TAXONOMIC PARTITIONING OF CORAL REEFS IN MICRONESIA

BY

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ABSTRACT

A central goal of evolutionary and community ecology is to identify the general mechanisms maintaining the diversity of communities. Uncovering the taxonomic and ecological characteristics of species assemblages provides useful information for conservation and in testing theories about the processes that regulate community structure. Traditionally, the ratio of the number of a higher-taxon to the number of a lower-taxon (e.g., genus to species (G/S) or family to species ratio (F/S)) have provided a means to quantify the taxonomic structure of communities; with the majority of studies conducted on woody plant communities. However, due to their well-known sample size dependence, this metric has been commonly used and abused in ecology literature. Here, we shed light on the taxonomic structure of coral communities in Micronesia using taxonomic partitioning (i.e., taxon to subtaxon curve) – a scale-free metric of taxonomic structure within or across communities. We find the number of genera/families in coral communities to be a general power-function of species richness (consistent with woody plant communities), where the number of genera and families is significantly different (in most cases) from randomized assemblages. Traditionally, randomized assemblages (null communities) have generally been constructed by sampling species with equal probabilities (i.e., with replacement) from a pool of regionally available species with replacement. However, in testing more realistic Null Models we highlight pitfalls of constructing Null Models by sampling species with replacement. In general, we find there to be fewer genera in a community than would be expected by chance, suggesting that the dominant set of ecological mechanisms (e.g., environmental filtering and dispersal limitation) responsible in maintaining the diversity of coral assemblages in Micronesia

select for closely related communities. Within Micronesia, we find the taxonomic structure of the sub-region of the Marianas Islands to be the most evolutionary diverse region in Micronesia. Owing to this feature and a relatively high latitude, the Marianas Islands could act as a source pool for warmer lower latitude regions of Micronesia as coral bleaching increases at an unprecedented rate. Hence, given limited resources the Marianas Islands may be of importance in preserving the evolutionary diversity of coral reefs, despite species loss in years to come.

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CHAPTER 1

INTRODUCTION

A central focus in community ecology is the identification of specific ecological processes responsible in shaping biodiversity patterns (Cornell & Lawton, 1992; Gotelli, 2002), with most of the work conducted on woody plants and more recently on marine bivalves (Enquist et al., 2002; Krug et al., 2008). Studies on woody plants as well as algae (Enquist et al., 2002; Passy & Legendre, 2006), show that higher-taxon richness (e.g., number of genera/families) is a power function of species richness, invariant across temporal and spatial scales. Such functions that describe the partitioning of taxonomic subunits into higher taxonomic groups are useful to ecologists and conservationist requiring robust and quick estimates of local taxonomic richness (Heino & Soininen, 2007). Here, we examine if coral reefs follow similar relationships between the number of genera/families and the number of species in communities across Micronesia.

Coral reefs are among some of the most threatened ecosystems in the world, with one-third of all reef corals facing heightened extinction risk from climate change and anthropogenic impacts (Carpenter et al., 2008). In particular, recent bleaching events and disease-driven effects linked to increases in sea temperatures have impacted the diversity of coral communities (Bruno et al., 2007). Without appropriate management, future extinction events can drastically alter the topology of Scleractinian corals' (hard reef-building corals) phylogenetic diversity as extinction threats appear to be non-randomly distributed amongst the coral tree of life (Huang & Roy, 2015). Despite this knowledge, species richness is still frequently used as a metric in quantifying biodiversity and setting conservation priorities (Gaston, 2000; Hughes, 2012).

The problem with using species richness alone as a primary method in quantifying diversity and setting conservation efforts is that diversity is organized hierarchically (i.e., species into genera, and genera into families). So, while the local dog-park ‘community’ may have a wide variety of different breeds of dogs, they all belong to the same species (Canis familiaris); and thus, while there may be high diversity at the breed level per se, there is low diversity at the species level. Thus, a community with a high diversity at one taxonomic scale may be less diverse at higher-taxon scales. If biologists and conservationists want to use species richness to quantify diversity and allocate limited resources, diversity patterns at different taxonomic scales must also be considered (Huang & Roy, 2015).

Taxonomic Ratios

Taxonomic ratios or taxon-subtaxon ratios (e.g., genus to species (G/S) and family to species (F/S)) account for diversity patterns amongst taxonomic levels, providing a quick, and more comprehensive metric than species richness alone in quantifying biodiversity (Gotelli, 2002; Krug et al., 2008). Also, taxonomic ratios provide a method to quantify evolutionary relatedness of cohabitating species – a proxy for species similarity (Jarvinen, 1982; Webb, 2000), and thus reflect the taxonomic structure of a community (Lessard et al., 2012). Consequently, taxonomic ratios have been widely used to investigate ecological and evolutionary drivers across numerous taxa despite their well-known sample size dependence (Gotelli & Colwell, 2001).

The sample size dependence in taxonomic ratios was first observed empirically in plant communities by Maillefer (1929); and then proven analytically by Pólya (1930), who derived the mathematical expectation of the G/S ratio (but see Jarvinen, 1982).

Despite this knowledge, some early ecologist ignored the sample-size dependence of taxonomic ratios (e.g., Ashton, 1998). The problem with any taxon to subtaxon ratio is that it is an increasing function of sample size or area sampled (Gotelli & Colwell, 2001). For example, the number of species in a community increases as a power function of area (size) of a community. This increase in the number of species as a power function of the area is considered as one of the few laws in ecology (Lomolino & Rosenzweig, 1996; Lomolino, 2000). The same pattern is generally true for higher taxonomic ranks (e.g., genera and families), albeit with a slower accumulation in the number of a higher-taxon as a function of area (Enquist et al., 2002; Marignani et al., 2004). Consequently, there are fewer species per genus/family in a community of few species (small sample ~ small area) than there are in a community of many species (large sample ~ large area) - an inevitable pattern for any two taxonomic ranks (except in the unlikely case of only monobasic taxa) since higher ranks intuitively have fewer members than lower ranks (Gotelli & Colwell, 2001).

Taxonomic Partitioning

The power law model proposed by Arrhenius (1923, but see Marquet et al., 2005) has traditionally been used in biology to describe allometric relationships like body size and relative growth (Gotelli, 2002). These relationships take on the form:

$$y = \beta * x^{\alpha}$$

where y is some dependent variable, x represents an independent variable, $\beta$is a normalization constant (intercept parameter) and α the scaling coefficient. For example, in mammals, the relationship between body size (x) and organ size (y) can be explained using a power function. The exponent α (scaling coefficient) describes the differential growth ratio between organ size and body size. Under the condition where $\alpha > 1$ (positive allometry), organ size (y) has a more significant growth rate than body size (x). On the other hand, when $\alpha < 1$ (negative allometry), organ size (y) has a smaller growth rate than body size (x). Therefore, power laws provide a method to describe some quantity expressed as some power of another (Marquet et al., 2005).

In ecology, Enquist et al. (2002) found the relationship between the number of a higher-taxon and number of species in woody plant communities worldwide is not a constraint envelope as would be expected if specific taxa sometimes dominated locally species-rich communities. Alternatively, they found that higher-taxon (genera and families) membership is a simple power law relationship of number of species:

$$G \propto S^{\alpha}$$

$$F \propto S^{\alpha}$$

This relationship has been coined *taxonomic partitioning* by Enquist et al. (2002), but reffered to as the taxon-subtaxon curve by others (e.g., Marignani et al., 2004). Here, the scaling exponent α is limited to a range of values: $(1 \leq \alpha > 0)$, as a higher taxonomic rank intuitively has fewer members than any lower taxonomic rank (Gotelli & Colwell, 2001; Gotelli, 2002). While the power law model is merely a good fit rather than an exact mathematical model, it sufficiently approximates the expected taxon-subtaxon curve (Enquist et al., 2002; Marignani et al., 2004) and thus provides a measure of the taxonomic structure within or across communities (Enquist et al., 2002; Marignani et al., 2004, Wang et al., 2012).

A unique property of the taxon-subtaxon curve (typically modeled by a power law) is that it standardizes the information in taxonomic ratios allowing for meaningful comparisons of data sets across sample sizes. As shown by Marignani et al. (2004), the scaling exponents of taxon-subtaxon relationships do not depend on how the underlying taxon richness-area relationship. This is because a power law is able to account for the nonlinear differences between a higher-taxon and species accumulation as a function of area. Many studies have failed to note this property, including Enquist et al. (2002), and a more recent study by Fan et al. (2017). For example, Fan et al. (2017), utilized a highly standardized data set on woody plant communities in China where they found mean taxonomic ratios (G/S and F/S) to decrease across broad sample grain sizes owing to the scale dependence of taxonomic ratios. However, upon investigating the relationship between higher-taxon richness and number of species they found little-to-no variation in the scaling exponents of taxon-subtaxon relationships as sample grain fluctuated in size. These studies suggest that the exponents of the taxon to subtaxon relationships may not be scale dependent, and thus it is feasible to combine different grain sizes in generating taxon-subtaxon relationships (Marignani et al., 2004; Fan et al. 2017).

Taxonomic Structure and Ecological Processes

On a global scale, it appears that the taxonomic structure of clades and biotas do not vary randomly (Enquist et al., 2002; Krug et al., 2008, Harnik et al., 2010). However, at more local scales, the taxonomic structure of communities can vary dependent on strength of assembly forces (Wang et al., 2012). In nature, communities are thought to be assembled by an ensemble of various processes including regional history, ecological interactions, and historical contingency operating at a wide range of spatiotemporal scales (Enquist et al., 2002; Wang et al., 2012; HilleRisLambers, 2012). Community assembly is generally explained by a hierarchical filtering model, whereby potential community members in a regional species pool pass through a series of filters. At large regional scales, species are thought to be assembled into pools of regionally available species primarily through speciation, extinction, and migration (Zobel, 1997; Gotzenberger et al., 2012). At more local scales, given a regional species pool, various ecological mechanisms (e.g., dispersal, environmental filtering, and interspecific competition) further shape the diversity of communities. For example, species get filtered at a regional level through a climatic filter based on their tolerances for marginal conditions, then segregate into local communities according to the relative strength of habitat filtering and species interactions (Hillebrand & Blenckner, 2002; Kraft et al., 2015; Trivellone et al., 2017). Because much of the variation in diversity found at local scales is a result of regional diversity (Gotelli, 2002), factors regulating species pools (e.g., evolutionary history) could imprint onto the taxonomic structure of local communities (Poulin and Mouillot, 2004). Local communities are thus assumed to reflect the cumulative effects of these processes (HilleRisLambers, 2012).

At local scales, the identification of which ecological processes are most influential in constructing and regulating diversity patterns in communities can be assessed using Null Models (e.g., Simberloff, 1970; Enquist et al., 2002; Wang et al, 2012). Here, the null expectation is that empirical communities do not differ in their taxonomic structure from randomized assemblages. Although it is the subject of much debate (Cadotte & Tucker, 2017), ecology literature has largely relied on the paradigm of environmental filtering and competitive interactions, and more recently abiotic and biotic interactions, to explain why some communities are more closely or distantly related from randomized assemblages (Gotelli & Graves, 1996; Swenson et al., 2011, 2012; HilleRisLambers, 2012; Wang et al., 2012). With abiotic factors such as environmental filtering expected to select for more closely related assemblages, and biotic interactions such as competition expected to select for more distantly related ones.

In assuming the theory of niche conservatism, species belonging to a particular genus or family should have similar ecological traits and live in similar habitats (Dornelas et al., 2006; Jabot & Chave, 2011). Consequently, environmental filtering (abiotic filter) is expected to prevent species with incompatible traits from entering and persisting a community, and thus should decrease the diversity of local communities (Swenson, 2011; Jabot & Chave, 2011; Sommer B et al., 2017). In terms of taxonomic structure, environmental filtering is thus expected to decrease the number of genera/families (lower the scaling exponent in figure 1.) in a community by selecting for compatible traits, usually shared amongst closely related species (Wang et al., 2012; Fan et al., 2017). On the other hand, interspecific competition (biotic filter), could be especially strong between closely related species, due to similar niche preferences. This demand for similar resources could lead to competitive exclusion, and thus, limit the coexistence of similar species within a community (Darwin, 1859). Consequently, competition is expected to decrease congeneric/confamilial species (increase number of genera/families and thus increase the scaling exponent in figure 1.) in a community by selecting for species assemblages that are more distantly related (Wang et al., 2012; Fan et al., 2017).

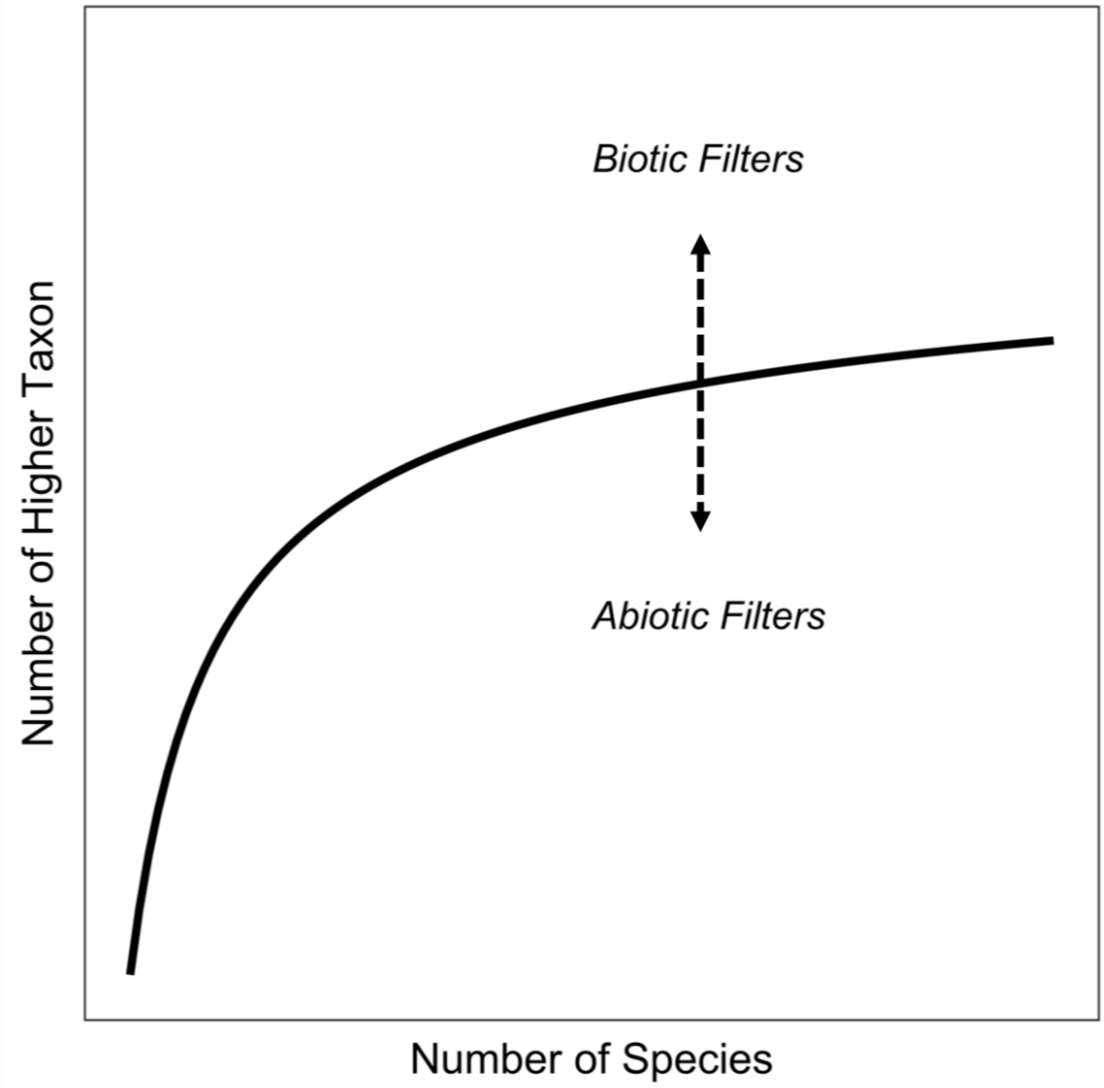

Figure 3. Expected power-law relationship between the number of higher-taxon and number of species in biological communities (black curve). Communities dominated by ecological processes like interspecific competition (Biotic Filters) are expected to increase the number of higher-taxon membership in communities, and thus increase the scaling exponent of the power law relationship (dashed arrow). In communities dominated by ecological processes like environmental filtering (Abiotic Filters), higher-taxon membership is expected to be limited, and thus the power law scaling exponent is expected to decrease.

While abiotic processes are generally expected to select for more closely related communities due to environmental filtering, and biotic processes are generally expected to select for more distantly related communities because of competitive exclusion; these are just two examples of numerous known (and potentially unknown) ecological mechanisms that regulate the diversity of communities. It is possible there may exist biotic interactions that select for more closely related communities, and abiotic interactions that favor more evolutionarily diverse assemblages. However, most abiotic and biotic processes are theorized to produce similar patterns as environmental filtering and competition (Fan et al., 2017), respectively. For example, dispersal limitation (like environmental filtering) is expected to decrease the diversity of communities, through a spatial filtering effect (Fan et al., 2017). Additionally, predation (biotic interaction) is expected to select for more distantly related species who are not preyed upon. Here, we keep consistent with more recent studies (e.g., Fan et al., 2017; Sommer et al., 2017)) by adopting the terms abiotic filtering (e.g. environmental filtering and dispersal limitation) and biotic filtering (e.g. competitive interactions and predation) to refer to sets of similar ecological processes expected to decrease or increase the diversity of communities, respectively.

Despite the presence of such explanations to describe why communities may be more or less closely related than expected by chance, most early studies (using G/S ratios) failed to differ significantly from null expectations (Simberloff, 1970; Harvey *et al*. 1983; Chase & Leibold, 2003). While others found evidence for more congeners than expected by chance, suggesting abiotic-like processes to be most important in assembling and regulating communities (Tofts & Silvertown 2000; Daehler 2001). Similarly, more recent studies using the relationship between the number of genera (GS) and/or families (FS), and the number of species within or across communities (e.g., Wang et al., 2012), have generally found communities to have less genera and families than would be expected by chance (Enquist et al., 2002; Fan et al., 2017). Like taxonomic ratios, the relationship between number of a higher-taxon and number of species (GS and FS) reflects the regulation from both regional and local processes (figure 1). At regional scales, the taxonomic structure is primarily regulated by the species pool, which can be quantified by a Null Modeling approach (Simberloff, 1970; Gotelli & Graves, 1996). Meanwhile, by examining the deviations from empirical patterns against Null Model expectations, the relative dominance of local ecological processes (abiotic filters and biotic interactions) can be assessed (e.g., Wang et al., 2012; Fan et al., 2017).

Ecological theory predicts that the relative importance of abiotic and biotic ecological processes driving biodiversity patterns varies along stress gradients (Krug et al., 2008). In particular, abiotic-like factors are generally predominant in abiotically stressful regions such as high latitude and high altitude, while biotic-like processes are predominant in abiotically benign regions (Darwin, 1859; Louthan et al., 2015; Sommer et al., 2017). A typical example of this is that negative biotic interactions should result in the co-occurrence of species dissimilar in their traits linked to competition and predation while environmental filtering and dispersal limitation should produce species co-occurring with similar traits related to abiotic gradients (Swenson et al., 2011). Moreover, the literature suggests that both abiotic and biotic filters operate at different spatial scales, with abiotic filtering more prevalent at large regional scales and biotic interactions dominating at smaller, more local scales (Weiher & Keddy, 1995; Swenson et al., 2012; Sommer et al., 2017).

In the case of coral reefs, the scientific community had long expected communities to be consistent with neutral theory, especially at larger scales. This expectation suggests that stochastic processes alone regulate coral assemblage diversity. However, Dornelas et al. (2006) suggested that coral reef diversity refutes the neutral theory of biodiversity, especially across abiotic gradients. Thus, it is likely the case that at large scales and across abiotic gradients, niche appointment rules are responsible in forming and stabilizing community structure over space and time (Dornelas et al. 2006; Swenson, 2011; Wang et al., 2012). However, for corals and other biotas, the influences of the species pool and local ecological processes on the structuring of communities have been primarily studied based on phylogenetic information (Cavender-Bares et al. 2006; Swenson et al. 2006; Kraft et al. 2007; Huang & Roy, 2015; Sommer et al., 2017), with few studies employing a pure taxonomic perspective (Enquist et al. 2002; Wang et al. 2012). Here, we investigate the community structure of coral reefs from a purely taxonomic standpoint (due to poor phylogenetic resolution, see Huang & Roy, 2015; Madin, 2016) using a data set collected by Peter Houk in the region of Micronesia (Northern & Southern Marianas Islands, Federated States of Micronesia, Marshall Islands and Palau). We address the following three hypotheses with respect to coral communities: (1) Communities exhibit similar relationships between number of a particular higher-taxon (genera and families) and number of species as woody plant communities (i.e., tight power-law fits); (2) The taxonomic structure reveals effects of local processes such as abiotic and biotic filtering; (3) The effect of local processes shaping taxonomic structure vary with respect to community and species pool size.

CHAPTER 2

MATERIALS & METHODS

Study Area

Coral assemblage data was collected in every significant jurisdiction of Micronesia from 2007-2018, primarily by Peter Houk (<75%), but also by three other calibrated observers (Steven Johnson, Christy Starsinic and Matthew Mclean). Specifically, the region encompasses 3,000,000 km^2 of the North Pacific Ocean, containing more than 6,000 km^2 (Andréfouët et al., 2006) of coral reefs. All in all, the data set contains 263 sites on 52 Islands throughout Micronesia spanning over 50,000 coral colonies located on four reef types (Outer, Patch/back, Channel and Inner) constrained to depths of 3-10 meters. At each site (excluding the Mariana Islands), reefs were surveyed using ten replicate 1 m^2 quadrat tossed at equal intervals along five transect lines each. On the reefs in the Mariana archipelago, 16 tosses of 0.25 m^2 were alternatively used to account for inherent differences in the mean coral colony sizes. See Houk et al. (2015) for more information.

In order to capture specific regional differences within Micronesia, we divided the data set into four distinct geographical regions: Marianas, West Carolines, East Carolines, and Marshall Islands (figure 2). In doing so, we analyzed each region separately (Regions) and combined (Micronesia). To provide the most realistic representation of coral assemblages, we first selected only Scleractinia corals (reef-building corals) and removed all juvenile species counts. Furthermore, in our study, we only considered the presence/absence of species and not their abundances. Since coral taxonomy has had considerable revisions over the past two decades (Huang et al., 2014), we further standardized the PH data set to the World Register of Marine Species (WORMS) as of June 1st, 2019.

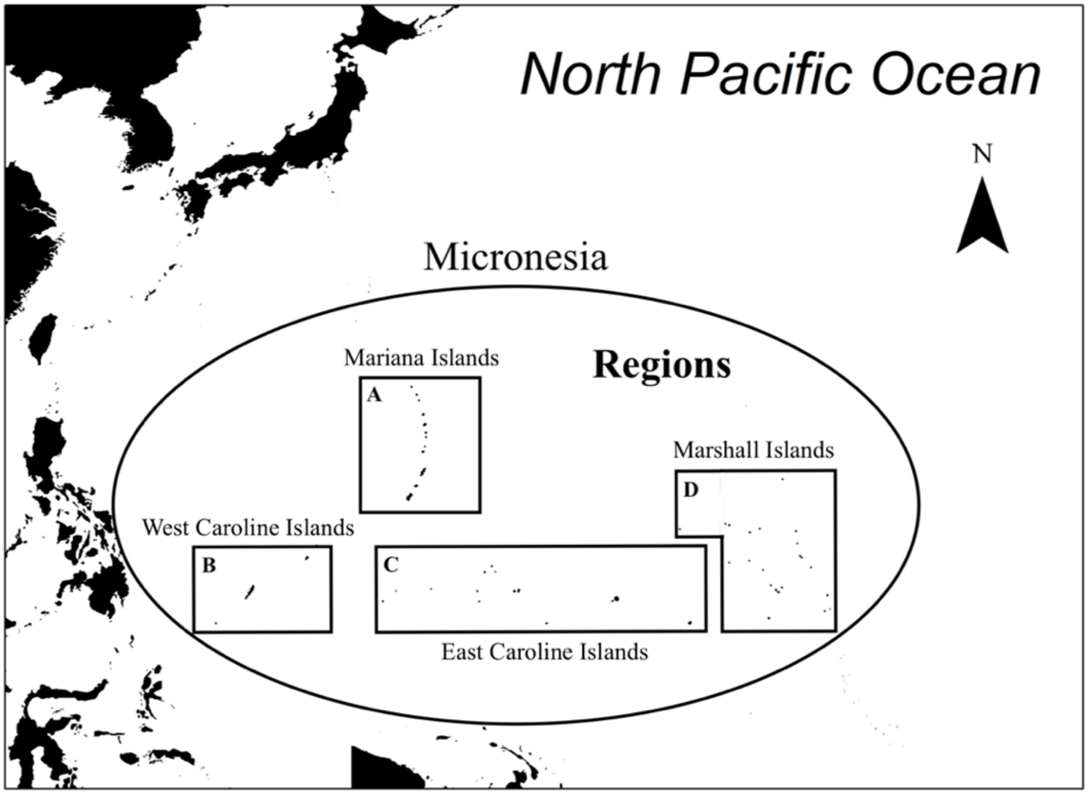

Figure 4. Map of study area including subdivisions of Micronesia into four distinct Regions: A) the Mariana Islands, B) Palau and Yap representing the West Caroline Islands; C) The Federated States of Micronesia (excluding Yap) representing the East Caroline Islands; D) The Marshall Islands.

Analysis of Taxonomic Structure

Here, we used the scaling exponent (α) of species to higher-taxon relationships as an indicator of the taxonomic structure of communities. Studies have shown that these relationships generally follow a power law in the classical form (Enquist et al., 2002):

$$G = \beta * S^{\alpha}$$

$$F = \beta * S^{\alpha}$$

where S represents the number of species, and G and F represent the number of genera and families, respectively. A unique property of the power law is that it can be linearized by taking the log of both sides:

$$\log(G) = \log(\beta) + \alpha * \log\,(S)$$

$$\log(F) = \log(\beta) + \alpha * \log\,(S)$$

In order to preserve the biological reality of the species to higher-taxon relationship, we constrained the intercept parameter (β) to 0 because each species belongs to only one genus or family:

$$\log(G) = \alpha * \log\,(S)$$

$$\log(F) = \alpha * \log\,(S)$$

In this form, the exponent α of the species to higher-taxon relationship can be estimated through linear regression. Here, we used the form of the equation above to estimate the scaling parameter α through a linear least squares method, before presenting our results in final the form:

$$G = S^{\alpha}$$

$$F = S^{\alpha}$$

In doing so, we preserved the biological realism of these taxonomic relationships while simultaneously reducing the parameters of the power law model allowing for more intuitive comparisons.

We further investigated the relationship between taxonomic structure and compounded community size at three geographic scale sizes: Regional, Island, and Site; where each scale size contains communities of a specific size (e.g., at Island level all sites found within a particular Island form the community). Consequently, the number of communities decreased from 263 to 52 to 4, as the geographic scale size increased (Sites within Islands, which are within Regions). Put simply; we assigned a ‘macro’ taxonomic ratio to each Island and each Region based on the surveyed sites within each geographic scale size. Thus, compounded community size measures the ratio of higher taxa to species that are available to populate each Island and each Region, respectively. Because any taxonomic ratio is an increasing function of the area sampled, comparing one Island’s ratio to another’s is not feasible. Therefore, we assume that the taxon-subtaxon curve (relationship) standardizes the information in taxonomic ratios as proposed by Marignani et al. (2004).

Inferring Ecological Processes from Taxonomic Structure

To test the relative dominance of ecological processes involved in community assembly, we applied a Null Modeling approach. In this context, a Null Model is a pattern-generating model based on the randomization of species assemblages. Here, some aspects of the data are held constant (species richness) while others (generic richness and familial richness) are allowed to vary stochastically. Specifically, the randomization is designed to produce an assemblage of species observed in nature in the absence of particular ecological mechanisms (Gotelli & Graves, 1996). In comparing these null communities to empirical communities, any deviation from the null expectation that these communities are indifferent, confirms the presence of ecological mechanisms. Here, communities where strong abiotic effects dominate (e.g., environmental filtering), should exhibit lower taxonomic relationship scaling exponents than that of null communities; ultimately selecting for more congeneric/confamilial species assemblages. Conversely, communities dominated by strong biotic effects (e.g., competitive exclusion) should have more substantial taxonomic relationships than those generated by the Null Model, as these ecological processes promote assemblages where closely related species are not present.

While local ecological processes and their relative importance have been used to explain why communities appear to be more/less diverse than would be expected by chance, it could be the case that these patterns are mainly a result of regional level diversity patterns (Gotelli, 2002). Since communities are generally thought to be assembled from a pool of regionally available species, factors regulating regional level diversity patterns (e.g., evolutionary history and species range size) could be responsible in producing patterns seen in local communities (Wang et al., 2012). Traditionally, ecologist have used Null Model approach has been used to examine the effects of the species pool (regional diversity) on taxonomic structure (Gotelli & Graves, 1996), while the effects of local ecological processes are usually assessed by deviations of empirical patterns from null expectations (Wang et al., 2012). Therefore, in applying a Null Model approach to investigate the importance of local ecological processes, results should always be interpreted in the context of a particular species pool. However, accurately defining a pool of regionally available species is not always an intuitive task (Swenson et al., 2006; Wang et al., 2012).

Historically, pioneer studies employing Null Models considered the regional pool of available species to be all species found within a particular area of interest (e.g., Simberloff, 1970; Enquist et al., 2002). From this pool, early studies generally sampled species without replacement (hypergeometric fashion, e.g., Simberloff, 1970). However, some have constructed communities by sampling species with replacement (binomial fashion) despite the literature warning against it (Gotelli & Graves, 1996). In the context of taxonomic partitioning, some earlier studies have fallen susceptible to sampling species with replacement (e.g., Enquist et al., 2002). Moving forward, more recent studies have ditched these somewhat archaic Null Models for more advanced ones (e.g., Wang et al., 2012).

The problem with early Null Models in ecology is that simply sampling species with or without replacement from a regional pool of available species fails to account for the dispersion fields of species in nature (Gotelli, 2002). For example, some species may be better dispersers than others, and thus, empirical communities are more likely to be populated by good dispersers than poor ones. More recent studies have come to design more complex Null Models to account for this issue of unequal dispersion limitations among species (e.g., Wang et al., 2012; Fan et al., 2017).

In choosing an appropriate Null Model, we considered the fact that coral communities are distributed non-randomly in space (Dornelas et al., 2006). Dispersal limitation and environmental factors may be involved in shaping community landscapes, and thus, empirical communities should share more species with nearby ecologically similar communities than with more distant dissimilar communities (Fan et al., 2017). Consequently, we must account for this spatial autocorrelation of species occurrence when constructing a Null Model (Wang et al., 2012). We addressed this issue by applying three different Null Models, and three different species pools:

(1) For a focal community, we constructed a null community by sampling species the same number of species as the focal community without replacement from a given species pool. Here, every species can only be chosen once to populate a given community, and thus should follow a hypergeometric distribution (Simberloff, 1970).

(2) For a given community, we assume that every species has an equal probability of being selected for a community but may be chosen more than once (binomial distribution). Thus, we sampled the same number of species as the focal community with replacement from a given source pool (Gotelli & Graves, 1996; Enquist et al., 2002).

(3) We adopted a Null Model based on ecological realism, as presented by Fan et al. (2017). Here, we sample species for each null community considering the dispersion fields of species (Gotelli, 2000; Burns & Strauus, 2011; Fan et al., 2017). For each observed community, we first sampled a community from all other communities weighted by the number of shared species. From the community chosen, we then sampled one species. We repeated this process until the number of distinct species present in the constructed community is equal to that of the observed community. In doing so, we aimed to weaken the effects of abiotic factors such as environmental filtering and dispersal limitation.

For each of the Null Models, we computed the species and higher taxa richness and calculated the scaling exponent α using least-squares linear regression on log10 transformed data. We repeat this process 1000 times for each Null Model in order to generate a null distribution of scaling exponents. To test whether empirical scaling exponents differed significantly from null expectations, we used an empirical cumulative distribution function to calculate P-values, and quantiles to estimate the 95% confidence limits of the null distributions.

Intuitively, species pools will have adverse effects on this type of experiment, particularly at the regional level (Simberloff, 1970; Gotelli & Graves, 1996), and thus, to accurately infer the effects of regional ecological processes, deviations from the null expectation must also be considered in the context of the species pool. Therefore, for Null Models 1 & 2, we applied three different sizes of species pools: Micronesia, Regional, and Island (i.e., all species present in the PH dataset at one of these distinct scales makes up the species pool). While most studies utilizing Null Models have typically used all the species present in the data (Enquist et al., 2002; Fan et al., 2017), we hoped to more accurately depict ecological realism in limiting the effects of environmental filtering and dispersal limitation by using smaller species pools.

We further investigated if local ecological processes shaping taxonomic structure (qualitatively) vary with spatial scale, by applying the approach above to Micronesia as a whole (figure 2.), and each Region. Because site grain size varied between the Marianas Region and the rest of Micronesia; in assessing Micronesia as a whole we assumed that these species to higher-taxon relationships are not scale-dependent as indicated by Marignani et al. (2004) and Fan et al. (2017). Similarly, we also investigated if local ecological processes shaping taxonomic structure (qualitatively) vary at different scales of compounded community size by applying each Null Model and available pool size to compounded communities (i.e., we only consider pool sizes large than the compounded community size). All data in this project was manipulated and computed using R version 3.5.2 (R Core Team., 2017).

CHAPTER 3

RESULTS

Taxonomic Structure

Previous studies have shown that taxonomic ratios are correlated with environmental variables (Enquist et al., 2002; Fan et al., 2017) and thus we tested the taxonomic ratios of sites against a myriad of environmental variables. However, taxonomic ratios have known sample size dependence, and sample grain varied between the sites in the Marianas and the rest of Micronesia, and thus, we correlated taxonomic ratios and environmental variables for the Mariana Islands separately (Appendix A.). A Pearson correlation test revealed both G/S and F/S ratios in the Mariana Islands to correlate with Longitude, Latitude, Island size, and Island Population (Appendix A1. & A3.). The rest of Micronesia's taxonomic ratios (G/S and F/S) correlated with Longitude and Latitude, and Island Population for just the F/S ratio. Furthermore, a One-way ANOVA revealed significant differences between Windward/Leeward and Reef Type for the G/S ratio in the rest of Micronesia (Appendix A2. & 1d). A One-way ANOVA ($P < 0.001$) and Tukey HSD test showed the Mariana Islands' G/S ratio to be distinct from all other Regions, and East Caroline Islands' ratios to be distinct from West Caroline Islands' ratios. Furthermore, we found the West Caroline F/S ratios to be distinct from all other Regions (One-way ANOVA ($P < 0.001$)).

We used a power law to estimate both generic/familial-to-species relationships in coral communities across all sites in Micronesia (figure 3). We found that both GS and FS relationships fit a power function regardless of the number of sites (N_{20}^{263}), with ($R^2 > 0.98$) in Micronesia and all four Regions (Appendix B.).

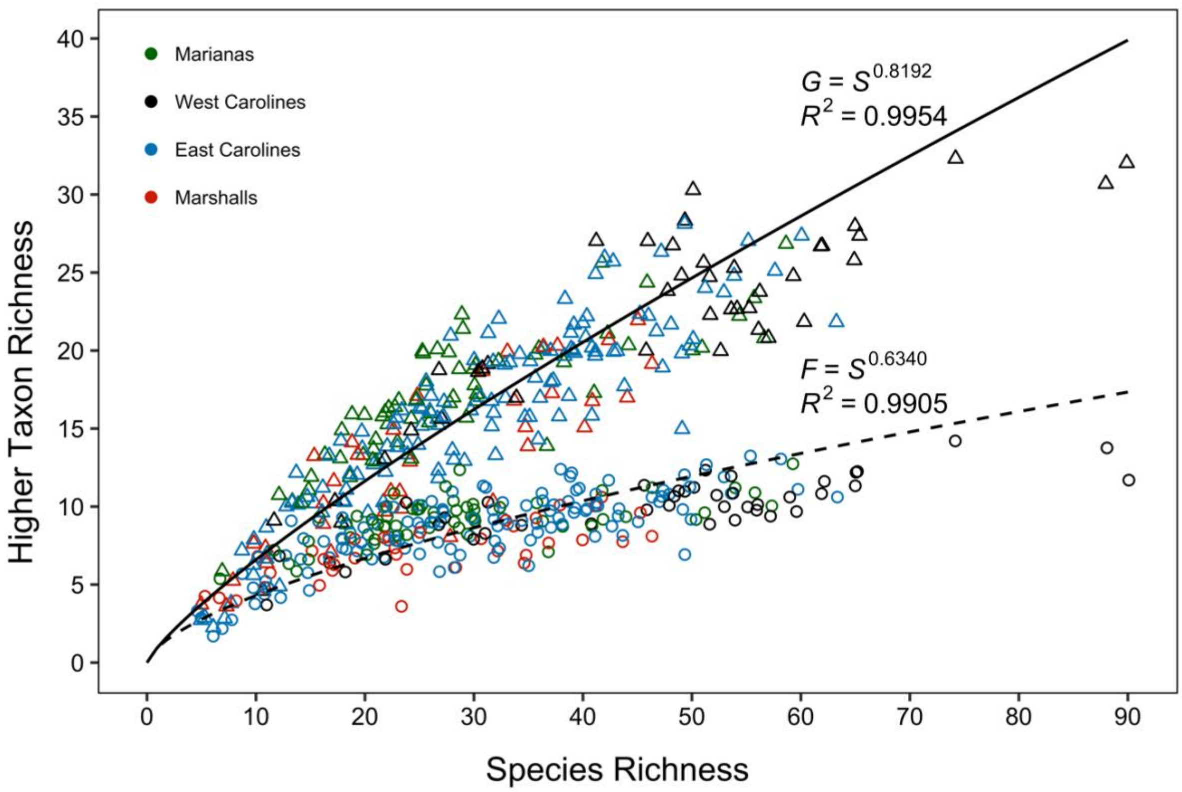

Figure 3. Relationship between the number of higher taxa (genera – triangles, families – circles) and number of species across coral reef sites in Micronesia fit to a power law (GS, black solid line; FS, black dashed line) constrained through the origin. G represents the number of genera; S, the number of species and F, the number of families. Species richness at individual sites ranged from (5-90) across 263 sites. Scaling exponents proved to be statistically invariant across reef types (Appendix C); but not across Regions as both the West Caroline and Mariana archipelagos proved to be statistically different from Micronesia as a whole (Appendix B).

Of the four Regions, the Mariana archipelago displayed the largest scaling exponents for both higher-taxon to subtaxon relationships, with the Marshall Islands having the lowest exponents for the GS relationship and the West Caroline Islands for the FS relationship (Appendix B.). The FS relationship in the Marianas and West Carolines Regions proved to be significantly different from Micronesia as a whole, and just Marianas' exponent for the GS relationship (confirmed by no 95% confidence interval overlap in Appendix B). Additionally, the taxonomic structure of coral communities (α) across Micronesia proved to be statistically invariant across the four reef types (Outer, Patch/back, Channel and Inner) surveyed in the PH data set (Appendix C).

We further investigated the effect of community size by combining all species observed on a particular Island or geographic Region to represent a community. For both Island and Region community scales, the higher-taxon to species relationships scale to a power-law sufficiently ($R^2 > 0.990$). At the Island scale, we found the GS and FS relationships scaling exponents to be 0.8198 and 0.6190, respectively (Appendix D). Furthermore, at the Region scale, we found the GS and FS relationships to be 0.7559 and 0.5521, respectively.

In recent years coral taxonomy has undergone considerable revisions (Huang et al., 2014). Thus, we also tested if different taxonomic revisions had adverse effects on the scaling exponents of the taxonomic structure of coral communities throughout Micronesia. We found the taxonomic structure of communities to change significantly at all community sizes for both the GS and FS relationships (except for the FS relationship when Community: Region) between the WORMS and COTW taxonomic revisions. In general, we found the WORMS taxonomic revision to have larger GS relationship exponents for all community-scale sizes, and smaller FS relationship exponents than COTW (Appendix D). By fitting the power-law through the origin, both the GS and FS relationships at each community-scale for both taxonomic revisions proved to have an R^2 higher than 0.99, and thus one revision does not fit a power-law better than the other, per se. Furthermore, when the power-law is not constrained through the origin, we generally found little to no difference in R^2 between taxonomic revisions; with the most considerable differences being at the site scale, with the COTW revision (GS $R^2 = 0.7814$, FS $R^2 = 0.5509$) fitting a power-law slightly worse than the WORMS taxonomic revision (GS $R^2 = 0.8066$, FS $R^2 = 0.5780$).

Lastly, we tested two different reproductive trait subsets to unveil their taxonomic structure. We collected trait data from the Coral Traits website (see Madin et al., 2016), and assigned traits to the Genera level. In the context of coral's Sexual System (gonochoric & hermaphroditic corals), we found coral communities in Micronesia to generally be composed of corals with a hermaphroditic mode of reproduction (Appendix E1.). The taxonomic structure for the GS relationship proved to be statistically indifferent between the two modes of the sexual system. However, for the FS relationship, we found the mode of gonochorism to exhibit significantly larger exponents for FS relationships than hermaphroditic corals (Appendix E1.). For the reproductive trait Larval Development (brooding & spawning corals), we found coral communities in Micronesia to generally be composed of much more spawning corals than brooding corals. For both the GS and FS relationships, we found brooding corals to exhibit significantly larger scaling exponents than spawning corals (Appendix E2.).

Inferring Local Ecological Processes

We used three different Null Models, three different sizes of species pools (Pool: Micronesia, Pool: Region, and Pool: Island), and three community sizes (Community: Site, Community: Island, and Community: Region) to infer ecological processes in Micronesia and within four regions. For Micronesia, Null Model 1 revealed the GS relationship to deviate significantly below null expectations ($P < 0.05$) across all compounded community sizes and pool sizes (except Community: Island and Pool: Region); while the FS relationship showed no deviation from null expectations ($P>0.05$) across all community scales and pool sizes (Appendix F1. & F4.). Null Model 2 showed quite different results for the GS empirical exponent which switched from deviating below null expectations in the general case where Community: Site and Pool: Micronesia to deviating above null expectations as community size increased and pool size decreased, albeit with intermediate steps of no deviation from null expectations (Appendix F2.). For the FS relationship, Null Model 2 proved to deviate above null expectations across all community and pool sizes (except when Community: Region ($P = 0.06$)), indicating there to be more families than expected by chance (Appendix F5.). For Null Model 3, we found the GS relationship for Micronesia to have fewer genera than expected by chance across all compounded community-scale sizes, albeit with Community: Island not deviating significantly from null expectations. For the FS relationship, we found no significant deviations from null expectations across all scales (Appendix F3. & F6.).

A within region analysis of local ecological processes revealed the Marianas Islands GS relationship to have no deviations from null expectations for Null Model 1, except when Community: Site & Pool: Region indicating there to be more genera than expected by chance (Appendix G1.). The FS relationship deviated above null expectations at all community sizes and pool sizes except when Pool: Region (Appendix G4.). Null Model 2 consistently showed there to be more genera and families than expected by chance, except at the Community: Island scale (Appendix G2. & G5.). Here, there were no deviations from null expectations when Pool: Micronesia and Pool: Region for the GS and FS relationships, respectively. Null Model 3 showed no deviations from null expectations in most cases for both taxonomic relationships, deviating above null expectations only when Community: Site for the FS relationship (Appendix G3. & G6.).

For the West Caroline Islands, Null Model 1 consistently had fewer genera than expected by chance across all pool sizes for the GS relationship (Appendix G1.), albeit with mild significance when Community: Island and Pool: Micronesia ($P = 0.06$). The FS relationship failed to deviate from null expectations across all pool and community sizes (Appendix G4.). For Null Model 2, both relationships showed no deviations from null expectations except at the Community: Site scale where the GS relationship had fewer genera than expected by chance when Pool: Region, and the FS relationship had more families than expected by chance when Pool: Island (Appendix G2. & G5.). Null Model 3 showed no significant deviations from null expectations for both taxonomic relationships, except for the GS relationship when Community: Site deviating below null expectation (Appendix G3. & G6.).

For Null Model 1 the East Caroline Islands appear to have fewer genera than expected by chance, with significant deviations below null expectations at all community and pool scales except for no deviation from null expectation when Community: Site and

Pool: Island (Appendix G1.). For the FS relationship, we found no deviations from null expectations across all community and pool sizes (Appendix G4.). Null Model 2 revealed different results for the GS relationship as community size increased (Appendix G2.), with deviations below null expectations at the Community: Site scale except when Pool: Island (no deviation from null expectation). As the community size increased to the Island scale, there appear to be more genera than expected by chance but only when Pool: Region with no deviations from null expectation when Pool: Micronesia. For the FS relationship, we found more families than expected by chance but only at the Community: Site scale regardless of pool size, with no deviations from null expectations at the Community: Island scale (Appendix G5.). For Null Model 3, only the GS relationship when Community: Site deviated from null expectations (below), indicating there to be fewer genera than expected by chance (Appendix G3. & G6.).

We found for Null Model 1, the Marshall Islands to have fewer genera than expected by chance across all community and pool sizes, except for no deviation from null expectations when Community: Island and Pool: Region (Appendix G1.). For the FS relationship, we found there to be fewer families than expected by chance only when Community: Site and Pool: Micronesia, with no deviations from null expectations across all other community and pool sizes (Appendix G4.). For Null Model 2, both the GS and FS relationships deviated below null expectations when Community: Site and Pool: Micronesia (Appendix G2. & G5.). At all other community and pool sizes, both taxonomic relationships showed no deviations from null expectations, except for the GS relationship when Community: Island. Here, when Pool: Micronesia there appear to be fewer genera than expected by chance, but more genera when Pool: Region. Null Model

3 revealed there to fewer genera and families than expected by chance at both community scales, except for no deviation from null expectation for the FS relationship when Community: Island (Appendix G3. & G6.).

In the most general of cases (Community: Site, Pool: Micronesia) we found Micronesia's empirical communities to contain less genera and similar number of families than would be expected by chance across the three Null Models. For most of the Null Models (1 & 3), it appears that this feature does not change as pool sizes and communities' sizes change. However, upon evaluating regions of Micronesia individually we found varying results. Specifically, trend of fewer genera in Micronesia is driven by signals of fewer genera in the West Carolines, East Carolines and Marshalls, with no deviations from null expectations in the Marianas. For the number of families, the result of no deviation from null expectation in Micronesia is driven by their being no deviations from null expectation in the West and East Carolines; and by the Marianas and Marshalls having more and less families than would be expected by chance, effectively producing a no deviation from null expectation like signal. In total, these results indicate that coral communities in Micronesia are generally more closely related than would be expected by chance, except in the Marianas where they appear to be more distantly related.

CHAPTER 4

DISCUSSION

Taxonomic Structure

Enquist et al. (2002) used woody plant communities to show a general pattern in the taxonomic structure of biological communities and found that the genus/family-species relationship can be adequately modeled using a power law. Specifically, they came up with equations where species richness explains 90% or more of the variation in higher-taxon richness; regardless of taxonomic realism (power-law constrained through the origin). Since then this type of analysis has been applied to communities of parasites, microbes, animals, and plants (Poulin & Mulliot, 2004; Passy & Legendre, 2006; Krug et al. 2008; Fan et al., 2017); with most studies constraining the power-law through the origin. Intuitively, it is known a priori that when there is one organism (species), there is also one higher-taxon present. By constraining the power-law function through the origin, it passes through the point (1,1) satisfying the taxonomic realism of the higher-taxon to species relationship. However, in constricting the fit through the origin R_2 can become more robust than would be if an intercept parameter was included (Bartels, 2015) because the explained sum of squares and the total sum of squares are taken around zero rather than around the mean.

We found very high R_2 values when accounting for taxonomic realism (constricting fit through the origin), and thus to some degree our results confirm that like other taxa, a power-law sufficiently describes the taxonomic structure of coral communities. However, when adding in an intercept parameter, as Enquist et al. (2002) did, we found much lower R_2 values (GS $R_2 = 0.83$, FS $R_2 = 0.63$). One possible explanation for lower R_2 values is that in coral communities, environmental and ecological processes regulating higher-taxon membership may not be as robust as in woody plant communities (Enquist et al., 2002; Fan et al., 2017). Nonetheless, we found that as the number of species increases, the number of genera/families also increases in a monotonic fashion rather than a constraint envelope. Therefore, these relationships pertaining to taxonomic structure represent the rate of diversification of a particular higher-taxon relative to the species taxonomic level (Passy & Legendre, 2006; Mayfield & Levine, 2010), and could be essential to ecologists requiring quick and robust estimates of local taxonomic richness (Roy et al., 1996; Enquist et al., 2002).

Unlike woody plant communities, coral reefs appear to be more variant in their taxonomic structure among regions. Seminal work by Stelhi & Wells (1972), recorded there to be a general decrease in diversity eastward across the Pacific. Consistent with their study, we found sites in Micronesia to exhibit a similar trend (Appendix H). Here, the most western Region of Micronesia (West Carolines) had on average the most considerable numbers of species, genera, and families, while the most eastern Region (Marshall Islands) had the least. Besides this trend, other studies have found coral reefs to be somewhat invariant in their biodiversity patterns at regional scales in the availability of (>50m) shallow-water habitats (Bellwood & Hughes, 2001). In Micronesia, we found significant differences in the taxonomic structure between Regions while only surveying shallow-water habitats (<10m), indicating that coral communities may be more variable than previously thought. Furthermore, the differences in taxonomic structure between Regions showed no clear trend along the expected (decreasing) gradient in taxonomic richness eastward across the Pacific, suggesting that the partitioning of diversity does not necessarily increase or decrease consistently with species and taxonomic richness.

Ultimately the differences in taxonomic structure between Regions can be attributed to different relative strengths of ecological processes and environmental factors (Wang et al., 2012). By investigating if taxonomic ratios of coral communities' correlate with environmental variables, we found the Mariana Islands to correlate differently from the rest of Micronesia. This result suggests that different environmental processes can regulate taxonomic structure between Regions. Furthermore, this suggests that the differences between the taxonomic structure of communities in the Mariana Islands and the rest of Micronesia may be due to environmental differences. For example, the Mariana Islands contain larger Islands with much higher elevations, while other Regions contain much lower lying Islands and atolls. Intuitively, larger Islands have more available habitats, and with more available habitats there is a higher chance of encountering an array of species.

In analyzing how environmental processes affect the taxonomic structure of communities in Micronesia, a negative correlation with Island Size in the Marianas proved to be quite interesting. Specifically, we found the taxonomic ratios (G/S and F/S to decrease as the size of Islands increase, indicating that biotic-like interactions (e.g. interspecific competition) weaken and abiotic-like processes increase in strength along this gradient. Furthermore, this result suggests that the overall evolutionary diversity of corals decreases as a function of Island Size (Appendix A1.) However, Houk and Starmer (2010) found a contradictory result with a positive correlation between diversity (species richness) and Island Size in the Marianas. Previous studies on marine mollusks found similar results, where taxonomic ratios increase as an inverse function of species richness (e.g., Roy et al., 1996). Therefore, one possible explanation is that the number of genera and families stays relatively constant as the number of species increases, hence lowering the value taxonomic ratios and creating a negative correlation in taxonomic ratios along an increasing gradient of species richness. A Pearson correlation revealed species ($r=0.56$, $p<0.001$), generic ($r=0.46$, $p<0.001$), and familial ($r=0.30$, $p=0.017$) richness to increase as a function of Island area. This result implies that evolutionary diversity increases as a function of Island size. Consequently, the negative correlation between taxonomic ratios and Island size is likely due to the number of species per community increasing at faster rate than the number of genera and families as a function of Island size.

In terms of the higher-taxon to species relationships in the Marianas, we found higher scaling exponents in the smaller northern Islands than the larger southern Islands (albeit not significantly different). While we found taxonomic richness to increase as function of Island size at the family, genus and species scales; the presence of larger scaling exponents on smaller Islands means that for a given species richness the smaller northern Marianas contain a higher number of genera and families than southern Islands. That is the evolutionary diversity of coral reefs for a given species richness is higher in the northern smaller Mariana Islands. Because we found negative correlations between taxonomic ratios with Island size and Island population (Appendix A1.), it is likely the case that these two factors (among others) are responsible in partitioning diversity for a given species richness within the Marianas.

The presence of larger scaling exponents in the Marianas indicates that this Region may be the most evolutionarily diverse in Micronesia, although further phylogenetic analysis may be needed (Huang & Roy, 2015; Sommer et al., 2017). That is, communities in the Mariana's contain a higher number of genera and families for a given species richness than other regions throughout Micronesia. Because differences in the taxonomic structure of communities are a result of a combination of processes (e.g., ecological, environmental, oceanographic), it may be the case that the Mariana Islands are more environmentally akin to diverse assemblages than other Regions in Micronesia (Gotelli, 2002; Dornelas et al., 2006; Wang et al., 2012; Fan et al., 2017). For example, we found higher scaling exponents in the Regions containing Islands with relatively high elevations (Marianas and the East Carolines), while regions containing atolls and lower lying Islands (West Carolines and Marshalls) proved to have lower scaling exponents. And thus, one mechanism leading to more diverse taxonomic structures is likely dependent on the elevation and size land masses within Regions.

Furthermore, we found the Mariana Islands to be the only region that showed signs of biotic-like interactions being the dominant set of ecological processes (similar numbers of genera and more families than would be expected by chance). This suggests, abiotic-like interactions (e.g. environmental filtering) appear to be weakest in the Marianas. Conversely, biotic-like interactions (e.g. interspecific competition) are expected to be the strongest in this region. This result proved interesting as abiotic-like processes are generally stronger at higher latitudes and the Marianas' has the highest latitude of Regions in this study (Louthan et al., 2015; Sommer et al., 2017). At the same time, this region has quite a large span of latitude which could support a more diverse range of species suitable to climactic conditions (Sommer et al., 2017), ultimately leading to higher scaling exponents. Therefore, the high scaling exponents in the Marianas suggests that ecological and environmental factors select in this region select for coral assemblages composed of more distantly related species than any other region.

It has become increasingly apparent in recent years that not every species can be saved. Because the Marianas contain the largest amounts of genera and families for a given species richness, this Region should be the best candidate to preserve the evolutionary diversity of coral reefs in Micronesia (Huang & Roy, 2015) despite species loss in years to come. This result is vital to conservationists and ecologist in Micronesia as the frequency of bleaching events has increased drastically in recent years (Bruno et al., 2007). For example, coral communities at higher latitudes are expected to help mitigate phylogenetic diversity loss in lower latitude (warmer water) communities by acting as sources pools (Sommer et al., 2017). Since the Mariana Islands have the most diverse taxonomic structure and have the largest latitudes in Micronesia, this Region could play an essential role in mitigating the loss of diversity in Micronesia in years to come.

In investigating the effect of compounding communities (sites), we found a significant decrease in the scaling exponents of coral communities as community size increased. While some studies have attributed this decrease in scaling exponents to be an issue associated with sample size dependence (e.g., Gotelli & Graves, 2001), others have shown evidence for no sample size dependence in taxonomic partitioning relationships (e.g., Marignani et al., 2004; Fan et al., 2017). In assuming the latter, the decreases we observed in scaling exponents as community sizes increased are likely due to a sampling effect rather than biological implications. For example, as community size increases the number of communities decreases (N: 263 for sites, 52 for Islands and 4 for regions), as the number of species per community increases. The accumulation in higher taxa membership as a function of species richness is asymptotic by nature (Polya, 1930; but see Gotelli & Colwell, 2001); when there are few large communities (high species richness), only a small asymptotic portion of the relationship is measured leading to smaller scaling exponents.

In addition to analyzing the taxonomic structure of coral communities, we further investigated the effect of taxonomic revisions on the taxonomic structure. The WORMS taxonomic revisions proved to be more significant for GS relationships at all compounded community sizes and smaller for FS relationships than the COTW taxonomic revision. This trend suggests that taxonomy is moving in the direction of splitting at the genus taxonomic level and lumping at the family level. Despite there being considerable changes to coral taxonomy between these revisions (Huang et al., 2014), there appear to be minimal differences in how well they fit a power law. This result suggests the changes made to coral taxonomy in the last 15 years have had little to no effect on the ability to predict the number of a particular taxonomic rank in a community given the number of another taxonomic rank in Micronesia.

Lastly, we analyzed the taxonomic structure of subsets of coral communities of particular reproductive traits (Appendix E) at the site scale for Micronesia as a whole. For the reproductive trait of Sexual System, we found there to be more species of hermaphroditic corals than gonochoric corals within communities in Micronesia (Appendix E1.). This result proved quite impressive, considering that the proportions of classified hermaphroditic and gonochoric corals are roughly 50:50 (see coraltraits.org). Furthermore, we found the scaling exponents of the GS relationship to be statistically indifferent between the two trait subsets indicating that at the genus level, their taxonomic structures are somewhat similar. However, for the FS relationship, we found gonochoric corals to have a much higher scaling exponent despite hermaphrodites having a generally higher number of species. Although further phylogenetic testing may be necessary (e.g., NTI & NRI metrics), it appears that gonochoric corals in Micronesia are much more evolutionarily diverse than hermaphroditic corals, at least for a particular species richness.

In the case of Larval Development, we found many more species of spawning coral than brooding corals across Micronesia. Due to a minimal number of species, brooding corals proved to have quite large scaling exponents for both taxonomic relationships. This is because there exist very few genera and families for brooding corals compared to spawning corals. Consequently, the relationship between the number of a particular higher-taxon (genera/families) and the number of species for brooding corals appears to be much more linear than spawning coral.

For evolutionary diversity, a higher scaling exponent for brooding corals would suggest that this group is more evolutionarily diverse than spawning corals. To some extent, this is true, but likely only in depauperate communities. As communities become speciose, the lack of diversity in brooding corals limits finding new species. For spawning corals, there exist many more genera and families of corals, and thus as communities become speciose (SR>10) spawning communities contain roughly the same or higher number of families/genera and species than brooding communities. This result suggests that within moderate to severely pupariate coral communities in Micronesia, spawning corals appear to be more diverse (high SR) and evolutionarily diverse than brooding corals, despite having lower scaling exponents.

More and more studies are incorporating trait analyses into measuring the relatedness of communities (Madin et al., 2017). However, most if not all studies utilizing taxonomic partitioning to quantify taxonomic structure have ignored incorporating a trait-based analysis (e.g., Enquist et al., 2002; Mulliot et al., 2004; Fan et al., 2017). One possible explanation may be that it is somewhat complicated and not straightforward. For example, in the case of coral's reproductive system, a higher scaling exponent for gonochoric corals (FS relationship) indicates the group to be more evolutionary diverse than hermaphroditic corals; as there generally exist a higher number of families for gonochoric corals than hermaphrodites regardless of the number of species. However, in the case of larval development, it is not so straight forward as there are very few numbers at any taxonomic rank (family, genus, species) of brooders compared to spawners. Consequently, the larger scaling exponent in brooding corals is somewhat misleading as brooding corals appear to be only more evolutionarily diverse than spawning corals at deficient number species. This feature highlights a potential pitfall when analyzing and comparing the taxonomic structures of trait subsets using taxonomic partitioning as a metric.

Our trait analysis should prove useful to ecologists and conservationists in the area looking to protect the evolutionary diversity of coral reefs. For example, broadcast spawning corals have been shown to have higher settlement success in less diverse communities, indicating that interspecific competition may play a substantial role in regulating diversity patterns of spawning coral (Sims et al., 2002). Furthermore, some believe that broadcast spawners have more extensive dispersal ranges than brooding corals, and thus may be better long-distance dispersers (Harii et al., 2002; Ayre & Miller, 2004). However, other studies have shown that brooding corals may be better long-distance dispersers than spawning corals (e.g., Richmond, 1988) and that the loss of adult brood-stock can disproportionately affect recruitment success on isolated reefs (Gilmour et al., 2013). Our data suggest that there is a surprisingly limited amount of brooding corals within the region, and if not appropriately managed bleach susceptible brooding species could go extinct in future bleaching events (Bruno et al., 2007; Huang & Roy, 2015).

Inferring Local Ecological Processes

In this study, we applied a taxonomic approach to infer community assembly processes despite the availability of phylogenetic approaches. Specifically, we employed a purely taxonomic approach because the PH data set contained phylogenetically undescribed species, resulting in poor phylogenetic resolution. Despite the differences in these approaches, a recent study on woody plant communities has shown that both approaches generally infer the same result (Fan et al., 2017). For Micronesia as a whole, we mostly found the empirical scaling exponent of the GS relationship to be significantly lower than that of null expectations across all three Null Models, community sizes, and pool sizes. Furthermore, we found the FS relationship to not deviate from null expectations in most cases. The difference in results between the GS and FS relationships, suggests that processes regulating higher-taxon membership in communities affect the genus and family taxonomic scales differently. Together, these results indicate that higher-level diversity in coral communities accumulates relatively slowly (Gotelli, 2002), a pattern first noted by C. B. Williams (1964). Consequently, for a given species richness observed communities have fewer numbers of genera than expected by chance indicating abiotic-like filters (e.g., environmental filtering & dispersal limitation) filters to be the dominant set of ecological processes regulating taxonomic structure in the region of Micronesia.

The first Null Model (1) we used in this study sampled species without replacement from a regionally available pool of species. While Micronesia as a whole showed there to be fewer genera than expected by chance at almost every pool and scale size, at one scale (Community: Island and Pool: Region) there were no deviations from null expectations. Such a result suggests that coral communities (at this particular scale) form in a manner consistent with neutral theory (Hubbell, 2000). However, others have shown coral communities to refute neutral theory (Dornelas et al., 2006), albeit when considering abundances. Therefore, it is more likely that the pattern of no deviation from null expectation at this particular scale is the scale at which both abiotic-like and biotic-like filtering are relatively similar (i.e., one is not dominant over the other), producing a neutral like pattern (Dornelas et al., 2006).

For Null Model 2, we found the GS relationship to have an entirely different result from Null Model 1 as the dominant ecological processes went from abiotic-like to biotic-like as pool size decreased, and community size increased. One possible explanation for this trend is that as the pool size decreases, the pool of available species allowed to populate null communities becomes restricted to only very local species (i.e. closer to approximating empirical assemblages). Since abiotic-like processes are hypothesized to be stronger at larger scales relative to biotic-like processes (Weiher et al., 2011); at very local scales (e.g. Island pool size) species may have already been filtered based on their environmental tolerances, and thus, biotic-like processes could become the main factors in regulating higher-taxon membership. Similar studies have shown in woody plants that as the species pool size decreases the primary processes shaping taxonomic structure can shift from abiotic filtering to biotic competition (Swenson et al. 2006, Kraft et al. 2007), and thus our results are in accordance.

Despite similar observations with other studies, Null Model 2 sampled species with replacement (binomial fashion) which may be problematic, especially when dealing with small species pools (Gotelli & Graves, 1996). For example, every time a species is sampled from a species pool with replacement, there is a slight statistical chance that the same species could be drawn again, thus decreasing the probability of receiving a new higher-taxon. Conversely, without replacement (hypergeometric), each time a new species is sampled, we are guaranteed a different species and thus have a higher chance of gaining a newer higher-taxon. When a particular species pool has many species the probability of sampling with replacement the same species twice to populate a null community is relatively small. However, as the number of species in the pool decreases (more local scales), this probability increases and can potentially cause misleading results (Gotelli & Graves 1996). Consequently, this is why we found Null Model 1 and 2 to have consistent results for the GS relationship when the pool size was large (Micronesia), but the results to differ as the pool size decreased (e.g., Pool: Island).

Intuitively, by decreasing the pool size of available species in Null Model 1 and 2 to the Region and Island level, we accounted for an increasingly accurate subset of species that were allowed to colonize their respective local communities. However, closely related species should have similar dispersal abilities; it could be the case that communities come to be dominated by higher taxa containing good dispersers (Gotelli, 2002). Because both Null Model 1 and 2 assumed that species colonize randomly with equal probability, they did not incorporate differences in dispersal abilities among species. In testing Null Model 3, which incorporated to dispersion fields of species in space (Fan et al., 2017), we generally found there to be fewer genera than would be expected by chance. Computationally, the way Null Model 3 sampled species from communities limited the exploration of smaller pool sizes (i.e., we could not test pool sizes per se). Nevertheless, we found striking similarities between Null Model 1 and Null Model 3 in Micronesia as a whole and within individual Regions.

For Micronesia as a whole, both the GS and FS relationships generally produced the same result for both Null Models 1 and 3. Here, we found there to be fewer genera than would be expected by chance and there to similar numbers of families than would be expected by chance (no empirical deviation from null expectation) across all community-scale sizes. Even as the pool size decreased for Null Model 1, results remained consistent with Null Model 3 in all cases. This result suggests that Null Model 1 (hypergeometric sampling) may be more accurate than previously thought (Gotelli, 2002), despite its failure to account for the variation in species dispersal abilities. On the other hand, the deviations in results from Null Model 1 & 3 with Null Model 2 confirms that the commonly used Null Model (2, sampling with replacement) can result in misleading findings.

In particular, we found real communities in the Marianas Islands to have more families than would be expected by chance at both Site and Island community scales while sampling species from a pool of all available species in Micronesia in Null Models

1 & 3. Furthermore, this pattern proved to persist in Null Model 1 as the pool size decreased at the Site community scale, albeit with mild significance when the pool size was constrained to the Marianas Region. All the while, the empirical communities of other Regions failed to deviate from null expectations or deviate below null expectations, indicating there to be similar or fewer families than would be expected by chance.

For the GS relationship in the Mariana Islands, we generally found there to be no deviation from null expectations for both Null Models 1 & 3. Furthermore, the one case that did deviate significantly from null expectations (Community: Site, Pool: Region) proved to indicate that there were more genera than would be expected by chance in empirical communities. All the while, the three other Regions (West Carolines, East Carolines, and Marshalls) generally showed empirical communities to contain fewer genera than would be expected by chance. Therefore, while the three other Regions generally contain assemblages more closely related than by chance, the Mariana Islands appear to have assemblages more distantly related than expected by chance.

One possible explanation is that biotic-like processes are truly more dominant in the Marianas than the other Regions. However, the Mariana Islands were surveyed at a smaller grain size compared to the three other Regions, and the relative dominance of biotic-like and abiotic-like have been shown to vary with sample grain. For example, in woody plant communities, multiple studies have shown that abiotic-like processes generally affect taxonomic structures more so than biotic-like processes (Claire et al., 2013; Fan et al. 2017). Furthermore, others have found that the effect of biotic-like processes can be dominant in woody plant assemblages, but usually only at scales less than 5 m$_2$ (Swenson et al., 2007). Since the Marianas was surveyed at 4 m$_2$ at every Site compared to 10 m^2 for the three other Regions, the result of more diverse assemblages than would be expected by chance may be due to this reduction in sample grain. More interestingly, these results suggest that like woody plant communities, the scale size at which biotic-like processes become dominant may be approximately 5 m^2.

In examining the ecological processes of Micronesia as a whole, we for the difference in sample grain between the Marianas and the rest of Micronesia by assessing regions individually. In doing so, our results show the patterns we observed in Micronesia as a whole broken down into the sum of its parts. For example, in the case of Micronesia, we found there to fewer genera than would be expected by chance at almost every scale for Null Models 1 & 3. A within Region analyses revealed that this trend is driven by fewer genera than expected by chance in the West Carolines, East Carolines, and the Marshall Islands, with no deviations from null expectations in the Mariana Islands. For the FS relationship, we found the trend of no deviation from null expectations in Micronesia to be driven by the same result in West Caroline and East Caroline Islands. However, we found the Marshal Islands to have fewer families than would be expected by chance and the Marianas to have more. Thus, it appears the case that these two regions essentially canceled each other out, producing the overarching result of no deviations from null expectations in Micronesia.

The presence of communities with more or less family/genera than would be expected by chance have been attributed to either biotic-like or abiotic-like processes being dominant. This is because biotic-like processes (e.g., competition) are expected to limit similarity within a community selecting for species which are more distantly related or the presence of more family/genera within a community. On the other hand, abiotic-like processes (e.g., environmental filtering) are expected to decrease the number of genera/family in a community by selecting for more closely related species. Thus, in the case of Micronesia as a whole, we found the dominant set of ecological processes to be abiotic-like, ultimately selecting for more closely related communities. Furthermore, we found abiotic-like processes to especially active in the Marshall Islands and biotic-like processes to be exceptionally robust in the Mariana Islands, although, the latter may be a result of reduced sample grain. Of interest, we found this trend to be primarily present at the genus taxonomic rank and less so at the family rank, suggesting that local processes operate differently on different taxonomic ranks. While we were able to distinguish between diversity patterns and the relative importance of ecological processes using a purely taxonomic approach, the rise of genetics and phylogenetic approaches may provide more clarity in years to come. Specifically, as phylogenies become increasingly extensive and begin to cover more of Micronesia's genetically undescribed species, the ability to accurately quantify the relatedness of communities using NTI or NRI indices (Sommer et al., 2017) will lead to more accurate results. Following this, the scales at which local ecological processes operate should become less elusive.

A Cautionary Note on Null Models

By comparing three Null Models: (1) sampling without replacement, (2) sampling with replacement, and (3) sampling to account for the spatial autocorrelation of species, we were able to observe key similarities and differences in our results. The most interesting being that Null Model 1 and 3 proved yielded similar results, despite the former not accounting for the unequal dispersal abilities of species. This was a key concern for Gotelli (2002) who reviewed the first taxonomic partitioning study conducted by Enquist et al. (2002). More interestingly, Gotelli failed to comment on the choice of Null Model (sampling with replacement) used by Enquist et al. (2002), despite repeatedly warning against using such Null Model in *Null Models in Ecology* (1996).

In the case of Enquist et al., (2002), their choice in using a Null Model which sampled species with equal probabilities (with replacement) proved to not be detrimental to their results. This is because they generally found there to be fewer genera and families than would be expected by chance. Since sampling with replacement (our Null Model 2) has the ability to over predict higher-taxon membership in communities (as demonstrated here), their result of fewer higher-taxon membership than would be expected by chance is likely correct. Perhaps this is why they chose to sample species with replacement, as it would provide a more conservative Null Model in testing if assemblages have fewer numbers of a particular higher-taxon than one which samples without replacement.

Here, we observed Null Model 2 to differ from the other Null Models (1 & 3) in three cases: small pool sizes (mentioned earlier), large community sizes, and taxonomic ranks with few taxonomic units. The discrepancies in results are ultimately caused by a sampling effect (mentioned earlier) that becomes exacerbated as the number of sampling units' available decreases relative to the number of samples drawn for a community. For example, as the size of communities increases the chance of drawing the same species per community also increases, despite the pool size remaining constant. Consequently, our results showed there to be more genera than would be expected by chance at the most extensive community-scale size (Region) for Null Model 2.

Furthermore, we observed for Null Model 2 there to always be fewer families than would be expected by chance, at all community and pool sizes. While we did observe Null Model 1 and 3 to show the same result as Null Model 2 for the GS relationship when the community size and pool size were Site and Micronesia, respectively; the discrepancies we observed between Null Models at this particular community-pool scale for the FS relationship are likely due to a decrease in taxonomic units from the genus to family rank. That is when sampling with replacement and using fewer taxonomic units (a consequence of high taxonomic rank), the probability of drawing the same taxonomic unit twice increases. Consequently, Null Model 2 can potentially underestimate the number of genera and families that would be expected in a community by chance, and we observed this feature quite clearly in our results.

Numerous studies, primarily those focused on woody plant communities, have used taxonomic structure to investigate the relative importance of local processes in real communities (e.g., Krug et al., 2008; Wang et al., 2012; Fan et al., 2017). These studies have found little to no statistically robust evidence for empirical communities having more congeners/confamilial species than would be expected by chance (e.g., Enquist et al., 2002) - a rare result as noted by Jarvinen (1982). While we did find some evidence (Null Model 2) supporting this elusive feature, it appears that it might have just been due to a sampling effect more so than biological implications. Consequently, our results for Null Model 2 should be taken with caution. More accurately, Null Models 1 & 3 provide better indicators for determining the relative importance of ecological processes associated with shaping community structure.

Conclusion (Future Work)

In this study, we have shown that higher-taxon (genus and family) to species relationships in coral reef communities fit a power law in a similar fashion to woody plants and other biotas. Furthermore, the GS and FS relationships are significantly different among Regions in Micronesia. Ultimately these differences are a result of environmental variables and ecological processes acting in concert to shape local level diversity, but more research is needed (Gotelli, 2002). One caveat of the PH dataset is that multiple observers collected data, and thus, there could be an observer effect. Furthermore, sites were surveyed disproportionately between regions regarding exposure to harsh environments (e.g., different proportions of high and low wave exposure sides of Islands). Consequently, these factors could alter the scaling exponents we found in this study.

Despite the tight power-law relationships we found between taxonomic ranks in coral communities, woody plants appear to fit a power law better in the case where the power-law origin is unconstrained. This discrepancy suggests that the governing processes regulating taxonomic structure in woody plant communities produce a more predictable pattern than they do in coral reefs (Enquist et al., 2002). However, when accounting for taxonomic realism (power-law constrained through the origin), the number of higher taxa in a coral community is highly predictable given the number of species. Therefore, these relationships should prove useful to ecologists and conservationists alike requiring quick and robust estimates of species richness given higher taxa observations (Enquist et al., 2002). For example, NASA has recently taken on a project to map and classify the reefs of the world using a machine learning algorithm (NEMO-NET); and is currently testing out their technology in the Mariana Islands (Chirayath & Earl, 2016; but see NASA website for more recent information).

Specifically, NASA is currently using drones to survey reefs, where feed their data is fed into a machine learning algorithm capable of quantifying coral colonies to the family level. Given the allometric scaling exponents we have generated between the number of families and number of species, one could predict the number of species present, and eventually the number of genera. Furthermore, as the machine learning algorithm develops to quantifying the genus and species levels of coral colonies, our data could provide realistic bounds on the expected number of species and number of in a survey site.

In addition to quantifying the taxonomic structure of corals using higher-taxon to subtaxon relationships, we also investigated how sensitive these relationships were to taxonomic revisions. Generally, we found the most recent taxonomic revisions provided by WORMS to be more accurate (than COTW) in fitting a power to GS and FS relationships. Because taxonomic partitioning records the accumulation in higher taxa as a function of species richness, the scaling exponent provides a means to quantify differences in taxonomic revisions. Despite more recent genetic and molecular-clock work, the coral taxonomic system seems to have benefited only slightly in its ability to use higher-taxon richness as a surrogate for species richness. While we found marginal differences between revisions separated by approximately 15 years, it could be the case that more distant taxonomic changes (e.g., Vaughan & Wells, 1943) are much less accurate at predicting the number of higher taxa given some amount of species.

Of interest, we found gonochoric corals to be more diverse than hermaphroditic corals across Micronesia. We also found brooding corals to be extremely limited (compared to spawning corals) not only in their number of families and genera but also species across the region. Recent studies have shown as sea surface temperatures rise and bleaching events become more frequent, more northern latitude (colder water) reefs may be essential in acting as source pools for more lower latitude regions (Sommer et al., 2017). Because we found there to generally be more genera than expected by chance (suggesting abiotic-filtering-like ecological processes to be dominant) the different trait groups of coral's dispersal abilities should be considered in future conservation efforts (Huang and Roy, 2015; Sommer et al. 2017). Given that the loss of adult brood-stock can disproportionately affect recruitment success on isolated reefs (Gilmour et al., 2013), protecting the diversity of this less diverse group of coral may prove to be essential in mitigating diversity loss in years to come (Huang & Roy, 2015).

Enquist et al. (2002) used power laws to explain higher taxa membership in woody plant communities and found through a Null Modeling approach that there are fewer genera and families than would be expected by chance. Specifically, they constructed their Null Model by drawing species with replacement from an available pool, despite others insisting that drawing without replacement is more appropriate (Gotelli & Graves, 1996). Here, we found that sampling with replacement tends to underestimate the number of higher taxa in a community when compared to sampling without replacement. Therefore, sampling with replacement is more sensitive to suggesting that empirical communities have more genera/families than would be expected by chance. Since Enquist et al. (2002) found there to be fewer genera/families than expected by chance, their result is still correct despite the use of a problematic Null Model. While Gotelli (2002) failed to mention this artifact upon reviewing Enquist et al. (2002), he did mention that their Null Model failed to account for the dispersal limitations of species. By incorporating a Null Model from more recent work (Fan et al., 2017) on woody plants, we were able to test early Null Models (sampling with and without replacement) which do not account for unequal dispersal limitations of species against a Null Model which does. Interestingly enough, we found that in almost all cases sampling without replacement yielded the same results as a Null Model which accounts for the spatial autocorrelation of species, suggesting earlier more archaic Null Models to hold up to more recently developed ones.

Of the four regions we tested in Micronesia, the Marianas Islands proved to be the most compelling case of preserving diversity not only in terms of taxonomic structure (largest scaling exponents) but also dominant ecological processes. This Region should prove vital in years to come, considering scientists and conservationists have concluded that with limited resources not every species can be saved. This realization has prompted a shift from managing for diversity (species richness) to managing for evolutionary variety (Vane-Wright et al., 1991; Mace et al., 2010; Huang and Roy, 2015). While the West Caroline Islands contain more species than other Regions in this study and thus if conservationists want to preserve species, the best place to allocate resources is the West Caroline Islands. However, this approach could negatively influence the topology of Scleractinia’s (hard reef-building corals) phylogenetic diversity. In the more realistic approach where managing for evolutionary diversity is a priority, our results indicate that the Mariana Islands may be the most critical Region in Micronesia.

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APPENDIX:

A) Environmental Data: We collected environmental data from various sources: 1) Island Size was estimated using Google Earth, only land area was considered. 2) Island population was taken from various census reports (References: 14, 49, 50, 60). 3) Island Elevation was approximated to be 1-3m for all atolls, for higher Islands data was collected from PacIOOS USGS 10-m Digital Elevation Model archives. 5) Longitude was recorded in the PH data set for each site. 6) Latitude was recorded in the PH data set for each site. 7) Reef Type was recorded in the PH data set for each site. 8) Windward/Leeward side was approximated using Google Earth (i.e. whether a site was on the east or west side of an Island). Below, we present two tables containing Pearson correlations between quantitative environmental variables and taxonomic ratios (G/S & F/S) for a) Mariana Islands and b) Micronesia excluding the Mariana Islands. For qualitative observations we present two tables below containing One-way ANOVA results between qualitative environmental variables and taxonomic ratios (G/S & F/S) for a) Mariana Islands and b) Micronesia excluding the Mariana Islands.

Table A1. Pearson correlations (95% CI in parentheses) between quantitative environmental variables and the taxonomic ratios (G/S & F/S) of sites in the Mariana Islands.

Environmental Variable	*G/S*	*F/S*
Island Size	-0.41**(-0.60, -0.17)	-0.46***(-0.64, -0.24)
Island Population	-0.61***(-0.75, -0.43)	-0.60***(-0.74, -0.42)
Island Elevation	0.14(-0.12, 0.38)	-0.01(-0.26, 0.24)
Longitude	-0.47***(-0.65, -0.25)	-0.53***(-0.69, -0.33)
Latitude	0.34**(0.09, 0.54)	0.40**(0.16, 0.59)

*** Indicates $p < 0.001$, ** indicates $p < 0.01$, * indicates $p < 0.05$

Table A2. Pearson correlations (95% CI in parentheses) between quantitative environmental variables and the taxonomic ratios (G/S & F/S) of sites in Micronesia excluding Mariana Islands.

Environmental Variable	*G/S*	*F/S*
Island Size	-0.03(-0.17, 0.10)	-0.11(-0.24, 0.03)
Island Population	0.03(-0.11, 0.17)	0.17*(0.03, 0.30)
Island Elevation	0.05(-0.09, 0.18)	0.05(-0.09, 0.19)
Longitude	0.18*(0.04, 0.31)	0.29***(0.15, 0.41)
Latitude	-0.37***(-0.49, -0.25)	-0.32***(-0.44, -0.19)

*** Indicates $p < 0.001$, ** indicates $p < 0.01$, * indicates $p < 0.05$

Table A3. One-way ANOVA results between qualitative environmental variables and taxonomic ratios (G/S & F/S) of sites in the Mariana Islands.

Taxonomic Ratio	*Environmental Variable*	*DF*	*SS*	*MS*	*F*	*P-value*
F/S	Reef Type	1	0.0013	0.0013	0.1082	0.7433
	Residuals	59	0.7150	0.0121		
F/S	Windward/Leeward	4	0.0458	0.0115	0.9569	0.4384
	Residuals	56	0.6705	0.0120		
G/S	Reef Type	1	0.0009	0.0009	0.0513	0.8215
	Residuals	59	1.0462	0.0177		
G/S	Windward/Leeward	4	0.0148	0.0037	0.2007	0.9369
	Residuals	56	1.0323	0.0184		

Table A4. One-way ANOVA results between qualitative environmental variables and taxonomic ratios (G/S & F/S) in Micronesia excluding Mariana Islands.

Taxonomic Ratio	*Environmental Variable*	*DF*	*SS*	*MS*	*F*	*P-value*
F/S	Reef Type	3	0.4521	0.1507	12.2673	> 0.0001
	Residuals	198	2.4324	0.0123		
F/S	Windward/Leeward	3	0.0777	0.0259	1.8259	0.1437
	Residuals	198	2.8069	0.0142		
G/S	Reef Type	3	0.1611	0.0537	4.1116	0.0074
	Residuals	198	2.5857	0.0131		
G/S	Windward/Leeward	3	0.1254	0.0418	3.1584	0.0258
	Residuals	198	2.6213	0.0132		

B) Taxonomic Structure: Table containing the scaling exponents of the species to higher-taxa relationship for various regions and countries throughout Micronesia.

Table B1. The power law relationship between number of genera/families to number of species across various regions and countries in Micronesia. Here, n represents the number of sites and S the range of species richness. The four regions of focus and Micronesia as a whole are highlighted in bold.

Region	*n*	*S range*	*Generic Exponent*	*R^2*	*95% CI*	*Familial Exponent*	*R^2*	*95% CI*
North Marianas	36	7-44	0.8691	0.9982	0.8568-0.8815	0.6902	0.9959	0.6751-0.7053
South Marianas	25	16-59	0.8283	0.9945	0.8029-0.8538	0.6366	0.9901	0.6103-0.6629
Marianas	**61**	**7-59**	**0.8501**	**0.9961**	**0.8365-0.8638**	**0.6652**	**0.9919**	**0.6498-0.6806**
Palau	20	17-65	0.8078	0.9977	0.7895-0.8261	0.5986	0.9974	0.5843-0.6130
West Carolines	**41**	**11-90**	**0.8067**	**0.9974**	**0.7938-0.8196**	**0.6021**	**0.9959**	**0.5899-0.6143**
East Carolines	**125**	**5-63**	**0.8168**	**0.9958**	**0.8074-0.8263**	**0.6381**	**0.9910**	**0.6273-0.6488**
F.S.M.	146	5-90	0.8149	0.9960	0.8064-0.8233	0.6324	0.9912	0.6226-0.6421
Marshalls	**36**	**5-46**	**0.7922**	**0.9928**	**0.7694-0.8150**	**0.6127**	**0.9868**	**0.5888-0.6367**
Micronesia	**263**	**5-90**	**0.8192**	**0.9954**	**0.8125-0.8260**	**0.6340**	**0.9905**	**0.6264-0.6415**

C) Taxonomic Structure Across Reef Types: Taxonomic Structure across four reef types: Outer, Patch/back, Channel and Inner across 263 sites in Micronesia.

Table C1. The power law relationship between number of genera/families to number of species across Outer, Patch/back, Channel and Inner reef types throughout Micronesia. Here, n represents the number of sites. The scaling exponent for both the GS and FS relationship proved to be invariant across the four reef types (95% CI overlap).

Reef Type	*n*	*Generic Exponent*	R^2	*95% CI*	*Familial Exponent*	R^2	*95% CI*
Channel	28	0.8095	0.9927	0.7827-0.8363	0.6124	0.9915	0.5905-0.6344
Inner	33	0.8112	0.9911	0.7840-0.8384	0.6437	0.9831	0.6138-0.6737
Outer	135	0.8226	0.9962	0.8139-0.8313	0.6343	0.9926	0.6249-0.6436
Patch/Back	67	0.8195	0.9963	0.8074-0.8317	0.6401	0.9886	0.6233-0.6569

D) Taxonomic Revisions and Community Size Taxonomic Structure: Taxonomic structure of coral communities in Micronesia at different compounded community scale sizes for two different taxonomic revisions.

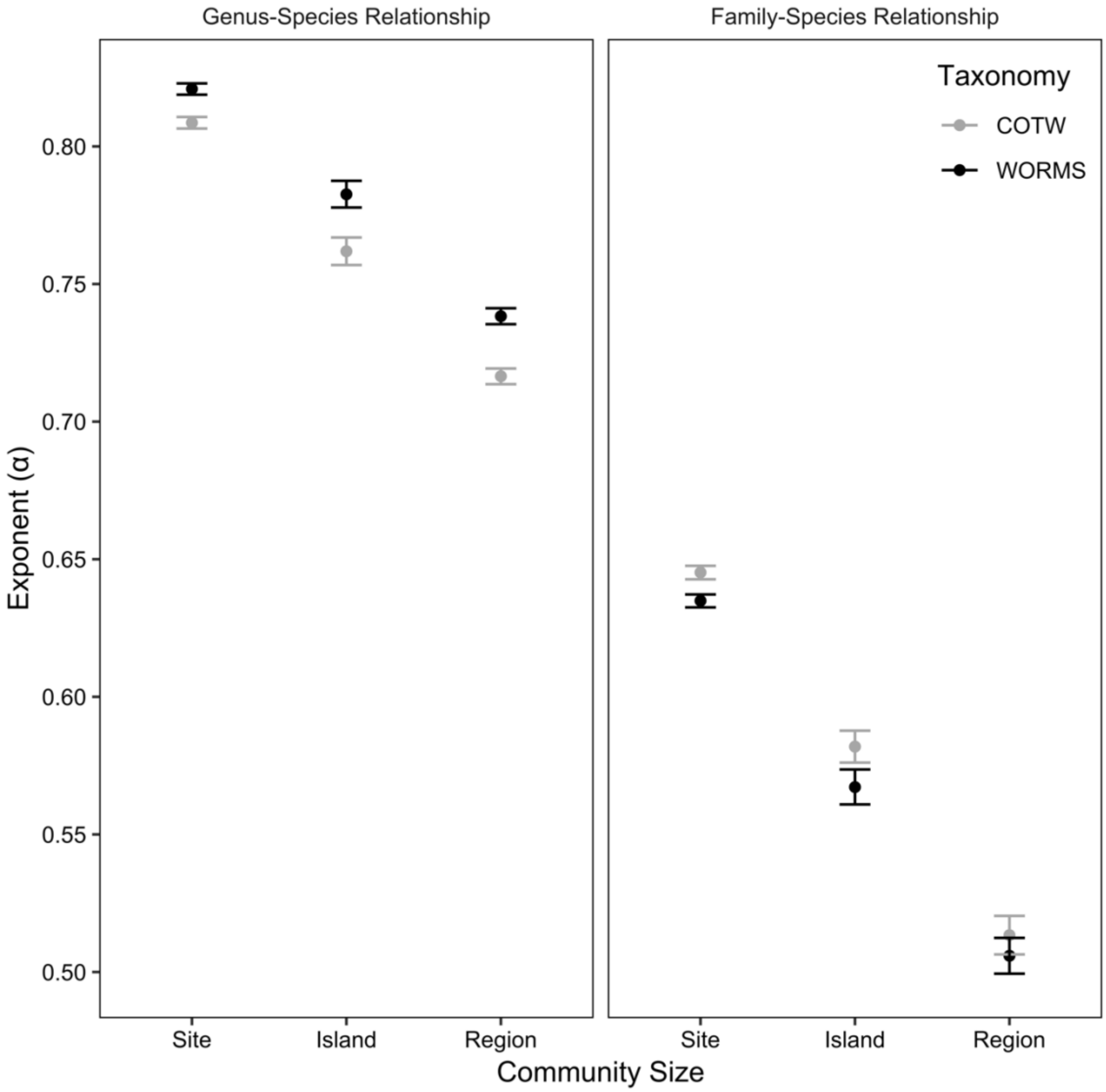

Figure D1. Exponents of the genus-to-species and family-to-species relationships of two different taxonomic revisions at different compounded community scale sizes. Black represents the World Register of Marine Species (WORMS) taxonomic revision, while gray represents Veron's Corals of The World (COTW) taxonomic revision. In the PH data-set the WORMS taxonomic revision contained 337 Species, 67 Genera, and 16 Families (including scleractinian incertae sedis). The COTW taxonomic revision contained 344 Species, 60 Genera, and 16 Families.

E) Trait Taxonomic Structure: The relationship between number of Genera (top) and number of Families (bottom) to number of species across 263 sites in Micronesia for subsets of two reproductive traits (sexual system & Larval Development). Trait data was downloaded from https://coraltraits.org, and traits were assigned to the genus level.

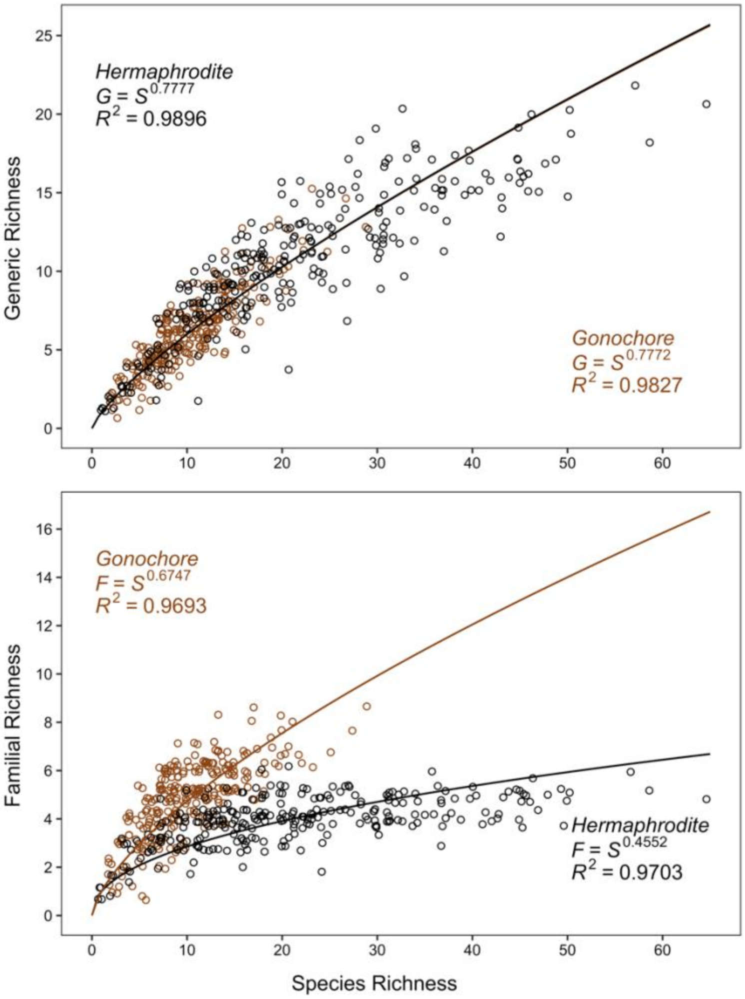

Figure E1. The relationship between number of genera (top) and number of families (bottom) to number of species across 263 sites in Micronesia for subsets (Gonochore & Hermaphrodite) of the coral reproductive trait of sexual system. Gonochore communities are represented in light brown, while Hermaphrodite communities are represented in black. Specifically, Gonochore (GS 95% CI: 0.7646-0.7897, FS 95% CI: 0.6601-0.6893) and Hermaphrodite (GS 95% CI: 0.7680-0.7874, FS 95% CI: 0.4455-0.4649) communities proved to statistically indifferent for the GS relationship and statistically different for the FS relationship, as measured by 95% CI overlap (or lack thereof).

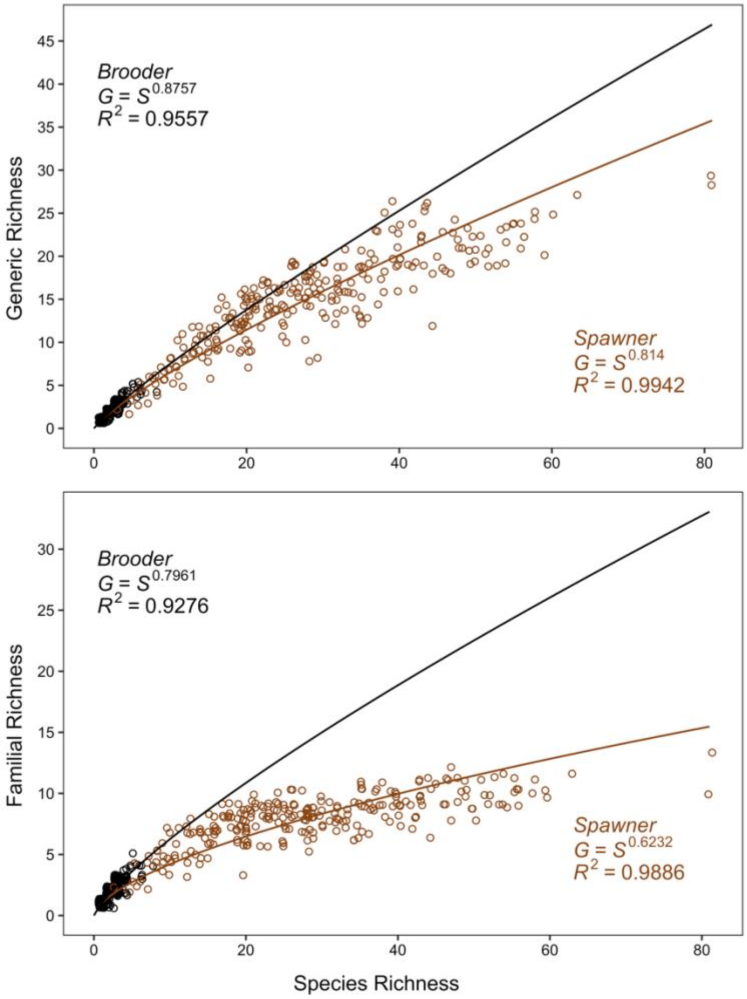

Figure E2. The relationship between number of genera (top) and number of families (bottom) to number of species across 263 sites in Micronesia for subsets (Brooders & Spawners) of the coral reproductive trait of larval development. Communities of Spawners are represented in light brown, while communities of Brooders are represented in black. Specifically, communities of Brooding corals (GS 95% CI: 0.8503-0.9011, FS 95% CI: 0.7661-0.8260) have statistically larger scaling exponents than communities of Spawning corals (GS 95% CI: 0.8064-0.8215, FS 95% CI: 0.6151-0.6314).

F) Null Model Graphical Results: Graphical representation of three Null Model approaches inferring local ecological processes shaping community structure in Micronesia. For each higher-taxon, we plotted species richness against higher taxa richness and applied a power law fit.

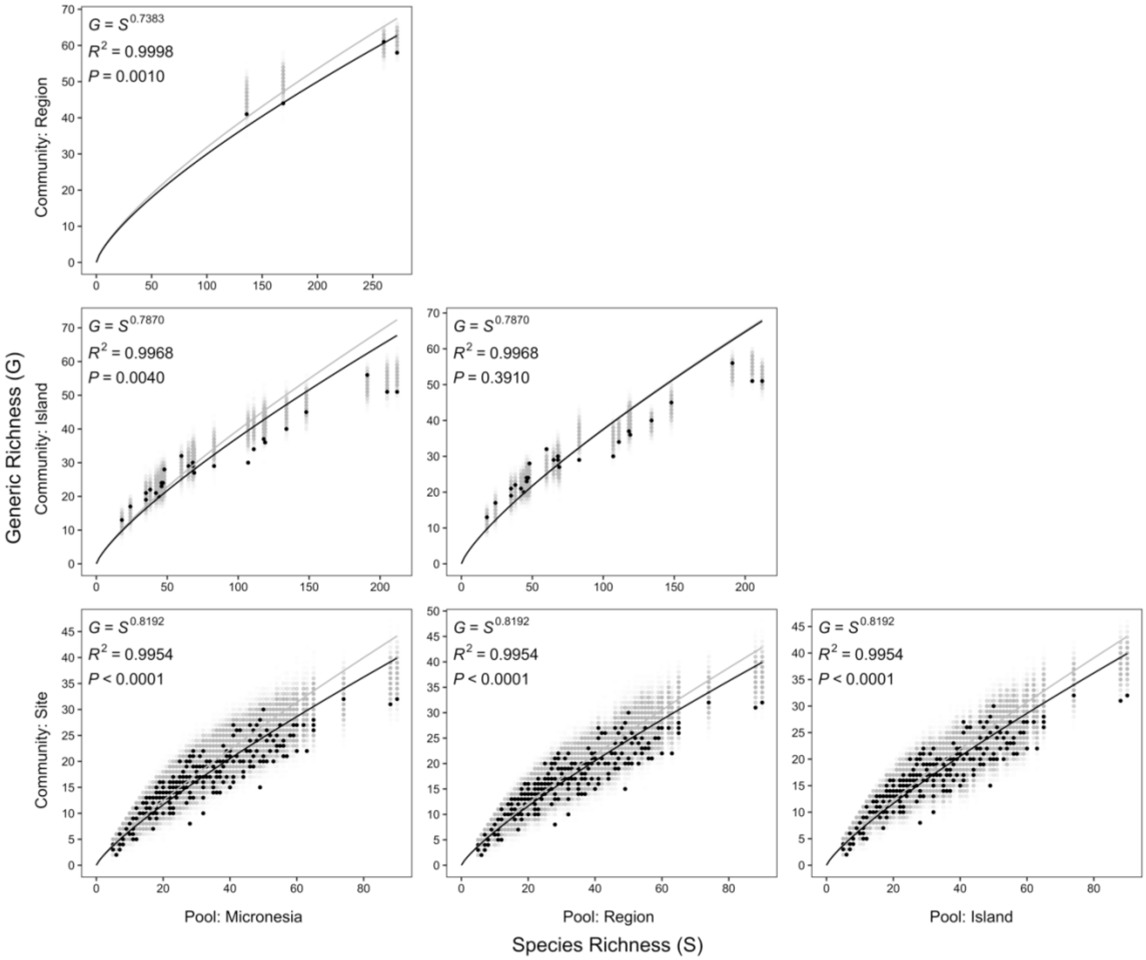

Figure F1. Matrix of graphical representations of Null Model 1 approach at different compounded community sizes (rows) and species pool sizes (columns). Black: relationship between the number of genera and number of species fit to a power law, with displayed fit equation, R2, and P-value indicating the empirical fit deviation from null expectations. Gray: Null Model simulations (1000) with mean simulation fit.

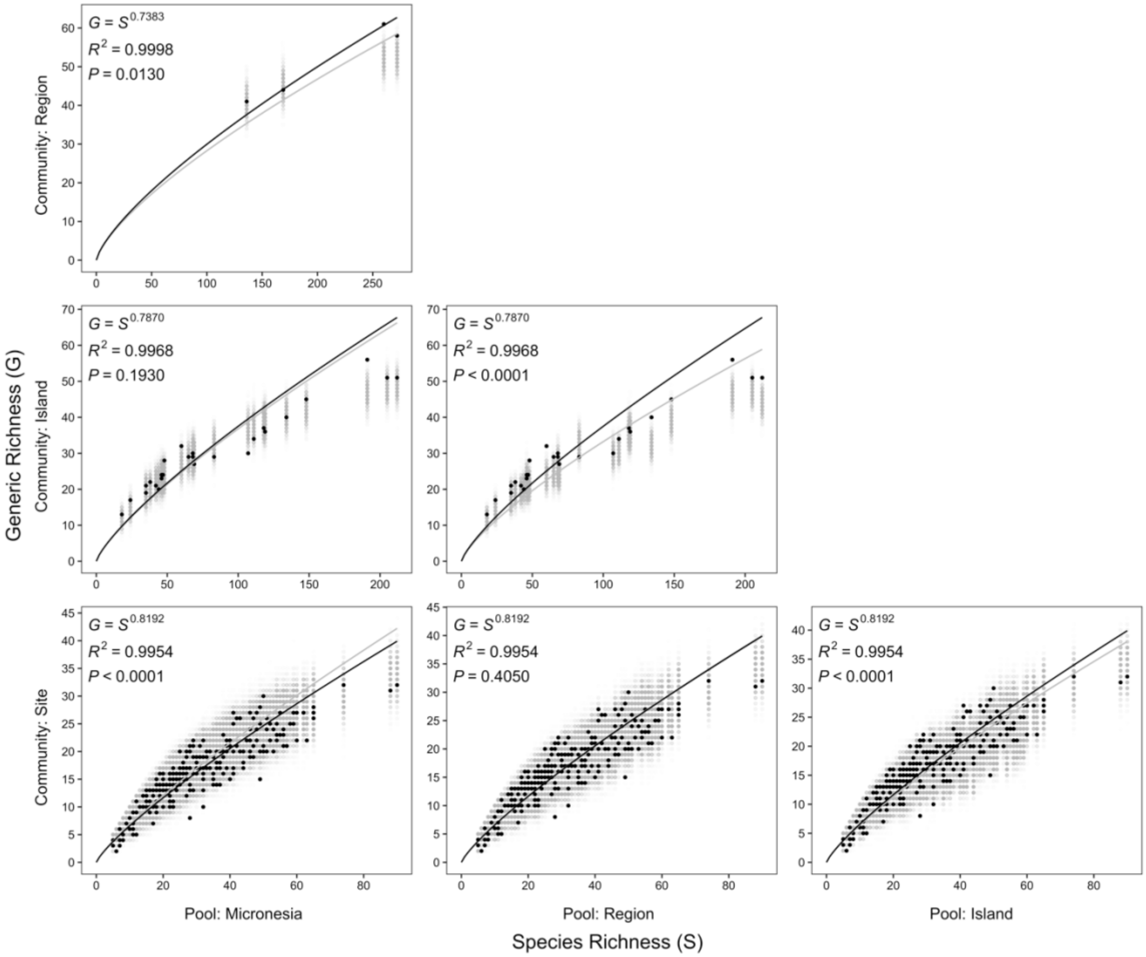

Figure F2. Matrix of graphical representations of Null Model 2 approach at different compounded community sizes (rows) and species pool sizes (columns). Black: relationship between the number of genera and number of species fit to a power law, with displayed fit equation, R_2, and P-value indicating the empirical fit deviation from null expectations. Gray: Null Model simulations (1000) with mean simulation fit.

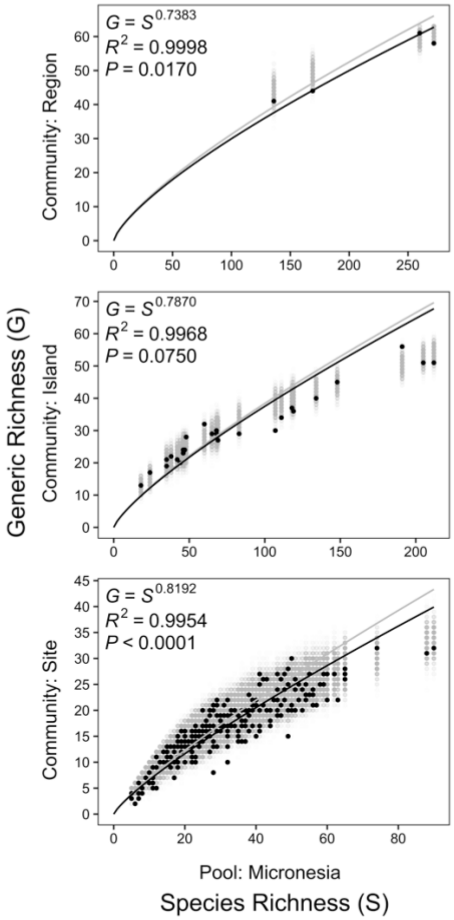

Figure F3. Matrix of graphical representations of Null Model 3 approach at different compounded community sizes (rows). Black: relationship between the number of genera and number of species fit to a power law, with displayed fit equation, R_2, and P-value indicating the empirical fit deviation from null expectations. Gray: Null Model simulations (1000) with mean simulation fit.

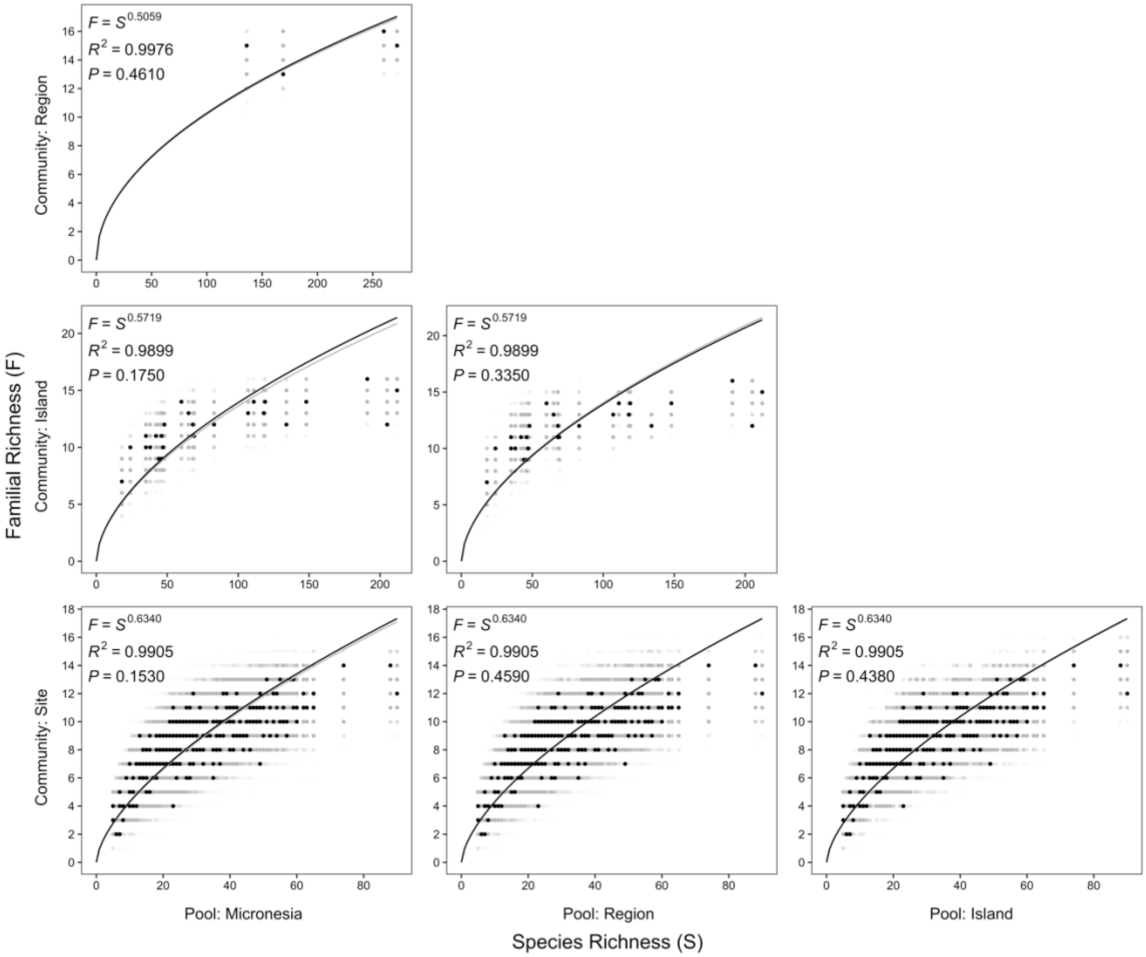

Figure F4. Matrix of graphical representations of Null Model 2 approach at different compounded community sizes (rows) and species pool sizes (columns). Black: relationship between the number of families and number of species fit to a power law, with displayed fit equation, R2, and P-value indicating the empirical fit deviation from null expectations. Gray: Null Model simulations (1000) with mean simulation fit.

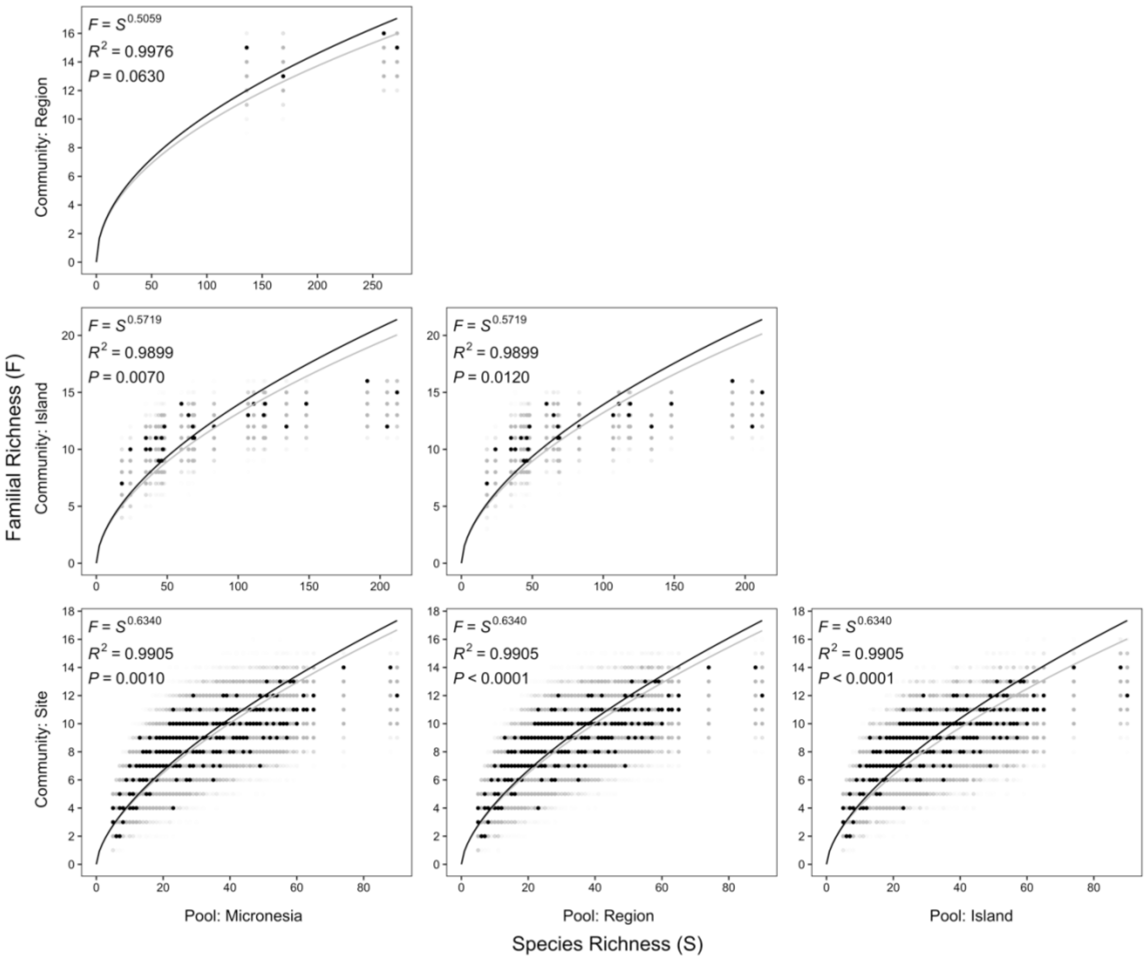

Figure F5. Matrix of graphical representations of Null Model 2 approach at different compounded community sizes (rows) and species pool sizes (columns). Black: relationship between the number of families and number of species fit to a power law, with displayed fit equation, R_2, and P-value indicating the empirical fit deviation from null expectations. Gray: Null Model simulations (1000) with mean simulation fit.

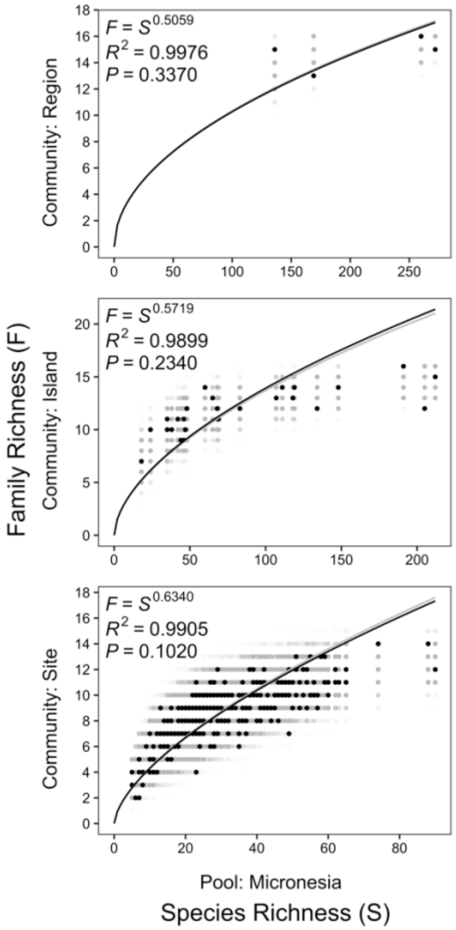

Figure F6. Matrix of graphical representations of Null Model 3 approach at different compounded community sizes (rows). Black: relationship between the number of families and number of species fit to a power law, with displayed fit equation, R2, and P-value indicating the empirical fit deviation from null expectations. Gray: Null Model simulations (1000) with mean simulation fit.

G) Null Model Table Results: Table representation of three Null Model approaches inferring local ecological processes shaping community structure in Micronesia and the four Regions of interest in this study.

Table G1. Null Model 1 results for the relationship between number of genera and number of species for Micronesia and the four Regions of interest at different compounded community scales and species pool sizes. Here, the P-value represents the significance of empirical exponent deviation from the null distribution of exponents generated from 1000 simulations, computed via an empirical distribution function. 95% CI are estimated using quantiles from the null distribution.

Region	*Community Scale*	*Exponent*	*R^2*	*Pool*	*Mean Null Exponent*	*R^2*	*P-value*	*95% CI*
Micronesia	Site	0.8192	0.9954	Micronesia	0.8417	0.9974	$p < 0.001$***	0.8372-0.8458
Micronesia	Site	0.8192	0.9954	Region	0.8350	0.9974	$p < 0.001$***	0.8306-0.8395
Micronesia	Site	0.8192	0.9954	Island	0.8365	0.9968	$p < 0.001$***	0.8324-0.8405
Micronesia	Island	0.7870	0.9968	Micronesia	0.7994	0.9977	0.0040**	0.7916-0.8072
Micronesia	Island	0.7870	0.9968	Region	0.7880	0.9977	0.3910	0.7811-0.7952
Micronesia	Region	0.7383	0.9998	Micronesia	0.7513	0.9994	0.0010**	0.7427-0.7597
Marianas	Site	0.8501	0.9961	Micronesia	0.8467	0.9974	0.2540	0.8368-0.8562
Marianas	Site	0.8501	0.9961	Region	0.8396	0.9975	0.0120*	0.8304-0.8485
Marianas	Site	0.8501	0.9961	Island	0.8510	0.9964	0.4190	0.8432-0.8587
Marianas	Island	0.8198	0.9980	Micronesia	0.8235	0.9984	0.3140	0.8074-0.8387
Marianas	Island	0.8198	0.9980	Region	0.8102	0.9983	0.0840	0.7969-0.8230
West Carolines	Site	0.8067	0.9975	Micronesia	0.8258	0.9983	$p < 0.001$***	0.8170-0.8343
West Carolines	Site	0.8067	0.9975	Region	0.8362	0.9984	$p < 0.001$***	0.8283-0.8444
West Carolines	Site	0.8067	0.9975	Island	0.8335	0.9983	$p < 0.001$***	0.8255-0.8411
West Carolines	Island	0.7548	0.9997	Micronesia	0.7659	0.9991	0.0620	0.7522-0.7791
West Carolines	Island	0.7548	0.9997	Region	0.7705	0.9990	0.0020**	0.7595-0.7806
East Carolines	Site	0.8168	0.9958	Micronesia	0.8440	0.9974	$p < 0.001$***	0.8378-0.8504
East Carolines	Site	0.8168	0.9958	Region	0.8374	0.9973	$p < 0.001$***	0.8305-0.8442
East Carolines	Site	0.8168	0.9958	Island	0.8367	0.9970	$p < 0.001$***	0.8310-0.8426
East Carolines	Island	0.7794	0.9969	Micronesia	0.7915	0.9979	0.0320*	0.7788-0.8035
East Carolines	Island	0.7794	0.9969	Region	0.7814	0.9976	0.3760	0.7697-0.7937
Marshalls	Site	0.7922	0.9930	Micronesia	0.8496	0.9970	$p < 0.001$***	0.8359-0.8636
Marshalls	Site	0.7922	0.9930	Region	0.8156	0.9963	0.0020**	0.8009-0.8294
Marshalls	Site	0.7922	0.9930	Island	0.8139	0.9954	0.0010**	0.7998-0.8273
Marshalls	Island	0.7516	0.9993	Micronesia	0.7905	0.9994	$p < 0.001$***	0.7717-0.8087
Marshalls	Island	0.7516	0.9993	Region	0.7622	0.9995	0.1100	0.7448-0.7774

Table G2. Null Model 2 results for the relationship between number of genera and number of species for Micronesia and the four Regions of interest at different compounded community scales and species pool sizes. Here, the P-value represents the significance of empirical exponent deviation from the null distribution of exponents generated from 1000 simulations, computed via an empirical distribution function. 95% CI are estimated using quantiles from the null distribution.

Region	*Community Scale*	*Exponent*	*R^2*	*Pool*	*Mean Null Exponent*	*R^2*	*P-value*	*95% CI*
Micronesia	Site	0.8192	0.9954	Micronesia	0.8318	0.9971	$p < 0.001$***	0.8270-0.8360
Micronesia	Site	0.8192	0.9954	Region	0.8198	0.9968	0.4050	0.8153-0.8245
Micronesia	Site	0.8192	0.9954	Island	0.8087	0.9961	$p < 0.001$***	0.8042-0.8130
Micronesia	Island	0.7870	0.9968	Micronesia	0.7829	0.9969	0.1900	0.7746-0.7913
Micronesia	Island	0.7870	0.9968	Region	0.7608	0.9967	$p < 0.001$***	0.7522-0.7689
Micronesia	Region	0.7383	0.9998	Micronesia	0.7258	0.9990	0.0130*	0.7137-0.7364
Marianas	Site	0.8501	0.9961	Micronesia	0.8376	0.9972	0.0050**	0.8275-0.8475
Marianas	Site	0.8501	0.9961	Region	0.8184	0.9967	$p < 0.001$***	0.8083-0.8289
Marianas	Site	0.8501	0.9961	Island	0.8041	0.9957	$p < 0.001$***	0.7938-0.8131
Marianas	Island	0.8198	0.9980	Micronesia	0.8111	0.9981	0.1510	0.7947-0.8270
Marianas	Island	0.8198	0.9980	Region	0.7817	0.9974	$p < 0.001$***	0.7666-0.7972
West Carolines	Site	0.8067	0.9975	Micronesia	0.8138	0.9980	0.0780	0.8039-0.8226
West Carolines	Site	0.8067	0.9975	Region	0.8208	0.9981	0.0020**	0.8111-0.8293
West Carolines	Site	0.8067	0.9975	Island	0.8117	0.9975	0.1420	0.8033-0.8204
West Carolines	Island	0.7548	0.9997	Micronesia	0.7441	0.9986	0.0860	0.7270-0.7596
West Carolines	Island	0.7548	0.9997	Region	0.7431	0.9984	0.0620	0.7269-0.7576
East Carolines	Site	0.8168	0.9958	Micronesia	0.8343	0.9971	$p < 0.001$***	0.8277-0.8414
East Carolines	Site	0.8168	0.9958	Region	0.8256	0.9969	0.0060**	0.8188-0.8320
East Carolines	Site	0.8168	0.9958	Island	0.8150	0.9965	0.3040	0.8083-0.8215
East Carolines	Island	0.7794	0.9969	Micronesia	0.7735	0.9971	0.2070	0.7580-0.7877
East Carolines	Island	0.7794	0.9969	Region	0.7591	0.9966	0.0040**	0.7439-0.7732
Marshalls	Site	0.7922	0.9930	Micronesia	0.8409	0.9967	$p < 0.001$***	0.8271-0.8538
Marshalls	Site	0.7922	0.9930	Region	0.7989	0.9955	0.1860	0.7840-0.8137
Marshalls	Site	0.7922	0.9930	Island	0.7877	0.9941	0.2840	0.7719-0.8031
Marshalls	Island	0.7516	0.9993	Micronesia	0.7725	0.9991	0.0280*	0.7512-0.7941
Marshalls	Island	0.7516	0.9993	Region	0.7273	0.9989	0.0090**	0.7054-0.7478

Table G3. Null Model 3 results for the relationship between number of genera and number of species for Micronesia and the four Regions of interest at different compounded community scales. Here, the P-value represents the significance of empirical exponent deviation from the null distribution of exponents generated from 1000 simulations, computed via an empirical distribution function. 95% CI are estimated using quantiles from the null distribution.

Region	*Community Scale*	*Exponent*	*R^2*	*Pool*	*Mean Null Exponent*	*R^2*	*P-value*	*95% CI*
Micronesia	Site	0.8192	0.9954	Micronesia	0.8375	0.9973	$p < 0.001$***	0.8336-0.8415
Micronesia	Island	0.7870	0.9968	Micronesia	0.7921	0.9974	0.0750	0.7851-0.7988
Micronesia	Region	0.7383	0.9998	Micronesia	0.7475	0.9995	0.0170*	0.7393-0.7551
Marianas	Site	0.8501	0.9961	Micronesia	0.8459	0.9974	0.1600	0.8374-0.8543
Marianas	Island	0.8198	0.9980	Micronesia	0.8185	0.9982	0.4260	0.8048-0.8322
West Carolines	Site	0.8067	0.9975	Micronesia	0.8159	0.9981	0.0060**	0.8084-0.8229
West Carolines	Island	0.7548	0.9997	Micronesia	0.7573	0.9991	0.3530	0.7456-0.7696
East Carolines	Site	0.8168	0.9958	Micronesia	0.8404	0.9974	$p < 0.001$***	0.8340-0.8461
East Carolines	Island	0.7794	0.9969	Micronesia	0.7840	0.9976	0.2310	0.7722-0.7952
Marshalls	Site	0.7922	0.9930	Micronesia	0.8462	0.9970	$p < 0.001$***	0.8339-0.8584
Marshalls	Island	0.7516	0.9993	Micronesia	0.7793	0.9994	0.0010**	0.7617-0.7958

Table G4. Null Model 1 results for the relationship between number of families and number of species for Micronesia and the four Regions of interest at different compounded community scales and species pool sizes. Here, the P-value represents the significance of empirical exponent deviation from the null distribution of exponents generated from 1000 simulations, computed via an empirical distribution function. 95% CI are estimated using quantiles from the null distribution.

Region	*Community Scale*	*Exponent*	*R^2*	*Pool*	*Mean Null Exponent*	*R^2*	*P-value*	*95% CI*
Micronesia	Site	0.6340	0.9905	Micronesia	0.6311	0.9914	0.1530	0.6254-0.6366
Micronesia	Site	0.6340	0.9905	Region	0.6337	0.9914	0.4590	0.6276-0.6391
Micronesia	Site	0.6340	0.9905	Island	0.6336	0.9906	0.4380	0.6285-0.6388
Micronesia	Island	0.5719	0.9899	Micronesia	0.5672	0.9917	0.1750	0.5576-0.5769
Micronesia	Island	0.5719	0.9899	Region	0.5737	0.9901	0.3350	0.5653-0.5825
Micronesia	Region	0.5059	0.9976	Micronesia	0.5044	0.9983	0.4610	0.4927-0.5155
Marianas	Site	0.6652	0.9920	Micronesia	0.6394	0.9918	$p < 0.001$***	0.6271-0.6518
Marianas	Site	0.6652	0.9920	Region	0.6567	0.9929	0.0930	0.6434-0.6689
Marianas	Site	0.6652	0.9920	Island	0.6562	0.9915	0.0330*	0.6460-0.6659
Marianas	Island	0.6191	0.9968	Micronesia	0.6016	0.9946	0.0300*	0.5838-0.6195
Marianas	Island	0.6191	0.9968	Region	0.6218	0.9955	0.3720	0.6039-0.6395
West Carolines	Site	0.6021	0.9960	Micronesia	0.6053	0.9943	0.2880	0.5955-0.6157
West Carolines	Site	0.6021	0.9960	Region	0.6049	0.9942	0.2800	0.5948-0.6148
West Carolines	Site	0.6021	0.9960	Island	0.6021	0.9938	0.4960	0.5918-0.6126
West Carolines	Island	0.5139	0.9943	Micronesia	0.5222	0.9968	0.1250	0.5048-0.5387
West Carolines	Island	0.5139	0.9943	Region	0.5260	0.9973	0.0660	0.5090-0.5389
East Carolines	Site	0.6381	0.9910	Micronesia	0.6345	0.9915	0.2090	0.6259-0.6428
East Carolines	Site	0.6381	0.9910	Region	0.6381	0.9917	0.4960	0.6296-0.6463
East Carolines	Site	0.6381	0.9910	Island	0.6387	0.9909	0.4380	0.6309-0.6464
East Carolines	Island	0.5596	0.9906	Micronesia	0.5560	0.9919	0.3430	0.5395-0.5711
East Carolines	Island	0.5596	0.9906	Region	0.5566	0.9915	0.3430	0.5425-0.5708
Marshalls	Site	0.6127	0.9872	Micronesia	0.6443	0.9902	$p < 0.001$***	0.6270-0.6617
Marshalls	Site	0.6127	0.9872	Region	0.6216	0.9893	0.1490	0.6020-0.6389
Marshalls	Site	0.6127	0.9872	Island	0.6237	0.9901	0.0950	0.6072-0.6405
Marshalls	Island	0.5382	0.9979	Micronesia	0.5513	0.9978	0.1580	0.5302-0.5718
Marshalls	Island	0.5382	0.9979	Region	0.5369	0.9982	0.4330	0.5173-0.5501

Table G5. Null Model 2 results for the relationship between number of families and number of species for Micronesia and the four Regions of interest at different compounded community scales and species pool sizes. Here, the P-value represents the significance of empirical exponent deviation from the null distribution of exponents generated from 1000 simulations, computed via an empirical distribution function. 95% CI are estimated using quantiles from the null distribution.

Region	*Community Scale*	*Exponent*	*R^2*	*Pool*	*Mean Null Exponent*	*R^2*	*P-value*	*95% CI*
Micronesia	Site	0.6340	0.9905	Micronesia	0.6252	0.9909	0.0010**	0.6193-0.6308
Micronesia	Site	0.6340	0.9905	Region	0.6245	0.9906	$p < 0.001$***	0.6188-0.6296
Micronesia	Site	0.6340	0.9905	Island	0.6165	0.9895	$p < 0.001$***	0.6107-0.6218
Micronesia	Island	0.5719	0.9899	Micronesia	0.5597	0.9908	0.0070**	0.5490-0.5692
Micronesia	Island	0.5719	0.9899	Region	0.5605	0.9894	0.0120*	0.5498-0.5707
Micronesia	Region	0.5059	0.9976	Micronesia	0.4943	0.9978	0.0630	0.4810-0.5064
Marianas	Site	0.6652	0.9920	Micronesia	0.6337	0.9914	$p < 0.001$***	0.6200-0.6460
Marianas	Site	0.6652	0.9920	Region	0.6421	0.9917	$p < 0.001$***	0.6286-0.6548
Marianas	Site	0.6652	0.9920	Island	0.6236	0.9890	$p < 0.001$***	0.6112-0.6365
Marianas	Island	0.6191	0.9968	Micronesia	0.5956	0.9941	0.0050**	0.5750-0.6135
Marianas	Island	0.6191	0.9968	Region	0.6052	0.9944	0.0810	0.5848-0.6247
West Carolines	Site	0.6021	0.9960	Micronesia	0.5989	0.9938	0.2700	0.5877-0.6097
West Carolines	Site	0.6021	0.9960	Region	0.5974	0.9936	0.1860	0.5868-0.6081
West Carolines	Site	0.6021	0.9960	Island	0.5916	0.9928	0.0230*	0.5805-0.6020
West Carolines	Island	0.5139	0.9943	Micronesia	0.5126	0.9964	0.4920	0.4933-0.5323
West Carolines	Island	0.5139	0.9943	Region	0.5124	0.9963	0.4920	0.4888-0.5298
East Carolines	Site	0.6381	0.9910	Micronesia	0.6288	0.9910	0.0230*	0.6196-0.6378
East Carolines	Site	0.6381	0.9910	Region	0.6312	0.9911	0.0430*	0.6229-0.6390
East Carolines	Site	0.6381	0.9910	Island	0.6258	0.9900	0.0010**	0.6178-0.6336
East Carolines	Island	0.5596	0.9906	Micronesia	0.5479	0.9912	0.0730	0.5300-0.5637
East Carolines	Island	0.5596	0.9906	Region	0.5482	0.9908	0.0840	0.5318-0.5636
Marshalls	Site	0.6127	0.9872	Micronesia	0.6385	0.9896	0.0040**	0.6203-0.6564
Marshalls	Site	0.6127	0.9872	Region	0.6109	0.9879	0.4340	0.5923-0.6292
Marshalls	Site	0.6127	0.9872	Island	0.6081	0.9882	0.3040	0.5902-0.6250
Marshalls	Island	0.5382	0.9979	Micronesia	0.5438	0.9976	0.3560	0.5175-0.5663
Marshalls	Island	0.5382	0.9979	Region	0.5223	0.9976	0.0630	0.4963-0.5439

Table G6. Null Model 3 results for the relationship between number of families and number of species for Micronesia and the four Regions of interest at different compounded community scales. Here, the P-value represents the significance of empirical exponent deviation from a null distribution of exponents generated from 1000 simulations, computed via an empirical distribution function. 95% CI are estimated using quantiles from the null distribution.

Region	*Community Scale*	*Exponent*	*R^2*	*Pool*	*Mean Null Exponent*	*R^2*	*P-value*	*95% CI*
Micronesia	Site	0.6340	0.9905	Micronesia	0.6374	0.9918	0.1020	0.6322-0.6423
Micronesia	Island	0.5719	0.9899	Micronesia	0.5686	0.9913	0.2340	0.5601-0.5774
Micronesia	Region	0.5059	0.9976	Micronesia	0.5071	0.9986	0.3370	0.4962-0.5156
Marianas	Site	0.6652	0.9920	Micronesia	0.6457	0.9926	$p < 0.001$***	0.6339-0.6564
Marianas	Island	0.6191	0.9968	Micronesia	0.6055	0.9947	0.0710	0.5873-0.6230
West Carolines	Site	0.6021	0.9960	Micronesia	0.6094	0.9945	0.0680.	0.5992-0.6184
West Carolines	Island	0.5139	0.9943	Micronesia	0.5214	0.9967	0.1350	0.5051-0.5344
East Carolines	Site	0.6381	0.9910	Micronesia	0.6417	0.9919	0.1840	0.6340-0.6491
East Carolines	Island	0.5596	0.9906	Micronesia	0.5561	0.9916	0.3170	0.5416-0.5708
Marshalls	Site	0.6127	0.9872	Micronesia	0.6506	0.9906	$p < 0.001$***	0.6348-0.6661
Marshalls	Island	0.5382	0.9979	Micronesia	0.5512	0.9980	0.1210	0.5318-0.5713

H) Taxonomic Richness by Region: Taxonomic Richness of each Region for each taxonomic rank (Species, Genus, Family).

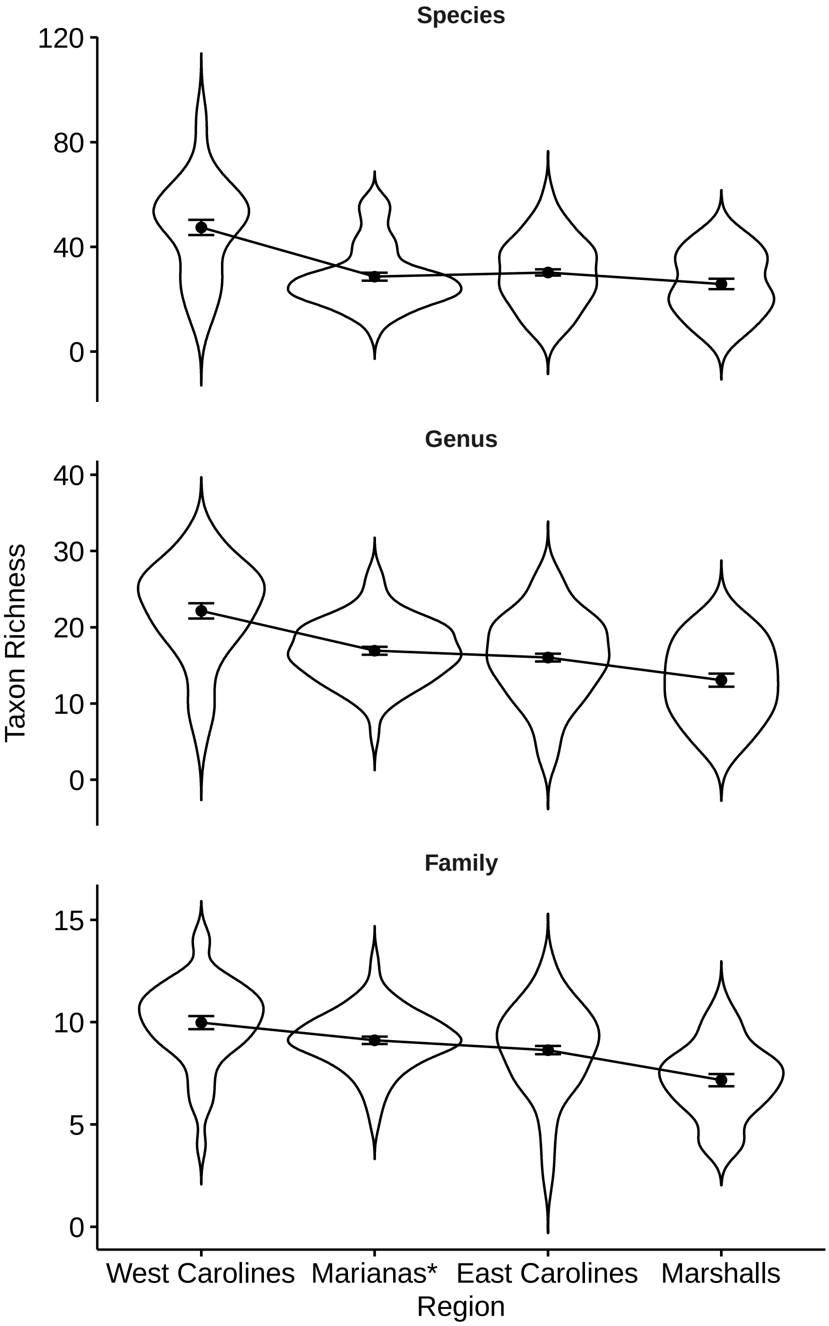

Figure H1. Violin plot of the taxonomic richness (species, genus, family) of coral reef communities in each Region surveyed arranged by increasing longitude, with mean and standard deviation. The Marianas* data was collected with different size quadrats than other regions. Despite this, there exists a general decrease in taxonomic richness from East Asia Westward across the Pacific, a pattern first noted by Vaughan & Wells, 1943.