se, i.e. positive fragmentation effects. In a large, multi-taxa study in the Brazilian Atlantic Forest, Püttker et al. (2020) similarly found no significant effects of forest fragmentation per se on species density, when fragmentation was measured as the number of forest patches. However, at high levels of forest cover they found negative effects of fragmentation per se, when fragmentation was measured as edge density.

2.2 | Habitat configuration in the region

The main contribution of Saura (2020) was to use the HAH to predict the effect of habitat configuration in a region (rather than in a local landscape) on mean and maximum species density across sites over the region. Note here I use "region" rather than "landscape" to avoid confusion with "local landscape." Saura used regions with different hypothetical habitat patterns to show that regional habitat fragmentation per se can result in most sample sites having low amounts of habitat in their local landscapes (compare Region A to Region B in Figure 2). As the HAH predicts a positive relationship between habitat amount in the local landscape and species density at a sample site, a lower mean and maximum habitat amount across sample sites in a region should lead to a lower mean and maximum species density across sites in a more fragmented region than in a less fragmented region with the same total amount of habitat.
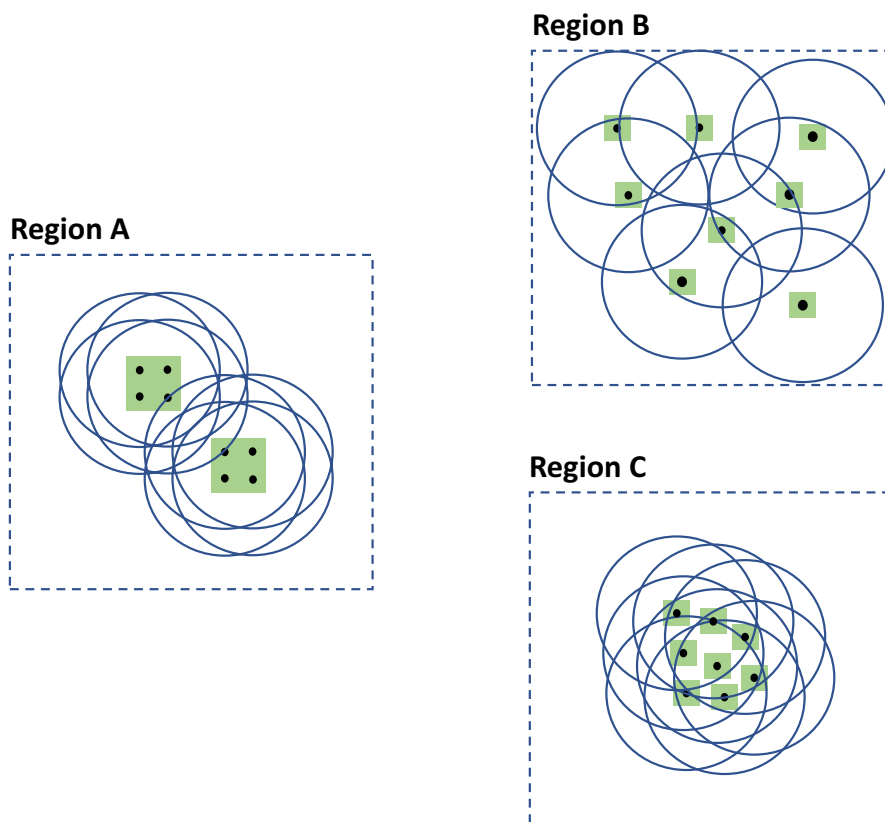

FIGURE 2 The habitat amount hypothesis (HAH) predicts negative, positive (or no) effect of habitat fragmentation per se on mean and maximum species density across sites in a region. Regions A, B and C have the same total amount of habitat; fragmentation is higher (more, smaller patches) in B and C than in A. The mean habitat amount within the eight local landscapes (circles) of the eight sample sites (black dots) in Region A is 52% of all habitat in the region. In Region B the mean habitat amount is 23%, and in Region C the mean habitat amount is 85%. If we assume (as does Saura, 2020) a proportional relationship between species density and habitat amount in the local landscape, then the predicted mean species density across sample sites is 56% lower in Region B than in Region A (negative fragmentation effect), and 63% higher in Region C than in Region A (positive fragmentation effect). Maximum species density across sample sites is 44% lower in Region B than in Region A, and 73% higher in Region C than in Region A [Colour figure can be viewed at wileyonlinelibrary.com]

This prediction is correct for the hypothetical habitat patterns provided by Saura (2020). However, it is important to note that in Saura's habitat patterns, the patches in the more fragmented regions were farther apart than those in the less-fragmented regions (e.g. compare Saura's figures 3a and 3c; see also Region A versus. Region B in Figure 2). When the reverse is true, i.e. when the patches in the more fragmented region are closer together than the patches in the less fragmented region, the HAH can predict higher mean and maximum species density across sites in a more fragmented region than in a less fragmented region, i.e. positive fragmentation effects (compare Region A to Region C in Figure 2). While theoretical studies often assume that patches in a more fragmented region are farther apart than patches in a less fragmented region (e.g. Tjørve, 2010), the empirical support for this assumption is unclear. Indeed, J.I. Watling (pers. comm.) found no consistent relationship across landscapes between the maximum distance between habitat edges and the number of patches (fragmentation), for the 32 studies included in Watling et al. (2020). Therefore, Saura's statement that the HAH "implies clearly negative effects of habitat fragmentation... on species richness" is not entirely accurate. Depending on how far apart the patches are, the HAH predicts that fragmentation per se can increase or decrease (or have no effect on) mean and maximum species density across sites in a region.

While these are interesting geometric thought experiments, it is important to note their limitations. Most importantly, these predictions are *not* about total species richness (gamma diversity) in a region. As noted by Saura (2020), the HAH makes predictions about species richness at an individual sample site, i.e. species density. Such site-scale predictions cannot be used to estimate total species richness in a region without information about how species composition changes between sites, which the HAH does not predict (see Section 3). Nevertheless, Saura's predictions and the predictions in Figure 2 about effects of habitat fragmentation per se on mean and maximum species density across sites in a region are interesting and should be tested empirically.

3 | WHAT THE HAH DOES NOT PREDICT ABOUT SAR SLOPES AND SLOSS

Two observations contributed to development of the HAH (Fahrig, 2013): (a) lack of empirical support for the prediction that the slope of the SAR should generally be steeper for sets of habitat patches than for sets of sample areas within continuous habitat; and (b) lack of empirical support for the prediction that there should generally be more species in a single large patch than in several small ones of the same total area (SLOSS). These observations led me to infer that habitat patches are not analogous to the islands of MacArthur and Wilson's (1967) theory of island biogeography. Note that these observations about SAR slopes and SLOSS are not predictions from the HAH but rather observations that led to its development. However, in Fahrig (2013) I incorrectly proposed comparing

SAR slopes as a way of testing the HAH. I am grateful for this opportunity to correct that statement.

In fact, predictions for SAR slopes and SLOSS cannot be derived from the HAH because they require a model that can predict cumulative species richness over sites and patches. As has long been recognized (e.g., Higgs & Usher, 1980; Margules et al., 1982; Nekola & White, 1999), this requires knowledge of how species composition changes over space, both within patches (for SAR slopes) and across patches (for SLOSS). For example, Giladi and Ziv (2020) found lower between-site differences in species composition within large patches than within small patches. The HAH only predicts species density at individual sites, and makes no assumptions or predictions about how species composition changes over space, within or across patches.

Consistent with this, Saura (2020) correctly stated: "the HAH cannot be used to make any direct statement on species richness at any scale different from (larger than) the site scale"; and, "it is not possible to use the HAH predictions to determine the slope of the SAR"; and, "it is not possible to determine, using the HAH, the total species richness in the landscape." However, in apparent contradiction to these statements, he then went on to conclude that "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)." Importantly, Saura included this last statement (but not the previous ones) in the Abstract of his paper. While "compatible with" does not necessarily imply a prediction, readers of Saura's Abstract are likely to incorrectly infer that the HAH predicts steeper SAR slopes for fragmented than continuous habitat and higher species richness for a single (or few) large than several small patches. In the remainder of this section I summarize Saura's arguments for SAR slopes and SLOSS, and I present plausible arguments resulting in opposite patterns to those suggested by Saura. I do this to illustrate that the HAH is equally compatible with either a steeper or shallower SAR slope for fragmented than for continuous habitat, and is equally compatible with either outcome of SLOSS.

Saura's arguments supporting his suggestions about SAR slopes and SLOSS involved extrapolations from species density at sites to species richness over patches (for SAR slopes) and species richness over regions (for SLOSS). In support of his suggestion regarding SAR slopes, Saura noted that the HAH will often predict higher species density at sites in large patches than at sites in small patches (supported in Chase et al., 2020; Watling et al., 2020), because the former often have more habitat in their local landscapes than the latter. He also noted that in a region of continuous habitat, the HAH predicts the same species density everywhere, as all sites have 100% habitat in their local landscapes. He then extrapolated from species density at sites to species richness over patches, suggesting that the slope of the SAR should be steeper for a set of patches than for a set of sample areas in continuous habitat. In support of his suggestion regarding SLOSS, Saura extrapolated from higher predicted species density at sites in large than small patches, to suggest that a region

containing few large patches should hold more species than a region containing several small patches of the same total area.

Here, I argue that consideration of how species composition changes over space can produce patterns opposite to those suggested by Saura (2020). For SAR slopes, the opposite pattern would occur if between-site differences in species composition across a habitat patch are lower than between-site differences in species composition across a sample area of the same size within continuous habitat. This is a reasonable expectation, especially for large patches and sample areas. Based on the distance effect (Nekola & White, 1999), the difference in species composition of habitat specialists at the centre versus edge of a patch should increase with increasing patch size. The same is true for the centre versus edge of a sample area within continuous habitat. However, this distance effect should be larger for sample areas in continuous habitat than for patches. This is because most or all of the habitat in the local landscape of a site at the edge of a large habitat patch is comprised of the patch itself, while no more than 50% of the habitat in the local landscape of a site at the edge of a large sample area in continuous habitat is comprised of habitat within that sample area. This means that the species pools contributing to edge and centre sites should be more similar for a habitat patch than for a sample area of the same size within continuous habitat. Between-site differences in composition of habitat specialist species across a habitat patch should thus be lower than between-site differences in species composition across a sample area of the same size within continuous habitat. And, this difference should increase with the size of the patch/sample area, which should steepen the SAR for sample areas in continuous habitat relative to the SAR for habitat patches. This would counter the suggested pattern described by Saura, and could lead to the common empirical finding of no difference in SAR slopes between habitat patches and sample areas within continuous habitat (reviewed in Fahrig, 2013).

Reasonable assumptions of how species composition changes over space can also lead to the opposite pattern to that suggested by Saura for SLOSS. May et al. (2019) showed that a set of small patches will generally intersect more species distributions than will a set of large patches. In other words, variation in species composition among sample sites should be higher across several small patches than across a few large patches of the same total area. This should result in more species over several small than few large patches. This prediction is supported in my recent review of empirical SLOSS studies (Fahrig, 2020), in which I found five times as many cases where several small patches hold more species than few large patches, than the reverse.

To reiterate, predictions about SAR slopes and SLOSS cannot be derived from the HAH. They require models that can predict cumulative species richness over sites and patches. This requires information about how species composition changes over space, while the HAH only predicts species density at individual sites. Thus, the HAH is equally compatible with either a steeper or shallower SAR slope for fragmented than for continuous habitat, and is equally compatible with either outcome of the SLOSS question.

4 | CONSERVATION IMPLICATIONS

What are the implications of the HAH for biodiversity conservation? In his concluding remarks, Saura (2020) stated that his analyses support Hanski's (2015) conclusion that "habitat fragmentation poses a threat to biodiversity, in addition to the threat posed by the loss of the total amount of habitat." I suggest that this conclusion is not strongly supported by the HAH.

Altering the level of habitat fragmentation per se can be an objective for conservation of biodiversity at each of two spatial scales relevant to management (Gaston et al., 2006). On one hand, the manager of a small park may be concerned about how fragmentation of habitat in the landscape surrounding that park will affect the biodiversity within it. This is where the predictions of the HAH are relevant to conservation. If we consider the park itself as a sample site, then the HAH predicts that the amount of habitat surrounding the park, within a relevant distance (its local landscape), will influence the biodiversity in the park, but the configuration of that habitat will not. On the other hand, a conservation agency may be concerned about protecting biodiversity over a region, e.g. an ecoregion, a province, a country etc. In this case the objective is to protect gamma diversity by ensuring that every species is protected somewhere within a set of protected areas, for instance using gap analysis and systematic conservation planning (e.g., Smith et al., 2019). As discussed above, the HAH makes no predictions about gamma diversity and so is not relevant in this situation.

What then are the conservation implications of Saura's (2020) observation that the HAH can predict negative effects of habitat fragmentation per se on mean and maximum species density across sites in a region? This prediction is relevant to neither the manager of a small park who is concerned about the influence of the surrounding landscape on biodiversity in the park, nor to the manager of a region who wants to maximize total species richness in the region. It might be relevant for a manager who aims to maximize mean species density across sites in a region, though this seems to me an unlikely objective. Even in this case, the effect of fragmentation per se, and the implications for management, will depend on the distances among patches in the region (Figure 2).

To conclude, Saura (2020) showed that the HAH can predict negative effects of fragmentation per se on mean and maximum species density across sites in a region. However, these predictions are incomplete; the HAH can also predict the opposite, depending on the distances among patches (Figure 2). I suggest that these predictions are interesting and worthy of empirical study. Saura also argued that 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). I emphasize that the HAH does not actually make predictions about SAR slopes or SLOSS. Such predictions require information about how species composition changes over space, while the HAH only makes predictions about species density at individual sites. As such, the opposite patterns to those suggested by Saura are equally compatible with the HAH. Finally, I agree with Saura on an important point: there are "misunderstandings on

what the HAH really implies." I hope that this reply to Saura's paper will help to correct some of those misunderstandings.

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