Disentangling the mechanisms underlying the island species-area relationship (ISAR)

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“Islands only produce a greater or less number of species, as their circumference is more or less extensive.”

J.R. Forster, 1778, Chapter V, p. 169.

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SUMMARY

The island species-area relationship (ISAR), that is, the increase in the number of species with increasing island size, is one of the most well known patterns in biogeography. The ISAR emerged as a key component in the development of theories on insular biogeography and has become a common focus of habitat fragmentation research. Understanding and predicting how species respond to changes in island/habitat size is critical in the realm of conservation as reduction in habitat area is one of the key drivers of species extinctions. Despite its importance in the context of conservation and habitat loss, there is a lack of consensus on how to measure the ISAR, as well as some ambiguity surrounding the mechanisms that shape it. One of the primary reasons for the uncertainty surrounding both the shape and underlying mechanisms of the ISAR is that data are not consistent or comparable within and across studies. The overall aim of this dissertation is to provide a deeper understanding of the ISAR using a framework that uses a scale-explicit approach to understand and disentangle the possible mechanisms underlying ISAR relationships in natural and fragmented island ecosystems. The chapters throughout this dissertation provide various tests of this framework across various systems such as: lakes, oceanic islands and other island-like habitats, and finally provides a synthesis of the mechanisms underlying the ISAR (Chapter 5).

In **Chapter 2,** I introduce a framework to dissect ecological mechanisms underlying the island species-area relationship. Here, the framework is tested using case studies from different types of islands (oceanic, glades and fragments) across different taxa. The main results suggest that plants in fragmented habitats are most likely influenced by random sampling effects, while the ISARs of grasshoppers in glades and lizards on oceanic islands

tend to be driven by non-random mechanisms. When comparing diversity measures at the local scale, I additionally find that rare lizard species are disproportionately favoured on larger islands in the Andaman Islands.

In **Chapter 3**, using lakes as islands, I assemble published datasets of zooplankton abundance at the local and whole-lake level across North American and European lakes and use the framework presented in Chapter 2 to disentangle the hypotheses. Results from this chapter show that random sampling effects are most probably driving the SAR of zooplankton in both North American and European lakes. Further, I was able to reject habitat heterogeneity hypothesis when analyzing a subset of lakes where multiple samples across the lakes were pooled.

In **Chapter 4**, I provide another test of the framework (Chapter 2) to try and disentangle the mechanisms underlying the ISARs of four taxa : birds, butterflies, frogs and lizards in the same archipelago, the Andaman and Nicobar islands. The main findings from this chapter show that the ISARs of all four taxa are influenced by non-random mechanisms and therefore emphasize the importance of larger islands as sources of rare species.

Finally, in **Chapter 5**, I present a synthesis of the mechanisms underlying the ISAR, where I gathered 35 relative abundance datasets across a variety of taxa on different types of islands and used the methods from Chapter 2 to specifically examine the mechanisms underlying the ISARs. The synthesis reveals that random sampling effects are driving the ISARs of most studies, suggesting that there is no difference between a large and small island other than larger islands passively sample more individuals of the regional species pool and therefore more species than smaller islands.

CHAPTER 1

INTRODUCTION

1.1 The species-area relationship (SAR)

The relationship between the area sampled and the number of species in that area - the species-area relationship - is one of the oldest laws in ecology (Arrhenius 1921, Lawton 1999, Lomolino 2000, Drakare et al. 2006). The species-area relationship (SAR) shows a non-linear increase in species richness as sampling area increases. This observation seems to have first occurred in the late eighteenth century and slowly taken hold in the nineteenth century. The SAR was first quantified by (Watson 1835) - through quantification of the geographical distribution of British plants - who later made the first plot relating species number with area (Watson 1859). We now refer to this as the species-area curve.

The species-area relationship (SAR) is mathematically described by a power curve equation (Arrhenius 1920, 1921):

$$S = cA^z$$

Where S is the number of species, A is the area and c and z are constants. Constant c describes the number of species in one unit of area, while constant z is the rate of change in the number of species with increasing area (Tjørve and Tjørve 2008).

In practice, however, this equation is often log-transformed in order to obtain a linear relationship:

$$log\, S = z log A + log\, c$$

Where z is the slope of the relationship and c is the y-intercept.

1.2 The island species-area relationship (ISAR)

The species-area relationship has been a fundamental underlying feature in the development of many ecological theories (e.g., MacArthur & Wilson 1963, 1967, Hanski and Gyllenberg 1997, Harte et al. 1999, Hubbell 2001). The SAR can take on many forms, depicting distinct patterns and processes (Scheiner et al. 2001, Scheiner 2003). In fact, Scheiner (2003) described 6 types of the SAR curves: Nested (Type I), contiguous (Type IIA, IIB), non-contiguous (Type IIIA, IIIB) and island (Type IV).

In this dissertation I focus on the Type IV curve, the island species-area relationship (ISAR), which describes how the total number of species changes as a function of island size. Like other types of SARs, the ISAR is generally positive (MacArthur and Wilson 1967, Connor and McCoy 1979, Watling and Donnelly 2006, Triantis et al. 2012). However, varying relationships between species number and island area have also been observed, including no influence of area on species richness or even negative relationships (Watling and Donnelly 2006, Baldi 2008, Hatteland et al. 2008, Nentwig et al. 2019).

1.3 Conservation and habitat fragmentation

MacArthur and Wilson's (1963, 1967) *Theory of Island Biogeography* (TIB) describes species patterns on islands as being a function of two main factors: island area and isolation, where a larger, less isolated island is more likely to have a higher total number of species than a smaller, more isolated island. This theory also inspired the Single Large or Several Small (SLOSS) debate, i.e., whether a single large reserve will conserve more species than several small reserves, and was subsequently used in the design of natural reserves (Diamond 1975). However, the SLOSS debate remains unresolved as it was difficult to reduce it to one general conservation strategy as species differ in many aspects (e.g., dispersal ability, habitat dependency, resilience, etc.), all of which define how susceptible is a species is to extinction (e,g., Gilpin and Diamond 1980, Simberloff and Abele 1982, Harrison and Bruna 1999, Fahrig 2017). The TIB has not only served as a key piece of the puzzle in understanding the processes that drive species distribution patterns in insular biogeography, but has even transcended habitat fragmentation research, being used as a cornerstone for the design of many conservation interventions (Laurance 2008). Indeed, islands have been studied as model systems as they provide comparatively small areas of land that are geographically distinct and isolated from other areas (Warren et al. 2015). In contexts where species endangerment and biodiversity decline is mainly driven by habitat loss and fragmentation (Pimm et al. 1995, Wilcove et al. 1998, Dirzo and Raven 2003, Pereira et al. 2012), understanding how specific mechanisms shape the ISAR can aid in effectively protecting species from extinction.

1.4 Mechanisms underlying the ISAR

Despite being one of the most well-known patterns in biogeography, there is a lack of consensus concerning the mechanisms underlying the ISAR, across different taxa, environmental conditions and spatial scales (Whittaker and Fernandez-Palacios 2007). Connor and McCoy (1979) outlined three main mechanisms underlying the island species-area relationship:

1) ***Passive sampling or random sampling effects*** (also called the ‘more individuals hypothesis’): This is the simplest mechanism of the ISAR where larger islands tend to passively sample more individuals and therefore have a higher likelihood of sampling more species from the regional pool than smaller islands (Connor and McCoy 1979). Here, the increase in species number with island size is merely due to a non-biological, random sampling phenomenon and is not influenced by biological factors such as habitat characteristics or population dynamics. Indeed, the passive sampling hypothesis is often considered as a null model when testing for ISARs (Hill et al. 1994). Coleman (1981) provided an analytical approach to evaluate this null model, which he called the “random placement model” and subsequently tested it with bird abundances on islands in a lake (Coleman 1982).
2) ***Disproportionate effects:*** These were referred to as ‘area per se’ in Connor and McCoy (1979), but in the intervening years, the term has become confused in the literature. **Disproportionate effects** emerge where the number of individuals and species are expected to increase disproportionately with island size, in contrast to the proportional increase observed with passive sampling. In the case of disproportionate effects, one would expect an increase in species number as island size increases in a given, fixed sampling area (in the absence of heterogeneity). Here, it is possible

that more species are able to persist on larger islands than smaller islands due to colonization-extinction dynamics as described by MacArthur and Wilson's equilibrium theory of island biogeography, where larger islands are able to sustain larger populations (due to lower extinction rates) and therefore more species than smaller islands. Other population-level processes, as Allee-effects or demographic stochasticity, are more likely to affect smaller rather than larger islands (e.g., Hanski and Gyllenberg 1993, Orrock and Wattling 2010), thus contributing to lower diversity on smaller islands.

3) ***Habitat heterogeneity***: The habitat diversity hypothesis (Williams 1964) describes an increase in the number of habitats with island size, thus resulting in the increase of species number with island size. Larger islands tend to include more habitat types (e.g. mountains, rivers and forests), and therefore more species that can specialize in these habitats than smaller islands with fewer habitats. Moreover, heterogeneity effects can occur through compositional heterogeneity due to dispersal limitation, where species movement can be hindered by a number of spatial mechanisms (Condit et al. 2002, Leibold and Chase 2017). Here, larger islands are expected to have higher levels of dispersal limitation therefore providing a greater likelihood for individuals of the same species to aggregate, leading to greater heterogeneity in species compositions.

Although these mechanisms have been described as separate hypotheses above, they are not mutually exclusive. For instance, island size and heterogeneity are often correlated, and together can sometimes better explain variability in species patterns across islands (Ricklefs and Lovette 1999, Davidar et al. 2001, Triantis et al. 2003, Kadmon and Allouche 2007), thus making it challenging to separate these two hypotheses. The relative importance of disproportionate effects versus heterogeneity has been explored throughout numerous studies (Nilsson et al. 1988, Ricklefs & Lovette 1999, Davidar et al. 2001, Triantis et al. 2003, Allouche et al. 2012), with no general trend as results tend to differ between taxonomic groups due to varying dispersal abilities and habitat requirements. Although larger islands commonly have higher levels of habitat heterogeneity (Kohn and Walsh 1994, Hortal et al 2009), there are many cases where island size and heterogeneity do not covary positively, i.e., when smaller islands have higher habitat heterogeneity than larger islands, and therefore more species (Baldi 2008, Hatteland et al. 2008, Nentwig et al. 2019). Another possible explanation for the lack of a positive species-area relationship in some studies could be the "small island effect" (SIE) (Lomolino 2000). The SIE predicts that stochastic disturbance events, unrelated to area-dependent island properties, drive patterns of species densities and richness on small islands. For example, in a study evaluating patterns of invertebrate density on small lake islands in Sweden, Jonsson et al. (2009) found that larger islands had higher levels of disturbance compared to smaller islands as they were more likely to be struck by lightning and therefore more susceptible to fire (Wardle et al. 1997, 2003b). As a result, invertebrate density and richness were higher in smaller rather than larger islands.

Despite the ISAR's importance in the context of island biogeography and conservation, there remains a great deal of ambiguity surrounding the ISAR and the processes that shape it (Scheiner et al. 2011). The main reason behind this uncertainty is heterogeneous sampling methods across studies. For instance, ISAR theories, such as the theory of island biogeography (MacArthur and Wilson 1967), were specifically developed to describe changes in ***total*** species richness of islands with increasing island size. Although a few studies actually measure total species richness on islands (derived from species lists) to quantify the ISAR (Triantis et al. 2012, Matthews et al. 2014, 2016), many others actually consider the relationship between island size and the number of species in a fixed sampling area to be an accurate quantification of the ISAR. Failure to recognize these differences can lead to improper conclusions about what is actually driving species patterns in islands, as different studies are not measuring the same thing. Here, we tackle this problem by adopting a scale-explicit approach to the ISAR that accounts for sampling effort through the means of individual-based rarefaction.

1.5 Individual-based rarefaction curves and the ISAR

In general, the more individuals are randomly drawn from an area, the more species we encounter. This is known as the species accumulation curve - the curve grows rapidly at first as the more common species are encountered before reaching a saturation point when all the species in a community have been sampled. The shape of this curve depends on the total number of species as well as the relative abundances of species in an assemblage. The more even the species abundance distribution, the more rapidly this curve will rise. In contrast, if the species abundance distribution is highly uneven (i.e., with a few common species and many rare ones), the curve will rise more slowly. Individual-based rarefaction is a method to standardize species richness that accounts for this nonlinear scaling relationship (Gotelli & Colwell, 2001). Here, the expected number of species is computed for a common number of individuals, *n* (i.e., *n* individuals are randomly drawn from each island)(Figure 1A).

The majority of ISAR studies – including those concerning habitat fragmentation – use the total number of species recorded on islands or island-like habitat as the principal measure of biodiversity. However, a focus on total richness may be inadequate as it ignores the fact that biodiversity is multidimensional and scale-dependent. Therefore, throughout this dissertation, I will not only look at classic log-log island species-area relationships (Figure 1B), which focuses merely on the total number of species encountered per area, but I will also focus on metrics derived from individual-based rarefaction curves at multiple spatial scales. This will allow meaningful comparisons of metrics of biodiversity based on equivalent numbers of individuals (Gotelli and Colwell 2001). These individual-based rarefaction methods account for the sampling bias by adjusting or controlling for differences in the number of individuals (i.e, rarefaction). Using these methods could therefore allow us to more explicitly separate the mechanisms underlying the island species-area relationship.

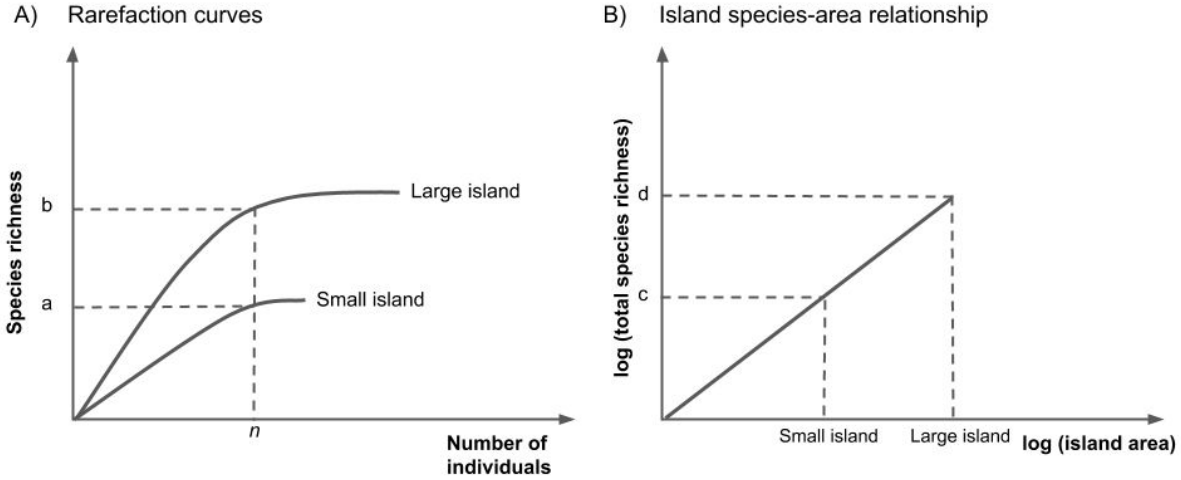

Figure 1. A) Individual-based rarefaction curve where a and b are the expected number of species for *n* randomly drawn number of individuals respectively. B) The island species-area relationship on a log-log scale, where the total species richness of the small and large islands are c and d respectively.

1.6 Objectives of the dissertation

Although island species-area relationship (ISAR) is of central importance for biodiversity conservation, specifically in the context of habitat loss and fragmentation, there remains an uncertainty surrounding the processes that shape it, thus rendering the ISAR difficult to synthesize. The overarching aim of this dissertation is to provide a better understanding of the ISAR by means of a framework to disentangle the main mechanisms underlying the ISAR (**Chapter 2)** as well as a test of this framework by applying it to many different case studies across a variety of island-like systems and taxa. Chapter 2 was published as : Chase, J. M., L. Gooriah, F. May, W. A. Ryberg, M. S. Schuler, D. Craven, and T. M. Knight. 2019. A framework for disentangling ecological mechanisms underlying the island species–area relationship. Frontiers of Biogeography 11.

In **Chapter 3**, lakes are considered as islands. In this chapter, datasets on zooplankton abundance from European and North American lakes were collated from the literature and online data portals. To determine which mechanism was driving the ISAR in European and North American lakes, I compared standardized estimates of diversity (derived from sample-level data) across lake size. I further tested a subset of lakes that were sampled at multiple stations in order to test for heterogeneity effects. Chapter 3 was published as : Gooriah, L., J. M. Chase 2019. Sampling effects drive the species-area relationship in lake zooplankton. Oikos. https://doi.org/10.1111/oik.06057

Chapter 4 focuses on a specific archipelago - The Andaman and Nicobar islands - where abundance-level data were available for four taxa : birds, butterflies, frogs and lizards. With additional data at the local scale, I was able to explore whether disproportionate effects or habitat heterogeneity were driving frog and lizard ISARs.
The work presented in Chapter 4 (Gooriah, L., P. Davidar and J. M. Chase 2019. Species-Area Relationships in the Andaman and Nicobar archipelago emerge because rarer species are disproportionately favored on larger islands) has been submitted to *Ecology and Evolution* and is currently in review.

Chapter 5, provides a synthesis of the ISAR using the framework developed in chapter 2. Here, I examine the variation in the ISARs of taxa across 35 studies on a variety of natural islands (true islands, atolls, forest islands and lake islands). The work presented in this chapter (Gooriah, L., S. A. Blowes, J. Schrader, D. N. Karger, H. Kreft, J. M. Chase 2019. Synthesis of the mechanisms underlying the Island Species-Area Relationship) is currently in preparation for submission to *Ecography*.

And finally **Chapter 6** summarizes the main findings of this dissertation and provides recommendations for future research.

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CHAPTER 2

A framework for disentangling ecological mechanisms underlying the island species–area relationship

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RESEARCH ARTICLE

A framework for disentangling ecological mechanisms underlying the island species–area relationship

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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 that drive it — random sampling, disproportionate effects, and heterogeneity. 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 disentangling the possible ecological mechanisms underlying the ISAR using parameters derived from individual-based rarefaction curves estimated across spatial scales. 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 random sampling. However, if the derived metrics change with island area, we can reject random sampling as the only operating mechanism and infer that effects beyond sampling (i.e., disproportionate effects and/or heterogeneity) are also operating. Finally, if parameters indicative of within-island spatial variation in species composition (i.e., β-diversity) increase with island area, we can conclude that 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.

Key Words: Area per se, Alpha-diversity, Beta-diversity, Biodiversity, Gamma-Diversity, Heterogeneity, Fragmentation, Island, Sampling Effects, Scale, Species–Area Relationship, Individual-Based Rarefaction.

Introduction

The relationship between the area sampled and the number of species in that area —the species–area relationship (SAR)— is one of the oldest laws in ecology (e.g., Arrhenius 1921, Lawton 1999, Lomolino 2000, Drakare et al. 2006). There are many forms of SARs that represent rather distinct patterns and processes (e.g., Scheiner 2003, Scheiner et al. 2011), but here we focus specifically on one type, the Island Species–Area Relationship (hereafter ISAR). The ISAR correlates how the numbers of species (species richness) varies with the size of islands or by extension, distinct habitat patches (natural or fragmented due to human activities). Like other types of SARs, the ISAR is usually positive for both islands and habitat patches (e.g., MacArthur and Wilson 1963, 1967, Connor and McCoy 1979, Triantis et al. 2012, Mathews et al. 2014, 2016). However, complexities such as island age, habitat heterogeneity, and/or isolation can complicate this simple expectation (Kreft et al. 2008, Borregaard et al. 2016).

We refer to 'islands' in the ISAR as any insular system, including true islands or habitat patches that are surrounded by distinctly different habitats (matrix) (e.g., lakes, edaphically delimited habitats) and habitat fragments that have been insularized by human activities. In addition to being an important biogeographic pattern in its own right, the ISAR and concepts closely related to it play an important role in understanding how biodiversity changes when habitat is lost and/or fragmented into smaller island-like habitats (e.g., Diamond 1975, Simberloff and Abele 1976, Hanski et al. 2013, Matthews et al. 2014, 2016, Fahrig 2017). As a result, understanding the patterns and the processes underlying ISARs and their derivatives would seem to be an important endeavor in the context of island biogeography and conservation.

Despite its conceptual importance, there remains a great deal of ambiguity regarding ISAR patterns, as well as its underlying processes (e.g., Scheiner et al. 2011). When describing ISAR patterns, authors report and analyze different aspects of species richness regressed against total island size, including total numbers of species and the number of species found within a constantly-sized sub-sampled area. Such different sampling designs have created confusion when comparing slopes of ISARs; an increasing number of species measured in a fixed-area plot with increasing island area means something quite different than an increasing number of species on the entire island (see also Hill et al. 1994, Gilaldi et al. 2011, 2014). In terms of processes underlying the ISAR, there is similar confusion. Multiple mechanisms, including passive sampling, colonization/extinction (i.e., metacommunity) dynamics, and habitat heterogeneity, as well as their interactions, have been invoked to explain ISARs (e.g., McGuiness 1984, Scheiner et al. 2011). Unfortunately, the exact ways by which these mechanisms operate and how they can be disentangled using observational data remain in question.

Following others (e.g., Triantis et al. 2012, Mathews et al. 2014, 2016), we refer to the ISAR as the relationship between the total species richness on a given island (or habitat patch) and the size of that island. However, simply knowing the shape of the relationship between the size of an island and the total species richness (hereafter S_{total}) on that island can tell us very little about the possible mechanisms underlying the ISAR. In order to understand the mechanisms underlying the ISAR, it is necessary to collect and analyze data at the level below the scale of the entire island (see also Hill et al. 1994, Yaacobi et al. 2007, Stiles and Scheiner 2010, Gilaldi et al. 2011, 2014). Specifically, we recommend collecting data from multiple standardized plots where both the numbers and relative abundances of species are available, as well as compositional differences of species among locations within an island. We recognize that this requires extra data often not available for many biogeographical and macroecological studies of island systems but emphasize that the extra effort involved allows a much deeper understanding of the possible processes underlying the ISAR patterns observed.

We overview three general classes of potential mechanisms underlying the ISAR —passive sampling, disproportionate responses, and heterogeneity— from least complex to most complex (see also Connor and McCoy 1979, McGuinness 1984, Scheiner et al. 2011 for deeper discussions of these mechanisms for all types of SARs). Then we discuss how they can be detected using a multi-scale and multi-metric approach. Importantly, there remains much confusion in the literature regarding exactly which mechanisms can create the ISAR, which patterns these mechanisms generate, and how to disentangle them. Thus, we begin with a general overview of the general classes of mechanisms and discuss how they can be disentangled with a more directed sampling approach.

Mechanisms underlying the ISAR

In brief, ***passive sampling*** (sometimes called the 'more individuals hypothesis') emerges when larger islands have more species than smaller islands via passive sampling of individuals (and thus species) from a larger regional pool. ***Disproportionate response*** (sometimes called 'area per se') include a large array of possible mechanisms whereby some species are favored, and others disfavored, on islands of different sizes such that they achieve different relative abundances on different-sized islands. ***Heterogeneity*** also leads to disproportionate responses and altered relative abundances of species, but these emerge at larger scales via clumping of species that can emerge because of habitat differences and/or dispersal limitation. In the following sections we discuss each of these mechanisms and possible ways to detect them from within-island surveys.

Passive sampling

The simplest mechanism of the ISAR is that islands passively sample individuals from a larger 'regional' pool of individuals of different species. Larger islands passively sample more individuals and thus more species from the regional pool. This is essentially a 'null' hypothesis but one that can be tested using standard methods, which provides important insights about the potential underlying processes leading to the ISAR. The influence of passive sampling on the ISAR was first described by Arrhenius (1921) in one of the first quantitative explorations of this relationship. It is important to emphasize that sampling effects are sometimes thought of as an artifact of limited sampling for uncovering the true numbers of species. This is not the case for this passive sampling null hypothesis. It is also implicit in several early quantitative explorations of the ISAR where the regional pool consists of few common and many rare species, and smaller islands passively sample fewer individuals, resulting in fewer species than on larger islands (e.g., Preston 1960, May 1975).

Coleman (1981) developed an analytical formula for this process based on random placement of individuals on islands, and Coleman et al. (1982) applied it to data from samples of breeding birds on islands in a reservoir to suggest that this passive sampling mechanism most likely explained the ISAR in this system. 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 do not change from small to large islands). Importantly, this random placement method is nearly identical to individual-based rarefaction methods (e.g., Gotelli and Colwell 2001), which we use below to test the random sampling hypothesis.

Several authors have tested the passive sampling hypothesis by measuring the numbers of species in a given fixed area on islands of different sizes and correlating that density with the total area of the island (e.g., Hill et al. 1994, Kohn and Walsh 1994, Yaacobi et al. 2007, Gilaldi et al. 2011, 2014). If the number of species in a fixed area sample does not vary as island size varies, this is taken to imply that passive sampling is most likely the only mechanism acting. However, if the number of species in a fixed area increases as island size increases, we would instead conclude that there is some biological effect, beyond sampling, that allows more species to persist in a given area on larger than smaller islands.

While fixed-area sampling can be useful for inferring whether ISAR patterns deviate from patterns expected from pure sampling effects, this method is unfortunately not as powerful a 'null hypothesis' as has often been suggested. There are at least two common factors that can lead to patterns that appear consistent with the passive sampling hypothesis that in fact emerge from effects that are beyond sampling. First, when disproportionate 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 significantly increased at the largest sampling grain (6400 m^2). Second, it is possible that species richness 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 cases, simply measuring standardized species richness in small plots across islands of different sizes may have led to the faulty conclusion of random sampling effects.

Disproportionate effects

When disproportionate effects underlie the ISAR, there are more species on larger islands because species from the regional pool differentially respond to island size (as opposed to the passive sampling hypothesis, where species are proportionately influenced by island size). Disproportionate effects include a number of different sub-mechanisms whereby some species are favored, and others disfavored, by changes in island size.

Most such mechanisms predict that the numbers of species in a fixed sampling area should increase with increasing island size (sometimes called 'area per se' mechanisms; Connor and McCoy 1979). The mostly widely considered of these mechanisms is MacArthur and Wilson's (1963, 1967) theory of island biogeography. Here, the colonization rates of species increase with island size, and the rates of extinction decrease with island size, leading to the expectation that more species should often be able to persist in a fixed area on larger islands. Several other kinds of spatial models can also predict similar patterns whereby the coexistence of several species is favored when the total area increases (e.g., Hanski et al. 2013) or when population-level processes, such as Allee-effects or demographic stochasticity, are less likely on larger relative to smaller islands (e.g., Hanski and Gyllenberg 1993, Orrock and Wattling 2010). Disproportionate effects can also emerge when island size influences within-island environmental and/or biotic processes. For example, smaller islands are often more likely to experience disturbances and/or have lower productivity (McGuinness 1984), and in the context of habitat fragmentation, smaller island fragments often have edge effects whereby habitat-specialist species are negatively impacted (Ewers and Didham 2006). Likewise, smaller islands and habitat fragments may have fewer trophic levels, which can in turn influence species richness at lower trophic levels (e.g., Gravel et al. 2011). Finally, island size can also influence within-island speciation dynamics (e.g., Losos and Schluter 2000, Whittaker et al. 2008). If higher speciation rates on larger islands leads to sympatric coexistence of more species than expected from random, this would lead to disproportionate effects. If speciation instead leads largely to allopatry of the incipient species, this would alternatively lead to patterns more consistent with heterogeneity effects (below)

Although often less well appreciated, mechanisms similar to those described above can favor multiple species in smaller rather than larger habitats. For example, it is possible that more widespread species can dominate larger habitats via high rates of dispersal and mass effects. Likewise, especially in the context of habitat islands formed via habitat fragmentation, disproportionate effects favoring species in smaller islands can include the disruption of interspecific interactions (e.g., via pathogens, predators or competitors) or more species favored by edges and heterogeneity created in smaller habitats (Fahrig 2017). In such cases, we might expect a weaker or even negative ISAR depending on whether random sampling effects (which are always operating) outweigh the disproportionate effects.

Heterogeneity

The last family of mechanisms that can lead to the ISAR involve heterogeneity in the composition of species within islands. These mechanisms are centered on the supposition that larger islands can have more opportunity for individuals of the same species to aggregate (leading to heterogeneity in species composition) than smaller islands. This can emerge from two distinct sub-mechanisms:

(i) *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. These mechanisms can operate even if the same number habitat types are present on each island because their absolute and relative abundances can change with island size and, on smaller islands, it may be below the threshold amount needed for particular species to persist on those habitat types.

(ii) *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. In the longer term, and on more isolated islands, this can also lead to within-island speciation (e.g., Losos and Schluter 2000, Whittaker et al. 2008), reinforcing the disproportionate number of species on larger 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, as well as how species respond to that heterogeneity. While we do not explicitly consider it further here, the spatial versus environmental drivers of compositional heterogeneity (β-diversity) can be more specifically disentangled if site-level environmental conditions and spatial coordinates are known by using standard methods in metacommunity ecology (e.g., Peres-Neto et al. 2006, Ovaskainen et al. 2017).

Finally, as with disproportionate effects above, opposite patterns are also possible. While we typically assume that heterogeneity increases with island area, leading to the positive ISAR, this need not be true. For example, smaller islands have higher perimeter:area ratios (i.e., edge effects), and thus can have higher levels of heterogeneity than larger islands by some measures.

Disentangling ISAR mechanisms with observational data

As a result of the difficulty of performing field experiments on ISAR mechanisms at realistic scales (but see Simberloff 1976), considerable attention has been paid to developing a sampling and analytical methodology to disentangle potential ISAR mechanisms from observational data. However, these approaches have appeared piecemeal in the literature, are incomplete, and have not yet been synthesized into a single analytical framework. Furthermore, two or more of these mechanisms can act in concert and are non-exclusive (e.g., Chisholm et al. 2016). For example, the influence of passive sampling is likely always occurring in the background, even when disproportionate effects and/or heterogeneity also influence ISAR patterns. Thus, even if we reject passive sampling as the sole mechanism leading to the ISAR via deviations from the null expectation, we cannot say that passive sampling does not at least partially influence the observed patterns. The same is true for any null modelling approach. Likewise, it is possible that disproportionate responses of species via alterations to spatial or local conditions can act in concert with changes in habitat heterogeneity. In this case, however, we can more completely falsify these processes by comparing patterns both within communities (α-diversity) and among communities (β-diversity), as we discuss in more detail below.

Here, we overview a generalized approach for disentangling the possible mechanisms underlying the ISAR. Our approach is based on recent work that uses an individual-based rarefaction framework (e.g., Gotelli and Colwell 2001) to calculate several measures of biodiversity at multiple spatial scales (e.g., Chase et al. 2018, McGlinn et al. 2019) and then to relate these measures to variation in island size. In a sense, then, we propose the use of within-island species richness relationships (Type II or Type III curves from Scheiner 2003, Scheiner et al. 2011) to evaluate the mechanisms underlying among-island ISAR relationships (Type IV curves from Scheiner 2003, Scheiner et al. 2011).

Figure 1a overviews the sampling design necessary on an island in order to calculate the parameters necessary to disentangle ISAR mechanisms. Specifically, in addition to estimating the total numbers of species on an island (S_{total}), we advocate sampling multiple standardized plots within a given island (ideally stratified across the island and any potential habitat heterogeneity) so that a number of parameters can be derived and compared with island size. These parameters are described in Table 1 and can be visualized as components along individual-based rarefaction curves as in Figure 1b.

From the combination of all sampled plots within an island, one can generate a γ-rarefaction curve. From this curve, we derive three diversity parameters that can be visualized, which place a different emphasis on common versus rare species. First, the upper-right of the curve (assuming adequate sampling or appropriate extrapolation technique) represents the total number of species on the island, S_{total}. Second, the rarefied number of species expected from *n* randomly sampled individuals from the γ-rarefaction curve, which we term ${}^{\gamma}S_n$. Because the γ-rarefaction curve is generated by combining all sample plots on a given island and randomly choosing individuals, any spatial heterogeneity in species associations is broken when calculating ${}^{\gamma}S_n$ for a given island. In practice, ${}^{\gamma}S_n$ is calculated either by using the traditional approach of taking the minimum *n* observed among samples to be compared (islands in this case) and calculating the expected number of species for that *n*, either as a resampling or using analytical approximations, or by using a slightly more complicated approach that includes extrapolations (e.g., Chao et al. 2014, McGlinn et al. 2019); below, we advocate the later. Third, the slope at the base of the individual-based rarefaction curve is equivalent to Hurlbert's (1971) Probability of Interspecific Encounter (PIE), a measure of evenness (illustrated by the gray arrows in Figure 1b (e.g., Gotelli and Graves 1996, Olszewski 2004). Here, we advocate using the bias-corrected version, $\mathrm{PIE} = \left(\frac{\mathrm{N}}{\mathrm{N}-1}\right) * \left(1 - \sum_{i=1}^{S} \mathrm{p}_i^{\,2}\right)$, 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*.

Importantly, these diversity parameters that can be derived from the individual-based rarefaction curve have a great deal of similarity to the Hill (1973) continuum of diversity measures that place greater emphasis on rarer species (i.e., species richness) or greater emphasis on more common species (i.e., Simpson's diversity index which is 1- PIE). However, at the risk of continuing to differentiate, rather than agglomerate similar measures, we prefer using the rarefaction-derived parameters (e.g., S_n, *PIE*) rather than Hill numbers for this application (see also Chase et al. 2018, McGlinn et al. 2019

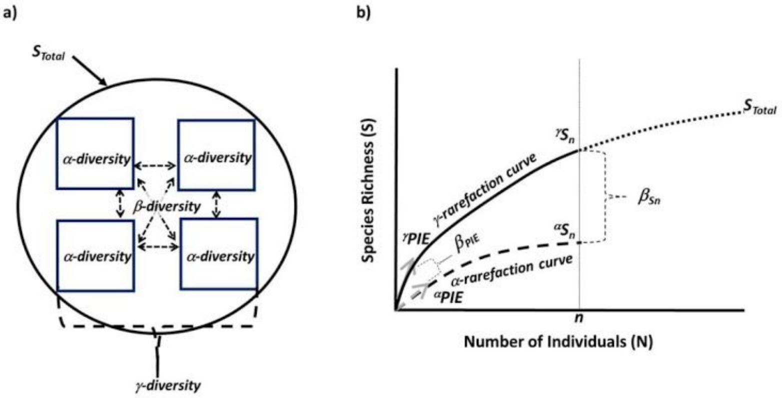

Figure 1. (a) Overview of a sampling scheme appropriate for applying the analytical approach outlined in this paper. The circle represents a hypothetical island, and each of the four squares represents individual sampling plots from which α-diversity metrics can be derived. The addition of all of the individuals sampled in all of the plots allows the calculation of γ-diversity metrics, while the differences among the α-diversity plots is β-diversity. S_{total} represents the total number of species on the island, including those that were not observed in any of the sampled plots. (b) Illustration of how these diversity indices can be visualized graphically from individual-based rarefaction curves that plot species richness (*S*) against the numbers of individuals (*N*) across 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, the dashed line allows us to visualize the total number of species on the island including up to S_{total}. We can also visualize: (i) the numbers of species expected from a given number of individuals (*n*), γS_n (where the vertical dashed line at *n* intersects the solid curve); (ii) the probability of interspecific encounter (PIE), which 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, and similar parameters can be derived —${}^{\alpha}S_n$ (vertical dashed line intersects the dashed curve at *n* individuals) and ${}^{\alpha}PIE$ (dashed grey arrow). 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.

Table 1. Parameters used to disentangle island species–area relationship patterns

Parameter	Description
Island-level patterns	
S_{total}	Total number of species on an entire island. Estimated independently from checklists or with extrapolations from samples.
N	Number of individuals of all species found in a given sampling plot (usually expected to scale linearly with effort)
γ-level patterns (derived by combining all sample plots on an island)	
$^{\gamma}S_n$	Number of species expected from n randomly sampled individuals from the γ-rarefaction curve
$^{\gamma}S_{PIE}$	Effective number of species given the probability of interspecific encounter (PIE) from the γ-rarefaction curve.
α-level patterns (derived from a single sampling plot or subset of plots on an island)	
$^{\alpha}S_n$	Number of species expected from n randomly sampled individuals from the α-rarefaction curve
$^{\alpha}S_{PIE}$	Effective number of species given the probability of interspecific encounter (PIE) from the α-rarefaction curve
β-level patterns (derived from comparing γ- to α-level patterns)	
β_{S_n}	Ratio of numbers of species expected for a given n from γ-rarefaction curve to those expected for a given n from α-rarefaction (a measure of compositional heterogeneity) ($^{\gamma}S_n / {}^{\alpha}S_n$)
$\beta_{S_{PIE}}$	Ratio of numbers of effective number of species for a given PIE from γ-rarefaction curve to the effective number of species for a given PIE from α-rarefaction (a measure of compositional heterogeneity emphasizing common species) ($^{\gamma}S_{PIE} / {}^{\alpha}S_{PIE}$).

for more discussion on the similarities/differences between the approaches). This is because PIE has a meaning (probability of interspecific encounter) that is quite intuitive and easily visualized as the slope at the base of the rarefaction curve. Nevertheless, when we statistically analyze PIE, we follow Jost's (2006) recommendation of converting to an effective number of species (the number of species that would be observed if all the species in a sample were equally abundant), which we call S_{PIE} $(=1/(1-PIE))$. When S_{PIE} is calculated from the γ-rarefaction curve, we refer to the effective number of species as $^{\gamma}S_{PIE}$. Note that only PIE, not S_{PIE}, is illustrated in Figure 1b because the forms of S_{PIE} are not readily illustrated in the individual-based rarefactions construct. For authors that prefer to think about Hill numbers rather than rarefaction curves, S_{PIE} is equivalent to the Hill number when q=2. An interesting exercise could be to explore the variation among island size in measures of the Hill number framework which differentially emphasize common to rare species along a continuum. However, this is beyond the scope of what we hope to accomplish here and is less easily connected to the rarefaction framework that we advocate.

To discern whether any of the ISAR patterns emerge from within-island heterogeneity in species composition, we need to derive estimates of β-diversity. To do so, we can generate an α-rarefaction curve and estimate diversity parameters similar to those above, but at the local (within plot) scale. From this, we can compare the parameters from the γ-rarefaction curve, which eliminates any plot-to-plot variation due to heterogeneity in species composition, by randomizing across the plots to the α-rarefaction curve calculated from individual plots (or a spatially defined subset of plots), which contains local information only (dashed line in Figure 1b). The degree to which the γ-rarefaction curve (which eliminates spatial heterogeneity) differs from the α-rarefaction curve (which keeps spatial heterogeneity), tells us how much local variation there is in species composition across sites, providing an index of β-diversity resulting from species aggregations (see Olszewski 2004, Chase et al. 2018, McGlinn et al. 2019). If the γ-and α-rarefaction curves are on top of each other, then we can conclude that there is no heterogeneity in the region. Alternatively, if the α-rarefaction curve is far below the γ-rarefaction curve, this implies that intraspecific aggregation has created compositional heterogeneity in the community. Two β-diversity parameters are informative in this context: β_{S_n} $(={}^{\gamma}S_n / {}^{\alpha}S_n)$, which indicates the influence of aggregation of all species, and $\beta_{S_{PIE}}$ $(={}^{\gamma}S_{PIE} / {}^{\alpha}S_{PIE})$, which indicates aggregations primarily by more common species (i.e., the effective number of unique communities; Tuomisto 2010).

In what follows, we discuss how this analytical framework can disentangle ISAR relationships where explicit sampling information from within and among islands is available. At the outset, it is important to note that in most of what follows, we focus exclusively on island systems where the primarily independent variable influencing species diversity is island size, with minimal variation in other diversity drivers. We focus on this because our goal is to elucidate and disentangle the ISAR, which describes a bivariate relationship between island size and species richness, and for which there remains much confusion and little synthesis. Nevertheless, as with all diversity studies, focusing on a single independent driver is a limiting case. In many island systems, islands vary in size as well as other drivers (e.g., productivity, isolation). Nevertheless, it is quite straightforward to extend the approach that we advocate below to include these complexities and still disentangle the influence of island size in the context of the ISAR. In such cases, one could simply use these other potential drivers as covariates with island size in an analysis focusing on the response variables, we overview in Table 1 and Fig. 1, using the same framework as described below. Or one could add more complexity by including these independent variables in a hierarchical model or structural equation model with the same response variables, which we discuss in more detail in the conclusions below (see e.g., Blowes et al. 2017, Chase et al. 2018 for similar analyses in a different context).

Question 1: What is the shape of the overall ISAR?

Parameter analyzed: Total number of species on an island (S_{total})

S_{total} is the most straightforward ISAR variable one can measure. The ideal way to estimate S_{total} is from independent information, such as exhaustive searching or checklists of species known to occur on a given island. However, because this information is often unavailable, S_{total} can be estimated via techniques for predicting the number of species in a given extent (e.g., Colwell and Coddington 1994, Harte et al. 2009, Chao and Jost 2012, Chao and Chiu 2014, Azaele et al. 2015). None of these approaches is perfect, and we are agnostic as to which approach is best for estimating S_{total} when complete species lists are not available. However, 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 (Colwell et al. 2012). However, this can only be viewed as a minimum and will likely underestimate the true S_{total}.

While S_{total} is the fundamental parameter of interest to calculate an ISAR, it alone provides little information as to the nature of its potential underlying mechanisms. This is because S_{total} is influenced by a number of underlying parameters, including the density of individuals, the relative abundances of species, and the intraspecific aggregation or spatial heterogeneity exhibited by species. Thus, to disentangle the factors underlying variation in S_{total}, we need to look deeper into these underlying components, which we can do using the parameters overviewed in Table 1 and Fig. 1b (see also Chase et al. 2018, McGlinn et al. 2019).

Question 2: Does the ISAR result differ from what is expected from random sampling?

Parameter Analyzed: Number of species expected from the γ-rarefaction curve (${}^{\gamma}S_n$)

If patterns of the ISAR were generated simply by the random sampling hypothesis, we would expect that γ-rarefaction curves of small and large islands would fall right on top of each other (whereas the curve would go farther along the x-axis for the larger island because more total N are present on larger islands) (Figure 2a).

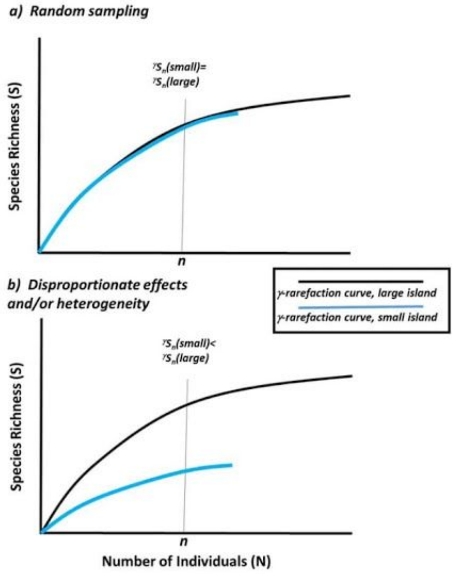

Figure 2. a) Hypothetical case where a large island has more species than a smaller island in total, but this is entirely because of random sampling (the larger island has more total individuals). Note that the rarefaction curves for each island fall on top of each other and the parameters derived from it, including ${}^{\gamma}S_n$ and ${}^{\gamma}S_{PIE}$ (not shown), are the same between larger and smaller islands. b) Hypothetical case where a large island has more species than a smaller island, and this results because both a sampling effect (the larger island has more *N* and goes farther down the x-axis) and a disproportionate effect (whereby ${}^{\gamma}S_n$ is lower on the smaller than the larger island). ${}^{\gamma}S_{PIE}$ in this case (not illustrated) is also smaller on the smaller island (because it has a shallower slope), but this need not be the case if only rarer species are affected.

If the γ-rarefaction curves between smaller and larger islands differ, which we can quantify by comparing ${}^{\gamma}S_n$ among islands (Figure 2b), then we can conclude that something other than random sampling influences the ISAR. This is essentially the same procedure as that described by the random placement approach (Coleman 1981, Coleman et al. 1982).

If ${}^{\gamma}S_n$ increases with increasing island area, this means that more species can persist for a given sampling effort on larger than smaller islands. In practice, however, exactly how ${}^{\gamma}S_n$ varies with island size will depend on the minimum number of individuals captured in all samples across islands, and the slope of the ${}^{\gamma}S_n$ relationship with island size depends on exactly which n is used in the calculations, with steeper slopes observed at higher n. This is similar to what was observed by Karger et al. (2014) on islands in Southeast Asia. Nevertheless, when an adequate number of individuals are sampled, we can also derive measures from the rarefaction curve that allow us to go one step further in describing how island size influences the relative commonness and rarity of species. If island area influences the γ-rarefaction curve via an overall decrease in evenness of both common and rare species (as shown in Figure 2b), we would expect that both ${}^{\gamma}S_n$ and ${}^{\gamma}S_{PIE}$ would change. However, if only relatively rarer species are disproportionately influenced by island area (not shown in figure), we would expect that ${}^{\gamma}S_n$ would increase with increasing island area, but there should be little to no effect on ${}^{\gamma}S_{PIE}$. While we advocate that a majority of information on any changes in relative abundances can be gleaned by comparing these two measures representing different parts of the rarefaction curve (see also Chase et al. 2018, McGlinn et al. 2019), one could also derive other parameters that differentially weight common and rare species (e.g., Shannon's entropy, which represents a more central position in the Hill numbers continuum; Jost 2006).

It is important to note that the hypotheses of increasing ${}^{\gamma}S_n$ and/or ${}^{\gamma}S_{PIE}$ with increasing island area, as illustrated in Fig. 2b, are not the only possibilities. Estimates of diversity from samples, such as ${}^{\gamma}S_n$ and/or ${}^{\gamma}S_{PIE}$, could certainly decrease with increasing island size. For example, on islands that result from habitat fragmentation and/or those that are surrounded by a relatively hospitable matrix, there are several mechanisms (e.g., habitat spillover) that can lead to higher levels of diversity (both in S_{total} as well as from samples [${}^{\gamma}S_n$ and/or ${}^{\gamma}S_{PIE}$]) in smaller relative to larger islands (e.g., Ewers and Didham 2006, Fahrig 2017).

Even if the numbers of species (and evenness) for a given sampling effort (${}^{\gamma}S_n$ and/or ${}^{\gamma}S_{PIE}$) declines, this can be outweighed by the random sampling effect, leading to an overall increasing ISAR even with decreasing components of diversity with increasing area. This emphasizes the fact that ISAR mechanisms are not mutually exclusive. That is, random sampling effects are likely always operating (as evidenced by the increase in species richness with increasing N along the rarefaction curve), even when disproportionate effects and/or heterogeneity also influence the ISAR pattern. As such, we can use rarefaction curves to examine whether random sampling is the only mechanism operating, as it would be if there is no influence of island size on ${}^{\gamma}S_n$, and, as a result, conclude that differential effects and/or heterogeneity are not operating. However, we cannot conversely say that random sampling is not operating if there is a relationship between ${}^{\gamma}S_n$ and island size. This is because random sampling effects are always operating anytime there are fewer species on a given island than the total numbers of species in the regional species pool.

Finally, our discussion above implicitly assumed that island size changes the total number of individuals on an island via passive sampling but not the density of individuals in a given sampled area. However, there are also reasons that island size can influence individual density. For example, if larger islands are more favorable for some reason, the total numbers of individuals would increase both because island size increases, as well as because the density in a given sampled area increases. Alternatively, smaller islands could contain more individuals for a given area (higher density) if there is high spillover from the matrix into smaller islands or if larger islands have less favorable habitats. In such cases, comparisons of ${}^{\gamma}S_n$ are still necessary to test the null hypothesis of whether the ISAR results from random sampling or not. However, when N varies with island size, it will also be useful to compare estimates of S at the scale of the sample rather than the number of individuals (i.e., sampled-based estimates sensu Gotelli and Colwell 2001, McGlinn et al. 2019) to determine how changes in N influence the ISAR.

Question 3: Does the ISAR result from disproportionate effects or from heterogeneity?

Parameter analyzed: β-diversity as the difference between the γ-rarefaction curve and α-rarefaction curve.

If there is a relationship between ${}^{\gamma}S_n$ and/or ${}^{\gamma}S_{PIE}$ and island area, we can conclude that there is something other than random sampling influencing the ISAR. With only the parameters from the γ-rarefaction curve, however, we cannot yet discern whether this is due to disproportionate effects that are equally distributed across the island or whether these effects emerge because of heterogeneity in species composition across the island (i.e., different species and relative abundances in different parts of the island). To disentangle disproportionate effects from heterogeneity, we must look more closely into the variation in species abundances and composition within an island—that is, within-island β-diversity.

If β_{S_n} has no relationship with island size, then we can reject the heterogeneity hypothesis (Fig. 3a; note, in the figure, we have illustrated that β_{S_n} is 1, indicating there is no heterogeneity due to aggregation; however, this hypothesis would also be true if $\beta_{S_n} > 1$ but does not significantly vary with island size). However, if β_{S_n} increases with island size, then we conclude that heterogeneity

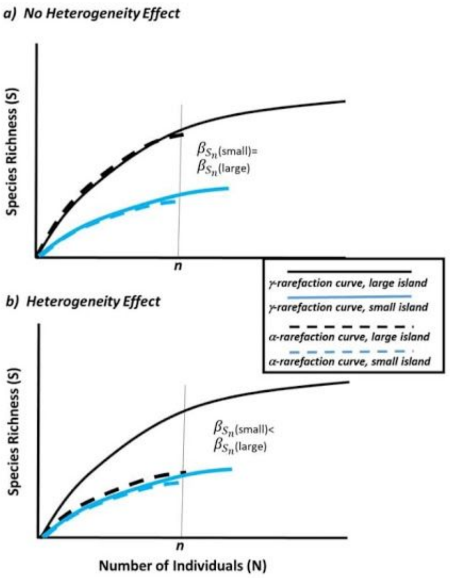

Figure 3. a) A hypothetical case where there is no heterogeneity in species composition within islands (the α- and γ-rarefaction curves completely overlap) such that β_{S_n} =1. And this does not vary with island size. Note, that it is also possible that β_{S_n} and/or $\beta_{S_{PIE}}$ >1, but we would conclude no heterogeneity effect underlying the ISAR if this is not influenced by island size. b) A case where there is heterogeneity in species composition in the larger island (the α- and γ-rarefaction curves differ) but not the smaller. And thus, there is a positive relationship between compositional heterogeneity (β_{S_n} and/or $\beta_{S_{PIE}}$) island size. In this case, note that the α- rarefaction curves between the larger and smaller island overlap, and the island-effect is only observed at the γ-level, indicating the ISAR results solely from heterogeneity. This need not be the case, however, and other complexities can arise (see text).

plays at least some role in the generation of the ISAR. If the ISAR is primarily driven by heterogeneity, we would expect there to be no relationship between $^{\alpha}S_n$ and island size but a strong relationship with $^{\gamma}S_n$, giving us a significant β_{S_n} relationship with island size (Fig. 3b). Such a pattern was observed by Sfenthourakis and Panitsa (2012) for plants on Greek islands in the Aegean Sea. In Fig. 3b, we have illustrated a case where heterogeneity influences rare as well as common species, indicating an effect on both β_{S_n} and $\beta_{S_{PIE}}$ (not shown, but implied because the slope at the base of the curve [i.e., PIE] is influenced). However, it is also possible that heterogeneity can influence just the rarer but not more common species, wherein we would expect an effect on β_{S_n} but not $\beta_{S_{PIE}}$ (not shown in Fig. 3).

It is quite possible that both disproportionate effects and heterogeneity occur simultaneously and in the same direction, in which case we would expect a significant relationship between $^{\alpha}S_n$ and island size (indicating disproportionate effects) and stronger relationship between $^{\gamma}S_n$ and island size, giving a significant relationship between island size and β_{S_n} (not shown in Fig. 3). On the other hand, disproportionate effects 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 disproportionate effects (not shown).

Finally, if there is a significant relationship between island area and β_{S_n} and/or $\beta_{S_{PIE}}$, 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, 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).

Caveat: Our approach, like all rarefaction-based analyses, assumes that sampling strategies can clearly identify and enumerate individuals of each species. Unfortunately, enumeration of individuals is difficult or impossible in certain kinds of communities (e.g., herbaceous plants, corals), and when individuals can be clonal. Nevertheless, there are some 'workaround' solutions that can be used to apply the rarefaction techniques we have advocated for when the numbers of individuals are not available but other measures of relative abundance are (e.g., percent cover or occupancy). For example, one can convert percentages of a species to individuals via a multiplier. In such a case, the meaning of *PIE*, S_n and β-diversity measures change slightly but can be calculated. Alternatively, one can collect presence–absence data on species in many quadrats within a locality. The presence of a species in a quadrat can be taken as a proportion and given the often-strong correlation between abundance and occupancy (e.g., Gaston et al. 2000, Borregaard and Rahbek 2010), converted to an estimate of percent cover and converted as above. Again, while the interpretation of the parameters measured above cannot be taken literally, they provide a useful way to compare multiple diversity measures (at multiple scales) so that the framework we advocate can be applied.

Case studies

Next, we illustrate how to use our analytical framework to test the 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 2015a,b); (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, Ryberg 2009); (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. We only used data from islands where multiple plots were censused. Results are presented in Table 2 and Fig. 4.

In each system, γ-measures for each island were estimated by pooling all of the samples across a given island; α-measures were taken as the average across individual-based rarefactions in each plot on an island. Because we did not have independent estimates of S_{total}, we extrapolated the γ-rarefaction curve of all of available samples on an island to estimate the total number of expected species on an island using the well-known Chao1 estimator, which provides a lower-bound of total richness (Chao 1984); these calculations were performed using the '*iNext*' package (Hseih et al. 2018). We used the '*mobr*' package (McGlinn et al. 2019) to calculate γ- and α-scale S_n and S_{PIE}, as well as their ratio to calculate β-diversity (β=γ/α); these are calculated via analytical formula rather than the more classical approach of resampling. Note that despite its utility, one must carefully consider sampling when calculating rarefactions, especially because minimum sample size can greatly influence qualitative results (see e.g., Chao et al. 2014, Hseih et al. 2018, McGlinn et al. 2019). Because minimum values of *n* are often small, particularly on small islands, we suggest using the approach recommended by Chao et al. (2014), which uses both rarefaction and extrapolation to create an overall rarefaction curve. From this, calculate the base *n* for S_n calculations by taking the value of whichever of the following is smallest: (i) double the *n* from the smallest sample size, or (ii) the largest sample *n*. For more details on the specific analytical procedures and conceptual reasons for them, see McGlinn et al. (2019). All metrics were calculated using R version 3.5.0 (R Core Team (2018). Code tailored to these specific analyses, as well as the data used, are available at https://github.com/Leana-Gooriah/ISAR_analysis and mirrored at https://zenodo.org/record/2633940.

Table 2: Linear regression coefficients and fits for each response in each case study. In all cases, log(area) was the explanatory variable against the log of the diversity measure. Coefficients are given only when the slope was significantly different from zero.

System	Response	Intercept	Slope	R^2	p-value
Lizards on Oceanic Islands	S_{total}	0.61	0.23	0.77	0.0004
	$^{\gamma}S_n$	0.72	0.18	0.75	0.0005
	$^{\gamma}S_{PIE}$	-	-	-	0.11
	$^{\alpha}S_n$	0.58	0.14	0.60	0.005
	$^{\alpha}S_{PIE}$	0.61	0.10	0.28	0.07
	β_{S_n}	-	-	-	0.27
	$\beta_{S_{PIE}}$	-	-	-	0.41
Grasshoppers in Ozark Glades	S_{total}	0.78	0.26	0.36	0.0007
	$^{\gamma}S_n$	-	-	-	0.1
	$^{\gamma}S_{PIE}$	0.18	0.18	0.37	0.0005
	$^{\alpha}S_n$	0.24	0.20	0.24	0.008
	$^{\alpha}S_{PIE}$	-0.016	0.20	0.37	0.0006
	β_{S_n}	2.37	-0.21	0.27	0.004
	$\beta_{S_{PIE}}$	-	-	-	0.43
Plants in fragmented scrubland	S_{total}	3.55	0.37	0.65	0.03
	$^{\gamma}S_n$	-	-	-	0.19
	$^{\gamma}S_{PIE}$	-	-	-	0.85
	$^{\alpha}S_n$	-	-	-	0.13
	$^{\alpha}S_{PIE}$	-	-	-	0.71
	β_{S_n}	-	-	-	0.79
	$\beta_{S_{PIE}}$	-	-	-	0.23

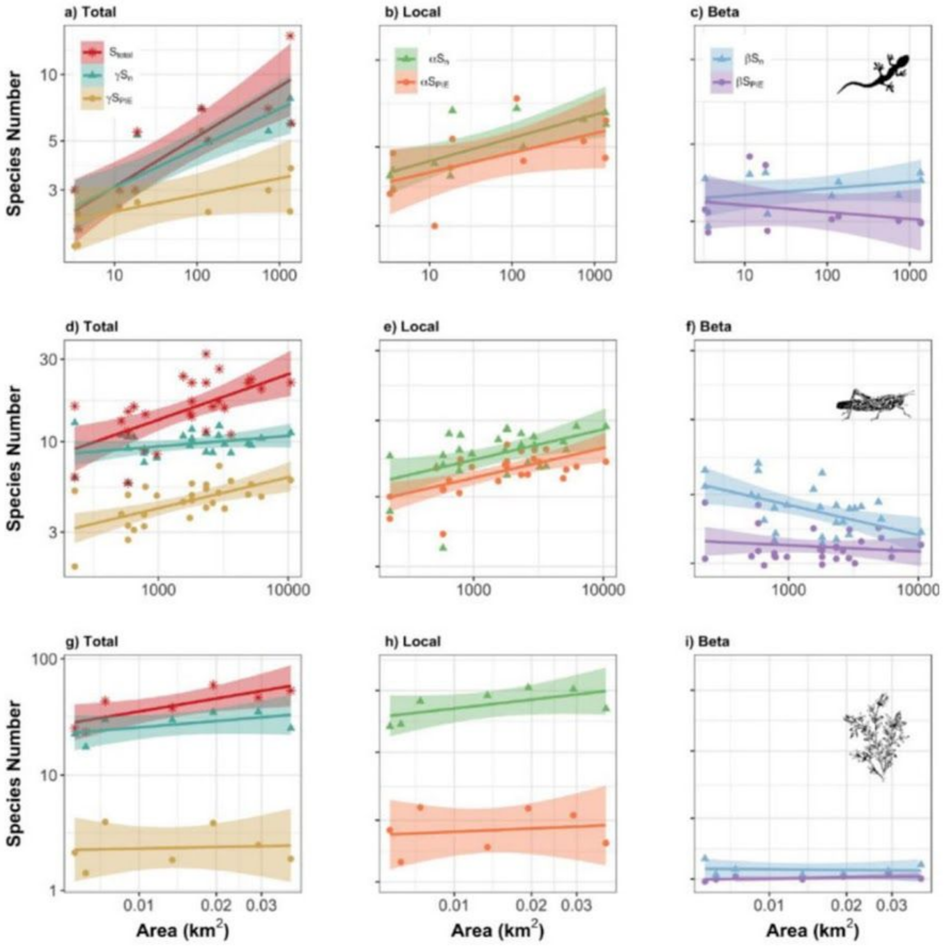

Figure 4. Log-log plots from the three case studies. Each row represents results from a different case study; top row is for the lizards on the Andaman Islands; middle row is for the grasshoppers in Ozark glades; bottom row is for plants in Israeli fragments. Panels a), d), and g) represent parameters 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), and 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), and 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 island biogeography studies, including ISAR studies (e.g., Davidar et al. 2001, 2002). Here, we used data from Surendran and Vasudevan (2015a, b) who intensively sampled lizards in several 100 m^2 quadrats on multiple islands. For this study, we only used data from islands where two or more quadrats were censused; this gave us data from 11 islands that varied from 3.3 to 1375 km^2 in area. The number of quadrats per island ranged from two to ten.

As expected, we found a strong increase in our estimate of S_{total} as island size increased. We also found that ${}^{\gamma}S_n$ increases significantly with island area, allowing us to reject the null hypothesis that the ISAR is driven only by random sampling effects. However, the relationship between ${}^{\gamma}S_{PIE}$ and island area was not significant (Table 2, Fig. 4a). A slightly different pattern emerged at the local scale (Fig. 4b), 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 disproportionate effects played at least some role in driving the ISAR on these islands. Without additional information, we cannot say for certain exactly which spatial mechanisms are operating to allow more even communities and more species co-occurring in local quadrats on larger compared to smaller islands. However, because β_{S_n} also increased with island size, this indicates that there was at least some influence of heterogeneity on the ISAR. This heterogeneity effect was only observed among the rarer species because there was no concomitant relationship between $\beta_{S_{PIE}}$ and island size. From other studies in these islands, we know that habitat heterogeneity generally increases with island size (Davidar et al. 2001, 2002), and so we suspect this relationship influenced heterogeneity in lizard composition from quadrat to quadrat, with higher effect on larger than smaller islands.

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 by Ryberg (2009) from area-standardized sweep sample transects (each sample represented 50 sweeps taken from a transect covering approximately 50 m^2) taken from within glades without predatory lizards. Glades ranged from 0.02 to 1.05 ha, and the number of transects ranged from four transects on the smallest glade to 32 on the largest.

Here, we find that S_{total} increases with island size but that ${}^{\gamma}S_n$ has a weak signal (slope of regression with a P=0.1). However, ${}^{\gamma}S_{PIE}$ increases with island area as does ${}^{\alpha}S_n$ and ${}^{\alpha}S_{PIE}$. Given this weight of evidence (Table 2, Fig. 4d), we can likely reject the null hypothesis that the ISAR emerges only from random sampling but that instead disproportionate effects influence the number of species and their relative abundances. We suspect that one reason for this was because we only used glades that were relatively isolated from one another, and these grasshoppers do not readily disperse through the matrix. Thus, local processes likely outweighed any regional-level sampling effects. Interestingly, however, we found glade size actually has a negative relationship with β-diversity of grasshoppers within a glade (Fig. 4f). One reason for this could be that smaller glades may have higher levels of habitat heterogeneity via edge effects (i.e., edges of glades are cooler and have different plant species than centers) than larger glades. Although our current data do not allow us to explicitly test this hypothesis, results from this framework allows us to develop hypotheses that can be tested with additional data and/or analyses.

Plants in Fragmented Scrubland

Xeric scrub habitat in Israel was once quite extensive but has been severely fragmented such that remnant habitats can be thought of as 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) on plants. Plants were enumerated in two to three 225 m^2 quadrats within seven fragments varying from 0.56 to 3.90 ha.

As above, we found that S_{total} increased with fragment area, indicating a positive ISAR relationship. Here, however, there were no significant relationships with ${}^{\gamma}S_n$ or ${}^{\gamma}S_{PIE}$ (Table 2, Fig. 4g), any of the metrics from the α-rarefaction curve (Fig. 4h), nor any of the β-scale metrics (Fig. 4i). In this case, then, we are not able to reject the null hypothesis and instead conclude that the ISAR in these fragmented habitats is most consistent with the idea of random sampling. Even though we used different (and in our opinion, more robust) analytical tools, our results are qualitatively similar to those derived by the authors of the original study (Giladi et al. 2011). In this case, these results would indicate one of two general possibilities. First, it could be that these plants disperse well enough across the matrix that habitat size does not strongly influence local population dynamics. Second, it could be that local population dynamics do not depend on the numbers of individuals and types of species in local neighborhoods, at least during the time scale in which habitat fragmentation has taken place.

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, it 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., Smith et al. 2005, Drakare et al. 2006, Fahrig 2017). As we have shown here, it is important to understand and report how species richness is 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 a 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 the 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, our approach, using metrics derived from γ- and α-rarefaction curves, provides an important advance over previous approaches by allowing one to more explicitly examine the influence of sampling and scale on the outcome. As our case studies illustrate, we can use this approach to disentangle the main hypotheses suspected to underlie the ISAR (random sampling, disproportionate effects, and heterogeneity). For example, the case study on fragmentation in Israeli scrub habitats indicated that random sampling was primarily responsible for the ISAR. Interestingly, this result is similar to that found by Coleman et al. (1982) in their use of this approach on islands within a flooded reservoir. Such results might occur if species can readily use the matrix between habitat islands or can easily disperse among habitats. Alternatively, in both the lizard and grasshopper systems, species are less likely to use the matrix and dispersal is likely lower, influencing the observation that disproportionate effects and heterogeneity influence the ISAR. These are just a few case studies where appropriate data were available. A more complete exploration of the generality of the patterns and potential mechanisms leading to the ISAR will require more thorough analyses of natural islands and patchy landscapes, as well as habitat islands that 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 island landscapes, but it 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.

Clearly, there are several extensions to the approach that we have presented. When measuring ISARs in the real world, there are often many other mechanisms that can influence diversity patterns in addition to island size. For example, another important variable that influences diversity on islands is the isolation (distance) of those islands from others (e.g., MacArthur and Wilson 1967, Kreft et al. 2008). Habitat area can also influence trophic structure (e.g., larger islands may be more likely to have top predators), which in turn will feed back 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 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., Whittaker et al. 2008, Gillespie and Baldwin 2010). In addition, islands can vary in a number of other environmental and biological features, all of which can interact with island area. The metrics used herein, which explicitly incorporate sampling theory and scale (see also Chase et al. 2018), can be analyzed in more complex models than the simple regressions that we have presented above. For example, hierarchical models can be applied to each of these metrics, analyzing the influence of island area along with a number of potential independent variables (see e.g., Blowes et al. 2017 for such analyses addressing a different set of questions). Likewise, structural equation models comparing patterns of ISARs along with several other covariables (e.g., Stiles and Scheiner 2010) can be applied to these metrics to disentangle area effects from other drivers.

Despite its advantages, it is important to note that our approach is purely observational. As such, although it can provide deeper insights into the likely mechanisms that influence the ISAR than previous observational approaches, it cannot definitively discern process from these patterns. To more definitively test the primary ISAR mechanisms described here, we would need to go a step or two further. This could include, for example, observational studies that take advantage of existing variation, 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, Stiles and Scheiner 2010), but also disentangling patterns of species richness in a more scale-explicit way as we have outlined here. Alternatively, it could include manipulative experiments that directly alter island size and/or heterogeneity (e.g., Simberloff 1976, Douglas and Lake 1994, Matias et al. 2010) or disrupt the processes occurring within islands (e.g., altering patterns of within-island dispersal and/or extinction).

Data and Code Accessibility: The code to run the analyses described here, as well as the data for the case studies, are available on https://github.com/Leana-Gooriah/ISAR_analysis and mirrored at https://zenodo.org/record/2632940.

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CHAPTER 3

Sampling effects drive the species-area relationship in lake zooplankton

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The island species–area relationship (ISAR) describes how the numbers of species increases with increasing size of an island (or island-like habitat, such as lakes), and is one of the oldest laws in ecology. Despite its conceptual importance, there remains a great deal of ambiguity regarding the ISAR and its underlying processes. We compiled data from sampled zooplankton assemblages from several hundred lakes in North America and Europe to examine the influence of the three main hypothesized mechanisms leading to ISARs – passive sampling, disproportionate effects and habitat heterogeneity. We compiled data on lake zooplankton assemblages that reported sample-level and lake level species richness estimates, as well as relative abundance data. In both North American and European lakes, we found a consistent and strong increase in total species richness with increasing lake area. However, when we compared the number of species standardized by number of individuals, there was no relationship between lake area and sample-level species richness or an estimate of species relative abundances, calculated as the probability of interspecific encounter (PIE; a measure of evenness). This was true even when multiple samples were taken across lakes and combined, reducing the likelihood that habitat heterogeneity was driving the results. Overall, our results suggest that the ISAR of zooplankton in these lakes was most likely determined by sampling effects rather than disproportionate effects or habitat heterogeneity leading to more species in larger lakes. Understanding the mechanisms driving ISAR results such as ours can also help us develop predictions for biodiversity change when the area of these habitats changes.

Keywords: biodiversity, disproportionate effects, freshwater zooplankton, heterogeneity, island biogeography, sampling effects, species–area relationship

Introduction

The relationship between the area sampled and the number of species in that area, known as the species–area relationship (SAR), is one of the oldest laws in ecology (Arrhenius 1922, Schoener 1976, Lawton 1999, Lomolino 2000, Drakare et al. 2006). The island species area relationship (ISAR) is one of several types of SAR that specifically addresses how the numbers of species on an island or island-like habitat

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(e.g. ponds and lakes) varies with increasing total area of that island (Scheiner 2003, Scheiner et al. 2011). The ISAR has served as a basis for some of the most important theories in biodiversity studies, such as the theory of island biogeography (MacArthur and Wilson 1967, Warren et al. 2015), as well as more applied questions, such as the influence of habitat loss and fragmentation on biodiversity (Fahrig 2003, Haddad et al. 2015).

Despite its central importance to both basic and applied questions in biodiversity studies, and in contrast to the relatively well understood nested mainland species–area relationships (Storch 2016), the exact nature of the ISAR shape, as well as the processes underlying it, remains in question (Kreft et al. 2007, Triantis et al. 2012, Matthews et al. 2016). One of the primary reasons for the uncertainty in both the patterns and underlying processes of the ISAR is that data are not consistent or comparable within and across studies. For example, the ISAR is often calculated via species checklists, which likely provides a good estimate of the total number of species on an island. However, in other cases, the number of species on an island (ISAR) is estimated via sampling subsets within a given island; this sampling is sometimes (semi-) proportional to the size of that island, but other times, sampling effort is held constant as island size varies. For example, in ponds and lakes, ISARs of planktonic species have been calculated from species lists collected from entire lakes (Dodson 1991, 1992, Dodson et al. 2000, Viana et al. 2014), from semi-proportional sampling (i.e. more samples from larger lakes, but not precise in proportionality) (Søndergaard et al. 2005), from fixed sampling effort regardless of lake area (Hobæk et al. 2002, Hessen et al. 2006), and from a mix of sampling methodologies (Smith et al. 2005).

Here, we reserve the term ISAR to represent the relationship between the total richness of species in a given lake and the size of that lake (similar to Triantis et al. 2012 for true islands). Alternatively, one can compare samples from scales smaller than the entire island to differentiate among three broad classes of mechanisms (overviewed by Connor and McCoy 1979) that could underlie the ISAR (Kohn and Walsh 1994, Yaacobi et al. 2007, Gilaldi et al. 2011, 2014, Sfenthourakis and Panitsa 2012, Karger et al. 2014, Chase et al. 2019).

1) Random sampling. With this mechanism, there are more species in larger islands simply because larger islands passively sample more individuals, and as a result, more species from a regional pool, than smaller islands (Arrhenius 1921, Coleman 1981). Sampling effects are often thought to be a result of limited sampling for uncovering the true numbers of species. However, this does not apply to the random sampling hypothesis as it is a natural phenomenon, and if this mechanism were driving the overall ISAR, we would expect the numbers of species to be exactly the same in smaller versus larger islands from an area or volume-controlled sample, or when the same number of individuals are compared via rarefaction (see also Coleman et al. 1982, Gilaldi et al. 2011, Chase et al. 2019).

2) Disproportionate effects (as opposed to the proportionate effects that happen with random sampling) occur when the number of species that can coexist in a given fixed area increases when the overall size of the island increases (e.g. due to colonization/extinction dynamics, MacArthur and Wilson 1967, or a number of other metacommunity-level processes). If this mechanism were operating, we would expect that the numbers of species in an area-controlled sample would increase with increasing island area.

3) Higher levels of heterogeneity in species composition on larger compared to smaller islands. For example, larger islands can have higher levels of habitat heterogeneity, and thus more opportunities for habitat specialists, than smaller islands (Williams 1964). Alternatively, larger islands can have higher compositional heterogeneity than smaller islands as simply because dispersal limitation becomes more likely as habitats become larger (Hubbell 2001). If this mechanism were operating, we would expect that within-island heterogeneity in species composition (i.e. β-diversity) would increase with increasing island area. However, one should exercise caution when inferring which of the mechanisms (i.e. random sampling, disproportionate effects and heterogeneity) are driving the ISAR as they are not mutually exclusive (i.e. two or more of these mechanisms could be operating simultaneously). For instance, the influence of passive sampling is always operating in the background even when disproportionate effects and/or heterogeneity are driving ISAR patterns (Chase et al. 2019).

Here, we examine the ISAR among freshwater zooplankton in lakes that vary across several orders of magnitude in size (owing to availability of data, we focus only on crustacean zooplankton [copepods and cladocerans], not rotifers). Zooplankton communities are amenable to the analytical framework we use (Chase et al. 2019) based on rarefaction curves and their associated diversity measures from local samples. Importantly, there has been much confusion and debate about the importance of area as a driver of zooplankton diversity in lakes, much of it likely due to differences in sampling approaches. A number of studies have found positive ISARs in lake zooplankton (i.e. more species in larger lakes) on several different continents and in several different contexts (Patalas 1971, Browne 1981, Dodson 1991, 1992, Keller and Conlon 1994, Dodson and Silva-Briano 1996, O'Brien et al. 2004, Ryberg and Chase 2007, Tavernini et al. 2009, Merrix-Jones et al. 2013, Horváth et al. 2017). Furthermore, multivariate tests comparing the influence of lake area along with other important drivers of diversity (e.g. nutrient inputs, landscape factors) often find that area has the strongest influence (Dodson et al. 2000, Hobæk et al. 2002, Shurin et al. 2007). However, other studies find much weaker influence of lake area on zooplankton species richness relative to other drivers (Shurin et al. 2000, Søndergaard et al. 2005, Viana et al. 2014, Lyons and Vinebrooke 2016, Magalhães Braghin et al. 2016). Some have even suggested that there is no influence of lake area on zooplankton species richness (Soto and Zùñiga 1991, De los Ríos and Soto 2007, Hessen et al. 2006, Aranguren-Riaño et al. 2011, De los Ríos-Escalante 2013). Finally, at least one study purported to show a negative relationship (albeit a weak one) of lake area on total zooplankton richness from a study of more than 400 Belarusian lakes (Karatayev et al. 2005). It is important to note, however, that because these studies all used different sampling and analytical methodologies (some sampled total zooplankton, others sampled zooplankton in a fixed volume), these results are not directly comparable. Nor can they help us to elucidate the possible mechanisms that could underlie the ISAR shape.

To explicitly evaluate the ISAR and the possible mechanisms underlying it, we compiled two types of data from online and published sources of zooplankton diversity from North America and Europe to limit biogeographical effects and focus mainly on the influence of lake size via the ISAR. First, we compiled data from lakes where species lists were available from multiple sampling periods, in order to generate the overall ISAR. Second, we compiled data from standardized (volume-controlled) samples to explicitly test whether there were the same number of species per volume (and per number of individuals), as would be expected from the random sampling hypothesis (Coleman 1981, Coleman et al. 1982, Chase et al 2019, Gilaldi et al. 2019). Or instead, whether there were more species in standardized samples, which would imply that disproportionate effect, or habitat heterogeneity, played a role in the ISAR. In all, we find support for a strong ISAR in lake zooplankton when species richness was measured at the scale of the entire lake. However, we found no influence of lake size on standardized sample-level species richness, even when different subsets of the data with different sampling strategies were analyzed. As a result, we conclude that random sampling effects are most likely the predominant mechanism leading to the positive ISAR in these freshwater lakes. That is, from a zooplankter's perspective, we suggest that there is nothing different about being in a large lake compared to a small lake for species coexistence and diversity, other than simply that there is more volume of water available for the random sampling of individuals from the species pool.

Methods

We searched the literature for studies on freshwater zooplankton having abundance and/or richness data in European and North American lakes using Google Scholar and a variety of open access online databases (e.g. Dryad, FigShare, DataONE) with the following keywords: 'zooplankton', 'abundance', 'richness', 'species', 'freshwater' and 'lakes'; other data sources were known to us or referred to us by colleagues. Data for each lake were obtained from tables and figures in the publications, from appendices of those papers, or from open access online databases such as the Long Term Ecological Research, LTER (<https://lter.limnology.wisc.edu/data>) and the National Lakes Assessment, NLA (<www.epa.gov/national-aquatic-resource-surveys/nla>). Data were also obtained through the International Institute for Sustainable Development – Experimental Lakes Area (IISD-ELA) via data request, and we contacted several authors who supplied supplemental data from their published studies (OnDryad: http://dx.doi.org/10.5061/dryad.9cnp5hqdc).

Lake surface area ranged from 1 ha to 824 000 ha in North America and from 1 ha to 3 172 200 ha in Europe. Figure 1 shows the geographical distribution of lakes that were included in our analysis (OnDryad: http://dx.doi.org/10.5061/dryad.9cnp5hqdc). At the scale of the entire lake (total species richness), we found species lists from 98 lakes in North America (many from Dodson 1992) and 41 lakes in Europe (mostly from Dodson 1991). At the scale of standardized samples where we could analyze zooplankton relative abundance data and derive volume-standardized diversity estimates, we found data from 173 North American and 120 European lakes (On Dryad: http://dx.doi.org/10.5061/dryad.9cnp5hqdc). We did not include data from fishless lakes, or from highly acidic or eutrophic lakes, as our goal was to focus specifically on the influence of lake area on zooplankton diversity without strong effects of covarying factors. Though there were clearly a number of covarying factors that might influence zooplankton diversity in addition to lake area, we performed several analyses to try to minimize the influence of this covariation.

To determine whether there was an overall ISAR relationship at the scale of the entire lake, we regressed the log of the total numbers of species measured in the lake, S_{total}, against the log of lake area separately for each continent. We also evaluated whether there were any systematic differences in the shape of the ISAR in lakes between the two continents. S_{total} estimates were taken from studies that reported the total number of species censused in a given lake from multiple sampling locations, seasons and years, so that we could be reasonably confident of the total species number in a given lake. For consistency, we only included species in these lists that were considered by the authors, or by independent sources, to be largely pelagic (free-swimming) species (see Dodson 1992, Dodson et al. 2000 for methodology to generate these species lists). We made no attempt to evaluate how likely these species lists were to have captured the 'true' richness of each lake, but rather took the authors at faith that these were reasonably complete samples. While this allows us to detect the overall ISAR among these lakes, it is also important to note that it was not our main goal to evaluate the accuracy of these whole lake estimates, but rather to evaluate the potential underlying mechanisms of the ISAR using sample data.

To evaluate the potential underlying mechanism leading to the ISAR, we collated data from studies where data could be compared on a standardized (per unit volume) basis. Here, our interest was not to compare how species richness varied as sampling increased within a lake, but rather was to compare how diversity within a standardized volume of water (and standardized number of individuals) differed among lakes that varied in size. We used sampling data from lakes where samples consisted of one to many zooplankton tows (net mesh diameter: 53–243 μm), and where the relative abundances of

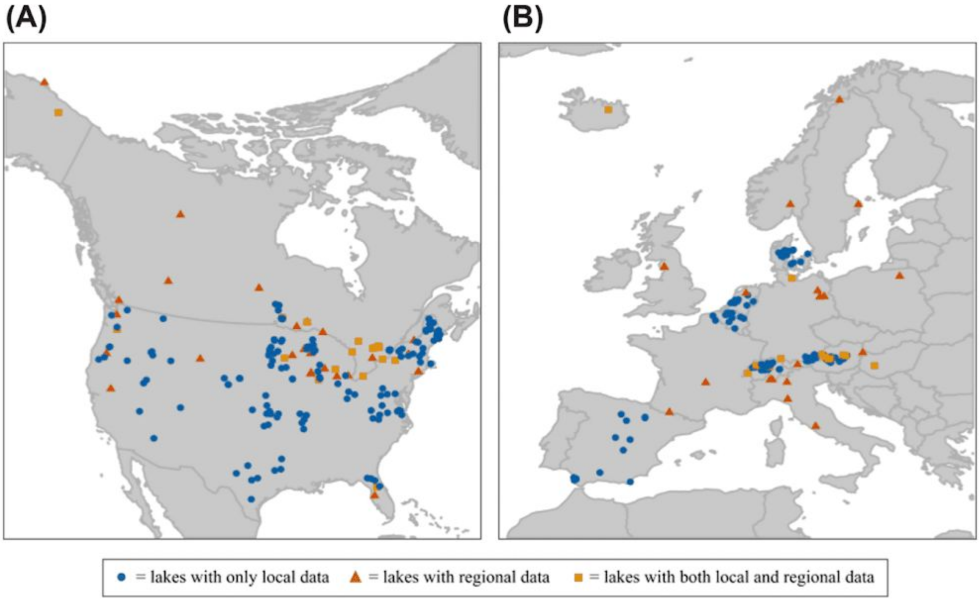

Figure 1. Map of study lakes across Europe and North America from which we were able to obtain data on total zooplankton species richness in the entire lake (red triangles), local zooplankton data on relative abundances on a litre basis (blue circles), and both total and local zooplankton data (yellow squares).

each species was enumerated and reported and could be standardized on a per volume basis. Specifically, the volume of water the tow collected was reported (typically between 45 and 48 l), from which the relative abundances of each species were reported on a per litre basis. Sampling methods varied among studies on exactly how and where tows were taken; two main types of sampling methodology were used: 1) one or several tows taken once or several times across the season from a single sampling location in the lake, 2) multiple tows at different locations from across the lake. For both sampling types, we took the average (not total) from multiple samples to standardize estimates on a per litre basis.

To dissect the possible underlying mechanisms influencing the ISAR at the whole lake level, we compared standardized estimates of species richness from within lakes that vary in size. If these estimates do not differ between small and large lakes, then we can reject the disproportionate effects hypothesis, which instead predicts that there should be more species in a given sample in larger lakes. For each lake, we calculated three diversity measures that capture different aspects how species richness might differ among lakes (Chase et al. 2019): 1) the average number of species per litre (species richness; S); 2) the richness of species rarefied to a common number of individuals (rarefied richness, S_n) (because the numbers of zooplankton per litre did not vary with lake size, we did not expect these relationships to differ). We calculated S_n from the analytical formula given in Chao et al. (2015); 3) a measure of evenness that is relatively robust to sample size, Hurlbert's (1971) probability of interspecific encounter (PIE), $\left(\mathrm{PIE} = \frac{N}{N-1} \times \left(1 - \sum_{i=1}^{S} p_i^2\right)\right)$ 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. For analyses, we converted PIE into an effective number of species, ENS of PIE (sensu Jost 2006), which we hereafter refer to as S_{PIE}. For each standardized measure of diversity (S, S_n and S_{PIE}), we regressed the log of the diversity value against the log of lake area.

If these standardized diversity measures are not related to lake area, we cannot reject the null hypothesis that the ISAR results from random sampling (see also Coleman et al. 1982, Chase et al. 2019). Alternatively, if there is a relationship between any of these standardized diversity measures and lake area, then we can reject the hypothesis that the ISAR is solely due to sampling, and that instead some biological mechanism related to habitat heterogeneity and/or disproportionate effects plays a role in generating the overall ISAR. However, because sample data were only collected from one part of several of the lakes in our study, we cannot reject the heterogeneity hypothesis with these data alone. This is because, if samples are taken from a single location within a lake, and if habitat heterogeneity were underlying the ISAR, we might observe no change from a given sample with lake size, even though different parts of the lake may have different species, leading to the ISAR at the whole lake level (Sfenthourakis and Panitsa 2012, Chase et al. 2019). We explicitly tested this hypothesis using 92 lakes from the BIOMAN dataset (Declerk et al. 2005, Lemmens et al. 2017) from Europe. In this dataset, zooplankton samples were collected from a number of different points across each lake and pooled. Because samples from across each lake were pooled, estimates of S_n and S_{PIE} in these lakes are calculated from the combined abundances of species from the whole lake, allowing us to explicitly test the random sampling hypothesis. If heterogeneity were driving the ISAR results, we would expect a positive relationship between lake area and S_n and S_{PIE}, even if results from samples of a single point in the lake might show no such relationship. A negative result for this scenario, then, showing no relationship between lake area and the sample-level estimates (S_n and S_{PIE}) from the samples pooled across lakes, would indicate that we could reject both the disproportionate and heterogeneity effects hypotheses, but not the random sampling hypothesis.

Finally, it is important to note that these hypotheses are not the only possibilities. The ISAR, and the biodiversity parameters (e.g. S_n, S_{PIE}) underlying it need not show simple neutral or positive relationships (i.e. they can be negative), nor need they be linear (i.e. they can be asymptotic or unimodal). In such cases, the conclusions would be more complex, but the analytical approach discussed here can still be useful for inferring possibly processes underlying these patterns (Chase et al. 2019).

We used the 'mobr' package (McGlinn et al. 2019) to calculate S_n and S_{PIE}. The effects of the log-transformed lake area on log-transformed biodiversity metrics (S_{total}, S_n and S_{PIE}) were assessed using linear regressions. We analyzed data from both continents separately using simple linear regression models. All analyses were done using R ver. 3.5.0 (<www.r-project.org>).

Results

We observed a strong relationship between the log-transformed variables lake area and total species richness (S_{total}) at the whole-lake scale in both European and North American lakes (Fig. 2). Additionally, the slope of the ISAR at the whole lake scale was steeper for the European lakes, that is, zooplankton species richness increased slightly more with lake area in Europe compared with North America (Table 1). Because the largest lakes for which we had S_{total} data were larger than those for which we had sample data, we removed the largest lakes (>30 000 ha for North American lakes and >20 000 ha for European lakes) from which we had S_{total} data and again found a significant relationship between log S_{total} and log lake area in both European ($p = 0.018$) and North American ($p = 0.04$) lakes.

When we compared standardized estimates of diversity (i.e. per litre), we found no significant relationships between the log of species richness per litre (not shown), S_n or S_{PIE} for either North America or Europe (Table 1, Fig. 2). That is, the numbers of species in a given standardized volume, as well as their relative abundances, did not appear to vary even as lake size varied by many orders of magnitude.

Because the geographic range of lakes was quite large, including lakes in very different climate zones, we ran the analysis on a subset lakes that were found in similar climatic and biogeographic zones (just within the temperate zones of North America and Europe), and found a similar positive ISAR relationship between the log S_{total} and log lake area in both European ($p = 0.01$) and North American ($p = 0.04$) lakes. However, we again found no significant relationships between the standardized estimates of diversity and lake area even within these more narrowly defined regions ($p > 0.1$). To examine potentially confounding factors that may have influenced species richness, we examined patterns of zooplankton biodiversity in response to phosphorus and nitrogen levels and other environmental factors such as: temperature,

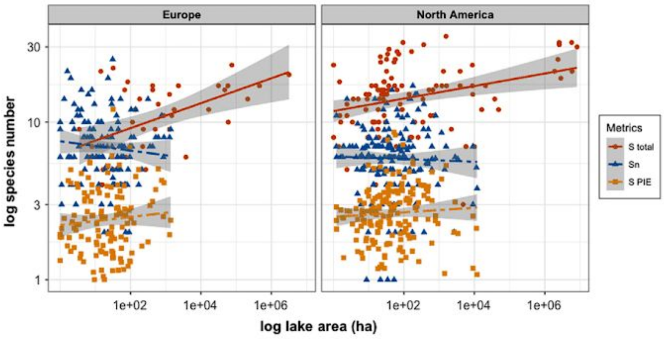

Figure 2. Linear regressions of log-transformed biodiversity metrics against log lake area (hectares). Variables include the total numbers of species observed in the entire lake (S_{total}), the rarefied number of species (S_n) and the effective number of species given the probability of interspecific encounter (S_{PIE}) (see text for explanation).

Table 1. Regression models and their estimates of intercept, slope and R^2. Entries in bold significant at $p < 0.05$.

Response	Continent	lgC ± SE	z ± SE	R^2	p-value
log S_n ~ log area	North America	4.06 ± 0.51	−0.11 ± 0.28	−0.005	0.68
log S_{PIE} ~ log area	North America	3.65 ± 0.43	0.343 ± 0.32	0.001	0.280
log S_{total} ~ log area	**North America**	**−2.46 ± 1.60**	**0.04 ± 0.12**	**0.08**	**0.0018**
log S_n ~ log area	Europe	3.67 ± 0.61	−0.34 ± 0.30	0.002	0.260
log S_{PIE} ~ log area	Europe	2.82 ± 0.32	0.25 ± 0.32	−0.003	0.43
log S_{total} ~ log area	**Europe**	**−1.77 ± 2.21**	**3.47 ± 0.92**	**0.269**	**0.0006**

chlorophyll a, pH and maximum depth and lake volume (We carried out a multivariate analysis using a linear model of the biodiversity indices (S_n and S_{PIE}) against their corresponding environmental variables, including area, and found no significant effect on zooplankton S_n, or S_{PIE} in both European and North American lakes (Supplementary material Appendix 1 Table A1).

Finally, to evaluate whether within-lake heterogeneity may have influenced our overall patterns, we used data from 92 lakes from the BIOMAN dataset (Declerk et al. 2005, Lemmens et al. 2017) where zooplankton were collected from multiple sampling stations across each lake and pooled. Here again, we found no significant relationship between S_n and lake area $[\log(S_n) = \log(2.09) + -0.04 \times \log(\text{Area}) p = 0.2433]$ or S_{PIE} and lake area $[\log(S_{PIE}) = \log(0.799) + 0.034 \times \log(\text{Area}), p = 0.3394]$ (Fig. 3).

Discussion

Overall, we observed a statistically significant positive zooplankton ISAR for both North American and European lakes when species richness was measured at the whole lake scale (S_{total}) (Fig. 2). This result is certainly not surprising, as the ISAR is expected from a number of theoretical predictions (MacArthur and Wilson 1967, Connor and McCoy 1979), and is a rather general phenomenon on both natural islands (Triantis et al. 2012) and habitat islands (Matthews et al. 2016). Further, our results confirm several previous studies that have found positive ISAR relationships of zooplankton when species richness was measured at the scale of the whole lake (Browne 1981, Fryer 1985, Dodson 1991, 1992, Dodson et al. 2000, O'Brien et al. 2004).

However, as we have argued here, such positive ISARs at the level of the whole island or lake can be explained by a number of different possible mechanisms, including random sampling effects, disproportionate effects and habitat heterogeneity. This evidences the need for more detailed information dissecting these patterns of species richness in order to disentangle these mechanisms (see also Gilaldi et al. 2014, Chase et al. 2019). Indeed, Hill et al. (1994) suggested that the sampling effect should be viewed as a null hypothesis to be rejected before inferring that non-sample-based ecological processes (such as disproportionate effects or heterogeneity) underlie the ISAR (see also Coleman 1981, Coleman et al. 1982). When compiling data from lakes, we found no influence of lake area on standardized estimates of species richness when estimated on a per litre basis, on rarefied species richness (S_n), nor on a measure that accounts for the evenness of species in the sample (S_{PIE}) (Fig. 2). From this, we can reject the hypothesis that disproportionate effects allow more species to persist in a given sample volume in larger lakes, leading to the ISAR. Further, we can reject the heterogeneity hypothesis, at least from a large number of European lakes, because we found no relationship between S_n and S_{PIE} and lake size when multiple samples from across the lake were pooled (Fig. 3). As a result, we conclude that the most likely mechanism underlying the ISAR in these lakes is random sampling; that is, larger lakes have more species because they passively sample more of the regional species pool.

Our results can help reconcile some of the seemingly contradictory evidence regarding the influence of lake area on zooplankton diversity. Although there is typically strong evidence for ISAR in lakes when zooplankton data are summarized at the whole lake level, results from studies where data are collected and analyzed at the sample level are less clear

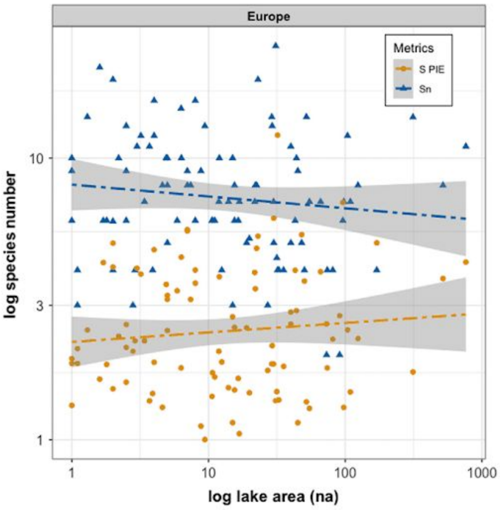

Figure 3. Log-transformed S_n and S_{PIE} as a function of log-transformed lake area from a subset of lakes that were sampled at multiple stations across each lake (points plotted represent S_n and S_{PIE} calculated from pooled values across sampling stations per lake).

and often show weak to non-existent relationships between sample-level estimates of species richness and lake area (Soto and Zùñiga 1991, De los Ríos and Soto 2007, Hessen et al. 2006, Aranguren-Riaño et al. 2011, De los Ríos-Escalante 2013). Indeed, such positive effects of lake area on total species richness, but weak to no effects on lake area on standardized estimates of species diversity would be expected if the ISAR were primarily driven by random sampling effects (Chase et al. 2019).

In our analyses, we only considered lake area as a driver of zooplankton species richness, although clearly this is an oversimplification of the factors that can influence biodiversity in these communities. Because we were primarily interested in the effect of area in driving the ISAR, not factors that influence zooplankton diversity in general, we deliberately eliminated several factors known to influence zooplankton diversity. For example, we only selected lakes that were not unusually acidic or eutrophic. Unfortunately, the full suite of environmental data that could influence zooplankton communities were not available for most of the lakes in our analysis, and so we could not more explicitly examine their role in creating residual effects of the ISAR. As a result, variation in these factors certainly could have played a role in obscuring any small effects lake area might have had on measures of diversity at the sample level. We did, however, have data for nitrogen and phosphorus, two of the most important drivers of lake productivity, from a number of lakes, as well as, pH, temperature, chlorophyll a, maximum depth and lake volume from others, and found that this had no influence on our observed patterns (Supplementary material Appendix 1 Table A1). Thus, given the fact that standardized sample-level estimates were clearly unrelated to lake area across many orders of magnitude of lake size, ranging from a hectare to some of the largest lakes in the world, we believe the interpretation that sampling effects are a primary driver of lake ISARs is likely a robust one.

Nevertheless, caution must be taken in interpreting results from studies on standardized estimates of diversity, because the sampling process itself can influence the results. For example, comparing standardized species richness at small spatial grains may underestimate the possible influence of disproportionate effects if rare species are the ones mostly influenced by increasing island area. For instance, Karger et al. (2014) found that fern species richness on southeast Asian islands increased significantly with island size at the whole island scale but did not increase when measured at the smallest spatial grains in their study (400 m^2). However, when richness was measured at larger spatial grains within their study, they found increasing S_n with island area. This suggests that larger islands favor rare species more than would be expected just by random sampling (e.g. disproportionate effects), but that it can only be detected at the larger sampling grains (because rare species are not well sampled in smaller grains). Unfortunately, our data were typically limited in this respect because zooplankton richness and abundance data were standardized on a per litre basis by the authors of the original studies. Therefore, we were unable to explore the influence of sampling grain on our results.

Despite our result that random sampling effects are most likely underlying the positive ISAR of zooplankton in lakes in both Europe and North America, we do not wish to imply that sampling effects generally drive ISARs. In a review of habitat fragmentation effects on plants (fragments were considered as islands), Gilaldi et al. (2014) showed that sample level richness was not significantly related to fragment area in more than 60% of the studies measured, suggesting sampling effects. However, this means that ~40% of the studies were more likely to be driven by disproportionate effects and/or heterogeneity effects. On the other hand, Chase et al. (2019) identified several case studies where disproportionate effects and/or heterogeneity were more likely leading to the positive ISAR. The generality of these results, thus, will remain unknown until a more thorough meta-analysis can be performed.

Even in freshwater zooplankton assemblages, different results have been observed. For example, in experimental mesocosms where volume was varied from 300 to 900 l, Schuler et al. (2017) found a likely disproportionate effects mechanism underlying the ISAR in some treatments. We hypothesize that the main difference between the results of our study, which suggest sampling effects predominate zooplankton ISARs and those of Schuler et al. (2017) which show some support for mechanisms beyond sampling effects is in the difference in the size of habitats between the different studies. Given the small size of zooplankton and the resulting vast population sizes that occur even in the smallest lakes from our surveys (e.g. n = 187 in a smallest lake of 1 ha), it might not be surprising that past a certain threshold disproportionate effects and heterogeneity mechanisms are no longer important for ISAR relationships, and only sampling effects can create ISARs. However, the mesocosms used by Schuler et al. (2017) were orders of magnitude smaller than even the smallest lakes in our surveys. The smaller sizes of these habitats, which would result in much smaller population sizes of the species, could easily have led to disproportionate effects or heterogeneity mechanisms in these smaller habitats that did not emerge in the larger lakes.

Overall, our results emphasize the importance of using multiple measures of diversity at multiple scales, while explicitly accounting for the nature of random sampling effects in driving those results, in order to understand the factors that underlie ISAR relationships. Importantly, we can use these results to reconcile conflicting results from a number of previous studies regarding the shape and strength of the ISAR in lake ecosystems. In doing so, we provide a strong test of a template (Chase et al. 2019) that has been developed to explicitly understand and disentangle the possible mechanisms underlying ISAR relationships in natural and fragmented island ecosystems.

Data availability statement

Data are available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.9cnp5hqdc> (Gooriah and Chase 2019).

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Supplementary material (available online as Appendix oik-06057 at <www.oikosjournal.org/appendix/oik-06057>). Appendix 1.

CHAPTER 4

Island species-area relationships in the Andaman and Nicobar archipelago emerge because rarer species are disproportionately favored on larger islands

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Island species-area relationships in the Andaman and Nicobar archipelago emerge because rarer species are disproportionately favored on larger islands.

Abstract

The Island Species-Area relationship (ISAR) describes how the number of species increases with increasing size of an island (or island-like habitat), and is of fundamental importance in island biogeography and conservation. Here, we use a framework based on individual-based rarefactions to infer whether ISARs result from random sampling, or whether some process are acting beyond sampling (e.g., disproportionate effects and/or habitat heterogeneity). Using data on total and relative abundances of four taxa (birds, butterflies, amphibians and reptiles) across the Andamans and Nicobar archipelago, we examine how different metrics of biodiversity (total species richness, rarefied species richness, and abundance-weighted effective numbers of species emphasizing common species) vary with island area. Total species richness increased for all taxa, as did rarefied species richness for a given sampling effort. This indicates that the ISAR did not result because of random sampling, but that instead, species were disproportionately favored on larger islands. For most taxa, this disproportionate effect was primarily due to changes in the abundance of rarer species, because there was no effect on the abundance-weighted diversity measure for all taxa except butterflies. Furthermore, for the two taxa for which we had plot-level data (lizards and frogs), within-island β-diversity did not increase with island size, suggesting that heterogeneity effects were unlikely to be driving these ISARS. Overall, our results indicate that the ISAR of these taxa is most likely because rarer species are more likely to survive and persist beyond that which would have been expected by random sampling alone, and emphasizes the role of these larger islands in the preservation and conservation of species.

Keywords: Alpha-diversity, Beta-diversity, Disproportionate effects, Gamma-diversity, Heterogeneity, Individual-based rarefaction, Island biogeography, Random sampling, Species-area relationship.

Introduction

The Island Species-Area relationship (ISAR) describes the relationship between the number of species on an island and the area of that island, and has served as a basis for some of the most important theories in biodiversity studies, such as the theory of island biogeography (MacArthur and Wilson 1967, Warren et al. 2015). While the general pattern and shape of the ISAR is generally positive and its shape is described by a few key parameters (e.g., Triantis et al. 2012, Matthews et al. 2016), there remains uncertainty about the mechanisms underlying the ISAR and how they shape it (e.g., Chase et al. 2019). A deeper understanding of these mechanisms will not only provide insight into the processes that shape biodiversity and its variation on islands, but will also be important for devising plans for conserving biodiversity on islands, which house a disproportionate amount of diversity compared to their land area, but are also disproportionately influenced by human impacts and global change (Vitousek et al. 1997, Tershy et al. 2015).

The simplest explanation leading to the positive ISAR is random sampling—where larger islands have more individuals and as a result, a higher likelihood of passively sampling more species from the regional pool than smaller islands (Connor and McCoy 1979). Coleman (1981) provided an analytical approach to evaluate this null model, which Coleman et al. (1982) subsequently tested with bird abundances on islands, finding that they did not reject the random sampling hypothesis. Indeed, when appropriate data were available, random sampling has been implicated in a number of empirical studies of ISAR patterns (e.g., Haila 1983, Hill et al. 1994, Ouin et al. 2006, Bidwell et al. 2014, Gooriah and Chase in revision), though other studies have rejected the random sampling hypothesis (e.g., Ranta and As 1982, Bolger et al. 1991, Schoereder et al. 2004, Wang et al. 2010, Xu et al. 2017).

If the random sampling effect is rejected, two classes of biological mechanisms beyond random sampling can be invoked. First, island size can disproportionately influence some species relative to others (when random sampling is operating, effects are proportional); Connor and McCoy (1979) called these '*area per se'* effects to indicate that island area itself influences the relative abundances and likelihood of co-occurrence among species, and Chase et al. (2019) more generally called these 'disproportionate' effects. One prominent mechanism leading to disproportionate effects is the colonization-extinction dynamics inherent to MacArthur and Wilson's (1963, 1967) theory of island biogeography. Likewise, population-level processes (Allee-effects or demographic stochasticity), which tend to be more pronounced on smaller rather than larger islands, can also lead to disproportionate effects.

Second, an increasing number of habitats, or an increase in habitat heterogeneity, with island area can also lead to more species on bigger islands (Kohn and Walsh 1994), particularly if species require specific or multiple habitat types (Williams, 1964, Hart and Horwitz, 1991, Guadagnin and Malchik 2007). However, disentangling disproportionate effects from habitat diversity can prove to be quite challenging as they can easily be confounded (Connor and McCoy 1979, Gilbert 1980, Boecklen and Gotelli 1984, Kohn and Walsh 1994); that is, bigger islands tend to have more diverse habitats (Hortal et al 2009). Furthermore, it is possible that area and habitat diversity together can better explain the variation of species patterns across islands (Ricklefs and Lovette 1999, Davidar et al. 2001, Triantis et al. 2003, Kadmon and Allouche 2007). Even within the same island archipelago, it is possible that different mechanisms underlie the response of different taxa to island area, depending, for example, on their dispersal capacity. For example, in a study of the ISAR of Caribbean islands, Ricklefs and Lovette (1999) suggested that birds were more likely responding to area alone, while habitat diversity effects were stronger for butterflies, amphibians and reptiles.

In this study, we use previously collected abundance data from four taxa that differ in their dispersal capacity—birds, butterflies, frogs and lizards—from the Andaman and Nicobar archipelago in the Bay of Bengal to examine the possible mechanisms underlying their respective ISARs. For birds and butterflies, we were able to explicitly test the null hypothesis of random sampling against more ecological mechanisms underlying the ISAR of these taxa using the individual-based rarefaction framework outlined in Chase et al. (2019). For frogs and lizards, we additionally had spatially-explicit plot level data, which allowed us to additionally test the potential role of habitat heterogeneity.

Material & Methods

Study site and sampling methods

The Andaman and Nicobar archipelago includes 556 islands, islets and rocks and is made up of four large contiguous regions: North, Middle, Baratang and South Andamans forming of over 5000 km^2 in total area, surrounded by many isolated islands. The forest types across islands are diverse, ranging from evergreen forests to deciduous forests and mangroves (Champion and Seth, 1968, Davidar et al 2002). Bird and butterfly surveys were carried out on 38 and 25 of these islands respectively (varying in size from 0.03 to 1375 km^2) in 1992 as part of the studies by Davidar et al. (1996) and Devy et al. (1998); data on the abundances of species from these surveys were previously unpublished (provided here in the Appendix). Frog and lizard surveys were carried out on 15 of these islands (varying in size from 0.03 to 1375 km^2) between 2010-2012 and were previously published by Surendran and Vasudevan (2015).

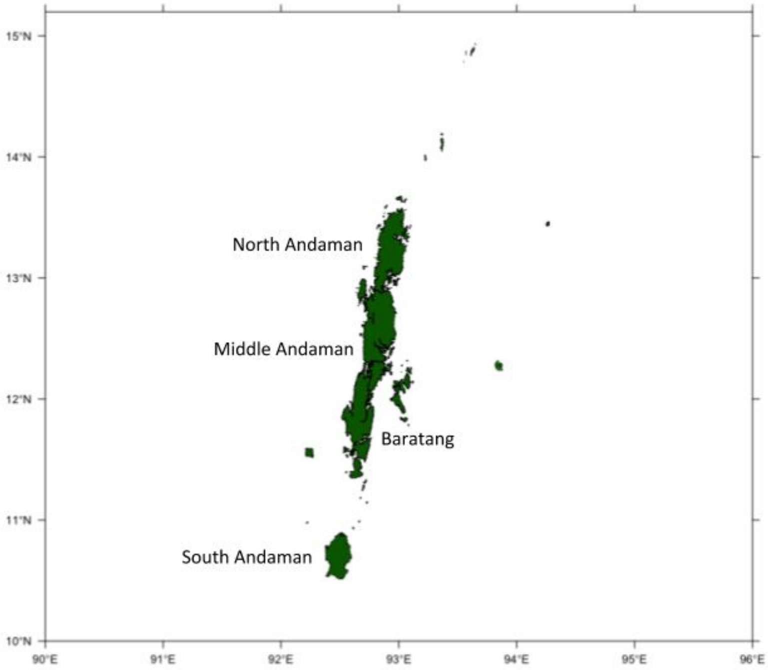

Figure 1. Map of Andaman island group, the four main regions: North, Middle, Baratang and South Andamans.

Transect methods were used to sample forest birds and butterflies (for more details, see Davidar et al. 1996, Devy et al. 1998). Bird sampling was conducted between 1992-1994 during the dry seasons, along 1 km length transects laid within each habitat type on the bigger islands. On smaller islands, transects cut through all the habitat types. The number of transects placed increased with the size of that habitat. Butterflies were sampled from 1992-1994 during the dry seasons. Variable length transects laid in different habitats on large islands or across small islands (Devy et al. 1998), where the number and length of transects depended on the size of the island. Information on the numbers of individuals from each transect was not retained, and so we pooled the total numbers of individuals of all species from all transects on a given island for the analyses we present below.

Lizards and frogs were surveyed using bounded quadrats (10 m x 10 m) from November to May 2010–2011 and 2011–2012 (for more details, see Surendran and Vasudevan 2015). Forty-nine quadrats per taxa were placed in rainforests on relatively flat terrain. The number of quadrats sampled was proportional to island size. We used data from 10 islands for frogs, and 11 islands for lizards (we removed islands where either no species were recorded or where only one quadrat was sampled). Here, sample data retained information on the numbers of individuals within each plot, allowing us to calculate patterns of local and regional diversity on each island.

Hypotheses and analyses

We follow the framework for hypotheses and analyses outlined in Chase et al. 2019 for untangling the potential mechanisms underlying the ISAR for these groups.

First, we estimated the total number of species on each island, which we refer to as S_{total}. Because we did not have independent estimates of S_{total} from each island, we combined abundance data from all plots and extrapolated that to an estimated number of species using the Chao1 estimator (Chao 1984, Hseih et al. 2016); this value should be taken as a minimum possible number of species on each island. We then regressed S_{total} against island size to derive an overall ISAR. While useful as a starting point, the relationship between S_{total} and island area cannot be used to go further into dissecting the possible mechanisms underlying the ISAR relationship.

Can we reject the null hypothesis of random sampling? We used individual-based rarefaction to evaluate whether the ISAR results deviate from random sampling, or if instead some biological mechanism can be invoked. This approach, similar to the random-placement model of Coleman (1981), uses the individual-based rarefaction curve calculated from all of the transects/quadrats taken from each island. From this island-wide individual-based rarefaction curve, we can then calculate the numbers of species expected for a given number of individuals (n), which we term S_n. These values (S_n) were interpolated or extrapolated from the island-wide individual-based rarefaction curves for each island at a common number of individuals (n). In this case, we rarefied S to a reference n, which we calculated as the product of two times the minimum total number of individuals found in an island per dataset (for more details see Chao et al. 2014).

If there is no relationship between S_n and island size, then we cannot reject the null hypothesis that the ISAR results from random sampling alone. Alternatively, if S_n increases with island size, we can conclude that there is some other mechanism operating that allows more species to co-occur within a given n on larger than smaller islands, which allows us to reject the null hypothesis of random sampling, and indicates that disproportionate effects and/or heterogeneity are playing a role in driving the patterns.

In order to further discern whether any changes in S_n were due to changes in the overall evenness of the community, or rather just changes to the rarest species in the community, we calculated a metric of diversity that is primarily sensitive to changes in the most common species, but insensitive to rarer species. Specifically, we used the pooled data to estimate Hurlbert's (1971) Probability of Interspecific Encounter (PIE),

$$PIE = \left(\frac{N}{N-1}\right) * \left(1 - \sum_{i=1}^{S} p_i^2\right)$$

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. For analyses, we convert PIE to an effective number of species, S_{PIE} which is described as the number of species that would be observed in a community if all of the species in it were equally abundant (Jost 2006) (S_{PIE}= 1/1-PIE, and is proportional to Simpson's index; Hill 1973, Jost 2006). A relationship between S_{PIE} and island area indicates that larger islands have overall more even abundance distributions. Alternatively, if S_n increases with island area, but S_{PIE} does not vary with island area, then we would conclude that only the rarer species are influenced by island area (Chase et al. 2019).

Within-island β-diversity

A significant relationship between island area and both S_n and S_{PIE} can allow us to reject the null hypothesis of random sampling driving the ISAR, but when these values are calculated from pooled data across each island, we cannot differentiate between disproportionate effects and heterogeneity. To disentangle the potential influence of heterogeneity, it is necessary to compare differences in species composition within islands (i.e, β-diversity) that differ in size (Chase et al. 2019). While we only had island-level information on relative abundances for the birds and butterflies, we were able to calculate β-diversity measures from the frog and lizard data where spatially-explicit plot level data were available. To do so, we compared the values of S_n when calculated within a single quadrat with the value of S_n when calculated from the pooled individuals across all plots. The difference between these two values indicates the degree to which species are clumped in the landscape (i.e., β-diversity). The same can also be done for S_{PIE} to determine whether the clumping is due to more common or rare species. If there is no relationship between either of these β-diversity and island size, we can reject the heterogeneity hypothesis, whereas if measures of β-diversity increases with island size, we can conclude that heterogeneity plays a role underlying the ISAR.

Statistical analysis

We calculated total estimated species richness (S_{total}), the rarefied number of species expected at a common number of individuals (S_n) and the effective number of species (S_{PIE}) using the R package mobr (McGlinn et al. 2019); for lizards and frogs, we calculated these from the pooled data across each island, as well as the plot-level data in order to derive β-indices. Code specifically for ISAR analyses are available on GitHub https://github.com/LeanaGooriah/ISAR_analysis. For each taxa, we used linear regressions to evaluate the relationship between the various diversity indices (S_{total}, S_n, S_{PIE}) and island size.

Results

Figure 2 illustrates the ISAR relationship for each taxa for each diversity measure and Table 1 gives the regression coefficients. For all four taxa, total species richness (S_{total}) increased with island size. Likewise, rarefied species richness, S_n, increased with island size, allowing us to reject the null hypothesis of random sampling for each taxa. However, we only found a significant increase of S_{PIE}, which emphasizes changes in the overall evenness of the community, with island size for butterflies, but not the other three taxa.

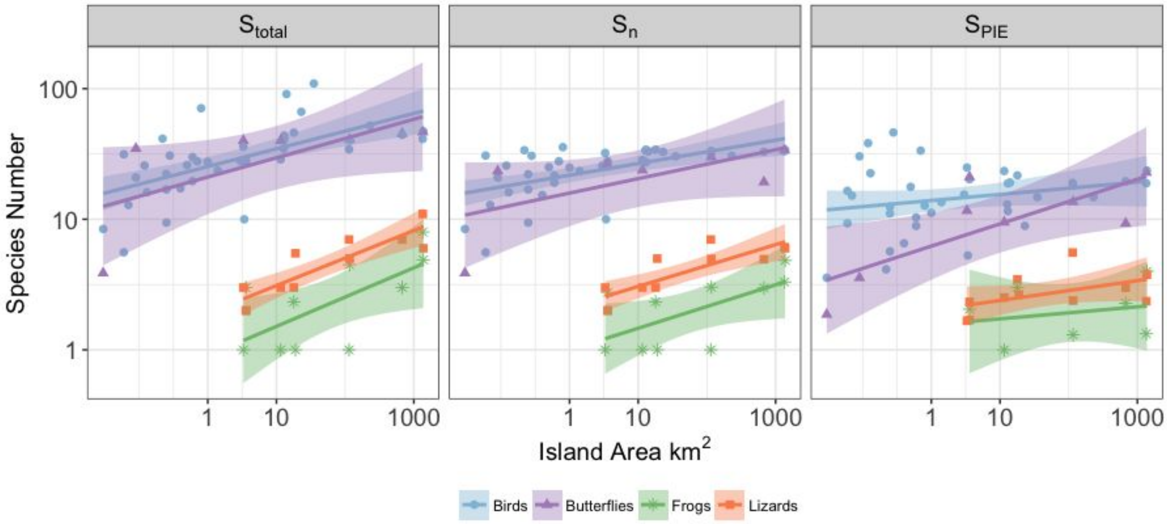

Figure 2: Linear regressions of log-transformed biodiversity metrics against the log of island area (km^2) for all four taxa. Variables include the total number of species estimated per island from the pooled abundance data (S_{total}), the number of species expected at a specific number of individuals (S_n) and the corresponding effective number of species of the probability of interspecific encounter (S_{PIE}).

Table 1. Regression models and their estimates of intercept, slope and R^2.

Taxa	Response	lgC ± SE	z ± SE	R^2	*p*-value
Birds	**log S_{total} ~ log Area**	**3.23 ± 0.08**	**0.14 ± 0.03**	**0.38**	**2.42e-05**^{9}
	log S_n ~ log Area	**3.07 ± 0.06**	**0.08 ± 0.02**	**0.31**	**0.0001**
	log S_{PIE} ~ log Area	2.63 ± 0.10	0.05 ± 0.03	0.03	0.15
Butterflies	**log S_{total} ~ log Area**	**3.04 ± 0.27**	**0.14 ± 0.06**	**0.39**	**0.05**
	log S_n ~ log Area	**2.76 ± 0.23**	**0.11 ± 0.05**	**0.29**	**0.09**
	log S_{PIE} ~ log Area	**1.82 ± 0.24**	**0.17 ± 0.05**	**0.53**	**0.02**
Lizards	**log S_{total} ~ log Area**	**0.64 ± 0.16**	**0.21 ± 0.03**	**0.77**	**0.0002**
	log S_n ~ log Area	**0.75 ± 0.15**	**0.16 ± 0.03**	**0.67**	**0.001**
	log S_{PIE} ~ log Area	0.70 ± 0.18	0.07 ± 0.04	0.18	0.10
Frogs	**log S_{total} ~ log Area**	**-0.10 ±0.41**	**0.22 ± 0.08**	**0.37**	**0.03**
	log S_n ~ log Area	**-0.002 ± 0.34**	**0.16 ± 0.07**	**0.31**	**0.05**
	log S_{PIE} ~ log Area	0.44 ± 0.45	0.046 ± 0.08	-0.13	0.62

Lizards and frogs

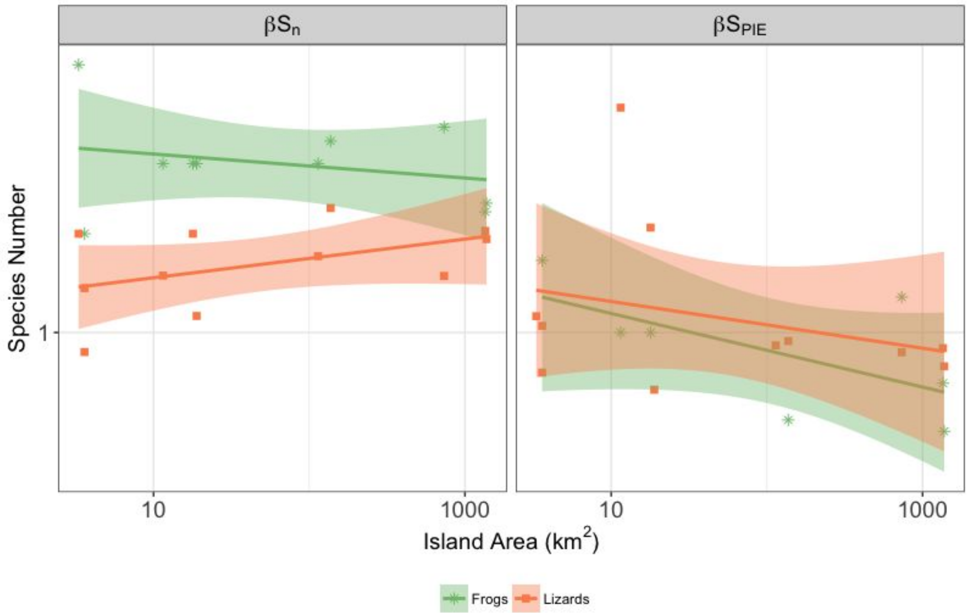

Figure 3: Linear regressions of log-transformed variables S_n and S_{PIE} at the β-scale against the log of island area (km^2) for frogs and lizards.

For frogs and lizards, we regressed S_n and S_{PIE} measured from individual plots (rather than the whole island, as above) against the log of island area and found similar results to the whole-island scale. As a result, we found no difference in either of the β-diversity measures (estimated by taking the regional level estimate divided by the plot-level estimate) with increasing island size for these two taxa (Figure 3, for all four linear regression lines : p-values > 0.1).

Discussion

Our results showed that island size had a positive significant effect on bird, butterfly, frog and lizard species richness at the whole island scale (S_{total}). This result is not surprising and such a positive ISAR is expected as a result of a number of theoretical expectations and is the most frequently observed pattern (e.g., MacArthur and Wilson 1967, Connor and McCoy 1979, Triantis et al. 2012). However, while significant attention has been paid towards describing the shape of this relationship at the whole island scale, it tells us little about the potential underlying mechanisms of the ISAR.

When we dissected the ISARs of these taxa to discern possible underlying mechanisms, we found an overall consistent pattern that the island-wide rarefied species richness (S_n) increased with island size. This means more species persist for a given number of individuals than would be expected from a random sampling effect, thus inferring that processes beyond sampling are operating. We used our measure of evenness (the Probability of Interspecific Encounter, PIE), which is relatively insensitive to rare species, and its conversion to an effective number of species to discern whether any changes in Sn were primarily due to an increased probability of rare species persisting beyond sampling expectations on larger islands (in which case, S_{PIE} would not be expected to change), or instead due to changes in both rarer and more common species (in which case, S_{PIE} would increase with island size). For three taxa (birds, frogs and lizards), S_n increased with island size, while S_{PIE} did not. From this, we can infer that it was primarily the rarer species that were able to disproportionately persist on larger rather than smaller islands. This could have emerged, for example, because populations on larger islands were more likely to persist by avoiding Allee-effects and/or demographic stochasticity (Hanski and Gyllenberg 1993, Orrock and Watling 2010), or through the increased likelihood of specialized habitats on larger islands (Williams 1964, Kohn and Walsh 1994, Davidar et al. 2001). For butterflies, both S_n and S_{PIE} increased with island size, suggesting that not only were rarer species disproportionately favored on larger islands, but that entire shape of the relative abundance distribution became more even on larger islands. Without further information, we cannot explicitly test why butterflies might have differed in their responses to island size compared to the other taxa, but might speculate that owing to their larger population sizes and higher levels of specialization (especially in the larval stage), they were able to more readily alter their relative abundance distributions on larger islands.

Because plot-level data were available for the frogs and lizards, we were able to compare the different biodiversity metrics across scales to explicitly test whether habitat heterogeneity, which would leave a signature in the derived β-diversity measures, played a role in driving the ISARs of these taxa. Perhaps surprisingly given the fact that larger islands in this archipelago do have more heterogeneity in habitat types and have a higher proportion of wet evergreen forests that support rarer species (Davidar et al. 2001, Yoganand and Davidar 2000), we found no influence of island size on β-diversity of these two taxa despite the fact that they are relatively poor dispersers (Quinn and Harrison 1988, Cook and Quinn 1995, Watling and Donnelly 2006). Thus, at least for these taxa, we can conclude that some mechanism is allowing rarer species to have a higher probability of persistence on larger islands, rather than a mechanism associated with habitat heterogeneity and/or dispersal limitation.

While our results point to a strong influence of island size on both the total number of species (S_{total}) as well as the numbers of species persisting when the numbers of individuals are controlled with rarefaction (S_n), we cannot exclude other variables influencing the species diversity relationships other than area. For example, in a study involving plants on small islands, Panitsa et al. (2006) found strong island species-area relationships but factors such as elevation and the presence of grazing species also explained some of the variance. Another important variable influencing island species-area relationships is isolation, that is, the distance of islands with regard to each other and the mainland (MacArthur and Wilson 1967, Kreft et al 2008). Most of the islands included in our analysis and the Andaman island group in general are quite close to the mainland, so isolation may not have been a likely contributing factor in this case.

In conclusion, we found positive ISARs for all four taxa, but no evidence for sampling effects. These findings suggest that larger islands are important sources of biodiversity, where more species are able to persist than expected from random sampling. Rare species seem to be important drivers of the ISAR, suggesting that rare species are more likely to persist on larger islands either due to disproportionate effects or the availability of more diverse habitats. Moreover, comparing species composition within islands (i.e., β-diversity) can give us additional insight on what drives diversity patterns by allowing us to test for disproportionate vs heterogeneity effects. Overall, our results highlight the importance of larger islands as sources of rare species. This is especially important in nature conservation and planning since smaller islands are usually given higher priority mainly when establishing nature reserves. The protection and presence of nature reserves on larger islands could therefore be a more effective way of protecting rare species from extinction.

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CHAPTER 5

Synthesis of the mechanisms underlying the island species-area relationship

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Synthesis of the mechanisms underlying the island species-area relationship

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ABSTRACT

The species-area relationship is one of the most general patterns in ecology, and is one of ecology's oldest laws. One form of the species-area relationship, the Island Species-Area relationship (ISAR), describes how the number of species increases with increasing size of an island (or island-like habitat). The ISAR and its underlying theories have played an important role in understanding biodiversity loss due to habitat fragmentation. However, there remains a great deal of confusion surrounding the ISAR and the mechanisms that shape it. Here, we synthesize the potential processes underlying the ISAR by applying a framework that uses individual-based rarefaction curves to infer whether ISARs result from species on small islands being random samples of those found on larger islands, or from biological processes (e.g., due to larger islands disproportionately favouring some species or habitat heterogeneity). To do so, we collated data from 35 studies on local-scale species abundances on oceanic, barrier, lake and forest islands across a wide range of taxa. We find that random sampling effects seem to be predominantly driving the ISARs across most of the studies (~80%) in our analysis, and that non-oceanic islands are slightly more likely to be influenced by random sampling effects. The ISARs of the remaining studies are influenced by non-random effects, including habitat heterogeneity or disproportionate effects, where there are disproportionately more species on larger rather than smaller islands.

INTRODUCTION

The relationship between species number and area - the species-area relationship - is one of the oldest laws in ecology (e.g., Arrhenius 1922, Schoener 1976, Lawton 1999, Lomolino 2000, Drakare et al. 2006). The island species-area relationship (ISAR) is one of several types of SAR (Scheiner 2003) and describes the increase in the number of species encountered as island size increases. However, unlike some other types of species-area relationships (e.g., nested), the slope of the ISAR is not always positive. In fact, in some cases there is no influence of island area on species diversity, or even negative relationships

(Kimmerer and Driscoll 2000, Nentwig et al. 2019, Tielens et al. 2019). The ISAR has been of central importance in the development of some of the most important concepts and theories in biodiversity studies, such as the theory of island biogeography (MacArthur and Wilson 1967, Warren et al. 2015), and has even transcended habitat fragmentation research (e.g., Fahrig 2003, Laurance 2008, Haddad et al. 2015). Island species-area relationships have been observed across vast ranges of taxa, differing in their dispersal abilities, body size and habitat requirements, ranging from microbes (Peay et al 2007) to mammals (Lomolino 1982). Moreover, positive ISARs have been observed in not only oceanic or 'true' islands (Kreft et al. 2007, Triantis et al. 2012, Matthews et al. 2016), but also in many island-like systems such as lakes (Browne 1981, Hobæk et al. 2002, Shurin et al. 2007), habitat islands (Matthews et al. 2014, 2016), mountain tops (Dawson et al. 2016), natural forest patches (Lövei et al. 2006, Azeria et al. 2009) and inselbergs (Porembski and Barthlott 2012).

Despite being one of the most general and well-known patterns in biogeography, the mechanisms that underlie the ISAR are still unclear (Chase et al 2019), and there is a lack of consensus on what exactly shapes species patterns on islands (Whittaker and Fernandez-Palacios 2007). One of the main reasons for this uncertainty lies in the way biodiversity is measured. For example, theories underlying species-area relationships on islands were specifically developed to describe the total number of species on islands (MacArthur and Wilson 1963, 1967). Yet, a large number of studies that appear to be measuring the ISAR are actually quantifying the number of species in a fixed area within an island or island-like system, and not the total number of species on that island, and are therefore not accurately representing the ISAR. These heterogeneous sampling designs can lead to misleading results as data are not consistent or comparable within and across studies. This distinction between sampling procedures is particularly important when comparing studies in the realm of conservation biology, where the influence of habitat loss and fragmentation on biodiversity remains a controversial topic (Haddad et al. 2015, 2017, Hanski 2015, Fahrig 2013, 2017).

The ISAR is primarily shaped by three mechanisms (Connor and McCoy 1979): 1) Random sampling (also known as the more individuals hypothesis), 2) Disproportionate effects (referred to as Area *per se* by Connor and McCoy 1979) and 3) Habitat heterogeneity. The random sampling hypothesis is the simplest mechanism underlying a positive ISAR, where larger islands passively sample more individuals from the regional pool and therefore more species than smaller islands. Here, one would expect an increase in species richness with island area with no change in the relative abundances of species with increasing island size (i.e., smaller islands are random samples of larger islands). Second, island size can disproportionately influence some species relative to others (as opposed to random sampling which is proportional). Prominent mechanisms leading to disproportionate effects include colonization-extinction dynamics such as those inherent to MacArthur and Wilson's (1963, 1967) theory of island biogeography. Additionally, population-level processes (e.g., Allee-effects or demographic stochasticity), which tend to be more prominent on smaller rather than larger islands, can also lead to disproportionate effects. Finally, an increase in the number of habitats, or an increase in habitat heterogeneity, with island area can also lead to more species on bigger islands (Kohn and Walsh 1994), particularly when species are habitat-specialists (Williams, 1964, Hart and Horwitz, 1991, Guadagnin and Malchik 2007). In fact, Tews et al. (2004) suggested that habitat heterogeneity could be the most important factor shaping species–area relationships.

Here, we provide a quantitative synthesis of the ISAR by using an individual-based rarefaction framework (Chase et al. 2019) that compares how rarefied richness and evenness vary with island size. These methods can allow us to explicitly test whether the ISAR is a result of random sampling or whether ecological mechanisms (i.e.,. disproportionate effects and/or heterogeneity) are driving species patterns on islands. In this paper, we synthesize the ISAR, by compiling species abundance datasets on a variety of '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). Our findings suggest that the ISAR is predominantly influenced by random sampling effects. That is, in most studies, larger islands simply sample more individuals and therefore more species than smaller islands. Moreover, we show that taxa on island-like systems (e.g forest islands, lake islands etc…) are more likely to be influenced by sampling effects than those found on oceanic islands.

METHODS

Data search

To search for abundance-level data, we used search engines such as Google Scholar, Web of Science (WoS) and entered the following keywords : species AND abundance OR survey AND islands OR archipelago. We selected studies that reported species abundances for multiple taxa within assemblages across islands in an archipelago, forest islands or lake islands. Data from some studies were already available either in the article itself or as supplementary material. We contacted the corresponding authors for raw abundance data if they were not available in the supplementary material. Data were also obtained through data requests. We additionally extended our search to data portals such as : DRYAD (https://datadryad.org/),KnB (https://knb.ecoinformatics.org/), Figshare (https://figshare.com/) using the following keywords : species, abundance, islands and archipelagos.

All data were screened to ensure that they met the following criteria :

1. The islands in the dataset were natural fragments surrounded by water, or natural forest patches. In our study, we have four island types: true islands (this includes islands in archipelagos and atolls), barrier islands, lake islands and forest islands.
2. There were more than two islands surveyed in the study.
3. The studies had recorded relative species abundances.
4. Sampling methods were consistent within a study.

In total, we compiled 35 datasets (Figure 1) documenting species abundances on oceanic islands (22/35), atolls (2/35), barrier islands (3/35), forest islands (4/35) and lake islands (4/35). Datasets selected included studies on invertebrates (17/35), birds (7/35), herpetofauna (7/35), plants (2/35) and mammals (2/35). The area of the islands were extracted from the respective papers if available. Otherwise, island area was acquired using either Google Earth (https://www.google.com/earth/), Wikipedia (https://www.wikipedia.org/), along with other resources (e.g., the literature, data owners). Other characteristics (e.g., elevation, geographic coordinates, sampling effort and methods) of all islands in our study were compiled into one dataset for analyses.

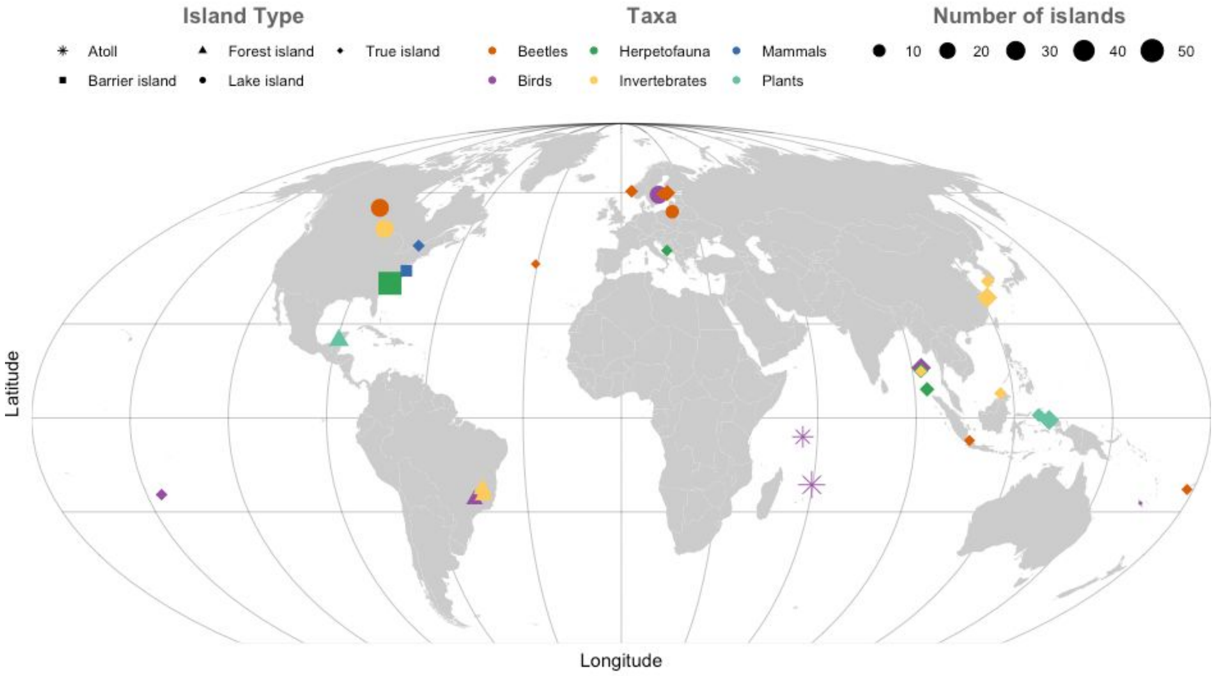

Figure 1 : A global map of the 35 studies included in the analysis. Point size indicates the number of islands in a dataset, colour indicates focal taxonomic group, and shape represents island type.

Estimation of biodiversity parameters from each study

Here, following a framework based on individual-based rarefaction methods (see Chase et al. 2019), we used the ‘mobr’ package (McGlinn et al. 2019) to calculate the following parameters:

S_n - the number of species expected for a specific number of individuals, *n*. Here, *n* (i.e., the reference sample) 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).
S_{PIE} - The effective number of species conversion of the probability of interspecific encounter (PIE).

Robust estimates of total species richness per island, that is, species lists derived from islands that were completely surveyed were not available and we were therefore unable to evaluate the relationship between total species richness (S_{total}) and island area. We used these parameters to test the following questions.

Question 1: Can we reject the null hypothesis that the ISAR results from random sampling?
To evaluate this question, we quantified the relationship of S_n to island area. If we assume that the total number of species increases with island area (as is typical; e.g., Triantis et al. 2012), no relationship between S_n and island size would indicate that we cannot reject the random sampling hypothesis. However, if S_n increases with island size (i.e., the slope estimate is greater than zero), we can reject the random sampling hypothesis and we conclude that some other mechanism (e.g., disproportionate effects or heterogeneity) is driving the ISAR. While we often expect these 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.

Question 2 : If there is a non-random sampling effect, what role do rare species play in this relationship?
To address this question, we used a metric based on the probability of interspecific encounter (PIE) (Hurlbert 1971), as a measure of evenness that is equivalent to the slope at the base of the rarefaction curve (Olszewski 2004). We convert the PIE into S_{PIE} , the effective number of species conversion (see Jost 2006) which is strongly influenced by the most common species in a community (and relatively insensitive to rare species). Thus, in cases where S_n increases with island size, we can examine the influence of rare species on this relationship. If island area has a positive influence on both S_n and S_{PIE}, we would expect both common and rare species to be driving the ISAR. On the other hand, if S_n increases with island area, but S_{PIE} does not change, the observed positive ISAR would largely be a result of there being disproportionately more rare species on larger islands.

Statistical analysis

To evaluate the relationship between the biodiversity variables and island area, we fit a single hierarchical linear model, where island area was fit as a continuous explanatory covariate, and the biodiversity metrics described above, designed to answer our questions (i.e., S_n and S_{PIE}), were used as a multivariate response. We log-transformed our response variables (S_n and S_{PIE}), and island area was also log-transformed and centered by subtracting the mean from each observed island area prior to model fitting. Island area was allowed to vary for each study, but was not fit as a non-varying parameter. We chose this model form for two reasons: we did not want the study-level estimates to be pulled back (regularized) towards some overall relationship between island area and diversity, and as we are most interested in the relationship between island area and diversity within each study. Models were fit with 2 chains, 2,000 iterations with 1000 used as a warmup. We used the default, weakly regularising priors for all the parameters. Visual inspection of the chains showed excellent convergence, and all Rhat values were less than 1.02 (Gelman et al. 2013). All analyses were conducted in a Bayesian framework in R (version 3.5.3) using the Hamilton Monte Carlo sampler Stan (Carpenter et al. 2017); models were coded using the “brms” package (Bürkner 2018).

To visualize the results, we plotted regression lines for each study using intercepts and slopes estimated by the model (Fig. 2A and 2B). To examine and separate the hypotheses (random sampling versus disproportionate or heterogeneity effects), we plotted the slopes (estimated by our bayesian model) of the relationship between the biodiversity variables (S_n and S_{PIE}) and island area, as well as their corresponding lower (2.5%) and upper (97.5%) credibility intervals (Fig. 3). If the lower credible value of S_n was not positive or was equal to zero, we can conclude that sampling effects were most likely driving the ISAR. In the cases where the lower credible interval of S_n were positive, then some other mechanism (disproportionate effects or heterogeneity) is driving the ISAR. For studies where we could reject random sampling as the driver of a positive ISAR, if the lower credible value of S_{PIE} was not positive or equal to zero, we can conclude that rare species were strongly influencing the ISAR. Whereas, positive lower credible values of S_{PIE} allow us to infer that the ISAR was influenced by both common and rare species.

Results

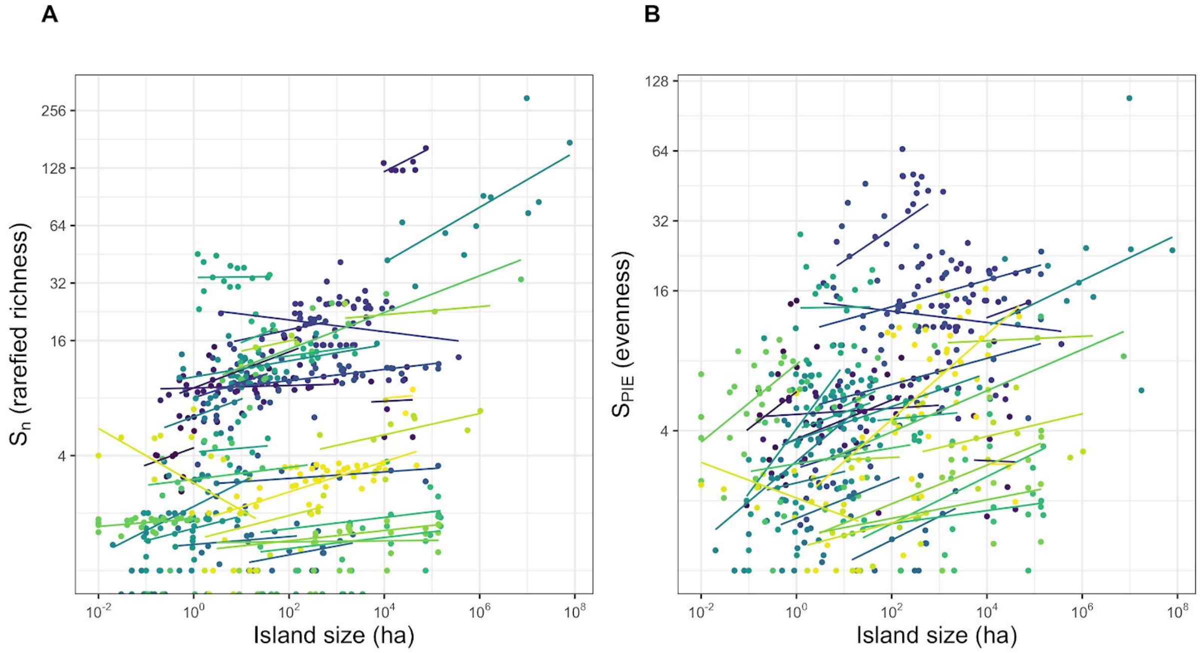

Figure 2. Panels A and B show model plots for the two variables studied across 35 ISAR studies.

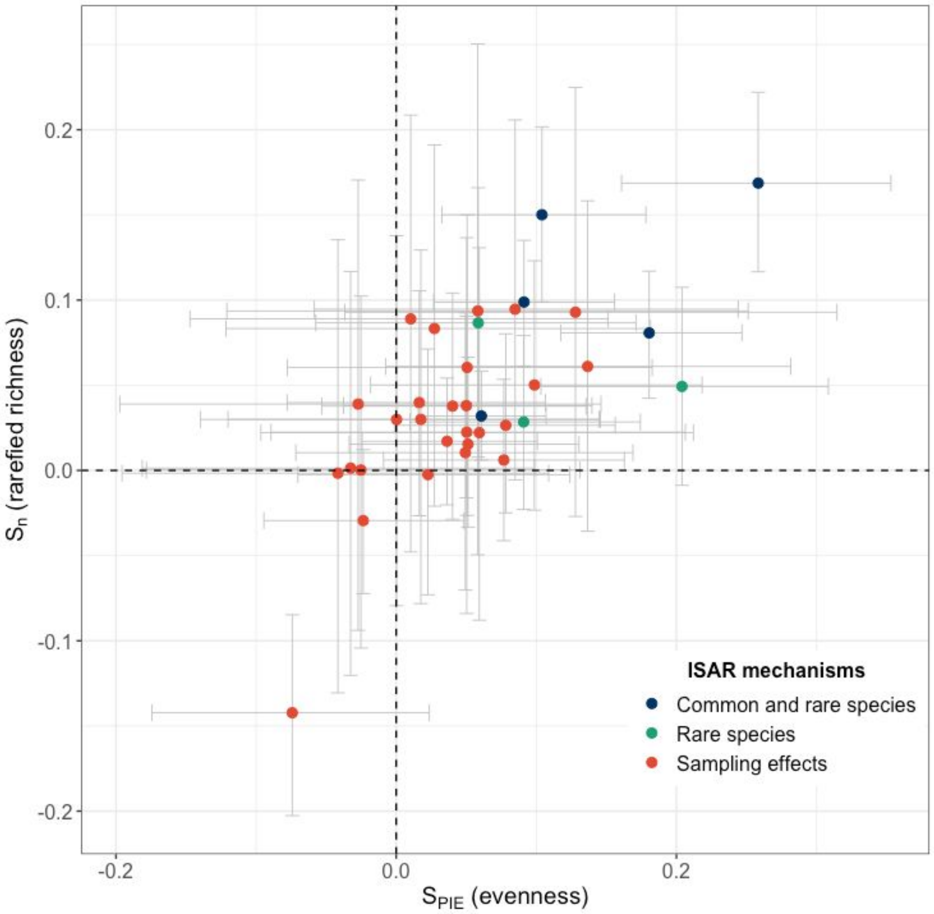

Figure 3. Comparisons of slope estimates of S_n and S_{PIE} (colored according to ISAR mechanisms) with their corresponding credible intervals.

Figures 2A and 2B show variable relationships between the biodiversity variables (S_n and S_{PIE}) and island size slopes among studies, even negative ones. For 27 of the 35 (77%) datasets, the slopes of the relationship between S_n and island area were non-significant (i.e., the lower credible interval is less than or equal to zero), indicating that we cannot reject the hypothesis of random sampling effects (Fig. 3). For those studies where S_n increases significantly with island size (i.e., the eight remaining studies), five show a significant positive relationship between S_{PIE} and island area (labelled as “common and rare species”), and the three remaining studies a non-significant relationship between S_{PIE} and island area (labelled as “rare species”) (Fig. 3).

What other factors could be influencing the observed patterns? (Taxonomic group and island type)

To evaluate whether additional factors could be underlying the patterns observed, we grouped posterior samples of the model by taxonomic group and island type (Fig. 4A and 4B). We divided the taxonomic groups into 6 categories and separated beetles from the other invertebrates in our analysis as we had numerous invertebrate datasets (7 out of 17) involving beetles. We separated islands into two categories: “True islands”, which are oceanic islands/archipelagos, the remaining islands were grouped into the “Other islands” type as they include forest islands, lake islands and barrier islands, which are close to the mainland or surrounded by a matrix. We also included atolls in this category since islands that make up an atoll are often highly connected.

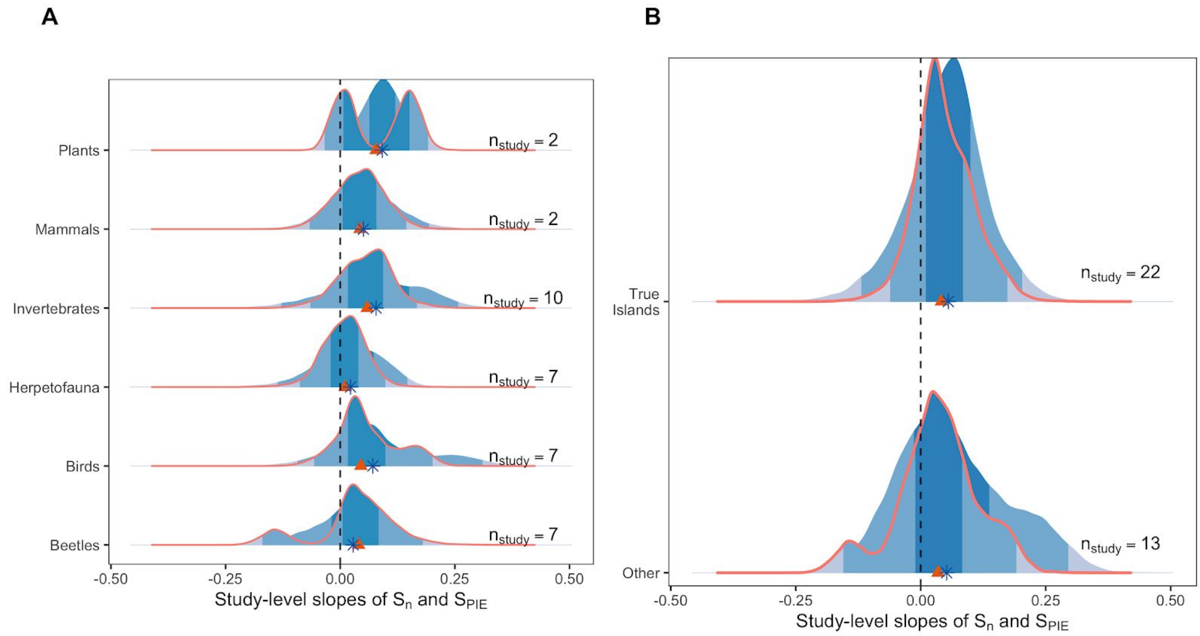

Figure 4. A-B : Posterior density plots (S_n and S_{PIE}) grouped by taxa and island type; Points represent the mean values of the posterior samples, where ▲ = S_n and ✱ = S_{PIE} and the different shadings represent the different quantiles ranging from the 2.5th percentile to the 97.5th percentile.

Based on the posterior density plots in Figure 4A, the slope estimates of S_n and S_{PIE} have a higher probability of being positive for most taxa except for beetles and herpetofauna, with beetles showing a tendency of having negative slope values. In contrast, the study-level slopes for island size and S_n tended to be positive for mammals, plants, invertebrates and birds. Moreover, the two studies involving plants showed contrasting results (a bimodal relationship) for the relationship between island size and S_n. When exploring the differences between ‘true’ and other types of islands, we observe a slightly higher probability of positive relationship between the variables (S_n and S_{PIE}) and island size for ‘true’ islands.

DISCUSSION

The ISAR is one of biogeography’s most well known patterns and yet there remains some ambiguity surrounding the mechanisms shaping this pattern. Several previous syntheses have addressed ISARs of many taxa across many contexts (conservation, habitat fragmentation) and have focused on total species richness at the whole island scale on ‘true islands’ (Triantis et al. 2012) and habitat islands (Matthews et al. 2016). In our synthesis, we focus on locally measured metrics of biodiversity (rarefied richness and a measure of evenness) to examine the likely mechanisms influencing the ISAR. Our main results show that random sampling effects are predominant in ISARs.

Random sampling effects were the main mechanism underlying the ISARs in our analysis, meaning that more species occur on larger islands most because larger islands passively sample more individuals and therefore record more of the regional pool (i.e., more species) than smaller islands. Indeed, random sampling has been previously implicated in a number of empirical studies of ISAR patterns (e.g., Haila 1983, Hill et al. 1994, Ouin et al. 2006, Bidwell et al. 2014, Gooriah and Chase 2019). Further, in a review examining the effects of habitat fragmentation on plants, Gilaldi et al. 2014 showed that 60% of the studies were most likely influenced by sampling effects. While nearly 80% of the studies included in our analysis showed random sampling effects, we were able to explore several other aspects such as island type and taxa. We found that species on true islands were slightly less likely to be influenced by random sampling effects. This result may be unsurprising as island-like systems, such as forest islands, are often less isolated than 'true' islands (Itescu 2019), thus allowing species to use the matrix around to disperse between islands/natural patches. This matrix permeability can contribute to the 'rescue effect' (Brown and Kodric-Brown 1977) by reducing the likelihood of species going extinct on smaller islands as well as the likelihood of having disproportionately fewer species than larger islands, thus leading to random sampling effects. Moreover, lake islands, though surrounded by water, are typically closer to the mainland as compared to oceanic islands and could also experience a rescue effect through colonization of species from the mainland, thus explaining the higher probability of random sampling effects occurring on these types of islands.

Perhaps surprisingly, we find that herpetofauna were more likely to be influenced by random sampling effects compared to other taxa. This is because herpetofauna tend to have lower dispersal rates with specific habitat requirements, whereas we might expect random sampling effect among species with greater dispersal ability and can readily use the matrix. Amphibians, for instance, tend to have narrow habitat distributions, particularly with respect to breeding sites and might be expected to be primarily influenced by habitat heterogeneity (Ricklefs & Lovette 1999). One explanation could be that close proximity between islands in herpetofauna studies could have led to higher dispersal rates and therefore more even communities. Beetles usually have higher dispersal rates, and were also more likely to be influenced by random sampling effects. Differences in dispersal traits have been shown to highly influence beetle diversity patterns (Zalewski and Ulrich 2006). For instance, Bell et al. 2017 showed that beetles on lake islands differing in body size and dispersal ability exhibited contrasting relationships between diversity and island area and isolation. Larger beetles with lower dispersal abilities (i.e., flightless) were more sensitive to changes in island area and less sensitive to isolation, while smaller beetles with higher dispersal abilities tended to decrease with island area and increase with isolation. The high dispersal abilities of macropterous beetles and other invertebrates in our analysis most probably contributed to the observation that random sampling effects are more likely to drive the ISARs of beetles and other invertebrates.

One study showed negative slopes of the relationship between the variables and island area, suggesting that rarefied richness and/or evenness was decreasing with island size.

Here, it is possible that some disproportionate effects favor species in 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 (Baldi 2008, Hatteland et al. 2008, Nentwig et al. 2019). In such cases, we might expect a weaker or even negative ISAR depending on whether random sampling effects (which are always operating) outweigh the disproportionate or heterogeneity effects. Further, it is possible that other factors that may be driving species patterns on islands. Typically, isolation is an important factor influencing diversity on islands (MacArthur and Wilson 1967, Kreft et al. 2008). Moreover, island age can also influence species diversity patterns where larger, younger islands tend to have had less time for diversification as compared to smaller, older islands. Nevertheless, given that we found that ~80% of studies in our analysis show random sampling effects across a variety of studies across different taxa and island systems, we conclude that random sampling effects are a primary driver of the ISAR.

Using local-scale data and individual-based rarefaction methods provides an important advance over previous approaches by allowing a more explicit examination of relative influence of random sampling effects versus biological processes underlying the ISAR. Though our synthesis shows that random sampling effects are a primary driver of ISAR patterns, it evidences the need for a more complete picture of the ISAR. Previous syntheses of the ISAR have been hampered by the lack of consensus on how to measure and interpret the ISAR. Therefore, we advocate a more careful consideration of sampling when measuring and interpreting ISARs as well as the advantages of using and presenting abundance data at multiple scales as they are rarely collected or published. A deeper understanding of what exactly drives species patterns on islands could therefore allow us to effectively protect and manage biodiversity on islands which are important hotspots of biodiversity.

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CHAPTER 6

SYNTHESIS

This dissertation presents several approaches for disentangling the main hypothesized mechanisms underlying the Island Species-Area Relationship (ISAR) using individual-based rarefaction methods at multiple scales. The application of this framework introduced in Chapter 2 is demonstrated in various case studies across a variety of ‘true’ islands and island-like systems (e.g., lakes, glades, lake islands, forest patches, atolls and oceanic islands) throughout the different chapters of this dissertation, with the main goal being to provide an overall data-based synthesis of the ISAR (Chapter 5). Our main findings indicate that random sampling effects are predominantly driving the ISARs of ‘true’ islands as well as island-like systems (e.g., lakes, forest patches, etc.), suggesting that there is no difference between large and small islands other than larger islands passively sample more individuals of the regional species pool and therefore more species than smaller islands.

6.1 Addressing the multidimensional nature of biodiversity and its scale-dependency

The island species-area relationship (ISAR) is one of the most well-known patterns in biogeography. Yet, despite its universality and its importance in the context of habitat loss and fragmentation, there remains some ambiguity around the shape of the ISAR and the mechanisms underlying it (Scheiner et al. 2011). This uncertainty can be mostly attributed to a lack of consensus on how to measure biodiversity. For instance, most studies continue to rely on comparisons of only one biodiversity variable, typically species richness, thus ignoring other major components such as changes in abundance, composition, and community structure that can provide a deeper understanding of the multidimensional nature of species diversity patterns. Therefore, the framework presented in Chapter 2 uses a combination of the total numbers of species in a given area as well as the total and relative abundances of those species in that area, and addresses the scale-dependency of biodiversity by comparing diversity patterns at different spatial scales. Our approach, using rarefied metrics of biodiversity derived at different scales (i.e., from γ- and α-rarefaction curves), provides an important advance over previous approaches by allowing for the specific examination of the influence of sampling and scale on the ISAR (Chase et al. 2019). Further, the use of a variable that accounts for changes in evenness of communities, S_{PIE}, the effective number of species of the probability of interspecific encounter (PIE), allows one to examine whether the non-random processes driving the ISAR are a result of rare species being disproportionately favoured on larger islands, or whether species from the whole of the species abundance distribution are altered. Overall, the rarefied and evenness metrics can allow us to effectively disentangle the main mechanisms underlying the ISAR. Although the framework is used to separate the main hypotheses, it is important to note that they are not mutually exclusive, as two or more mechanisms could be operating simultaneously to produce a positive ISAR.

6.2 Summary of findings

First, using case studies with available plot-level and whole-island scale data, we demonstrate how the framework presented in Chapter 2 can be used to separate the different hypotheses by deriving individual-based rarefaction metrics and an evenness metric at different spatial scales. We find that plants in fragmented habitats are influenced by random sampling effects, while grasshoppers and lizards in other island systems tend to be influenced by non-random mechanisms. We additionally find that rare lizard species are disproportionately favoured on larger islands in the Andamans.

Second, considering lakes as islands, we provide another test of this framework in Chapter 3 by applying it to datasets amassed on zooplankton densities in North American and European lakes. Our results indicate that random sampling effects are most likely driving the species-area relationship of zooplankton in both North American and European lakes. Further, we were able to reject habitat heterogeneity hypothesis when analyzing a subset of lakes where multiple samples across the lakes were pooled.

Third, we apply the framework to a specific group of islands, the Andaman islands, in Chapter 4. Here, we reject the random sampling hypothesis and find that larger islands have disproportionately more rare species than smaller islands. These results highlight the importance of larger islands as sources of rare species.

And finally, we synthesize patterns across ISAR datasets on species abundances from 35 island, and island-like, archipelagos. Our main results indicate that random sampling effects are predominantly driving the ISAR (~80% of the datasets analysed). Further, species on islands such as atolls, lake islands and forest islands were slightly more likely to be influenced by sampling effects as compared to species on ‘true’ islands.

With the framework presented here, we provide methods to disentangle the main mechanisms underlying the island species-area relationship and emphasize the importance of taking into account the influence of both sampling and spatial scale on species diversity patterns. Overall, our results tend to show that most ISARs tend to be more influenced by sampling effects (Chapters 3 and 5), albeit with some important exceptions (Chapters 2 and 4).

6.3 Conservation implications

Throughout the history of biogeography, the island species-area relationship has served as a basis for many important theories that played important roles in designing effective strategies for conserving biological diversity (Diamond 1975), as well as predicting the number of species likely to go extinct as a result of habitat loss. The ISAR inspired the Single Large Or Several Small (SLOSS) debate that was never formally resolved as it was impossible to determine a general strategy across different species. Indeed, species ecological traits, habitat dependency and resilience to disturbance define how susceptible a species is to fragmentation and cannot be limited to one conservation strategy. Habitat loss is one of the biggest threats to biodiversity (Pimm et al. 1995, Wilcove et al. 1998, Dirzo and Raven 2003, Pereira et al. 2012), it is therefore important to effectively quantify and predict how species patterns will vary as a result of decreasing habitat size. The framework presented in this dissertation allows the non-confounding comparisons of studies across different island systems and taxa. Insights gained from Chapter 4, for example, showed the importance of preserving larger islands in the Andaman archipelago, when it is common practice to turn smaller islands into natural reserves (Davidar et al. 1995).

6.4 Limitations

Although the methods used throughout this dissertation allow us to separate the main hypothesized mechanisms, it is limited with respect to other factors that may be influencing species diversity on islands. Isolation, for instance, is an important variable in island biogeography (MacArthur and Wilson 1967, Kreft et al. 2008) and could have a significant influence on species diversity patterns on islands. In addition, island age can also be an important factor when examining volcanic archipelagos, as larger islands tend to be younger and therefore have had less time for diversification than smaller, older islands (Whittaker et al. 2008, Gillespie and Baldwin 2010). Moreover, islands differ across a number of environmental and biological attributes (elevation, climate, etc.), all of which can interact with island area. However, the metrics used throughout this dissertation can also be analyzed in more complex models that include other possible variables than we have presented in the chapters of this dissertation. Another limitation is that our approach relies on estimates of relative abundances of species, therefore assuming that sampling strategies can effectively detect individuals of each species. However, it can be quite challenging to enumerate individuals of certain species, especially when individuals can be clonal.

6.5 Recommendations for future research

As we stressed previously, it is important to report how species richness is sampled to effectively compare studies that quantify the ISAR in various ways. Similarly, many others have called 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). Accounting for differences in sampling strategies across studies is especially important in the realm of conservation biology, where the influence of habitat loss and fragmentation on biodiversity is often controversial (e.g., Haddad et al. 2015, 2017, Hanski 2015, Fahrig 2013, 2017). We recommend collecting and reporting abundance data from standardized plots at multiple scales. Although it requires more effort (i.e., sampling spatially explicit data of total and relative abundances of species), we emphasize that the additional data could provide a much deeper understanding of the potential processes underlying the ISAR. It is also important to note that our approach is only observational and that in order to effectively test the framework one would have to apply it to groups of islands that vary naturally in size and heterogeneity levels (Nilsson et al. 1988, Ricklefs and Lovette 1999, etc.). Moreover, manipulative experiments where one can directly alter island size and/or heterogeneity could also be used to more specifically tease apart the different hypotheses.

6.6 Final remarks

The ISAR framework presented here emerges as a novel framework that accounts for the multidimensionality and scale-dependency of biodiversity. It can be used to gain a deeper understanding of what exactly shapes the ISARs on islands and island-like habitats. This dissertation specifically addresses the importance of accounting for differences in sampling strategies when measuring and interpreting the ISAR. Finally, insights gained from this work can be used in different contexts, including habitat loss and fragmentation (understanding how species patterns change when fragments become smaller) and conservation biology (predicting which species will be more susceptible to extinction). Overall, our results indicate the importance of sampling scale and the use of multiple biodiversity measures when examining species patterns, as well as a need for future research by means of experimental studies to further test the hypotheses. In addition, the various chapters of this dissertation contribute towards building a consensus on how to measure and interpret island species-area relationships. Finally, the findings from the synthesis in Chapter 5 brings us one step closer to understanding what drives species patterns on islands or island-like habitats.

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APPENDIX

A. Supplementary material for chapter 3

Table S1 Regression models for lakes with environmental variables (128 European lakes and 109 North American lakes).

Continent	**Model**	**Estimate**	**SE**	**t**	***p*-value**
North America	log S_n ~ log Area +log N + log P + …				
	Intercept	2.16	0.965	2.24	0.02
	log(Area)	-0.008	0.024	-0.340	0.73
	log(N)	0.063	0.077	0.82	0.41
	log(P)	0.001	0.059	0.030	0.97
	log((max_depth)	0.06	0.078	0.792	0.43
	log(Temperature)	-0.27	0.179	-1.507	0.13
	log(Chl a)	-0.019	0.047	-0.409	0.68
	log(pH)	-0.034	0.328	-0.105	0.92
North America	log S_{PIE} ~ log Area +log N + log P + …				
	Intercept	1.80	0.89	2.01	0.046
	log(Area)	-0.02	0.023	-0.92	0.36
	log(N)	-0.08	0.071	-1.08	0.28
	log(P)	-0.008	0.054	-0.15	0.88
	log(max_depth)	0.064	0.072	0.90	0.37
	log(Temperature)	0.095	0.165	0.58	0.56
	log(Chl a)	0.061	0.044	1.39	0.17
	log(pH)	-0.21	0.302	-0.70	0.49
Europe	log S_n~ log Area +log N + log P + ...				
	Intercept	-1.24	2.14	-0.58	0.57
	log Area	0.10	0.24	0.45	0.66
	log(P)	0.15	0.24	0.62	0.54
	log(N)	0.31	0.22	1.41	0.17
	log(max_depth)	0.26	0.29	0.88	0.39
	log(lake_volume)	-0.15	0.23	-0.62	0.54
	log(Chla)	-0.18	0.18	-1.02	0.32
Europe	log S_{PIE} ~ log Area +log N + log P + ...				
	Intercept	-4.96	3.14	-1.58	0.13
	log Area	0.42	0.35	1.19	0.25
	log(P)	-0.01	0.35	-0.03	0.97
	log(N)	0.39	0.32	1.21	0.24
	log(max_depth)	0.72	0.43	1.68	0.11
	log(lake_volume)	-0.38	0.35	-1.09	0.29
	log(Chla)	0.04	0.26	0.17	0.87

B. Curriculum vitae (CV)

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Curriculum vitae

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2014–2016	**Master's degree**, *Terrestrial Ecosystem Functioning.* University of Bordeaux
2011–2014	**Bachelor's degree**, *Animal and Environmental Biology.* University of Bordeaux
2009–2011	**Two first years of medical studies**, *PACES.* University Bordeaux Segalen Bordeaux, France
2008	**Higher School Certificate**, *(Cambridge A-levels).* Dr Maurice Curé State Secondary School Mauritius

Internships

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Country, City	Germany, Freiburg
Title	*IDENT project: Does tree diversity increase crown packing and wood biomass production?*
Supervisor	Dr Charles A.Nock
Tasks	Measuring height, diameter and crown dimensions of trees in the IDENT project(Group of Prof. Dr. Michael Scherer-Lorenzen). Using R statistics to analyse the data from this year and last year so as to observe changes in biomass production and canopy structure.
	May to July 2015
Country, City	Amsterdam, The Netherlands
Title	*How do life history traits differ across an elevation gradient between four sub-populations of Orchestia gammarellus (Crustacea, Talitridae)?*
Supervisor	Prof.dr. Matty P. Berg
Tasks	Dissecting female specimens under a microscope. Using digital, analyzing techniques to measure traits such as body length, age and reproductive output. Using R statistics to compare the four sub-populations.
	June to July 2014

Country	Mauritius
Title	Conservation of endemic species of Mauritius : The Pink Pigeon project.
Supervisor	Dr.sc.nat.Nicolas Zuël
Tasks	Hopper and nest watch. Feeding the birds and bats and disinfecting the cages. Bird banding. Putting bait in live traps (predator control).

Work experience

September 2013–April 2015	**Private Tutor**, *Mainly English lessons* , Help with other homework: Maths, Science and Geography High-School level, Bordeaux, France. Employer: Michel Mazaud,+33677980765
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July 2011	**Waitress at a wine event**, *Salon Vinexpo*, Private wine tasting saloon, Bordeaux. Employer: HRC agency

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English	**Fluent**	*Native language*
French	**Fluent**	*Second language*

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C. List of publications and conference participations

Publications of the dissertation

Chase, J. M., **L. Gooriah**, F. May, W. A. Ryberg, M. S. Schuler, D. Craven, and T. M. Knight. 2019. A framework for disentangling ecological mechanisms underlying the island species–area relationship. Frontiers of Biogeography 11.

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Gooriah, L., S. Blowes, J. Schrader, D. N. Karger, H. Kreft, J. M. Chase (*in preparation*). Synthesis of the mechanisms underlying the island species-area relationship.

Conference talks

Chase, J. M., **L. Gooriah**, F. May, W. A. Ryberg, M. S. Schuler, D. Craven, and T. M. Knight. 2018. A framework for disentangling ecological mechanisms underlying the island species–area relationship. 4th iDiv Conference, Leipzig, Germany. (talk)

Gooriah, L., Davidar, P., Chase, J.M. (2019) Understanding the mechanisms that drive bird, butterfly, frog and lizard species-area relationships in the Andaman archipelago. 9th Biennial International Biogeography Society (IBS) conference, Malaga, Spain. (talk)

D. Authors' contributions

Chapter 2

Chase, J. M., **L. Gooriah**, F. May, W. A. Ryberg, M. S. Schuler, D. Craven, and T. M. Knight. 2019. A framework for disentangling ecological mechanisms underlying the island species–area relationship. Frontiers of Biogeography 11.

Design/Analysis: L. Gooriah (30%), J.M.Chase (20%), D. Craven (15%), F. May (15%), T. M. Knight (10%), W. A. Ryberg (5%), M. S. Schuler (5%).

Writing: J.M.Chase (70%), F. May (5%), D. Craven (5%), L. Gooriah (5%), W. A. Ryberg (5%), M. S. Schuler (5%), T. M. Knight (corrections).

Chapter 3

Gooriah, L., J. M. Chase 2019. Sampling effects drive the species-area relationship in lake zooplankton. Oikos. https://doi.org/10.1111/oik.06057

Analysis: L. Gooriah (75%), J. M. Chase (25%)

Writing: L. Gooriah (60%), J. M. Chase (40%)

Chapter 4

Gooriah, L., P. Davidar, J. M. Chase (under review - *submitted to Ecology and Evolution in September 2019*). Island species-area relationships in the Andaman and Nicobar archipelago emerge because rarer species are disproportionately favored on larger islands.

Analysis: L. Gooriah (60%), P. Davidar (15%), J. M. Chase (25%)

Writing: L. Gooriah (65%), J. M. Chase (35%), P. Davidar (corrections)

Chapter 5

Gooriah, L., S. Blowes, J. Schrader, D. N. Karger, H. Kreft, J. M. Chase (*in preparation*). Synthesis of the mechanisms underlying the island species-area relationship.

Analysis: L. Gooriah (45%), S. Blowes (35%), J. M. Chase (20%), J. Schrader, D. N. Karger and H. Kreft (provided data).

Writing: L. Gooriah (70%), S. Blowes (15%), J. M. Chase (15%)

Halle (Saale), den 15.11. 2019

Leana Gooriah

E. Eigenständigkeitserklärung

Hiermit erkläre ich, dass die Arbeit mit dem Titel "Disentangling the mechanisms underlying the island species-area relationship (ISAR)" bisher weder bei der Naturwissenschaftlichen Fakultät III Agrar und Ernährungswissenschaften, Geowissenschaften und Informatik der Martin-Luther-Universität Halle-Wittenberg noch einer anderen wissenschaftlichen Einrichtung zum Zweck der Promotion vorgelegt Wurde.

Ferner erkläre ich, dass ich die vorliegende Arbeit selbstständig und ohne fremde Hilfe verfasst sowie keine anderen als die angegebenen Quellen und Hilfsmittel benutzt habe. Die den Werken wörtlich oder inhaltlich entnommenen Stellen wurden als solche von mir kenntlich gemacht. Ich erkläre weiterhin, dass ich mich bisher noch nie um einen Doktorgrad beworben habe.

Halle (Saale), den 15.11. 2019

Leana Gooriah