SYNTHESIS

Rethinking patch size and isolation effects: the habitat amount hypothesis

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ABSTRACT

I challenge (1) the assumption that habitat patches are natural units of measurement for species richness, and (2) the assumption of distinct effects of habitat patch size and isolation on species richness. I propose a simpler view of the relationship between habitat distribution and species richness, the 'habitat amount hypothesis', and I suggest ways of testing it. The habitat amount hypothesis posits that, for habitat patches in a matrix of non-habitat, the patch size effect and the patch isolation effect are driven mainly by a single underlying process, the sample area effect. The hypothesis predicts that species richness in equal-sized sample sites should increase with the total amount of habitat in the 'local landscape' of the sample site, where the local landscape is the area within an appropriate distance of the sample site. It also predicts that species richness in a sample site is independent of the area of the particular patch in which the sample site is located (its 'local patch'), except insofar as the area of that patch contributes to the amount of habitat in the local landscape of the sample site. The habitat amount hypothesis replaces two predictor variables, patch size and isolation, with a single predictor variable, habitat amount, when species richness is analysed for equal-sized sample sites rather than for unequal-sized habitat patches. Studies to test the hypothesis should ensure that 'habitat' is correctly defined, and the spatial extent of the local landscape is appropriate, for the species group under consideration. If supported, the habitat amount hypothesis would mean that to predict the relationship between habitat distribution and species richness: (1) distinguishing between patch-scale and landscape-scale habitat effects is unnecessary; (2) distinguishing between patch size effects and patch isolation effects is unnecessary; (3) considering habitat configuration independent of habitat amount is unnecessary; and (4) delineating discrete habitat patches is unnecessary.

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THE HABITAT PATCH CONCEPT

Over the years following publication of the theory of island biogeography (MacArthur & Wilson, 1963, 1967), the idea that patches of habitat are analogues of islands took root, becoming a central theme in conservation biology. Patch size and isolation, analogous to island size and isolation, became viewed as primary determinants of species richness in habitat patches. As an important outcome, the habitat patch has been widely adopted as the 'natural' area for measuring and recording species richness, as well as the abundance and occurrence of individual species. In the habitat patch framework, sampling effort is usually scaled to patch size, and species richness (or abundance or occurrence) is reported and analysed on a per-patch basis, even if the original data are based on sample sites or quadrats. The resulting data points therefore represent values from areas that may range in size over two or three orders of magnitude (e.g. Rosin *et al.*,

2011; Robles & Ciudad, 2012), a significant departure from the equal-sized sample sites or quadrats in classical ecological studies (Fig. 1).

The notion that the habitat patch is the natural spatial unit for recording and analysing species richness, abundance and occurrence comes from the implicit assumption that habitat patch boundaries contain or delimit populations and communities, such that each patch represents a meaningful ecological entity. I refer to this idea as the 'habitat patch concept'. A persistent difficulty with the habitat patch concept has been uncertainty in how to delineate ecologically relevant patches. If two patches are very close together, should they be analysed as a single patch? At what distance apart should they be recognized as two patches (Fig. 1b vs. 1bi)? As 'habitat' implies the particular cover types used by a given species or species group, does the inclusion of more detailed information on cover types within patches require subdivision of patches into smaller patches of uniform type (Fig. 1b vs. 1bii)? Also, more generally, should the habitat associations of species and species groups determine habitat patch delineation (Fig. 1b vs. 1biii)?

Even if patches could be delineated 'correctly', many studies have challenged the notion that patch boundaries contain or delimit populations (Harrison, 1991; reviewed in Bowne & Bowers, 2004). Animals make frequent movements into and through the non-habitat parts of the landscape, the 'matrix', including not only dispersal movements but also seasonal movements and even daily movements (e.g. Baguette *et al.*, 2000; Broome, 2001; Fraser & Stutchbury, 2004; Petranka & Holbrook, 2006; Roe *et al.*, 2009; Schultz *et al.*, 2012). If animals move frequently in the matrix and between habitat patches, their populations are not bounded by them. On the other hand, habitat patch boundaries do constrain

the movements of some species (Stasek *et al.*, 2008; Franzén *et al.*, 2009; Jackson *et al.*, 2009).

Here, I challenge (1) the assumption that habitat patches are natural units of measurement for ecological responses, in particular for species richness, and (2) the assumption of distinct effects of habitat patch size and isolation on species richness. I propose a simpler view of the relationship between habitat distribution and species richness, the 'habitat amount hypothesis', and I suggest ways of testing it. Although I focus here exclusively on habitat patches, the ideas I present may also apply to many island clusters and islands within lakes, or sets of islands near the coast such as barrier island systems. Also, I limit my treatment here to species richness, but I suggest that, if habitat patches are not natural units for studying species richness, they are also probably not natural units for studying species abundance and occurrence.

PATCH SIZE EFFECT OR SAMPLE AREA EFFECT?

In their opening sentence, MacArthur & Wilson, [1963; p. 373 (with reference to Preston, 1962)] state: '[as] the area of sampling A increases in an ecologically uniform area, the number of plant and animal species s increases in an approximately logarithmic manner'. The simplest explanation for this increase in species number is the sample area effect: in any region of continuous habitat, larger sample areas will contain more individuals and, for a given abundance distribution, this will imply more species (Fig. 2a). If one were subsequently to remove large amounts of habitat from the region, leaving habitat patches of different sizes, the species–area relationship would still hold across these patches, owing to the sample area effect (Fig. 2b), and the level of the curve would subsequently drop over time as species disappear from
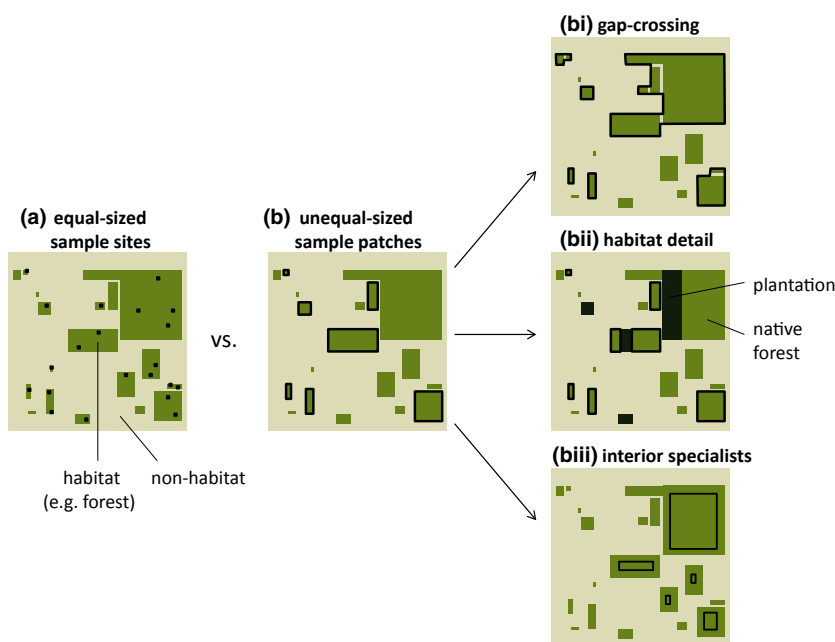

Figure 1 (a) Equal-sized sample sites versus (b) unequal-sized sample patches, where patch delineation depends on: the minimum distance between patches (b vs. bi); the level of cover type detail in habitat mapping (b vs. bii); and the specific habitat association of the species group (b vs. biii).

Figure 2 Comparison of the species–area relationship for (a) sample areas within continuous habitat, (b) habitat patches and (c) islands. Species richness increases with increasing sampled area within continuous habitat, because of the sample area effect. The species–area relationship is steeper for islands than for sample areas within continuous habitat because of the island effect. The sample area effect alone predicts that the species–area relationship for habitat patches should be lower, but have the same slope, as the relationship for sample areas within continuous habitat. In contrast, the island effect for habitat patches predicts that the species–area relationship for habitat patches should be steeper than for sample areas within continuous habitat.
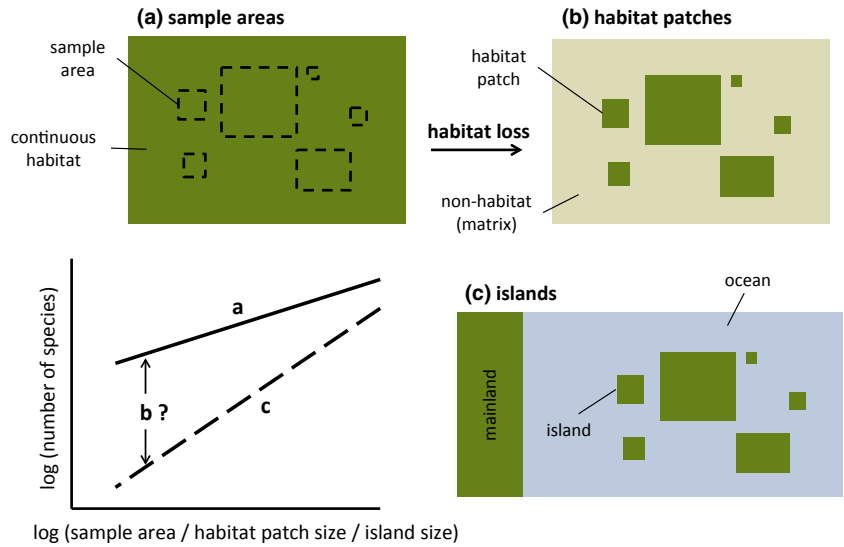
the region (faunal relaxation). Many researchers have constructed species–area curves across habitat patches of different sizes (i.e. Type IV curves *sensu* Scheiner, 2003; or island species–area curves, ISARs; Triantis *et al.*, 2012), confirming the species–area relationship for habitat patches, for a wide range of taxa, including plants (Piessens *et al.*, 2004; Galanes & Thomlinson, 2009), birds (Freemark & Merriam, 1986; van Dorp & Opdam, 1987; Beier *et al.*, 2002; Uezu & Metzger, 2011), mammals (Holland & Bennett, 2009), amphibians (Parris, 2006), and insects (Fenoglio *et al.*, 2010; Öckinger *et al.*, 2012).

Importantly, the species–area relationship, as predicted from the sample area effect, does not require that the area sampled for each data point on the species–area curve be spatially contiguous. In a region of continuous habitat, the number of species present in a contiguous sample area of a given size will be the same (on average) as the number present in two or more smaller sample areas of the same total size as the single contiguous sample area (Fig. 3). Similarly, due to the sample area effect, as habitat loss proceeds, the number of species in a given habitat type in a whole land-scape will decline with the total remaining area of that habitat type in the landscape (Fig. 4), irrespective of the individual sizes of the remaining patches. As stated by Helliwell (1976), '[o]bviously there will be a better chance of finding almost any species in a sample of larger size, whether this sample is made up of a single large unit or several smaller units, and regardless of any island effect'. Therefore, the occurrence of a species–area relationship across a set of patches is not necessarily related to the delineation of those areas as patches. While this has been pointed out previously (Helliwell, 1976; Haila, 1988), it has been 'all but neglected in the fragmentation literature' (Haila, 2002).

MacArthur & Wilson (1967: Chapter 2) noted that remote islands differ from sample areas in continuous habitat, in that the species–area relationship across a set of remote islands is typically steeper than the species–area relationship across a set of sample areas in continuous habitat (confirmed in a review by Watling & Donnelly, 2006). Remote islands have a higher extinction : colonization ratio than areas of the same size on continents, and this difference is greater when the island and its corresponding sample area

Figure 3 Different sized sample areas in an area of continuous habitat. The number of species in equal-sized quadrats is the same (on average), irrespective of the sample area containing the quadrat. The number of species in a given amount of sampled habitat is the same, irrespective of the sizes of individual sample areas included in the total sample area; e.g. number of species in G = number of species in A + B + C + D + E.
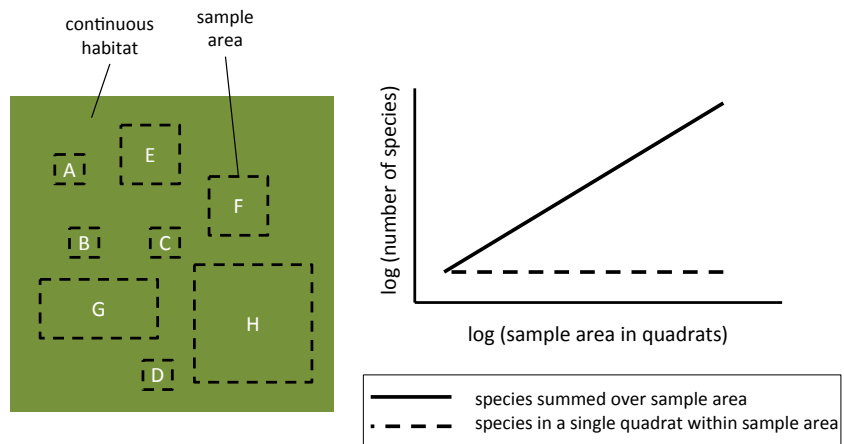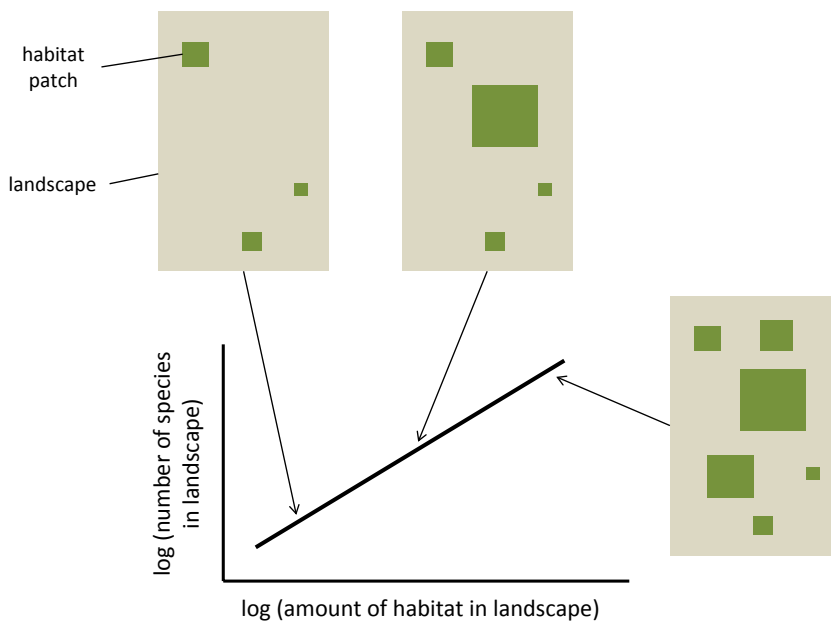
Figure 4 Due to the sample area effect, the total number of species in a given habitat type within a landscape increases with the total amount of that habitat in the landscape, irrespective of the sizes of individual habitat patches in the landscape.

are small than when they are large. The smaller and more isolated the island, the less likely it is to contain 'transient' or 'sink' species, whose persistence on the island would depend on frequent immigration from elsewhere (MacArthur & Wilson, 1967: Chapter 2; Rosenzweig, 2004). The steeper slope for islands than for sample areas in continuous habitat (the 'island effect') means that the species–area relationship for islands results from more than just the sample area effect.

The island effect also implies that smaller islands have fewer species in randomly selected quadrats of a given size than do larger islands. Imagine that the islands and the area of continuous habitat are divided into quadrats, all the same size. In continuous habitat, all quadrats contain (on average) the same number of species (Fig. 3), so in continuous habitat the ratio of the number of species in a random quadrat in the largest sample area to the number of species in a random quadrat in the smallest sample area is one. In addition, since the log–log species–area slope for the islands is steeper than the slope for sample areas within continuous habitat, the ratio of the total number of species on the largest island to the total number of species on the smallest island is higher than the ratio of the total number of species in the largest sample area to the total number of species in the smallest sample area within continuous habitat. Taken together, these two points imply that the ratio of the number of species in a random quadrat on the largest island to the number of species in a random quadrat on the smallest island must be greater than one, i.e. greater than the ratio for continuous habitat. Essentially, the species pool sampled by a random quadrat is smaller on a small island than on a large island (e.g. Stiles & Scheiner, 2010), whereas the sampled species pool is the same for all quadrats in continuous habitat. In other words, the island effect implies declining number of species in equal-sized quadrats with declining island size.

Is the species–area curve across habitat patches steeper (like the curve for islands) or shallower (like the curve for sample areas within continuous habitat)? If the latter, we can hypothesize that the species–area curve for habitat patches primarily results from the sample area effect, where larger patches represent larger sample areas. This is an important question because, if the patch size effect were due only to the sample area effect then, for biodiversity conservation, only the total amount of habitat in the landscape would matter (Fig. 4), and not the sizes of the individual patches that make up that total.

I attempted an exhaustive search for studies that compared the slope of the species–area relationship across a set of different-sized habitat patches with the slope of the species–area relationship across a set of sample areas equal in size to these habitat patches but embedded in a region of continuous habitat. If habitat patches are analogous to remote islands, the slope of the former should be steeper than the slope of the latter (Fig. 2). I found remarkably few such studies, six in all. Middleton & Merriam (1983) compared species richness of small mammals, plants and insects along a 6-km transect within continuous woods, with a similar total transect length within 15 small forest patches. Consistent with the sample area effect, the total number of species was greater in the continuous forest, but inconsistent with the island effect, the slopes of the species–area curves were essentially identical. Similarly, Schmiegelow *et al.* (1997) and Laurance *et al.* (2002) found almost identical species–area slopes for boreal forest birds and for tropical forest birds, respectively, across control sites within continuous forest compared with species–area slopes across experimental fragments. Collinge (2000) found no difference in insect species richness between experimentally created grassland plots and sample areas of the same sizes within continuous grassland. Shirley & Smith (2005), studying birds in uncut riparian buffer strips retained

after clear-cutting, found no evidence for a steeper slope in the species number versus buffer-width relationship among remnant buffers than at control sites. Finally, Paciencia & Prado (2005) found no difference in pteridophyte species-accumulation curves across small versus large tropical forest fragments. In summary, these six studies suggest that the species–area relationship across habitat patches could be simply due to the sample area effect.

An indirect way to test for the island effect on habitat patches is to compare species richness in one large patch with total species richness in many small patches equal in total area to the large patch (i.e. single large or several small: SLOSS). This has been done empirically by calculating cumulative species number over cumulative area, summing over patches in two ways, first where patch areas are accumulated from smallest to largest patch, and second where they are accumulated from largest to smallest patch (Fig. 5). If the patch size effect is due only to the sample area effect, these two curves should coincide, whereas if there is an additional island effect, species should accumulate more quickly when area is accumulated from the largest to smallest patch than when area is accumulated from the smallest to largest patch (Fig. 5). Using the search term 'SLOSS' in the Web of Knowledge database, I found 14 empirical studies of this type. One of these (Hoyle & Harborne, 2005) was based on experimentally created patches, 12 were based on observational data from sets of pre-existing patches (McCoy & Mushinsky, 1994; Sætersdal, 1994; Baz & Garcia-Boyero, 1996; Virolainen et al., 1998; Oertli et al., 2002; Tscharntke et al., 2002; Hokkanen et al., 2009; Fattorini, 2010; Hattori

& Shibuno, 2010; Gavish et al., 2011; Martínez-Sanz et al., 2012), and one had both observational and experimental data (McNeill & Fairweather, 1993). All thirteen of the observational studies found the opposite pattern to that predicted by the island effect: several small patches had higher species richness than a single large patch of the same total area. This result held true even when authors evaluated only rare, threatened or specialist species groups (McCoy & Mushinsky, 1994; Sætersdal, 1994; Virolainen et al., 1998; Oertli et al., 2002; Tscharntke et al., 2002; Peintinger et al., 2003; Hokkanen et al., 2009). As suggested by several of the SLOSS authors, and shown theoretically by Tjørve (2010), it seems likely that at least part of the reason for higher species richness in several small than in one large patch is that several small patches are spread over a larger extent (Fig. 5), so they intersect the distributions of more species. Interestingly, the two experimental SLOSS studies (McNeill & Fairweather, 1993; Hoyle & Harborne, 2005) found no difference between species richness on single large versus several small patches. This is consistent with this explanation, because these two experiments were conducted over much smaller spatial extents than were the 13 observational studies.

A slightly different way to test SLOSS, which does not confound the several-small scenario with the spatial extent sampled, is to extrapolate the species–area curve to predict the number of species that should occur in a single hypothetical patch equal in size to the sum of the sizes of the actual sampled patches, and then compare this with the total species richness over the actual patches. The island effect would predict lower species richness summed over the actual
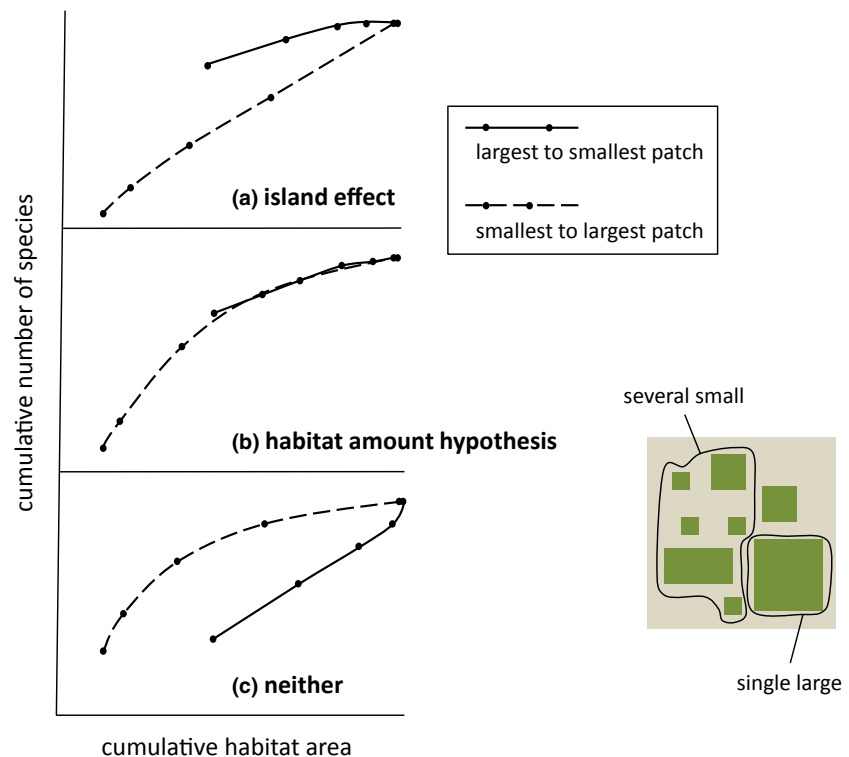

Figure 5 Method for empirically evaluating single large versus several small (SLOSS). Species richness is accumulated over area either beginning with the largest patch and adding patches in order of decreasing size (solid lines), or beginning with the smallest patch and adding patches in order of increasing size (dashed lines). (a) The island effect predicts more species in a single large patch than in several small patches of the same total area as the single large one. (b) The habitat amount hypothesis predicts that species number should increase with total area, irrespective of the number of patches making up that total. (c) A third possibility is that several small patches contain more species than a single large patch equal in area to the sum of the areas of the small ones.

patches than the species richness predicted for the hypothetical single large patch. Rosenzweig (2004) conducted this sort of analysis for 37 datasets and found equal numbers (19 vs. 18) of situations in which the actual value was higher versus lower than the predicted value. In summary, empirical tests of the SLOSS question do not support the island effect for habitat patches.

Overall then, empirical studies so far are consistent with the idea that the species–area relationship across habitat patches is mainly due to the sample area effect. If this is widely true then its significance is clear: when the conservation objective is to maximize species richness in a given habitat type, what matters is the total amount of that habitat in the landscape and not the sizes of individual patches that make up that total.

PATCH ISOLATION EFFECT OR SAMPLE AREA EFFECT?

MacArthur & Wilson (1963, p. 373) described the colonization of remote islands as occurring by immigration from the 'primary faunal source area', which later authors shortened to the 'mainland'. The mainland community determined the total species pool available for colonization, and islands more distant from the mainland were predicted to have fewer colonists and therefore fewer species than islands closer to the mainland. In contrast, in most patchy habitat situations (and some island situations: Kalmar & Currie, 2006; Weigelt & Kreft, 2013), immigration occurs predominantly from habitat within the neighbourhood of the patch, rather than from a common mainland area. Each patch effectively has its own mainland, which is sometimes assumed to be the nearest patch, sometimes the nearest patch weighted by area or occupancy, sometimes the summed areas of all patches within an appropriate distance (see 'Caution 2: appropriate spatial scale', below, for a discussion of appropriate distance), and sometimes the summed areas of all patches within an appropriate distance, with the summation weighted inversely by the distances of the patches from the focal patch. Each patch thus has a different potential pool of immigrants, and the isolation of a patch depends not just on the distance to, but also, and probably more importantly (see below), on the area represented by the nearby patch(es). In other words, patch isolation depends on the amount of habitat within some distance of the patch (Fig. 6). Many studies have found negative effects of such measures of patch isolation on species richness (e.g. van Dorp & Opdam, 1987; Beier et al., 2002; Piessens et al., 2004; Bailey et al., 2010; Galanes & Thomlinson, 2011; Schüepp et al., 2011; Uezu & Metzger, 2011; Öckinger et al., 2012).

Of the various measures of patch isolation (above), the amount of habitat within an appropriate distance of a patch (and measures that are highly correlated with it) best predicts patch immigration rate and related ecological responses (Moilanen & Nieminen, 2002; Bender et al., 2003; Tischendorf et al., 2003; Prugh, 2009; Ranius et al., 2010; Figure 2 in Thornton et al., 2011; Martin & Fahrig, 2012), including species richness (Piessens et al., 2004). The amount of occupied habitat is a slightly better measure than simply total habitat amount (Prugh, 2009), but such measures are usually not practical as information on occupancy in all habitat is usually not available; in any case, the amount of occupied habitat is typically highly correlated with total habitat amount. Measures of patch isolation that rely entirely on distance, particularly the distance to the single nearest patch, are generally poor predictors of species richness, except when highly correlated with habitat amount (van Dorp & Opdam, 1987; Piessens et al., 2004; Fenoglio et al., 2010; Schüepp et al., 2011; but see Bailey et al., 2010). Generally, the more information about the amount of habitat, particularly occupied habitat, that is contained in the isolation measure, the better it predicts species richness.

What drives this relationship between species richness in a patch and the amount of habitat within an appropriate distance of the patch? As discussed above, landscapes containing less habitat should contain fewer species associated with that habitat type, due to the sample area effect (Fig. 4). Therefore, landscapes surrounding more isolated patches (i.e. landscapes containing less habitat) should contain fewer species than landscapes surrounding less isolated patches, again due
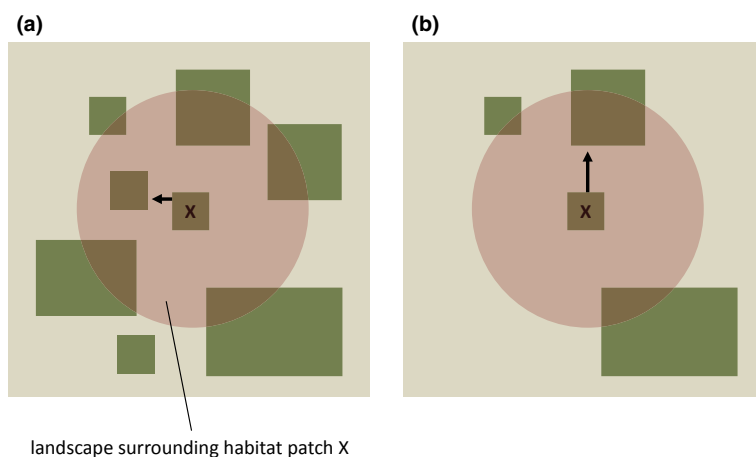

(a)   (b)

landscape surrounding habitat patch X

Figure 6 Habitat patch isolation depends not only on the distance to the nearest patch (arrows), but also, and probably more strongly, on the amount of habitat within an appropriate distance of the sampled patch. The species pool available to colonize the central patch X is lower in panel (b) than in panel (a), making X more isolated in (b) than in (a).

to the sample area effect. The habitat in the landscape surrounding a patch is its primary source of colonists, so fewer individuals and species colonize a more isolated patch (Püttker et al., 2011), reducing its species richness compared with a less isolated patch. Therefore, the patch isolation effect is indirectly due to the sample area effect. Of course, less habitat in the landscape surrounding a patch also means that individuals must travel further, on average, to reach the patch (Andrén, 1994; Fahrig, 2003) (Fig. 6). The isolation effect is thus due to the combination of distance and reduced habitat amount in the surrounding landscape, the latter most likely outweighing the former (as argued above).

THE HABITAT AMOUNT HYPOTHESIS

This leads to a simple hypothesis, that the patch size effect and the patch isolation effect are driven mainly by a single underlying process, the sample area effect. The number of species in a patch is a function of both the size of the patch (i.e. the sample area represented by the patch), and the area of habitat in the landscape surrounding the patch (i.e. the sample area represented by the surrounding habitat), which affects the colonization rate of the patch. We can combine these two sample area effects to predict that species richness in equal-sized sample sites should increase with the total amount of habitat in the 'local landscape' of the sample site (Fig. 7), where the local landscape is the area within an appropriate distance of the sample site.

Several studies have shown such positive effects of the amount of habitat in the local landscape on species richness within sample sites (Holland & Fahrig, 2000; Fischer et al., 2005; Hendrickx et al., 2009; Bailey et al., 2010; Garden et al., 2010; Smith et al., 2011; Flick et al., 2012; Rodríguez-Loinaz et al., 2012). The habitat amount hypothesis further predicts that species richness in a sample site is independent of the area of the particular patch in which the sample site is located (its 'local patch'), except insofar as the area of that patch contributes to the amount of habitat in the local landscape of the sample site. In other words, the hypothesis replaces two predictor variables, patch size and isolation, with a single predictor variable, habitat amount, when species richness is measured and analysed in equal-sized sample sites rather than in unequal-sized habitat patches (Fig. 7).

Note that in proposing the habitat amount hypothesis I do not deny that extinction and colonization drive observed species richness. This has to be true on any spatial scale, including in sample sites within patches, as has been recognized in theoretical work for quite some time. For example, Lande (1987) modelled individual territories as the spatial units of local extinction and colonization, and Holt (1992) modelled colonization–extinction dynamics of equal-sized areas within patches. The habitat amount hypothesis implies that there is nothing special about the habitat patch that would require extinction–colonization dynamics to be assessed at the scale of individual patches.
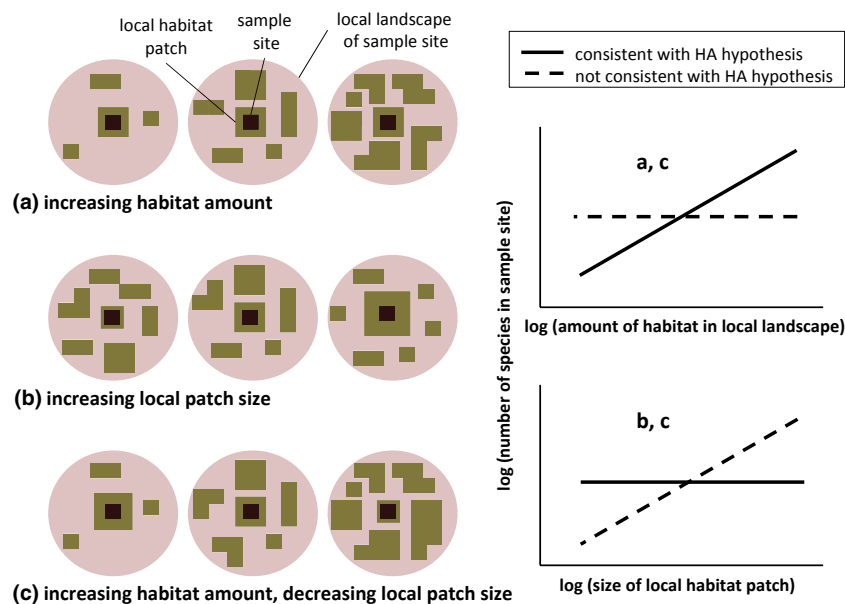

Figure 7 Predictions of the habitat amount (HA) hypothesis. The HA hypothesis predicts that species richness in a given sample site (central black squares) increases with the amount of habitat in the local landscape (scenarios (a) and (c); shown in upper graph). Furthermore, if the amount of habitat in the local landscape remains constant, species richness in the sample site should be independent of the size of the habitat patch containing the sample site (the local patch) (scenario (b), shown in lower graph), and species richness in the sample site should increase with increasing habitat amount in the local landscape, even if the size of the local patch decreases (scenario (c), shown in upper 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.

TWO CAUTIONS AND A CAVEAT

Caution 1: habitat definition and species group selection

Testing the habitat amount hypothesis requires that 'habitat' be correctly defined for the species group under consideration (Fig. 8). For example, if habitat amount is equal to the amount of forest, then the species included in the test should be those that can occur in all forest stand types; species that specialize on particular stand types should not be included, or should be analysed in separate tests where habitat amount is the amount of the particular stand type (Fig. 8). Similarly, only edge habitat amount should be used for tests involving edge specialists and only interior habitat amount should be used for tests involving interior specialists (e.g. Bailey *et al.*, 2010) (Fig. 8).

Of course any single delineation of 'habitat' for a species group will contain errors for at least some of the species in the group. A species may use other cover types in the landscape, but with reduced likelihood or reduced breeding success in them. In a single-species context, these issues can be dealt with using habitat suitability mapping (e.g. Betts *et al.*, 2007). Probabilities of species occurrence are estimated for different cover types, and the total amount of habitat for the species in the local landscape of a sample site is then the sum of these probabilities over all points within the local landscape. While this is a reasonable approach for a single species, it is difficult to imagine how one could apply it to species richness. To test the habitat amount hypothesis directly, we need a single value of habitat amount for each sample site; it is not clear what that value would be if the habitat amount available to each species (both present and absent) is different. Therefore, tests of the habitat amount hypothesis will generally rely on a habitat/non-habitat view of the landscape, where only the species that are expected to use predominantly the same cover type should be included in the species richness estimate. Note that, as this cover type must occur (in varying amounts) over the whole spatial extent of the test, the habitat amount hypothesis applies within, but not across, ecoregions, i.e. it applies within regions containing the focal cover type.

Caution 2: appropriate spatial scale

To test the habitat amount hypothesis, the amount of habitat must be estimated in the local landscape surrounding each sample site. But what is the appropriate spatial extent of this local landscape? We know that landscape structure affects different species most strongly at different spatial scales, the 'scale of effect' (e.g. Holland *et al.*, 2005; Eigenbrod *et al.*, 2008; Martin & Fahrig, 2012), and that if landscape structure is measured at an inappropriate scale, relationships may go undetected (Holland *et al.*, 2005). Most authors assume, intuitively, that the scale of effect is related to the movement range of the study species. This is confirmed by modelling work, which suggests that for simple random dispersal, the scale of effect should occur at about 4–9 times the species' median dispersal distance (Jackson & Fahrig, 2012). More complex, decision-based movement generally leads to smaller scales of effect (Jackson & Fahrig, 2012).

What is the appropriate scale for the local landscape when the response variable is species richness? Interestingly, multi-scale analyses suggest that the response of species richness to habitat amount in the local landscape is strongest within a particular range of scales, at least for taxonomically related groups (e.g. Ricketts *et al.*, 2001; Horner-Devine *et al.*, 2003; Flick *et al.*, 2012). This scale is presumably related in some way to the average movement ranges of the species in the species group. Because this scale will often be impossible to predict a priori, in practice a multi-scale analysis will be necessary (Fig. 9), where the species richness–habitat amount
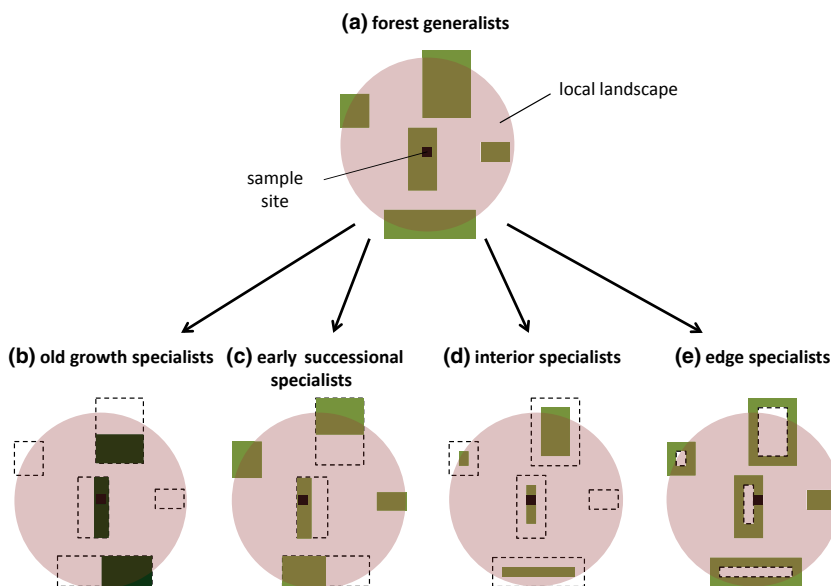

(a) forest generalists

local landscape

sample site

(b) old growth specialists **(c) early successional specialists** **(d) interior specialists** **(e) edge specialists**

Figure 8 The amount of habitat in the local landscape of a sample site (black squares) within forest depends on whether the study species are (a) forest generalists, (b) old growth specialists, (c) early successional forest specialists, (d) forest interior specialists, or (e) forest edge specialists.
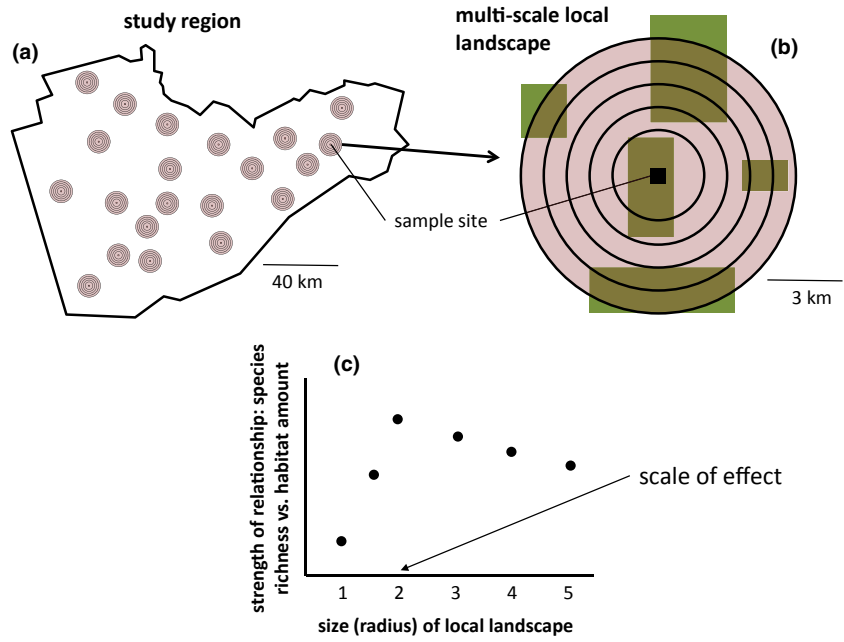
Figure 9 Multi-scale analysis, when the appropriate local landscape scale is unknown. (a) Species richness is sampled in multiple sample sites within a study region. (b) Habitat amount is measured within nested local landscapes at multiple spatial extents surrounding each sample site. (c) The scale of effect is the spatial extent where the strength of the relationship between species richness and habitat amount peaks.

relationship is evaluated for habitat amount estimated at multiple nested extents around the sample sites. As habitat amount is highly correlated between adjacent nested extents, if there is an effect of habitat amount, the fit of the richness–habitat amount relationship should increase smoothly to the scale of effect and then gradually decrease (e.g. Ricketts *et al.*, 2001; Horner-Devine *et al.*, 2003; Eigenbrod *et al.*, 2008).

Caveat: habitat amount isn't everything

Omission of matrix effects from the habitat amount hypothesis does not suggest that they are unimportant. The hypothesis posits that habitat patch size and isolation effects on species richness are due to the sample area effect. However, in addition to the sample area effect, there is ample evidence that the matrix can influence species richness in habitat (Fig. 10; reviewed in Prevedello & Vieira, 2010). For example, fewer species of amphibians are found in ponds, and fewer species of Neotropical migrant birds are found in forests, when the pond or forest is situated in a predominantly urban local landscape than in a predominantly agricultural local landscape (Dunford & Freemark, 2004; Gagné & Fahrig, 2007). Therefore, in proposing the habitat amount hypothesis, I am not suggesting that habitat amount is the only driver of species richness, although it is usually the most important (Prevedello & Vieira, 2010).
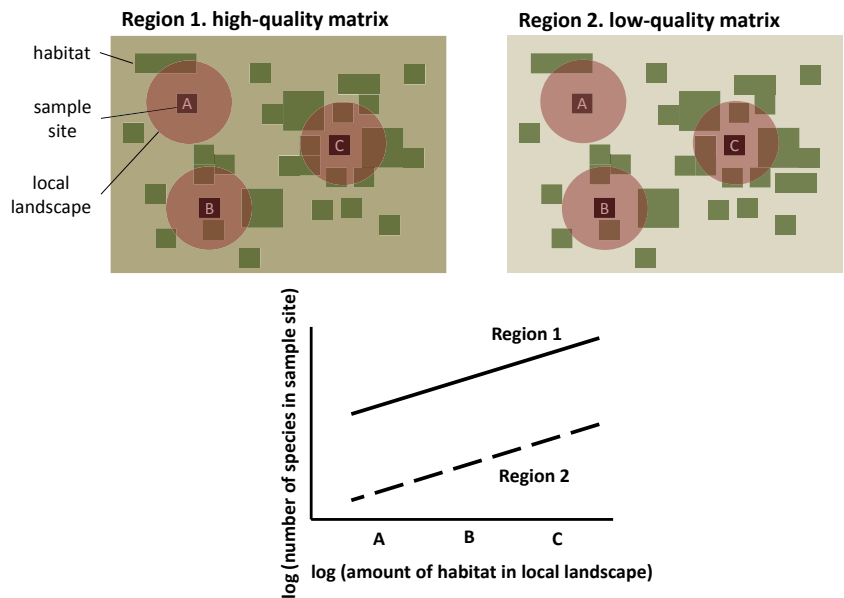

Figure 10 Effect of matrix quality on the relationship between species richness in a sample site (A, B, C) and habitat amount in the local landscape. Reducing matrix quality reduces species richness in a sample site, for a given amount of habitat in the local landscape (Region 1 versus Region 2), thus reducing the overall level of the curve.

HOW TO TEST THE HABITAT AMOUNT HYPOTHESIS

The habitat amount hypothesis posits that the patch size effect and the patch isolation effect are both due mainly to the sample area effect. The former can be tested by comparing the slope of the species–area relationship across a set of different-sized patches with the slope of the relationship across a set of sample areas equal in size to these patches but contained within a region of continuous habitat. If the patch size effect is due to the sample area effect, there should be no difference between these slopes; a steeper slope for the patches would be consistent with the island effect and inconsistent with the habitat amount hypothesis. Because several factors can affect the slope of a species–area curve – the species group, the sampling effort per area, and the size of the study region (Azovsky, 2011; Triantis *et al.*, 2012) – these factors would need to be identical for the set of patches and the set of sample areas in continuous habitat. In addition, it would be important that the patches were created sufficiently long ago such that if the island effect were operating, its effect on the slope would be detectable. Difficulty in finding such directly comparable sets may be the reason that there are few such studies to date.

Testing the assertion that the patch isolation effect on species richness is mainly due to the sample area effect (rather than to inter-patch distances) would require an experiment (or quasi-experiment), where sample sites are created (or selected) such that the distance from the local patch to the next nearest patch, and the amount of habitat within the local landscape are varied independently across sample sites (Fig. 11). A much stronger effect of habitat amount than nearest-neighbour distance on species richness in sample sites would be consistent with the habitat amount hypothesis (Fig. 11).

The habitat amount hypothesis also implies two predictions that could be tested using experiments (or quasi-experiments). First, a set of landscapes could be created (or selected) such that they all contain the same total amount of habitat in the local landscapes around sample sites, but there is variation in the sizes of the local patches containing the sample sites. In this case, the hypothesis predicts that there should be no effect of increasing local patch size on species richness in the sample sites (Fig. 7b). A positive effect would be consistent with the island effect and inconsistent with the habitat amount hypothesis. Second, a set of landscapes could be created (or selected) such that there is a negative correlation between the sizes of the local patches and the total amount of habitat in the local landscapes of the sample sites. In this case, the hypothesis predicts a positive effect of habitat amount in the local landscapes on species richness in the sample sites, even though the size of the local patch decreases (Fig. 7c). Here, a lack of effect of habitat amount (given sufficient statistical power) would be inconsistent with the habitat amount hypothesis.
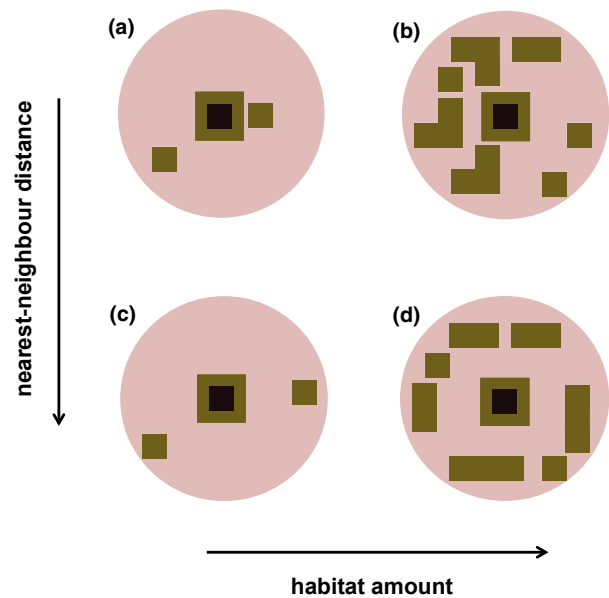

Figure 11 Study design for estimating the independent effects of habitat amount and nearest-neighbour distance on species richness in a sample site (black squares). Given an appropriate local landscape scale (circles), the habitat amount hypothesis predicts that the effect of habitat amount (a vs. b, or c vs. d) should be much stronger than the effect of nearest-neighbour distance (a vs. c, or b vs. d).

An indirect way to test the hypothesis is to test the above predictions for each of a large number of species individually, using the study designs suggested above, but where the response is species occurrence rather than species richness. Because species richness is the sum of the occurrences of individual species, the hypothesis implies that, for most species, the effects of patch size and isolation on species occurrence are due to the sample area effect. Ultimately it may be more valid to test the hypothesis indirectly by accumulating such tests across many species, than by conducting tests on species richness, because the habitat of individual species can be defined a priori using habitat suitability modelling, as discussed above (Betts *et al.*, 2007).

Population processes and patch size

At this point the reader may be wondering about the role of the numerous population processes that can affect population size, and that have been linked to patch size. Examples include pairing and reproductive success (e.g. Fraser & Stutchbury, 2004; Butcher *et al.*, 2010), conspecific attraction (Fletcher, 2009; Schipper *et al.*, 2011) and predation by generalist predators (Møller, 1988; Beier *et al.*, 2002; but see Huhta *et al.*, 1998; Loman, 2007). It has been argued that these processes and others lead to reduced abundances in smaller patches. If true, this should lead to reduced persistence and therefore reduced species occurrence, which, summed over species, should lead to lower species richness

in smaller patches. In other words, one might argue that these processes imply that the patch size effect is due to more than the sample area effect, which is inconsistent with the habitat amount hypothesis. However, this inference requires that these processes are linked specifically to patch size, and not indirectly to patch size through its (usual) correlation with local habitat amount. These processes would be inconsistent with the habitat amount hypothesis if: (1) they are related to patch size even when habitat amount in the local landscape remains constant or decreases; and (2) species richness is lower in sample sites within smaller habitat patches than in sample sites of the same size within larger patches, even when the amount of habitat in the local landscape is the same (i.e. Fig. 7b).

It has also been suggested that species should be absent from patches that are too small to hold a single territory, on the assumption that a territory must be contained within a single habitat patch ('minimum patch size requirement': Hinsley *et al.*, 1996; Lindenmayer *et al.*, 1999; Beier *et al.*, 2002). If true, then a subset of the regional species pool (those with larger territories) should be absent from smaller patches and this should lead to effects of patch size on species richness beyond the sample area effect. Some have argued that this is shown by 'nested subset' structuring of species, when the species matrix is ordered by patch area (Berglund & Jonsson, 2003; Fischer & Lindenmayer, 2005; Soga & Koike, 2012; but see Honnay *et al.*, 1999). Species nestedness patterns would be inconsistent with the habitat amount hypothesis only if the nestedness pattern with increasing patch size remains, even when the local habitat amount is constant or decreases. To summarize, the existence of these population processes and nestedness patterns is not in itself inconsistent with the habitat amount hypothesis. In proposing the hypothesis, I am implicitly questioning both their linkage to patch size itself (rather than to local habitat amount) and their impact on species richness.

IMPLICATIONS

Of course, in reality, fragmented ecological systems are complex webs of interacting processes affecting complex webs of interacting species (Didham *et al.*, 2012). One role of research is to catalogue these processes. However, another, important role is to identify the *dominant* processes and, by subtraction, those that can be safely ignored in most situations. This simplification is needed in the context of pressing conservation challenges, where simple yet effective advice is needed. The habitat amount hypothesis is one such simplification. It posits that patch size and patch isolation can be replaced with a single predictor, habitat amount, when species richness is measured in sample sites rather than over whole patches. Patch area only affects species richness in sample sites through its contribution to habitat amount, and patch isolation affects species richness in sample sites predominately through habitat amount rather than through inter-patch distance effects.

The habitat amount hypothesis can also be viewed as positing that the relevant spatial extent for evaluating extinction is much larger than individual habitat patches. Faunal relaxation following habitat loss may be observed for a whole region or landscape, but movement rates among patches are too high for there to be additional effects of patch size beyond these effects of regional habitat loss. In another sense, the hypothesis posits a shift, from remote islands, where island size and island isolation are independent predictors of species richness (Kalmar & Currie, 2006), to much less isolated continental habitat, where patch size and isolation can be replaced with habitat amount in the local landscapes of sample sites. An intermediate situation probably occurs for islands in tight clusters or spread over small areas, and continental island-like habitats such as mountain-tops. Consistent with this idea, a comprehensive review of species–area relationships for sets of true islands showed that the species–area slopes for inland islands, such as those in lakes, are shallower than the species–area slopes for oceanic islands (Triantis *et al.*, 2012).

If the habitat amount hypothesis turns out to be generally supported, it would mean that the habitat patch concept is flawed and that ecological communities are not spatially bounded entities (Ricklefs, 2008). It would also lead to some fairly radical implications. First, it would mean that the commonly made distinction between patch-scale and landscape-scale habitat effects (e.g. reviewed in Thornton *et al.*, 2011) is unnecessary: all habitat within the local landscape of a sample site, including the local patch, contributes to the habitat amount effect. Second, it would mean that distinguishing between patch size and patch isolation effects on species richness in sample sites is also unnecessary, as both are components of habitat amount in the local landscape, affecting species richness mainly through a single process, the sample area effect. Third, it would mean that the configuration of habitat in the landscape (e.g. fragmentation per se; Fahrig, 2003) generally has little or no effect on species richness in sample sites. Finally, it would even mean that the identification of discrete habitat patches is unnecessary for understanding the relationships between habitat distribution and species richness in sample sites.

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REFERENCES

Andrén, H. (1994) Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. *Oikos*, **71**, 355–366.

Azovsky, A.I. (2011) Species–area and species–sampling effort relationships: disentangling the effects. *Ecography*, **34**, 18–30.

Baguette, M., Petit, S. & Quéva, F. (2000) Population spatial structure and migration of three butterfly species within the same habitat network: consequences for conservation. *Journal of Applied Ecology*, **37**, 100–108.

Bailey, D., Schmidt-Entling, M.H., Eberhart, P., Herrmann, J.D., Hofer, G., Kormann, U. & Herzog, F. (2010) Effects of habitat amount and isolation on biodiversity in fragmented traditional orchards. *Journal of Applied Ecology*, **47**, 1003–1013.

Baz, A. & Garcia-Boyero, A. (1996) The SLOSS dilemma: a butterfly case study. *Biodiversity and Conservation*, **5**, 493–502.

Beier, P., van Drielen, M. & Kankam, B.O. (2002) Avifaunal collapse in West African forest fragments. *Conservation Biology*, **16**, 1097–1111.

Bender, D.J., Tischendorf, L. & Fahrig, L. (2003) Using patch isolation metrics to predict animal movement in binary landscapes. *Landscape Ecology*, **18**, 17–39.

Berglund, H. & Jonsson, B.G. (2003) Nested plant and fungal communities; the importance of area and habitat quality in maximizing species capture in boreal old-growth forests. *Biological Conservation*, **112**, 319–328.

Betts, M.G., Forbes, G.J. & Diamond, A.W. (2007) Thresholds in songbird occurrence in relation to landscape structure. *Conservation Biology*, **21**, 1046–1058.

Bowne, D.R. & Bowers, M.A. (2004) Interpatch movements in spatially structured populations: a literature review. *Landscape Ecology*, **19**, 1–20.

Broome, L.S. (2001) Density, home range, seasonal movements and habitat use of the mountain pygmy-possum *Burramys parvus* (Marsupialia: Burramyidae) at Mount Blue Cow, Kosciuszko National Park. *Austral Ecology*, **26**, 275–292.

Butcher, J.A., Morrison, M.L., Ransom, D., Slack, R.D. & Wilkins, R.N. (2010) Evidence of a minimum patch size threshold of reproductive success in an endangered songbird. *Journal of Wildlife Management*, **74**, 133–139.

Collinge, S.K. (2000) Effects of grassland fragmentation on insect species loss, colonization, and movement patterns. *Ecology*, **81**, 2211–2226.

Didham, R.K., Kapos, V. & Ewers, R.M. (2012) Rethinking the conceptual foundations of habitat fragmentation research. *Oikos*, **121**, 161–170.

van Dorp, D. & Opdam, P.F.M. (1987) Effects of patch size, isolation and regional abundance on forest bird communities. *Landscape Ecology*, **1**, 59–73.

Dunford, W. & Freemark, K. (2004) Matrix matters: effects of surrounding land uses on forest birds near Ottawa, Canada. *Landscape Ecology*, **20**, 497–511.

Eigenbrod, F., Hecnar, S.J. & Fahrig, L. (2008) The relative effects of road traffic and forest cover on anuran populations. *Biological Conservation*, **141**, 35–46.

Fahrig, L. (2003) Effects of habitat fragmentation on biodiversity. *Annual Reviews of Ecology, Evolution and Systematics*, **34**, 487–515.

Fattorini, S. (2010) The use of cumulative area curves in biological conservation: a cautionary note. *Acta Oecologica*, **36**, 255–258.

Fenoglio, M.S., Salvo, A., Videla, M. & Valladares, G.R. (2010) Plant patch structure modifies parasitoid assemblage richness of a specialist herbivore. *Ecological Entomology*, **35**, 594–601.

Fischer, J. & Lindenmayer, D.B. (2005) Nestedness in fragmented landscapes: a case study on birds, arboreal marsupials and lizards. *Journal of Biogeography*, **32**, 1737–1750.

Fischer, J., Lindenmayer, D.B., Barry, S. & Flowers, E. (2005) Lizard distribution patterns in the Tumut fragmentation "Natural Experiment" in south-eastern Australia. *Biological Conservation*, **123**, 301–315.

Fletcher, R.J. (2009) Does attraction to conspecifics explain the patch-size effect? An experimental test. *Oikos*, **118**, 1139–1147.

Flick, T., Feagan, S. & Fahrig, L. (2012) Effects of landscape structure on butterfly species richness and abundance in agricultural landscapes in eastern Ontario, Canada. *Agriculture, Ecosystems and Environment*, **156**, 123–133.

Franzén, M., Larsson, M. & Nilsson, S. (2009) Small local population sizes and high habitat patch fidelity in a specialised solitary bee. *Journal of Insect Conservation*, **13**, 89–95.

Fraser, G.S. & Stutchbury, B.J.M. (2004) Area-sensitive forest birds move extensively among forest patches. *Biological Conservation*, **118**, 377–387.

Freemark, K.E. & Merriam, H.G. (1986) Importance of area and habitat heterogeneity on bird assemblages in temperate forest fragments. *Biological Conservation*, **36**, 115–141.

Gagné, S.A. & Fahrig, L. (2007) Effect of landscape context on amphibian communities in breeding ponds. *Landscape Ecology*, **22**, 205–215.

Galanes, I.T. & Thomlinson, J.R. (2009) Relationships between spatial configuration of tropical forest patches and woody plant diversity in northeastern Puerto Rico. *Plant Ecology*, **201**, 101–113.

Galanes, I.T. & Thomlinson, J.R. (2011) Soil millipede diversity in tropical forest patches and its relation to landscape structure in northeastern Puerto Rico. *Biodiversity Conservation*, **20**, 2967–2980.

Garden, J.G., McAlpine, C.A. & Possingham, H.P. (2010) Multi-scaled habitat considerations for conserving urban

biodiversity: native reptiles and small mammals in Brisbane, Australia. *Landscape Ecology*, **25**, 1013–1028.

Gavish, Y., Ziv, Y. & Rosenzweig, M.L. (2011) Decoupling fragmentation from habitat loss for spiders in patchy agricultural landscapes. *Conservation Biology*, **26**, 150–159.

Haila, Y. (1988) Calculating and miscalculating density: the role of habitat geometry. *Ornis Scandinavica*, **19**, 88–92.

Haila, Y. (2002) A conceptual genealogy of fragmentation research: from island biogeography to landscape ecology. *Ecological Applications*, **12**, 321–334.

Harrison, S. (1991) Local extinction in a metapopulation context: an empirical evaluation. *Biological Journal of the Linnean Society*, **42**, 73–88.

Hattori, A. & Shibuno, T. (2010) The effect of patch reef size on fish species richness in a shallow coral reef shore zone where territorial herbivores are abundant. *Ecological Research*, **25**, 457–468.

Helliwell, D.R. (1976) The effects of size and isolation on the conservation value of wooded sites in Britain. *Journal of Biogeography*, **3**, 407–416.

Hendrickx, F., Maelfait, J.-P., Desender, K., Aviron, S., Bailey, D., Diekotter, T., Lens, L., Liira, J., Schweiger, O., Speelmans, M., Vandomme, V. & Bugter, R. (2009) Pervasive effects of dispersal limitation on within- and among-community species richness in agricultural landscapes. *Global Ecology and Biogeography*, **18**, 607–616.

Hinsley, S.A., Pakeman, R., Bellamy, P.E. & Newton, I. (1996) Influences of habitat fragmentation on bird species distributions and regional population sizes. *Proceedings of the Royal Society B: Biological Sciences*, **263**, 307–313.

Hokkanen, P.J., Kouki, J. & Komonen, J. (2009) Nestedness, SLOSS and conservation networks of boreal herb-rich forests. *Applied Vegetation Science*, **12**, 295–303.

Holland, G.J. & Bennett, A.F. (2009) Differing responses to landscape change: implications for small mammal assemblages in forest fragments. *Biodiversity Conservation*, **18**, 2997–3016.

Holland, J. & Fahrig, L. (2000) Effect of woody borders on insect density and diversity in crop fields: a landscape-scale analysis. *Agriculture, Ecosystems and Environment*, **78**, 115–122.

Holland, J.D., Fahrig, L. & Cappuccino, N. (2005) Body size affects the spatial scale of habitat–beetle interactions. *Oikos*, **110**, 265–270.

Holt, R.D. (1992) A neglected facet of island biogeography: the role of internal spatial dynamics in area effects. *Theoretical Population Biology*, **41**, 354–371.

Honnay, O., Hermy, M. & Coppin, P. (1999) Nested plant communities in deciduous forest fragments: species relaxation or nested habitats? *Oikos*, **84**, 119–129.

Horner-Devine, M.C., Daily, G.C., Ehrlich, P.R. & Boggs, C.L. (2003) Countryside biogeography of tropical butterflies. *Conservation Biology*, **17**, 168–177.

Hoyle, M. & Harborne, A.R. (2005) Mixed effects of habitat fragmentation on species richness and community structure in a microarthropod microecosystem. *Ecological Entomology*, **30**, 684–691.

Huhta, E., Jokimaki, J. & Helle, P. (1998) Predation on artificial nests in a forest dominated landscape – the effects of nest type, patch size and edge structure. *Ecography*, **21**, 464–471.

Jackson, H.B. & Fahrig, L. (2012) What size is a biologically relevant landscape? *Landscape Ecology*, **27**, 929–941.

Jackson, H.B., Baum, K.A., Robert, T. & Cronin, J.T. (2009) Habitat-specific movement and edge-mediated behavior of the saproxylic insect *Odontotaenius disjunctus* (Coleoptera: Passalidae). *Environmental Entomology*, **38**, 1411–1422.

Kalmar, A. & Currie, D.J. (2006) A global model of island biogeography. *Global Ecology and Biogeography*, **15**, 72–81.

Lande, R. (1987) Extinction thresholds in demographic models of territorial populations. *The American Naturalist*, **130**, 624–635.

Laurance, W.F., Lovejoy, T.E., Vasconcelos, H.L., Bruna, E.M., Didham, R.K., Stouffer, P.C., Gascon, C., Bierregaard, R.O., Laurance, S.G. & Sampaio, E. (2002) Ecosystem decay of Amazonian forest fragments: a 22-year investigation. *Conservation Biology*, **16**, 605–618.

Lindenmayer, D.B., Cunningham, R.B., Pope, M.L. & Donnelly, C.F. (1999) The response of arboreal marsupials to landscape context: a large-scale fragmentation study. *Ecological Applications*, **9**, 594–611.

Loman, J. (2007) Effect of woodland patch size on rodent seed predation in a fragmented landscape. *Web Ecology*, **7**, 47–52.

MacArthur, R.H. & Wilson, E.O. (1963) An equilibrium theory of insular zoogeography. *Evolution*, **17**, 373–387.

MacArthur, R.H. & Wilson, E.O. (1967) *The theory of island biogeography*. Princeton University Press, Princeton, NJ.

Martin, A.E. & Fahrig, L. (2012) Measuring and selecting scales of effect for landscape predictors in species–habitat models. *Ecological Applications*, **22**, 2277–2292.

Martínez-Sanz, C., Cenzano, C.S.S., Fernández-Aláez, M. & García-Criado, F. (2012) Relative contribution of small mountain ponds to regional richness of littoral macroinvertebrates and the implications for conservation. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **22**, 155–164.

McCoy, E.D. & Mushinsky, H.R. (1994) Effects of fragmentation on the richness of vertebrates in the Florida scrub habitat. *Ecology*, **75**, 446–447.

McNeill, S.E. & Fairweather, P.G. (1993) Single large or several small marine reserves? An experimental approach with seagrass fauna. *Journal of Biogeography*, **20**, 429–440.

Middleton, J. & Merriam, G. (1983) Distribution of woodland species in farmland woods. *Journal of Applied Ecology*, **20**, 625–644.

Moilanen, A. & Nieminen, M. (2002) Simple connectivity measures in spatial ecology. *Ecology*, **83**, 1131–1145.

Møller, A.P. (1988) Nest predation and nest site choice in passerine birds in habitat patches of different size – a study of magpies and blackbirds. *Oikos*, **53**, 215–221.

Öckinger, E., Lindborg, R., Sjödin, N.E. & Bommarco, R. (2012) Landscape matrix modifies richness of plants and insects in grassland fragments. *Ecography*, **35**, 259–267.

Oertli, B., Joye, D.A., Castella, E., Juge, R., Cambin, D. & Lachavanne, J.-B. (2002) Does size matter? The relationship between pond area and biodiversity. *Biological Conservation*, **104**, 59–70.

Paciencia, M.L.B. & Prado, J. (2005) Effects of forest fragmentation on pteridophyte diversity in a tropical rain forest in Brazil. *Plant Ecology*, **180**, 87–104.

Parris, K.M. (2006) Urban amphibian assemblages as meta-communities. *Journal of Animal Ecology*, **75**, 757–764.

Peintinger, M., Bergamini, A. & Schmid, B. (2003) Species–area relationships and nestedness of four taxonomic groups in fragmented wetlands. *Basic and Applied Ecology*, **4**, 385–394.

Petranka, J.W. & Holbrook, C.T. (2006) Wetland restoration for amphibians: should local sites be designed to support metapopulations or patchy populations? *Restoration Ecology*, **14**, 404–411.

Piessens, K., Honnay, O., Nackaerts, K. & Hermy, M. (2004) Plant species richness and composition of heathland relics in north-western Belgium: evidence for a rescue-effect? *Journal of Biogeography*, **31**, 1683–1692.

Preston, F.W. (1962) The canonical distribution of commonness and rarity: parts I, II. *Ecology*, **43**, 185–215, 410–432.

Prevedello, J.A. & Vieira, M.V. (2010) Does the type of matrix matter? A quantitative review of the evidence. *Biodiversity Conservation*, **19**, 1205–1223.

Prugh, L.R. (2009) An evaluation of patch connectivity measures. *Ecological Applications*, **19**, 1300–1310.

Püttker, T., Bueno, A.A., de Barros, C.D., Sommer, S. & Pardini, R. (2011) Immigration rates in fragmented landscapes – empirical evidence for the importance of habitat amount for species persistence. *PLoS ONE*, **6**, e27963.

Ranius, T., Johansson, V. & Fahrig, L. (2010) A comparison of patch connectivity measures using data on invertebrates in hollow oaks. *Ecography*, **33**, 1–8.

Ricketts, T.H., Daily, G.C., Ehrlich, P.R. & Fay, J.P. (2001) Countryside biogeography of moths in a fragmented landscape: biodiversity in native and agricultural habitats. *Conservation Biology*, **15**, 378–388.

Ricklefs, R.E. (2008) Disintegration of the ecological community. *The American Naturalist*, **172**, 741–750.

Robles, H. & Ciudad, C. (2012) Influence of habitat quality, population size, patch size, and connectivity on patch-occupancy dynamics of the Middle Spotted Woodpecker. *Conservation Biology*, **26**, 284–293.

Rodríguez-Loinaz, G., Amezaga, I. & Onaindia, M. (2012) Does forest fragmentation affect the same way all growth-forms? *Journal of Environmental Management*, **94**, 125–131.

Roe, J.H., Brinton, A.C. & Georges, A. (2009) Temporal and spatial variation in landscape connectivity for a freshwater turtle in a temporally dynamic wetland system. *Ecological Applications*, **19**, 1288–1299.

Rosenzweig, M.L. (2004) Applying species–area relationships to the conservation of species diversity. *Frontiers in biogeography: new directions in the geography of nature* (ed. by M.V. Lomolino and M.V. Heaney), pp. 325–344. Sinauer Associates, Sunderland, MA.

Rosin, Z.M., Skórka, P., Lenda, M., Morón, D., Sparks, T.H. & Tryjanowski, P. (2011) Increasing patch area, proximity of human settlement and larval food plants positively affect the occurrence and local population size of the habitat specialist butterfly *Polyommatus coridon* (Lepidoptera: Lycaenidae) in fragmented calcareous grasslands. *European Journal of Entomology*, **108**, 99–106.

Sætersdal, M. (1994) Rarity and species/area relationships of vascular plants in deciduous woods, western Norway – applications to nature reserve selection. *Ecography*, **17**, 23–38.

Scheiner, S.M. (2003) Six types of species–area curves. *Global Ecology and Biogeography*, **12**, 441–447.

Schipper, A.M., Koffijberg, K., van Weperen, M., Atsma, G., Ragas, A.M.J., Hendriks, A.J. & Leuven, R.S.E.W. (2011) The distribution of a threatened migratory bird species in a patchy landscape: a multi-scale analysis. *Landscape Ecology*, **26**, 397–410.

Schmiegelow, F.K.A., Machtans, C.S. & Hannon, S.J. (1997) Are boreal birds resilient to forest fragmentation? An experimental study of short-term community responses. *Ecology*, **78**, 1914–1932.

Schüepp, C., Herrmann, J.D., Herzog, F. & Schmidt-Entling, M.H. (2011) Differential effects of habitat isolation and landscape composition on wasps, bees, and their enemies. *Oecologia*, **165**, 713–721.

Schultz, C.B., Franco, A.M.A. & Crone, E.E. (2012) Response of butterflies to structural and resource boundaries. *Journal of Animal Ecology*, **81**, 724–734.

Shirley, S.M. & Smith, J.N.M. (2005) Bird community structure across riparian buffer strips of varying width in a coastal temperate forest. *Biological Conservation*, **125**, 475–489.

Smith, A.C., Fahrig, L. & Francis, C.M. (2011) Landscape size affects the relative importance of habitat amount, habitat fragmentation, and matrix quality on forest birds. *Ecography*, **34**, 103–113.

Soga, M. & Koike, S. (2012) Life-history traits affect vulnerability of butterflies to habitat fragmentation in urban remnant forests. *Écoscience*, **19**, 11–20.

Stasek, D.J., Bean, C. & Crist, T.O. (2008) Butterfly abundance and movements among prairie patches: the roles of habitat quality, edge, and forest matrix permeability. *Environmental Entomology*, **37**, 897–906.

Stiles, A. & Scheiner, S.M. (2010) A multi-scale analysis of fragmentation effects on remnant plant species richness in Phoenix, Arizona. *Journal of Biogeography*, **37**, 1721–1729.

Thornton, D.H., Branch, L.C. & Sunquist, M.E. (2011) The influence of landscape, patch, and within-patch factors on species presence and abundance: a review of focal patch studies. *Landscape Ecology*, **26**, 7–18.

Tischendorf, L., Bender, D.J. & Fahrig, L. (2003) Evaluation of patch isolation metrics in mosaic landscapes for specialist vs. generalist dispersers. *Landscape Ecology*, **18**, 41–50.

Tjørve, E. (2010) How to resolve the SLOSS debate: lessons from species–diversity models. *Journal of Theoretical Biology*, **264**, 604–612.

Triantis, K.A., Guilhaumon, F. & Whittaker, R.J. (2012) The island species–area relationship: biology and statistics. *Journal of Biogeography*, **39**, 215–231.

Tscharntke, T., Steffan-Dewenter, I., Kruess, A. & Thies, C. (2002) Contribution of small habitat fragments to conservation of insect communities of grassland-cropland landscapes. *Ecological Applications*, **12**, 354–363.

Uezu, A. & Metzger, J.P. (2011) Vanishing bird species in the Atlantic Forest: relative importance of landscape configuration, forest structure and species characteristics. *Biodiversity Conservation*, **20**, 3627–3643.

Virolainen, K.M., Suomi, T., Suhonen, J. & Kuitunen, M. (1998) Conservation of vascular plants in single large and several small mires: species richness, rarity and taxonomic diversity. *Journal of Applied Ecology*, **35**, 700–707.

Watling, J.I. & Donnelly, M.A. (2006) Fragments as islands: a synthesis of faunal responses to habitat patchiness. *Conservation Biology*, **20**, 1016–1025.

Weigelt, P. & Kreft, H. (2013) Quantifying island isolation – insights from global patterns of insular plant species richness. *Ecography*, **36**, 417–429.

BIOSKETCH

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