

CONTRIBUTED PAPERS

Obstruction of biodiversity conservation by minimum patch size criteria

Federico Riva¹  | Lenore Fahrig²

¹Spatial Ecology Group, Department of Ecology and Evolution, Université de Lausanne, Lausanne, Switzerland

²Geomatics and Landscape Ecology Laboratory, Department of Biology, Carleton University, Ottawa, Ontario, Canada

Correspondence

Lenore Fahrig, Geomatics and Landscape Ecology Laboratory, Department of Biology, Carleton University, Ottawa, Ontario, Canada.
Email: lenorefahrig@cunet.carleton.ca

Article impact statement: Minimum patch size criteria are inconsistent with actions designed to bolster landscape-scale biodiversity conservation.

Funding information

Mitacs, Grant/Award Number: Accelerate fellowship; European Commission Horizon 2020 Marie Skłodowska-Curie Actions, Grant/Award Number: grant101024579toFR.

Abstract

Minimum patch size criteria for habitat protection reflect the conservation principle that a single large (SL) patch of habitat has higher biodiversity than several small (SS) patches of the same total area (SL > SS). Nonetheless, this principle is often incorrect, and biodiversity conservation requires placing more emphasis on protection of large numbers of small patches (SS > SL). We used a global database reporting the abundances of species across hundreds of patches to assess the SL > SS principle in systems where small patches are much smaller than the typical minimum patch size criteria applied for biodiversity conservation (i.e., ~85% of patches <100 ha). The 76 metacommunities we examined included 4401 species in 1190 patches. From each metacommunity, we resampled species–area accumulation curves to evaluate how biodiversity responded to habitat existing as a few large patches or as many small patches. Counter to the SL > SS principle and consistent with previous syntheses, species richness accumulated more rapidly when adding several small patches (45.2% SS > SL vs. 19.9% SL > SS) to reach the same cumulative area, even for the very small patches in our data set. Responses of taxa to habitat fragmentation differed, which suggests that when a given total area of habitat is to be protected, overall biodiversity conservation will be most effective if that habitat is composed of as many small patches as possible, plus a few large ones. Because minimum patch size criteria often require larger patches than the small patches we examined, our results suggest that such criteria hinder efforts to protect biodiversity.

KEYWORDS

2050 Vision for Biodiversity, habitat fragmentation, landscape planning, minimum patch area, Post-2020 Biodiversity targets, reserve design

Obstrucción de la conservación de la biodiversidad por el criterio del tamaño mínimo del fragmento

Resumen: Los criterios de tamaño mínimo de los fragmentos para la protección de los hábitats reflejan el principio de conservación según el cual un fragmento único grande (UG) de hábitat tiene mayor biodiversidad que varios fragmentos pequeños (VP) de la misma superficie total (UG > VP). Sin embargo, este principio a menudo es incorrecto; en su lugar, la conservación de la biodiversidad debería enfatizar más la protección de un gran número de pequeñas parcelas (VP > UG). Utilizamos una base de datos mundial que recopila la abundancia de especies en cientos de fragmentos para evaluar el principio UG > VP en sistemas donde los fragmentos pequeños son mucho menores que los criterios comunes de tamaño mínimo de fragmento aplicados para la conservación de la biodiversidad (es decir, ~85% de parches <100 ha). Las 76 metacomunidades analizadas

This is an open access article under the terms of the [Creative Commons Attribution](https://creativecommons.org/licenses/by/4.0/) License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited and is not used for commercial purposes.

© 2023 The Authors. Conservation Biology published by Wiley Periodicals LLC on behalf of Society for Conservation Biology.

incluyeron 4,401 especies en 1,190 parcelas. Volvimos a muestrear las curvas de acumulación especie-área en cada metacomunidad para evaluar cómo respondía la biodiversidad al hábitat: como unas pocas manchas grandes o como fragmentos de muchas manchas pequeñas. Contrario al principio $UG > VP$ y en congruencia con síntesis anteriores, la riqueza de especies se acumuló con mayor rapidez al añadir varios fragmentos pequeños (45.2% $VP > UG$ frente a 19.9% $UG > VP$) para alcanzar la misma área acumulada, incluso para los fragmentos muy pequeños de nuestro conjunto de datos. Las respuestas de los taxones a la fragmentación del hábitat fueron diferentes, lo que sugiere que, cuando se trata de proteger una determinada superficie total de hábitat, la conservación global de la biodiversidad será más efectiva si ese hábitat está compuesto por el mayor número posible de pequeños fragmentos, más unos cuantos fragmentos grandes. Dado que los criterios de tamaño mínimo exigen a menudo fragmentos más grandes que los pequeños que examinamos, nuestros resultados sugieren que tales criterios dificultan los esfuerzos por proteger la biodiversidad.

PALABRAS CLAVE

área mínima de fragmento, diseño de reservas, fragmentación del hábitat, objetivos del Marco Mundial de Biodiversidad Post 2020, planeación del paisaje, Visión 2050 para la Biodiversidad

【摘要】

生境保护的最小斑块面积标准反映了一项保护原则,即单个大生境斑块(SL)比总面积相同的多个小斑块(SS)具有更高的生物多样性($SL > SS$)。然而,这一原则往往并不正确;相反,生物多样性保护更需要强调对大量小斑块的保护($SS > SL$)。我们使用了一个报告了数百个斑块物种丰度的全球数据库,以评估面积远小于生物多样性保护的典型最小斑块面积标准(约85%的斑块小于100公顷)的小斑块系统是否符合 $SL > SS$ 原则。本研究共分析了包含1190个斑块、4401个物种的76个集合群落。在每个集合群落中,我们对物种-面积累积曲线进行重取样,以评估生物多样性对大斑块生境或多个小斑块破碎化生境的响应。与 $SL > SS$ 原则相反,且与以前的综合性研究相一致,我们发现在增加多个小斑块以达到相同的累积面积时,物种丰度累积上升更快(45.2% $SS > SL$ 比19.9% $SL > SS$),即使对于我们数据集中非常小的斑块也是如此。不同类群对生境破碎化的响应也存在差别,表明当需要保护给定面积的生境时,如果该生境由几个大斑块和尽可能多的小斑块组成,则整体的生物多样性保护将最为有效。由于目前的最小斑块面积标准通常要求保护比本研究分析的小斑块面积更大的斑块,因此我们的结果表明,这种标准阻碍了生物多样性保护的 efforts。【翻译:胡怡思;审校:聂永刚】

关键词: :2020年后生物多样性目标,2050年生物多样性愿景,生境破碎化,保护区设计,景观规划,最小斑块面积

INTRODUCTION

Human societies are under increasing pressure to halt ongoing biodiversity loss (Caro et al., 2022; Kremen & Merenlender 2018). Given the magnitude of current environmental impacts, this will require quickly protecting a considerable portion of Earth's biomes (Dinerstein et al., 2019). Yet, understanding of natural phenomena remains at best partial across most of the planet (Hortal et al., 2015; Hughes, Orr, Ma et al. 2021). There is, therefore, an urgent need to evaluate general conservation principles for habitat protection in the face of limited knowledge about most ecosystems (Arroyo-Rodríguez et al., 2020; Fahrig et al., 2022).

One of the most widely applied general principles for biodiversity conservation is the $SL > SS$ principle that a single large (SL) patch—or a few large patches—has higher biodiver-

sity than several small (SS) patches of the same cumulative area. The $SL > SS$ principle, initially proposed by Wilson and Willis (1975) and Diamond (1975), was inspired by island biogeography theory and seems intuitive. However, historical (Quinn & Harrison 1988; Simberloff & Abele 1976) and more recent (Deane et al., 2020; Fahrig, 2020; Hammill & Clements 2020; Riva & Fahrig 2022) evidence shows the opposite $SS > SL$ pattern: for the same cumulative area, a set of many small patches usually harbors more species than a set of a few large patches (Figure 1). In addition to the prevalence of the $SS > SL$ pattern, many studies demonstrate high potential of small patches for conservation of rare species, provision of ecosystem services, landscape connectivity, and optimal reserve design (Bennett & Arcese 2013; Deane & He 2018; Han et al., 2022; Hunter et al., 2017; Riva & Fahrig 2023; Shafer, 1995; Tulloch et al., 2016; Valdés et al. 2020; Wintle et al., 2019; Yan et al., 2021).

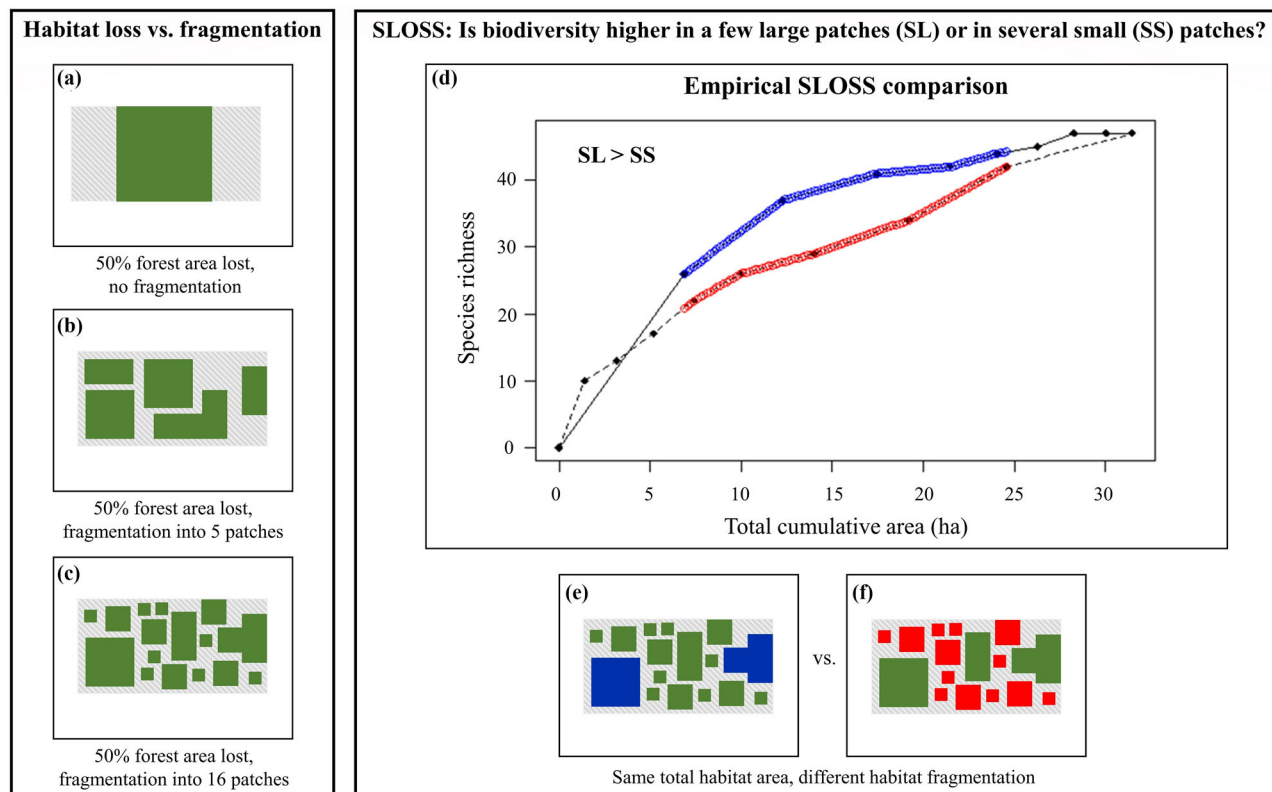


FIGURE 1 (a, b, c) Degrees of habitat fragmentation in 3 hypothetical landscapes in which the same amount of habitat is lost (green, patches of habitat; gray, habitat lost from an original, continuous area of habitat). (d) Empirical comparison proposed by Quinn and Harrison (1988) that is traditionally used to answer the SLOSS question (i.e., For the same total habitat area, is biodiversity higher in 1 or a few large patches or in several small patches?). The method consists of a comparison of 2 curves of cumulative species richness—one with patches ordered in increasing size (dotted line) and the other with patches ordered in decreasing size (continuous line)—with cumulative area. Set of (e) 2 and (f) 13 habitat patches comprising the same cumulative area that pertain to blue and red shading in panel (d).

Despite this body of evidence, the idea that habitat in large patches must be disproportionately important for biodiversity remains strongly entrenched in conservation (Fahrig et al., 2022; Wintle et al., 2019). Many environmental policies worldwide emphasize protection of large patches—a standard that stems from the SL > SS principle—with minimum patch sizes in habitat protection policies typically ranging from hundreds to thousands of hectares. For instance, in Mexico, forests must be > 100 ha to be eligible for the payment for ecosystem services program (CONAFOR, 2021). In the United States, protection of upland forests > 3000 ha is recommended for biodiversity conservation (Wallace & Tarr 2012). In Europe, a “core area” > 10,000 ha is considered necessary for rewilding (Europarc Federation 2013). Finally, globally, contiguous areas > 50,000 ha are recommended by the High Conservation Value Resource Network (Brown et al., 2013). These minima are typically much larger than many patches of native habitat, especially in anthropogenic landscapes (Taubert et al., 2018). It is likely that minimum patch size criteria are at least partly blame for documented higher rates of habitat loss from small patches than from large patches around the world (Birch et al., 2022; Riva et al., 2022).

Empirical evidence suggesting that SS > SL could be a ubiquitous pattern elicits the question of whether this pattern can safely inform habitat protection decisions in understudied systems (Fahrig et al., 2022). However, skepticism persists around using the SS > SL pattern in conservation (Deane, 2022; Fletcher et al., 2018; Haddad et al., 2015). One reason underlying this might be that some studies suggest sensitivity to habitat fragmentation in some taxa. For instance, Krauss et al. (2010) suggest that fragmentation negatively affects vascular plants but not butterflies, whereas Keinath et al. (2017) suggest that amphibians are the most sensitive vertebrate taxon to habitat fragmentation. Nevertheless, the vast body of literature purporting to address fragmentation effects relies mainly on extrapolation of patch size effects measured using individual patches, assuming that such patch-scale effects must translate to analogous landscape-scale patterns (Hadley & Betts 2016; Riva & Fahrig, 2023). This approach has been long identified as causing confusion in the conservation literature because it confounds effects of habitat area (loss) with effects of habitat configuration (fragmentation) (Fahrig, 2003; Hadley & Betts 2016) (Figure 1; Wang et al., 2014). In turn, this confusion might have contributed to a premature shelving of the SLOSS

(Is biodiversity better protected in single large or several small patches?) research avenue, even though the SLOSS question accounts for cumulative habitat area when comparing large and small patches (Fahrig, 2017).

For the reasons described above, we, along with coauthors, recently called for a reevaluation and development of SLOSS research, particularly to better understand the conditions in which one can reasonably expect to find negative responses of biodiversity to habitat fragmentation (i.e., $SL > SS$) (Fahrig et al., 2022). We evaluated the SLOSS question with data from a relatively new database (Chase et al., 2019). Our analysis included 76 metacommunities, including 4401 species from a wide range of taxonomic groups and 1190 habitat patches. Because the smaller patches in these data sets are comparatively small relative to minimum patch size criteria, we used these data to test the utility of such criteria. We asked whether there are more species in several small than few large patches even when the small patches are much smaller than typical minimum patch size criteria. In our analysis, individuals in patches were sampled proportionally to their area, thus avoiding sampling bias that favors groups of many small patches over a few large ones in some analyses (Fahrig, 2020; Gavish et al., 2012). We repeated the analyses using random resamples, which allowed us to estimate uncertainty in the answer to the SLOSS question, for the first time. We also accounted for the relative sizes of small and large patches in each data set, a property recently demonstrated to influence the answer to the SLOSS question (Riva & Fahrig 2022).

METHODS

SLOSS comparisons

We assessed biodiversity responses to habitat fragmentation with SLOSS comparisons (Quinn & Harrison 1988), which juxtapose 2 species–area accumulation curves generated from a metacommunity of species inhabiting a set of patches (Figure 1d). In SLOSS comparisons, the 2 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, for a given total habitat area, biodiversity is higher across more fragmented than less fragmented habitat (small-to-large curve above large-to-small curve, $SS > SL$); is higher across less fragmented than more fragmented habitat (large-to-small curve above small-to-large curve, $SL > SS$); or is not clearly related to fragmentation (curves cross, $SS = SL$). We define *degree of fragmentation* as the number of patches into which a given total area of habitat is divided (Figure 1). We chose SLOSS comparisons because they are one of the most conservative approaches to assess responses of biodiversity to habitat fragmentation. To report a positive (or negative) response of species richness to fragmentation, the accumulation curve representing SS (or SL) has to be higher across the entire species richness accumulation plot (Figure 1d). When this occurs, there is strong support for $SS > SL$ (or $SL > SS$).

Data set characteristics and preparation

In the analyses, we used the FragSAD open data set (Chase et al., 2019). FragSAD includes 117 metacommunities defined by abundance estimates of species recorded in several habitat patches of (usually) known sizes. FragSAD includes data from different studies that assessed many different taxa, classified across 5 major taxonomic groups (plants, invertebrates, birds, mammals, and amphibians and reptiles [hereafter herptiles]). The data sets come from across the world and a diversity of environments (Figure 3; Appendix S1). We excluded FragSAD data sets containing too few patches for SLOSS comparisons. We also excluded patches for which area was missing, because SLOSS comparisons are strictly area based, and we excluded patches that were larger than 50% of the total area sampled in a data set, because these patches cannot be compared with an equal total area made up of smaller patches.

Although the FragSAD studies are heterogeneous in design (e.g., sampling effort and method), the database includes information on the species abundance distribution sampled in each patch from each data set, thereby allowing one to control sampling effort effects while synthesizing disparate data sets. This is important because sampling effort can cause bias in SLOSS analyses, specifically by inflating biodiversity in sets of many small patches when sampling intensity across patches is not proportional to patch area (Deane, 2022; Fahrig, 2020; Gavish et al., 2012).

In other words, 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) (Fahrig, 2020; Gavish et al., 2012). When comparing an equal total habitat area made of many small or a few large patches, one must also compare the same total sampling effort. We controlled for the number of individuals sampled in each patch as a way to ensure the same sampling effort across sets of patches totaling the same area. We also considered that in different data sets, the number of individuals sampled per unit effort might itself be related to patch area (Chase et al., 2020); therefore, we corrected the number of individuals sampled to account for such relationships, which were typically very weak (see also Riva & Fahrig 2023).

Removing sampling bias

Most ecological data sets—including many collected in FragSAD—are sampled more intensively in small patches than in large patches on a per-area basis. For instance, when all patches have the same sampling effort (e.g., the same number of transects), SLOSS comparisons are biased in favor of SS . To remove this bias and to estimate the uncertainty in the answer to SLOSS, we implemented a novel resampling procedure that generated 100 metacommunities from each data set, 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 patches in the given metacommunity. This was then multiplied by the area of each patch and adjusted for effects of patch size on the density of individuals, that is, for any relationship between patch size and the number of individuals sampled for an equal sampling effort in small and large patches (Chase et al., 2020) (Appendix S3). The procedure generates species lists across sets of patches derived from a constant sampling effort per area and accounts for any effect of patch size on the density of individuals. Importantly, the original lists are not estimated populations, but rather numbers of individuals of different species sampled per unit effort. Our sampling bias correction is based on a null expectation that the number of individuals of a given species in a patch is proportional to patch area. If a large patch A is 10 times the size of a small patch B, the population size of a given species will be approximately 10 times larger on patch A than on patch B.

The workflow was developed in R 4.1.3 (R Core Team, 2022). First, we filtered the data and retained 76 metacommunities inhabiting 1190 patches. Then, we implemented the bias control procedure by generating 100 unbiased samples for each metacommunity. From these, we performed 7600 SLOSS comparisons (Appendices S3 & S4). The 100 samples for each data set represented uncertainty in the SLOSS outcomes due to resampling of the original individuals observed in each patch. Next, we developed a script that automatically classified the SLOSS comparisons into $SS > SL$, $SS = SL$, or $SL > SS$ (positive, uncertain, and negative relationship between biodiversity and fragmentation, respectively) (Figure 1d). This procedure indirectly accounts for the sizes of the populations found in sets of small and large patches because it is based on the species–abundance distribution of the metacommunities analyzed.

Modeling outcome of SLOSS comparisons across metacommunities

With the outcomes for the 7600 SLOSS comparisons as the response variable, we then fitted generalized linear mixed-effects models, including taxon and patch size evenness as fixed effects and a data set (metacommunity) identifier as a random effect. Patch size evenness of each data set was measured as Pielou's evenness ($J' = H'/H'_{\max}$, where H' is the Shannon entropy calculated as $-\sum(p_i) \log(p_i)$, where p_i is the proportion of the total area sampled in a data set accounted for by each patch i [Pielou, 1966]). We included patch size evenness in the model because previous work suggests that the answer to the SLOSS question strongly depends on the differences in size between the small and large patches of a given metacommunity (Riva & Fahrig 2022). The random effect for data set accounted for the dependency among the 100 SLOSS comparisons for each metacommunity. More details on model fitting and diagnostics are in Appendix S6. Data analyzed are openly available at <https://datadryad.org/stash/datasethttps://doi.org/10.5061/dryad.595718c>, and the

R script is in Appendix S8 and at https://github.com/FedericoRiva/SLOSS_3.

RESULTS

Our synthesis included 4401 species and 1190 patches from 76 data sets—37 invertebrate, 12 mammal, 9 bird, 9 herptile, and 9 plant metacommunities (Figures 2–4). These metacommunities inhabited comparatively small patches; 85.4% of the patches were <100 ha (1 km^2) and 97.8% were <1000 ha (10 km^2) (Figure 2). The range in patch sizes was similar across taxa: mean (SD) of \log_{10} area ranged across taxa from 0.8 (0.6) to 1 (1.3) (Figure 2; Appendix S2).

In 19.9% of the SLOSS comparisons, biodiversity accumulated more rapidly in less fragmented than more fragmented habitat ($SL > SS$); there was no clear difference ($SS = SL$) in 34.7% of the comparisons; and biodiversity accumulated more rapidly in more fragmented than less fragmented habitat ($SS > SL$) in 45.2% of the comparisons (Figure 4; Appendices S4 & S5). Species richness was typically higher in sets of many small than few large patches for plants (81% vs. $<1\%$), invertebrates (45.2% vs. 18.4%), birds (44.3% vs. 17.5%), and mammals (36.7% vs. 19.5%). Conversely, species richness of herptiles was typically higher in sets of a few large patches (21.6% vs. 48.8%).

Models confirmed the influence of taxonomic identity and patch size evenness on the answer to the SLOSS question (Figure 5; Appendices S6 & S7). For plants, invertebrates, birds, and mammals, the effects of taxon on the probability of $SS > SL$ were positive, and the effects of taxon on the probability of $SL > SS$ were negative, whereas the reverse was true for herptiles (Appendix S7). Responses of biodiversity to fragmentation were amplified at low patch size evenness (i.e., when small patches were much smaller than large patches within a data set). Thus, when more small patches were required to total the same area of a large patch, the difference between biodiversity in SS and SL was larger (Appendix S7). No clear fragmentation effect ($SS = SL$) was the most common outcome at high patch size evenness (e.g., evenness > 0.9) for every taxon except for plants, where $SS > SL$ remained the most common outcome even at high patch size evenness. The $SS = SL$ outcome became increasingly rare, generally in favor of $SS > SL$ at low patch size evenness (e.g., evenness < 0.8), except in herptile data sets (Figure 5). The 89% credible intervals of parameter estimates did not overlap zero or overlapped zero only at the tail of the posterior parameter distribution (Appendix S7), confirming that the observed effects were substantial despite the broad array of metacommunities included in the analysis (Appendix S1).

DISCUSSION

Our results suggest that minimum patch size criteria do a disservice to biodiversity conservation. Like previous syntheses based on different data sets (Deane et al., 2020; Fahrig, 2020; Quinn & Harrison 1988), we found that, for the same total

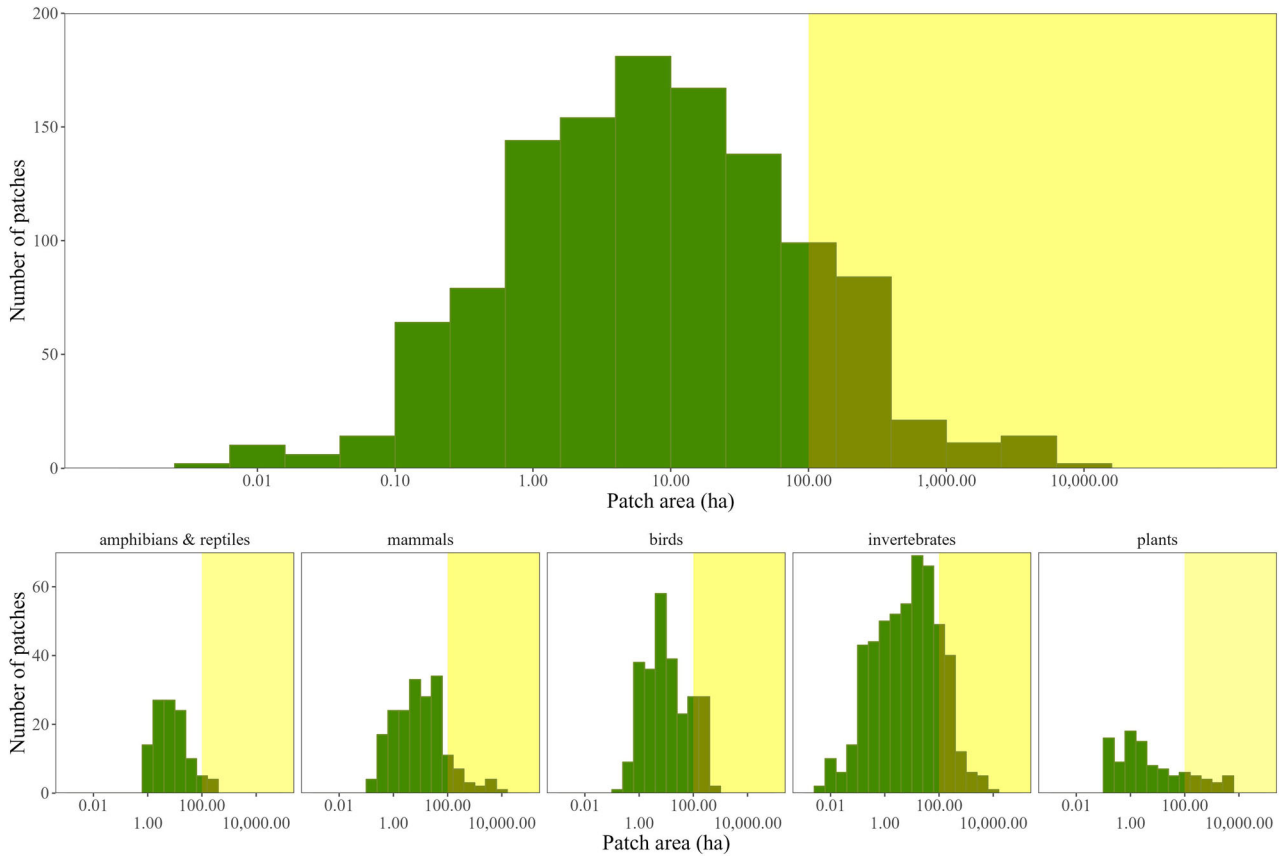


FIGURE 2 Distributions of habitat patch sizes reported in FragSAD (Chase et al., 2019) relative to typical minimum patch size criteria for all data sets combined (top) and for herptiles (111 patches), mammals (192 patches), birds (262 patches), invertebrates (524 patches), and plants (101 patches) (green bars below yellow shading, patches considered too small to have conservation value based on typical minimum patch size criteria [details in INTRODUCTION]).

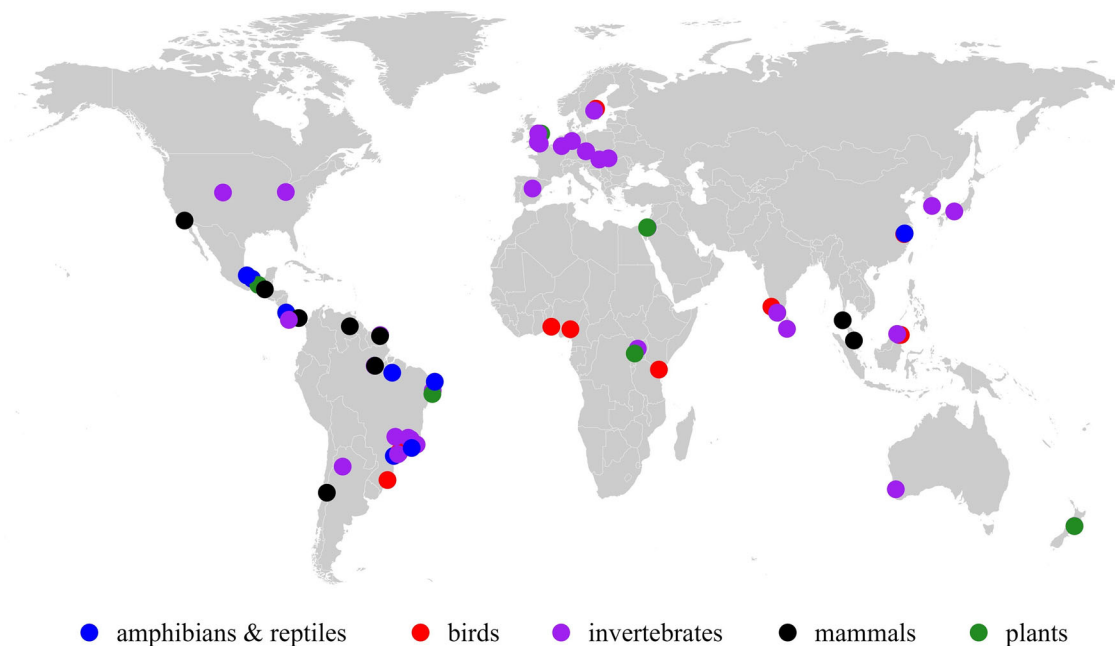


FIGURE 3 Spatial distribution of the 76 metacommunities in the analysis of species richness patterns. The SLOSS comparisons were conducted contrasting cumulative species richness pattern within sets of habitat fragments accumulated from small to large (SS) and from large to small (SL).

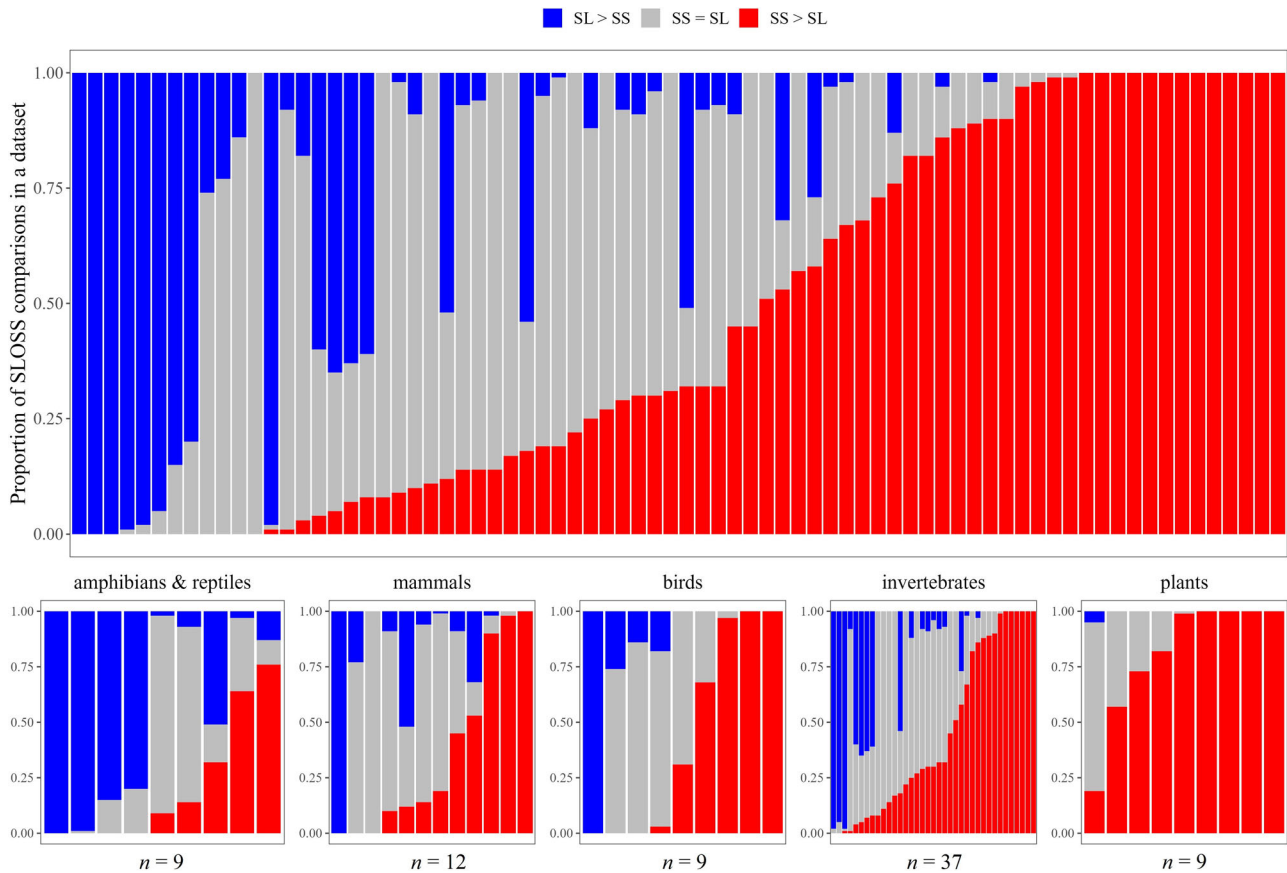


FIGURE 4 Results of empirical comparisons of cumulative species richness in single large (SL) or several small (SS) (SLOSS) areas performed on each of 100 resampled communities generated for each of the 76 metacommunities assessed (bars), overall (top), and separately for major taxa (bottom) (blue, species richness higher in sets of large patches, $SL > SS$ for 19.9% of comparisons; red, species richness higher in sets of small patches, $SS > SL$ for 45.2% of comparisons; gray, no clear difference in species richness between sets of small and sets of large patches, $SS = SL$ for 34.7% of comparisons).

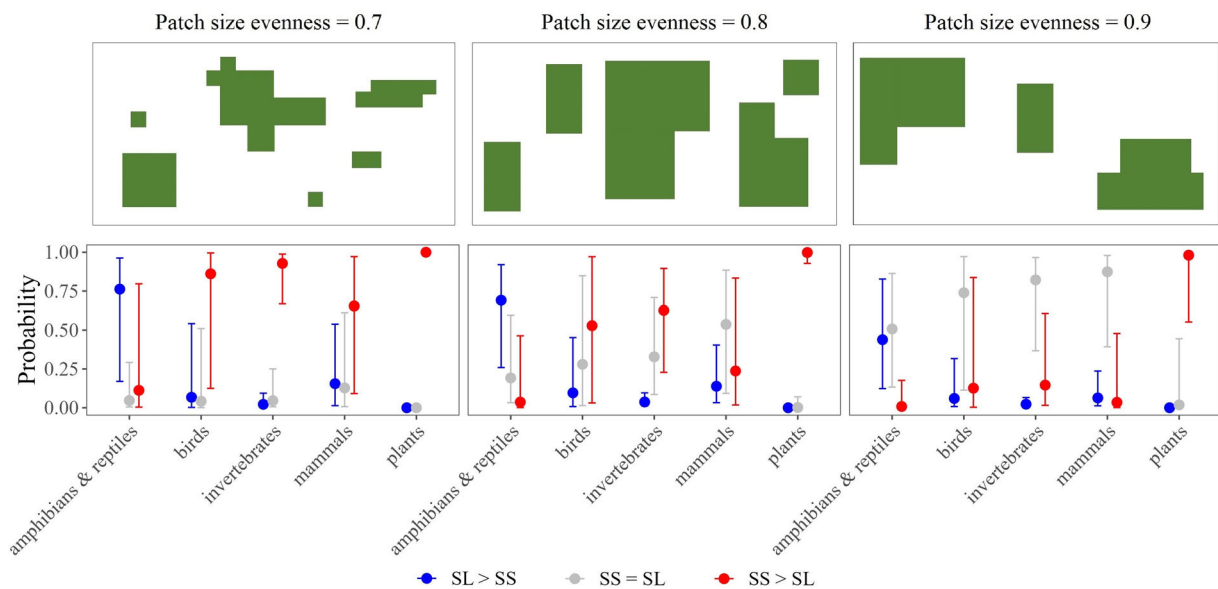


FIGURE 5 Probability of observing negative (blue), positive (red), and no (grey) relationships between biodiversity and habitat fragmentation as a function of taxon and habitat patch size evenness (SL, single large; SS, several small; error bars, 89% credible intervals). Patch size evenness is a continuous covariate (mean = 0.79 [SD 0.10]), but predictions are shown for 3 values (0.7, metacommunity patch size evenness relatively low, with patches in a metacommunity of very different sizes; 0.9, patch size evenness relatively high, with patches in a metacommunity of similar sizes).

habitat area, more species accumulated over many small patches than few large ones. Furthermore, in our data the individual patches making up the small-patch accumulations were much smaller than typical patch size criteria (Figure 2). This means the patches that contributed most to biodiversity on a per-area basis were those that would not qualify for protection under most minimum patch size criteria. Additionally, it strongly suggests that imposing minimum patch size criteria is counterproductive for biodiversity conservation. Although such criteria may be imposed for practical reasons (Fahrig et al., 2022; Shafer, 1995), there is no evidence supporting the biodiversity arguments that are often used to justify them. Importantly, this does not mean that large habitat remnants should be reduced in size. Instead, it means that many conservation opportunities are being lost because small patches are not recognized for their large biodiversity potential on a per-area, cumulative basis.

Interesting differences emerged among major taxonomic groups. For instance, our results suggest that conserving small patches is especially important for protecting Earth's flora because $SL > SS$ was extremely rare when assessing plants (Figures 4 & 5). This result is consistent with the fact that plants have higher intercepts than animals in species–area relationships (Blackburn et al., 2021). Perhaps the same patch area is functionally larger for plants than for animals because plants are sessile, and thus many plant populations can occur in smaller areas than many animal populations. In addition, the higher microhabitat heterogeneity expected across sets of many small patches than expected with few large ones (Lasky & Keitt 2013) might more strongly increase plant biodiversity. Although positive relationships between biodiversity and habitat fragmentation are also common for birds, invertebrates, and mammals, where $SS > SL$ was at least twice as likely as $SL > SS$, the opposite pattern occurred for herptiles (Figures 4 & 5). We speculate that negative fragmentation effects on herptiles might be due to their high mortality in the nonhabitat or matrix portions of landscapes. Consistent with this, herptiles are the group of vertebrates whose populations are most affected by roads and traffic (Rytwinski & Fahrig, 2012). Therefore, when implementing a policy meant to benefit biodiversity, protection should be extended to as many small patches as possible, while also including 1 or a few large patches suitable for herptiles. Thus, our results support the landscape planning strategy proposed by Arroyo-Rodríguez et al. (2020): in human-dominated, naturally forested regions, protected and restored forest should occur mainly in small patches but there should also be at least a single large patch.

Although some species requiring large amounts of habitat likely have already disappeared from human-dominated regions (Chetcuti et al., 2020; Riva et al., 2023; Vellend et al., 2017), there is little evidence that these species are generally negatively affected by fragmentation if sufficient habitat is available, such that remnant patches are within reach for dispersal. On the contrary, empirical and theoretical work demonstrates that biodiversity in some metacommunities persists more readily in large numbers of small patches, even if populations inhabiting such small patches are isolated and exposed to higher extinction risks (Hammill & Clements 2020; Luo et al., 2022; Wang

& Altermatt 2019). In addition, many small patches harbor more specialist species and more species of conservation concern than few large patches (Fahrig, 2020; Riva & Fahrig 2023). And finally, there is currently no support for the assumption that extinction debt depletes biodiversity in sets of small patches more than in a few large patches (Riva & Fahrig, 2022). In all, 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 most species (Riva & Fahrig 2023). This also applies in unexpected conditions; for example, carnivores across Europe are expected to rely strongly on large patches, but are currently showing widespread population recovery across patchy anthropogenic landscapes (Chapron et al., 2014). Importantly, for a given landscape extent, matrix quality, and cumulative habitat area, patches of habitat fragmented into many small patches are more connected than a few patches of continuous habitat because the former are typically closer together (Chetcuti et al., 2020; Fahrig et al., 2022). The higher landscape-scale connectivity of fragmented habitat might partly explain the high potential of many small patches for meta-community persistence (Luo et al., 2022; Wang & Altermatt 2019).

Why are the small patches in the Chase et al. (2019) data compilation so much smaller than typical minimum patch size criteria? One hint is the fact that the data sets for the different taxa analyzed had similar patch size distributions (Figure 2; Appendix S2). This suggests that the patches assessed in conservation research typically reflect the land-use patterns of the study region, which can be remarkably consistent globally (e.g., Taubert et al., 2018), rather than researchers selecting patch sizes to match assumed area requirements of the studied taxa (Hendriks et al., 2009). For studies in human-dominated regions, where most patches are small, this will result in studied patches that are much smaller than minimum patch size criteria. The resulting large number of such small patches in the data set was ideal for testing the minimum patch size concept.

For herptiles, the only taxonomic group differing from the $SS > SL$ pattern, the large patches were slightly smaller than for the other taxa (Figure 2). However, it is unlikely that the higher prevalence of $SL > SS$ for herptiles was an artifact of these smaller large patches. If anything, we would have expected the opposite of our finding that these smaller large patches harbored more species than sets of smaller patches because we would have expected them to be subject to high extinction risk (Riva & Fahrig 2022). Furthermore, creation of large numbers of small (typically <0.1 ha) ponds has been a successful strategy to bolster the recovery of amphibians in Switzerland (Moor et al., 2022). Perhaps, herptiles diverged from the general $SS > SL$ pattern in our analysis because the metacommunities we studied occurred in landscapes with low amounts of remnant habitat. We could not evaluate this possibility because the locations of the patches are not provided in the FragSAD database.

Ultimately, our results suggest that minimum patch size criteria should be abandoned when the goal is to protect biodiversity in human-dominated landscapes. We acknowledge that defining what exactly patches and habitats are is an ongoing

conversation in ecology and conservation (Dennis et al., 2006; Fahrig, 2013). Bypassing these important debates, the major take-home message of our results is that bits of habitat as small as 0.1–1 ha (Figure 2) consistently contribute to cumulative biodiversity across a variety of systems and taxa (see also Deane & He [2018]) and should therefore be valued. This will not be possible until policy and management targeting biodiversity conservation break free from minimum patch size criteria.

ACKNOWLEDGMENTS

We acknowledge the support of a Mitacs Accelerate Fellowship awarded to F.R. in partnership with Carleton University and eButterfly, the community science platform hosted by the Montreal Insectarium, and of a Marie Curie Reintegration Fellowship (European Commission Horizon 2020 Marie Skłodowska-Curie Actions, grant 101024579) awarded to F.R.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

ORCID

Federico Riva  <https://orcid.org/0000-0002-1724-4293>

REFERENCES

- Arroyo-Rodríguez, V., Fahrig, L., Tabarelli, M., Watling, J. I., Tischendorf, L., Benchimol, M., Cazetta, E., Faria, D., Leal, I. R., Melo, F. P. L., Morante-Filho, J. C., Santos, B. A., Arasa-Gisbert, R., Arce-Peña, N., Cervantes-López, M. J., Cudney-Valenzuela, S., Galán-Acedo, C., San-José, M., Vieira, I. C. J., ... Slik, J. W. F. (2020). Designing optimal human-modified landscapes for forest biodiversity conservation. *Ecology letters*, 23, 1404–1420.
- Bennett, J. R., & Arcese, P. (2013). Human influence and classical biogeographic predictors of rare species occurrence. *Conservation biology*, 27, 417–421.
- Birch, W. S., Drescher, M., Pittman, J., & Rooney, R. C. (2022). Trends and predictors of wetland conversion in urbanizing environments. *Journal of environmental management*, 310, 114723.
- Blackburn, T. M., Cassey, P., & Pyšek, P. (2021). Species–area relationships in alien species: Pattern and process. In T. J. Matthews, K. A. Triantis, & R. J. Whittaker *The species-area relationship: Theory and application*. Cambridge University Press, pp. 133–154.
- Brown, E., Dudley, N., Lindhe, A., Muhtaman, D. R., Stewart, C., & Synnott, T. (2013). *Common guidance for the identification of high conservation values*. HCV Resource Network.
- Caro, T., Rowe, Z., Berger, J., Wholey, P., & Dobson, A. (2022). An inconvenient misconception: Climate change is not the principal driver of biodiversity loss. *Conservation letters*, 15, e12868. <https://doi.org/10.1111/conl.12868>
- Chapron, G., Kaczensky, P., Linnell, J. D. C., von Arx, M., Huber, D., Andrén, H., López-Bao, J. V., Adamec, M., Álvares, F., Anders, O., Balčiauskas, L., Balys, V., Bedó, P., Bego, F., Blanco, J. C., Breitenmoser, U., Brøseth, H., Bufka, L., Bunikyte, R., ... Boitani, L. (2014). Recovery of large carnivores in Europe's modern human-dominated landscapes. *Science*, 346, 1517–1519.
- Chase, J. M., Liebergesell, M., Sagouis, A., May, F., Blowes, S. A., Berg, A., Bernard, E., Brosi, B. J., Cadotte, M. W., Cayuela, L., Chiarello, A. G., Cosson, J.-F., Cresswell, W., Dami, F. D., Dauber, J., Dickman, C. R., Didham, R. K., Edwards, D. P., Farneda, F. Z., ... Ziv, Y. (2019). FragSAD: A database of diversity and species abundance distributions from habitat fragments. *Ecology*, 100, e02861.
- Chase, J. M., Blowes, S. A., Knight, T. M., Gerstner, K., & May, F. (2020). Ecosystem decay exacerbates biodiversity loss with habitat loss. *Nature*, 584, 238–243.
- Chetcuti, J., Kunin, W. E., & Bullock, J. M. (2020). Habitat fragmentation increases overall richness, but not of habitat-dependent species. *Frontiers in Ecology and Evolution*, 8, 12.
- Comisión Nacional Forestal (CONAFOR). (2021). *Reglas de Operación del Programa Apoyos para el Desarrollo Forestal Sustentable 2021*. Diario Oficial de la Federación (DOF).
- Deane, D. C. (2022). Species accumulation in small-large vs large-small order: More species but not all species? *Oecologia*, 200, 273–284. <https://doi.org/10.1007/s00442-022-05261-1>
- Deane, D. C., & He, F. (2018). Loss of only the smallest patches will reduce species diversity in most discrete habitat networks. *Global change biology*, 24, 5802–5814.
- Deane, D. C., Nozohourmehrabad, P., Boyce, S. S. D., & He, F. (2020). Quantifying factors for understanding why several small patches host more species than a single large patch. *Biological conservation*, 249, 108711.
- Dennis, R. L. H., Shreeve, T. G., & Van Dyck, H. (2006). Habitats and resources: The need for a resource-based definition to conserve butterflies. *Biodiversity & Conservation*, 15, 1943–1966.
- Diamond, J. M. (1975). The island dilemma: Lessons of modern biogeographic studies for the design of natural reserves. *Biological conservation*, 7, 129–146.
- Dinerstein, E., Vynne, C., Sala, E., Joshi, A. R., Fernando, S., Lovejoy, T. E., Mayorga, J., Olson, D., Asner, G. P., Baillie, J. E. M., Burgess, N. D., Burkart, K., Noss, R. F., Zhang, Y. P., Baccini, A., Birch, T., Hahn, N., Joppa, L. N., & Wikramanayake, E. (2019). A Global Deal For Nature: Guiding principles, milestones, and targets. *Science advances*, 5, eAaw2869.
- Europarc Federation. (2013). *Wild Europe. A working definition of European wilderness and wild areas*. <https://www.europarc.org/wp-content/uploads/2015/05/a-working-definition-of-european-wilderness-and-wild-areas.pdf>
- Fahrig, L. (2003). Effects of habitat fragmentation on biodiversity. *Annual review of ecology, evolution, and systematics Annual Reviews*, 34, 487–515.
- Fahrig, L. (2013). Rethinking patch size and isolation effects: The habitat amount hypothesis. *Journal of biogeography*, 40, 1649–1663.
- Fahrig, L. (2017). Ecological responses to habitat fragmentation per se. *Annual Reviews*, 48, <https://doi.org/10.1146/annurev-ecolsys-110316-022612>
- Fahrig, L. (2020). Why do several small patches hold more species than few large patches? *Global ecology and biogeography*, 29, 615–628.
- Fahrig, L., Watling, J. I., Arnillas, C. A., Arroyo-Rodríguez, V., Jörgen-Hickfang, T., Müller, J., Pereira, H. M., Riva, F., Rösch, V., Seibold, S., Tscharnkte, T., & May, F. (2022). Resolving the SLOSS dilemma for biodiversity conservation: A research agenda. *Biological reviews of the Cambridge Philosophical Society*, <https://doi.org/10.1111/brv.12792>
- Fletcher, R. J. Jr, Didham, R. K., Banks-Leite, C., Barlow, J., Ewers, R. M., Rosindell, J., Holt, R. D., Gonzalez, A., Pardini, R., Damschen, E. I., Melo, F. P. L., Ries, L., Prevedello, J. A., Tscharnkte, T., Laurance, W. F., Lovejoy, T., & Haddad, N. M. (2018). Is habitat fragmentation good for biodiversity? *Biological conservation*, 226, 9–15.
- Gavish, Y., Ziv, Y., & Rosenzweig, M. L. (2012). Decoupling fragmentation from habitat loss for spiders in patchy agricultural landscapes. *Conservation biology*, 26, 150–159.
- Haddad, N. M., Brudvig, L. A., Clobert, J., Davies, K. F., Gonzalez, A., Holt, R. D., Lovejoy, T. E., Sexton, J. O., Austin, M. P., Collins, C. D., Cook, W. M., Damschen, E. I., Ewers, R. M., Foster, B. L., Jenkins, C. N., King, A. J., Laurance, W. F., Levey, D. J., Margules, C. R., ... Townshend, J. R. (2015). Habitat fragmentation and its lasting impact on Earth's ecosystems. *Science advances*, 1, e1500052.
- Hadley, A. S., & Betts, M. G. (2016). Refocusing habitat fragmentation research using lessons from the last decade. *Current landscape ecology reports*, 1, 55–66.
- Hammill, E., & Clements, C. F. (2020). Imperfect detection alters the outcome of management strategies for protected areas. *Ecology letters*, 23, 682–691.
- Han, L., Wang, Z., Wei, M., Wang, M., Shi, H., Ruckstuhl, K., Yang, W., & Alves, J. (2022). Small patches play a critical role in the connectivity of the Western Tianshan landscape, Xinjiang, China. *Ecological indicators*, 144, 109542.
- Hendriks, A. J., Willers, B. J. C., Lenders, H. J. R., & Leuven, R. S. E. W. (2009). Towards a coherent allometric framework for individual home ranges, key population patches and geographic ranges. *Ecography*, 32, 929–942.
- Hortal, J., de Bello, F., Diniz-Filho, J. A. F., Lewinsohn, T. M., Lobo, J. M., & Ladle, R. J. (2015). Seven shortfalls that beset large-scale knowledge of biodiversity. *Annual review of ecology, evolution, and systematics Annual Reviews*, 46, 523–549.

- Hughes, A. C., Orr, M. C., Ma, K., Costello, M. J., Waller, J., Provoost, P., Yang, Q., Zhu, C., & Qiao, H. (2021). Sampling biases shape our view of the natural world. *Ecography*, *44*, 1259–1269.
- Hunter, M. L., Acuña, V., Bauer, D. M., Bell, K. P., Calhoun, A. J. K., Felipe-Lucía, M. R., Fitzsimons, J. A., González, E., Kinnison, M., Lindenmayer, D., Lundquist, C. J., Medellín, R. A., Nelson, E. J., & Poschold, P. (2017). Conserving small natural features with large ecological roles: A synthetic overview. *Biological conservation*, *211*, 88–95.
- Keinath, D. A., Doak, D. F., Hodges, K. E., Prugh, L. R., Fagan, W., Sekercioglu, C. H., Buchart, S. H. M., & Kauffman, M. (2017). A global analysis of traits predicting species sensitivity to habitat fragmentation. *Global ecology and biogeography*, *26*, 115–127.
- Krauss, J., Bommarco, R., Guardiola, M., Heikkinen, R. K., Helm, A., Kuussaari, M., Lindborg, R., Öckinger, E., Pärtel, M., Pino, J., Pöyry, J., Raatikainen, K. M., Sang, A., Stefanescu, C., Teder, T., Zobel, M., & Steffan-Dewenter, I. (2010). Habitat fragmentation causes immediate and time-delayed biodiversity loss at different trophic levels. *Ecology letters*, *13*, 597–605.
- Kremen, C., & Merenlender, A. M. (2018). Landscapes that work for biodiversity and people. *Science*, *362*, <https://doi.org/10.1126/science.aau6020>
- Lasky, J. R., & Keitt, T. H. (2013). Reserve size and fragmentation alter community assembly, diversity, and dynamics. *The American Naturalist*, *182*, 142–160.
- Luo, M., Wang, S., Saavedra, S., Ebert, D., & Altermatt, F. (2022). Multispecies coexistence in fragmented landscapes. *Proceedings of the National Academy of Sciences of the United States of America*, *119*(42), e2123070119.
- Moor, H., Bergamini, A., Vorburger, C., Holderregger, R., Buhler, C., Egger, S., & Schmidt, B. R. (2022). Bending the curve: Simple but massive conservation action leads to landscape-scale recovery of amphibians. *Proceedings of the National Academy of Sciences of the United States of America*, *119*(37), e2201503119.
- Pielou, E. C. (1966). The measurement of diversity in different types of biological collections. *Journal of Theoretical Biology*, *13*, 131–144.
- Quinn, J. F., & Harrison, S. P. (1988). Effects of habitat fragmentation and isolation on species richness: Evidence from biogeographic patterns. *Oecologia*, *75*, 132–140.
- R Core Team. (2022). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. <https://www.R-project.org/>
- Riva, F., & Fahrig, L. (2022). The disproportionately high value of small patches for biodiversity conservation. *Conservation Letters*, *15*(3), e12881.
- Riva, F., & Fahrig, L. (2023). Landscape-scale habitat fragmentation is positively related to biodiversity, despite patch-scale ecosystem decay. *Ecology Letters*, *26*(2), 268–277.
- Riva, F., Martin, C. J., Millard, K., & Fahrig, L. (2022). Loss of the world's smallest forests. *Global change biology*, *28*(24), 7164–7166.
- Riva, F., Barbero, F., Balletto, E., & Bonelli, S. (2023). Combining environmental niche models, multi-grain analyses, and species traits identifies pervasive effects of land use on butterfly biodiversity across Italy. *Global change biology*, *29*, 1715–1728. <https://doi.org/10.1111/gcb.16615>
- Rytwinski, T., & Fahrig, L. (2012). Do species life history traits explain population responses to roads? A meta-analysis. *Biological Conservation*, *147*(1), 87–98.
- Shafer, C. L. (1995). Values and shortcomings of small reserves. *Bioscience*, *45*, 80–88.
- Simberloff, D. S., & Abele, L. G. (1976). Island biogeography theory and conservation practice. *Science*, *191*, 285–286.
- Taubert, F., Fischer, R., Groeneveld, J., Lehmann, S., Müller, M. S., Rödig, E., Wiegand, T., & Huth, A. (2018). Global patterns of tropical forest fragmentation. *Nature*, *554*, 519–522.
- Tulloch, A. I. T., Barnes, M. D., Ringma, J., Fuller, R. A., & Watson, J. E. M. (2016). Understanding the importance of small patches of habitat for conservation. *The journal of applied ecology*, *53*, 418–429.
- Valdés, A., Lenoir, J., De Frenne, P., Andrieu, E., Brunet, J., Chabrierie, O., Cousins, S. A. O., Deconchat, M., De Smedt, P., Diekmann, M., Ehrmann, S., Gallet-Moron, E., Gärtner, S., Giffard, B., Hansen, K., Hermy, M., Kolb, A., Le Roux, V., Liira, J., ... Decocq, G. (2020). High ecosystem service delivery potential of small woodlands in agricultural landscapes. *The journal of applied ecology*, *57*, 4–16.
- Vellend, M., Baeten, L., Becker-Scarpitta, A., Boucher-Lalonde, V., McCune, J. L., Messier, J., Myers-Smith, I. H., & Sax, D. F. (2017). Plant biodiversity change across scales during the Anthropocene. *Annual review of plant biology*, *68*, 563–586.
- Wallace, J., & Tarr, N. (2012). *Conservation recommendations for priority terrestrial wildlife species and habitats in North Carolina*. <https://www.ncwildlife.org/Portals/0/Conserving/documents/ConservingTerrestrialHabitatandSpecies.pdf>
- Wang, X., Blanchet, F. G., & Koper, N. (2014). Measuring habitat fragmentation: An evaluation of landscape pattern metrics. *Methods in ecology and evolution*, *5*, 634–646.
- Wang, S., & Altermatt, F. (2019). Metapopulations revisited: The area-dependence of dispersal matters. *Ecology*, *100*(9), e02792.
- Wilson, E. O., & Willis, E. O. (1975). Applied biogeography. Pages 422–534 in M. L. Cody & J. M. Diamond editors. *Ecology and evolution of communities*. Harvard University Press.
- Wintle, B. A., Kujala, H., Whitehead, A., Cameron, A., Veloz, S., Kukkala, A., Moilanen, A., Gordon, A., Lentini, P. E., Cadenhead, N. C. R., & Bekessy, S. A. (2019). Global synthesis of conservation studies reveals the importance of small habitat patches for biodiversity. *Proceedings of the National Academy of Sciences of the United States of America*, *116*, 909–914.
- Yan, Y., Jarvie, S., Zhang, Q., Zhang, S., Han, P., Liu, Q., & Liu, P. (2021). Small patches are hotspots for biodiversity conservation in fragmented landscapes. *Ecological indicators*, *130*, 108086.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Riva, F., & Fahrig, L. (2023). Obstruction of biodiversity conservation by minimum patch size criteria. *Conservation Biology*, *37*, e14092. <https://doi.org/10.1111/cobi.14092>

