CORRESPONDENCE

Habitat fragmentation and species richness

ABSTRACT

In a recent article in this journal, Fahrig (2013, *Journal of Biogeography*, **40**, 1649–1663) concludes that variation in species richness among sampling sites can be explained by the amount of habitat in the 'local landscape' around the sites, while the spatial configuration of habitat within the landscape makes little difference. This conclusion 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. Fragmentation effects are best tested with studies on individual species rather than on communities, as the latter typically consist of species with dissimilar habitat requirements. The total amount of habitat and the degree of fragmentation tend to be correlated, which poses another challenge for empirical studies. I conclude that fragmentation poses an extra threat to biodiversity, in addition to the threat posed by loss of habitat area.

Keywords Biodiversity conservation, connectivity, conservation biogeography, extinction threshold, fragmentation, habitat loss, habitat patch, species richness.

Ecologists agree that the regional distribution and abundance of species, as well as species richness in communities, are greatly influenced by the amount and quality of habitat. The fundamental role of habitat in limiting species richness is underscored by the fact that habitat loss is the main cause of declining biodiversity worldwide (Hanski, 2005; Millennium Ecosystem Assessment, 2005; Pimm *et al.*, 2014). Habitat loss is typically accompanied by fragmentation (Tscharntke *et al.*, 2012), and many ecologists, myself included, have concluded that fragmentation poses an

extra threat to biodiversity, in addition to and on top of the threat posed by declining total amount of habitat. However, this conclusion is not accepted by everybody. One prominent critic of fragmentation effects is Lenore Fahrig. In her early papers, Fahrig stressed the independent effects of fragmentation and the total amount of habitat (Fahrig & Merriam, 1985, 1994; Taylor *et al.*, 1993), but following a modelling study that she published in 1997 (Fahrig, 1997) she has consistently concluded that what really matters is the total amount of habitat, while fragmentation makes little difference (Fahrig, 2001, 2003). In her latest contribution, Fahrig (2013) proposes the 'habitat amount hypothesis', under which it is unnecessary to consider habitat configuration independent of habitat amount. I challenge that conclusion. Below, I make four main points, and I draw attention to the need for more interactions between landscape ecology and other approaches to spatial population dynamics, the need for a combination of theoretical and empirical approaches in the study of the biological consequences of habitat fragmentation, and the need to consider the implications for biodiversity conservation.

Fahrig (2013) suggests that the 'habitat patch concept' – where habitat patches are terrestrial 'habitat islands' containing discrete populations – is not needed to explain patterns of species richness nor variation in the occurrence and abundance of individual species in fragmented landscapes. Instead, she proposes the habitat amount hypothesis, according to which one can explain species richness at sampling sites simply by the total amount of habitat in the 'local landscape' around those sites (Fahrig, 2013). She recommends defining the size of the local landscape by the spatial scale at which the amount of habitat explains most of the variation in species number (Fahrig, 2013: figure 9). The habitat amount hypothesis lacks any mechanism that may underlie species' responses to habitat availability, other than the 'sample area effect', meaning that there

are more individuals and thereby more species in local landscapes with more habitat area.

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. 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 were not to make a difference to the occurrence of the species. To take a real example, Pardini *et al.* (2010) have reported on the occurrence of non-volant forest specialist small mammal species in multiple landscapes of 100 km^2 in the Atlantic forest in Brazil. A large fraction of the species have persisted in a landscape with 30% forest cover, but just a single species occurred in a landscape with 10% forest cover (for further discussion see Hanski, 2011a), apparently because the habitat in the latter landscape is below the extinction threshold for these species. Now, consider a landscape of 300 km^2 with 10% forest cover, which, based on Pardini *et al.*'s (2010) data, has just a single species, because the landscape is below the extinction threshold for the other species. Then imagine that the habitat of the 300 km^2 landscape is concentrated within one-third of the area, where there would be now 30% forest cover and many species would be above their extinction threshold and would persist. This example highlights the significance of the spatial configuration of habitat across large areas. The habitat amount hypothesis, focused as it is on 'local landscapes', does not help us understand the large-scale processes and patterns.

Second, Fahrig (2013) applies the habitat amount hypothesis to pooled data for

many species, although it could as well be applied to individual species, as there are no assumptions about interactions among the species and hence species number is simply the sum of the incidences of occupancy by individual species. Analysing multispecies communities is problematic, because different species typically have somewhat different habitat requirements (which is acknowledged by Fahrig, 2013). With a given definition of habitat, some species in a study assemblage are likely not to be entirely confined to the focal habitat: they may use habitat edges or even the matrix surrounding the habitat. They will respond to fragmentation, but not just to the spatial configuration of the habitat like strict habitat specialists, and changes in species richness reflect all the various responses by all the species in the community. One might argue that this is not a problem when the aim is to develop a phenomenological model for species richness, which is what Fahrig (2013) does, rather than to explain the dynamics of particular species. But there is a problem if such non-mechanistic community-level analysis is the basis for concluding that habitat fragmentation in the sense of the spatial configuration of the habitat makes little or no difference to the occurrence of individual species or species richness. Before such conclusions are drawn, we need to understand the processes that influence the dynamics of species in fragmented landscapes; it is not enough to construct regression models for heterogeneous species assemblages that lack both biological mechanisms and predictive power beyond the system to which the model was fitted.

The alternative to community-level analyses is to focus on single species with well-known ecologies, in order to dissect the mechanisms that underlie species' responses to habitat fragmentation. This is the approach that we have taken in a long-term research project on the Glanville fritillary butterfly (Hanski, 2011b; Ojanen et al., 2013). Naturally, in-depth understanding of just a single species is not enough, but knowledge stemming from multiple studies on multiple species will advance our general understanding of the consequences of habitat loss and fragmentation. I am also calling for more communication between different and complementary approaches to spatial population ecology. I conjecture that the disconnection of Fahrig's habitat amount hypothesis from the population and evolutionary ecology literature on the effects of

fragmentation reflects the largely independent research traditions of landscape ecology and metapopulation biology, which have persisted for more than two decades – to the detriment of both disciplines.

Third, the habitat amount hypothesis is problematic as an empirical model of species richness. The total amount of habitat and the degree of fragmentation are typically closely correlated, which makes it hard to tease apart their effects with observational data. In this situation, and to improve our general understanding of the biological mechanisms, it is helpful to employ models, where one can contrast dissimilar hypothetical landscapes in which the amount and fragmentation of habitat can be varied independently of each other. Naturally, one should attempt to construct realistic models when the aim is to study what is likely to happen in natural populations. Fahrig (1997) constructed an individual-based, stochastic model for a single species, which showed very little effect of fragmentation on extinction probability in addition to the effect of habitat loss. My concern with this model is the small scale of the landscape (30 × 30 grid cells) in relation to the movement range of individuals (up to 4 grid cells). Given the parameter values, there is a good chance of individuals moving in the model across the entire landscape before dying; the model is focused more on individual movements and reproduction rather than the dynamics of spatially structured populations. I suspect that the model was stimulated by Fahrig's early study on movements and oviposition of the cabbage butterfly (Pieris rapae) in a system of nearby cabbage patches (Fahrig & Paloheimo, 1988). In a more complex version of the model, Fahrig (1998) actually found a distinct effect of fragmentation on the survival time of the population, but she curiously dismissed this result as an unlikely special case, because it required, in her simulations, that dispersal distances are not very long, that the pooled amount of habitat is less than 20% of the landscape area, and that individuals show habitat selection, that is, they tend to stay in the breeding habitat (for further details see Fahrig, 1998). To me these are features that characterize the majority of species living in highly fragmented landscapes.

Figure 1 shows the results of another model by Rybicki & Hanski (2013). We simulated the dynamics of a large number of species in a large heterogeneous landscape, modelled as a grid of 512 × 512

cells. To make the simulations realistic, we assumed interspecific differences in species' ecological traits, that there is spatial variation in habitat type, and that the match between a species' phenotype and the local habitat type (in a given grid cell) influences population dynamics. The habitat type may be spatially correlated, and the model allows for spatially correlated environmental stochasticity, both of which are ubiquitous features of real landscapes. The size of the simulated landscape is much greater than the spatial scale of movements. We modelled the presence or absence of each species in each grid cell, while habitat patches in this model are simply contiguous groups of cells with appropriate habitat. The model can therefore be applied to any kind of landscape, patchy or not. One indication of the realism of the model is that it predicts realistic species–area relationships (Rybicki & Hanski, 2013).

In the examples in Fig. 1, the amount of habitat was varied from 1% to 30% of the total landscape area, and the habitat was split up into a smaller or larger number of randomly located, equally large fragments, as indicated by the legend to the right of the figure. As expected, species richness is strongly affected by the total amount of habitat in the landscape, but it is also strongly affected by the degree of fragmentation when the total habitat amount is small. Thus in Fig. 1a, species richness is high when 5% of the landscape area is covered by habitat that occurs in one or a few fragments, but no species persist when the same amount of habitat is split up into a very large number of small fragments. Changing the values of model parameters would affect the quantitative details, but the qualitative result would remain the same. Another feature to notice is the effect of spatial autocorrelation in habitat type. In Fig. 1a there is weak autocorrelation, whereas in Fig. 1b autocorrelation is strong. In the latter case, moderate amount of fragmentation actually increases the number of species surviving at the landscape level, because now the fragments are spread out and have dissimilar habitat composition (because of autocorrelation in habitat type) and hence support somewhat different assemblages of species (beta diversity) than a single or a few large pieces of habitat with the same total area. Nonetheless, even in this case a high level of fragmentation leads to a reduction in species number (Fig. 1b). To describe the effect of fragmentation, we have extended
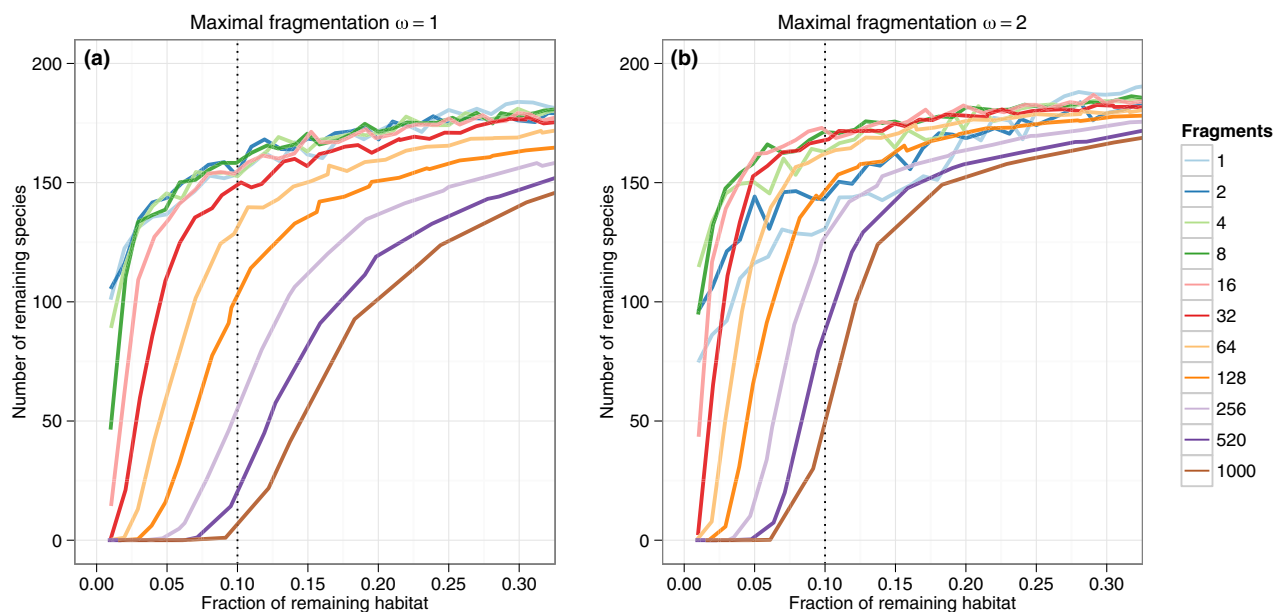
Figure 1 The effects of the fraction of remaining habitat out of the total landscape area and its degree of fragmentation on species richness in the model described in the text (for further details see Rybicki & Hanski, 2013). The coloured lines indicate into how many equally large and randomly located fragments the given amount of habitat (horizontal axis) is split (see the legend on the right). In panel (a) there is weak spatial autocorrelation in habitat type, in panel (b) autocorrelation is strong.

the power-law island species–area relationship (SAR) to the species–fragmented area relationship (SFAR), which explicitly accounts for the effect of fragmentation (Hanski *et al.*, 2013). SFAR described well the effects of both habitat amount and fragmentation on species richness in simulation results such as shown in Fig. 1 (Hanski *et al.*, 2013).

From these examples, it is clear that the effect of fragmentation on species richness can be demonstrated with plausible models, but what about real populations and communities? We applied the SFAR approach to an empirical dataset for specialist subtropical forest birds surveyed in large landscapes, each 100 km^2 in area (Hanski *et al.*, 2013). In 14 landscapes with forest cover less than 40%, the SAR explained 65% of the variation in species number, while the SFAR explained 81%. This is not a huge improvement over the SAR, but because the amount of habitat and the level of fragmentation are closely correlated in this example, as they are in empirical data in general, it is difficult to tease apart their independent effects. Notably, in this case the slope of the power-law SAR was $z = 1.38$, which is an unusually large value (e.g. Connor & McCoy, 1979; Rosenzweig, 1995). It is probable that the large z value reflects the effect of fragmentation, which reduces species richness in landscapes with a small amount of

highly fragmented habitat. The lesson from this example is that even if habitat amount alone might explain relatively well species richness in a simple regression model, such as the SAR or the model advocated by Fahrig (2013), one should not jump to the conclusion that this result alone suffices to demonstrate lack of any fragmentation effects. I emphasize the importance of developing theoretical understanding of fragmentation effects combined with ecologically well-informed analyses, to advance our general understanding and to construct predictive models.

My fourth problem with Fahrig's criticism of the habitat patch concept is that, as a matter of fact, distinct patches of habitat are more than just a concept, they are the reality in countless landscapes, although by no means everywhere. In particular, whenever the total amount of habitat is small across a large area, the degree of fragmentation tends to be high and the remaining habitat often occurs in discrete patches. In such landscapes, most dispersing individuals do not visit multiple habitat fragments in their life-time. Many individuals, if they disperse at all, perform only one dispersal event, and the connectivity of many fragments is so low that, in any one generation, no dispersing individuals arrive from outside. Highly fragmented landscapes are becoming ever more common with continuing anthropogenic habitat conversion. To

take an example from practical conservation, in Finland more than 100,000 'woodland key habitats' (WKH) have been delimited in managed forests, and they are left untouched while the rest of the forest is clear-cut, for the explicit purpose of protecting forest biodiversity (Hanski, 2008). There are thus very many patches of WKH, but they are all very small, with an average area of 0.7 ha, and they are very widely scattered across 20 million ha of forested land. A meta-analysis found no difference in the numbers of threatened species in WKHs and in equal-sized control plots in the surrounding managed forest – both had almost none (Timonen *et al.*, 2011). A single protected area of 70,000 ha would retain large numbers of threatened species, although I admit that more data would be needed to rigorously test which alternative, the WKHs or a few large protected areas with the same total area, protect more species. Nonetheless, given the theoretical understanding of the viability of very small, isolated populations, I venture to predict that WKHs exemplify the loss of species in Fig. 1 when habitat becomes highly fragmented. Another factor reducing the value of WKHs in supporting biodiversity is a massive edge effect and hence reduced habitat quality, which is a generic problem with many highly fragmented habitats. The WKHs may represent an extreme example, but this is also an example of

how managers claim to protect biodiversity in practice, in spite of extreme fragmentation of the habitat. Should we endorse such an approach to biodiversity conservation, and on what basis – because habitat fragmentation does not matter? Unfortunately, the WKHs exemplify the direction towards which habitat loss is transforming many landscapes. To take another example, vast areas of tropical forest are being converted to oil palm plantations in Southeast Asia, where recommendations have been made to reduce species loss by the retention of natural forest patches within plantations (Lucey *et al.*, 2014). How large these fragments should be, and what should their density be across large areas, to protect even a fraction of the original biodiversity, are hugely important questions for conservation.

I offer a few conclusions. First, I agree with Fahrig that habitat patches are not fundamental entities, but I maintain that it is often convenient and helpful to analyse the dynamics of species in highly fragmented landscapes at the level of local populations inhabiting discrete habitat patches. Second, everybody agrees that in the case of land-covering habitats such as forests, fragmentation makes little or no difference if the amount of habitat is large, roughly more than 20–30% of the landscape area (Lande, 1987; Andrén, 1994; Fahrig, 1998; Hanski, 2005), simply because all habitat is then relatively well connected. However, if the amount of habitat is smaller, fragmentation effects kick in and should not be ignored; this threshold is often referred to as the '20% rule', although the value of the threshold naturally depends on the ecology of the species (see Fig. 1). Moreover, this level of habitat amount should not be confused with the extinction threshold, which sets the limit below which a species goes deterministically extinct at the landscape level. It should also be noted that the 20% rule applies to land-covering habitats, which originally covered most of the landscape. In contrast, many habitat types are naturally sparse and patchy, and the species inhabiting them may have become adapted, in one way or another, to extreme fragmentation, in which case much less habitat out of the total landscape area is sufficient for viable populations. The well-studied Glanville fritillary butterfly metapopulation is a good example, with roughly 1% of the total landscape area representing the appropriate habitat (dry meadows; Ojanen *et al.*, 2013). Nonetheless, even species adapted to living in highly fragmented landscapes lose their

viability when the density of habitat patches becomes very low, that is, these species too have an extinction threshold (for the Glanville fritillary see Hanski & Ovaskainen, 2000). The landscape-level extinction threshold has enormous practical importance for conservation and habitat restoration, as much as the analogous concept of eradication threshold in epidemiology (Anderson & May, 1991), which explains why vaccination works although not every individual can be vaccinated. I conclude 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.

I l k k a   H a n s k i *

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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
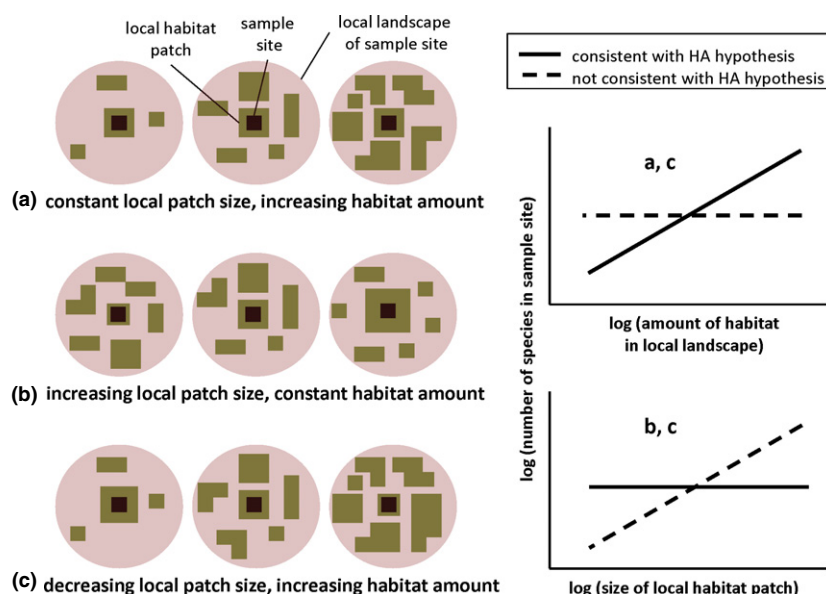
Figure 1 Predictions of the habitat amount (HA) hypothesis. The HA hypothesis predicts that species richness in a given sample site (central black squares) increases with the amount of habitat in the local landscape [scenarios (a) and (c); shown in upper graph]. Furthermore, if the amount of habitat 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.