Research Article: A framework for dissecting ecological mechanisms underlying the island species-area relationship

Jonathan M. Chase[1,2,*], Leana Gooriah[1], Felix May[1,3], Wade A. Ryberg[4], Matthew S. Schuler[5], Dylan Craven[6,1,7], Tiffany M. Knight[6,8,1]

[1]German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig. Deutscher Platz 5e, Leipzig, 04103, Germany

[2]Department of Computer Science, Martin Luther University, 06099, Halle, Germany

[3]Leuphana University Lüneburg, Universitätsallee 1, D-21335 Lüneburg, Germany

[4]Texas A&M Natural Resources Institute, College Station, Texas, USA

[5]Department of Biological Sciences, Darrin Fresh Water Institute, Rensselaer Polytechnic Institute, Troy, NY 12180, USA

[6]Department of Community Ecology, Helmholtz Centre for Environmental Research - UFZ, Halle (Saale), Germany

[7]Biodiversity, Macroecology & Biogeography, Faculty of Forest Sciences and Forest Ecology, University of Göttingen, Göttingen, Germany

[8]Institute of Biology, Martin Luther University Halle-Wittenberg, Halle (Saale), Germany

*Corresponding author: jonathan.chase@idiv.de

URL: https://www.idiv.de/groups_and_people/employees/details/eshow/chase_jonathan.html

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Abstract:

The relationship between an island's size and the number of species on that island—the island species-area relationship (ISAR)—is one of the most well-known patterns in biogeography, and forms the basis for understanding biodiversity loss in response to habitat loss and fragmentation. Nevertheless, there is contention about exactly how to estimate the ISAR, and the influence of the three primary ecological mechanisms—sampling, area *per se*, and heterogeneity— that drive it. Key to this contention is that estimates of the ISAR are often confounded by sampling and estimates of measures (i.e., island-level species richness) that are not diagnostic of potential mechanisms. Here, we advocate a sampling-explicit approach for dissecting the possible ecological mechanisms underlying the ISAR using individual-based rarefaction curves estimated across spatial scales. Specifically, we show how ISAR mechanisms can be inferred by comparing the relationship between island area and diversity indices derived from regional (γ-) and local (α-) individual-based rarefaction curves. If the parameters derived from rarefaction curves at each spatial scale show no relationship with island area, we cannot reject the hypothesis that ISARs result only from sampling effects. However, if the parameters derived from the rarefactions change with island area, effects beyond sampling (i.e., area per se or heterogeneity) are operating. Additionally, if parameters indicative of within-island spatial variation in species composition (i.e., β-diversity) increase with island area, intra-island compositional heterogeneity plays a role in driving the ISAR. We illustrate this approach using representative case studies, including oceanic islands, natural island-like patches, and habitat fragments from formerly continuous habitat, illustrating several combinations of underlying mechanisms. This approach will offer insight into the role of sampling and other processes that underpin the ISAR, providing a more complete understanding of how, and some indication of why, patterns of biodiversity respond to gradients in island area.

Introduction:

The relationship between the area sampled and the number of species in that area—the species-area relationship—is one of the few general laws in ecology (e.g., Arrhenius 1921, Lawton 1999, Lomolino 2000, Drakare et al. 2006). Here, we focus specifically on the Island Species-Area Relationship (hereafter ISAR), which correlates how the numbers of species (species richness) varies with the size of islands or distinct habitat patches (natural or fragmented due to human activities). Like other types of species-area relationships, the ISAR is usually positive (e.g., MacArthur and Wilson 1963, 1967, Connor and McCoy 1979, Triantis et al. 2012). However, various complexities, such as covariation with island age, habitat heterogeneity or isolation can complicate this simple expectation (Kreft et al. 2008, Borregard et al. 2016).

There is ambiguity in the literature regarding the ISAR and its measurement, most notably, because there are dramatic differences in how species richness is sampled and analyzed among studies. For example, some studies regress island size against the total number of species on an entire island, while other studies compare island size to the numbers of species within a sub-sampled area of the island (e.g., quadrat, transect). Further, the number of sub-samples per island

can be constant or proportional to the island area. Here, we follow others (e.g., Triantis et al. 2012, Mathews et al. 2014, 2016) to describe the ISAR as the relationship between the total species richness on a given island (or habitat patch) and the size of that island. Different, but complementary, relationships such as the number of species found within a constantly-sized sub-sampled area regressed against total island size (e.g., sometimes called species density area relationships; Giladi et al. 2014) are treated as sub-components that allow us to discern possible mechanisms of the overall ISAR.

Connor and McCoy (1979) discussed three general mechanisms that could underlie the ISAR, which we overview, update, and extend here:

(1) *Sampling effects*. The simplest mechanism of the ISAR is that islands passively sample individuals from a larger 'regional' pool of individuals of different species. Smaller islands will sample fewer individuals in total than larger islands. And because the regional pool consists of few common and many rare species (i.e., Preston 1960, May 1975, McGill et al. 2007), smaller islands will have fewer species than larger islands. This will create a positive ISAR with more rare species being present on larger islands, but only in proportion to their abundance in the total pool (i.e., the relative proportions of species does not change from small to large islands).

(2) *Area per se*. This mechanism derives from theories that account for local and spatial processes allowing for more species to persist in large areas relative to small areas. This can include dispersal-enabled coexistence mechanisms such as those inherent to the theory of island biogeography (e.g., MacArthur and Wilson 1963, 1967) and other mechanisms of spatial coexistence via metacommunity dynamics (e.g., Tilman 1994, Hanski et al. 2013). Area per se can also include population-level processes, such as Allee-effects or demographic stochasticity, which are more likely to increase extinction or decrease establishment probabilities on smaller islands (e.g., Levin 1974, Hanski and Gyllenberg 1993, Orrock and Wattling 2010).

(3) *Heterogeneity*. Heterogeneity leads to intraspecific aggregation (clumping), and larger islands should have more opportunities for such aggregation. This can emerge from two distinct sub-mechanisms:

(a) *Habitat heterogeneity*. Habitat heterogeneity leads to dissimilarities in species composition via the 'species sorting' process inherent to niche theory (e.g., Whittaker 1970, Tilman 1982, Chase and Leibold 2003). As a mechanism for the ISAR, larger islands are often assumed to have higher levels of habitat heterogeneity than smaller islands (e.g., Williams 1964, Hortal et al. 2009). For example, larger oceanic islands typically have multiple habitat types, including mountains, valleys, rivers, etcetera, allowing for multiple types of species to specialize on these habitats, whereas smaller islands only have a few habitat types. Likewise, in freshwater lakes, which can be thought of as aquatic islands in a terrestrial 'sea', larger lakes typically have more habitat heterogeneity (e.g., depth zonation) than smaller lakes.

(b) *Compositional heterogeneity due to dispersal limitation*. Dispersal limitation can also lead to compositional heterogeneity through a variety of spatial mechanisms, including ecological drift, colonization and competition tradeoffs, and the like (e.g., Condit et al.

2002, Leibold and Chase 2017). If dispersal limitation is more likely on larger islands, we might expect greater within-island spatial coexistence via dispersal limitation, higher compositional heterogeneity, and thus greater total species richness on larger than on smaller islands.

Patterns of species compositional heterogeneity that emerge from these two distinct mechanisms are difficult to distinguish without explicit information on the characteristics of habitat heterogeneity itself (e.g., habitat maps, environmental data), and how species respond to that heterogeneity. And thus, in the absence of information about environmental conditions, we cannot disentangle these mechanisms.

While the above ecological mechanisms can independently determine the ISAR, it is also quite possible that two or more of these mechanisms act in concert (e.g.., Chisholm et al. 2016). Connor and McCoy (1979) suggested that experimental approaches were the primary way that the ISAR mechanisms could be disentangled (e.g., Simberloff 1976, Douglas and Lake 1994, Matias et al. 2010, Schuler et al. 2015, 2017a,b). Such experiments, however, are exceptionally difficult to design, and usually represent artificial conditions (but see Simberloff 1976).

An alternative to explore the mechanisms underlying the ISAR is to use observational data to estimate species richness and other diversity measures at multiple sampling scales (e.g., Hill et al. 1994, Kohn and Walsh 1994, Yaacobi et al. 2007, Sfenthourakis and Panitsa 2012, Gilaldi et al. 2011, 2014, Karger et al. 2014, Leibold and Chase 2017). Here, we synthesize and extend these approaches to provide a more complete way to disentangle the mechanisms underlying ISARs via the use of individual-based rarefaction curves (e.g., Heck et al. 1975, Gotelli and Colwell 2001), and the metrics that can be derived from them, at multiple spatial scales.

Testing ISAR Mechanisms with Individual-Based Rarefactions of Sample Data:

We show that it is possible to disentangle the three ecological mechanisms leading to the ISAR —sampling, area per se, and heterogeneity—by measuring several parameters from the individual-based rarefaction curves collected from larger and smaller scales (see Chase et al. 2018, McGlinn et al. 2018 for a generalized version of this approach) (illustrated in Figure 1).

Figure 1.

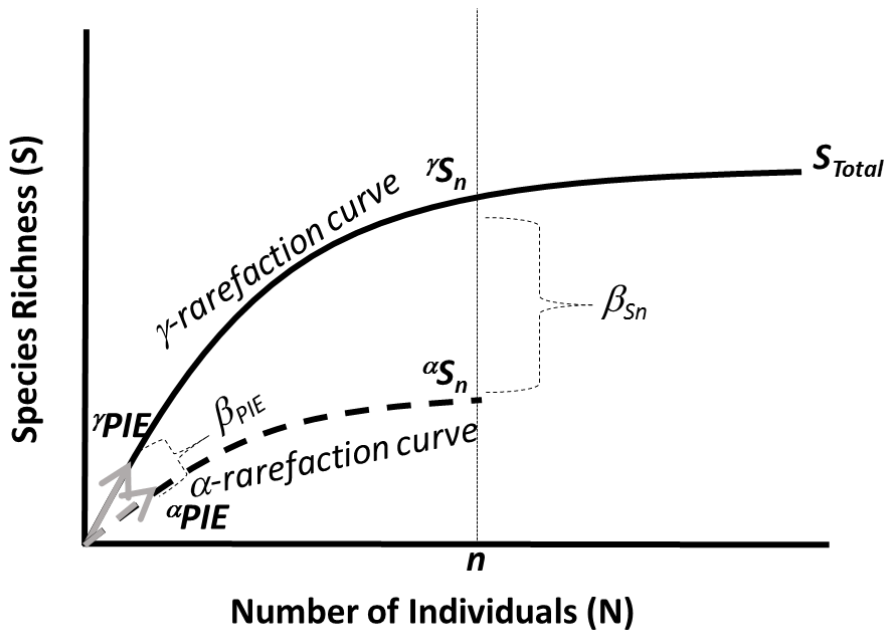

Figure 1. Conceptual illustration of how the diversity indices can be visualized graphically from individual-based rarefaction curves that plot species richness (S) against the numbers of individuals (N) at multiple spatial scales. The γ-rarefaction curve (solid line) is derived by combining all individuals from all plots measured on a given island and randomizing individuals to generate the curve. From this curve, we can visualize the total number of species on the island (S_{Total}), which can be derived from a extrapolation techniques or from independent data (i.e., checklists). We can also visualize two other parameters of interest for dissecting the ISAR: (i) the numbers of species expected from a given N, γS_n (where the vertical dashlined line at n intersects the solid curve) (ii) the probability of interspecific encounter (PIE), which when bias-corrected, represents the slope at the base of the rarefaction curve, $^{\gamma}$PIE (solid grey arrow). The α-rarefaction curve (dashed line) is derived by randomizing individuals from a single plot or subset of plots that constitute a restricted part of the island, and similar parameters—$^{\alpha}S_n$ (vertical dashed line intersects the dashed curve) and $^{\alpha}$PIE (dashed grey arrow)—can be derived from this scale. The ratio between the γ− and α-rarefaction curves provides estimates of β-diversity that indicate the degree of intraspecific aggregation on the island. Note, in text, we advocate converting PIE values into effective numbers of species (S_{PIE}), but only illustrate PIE in the figure, as it is not straightforward to illustrate S_{PIE} on these axes.

First, we derive an individual-based rarefaction curve by combining all individuals from all representative samples (e.g., transects, quadrats) measured on a given island and randomizing individuals to generate the curve. Because this curve extends out to the regional extent of

samples, we refer to it as the γ-rarefaction curve (solid line in Figure 1). This γ-rarefaction curve allows us to estimate the first parameter of the ISAR:

1) The total number of species on a given island, S_{total}. Because the γ-rarefaction curve comes from samples, it is not a complete survey. Thus, the most straightforward way to estimate S_{total} is from independent information, such as checklists of species known to occur on a given island. However, because this information is often unavailable, S_{total} can simply be the total number of species observed in the sampled plots (if sampling effort is proportional to island size), or it can be estimated via techniques for predicting the number of species in a given extent via sampling from within that extent (e.g., Colwell and Coddington 1994, Harte et al. 2009, Chao and Jost 2012, Chao and Chiu 2014, Azaele et al. 2015). Here, we are agnostic on which approach is best for estimating S_{total} on a given island when complete species lists are not available, as there are costs and benefits of each. In our case studies below, we use the Chao (1984) non-parametric estimator to extrapolate the total number of species on a given island, because it can be mathematically and conceptually linked to the rarefaction curves that we use for dissecting the ISAR (Colwell et al. 2012).

Independent of S_{total}, we can estimate two other parameters from the γ-rarefaction curve of samples from across the island that are useful for dissecting ISAR patterns:

2) The numbers of species expected from a rarefaction to a common number of individuals (S_n). Because this value is calculated from the individual-based rarefaction curve from the larger group of samples from across the island (i.e., the γ-rarefaction curve), we refer to this as the rarefied number of species expected from the γ-rarefaction curve, ${}^{\gamma}S_n$.
3) Hurlbert's (1971) Probability of Interspecific Encounter (PIE). We use the bias-corrected version, $PIE = \left(\frac{N}{N-1}\right) * \left(1 - \sum_{i=1}^{S} {p_i}^2\right)$, where N is the total number of individuals in the entire community, S is the total number of species in the community, and p_i is the proportion of each species i. The bias-corrected PIE is a measure of evenness in the community and is equivalent to the slope of the rarefaction curve at its base, as illustrated by the gray arrow in Figure 1a (e.g., Gotelli and Graves 1996, Olszewski 2004). PIE is converted to an effective number of species (the number of species that would be observed if all of the species in a sample were equally abundant) (Jost 2006), which we call S_{PIE} (=1/(1-PIE)). PIE is the same as 1-Simpson's diversity index, and when converted to an effective number of species, is part of the Hill continuum of diversity numbers that places more weight on common species (whereas richness places equal weight on common and rare species) (e.g., Hill 1973, Jost 2006). When S_{PIE} is calculated from the γ-rarefaction curve, we refer to the effective number of species from PIE as ${}^{\gamma}S_{PIE}$. Note that only PIE, not S_{PIE}, is illustrated in Figure 1, because the forms of S_{PIE} are not readily illustrated in the same individual-based rarefactions construct.

At the scale of the γ-rarefaction curve, ${}^{\gamma}S_n$ and ${}^{\gamma}S_{PIE}$ provide important information on separating the influence of the sampling effects from other mechanisms. However, the γ-rarefaction curve averages across the entire set of plots, and thus eliminates any plot-to-plot variation due to heterogeneity in species composition. We calculate a second rarefaction curve from individual

plots (or a defined subset of plots), which we call the α-rarefaction curve (dashed line in Figure 1). From the α-rarefaction curve, we can derive two more parameters, which are similar to those described above but measured from within a given locality, rather than from across the entire island.

4) The numbers of species expected from a rarefaction to a common number of individuals from individual plots, which we refer to as ${}^{\alpha}S_n$.
5) The effective number of species from PIE as above, but calculated from the α-rarefaction curve, which we refer to as ${}^{\alpha}S_{PIE}$.

These metrics from the α-rarefaction curve can be taken from every replicate sample so that these parameters have a mean and variance.

Finally, we take the ratio of these parameters measured from the γ- and α-rarefaction curves to derive two indices of β-diversity that provide an estimate of the amount of interspecific aggregation or clumping (i.e., compositional heterogeneity) within the region (indicated by comparing parameters of the curves as in Figure 1) (see also Olszewski 2004, Chase et al. 2018, McGlinn et al. 2018). These two indices also capture the relative influences of common and rare species on that aggregation.

6) β_{S_n} (${}^{\alpha}S_n$:${}^{\gamma}S_n$), which indicates the ratio of the numbers of individuals expected for a given N from the entire γ- rarefaction curve (${}^{\gamma}S_n$) to that actually observed in a given locality from the α-rarefaction (${}^{\alpha}S_n$).
7) $\beta_{S_{PIE}}$ (${}^{\alpha}S_{PIE}$:${}^{\gamma}S_{PIE}$), which is similar to β_{S_n}, but accounts for differences in the relative abundances of common species via PIE.

Next, we discuss how we can dissect the patterns underlying the ISAR, and the influence of the three underlying ecological mechanisms (sampling, area per se, and heterogeneity), by comparing how each of these diversity indices changes as island area varies. The suite of these hypotheses are presented in Figure 2, and discussed in detail below. Importantly, for each case, we assume that N increases proportionately with island size, but that density (the numbers of individuals per unit area) remains the same. This assumption is not a prerequisite, and island area can directly influence the density of individuals per unit area, which in turn can influence the numbers of species observed in a given plot. In such cases, in order to fully dissect any island-size effects on species richness (S) that are mediated by changes in density of individuals (N), sampling effort needs to be accounted for at the plot scale (by estimating S_n) when comparing patterns of S (see e.g., Schuler et al. 2015, 2017a,b).

Figure 2.

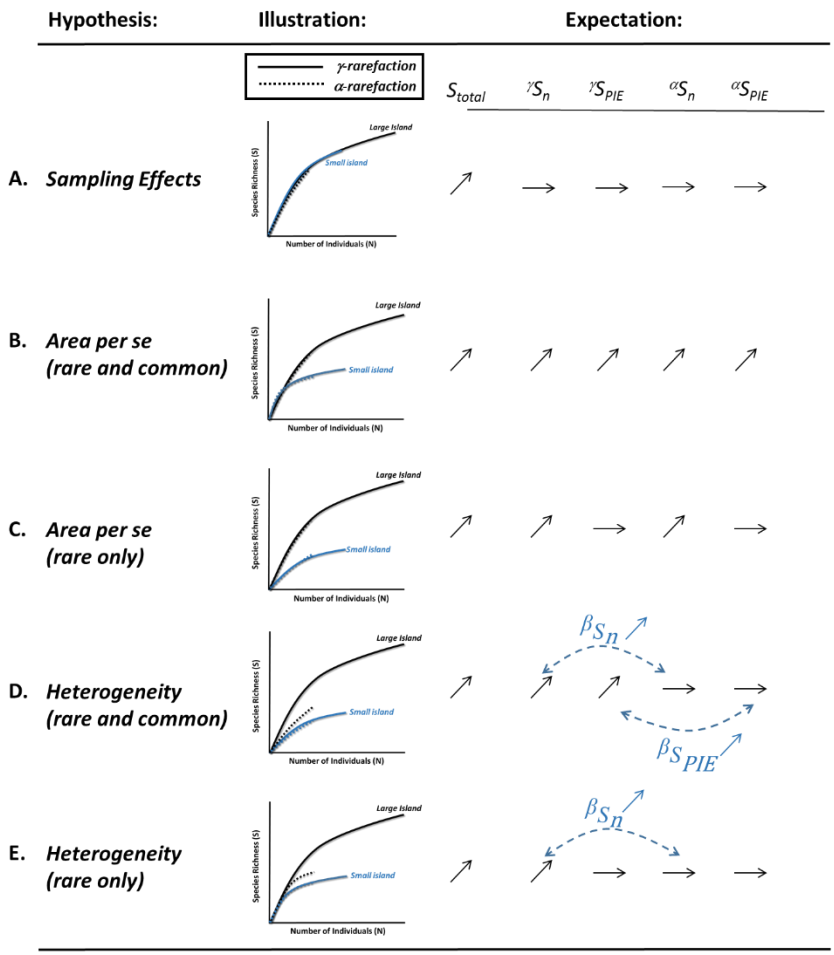

Figure 2. Illustration and expectation for individual-based rarefaction curves, and parameters derived from them, to tease apart the ecological mechanisms of ISARs (note, these are only the canonical hypotheses, and combinations of them can occur). In each case, S_{total} is expected to increase with island area, though this expectation could differ if there are covariation between island size and other environmental or biotic features. A. Sampling effects, whereby the ISAR is determined totally by more individuals being present on larger islands. In this case, none of the parameters sampled from the rarefaction curves differ among islands. B. Area per se, where the rarefaction curves differ. In this case, both common and rare species are influenced, and thus the parameters of S_n and S_{PIE} increase with island area. C. Area per se where only rare species are more likely to persist on larger islands, so that S_n increases, but S_{PIE} does not vary. D. Heterogeneity where both rare and common species are influenced. Depicted by a difference between the α-parameters, which do not vary with island area, and the γ-parameters, which do differ. This also leads to significant effects on both β-parameters (indicated in blue). E. Heterogeneity where only rare species are influenced. Depicted by a difference in S_n, but not S_{PIE}, from the α- to γ-levels, also leading to a difference in β_{S_n} (indicated in blue).

Separating sampling effects from area per se and heterogeneity—The most straightforward mechanism to test is that of sampling effects. Several previous studies have advocated that measuring the numbers of species in standardized samples and comparing it across islands that vary in area can provide information on the influence of sampling (e.g., Hill et al. 1994, Kohn and Walsh 1994, Yaacobi et al. 2007, Giladi et al. 2011, 2014). We advocate a similar, but more detailed approach. To robustly test the sampling effects hypothesis, it is necessary to calculate ${}^{\gamma}S_n$ and ${}^{\gamma}S_{PIE}$ from the entire γ-rarefaction curve. If the ISAR is driven by sampling effects, then we would expect there to be no relationship between island area and either ${}^{\gamma}S_n$ or ${}^{\gamma}S_{PIE}$ (Figure 2a). If, instead, there is a relationship between island area with ${}^{\gamma}S_n$ and/or ${}^{\gamma}S_{PIE}$, then we can falsify the sampling effects mechanism and dive deeper into questions about area per se and heterogeneity. Specifically, if either area per se or heterogeneity are operating, we would expect ${}^{\gamma}S_n$ to increase with increasing island area indicating an effect beyond sampling alone; if ${}^{\gamma}S_{PIE}$ also increases with island area, then we would conclude that the increase in species richness with island area occurred via shifts in dominance of species from smaller to larger islands.

Separating area per se from heterogeneity—While a relationship between ${}^{\gamma}S_n$ and/or ${}^{\gamma}S_{PIE}$ with area can falsify the sampling effects hypothesis, this cannot yet distinguish the role of area per se or within-island compositional heterogeneity. To disentangle these, we can compare the parameters derived from the γ-rarefaction curve to the same parameters from the α-rarefaction curve. If the γ-rarefaction curve and α-rarefaction curve fall on top of each other (i.e., have the same shape), this indicates that there is no aggregation or heterogeneity in species composition (β_{S_n}or $\beta_{S_{PIE}}$ are 1) and the effect is most likely due to area per se alone (Figure 2b, 2c). Additionally, even if β measures are greater than 1, but there is no relationship between these values and island area, we can eliminate the heterogeneity hypothesis. Alternatively, if is a significant positive relationship between β_{S_n}or $\beta_{S_{PIE}}$ and island area, we can deduce that larger islands have higher levels of compositional heterogeneity than smaller islands, and that at least some of the ISAR is due to mechanisms of heterogeneity changing with island size (Figure 2d,e).

Finally, if there is a significant relationship between $\beta_{S_n}$and/or $\beta_{S_{PIE}}$ with island area, we can conclude that compositional heterogeneity likely underlies the ISAR, but we cannot infer whether this is due to habitat heterogeneity or dispersal limitation. To disentangle the relative importance of these mechanisms, it would be necessary to have additional information; for example, on the environmental conditions from different locations from within an island, and how species compositional heterogeneity was related to those conditions (see e.g., Leibold and Chase 2017 for an overview of approaches aimed at disentangling these).

Interactions between area per se and heterogeneity—Although we have discussed area per se and heterogeneity as competing mechanisms, they can both influence the ISAR simultaneously (possibly to varying degrees). In such cases, we might expect more habitats (heterogeneity) per island, but also more area of each given habitat, on larger relative to smaller islands. As a result, area per se effects with increasing size of different habitat types can act in concert with heterogeneity effects. Here, we would expect that ${}^{\alpha}S_n$ and/or ${}^{\alpha}S_{PIE}$, ${}^{\gamma}S_n$ and/or ${}^{\gamma}S_{PIE}$, and $\beta_{S_n}$and/or $\beta_{S_{PIE}}$ would increase with increasing island area (not shown).

On the other hand, area per se and heterogeneity mechanisms can act in opposition to one another. For example, the area-heterogeneity trade-off hypothesis assumes that as heterogeneity increases, the amount of area of each habitat type declines when total area is held constant (Kadmon and Allouche 2007, Allouche et al. 2012). Although perhaps not a common scenario (e.g., Hortal et al. 2009), if the types of habitats increase with island area, while the total amount of each habitat type declines, we might expect ${}^{\alpha}S_n$ and/or ${}^{\alpha}S_{PIE}$ to decline, while ${}^{\gamma}S_n$ and/or ${}^{\gamma}S_{PIE}$ can increase, remain unchanged or decrease, depending on the degree to which the heterogeneity effect is overcome by the area per se effect (not shown).

***Other confounding mechanisms*—**The scenarios that we described above represent a conceptual overview of mechanisms underlying the ISAR when only island area varies, and each island has the same likelihood of receiving individuals from the species pool. However, when measuring ISARs in the real world, there are many other mechanisms that can influence ISAR patterns. These include a number of variables that can often be confounded with island area, such as island isolation, trophic structure, age, historical landscape features, and many others. For each of these, hypotheses about how the metrics calculated from the γ-rarefaction curve and α-rarefaction curve will differ with island area and other variables will need to be modified. For example, larger islands may have more trophic structure (e.g., may be more likely to have top predators), which in turn will feedback to influence the shapes of the rarefaction curves and patterns of diversity (e.g., Östman et al. 2007, Gravel et al. 2011). Likewise, in volcanic archipelagos, larger islands tend also to be younger and may have not had as much time for diversification as smaller/older islands, and this confounding factor can also greatly influence the shape of the ISAR (e.g., Gillespie and Baldwin 2010). Nevertheless, these complexities, and many others, can still be usefully dissected with the generic approach we advocate, comparing metrics derived from rarefaction curves at multiple spatial scales (see also Chase et al. 2018 for discussion of using this approach to analyze several other ecological drivers of biodiversity).

Case studies:

Next, we illustrate how to use our analytical framework to test the three principal ecological mechanisms underlying the ISAR with examples from three datasets representing different taxa and island settings. (1) Lizards sampled from several islands in the Andaman and Nicobar archipelago in the Indian Ocean (data from Surendran and Vasudevan 2015); (2) Grasshoppers (Orthoptera) from Ozark glades, which are rocky outcrop prairies that represent island-like patches in a forested 'sea' (data from Ryberg and Chase 2007); (3) plants from island-like habitat fragments of desert/Mediterranean scrub within an agriculture matrix (data from Giladi et al. 2011). For each case study, we present a brief overview of the system, results, and an interpretation of the results. Results are presented in Table 1 and Figure 3.

All analyses were performed in R version 3.5.0 (R Core Team (2018); diversity indices (i.e., S_{PIE}) were calculated using the Vegan R package (Oksanen et al. 2017) and rarefactions (S_n) and extrapolations (S_{Chao}) were calculated using the iNEXT R package (Hsieh et al. 2018). Plots were generated using ggplot2 (Wickham 2016). Code and raw data for these analyses are available at https://github.com/Leana-Gooriah/ISAR_analysis

Table 1: Regression coefficients and fits for each response in each case study. Coefficients are only given when slope was significantly different from zero.

System	Response	Intercept	Slope	R^2	p-value
Lizards on Oceanic Islands	S_{total}	0.55	0.24	0.88	**<0.0001**
	γS_n	0.49	0.16	0.76	**<0.0001**
	γS_{PIE}	0.47	0.12	0.56	**0.002**
	αS_n	0.71	0.12	0.63	**0.001**
	αS_{PIE}	0.44	0.13	0.61	**0.001**
	β_{S_n}	-0.22	0.04	0.28	**0.03**
	$\beta_{S_{PIE}}$	-	-	-	0.48
Grasshoppers in Ozark Glades	S_{Total}	0.87	0.25	0.30	**0.0001**
	γS_n	0.45	0.16	0.19	**0.01**
	γS_{PIE}	0.18	0.18	0.35	**0.0005**
	αS_n	-0.02	0.2	0.18	**0.013**
	αS_{PIE}	-0.39	0.22	0.25	**0.004**
	β_{S_n}	-	-	-	0.54
	$\beta_{S_{PIE}}$	-	-	-	0.33
Plants in fragmented scrubland	S_{total}	3.61	0.24	0.37	**0.03**
	γS_n	3.02	0.18	0.32	**0.04**
	γS_{PIE}	-	-	-	0.75
	αS_n	-	-	-	0.12
	αS_{PIE}	-	-	-	0.50
	β_{S_n}	-0.05	0.05	0.57	**0.005**
	$\beta_{S_{PIE}}$	-	-	-	0.20

Figure 3.

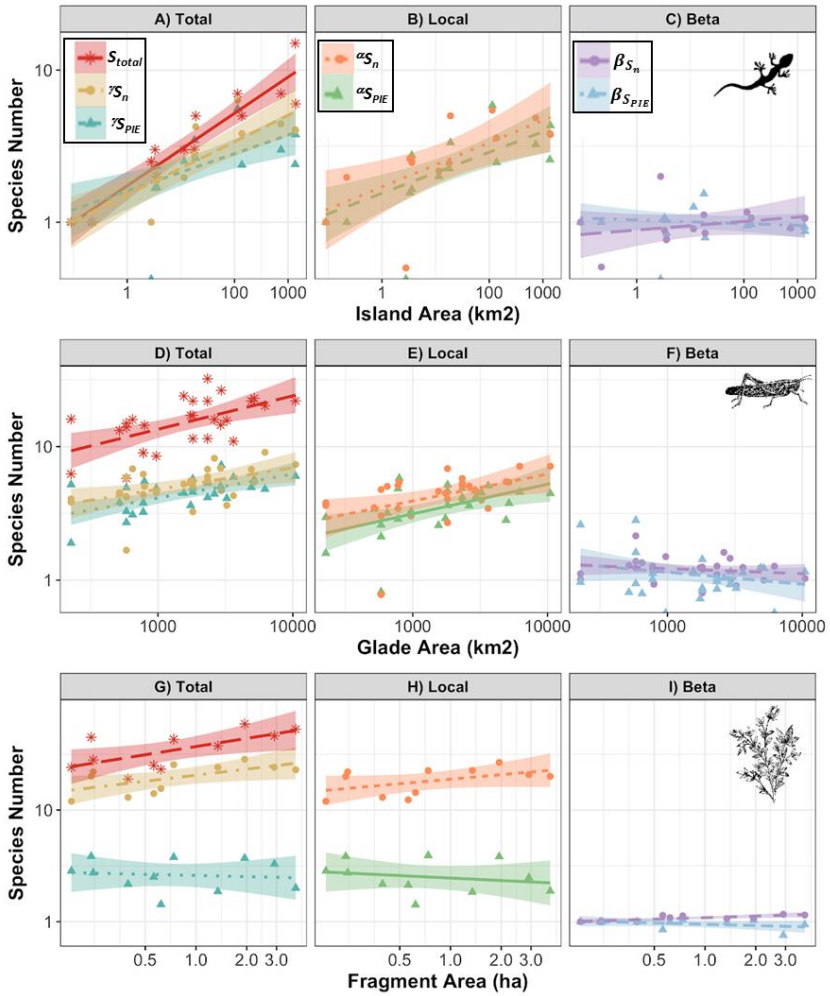

Figure 3. Results from the three case studies provided above. Each row represents results from a different case study; top row is for the lizards on the Andaman Islands; middle row is for the grasshoppers in Ozark glades; bottom row is for plants in Israeli fragments. Panels A,D,G represent parameters derived from the regional scale, including S_{Total} (the number of species estimated on the total island), ${}^{\gamma}S_n$ (the number of species expected for a minimum N measured across plots), and ${}^{\gamma}S_{PIE}$ (the effective number of species given PIE across plots) (see text for explanation). Panels B, E, H represent parameters derived from the local scale, including ${}^{\alpha}S_n$ (the number of species expected for a minimum N measured in a single plot) and ${}^{\alpha}S_{PIE}$ (the effective number of species given PIE within a plot). Panels C, F, I represent parameters derived from comparing the local and regional scale (=β-diversity), including β_{S_n} (the difference which represents heterogeneity in rare and common species), and $\beta_{S_{PIE}}$ (the difference which represents heterogeneity in common species). Coefficients and significance values are given in Table 1. Images are CC0 Creative Commons, with no attribution required.

Lizards on Oceanic Islands—The Andaman and Nicobar islands are a relatively pristine island archipelago in the Indian Ocean. A variety of taxa on these islands have been the subject of a number of island biogeography studies, including ISAR studies (e.g., Davidar et al. 2002). Here, we used data from lizards collected from intensively sampled quadrats (10 m x 10 m) across 15 islands that varied from 0.09 to 1375 km^2 in area (Surendran and Vasudevan 2015).

In this system, we find that S_{total} increases with island area, as expected. Furthermore, both ${}^{\gamma}S_n$ and ${}^{\gamma}S_{PIE}$ increase with island area (Figure 3a). Thus, we can reject the null hypothesis that the ISAR is driven by sampling effects. Instead, there is a clear signal that the number of species increases with island area, even when sampling is controlled for, and that part of this effect is because larger islands have more even communities (indicated by increasing ${}^{\gamma}S_{PIE}$) at the scale of the entire island. A similar pattern emerged at the local scale (Figure 3b), with individual quadrats on larger islands having more species (${}^{\alpha}S_n$) that were less uneven in species composition (${}^{\alpha}S_{PIE}$) than on smaller islands. Because there were significant relationships between island size and both the γ-scale and α-scale measures, we can conclude that area per se played at least some role in driving the ISAR on these islands. However, β_{S_n} increases with increasing island size, indicating some influence of heterogeneity on the ISAR in addition to area per se. This indicates that the quadrat to quadrat variation in the composition of lizard species increased with island size. Interestingly, this heterogeneity effect was only observed among the rarer species, but not the more common species, because there was no concomitant relationship between $\beta_{S_{PIE}}$ and island size.

Grasshoppers in Ozark Glades—Ozark glades are patchy island-like habitats within Midwestern forested ecosystems that contain xeric adapted herbaceous plant communities together with associated fauna (Ware 2002). Grasshoppers are diverse and abundant herbivores that are known to respond to local and spatial processes in these patchy ecosystems (e.g., Östman et al. 2007, Ryberg and Chase 2007). Here, we use data collected from area-standardized sweep samples taken from within glades without top predatory lizards that varied from 0.02 to 1.05 ha.

Here, like the lizards above, we find that S_{total}, ${}^{\gamma}S_n$ and ${}^{\gamma}S_{PIE}$ increase with island area (Figure 3d), and this pattern is reflected at the local scale (Figure 3e). Thus, again, there is a clear signal for an influence of area per se influencing both the number of species and their relative abundances. Unlike the lizards, however, here we found no effect of glade size on β-diversity between sweep samples within a glade (Figure 3F), suggesting that the ISAR did not likely result from increased levels of heterogeneity in larger glades, but rather from spatial processes associated with area per se effects.

Plants in fragmented scrubland—Xeric scrub habitat in Israel was once quite extensive, but has been severely fragmented such that remnant habitats are currently small islands within a sea of agriculture (mostly wheat fields). These fragments have been the subject of intensive research on a number of organisms, including plants and several groups of animals (e.g., Yaacobi et al. 2007, Giladi et al. 2011, 2014, Gavish et al. 2012). Here, we used data from the Dvir region from the study by Giladi et al. (2011), consisting of 11 fragments varying from 0.18 to 3.90 ha. Plants were identified and enumerated in 15 x 15 m plots within each fragment.

We found that ${}^{\gamma}S_n$ increased with fragment area (Figure 3g), but that there was no significant influence of fragment area on ${}^{\alpha}S_n$ (Figure 3h) or on any of the measures involving PIE. Further, the fact that there was a significant area effect on ${}^{\gamma}S_n$ but not ${}^{\alpha}S_n$ indicates there was a significant effect on β_{S_n} (Figure 3i). The results observed at the α-scale imply that sampling effects underlie the ISAR, as concluded by Giladi et al. (2011) (see also Giladi et al. 2014). However, our more complete analyses indicate that heterogeneity is more likely playing a role by creating compositional variation among the rarer species (i.e., as indicated by the effect of fragment size on β_{S_n}, but not $\beta_{S_{PIE}}$).

Synthesis of case studies—In the original studies, which primarily focused just on species richness and not relative abundances, little more than describing the shape of the ISAR could be discerned. However, from our more in depth analyses, we see consistent patterns in S_{total}, but distinct features in the metrics underlying this overall pattern, allowing us to delve deeper into the possible mechanisms underlying these patterns. First, we can see that the ISARs of each taxa/system result from more than just sampling effects. That is, for each system, larger islands/patches have more species (indicated by a significant ${}^{\gamma}S_n$ relationship) than would have been expected from a simple sampling process from the regional species pool. This effect influenced both common and rare species for the island lizards and glade grasshoppers (indicated by a significant ${}^{\gamma}S_{PIE}$ relationship). Alternatively, only the rarer plant species were influenced by fragment size in the terrestrial fragmented system in Israel (because there was no significant ${}^{\gamma}S_{PIE}$ relationship). Indeed, this may explain why the plot-level analyses by the authors failed to detect any change in plot-level measures, and concluded that sampling effects were likely, even though our analyses indicated that area per se played a role, at least for the rarer species.

Going a step further, by deriving β-diversity measures to capture within-island aggregation, we see that lizards on islands and plants in fragments appeared to show higher levels of within-island aggregation on larger islands, at least among the rarer species (i.e., significant β_{S_n} results). This suggests that at least some amount of the ISAR in these two systems was influenced by compositional heterogeneity. Without additional environmental data, however, we cannot tell if that heterogeneity is due to dispersal limitation or environmental variation. Grasshoppers in glades, however, do not appear to show any divergent β-diversity patterns across different sized glades, suggesting that variation in heterogeneity among different sized glades was not a primary driver of the ISAR, but that area per se effects were primarily operating. Unfortunately, however, without further information, we cannot say exactly what sorts of area per se mechanisms allowed more species of grasshoppers to persist in larger glades than expected from sampling.

We used the selected case studies to demonstrate the utility of our framework to provide insight for the possible ecological mechanisms that underpin ISARs. A more complete exploration of the generality of the different patterns and potential mechanisms leading to the ISAR will require a much more thorough analysis of natural islands and patchy landscapes, as well as habitat islands that are created by habitat loss and fragmentation. Such analyses will allow us to achieve a more general synthesis of the patterns and possible processes creating ISARs in natural and fragmented landscapes, but will also require more data (i.e., spatially explicit data of total and

relative abundances of species as well as spatially explicit environmental data) than is typically analyzed in such studies.

Discussion and Conclusions

The island species-area relationship (ISAR)—depicting how the numbers of species increase with the size of the island or habitat patch—is one of the most well-known patterns in biogeography. Understanding the ISAR and the processes leading to it is not only important for basic ecological knowledge, but is also of critical importance for biodiversity conservation in the context of habitat loss and fragmentation. Despite this, the study of the ISAR continues to be difficult to synthesize, primarily because of the confusion about the confounding influence of sampling effects and spatial scale on the ISAR. For example, previous syntheses of the ISAR in natural and fragmentation contexts have focused on estimates of species richness at the entire island scale (e.g., Triantis et al. 2012, Matthews et al. 2016). Other syntheses, however, have confounded species richness measurements from multiple scales and contexts, making comparisons within and among studies difficult (e.g., Drakare et al. 2006, Smith et al. 2009, Fahrig 2017). As we have shown here, it is important to understand and report how species richness was sampled in order to interpret ISAR results. This is particularly true in the realm of conservation biology, where the influence of habitat loss and fragmentation on biodiversity is a critically important, but also controversial topic. In fact, a great deal of the controversy (e.g., Haddad et al. 2015, 2017, Hanski 2015, Fahrig 2013, 2017, Fletcher et al. 2018) is likely attributable to different investigators using different sampling procedures, different analyses, and different spatial scales for their comparisons, and thus comparing apples to oranges.

We are not alone in this call for a more careful consideration of sampling when measuring and interpreting ISARs (Hill et al. 1994, Schroeder et al. 2004, Yaacobi et al. 2007, Giladi et al. 2011, 2014, Sfenthourakis and Panitsa 2012, Karger et al. 2014). However, we argue that our approach, using metrics derived from γ- and α-rarefaction curves, provides an important advance over previous approaches, which we overview next.

Several authors have advocated for comparing how the numbers of species in a fixed area (similar to our S_n) varies with area of islands or habitat fragments in order to determine whether ISAR patterns 'beyond sampling effects' emerged. For example, using this approach, Hill et al. (1994) showed that area had a small influence on tree species richness when sample area was standardized (number of plots) in forest fragments in Ghana, indicating predominantly sampling effects. Alternatively, Kohn and Walsh (1994) found a strong increase in plant species richness in quadrats on larger relative to smaller oceanic islands off of Shetland (UK), suggesting area per se played some role in driving the ISAR on these islands. In an overview of plant fragmentation studies, Giladi et al. (2014) showed that of the 28 studies that measured the number of species in standardized plots, 64% showed no relationship with habitat area, suggesting a predominant role for sampling effects, while the remaining 36% showed increasing standardized species richness with increasing fragment area, indicating a role for area per se and/or heterogeneity.

However, caution must be taken when inferring sampling effects when only species richness is measured in fixed area samples. First, when area per se effects are primarily experienced by rare

species, sampling at small spatial grains may miss this effect, especially when averages of the numbers of species are taken from the smallest spatial scale. For example, Karger et al. (2014) found that fern species richness in standardized plots did not increase with island area when measured at small spatial grains (i.e., $400m^2$-$2400m^2$), but that the slope became significantly increasing at the largest sampling grain (6400 m^2). Second, it is possible that S measured in standardized plots may not vary with island size, but that habitat heterogeneity leads to different species present in different habitat types, creating the ISAR. For example, Sfenthourakis and Panitsa (2012) found that plant species richness on Greek islands measured at local ($100m^2$) scales did not change with island area, but that there were high levels of β-diversity on islands that were larger, likely due to increased heterogeneity. In both of these studies, simply measuring standardized species richness in small plots across islands of different spatial grains may have led to the faulty conclusion that sampling effects predominated (i.e., no relationship of S with island area). This is because area per se and/or habitat heterogeneity can generate patterns that are largely indistinguishable from sampling effects when sampling grain, and habitat heterogeneity are not considered. However, our approach, which explicitly considers these scaling effects, provides a more definitive way to test amongst these alternative mechanisms. Indeed, this is exactly what we found in our case study on fragments in Israel (Figure 3g, h, i). While local scale results imply sampling effects, as concluded by the original authors, larger scale results actually suggest heterogeneity underlies the ISAR.

In an approach similar to our own to disentangle the role of sampling effects from ISAR studies, Yaacobi et al. (2007) advocated the use of Fisher's α as a measure intended to capture the relative abundances of species in addition to area-standardized species richness. They used this approach to examine the influence of habitat fragmentation on plants and beetles in the same fragmented Mediterranean scrubland described above. Like our approach, comparing Fisher's α across islands or habitat patches can provide an indicator of how commonness and rarity (i.e., evenness) varies across islands, and Yaacobi et al. (2007) found no change in Fisher's α, which they interpreted to indicate that sampling was primarily responsible for differences in S among habitat fragments. While this approach was quite similar to ours in spirit, the use of Fisher's α as a measure of diversity is predicated on the implicit assumption that the distribution of commonness and rarity follows a log-series distribution; when it does not, the metric can give highly suspect results (e.g., Jost 2007). Thus, we prefer the use of PIE and its conversion to an effective number of species S_{PIE}, for capturing differences in the relative abundances of species, which makes no such assumptions, can be more directly compared to changes in S along the Hill number continuum, and can be more meaningfully compared across spatial scales (e.g., Jost 2007, Chase and Knight 2013).

Despite its advantages, it is important to note that our approach is purely observational and dissects the island-wide ISAR into metrics that capture different elements of how biodiversity scales with sampling. As such, it cannot definitively discern process from these patterns, although it can provide deeper insights into the likely mechanisms that influence the ISAR than previous observational approaches. To more definitively test the primary ISAR mechanisms described here (e.g., sampling, area per se, and heterogeneity; see Connor and McCoy 1979), we would need to go a step or two further. This could include, for example, observational studies

that took advantage of natural experiments such as islands that varied semi-orthogonally in both area and heterogeneity (Nilsson et al. 1988, Ricklefs and Lovette 1999, Kallimanis et al. 2008, Hannus and Von Numers 2008), but also dissecting patterns of species richness in a more explicit way as we have outlined here. Or it could include manipulative experiments that directly alter island size and/or heterogeneity (e.g., Simberloff 1976, Matias et al. 2010), or disrupt the processes occurring within islands (e.g., altering patterns of within-island dispersal and/or extinction).

Finally, we note that the approach that we advocate here is only one step towards creating a deeper understanding of patterns of diversity on islands and island-like habitats. We have only focused on the simplest pattern of diversity on islands, the ISAR. We hope that new analyses and meta-analyses will emerge along the lines of what we have presented above in the 'case studies' section, so that we might start to see some generalities emerge. However, there are many other features of islands that vary in addition to and in conjunction with island area (and associated habitat heterogeneity), that influence patterns of diversity. These include variations in trophic structure (e.g., Gravel et al. 2011), variations in island isolation (Kreft et al. 2008) and variation in island age (Baldwin and Gillespie 2009), among many others. Nevertheless, generalizations of the approach that we advocate, which explicitly derives parameters that capture different elements of diversity from rarefaction curves at different spatial scales (see also Chase et al. 2018, McGlinn et al. 2018), should be invaluable in capturing key features for how and why diversity varies across islands and contexts.

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JMC and TMK developed the initial conceptualization of the framework presented here, with significant input from WAR, MAS, FM, DC and LG at different stages. WAR provided the data for the grasshopper case study; FM provided the data for the fragmentation case study. LG wrote the code, with help from DC and FM, and did the analyses. JMC wrote the first draft of the manuscript, and all authors contributed significantly to revisions.

Data and Code Accessibility:

The code to run the analyses described here, as well as the data for the case studies, are freely available on https://github.com/Leana-Gooriah/ISAR_analysis.

Literature Cited:

Allouche, O., M. Kalyuzhny, G. Moreno-Rueda, M. Pizarro, & R. Kadmon. (2012). Area-heterogeneity tradeoff and the diversity of ecological communities. Proceedings of the National Academy of Sciences USA, 109, 17495–17500.

Arrhenius, O. (1921). Species and area. Journal of Ecology 9, 95-99.

Azaele, S., A. Maritan, S. J. Cornell, S. Suweis, J. R. Banavar, D. Gabriel, & W. E. Kunin. (2015). Towards a unified descriptive theory for spatial ecology: predicting biodiversity patterns across spatial scales. Methods in Ecology and Evolution, 6, 324–332.

Borregaard, M. K., T. J. Matthews, and R. J. Whittaker (2016). The general dynamic model: towards a unified theory of island biogeography? Global Ecology and Biogeography, 25, 805–816.

Chao, A. (1984). Nonparametric estimation of the number of classes in a population. Scandinavian Journal of Statistics, 11, 265–270.

Chao, A., & C.-H. Chiu. (2016). Species Richness: Estimation and Comparison. Pages 1–26 *in* N. Balakrishnan, T. Colton, B. Everitt, W. Piegorsch, F. Ruggeri, and J. L. Teugels, editors. Wiley StatsRef: Statistics Reference Online. John Wiley & Sons, Ltd, Chichester, UK.

Chao, A., & L. Jost. (2012). Coverage-based rarefaction and extrapolation: standardizing samples by completeness rather than size. Ecology, 93, 2533–2547.

Chase, J. M., & M. A. Leibold. (2003). Ecological Niches: linking classical and contemporary approaches. University of Chicago Press, Chicago, Illinois, USA.

Chase, J., B. McGill, D. J. McGlinn, F. May, S. A. Blowes, X. Xiao, T. M. Knight, O. Purschke, & N. J. Gotelli. (2018). Embracing scale-dependence to achieve a deeper understanding of biodiversity and its change across communities. Ecology Letters. https://doi.org/10.1111/ele.13151

Chisholm, R. A., T. Fung, D. Chimalakonda, & J. P. O'Dwyer. (2016). Maintenance of biodiversity on islands. Proceedings of the Royal Society B: Biological Sciences, 283, 20160102.

Colwell, R. K., A. Chao, N. J. Gotelli, S.-Y. Lin, C. X. Mao, R. L. Chazdon, & J. T. Longino. (2012). Models and estimators linking individual-based and sample-based rarefaction, extrapolation and comparison of assemblages. Journal of Plant Ecology, 5, 3–21.

Condit, R., Pitman, N., Leigh, E.G., et al., (2002). Beta-diversity in tropical forest trees. Science, 295, pp.666-669.

Connor, E. F., & E. D. McCoy. (1979). The statistics and biology of the species-area relationship. American Naturalist 113, 791–833.

Davidar, P., K. Yogananad, T. Ganesh, & S. Devy. (2002). Distributions of forest birds and butterflies in the Andaman islands, Bay of Bengal: nested patterns and processes. Ecography, 25, 5–16.

Dengler, J. (2009). Which function describes the species-area relationship best? A review and empirical evaluation. Journal of Biogeography 36, 728–744.

Douglas, M. & P. S. Lake. (1994). Species richness of stream stones: An investigation of the mechanisms generating the species-area relationship. Oikos, 69, 387-396.

Drakare, S., J. J. Lennon & H. Hillebrand. (2006). The imprint of the geographical, evolutionary and ecological context on species-area relationships. Ecology Letters, 9, 215–227.

Fahrig, L. (2013). Rethinking patch size and isolation effects: the habitat amount hypothesis. Journal of Biogeography, 40, 1649–1663.

Fahrig, L. (2017). Ecological responses to habitat fragmentation per se. Annual Review of Ecology, Evolution, and Systematics 48, 1–23.

Giladi, I., F. May, M. Ristow, F. Jeltsch, & Y. Ziv. (2014). Scale-dependent species-area and species-isolation relationships: a review and a test study from a fragmented semi-arid agro-ecosystem. Journal of Biogeography 41, 1055–1069.

Giladi, I., Y. Ziv, F. May, & F. Jeltsch. (2011). Scale-dependent determinants of plant species richness in a semi-arid fragmented agro-ecosystem: Scale-dependent plant diversity in an agro-ecosystem. Journal of Vegetation Science, 22, 983–996.

Gillespie, R. G., & B. G. Baldwin. (2009). Island biogeography of remote archipelagoes: Interplay between ecological and evolutionary Processes. Page *in* J. B. Losos and R. E. Ricklefs, editors. The Theory of Island Biogeography Revisited. Princeton University Press, Princeton, New Jersey, USA.

Gotelli, N. J., & R. K. Colwell. (2001). Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecology Letters, 4, 379–391.

Gotelli, N. J., & G. R. Graves. (1996). Null models in ecology. Smithsonian Institute Press, Washington, D.C., USA.

Gravel, D., F. Massol, E. Canard, D. Mouillot, & N. Mouquet. (2011). Trophic theory of island biogeography: Trophic theory of island biogeography. Ecology Letters, 14, 1010–1016.

Haddad, N. M., L. A. Brudvig, J. Clobert, et al. (2015). Habitat fragmentation and its lasting impact on Earth's ecosystems. Science Advances, 1, e1500052–e1500052.

Haddad, N. M., A. Gonzalez, L. A. Brudvig, M. A. Burt, D. J. Levey, & E. I. Damschen. (2017). Experimental evidence does not support the Habitat Amount Hypothesis. Ecography, 40, 48–55.

Hannus, J.-J., & M. Von Numers. (2008). Vascular plant species richness in relation to habitat diversity and island area in the Finnish Archipelago. Journal of Biogeography, 35, 1077–1086.

Hanski, I. (2015). Habitat fragmentation and species richness. Journal of Biogeography, 42, 989–993.

Hanski, I., & M. Gyllenberg. (1993). Two general metapopulation models and the core-satellite species hypothesis. American Naturalist, 142, 17–41.

Hanski, I., G. A. Zurita, M. I. Bellocq, & J. Rybicki. (2013). Species-fragmented area relationship. Proceedings of the National Academy of Sciences 110, 12715–12720.

Harte, J., A. B. Smith, & D. Storch. (2009). Biodiversity scales from plots to biomes with a universal species-area curve. Ecology Letters 12, 789–797.

Heck, K. L., G. van Belle, & D. Simberloff. (1975). Explicit calculation of the rarefaction diversity measurement and the determination of sufficient sample size. Ecology, 56, 1459–1461.

Hill, J. L., P. J. Curran, & G. M. Foody. (1994). The effect of sampling on the species-area curve. Global Ecology and Biogeography Letters, 4, 97-106.

Hill, M. O. (1973). Diversity and evenness: A unifying notation and its consequences. Ecology, 54, 427–432.

Hortal, J., K. A. Triantis, S. Meiri, E. Thébault, & S. Sfenthourakis. (2009). Island species richness increases with habitat diversity. American Naturalist, 174, E205–E217.

Hurlbert, S. H. (1971). The nonconcept of species diversity: A critique and alternative parameters. Ecology, 52, 577–586.

Hsieh, T. C., K. H. Ma & A. Chao. (2018). iNEXT: iNterpolation and EXTrapolation for species diversity. R package version 2.0.15.

Jost, L. (2006). Entropy and diversity. Oikos, 113, 363–375.

Jost, L. (2007). Partitioning diversity into independent alpha and beta components. Ecology, 88, 2427–2439.

Kadmon, R., & O. Allouche. (2007). Integrating the effects of area, isolation, and habitat heterogeneity on species diversity: A unification of island biogeography and niche theory. American Naturalis, 170, 443–454.

Kallimanis, A. S., A. D. Mazaris, J. Tzanopoulos, J. M. Halley, J. D. Pantis, & S. P. Sgardelis. (2008). How does habitat diversity affect the species–area relationship? Global Ecology and Biogeography, 17, 532–538.

Karger, D. N., P. Weigelt, V. B. Amoroso, D. Darnaedi, A. Hidayat, H. Kreft, & M. Kessler. (2014). Island biogeography from regional to local scales: evidence for a spatially scaled echo pattern of fern diversity in the Southeast Asian archipelago. Journal of Biogeography, 41, 250–260.

Kohn, D. D., & D. M. Walsh. (1994). Plant species richness: The effect of island size and habitat diversity. Journal of Ecology, 82, 367-377.

Kreft, H., W. Jetz, J. Mutke, G. Kier, & W. Barthlott. (2007). Global diversity of island floras from a macroecological perspective. Ecology Letters, 11, 116–127.

Lawton, J. H. (1999). Are there general laws in ecology? Oikos, 84, 177-192.

Leibold, M. A., & J. M. Chase. (2017). Metacommunity ecology. Princeton University Press, Princeton, New Jersey, USA.

Levin, S. A. (1974). Dispersion and Population Interactions. American Naturalist, 108, 207–228.

Lomolino, M. V. (2000). Ecology's most general, yet protean pattern: the species-area relationship. Journal of Biogeography, 27, 17–26.

MacArthur, R. H., & E. O. Wilson. (1963). An equilibrium theory of insular zoogeography. Evolution, 17, 373–387.

MacArthur, R. H., & E. 0. Wilson. (1967). The theory of island biogeography. Princeton University Press, Princeton, New Jersey, USA.

Matias, M. G., A. J. Underwood, D. F. Hochuli, & R. A. Coleman. (2010). Independent effects of patch size and structural complexity on diversity of benthic macroinvertebrates. Ecology, 91, 1908–1915.

Matthews, T. J., F. Guilhaumon, K. A. Triantis, M. K. Borregaard, & R. J. Whittaker. (2016). On the form of species-area relationships in habitat islands and true islands: Species-area relationships in islands and habitat islands. Global Ecology and Biogeography, 25, 847–858.

Matthews, T. J., M. J. Steinbauer, E. Tzirkalli, K. A. Triantis, & R. J. Whittaker. (2014). Thresholds and the species-area relationship: a synthetic analysis of habitat island datasets. Journal of Biogeography, 41, 1018–1028.

May, R. M. (1975). Patterns of species abundance and diversity. Pages 81–120 *in* M. L. Cody and J. M. Diamond, editors. Ecology and Evolution of Communities. Belknap Press of Harvard University, Cambridge, Massachusetts, USA.

McGill, B. J., R. S. Etienne, J. S. Gray, et al. (2007). Species abundance distributions: moving beyond single prediction theories to integration within an ecological framework. Ecology Letters, 10, 995–1015.

McGlinn, D. J., X. Xiao, F. May, N. J. Gotelli, S. Blowes, T. Knight, O. Purschke, J. Chase, & B. McGill. (2018). MoB (Measurement of Biodiversity): a method to separate the scale-dependent effects of species abundance distribution, density, and aggregation on diversity change. bioRxiv doi: https://doi.org/10.1101/244103.

Nilsson, S. G., J. Bengtsson, & S. As. (1988). Habitat diversity or area per se? Species richness of woody plants, carabid beetles and land snails on islands. Journal of Animal Ecology, 57, 685-704.

Oksanen et al. (2018). vegan: Community Ecology Package. R package version 2.4-5.

Olszewski, T. D. (2004). A unified mathematical framework for the measurement of richness and evenness within and among multiple communities. Oikos, 104, 377–387.

Orrock, J. L., & J. I. Watling. (2010). Local community size mediates ecological drift and competition in metacommunities. Proceedings of the Royal Society B: Biological Sciences 277, 2185–2191.

Östman, Ö., N. W. Griffin, J. L. Strasburg, J. A. Brisson, A. R. Templeton, T. M. Knight, & J. M. Chase. (2007). Habitat area affects arthropod communities directly and indirectly through top predators. Ecography, 30, 359–366.

Preston, F. W. (1960). Time and space and the variation of species. Ecology, 41, 611–627.

R Core Team. (2018). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Ricklefs, R. E., & I. J. Lovette. (1999). The roles of island area per se and habitat diversity in the species-area relationships of four Lesser Antillean faunal groups. Journal of Animal Ecology, 68, 1142–1160.

Ryberg, W. A., & J. M. Chase. (2007). Predator-dependent species-area relationships. American Naturalist 170, 636–642.

Schuler, M. S., J. M. Chase & T. M. Knight. (2015). More individuals drive the species energy-area relationship in an experimental zooplankton community. Oikos, 124, 1065–1070.

Schuler, M. S., J. M. Chase & T. M. Knight. (2017a). Habitat size modulates the influence of heterogeneity on species richness patterns in a model zooplankton community. Ecology, 98, 1651–1659.

Schuler, M. S., J. M. Chase & T. M. Knight. (2017b). Habitat patch size alters the importance of dispersal for species diversity in an experimental freshwater community. Ecology and Evolution 7, 5774–5783.

Sfenthourakis, S. & M. Panitsa. (2012). From plots to islands: species diversity at different scales: Diversity patterns in insular plants communities. Journal of Biogeography, 39, 750–759.

Simberloff, D. (1976). Experimental zoogeography of islands: Effects of island size. Ecology, 57, 629–648.

Simberloff, D. S. (1974). Equilibrium theory of island biogeography and ecology. Annual Review of Ecology and Systematics 5, 161–182.

Smith, V. H., B. L. Foster, J. P. Grover, R. D. Holt, M. A. Leibold, & F. deNoyelles. (2005). Phytoplankton species richness scales consistently from laboratory microcosms to the world's oceans. Proceedings of the National Academy of Sciences USA, 102, 4393–4396.

Surendran, H., & K. Vasudevan. (2015). The devil is in the detail: estimating species richness, density, and relative abundance of tropical island herpetofauna. BMC Ecology, 15, 18.

Tilman, D. (1994). Competition and biodiversity in spatially structured habitats. Ecology, 75, 2–16.

Tjørve, E. (2009). Shapes and functions of species-area curves (II): a review of new models and parameterizations. Journal of Biogeography 36, 1435–1445.

Triantis, K. A., F. Guilhaumon, & R. J. Whittaker. (2012). The island species-area relationship: biology and statistics. Journal of Biogeography, 39, 215–231.

Whittaker, R. H. (1972). Communities and ecosystems. Macmillan, New York, New York, USA.

Ware, S. (2002). Rock outcrop plant communities (Glades) in the Ozarks: A synthesis. Southwestern Naturalist 47, 585-597.

Williams, C. B., (1964). Patterns in the balance of nature and related problems of quantitative ecology. Academic Press, London, UK.

Yaacobi, G., Y. Ziv, & M. L. Rosenzweig. (2007). Habitat fragmentation may not matter to species diversity. Proceedings of the Royal Society B: Biological Sciences, 274, 2409–2412.

Wickham, H., 2016. ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag, New York, USA.