

1 **Resolving the SLOSS dilemma for biodiversity conservation: a research agenda**

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45

46

47 **Abstract**

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

62

63 **INTRODUCTION**

64

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

70 reserves (SS) of the same total area, the "SL > SS principle" (see also May 1975, Diamond
71 1976). The SL > SS principle became a standard in conservation planning worldwide following
72 its reiteration in the IUCN's (1980) highly influential *World Conservation Strategy*.

73

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

84

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

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

94

95 In contrast to the frequent empirical result that $SS > SL$, theoretical work related to the SLOSS
96 question suggests a more complex picture. Several hypotheses predict either $SL > SS$ or $SS >$
97 SL , depending on traits of the organisms (e.g., behavior, life history) or the landscapes (e.g., total
98 habitat amount, disturbances). These are summarized in **Box 1** (also reviewed in Ovaskainen
99 2002; Fahrig 2020). We also note that these conditions can occur together and may interact,
100 resulting in a plethora of possible scenarios. Given this diversity of predictions, most ecologists
101 have concluded that the answer to the SLOSS question "depends" (Kingsland 2002). For
102 example, Sarkar (2012) states that there is "no non-contextual answer to the SLOSS question",
103 and the Wikipedia entry for "SLOSS debate" concludes that "[t]he general consensus of the
104 SLOSS debate is that neither option fit[s] every situation and that they must all be evaluated on a
105 case to case basis." The SLOSS debate has therefore largely disappeared from the ecological
106 literature: Google Ngram Viewer indicates that the proportional occurrence of the term "SLOSS
107 debate" peaked in 2006 and has declined steadily since (**Appendix 1**; Michel *et al.* 2011).

108

109 ***Box 1 here***

110

111 Despite the fact that most researchers have shelved the SLOSS debate, it remains relevant
112 because many conservation agencies continue to prioritize protection of large, contiguous areas
113 of habitat, while small patches of natural habitat are less likely to be protected (reviewed in
114 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

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

141

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

158

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

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

171
172 Here we propose a research agenda to resolve the SLOSS dilemma, addressing the question, "are
173 there consistent, empirically-demonstrated conditions in which few large patches hold more
174 species than several small ones?" We begin by reviewing the relevant theory (**Box 1**). We then
175 propose a hypothesis, the "SLOSS cube hypothesis," which summarizes existing theory and
176 empirical work, and finally we use that hypothesis to propose a research agenda. Our aim is to
177 encourage future research in a direction that will resolve the SLOSS dilemma.

178

179 **REVIEW OF SLOSS PREDICTIONS**

180

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

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

187

188 **Extinction-colonization-based theory where variation in extinction dominates**

189

190 Most predictions of $SL > SS$ derive from the assumption that variation in extinction rate
191 dominates the outcome of the extinction-colonization dynamic. This is expected when
192 populations in separate patches are largely independent of each other because movements among
193 patches are rare such that colonization events are infrequent. Such isolation among patches
194 should occur when: (i) patches are far apart; (ii) the matrix is hostile and leads to very high
195 dispersal mortality; (iii) the species avoid entering the matrix (as might occur for habitat interior
196 specialists); or (iv) the species have very low innate mobility. As small patches are expected to
197 have smaller populations than large patches, they should have higher extinction rates from
198 demographic stochasticity. The persistence of any given species on a set of isolated patches will
199 then be driven by the size of the largest patch (Burkey 1989; Etienne & Heesterbeek 2000; Jagers
200 & Harding 2009). This effect will be accentuated for habitat interior species because the
201 proportion of a patch that is interior habitat declines with decreasing patch size (Preston 1960;
202 Laurance 1991; Williams *et al.* 2005; Moilanen & Wintle 2007). This effect is also expected to
203 be accentuated in situations where the matrix is hostile, for species that readily emigrate from
204 patches. Emigration rate should be higher from SS than SL due to the larger edge-to-area ratio
205 for SS, and therefore the mortality rate in the hostile matrix will be higher for SS than SL (Willis
206 1984; Atmar & Patterson 1993; Fahrig 1998, 2002; Flather & Bevers 2002; Martin & Fahrig

207 2016). The $SL > SS$ pattern is also predicted to be stronger when species within a group have
208 different patch size requirements, leading to selective extinction of particular species from small
209 patches (Diamond 1976; Terborgh 1976; Cole 1981; Patterson & Atmar 1986; Atmar &
210 Patterson 1993; McCarthy *et al.* 2006; Tjørve 2010).

211
212 On the other hand, theory can predict $SS > SL$ in extinction-dominated systems when extinctions
213 are caused by an antagonistic species or by a disturbance, leading to spreading-of-risk across SS .
214 Division of habitat into many small patches is predicted to reduce interspecific competition, such
215 that poor competitors can persist on some small, isolated patches due to the absence of stronger
216 competitors (e.g., Heilmann-Clausen & Christensen 2004; Hernández-Ruedas *et al.* 2018). This
217 could increase the overall number of species across a set of small patches, leading to $SS > SL$
218 (Levins & Culver 1971). SS can also stabilize predator-prey or host-parasitoid interactions as
219 prey or hosts can escape to patches that are temporarily unoccupied by the predator or parasitoid
220 (Huffaker 1958; Levins 1969; Wiens 1976; Morrison & Barbosa 1987). This should lead to $SS >$
221 SL for groups of predators and their prey, or parasitoids and their hosts. And, SS are predicted to
222 reduce the risk of simultaneous extinction due to disturbances that do not spread from patch to
223 patch through the matrix (den Boer 1968; Levins 1969; Andrewartha 1984; Kallimanis *et al.*
224 2005; Tschardtke *et al.* 2008), again leading to $SS > SL$.

225

226 **Extinction-colonization-based theory where variation in colonization dominates**

227

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

230 higher immigration rate in SS than SL, and a larger species pool in the proximity of SS than SL.
231 If a species has a very high rate of emigration from patches (e.g. larval fish: Fovargue *et al.*
232 2018), then SS are predicted to intercept more dispersers than SL because of the higher edge-to-
233 area ratio of SS than SL, leading to higher immigration and therefore higher colonization rates in
234 SS than SL (Bowman *et al.* 2002a; Grez *et al.* 2004; Tischendorf *et al.* 2005; Puckett &
235 Eggleston 2016). In other words, in this situation SS are predicted to have higher functional
236 connectivity (sensu Taylor *et al.* 1993) than SL. For species that need to access resources outside
237 of habitat patches during some part of their life cycle (e.g. Pope *et al.* 2000), access to those
238 resources will be higher in a landscape with SS than SL (Dunning *et al.* 1992; Duelli 1997;
239 Fahrig *et al.* 2011), which could also lead to SS > SL.

240

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

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

254

255 *Figure 1 here*

256

257 **Theory based on beta diversity**

258

259 All of the SLOSS predictions discussed so far derive from assumptions about how
260 extinction/mortality and colonization/immigration dynamics interact with sizes of individual
261 patches and with sets of patches. In general, $SL > SS$ is predicted when extinction dominates
262 these dynamics, except when spreading-of-risk plays an important role in population dynamics.
263 $SS > SL$ is generally predicted when colonization/immigration dominates the dynamics.

264

265 A different set of SLOSS theory asks how the number of patches (for a given total habitat
266 amount) is expected to affect beta diversity. The fact that species distributions in continuous
267 habitat are usually clumped or spatially autocorrelated leads to a prediction of $SS > SL$ (May *et*
268 *al.* 2019; **Fig. 2**). One of the most general patterns in ecology is that species distributions are
269 clumped, due to both extrinsic and intrinsic reasons (Nekola & White 1999; Tuomisto *et al.*
270 2003; Seidler & Plotkin 2006; Morlon *et al.* 2008; McGill 2010, 2011). Extrinsic environmental
271 conditions (e.g. soil type or microclimate) are often spatially autocorrelated (heterogeneous in
272 space), creating clumped species distributions in response. Intrinsic factors that lead to clumped
273 species distributions include limited dispersal from occupied sites, creating population centres
274 (Hubbell 2001; Tuomisto *et al.* 2003), conspecific attraction (e.g., Vité & Francke 1976; Ramsay

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

283

284 Note that the prediction of higher beta diversity across SS than SL does not assume or imply that
285 small patches are farther apart than large patches. Indeed, when the landscape size and the
286 amount of habitat are held constant, there is no consistent difference in maximum distance
287 between habitat edges between SS and SL (**Appendix 2**). Spatial clumping of species
288 distributions is nevertheless expected to lead to more species sampled over SS than SL because
289 SS will cover a given area more evenly than SL, thus intersecting more species distributions
290 (**Fig. 2a vs. 2b**; Tschardtke *et al.* 2002; May *et al.* 2019). May *et al.* (2019) referred to this
291 spatial sampling effect as a "geometric effect" because it emerges from the geometric distribution
292 of habitat patches and the assumption that species have clumped distributions. The prediction
293 that differences in beta diversity play an important role in SLOSS was confirmed by Deane *et al.*
294 (2020), who found that beta diversity was the strongest predictor of $SS > SL$ after accounting for
295 sampling bias.

296

297 **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 al.*
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**

321

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

326

327 **The SLOSS cube hypothesis**

328

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

341

342 *Figure 3 here*

343

344 To summarize empirical work to date based on classical SLOSS studies (Quinn & Harrison
345 1988): about 50% of apparently unbiased (see below) empirical SLOSS studies find $SS > SL$ and
346 about 10% find $SL > SS$, while the remaining 40% find no difference (Fahrig 2020). These
347 proportions are represented as the coloured volumes in **Fig. 3**. Given the relative rarity of $SL >$
348 SS results, the SLOSS cube hypothesis predicts that $SL > SS$ will occur predictably only when
349 *all* of the following are met: between-patch movements are rare, spreading-of-risk is not
350 important in population dynamics, *and* across-habitat heterogeneity is low (blue volume in **Fig.**
351 **3**). The prediction that all three conditions must hold to obtain $SL > SS$ derives not only from the
352 relative rarity of $SL > SS$, but also from preliminary summaries of relevant empirical work
353 suggesting that when only one of these conditions holds we still find a predominance of $SS > SL$
354 (reviewed in Fahrig 2020). In particular, $SS > SL$ is more common than $SL > SS$ in situations
355 with high matrix hostility, suggesting that low between-patch movement rate alone is insufficient
356 to reliably produce $SL > SS$. And, many cases of $SS > SL$ occur in situations where across-
357 habitat heterogeneity is low (Fahrig 2020), suggesting that low spatial autocorrelation in
358 environmental characteristics alone is not sufficient to reliably produce $SL > SS$. However, the
359 *combination* of factors – low between-patch movement, low role of spreading-of-risk, and low
360 across-habitat heterogeneity – has not yet been explicitly tested across a range of systems.

361

362 **Testing the SLOSS cube hypothesis**

363

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

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

375

376 The frequency of between-patch movements is unknown and hard to measure for nearly all
377 species groups and regions. While relative innate mobility of different species groups can often
378 be estimated using morphological or life history correlates (Bowman *et al.* 2002b; Stevens *et al.*
379 2004; Beckman *et al.* 2018), the realized frequency of between-patch movements is related not
380 only to innate mobility but also to landscape attributes such as habitat configuration and matrix
381 quality. Therefore, we propose a combination of two steps for selecting species groups with low
382 (or high) between-patch movement frequency in the selected region. First, species groups would
383 be categorized into low vs. high innate mobility based on morphology and life history traits such
384 as wing presence/absence, territory size, etc. The purpose of the second step is then to confirm
385 that, in the selected region, the low-mobility group does in fact show low between-patch
386 movement and/or the high-mobility group does in fact show high between-patch movement. This
387 can be done indirectly by comparing mean species density (number of species per sample site) of
388 the mobility group in landscapes with SS vs. SL. If, for the low mobility group, movement is
389 lower between patches than within patches in the selected region, then we should find lower

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

392

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

403

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

410

411 *Box 2 here*

412 *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

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

445

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

448

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

457

458 Addressing this question requires multiple empirical tests, using appropriate study designs (**Box**
459 **2**), focused on species groups and environments where between-patch movements are rare,
460 spreading-of-risk is likely unimportant, and habitat is homogeneous. In other words, studies
461 should focus on the blue portion of the SLOSS cube in **Fig. 3**. If the majority of studies in this
462 space find $SL > SS$ then we can conclude that the $SL > SS$ principle is generally valid in those
463 conditions. As discussed above, estimates of realized interpatch movement rates for groups of
464 species are usually not available for a given region, but movement rates should be low when
465 patches are very far apart or the matrix is hostile, or when the species group is comprised of
466 sedentary species. Therefore, SLOSS tests should focus on regions where (i) habitat is rare i.e.,
467 patches - both large and small - are far apart, (ii) habitat is spatially homogeneous, and (iii)
468 matrix is hostile (e.g. urban areas, high-intensity agriculture). The groups of species selected
469 should be those assumed to have low innate mobility, and those for whom spreading-of-risk
470 likely plays a minor role in population dynamics, i.e. strong competitors under bottom-up control
471 that are not subject to frequent local disturbances (see above). Once a region and a species group
472 have been selected, multiple sample landscapes should be selected within that region, that vary in
473 the numbers and sizes of patches and do not vary in total habitat amount (**Fig. 4**), or for which
474 there is no relationship between habitat amount and the numbers and sizes of patches across the
475 landscapes. Sample sites should then be randomly placed in the habitat within each landscape,
476 and the species group sampled at each site. Average species density (mean number of species per
477 site) should be compared between SS and SL to confirm the assumption of low between-patch
478 movement in the selected region (see above). Total species richness (gamma diversity) should
479 then be estimated across the habitat in each landscape to determine whether there are more
480 species in landscapes with SL than SS .

481

482 **Note on negative edge effects and SLOSS**

483

484 As indicated in **Box 1**, habitat interior species, i.e. those that show negative edge effects, should
485 be particularly susceptible to the effects of patch size on extinction probability. In addition, they
486 may have low mobility between patches if they are averse to leaving interior habitat and entering
487 the matrix. For this reason, patch-scale evidence of negative edge effects on a species group is
488 often taken as evidence of $SL > SS$ for that group (Fletcher *et al.* 2018). However, we note that
489 $SL > SS$ cannot be directly inferred for groups of habitat interior species based only on patch-
490 scale evidence. Such an inference would entail cross-scale extrapolation from local edge effects
491 to landscape-scale effects. This extrapolation is a prediction that must be tested at a landscape-
492 scale because other mechanisms in **Box 1**, operating at a landscape scale, may outweigh negative
493 local edge effects in influencing species richness across a landscape (Fahrig *et al.* 2019). Such
494 tests would compare gamma diversity of species groups known to show negative edge effects
495 (and thus assumed to fall into the blue portion of the SLOSS cube in **Fig. 3**), across multiple
496 landscapes as in **Fig. 4** and **Box 2**.

497

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

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

507

508 **Need for many studies**

509

510 Here we emphasize that a single study on a particular species group in a particular region cannot
511 answer the question "are there consistent, empirically-demonstrated conditions that lead to $SL >$
512 SS ?" $SL > SS$ was conceived and is used as a general principle. We know it is not universally
513 valid, because most empirical studies do not support it. However, it may still apply in general
514 when certain conditions hold, specifically the combination of low between-patch movement, low
515 spreading-of-risk, and low across-habitat heterogeneity. Testing this prediction will require
516 multiple studies on a range of taxa and regions that match these conditions (Seibold *et al.* 2018).
517 $SL > SS$ would be upheld as a principle if we find more species in habitat within landscapes with
518 SL than SS , in most of these studies.

519

520 **DISCUSSION**

521

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

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

535

536 There are two possible outcomes of research aimed at testing the SLOSS cube hypothesis. First,
537 empirical studies might generally support the hypothesis. This would have different implications
538 for conservation decision-making, depending on the conservation goal. In situations where the
539 goal is general conservation of biodiversity, support for the hypothesis would suggest that a
540 mixed strategy of mainly small patches and a few large patches would maximize biodiversity, as
541 suggested by Arroyo-Rodríguez *et al.* (2020). On the other hand, when the goal is conservation
542 of a particular species group, then support for the hypothesis would indicate what research the
543 conservation agency needs to carry out, to determine whether the particular conditions in their
544 system fall within the range of conditions where $SL > SS$ is valid. In particular, do the level of
545 between-patch movement, the role of spreading-of-risk, and the level of across-habitat
546 heterogeneity place the system within the blue portion of the SLOSS cube in **Fig. 3**? If so then,
547 for biodiversity conservation, large patches should be prioritized and small patches should be
548 down-weighted, but if not, then total habitat amount should be maximized irrespective of the
549 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).

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

578

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

591

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

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

604
605 We also note that, if there are no consistent, empirically-demonstrated conditions leading to $SL >$
606 SS , this does not invalidate the mechanisms proposed in **Box 1**. Rather, it would mean that the
607 mechanisms predicting $SS > SL$ outweigh the mechanisms predicting $SL > SS$ in nature. Put
608 differently, it would mean that, for a mechanism to result in $SL > SS$, the conditions would need
609 to be so extreme - e.g. perfectly homogeneous habitat and essentially no between-patch
610 movement - that they are almost never observed except in models.

611
612 We emphasize that SLOSS is explicitly not about the role of habitat amount. Rather, it is about
613 the influence of the pattern or configuration of a given amount of habitat (several small vs. few
614 large patches). Habitat loss is the main cause of species declines, and so habitat preservation and
615 restoration are the top priorities for biodiversity conservation. If, in a particular situation, a
616 choice is presented between conserving one large patch vs. several small patches, but the small
617 patches have much less habitat in total, then the decision should be to conserve the large patch.
618 For example, in the Steigerwald forest in Southern Germany there is an ongoing discussion about

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

626

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

639

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641

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644

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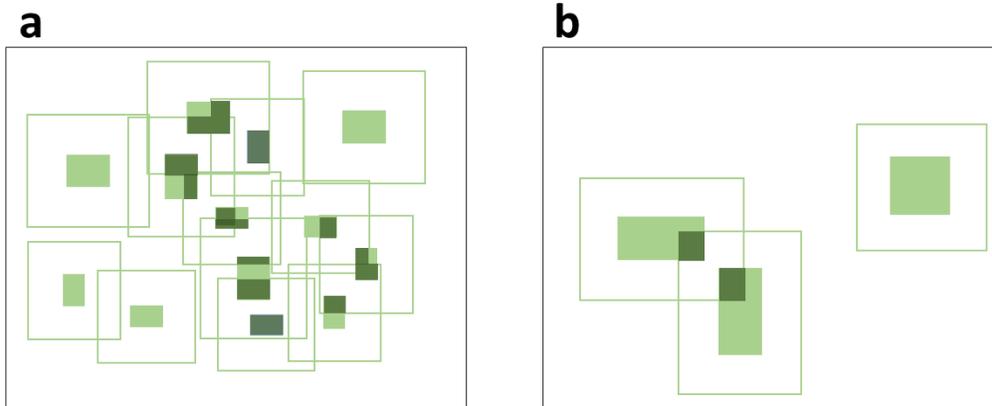
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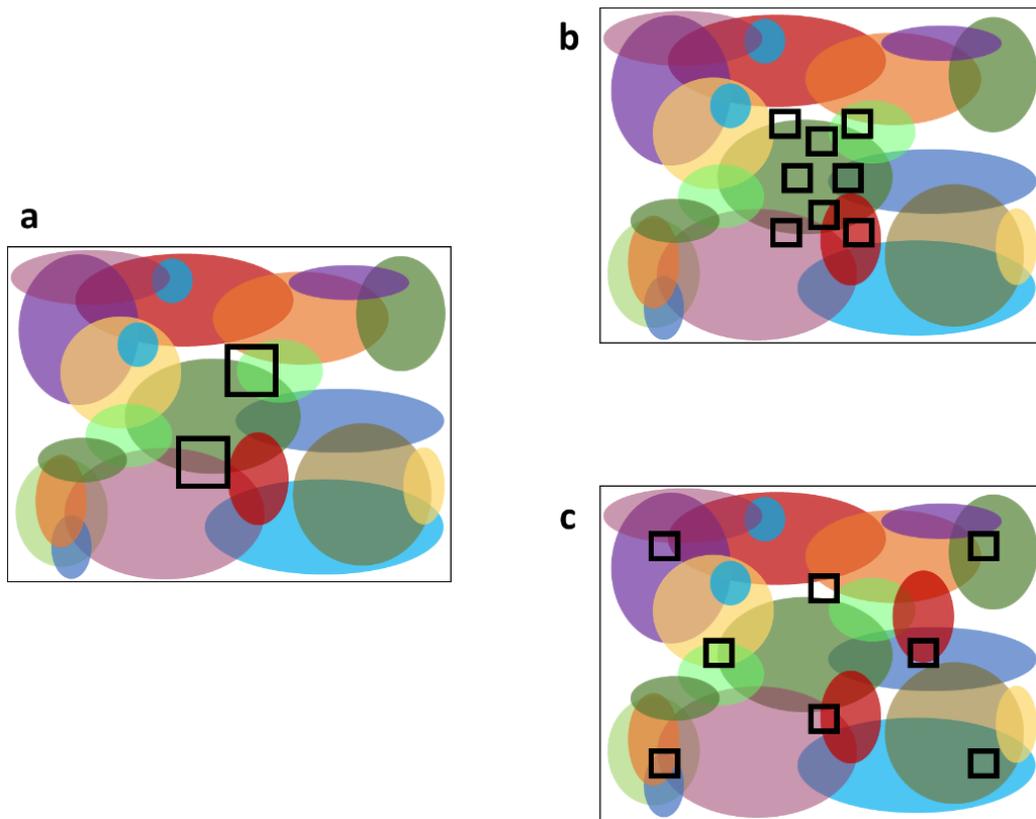


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972 **Figure 1.** The total area contributing the species pool available to colonize a set of several small
973 patches (a) is larger than the total area contributing the species pool available to colonize a set of
974 few large patches (b). Light 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.

977



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980

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

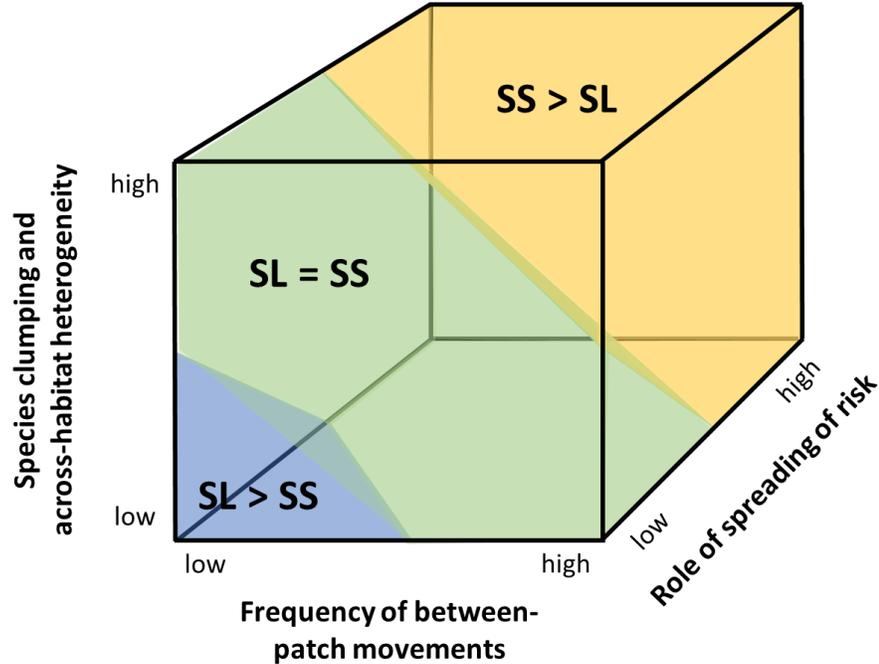
986 small patches (a vs. b), several small patches will cover the area more evenly and will therefore

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).



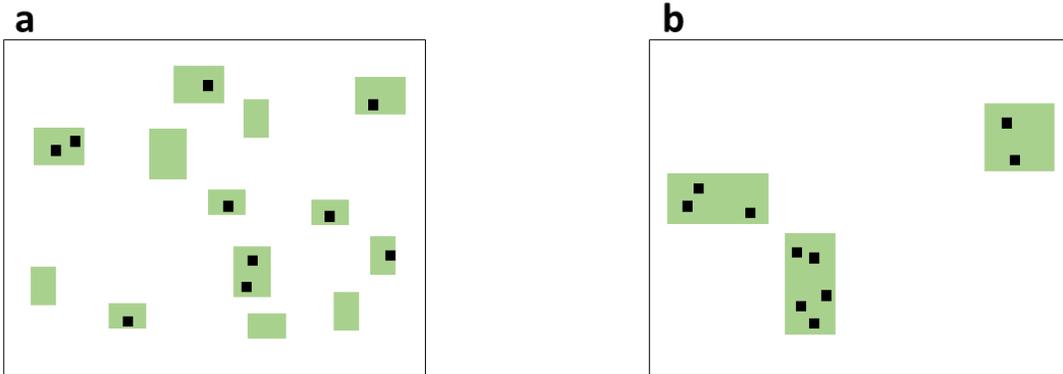
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994 **Fig. 3.** Illustration of the "SLOSS cube," combining SLOSS-relevant theory and empirical
 995 SLOSS studies. The axes are based on the theory summarized in **Box 1**. The proportional
 996 volumes of the three outcomes are based on their proportions 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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1005

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

1015 **Box 1.** Theory related to the SLOSS debate; i.e. whether several small patches (SS) contain more
1016 species than a single (or few) large patches (SL) of the same total area ($SS > SL$), or the opposite
1017 ($SL > SS$). Note that many predictions require extrapolation from single species to multiple
1018 species.

1019

1020 I. PREDICTIONS BASED ON EXTINCTION-COLONIZATION DYNAMICS

1021

1022 **Assumption A. Variation in extinction rate dominates the outcome of extinction-**
1023 **colonization dynamics.**

1024

1025 Ecological pattern 1: Extinction rate per patch decreases with increasing patch size.

1026 Prediction: $SL > SS$.

1027 Potential mechanisms:

- 1028 • Demographic stochasticity decreases with patch size.¹
- 1029 • Species have minimum patch size requirements.¹
- 1030 • Negative edge effects accentuate both of the previous mechanisms because patch edge-to-
1031 area ratio decreases with patch size. This disproportionately reduces patch size and increases
1032 demographic stochasticity for small patches compared to large patches.²
- 1033 • Higher per-unit-area emigration rate from small than large patches, due to higher edge-to-
1034 area ratio, leads to higher dispersal mortality in the matrix over SS than over SL.³

1035

1036 Ecological pattern 2: Extinction probability over the landscape is lower for SS than SL.

1037 Prediction: $SS > SL$.

1038 Potential mechanisms:

- 1039 • Between-patch movements of a competitor/predator/parasitoid are lower than their within-
1040 patch movements, and lower than between-patch movements of the affected species. This
1041 results in spreading-of-risk to that species from antagonists, over SS.⁴
- 1042 • Disturbances cannot spread through the matrix, resulting in spreading-of-risk from
1043 disturbances over SS.⁵

1044

1045 **Assumption B. Variation in colonization rate dominates the outcome of extinction-**
1046 **colonization dynamics.**

1047

1048 Ecological pattern: Colonization rates are higher across SS than SL.

1049 Prediction: SS > SL.

1050 Potential mechanisms:

- 1051 • Higher per-unit-area immigration rate over SS than SL due to: lower patch-to-patch distances
1052 in SS than SL; and higher edge-to-area ratio over SS than SL.⁶
- 1053 • Larger species pool available to SS than SL, due to the larger amount of habitat within an
1054 accessible distance of SS than SL.⁷

1055

1056 **II. PREDICTIONS BASED ON BETA DIVERSITY**

1057

1058 Ecological pattern: Beta-diversity is higher over SS than over SL.

1059 Prediction: SS > SL.

1060 Potential mechanisms:

- 1061 • Species distributions in continuous habitat are clumped due to: limited dispersal from
1062 occupied sites, conspecific attraction, and habitat heterogeneity. When patches are created by
1063 removal of habitat, SS intersect more pre-existing species distributions than SL.⁸
- 1064 • Different successional trajectories in different patches produce higher heterogeneity and
1065 higher beta diversity over SS than SL.⁹

1066

1067 *Studies that contributed to SLOSS-relevant theory or to part of the theory:*

1068 ¹Skellam (1951); Diamond (1976); Whitcomb *et al.* (1976); Terborgh (1976); Cole (1981); Blake
1069 & Karr (1984); Willis (1984); Patterson & Atmar (1986); Burkey (1989); Atmar & Patterson
1070 (1993); Hill & Caswell (1999); With & King (1999); Etienne & Heesterbeek (2000); Pereira *et al.*
1071 (2004); McCarthy *et al.* (2006); Moilanen & Wintle (2007); Jagers & Harding (2009);
1072 Pardini *et al.* (2010); Tjørve (2010).

1073 ²Preston (1960); Laurance (1991); Williams *et al.* (2005); Moilanen & Wintle (2007).

1074 ³Willis (1984); Atmar & Patterson (1993); Fahrig (1998, 2002); Flather & Bevers (2002); Martin
1075 & Fahrig (2016).

1076 ⁴Huffaker (1958); Levins (1969); Levins & Culver (1971); Simberloff & Abele (1976); Wiens
1077 (1976); Morrison & Barbosa (1987); Amarasekare & Nisbet (2001); Hernández-Ruedas *et al.*
1078 (2018); Ben-Hur & Kadmon (2020); Deane *et al.* (2020).

1079 ⁵den Boer (1968); Levins (1969); Andrewartha (1984); Kallimanis *et al.* (2005); Tschardtke *et al.*
1080 (2008).

1081 ⁶Dunning *et al.* (1992); Duelli (1997); Bowman *et al.* (2002a); Grez *et al.* (2004); Tischendorf *et al.*
1082 (2005); Puckett & Eggleston (2016); Fovargue *et al.* (2018); Fahrig *et al.* (2011).

1083 ⁷Preston (1962); Tschardtke *et al.* (2012); Fahrig (2013).

1084 ⁸Hutchinson (1959); Preston (1960); Diamond (1975); Higgs & Usher (1980); Margules *et al.*
1085 (1982); Nekola & White (1999); Kallimanis *et al.* (2005); Tjørve (2010); Socolar *et al.* (2016);
1086 May *et al.* (2019); Simberloff & Gotelli (1984); Lasky & Keitt (2013); del Castillo (2015);
1087 Socolar *et al.* (2016); Nekola & White (2002); Arroyo-Rodríguez *et al.* (2017).
1088 ⁹Laurance (2002); Laurance *et al.* (2007); Ewers *et al.* (2013); del Castillo (2015); Arroyo-
1089 Rodríguez *et al.* (2017).

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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

1116 effects caused by a crowding effect on small patches following patch creation (Gre z *et al.* 2004),
1117 and (ii) sufficient time for any extinctions to play out.

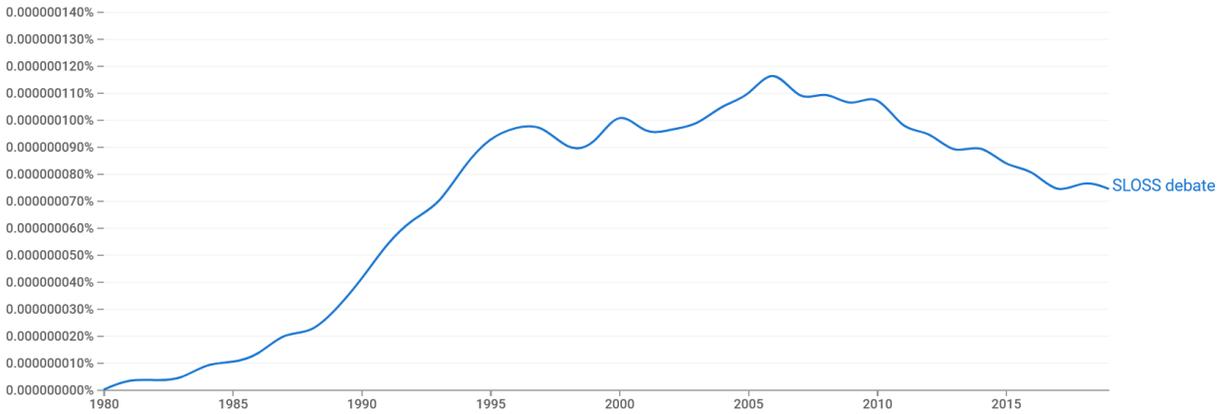
1118 8. Differences in species detectability (MacKenzie *et al.* 2002) between SS and SL should be
1119 estimated and accounted for if present.

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1122 **Appendix 1.** Use of the term "SLOSS debate" as a proportion of all English-language literature,
1123 per year since 1980, estimated using Google Ngram (Michel *et al.* 2011).

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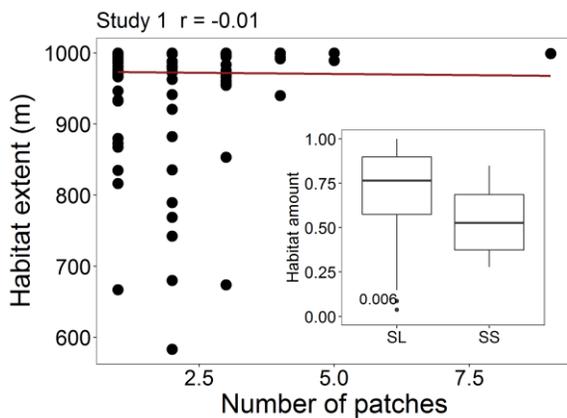
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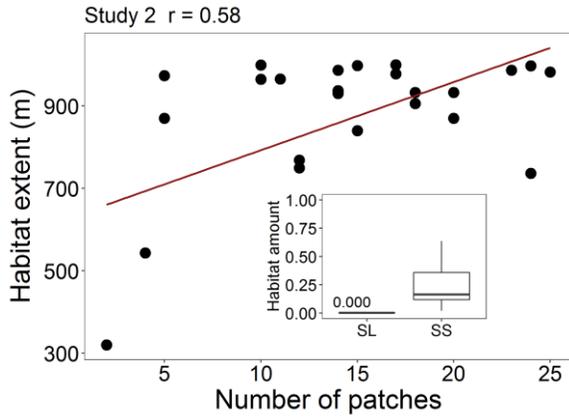
1127 **Appendix 2**

1128 Habitat extent (maximum distance between habitat edges in a landscape) vs. number of patches
1129 in the landscape, for landscapes within each of 32 studies included in the main analysis in
1130 Watling *et al.* (2020). For each study, each point represents a circular landscape within which
1131 habitat extent and patch number were calculated. Landscape size was constant within each study,
1132 but varied among studies from about 13 ha to over 11000 ha. Boxplots in insets are the medians
1133 of the total habitat amount per landscape, for landscapes with few (1-3) vs. many (> 3) patches.
1134 The strength and direction of the correlation between habitat extent and the number of patches
1135 per landscape were inconsistent across studies. This was true for all studies, and for those in
1136 which there was no significant difference in habitat area between SL and SS (Studies 3, 14, 19,
1137 26, 28, and 34), i.e. studies appropriate for a SLOSS comparison. Note that three of an original
1138 35 studies were omitted from Watling *et al.* (2020) due to insufficient information, or insufficient
1139 variation in predictor variables.

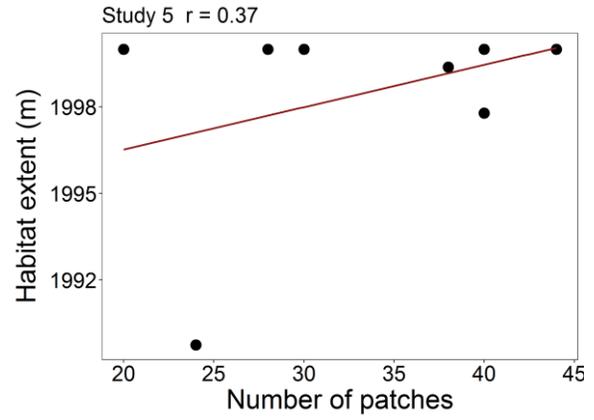
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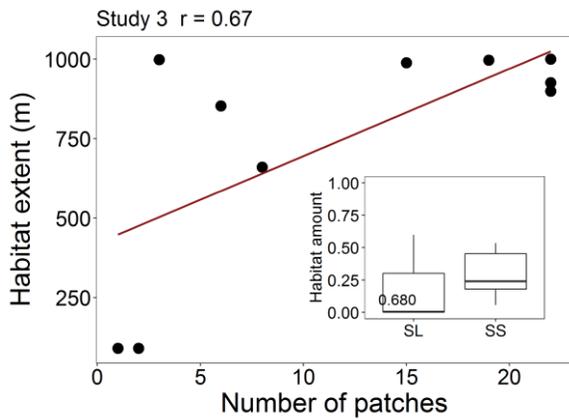
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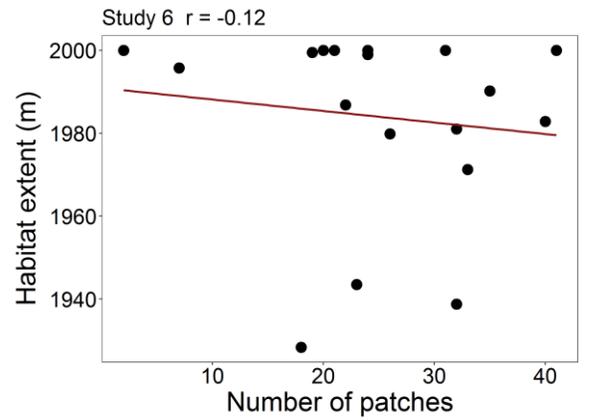
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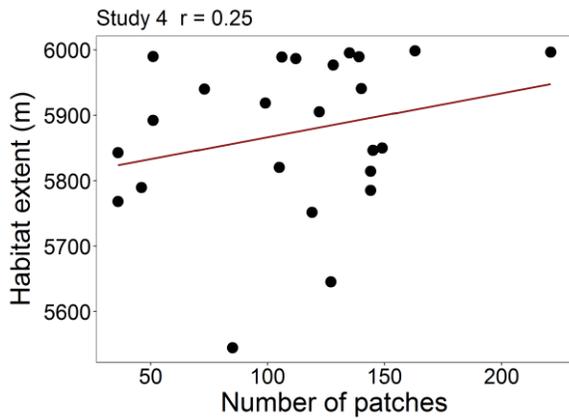
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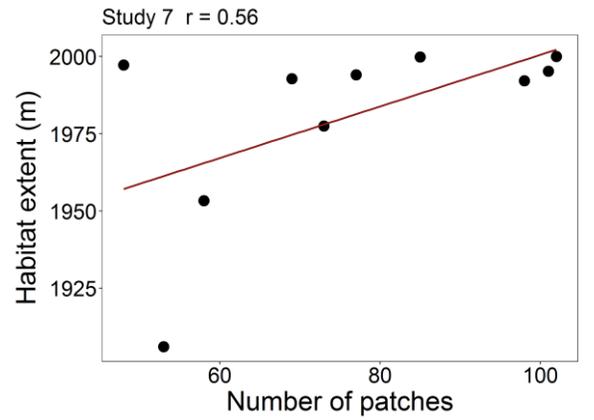
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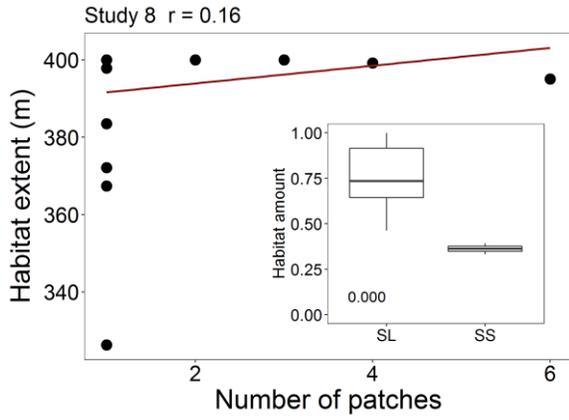
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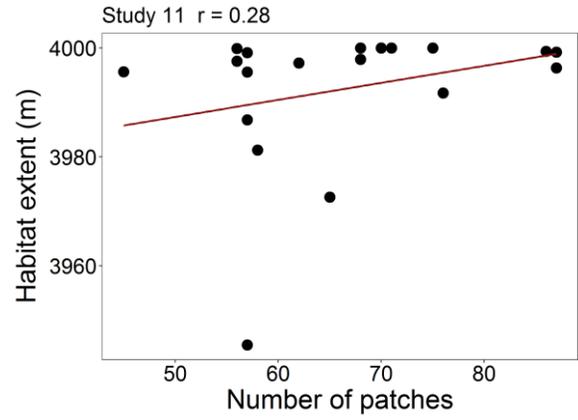
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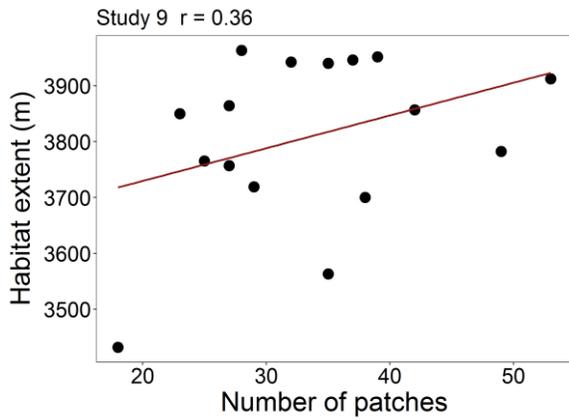
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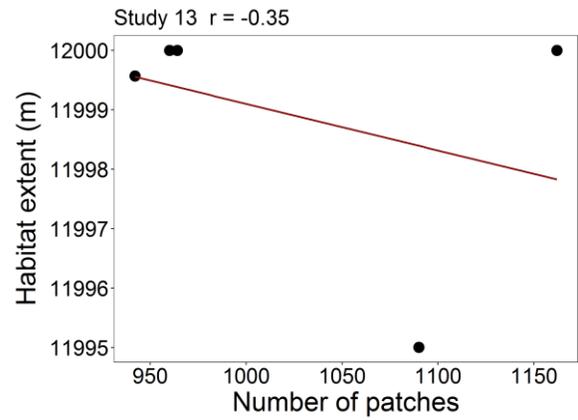
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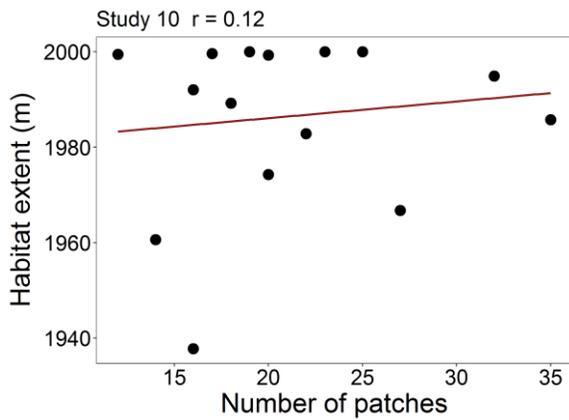
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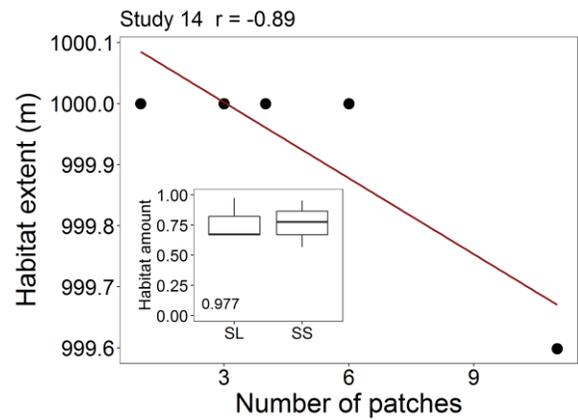
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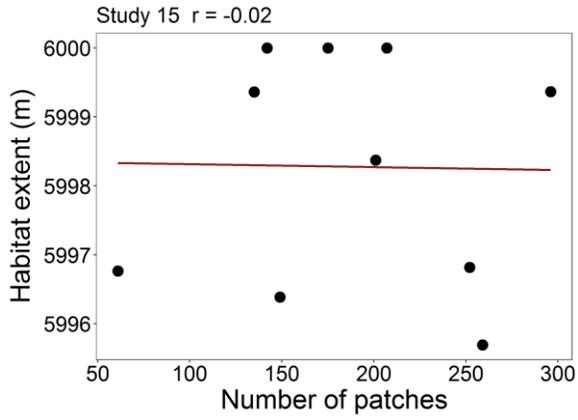
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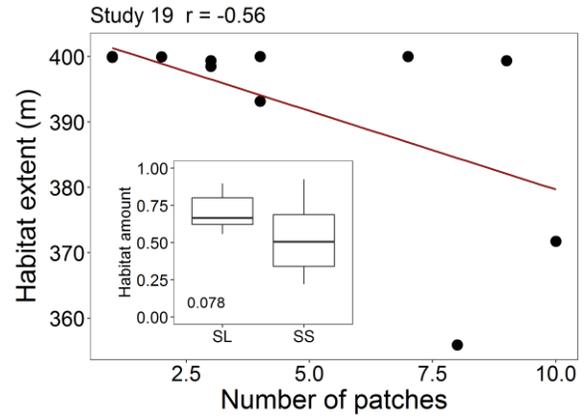
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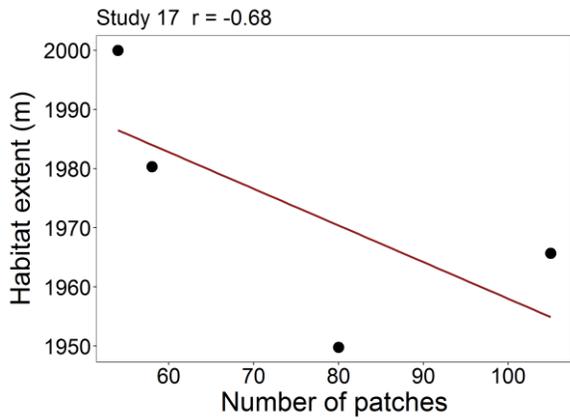
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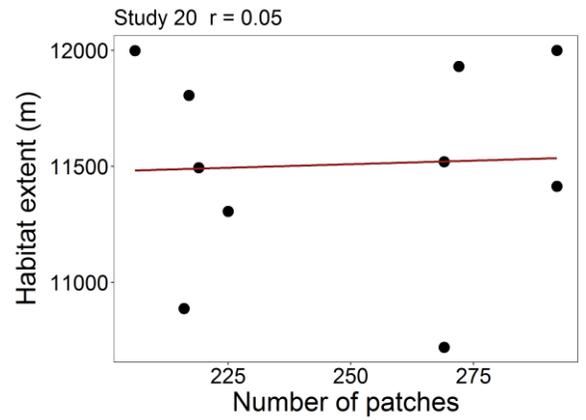
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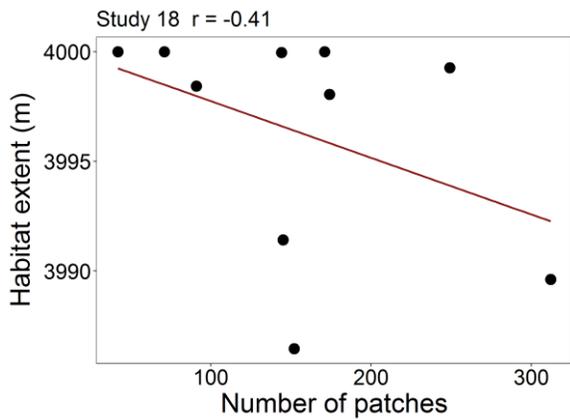
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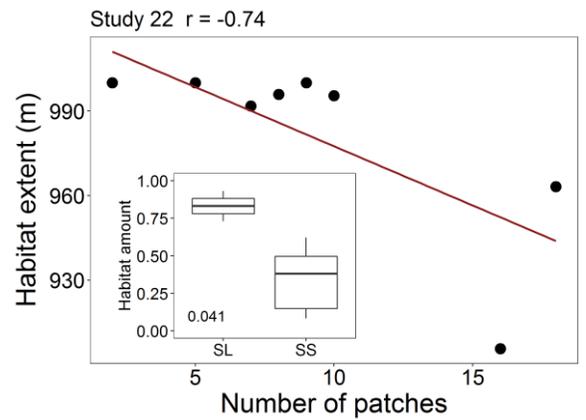
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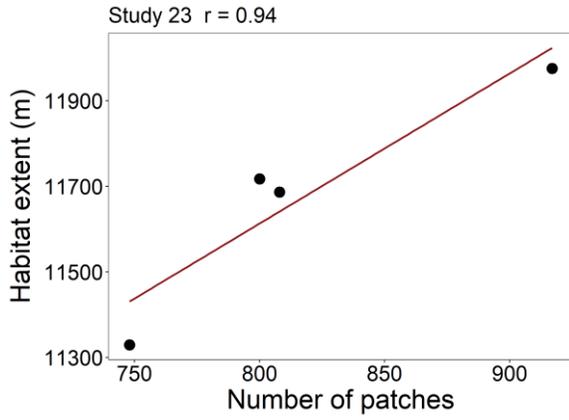
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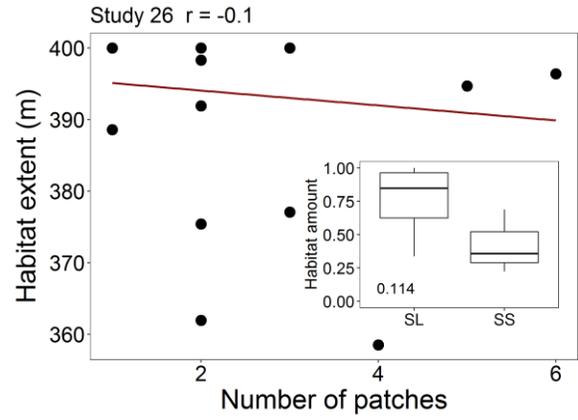
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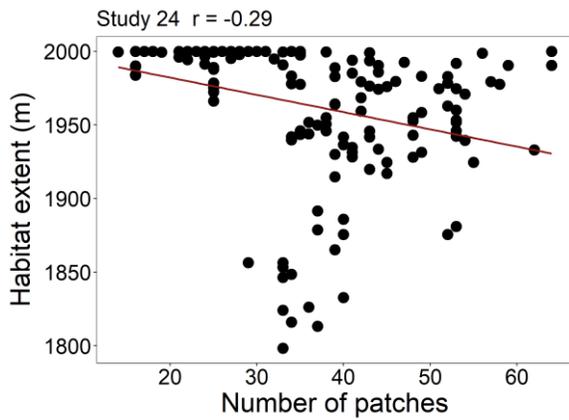
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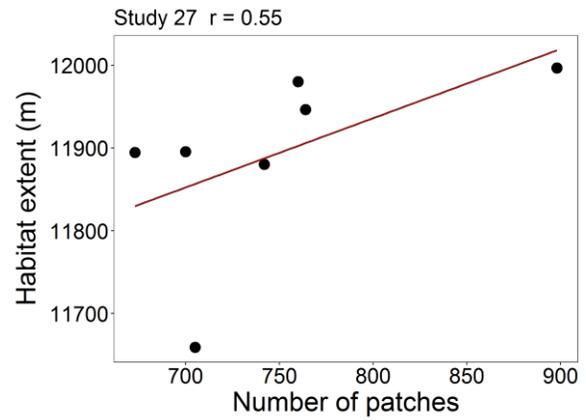
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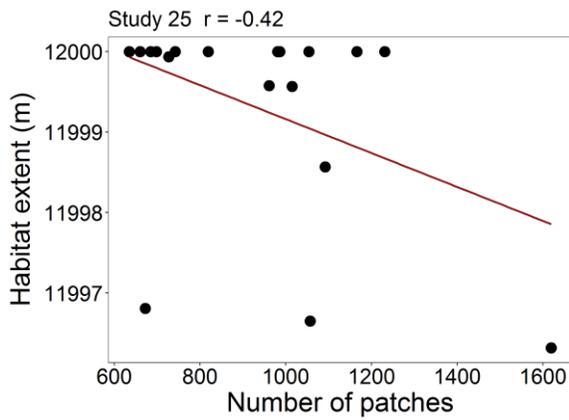
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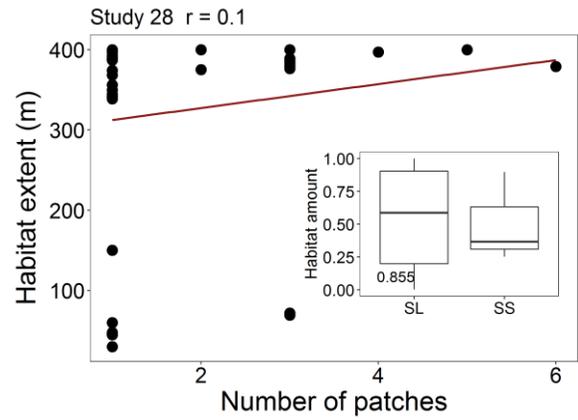
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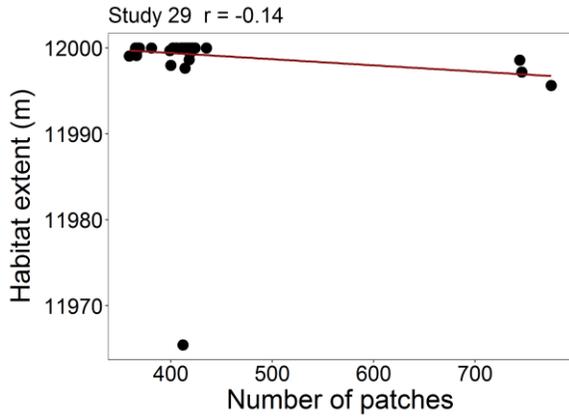
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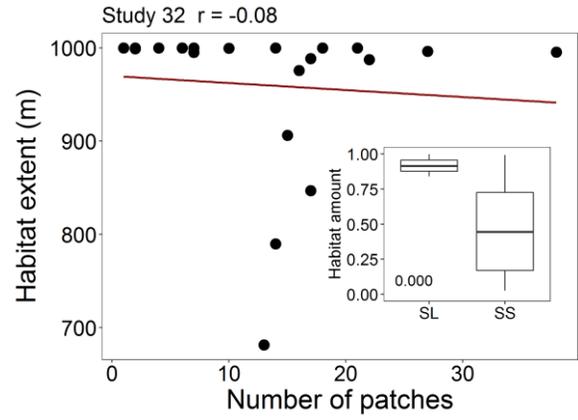
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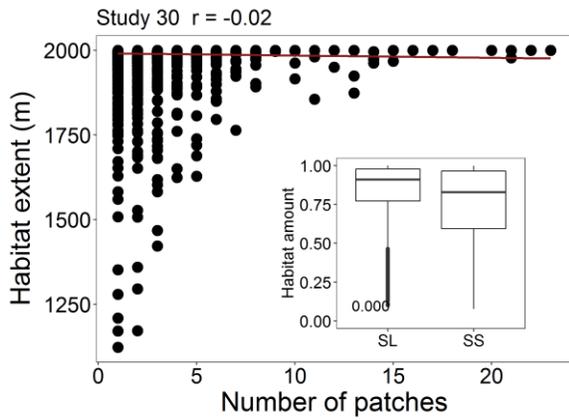
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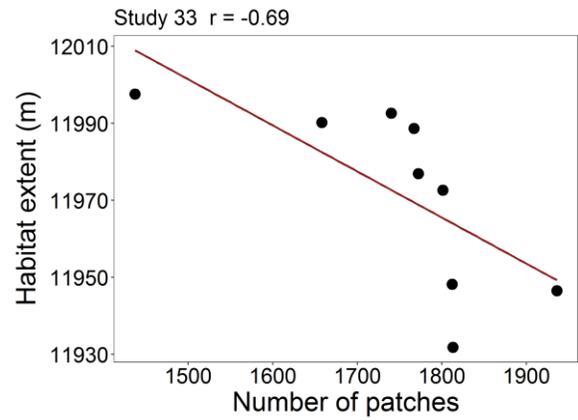
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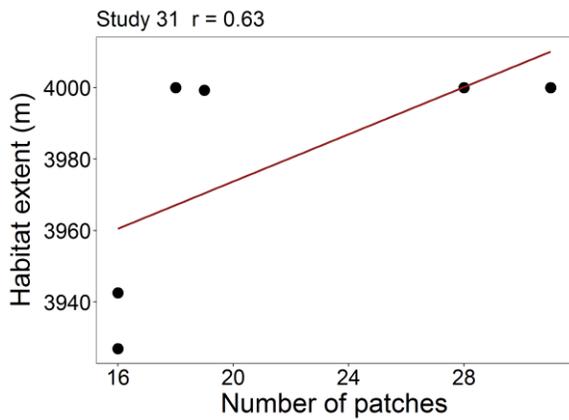
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