

# Protecting many small patches will maximize biodiversity conservation for most taxa: the $SS > SL$ principle

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## Abstract

The principle that a single large patch has higher value for biodiversity than several small patches of the same total area ( $SL > SS$ ) is widely applied in conservation. We show this principle is incorrect, and that biodiversity conservation requires placing more emphasis on protection of large numbers of small patches ( $SS > SL$ ). Analyzing 76 metacommunities (4401 species, 1190 patches) we demonstrate that, at equal habitat area, species richness accumulates more rapidly in large numbers of small patches twice as often as in few large patches (45.2% vs 19.9% of cases). This pattern is clear for plants, birds, mammals, and invertebrates, but reversed for herptiles. We therefore propose a new principle: for a given area, protecting the largest possible number of patches will maximize biodiversity for most taxa. Our findings indicate large untapped potential for biodiversity conservation worldwide, highlighting the need for a paradigm shift in conservation policy.

## Introduction

Human societies are under increasing pressure to halt unprecedented biodiversity loss (Caro *et al.* 2022; Cowie *et al.* 2022). Given the magnitude of current environmental impacts, this will require quickly protecting a considerable portion of the Earth's biomes, moving from the currently protected  $\sim 17\%$  of the planet surface to 30% before 2030 (Dinerstein *et al.* 2019; Maxwell *et al.* 2020). Yet, our understanding of natural phenomena remains at best partial across most of the planet (Hortal *et al.* 2015; Hughes *et al.* 2021). There is, therefore, an urgent need to identify general conservation principles that would allow the most effective habitat protection in the face of limited knowledge about particular ecosystems (Currie 2019; Arroyo-Rodríguez *et al.* 2020; Fahrig *et al.* 2022).

One of the most widely applied such general principles for biodiversity conservation, first proposed by Diamond (1975), is the  $SL > SS$  principle that a single large patch (or a few large patches) has higher conservation value than several small patches. Although the  $SL > SS$  principle seems intuitive, both historical (Simberloff & Abele 1976; Quinn & Harrison 1988) and recent (Deane *et al.* 2020; Fahrig 2020; Hammill & Clements 2020; Riva & Fahrig 2022) evidence support the opposite  $SS > SL$  pattern, that a set of many small patches usually harbors more species than a set of few large patches totaling the same area. In addition, many studies suggest high potential of small patches for conservation of rare species, provision of ecosystem services, and optimal reserve design (Bennett & Arcese 2013; Tulloch *et al.* 2016; Hunter *et al.* 2017; Deane & He 2018; Wintle *et al.* 2019; Valdés *et al.* 2020; Yan *et al.* 2021). Nevertheless, the idea that habitat in large patches is disproportionately important for biodiversity is strongly entrenched in conservation research and practice (Wintle *et al.* 2019; Fahrig *et al.* 2022).

Persistence of the  $SL > SS$  principle over more than four decades despite evidence to the contrary is largely due to the assumption that the  $SL > SS$  principle is valid for species of conservation concern, many of which are habitat specialists that require large expanses of continuous habitat. The  $SL > SS$  inference is also expected to hold when the matrix separating habitat patches is hostile to those species. Nevertheless, recent

tests do not support these ideas. Species richness of habitat specialists and of threatened or declining species is generally higher across several small than few large patches, and the direction of this relationship does not change when the matrix is hostile (Fahrig 2017, 2020; Riva & Fahrig 2022). Thus, it seems reasonable to ask – *should the  $SL > SS$  principle be reversed?* In other words, when a choice must be made, should the default principle be to protect many small patches, i.e.,  $SS > SL$ ? The evidence to date supports such a shift, but science is conservative, erring on the side of the status quo unless and until the evidence is overwhelming.

Here we bring the evidence to that tipping point by adding analyses of 76 metacommunities, including 4401 species and 1190 patches, from the database compiled by Chase *et al.* (2019). Implementing a novel resampling algorithm, we synthesize the largest unbiased (rarefied) metacommunity dataset generated to date for the “SLOSS” question: for the same total area, is biodiversity higher in several small patches or in one or a few large patches? Based on the results, we propose a new principle for biodiversity conservation – *for a given total area, protecting the largest possible number of patches, including very small ones, will maximize biodiversity for most taxa*. This is opposite to current strategies that typically target for protection patches orders of magnitude larger than the smaller patches in the database we analyzed. Immediate recognition of the value of small patches is therefore fundamental to global biodiversity conservation.

## Material and methods

### *Assessing biodiversity in fragmented landscapes using SLOSS comparisons*

We used SLOSS comparisons (Quinn & Harrison 1988), which juxtapose two species-area accumulation curves generated from a metacommunity of species inhabiting a set of patches (Fig. 1-d). The two curves describe the cumulative number of species as a function of cumulative area, adding patches either from smallest to largest or from largest to smallest. From the relative position of the curves, one can infer that biodiversity increases with habitat fragmentation (small-to-large curve above large-to-small curve;  $SS > SL$ ), decreases with fragmentation (large-to-small curve above small-to-large curve;  $SL > SS$ ), or is unrelated to fragmentation (curves cross;  $SS = SL$ ). This method for estimating effects of habitat fragmentation on biodiversity is conservative, because it identifies fragmentation effects only when they occur consistently across an entire dataset (Fahrig *et al.* 2019).

### *Datasets*

We analyzed data available in the FragSAD open dataset compilation (Chase *et al.* 2019). FragSAD includes 117 metacommunities defined by counts of species recorded in several habitat patches of (usually) known sizes. We excluded from FragSAD (i) datasets containing an insufficient number of patches for SLOSS comparisons, i.e., [?] 2 patches; (ii) patches for which area was missing or roughly imputed, because SLOSS comparisons are area-based; and (iii) patches that were larger than 50% of the total area sampled in a dataset, because these patches cannot be compared to an equal total area made of smaller patches. Given that the studies recorded in FragSAD were originally designed to compare metacommunities across gradients of fragment sizes (Chase *et al.* 2019), we assumed that the patches within each dataset were within a given landscape and were of meaningful sizes for the taxa sampled – a corollary being that “large” and “small” patches vary depending on the system studied.

### *Controlling sampling bias*

SLOSS comparisons are unbiased only when sampling effort is constant on a per-area basis, i.e., when sets of patches that add to the same total area also add to the same total sampling effort (Gavish *et al.* 2012; Fahrig 2020). However, most ecological datasets – including many collected in FragSAD – are sampled more intensively in small patches than in large patches, on a per area basis. For example, patches differing in size are often sampled with the same number of plots, traps, or transects. To remove this bias in favor of small patches, we implemented a novel resampling (rarefaction) procedure that generated 100 simulated metacommunities from each dataset, where the number of individuals “sampled” in each patch was proportional to patch size, and individuals were resampled randomly without replacement. The number of individuals sampled in each patch was determined by the lowest density of individuals per unit area observed

across all the patches in the given metacommunity (usually the density of individuals in the largest patch), multiplied by the area of each patch, and adjusted for effects of patch size on the density of individuals (Chase *et al.* 2020a) (Appendix). This procedure resulted in species lists across sets of patches derived from a constant sampling effort per area, and accounted for effects of patch size on the density of individuals.

### Analysis

Our analysis was developed in R 4.1.3 (R Core Team 2021). We began by filtering the data, retaining only datasets and patches compatible with our criteria, resulting in 76 metacommunities containing 1190 patches. Then, we implemented the bias control procedure (Appendix), which resulted in 100 unbiased samples for each metacommunity. From these we generated 7600 SLOSS comparisons. The 100 samples for each dataset represent uncertainty in the SLOSS outcomes in each metacommunity due to resampling. We developed an algorithm that automatically classified the SLOSS comparisons into  $SS > SL$  (positive responses of biodiversity to fragmentation),  $SS = SL$  (no evidence of a biodiversity responses to fragmentation), or  $SL > SS$  (negative responses of biodiversity to fragmentation). The algorithm classifies each SLOSS comparison based on the difference between the two species accumulation curves in the interval between the areas of (i) the largest patch on the large-to-small curve and (ii) all patches except the largest patch on the small-to-large curve (Fig. 1-d).

Next, we fitted generalized linear mixed effects models to determine whether the SLOSS outcome depended on the general taxon of the metacommunity. We assumed a binomial distribution of the response in our models, predicting the likelihood of a dataset being  $SS > SL$ . Because  $SL > SS$  was much rarer than  $SS > SL$ , modelling  $SL > SS$  would result in poor model fit. We therefore only present models predicting  $SS > SL$ , but we note that results for  $SL > SS$  are opposite to those for  $SS > SL$ , as expected (Fig. 2). We also included patch size evenness in the model because previous work suggested that the likelihood of observing  $SS > SL$  strongly increases with decreasing patch size evenness, i.e., as the difference in size between small and large patches increases (Riva & Fahrig 2022). The model included a random effect for metacommunity to account for the dependency among the 100 SLOSS comparisons generated for each metacommunity.

### Results

Our analysis included 76 datasets – 37 invertebrate, 12 mammal, 9 bird, 9 herptile, and 9 plant metacommunities – totaling 4401 species and 1190 patches (Fig. 2). Biodiversity declined with habitat fragmentation ( $SL > SS$ ) in 19.9% of the SLOSS comparisons, showed no response ( $SS = SL$ ) in 34.7% of the comparisons, and increased with fragmentation ( $SS > SL$ ) in 45.2% of the comparisons (Fig. 2). If we consider only cases where one of the three SLOSS outcomes was at least twice as likely to occur as the other two outcomes (i.e.,  $> 66\%$  of the comparisons), we found negative fragmentation effects in 9 metacommunities (11.8%), no effect in 20 metacommunities (26.3% of the sample), and positive fragmentation effects in 28 metacommunities (36.8%). Biodiversity was typically higher in sets of many small patches than in sets of a few large patches in plants (81% vs.  $< 1\%$ ), invertebrates (45.2% vs. 18.4%), birds (44.3% vs. 17.5%), and mammals (36.7% vs. 19.5%). Conversely, biodiversity of amphibians and reptiles was typically higher in sets of a few large patches (21.6% vs. 48.8%).

Taxonomic identity had a significant effect on the SLOSS outcome, explaining 19% of the variation, with variation explained increasing to 27% when including an additive effect of patch size evenness in the model (marginal  $R^2$ ). The probability of observing positive responses to fragmentation in biodiversity increased from herptiles ( $\beta_{\text{amp\&rep}} = 7.95$ ;  $SD = 3.98$ ;  $z = 1.99$ ;  $p = 0.04$ ) to mammals ( $\beta_{\text{mamm}} = 10.01$ ;  $SD = 3.79$ ;  $z = 2.64$ ;  $p < 0.01$ ), birds ( $\beta_{\text{birds}} = 10.80$ ;  $SD = 3.97$ ;  $z = 2.72$ ;  $p < 0.01$ ), invertebrates, ( $\beta_{\text{invert}} = 11.31$ ;  $SD = 3.64$ ;  $z = 3.10$ ;  $p < 0.01$ ), and plants ( $\beta_{\text{plants}} = 16.46$ ;  $SD = 4.19$ ;  $z = 3.92$ ;  $p < 0.01$ ).

### Discussion

Our results suggest that including a large number of small patches in area-based conservation actions will usually result in higher biodiversity protection than expected based solely on their cumulative area (Deane *et al.* 2020; Fahrig 2020; Riva & Fahrig 2022). Furthermore, we find this for all taxa except herptiles

(Figs. 2, 3). Positive fragmentation effects on biodiversity were apparent for plants, birds, invertebrates, and mammals, where  $SS > SL$  was at least twice as likely as  $SL > SS$  (Fig. 2). Mechanisms underlying biodiversity patterns across sets of patches are reviewed in Fahrig (2020) and Fahrig *et al.* (2022), particularly in relation to extinction-colonization dynamics and species turnover across patches. We first speculate on how these mechanisms might have determined the taxonomic differences observed in our study (Fig. 2, 3), and then discuss the implications of our results for biodiversity conservation.

### *Responses to habitat fragmentation across taxa*

Except for herptiles, all taxa assessed in our analysis typically accumulate more species across a large number of small patches than a few large patches of the same total area. Conserving small patches will be especially important for conservation of the Earth's flora, given that the  $SL > SS$  was extremely rare when assessing plants (Fig. 2). One reason for this pattern might be that plants were the most diverse taxon in our analysis, with typically more than 100 species in their metacommunities. Communities with more species usually have higher turnover due to niche partitioning (Finke & Snyder 2008; Chesson 2018), and high turnover is an important process determining  $SS > SL$  (Deane *et al.* 2020; Fahrig *et al.* 2022). In addition, plants might be especially likely to display  $SS > SL$  due their tendency to aggregate in space. More specifically, several small patches are more likely to intersect with more species distributions than few large patches when those distributions are clumped in space (May *et al.* 2019; Fahrig *et al.* 2022).

We also found that mammals, birds, and invertebrates were more speciose in sets of many small patches than few large ones (Figs. 2,3). This might seem inconsistent with evidence that, for these taxa, occurrence probability is typically higher in large than small patches (e.g., Schultz & Crone 2005; Keinath *et al.* 2017). Indeed, based on this pattern Timmers *et al.* (2022) recently concluded that “[c]onservation of threatened bird species in fragmented landscapes should preferably focus on strict protection of large forest”. However, this type of inference is based on comparing single small to single large patches. Using Timmers *et al.* (2022) estimates it is in fact more likely to encounter a threatened bird species somewhere in a set of a thousand 1-ha forest patches than in one 1000-ha patch. This example highlights how recommendations on reserve design at the landscape scale must be based on landscape-scale analyses (Fahrig *et al.* 2019).

In contrast with all other taxa, for herptiles  $SL > SS$  was over twice as likely as  $SS > SL$  (Fig. 2, 3). We speculate that these species are particularly vulnerable to dispersal mortality in the matrix. Many amphibians and reptiles require disjunct habitats at different times of the year and so must move between them, and in a landscape with many small patches, such movements are likely to take them through the matrix. Being non-volant and slow-moving, they may be more at risk from various mortality factors in the matrix than other taxa. For example, Rytwinski & Fahrig (2012) found that amphibians and reptiles are the taxa most impacted by roads and traffic, likely through road kill. The high dispersal mortality would lead to smaller populations of these species across many small patches than few large ones, increasing the likelihood of extinction. We note, however, that even for herptiles there are more species in several small than few large patches in nearly half of the datasets (4 of 9).

In addition to taxonomic effects, we found negative effects of patch size evenness on the likelihood of finding positive fragmentation effects on biodiversity (Riva & Fahrig 2022) (Fig. 3). In other words, as the sizes of small and large patches in a dataset become more different, and thus more small patches are needed to equal the area of a large patch, it becomes more likely that sets of small patches will consistently harbor more species than a set of a few large patches. This result is important because it contradicts a major theoretical argument used to prioritize large patches in conservation, i.e., that patch-level extinction risk determines biodiversity in sets of patches (Diamond 1975; Riva & Fahrig 2022). Landscape-scale processes, e.g., turnover or metacommunity dynamics (Chase *et al.* 2020b; Deane *et al.* 2020; Fahrig *et al.* 2022), appear to be more important than patch-scale extinction risk in determining biodiversity in fragmented landscapes.

### *Implications for biodiversity conservation in fragmented landscapes*

Our results are consistent with the landscape planning strategy proposed by Arroyo-Rodríguez *et al.* (2020) for forest biodiversity protection in human-dominated naturally forested regions. They suggested that 40%

of the landscape should be dedicated to forest, and that three quarters of that forest should be in small patches while the remaining quarter should be in a single large patch (or a few large patches). Retaining a large patch would support the persistence of herptile populations, while small patches would maximize the diversity and persistence of other taxa.

Most notably, patch-size thresholds used to prioritize habitat for biodiversity protection are orders of magnitude larger than the sizes of the small patches that we found to have disproportionately high biodiversity value on a per-area basis (Fig. 4, vertical lines; reviewed in Fahrig *et al.* (2022)). These thresholds may be imposed for practical reasons (Armsworth *et al.* 2018), but they are not supported by biological evidence. In addition, while some species requiring large amounts of habitat likely have already disappeared from human-dominated regions, there is no evidence that these species are generally negatively affected by fragmentation per se (independent of habitat loss, Fahrig (2017); Fig. 1, left panel). If anything, the opposite is confirmed in previous analyses suggesting that many small patches harbor both more specialist species and more species of conservation concern than few large patches (Fahrig 2020; Riva & Fahrig 2022). Therefore, protecting a very large number of small patches that sum to a high total habitat density across a landscape appears to be an effective solution for sustaining populations of most species. This seems to be the case for carnivores across Europe, a group expected to rely strongly on large patches, but in fact showing widespread population recoveries across patchy anthropogenic landscapes (Chapron *et al.* 2014).

We caution that our results apply in regions with patches similar in size to those analyzed here, which were generally centered around 10-ha (Fig. 4). It is possible that analyses using much smaller patches would not show the predominant  $SS > SL$  pattern. However, as the small patches in the datasets were generally much smaller than those normally considered for protection, our conclusion that the default priority for habitat protection should shift to several small patches seems robust. Additionally, we lack detailed information about the spatial extents of the studies, which could conceivably affect the SLOSS outcomes. A recent meta-analysis suggests that the extent of most studies in ecology is  $< 100,000$  ha (Estes *et al.* 2018). The datasets we used here from Chase *et al.* (2019) appear to be consistent with this pattern based on inspection of maps in the papers describing each dataset. Further work is needed to determine whether the generality of our results is affected by the spatial extent of the study area or by the spatial arrangement of small and large patches.

## Conclusions

This study adds strong evidence to a body of literature (Bennett & Arcese 2013; Tulloch *et al.* 2016; Hunter *et al.* 2017; Deane & He 2018; Wintle *et al.* 2019; Deane *et al.* 2020; Fahrig 2020; Valdés *et al.* 2020; Yan *et al.* 2021; Riva & Fahrig 2022) suggesting it is time to reconsider the widespread principle that large patches should always be prioritized in conservation. We suggest instead a new principle: *For a given total area, protecting the largest possible number of patches, including very small ones, will maximize biodiversity for most taxa.* This conclusion is grounded in a synthetic analysis of a large biodiversity dataset that includes information on both the taxonomic identities and relative size of small and large patches, two factors that have been so far poorly understood in the context of SLOSS meta-analyses (Deane *et al.* 2020; Fahrig 2020; Riva & Fahrig 2022).

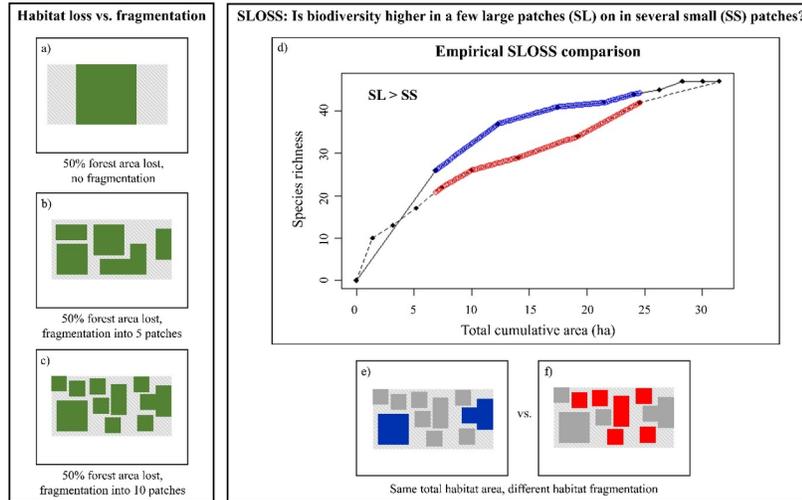
We stress that consideration of patch sizes cannot compensate for loss of habitat. When the goal is to protect biodiversity, the priority should be to maximize the total area of habitat protected regardless of patch sizes. This also implies that continuous habitat should not be fragmented for biodiversity conservation, because this would entail habitat loss, the most important contributor to biodiversity declines (Caro *et al.* 2022). Furthermore, large habitat patches are now very rare in human-dominated regions (Taubert *et al.* 2018) and can fulfill specific roles (Arroyo-Rodríguez *et al.* 2020; Fahrig *et al.* 2022). For instance, here we find that they are important for conservation of amphibians and reptiles.

That being said, the cumulative value of small patches for biodiversity has long been underappreciated. Recognizing this value will allow conservation agencies to capitalize on all opportunities for habitat protection, independent of patch sizes, facilitating habitat protection in regions where the only remaining patches left

are small (Shafer 1995; Fahrig 2020; Riva & Fahrig 2022), and empowering individuals and communities to protect the nature that they experience in their daily lives (Fahrig 2019; Riva & Fahrig 2022). In a best-case scenario, acknowledging the benefits of small patches could trigger a new epoch of bottom-up conservation actions, driven by the efforts of communities and large numbers of local conservation initiatives.

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## Figures



*Fig. 1: Left panel – the same loss of habitat can result in different degrees of habitat fragmentation, as shown in three hypothetical landscapes (a-c) totaling the same habitat area. Green areas symbolize patches of habitat, whereas areas shaded in grey symbolize habitat lost from an original, continuous habitat patch. Right panel – the empirical comparison (d) (Quinn & Harrison 1988)*

*traditionally used to answer the SLOSS question, i.e., “for the same total habitat area, is biodiversity higher in one or a few large patches, or in several small patches?” The method consists in comparing two curves of cumulative species richness vs. cumulative area, ordering patches in either increasing (dotted line) or decreasing (continuous line) sizes. Cumulative areas on the x axis correspond to sets of multiple patches, e.g., the two blue patches in (e) vs. the six red patches in (f). When one of the two curves in (d) is consistently above the other, one can infer that in the system under consideration biodiversity responds negatively (continuous line above) or positively (dotted line above) to habitat fragmentation (negative fragmentation effect shown in the example).*

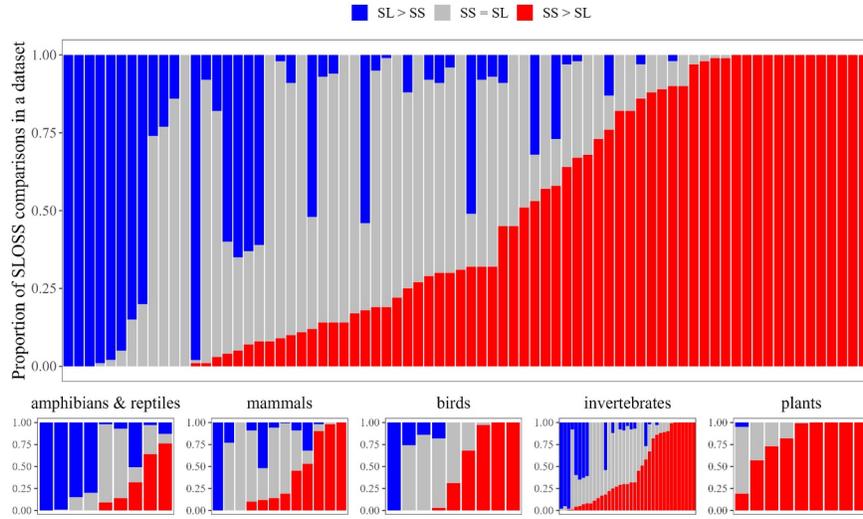


Fig. 2: Results of empirical SLOSS comparisons (colors) performed in each of 100 resampled communities generated for the 76 metacommunities assessed in this study (bars). Colors represent the three possible outcomes of SLOSS, i.e., species richness higher in sets of large patches ( $SL > SS$  in blue; 19.9% of comparisons), species richness higher in sets of small patches ( $SS > SL$  in red; 45.2% of comparisons), or no clear difference in species richness between sets of small patches and sets of large patches ( $SS = SL$  in grey; 34.7% of comparisons).

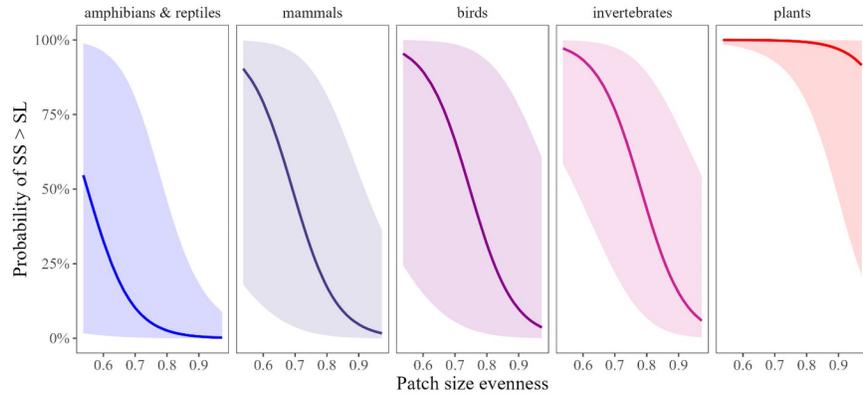


Fig. 3: Probability of observing positive responses of biodiversity to habitat fragmentation ( $SS > SL$ , i.e., higher biodiversity in sets of many small patches than in a few large patches totaling the same area) as a function of taxon and patch size evenness.

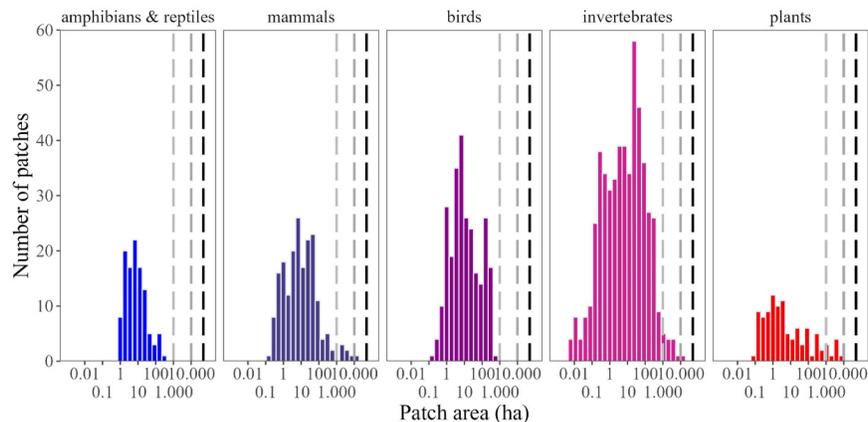


Fig.4: Distributions of patch sizes for the different taxonomic groups analyzed in this study. Herptiles: 111 patches; mammals: 192 patches; birds: 262 patches; invertebrates: 524 patches; plants: 101 patches. Vertical dotted lines represent examples of three widely adopted thresholds for the smallest patch size considered to have conservation value (i.e., 1000 ha, 10,000 ha and 50,000 ha; reviewed in Fahrig et al. 2022).

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