META-ANALYSIS

Synthesis reveals that island species–area relationships emerge from processes beyond passive sampling

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Abstract

Aim: The island species–area relationship (ISAR) quantifies how the number of species increases as the area of an island or island-like habitat gets larger and is one of the most general patterns in ecology. However, studies that measure the ISAR often confound variation in sampling methodology and analyses, precluding appropriate syntheses of its underlying mechanisms. Most ISAR studies use only presence–absence data at the whole-island scale, whereas we planned to use a framework that applies individual-based rarefaction to synthesize whether and how the ISAR differs from the null expectation of the passive sampling hypothesis.

Location: Five hundred and five islands from 34 different archipelagos across the world, including oceanic islands, lake islands and forest islands.

Major taxa studied: Local assemblages of plants, invertebrates, herpetofauna, birds and mammals.

Methods: We collated local-scale species abundance data from multiple archipelagos (median of 12 islands per study) and used a rarefaction-based approach to synthesize the relationship between island size and (1) sample effort-controlled rarefied species richness, or (2) an effective number of species derived from the probability of interspecific encounter (an index of community evenness).

Results: When we applied rarefaction to control for sampling effort, the numbers of species and their relative abundances across all studies differed from the passive sampling hypothesis. Our measure of evenness also increased with island size, suggesting that the disproportionate effects we observed influenced both rarer and more common species. We found few associations between the slope of this effect and island type or taxon, but we did find that island archipelagos with greater elevational heterogeneity also deviated more from the null expectation than those with less heterogeneity.

Main conclusions: Using a synthetic approach across island archipelagos, we reject the null expectation that passive sampling causes the ISAR and instead suggest that ecological mechanisms leading to disproportionate (non-random) effects on larger relative to smaller islands are predominant.

1 | INTRODUCTION

The island species–area relationship (ISAR) describes how the numbers of species on an island or island-like habitat increases with island area. The ISAR is typically positive (e.g., Arrhenius, 1921; Drakare et al., 2006; Lomolino, 2000; Matthews et al., 2019; Schoener, 1976; Triantis et al., 2012), except in unusual circumstances, such as when larger islands have lower habitat heterogeneity than smaller islands, when sampling is less complete in larger than smaller islands, or on particularly small islands where stochastic processes predominate (i.e., the small island effect; Wang et al., 2018). ISARs occur across taxa and appear on islands (Kreft et al., 2008; Matthews et al., 2016; Triantis et al., 2012), island-like systems, such as lakes (Browne, 1981; Dodson, 1992; Hobæk et al., 2002), habitat fragments (Matthews et al., 2014, 2016), mountain tops (Brown, 1971), natural forest patches (Azeria et al., 2009; Lövei & Magura, 2006) and inselbergs (Porembski & Barthlott, 2012). Indeed, the ISAR has been of central importance in the development of some of the most influential concepts in ecology, such as the theory of island biogeography (MacArthur & Wilson, 1967; Warren et al., 2015), and has transcended research on the influence of habitat loss and fragmentation on biodiversity patterns (e.g., Chase et al., 2020; Fahrig, 2003; Haddad et al., 2015; Laurance, 2008).

Despite being one of the most general and well-known patterns in biogeography, there is a lack of consensus on what shapes diversity patterns such as the ISAR on islands (Whittaker & Fernández-Palacios, 2007). One of the main reasons for this uncertainty lies in the different ways in which biodiversity is estimated on islands for analyses. Theories underlying the ISAR were developed to describe the total number of species that occur on an island (MacArthur & Wilson, 1963, 1967). To date, syntheses of ISARs have focused on studies of whole island-level data of species richness patterns (e.g., Matthews et al., 2016; Triantis et al., 2012), which provide useful information regarding the overall shape of the ISAR but are less useful for evaluating the potential mechanisms creating them. One important way to examine the possible mechanisms underlying the ISAR is to measure patterns of diversity and relative abundances of species at areas less than the total island (Chase et al., 2019). Unfortunately, ISAR studies are fraught with highly variable sampling designs that strongly influence its observed shape (Scheiner, 2003; Scheiner et al., 2011; Schrader et al. 2019) and have heretofore precluded meaningful synthesis.

The simplest explanation for a positive ISAR is passive sampling (Connor & McCoy, 1979). With passive sampling, larger islands passively sample more individuals from the regional pool and therefore have more species than smaller islands. Passive sampling was noted in some of the earliest discussions of the ISAR (e.g., Arrhenius, 1921) and is often considered a "null" expectation for the ISAR (e.g., Coleman et al., 1982; Hill et al., 1994; McGuiness 1984a). Passive

sampling can be detected (or refuted) by comparing the numbers of species observed with a fixed sampling area across islands that vary in area (e.g., Giladi et al., 2014; Hill et al., 1994; Kohn & Walsh, 1994) or by using null models and rarefaction-based approaches (e.g., Chase et al., 2019; Coleman et al., 1982). When passive sampling is the only mechanism operating, we expect an increase in whole-island species richness with island area, but no change in the relative abundances of species or the number of species with a fixed sampling effort (i.e., smaller islands are passive samples of larger islands). Although often discounted as a real mechanism underlying the ISAR, but simply one that should be accounted for, a number of empirical studies have suggested evidence for passive sampling as a main driver of ISARs using effort-controlled methods. These include breeding birds on islands in a reservoir (Coleman et al., 1982), colonists of intertidal boulders (McGuiness, 1984b), trees in forest fragments (Hill et al., 1994), several studies on plants in island and island-like fragments (Gilaldi et al. 2014), and zooplankton in freshwater lakes (Gooriah & Chase, 2020). Furthermore, although mechanisms other than passive sampling are often invoked, many models of ISARs implicitly assume that individuals and species are randomly pulled from a distribution in a way similar to passive sampling; such models are often used when, for example, making projections of species losses with habitat loss (e.g., Chase et al., 2020).

If the null hypothesis of passive sampling is rejected, we can invoke ecological mechanisms that determine the magnitude by which it deviates, and the relative abundances of some species increase (or decrease) more than would have been expected by random sampling. Hereafter, we call these "disproportionate effects", and they can include the influence of area per se (Connor & McCoy, 1979), such as variable colonization–extinction dynamics (e.g., MacArthur & Wilson, 1963, 1967), or population-level processes that tend to be more prominent in communities on smaller rather than larger islands (e.g., Allee effects or demographic stochasticity) (e.g., Courchamp et al., 2008; Lande, 1998). When larger islands have higher colonization rates and lower extinction rates or demographic stochasticity is much less likely on larger islands, we would often expect there to more species on an island and in any given sample within that island than would have been expected from a passive sampling hypothesis from the regional species pool. It is also possible that when colonization rates are very low and extinction rates very high, smaller islands can have fewer species than would have been expected in any given sample. In either case, we would expect a positive relationship between the numbers of species found in a given effort-controlled sample and the area of that island. Disproportionate effects leading to the ISAR can arise when habitat heterogeneity increases with island area, particularly when species have some degree of habitat specialization (Guadagnin & Malchik 2007; Hart & Horwitz, 1991; Hortal et al., 2009; Triantis et al., 2003; Williams, 1943). Here, if

multiple samples are taken from across a larger island that has higher habitat heterogeneity, the number of species for a given sampling effort (e.g., rarefied richness) would increase with increasing island size. Empirical support for disproportionate effects where effort-controlled samples of species richness increase with increasing island size, leading to the ISAR, include studies of plants on an island archipelago off the British coast (Kohn & Walsh, 1994), birds, butterflies, lizards and frogs on the Andaman and Nicobar islands in the Indian Ocean (Gooriah et al., 2020), and grasshoppers from patch-like grassland openings in the Midwestern USA (Chase et al., 2019).

Although comparing effort-controlled patterns of species richness with island area is a useful way to test the null expectation of passive sampling, some caveats need to be considered. For example, Karger et al. (2014) found no influence of island area on the number of species in a small fixed-area plot, but a positive relationship with larger plot sizes owing to the inclusion of more rare species, allowing them to reject passive sampling. Likewise, Sfenthourakis and Panitsa (2012) found no influence of island area on the numbers of species in fixed-area plots, but did find strong compositional variation among plots, suggesting strong habitat heterogeneity effects. Finally, it is important to note that rejecting the null hypothesis of passive sampling by comparing effort-controlled species richness in individual studies with a limited number of islands can be difficult when there are many sources of variation. A quantitative synthesis of multiple islands from multiple studies can provide a more robust test of the null and alternative hypotheses.

Here, we take a step towards circumventing some of the limitations of previous studies by applying parts of a recently developed individual-based, rarefaction-based approach for evaluating the null expectation of passive sampling against the alternative (Chase et al., 2019). It also allows us to evaluate the effects of island area on multiple components of species diversity that account differentially for relative commonness and rarity of species (i.e., species richness vs. an effective number of species). Specifically, we compiled species abundance information from 505 "true" islands and natural island-like habitats (barrier islands, lake islands and forest islands) across a wide range of taxa (birds, herpetofauna, invertebrates, mammals and plants) from 34 separate datasets of archipelagos. Although 34 multiple-island datasets is many fewer than previous syntheses on the ISAR calculated at the whole-island level (e.g., Matthews et al., 2019; Triantis et al., 2012), the data needs for our approach (sample-level data including total and relative abundances across multiple islands) are much more stringent, and our synthesis represents a thorough search of the openly available data (and some previously unavailable data). Our focus here is specifically on "natural" islands rather than habitat islands that are formed after habitat destruction and fragmentation, which have had less time to achieve equilibrium and were the subject of a different (albeit related) project (Chase et al., 2020).

1.1 | Questions and hypotheses

Given that it is rare for studies to present both information on the total numbers of species per island and data on their abundances from samples within islands, we focused only on datasets with information on the latter; that is, we did not quantify the ISAR of total species richness, which has been well studied and synthesized previously, although we expect that it was operating at the scale of the entire island for most of these studies, because this is a very general pattern (e.g., Matthews et al., 2016, 2019; Triantis et al., 2012). Instead, we focused on identifying potential mechanisms underlying the ISAR by estimating diversity parameters from standardized sampling regimes within islands of an archipelago. To do so, we used parts of an individual-based rarefaction framework overviewed by Chase et al. (2019). Figure 1 presents a conceptual overview of the questions we asked and hypotheses we tested, which were as follows.

1.1.1 | Question 1: Can we reject the null hypothesis that the ISAR results from passive sampling?

To evaluate whether species diversity on small islands and larger islands results from passive sampling of individuals from a larger species pool, we analysed the rarefied number of species, S_n, expected from a sample of n (e.g., Chao et al. 2014; Gotelli & Colwell, 2001) from each island. Here, n was taken as the product of two times the minimum number of individuals (of all species combined) observed on an island within each dataset (see Chao et al., 2014). By comparing S_n with island area, we can test the null expectation of the passive sampling hypothesis. With passive sampling, the numbers of species from an effort-controlled sample, S_n, should be unchanged with increasing island area (Chase et al., 2019). Although passive sampling might seem unrealistic in the face of many ecological processes that could differ between larger and smaller islands, it has not been rejected in a number of studies (e.g., Coleman et al., 1982; Gilaldi et al., 2014; Gooriah & Chase, 2020; Hill et al., 1994; McGuiness 1984b). Furthermore, passive sampling is often assumed implicitly in species–area modelling and how to project species losses with habitat losses (e.g., He & Hubbell, 2011), which can underestimate losses if passive sampling is not the only mechanism acting (Chase et al., 2020).

If, instead, S_n increases with island area (i.e., if the slope estimate of the relationship between S_n and island area is greater than zero), we can reject the passive sampling hypothesis and conclude that some other mechanism (e.g., disproportionate effects or heterogeneity) is driving the ISAR. Given that we combine individuals from plots sampled from across multiple habitats across each sampled island, this approach can capture disproportionate effects that emerge owing to a number of possible mechanisms, including those attributable to area per se (e.g., colonization–extinction dynamics, dispersal limitation and Allee effects), in addition to habitat heterogeneity, which will create opportunities for different species in different localities. We can then estimate the magnitude of any deviation from the null expectation to discern whether differences in taxa, island type or island characteristics might be important. Finally, although we often expect these
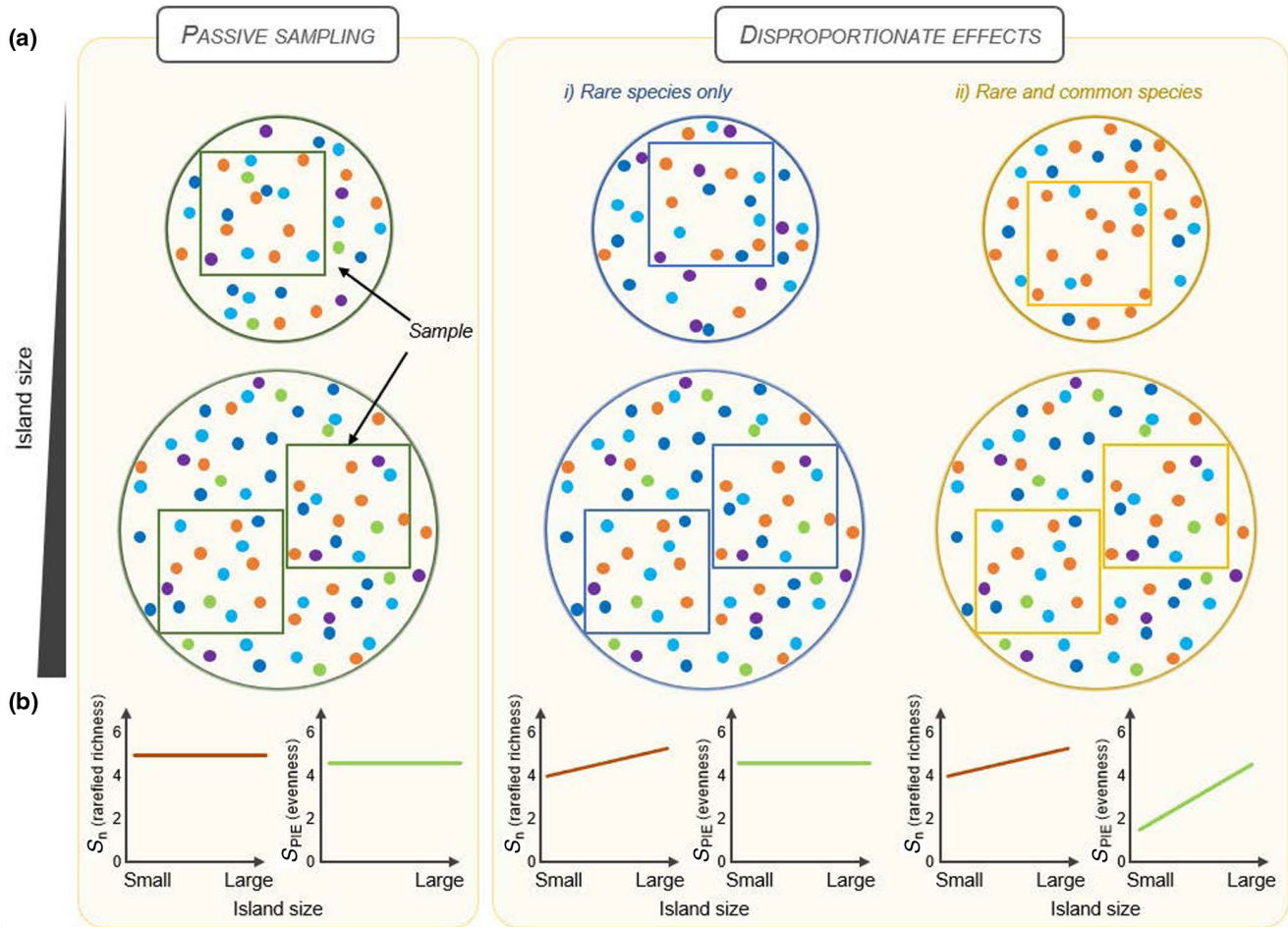
FIGURE 1 (a) Conceptual schematic diagram for the three hypotheses overviewed in the text. Passive sampling (left panels) is when the smaller island (smaller circle) has a passive sample of the individuals on the larger island (larger circle). Disproportionate effects (right two panels) illustrate a case where the smaller island has fewer species (rare species only) or fewer species and less even communities (rare and common species) than expected from a random sample of the larger island. Dots represent individuals on a given island, and colours indicate different species. Within each island, standardized samples are depicted here with square "quadrats" taken (note that the real sampling design varied among studies but was standardized for analyses). (b) Expected relationships with island size from the different hypotheses for the rarefied number of species (S_n) and the effective number of species given the probability of interspecific encounter (S_{PIE}; an estimate of evenness) (modified from Chase et al., 2019, 2020)

disproportionate effects to lead to positive relationships, S_n can also have a negative relationship with island area, for example, if habitats are less heterogeneous or species coexistence is less likely in larger areas.

1.1.2 | Question 2: If there is a disproportionate effect, what role do rare species play in this relationship?

To determine whether any deviations from the null expectation emerged because of changes only to rare species (in which case, we would expect a change in S_n with island area) or owing to changes in the entire shape of the relative abundance distribution, we calculated another metric intended to capture changes in the relative abundances of more common species. Specifically, we used the

effective numbers of species (*sensu* Jost, 2006) conversion of the probability of interspecific encounter [PIE; Hurlbert, 1971; PIE is the complement of Simpson's diversity, and the inverse of PIE is a Hill (1973) number with $q = 2$], which we refer to as S_{PIE} (see Chase et al., 2019). S_{PIE} represents a metric of "evenness" that is strongly influenced by changes in the overall dominance of the most common species in a community and is relatively insensitive to rare species. If island area has a positive influence on both S_n and S_{PIE}, we would surmise that overall evenness is changing with island area and that both common and rare species are increasing more than expected from sampling to drive the ISAR. Instead, if S_n increases with island area but S_{PIE} does not change, we would surmise that an observed positive ISAR would largely be a result of there being disproportionately more rare species on larger islands. Finally, as with S_n above, S_{PIE} can also decrease with increasing island area if larger islands support less even communities.

2 | METHODS

2.1 | Data search and compilation

To search for studies that contained abundance-level data of assemblages from multiple islands, we used Google Scholar and Web of Science (WoS) and entered the following keywords: species AND abundance OR survey AND islands OR archipelago. We selected studies for multiple taxa that reported species abundances across islands in an archipelago, forest islands or lake islands. If these data were not immediately available in the article or associated supplemental material, we contacted the corresponding authors to ask whether they could supply the required abundance data. Additionally, we extended our search to include several data portals, including Dryad (https://datadryad.org/), Knowledge Network for Biocomplexity (KNB); https://knb.ecoinformatics.org/), the Environmental Data Initiative (https://environmentaldatainitiative.org/) and FigShare (https://figshare.com/), using the following keywords: species, abundance, islands and archipelagos.

We ensured that each included dataset met the following criteria. First, the islands in the dataset were natural landmasses surrounded by water, or natural forest patches surrounded by a matrix of habitats that are less hospitable to these organisms. We identified four island types: (1) oceanic islands (this includes islands in archipelagos and atolls); (2) barrier islands; (3) islands within lakes; and (4) forest islands. Second, there were more than two islands surveyed in the study, and surveys used consistent methodology where sampling effort could be evaluated and controlled. Third, the studies recorded

abundances of each species in an assemblage such that rarefaction and relative abundances could be estimated.

In total, we compiled data from assemblages on 505 islands from 34 separate datasets (Figure 2). These datasets come from the following 32 publications (two publications had two datasets each): Andrade and Marini (2002); As (1984); Barun et al. (2010), Bell et al. (2017); Borges et al. (2016); Choi and An (2011); Da Silva et al. (2019); Davidar et al. (2001); Devy et al. (1998); Dueser et al. (1979); Evans et al. (2016); Hatteland et al. (2008); Jonsson et al. (2011); Karger et al. (2014); Kotze et al. (2000); MacDonald et al. (2018); Pereira et al. (2017); Perillo et al. (2020; data in the paper by Perillo (2017); Pierce et al. (2003); Puspitasari (2016); Rangasamy et al. (2014); Rocamora et al. (2003); Schilthuizen et al. (2013); Schrader et al. (2019); Surendran and Vasudevan (2015); Theuerkauf et al. (2017); Usher and Edwards (1986); Waqa-Sakiti et al. (2018); Werden (2012); Xu et al. (2017); Žagar et al. (2013); and Zalewski and Ulrich (2006). Studies included datasets on volcanic islands ($n = 17$), continental islands ($n = 9$), islands within lakes ($n = 4$) and natural forest islands ($n = 4$) across several different taxonomic groups (invertebrates, $n = 16$; birds, $n = 7$; herpetofauna, $n = 7$; plants, $n = 2$; and mammals, $n = 2$). The number of islands per dataset ranged from 3 to 42, with a mean of 14.5 islands and a median of 12 islands per dataset.

Sampling effort varied across studies, but could be categorized broadly into two methods: (1) fixed sampling, whereby sampling effort was the same across all islands in a dataset ($n = 7$); and (2) proportional sampling ($n = 27$), whereby sampling effort varied with island size. Island area and other pertinent characteristics
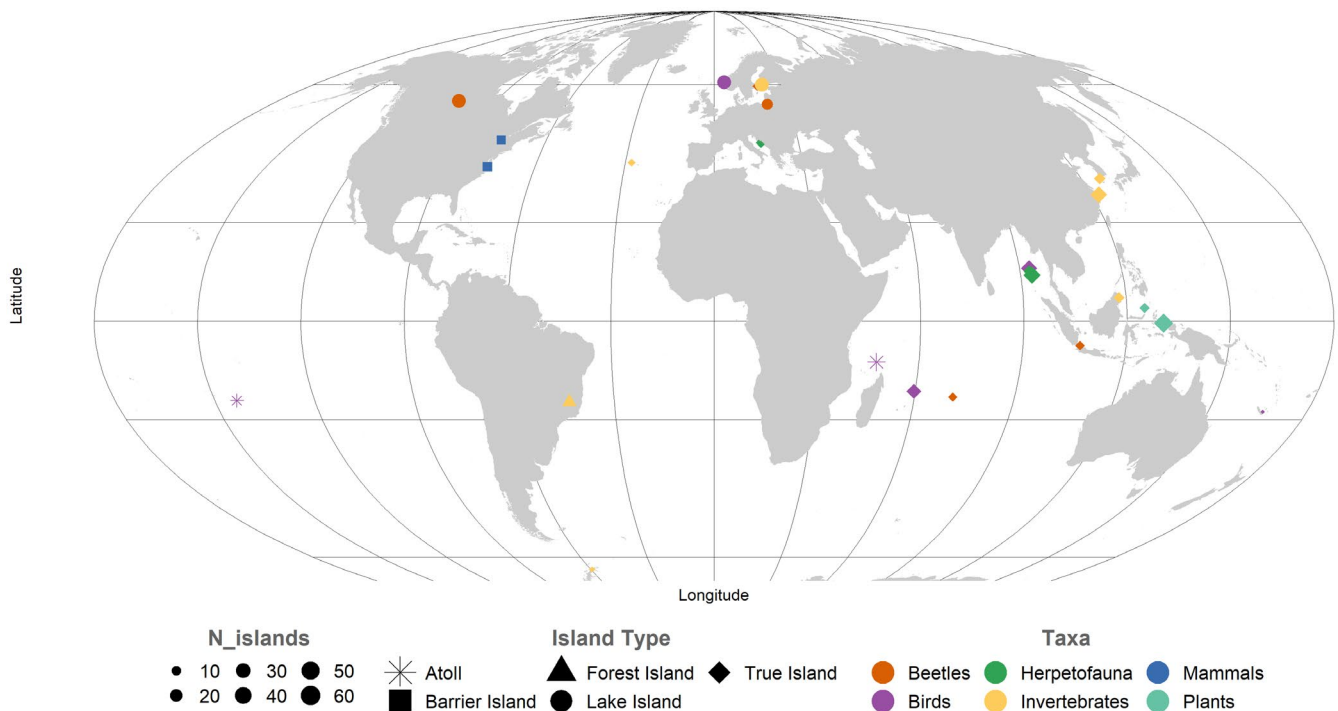

FIGURE 2 Locations of the 34 datasets included in the analysis. Point size indicates the number of islands in a dataset, colour indicates focal taxonomic group, and shape represents island type

(e.g., elevation, coordinators and sampling effort) were extracted from the respective papers, from data providers and/or from online resources (e.g., https://www.google.com/earth/, https://www.wikipedia.org/ and https://www2.jpl.nasa.gov/srtm/). Most datasets have been published previously, but we provide them here for ease of reuse and reproducibility. Species abundances in a few of the datasets were previously unpublished (Jonsson et al., 2011; Karger et al., 2014; Schrader et al., 2019; Zalewski & Ulrich, 2006), but are made available here in an accompanying repository link. The R code used for standardizing the data and the analyses described below are available at: https://github.com/chase-lab/ISAR_synthesis. They are also mirrored and archived along with the data at https://zenodo.org/record/5037070#.YNrQPOgzY2w. Finally, the data are available at the following Dryad link: https://doi.org/10.5061/dryad.pnvx0k6n0.

2.2 | Statistical analyses

From each island, we estimated S_n using the "mobr" package (McGlinn et al., 2019) and S_{PIE} using the "vegan" package (Oksanen et al., 2019). To evaluate the relationship between island area and S_n and S_{PIE}, we fitted hierarchical linear models to each metric as a function of island area. Island area was $\log_{10}$-transformed and centred by subtracting the mean from each observed island area before model fitting. Both our response metrics took positive, non-integer values, and we fitted models to both metrics that assumed log-normal error distributions and identity link functions. We fitted models that estimated an overall relationship with island area and also allowed the slope and intercept of the relationship to vary among datasets (i.e., the slope and intercept were estimated as fixed effects, in addition to random effects for each study).

To evaluate whether additional factors could be underlying the patterns observed, we examined study-level posterior samples of the slope estimates as a function of taxonomic groups, island types and elevation (a.s.l.) range. Taxonomic groups were simplified into five categories (plants, invertebrates, herpetofauna, birds and mammals). For our analyses, we did not have enough islands of each island type to evaluate variation among all island types fully. However, in order to test a key hypothesis that more isolated islands might experience different mechanisms from island archipelagos that were more connected, we separated islands into two categories. First, we defined "true islands" ($n = 17$) as volcanic oceanic islands within archipelagos that are isolated and separated by a harsh oceanic matrix. Second, "other islands" ($n = 17$) included continental islands, forest islands, lake islands and barrier islands, which are close to the mainland and have fewer dispersal barriers and/or are surrounded by a more hospitable matrix. We included atolls in this category because it is typical for islands that make up an atoll to be highly connected (note that decisions on how to categorize island type did not influence the results qualitatively).

In order to evaluate a potential role of habitat heterogeneity in any potential deviations from the null expectation, we used the elevational range as a measure of within-island heterogeneity. This is because some islands are flat, with little habitat heterogeneity, whereas others are variable in elevation, containing many habitat types, and this elevational difference among islands can strongly influence the ISAR (e.g., Ricklefs & Lovette, 1999). We calculated the range of elevations spanned by the islands for 31 of the 34 datasets (elevation data were unobtainable for islands in three studies). We calculated elevational range as the difference between the highest and lowest maximum elevations among islands within each dataset. To quantify the relationship between elevational range and study-level slope estimates, we fitted random-effects meta-analytical models that incorporated study-level uncertainty (i.e., the standard error of the posterior distributions). Elevational range was $\log_{10}$-transformed before model fitting, study was included as a random intercept, and both the models assumed Gaussian error distributions and identity link functions.

For Bayesian inference and estimates of uncertainty, models were fitted using the Hamilton Monte Carlo sampler, Stan (Carpenter et al., 2017), and coded with the "brms" package (Bürkner, 2018). All models were fitted with four chains and 3,000 iterations, with 1,500 used as a warm-up. We used the default, weakly regularizing priors for all the parameters. Visual inspection of the chains showed excellent convergence, and all Rhat values were < 1.02 (Gelman et al., 2013).

3 | RESULTS

After controlling for sampling effort within studies, we observed an overall positive trend, whereby the slopes of the relationship between the biodiversity variables (S_n and S_{PIE}) and island area were different from zero across all studies; that is, standardized species richness, S_n (Figure 3a), in addition to our metric of evenness, S_{PIE} (Figure 3b), increased with island area, allowing us to reject the null hypothesis of passive sampling effects.

As with any synthetic analysis, one concern with combining studies lies with the combination of studies having different sampling methodologies. Although individual-based rarefactions that we use here are generally robust to differences in sampling, they can be biased when low numbers are sampled. In our analyses, some datasets collected data from a fixed sampling area, whereas others collected data from more plots on larger islands. It is plausible that the latter data types would be more likely to find divergence from the null expectation because they sample larger extents (hence, larger environmental characteristics) than studies with fixed samples. As a result, we removed the seven datasets with fixed sampling and re-ran the analyses on the 27 remaining datasets (with 403 islands) that used sampling proportional to area. In the Supporting Information (Table S1), we show that the overall slope of the relationship between S_n and S_{PIE} was largely unchanged when these datasets were removed. Another potential concern is that when the number of individuals on an island is very small, individual-based rarefaction will be limited in its ability to
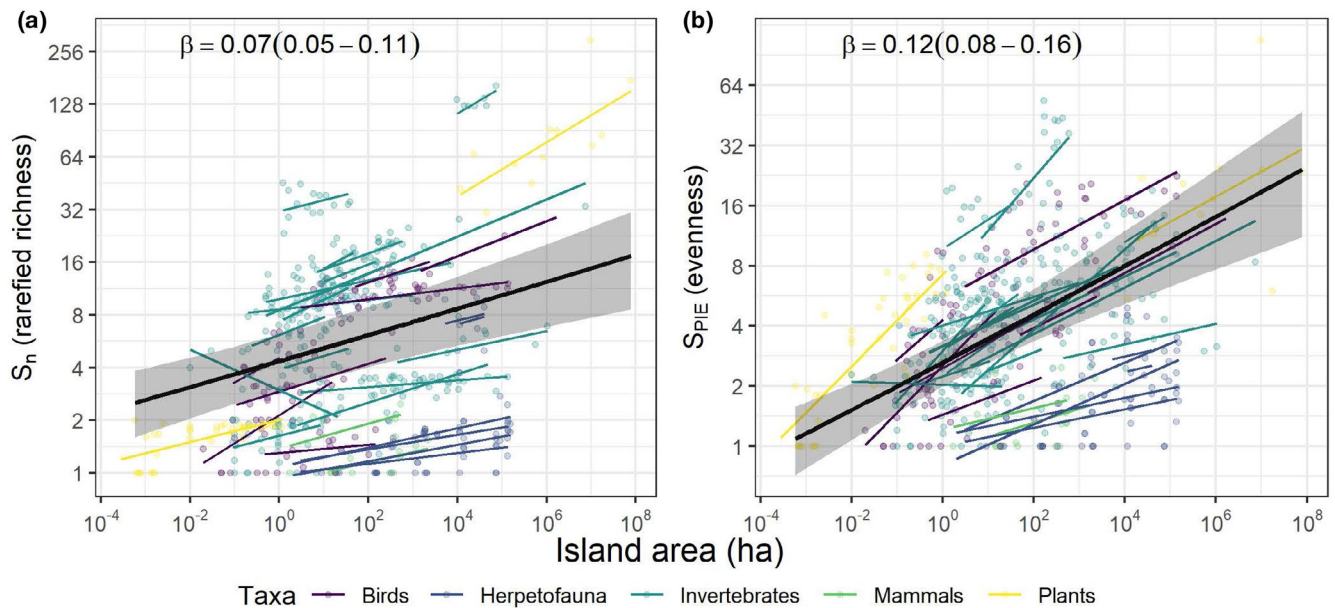
FIGURE 3 Relationship between (a) rarefied richness (S_n) and (b) evenness measured by the effective number of species given the probability of interspecific encounter (S_{PIE}) and island area for each study ($n = 34$). The overall slope (β) coefficient for each metric and its corresponding 95% credible interval are shown at the top-left corner and represented by the continuous black line and surrounding shading. Colours denote different taxonomic groups listed in the key

detect differences in species richness relative to cases where the numbers of individuals are very high. To discern whether there was any effect of very low numbers of individuals on our results, we sequentially removed any island from the entire analysis that had < 10 or < 20 total individuals in a sample. In either case, removal of islands with very low numbers of individuals had no overall influence on the slopes estimated from our analyses for either S_n or S_{PIE} (Supporting Information Table S1).

To examine how the biodiversity variables (S_n and S_{PIE}) varied with island area according to taxa and island types, we examined the posterior density plots of study-level variation in the slopes of S_n and S_{PIE}. Although the mean slope values were different from zero across all taxa and island types, we did find that herpetofauna had weaker relationships between both S_n and S_{PIE} and island area than other taxa where there were enough data to evaluate (i.e., $n > 5$; Figure 4a). We found no clear differences in ISAR relationships between islands of different types (Figure 4b). Finally, using elevational range as a proxy for within-archipelago heterogeneity, we found a slight positive relationship for study-level ISARs and elevational range for both S_n and S_{PIE}, although the 95% credible intervals overlapped zero for both metrics (Figure 5).

4 | DISCUSSION

The ISAR is one of the most well-known patterns in biogeography, with much speculation regarding its underlying mechanisms. However, previous syntheses have primarily examined the relationship at the whole-island scale (e.g., Matthews et al., 2016; Triantis et al., 2012) or have been ambiguous about the scale of

measurement (Drakare et al., 2006). With the combination of our individual rarefaction-based tools for hypothesis testing, in addition to a synthetic approach that allows us to take advantage of the combined information across multiple studies, we were able to reject the null hypothesis that the ISAR largely results only from passive sampling effects; that is, across studies, we found generally more species for a given sample of individuals (S_n), in addition to more even communities (higher S_{PIE}, indicating more relatively common species), with increasing island area.

Consistent with our overall result, a number of individual studies have found some indication of ecological mechanisms allowing more species (and more even and/or heterogeneous communities) beyond that expected from passive sampling (e.g., Gooriah et al., 2020; Kohn & Walsh, 1994; Sfenthourakis & Panitsa, 2012). In short, this suggests that within-island metacommunity-level processes vary with island area. Such processes could include dispersal limitation and dispersal surplus, local demographic factors (e.g., stochasticity and Allee effects) and/or geometric effects (e.g., edge effects or habitat heterogeneity) that would differentially influence species on smaller islands relative to larger islands and therefore diverge from the null expectation (Burns & Neufeld, 2009; Schrader et al., 2020). Owing to the limitations of data available from many studies, we cannot rule out a "breakpoint" consistent with a small island effect in some studies, where rarefied richness does not increase with island area in the smaller islands but does so among larger islands. Furthermore, given that our analyses are on patterns that are aggregates of the dynamics of many different species across scales (i.e., metrics of biodiversity), we are unable to test any of these mechanisms explicitly for each dataset. Further insights would need more information, for example, on among-site variation in species composition (i.e., β-diversity) and,
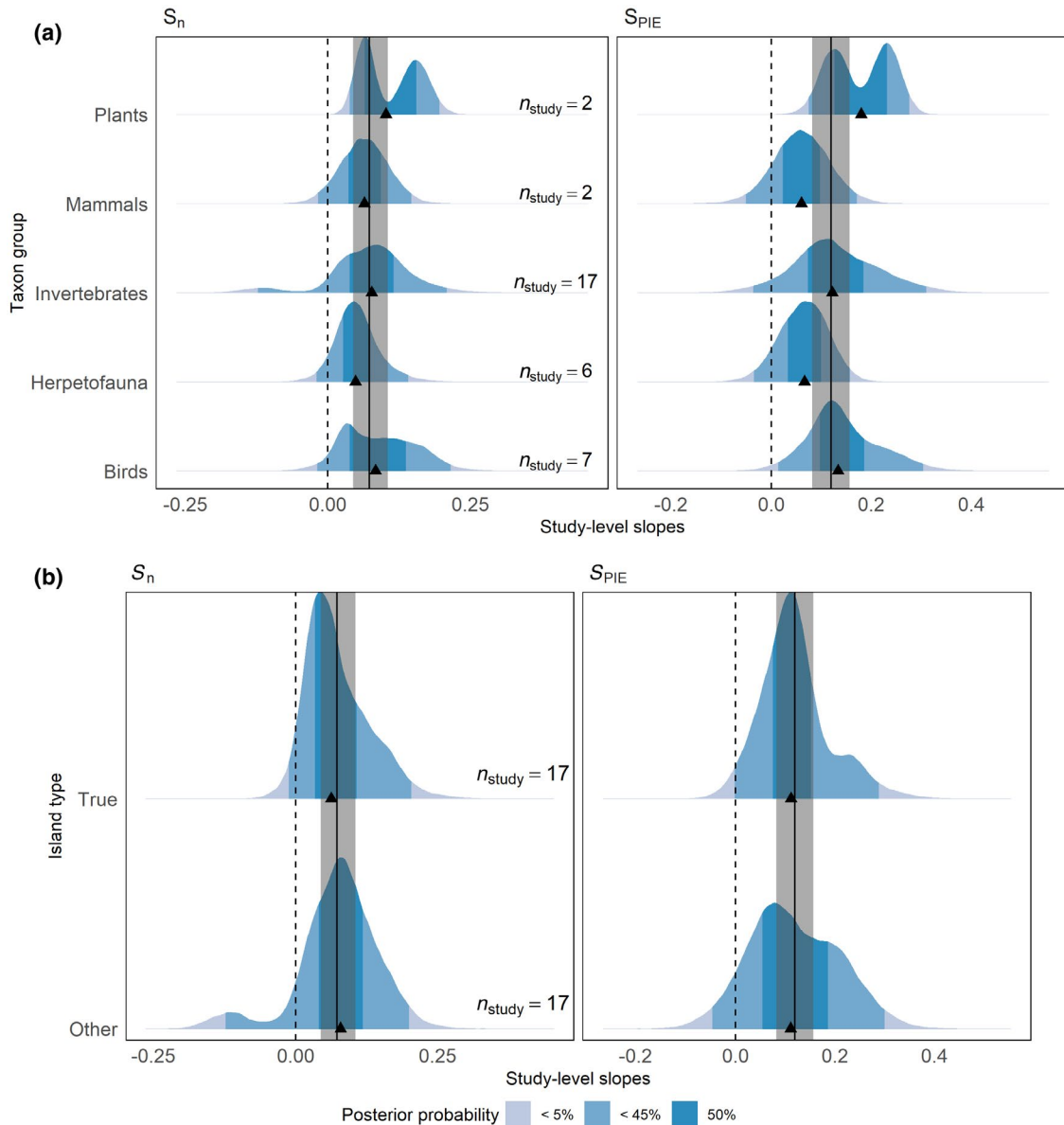
FIGURE 4 Study-level variation in the island species–area relationship (ISAR). Posterior density plots of study-level variation in the slopes of the rarefied number of species (S_n) and the effective number of species given the probability of interspecific encounter (S_{PIE}) grouped by (a) taxon group and (b) island type. The continuous black line and shading shows the overall slope and 95% credible interval. Each density plot is based on 1,000 samples from the posterior distribution of the study-level slope estimates. Black triangles indicate the median values, and densities are shaded by quantiles

possibly, the variation in environmental conditions among sampling points, which we were unable to obtain from most of these studies.

Our overall results that larger islands house more species than expected by passive sampling and that much of this arises because larger islands have more habitat heterogeneity might not be particularly surprising to many. However, testing (and rejecting) the passive sampling hypothesis will allow us to provide better predictive power when predicting how species richness should change with increasing or decreasing island size (e.g., when habitats are lost or restored). Furthermore, passive sampling has been a long-held "null" expectation for the ISAR that has not yet been refuted fully. In fact, passive sampling has been identified as the likely mechanism

behind a number of empirical studies of the ISAR in both natural islands and island-like habitat fragments (e.g., Bidwell et al., 2014; Coleman et al., 1982; Gooriah & Chase, 2020; Haila, 1983; Hill et al., 1994; Ouin et al., 2006). Likewise, using different methods, Giladi et al. (2014) synthesized data from 28 studies on fragmentation in vegetated systems and suggested that 64% of them could not reject the null expectation of passive sampling. Without the power of our cross-site synthesis, a more nuanced picture would also have emerged from our analyses if we had taken a "vote-counting" approach. Specifically, when looking at the individual studies in our synthesis of islands, we find that c. 50% of them (17 of 34) could not individually be used to reject the passive sampling hypothesis.
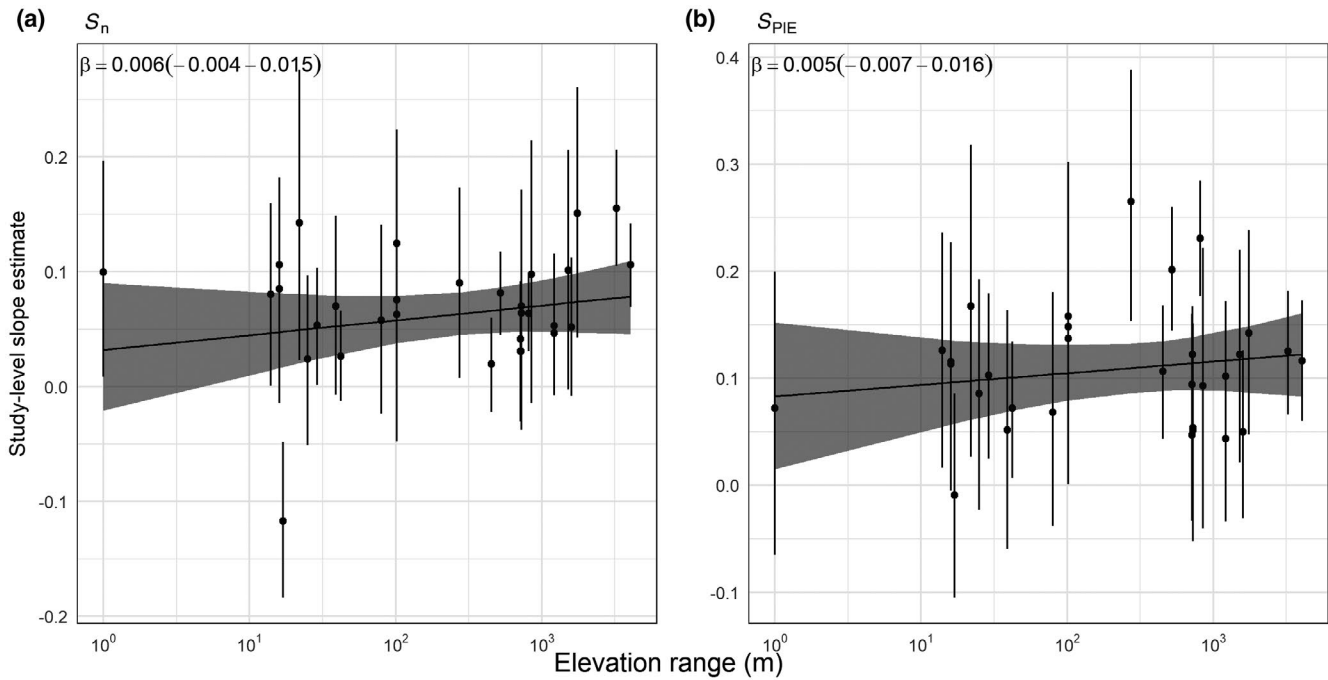
(a) S_n

$\beta = 0.006(-0.004 - 0.015)$

(b) S_{PIE}

$\beta = 0.005(-0.007 - 0.016)$

Study-level slope estimate

Elevation range (m)

FIGURE 5 Study-level slope estimates as a function of elevational range per archipelago. Study-level slope estimates for (a) rarefied richness (S_n) and (b) evenness (S_{PIE}) as a function of the elevational range for each archipelago. The elevational range was calculated as the difference between the highest and lowest maximum elevation within each archipelago. Each point shows the median and 95% credible interval from the island species–area relationship (ISAR) models, and the line and shading show the regression and 95% credible interval for study-level slope estimates as a function of elevational range

However, by combining the studies into a single overarching analysis, we were able to achieve a more conclusive test and rejection of the passive sampling hypothesis.

When we compared differences in the slopes among the studies in our synthesis, we found little clear variation among taxonomic groups or island types. This is, at least in part, because of the small sample size within individual categories. However, we had considerable power ($n = 17$) to evaluate differences among "true islands", which are typically more likely to be more isolated from one another and other island types that might be more likely to experience "rescue effects" (Brown & Kodric-Brown, 1977) from higher dispersal rates and/or higher matrix permeability (Itescu, 2019). As a result, we hypothesized that "true islands" might have a stronger relationship between island area and effort-controlled diversity measures. However, we found no such patterns, as seen in Figure 4b. We did, however, find a slight tendency for herpetofauna to have lower slopes for both S_n and S_{PIE} than other taxa; that is, although there was an overall positive relationship, on a per sample-effort basis, this taxon was less strongly influenced by island area per se than other taxa. We can only speculate regarding possible reasons, including potentially lower dispersal rates that would act against strong metacommunity-like processes such that sampling effects could play a stronger role.

Interestingly, we found that the deviation from the null expectation (magnitude of the slope) of both S_{PIE} and S_n was greater when heterogeneity (measured with elevational range as a proxy) within an island archipelago was larger (Figure 5). This suggests that at least

some of the overall positive relationship between effort-controlled biodiversity measures and island area resulted when larger islands had higher levels of habitat heterogeneity. This is consistent with the conclusions of Triantis et al. (2003), who used different methodology also to suggest a predominant role for habitat heterogeneity in driving the ISAR (Triantis et al., 2003).

Although most studies in our analysis showed positive or weakly positive effects of island area on sample effort-controlled patterns of diversity, one study on ground beetles (Coleoptera: Carabidae) on lake islands showed a strongly negative relationship between sample effort-controlled diversity estimates and island area (Zalewski & Ulrich, 2006). Here, it is possible that some disproportionate effects favour many beetles species on smaller islands, such as the disruption of interspecific interactions (e.g., via pathogens, predators or competitors). It is also possible that heterogeneity was higher in smaller islands, as has been observed elsewhere (Báldi, 2008; Hatteland et al., 2008; Nentwig et al., 2019). In such cases, we might expect a weaker or even negative ISAR depending on whether passive sampling effects (which are always operating) outweigh the disproportionate or heterogeneity effects. Most archipelagos in our dataset, however, had increasing heterogeneity with increasing island area, including the study by Zalewski and Ulrich (2006), suggesting that this was not likely to be the cause.

Overall, we find that processes beyond passive sampling effects seem to be a primary driver of ISAR patterns. Previous syntheses of the ISAR have been hampered by the lack of consensus on how to measure and interpret the ISAR. Moreover, most ISAR studies

commonly use the total number of species on islands as the main variable when evaluating species–area relationships; therefore, most available data on islands do not include species abundances from local samples. An important caveat of our synthesis, however, is that our analyses were only able to examine local-level processes, because these data together with data on within-island variation and total island species richness are rarely collected at the same times/places. Future studies able to examine data fully, from local samples to the entire island, would allow a much deeper analysis of the drivers of the ISAR. This will give us a deeper understanding of the potential underlying factors influencing species patterns on islands, hence providing an important step toward effectively protecting and managing biodiversity on islands and island-like habitats.

AUTHOR CONTRIBUTIONS

L.G. and J.M.C. conceived the study. L.G. performed the literature search and data compilation. A.S., L.G. and S.A.B. cleaned and finalized the data and code. D.N.K., J.S. and H.K. collected data from some archipelagos. L.G., S.A.B. and A.S. did the analyses. L.G. and J.M.C. wrote the first draft of the manuscript and revisions, with input from all authors.

DATA AVAILABILITY STATEMENT

Data and code are available at the following Zenodo link: https://zenodo.org/record/5037070#.YNrQPOgzY2w. Data are further mirrored and available at Dryad: https://doi.org/10.5061/dryad.pnvx0k6n0

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BIOSKETCH

This collaboration consists of scientists interested in synthesizing patterns of diversity and its possible underlying causes using multiple data sources and analytical techniques.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the Supporting Information section.