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RESEARCH ARTICLE

SLOSS-based inferences in a fragmented landscape depend on fragment area and species–area slope

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Abstract

Aims: Whether a Single Large Or Several Small (SLOSS) habitat patches contain more species is central to the debate about how habitat fragmentation threatens species diversity. However, the geographical and biogeographical variables that affect emergent SLOSS patterns remain poorly understood. Here, we quantified SLOSS-based diversity patterns of woody plant, bird and spider assemblages in a subtropical archipelago of land bridge islands.

Location: Thousand Island Lake, Zhejiang Province, China.

Taxon: Woody plants, birds and spiders.

Methods: We analysed species accumulation curves and species–area relationships (SARs) to quantify SLOSS-based patterns of all, common and rare species for each taxon across different groupings of islands. Differences in the number of species between a single large island and sets of several small islands were measured in these analyses using a Saturation index (SI) and SLOSS index. Generalized additive models were used to assess the relationships between SI and SLOSS index values and the maximum area of islands included in the analysis, the slope of SARs (i.e. *z*-score) and the degree of nestedness.

Results: SI values increased with the maximum area of islands for three taxa, while SLOSS index values only increased with the maximum island area for woody plants. SI values increased as *z*-scores of woody plants decreased, and showed a quadratic relationship for birds and spiders. SLOSS index values decreased as *z*-scores of three taxa increased. The degree of nestedness and SI values or SLOSS index values were weakly correlated with all, rare and common species in the three taxa.

Main conclusions: SLOSS-based inferences of fragmentation effects are contingent on variation in the maximum area of patches included in analyses and the slope of SARs in fragmentated landscapes. Whether conservation efforts should prioritize a single large or several small patches depends on the geographical (e.g. maximum fragment area) and biogeographical (e.g. slope of SAR) attributes of a fragmentated landscape.

KEYWORDS
biodiversity conservation, habitat fragmentation, habitat heterogeneity, land-bridge islands, nestedness, rare species, species accumulation curve, species area relationship, species composition

1 | INTRODUCTION

SLOSS-based inferences, which address whether a single large (SL) or several small (SS) habitat patches contain more species, have been widely applied to conservation decision-making, from the management of fragmented landscapes to the design of nature reserves (Diamond, 1975; Fahrig, 2017; Lasky & Keitt, 2013; Tjorve, 2010; Wintle et al., 2019). Generally, three SLOSS patterns are recognized as indicators of how habitat fragmentation—the breaking apart of continuous habitat into smaller habitat fragments—affects species richness (Fahrig, 2017; MacDonald et al., 2018b): (1) a single large habitat patch contains greater species richness than several small fragments of the same total area, equating to a 'negative fragmentation effect' (SS < SL); (2) several small patches support a greater number of species than a single large patch with an area equal to the sum of the small patches, equating to a 'positive fragmentation effect' (SS > SL); and (3) a single large patch and several small patches contain an equivalent number of species, equating to a 'neutral fragmentation effect' (SS = SL).

A plethora of studies have quantified patterns of SLOSS across a variety of landscapes (e.g. Quinn & Harrison, 1998; Gavish et al., 2012; Lindenmayer et al., 2015; MacDonald et al., 2018a, and see reviews by Fahrig, 2017, 2019, 2020; Fahrig et al., 2022). In a recent review of 157 SLOSS-based comparisons, Fahrig (2020) reported that several small patches contained more (SS > SL), equivalent (SS = SL) and fewer (SS < SL) species than single large patch in 72%, 22% and 6% of instances, respectively. When removing studies with biased sampling effort across patches of different areas, several small patches contained more, equivalent and fewer species in 58%, 37% and 5% on instances, respectively. Therefore, even when sampling is standardized to survey area, in order to control for sampling artefacts, it is clear that the species richness of several smaller habitat patches is generally higher than that in a single larger habitat patch. However, the geographical and biogeographical variables underling this observed variation in SLOSS-based inferences are still poorly understood (Deane et al., 2020).

Understanding the geographical and biogeographical variables that affect emergent SLOSS patterns is integral to address their ecological significance and importance to conservation planning (Deane et al., 2020; Fahrig, 2019; Fahrig et al., 2019; Fletcher et al., 2018). Three geographical and biogeographical variables are hypothesized to be related to SLOSS patterns: (1) the maximum area of patches included in analyses (geographical variable) (Allouche et al., 2012; Fattorini, 2010; MacDonald et al., 2018b; Tjorve, 2010); (2) the slope of SAR (biogeographical variable) (Deshaye & Morisset, 1989; Haddad et al., 2017; Ovaskainen, 2002); and (3) the degree of nestedness in relation to patch area (i.e. whether depauperate species assemblages tend to be proper subsets of richer species assemblages) (biogeographical variable) (Gao & Perry, 2016; Matthews et al., 2015). There are several mechanistic hypotheses that link these three variables together and relate them to SLOSS-based inferences of fragmentation effects. The maximum area of patches included in SLOSS-based analyses may affect inference of fragmentation effects if species differ in minimum area requirements. For example, large minimum area requirements of certain species may lead to their complete exclusion from small patches, producing a nested pattern of species diversity in relation to patch area (Fattorini, 2010). Failure to include larger patches in SLOSS-based studies may thereby result in failure to detect important fragmentation effects because species with large minimum area requirements are excluded from analyses (Gotelli & Graves, 1996; Soulé & Simberloff, 1986). Interspecific variation in minimum area requirements may also steepen the slope of the SAR, which has been inferred to be an indicator of negative fragmentation effects (Haddad et al., 2017). In spite of our theoretical understandings of these relationships, the extent to which inferences drawn from SLOSS-based analyses vary with the area of patches included in analyses, and how this, in turn, relates to the slope of SARs and patterns of nestedness, remains largely unresolved.

To assess what geographical and biogeographical variables were related to variation in SLOSS-based inferences, we quantified relationships between SLOSS patterns and (1) the maximum area of island included in analyses; (2) the slope of SAR; and (3) the degree of nestedness in relation to island area in a subtropical hydroelectric reservoir in Zhejiang Province, China (Hu et al., 2021). To further examine whether these relationships were consistent across taxa, we quantified SLOSS patterns for woody plants, birds and spiders occurring in the archipelago. We also analysed common and rare species in each taxon separately to investigate the effect of species rarity on SLOSS-based inferences.

2 | MATERIALS AND METHODS

2.1 | Study site

Islands included in this study are within the Thousand Island Lake (29°220–29°500 N, 118°340–119°150 E), a hydroelectric reservoir in Zhejiang Province, eastern China. This reservoir was formed by the construction of the Xin'an River Dam in 1959, resulting in a freshwater impoundment of 573 km^2 and the formation of 1078 land-bridge islands with areas >0.25 ha when the water reaches its highest level (108 m) (Hu et al., 2021). All islands included within this study are identical in the time since isolation, beginning with the damning of the Xin'an River and subsequent flooding of the landscape (Liu et al., 2020). Forests were clear-cut on the selected islands, and the major vegetation type on all selected islands is now secondary successional forest dominated by Masson pine (*Pinus massoniana*) (Hu et al., 2021; Liu et al., 2018). The climate of study area is characterized by a subtropical, monsoon climate with hot, wet summers and cool, dry winters. The mean annual temperature is 17.0°C, and daily temperatures range from −7.6°C in January to 41.8°C in July. The mean annual precipitation is 1430 mm, with 155 days of precipitation per year, mostly between April and June (Liu et al., 2018).

2.2 | Data collection

Species richness of woody plants was surveyed on 28 islands (area ranges from 0.08 ha to 47.98 ha) from 2014 to 2015. Islands with an area of less than 1 ha were covered by subplots of 5 × 5 m in the entire forest area; islands with an area of more than 1 ha were covered by 2–3 transects (the length of each transect depended on the area and shape of the island), which were set from the edge to the interior of the island, and each transect was covered by 5 × 5 m subplots. The number of sampling subplots on each island increased linearly in proportion to the area of the island (linear regression: $F = 285.249$, $R_{\text{adj}}^2 = 0.910$, $p < 0.001$). On all islands, all woody plants with a diameter at breast height (DBH) ≥1 cm in the 5 × 5 m subplots were identified to species (see Liu et al., 2018 and 2020 for further description of the method). SACs analyses indicated that sampling protocols were sufficient to capture most woody plant species on the islands (Yu et al., 2012).

Species richness of breeding birds was surveyed on 36 islands, with size ranging from 0.57 to 143.19 ha, during the breeding season (April–June) annually from 2007 to 2012 (Si et al., 2015). In each survey, the observer walked each transect at a constant speed (approximately 2.0 km/h) and recorded all breeding birds seen or heard on the survey island, excluding the high-flying species passing over the island and water birds during the survey. Most transects were 400 m and in straight lines wherever possible, except for small islands. The sampling effort of each island was approximately proportional to island area: four transects each on islands with areas greater than 100 ha, two transects each on islands with areas greater than 10 ha and less than 100 ha, and one transect on each of the remaining small islands (~1 ha for most islands). If the island has more than one habitat type, stratified random placement of transect locations were used to capture all types. In total, each transect on these islands was surveyed 78 times over the course of the entire study. These surveys produced occupancy data of forest breeding birds along transects, excluding diving birds, ducks, gulls, shorebirds, herons and kingfishers, which extensively rely on resources provided by the open-water matrix. The completeness of surveys for the islands was assessed by examining species accumulation curves for each of the 6 years. All curves levelled off before the completion of the surveys, indicating that the sampling effort was sufficient and comparable among islands (Si et al., 2014, 2015).

Spider species richness was surveyed on 30 islands, with size ranging from 0.57 to 55.08 ha, from April 2013 to September 2014 except for winter times (from 26th December 2013 to 20th March 2014) (Wu et al., 2017). Ground-dwelling spiders were sampled using pitfall traps placed in groups of three, positioned 2 m apart at the vertices of an equilateral triangle. The distance between groups was approximately 50 m to achieve group independence along the transect trails that traversed the highest points on each study island (Larsen, 2005). The total number of pitfall traps on island increased linearly proportional to the island area (linear regression: $F = 215.552$, $R_{\text{adj}}^2 = 0.877$, $p < 0.001$). Visual searches were carried out for web spiders within 2 m of the trail along the same transect(s) on each island. Each island was surveyed two times per month on days without precipitation. Only adult individuals were included in our analyses due to the difficulty of assigning most juvenile spiders to species level. The order in which the islands were sampled was randomized within each sampling period. The final slopes of the observed and estimated species accumulation curves for ground-dwelling spiders and web spiders for each island were close to asymptotic, indicating that sampling completeness was high and comparable among islands (Wu et al., 2017).

All species were further divided into rare and common based on their island occupancy and all analyses detailed below were repeated separately for each category. That is, species recorded on ≤25% of the study islands were classified as rare, while species recorded on >25% of the study islands were classified as common.

2.3 | Inferring SLOSS patterns

For each of the three taxa surveyed, we used species accumulation curves (SACs) to infer the SLOSS patterns of our study islands (including SLOSS patterns based on all, common and rare species). To build SACs, we plotted the cumulative number of species against cumulative island area when islands were sequentially added in increasing order of island area (small-to-large SAC) and decreasing order of island area (large-to-small SAC). Plotted data points corresponding to cumulative species and area were connected with straight lines, which passed through the origin to allow area-under-the-curve comparisons (estimated using the trapezoidal rule) (Gavish et al., 2012; Quinn & Harrison, 1998). If large-to-small SAC lies above small-to-large SAC, single/fewer larger islands contain more species than a set of several smaller islands summing to equivalent area (we refer to this pattern as negative fragmentation effect). Alternatively, if large-to-small SAC lies below the small-to-large SAC, single/fewer larger islands contain fewer species than a set of several smaller islands (i.e. positive fragmentation effect). The third possibility is that the overlap of SAC from large-to-small and small-to-large suggests that species richness increases with the increase in the total island area, and is independent of the spatial configuration of the island. Difference between large-to-small and small-to-large SAC was quantitatively estimated using Quinn and Harrison's (1998) saturation index (SI), and was estimated as the area under the small-to-large SAC divided by that of the large-to-small SAC. For this index, estimates less than, equal to and greater than one suggest negative, neutral and positive fragmentation effects, respectively. However, connecting the small-to-large and large-to-small curves to the origin has been criticized, because it is unrealistic to assume linear species accumulation between the largest island and the origin (Fahrig, 2020). We therefore devised an additional saturation index, in which the area under the small-to-large and large-to-small curves was calculated only between the area of the largest island and the cumulative area of all islands included in the analysis (see a graphical example of saturation index and modified saturation index in Appendix Figure S1).

As a second analysis of fragmentation effects, we used a SLOSS index based on the SAR extrapolation method (Gavish et al., 2012; MacDonald et al., 2018b). First, we applied log–log least-squares linear regression to observed species richness and island area. Then we substituted the total area of all study islands into the SAR regression to yield the predicted species richness (S_{sl}) of a single large, theoretical habitat patch equal to the area of all the study islands combined. This value was then compared to the observed total species richness across all study islands (S_{ss}) using a SLOSS index, estimated as $100\% \times (S_{ss} - S_{sl})/S_{ss}$. Here, estimates less than, equal to and greater than zero are indicated as negative, neutral and positive fragmentation effects, respectively.

To assess whether SLOSS-based inferences of fragmentation effects varied with the range of patch areas, we iteratively estimated the saturation index for the subset of islands generated with a threshold maximum area. As the threshold maximum area decreased, the number of islands that may be included in our analysis decreased. To control for this and to address whether the number of islands included in SAC analyses affected inferred fragmentation effects, we estimated the saturation index using 999 repeats of 5 and 10 islands that were randomly selected from all study islands for each taxon. The maximum island area included in each random repeat of 5 or 10 islands was recorded.

Using the 999 random 5- and 10-island subsets, we calculated the slope of SAR (i.e. *z*-score in a power model) and the degree of nestedness. We calculated the *z*-scores from a linear model after logarithmic transformation, $\log(S) = z \log(A) + c$, where S and A represent the richness and the area of individual islands.

We used the NODF (Nestedness based on Overlap and Decreasing Fill, Almeida-Neto et al., 2008) metric to estimate the degree of assemblage nestedness in relation to island area. This was estimated using the 'vegan' package in R (Almeida-Neto & Ulrich, 2011). To determine whether the NODF value was significantly higher or lower than expected by chance, we simulated 999 random matrices using the 'quasiswap' algorithm (Miklos & Podani, 2004), and generated standard effect sizes (SES) using our observed NODF value and NODF values calculated using the null matrices (SES = [observed-expected]/SD) (Ulrich & Gotelli, 2012). When a set of N matrices are simulated using the quasiswap algorithm, the row and column frequencies and marginal totals for each simulated matrix are preserved (Miklos & Podani, 2004). The degree of nestedness increases across increasing SES values; values greater than 1.96 indicate a significant nestedness, while values lower than −1.96 indicate significant anti-nestedness (i.e. less nested than random assemblages) (Ulrich & Gotelli, 2012).

2.4 | Statistical analysis

To evaluate the relationships between SLOSS patterns and our geographical and biogeographical variables of interest, we used the 'mgcv' package (Wood, 2006) in R (version 3.6.3) (R Development Core Team 2018) to fit the generalized additive model (GAM), with the saturation index or SLOSS index as the response variable, and maximum island area, *z*-scores of SARs, and degree of nestedness as explanatory variables. Variance inflation factors (VIFs) were used to assess multicollinearity among explanatory variables in GAMs. A VIF of 10 was used as a maximum cut-off value (Craney & Surles, 2002; MacDonald et al., 2018a), beyond which individual coefficients were considered uninterpretable. Generalized cross-validation (GCV) optimization was used to choose appropriate degrees of freedom (Zuur et al., 2009). The gamma penalty within in the gam function was set to 1.4 degrees of freedom to reduce effects of over-fitting associated with the GCV criterion (Kim & Gu, 2004). We also applied GAM fitting with 95% confidence interval to plot the relationship between the saturation index and the maximum island area, *z*-scores of SARs and the degree of nestedness of the richness of all, common and rare species of woody plants, birds and spiders when controlling the number of islands.

3 | RESULTS

Our general inferences were similar when using either the Quinn and Harrison's saturation index or our modified saturation index (See Figures S2, S3); here, we report results using Quinn and Harrison's saturation index. Relationships between saturation index values and maximum island area thresholds were similar for both 5- and 10-island random subsets for woody plant (Figure 1a, b), bird (Figure 1c, d) and spider assemblages (Figure 1e, f). Therefore, we completed all subsequent analyses using the 999 random 10-island subsets.

In GAMs, as maximum island area thresholds increased, the saturation index values generally increased and then stabilized for all (Figure 1), common (Figure S4a, d, h) and rare (Figure S5a, d, h) species for all three taxa. Saturation index values and *z*-scores of SAR were significantly negatively related for all (Figure 2a), common (Figure S4b) and rare (Figure S5b) species of wood plants, and showed quadratic relationship for all (Figure 2c), common (Figure S4e) and rare (Figure S5e) species of birds and for all (Figure 2e), common (Figure S4g) and rare (Figure S5g) species of spiders. When we used the 10-island subset in the analysis, we tested the significant relationship of SAR, and we found that all SARs of woody plants were significant, but some SARs of birds and spiders were not significant. To assess whether these insignificant *z*-scores affected our results, we removed them from the analysis, but we still found the same relationships. Saturation index values and the degree of nestedness (SES) showed weak relationships for all (Figure 2b, d, f; $R^2_{adj} < 0.02$), common (Figure S4c, f, k) and rare species (Figure S5c, f, k) for each of the three taxa. VIFs were less than 10 for all variables in all models (woody plants, min = 1.376, max = 3.994; birds, min = 1.240, max = 1.469; siders, min = 3.207, max = 5.536), suggesting that multicollinearity was not an issue.

In addition to SAC analysis, we also used the SAR extrapolation method to calculate a SLOSS index and found that values generally increased with the maximum island area for all species (Figure 3a) and common species (Figure S6a) of woody plants. SLOSS index values and the *z*-scores of SARs were significantly negatively correlated with all (Figure 3b, e, h), common (Figure S6b, e, g) and rare (Figure S7b, e, g) species for each of the three taxa. SLOSS index values and the degree of nestedness also showed a weak relationship for all (Figure 3c, f, k; $R^2_{adj} < 0.07$), common (Figure S6c, f, k) and rare (Figure S7c, f, k) species for each of the three taxa.

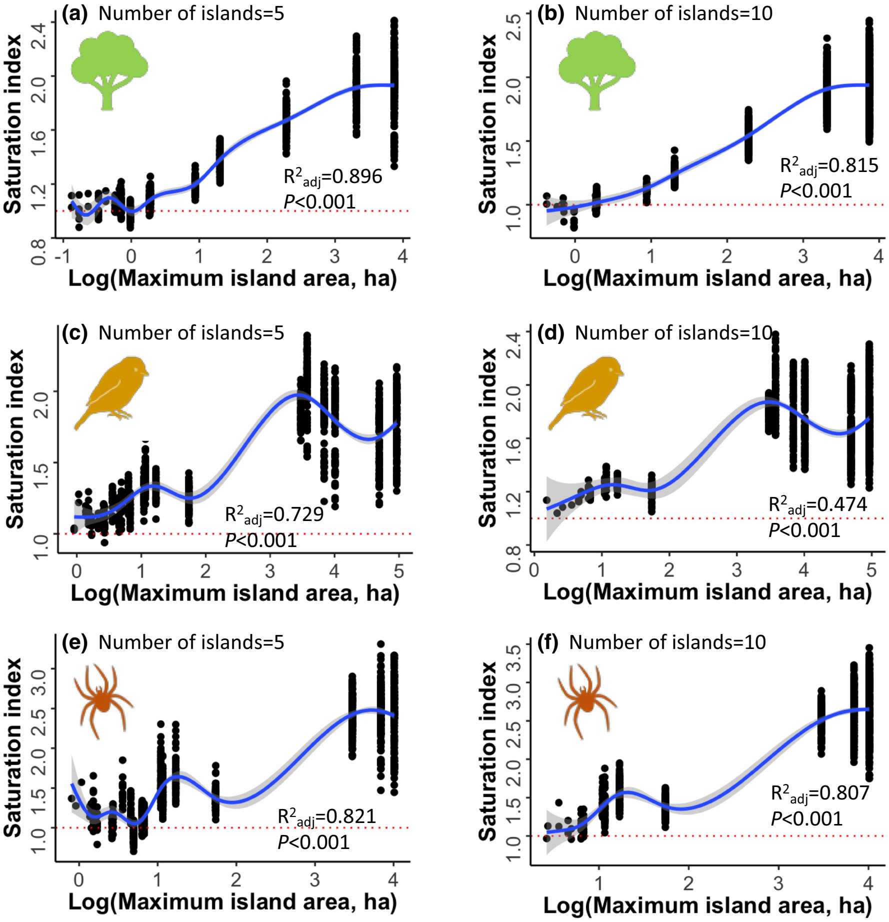

FIGURE 1 The fit of generalized additive models (GAM) with 95% confidence interval examining the relationship between saturation index and maximum island area in the selected islands for woody plants (a, b), birds (c, d) and spiders (e, f) species richness when controlling for the number of islands. Shaded area is standard error. Smoothed lines are fitted values. The black points refer to the saturation index calculated by randomly selecting 5 (a, c, e) or 10 (b, d, f) islands for 999 repeats

4 | DISCUSSION

A large number of studies have assessed whether single large or several small habitat patches of equal total area, contain a greater, equal or lesser number of species (Fahrig, 2017, 2020; Fahrig et al., 2022; Liu et al., 2018). In general, single large habitat patches have been found to contain an equal or lesser number species than several small habitat patches (SL ≤ SS), but there is still a substantial amount of variation in these inferences among both taxa and landscapes. In this study, SAC (saturation index) and SAR extrapolation (SLOSS index) analyses resolved that several small islands contained at least as many woody plant, bird and spider species as a single large island, suggesting a positive or neutral fragmentation effect. However, varying the size of islands that were included in these analyses resulted in variation in inferences, allowing us to examine geographical and biogeographical variables that affect emergent SLOSS patterns.

4.1 | Possible explanations for positive fragmentation effects

Our results indicated that several small islands contained at least as many woody plant, bird and spider species as a single large island in the research archipelago, indicating a positive fragmentation effect (saturation index >0). Several studies have also suggested that SLOSS patterns are related to habitat heterogeneity (e.g. Liu et al., 2018). If several small habitat patches contain a greater diversity of habitats than a single large island, they may also be expected to support a greater number of species (Nillson et al., 1988; Williams, 1964). In a previous study addressing islands of this archipelago, Liu et al. (2018) found that accumulation of both environmental heterogeneity and species richness was greater for sets of small islands than for sets of large islands with equivalent cumulative area. Given a positive relationship between environmental and habitat heterogeneity, several smaller islands are likely to contain a greater diversity of micro-habitats compared with fewer or single larger islands (Fahrig et al., 2022; Gavish et al., 2012; Liu et al., 2018; MacDonald et al., 2018a; Tscharntke et al., 2012). Additionally, even though species richness of individual small island may be lower than the species richness of an equal-sized sampling plot in a large island (Phillips et al., 2017), several small heterogeneous islands may harbour more species than a single large island if species turnover among small islands is substantial (Deane et al., 2020; Liu et al., 2018).

If several small habitat patches have higher immigration/colonization rate than a single large patch, then the positive fragmentation effect could also be supported (Fahrig et al., 2022). Previous studies have inferred that island area rather than isolation is the main variable driving the assembly of woody plants, birds and spiders in the research archipelago (Hu et al., 2021; Wilson et al., 2016). When dispersal is effectively connecting all islands, and species have a high immigration

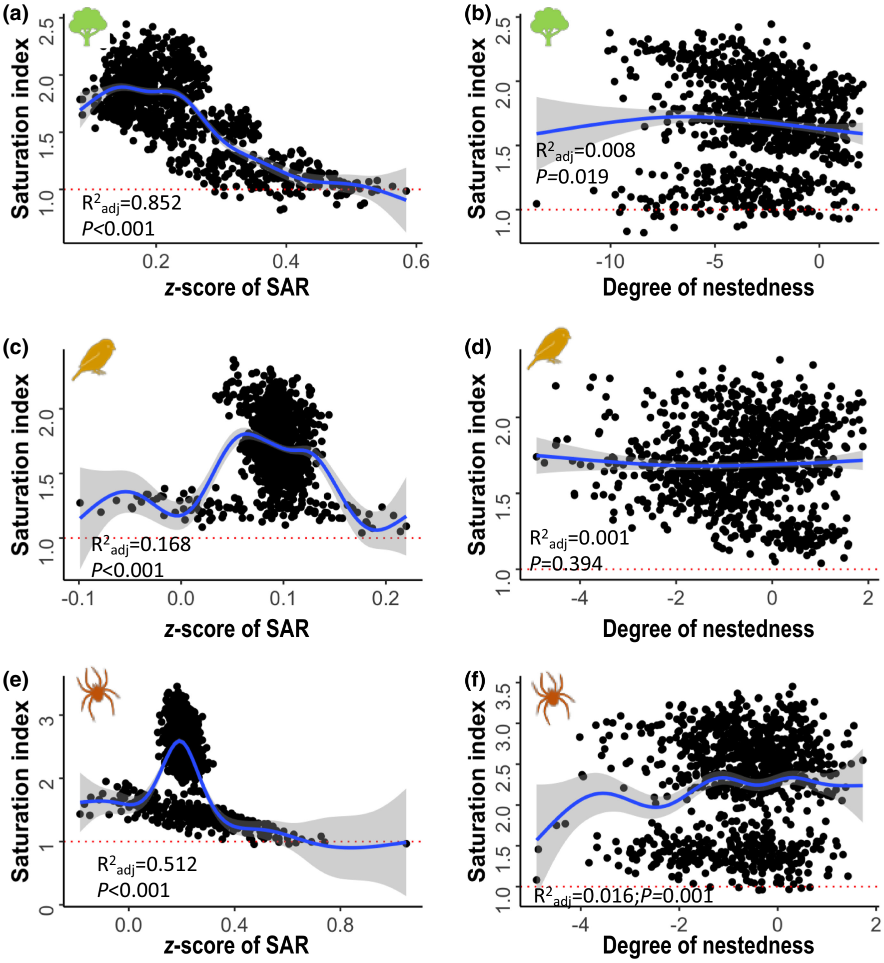

FIGURE 2 The fit of generalized additive models (GAM) with 95% confidence interval examining the relationship between the saturation index and slope of SAR (*z*-score), and degree of nestedness (SES) when randomly selecting 10 islands for 999 repeats for woody plants (a, b), birds (c, d) and spiders (e, f)

rate across islands, then for most dispersal and habitat searching behaviours, several small islands are predicted to intercept more dispersers than a single large island because of the higher edge-to-area ratio (Bowman et al., 2002; Fahrig et al., 2022). Several small islands may therefore experience a higher colonization rate than a single large island of a comparable area, increasing the species richness of several small islands relative to a single large island (Fahrig et al., 2022).

4.2 | Effects of maximum island area and *z*-score on SLOSS-based inferences

Our analyses showed that the maximum area of islands included in SLOSS-based analyses had a significant effect on inferences of fragmentation effects. Several small islands were more likely to contain an increasingly greater number of species relative to a single large island as the maximum area of islands included in SAC analyses was increased for all (Figure 1), common (Figure S4) and rare (Figure S5) species of all three taxa. The results do not support the prediction that inclusion of larger islands will result in the detection of species with large minimum area requirements (Gotelli & Graves, 1996; Soulé & Simberloff, 1986), indicating the distribution of species across islands is not limited by the minimum island area in this research system. As maximum island area increased, the increased same total area of several small islands probably has higher habitat heterogeneity to allow more species colonization than large islands do, resulting in an increase in species richness of several smaller islands relative to larger islands. Moreover, because rare species richness of several smaller islands also increased relative to larger islands as the maximum island area increases in SAC analysis, it is likely that more specific habitats for rare species could be contained on several small islands than on large islands when more small islands were included. While we also found that SAC analysis and SAR extrapolation analysis could produce different or even opposite results for birds (Figure 1c vs. Figure 3d) and spiders (Figure 1e vs. Figure 3g) as the maximum area of islands changes. This result highlighted that fragmentation effects inferred by the two analyses could be different and which affected by the maximum patch area in a fragmented landscape, especially for animal groups.

We also showed a significant negative relationship between the maximum area of islands included in analyses and the slope of SAR (*z*-scores) (Table 1). Our results indicate that the overall rate at which species richness changes with island area decreases as the maximum island area increases in the archipelago. Accordingly, we found that several small islands contain more species than a single large island increased in the system with lowest *z*-scores for all (Figures 2, 3), rare and common species (Figures S4, S5) in the three taxa when using the SAC and SAR extrapolation analysis. Generally, the island system with the lowest *z*-score has the least isolation such that species on smaller islands

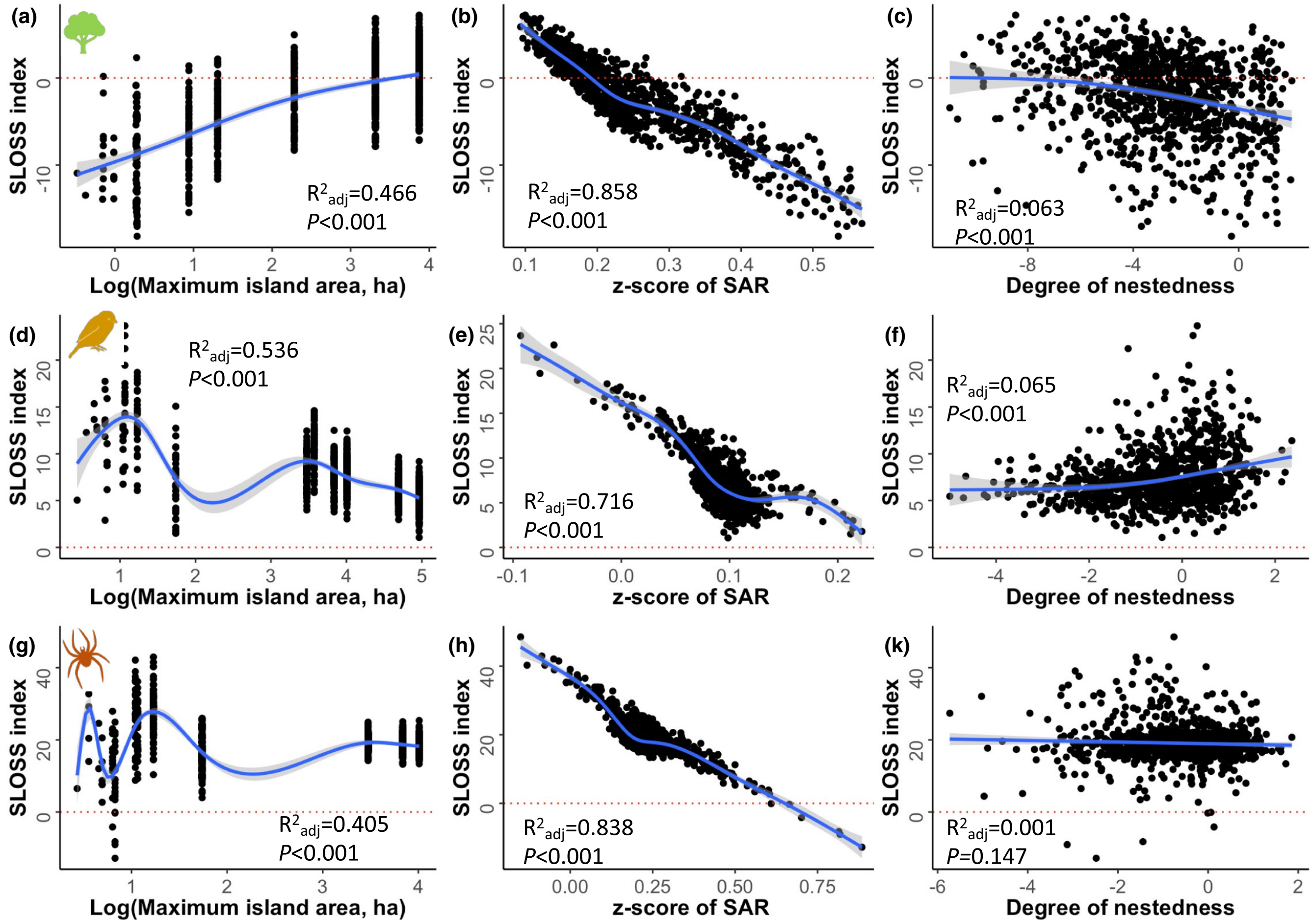

FIGURE 3 The fit of generalized additive models (GAM) with 95% confidence interval examining the relationship between SLOSS index and maximum island area, slope of SAR (*z*-score) and degree of nestedness (SES) when randomly selecting 10 islands for 999 repeats for woody plants (a, b, c), birds (d, e, f) and spiders (g, h, k)

TABLE 1 The Pearson's product–moment correlation for the maximum island area, z-score of SAR and degree of nestedness when randomly selected 10 islands

	Maximum island area	Degree of nestedness
z-score of SAR	−0.766***	0.041^{ns}
Degree of nestedness	−0.006^{ns}	1.00

Abbreviation: ns, no significance.

****p*-value <0.001.

usually have a higher immigration rate and are rapidly rescued from extinction through recolonization from the large island or mainland (i.e. rescue effects), therefore exhibiting comparatively high richness even on smaller islands (See 4.1 for more detailed explanation) (Matthews et al., 2021; Whittaker & Fernández-Palacios, 2007). The lower *z*-score may be due to the increased dispersal abilities of taxa, leading to more homogeneous biota between islands (Matthews et al., 2016). For example, MacDonald et al. (2018b) found that the inter-island movement of highly mobile species from larger islands or mainland habitats to small islands inflated the number of small island species observed. Hence, in systems that are characterized by a higher maximum island area and thus lower *z*-scores, since colonization process dominates the outcome of extinction–colonization dynamics (Fahrig et al., 2022), there will be more species on multiple small islands than on large islands of the same area (Figure 4c). By contrast, islands in systems with intermediate isolation and small size will have steeper slopes (higher *z*-scores). Theoretically, the smallest islands have low species richness in the higher *z*-scores systems, because their small, unreliable resource bases cannot sustain marginal populations of small size or permit the species recolonization (Matthews et al., 2021). Therefore, in higher *z*-score and smaller patch characterization systems, the number of species accumulated on smaller islands will be lower than the number of species on a larger island with comparable areas (Figure 4a, b).

4.3 | Effects of nestedness on SLOSS-based inferences

Theoretically, if species composition distribution across islands is perfectly nested, then several small islands cannot have more species than a single large island of comparable area. Working

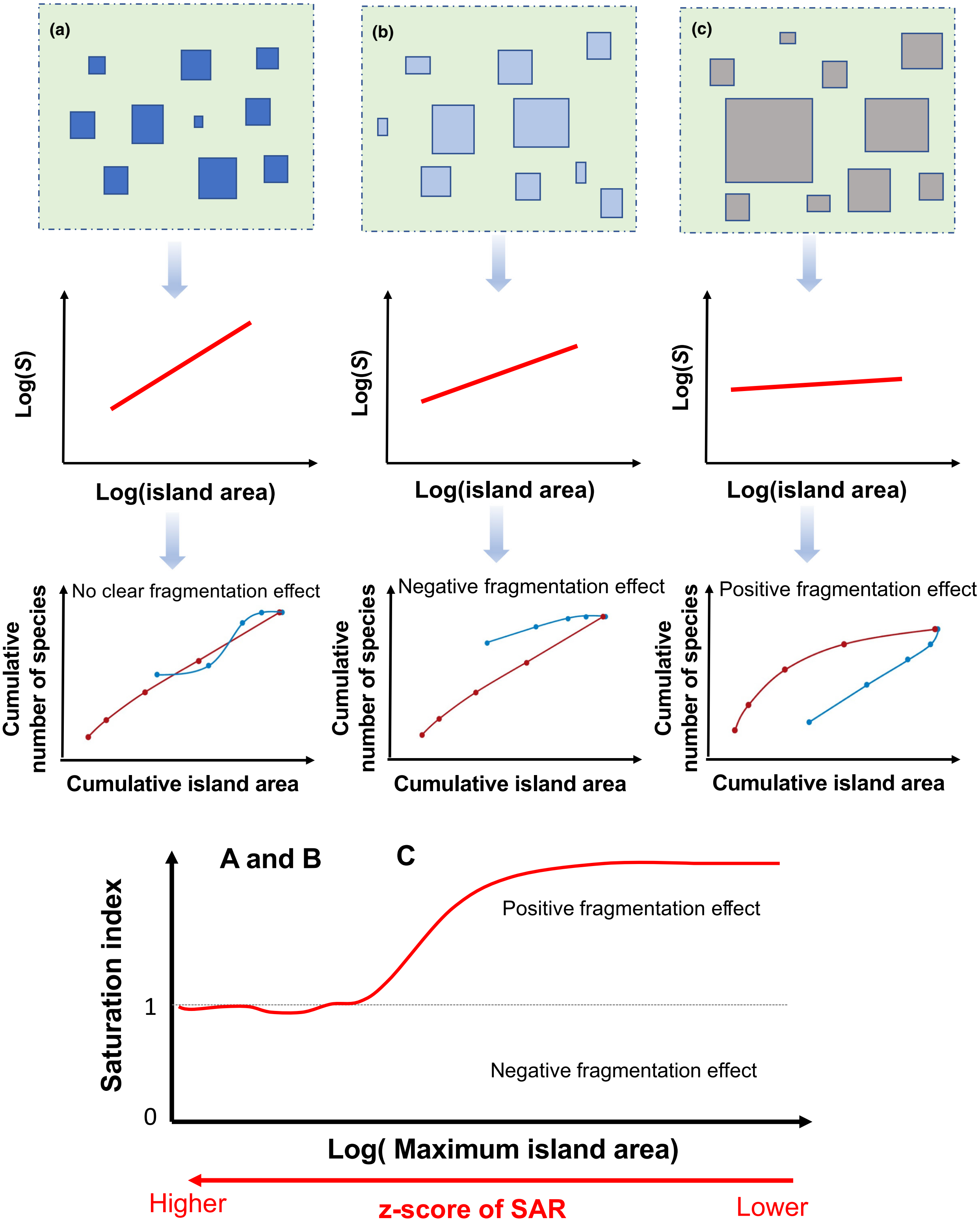

FIGURE 4 Examples of how maximum island area and slope of SAR may have profound effects on saturation index (i.e. SLOSS pattern). The dotted boxes correspond to fragmented systems. Changes from landscape (a) to (c) increase maximum island area and reduce *z*-score (slope of SAR). The number of species accumulated on several smaller islands will be equal to (no clear fragmentation effect) or lower (negative fragmentation effect) than the number of species on larger island with comparable area that are characterized by higher *z*-scores and with smaller maximum area (a and b). In contrast, multiple small islands may accumulate more species than that of few large islands of the same size (saturation index >1, positive fragmentation effect) that are characterized by lower *z*-scores and with larger maximum area (c)

backwards through this relationship, negative relationships between the degree of nestedness and saturation index (or SLOSS index) may be expected. Here we found that there was a weak correlation between the degree of nestedness and saturation index (or SLOSS index) for all, rare and common species of woody plants, birds and spiders (the low adjusted R^2 values in Figures 2, 3). In this study, almost all the SES values were deviating from significant nestedeness SES values (i.e. lower than 1.96) for woody plants (e.g. 38.2% SES values within the range of −1.96 and 1.96, and 61.5% SES values below −1.96), birds (87.5% SES values within the range of −1.96 and 1.96, and 12.0% SES values below −1.96) and spiders (87.3% SES values within the range of −1.96 and 1.96, and 12.6% SES values below −1.96) (Figure 2), indicating a random or anti-nestedness species distribution across islands (Matthews et al., 2015). Because isolation is not an important factor structuring the assembly of woody plants, birds, and spiders in the study archipelago (Hu et al., 2021; Wilson et al., 2016), the higher immigration/colonization rate of species among islands may lead to a weaker nestedness of species composition along the island size gradient (Fahrig et al., 2022; Matthews et al., 2015). In the future studies, the relationship between the degree of nestedness and SLOSS pattern can be further analysed in systems with different nestedness patterns.

5 | CONCLUSIONS AND CONSERVATION IMPLICATIONS

According to our results, we infer that several small islands contained at least as many species as a single large island with a comparable area. Variation in SLOSS-based inferences was related both to the maximum island area of islands included in analyses and the slope of SAR among islands. Therefore, we should be cautious of conclusions regarding the positive effect of fragmentation based on reviews of SLOSS studies, as these may be biased if the maximum patch area included in the analysis exceeds a certain threshold in these studies (Fletcher et al., 2018). This is especially important when deciding to protect a large patch or several small patches, as we should consider the maximum patch area or the slope of SAR in a fragmentated landscape. Based on our findings, when the maximum patch area is above a certain threshold area and the slope of SAR is low in a landscape, protecting only the largest patch is not enough. This is because the probability that multiple smaller fragments of comparable areas conserves more species increased as the patch area increased and the slope of SAR decreased (Oertli et al., 2002). In cases where there are patches smaller than a certain threshold area and thus with steep slope of SARs due to their intermediate isolation in a fragmented landscape, the largest patch could also conserve more species than several smaller patches of equivalent area because the largest patch could sustain the rarest specialist and occasional taxa or permit persistence of newly formed endemics (Deshaye & Morisset, 1989; Matthews et al., 2021). Therefore, in systems with higher slope of SARs (Matthews et al., 2021), the more efficient conservation strategy would be to protect the largest patch. Overall, whether to conserve a single large or several small patches depends on the geographical (e.g. maximum patch area) and biogeographical (e.g. slope of SAR) attributes in a fragmentated landscape. However, in this study, we only examined three variables, but other geographical and biogeographical factors can also play important role in explaining SLOSS patterns, such as geographical regions (tropical/temperate), habitat patch types (e.g. water ponds) and matrix types (e.g. shade coffee plantations surrounding forest fragments), spatial heterogeneity (e.g. lowlands/hilltops), taxonomic groups and associated species traits.

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CONFLICT OF INTEREST

The authors declare no competing interests.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in the Si et al. (2015) at https://doi.org/10.1371/journal.pone.0127692, Wu et al. (2017) at https://doi.org/10.1111/jbi.13007, and Liu et al. (2020) at https://doi.org/10.1111/13652745.13272.

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