

# The theory of island biogeography, the sample-area effect, and the habitat diversity hypothesis: complementarity in a naturally fragmented landscape of lake islands

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## Abstract

**Aim:** Investigate relationships between fragmentation and species diversity in the context of the theory of island biogeography, sample-area effect, and habitat diversity hypothesis.

**Location:** Lake of the Woods, Canada.

**Taxon:** Vascular plants

**Methods:** Vascular plant species diversity was inventoried on 30 islands, organized into two island sets. Each island set contained four size classes that varied in degree of fragmentation while controlling for the sample-area effect (small island set: 8 × 0.1-ha, 4 × 0.2-ha, 2 × 0.4-ha, and 1 × 0.8-ha islands; large island set: identical pattern utilizing 1.0-ha to 8.0-ha islands). Fragmentation effects were then examined using SLOSS-based analyses, addressing whether single large or several small islands contained more species/habitats: (a) direct comparisons of species and habitat richness across size classes; (b) extrapolations of species–area relationships; and (c) analyses of species and habitat accumulation curves. Multi-group path analysis was next used to quantify effects of habitat diversity, island area, and isolation on species richness for both island sets. Finally, pairwise and multiple-site dissimilarity was estimated for both species and habitats across 0.1-ha and 1.0-ha islands to investigate whether: (a) variation in species composition was related to habitat composition; and (b) species dissimilarity increased with inter-island distance.

**Results:** SLOSS-based analyses indicated that several small islands contained more species than single large islands in both island sets. This pattern was also observed for habitats, but only in the small islands set. Path analysis suggested that island area had significant direct and indirect (mediated by habitat diversity) effects on species richness. Habitat diversity and island isolation had significant positive and negative effects on species richness, respectively, independent of island area. Species and habitat dissimilarities were significantly related across 0.1-ha but not 1.0-ha islands, and showed no relationship to inter-island distance.

**Main conclusions:** The overall positive relationship between fragmentation and species richness may be attributed to greater habitat diversity and increased species dissimilarity across smaller islands relative to larger islands. However, negative isolation effects indicate that landscape configuration is still an important conservation



consideration. These results each align with different predictions of the theory of island biogeography, sample-area effect, and habitat diversity hypothesis, questioning the exclusivity of these theoretical frameworks.

#### KEYWORDS

habitat amount hypothesis, habitat diversity, habitat fragmentation, island biogeography, sample-area effect, SLOSS, small island effect, species–area relationship, structural equation model, vascular plants

## 1 | INTRODUCTION

The diversity of species on islands has been a topic of considerable research in ecology for well over a century (e.g., Darwin, 1859; Wilson & MacArthur, 1967), resulting in a variety of theoretical explanations for variation in insular communities (Gotelli & Graves, 1996; Rosenzweig, 1995; Watson, 2002). Ecologists have applied these explanations to diversity patterns on fragmented landscapes, interpreting isolated fragments as ecological islands situated in a sea of unsuitable habitat (Haila, 2002). However, fragmentation effects on individual species and entire communities appear to be largely idiosyncratic, limiting the generality of fragmentation–species diversity relationships (Debinski & Holt, 2000; MacDonald, Anderson, Acorn, & Nielsen, 2018). Still, a single recurrent pattern stands out; area is a good predictor of species richness at both the fragment and landscape level (Nilsson, Bengtsson, & As, 1988; Rosenzweig, 1995; Fahrig, 2013; but see Lomolino & Weiser, 2001). Three principal frameworks addressing distinct ecological processes have been proposed to account for this positive species–area relationship: (a) the theory of island biogeography (MacArthur & Wilson, 1963; Wilson & MacArthur, 1967); (b) the sample-area effect (Connor & McCoy, 1979; Fahrig, 2013); and (c) the habitat diversity hypothesis (Williams, 1964).

Developed in the context of oceanic islands, the theory of island biogeography interprets insular species richness as an equilibrium between extinction and immigration rates, arising from the effects of island area and isolation on demographic processes (MacArthur & Wilson, 1963; Wilson & MacArthur, 1967). Larger islands generally support larger populations relative to smaller islands, decreasing probabilities of inbreeding depression and stochastic extinction (Hanski, 1999). Gilpin and Diamond (1976) add that larger islands also present larger dispersal targets, increasing probabilities of colonization (i.e., the target area effect). Of conservation interest, summing probabilities of colonization and persistence across species provides a mechanistic explanation for the species–area relationship across ecological islands, whether they are oceanic or terrestrial. Island configuration is also invoked as a predictor of species richness, as rates of species immigration (Simberloff & Wilson, 1969) and rescue effects (Brown & Kodric-Brown, 1977) generally decrease as islands become further isolated from sources of species immigration, such as the mainland or other islands.

While lack of empirical evidence and a plethora of competing models have led many ecologists to infer that the theory of island

biogeography has been largely overturned (Gotelli & Graves, 1996; Lomolino, 2000), equilibristic interpretations of species richness on fragmented landscapes still appear to constitute a dominant scientific paradigm (*sensu* Kuhn 1967) in ecology (Haila, 2002; Mendenhall, Karp, Meyer, Hadly, & Daily, 2014). Demographic effects predicted by the theory of island biogeography suggest that decreasing fragment area and increasing fragment isolation pose considerable threats to species diversity, thereby warranting continued investigation (Diamond, 1975; Haddad et al., 2017; May, 1975; Rybicki & Hanski, 2013; Wilson & Willis, 1975). If fragmentation indeed reduces species diversity via processes predicted by the theory of island biogeography, “island effects” should ultimately result in several smaller fragments containing fewer species than single larger fragments of equal area (*sensu* Fahrig, 2013). Independent of fragment area, species richness is also predicted to decrease as fragment isolation increases (Diamond, 1975; Gotelli & Graves, 1996; Wilson & Willis, 1975). Such predictions are often framed in terms of the ongoing SLOSS debate, addressing whether conservation efforts should prioritize the protection of single large or several small conservation reserves (Diamond, 1975; Simberloff & Abele, 1982; Tjørve, 2010). If fragmentation reduces species richness, finite conservation efforts may be best allocated to “single large” conservation strategies (Simberloff & Abele, 1976, 1982) and maximizing connectivity within fragmented landscapes (Haddad et al., 2017; Rybicki & Hanski, 2013).

Contrasting with the theory of island biogeography, the habitat amount hypothesis (Fahrig, 2013) replaces fragment area and isolation with a single predictor of species richness, total habitat area. Not unlike the passive sampling hypothesis, developed in the context of oceanic islands (Connor & McCoy, 1979), the habitat amount hypothesis uses the sample-area effect to explain positive species–area relationships across isolated fragments: larger sample areas generally contain more individuals, belonging to more species (Burns, Berg, Bialynicka-Birula, Kratchmer, & Shortt, 2010; Fahrig, 2013). In SLOSS terms, the sample-area effect specifically predicts that single large and several small fragments will contain equivalent numbers of species when total area is held constant. The habitat amount hypothesis also interprets negative relationships between fragment isolation and species richness as sampling artefacts, based on two premises: (a) total habitat area is the principal determinant of local species pools because fragment edges do not typically delimit populations (i.e., extinction and colonization occur at the landscape level,

and not within individual fragments); and (b) fragment isolation generally increases as total habitat area decreases. Species richness may therefore decrease with fragment isolation simply because of reductions in total habitat area at the landscape level, rather than increases in degree of fragmentation per se (Fahrig, 2013).

Heuristics outlined by the habitat amount hypothesis offer a compelling gestalt switch (*sensu* Kuhn 1962) away from viewing fragments as natural spatial units for measuring and interpreting species richness. However, the hypothesis fails to account for variation in habitat composition both within and between fragments, as well as interspecific variation in habitat associations. Habitat associations differ considerably between species (Hortal, Triantis, Meiri, Thébault, & Sfenthourakis, 2009), challenging applications of single habitat definitions to entire communities and begging the question as to whether relationships between habitat amount and species richness are even meaningful (*sensu* Hanski, 2015). Indeed, there is a strong theoretical and empirical basis to suggest that habitat diversity is a principal determinant of species richness within islands, fragments, and entire landscapes (Hortal et al., 2009; Kadmon & Allouche, 2007; Rosenzweig, 1995).

The habitat diversity hypothesis (Williams, 1964) represents a third explanation of positive species–area relationships that is predicated on interspecific variation in habitat associations. Specifically, the habitat diversity hypothesis predicts that area per se has minor effects on demographic processes, and hence species richness, and instead serves as a surrogate variable for habitat diversity (Gotelli & Graves, 1996). Larger sample areas generally contain more habitats, which support more species (Rosenzweig, 1995; Williams, 1964). A specific and testable prediction of the habitat diversity hypothesis is that species diversity and habitat diversity will positively correlate independent of island or fragment area (e.g., MacArthur & MacArthur, 1961). Nevertheless, it remains controversial whether habitat diversity or area per se is more important in structuring patterns of species richness on fragmented landscapes, and the habitat diversity hypothesis makes no specific predictions of fragmentation effects. While there is support for effects of habitat diversity on species richness independent of area (Burns et al., 2010; Hortal et al., 2009; Kohn & Walsh, 1994), there is also support for direct effects of area per se on demographic processes affecting species richness (Buckley, 1982; Nilsson et al., 1988). An important consideration in such investigations is scale, as the relative importance of habitat diversity and area per se has been shown to vary with island or fragment area (Rosenzweig, 1995; Sfenthourakis & Triantis, 2009). For instance, species–area relationships often become unpredictable below threshold island or fragment sizes (i.e., the small island effect; Lomolino & Weiser, 2001; Triantis et al., 2006). Here, habitat diversity and isolation frequently replace area as the strongest predictor of species richness (Sfenthourakis & Triantis, 2009).

In this study, we estimated vascular plant species diversity and habitat diversity on 30 lake islands through repeated full-island surveys. We then used a series of SLOSS-based analyses, path analysis, and analyses of species and habitat dissimilarity ( $\beta$ -diversity) to investigate ecological processes underlying the species–area relationship

and their implicated fragmentation effects. While species and habitat dissimilarity are widely understood as principal determinants of aggregate species richness ( $\gamma$ -diversity) in a variety of insular systems (Gotelli & Graves, 1996; Rosenzweig, 1995; Simberloff, 1988), their importance is seldomly explicitly recognized in SLOSS-based investigations of fragmented landscapes (e.g., Yaacobi, Ziv, & Rosenzweig, 2007; Gavish, Ziv, & Rosenzweig, 2012; but see Wright & Reeves, 1992; Tjørve, 2010). Results of this study indicate that patterns of species and habitat dissimilarity are important considerations that warrant continued investigation in the context of fragmentation–species diversity relationships.

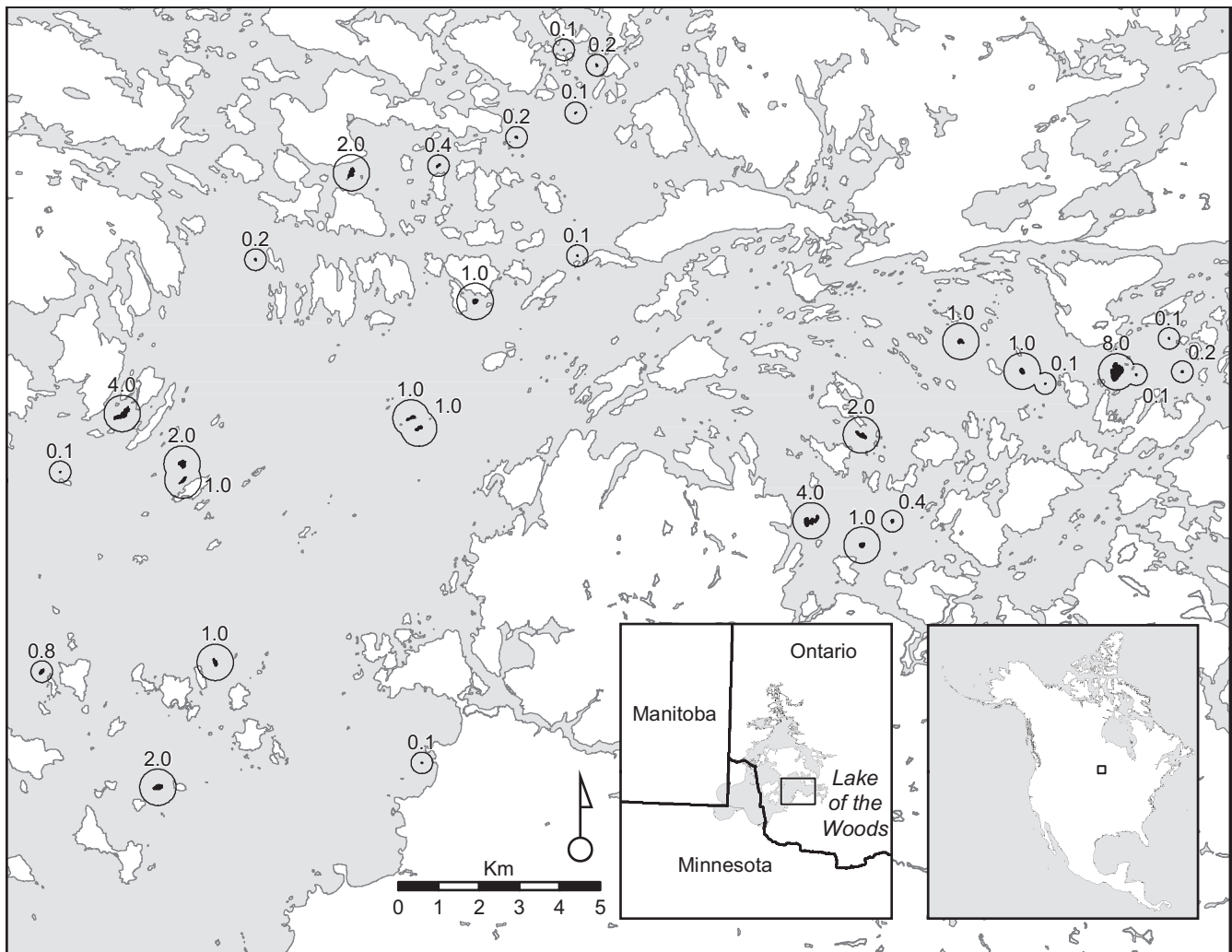
## 2 | MATERIALS AND METHODS

### 2.1 | Study area

Observations were made on islands within Sabaskong Bay at the southeastern corner of Lake of the Woods, Ontario, Canada (Figure 1). Sabaskong Bay is located in transitional zone between boreal forest to the north, Laurentian forest to the southeast, and, to a lesser extent, tallgrass prairie to the southwest. Local flora is therefore a mix of boreal tree species (e.g., *Pinus banksiana*, *Betula papyrifera*, and *Picea glauca*), Laurentian tree species (e.g., *Acer spicatum*, *Tilia americana*, and *Pinus strobus*), and few tree species from the Eastern prairies (e.g., *Quercus macrocarpa* and *Fraxinus pensylvanica*). All study islands are included within the Lake of the Woods Conservation Reserve, where residential and commercial developments are prohibited (Ontario Ministry of Natural Resources, 2006). Island isolation is hypothesized to have occurred between 3000 and 4000 years ago, when differential rates of isostatic rebound and outlet restriction caused the progressive southward transgression of the remnants of Glacial Lake Agassiz, inundating Sabaskong Bay (Yang & Teller, 2005). Islands within this system therefore represent “old high-contrast fragments,” appropriate for inferring long-term fragmentation effects on species richness (*sensu* Watson, 2002).

### 2.2 | Sampling design

A nested set sampling design was used to decouple the effects of island configuration from those of island area (i.e., decouple the effects of fragmentation per se from those of habitat loss; *sensu* Fahrig, 2003, 2013). Specifically, 30 study islands were randomly selected from a list of candidate islands and organized into two sets of non-overlapping size classes (Table 1; see Appendix S1 in Supporting Information for island selection criteria). Four size classes in the small island set consisted of eight 0.1-ha islands, four 0.2-ha islands, two 0.4-ha islands, and a single 0.8-ha island. The large island set followed an identical logarithmic pattern using islands ranging from 1.0 to 8.0 ha. Within each island set, degree of fragmentation decreased across increasing size classes, with the largest size class (a single island) representing the “single large” conservation strategy, and the smallest size class (a highly fragmented set of islands) representing the “several small” conservation strategy (*sensu* Gavish et al., 2012).



**FIGURE 1** Map of the study area, located in Lake of the Woods, Ontario, Canada. Study islands ( $n = 30$ ) in the small and large island sets are highlighted with small and large circles, respectively. Each island is labelled by size class (ha). Inset maps indicate the regional and continental location of the study area

Vascular plant species diversity was estimated on each island through repeated full-island surveys, conducted between 1 June 2015 and 20 August 2015. Handheld GPS units were used to ensure adequate coverage of all areas and habitats on islands during each survey. To maintain consistency in survey effort across all islands, survey time was standardized to 40 min per ha per survey. Four repeated surveys were completed on each island, resulting in a seasonal total of two hours and 40 min per ha. This is consistent with recent sampling-effort recommendations for boreal plant communities (Zhang et al., 2014). Specimens that could not be identified in the field were collected and identified with a microscope and keys (e.g., Chadde, 2013; Voss & Reznicek, 2012), and voucher specimens were deposited in the University of Alberta Vascular Plant Herbarium. Twenty-three unidentified specimens were recorded as distinct morphospecies and included in richness totals.

Habitat diversity was estimated on each island using the number and relative area of 14 distinct habitat types, defined using structural properties of vegetation and geological features. (See Supporting

Information Table S1.1 in Appendix S1 for habitat type descriptions.) While this habitat classification scheme is not entirely independent of plant diversity, no individual plant species were used in the delineation of habitat types. Only higher level taxonomic information was used (e.g., coniferous vs. deciduous forest), limiting the circularity of habitat diversity–species diversity relationships. The exclusion of all vegetation characteristics, in favour soil physical and chemical components, in a habitat classification scheme may be appropriate for testing environmental filtering and related hypotheses (e.g., Kraft et al., 2015), but not necessarily the habitat diversity hypothesis, which considers both biotic and abiotic factors affecting species richness (Nilsson et al., 1988; Rosenzweig, 1995; Williams, 1964).

### 2.3 | Comparisons of species and habitat richness

To investigate the effects of fragmentation while controlling for the sample-area effect, aggregate species richness was compared across island size classes within the small and large island set. If

**TABLE 1** Summary of the nested set sampling design used to decouple degree of fragmentation from total island area across two distinct ranges of island sizes. Within island sets, total island area is maintained across sizes classes by halving the number of replicates per twofold increase in the individual areas of constituent islands. Degree of fragmentation decreased across increasing size classes. Aggregate vascular plant species richness and habitat richness are reported by size class

Island Set	Size class (ha)	Number of islands	Total area (ha)	Species richness	Habitat richness
Small	0.1	8	0.8	114	9
Small	0.2	4	0.8	112	11
Small	0.4	2	0.8	95	8
Small	0.8	1	0.8	106	7
∑ Small		15	~3.2	179	12
Large	1.0	8	8.0	177	12
Large	2.0	4	8.0	195	13
Large	4.0	2	8.0	194	14
Large	8.0	1	8.0	167	12
∑ Large		15	~32.0	272	14
∑ Complete		30	~35.2	281	14

fragmentation reduced species richness via island effects (*sensu* Willis & Willis, 1975; May, 1975; Diamond, 1975), aggregate species richness should be lowest within the smallest size classes in each island set (highest degree of fragmentation), and increase across larger size classes (lower degrees of fragmentation). Any other arrangement of species richness would suggest that fragmentation did not reduce species richness, but would not necessarily support the habitat amount hypothesis. The underlying sample-area effect specifically predicts species richness as unrelated to degree of fragmentation when total area is held constant, equating to an even distribution of species richness across size classes. A third possible result is species richness increasing with degree of fragmentation. This positive fragmentation effect would align with the habitat diversity hypothesis if several smaller islands contained a greater number of habitats than fewer or single larger islands. To test for this possibility, aggregate habitat richness was compared across island size classes within each island set. Pearson product-moment correlations were then used to assess relationships between species richness and habitat richness across islands in the 0.1-ha and 1.0-ha size classes, effectively controlling for island area.

## 2.4 | Species–area relationship extrapolation

To further investigate the effects of fragmentation on species diversity, island species–area relationships (ISAR) were estimated using linear models for the small, large, and complete island sets (all 30 study islands together). As suggested by Rosenzweig (1995) for insular plant communities, semi-log ISARs were used. Each ISAR was extrapolated to generate a species richness estimate for a single theoretical island, equivalent in area to all islands used to generate the ISAR (3.21, 32.13, and 35.34 ha for the small, large, and complete

island set, respectively). This ISAR species richness estimate was then compared to the aggregate species richness of study islands used to generate the ISAR (e.g., Gavish et al., 2012; Matthews et al., 2016; Yaacobi et al., 2007). In SLOSS terms, the aggregate species richness of study islands is analogous to the “several small” conservation strategy ( $S_{ss}$ ), while the ISAR species richness estimate for a single theoretical island is analogous to the “single large” conservation strategy ( $S_{sl}$ ; Gavish et al., 2012; MacDonald et al., 2018). A SLOSS index, estimated as  $100\% \times (S_{ss} - S_{sl})/S_{ss}$ , was used to compare the aggregate species richness of study islands to the ISAR species richness estimate in each island set (Boecklen, 1997). Similar extrapolations were not used for island habitat–area relationships, as resulting habitat richness estimates for single theoretical islands exceeded the total number of defined habitat types in our a priori habitat classification scheme, indicating they were not meaningful.

If fragmentation reduced species richness at any given size scale (small, large, or complete island set), the aggregate species richness of study islands will be lower than the ISAR species richness estimate for the corresponding theoretical island ( $S_{ss} < S_{sl}$ ). If islands passively sampled species, as predicted by the habitat amount hypothesis, the aggregate species richness of study islands will be approximately equivalent to the ISAR species richness estimate ( $S_{ss} \approx S_{sl}$ ). If habitat fragmentation positively affected species richness, the aggregate species richness of study islands will be greater than the ISAR species richness estimate ( $S_{ss} > S_{sl}$ ). Extrapolated ISAR 95% confidence intervals were used to determine the significance of fragmentation effects (MacDonald et al., 2018).

## 2.5 | Accumulation of species and habitats

To assess patterns of species and habitat accumulation across islands in the small, large, and complete island set, cumulative species richness and habitat richness were plotted against cumulative island area in two ways: (a) increasing order of island area (small to large); and (b) decreasing order of island area (large to small; Quinn & Harrison, 1988). The resulting accumulation curves were made to pass through the origin, permitting direct area-under-the-curve comparisons (Gavish et al., 2012; Quinn & Harrison, 1988). A saturation index, estimated as the area under the small-to-large accumulation curve relative to that of the large-to-small accumulation curve, was used to quantitatively compare accumulation patterns. Integrals were calculated using the trapezoidal rule.

Steeper slopes of large-to-small accumulation curves relative to small-to-large accumulation curves (saturation index  $< 1$ ) may be driven by two diversity patterns: (a) a nested pattern of species or habitat richness with respect to island area (Matthews et al., 2016); or (b) fewer or single larger islands containing more species or habitats than several smaller islands (Gavish et al., 2012; Quinn & Harrison, 1988). In either case, steeper large-to-small accumulation curves would suggest that fragmentation negatively affected the richness of species or habitats. Similarity between the slopes of small-to-large and large-to-small accumulation curves (saturation index  $\approx 1$ ) would indicate that numbers of species or habitats



increased with cumulative area, irrespective of degree of fragmentation. This result would suggest that islands passively sampled species or habitats (Fahrig, 2013). A third possibility, steeper small-to-large accumulation curves (saturation index > 1), would indicate that several smaller islands contained more species or habitats than fewer or single larger islands, suggesting a positive fragmentation effect on species or habitat richness.

## 2.6 | Path analysis

If habitat diversity and island isolation contribute to patterns of insular species richness, they should make a statistical contribution to variation in species richness beyond that explained by area per se (Gotelli & Graves, 1996). However, strong collinearity between habitat diversity and area questions the efficacy of multiple and residual regression techniques (Connor & Simberloff, 1978; Freckleton, 2002). Furthermore, area is hypothesized to be a principal determinant of habitat diversity, thereby having both direct and indirect effects on species richness (Hortal et al., 2009; Rosenzweig, 1995; Triantis et al., 2006; Williams, 1964). We therefore used path analysis with correlated causes (a structural equation model) to assess both direct and indirect effects of predictor variables according to an a priori model structure (Grace & Pugsek, 1997, 1998; Li, 1975). Path analysis is particularly useful for distinguishing the effects of multiple collinear variables (e.g., habitat diversity and area per se) on multiple response variables (for similar applications, see Kohn & Walsh, 1994; Triantis, Mylonas, Weiser, Lika, & Vardinoyannis, 2005; Triantis et al., 2006; Sfenthourakis & Triantis, 2009; Burns et al., 2010). Multigroup path analysis, grouped by small and large island set, permitted comparisons of relationships between the two ranges of island sizes used in SLOSS-based analyses. This effectively determines the extent to which ecological processes within the small and large island set may be approximated by a single model.

Multigroup path analysis was completed by constructing an initial multigroup path model, wherein all path coefficients were estimated using maximum likelihood and permitted to vary between the small and large island set. Path coefficients were then iteratively constrained to a single estimate for the small and large island set together (complete island set), and chi-squared difference tests were used to assess whether model fit was significantly reduced ( $\alpha = 0.05$ ) relative to the unconstrained multigroup path model (Grace, 2003). If model fit was not significantly reduced by a given constraint, we retained the single estimate, as this represents a more parsimonious model. This result would indicate that ecological processes moderating the relationship in question were consistent across the small and large island set. Alternatively, if model fit was significantly reduced by constraining coefficients for a given path to a single estimate, the respective estimates were permitted to vary between the small and large island set. This result would suggest that underlying ecological processes significantly differed between the small and large island set, suggesting size scale-dependency of the relationship.

Our a priori multigroup path model structure consisted of four variables; vascular plant species richness, habitat diversity, island

area, and island isolation. Within this model structure, habitat diversity, island area, and island isolation each directly affects species richness. Island area also directly affects habitat diversity, thereby having an additional indirect effect on species richness. This indirect effect was estimated as the product of: (a) the direct effect of island area on habitat diversity; and (b) the direct effect of habitat diversity on species richness. The total effect of island area on species richness was then estimated by summing direct and indirect effects (e.g., Kohn & Walsh, 1994). Habitat diversity was included in competing models as either habitat richness or the exponential of Shannon's entropy, estimated using the relative area of habitat types on each island (Jost, 2006). The best-supported measure of habitat diversity was determined using both  $R^2_{SP\ RICH}$  and  $R^2_{HAB\ DIV}$ , estimated as 1 – the standardized variance unexplained by the path model (“residual variance”) for species richness and habitat diversity, respectively. This method effectively minimizes the proportion of variance in endogenous variables left unexplained by the path model. As with ISARs, island area was log-transformed to account for non-linear relationships (Rosenzweig, 1995). Island isolation was estimated at multiple scales as the proportion of water (1 – proportion of landmass) within 250-, 500-, 1000-, 2500-, and 5000-m buffers. Buffers were drawn from island edges, ensuring isolation estimates were independent from island area. Proportion-based measures have been shown to be better predictors of immigration rates and related ecological processes than distance-based measures to nearest neighbour or landmass (Fahrig, 2013). The best-supported isolation buffer size was determined using Akaike's information criterion (AIC), where smaller AIC values indicate higher relative model support (Burnham & Anderson, 2004). AIC comparison is possible in this instance because island isolation is exogenous within the multigroup path model. Finally, a likelihood ratio test was used to assess the overall fit of the multigroup path model. Here, a non-significant result ( $\alpha = 0.05$ ) indicates that the covariance structure of the multigroup path model did not significantly differ from the observed covariance structure, equating to good model fit (Grace, 2008; Grace, Anderson, Olf, & Scheiner, 2010). Multigroup path analysis and related statistical tests were completed using the R package ‘lavaan’ (Rosseel, 2012).

## 2.7 | Dissimilarity of species and habitats

The theory of island biogeography predicts that species composition may vary substantially across islands of comparable area and isolation, with little variation in species richness (MacArthur & Wilson, 1963; Simberloff & Wilson, 1969; Wilson & MacArthur, 1967). The same may be true for habitats. Cryptic turnover of species and habitats may therefore obscure relationships predicted by the habitat diversity hypothesis (e.g., positive correlations between species richness and habitat richness across islands of equal area). To account for the identities of individual species and habitats, pairwise dissimilarity was estimated for both species and habitats across islands in the 0.1-ha and 1.0-ha size classes using the Jaccard pairwise dissimilarity index:  $d_{J-PAIR} = [b + c / (a + b + c)]$ , where  $a$  is the number of

species or habitats shared between two islands ( $i$  and  $j$ ),  $b$  is the number of species or habitats occurring on  $i$  but not  $j$ , and  $c$  is the number of species or habitats occurring on  $j$  but not  $i$ . This index is a monotonic transformation of beta diversity, accounting for both turnover and nestedness, and reflects the proportion of unshared species or habitats observed on two islands (Anderson et al., 2011; Baselga, 2012). Positive relationships between species dissimilarity and habitat dissimilarity would indicate that species diversity and habitat diversity were positively related independent of area, supporting the habitat diversity hypothesis. To investigate whether overall rates of species and habitat dissimilarity changed with island area, multiple-site dissimilarity was estimated for the 0.1-ha and 1.0-ha size classes using the Jaccard multiple-site dissimilarity index, referred to here as  $d_{J-MULT}$ , derived by Baselga (2012). Averages of pairwise dissimilarities are shown to produce misleading results, justifying this approach (Baselga, 2012). All dissimilarity indices were estimated using the R package 'betapart' (Baselga & Orme, 2012).

Pairwise species dissimilarity was also compared with inter-island (Euclidean) distance across islands in the 0.1- and 1.0-ha size classes. Several smaller fragments may be more likely to intersect the distributions of more species than fewer or single larger fragments, effectively sampling a higher diversity of species (Fahrig, 2013; Tjørve, 2010). Given this possibility, the sample-area effect may theoretically result in the spurious observation of positive fragmentation effects when using SLOSS-based analyses. Positive relationships between pairwise species dissimilarity and inter-island distance would indicate that the expanded spatial distribution of several smaller islands, relative to fewer or single larger islands, contributed to their aggregate species richness. Lack of such relationships would suggest that islands did not significantly differ in their pools of potential immigrants, and that their diversities were not significantly spatially auto-correlated. Simple Mantel tests (999 permutations) were used to assess whether relationships between pairwise species dissimilarity, pairwise habitat dissimilarity, and inter-island distance were significant (Anderson et al., 2011). All statistical analyses were performed using the statistical software R version 3.4.3 (R Core Team, 2017).

### 3 | RESULTS

#### 3.1 | Comparisons of species and habitat richness

A total of 179 and 272 vascular plant species were observed within the small (0.1 to 0.8 ha) and large (1.0 to 8.0 ha) island sets, respectively (Table 1). Aggregate species richness across all 30 study islands was 281, indicating that vascular plant diversity of the small island set was largely nested within that of the large island set. Although aggregate species richness did not consistently increase or decrease with degree of fragmentation in the small island set, each of the two smallest size classes (0.1 and 0.2 ha) contained more species than the two largest size classes (0.4 and 0.8 ha). No clear trend in aggregate species richness was observed across size classes in the large island set.

Similar relationships were observed for comparisons of habitat richness across size classes. In the small island set, the two smallest

size classes contained more habitats than the two largest size classes, with habitat richness ranging from 7 to 12. Habitat richness was less variable in the large island set, ranging from 12 to 14 (all habitat types present). This suggests that a total area of 8.0 ha accumulates most of the defined habitat types to near saturation. There was no clear trend in habitat richness across size classes at this size scale. Species richness and habitat richness were positively correlated across 0.1-ha islands ( $r_{\text{Pearson}} = 0.893$ ,  $p = 0.003$ ), but not 1.0-ha islands ( $r_{\text{Pearson}} = 0.056$ ,  $p = 0.896$ ).

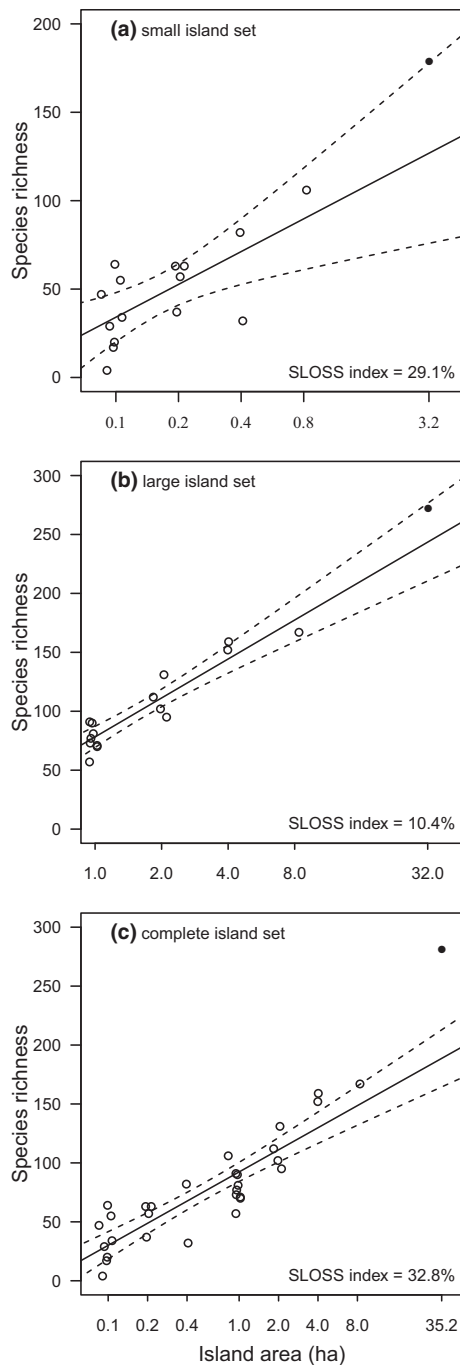
#### 3.2 | Species–area relationship extrapolation

The aggregate species richness of study islands was greater than the ISAR species richness estimate for a single theoretical island ( $S_{ss} > S_s$ ) for the small, large, and complete island set (Figure 2a–c, respectively). However, not all differences were significant. Aggregate species richness across islands in the small island set was observed to be 179; significantly higher than the ISAR species richness estimate of 126.93 for a theoretical 3.21-ha island (95% CI = [75.92, 177.94]). Here, the SLOSS index estimate indicated that a fragmented set of islands of this configuration is expected, on average, to contain 29.1% more species than a single large island of equal area. In the large island set, aggregate species richness was observed at 272, which did not significantly differ from the ISAR species richness estimate of 243.72 for a theoretical 32.13-ha island (95% CI = [210.73, 276.71]). Notwithstanding, the SLOSS index estimate indicated that a fragmented set of islands is expected to contain 10.4% more species than a single large island. In the complete island set (all 30 study islands), aggregate species richness was observed at 281; significantly greater than the ISAR species richness estimate of 188.78 for a theoretical 35.34-ha island (95% CI = [164.55, 213.01]). The SLOSS index estimate for the complete island set indicated that a fragmented set of islands is expected to contain 32.8% more species than a single large island.

#### 3.3 | Accumulation of species and habitats

When cumulative species richness was plotted against cumulative island area, the small-to-large accumulation curve lay above the large-to-small accumulation curve in the small, large, and complete island sets (Figure 3a–c). This visual inspection of curves aligns with saturation index estimates of 1.071, 1.097, and 1.161, respectively. These results suggest two diversity patterns: (a) species richness was not consistently nested in relation to island area; and (b) several smaller islands generally contained more species than fewer or single larger islands equivalent in areal extent. These observations equate to a positive effect of fragmentation on species richness (Gavish et al., 2012).

Visual inspection of habitat accumulation curves (Figure 3d–f) suggested that small-to-large and large-to-small curves only differed substantially in the small island set, where habitats accumulated with area more rapidly across small islands than large. In the large and complete island sets, habitats accumulated with area irrespective of island size, even though saturation index estimates were positive at



**FIGURE 2** ISARs derived from the (a) small ( $n = 15$ ), (b) large ( $n = 15$ ) and (c) complete ( $n = 30$ ) island sets. Open circles represent the observed vascular plant species richness for single islands, while filled circles represent the aggregate species richness of study islands used to generate the ISAR. Dashed lines represent 95% confidence intervals for ISAR regressions (estimated using least-squares). The SLOSS index was estimated as  $100\% \times (S_{ss} - S_{si})/S_{ss}$ , where  $S_{ss}$  is the aggregate species richness of study islands, and  $S_{si}$  is the ISAR species richness estimate for a single theoretical island of equal area

all size scales. It is clear that saturation index estimates  $> 1$  for the large and complete island sets stemmed from the constraint of passing accumulation curves through the origin (Gavish et al., 2012;

Quinn & Harrison, 1988). Saturation index estimates under these circumstances (large variation in island area with few types of accumulating entities) are therefore unreliable. Considering only visual inspection of habitat accumulation curves, it is interesting that the positive fragmentation effect on habitat richness observed in the small island set was not persevered when all 30 islands were used to build habitat accumulation curves for the complete island set. To explain this result, MacDonald et al. (2018) suggest that accumulation patterns across larger islands may dominate those across smaller islands; particularly, when the range of island sizes is great and the abundance of small islands is high.

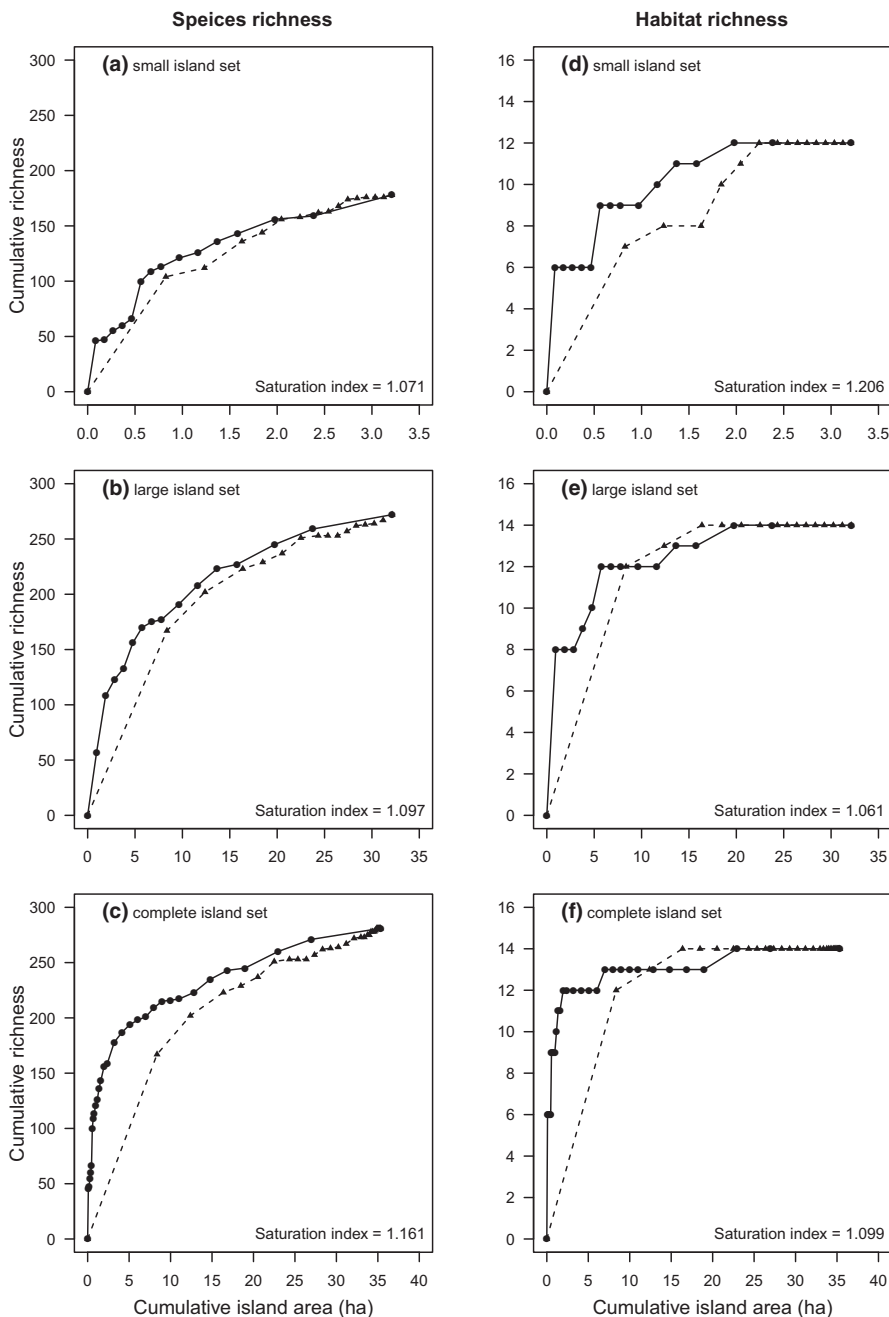
### 3.4 | Path analysis

Habitat richness and the proportion of water within a 500-m buffer were the best-supported measures of habitat diversity and island isolation, respectively. The final multigroup path model accounting for these variables yielded a non-significant likelihood ratio test, indicating that the model's covariance structure provided an adequate description of the total observed covariance matrix. All coefficient estimates, including those measuring the indirect effect of island area on species richness, were significant at  $\alpha = 0.05$  (Table 2, Figure 4). Unstandardized coefficients relating island area to habitat diversity, habitat diversity to species richness, and island isolation to species richness were constrained to single estimates for the small and large island set without significantly decreasing model fit (respective standardized coefficient estimates reported in Table 2 and Figure 4 vary between the small and large island set due to disparity in the variance of individual variables between the small and large island set). This result suggests that ecological processes underlying these relationships are approximately equivalent between the two ranges of island sizes. In contrast, constraining coefficients measuring the direct effect of island area on species richness to a single estimate for the small and large island set significantly reduced model fit. The direct effect of island area on species richness was therefore estimated for the small and large island set independently. This effect of area per se was greater across islands in the large island set, suggesting size scale-dependency. Overall, the final multigroup path model explained 81.2% and 91.6% of the variation in species richness and 34.4% and 55.3% of variation in habitat diversity (richness) in the small and large island set, respectively.

### 3.5 | Dissimilarity of species and habitats

Pairwise dissimilarities of species and habitats were significantly related across islands in the 0.1-ha size class ( $r_{\text{Mantel}} = 0.525$ ,  $p = 0.021$ ), but not in the 1.0-ha size class ( $r_{\text{Mantel}} = -0.186$ ,  $p = 0.756$ ). This size scale-dependency may be driven by partial habitat saturation in areas approaching 1.0 ha, resulting in reduced habitat dissimilarity across larger islands. Greater multiple-site habitat dissimilarity across islands in the 0.1-ha size class than in the 1.0-ha size class ( $d_{\text{J-MULT}} = 0.784$  and 0.583, respectively) corroborate this hypothesis. Multiple-site species dissimilarity was also greater across





**FIGURE 3** Cumulative number of vascular plant species (a, b and c) and habitats (d, e and f) relative to cumulative island area. Accumulation of species and habitats occurred from the smallest island to largest island (small-to-large curve, represented by closed circles connected by solid lines) and from the largest island to smallest island (large-to-small curve, represented by closed triangles connected by dashed lines). The saturation index was estimated as the area under the small-to-large curve relative to that of the large-to-small curve

islands in the 0.1-ha size class than in the 1.0-ha size class, although the difference was less pronounced ( $d_{J-MULT} = 0.887$  and  $0.792$ , respectively). No significant relationship was observed between pairwise species dissimilarity and inter-island distance across islands in either the 0.1-ha or 1.0-ha size class ( $r_{Mantel} = -0.221$ ,  $p = 0.839$  and  $r_{Mantel} = -0.093$ ,  $p = 0.659$ , respectively).

## 4 | DISCUSSION

Results of this study accord well with those of others, suggesting that fragmentation may not reduce species diversity (e.g., Yaacobi et al., 2007; Gavish et al., 2012; review in Fahrig, 2003, 2013, 2017).

This expanding literature has led some ecologists to infer that the sample-area effect may explain positive species–area relationships in the majority of fragmented landscapes (e.g., Fahrig, 2013, 2017). Unexplained by the sample-area effect, however, we observed a general trend of species richness actually increasing with degree of fragmentation after controlling for total area sampled with SLOSS-based analyses. This positive fragmentation effect was most pronounced in the small island set, where all SLOSS-based analyses indicated that species richness increased with increasing degrees of fragmentation. Fragmentation–species richness relationships were more ambiguous in the large island set, where no clear pattern in species richness was observed across size classes, and the aggregate species richness of study islands did not significantly differ from the



**TABLE 2** Standardized multigroup path coefficient estimates for the effects of habitat diversity (richness), island area (log-transformed), and island isolation (proportion of water within 500-m buffer) on vascular plant species richness. All unstandardized path coefficients were constrained to single estimates for the small and large island set, without significantly reducing model fit, except for those measuring the direct effect of island area on species richness, which were estimated for the small and large island set independently. The indirect effect of island area on species richness (mediated by habitat diversity) was estimated as the product of the direct effect of island area on habitat diversity and the direct effect habitat diversity on species richness. The total effect of island area on species richness was then estimated as the sum of its direct and indirect effects. Multigroup path analysis model structure is given in Figure 4

Island set	Variable	Direct effect	Indirect effect	Total effect
Small	Habitat diversity	0.491***		
	Area	0.502***	0.288*	0.790***
	Isolation	-0.146*		
Large	Habitat diversity	0.323***		
	Area	0.675***	0.240*	0.915***
	Isolation	-0.151*		

Significance is denoted by \* $p < 0.05$ ; \*\* $p < 0.01$ ; \*\*\* $p < 0.001$ .

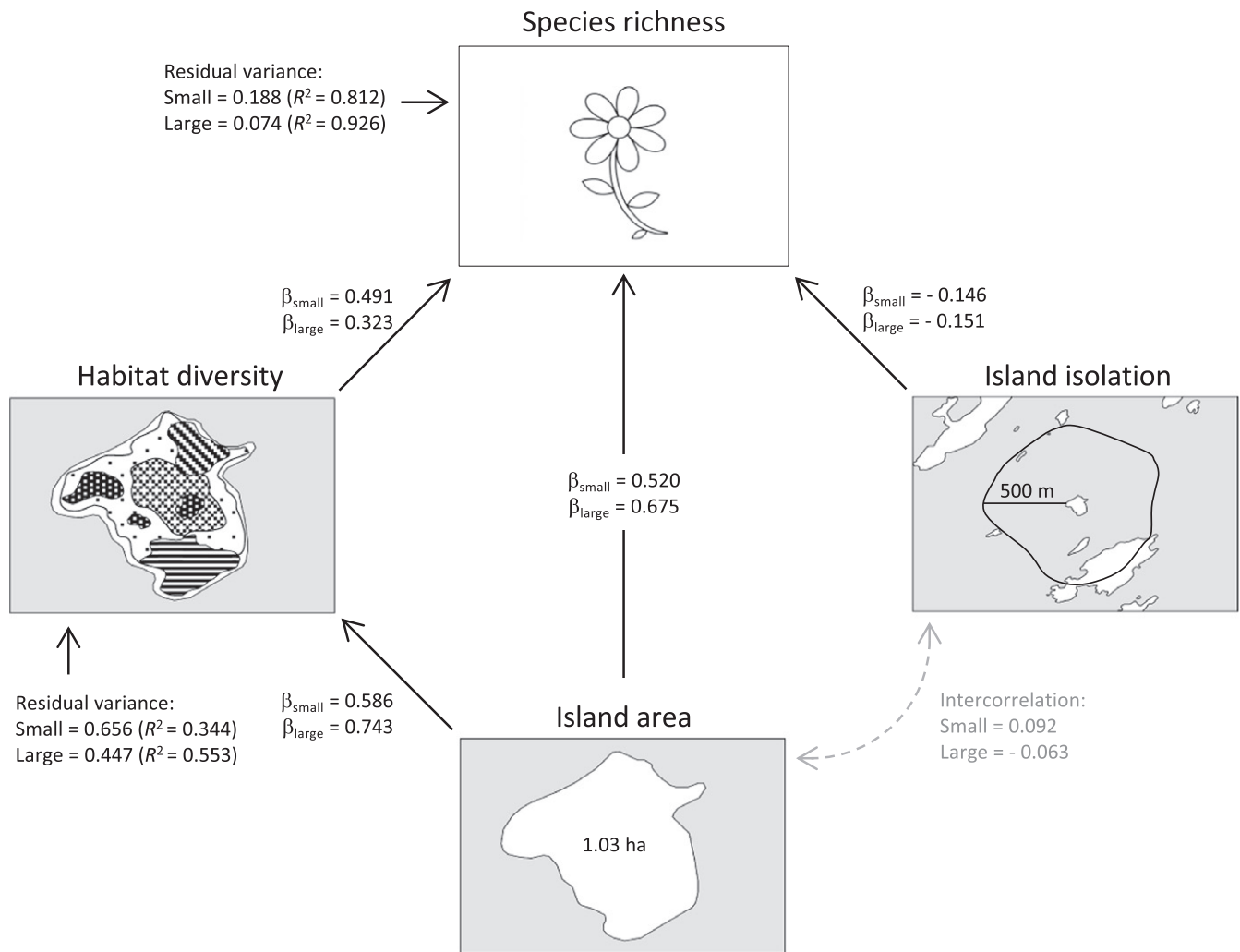
ISAR species richness estimate. However, the SLOSS index estimate indicated that a fragmented set of islands, equivalent in configuration to the large island set, is still expected to contain 10.4% more species than a theoretical single large island. Others have interpreted similar differences between aggregate species richness and ISAR species richness estimates as meaningful, so long as the ISAR was significant (e.g., Matthews et al., 2016; Yaacobi et al., 2007). While we have cautioned interpretation of SLOSS index estimates under these circumstances (e.g., MacDonald et al., 2018), species accumulation curves also indicated a weak positive fragmentation effect at this size scale, suggesting that the directionality of the SLOSS index estimate for the large island set was accurate. Considering all 30 islands together (complete island set), both ISAR extrapolation and species accumulation curves indicated that fragmented sets of smaller islands contained more species than fewer or single larger islands, suggesting that fragmentation at this scale may increase species richness.

To account for similar observations in the context of habitat amount hypothesis (i.e., sample-area effect), Fahrig (2013) points out that several smaller fragments may intersect the distributions of more species because of their expanded spatial distribution relative to fewer or single larger fragments. Several small fragments may thereby passively sample a higher diversity of species, resulting in the spurious observation of positive fragmentation effects. Indeed, theoretical species diversity models suggest that several small conservation reserves capture more species when species turnover increases with distance (Tjørve, 2010). However, such processes are unlikely to operate within single fragmented landscapes; the scale at which fragmentation effects are most often inferred (review in Debinski & Holt, 2000). In this

study, pairwise species dissimilarity was not related to inter-island distance at either of the two island sizes addressed. We therefore find it reasonable to conclude that: (a) the expanded spatial distribution of several small islands did not confound SLOSS-based analyses; and (b) the observation that several smaller islands contained a greater number of species than fewer or single larger islands is best interpreted as a positive effect of fragmentation on species richness. While the sample-area effect undoubtedly contributes to positive species–area relationships in a variety of systems, including this one, a more likely explanation of the positive fragmentation effect observed here involves a combination of habitat diversity and the small island effect.

In the small island set, SLOSS-based analyses of habitat richness suggested that several smaller islands contained more habitat types than fewer or single larger islands. This pattern of habitat richness aligned well with that of species richness, as would be predicted by the habitat diversity hypothesis. Further support for the habitat diversity hypothesis in the small island set is conferred by three additional relationships. First, species richness and habitat richness were positively correlated across 0.1-ha islands, demonstrating that species richness and habitat richness were positively related independent of island area at this size scale (MacArthur & Wilson, 1963; Rosenzweig, 1995; Williams, 1964). Second, pairwise species dissimilarity was significantly related to pairwise habitat dissimilarity across this same grouping of islands, indicating that the former correlation was not spurious. Third, path analysis demonstrated that habitat richness had a significant positive effect on species richness, independent of area per se. Together, these relationships suggest that the positive fragmentation effect on species richness may be at least partially attributed to a positive fragmentation effect on habitat richness. Several smaller islands contained more habitats than fewer or single larger islands, and more habitats supported more species. These relationships were more prominent across islands within the small island set than those within the large, supporting that both fragmentation effects and ecological processes underlying species–area relationships are size scale-dependent (*sensu* Rosenzweig, 1995; Lomolino & Weiser, 2001; Triantis et al., 2006).

An additional, and perhaps complimentary, explanation of positive fragmentation effects is contributed by the small island effect. The small island effect specifically predicts the existence of threshold island sizes, below which, species richness does not consistently increase with area (e.g., Lomolino & Weiser, 2001; Sfenthourakis & Triantis, 2009; Triantis et al., 2006). A more generalized prediction here may be that the effect of area per se on species richness will be less prominent for smaller islands than larger islands. Multigroup path analysis supported this generalized prediction, indicating that direct and total effects of island area on species richness were smaller in the small island set than in the large island set. Working backwards through these area effects, it is clear that losses of species associated with reductions in area should be less prominent across smaller islands than across larger islands. Fragmented sets of smaller islands may therefore be expected to contain more species than fewer or single larger islands; particularly, if the areas of individual small islands are below a small island effect threshold.



**FIGURE 4** Multigroup path model structure accounting for species richness, habitat diversity (richness), island area (log-transformed), and island isolation (proportion of water within 500-m buffer). Habitat diversity, island area, and island isolation each directly affects species richness. Island area also directly affects habitat diversity, thereby having an additional indirect effect on species richness. All unstandardized path coefficients were constrained to single estimates for the small and large island set, without significantly reducing model fit, except for those measuring the direct effect of island area on species richness, which were estimated for the small and large island set independently. Residual variances ( $1 - R^2$ ) for species richness and habitat diversity in the small and large island set are reported adjacent to arrows unconnected to other variables. Coefficients associated with the dashed double-headed arrow connecting island area and island isolation represent intercorrelation, which is not treated as a causal path. The direct, indirect, and total effects of habitat diversity, island area, and island isolation on species richness are reported in Table 2

Interestingly, this prediction that fragmented sets of smaller islands may contain more species than fewer or single larger islands may not be in opposition with the theory of island biogeography. In accordance with the small island effect, the theory of island biogeography predicts that extinctions will become increasingly frequent and stochastic as island size decreases, to the eventual extent that extinction rates are decoupled from island area (Wilson & MacArthur, 1967). These high, area-independent extinction rates may equilibrate with immigration rates at nonzero richness values, with particularly high rates of temporal species turnover. Assuming that demographic processes and assemblage dynamics are independent across islands (Hanski, 1999; Leibold et al., 2004; Wilson & MacArthur, 1967), high rates of temporal species turnover within small islands should translate to increased species dissimilarity across small islands, effectively

increasing their aggregate species richness. Evidence for these relationships was observed in our study system, wherein multiple-site species dissimilarity was greater across smaller islands (0.1 ha) than larger islands (1.0 ha). Together with the positive fragmentation effect on habitat diversity, the small island effect and increased species dissimilarity across small islands may explain why the positive fragmentation effect on species richness was most pronounced in the small and complete island set, which both contained our smallest study islands.

If there is validity to these relationships, species richness within and among small fragments may not consistently decrease with reductions in fragment area. However, this conclusion should not be interpreted as conclusive evidence that fragmentation does not threaten species diversity. Species richness within small fragments may be largely comprised of early seral species of low conservation



concern (Debinski & Holt, 2000), with threatened species with higher extinction thresholds restricted to larger fragments or extirpated from fragmented landscapes entirely (Fukamachi, Iida, & Nakashizuka, 1996; Rybicki & Hanski, 2013). Furthermore, the prediction that high extinction rates may equilibrate with immigration rates at nonzero richness values for small islands is predicated on the existence of a mainland within the dispersal ranges of species, serving as a continuous source of immigration (Wilson & MacArthur, 1967). In the absence of mainland equivalents on many fragmented landscapes, similar source-sink dynamics are also predicted among fragments by metapopulation and metacommunity theory; particularly, when ranges of fragment areas within single landscapes are great (e.g., “mass effects”; Hanski, 1999; Leibold et al., 2004). Ecologists should therefore proceed carefully when inferring the conservation significance of SLOSS, as large fragments may be necessary for the maintenance of species richness at the landscape level.

An additional shortfall of SLOSS-based analyses is that they do not permit direct investigation of the effects of isolation on species richness, which, in many respects, operate independent of the effects of area per se (Hanski, 1999; Wilson & MacArthur, 1967). Negative relationships between fragment isolation and species richness have been observed in other studies where SLOSS-based analyses suggested neutral to positive fragmentation effects overall (review in Fahrig, 2013, 2017). To account for these relationships in the context of the habitat amount hypothesis, Fahrig (2013) suggests that species richness may decrease with fragment isolation simply because of reductions in: (a) the total amount of habitat surrounding fragments; and (b) corresponding pools of potential immigrants (i.e., “source pools”, *sensu* Gotelli & Graves, 1996). However, we question whether it is reasonable to suppose that source pools vary within single landscapes, to the extent that individual fragments differ significantly in the number and composition of species they sample. If islands indeed sample species passively, dissimilarity in species composition between islands of similar areas should serve as an adequate proxy for dissimilarity in their respective source pools. In this study, pairwise species dissimilarity (accounting for both turnover and nestedness) was not related to inter-island distance. This suggests, but does not prove, a general homogeneity of source pools within our study area. The negative isolation effect observed may therefore be best interpreted as a negative fragmentation effect, as predicted by the theory of island biogeography, rather than a sampling artefact, as suggested by the habitat amount hypothesis.

## 5 | CONCLUSIONS

While SLOSS-based observations indicated that fragmentation increased species richness overall, it should not be assumed that all aspects of landscape configuration associated with the fragmentation construct align in the directionality of their effects. Increased habitat diversity, the small island effect, and increased species dissimilarity may all positively affect aggregate species richness among several small fragments, while increasing isolation negatively affects species richness

within individual fragments. The history of ecology is marked by an ongoing debate on the ecological processes moderating these relationships, and how our understandings of these processes are best applied to conservation. Within this debate, the theory of island biogeography, the sample-area effect, and the habitat diversity hypothesis are most often framed as addressing mutually exclusive processes representing opposing schools of thought. Indeed, the epistemological comfort afforded by exclusive subscription to a scientific paradigm is attractive due to the relative ease of operating under a single framework. However, such perspectives are generally incompatible with the complexity of ecological systems; particularly, when considering emergent ecological properties such as species diversity. Results of this study, among others (e.g., Buckley, 1982; Burns et al., 2010; Kadmon & Allouche, 2007), suggest that multiple processes operate simultaneously to structure species diversity in insular and fragmented systems, and ought to be viewed as mutually complementary, rather than exclusive.

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## DATA ACCESSIBILITY

All vascular plant occurrence data and voucher specimen information are accessible via the public data archive Dryad (<https://datadryad.org/>). Information on this dataset is as follows:

Title: Data from: The theory of island biogeography, the sample-area effect, and the habitat diversity hypothesis: complementarity in a naturally fragmented landscape of lake islands

DOI: <https://doi.org/10.5061/dryad.767tg03>

Journal: Journal of Biogeography

Journal manuscript number: none available

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#### BIOSKETCH

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#### SUPPORTING INFORMATION

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

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