Global Ecology and Biogeography | A Journal of Macroecology | WILEY

Why do several small patches hold more species than few large patches?

Lenore Fahrig [ORCID]

Geomatics and Landscape Ecology Laboratory, Department of Biology, Carleton University, Ottawa, Ontario, Canada

Correspondence
Lenore Fahrig, Geomatics and Landscape Ecology Laboratory, Department of Biology, Carleton University, Ottawa, Ontario, Canada K1S 5B6.
Email: lenore.fahrig@carleton.ca

Abstract

Background: The principle that a single large habitat patch should hold more species than several small patches totalling the same area (SL > SS) is used by conservation agencies to favour protection of large, contiguous areas. Previous reviews of empirical studies have found the opposite, SS > SL, creating the single large or several small (SLOSS) debate.

Aims: Review the empirical and theoretical SLOSS literature; identify potential mechanisms underlying the SS > SL pattern; evaluate these where possible.

Location: Global.

Time period: 1976–2018.

Major taxa: Plants, invertebrates, vertebrates.

Methods: Literature review.

Results: Like previous reviews, I found that SS > SL dominates empirical findings. This pattern remained, although it was somewhat weakened, in studies where sampling intensity was proportional to patch size. I found six classes of theory, and conducted five preliminary evaluations of theory. None of the predictions was supported. The SS > SL pattern held for specialist species groups, suggesting it does not result from incursion by generalists into small patches. I found no evidence for the prediction that the reverse pattern (SL > SS) becomes more common over time since patch creation, through gradual species losses from SS. I found no difference between results for natural and anthropogenic patches. There was also no evidence for predictions that SL > SS is more common when the matrix is more hostile, or for stable than ephemeral patches.

Main conclusions: Most empirical comparisons find SS > SL. While there are several potential causes, more empirical work is needed to identify those at play. Meanwhile, conservation practitioners should understand that there is no ecological evidence supporting a general principle to preserve large, contiguous habitat areas rather than multiple small areas of the same total size.

KEYWORDS
fragments, habitat amount, habitat fragmentation, islands, isolates, landscape configuration, landscape fragmentation, patch size, reserves, SLOSS debate

1 | INTRODUCTION

More than four decades ago, Diamond (1975) proposed the SL > SS 'principle', that a single large patch of habitat (SL) holds more species than several small patches (SS) of the same total area. Here I use 'patch' as a general term meaning a habitat area that can be delineated from others. Notably, Diamond did not provide any empirical support for his principle. In the applied world, conservation organizations immediately assumed that Diamond's principle was valid and began to use it. Of particular importance, the International Union for Conservation of Nature (IUCN) included the SL > SS principle in their World Conservation Strategy (IUCN, 1980), a very influential document used by countries around the world to guide conservation efforts.

Early reviews concluded that all empirical tests of Diamond's SL > SS principle had failed to support it (Quinn & Harrison, 1988; Simberloff & Abele, 1982). This ignited the now-longstanding 'single large or several small' (SLOSS) debate within the conservation research community. The lack of empirical support for SL > SS has continued over the past 40 + years. My review of significant responses to habitat fragmentation (Fahrig, 2017) included 60 SLOSS-type comparisons. All of them found more species in several small patches than in few large patches of the same total area (as in Figure 1a; see figure 9a in Fahrig, 2017). Several small patches have been found to contain more species than few large patches for a wide variety of taxonomic groups – trees, other vascular plants, bryophytes, liverworts, lichens, bracket fungi, aquatic plants, gastropods, crustaceans, aquatic invertebrates, butterflies, leafhoppers, crickets, dragonflies, ants, carabid beetles, saproxylic beetles, parasitoid wasps, micro-arthropods, reef fish, amphibians, lizards, small mammals, bats, and birds – and for a wide variety of different ecosystems and spatial scales.

Despite apparent consistency of the empirical results, SLOSS is still described either as a debate (e.g. Kendal et al., 2017; Le Roux, Ikin, Lindenmayer, Manning, & Gibbons, 2015; Lindenmayer, Wood, McBurney, Blair, & Banks, 2015; MacDonald, Anderson, Acorn, & Nielsen, 2018a, 2018b; Rösch, Tscharntke, Scherber, & Batáry, 2015), or researchers conclude that there is no single answer and that the answer depends on various conditions (reviewed in Kingsland, 2002). There are two reasons for this mismatch between the empirical findings and researchers' inferences about SLOSS. First, the validity of empirical SLOSS studies has been called into question. Early on, Ramsey (1989) and Mac Nally and Lake (1999) argued that the Quinn and Harrison (1988) 'saturation index' for testing SLOSS was biased. Some researchers incorrectly took this to mean that conclusions based on comparisons of the Quinn and Harrison (1988) species accumulation curves (Figure 1) were also biased. More recently, Gavish, Ziv, and Rosenzweig (2011) pointed out that many empirical SLOSS studies are biased in favour of SS > SL because small patches are often more intensively sampled for species than are large patches. The second reason for the mismatch between the consistent empirical findings of SS > SL and researchers'
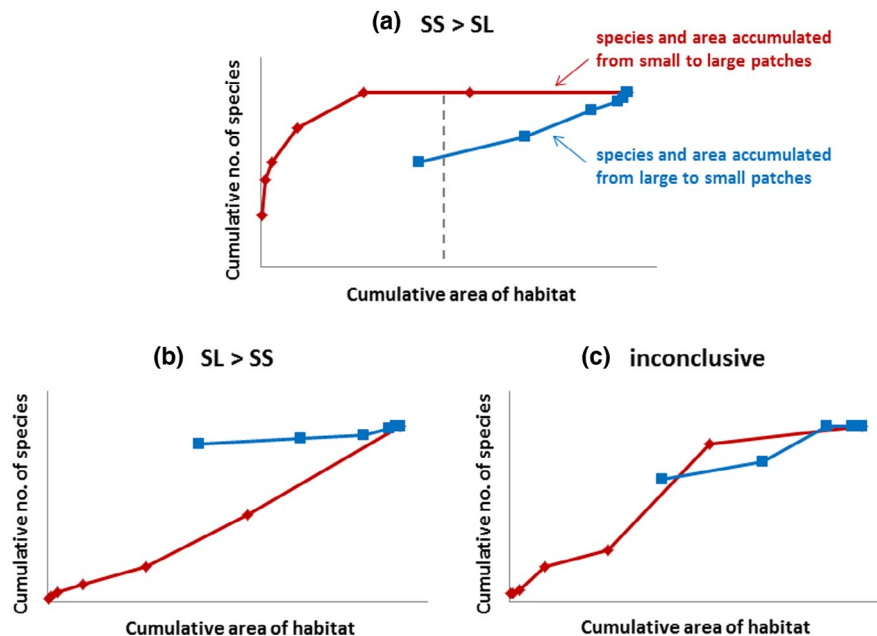

FIGURE 1 Empirical single large or several small (SLOSS) comparisons (Quinn & Harrison, 1988). The total number of species is accumulated with cumulative area across patches, ordered from smallest to largest (red curve) and from largest to smallest (blue curve). The two curves accumulate the same list of species (from all sampled patches), and so the maximum number of species, and the maximum habitat area, across all patches is identical for the two curves. Dashed grey line in panel (a): comparison of the two cumulative species values at a given total area of habitat indicates whether the total number of species in many small patches is higher or lower than the total number of species in few large patches, for that given total area of habitat. Panel headers indicate the conclusion drawn from each figure. If the small-to-large curve is entirely above the large-to-small curve (a), then SS > SL. If the large-to-small curve is entirely above the small-to-large curve (b), then SL > SS. If the curves cross (c) then the SLOSS comparison is inconclusive [Colour figure can be viewed at wileyonlinelibrary.com]

inferences about SLOSS is that many studies have proposed reasonable ideas and theories for why and how SLOSS should depend on various factors (e.g. Atmar & Patterson, 1993; Kallimanis, Kunin, Halley, & Sgardelis, 2005; Margules, Higgs, & Rafe, 1982; McCarthy, Thompson, & Williams, 2006; Ovaskainen, 2002; Pelletier, 2000; Tjørve, 2010). These have led to an expectation that there are predictable situations where SL > SS and others where SS > SL.

Importantly, SLOSS is not simply an abstract academic question. Global biodiversity is in precipitous decline due mainly to loss of natural habitats (Butchart et al., 2010). Conservation of biodiversity depends on the answer to SLOSS because at present, conservation agencies around the world are using the SL > SS principle for decisions about habitat preservation. Based on this principle, conservation agencies prioritize large, contiguous natural areas, and assume that small bits of habitat are not worth conserving (Fischer & Lindenmayer, 2002; Hernández-Ruedas et al., 2014; Hill et al., 2018), even when these add up to the same area as the large ones. If the SL > SS principle is not correct, the cumulative impact on biodiversity of the loss of small unprotected patches is much larger than conservation agencies have been led to believe.

Here, my overall goal was to understand why previous empirical reviews consistently find SS > SL. To this end, I conducted a review of empirical and theoretical SLOSS studies, to: (a) determine whether this pattern (SS > SL) holds for studies with unbiased sampling, that is, where sampling was proportional to patch size; (b) identify theories from the literature that might explain this pattern, and (c) use the empirical studies to conduct evaluations of predictions derived from some of these theories, where possible.

2 | LITERATURE SEARCH

The goal of the literature review was to build a complete picture of the SLOSS literature up to the end of 2018, including both empirical and theoretical studies. I began by searching on Web of Science using the following search string: ("several small" OR "several-small" OR "SLOSS") AND ("single large" OR "single-large" or "SLOSS"), refined by research area to environmental sciences and biodiversity and conservation. I retained all papers presenting SLOSS theory or SLOSS data. I did not retain review papers. For the empirical studies I retained only those that evaluated species richness, as the SLOSS debate is specifically about species richness. However, most of the theory related to the SLOSS question is actually based on single species models and mechanisms (Ovaskainen, 2002), which are then extrapolated to species richness. Therefore, I retained both single-species and multi-species SLOSS theory.

To ensure comparability among empirical studies I included only SLOSS studies of the type shown in Figure 1 (Quinn & Harrison, 1988) or equivalent, that is, combining species lists across patches to compare species richness in several small versus few large patches of the same total area. Hereafter I refer to a comparison based on Quinn and Harrison species accumulation curves (Figure 1) as a 'SLOSS comparison'. SLOSS comparisons are usually presented in figures but are sometimes presented in text or tables. Note I did not include papers that only reported the Quinn and Harrison (1988) saturation index without the species accumulation curves, because, as mentioned above, this index has been shown to be biased.

In addition to studies found through the Web of Science search, I looked for additional studies by reviewing the papers that cite Quinn and Harrison (1988), as this paper is the source of the graphical method for making SLOSS comparisons (Figure 1). I also looked for additional studies in the citations sections of retained papers. In cases where data were included in the paper but not presented in a SLOSS comparison figure (Figure 1), I extracted the data and made the SLOSS comparison figure. In cases where the data were not included in the paper and were not presented in a SLOSS comparison figure, I contacted the authors to request the data and/or SLOSS comparison figure. Some authors did not reply, some sent me their data so that I could make the figure, and some sent me one or more SLOSS comparison figures. In some cases these represented only a subset of the comparisons mentioned in the paper. I did not include comparisons mentioned in papers unless I had the actual SLOSS comparison figures (or data). I did not include data presented in review papers, to avoid double-counting. I included results separately for most subdivisions of the data made by the authors. For example, if the authors included separate figures for specialist and generalist species I included these as separate comparisons. When provided, I also included separate comparisons for different habitat types (e.g. natural versus man-made stones in Douglas & Lake, 1994), or for patches surrounded by different matrix types (e.g. a matrix of non-native pine plantation versus grazing lands in Fischer & Lindenmayer, 2002). I did this to allow evaluations of some of the predictions that emerged from my review of theory (below). However, I acknowledge that these evaluations are preliminary because multiple comparisons from the same study are not independent. Note that I did not include multiple comparisons from a study for the same species group in the same patches in different years, or for different groupings of patches (unless they differed by habitat type), or in different regions (unless the author indicated some difference between the regions, for example habitat type, matrix type).

As there is no effect size and no statistical test for SLOSS comparisons, I categorized each SLOSS comparison into one of the three categories shown in Figure 1. If the small-to-large curve was entirely above the large-to-small curve, I concluded that SS > SL. If the large-to-small curve was entirely above the small-to-large curve, I concluded SL > SS. If the curves crossed I concluded that the result was inconclusive. There were two situations in which I did not consider line-crossings as such, because they could be artefacts of connecting points by straight lines. First, if the author connected the first point in the large-to-small curve to the origin, I did not include instances of crossed lines within this extrapolated segment if this was the only instance of the lines crossing (e.g. see figure 2f in MacDonald et al., 2018a). Similarly, I did not include instances of crossed lines between the second last and last points on the small-to-large curve when this was the only instance of the lines crossing (e.g. see figure 4 in Lizee, Tatoni, & Deschamps-Cottin, 2016). The former would lead to

missing an instance where SL > SS (four cases), while the latter would lead to missing an instance where SS > SL (five cases).

3 | RESULTS AND DISCUSSION

3.1 | Overall review of empirical studies

I found 157 SLOSS comparisons, from 58 studies (data are in Supporting Information Table S1; reference for each study is in either the References section or in the Appendix). Seventy-two percent of SLOSS comparisons found SS > SL, 22% were inconclusive (i.e. the small-to-large and large-to-small lines crossed) and 6% found SL > SS (Figure 2a – left bar). The pattern was similar at the level of studies: 81% of studies found at least one comparison where SS > SL, 33% of studies found at least one comparison that was inconclusive and 9% of studies found at least one comparison where SL > SS (Figure 2a – right bar); note these add to > 100% of studies as some studies with multiple comparisons found more than one result. Of the comparisons where there was a clear difference between SL and SS, 93% found SS > SL (Figure 2a – left bar). These results are consistent with those of previous reviews, which found that SS > SL findings dominate the empirical literature.

There were no obvious similarities among the five studies that contained at least one instance of SL > SS. They were highly variable, including aquatic invertebrates, butterflies, forest birds, and vascular plants including exotic plants. They included studies of both true islands and habitat patches (both natural and human-created), and with different types of matrix – forest, water or agriculture.

3.2 | Effect of sampling bias

Gavish et al. (2011) pointed out that many SLOSS studies are likely biased toward finding SS > SL because in many studies the number of sampling points per unit area declines with patch size. Therefore, when combining patches into subsets of equal total area, subsets with many small patches often have more sampling points than subsets with few large patches. This would lead to a higher likelihood of finding a given species in the set of several small patches than in the few large patches.

To determine whether this is responsible for the predominance of SS > SL in the empirical literature, I categorized the sampling methods in each study into one of four categories: (a) no sampling bias, that is, either sampling was proportional to patch size or all patches were completely sampled; (b) sampling intensity decreased with patch size but there was some effort to compensate for potential bias; (c) the number of samples or sampling area was the same for all patches (i.e. strong sampling bias); or (d) the relationship between sampling intensity and patch size was unclear.

Just under half of the SLOSS comparisons (75) were from studies with clearly unbiased sampling, that is, where sampling increased in proportion to patch size. Fifty-two percent of comparisons from

these unbiased studies found SS > SL (Figure 2b – right bar). In contrast 91% of comparisons from the remaining studies (a combination of biased studies and possibly biased studies) found SS > SL (Figure 2b – left bar). Eleven percent of comparisons from unbiased studies found SL > SS while only 1% of comparisons in the remaining studies found SL > SS (Figure 2b). Therefore, while sampling bias does not 'explain away' the dominant finding of SS > SL, it is clearly producing an over-representation of this pattern in the empirical literature. Future empirical SLOSS studies need to ensure that sampling is proportional to patch size.

The SLOSS comparisons from studies with unbiased sampling were highly variable. They represent a wide variety of taxonomic groups – birds, butterflies, plants, fish, fungi, lichens, bryophytes, crustaceans, orthopterans and mites – and a wide variety of habitats—coral reefs, forests, grasslands, trees, moss, stones, mires and true islands – surrounded by different matrix types – water, clear-cuts, wetland, forest, agriculture, rock, and urban development. All of my preliminary evaluations of predictions from SLOSS theory (Figure 2c–g) were limited to the 75 comparisons from these unbiased studies.

3.3 | Review of SLOSS theory and predictions, and some evaluations

In my review of SLOSS theory I found a plethora of ideas, published over a 40-year span, that make predictions about the conditions in which we should expect SL > SS versus SS > SL. However, these predictions have not yet been compared to the empirical evidence. All reviews of the empirical SLOSS comparisons, including this one, have found that SS > SL dominates results: among the 75 SLOSS comparisons with unbiased sampling, I found about five times as many SS > SL results as SL > SS results (Figure 2b – right bar). Given this, the next step to resolving the SLOSS debate is to determine which mechanism or combination of mechanisms is responsible for this empirical pattern. Here I summarize the SLOSS theories I found in my review, and I extract predictions from each in light of the results of the empirical review (in italics below). For a few of these predictions there was sufficient information from the reviewed empirical studies to do an evaluation (Figure 2c–g). These evaluations are preliminary because the number of comparisons is often small and multiple comparisons from the same study are not independent. Again, for these evaluations I used only the 75 comparisons from studies with sampling clearly proportional to patch size, that is, unbiased sampling (see Section 3.2).

3.3.1 | Incursion by common, generalist species

Early on, proponents of the SL > SS principle recognized that the arguments predicting SL > SS only apply to species whose distributions are mainly limited to the habitat in question. They argued that common, habitat-generalist species are more likely to occur in small patches
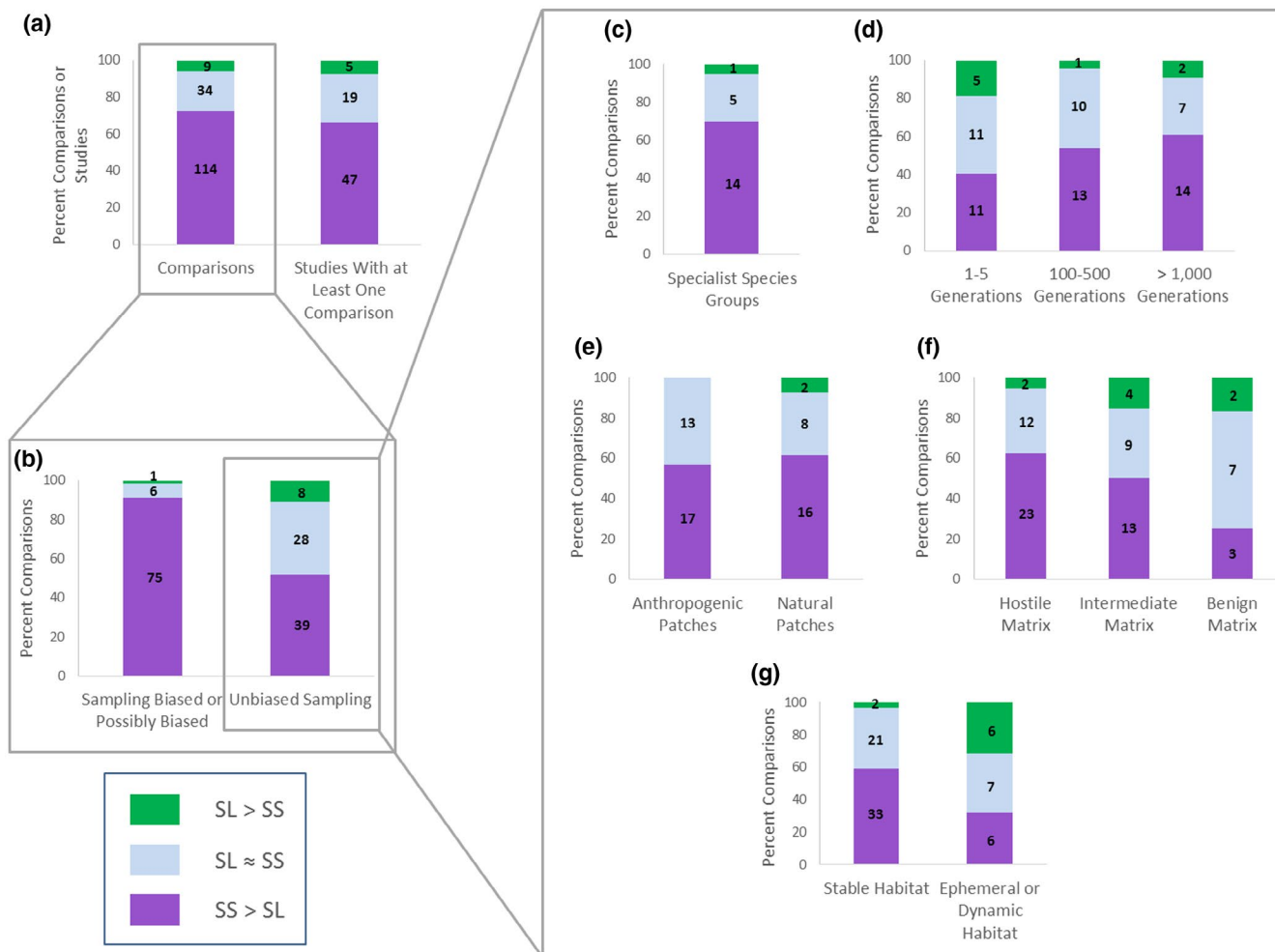
FIGURE 2 (a) Several small > single large (SS > SL) findings dominate the empirical literature. Of 157 single large or several small (SLOSS) comparisons, 72% found SS > SL, 22% were inconclusive and 6% found SL > SS. Of the comparisons where there was a clear difference between SL and SS, 93% found SS > SL. The pattern was similar at the level of studies. Of the 58 studies, 81% found at least one case where SS > SL, 33% found at least one case that was inconclusive and 9% found at least one case where SL > SS. (Note these add to > 100% of studies as some studies with multiple comparisons found more than one result.) (b) Sampling bias causes an over-representation of the SS > SL pattern in the empirical literature, but SS > SL is still the dominant pattern. Just under half of the SLOSS comparisons (75) were from studies with unbiased sampling, that is, where sampling increased in proportion to patch size. Fifty-two percent of these comparisons from unbiased studies found SS > SL and 11% found SL > SS, that is, about a fivefold difference. Ninety-one percent of comparisons from the remaining studies – biased studies and possibly biased studies – found SS > SL. (c) There was no evidence for the prediction that the SS > SL pattern is due to incursion of small patches by generalist species. Seventy percent of specialist/threatened species groups showed SS > SL, as compared to 52% for all species groups (compare to b – unbiased sampling). (d) There was no evidence for the prediction that SL > SS should become more likely over time following patch creation by habitat loss. If anything, the reverse seemed to be true. Each study was placed into one of four approximate categories, varying in order of magnitude in the number of generations (for the particular species group) since patch creation: 1–5 generations; 10–50 generations; 100–500 generations (omitted as there was only one comparison); > 1,000 generations. (e) The proportion of SS > SL results was about the same, irrespective of whether the patches were created by anthropogenic habitat loss and matrix alteration or natural in origin. Note, studies where the habitat was ephemeral or highly dynamic were excluded from this evaluation. (f) There was no evidence for the prediction that SL > SS when the matrix is more hostile and/or patches are farther apart. If anything, the reverse seemed to be true. (g) There was no evidence for the prediction that SS > SL should be more common for ephemeral or highly dynamic habitat than for stable habitat. Note, evaluations (c) through (g) were based only on the studies in which sampling was proportional to patch size, that is, unbiased sampling [Colour figure can be viewed at wileyonlinelibrary.com]

than large patches because of their high edge : area ratio, while the interior of large patches should be the abode of habitat specialists, including rare species and many threatened species (Blake & Karr, 1984; Diamond, 1976; Willis, 1984). Therefore, they suggested that the predominance of SS > SL results was due to incursion of small patches by generalist species, boosting the species richness across SS patches. If this is in fact the underlying reason for the dominance of SS > SL across empirical studies, then we should be *less likely to find SS > SL for groups of habitat specialist/threatened species than for groups of habitat generalists or for groups that combine specialists and generalists.*

From the studies in which sampling was proportional to patch size (i.e. unbiased sampling), there were 20 empirical SLOSS comparisons for specialist/threatened groups of species. Of these, 14 found SS > SL and only one found SL > SS (Figure 2c). Thus, empirical SLOSS studies to date do not support the idea that SL > SS for specialist and threatened species groups. If anything, specialists/threatened species groups show an even stronger tendency for SS > SL than the overall pattern: compare Figure 2c to Figure 2b – right bar. Therefore, it appears that incursion of small patches by generalist species does not explain the dominance of the SS > SL pattern.

3.3.2 | Minimum patch size, selective extinction, and nestedness

The earliest argument I found in my review of theory is the idea that species have minimum patch size requirements (Hanski, 1994). The idea is that when patches are created (through habitat loss), the species that need larger patches for persistence will be lost from the smaller patches over time, in a process of selective extinction. Small patches would then contain only a subset of species that occur in large patches, resulting over time in a pattern of species nestedness with respect to patch size (Atmar & Patterson, 1993; Margules et al., 1982; Patterson & Atmar, 1986). In addition, using a two-patch model, and assuming minimum patch size requirements, Tjørve (2010) predicted that selective extinction should lead to higher species density, that is, number of species per sampling plot, in large patches than small patches.

Occasionally, authors have used this theory to infer SL > SS from an observed pattern of species nestedness with patch size, without actually presenting a SLOSS comparison (e.g. Hecnar & M'Closkey, 1997). However, this inference entails cross-scale extrapolation, because nestedness is about the species composition of large versus small patches, not about the species composition of few large versus several small patches. Such cross-scale extrapolation can be problematic (Fahrig et al., 2019). In fact, many studies have found little or no relationship between the degree of nestedness and SLOSS (Berglund & Jonsson, 2003; Cook, 1995; Cutler, 1994; McLain & Pratt, 1999; Peintinger, Bergamini, & Schmid, 2003; Simberloff & Martin, 1991). In addition, it appears that most systems are either not nested or only weakly nested by patch size (Acosta & Robertson, 2002; Dauber, Bengtsson, & Lenoir, 2006; Hokkanen, Kouki, & Komonen, 2009; Mohd-Azlan & Lawes, 2011; Richardson et al., 2015; Rosch et al., 2015). This might be because species occurrence is not only affected by extinction, but is also affected by colonization (see Section 3.3.5). To produce a highly nested pattern, selective extinction would need to outweigh colonization.

The mechanisms of minimum patch size requirements and selective extinction predict dominance of SL > SS. Given that the empirical literature does not support this prediction, and given that species do require a minimum amount of habitat for persistence (Fahrig, 2001), the theory implies that *most species can persist across multiple patches rather than requiring a single patch for persistence*. In
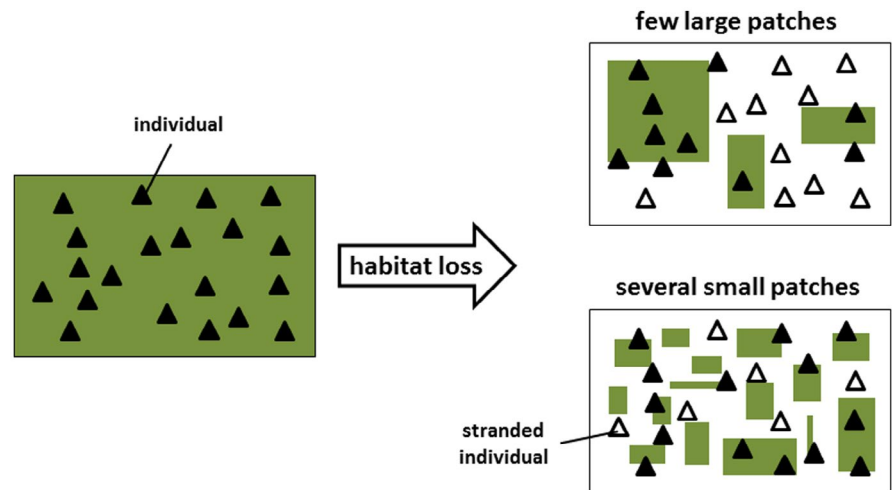
other words, minimum area requirements refer to a minimum total area (across all patches) rather than a minimum patch size. As long as patches are close enough together, persistence across multiple patches could occur by frequent immigration and/or by individual space use that incorporates multiple patches. Indeed, tracking studies of mammalian predators indicate that individuals often move through non-habitat, linking patches together (LaPoint, Gallery, Wikelski, & Kays, 2013; Scharf, Belant, Beyer, Wikelski, & Safi, 2018; Vanbianchi, Gaines, Murphy, & Hodges, 2018). The lack of support for the predicted dominance of SL > SS based on minimum patch size requirements also suggests that Tjørve's (2010) prediction of *higher species density on large patches than small patches is likely not supported*. This is at least qualitatively consistent with the fact that, among the papers in my SLOSS empirical review that included estimates of species density (in addition to species number per patch), Acosta and Robertson (2002) found higher fish species density on small than large reef patches, Arroyo-Rodríguez, Pidena, Escobar, and Benítez-Malvido (2009) found higher plant species density in small than large forest patches, and Leavesley and Cary (2013) and Hernandez-Ruedas et al. (2014) found no difference in species density between small and large patches for birds and trees in forest patches, respectively.

3.3.3 | Time since patch creation, accumulation of species losses

Noting the lack of empirical support for the expectation of SL > SS, Soulé and Simberloff (1986) were the first to propose the idea that perhaps SL > SS only several generations after the patches were created. This is again based on the idea that species with large patch size requirements will be lost from small patches (see previous section), and so ultimately more species should be lost from several small than few large patches. As these species losses will take some time, the SL > SS pattern may not be observed until several generations after the patches were created. This leads to the prediction that *the longer since patch creation, the higher the likelihood of observing SL > SS*. This idea also leads to the prediction that we should see *SL > SS in naturally patchy situations, except where patches are ephemeral*, as here the time since patch creation is longest, providing the most time for an accumulation of species losses.

Note that Soulé and Simberloff's argument does not actually predict SS > SL immediately following patch creation, so it cannot explain the preponderance of SS > SL in the empirical literature. However, modelling and empirical work on single species suggest that, as long as patches are close enough together, more individuals should be 'rescued' from habitat loss when the remaining habitat is in several small patches than a few large patches. This is because the higher edge length of several small patches should increase the likelihood that individuals stranded in the matrix following habitat loss will find habitat (Figure 3; Grez, Zaviezo, Tischendorf, & Fahrig, 2004; Tischendorf, Grez, Zaviezo, & Fahrig, 2005). This should produce *a short-term predominance of SS > SL following habitat creation*.

FIGURE 3 Modelling and empirical work on single species suggest that more individuals should be 'rescued' from habitat loss when the remaining habitat is in several small patches than a single large patch. This is because the higher edge length of several small patches should increase the likelihood that individuals stranded in the matrix following habitat loss will find habitat [Colour figure can be viewed at wileyonlinelibrary.com]

As a preliminary evaluation of these ideas I categorized each of the empirical studies with unbiased sampling into one of four approximate categories, varying in order of magnitude in the number of generations (for the particular species group) since patch creation: 1–5 generations; 10–50 generations; 100–500 generations; > 1,000 generations. Note that these categories are very approximate because most studies did not provide detailed information on the time since patch creation, and because species groups often include a mix of species with very different generation times. However, as the categories vary by orders of magnitude I suggest they do represent meaningful variation. I emphasize that these categories were not the number of years since patch creation, but (very approximately) the number of generations since patch creation. For example, I placed studies of arthropods 1 or 2 years following experimental creation of rock or moss patches (Douglas & Lake, 1994; Hoyle & Harbone, 2005) in the 1–5 generations since patch creation category. I also placed a study of shrubs and trees on a set of islands that were created 60 years ago by flooding (Hu, Wu, Feeley, Xu, & Yu, 2012) in the 1–5 generations category because of the relatively long generation time of woody plants, and especially considering that seed banks may be present. Again, this is a coarse categorization but I believe they are meaningful given the wide variation in study systems that I found in my review. In addition, for each study I determined whether the patches were created by human activities – either habitat loss or conversion of the matrix from natural to human-dominated covers (or both). I also identified the cases where the patches were ephemeral or highly dynamic, for example stones in the inter-tidal zone (Londoño-Cruz & Tokeshi, 2007), tree gaps that will fill in (Vargas et al., 2013), or patches created by clear-cuts that are allowed to regrow (Lindenmayer et al., 2015). I found no evidence for the predictions that SL > SS becomes more prevalent with increasing time since patch creation, and that instances of SS > SL should be more commonly observed shortly after patch creation. Interestingly, if anything the pattern was opposite to the predicted pattern (Figure 2d).

I also evaluated the prediction that we should see SL > SS in naturally patchy systems, except when habitat is ephemeral or highly dynamic (Figure 2e). As SS > SL was eight times more common than

SL > SS in this situation, there was no support for this prediction. Additionally, in conversation, some researchers have suggested the opposite prediction, arguing that species in naturally patchy systems should be adapted to them. It is not clear to me why this should lead to a predominance of SS > SL, but in any case the results so far do not support this idea (Figure 2e).

3.3.4 | Habitat heterogeneity, environmental clumping, patchy species distributions

In my review of theory, several authors pointed out that the pre-existing spatial distribution of species and habitat types might cause either SS > SL or SL > SS following habitat loss and patch creation, depending on whether those pre-existing distributions are spatially autocorrelated, that is, clumped (SS > SL) or even (SL > SS), and depending on the spatial scale of the spatial autocorrelation relative to the spatial scale of the patches. This idea was first implied by Diamond (1975), when he proposed the SL > SS principle and noted that 'Principle B [i.e. SL > SS] needs to be qualified by the statement that separate reserves in an inhomogeneous region may each favour the survival of a different group of species'. In other words, he expected SL > SS only if either habitat was homogeneous across all patches or if large patches were at least as heterogeneous as the set of small patches. Thus, if *sets of many small patches are more heterogeneous than sets of few large patches* then we might find SS > SL. In fact this was the most common explanation provided by authors for their findings of SS > SL in my review of empirical SLOSS studies (Baz & Garcia Boyero, 1996; Dauber et al., 2006; Dzwonko & Loster, 1989; Game & Peterken, 1984; Magura, Ködöböcz, & Tóthmérész, 2001; Martínez-Sanz, Cenzano, Fernández-Aláez, & García-Criado, 2012; McNeil & Fairweather, 1993; Peintinger et al., 2003; Richardson et al., 2015; Saetersdahl, 1994; Seibold et al., 2017; Simberloff & Gotelli, 1984; Tscharntke, Steffan-Dewenter, Kruess, & Thies, 2002; Virolainen, Suomi, Suhonen, & Kuitunen, 1998).

Similarly, Lasky and Keitt (2013) argued that, when the patches are created by habitat loss, one can consider the set of many small
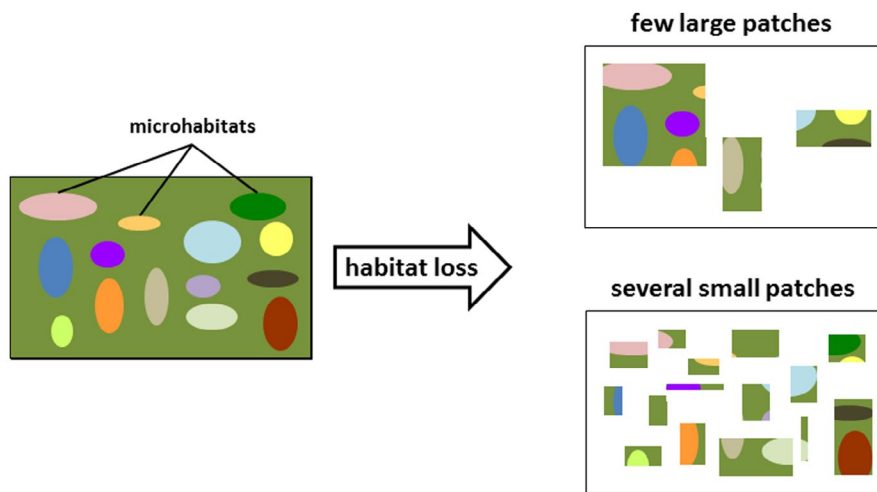
FIGURE 4 When the patches are created by habitat loss, we can consider the set of many small patches and the set of few large patches (of equal total area) as two samples of the previous distribution of cover types or micro-habitats in the landscape. If these micro-habitats are patchily distributed, a set of many small patches will intersect more of them than will a set of few large patches [Colour figure can be viewed at wileyonlinelibrary.com]

patches and the set of few large patches (of equal total area) as two samples of the previous distribution of cover types in the landscape (Figure 4). Given that cover types tend to be spatially autocorrelated and thus patchily distributed and/or distributed along gradients (Margules & Stein, 1989) then, depending on the spatial scaling of that distribution relative to patch sizes, the set of several small patches can represent 'more extensive environmental sampling' (Lasky & Keitt, 2013) than the set of few large patches, such that *the SS set will intersect more cover types.* Based on this they predicted that *the set of several small patches should have higher total species richness and higher beta diversity, even if it has lower plot-scale alpha diversity (i.e. species density).* Similarly, Kallimanis et al. (2005) argued that SLOSS depends on the spatial autocorrelation of disturbances, where *high spatial autocorrelation (clumping) of disturbances should lead to SS > SL.*

May, Rosenbaum, Schurr, and Chase (2019) also considered the set of many small patches and the set of few large patches as two samples of the pre-existing landscape. However, rather than the pre-existing distribution of cover types, they considered the pre-existing spatial distributions of the species themselves. May et al. (2019) predicted SS > SL when species are distributed in clumped patterns. Their argument is essentially the same as the argument of Lasky and Keitt (above) for a clumped distribution of cover types. However, the species distribution argument could apply even if the distribution of cover types is not clumped or heterogeneous but the species distributions are. For example, many species exhibit conspecific attraction (e.g. Peignier et al., 2019; Ramsay, Otter, & Ratcliffe, 1999; Schuck-Paim & Alonso, 2001), which leads to spatially autocorrelated (clumped) species distributions. Depending on the spatial scaling of this clumping with respect to the sizes of the patches, this could lead to SS > SL. Given the predominance of SS > SL, May et al.'s species-clumping argument predicts that *in most SLOSS comparisons to date, most species distributions are clumped at a spatial scale that is relevant to the scale of patchiness following habitat removal.* Note that species clumping independent of habitat heterogeneity might explain why some studies in my empirical review found SS > SL even in a homogeneous environment or where SL were more heterogeneous

than SS (Abele & Patton, 1976; Báldi & Kisbenedek, 2000; Gavish et al., 2011; Hu et al., 2012; O'Connell & Bolger, 1997; Robinson & Quinn, 1988).

To summarize this class of hypotheses: when species distributions are spatially autocorrelated (clumped), a set of many small patches should intersect with more species distributions than should a set of few large patches. One possible reason for clumped species distributions is because the environment is clumped, in which case a set of many small patches should have higher overall heterogeneity (and so more species) than a set of few large patches. Given the predominance of spatial aggregation in nature, May et al. (2019) argue that SS > SL should in fact be our null hypothesis.

3.3.5 | Dominance of colonization/immigration

The number of species in a single patch depends on the trade-off between colonization/immigration and extinction. Most of the theories I found in my review that predicted SL > SS relied (implicitly or explicitly) on the assumption that extinction dominates this trade-off (see Section 3.3.2). For a single species, if there is no colonization/immigration then extinction time for a population in a patch should depend on patch size, because a smaller patch holds a smaller population. This means that, in the absence of immigration, extinction should usually occur sooner in a large set of small patches than in a small set of large patches, as the populations in every one of the small patches is expected to go extinct before the population in a large patch, leading to SL > SS (Jagers & Harding, 2009; McCarthy, Thompson, & Possingham, 2005).

However, there are several theories that predict SS > SL in situations where *extinction does not dominate the trade-off between extinction and colonization/immigration.* Most of the theory I found in this area is based on single-species modelling (see also Ovaskainen, 2002) and so must be extrapolated across species to make SLOSS predictions. Ovaskainen (2002) predicted that the effect of colonization/immigration on population occurrence in SS and SL patches should depend on the shapes of the relationships between patch size

—**WILEY**—

and (a) emigration, (b) immigration, and (c) extinction. A set of small patches has higher edge : area and so a higher per capita emigration rate. Emigration represents a reduction of total population size across the set of patches, unless the emigrants successfully immigrate to another patch. On the other hand, the higher edge : area of several small patches should also lead to a higher per capita immigration rate in a set of several small than few large patches, when patches are close enough together (Bowman, Cappuccino, & Fahrig, 2002; Simberloff & Gotelli, 1984). Thus, Ovaskainen (2002) predicted SS > SL when *the exponential decrease in emigration with patch size is faster than the exponential increase in immigration with patch size*. In addition, he predicted SS > SL is likely if *extinction probability decreases more slowly than linearly with increasing patch size* because of higher per capita immigration into small patches (Ovaskainen, 2002). Similarly, Tischendorf et al. (2005) and Pucket and Eggleston (2016) hypothesized that in systems with *very high dispersal rates*, a larger proportion of emigrants will be retained in a system of several small than few large patches, leading to SS > SL.

The potential influence of colonization/immigration on the SLOSS question was recognized early on. Even proponents of the SL > SS principle realized that if the matrix was essentially benign then a higher rate of colonization across several small patches might outweigh the higher per-patch extinction rate of small patches (Atmar & Patterson, 1993; Willis, 1984). However, they expected this to be the exception rather than the rule. Given the dominance of SS > SL empirical results, these ideas would predict that *for most species in most systems dispersal success is high enough such that the effects of colonization outweigh the effects of extinction.* In other words, *the matrix is generally relatively benign.*

As a preliminary evaluation of this last idea, I categorized the matrix in the empirical studies from my review, relative to the ability of the species group to enter or cross it, as follows: (a) matrix very hostile and/or very large inter-patch distances, (b) matrix benign and/or very small inter-patch distances, or (c) matrix of intermediate hostility. For example, I categorized agriculture as hostile for woodland plants, benign for non-woodland plants, and intermediate for the combination of the two (Dzwonko & Loster, 1989). An urban matrix was considered hostile for plants (Godefroid & Koedam, 2003) but of intermediate hostility for birds (Kim, Chae & Koo, 2007). I considered water a benign matrix for aquatic species moving between patches of coral (Acosta & Robertson, 2002), but hostile for terrestrial plants on islands (Deshaye & Morisset, 1989). As in the other evaluations, I only included the studies with unbiased sampling. Oddly, the pattern was exactly opposite to that predicted (Figure 2f): findings of SS > SL were more common when the matrix was more hostile. Therefore, I found no support for the prediction that SS > SL results should be more common when the matrix is less hostile.

In my review of SLOSS theory I found two other ideas related to the dominance of colonization/immigration. Nekola and White (2002) combined the roles of habitat heterogeneity and colonization/immigration to predict that SS > SL when *both colonization/immigration is high and habitat heterogeneity is higher in several small than few large patches.* Cole (1981) hypothesized that when colonizing

abilities are very dissimilar across species we should find SL > SS. If species vary in colonizing ability then those with low colonizing ability should only occur in the largest patches where extinction probability is low, while those with strong colonizing abilities should occur in nearly all patches. Thus, Cole's idea is essentially a mechanism for selective extinction and nested species patterns (Section 3.3.2). Note, however, that it does not predict a situation where SS > SL; if colonizing abilities were identical across species, based on this idea one would expect SS = SL.

3.3.6 | Population variability, spreading of risk

Finally, some authors extrapolated across species the idea that a patchy environment reduces the risk of species extinction by spreading the risk over multiple sites (den Boer, 1968), to predict SS > SL. In a single species model, Fovargue, Bode, and Armsworth (2018) predicted *lower overall variability through time in population abundance over several small than few large patches.* Although the median abundance across the two systems was similar, higher variability over few large patches than many small patches increased the predicted probability of extinction there. In addition, Tscharntke et al. (2007) predicted *SS > SL when habitat is ephemeral*, as dividing the habitat into many small patches should reduce the probability that all habitat containing a given species disappears simultaneously.

As a preliminary test of this last idea, I identified the empirical studies in which patches were highly ephemeral or dynamic (e.g. rocks in a streambed, clear-cut forest stands that are allowed to regrow), relative to the generation time of the studied species group. I found no support for the predicted higher occurrence of SS > SL in ephemeral than stable habitats (Figure 2g). If anything, the pattern was opposite to predicted.

4 | SUMMARY AND CONCLUSIONS

The SLOSS literature of the past 40 years is rich in both empirical results and theory. Nevertheless, this paper represents the first attempt to confront the theory with the empirical results. In my review of empirical studies I found that several small patches usually hold more species than few large patches of the same total area, that is, SS > SL. This pattern remained, although it became somewhat weaker, when I included only the studies in which sampling was proportional to patch size, that is, unbiased sampling.

In my review of theory I found a wide array of predicted situations where SL > SS should dominate versus where SS > SL should dominate. However, in preliminary evaluations using the unbiased studies from my empirical review, I found no support for several of these predictions. First, the SS > SL pattern held for specialist and threatened species, which suggests that the dominance of SS > SL is not a result of incursion by generalist species into small patches. I also found no evidence for the prediction that results showing SL > SS should become more common over time since patch creation due

to gradual loss of species; if anything, the opposite appeared to be true. I also found no difference between natural and anthropogenic patches; they had similar rates of occurrence of SS > SL. There was also no evidence for the prediction that SL > SS should be more common when the matrix is more hostile, or that SS > SL should be more common in ephemeral than stable patches; the results suggested the reverse in both cases. These preliminary evaluations should not be considered conclusive, as the numbers of comparisons available for them were relatively small, and multiple SLOSS comparisons from the same study are not independent.

As discussed in Section 1, the SLOSS question is very important for conservation. The common assumption among conservation agencies, that SL > SS, has led to preferential protection of large, contiguous areas and little or no protection of small areas, even when numerous. The findings of this review suggest that this bias towards large, contiguous areas does a disservice to the conservation of biodiversity. Some authors have even argued that small patches have a particularly important role for biodiversity (Bennett & Arcese, 2013; Wintle et al., 2019). The results of this review support the notion that much more emphasis should be placed on conservation of small patches than is currently the case. None of this negates, in any way, the importance of preserving large quantities of natural habitat for biodiversity conservation. In addition, in some situations protecting large contiguous areas may be more practical than protecting the same area distributed over many small patches (Kim, Cho, Larson, & Armsworth, 2014). However, there is no evidence supporting a general principle that the former will protect more biodiversity than the latter. In fact, the data suggest the opposite. It is important that the research community recognizes this, and explains it clearly to conservation practitioners, for the sake of biodiversity.

By summarizing the theory and by starting a process of confronting the theory with data, the results here open the door to a wide array of future research needs, where the goal will be to understand the combination of mechanisms responsible for the dominant empirical pattern of SS > SL. First, we need many more empirical SLOSS studies in which sampling is proportional to patch size, and especially for habitat-specialist species groups. These need to be conducted in a wide range of situations, providing larger sample sizes for evaluations of theory such as those in Figure 2c–g. Most combinations of the conditions needed for simultaneously testing multiple theoretical predictions are missing from the empirical literature to date. This greatly constrained what I could accomplish in my preliminary evaluations of theory here. In particular, I could not evaluate the relative or combined roles of different potential mechanisms. Future SLOSS studies designed to fill in the gaps would pave the way for such evaluations. In addition, we need to test the remaining hypotheses discussed above (Section 3.3) with empirical data. For this we need long-term studies of population dynamics and persistence across many small versus few large patches of the same total area. We need comparisons of species density (number of species per sampling plot) in small versus large patches. We need studies that estimate habitat heterogeneity across several small versus few large patches. We need studies of net movement (immigration minus emigration)

in several small versus few large patches. And, we need all of these across a wide range of ecological situations, that is, different species groups, habitat types, landscape types and spatial scales.

In summary, there is so far no evidence to support the common assumption that SL > SS. The majority of empirical results suggest SS > SL, and there are, as yet, no clear conditions in which SL > SS. To move forward on SLOSS we need to recognize this pattern in the data. We must also subject the theory and ideas that predict SL > SS in various situations to empirical tests rather than accepting them without evidence. My hope is that this review will encourage further empirical tests. Meanwhile, it is critically important that conservation practitioners understand that there is no evidence supporting a general conservation principle that values preservation of large, contiguous habitat areas over multiple small areas of the same total area.

DATA ACCESSIBILITY

The data extracted from the reviewed papers are provided in Supporting Information Table S1.

ORCID

Lenore Fahrig iD https://orcid.org/0000-0002-3841-0342

REFERENCES

Abele, G., & Patton, W. K. (1976). The size of coral heads and the community biology of associated decapod crustaceans. *Journal of Biogeography*, *3*, 35–47. https://doi.org/10.2307/3038097

Acosta, C. A., & Robertson, D. N. (2002). Diversity in coral reef fish communities: The effects of habitat patchiness revisited. *Marine Ecology Progress Series*, *227*, 87–96. https://doi.org/10.3354/meps227087

Arroyo-Rodríguez, V., Pidena, E., Escobar, F., & Benítez-Malvido, J. (2009). Value of small patches in the conservation of plant-species diversity in highly fragmented rainforest. *Conservation Biology*, *23*, 729–739. https://doi.org/10.1111/j.1523-1739.2008.01120.x

Atmar, W., & Patterson, B. D. (1993). The measure of order and disorder in the distribution of species in fragmented habitat. *Oecologia*, *96*, 373–382. https://doi.org/10.1007/BF00317508

Báldi, A., & Kisbenedek, T. (2000). Bird species numbers in an archipelago of reeds at Lake Velence, Hungary. *Global Ecology and Biogeography*, *9*, 451–461.

Baz, A., & Garcia-Boyero, A. (1996). The SLOSS dilemma: A butterfly case study. *Biodiversity and Conservation*, *5*, 493–502. https://doi.org/10.1007/BF00056393

Bennett, J. R., & Arcese, P. (2013). Human influence and classical biogeographic predictors of rare species occurrence. *Conservation Biology*, *27*, 417–421. https://doi.org/10.1111/cobi.12015

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. https://doi.org/10.1016/S0006-3207(02)00329-4

Blake, J. G., & Karr, J. R. (1984). Species composition of bird communities and the conservation benefit of large versus small forests. *Biological Conservation*, *30*, 173–187. https://doi.org/10.1016/0006-3207(84)90065-X

Bowman, J., Cappuccino, N., & Fahrig, L. (2002). Patch size and population density: The effect of immigration behavior. *Conservation Ecology*, *6*, article 9. https://doi.org/10.5751/ES-00354-060109

Butchart, S. H. M., Walpole, M., Collen, B., van Strien, A., Scharlemann, J. P. W., Almond, R. E. A., ... Watson, R. (2010). Global biodiversity: Indicators of recent declines. *Science*, *328*, 1164–1168. https://doi.org/10.1126/science.1187512

Cole, B. J. (1981). Colonizing abilities, island size, and the number of species on archipelagoes. *The American Naturalist*, *117*, 629–638. https://doi.org/10.1086/283749

Cook, R. R. (1995). The relationship between nested subsets, habitat subdivision, and species diversity. *Oecologia*, *101*, 204–210. https://doi.org/10.1007/BF00317285

Cutler, A. H. (1994). Nested biotas and biological conservation: Metrics, mechanisms, and meaning of nestedness. *Landscape and Urban Planning*, *28*, 73–82. https://doi.org/10.1016/0169-2046(94)90045-0

Dauber, J., Bengtsson, J., & Lenoir, L. (2006). Evaluating effects of habitat loss and land-use continuity on ant species richness in seminatural grassland remnants. *Conservation Biology*, *20*, 1150–1160. https://doi.org/10.1111/j.1523-1739.2006.00373.x

den Boer, P. J. (1968). Spreading of risk and stabilization of animal numbers. *Acta Biotheoretica*, *18*, 165–194. https://doi.org/10.1007/BF01556726

Deshaye, J., & Morisset, P. (1989). Species-area relationships and the SLOSS effect in a subarctic archipelago. *Biological Conservation*, *48*, 265–276.

Diamond, J. M. (1975). The island dilemma: Lessons of modern biogeographic studies for the design of natural reserves. *Biological Conservation*, *7*, 129–146. https://doi.org/10.1016/0006-3207(75)90052-X

Diamond, J. M. (1976). Island biogeography and conservation: Strategy and limitations. *Science*, *193*, 1027–1029. https://doi.org/10.1126/science.193.4257.1027

Douglas, M., & Lake, P. S. (1994). Species richness of stream stones: An investigation of the mechanisms generating the species-area relationship. *Oikos*, *69*, 387–396. https://doi.org/10.2307/3545851

Dzwonko, Z., & Loster, S. (1989). Distribution of vascular plant species in small woodlands on the western Carpathian foothills. *Oikos*, *56*, 77–86. https://doi.org/10.2307/3566089

Fahrig, L. (2001). How much habitat is enough? *Biological Conservation*, *100*, 65–74. https://doi.org/10.1016/S0006-3207(00)00208-1

Fahrig, L. (2017). Ecological responses to habitat fragmentation per se. *Annual Review of Ecology, Evolution, and Systematics*, *48*, 1–23. https://doi.org/10.1146/annurev-ecolsys-110316-022612

Fahrig, L., Arroyo-Rodríguez, V., Bennett, J. R., Boucher-Lalonde, V., Cazetta, E., Currie, D. J., ... Watling, J. I. (2019). Is habitat fragmentation bad for biodiversity? *Biological Conservation*, *230*, 179–186. https://doi.org/10.1016/j.biocon.2018.12.026

Fischer, J., & Lindenmayer, D. B. (2002). Small patches can be valuable for biodiversity conservation: Two case studies on birds in southeastern Australia. *Biological Conservation*, *106*, 129–136. https://doi.org/10.1016/S0006-3207(01)00241-5

Fovargue, R., Bode, M., & Armsworth, P. R. (2018). Size and spacing rules can balance conservation and fishery management objectives for marine protected areas. *Journal of Applied Ecology*, *55*, 1050–1059. https://doi.org/10.1111/1365-2664.13043

Game, M., & Peterken, G. F. (1984). Nature reserve selection strategies in the woodlands of Central Lincolnshire, England. *Biological Conservation*, *29*, 157–181. https://doi.org/10.1016/0006-3207(84)90075-2

Gavish, Y., Ziv, Y., & Rosenzweig, M. L. (2011). Decoupling fragmentation from habitat loss for spiders in patchy agricultural landscapes. *Conservation Biology*, *26*, 150–159. https://doi.org/10.1111/j.1523-1739.2011.01799.x

Godefroid, S., & Koedam, N. (2003). How important are large vs. small forest remnants for the conservation of the woodland flora in an urban context? *Global Ecology and Biogeography*, *12*, 287–298.

Grez, A., Zaviezo, T., Tischendorf, L., & Fahrig, L. (2004). A transient, positive effect of habitat fragmentation on insect population densities. *Oecologia*, *141*, 444–451. https://doi.org/10.1007/s00442-004-1670-8

Hanski, I. (1994). A practical model of metapopulation dynamics. *Journal of Animal Ecology*, *63*, 151–162. https://doi.org/10.2307/5591

Hecnar, S. J., & M'Closkey, R. T. (1997). Patterns of nestedness and species association in a pond-dwelling amphibian fauna. *Oikos*, *80*, 371–380. https://doi.org/10.2307/3546605

Hernández-Ruedas, M. A., Arroyo-Rodríguez, V., Meave, J. A., Martínez-Ramos, M., Ibarra-Manríquez, G., Martínez, E., ... Santos, B. A. (2014). Conserving tropical tree diversity and forest structure: The value of small rainforest patches in moderately-managed landscapes. *PLoS ONE*, *9*, e98931. https://doi.org/10.1371/journal.pone.0098931

Hill, M., Hassall, C., Oertli, B., Fahrig, L., Robson, B., Biggs, J., ... Wood, P. (2018). New policy directions for global pond conservation. *Conservation Letters*, *11*, e12447.

Hokkanen, P. J., Kouki, J., & Komonen, A. (2009). Nestedness, SLOSS and conservation networks of boreal herb-rich forests. *Applied Vegetation Science*, *12*, 295–303. https://doi.org/10.1111/j.1654-109X.2009.01031.x

Hu, G., Wu, J., Feeley, K. J., Xu, G., & Yu, M. (2012). The effects of landscape variables on the species-area relationship during late-stage habitat fragmentation. *PLoS ONE*, *7*, e43894. https://doi.org/10.1371/journal.pone.0043894

IUCN (1980). *World conservation strategy: Living resource conservation for sustainable development*. Gland, Switzerland: International Union for Conservation of Nature and Natural Resources.

Jagers, P., & Harding, K. C. (2009). Viability of small populations experiencing recurring catastrophes. *Mathematical Population Studies*, *16*, 177–198. https://doi.org/10.1080/08898480903034694

Kallimanis, A. S., Kunin, W. E., Halley, J. M., & Sgardelis, S. P. (2005). Metapopulation extinction risk under spatially autocorrelated disturbance. *Conservation Biology*, *19*, 534–546. https://doi.org/10.1111/j.1523-1739.2005.00418.x

Kendal, D., Zeeman, B. J., Ikin, K., Lunt, I. D., McDonnell, M. J., Farrar, A., ... Morgan, J. W. (2017). The importance of small urban reserves for plant conservation. *Biological Conservation*, *213*, 146–153. https://doi.org/10.1016/j.biocon.2017.07.007

Kim, J., Chae, J., & Koo, T.-H. (2007). Variation in bird diversity in relation to habitat size in the urban landscape of Seoul, South Korea. *Acta Ornithologica*, *42*, 39–44.

Kim, T., Cho, S.-H., Larson, E. R., & Armsworth, P. R. (2014). Protected area acquisition costs show economics of scale with area. *Ecological Economics*, *107*, 122–132.

Kingsland, S. E. (2002). Creating a science of nature reserve design: Perspectives from history. *Environmental Modeling and Assessment*, *7*, 61–69.

LaPoint, S., Gallery, P., Wikelski, M., & Kays, R. (2013). Animal behavior, cost-based corridor models, and real corridors. *Landscape Ecology*, *28*, 1615–1630. https://doi.org/10.1007/s10980-013-9910-0

Lasky, J. R., & Keitt, T. H. (2013). Reserve size and fragmentation alter community assembly, diversity, and dynamics. *The American Naturalist*, *182*, E142–E160. https://doi.org/10.1086/673205

Le Roux, D. S., Ikin, K., Lindenmayer, D. B., Manning, A. D., & Gibbons, P. (2015). Single large or several small? Applying biogeographic principles to tree-level conservation and biodiversity offsets.

Biological Conservation, *191*, 558–566. https://doi.org/10.1016/j.biocon.2015.08.011

Leavesley, A. J., & Cary, G. J. (2013). The effect of patch area on birds in central Australian mulga (*Acacia aneura*) woodland of different time-since-fire. *Pacific Conservation Biology*, *19*, 28–38.

Lindenmayer, D. B., Wood, J., McBurney, L., Blair, D., & Banks, S. C. (2015). Single large versus several small: The SLOSS debate in the context of bird responses to a variable retention logging experiment. *Forest Ecology and Management*, *339*, 1–10. https://doi.org/10.1016/j.foreco.2014.11.027

Lizee, M.-H., Tatoni, T., & Deschamps-Cottin, M. (2016). Nested patterns in urban butterfly species assemblages: Respective roles of plot management, park layout and landscape feature. *Urban Ecosystems*, *19*, 205–224.

Londoño-Cruz, E., & Tokeshi, M. (2007). Testing scale variance in species–area and abundance–area relationships in a local assemblage: an example from a subtropical boulder shore. *Population Ecology*, *49*, 275–285.

Mac Nally, R., & Lake, P. S. (1999). On the generation of diversity in archipelagos: A re-evaluation of the Quinn-Harrison "saturation index". *Journal of Biogeography*, *26*, 285–295. https://doi.org/10.1046/j.1365-2699.1999.00268.x

MacDonald, Z. G., Anderson, I. D., Acorn, J. H., & Nielsen, S. E. (2018a). Decoupling habitat fragmentation from habitat loss: Butterfly species mobility obscures fragmentation effects in a naturally fragmented landscape of lake islands. *Oecologia*, *186*, 11–27. https://doi.org/10.1007/s00442-017-4005-2

MacDonald, Z. G., Anderson, I. D., Acorn, J. H., & Nielsen, S. E. (2018b). The theory of island biogeography, the sample-area effect, and the habitat diversity hypothesis: Complementarity in a naturally fragmented landscape of lake islands. *Journal of Biogeography*, *45*, 2730–2743. https://doi.org/10.1111/jbi.13460

Magura, T., Ködöböcz, V., & Tóthmérész, B. (2001). Effects of habitat fragmentation on carabids in forest patches. *Journal of Biogeography*, *28*, 129–138. https://doi.org/10.1046/j.1365-2699.2001.00534.x

Margules, C., Higgs, A. J., & Rafe, R. W. (1982). Modern biogeographic theory: Are there any lessons for nature reserve design? *Biological Conservation*, *24*, 115–128. https://doi.org/10.1016/0006-3207(82)90063-5

Margules, C. R., & Stein, J. L. (1989). Patterns in the distributions of species and the selection of nature reserves: An example from Eucalyptus forests in South-eastern New South Wales. *Biological Conservation*, *50*, 219–238.

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. https://doi.org/10.1002/aqc.2227

May, F., Rosenbaum, B., Schurr, F. M., & Chase, J. M. (2019). The geometry of habitat fragmentation: Effects of species distribution patterns on extinction risk due to habitat conversion. *Ecology and Evolution*, *9*, 2775–2790. https://doi.org/10.1002/ece3.4951

McCarthy, M. A., Thompson, C. J., & Possingham, H. P. (2005). Theory for designing nature reserves for single species. *The American Naturalist*, *165*, 250–257. https://doi.org/10.1086/427297

McCarthy, M. A., Thompson, C. J., & Williams, N. S. G. (2006). Logic for designing nature reserves for multiple species. *The American Naturalist*, *167*, 717–727. https://doi.org/10.1086/503058

McLain, D. K., & Pratt, A. E. (1999). Nestedness of coral reef fish across a set of fringing reefs. *Oikos*, *85*, 53–67. https://doi.org/10.2307/3546791

McNeill, S. E., & Fairweather, P. G. (1993). Single large or several small marine reserves? An experimental approach with sea-grass fauna. *Journal of Biogeography*, *20*, 429–440. https://doi.org/10.2307/2845591

Mohd-Azlan, J., & Lawes, M. J. (2011). The effect of the surrounding landscape matrix on mangrove bird community assembly in north

Australia. *Biological Conservation*, *144*, 2134–2141. https://doi.org/10.1016/j.biocon.2011.04.003

Nekola, J. C., & White, P. S. (2002). Conservation, the two pillars of ecological explanation, and the paradigm of distance. *Natural Areas Journal*, *22*, 305–310.

O'Connell, T., & Bolger, T. (1997). Stability, ephemerality and dispersal ability: Microarthropod assemblages on fungal sporophores. *Biological Journal of the Linnean Society*, *62*, 111–131. https://doi.org/10.1111/j.1095-8312.1997.tb01617.x

Ovaskainen, O. (2002). Long-term persistence of species and the SLOSS problem. *Journal of Theoretical Biology*, *218*, 419–433. https://doi.org/10.1016/S0022-5193(02)93089-4

Patterson, B. D., & Atmar, W. (1986). Nested subsets and the structure of insular faunas and archipelagos. *Biological Journal of the Linnean Society*, *28*, 65–82.

Peignier, M., Webber, Q. M. R., Koen, E. L., Laforge, M. P., Robitaille, A. L., & Vander Wal, E. (2019). Space use and social association in a gregarious ungulate: Testing the conspecific attraction and resource dispersion hypotheses. *Ecology and Evolution*, *9*, 5133–5145. https://doi.org/10.1002/ece3.5071

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. https://doi.org/10.1078/1439-1791-00181

Pelletier, J. D. (2000). Model assessments of the optimal design of nature reserves for maximizing species longevity. *Journal of Theoretical Biology*, *202*, 25–32. https://doi.org/10.1006/jtbi.1999.1030

Puckett, B. J., & Eggleston, D. B. (2016). Metapopulation dynamics guide marine reserve design: Importance of connectivity, demographics, and stock enhancement. *Ecosphere*, *7*, e01322. https://doi.org/10.1002/ecs2.1322

Quinn, J. F., & Harrison, S. P. (1988). Effect of habitat fragmentation and isolation on species richness: Evidence from biogeographic patterns. *Oecologia*, *75*, 132–140.

Ramsay, S. M., Otter, K., & Ratcliffe, L. M. (1999). Nest-site selection by female black-capped chickadees: Settlement based on conspecific attraction? *The Auk*, *116*, 604–617. https://doi.org/10.2307/4089322

Ramsey, F. L. (1989). Comments on a "saturation index". *Oecologia*, *81*, 569–570. https://doi.org/10.1007/BF00378971

Richardson, S. J., Clayton, R., Rance, B. D., Broadbent, H., McGlone, M. S., & Wilmshurst, J. M. (2015). Small wetlands are critical for safeguarding rare and threatened plant species. *Applied Vegetation Science*, *18*, 230–241. https://doi.org/10.1111/avsc.12144

Robinson, G. R., & Quinn, J. F. (1988). Extinction, turnover and species diversity in an experimentally fragmented California annual grassland. *Oecologia*, *76*, 71–82. https://doi.org/10.1007/BF00379603

Rösch, V., Tscharntke, T., Scherber, C., & Batáry, P. (2015). Biodiversity conservation across taxa and landscapes requires many small as well as single large habitat fragments. *Oecologia*, *179*, 209–222. https://doi.org/10.1007/s00442-015-3315-5

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

Scharf, A. K., Belant, J. L., Beyer, D. E., Wikelski, M., & Safi, K. (2018). Habitat suitability does not capture the essence of animal-defined corridors. *Movement Ecology*, *6*, article 18.

Schuck-Paim, C., & Alonso, J. (2001). Deciding where to settle: Conspecific attraction and web site selection in the orb-web spider *Nephilengys cruentata*. *Animal Behaviour*, *62*, 1007–1012. https://doi.org/10.1006/anbe.2001.1841

Seibold, S., Bässler, C., Brandl, R., Fahrig, L., Förster, B., Heurich, M., … Müller, J. (2017). An experimental test of the habitat-amount hypothesis for saproxylic beetles in a forested region. *Ecology*, *98*, 1613–1622. https://doi.org/10.1002/ecy.1819

Simberloff, D. S., & Abele, L. G. (1982). Refuge design and island biogeographic theory: Effects of fragmentation. *The American Naturalist*, *120*, 41–50. https://doi.org/10.1086/283968

Simberloff, D., & Gotelli, N. (1984). Effects of insularisation on plant species richness in the prairie-forest ecotone. *Biological Conservation*, *29*, 27–46. https://doi.org/10.1016/0006-3207(84)90012-0

Simberloff, D., & Martin, J.-L. (1991). Nestedness of insular avifaunas: Simple summary statistics masking complex species patterns. *Ornis Fennica*, *68*, 178–192.

Soulé, M. E., & Simberloff, D. (1986). What do genetics and ecology tell us about the design of nature reserves? *Biological Conservation*, *35*, 19–40. https://doi.org/10.1016/0006-3207(86)90025-X

Tischendorf, L., Grez, A., Zaviezo, T., & Fahrig, L. (2005). Mechanisms affecting population density in fragmented habitat. *Ecology and Society*, *10*, article 7. https://doi.org/10.5751/ES-01265-100107

Tjørve, E. (2010). How to resolve the SLOSS debate: Lessons from species-diversity models. *Journal of Theoretical Biology*, *264*, 604–612. https://doi.org/10.1016/j.jtbi.2010.02.009

Tscharntke, T., Bommarco, R., Clough, Y., Crist, T. O., Kleijn, D., Rand, T. A., … Vidal, S. (2007). Conservation biological control and enemy diversity on a landscape scale. *Biological Control*, *43*, 294–309.

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.

Vanbianchi, C., Gaines, W. L., Murphy, M. A., & Hodges, K. E. (2018). Navigating fragmented landscapes: Canada lynx brave poor quality habitats while traveling. *Ecology and Evolution*, *8*, 11293–11308. https://doi.org/10.1002/ece3.4605

Vargas, R., Gärtner, S., Alvarez, M., Hagen, E., & Reif, A. (2013). Does restoration help the conservation of the threatened forest of Robinson Crusoe Island? The impact of forest gap attributes on endemic plant species richness and exotic invasions. *Biodiversity Conservation*, *22*, 1283–1300.

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. https://doi.org/10.1046/j.1365-2664.1998.355344.x

Willis, E. O. (1984). Conservation, subdivision of reserves, and the antidismemberment hypothesis. *Oikos*, *42*, 396–398. https://doi.org/10.2307/3544410

Wintle, B. A., Kujala, H., Whitehead, A., Cameron, A., Veloz, S., Kukkala, A., … Bekessy, S. A. (2019). Global synthesis of conservation studies reveals the importance of small habitat patches for biodiversity. *Proceedings of the National Academy of Sciences USA*, *116*, 909–914. https://doi.org/10.1073/pnas.1813051115

BIOSKETCH

Lenore Fahrig studies how landscape structure affects species abundance, distribution, and diversity.

SUPPORTING INFORMATION

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

APPENDIX

Báldi, A., & Kisbenedek, T. (1999). Orthopterans in small steppe patches: An investigation for the best-fit model of the species-area curve and evidences for their non-random distribution in the patches. *Acta Oecologica*, 20, 125–132. https://doi.org/10.1016/S1146-609X(99)80025-3

Beckon, W. N. (1993). The effect of insularity on the diversity of land birds in the Fiji islands: Implications for refuge design. *Oecologia*, 94, 318–329.

Bouget, C., & Parmain, G. (2016). Effects of landscape design of forest reserves on Saproxylic beetle diversity. *Conservation Biology*, 30, 92–102.

Celada, C., & Bogliani, G. (1993). Breeding bird communities in fragmented wetlands. *Italian Journal of Zoology*, 60, 73–80.

Fattorini, S. (2007). Non-randomness in the species-area relationship: testing the underlying mechanisms. *Oikos*, 116, 678–689.

Gilpin, M. E., & Diamond, J. M. (1980). Subdivision of nature reserves and the maintenance of species diversity. *Nature*, 285, 567–568.

Hattori, A., & Shibuno, T. (2015). Total volume of 3D small patch reefs reflected in aerial photographs can predict total species richness of coral reef damselfish assemblages on a shallow back reef. *Ecological Research*, 30, 675–682.

Higgs, A. J., & Usher, M. B. (1980). Should nature reserves be large or small? *Nature*, 285, 568–569.

Honnay, O., Hermy, M, & Coppin, P. (1999). Effects of area, age and diversity of forest patches in Belgium on plant species richness, and implications for conservation and reforestation. *Biological Conservation*, 87, 73–84.

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

Hu, G., Wu, J., Feeley, K. J., Xu, G., & Yu, M. (2012). The effects of landscape variables on the species-area relationship during late-stage habitat fragmentation. *PloS ONE*, 7, e43894.

Järvinen, O. (1982). Conservation of endangered plant populations: Single large or several small reserves? *Oikos*, 38, 301–307.

Lumaret, R., Guillerm, J.-L., Maillet, J., & Verlaque, R. (1997). Plant species diversity and polyploidy in islands of natural vegetation isolated in extensive cultivated lands. *Biodiversity and Conservation*, 6, 591–613.

McCoy, E. D., & Mushinsky, H. R. (1994). Effects of fragmentation on the richness of vertebrates in the Florida scrub habitat. *Ecology*, 75, 446–457.

Mitsuo, Y., Tsunoda, H., Ohira, M., Doi, M., & Senga, Y. (2011). Nested subset patterns of species composition in a pond-dwelling fish fauna. *Ecological Research*, 26, 311–316.

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.

Ribas, C. R., Sobrinho, T. G., Schoereder, J. H., Sperber, C. F., Lopes-Andrade, C., & Soares, S. M. (2005). How large is large enough for insects? Forest fragmentation effects at three spatial scales. *Acta Oecologica*, 27, 31–41.

Richart, M., & Hewitt, N. (2008). Forest remnants in the Long Point region, Southern Ontario: Tree species diversity and size structure. *Landscape and Urban Planning*, 86, 25–37.

Struebig, M. J., Kingston, T., Petit, E. J., Le Comber, S. C., Zubaid, A., Mohd-Adnan, A., & Rossiter, S. J. (2011). Parallel declines in species and genetic diversity in tropical forest fragments. *Ecology Letters*, 14, 582–590.

Sun, Q., Lu, J., Wu, J., & Zhang, F. (2008). Effects of island area on plant species distribution and conservation implications in the Thousand Island Lake region. *Biodiversity Science*, 16, 1–7.