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Just a hypothesis: a reply to Hanski

ABSTRACT

Hanski's critique of the habitat amount hypothesis (Hanski, 2015, *Journal of Biogeography*, **42**, 989–993) does not actually constitute a test of the hypothesis, but rather a series of arguments for why he suspects that it is not correct. But the habitat amount hypothesis is exactly that – a hypothesis. It will remain 'just' a hypothesis until it has been rigorously tested against empirical data. To facilitate such testing, in Fahrig (2013, *Journal of Biogeography*, **40**, 1649–1663) I presented specific, testable predictions of the hypothesis. Here, I reiterate the main tests needed, in the hope that some readers will be encouraged to carry them out. I appreciate this opportunity to emphasize that the habitat amount hypothesis needs to be tested against empirical data, and I

look forward to seeing the results of such tests.

In his critique of Fahrig (2013), Hanski presents a series of arguments for why he suspects that the habitat amount hypothesis is not correct. I do not find Hanski's arguments convincing, but that is beside the point. The point is, rather, that the habitat amount hypothesis is 'just' a hypothesis. It will remain just a hypothesis until it has been rigorously tested against empirical data, preferably several times. The final verdict on the habitat amount hypothesis will depend on the results of such rigorous hypothesis testing.

To encourage such testing, in Fahrig (2013) I specify clear, testable predictions (see section 'How to test the habitat amount hypothesis' in Fahrig, 2013). The three main predictions, illustrated in Fig. 1 below and in Fig. 7 in Fahrig (2013), are as follows. First, across a set of same-sized sample sites, where the patches containing the sample sites (the 'local patches') are the same size, but the amount of habitat
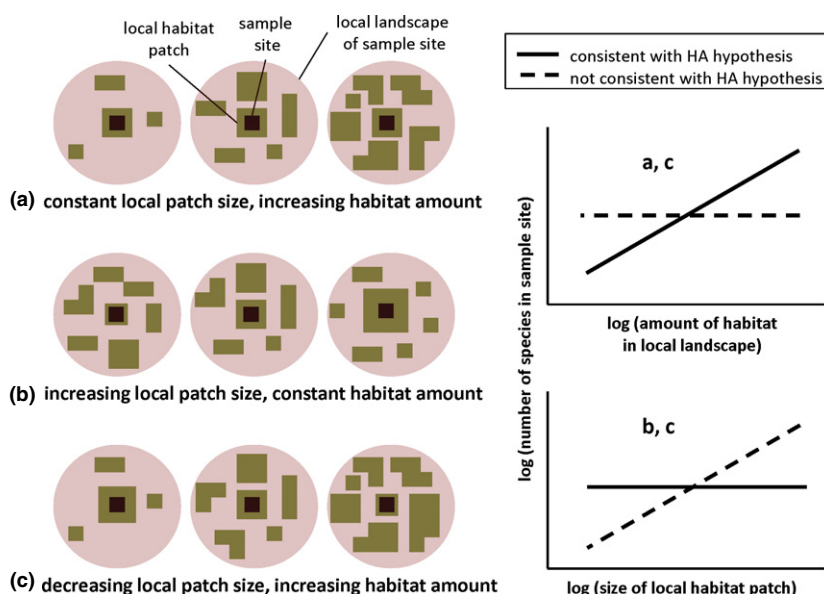

Figure 1 Predictions of the habitat amount (HA) hypothesis. The HA hypothesis predicts that species richness in a given sample site (central black squares) increases with the amount of habitat in the local landscape [scenarios (a) and (c); shown in upper graph]. Furthermore, if the amount of habitat in the local landscape remains constant, species richness in same-sized sample sites should be independent of the sizes of the habitat patches containing the sample sites (the local patches) [scenario (b); shown in lower graph], and species richness in the same-sized sample sites should increase with increasing habitat amount in the local landscapes, even if the size of the local patch decreases [scenario (c); shown in lower graph]. Note that there is no prediction for local patch size in scenario (a) or for habitat amount in scenario (b), because they do not vary in these scenarios. Scenario (c) varies in both local patch size and habitat amount.

in the landscapes surrounding the sample sites (the 'local landscapes') varies, the habitat amount hypothesis predicts a positive relationship between species richness and habitat amount in the local landscapes (Fig. 1a). Second, across a set of same-sized sample sites, where the local patches containing the sample sites vary in size but the amount of habitat in the local landscapes (including the local patches) is constant, the hypothesis predicts no relationship between species richness and local patch size (Fig. 1b). Finally, across a set of same-sized sample sites where the local patches vary in size inversely with the amount of habitat in the local landscapes, the hypothesis predicts no relationship between species richness and local patch size, and a positive relationship between species richness and habitat amount (Fig. 1c).

There are probably many existing data sets that could be used to perform such tests. All that is needed is (1) species richness values for a group of species associated with a given cover type, where the samples are taken at multiple, same-sized sample sites, in known locations distributed over a large region, and (2) an accurate regional map of that cover type. A multi-scale analysis (e.g. Holland *et al.*, 2005; see Fahrig, 2013) would first be performed to estimate the local landscape size (also called the 'scale of effect'; Jackson & Fahrig, 2012). Then, subsets of the sample sites would be selected to create the gradients in Fig. 1. For example, the North American Breeding Bird data, or one of the other large-scale breeding bird data sets, could be used, where the species group selected might be forest-breeding birds, and the land-cover type would then be forest.

In addition, as Hanski correctly states, the habitat amount hypothesis 'could as well be applied to individual species'. Therefore, the hypothesis can also be tested by combining the results of many tests on individual species, as described in Fahrig (2013). A candidate species for such a single-species test would be the Glanville fritillary butterfly (*Melitaea cinxia*), which Hanski and co-workers have studied for many years across a large number of sites. All that would be needed is (1) site-level (not patch-level) occurrence data, (2) accurate sample site locations, (3) habitat amount calculated at multiple extents around each sample site (not patch) to estimate the size of the local landscape (e.g. Holland *et al.*, 2005), and (4) the sizes of the local patches within which the sample sites are located.

Until its predictions have been tested, it is premature to pass judgement on the habitat amount hypothesis. In the end, science can only progress if we are willing to subject our hypotheses to rigorous empirical testing, and to accept the test results however they come out. For that reason, I am grateful to Hanski for providing this opportunity to emphasize the need to test the habitat amount hypothesis, and I look forward to seeing the results.

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