

Resolving the SLOSS dilemma for biodiversity conservation: a research agenda

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Abstract

In biodiversity conservation, the "SL > SS principle" that a single (or few) large habitat patches (SL) conserve more species than several small patches (SS) is used to prioritize protection of large patches while down-weighting small ones. However, empirical support for this principle is lacking; most studies find SS > SL. We propose a research agenda to resolve this dilemma by asking, "are there consistent, empirically-demonstrated conditions leading to SL > SS?" We develop a hypothesis to answer this question, the "SLOSS cube hypothesis," which predicts SL > SS only when all three of the following are true: between-patch movement is low, population dynamics are not influenced by spreading-of-risk, and large-scale across-habitat heterogeneity is low. We then propose methods to test this prediction. Many tests are needed, comparing gamma diversity across multiple landscapes varying in number and sizes of patches. If the prediction is not generally supported across tests, then either the mechanisms leading to SL > SS are extremely rare in nature, or they are outweighed by countervailing mechanisms leading to SS > SL (e.g. lower competition or higher immigration in SS), or both. In that case, the SL > SS principle should be abandoned.

INTRODUCTION

Conservation decision-making relies on a combination of local knowledge and general rules or principles (reviewed in Gagné *et al.* 2015; Arroyo-Rodríguez *et al.* 2020). Some of the first such general principles were those proposed by Diamond (1975) for the design of nature reserves. One of Diamond's principles, inspired by MacArthur and Wilson's (1963, 1967) theory of island biogeography, was that a single large reserve (SL) should hold more species than several small

reserves (SS) of the same total area, the "SL > SS principle" (see also May 1975, Diamond 1976). The SL > SS principle became a standard in conservation planning worldwide following its reiteration in the IUCN's (1980) highly influential *World Conservation Strategy*.

However, not all ecologists accepted Diamond's rationale for the SL > SS principle. Simberloff and Abele (1976) pointed out that the theory of island biogeography is in fact agnostic on the SLOSS question, i.e. "should conservation efforts be aimed at preserving a 'single large or several small' habitat patches?" (see also Simberloff & Abele 1982). Indeed, the number of species on several small patches compared to one or a few large patches will depend on the degree to which species composition varies among the small patches, i.e. beta diversity (Higgs & Usher 1980; Rösch *et al.* 2015). That is, the SLOSS question cannot be answered by comparing species richness on individual patches of different sizes; it must be addressed by comparing total species richness among sets of patches having the same total area but different numbers and sizes of patches.

Ecologists immediately began testing the SL > SS principle by comparing the number of species found in sets of habitat patches having the same total area but either few large (SL) or several small (SS) patches. Early reviews of these empirical studies showed lack of support for the principle. In particular, Simberloff and Abele (1982) found "... not a single case where one large site unequivocally excels several small ones, and many cases where several small sites clearly contain more species than one large one," and Quinn and Harrison (1988) found that "[i]n all cases where a consistent effect of subdivision is observed, the more subdivided collection of

islands or isolates contains more species." Studies over the past three decades have continued to find $SS > SL$ in most cases (reviewed in Deane *et al.* 2020; Fahrig 2020).

In contrast to the frequent empirical result that $SS > SL$, theoretical work related to the SLOSS question suggests a more complex picture. Several hypotheses predict either $SL > SS$ or $SS > SL$, depending on traits of the organisms (e.g., behavior, life history) or the landscapes (e.g., total habitat amount, disturbances). These are summarized in **Box 1** (also reviewed in Ovaskainen 2002; Fahrig 2020). We also note that these conditions can occur together and may interact, resulting in a plethora of possible scenarios. Given this diversity of predictions, most ecologists have concluded that the answer to the SLOSS question "depends" (Kingsland 2002). For example, Sarkar (2012) states that there is "no non-contextual answer to the SLOSS question", and the Wikipedia entry for "SLOSS debate" concludes that "[t]he general consensus of the SLOSS debate is that neither option fit[s] every situation and that they must all be evaluated on a case to case basis." The SLOSS debate has therefore largely disappeared from the ecological literature: Google Ngram Viewer indicates that the proportional occurrence of the term "SLOSS debate" peaked in 2006 and has declined steadily since (**Appendix 1**; Michel *et al.* 2011).

Box 1 here

Despite the fact that most researchers have shelved the SLOSS debate, it remains relevant because many conservation agencies continue to prioritize protection of large, contiguous areas of habitat, while small patches of natural habitat are less likely to be protected (reviewed in Armsworth *et al.* 2018). For example, the current emphasis on "rewilding" in Europe aims to

115 conserve and restore large contiguous areas of natural habitat having at least a 10,000 ha "core
116 area" (Europarc Federation 2013). Three studies in Peru prioritized larger patches over smaller
117 ones (Mindreau *et al.* 2013). Wetland conservation generally focuses on large wetlands, while
118 most small wetlands around the world have little or no protection (reviewed by Hill *et al.* 2018).
119 The same is true for small forest patches; forestry policy in Ontario, Canada, recommends
120 cutting patterns that "defragment" the remaining forest by removing small patches (OMNR
121 2002). And in Mexico, landowners and communities can be paid to preserve forest (payment for
122 ecosystem services), but only for patches larger than 25 ha (Hernández-Ruedas *et al.* 2014). The
123 continued prioritization of large, contiguous habitat areas is further entrenched in proposed
124 guidelines of the High Conservation Value Resource Network (Brown *et al.* 2013) for
125 "identification of HCVs [high conservation values] globally, for any type of ecosystem, and
126 across all natural resource sectors and standards." HCV 2 specifies "large landscape-level
127 ecosystems" and "intact forest landscapes," implying that small ecosystems or forest patches
128 (even in large numbers) have low conservation value. The HCV definition of a large ecosystem
129 is context-dependent but a "widely used" minimum size is 50,000 ha (Brown *et al.* 2013).

130
131 In many cases, decisions to favour large areas are based on practical reasons rather than
132 ecological ones. For example, large patches might be preferred for cultural, psychological, and
133 aesthetic reasons (Europarc Federation 2013; Perino *et al.* 2019). In addition, it may be cheaper
134 and easier to acquire and manage a few large patches than many small ones (Armsworth *et al.*
135 2018). However, ecological arguments still underlie at least part of the rationale for down-
136 weighting the conservation value of small patches. For example, Edwards *et al.* (2012)
137 recommend preferentially clearing forest patches that are smaller than 1,000 ha to meet future

agricultural demand in the tropics; they base this recommendation on assumed low biodiversity value of small patches. Brown *et al.* (2013) base their HCV 2 (above) exclusively on ecological value arguments, though they do not cite evidence for them.

Such down-weighting of small patches is problematic for conservation, because it places a disproportionate number of species at risk. In their analyses of 175 published datasets, Deane and He (2018) found that hypothetical removal of the smallest patches from each set of patches would result in species losses in almost all of the datasets, even if the large patches remain intact and even if 80% of the habitat remains. In fact, the loss of species resulting from removal of the smallest patches was 50% higher than predicted based on species-area relationships (Deane & He 2018). This is because these smaller patches have species that are unique to them, and thus higher beta-diversity across patches, than would have been expected from random sampling. The assumed low value of small patches for biodiversity conservation is particularly problematic in regions where most remaining habitat occurs only in small patches. These are often human-dominated ecoregions where most natural habitat has been lost to human uses and there are few protected areas (e.g. Taubert *et al.* 2018; Hannah *et al.* 2020). For example, small patches of habitat in and around urban areas often contain rare species and have high biodiversity value (Planchuelo *et al.* 2020). In such regions, the down-weighting of the relative conservation value of small habitat patches undermines habitat preservation where protection of biodiversity is most needed (e.g. Ribeiro *et al.* 2009).

In summary, even though most ecologists have moved on from the SLOSS debate, the implicit favoring of larger over smaller habitat patches in conservation decision-making suggests an

inherent expectation that $SL > SS$. Theory predicts $SL > SS$ under certain conditions (**Box 1**), but so far these are not well-supported in empirical studies (reviewed in Fahrig 2020). We suggest that this dilemma needs to be resolved for the sake of biodiversity conservation. In particular, we need to know whether the $SL > SS$ principle is consistently and predictably valid over a defined set of ecological conditions. If it is not, then the mechanisms leading to $SS > SL$ counterbalance or outweigh those predicted to lead to $SL > SS$. This would, in turn, suggest that the $SL > SS$ principle should be abandoned. In contrast, if there is a set of conditions in which SL consistently and predictably hold more species than SS , then conservation agencies should determine whether those conditions hold in a given situation, and thus whether they should prioritize conservation of large patches.

Here we propose a research agenda to resolve the SLOSS dilemma, addressing the question, "are there consistent, empirically-demonstrated conditions in which few large patches hold more species than several small ones?" We begin by reviewing the relevant theory (**Box 1**). We then propose a hypothesis, the "SLOSS cube hypothesis," which summarizes existing theory and empirical work, and finally we use that hypothesis to propose a research agenda. Our aim is to encourage future research in a direction that will resolve the SLOSS dilemma.

REVIEW OF SLOSS PREDICTIONS

SLOSS predictions are based on two general groups of theory (**Box 1**). The first group make predictions derived from extinction-colonization dynamics, which are then extrapolated to multiple species, while the second group make predictions derived from considerations about

differences in species composition across space (beta diversity). The extinction-colonization group can predict either $SL > SS$ or $SS > SL$, depending on assumptions, while the beta diversity group predicts $SS > SL$.

Extinction-colonization-based theory where variation in extinction dominates

Most predictions of $SL > SS$ derive from the assumption that variation in extinction rate dominates the outcome of the extinction-colonization dynamic. This is expected when populations in separate patches are largely independent of each other because movements among patches are rare such that colonization events are infrequent. Such isolation among patches should occur when: (i) patches are far apart; (ii) the matrix is hostile and leads to very high dispersal mortality; (iii) the species avoid entering the matrix (as might occur for habitat interior specialists); or (iv) the species have very low innate mobility. As small patches are expected to have smaller populations than large patches, they should have higher extinction rates from demographic stochasticity. The persistence of any given species on a set of isolated patches will then be driven by the size of the largest patch (Burkey 1989; Etienne & Heesterbeek 2000; Jagers & Harding 2009). This effect will be accentuated for habitat interior species because the proportion of a patch that is interior habitat declines with decreasing patch size (Preston 1960; Laurance 1991; Williams *et al.* 2005; Moilanen & Wintle 2007). This effect is also expected to be accentuated in situations where the matrix is hostile, for species that readily emigrate from patches. Emigration rate should be higher from SS than SL due to the larger edge-to-area ratio for SS, and therefore the mortality rate in the hostile matrix will be higher for SS than SL (Willis 1984; Atmar & Patterson 1993; Fahrig 1998, 2002; Flather & Bevers 2002; Martin & Fahrig

2016). The $SL > SS$ pattern is also predicted to be stronger when species within a group have different patch size requirements, leading to selective extinction of particular species from small patches (Diamond 1976; Terborgh 1976; Cole 1981; Patterson & Atmar 1986; Atmar & Patterson 1993; McCarthy *et al.* 2006; Tjørve 2010).

On the other hand, theory can predict $SS > SL$ in extinction-dominated systems when extinctions are caused by an antagonistic species or by a disturbance, leading to spreading-of-risk across SS . Division of habitat into many small patches is predicted to reduce interspecific competition, such that poor competitors can persist on some small, isolated patches due to the absence of stronger competitors (e.g., Heilmann-Clausen & Christensen 2004; Hernández-Ruedas *et al.* 2018). This could increase the overall number of species across a set of small patches, leading to $SS > SL$ (Levins & Culver 1971). SS can also stabilize predator-prey or host-parasitoid interactions as prey or hosts can escape to patches that are temporarily unoccupied by the predator or parasitoid (Huffaker 1958; Levins 1969; Wiens 1976; Morrison & Barbosa 1987). This should lead to $SS > SL$ for groups of predators and their prey, or parasitoids and their hosts. And, SS are predicted to reduce the risk of simultaneous extinction due to disturbances that do not spread from patch to patch through the matrix (den Boer 1968; Levins 1969; Andrewartha 1984; Kallimanis *et al.* 2005; Tschardtke *et al.* 2008), again leading to $SS > SL$.

Extinction-colonization-based theory where variation in colonization dominates

When movements among patches are common, population processes are generally predicted to lead to $SS > SL$ (**Box 1**). SS should have a higher rate of colonization than SL , for two reasons: a

higher immigration rate in SS than SL, and a larger species pool in the proximity of SS than SL. If a species has a very high rate of emigration from patches (e.g. larval fish: Fovargue *et al.* 2018), then SS are predicted to intercept more dispersers than SL because of the higher edge-to-area ratio of SS than SL, leading to higher immigration and therefore higher colonization rates in SS than SL (Bowman *et al.* 2002a; Grez *et al.* 2004; Tischendorf *et al.* 2005; Puckett & Eggleston 2016). In other words, in this situation SS are predicted to have higher functional connectivity (*sensu* Taylor *et al.* 1993) than SL. For species that need to access resources outside of habitat patches during some part of their life cycle (e.g. Pope *et al.* 2000), access to those resources will be higher in a landscape with SS than SL (Dunning *et al.* 1992; Duelli 1997; Fahrig *et al.* 2011), which could also lead to SS > SL.

The species pool available to colonize SS is also expected to be larger than the species pool available to colonize SL. If potential colonists can arrive from habitat within a given distance of a patch (the patch's "local landscape") then the species pool available to colonize a set of patches will depend on the sum of additional habitat outside of those patches, but within their local landscapes. This sum is expected to be larger for SS than SL because the total edge length in SS is larger than the total edge length in SL (**Fig. 1**). The species pool available to colonize SS will be larger not only due to the larger amount of habitat in the surrounding local landscapes but also because along with more habitat will likely come more micro-habitats, increasing heterogeneity and the species pool for SS relative to SL (Tscharntke *et al.* 2012). Notably, classical SLOSS studies (Quinn & Harrison 1988; reviewed in Fahrig 2020) do not account for such "landscape moderation" effects. This is because classical SLOSS studies compare species richness across

subsets of patches that are drawn from a single landscape in which the small and large patches are interspersed.

Figure 1 here

Theory based on beta diversity

All of the SLOSS predictions discussed so far derive from assumptions about how extinction/mortality and colonization/immigration dynamics interact with sizes of individual patches and with sets of patches. In general, $SL > SS$ is predicted when extinction dominates these dynamics, except when spreading-of-risk plays an important role in population dynamics. $SS > SL$ is generally predicted when colonization/immigration dominates the dynamics.

A different set of SLOSS theory asks how the number of patches (for a given total habitat amount) is expected to affect beta diversity. The fact that species distributions in continuous habitat are usually clumped or spatially autocorrelated leads to a prediction of $SS > SL$ (May *et al.* 2019; **Fig. 2**). One of the most general patterns in ecology is that species distributions are clumped, due to both extrinsic and intrinsic reasons (Nekola & White 1999; Tuomisto *et al.* 2003; Seidler & Plotkin 2006; Morlon *et al.* 2008; McGill 2010, 2011). Extrinsic environmental conditions (e.g. soil type or microclimate) are often spatially autocorrelated (heterogeneous in space), creating clumped species distributions in response. Intrinsic factors that lead to clumped species distributions include limited dispersal from occupied sites, creating population centres (Hubbell 2001; Tuomisto *et al.* 2003), conspecific attraction (e.g., Vité & Francke 1976; Ramsay

et al. 1999; Schuck-Paim & Alonso 2001; Peignier *et al.* 2019), and philopatry (Weatherhead & Forbes 1994). The spatial clumping of species distributions within continuous habitat leads to an expectation of $SS > SL$ following habitat loss and patch creation, because SS will intersect more species distributions than SL (Tschardt *et al.* 2002; May *et al.* 2019; **Fig. 2**). This prediction should be accentuated with increasing habitat heterogeneity and when disturbances are spatially autocorrelated, as these will increase spatial clumping or autocorrelation of species distributions (Diamond 1975; Simberloff & Gotelli 1984; Lasky and Keitt 2013; Nekola & White 2002; Kallimanis *et al.* 2005; Laurance *et al.* 2007).

Note that the prediction of higher beta diversity across SS than SL does not assume or imply that small patches are farther apart than large patches. Indeed, when the landscape size and the amount of habitat are held constant, there is no consistent difference in maximum distance between habitat edges between SS and SL (**Appendix 2**). Spatial clumping of species distributions is nevertheless expected to lead to more species sampled over SS than SL because SS will cover a given area more evenly than SL, thus intersecting more species distributions (**Fig. 2a** vs. **2b**; Tschardt *et al.* 2002; May *et al.* 2019). May *et al.* (2019) referred to this spatial sampling effect as a "geometric effect" because it emerges from the geometric distribution of habitat patches and the assumption that species have clumped distributions. The prediction that differences in beta diversity play an important role in SLOSS was confirmed by Deane *et al.* (2020), who found that beta diversity was the strongest predictor of $SS > SL$ after accounting for sampling bias.

Figure 2 here

298

299 If a set of several small patches happen to be more spread out than a set of few large patches (e.g.
300 Hill *et al.* 2011), beta diversity is predicted to increase even more over SS (Nekola & White
301 1999; Morlon *et al.* 2008; Anderson *et al.* 2011; compare **Fig. 2a** and **2c**). In other words, as
302 pointed out early on by Higgs and Usher (1980), we can expect $SS > SL$ if the proportional
303 species overlap between patches is lower for SS than SL. However, increasing the distance
304 among SS is also predicted to reduce inter-patch movements, increasing patch isolation, and
305 therefore to increase extinction dominance of extinction-colonization dynamics (**Box 1**). Thus,
306 the spatial spread of SS is predicted to have two opposing effects: (i) decreasing inter-patch
307 movement potentially leading to $SL > SS$, and (ii) decreasing species overlap leading to higher
308 beta diversity and $SS > SL$ (Tjørve 2010; Blowes & Connolly 2012; Arnillas *et al.* 2017).

309

310 There are two reasons why the role of beta diversity in producing $SS > SL$ may be even greater
311 than expected from the geometric effect. First, it has been predicted that higher beta diversity
312 across SS than across SL may be accentuated over time following patch creation if different
313 patches follow different successional trajectories (Laurance 2002; Laurance *et al.* 2007; Ewers *et*
314 *al.* 2013; del Castillo 2015; Arroyo-Rodriguez *et al.* 2017). Second, Giladi and Ziv (2020)
315 recently found an intriguing pattern of higher within-patch plant beta diversity in small patches
316 than in large patches, in sets of both homogeneous and heterogeneous patches. While this is an
317 empirical finding and not a prediction from theory, if it turns out to be a general pattern it would
318 reinforce the role of beta diversity in producing $SS > SL$.

319

320 **RESEARCH AGENDA**

Here we suggest a research agenda for resolving the SLOSS dilemma. We first propose a hypothesis that combines and summarizes theory and empirical studies. We then use this hypothesis to propose an agenda for future empirical studies to ask, "are there any consistent, empirically-demonstrated conditions that lead to $SL > SS$?"

The SLOSS cube hypothesis

The major features of SLOSS theory and data to date are illustrated in **Fig. 3**. To summarize theory: (i) arguments based on population processes generally predict $SL > SS$ when between-patch movements are assumed to be rare, such that variation in local (patch) extinctions dominates the extinction-colonization dynamic; (ii) an exception to this occurs where spreading-of-risk plays a large role in population persistence, leading to a prediction of $SS > SL$; (iii) arguments based on population processes generally predict $SS > SL$ when between-patch movements are assumed to be common such that variation in colonization dominates the extinction-colonization dynamic; and (iv) consideration of beta diversity generally leads to predictions of $SS > SL$. Therefore, SLOSS predictions can be largely characterized by the combination of three variables: the frequency of between-patch movements; the role of spreading-of-risk in landscape-scale population persistence; and the level of species clumping and across-habitat heterogeneity over habitat patches. These are the three axes in **Fig. 3**.

Figure 3 here

To summarize empirical work to date based on classical SLOSS studies (Quinn & Harrison 1988): about 50% of apparently unbiased (see below) empirical SLOSS studies find $SS > SL$ and about 10% find $SL > SS$, while the remaining 40% find no difference (Fahrig 2020). These proportions are represented as the coloured volumes in **Fig. 3**. Given the relative rarity of $SL > SS$ results, the SLOSS cube hypothesis predicts that $SL > SS$ will occur predictably only when *all* of the following are met: between-patch movements are rare, spreading-of-risk is not important in population dynamics, *and* across-habitat heterogeneity is low (blue volume in **Fig. 3**). The prediction that all three conditions must hold to obtain $SL > SS$ derives not only from the relative rarity of $SL > SS$, but also from preliminary summaries of relevant empirical work suggesting that when only one of these conditions holds we still find a predominance of $SS > SL$ (reviewed in Fahrig 2020). In particular, $SS > SL$ is more common than $SL > SS$ in situations with high matrix hostility, suggesting that low between-patch movement rate alone is insufficient to reliably produce $SL > SS$. And, many cases of $SS > SL$ occur in situations where across-habitat heterogeneity is low (Fahrig 2020), suggesting that low spatial autocorrelation in environmental characteristics alone is not sufficient to reliably produce $SL > SS$. However, the *combination* of factors – low between-patch movement, low role of spreading-of-risk, and low across-habitat heterogeneity – has not yet been explicitly tested across a range of systems.

Testing the SLOSS cube hypothesis

Testing the SLOSS cube hypothesis will require a large number of individual empirical studies, where each study represents a point within the cube in **Fig. 3**. For each study four things should be estimated: (i) the frequency of between-patch movements, (ii) the degree to which spreading-

of-risk is important for landscape-scale population persistence, (iii) the level of across-habitat heterogeneity; and (iv) gamma diversity over different landscapes characterized by SS vs. SL. Note empirical tests will measure across-habitat heterogeneity rather than spatial clumping of species because estimating the spatial distribution of multiple species over multiple landscapes (see below) is generally not feasible. In contrast, across-habitat heterogeneity is one of the major reasons for clumped species distributions, and can be measured from continuous rasters based on remotely-sensed data, using surface metrics (Riva & Nielsen 2020) such as metrics of spatial variance of the Normalized Difference Vegetation Index (NDVI; e.g. Duro *et al.* 2014).

The frequency of between-patch movements is unknown and hard to measure for nearly all species groups and regions. While relative innate mobility of different species groups can often be estimated using morphological or life history correlates (Bowman *et al.* 2002b; Stevens *et al.* 2004; Beckman *et al.* 2018), the realized frequency of between-patch movements is related not only to innate mobility but also to landscape attributes such as habitat configuration and matrix quality. Therefore, we propose a combination of two steps for selecting species groups with low (or high) between-patch movement frequency in the selected region. First, species groups would be categorized into low vs. high innate mobility based on morphology and life history traits such as wing presence/absence, territory size, etc. The purpose of the second step is then to confirm that, in the selected region, the low-mobility group does in fact show low between-patch movement and/or the high-mobility group does in fact show high between-patch movement. This can be done indirectly by comparing mean species density (number of species per sample site) of the mobility group in landscapes with SS vs. SL. If, for the low mobility group, movement is lower between patches than within patches in the selected region, then we should find lower

mean species density in sample sites across a landscape with SS than across a landscape with SL (Tjørve 2010).

The role that spreading-of-risk plays in landscape-scale population persistence is also unknown for most groups of species. However, it should be possible to roughly categorize species groups into those that are likely to benefit from spreading-of-risk vs. those that are not. Those that might benefit from spreading-of-risk would include: groups under strong top-down control from predators/parasitoids; groups of weak competitors; and groups subject to frequent local disturbances. These conditions do not guarantee that the species group benefits from spreading-of-risk. However, the absence of all three of these conditions would be a strong indicator of a species group that does not benefit from spreading-of-risk, and therefore of a potential species group to include in tests of the question, "are there any consistent, empirically-demonstrated conditions that lead to $SL > SS$?" as illustrated in **Fig. 3** (see next section).

In **Box 2** we describe the characteristics of individual empirical studies that together would test the SLOSS cube hypothesis (**Fig. 3**). Importantly, each study should be based on randomly distributed samples within each of multiple landscapes (**Fig. 4**), rather than using the classical SLOSS approach (Quinn & Harrison 1988) where species lists are combined across subsets of patches within the same landscape. Using random samples across multiple landscapes is preferable because it avoids two problems inherent in many empirical SLOSS studies to date.

Box 2 here

Figure 4 here

413

414 First, using multiple landscapes avoids the problem that, when all sampled patches are within the
415 same landscape, large patches are intermixed with small patches. This classical study design is
416 inconsistent with the inferences actually made from those studies, which are about whether many
417 small patches (alone) have more or fewer species than few large patches (alone). In addition,
418 when SLOSS is evaluated using subsets of intermixed patches, the link between the data and
419 several of the mechanisms in **Box 1** becomes unclear. For example, it is not clear how the
420 spreading-of-risk of predation over SS would play out in a landscape in which small and large
421 patches are intermixed. As another example, when small and large patches are intermixed, the
422 amount of habitat contributing the species pools for colonization of SS vs. SL (**Fig. 2**) includes
423 portions of large and small patches within the local landscapes, and so the link between SLOSS
424 and landscape moderation effects becomes unclear. Therefore, future empirical studies should
425 sample species in multiple landscapes, each containing either SS or SL (**Fig. 4**), rather than
426 subsets of SS or SL drawn from within a single landscape. The total habitat amount should be
427 either the same across sampled landscapes, or at least habitat amount should be uncorrelated to
428 the number of patches.

429

430 The second reason that using random samples across multiple landscapes is preferable to the
431 classical SLOSS study design is that it avoids the problem that sampling is often biased in favour
432 of SS (Gavish *et al.* 2012). Small patches often have more sample sites per area than large
433 patches, which means that the probability of detecting a given species is higher across SS than
434 SL. Only about half of all SLOSS studies to date have apparently unbiased sampling effort
435 (Fahrig 2020). This is due to logistical constraints when the range of patch sizes is large. For

example, if patches range in size from 5 ha to 1000 ha then, for equal sampling effort, the smallest possible number of sample sites in a 1000-ha patch would be 200, assuming there is only one sample site per 5-ha patch. For many species groups, such sample sizes would be impossible to accomplish. We note that if sampling effort information is available, patch size dependence in sampling effort can be estimated and controlled for in statistical models when using existing data (e.g., Deane *et al.* 2020). However, when designing a new empirical SLOSS study, the sampling effort problem can be best avoided using random samples across multiple landscapes (**Fig. 4**). Cumulative number of species (gamma diversity) (see below) can then be directly compared for landscapes with SS vs. landscapes with SL (**Fig. 4**).

Method for determining whether there are consistent, empirically-demonstrated conditions that lead to $SL > SS$

As discussed above, the $SL > SS$ principle continues to guide conservation decision-making in many situations, despite lack of empirical support for it as a general principle. To resolve this dilemma, we need to determine whether $SL > SS$ is in fact a valid principle in a predictable set of conditions. The principle could then be reworded as, "in general $SL > SS$ whenever conditions x hold." Such conditions have been suggested (**Box 1**, summarized in **Fig. 3**) but to date there is little supporting empirical evidence. Therefore, resolving the SLOSS dilemma means addressing the question, "are there any consistent, empirically-demonstrated conditions that lead to $SL > SS$?"

Addressing this question requires multiple empirical tests, using appropriate study designs (**Box 2**), focused on species groups and environments where between-patch movements are rare, spreading-of-risk is likely unimportant, and habitat is homogeneous. In other words, studies should focus on the blue portion of the SLOSS cube in **Fig. 3**. If the majority of studies in this space find $SL > SS$ then we can conclude that the $SL > SS$ principle is generally valid in those conditions. As discussed above, estimates of realized interpatch movement rates for groups of species are usually not available for a given region, but movement rates should be low when patches are very far apart or the matrix is hostile, or when the species group is comprised of sedentary species. Therefore, SLOSS tests should focus on regions where (i) habitat is rare i.e., patches - both large and small - are far apart, (ii) habitat is spatially homogeneous, and (iii) matrix is hostile (e.g. urban areas, high-intensity agriculture). The groups of species selected should be those assumed to have low innate mobility, and those for whom spreading-of-risk likely plays a minor role in population dynamics, i.e. strong competitors under bottom-up control that are not subject to frequent local disturbances (see above). Once a region and a species group have been selected, multiple sample landscapes should be selected within that region, that vary in the numbers and sizes of patches and do not vary in total habitat amount (**Fig. 4**), or for which there is no relationship between habitat amount and the numbers and sizes of patches across the landscapes. Sample sites should then be randomly placed in the habitat within each landscape, and the species group sampled at each site. Average species density (mean number of species per site) should be compared between SS and SL to confirm the assumption of low between-patch movement in the selected region (see above). Total species richness (gamma diversity) should then be estimated across the habitat in each landscape to determine whether there are more species in landscapes with SL than SS.

Note on negative edge effects and SLOSS

As indicated in **Box 1**, habitat interior species, i.e. those that show negative edge effects, should be particularly susceptible to the effects of patch size on extinction probability. In addition, they may have low mobility between patches if they are averse to leaving interior habitat and entering the matrix. For this reason, patch-scale evidence of negative edge effects on a species group is often taken as evidence of $SL > SS$ for that group (Fletcher *et al.* 2018). However, we note that $SL > SS$ cannot be directly inferred for groups of habitat interior species based only on patch-scale evidence. Such an inference would entail cross-scale extrapolation from local edge effects to landscape-scale effects. This extrapolation is a prediction that must be tested at a landscape-scale because other mechanisms in **Box 1**, operating at a landscape scale, may outweigh negative local edge effects in influencing species richness across a landscape (Fahrig *et al.* 2019). Such tests would compare gamma diversity of species groups known to show negative edge effects (and thus assumed to fall into the blue portion of the SLOSS cube in **Fig. 3**), across multiple landscapes as in **Fig. 4** and **Box 2**.

We note further that such studies will need to estimate gamma diversity, not species richness at a sample site, i.e. species density. For example, Pfeifer *et al.* (2017) and Püttker *et al.* (2020) documented negative effects on species density of "edge influence" and edge density (respectively) in the local landscapes surrounding sample sites. The observed reductions in local richness cannot be directly extrapolated to infer $SL > SS$ because other mechanisms, such as higher beta diversity across SS than SL , might outweigh the negative effect of edge density when

species richness is measured over the landscape. Again, the extrapolation to $SL > SS$ needs to be tested by comparing species richness (gamma diversity) across multiple landscapes with different numbers and sizes of patches.

Need for many studies

Here we emphasize that a single study on a particular species group in a particular region cannot answer the question "are there consistent, empirically-demonstrated conditions that lead to $SL > SS$?" $SL > SS$ was conceived and is used as a general principle. We know it is not universally valid, because most empirical studies do not support it. However, it may still apply in general when certain conditions hold, specifically the combination of low between-patch movement, low spreading-of-risk, and low across-habitat heterogeneity. Testing this prediction will require multiple studies on a range of taxa and regions that match these conditions (Seibold *et al.* 2018). $SL > SS$ would be upheld as a principle if we find more species in habitat within landscapes with SL than SS , in most of these studies.

DISCUSSION

In one sense, by proposing this research agenda, we are reviving a debate that most ecologists had set aside. Most ecologists believe that there is no general SLOSS principle and that each case must be evaluated individually. But at the same time the idea persists that the $SL > SS$ principle is generally valid under some conditions (**Box 1**), such as for groups of habitat-interior species and in landscapes with low matrix quality (Pfeifer *et al.* 2017; Fletcher *et al.* 2018), and that

these are the conditions where biodiversity is most threatened. For this reason, conservation planners often give lower priority to preservation of small patches, effectively applying the $SL > SS$ principle on the assumption that they are taking a conservative decision. However, empirical tests to date do not generally support the $SL > SS$ principle even in these conditions. If anything, the evidence so far suggests the reverse (Deane & He 2018; Deane *et al.* 2020; Fahrig 2020), though the number of tests is much smaller than needed for evaluating a general principle. We suggest that this contradiction needs to be resolved for the sake of biodiversity conservation, and we propose our research agenda as a path to resolving it.

There are two possible outcomes of research aimed at testing the SLOSS cube hypothesis. First, empirical studies might generally support the hypothesis. This would have different implications for conservation decision-making, depending on the conservation goal. In situations where the goal is general conservation of biodiversity, support for the hypothesis would suggest that a mixed strategy of mainly small patches and a few large patches would maximize biodiversity, as suggested by Arroyo-Rodríguez *et al.* (2020). On the other hand, when the goal is conservation of a particular species group, then support for the hypothesis would indicate what research the conservation agency needs to carry out, to determine whether the particular conditions in their system fall within the range of conditions where $SL > SS$ is valid. In particular, do the level of between-patch movement, the role of spreading-of-risk, and the level of across-habitat heterogeneity place the system within the blue portion of the SLOSS cube in **Fig. 3**? If so then, for biodiversity conservation, large patches should be prioritized and small patches should be down-weighted, but if not, then total habitat amount should be maximized irrespective of the sizes of patches comprising it.

550

551 The second possible outcome of the proposed research agenda is that the majority of studies find
552 either $SS > SL$ or $SL = SS$ throughout the SLOSS cube in **Fig. 3**, even when between-patch
553 movement, spreading-of-risk, and across-habitat heterogeneity are all low. In that case, we
554 should conclude that the SLOSS cube hypothesis is not supported, i.e. $SL > SS$ is not a general
555 principle under any predictable conditions, and therefore it should not be used in conservation
556 planning. Two lines of evidence suggest this outcome is at least possible. First, reviews of
557 empirical studies to date have not found predictable conditions leading to $SL > SS$; the majority
558 of results so far find higher biodiversity in SS than SL for habitat specialists, when the matrix is
559 hostile, when habitat amount is low, and when across-habitat heterogeneity is low (reviewed in
560 Fahrig 2017a, 2020). Second, simulations by Fronhofer *et al.* (2012) suggest that the main
561 mechanism proposed to lead to $SL > SS$ - extinction-colonization dynamics dominated by
562 variation in extinction rate - is likely very rare in nature. Fronhofer *et al.* (2012) predict this
563 situation is usually evolutionarily unstable, with systems either becoming extinct or between-
564 patch movement rates increasing such that variation in extinction rate no longer drives the
565 extinction-colonization dynamic.

566

567 We note that the idea that the $SL > SS$ principle could be abandoned seems to fly in the face of
568 the fact that there are documented empirical cases of $SL > SS$. Nevertheless, given the small
569 number of these cases to date, if they do not occur in predictable conditions, then we would not
570 be able to discount the possibility that they are due to statistical chance alone. In a review of
571 effects of fragmentation *per se* (of which SLOSS is one component), Fahrig (2017a) found that
572 24% of significant fragmentation effects were negative (i.e. $SL > SS$ in the context of SLOSS).

However, fewer than 30% of all effects were significant, suggesting that fewer than 7.2% of all effects are significantly negative. Furthermore, documented reporting biases (Fahrig 2017b) reduce this estimate to about 3 - 4.2% of all tests. Thus, if it turns out that there are no empirically-demonstrated, consistent conditions leading to $SL > SS$ then it would be reasonable to infer that the few $SL > SS$ findings to date may be due to statistical chance alone.

If there are no consistent conditions leading to $SL > SS$, this would confirm that small habitat patches have the same or greater biodiversity value as the same area of habitat in large patches. It would also mean that the overall goal for conservation should be to preserve or restore as much area as possible of each natural habitat type within a given ecoregion, intersecting the distributions of as many species as possible, irrespective of the patch sizes within which the habitat is distributed, as long as the patches are large enough to function as habitat for the species group (Rösch *et al.* 2015). Removing the constraint that a given amount of habitat must be in large contiguous patches would increase options for conservation, especially in regions dominated by people where there are no large, contiguous natural areas remaining. Collections of small reserves such as small forest patches and riparian and wetland buffers could have high biodiversity value in such ecoregions. This would provide a rationale for local small-scale conservation efforts, both public and private (Monteferri 2019; Shumba *et al.* 2020).

It is important to note, however, that even if there is no evidence for $SL > SS$ as a general principle, this will not necessarily translate into a higher priority for preservation of SS than SL *in a given situation*. As mentioned above, factors other than biodiversity enter into decisions about habitat preservation and restoration. For example, cultural, psychological and aesthetic

considerations may favour preservation of large, contiguous areas (Europarc Federation 2013; Perino *et al.* 2019). In addition, a few large areas may be easier to manage than many small ones, as suggested by Higgs and Usher (1980). Finally, for species that are prone to be killed legally or illegally when encountered by people (grizzly bear, jaguar, lynx, wolf), large contiguous natural areas may be the only way to ensure that such encounters are rare (e.g. Müller *et al.* 2014). Nevertheless, in such situations, prioritizing preservation of few large areas over many small ones would be taken not because the $SL > SS$ principle is valid, but in spite of the fact that it is not.

We also note that, if there are no consistent, empirically-demonstrated conditions leading to $SL > SS$, this does not invalidate the mechanisms proposed in **Box 1**. Rather, it would mean that the mechanisms predicting $SS > SL$ outweigh the mechanisms predicting $SL > SS$ in nature. Put differently, it would mean that, for a mechanism to result in $SL > SS$, the conditions would need to be so extreme - e.g. perfectly homogeneous habitat and essentially no between-patch movement - that they are almost never observed except in models.

We emphasize that SLOSS is explicitly not about the role of habitat amount. Rather, it is about the influence of the pattern or configuration of a given amount of habitat (several small vs. few large patches). Habitat loss is the main cause of species declines, and so habitat preservation and restoration are the top priorities for biodiversity conservation. If, in a particular situation, a choice is presented between conserving one large patch vs. several small patches, but the small patches have much less habitat in total, then the decision should be to conserve the large patch. For example, in the Steigerwald forest in Southern Germany there is an ongoing discussion about

establishing a national park of 10,000 ha vs. protecting a set of smaller areas of about 5,000 ha in total. Here, the large national park would probably be more effective for biodiversity conservation, because the total habitat preserved would be twice that of the set of small patches. We also emphasize that we would never recommend the intentional fragmentation of what is now continuous habitat. Such areas are increasingly rare globally (Watson *et al.* 2016), and fragmentation of them would entail loss of habitat. Large protected areas should remain, and to the extent possible, so should remaining large unprotected tracts of contiguous habitat.

In summary, we suggest that the SLOSS dilemma can be resolved by focusing future empirical studies on the question, "are there consistent, empirically-demonstrated conditions leading to $SL > SS$?" Answering this will require a large number of studies targeted at species groups and regions where between-patch movements are rare, spreading-of-risk is unimportant, and the habitat is homogeneous. These studies should be designed such that samples are randomly distributed across habitat over multiple equal-sized landscapes containing different numbers and sizes of patches but the same total amount of habitat. If the majority of studies in these conditions show more species in landscapes with few large than several small patches then this will delineate the situations in which the $SL > SS$ principle can be included as a criterion in reserve design. On the other hand, if the majority of studies in these conditions find more species in landscapes with several small patches, or no difference, then the $SL > SS$ principle should be abandoned.

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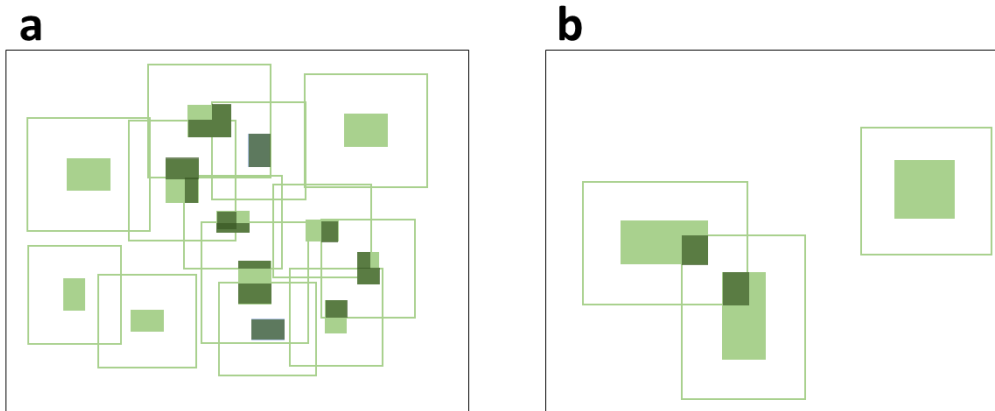
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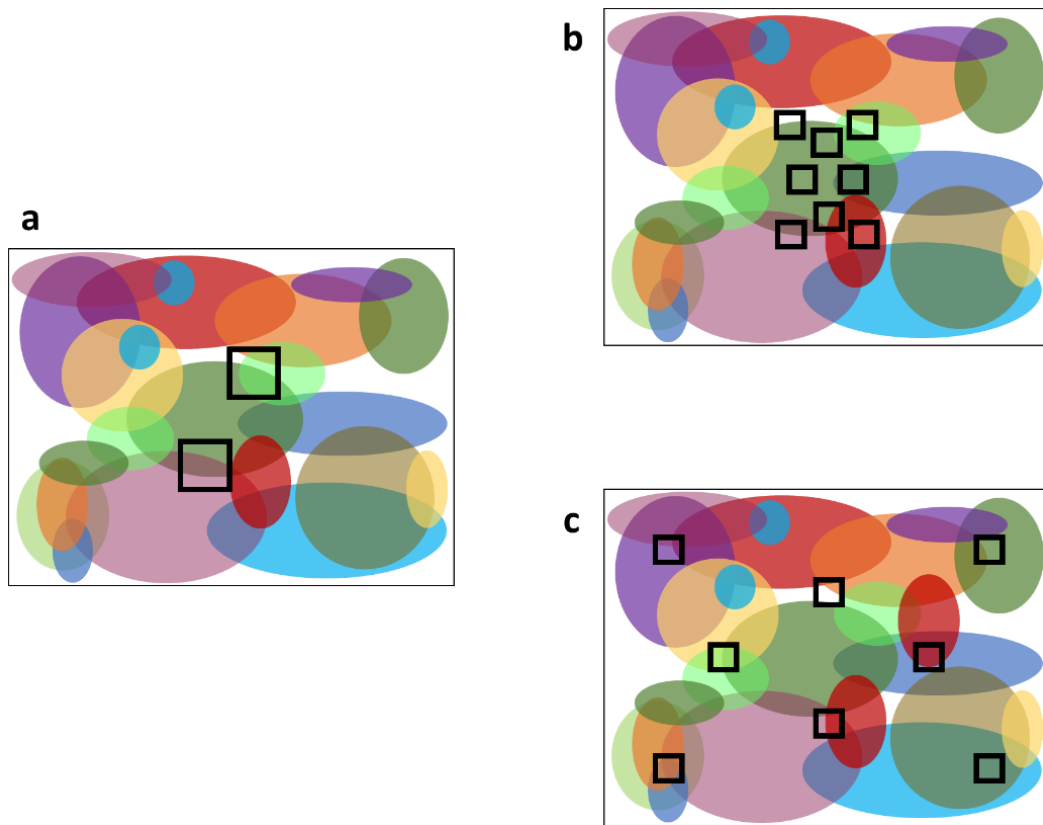


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972 **Figure 1.** The total area contributing the species pool available to colonize a set of several small
973 patches (a) is larger than the total area contributing the species pool available to colonize a set of
974 few large patches (b). Light coloured rectangles are patches. Boxes around them represent the
975 areas from within which habitat can contribute colonists to the patches. Dark coloured rectangles
976 are the areas of other habitat patches within the local landscape surrounding each patch.

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981 **Figure 2.** When species distributions are clumped or spatially autocorrelated, few large patches

982 (a) will intersect ("sample") fewer species than several small patches (b and c). Different colours

983 represent different species within continuous habitat in a single ecoregion before habitat loss

984 (large rectangles). Squares represent patches subsequently created by habitat loss. When the

985 landscape extent (maximum distance between patch edges) is the same for few large and several

986 small patches (a vs. b), several small patches will cover the area more evenly and will therefore

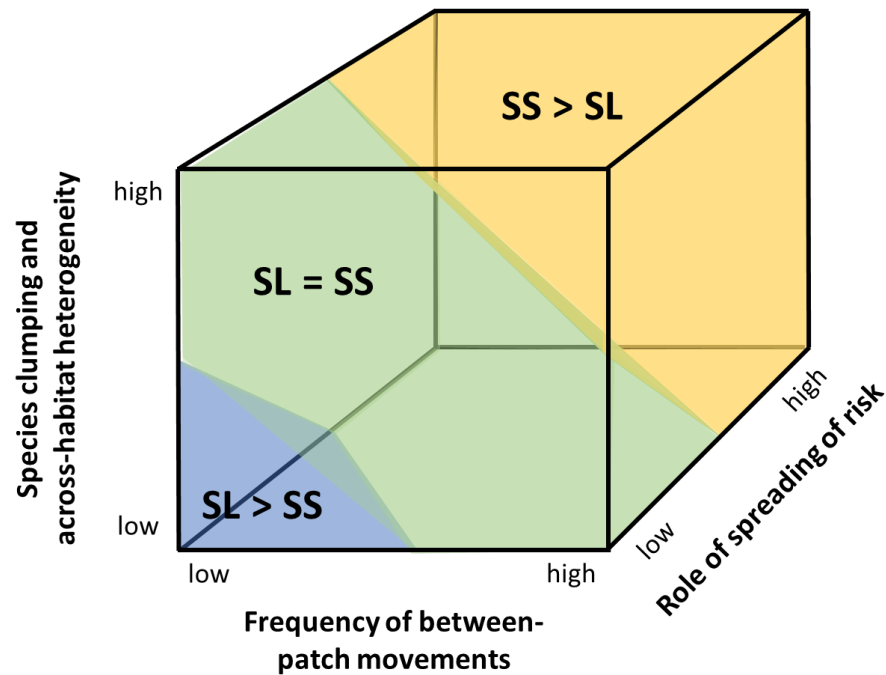
987 intersect more species: in (a) two large patches intersect 3 species while in (b) eight small

988 patches intersect 5 species. This effect is accentuated if the several small patches are farther apart

989 than the few large patches: in (c) eight small patches intersect 9 species compared to 3 species in

990 (a).

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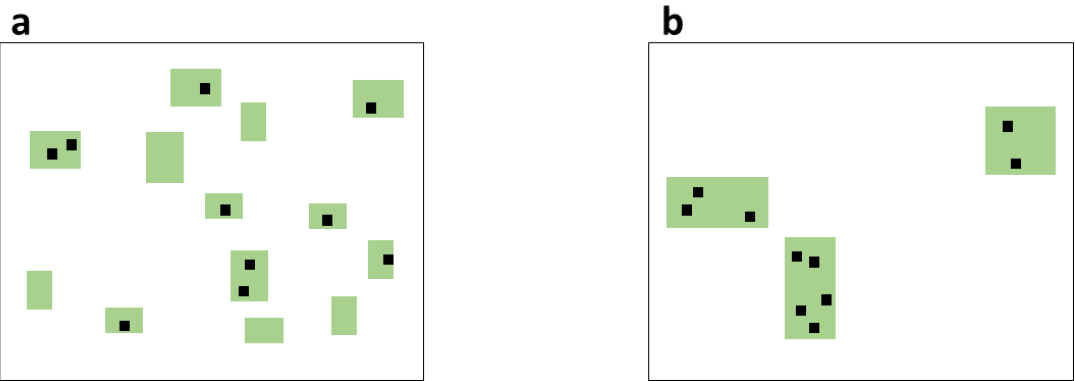
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994 **Fig. 3.** Illustration of the "SLOSS cube," combining SLOSS-relevant theory and empirical
995 SLOSS studies. The axes are based on the theory summarized in **Box 1**. The proportional
996 volumes of the three outcomes are based on their proportions found in a review of empirical
997 SLOSS studies in which sampling effort was unbiased, i.e. sampling proportional to area (see
998 Fig. 2b in Fahrig 2020): 50% $SS > SL$; 40% $SL = SS$; 10% $SL > SS$. The "SLOSS cube
999 hypothesis" predicts that $SL > SS$ will dominate when *all* of the following are true: between-
1000 patch movement rate is low, population dynamics are not influenced by spreading-of-risk, and
1001 across-habitat heterogeneity is low, i.e. the blue portion of the SLOSS cube.

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1006 **Fig. 4.** SLOSS can be evaluated by comparing cumulative species richness across the same
1007 number of sample sites (black squares) randomly placed within habitat (green rectangles) in
1008 multiple landscapes of the same size, each containing the same total area of habitat, but
1009 distributed in different numbers and sizes of patches. Two example landscapes are shown here,
1010 each with 10 sample sites placed randomly in habitat. Note that when the landscape has many
1011 small patches, some will not be sampled. This is not a problem because the unit of analysis in
1012 such a study is the landscape, not the patch.

1013

1014

Box 1. Theory related to the SLOSS debate; i.e. whether several small patches (SS) contain more species than a single (or few) large patches (SL) of the same total area ($SS > SL$), or the opposite ($SL > SS$). Note that many predictions require extrapolation from single species to multiple species.

I. PREDICTIONS BASED ON EXTINCTION-COLONIZATION DYNAMICS

Assumption A. Variation in extinction rate dominates the outcome of extinction-colonization dynamics.

Ecological pattern 1: Extinction rate per patch decreases with increasing patch size.

Prediction: $SL > SS$.

Potential mechanisms:

- Demographic stochasticity decreases with patch size.¹
- Species have minimum patch size requirements.¹
- Negative edge effects accentuate both of the previous mechanisms because patch edge-to-area ratio decreases with patch size. This disproportionately reduces patch size and increases demographic stochasticity for small patches compared to large patches.²
- Higher per-unit-area emigration rate from small than large patches, due to higher edge-to-area ratio, leads to higher dispersal mortality in the matrix over SS than over SL.³

Ecological pattern 2: Extinction probability over the landscape is lower for SS than SL.

Prediction: $SS > SL$.

Potential mechanisms:

- Between-patch movements of a competitor/predator/parasitoid are lower than their within-patch movements, and lower than between-patch movements of the affected species. This results in spreading-of-risk to that species from antagonists, over SS.⁴
- Disturbances cannot spread through the matrix, resulting in spreading-of-risk from disturbances over SS.⁵

Assumption B. Variation in colonization rate dominates the outcome of extinction-colonization dynamics.

Ecological pattern: Colonization rates are higher across SS than SL.

Prediction: SS > SL.

Potential mechanisms:

- Higher per-unit-area immigration rate over SS than SL due to: lower patch-to-patch distances in SS than SL; and higher edge-to-area ratio over SS than SL.⁶
- Larger species pool available to SS than SL, due to the larger amount of habitat within an accessible distance of SS than SL.⁷

II. PREDICTIONS BASED ON BETA DIVERSITY

Ecological pattern: Beta-diversity is higher over SS than over SL.

Prediction: SS > SL.

Potential mechanisms:

- Species distributions in continuous habitat are clumped due to: limited dispersal from occupied sites, conspecific attraction, and habitat heterogeneity. When patches are created by removal of habitat, SS intersect more pre-existing species distributions than SL.⁸
- Different successional trajectories in different patches produce higher heterogeneity and higher beta diversity over SS than SL.⁹

Studies that contributed to SLOSS-relevant theory or to part of the theory:

¹Skellam (1951); Diamond (1976); Whitcomb *et al.* (1976); Terborgh (1976); Cole (1981); Blake & Karr (1984); Willis (1984); Patterson & Atmar (1986); Burkey (1989); Atmar & Patterson (1993); Hill & Caswell (1999); With & King (1999); Etienne & Heesterbeek (2000); Pereira *et al.* (2004); McCarthy *et al.* (2006); Moilanen & Wintle (2007); Jagers & Harding (2009); Pardini *et al.* (2010); Tjørve (2010).

²Preston (1960); Laurance (1991); Williams *et al.* (2005); Moilanen & Wintle (2007).

³Willis (1984); Atmar & Patterson (1993); Fahrig (1998, 2002); Flather & Bevers (2002); Martin & Fahrig (2016).

⁴Huffaker (1958); Levins (1969); Levins & Culver (1971); Simberloff & Abele (1976); Wiens (1976); Morrison & Barbosa (1987); Amarasekare & Nisbet (2001); Hernández-Ruedas *et al.* (2018); Ben-Hur & Kadmon (2020); Deane *et al.* (2020).

⁵den Boer (1968); Levins (1969); Andrewartha (1984); Kallimanis *et al.* (2005); Tschardtke *et al.* (2008).

⁶Dunning *et al.* (1992); Duelli (1997); Bowman *et al.* (2002a); Grez *et al.* (2004); Tischendorf *et al.* (2005); Puckett & Eggleston (2016); Fovargue *et al.* (2018); Fahrig *et al.* (2011).

⁷Preston (1962); Tschardtke *et al.* (2012); Fahrig (2013).

⁸Hutchinson (1959); Preston (1960); Diamond (1975); Higgs & Usher (1980); Margules *et al.* (1982); Nekola & White (1999); Kallimanis *et al.* (2005); Tjørve (2010); Socolar *et al.* (2016); May *et al.* (2019); Simberloff & Gotelli (1984); Lasky & Keitt (2013); del Castillo (2015); Socolar *et al.* (2016); Nekola & White (2002); Arroyo-Rodríguez *et al.* (2017).
⁹Laurance (2002); Laurance *et al.* (2007); Ewers *et al.* (2013); del Castillo (2015); Arroyo-Rodríguez *et al.* (2017).

1093

1094 **Box 2. Recommended attributes of individual empirical studies**

1095 To test the SLOSS cube hypothesis in **Fig. 3**, many empirical studies are needed. In designing
1096 these studies researchers should pay attention to the following.

1097 1. Comparisons should be made across multiple landscapes that contain either SS or SL (**Fig. 4**),
1098 not across subsets of SS or SL within a single landscape.

1099 2. All sample landscapes should have the same spatial extent.

1100 3. Samples should be randomly distributed within the habitat in each landscape, with the number
1101 of samples in proportion to total habitat amount in the landscape.

1102 4. All sample landscapes should be within a single ecoregion to ensure the same overall species
1103 pool.

1104 5. The species included in the surveyed group should be those that are mainly associated to the
1105 particular habitat type studied. Significant attention should be paid to the definition of "habitat."

1106 For example, single trees may not be habitat patches for species groups that rely on humid forest
1107 understory conditions; however, single trees can be habitat patches for wood-boring beetles.

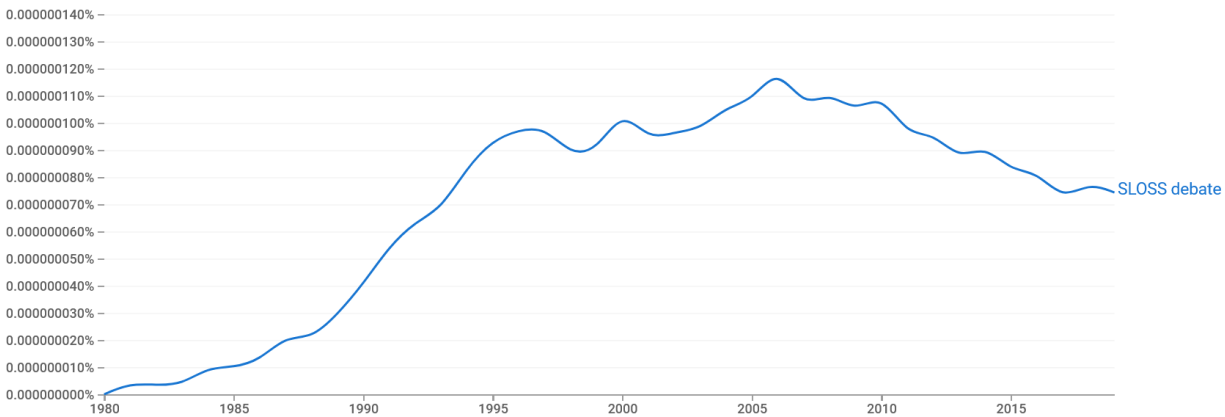
1108 6. Confounding of other variables with the SL vs. SS comparison should be avoided. For
1109 example, an apparent pattern of $SS > SL$ could be created where larger patches are more
1110 intensively managed or where smaller patches have more varied management approaches (e.g.
1111 grazed, mown, abandoned) than large ones, e.g. due to different ownership of different patches
1112 (Rösch *et al.* 2015). Conversely, an apparent pattern of $SL > SS$ could be created where small
1113 patches are more disturbed by humans than large patches (e.g., Barlow *et al.* 2016).

1114 7. The spatial pattern of patches should have been already in place for several generations of the
1115 surveyed species group. This is to ensure: (i) dissipation of transient positive fragmentation

effects caused by a crowding effect on small patches following patch creation (Gre \acute{z} *et al.* 2004),
and (ii) sufficient time for any extinctions to play out.

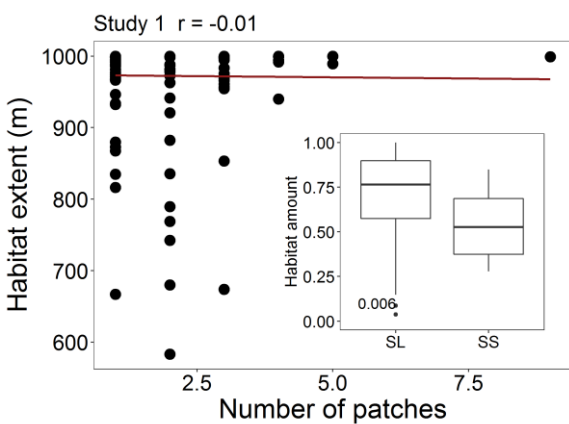
8. Differences in species detectability (MacKenzie *et al.* 2002) between SS and SL should be
estimated and accounted for if present.

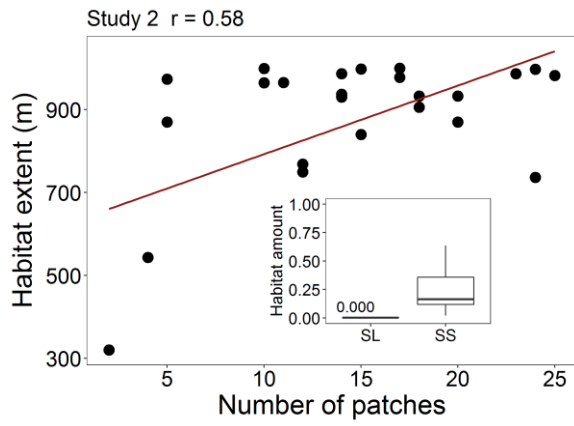
Appendix 1. Use of the term "SLOSS debate" as a proportion of all English-language literature, per year since 1980, estimated using Google Ngram (Michel *et al.* 2011).



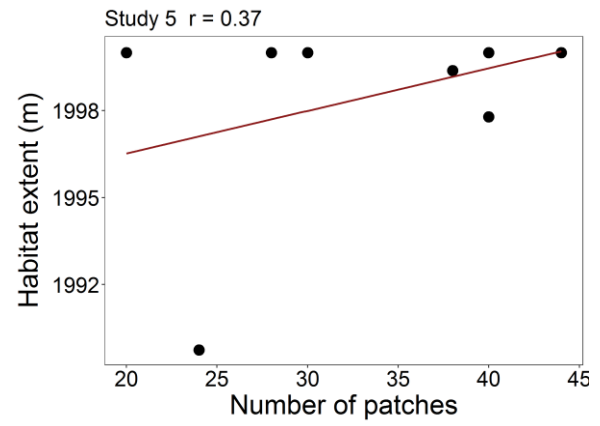
Appendix 2

Habitat extent (maximum distance between habitat edges in a landscape) vs. number of patches in the landscape, for landscapes within each of 32 studies included in the main analysis in Watling *et al.* (2020). For each study, each point represents a circular landscape within which habitat extent and patch number were calculated. Landscape size was constant within each study, but varied among studies from about 13 ha to over 11000 ha. Boxplots in insets are the medians of the total habitat amount per landscape, for landscapes with few (1-3) vs. many (> 3) patches. The strength and direction of the correlation between habitat extent and the number of patches per landscape were inconsistent across studies. This was true for all studies, and for those in which there was no significant difference in habitat area between SL and SS (Studies 3, 14, 19, 26, 28, and 34), i.e. studies appropriate for a SLOSS comparison. Note that three of an original 35 studies were omitted from Watling *et al.* (2020) due to insufficient information, or insufficient variation in predictor variables.

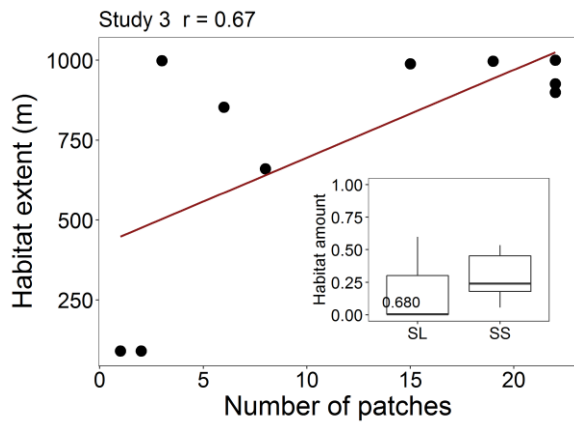




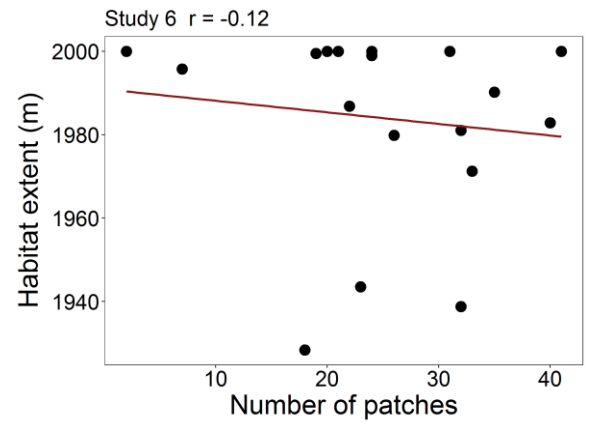
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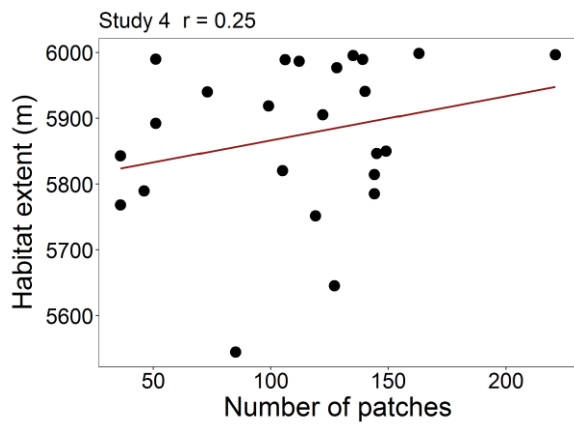
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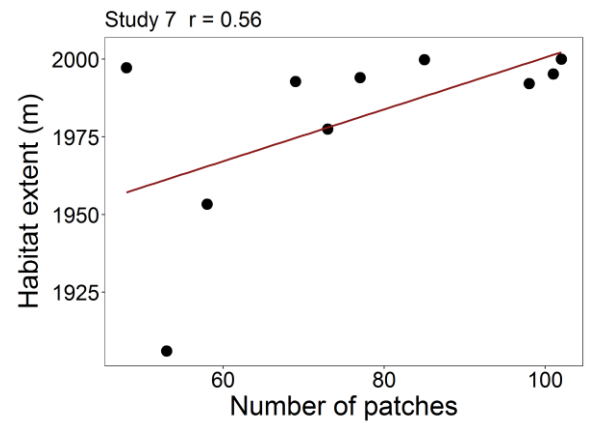
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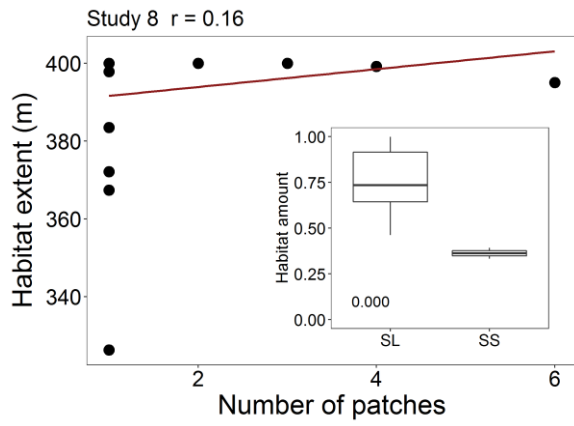
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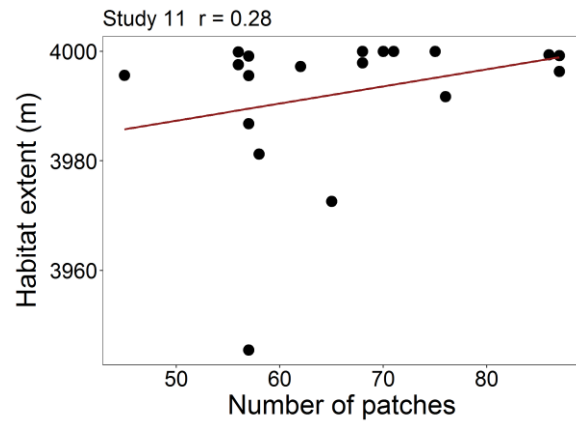
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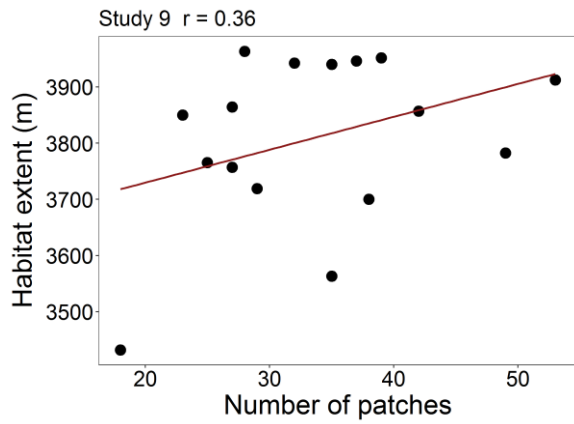
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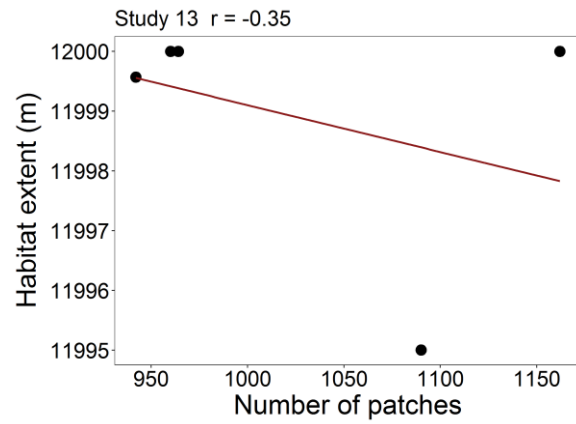
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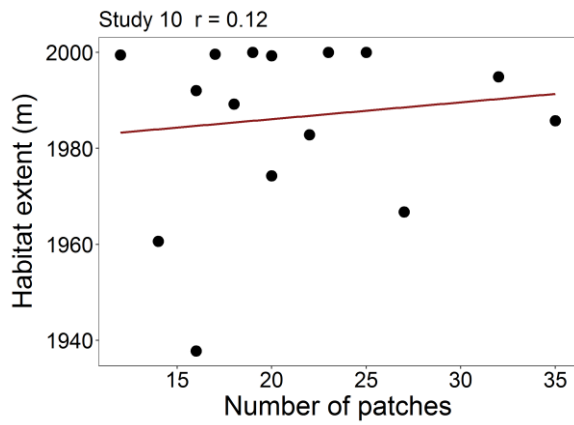
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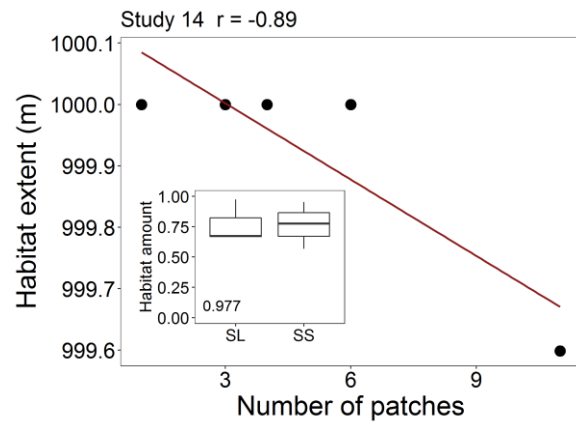
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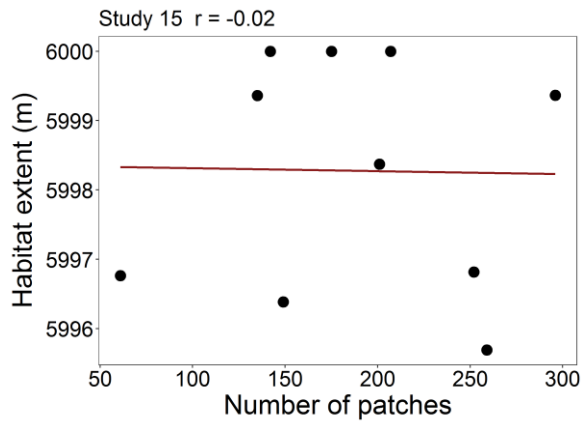
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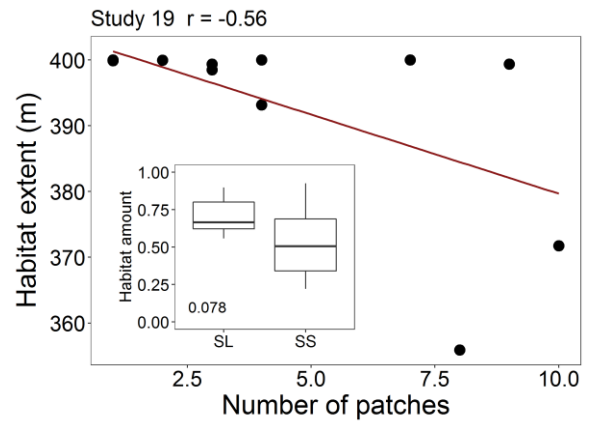
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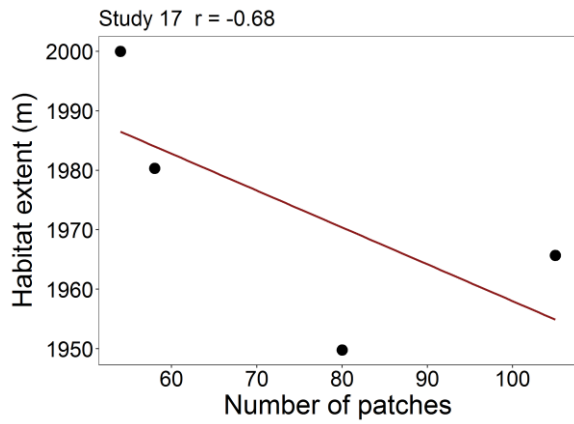
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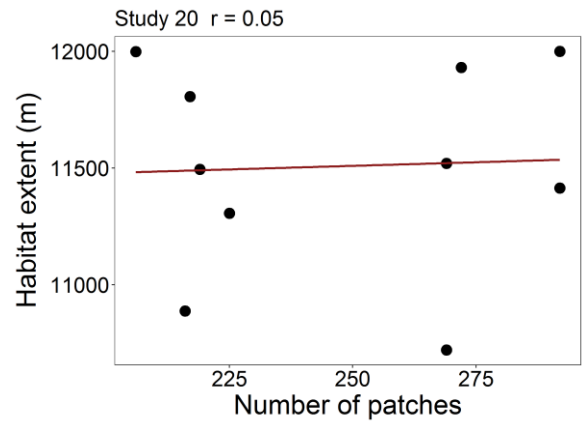
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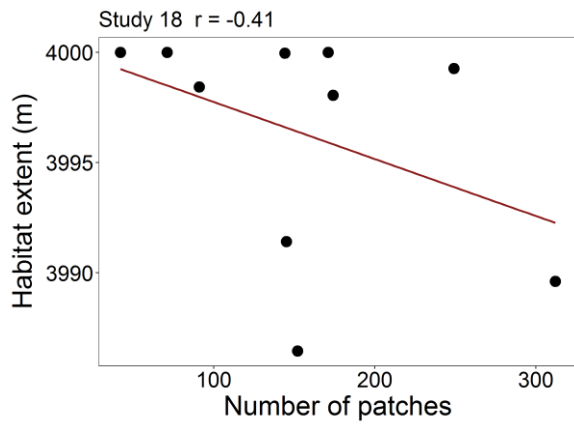
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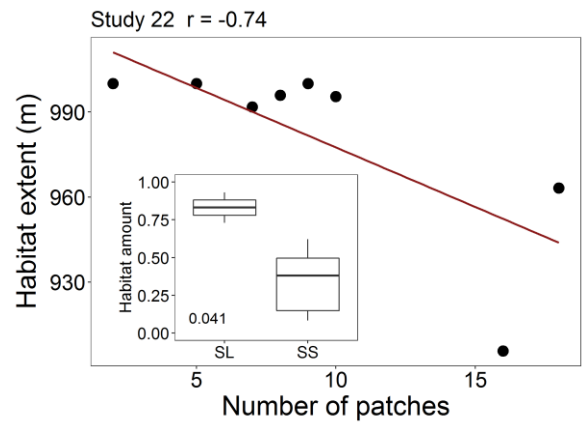
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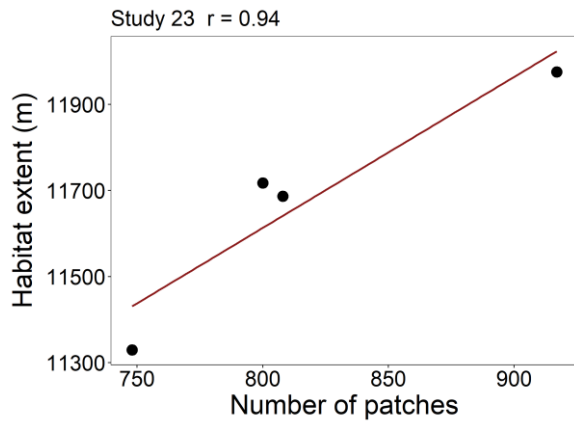
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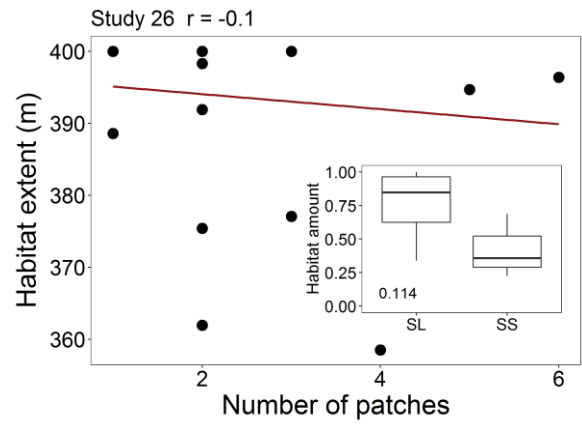
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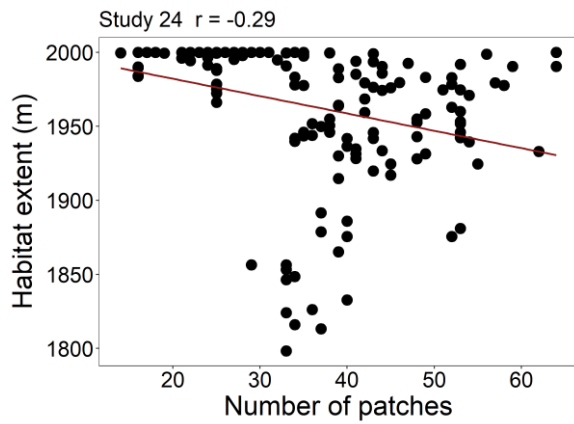
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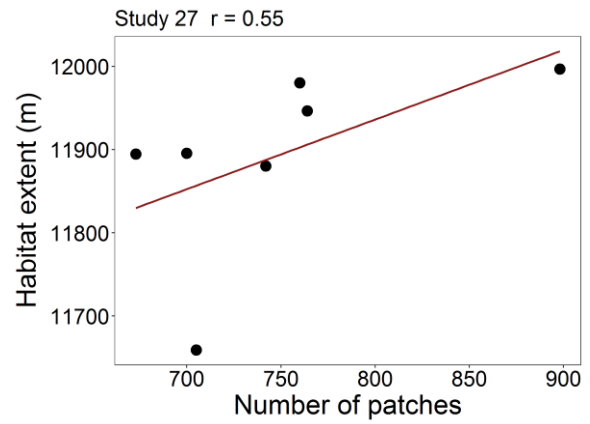
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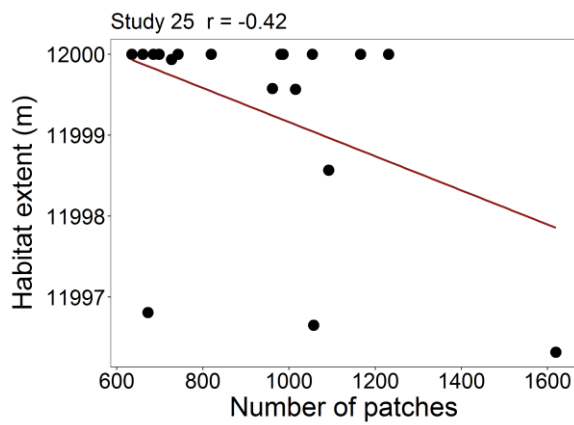
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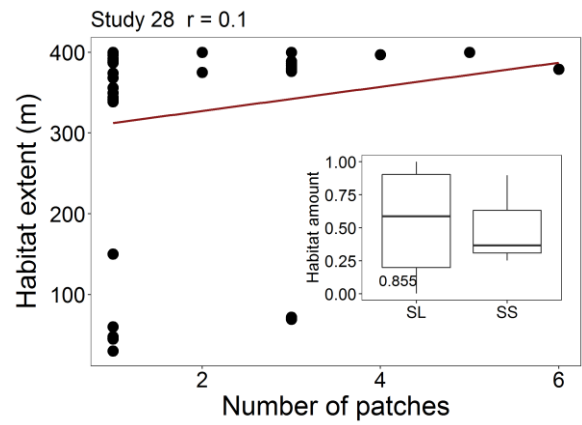
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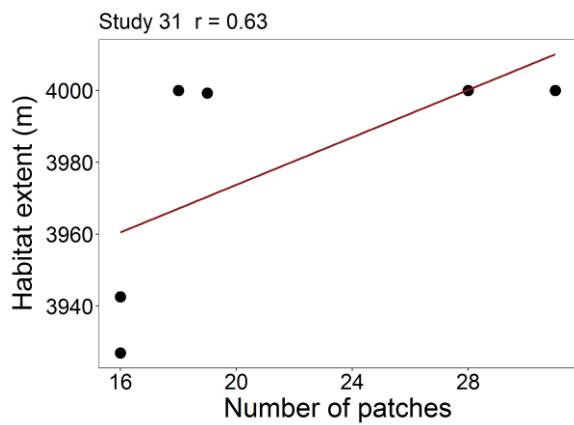
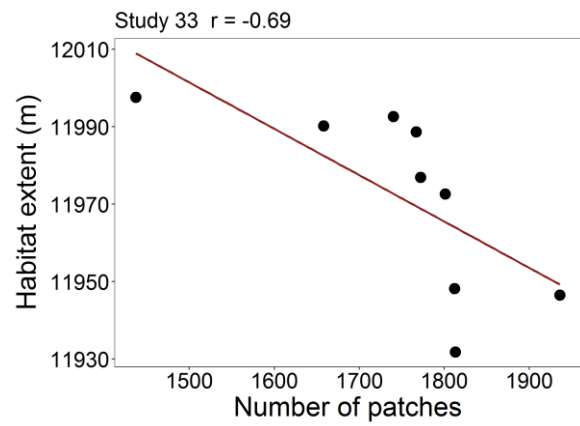
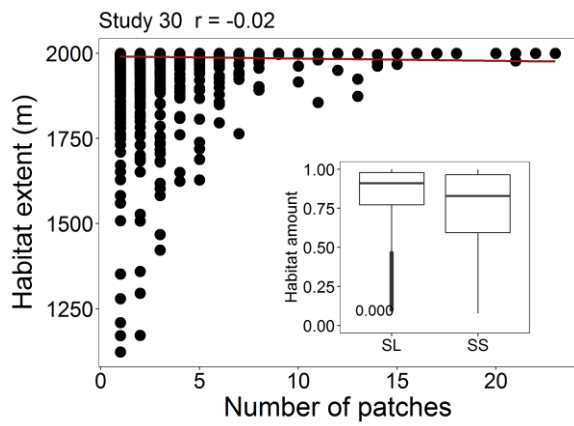
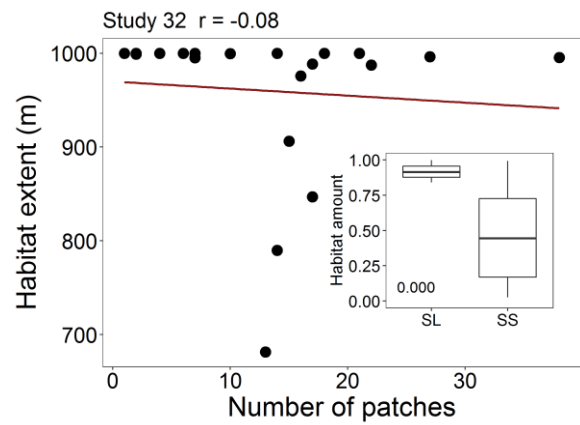
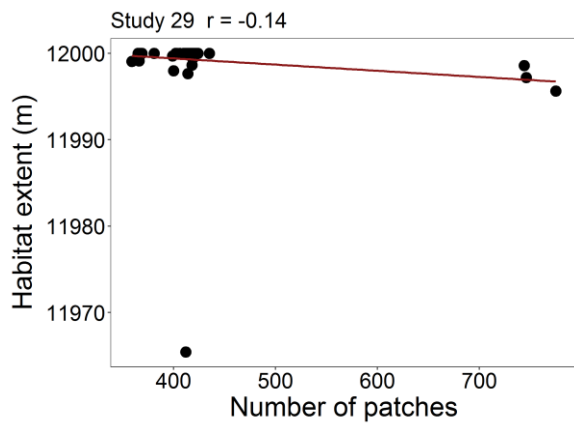
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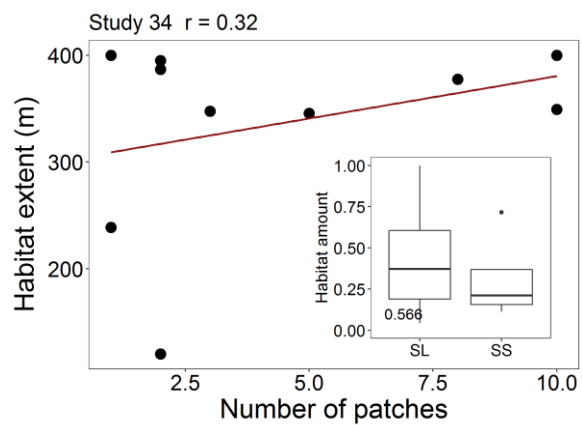


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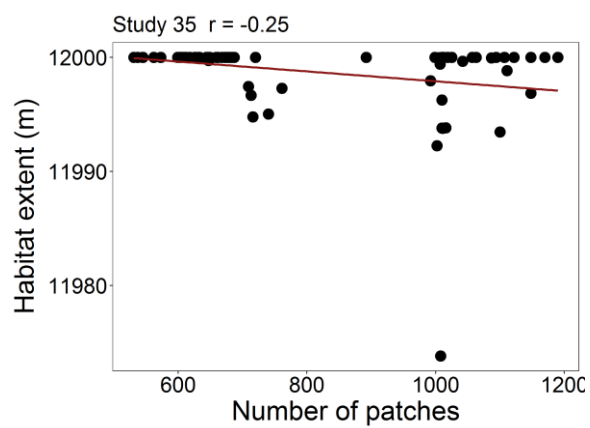


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