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A test of trophic and functional island biogeography theory with the avifauna of a continental archipelago

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Abstract

1. The classical MacArthur–Wilson theory of island biogeography (TIB) emphasizes the role of island area and isolation in determining island biotas, but is neutral with respect to species differences that could affect community assembly and persistence. Recent extensions of island biogeography theory address how functional differences among species may lead to non-random community assembly processes and different diversity–area scaling patterns. First, the trophic TIB considers how diversity scaling varies across trophic position in a community, with species at higher trophic levels being most strongly influenced by island area. Second, further extensions have predicted how trait distributions, and hence functional diversity, should scale with area. Trait-based theory predicts richness-corrected functional diversity should be low on small islands but converge to null on larger islands. Conversely, competitive assembly predicts high diversity on small islands converging to null with increasing size.

2. However, despite mounting interest in diversity–area relationships across different dimensions of diversity, these predictions derived from theory have not been extensively tested across taxa and island systems.

3. Here, we develop and test predictions of the trophic TIB and extensions to functional traits, by examining the diversity–area relationship across multiple trophic ranks and dimensions of avian biodiversity in the Ryūkyū archipelago of Japan.

4. We find evidence for a positive species– and phylogenetic diversity–area relationship, but functional diversity was not strongly affected by island area. Counter to the trophic TIB, we found no differences in the slopes of species–area relationships among trophic ranks, although slopes varied among trophic guilds at the same rank. We revealed differential assembly of trophic ranks, with evidence of trait-based assembly of intermediate predators but otherwise neutral community assembly.

5. Our results suggest that niche space differs among trophic guilds of birds, but that differences are mostly not predicted by current extensions of island biogeography theory. While predicted patterns do not fit the empirical data well in this case, the development of such theory provides a useful framework to analyse island patterns from new perspectives. The application of empirical datasets such as ours should help provide a basis for developing further iterations of island biogeography theory.

1 | INTRODUCTION

MacArthur and Wilson's (1967) theory of island biogeography (TIB) posits that ecological communities on islands are random samples from a shared regional species pool, with equilibrial richness determined by island area and isolation (MacArthur & Wilson, 1967; Patiño et al., 2017; Si, Baselga, Leprieur, Song, & Ding, 2016; Simberloff & Wilson, 1970). A positive relationship between island area and species richness is a widely observed pattern in ecology (e.g. Connor & McCoy, 1979; Lomolino, 2000). MacArthur and Wilson's (1967) theory implicitly assumes that while colonization–extinction dynamics drive the species–area relationship, community composition is random and unbiased by species identities or differences in traits. In other words, the TIB assumes functional equivalency of species, since all species present in the regional species pool are equally likely to colonize and persist on a given island.

Recent work has begun to address this limitation by incorporating functional and ecological dimensions into island biogeography theory. Ecological communities are hugely diverse, consisting of species which differ in their life histories, functional roles, trophic interactions and evolutionary histories (Wilson, 1999), all of which can affect colonization–extinction probabilities and community assembly (Diamond, 1975; MacArthur & Wilson, 1967; Simberloff & Wilson, 1970). Thus, island communities are unlikely to be randomly assembled, but MacArthur and Wilson's (1967) TIB serves as a null model against which to test extensions of this theory which relax the assumption of species equivalency.

One such extension is the trophic theory of island biogeography (trophic TIB) which builds upon classical island biogeography theory by considering the trophic structure of communities (Holt, 2010; Holt, Lawton, Polis, & Martinez, 1999; Matias et al., 2017; Stier, Hanson, Holbrook, Schmitt, & Brooks, 2014, see also Seibold, Cadotte, MacIvor, Thorn, & Müller, 2018). The trophic TIB predicts that species at higher trophic levels should be more strongly regulated by island area than species at lower trophic levels (Gravel, Massol, Canard, Mouillot, & Mouquet, 2011). This is primarily because of two mechanisms: one based on colonization and the other on extinction. (a) Predators necessarily depend on the presence of their prey on an island. If a prey species is not present on an island, then the predator cannot colonize that island (Gravel et al., 2011). (b) Often in nature, species at higher trophic levels are regulated via changes in the abundance of prey species populations (Alonso, Pinyol-Gallemí, Alcoverro, & Arthur, 2015). These systems are more prone to bottom-up trophic cascades which cause local extinction of predatory species in response to changes further down the food chain (Jacquet, Mouillot, Kulbicki, & Gravel, 2017; Massol et al., 2017). If a prey species is lost from an island,

then the predator cannot persist and faces extinction. So, predator colonization and persistence rely entirely on the presence and abundance of their prey. These processes should both be more pronounced on smaller islands, resulting in different species–area scaling relationships across trophic levels (Gravel et al., 2011; Holt, 2010; Massol et al., 2017). Indeed, of the few empirical tests of the trophic TIB to date, most find that species richness scales more steeply with island area at higher trophic levels (e.g. Gravel et al., 2011; Post, Pace, & Hairston, 2000; Roslin, Várkonyi, Koponen, Vikberg, & Nieminen, 2014). However, we still lack a robust diversity of tests of the trophic TIB's predictions across taxonomic groups and island systems.

Recently, Jacquet et al. (2017) presented a more general extension of island biogeography theory which considers the functional dimension of diversity beyond merely trophic position. Functional traits allow insight into niche space occupancy, since the diversity of these traits, measured as "functional diversity," accounts for the range of functional roles performed within a community (Petchey & Gaston, 2002; Tilman et al., 1997). Species' functional traits may bias their occurrence on an island if those traits affect colonization and extinction (McGill, Enquist, Weiher, & Westoby, 2006). The framework proposed by Jacquet et al. (2017) describes how a trait-based theory of island biogeography should influence functional trait distributions. They suggest that for any persistence-enhancing trait, the average value and variance of the trait should shift from underdispersion to converge on the mean of the regional pool as island area increases (Jacquet et al., 2017). This is because selection pressure scales inversely to island area since extinction likelihood decreases with island size (Hanski, 1989).

When considering the functional diversity of entire communities, we could thus predict a scaling of functional diversity with island area by applying the framework of Jacquet et al. (2017) to multiple traits simultaneously. If all focal traits are persistence-enhancing, then functional diversity should scale with island area in the same way as individual traits; functional diversity should be lower than expected on small islands, converging to the mean diversity of the regional species pool on larger islands, since extinction pressure is relaxed on larger islands. This would indicate a community assembly mechanism that favours trait similarity on small islands, since the trophic diversity of smaller islands should be lower initially (Jacquet et al., 2017).

Alternatively, if island community assembly is influenced by functional traits but those traits relate to competitive characteristics of species, then competitive interactions should dominate assembly mechanisms on small islands (Diamond, 1975). In this way, the functional diversity–area relationship might display the opposite trend to trait-based assembly; overdispersion on small islands converging to

mean values on large islands. Empirical tests of the functional diversity–area relationship are emerging (Ding, Feeley, Wang, Pakeman, & Ding, 2013; Karadimou, Kallimanis, Tsiripidis, & Dimopoulos, 2016; Triantis et al., 2016; Wang et al., 2013), and studies are beginning to explore the mechanisms behind this relationship (Jacquet et al., 2017; Si et al., 2017; Smith, Sandel, Kraft, & Carey, 2013; Whittaker et al., 2014).

While the functional dimension of diversity–area relationships – in terms of both trophic level (e.g. Harvey & MacDougall, 2014) and trait distributions (e.g. Jacquet et al., 2017) – has received a fair amount of attention in island biogeography, phylogenetic diversity–area scaling has been less studied (but see Helmus & Ives, 2012; Mazel et al., 2014; Si et al., 2017; Wang et al., 2013). If persistence-enhancing functional traits do not evolve too quickly, one may expect a subset of related lineages with that trait to persist on small islands, reducing phylogenetic diversity. Similarly, since small islands tend to have fewer habitat types, species sorting could reduce the range of species that can persist there. In these cases, if habitat affinity is phylogenetically conserved, then one would expect a steeper scaling of phylogenetic diversity with area than through random assembly (Helmus & Ives, 2012). Alternatively, competition should limit the persistence of related, and thus ecologically similar species on small islands, whereas larger islands could support more ecologically similar species (Diamond, 1975). All of the above hypotheses depend on some degree of phylogenetic niche conservatism, the condition that traits affecting colonization, extinction or competition do not evolve too quickly to lose phylogenetic signal. If phylogenetic signal is lost, phylogenetic structure would be random.

Non-random trophic, functional or phylogenetic processes may also interact to further bias island community composition in non-random ways. If trophic guilds are subject to differing assembly processes – either based solely on their trophic position following Gravel et al. (2011) or through the relationship between island size and trophic generalism (Piechnik, Lawler, & Martinez, 2008) – then we would expect to see different patterns of under/overdispersion scaling with island area for different trophic levels.

Here, we test recent theoretical extensions to MacArthur–Wilson's theory – which we informally term "extended island biogeography" – including the trophic theory of island biogeography (Gravel et al., 2011), and a trait-based theory of island biogeography (Jacquet et al., 2017), by examining the scaling of multiple dimensions of avian diversity across the Ryūkyū archipelago and identifying community assembly patterns across trophic levels. The Ryūkyū archipelago is a chain of continental relic islands spanning from Taiwan in the south to the Japanese main islands (southern Kyushu) in the north. Previous work in the Ryūkyūs has focused on patterns of beta diversity and island differences (e.g. Hirao, Kubota, & Murakami, 2015; Wepfer, Guénard, & Economo, 2016), but the above extensions to island biogeography theory have not been tested in this system. Theoretical predictions concerning extended island biogeography are relatively recent; thus, they have not been subject to extensive empirical tests. Accordingly, our study attempts to address this gap by testing the trophic TIB, the functional and phylogenetic diversity–area relationships and the relationship between community assembly processes and island area (Smith et al., 2013). To our knowledge, the trophic TIB has not been tested using birds as a model system. Although several studies have addressed avian diversity–area relationships (Ding et al., 2013; Si et al., 2016) and community assembly processes (Si et al., 2017), to our knowledge, the trophic TIB has not been tested with birds as a model system. Furthermore, we examine patterns of functional and phylogenetic diversity–area relationships and community assembly–area relationships across trophic levels, which to our knowledge has not been addressed in any system. This provides a framework for integrating multiple tests of extended island biogeography theory in one system and collectively allows us to begin to provide empirical feedback to interesting theoretical developments.

2 | MATERIALS AND METHODS

2.1 | Study location and species lists

Our study location was the Ryūkyū archipelago, spanning 660 miles (1,062.2 km) south from Kyushu, Japan, into the East China Sea towards Taiwan (Figure 1). The archipelago consists of 32 island groups of varying size and distance from the mainland. For each island or island group (see Figure 1), we used data from the Checklist of Birds of Okinawa (McWhirter, Ikenaga, Iozawa, Shoyama, & Takehara, 1996) and the Checklist of Japanese Birds (Ornithological Society of Japan, 2012), as organized on Avibase (Lepage, Vaidya, & Guralnick, 2014; see Supporting Information for additional citations). Species nomenclature follows the 4th edition of Howard and Moore's checklist (Christidis, 2014). From species checklists, we removed species considered accidental, extirpated or extinct, as well as species that were introduced but not established (the removal of extinct species from our study did not significant alter our results, see Supporting Information). The checklists were then split to create two distinct checklists, one for seabirds ($N = 41$, see Supporting Information) and one for all remaining species, herein termed "landbirds" ($N = 279$). As checklists were based on species occurrences, all data and indices were presence–absence rather than abundance-weighted.

2.2 | Spatial data

Data on island area were based on Adm2 shapefiles for Kyushu and Okinawa from DIVA-GIS. As most island groups fell within the universal transverse Mercator zone (UTM) 52N, data were projected to this zone, excluding those islands west of Ishigaki, which were projected to UTM zone 51N. The UTM projection minimized distortions among area, distance and geometry for a given zone of interest. Target islands were then selected and grouped according to the 32 island groups from the Japanese checklists above (McWhirter et al., 1996; Ornithological Society of Japan, 2012; see Figure 1). Latitude and longitude of island centroids were recorded, and total area for each island group was then measured using ArcGIS 10.3.
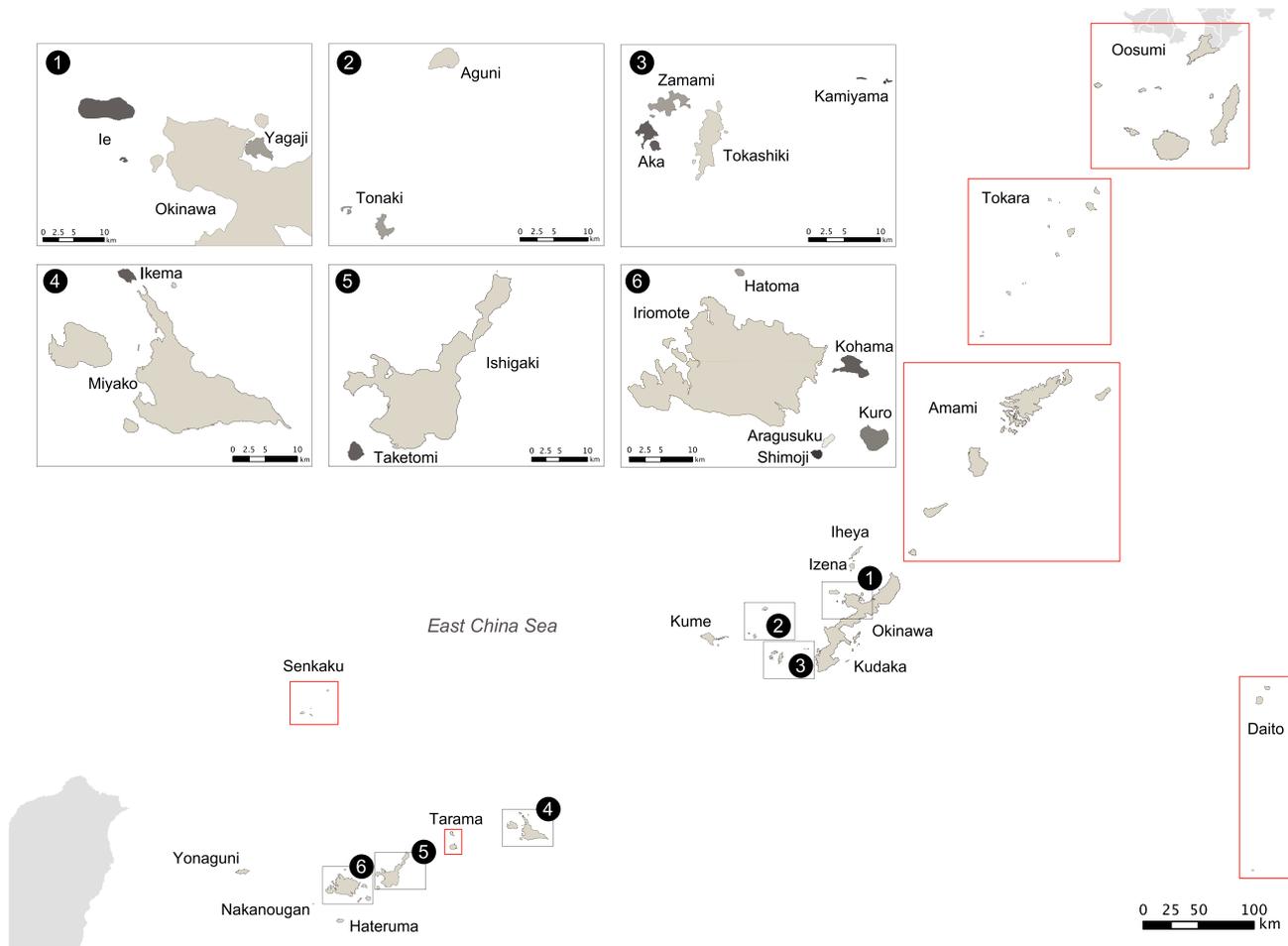
FIGURE 1 Study region: the Ryūkyū archipelago. Some "islands" are actually groups of nearby islands as included in the Avibase species checklists. Unlabelled landmasses in the bottom left and top right are Taiwan and Kyushu, Japan, respectively; neither are part of the study region. Boxes without numbers indicate island groups. Indented numbered boxes represent different islands/groups by shading

2.3 | Biodiversity indices

2.3.1 | Taxonomic diversity

We calculated taxonomic diversity for each island as the summed species richness of all bird species on a given island based on the island checklists as described above.

2.3.2 | Phylogenetic diversity

We calculated phylogenetic diversity using mean pairwise distances (PD_{MPD}) following Webb (2000), based on 1,000 phylogenetic trees downloaded from birdtree.org (Jetz, Thomas, Joy, Hartmann, & Mooers, 2012). Trees were constructed to initially match the species richness of the regional pool, with backbones constructed from Hackett et al. (2008). Trees were pruned to include only species detected on each island, and in each case, phylogenetic diversity was calculated as the mean PD_{MPD} between all species across all 1,000 transformed phylogenetic distance matrices (Webb, 2000). We also tested for phylogenetic signal of island occupancy (see Supporting Information).

2.3.3 | Functional diversity

We calculated functional diversity using mean pairwise distances (FD_{MPD}) of a functional dendrogram constructed using species' dissimilarities in their functional traits (Swenson, 2014). We selected 15 functional traits previously recognized to be functionally important in the partitioning of niche space based on resource requirements, foraging substrate use and dietary composition (Sekercioglu, 2006). Trait data were collected from Wilman et al. (2014) and Del Hoyo, Elliott, Sargatal, Christie, and Juana (2017) following methods in Ross et al. (2017), and no traits were assumed a priori to contribute more to ecosystem functioning than others (for a full list of traits and their sources, see Table S1). We first down-weighted correlated traits and scaled continuous traits (body mass and clutch size) so they approximated a Gaussian distribution. We used presence–absence community data and the Gower distance measure to calculate the functional distance between species pairs (Gower, 1971). We then performed a principal coordinates analysis (PCoA) on the distance matrix and used a subset of these PCoA axes (Table S2) as our "traits" for FD_{MPD} analysis (Laliberté & Legendre, 2010). We subset distance matrices

to include only the species detected on each island and calculated functional diversity as the FD_{MPD} between all species across each functional distance matrix (Wang et al., 2013). To check whether functional diversity analyses were diluted through use of multiple traits, we also tested for the scaling of body size with island area, since body size is expected to be under selection based on the allometric theory of island biogeography (Jacquet et al., 2017; Mazel et al., 2014).

2.4 | Null distributions

We chose the mean pairwise distance (MPD) approach to measure phylogenetic and functional diversity, since the expected value of these metrics does not change with species richness (Faith, 1992) and to make our measures of phylogenetic and functional diversity more comparable (Mazel et al., 2014). However, Swenson (2014) notes that the variance structure of these indices is not independent of species richness. We therefore used separate null distributions for both the phylogenetic and functional diversity–area relationships (see discussion in Webb, Ackerly, McPeek, & Donoghue, 2002) to determine whether observed diversity–area relationships scaled significantly differently than expected by random chance. That is, we asked whether diversity–area relationships scaled more or less positively than if their phylogenetic or functional data were randomly assigned from the Ryūkyū archipelago regional species pool. We also compared each observed island diversity value to its respective null distribution to determine whether observations were functionally and phylogenetically overdispersed or underdispersed.

2.4.1 | Phylogenetic diversity

To produce a null distribution for the PD_{MPD}–area relationship, we used an unconstrained phylogenetic swapping approach which maintains phylogeny topology (i.e. branch lengths and their distribution) but randomizes species positions in the phylogeny (Swenson, 2014). We produced null diversity–area slopes by first shuffling the species names on the constructed phylogeny 1,000,000 times (1,000 times per tree) while maintaining all other properties. We calculated PD_{MPD} for each iteration of this randomization procedure to produce 1,000,000 PD_{MPD} values for each island. We calculated standardized effect scores (see below) for the mean PD_{MPD} across all islands and the slope of the diversity–area relationship to reveal whether community assembly patterns were related to island area.

2.4.2 | Functional diversity

To produce a null distribution for the FD_{MPD}–area relationship, we used an unconstrained functional trait swapping approach which maintains island richness but randomizes species occupancy, and hence functional trait data (see Ding et al., 2013). We produced null diversity–area slopes by first shuffling the species names on the

transformed functional trait matrix 1,000,000 times, while maintaining all other properties, and calculating FD_{MPD} for each iteration. This produced 1,000,000 FD_{MPD} values for each island. As with PD_{MPD}, we then calculated standardized effect scores for the mean and slope of the diversity–area relationship to test for competitive or trait-based community assembly.

2.4.3 | Trophic ranks

For both the PD_{MPD} and FD_{MPD} null distributions of island and model slopes described above, we produced null distributions for trophic ranks individually, to compare deviation from null among trophic ranks. Distributions were generated as described except subset by species occupancy within individual trophic ranks.

2.5 | Statistical analysis

All analyses were performed in R version 3.3.2 (R Core Team, 2016) with packages *Picante* (Kembel et al., 2010) and *PhyloMeasures* (Tsirogiannis & Sandel, 2016). We performed all analyses on landbirds (presented here) and seabirds separately (see Supporting Information). To determine whether island area significantly predicted each dimension of diversity – taxonomic, phylogenetic and functional diversity – we fit generalized least squares (GLS) models to each biodiversity variable individually, using only the predictor variable island area. In all models, biodiversity values and island area values were $\log_{10}$-transformed so that model error structure was appropriate for the underlying data distribution; a Poisson fit then determined a linear diversity–area relationship in log–log space via the identity link function. In each case, the minimum adequate model was identified via Akaike's information criterion with small sample correction (AICc). Spatial coordinates were also included in all models to account for any autocorrelative effects.

To determine whether trophic ranks responded differently to island area, we calculated the diversity indices above for several subsets of our data. We grouped species into three trophic ranks based on five guilds from Wilman et al. (2014) and assigned trophic ranks based on trophic level (Roslin et al., 2014; van Noordwijk et al., 2015). Trophic ranks were apex predators (carnivores: N = 61, rank = 3), intermediate predators (insectivores: N = 159, rank = 2) and herbivores (granivores and frugivores: N = 63, rank = 1). Omnivores (N = 39) were not assigned a trophic rank as there was no clear a priori expectation about the scaling of this guild with island area. See Wilman et al. (2014) for descriptions of trophic guilds. Note that seabirds occupied only three trophic guilds (carnivores, insectivores and omnivores).

To test whether trophic ranks differed in their species–area relationships, we fit pairwise GLS models between pairs of ranks (e.g. apex predators vs. herbivores) and tested the significance of an interaction between trophic rank and island area. If interaction terms were significant, then pairs of trophic ranks differed significantly in their species–area slopes. To test whether the trophic TIB explained differences among ranks, we then fit GLS models to species richness

with an interaction between island area and trophic rank as predictor variables, where higher trophic levels were assigned larger numbers (van Noordwijk et al., 2015). We compared this model to a model where richness was predicted by island area and trophic rank additively, which assumes that species–area slopes do not differ among ranks (MacArthur & Wilson, 1967). We also asked whether there were different species–area relationships among trophic guilds of birds that were not captured by our trophic rank analysis (e.g. differences between frugivores and granivores within our herbivore rank). To do this, we conducted an exploratory analysis (see Supporting Information) to check for differences in the species–area relationship of our five trophic guilds (see above) but had no a priori prediction regarding the directionality of any differences.

For functional and phylogenetic diversity, we compared observed diversity values to their respective null distributions and identified community assembly processes by calculating standardized effect scores (SES) as the difference between the observed and expected values divided by the standard deviation of the null distribution. Standardized effect scores below −1.96 (above 1.96) indicate that communities are significantly underdispersed (overdispersed) at the alpha = 0.05 significance threshold (two-tailed test). While this tells us whether an individual island is over- or underdispersed relative to a null, it does not reveal whether the entire island set has higher or lower diversity than expected (mean across islands) or whether there is a trend with island area (Diversity ~ Area slope). Since island assemblages share species, island diversities do not vary independently in our null models, so we performed the regression on each realization of the null and generated a null distribution of mean and slope values. To determine whether trophic ranks/guilds were over- or underdispersed, we first calculated the SES of the mean PD_{MPD} or FD_{MPD} value across all islands in each null iteration. We then determined whether diversity–area relationships were more positive or negative than expected, by calculating the SES of the slope value for the relationship. Taken together, these values reveal whether communities exhibited trait-based assembly, that is underdispersion on smaller islands and converging on null with increasing island area (Jacquet et al., 2017), or whether communities exhibited assembly based on competitive exclusion, that is overdispersed and decreasing with island area (Weiher & Keddy, 1995; Figure S1). We compared these relationships assuming species equivalency and then for the three trophic ranks individually. Finally, both for all landbirds simultaneously and for each trophic rank, we fit a GLS model between mean body size of birds occupying each island and island area to test whether an individual functional trait scaled with island area, and we repeated the FD_{MPD} analysis with body size as the only trait in the analysis (see Supporting Information).

3 | RESULTS

For brevity, only landbird results are presented here, although diversity–area relationships and community assembly mechanisms differed between landbirds and seabirds in significance but mostly not directionality (see Supporting Information). We compared the fit of generalized least squares (GLS) models to test whether there was a significant influence of island area on multiple dimensions of biodiversity. The results of this test showed that island area was correlated with taxonomic diversity and phylogenetic diversity, but not with functional diversity (Figure 2). Taxonomic diversity exhibited the classical positive species–area relationship, following the Macarthur and Wilson (1967) theory of island biogeography ($GLS_{M\&W}$: $\Delta AICc = 0$, slope = 0.36 ± 0.03, intercept = −0.89 ± 0.24; GLS_{null}: $\Delta AICc = 25.8$). There was also a positive relationship between PD_{MPD} and island area (GLS_{PDAR}: $\Delta AICc = 0$, slope = 3.83 ± 1.17, intercept = 117.3 ± 8.65; GLS_{null}: $\Delta AICc = 9.01$). The best model for the relationship between FD_{MPD} and island area was the null model that functional diversity was not influenced by island size (GLS_{FDAR}: $\Delta AICc = 2.7$; GLS_{null}: $\Delta AICc = 0$).

Our model to test the trophic TIB was not a significantly better fit than the MacArthur and Wilson (1967) species–area relationship (GLS_{rank}: $\Delta AICc = 9.07$; $GLS_{M\&W}$: $\Delta AICc = 0$). This was corroborated by the fact that none of our pairs of trophic ranks differed significantly; AICc was always lower in the additive model where species–area slopes were identical among pairs (Figure 3a). However, our exploratory analysis of differences in the species–area relationship among trophic *guilds* revealed significant differences between the scaling of granivores and frugivores (see Supporting Information).

We compared the deviation of realized phylogenetic and functional diversity values and diversity–area slopes from their respective null distributions to infer community assembly mechanisms. When considering the PD_{MPD} of all landbirds, we found that values were non-significantly underdispersed and increasing with island area ($SES_{Mean} = −0.85$, $SES_{Slope} = 0.86$; Figure 2b). There was also no significant underdispersion or convergence on null for the functional diversity of all landbirds ($SES_{Mean} = −0.22$, $SES_{Slope} = 0.16$; Figure 2c).

We also tested diversity–area relationships for trophic ranks individually and found only three significant results (Figure 3). Phylogenetic diversity scaled positively with island area for intermediate predators (GLS_{PDAR}: $\Delta AICc = 0$, slope = 5.11 ± 0.99, intercept = 98.1 ± 7.34; GLS_{null}: $\Delta AICc = 18.6$) but negatively with area for herbivores (GLS_{PDAR}: $\Delta AICc = 0$, slope = −5.73 ± 2.52, intercept = 192.2 ± 19.5; GLS_{null}: $\Delta AICc = 4.4$; Figure 3b). The functional diversity of intermediate predators also scaled positively with island area (GLS_{FDAR}: $\Delta AICc = 0$, slope = −0.005 ± 0.0008, intercept = 0.23 ± 0.006; GLS_{null}: $\Delta AICc = 11.6$; Figure 3c). When examining the deviation from null island means and diversity–area slopes to infer community assembly patterns, we found two notable results. First, the PD_{MPD} of intermediate predators was underdispersed and converging on null ($SES_{Mean} = −2.03$, $SES_{Slope} = 2.43$; Figure 3b), indicating trait-based phylogenetic community assembly (Jacquet et al., 2017). Second, the functional diversity of intermediate predators tended towards underdispersion and was significantly more positive than expected ($SES_{Mean} = −1.73$, $SES_{Slope} = 2.26$; Figure 3c), also suggesting trait-based functional assembly. Neither apex predators nor herbivores had mean diversity values or diversity–area slopes that were different from null (Figure 3).
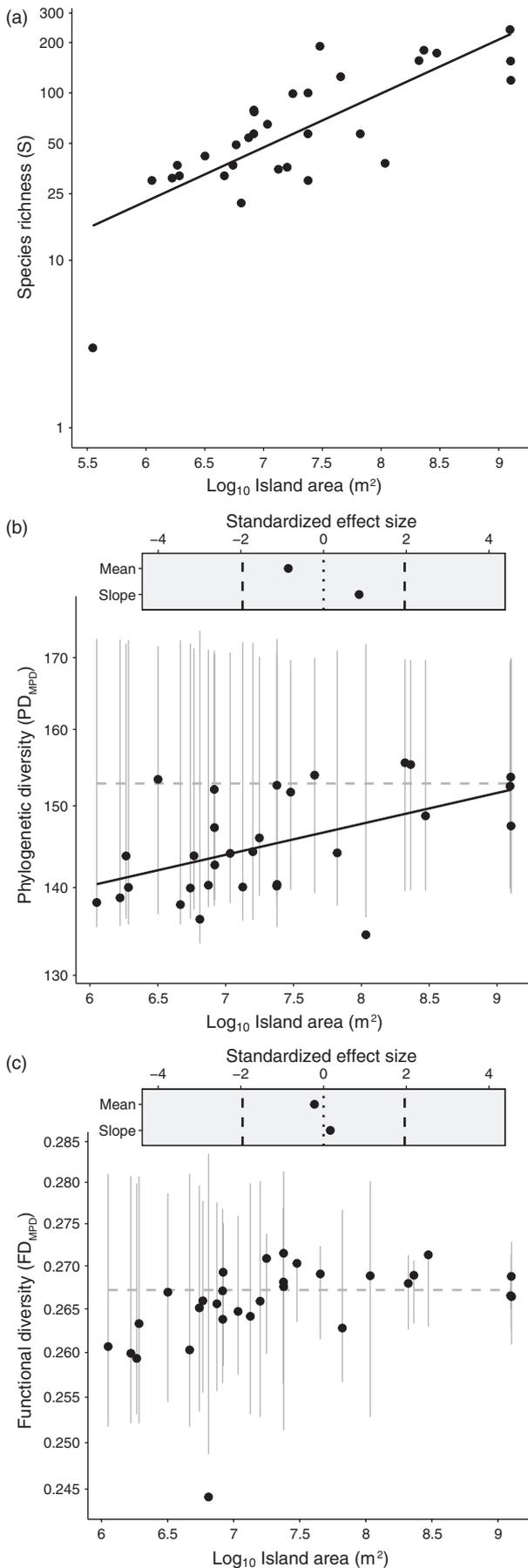
(a)

(b)

(c)

FIGURE 2 Diversity–area relationships for three dimensions of landbird biodiversity. Diversity–area relationships for log_{10}-transformed diversity indices: (a) taxonomic diversity [S], (b) phylogenetic diversity [PD_{MPD}] and (c) functional diversity [FD_{MPD}]. Black points are observed values of biodiversity for each island. Grey vertical lines represent the 95% confidence intervals for null distributions of 1,000,000 PD_{MPD} or FD_{MPD} values for each island. Grey dashed horizontal lines represent the expected mean PD_{MPD} or FD_{MPD} values of the null distributions for the regional pool. Black trend lines indicate significant diversity–area relationships when modelled as log–log linear models. For (b) and (c), inset plots represent standardized effect sizes for the mean PD_{MPD} or FD_{MPD} value across each island relative to null and the slope of the diversity–area relationship relative to null (see Materials and Methods). Data are for landbirds only (see Figure S4 for seabirds)

Our test to determine whether an individual functional trait (body size) scaled with island area found a significant relationship between body size and island area in all cases (Figure 4). When ignoring trophic differences, body-size scaled positively with island area (GLS_{Trait}: $\Delta AICc = 0$, slope = 0.06 ± 0.009, intercept = −0.66 ± 0.07; GLS_{null}: $\Delta AICc$ = 17.2). When considering trophic ranks individually, the mean body size of apex predators (GLS_{Trait}: $\Delta AICc = 0$, slope = 0.2 ± 0.03, intercept = −1.43 ± 0.21; GLS_{null}: $\Delta AICc$ = 21.2), intermediate predators (GLS_{Trait}: $\Delta AICc = 0$, slope = 0.02 ± 0.004, intercept = −0.47 ± 0.03; GLS_{null}: $\Delta AICc$ = 5.3) and herbivores (GLS_{Trait}: $\Delta AICc = 0$, slope = 0.13 ± 0.03, intercept = −1.07 ± 0.23; GLS_{null}: $\Delta AICc$ = 3.35) all scaled positively with island area. Body-size scaling relationships did not show significant patterns of assembly processes, although the mean body size of intermediate predators was significantly underdispersed (SES_{Mean} = −1.99; Figure 4c) and patterns across ranks qualitatively matched predictions from Jacquet et al. (2017).

4 | DISCUSSION

This study is an early empirical test of multiple extensions to island biogeography theory, including the trophic theory of island biogeography (Gravel et al., 2011) and trait-based theory (Jacquet et al., 2017). Overall, our tests reveal that non-neutral processes operate in island assembly across the Ryūkyū archipelago to some degree, but that these patterns are not all captured well by existing theory. We found that island area correlated positively with taxonomic diversity (i.e. the traditional species–area relationship, MacArthur & Wilson, 1967) and phylogenetic diversity (Si et al., 2017; Wang et al., 2013) but island area was not related to functional diversity. We did not find support for the trophic TIB here since trophic ranks did not differ significantly in their species–area relationships. However, we found evidence for trait-based island community assembly of body size and revealed differences in diversity–area relationships and community assembly mechanisms among trophic ranks for the first time.
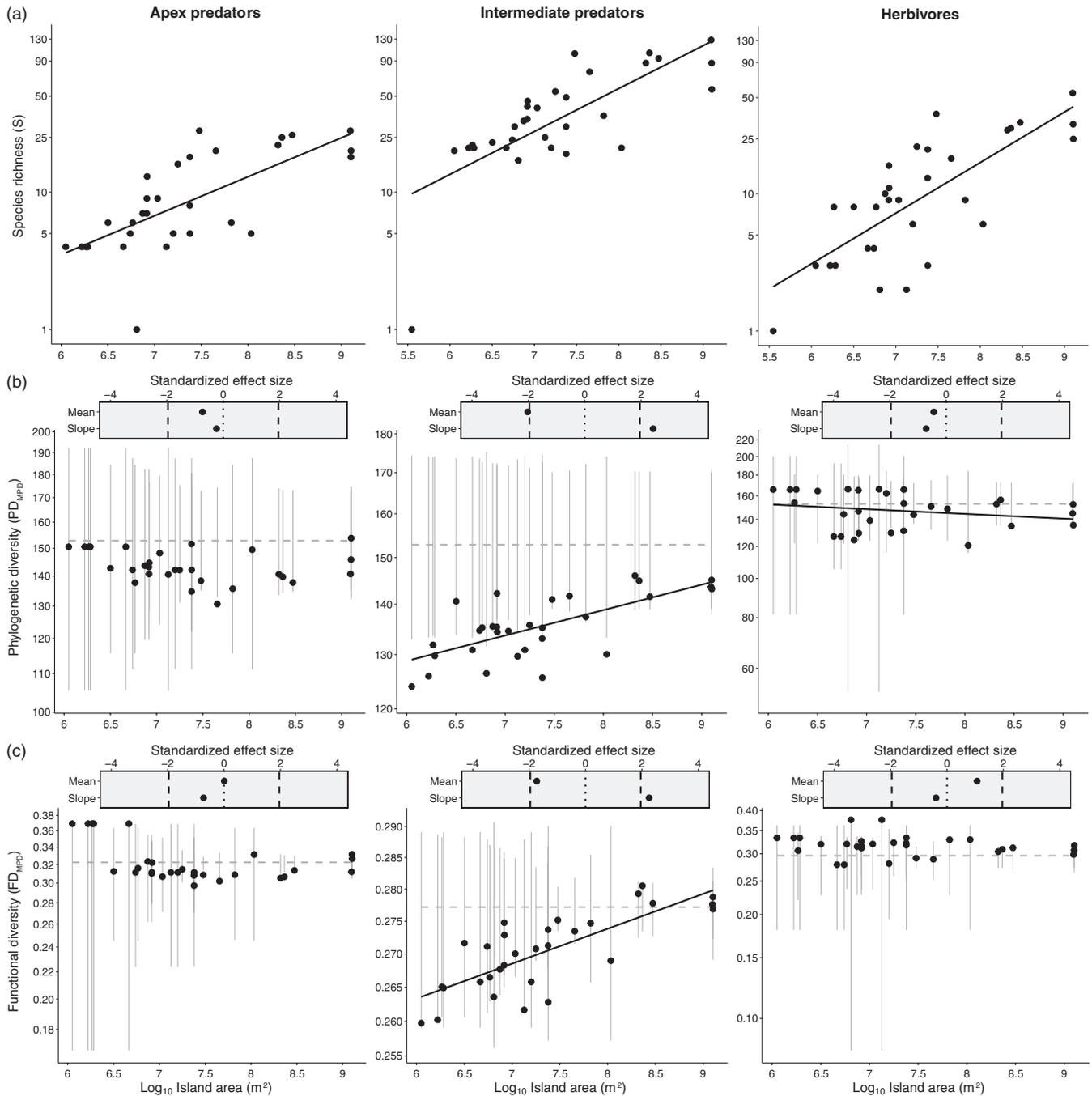
FIGURE 3 Diversity–area relationship for three dimensions of landbird biodiversity across trophic ranks. Diversity–area relationships for $\log_{10}$-transformed diversity indices: (a) taxonomic diversity [S], (b) phylogenetic diversity [PD_{MPD}] and (c) functional diversity [FD_{MPD}] split by trophic ranks with apex predators [carnivores, rank 3], intermediate predators [insectivores, rank 2] and herbivores [frugivores and granivores, rank 1]. Black points are observed values of biodiversity for each island. Grey vertical lines represent the 95% confidence intervals for null distributions of 1,000,000 PD_{MPD} or FD_{MPD} values for each island. Grey dashed horizontal lines represent the expected mean PD_{MPD} or FD_{MPD} values of the null distributions for the regional pool for each trophic rank. Black trend lines indicate significant diversity–area relationships when modelled as log-log linear models. For (b) and (c), inset plots represent standardized effect sizes for the mean PD_{MPD} or FD_{MPD} value across each island relative to null and the slope of the diversity–area relationship relative to null (see Materials and Methods). Data are for landbirds only (see Figure S5 for seabirds)

4.1 | Trophic theory of island biogeography

Our data do not support the idea that diversity at higher trophic levels scales more strongly with island area than at lower trophic

levels, which is a central prediction of the trophic TIB (Gravel et al., 2011; Holt et al., 1999). We found no significant differences among our trophic ranks in their species–area relationships. However, our exploratory analysis of trophic guilds of birds revealed differences
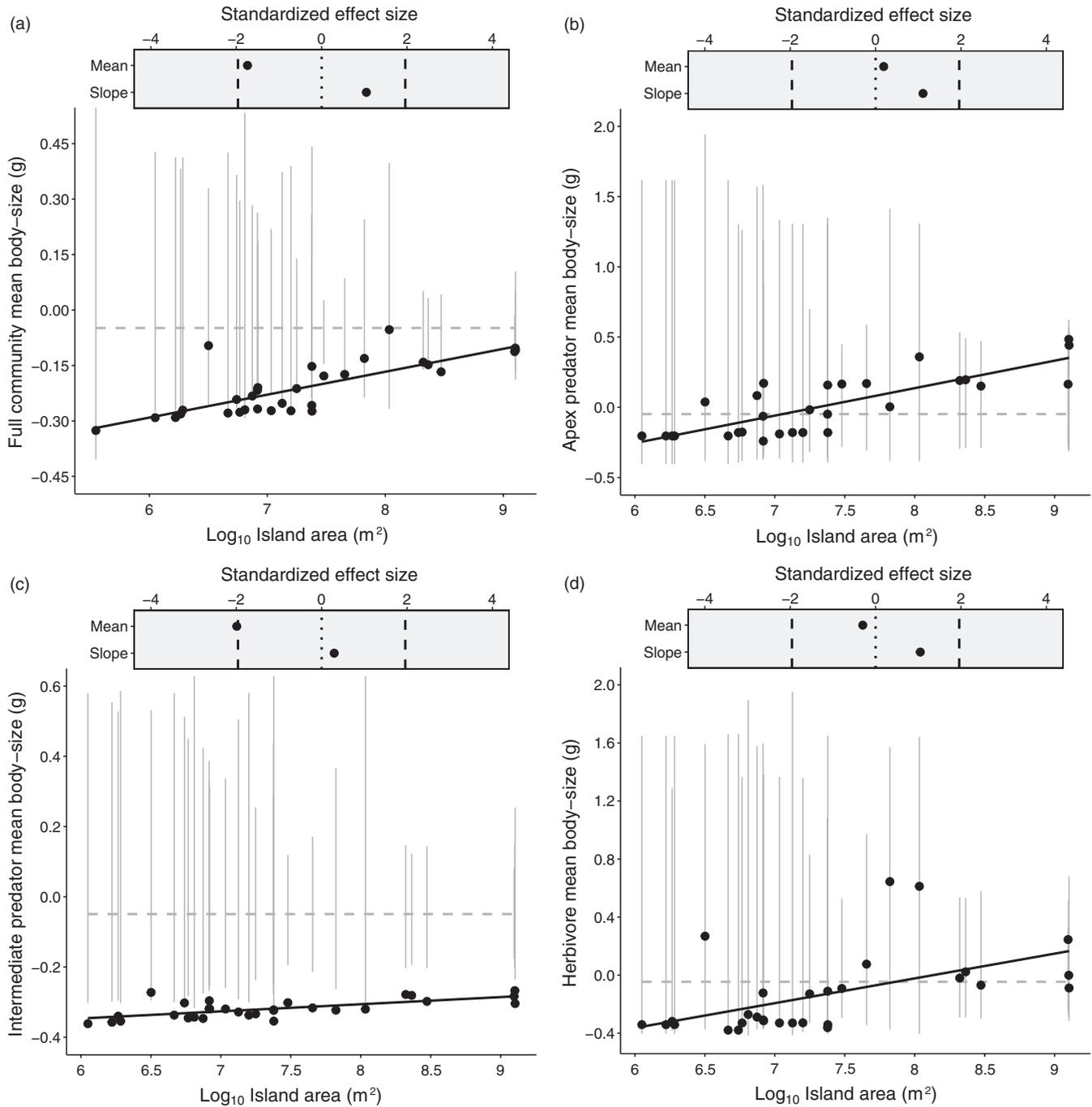
FIGURE 4 Relationship between mean body size and island area across trophic ranks. Influence of island area on scaled mean body size for (a) all landbirds, (b) apex predators, (c) intermediate predators and (d) herbivores. Black points are observed mean body-size values for each island. Grey vertical lines represent the 95% confidence intervals for null distributions of mean body-size values for each island. Grey dashed horizontal lines represent the expected mean body-size values of the null distributions for (a) the regional pool or (b-d) the pool of species assigned to each trophic rank. Black trend lines indicate significant body-size-island area relationships. Inset plots represent standardized effect sizes for the mean body-size value across each island relative to null and the slope of the mean body size-area relationship relative to null (see Materials and Methods). Data are for landbirds only

in the scaling of guilds that were not a function of rank. This is due to strongly divergent species–area relationships observed between granivores and frugivores (Figure S2), which are masked in the trophic rank model since both these guilds are included within the herbivore rank. If consumers are highly mobile, or if many species are trophic generalists (Holt et al., 1999), our analyses may not be sufficient to observe effects of the trophic TIB. However, we can perhaps rule out the widespread generalism since the few species that were considered "omnivorous" were not included in our trophic TIB analysis.

4.2 | Functional biogeography

Our tests of scaling of functional diversity with area, which were based on extensions of the trait-based theory proposed by Jacquet et al. (2017), found that neutral processes tend to govern island bird community assembly when considering the functional diversity of all landbirds. A range of studies document positive functional diversity–area relationships both for birds and other taxa (Mazel et al., 2014; Si et al., 2016; Si et al., 2017; Wang et al., 2013; Whittaker et al., 2014, but see Karadimou et al., 2016). However, we did not detect a diversity–area relationship that differed significantly from null, suggesting that perhaps our chosen functional traits did not scale with island area (i.e. were not persistence-enhancing). To further explore this, we tested for the scaling of body size with island area, since body-size scaling theory has been developed under the allometric theory of biogeography (Jacquet et al., 2017). We found that body size was positively related to island area regardless of the trophic rank considered. This suggests that this functional trait was persistence-enhancing, but that perhaps our ability to move from individual functional trait scaling relationships towards richness-corrected functional diversity–area scaling relationships may have been hindered by the addition of other functional traits, as also suggested when analysing the FD_{MPD} of a single trait (Figure S3). Our body-size analysis also revealed that the body size of intermediate predators was underdispersed regardless of island size, and that perhaps there was evidence of a tendency towards trait-based assembly of body-size (Jacquet et al., 2017). Alternatively, we may not see a relationship between functional diversity and area because our metric, MPD, is richness-corrected. Karadimou et al. (2016) explored the relationship between various metrics of functional diversity and island area, finding that the form of the FD–area relationship was dependent on the metric chosen. However, the functional diversity–area relationship itself is increasingly well-studied (e.g. Whittaker et al., 2014, Si et al., 2016; Si et al., 2017), and so was of less interest here than our ability to reveal community assembly mechanisms by testing how divergence from expected diversity values scales with island area (Smith et al., 2013).

Although we did not find trait-based community assembly when considering all landbirds (Jacquet et al., 2017), there were marked differences in assembly mechanisms among trophic ranks. Apex predators and herbivores each displayed neutral community assembly, with means and slopes not different from null. However, intermediate predators showed patterns of functional trait-based assembly, indicating that trait similarity is favoured on small islands. Extinction pressure on small islands may therefore be higher for intermediate predators than for other trophic ranks, resulting in stronger selection for trait similarity during the community assembly process. When considering further the diversity–area relationships and community assembly mechanisms of herbivorous birds, we found that functional diversity of granivores scaled steeply with island size, whereas frugivores were overdispersed, displaying competitive assembly (results not shown). This may be because larger islands support a greater diversity of plant species, thus allowing exploitation of a greater range of seed-eating niches. Different seed types may have different optimum feeding morphologies (Grant, Grant, Smith, Abbott, & Abbott, 1976), which could explain why functional diversity scales steeply for granivores. If different fruits also require different feeding morphologies, specialization and subsequent morphological divergence may explain the competitive assembly of frugivores across the Ryūkyūs.

4.3 | Phylogenetic diversity and community assembly

We found that phylogenetic diversity was fairly consistently underdispersed. This suggests evolutionary histories are more shared than expected from the regional species pool, since phylogenetic diversity is generally lower than null. We found an overall increase in phylogenetic diversity with island area, in accordance with previous studies finding positive PD–area relationships (e.g. Helmus & Ives, 2012; Mazel et al., 2014; Si et al., 2017; Wang et al., 2013). Community assembly mechanisms inferred from phylogenetic diversity–area relationships largely matched those of functional diversity. All trophic ranks exhibited some phylogenetic underdispersion (though the significance of such patterns differed), a pattern matching the phylogenetic clustering of birds in the Thousand Island Lake region of China (Si et al., 2017), although at different spatial scales. Particularly, intermediate predators were underdispersed, but the slope of the PD_{MPD}–area relationship was more positive than null. This suggests phylogenetic trait-based community assembly mechanisms operate for intermediate predators across the Ryūkyūs (Jacquet et al., 2017). Herbivores, on the other hand, did not exhibit patterns of increasing or decreasing divergence from null with island area for phylogenetic diversity, as with functional diversity, despite a significant species–area relationship. This suggests that for herbivores at least, the spatial scaling of species richness may be separate from the scaling of other biodiversity dimensions (Mazel et al., 2014; White, Montgomery, Pakeman, & Lennon, 2017).

Our tests of extended island biogeography theory revealed different patterns of coherence between seabirds and landbirds across biodiversity dimensions. Patterns of seabird species richness and functional diversity–area relationships across trophic groups generally followed landbird results. However, when inferring seabird community assembly mechanisms based on the form of the functional and phylogenetic diversity–area relationships relative to null, we found consistent underdispersion across trophic guilds. However, functional traits largely did not appear to reveal community assembly processes for seabirds. This may be due to the relative importance of selected traits. For all species, we chose traits a priori that have been demonstrated to influence resource requirements and foraging (Sekercioglu, 2006). However, if these traits had a more significant influence on persistence of landbirds than seabirds, then community assembly mechanisms would be more easily detected in landbirds. Alternatively, seabirds rely less on island size due to their life histories and ability to forage at sea. This could mean that

competitive pressure among similar species is lower, since seabirds are less bound by finite island resources. If the ocean allows for greater niche segregation than on islands, there is a lower cost to shared functional traits among seabirds than landbirds. This in turn may reduce competitive pressure, promoting phylogenetic and functional underdispersion and a reduced trend with island size (Mason, de Bello, Mouillot, Pavoine, & Dray, 2013).

4.4 | Context and future directions

Our study adds to the growing body of literature exploring community assembly processes across the biodiverse Ryūkyū archipelago (e.g. Hirao et al., 2015; Kubota, Hirao, Fujii, & Murakami, 2011; Wepfer et al., 2016), and we demonstrate for the first time how extensions of island biogeography theory might apply to the Ryūkyū archipelago. Previous work in this system has suggested that both current and historic environmental factors should be considered simultaneously when assessing diversity of the Ryūkyūs (Nakamura, Suwa, Denda, & Yokota, 2009) and that climate and historic land connectivity drives ant community composition across the islands of East Asia (Wepfer et al., 2016). Here, we were unable to differentiate between the effects of contemporary and historic processes. It is unlikely that land connectivity would influence distribution of avian groups as strongly as ants, but since we did not test for an influence of historic island biogeographical variables, we cannot rule out this possibility.

Our finding that trophic guilds differed in their diversity–area relationships and community assembly mechanisms has implications in the context of global change. As habitat destruction and fragmentation continue to degrade ecosystems globally (Brooks et al., 2002; Fahrig, 2003), diversity–area relationships will be useful in understanding and predicting the effects of global change on the multiple dimensions of biodiversity (Didham, Lawton, Hammond, & Eggleton, 1998; Keil, Storch, & Jetz, 2015; van Noordwijk et al., 2015). Specifically, as the size of natural habitats decreases through human action, the trophic TIB suggests that predatory species will be the first at risk of population reduction and local extinction (Didham et al., 1998; Dobson et al., 2006; Fountain-Jones et al., 2017; Roslin et al., 2014). The trophic TIB thus likely determines whether community disassembly occurs randomly or systematically. If the trophic TIB operates in a given system, we would observe systematic loss of predators followed by their prey with habitat destruction (Dobson et al., 2006; Fountain-Jones et al., 2017). Although seemingly not in operation for the avifauna of the Ryūkyū archipelago, the trophic TIB may broadly help to explain the pervasive trophic downgrading of ecosystems (Estes et al., 2011). Community assembly mechanisms can also help to predict disassembly rules under disturbance and recovery dynamics through recolonization (Alonso et al., 2015; Fountain-Jones et al., 2017). Trait-based assembly implies that as communities lose species in response to disturbance, even closely related species – in terms of their evolutionary histories or shared functional traits – are able to coexist, as would be the case for the avian

intermediate predators of the Ryūkyūs. Conversely, competitive assembly means that if habitat destruction reduces the carrying capacity of an island, biotic filters limit the similarity of any remaining species. Thus, competitive assembly may mean that functional and/or phylogenetic diversity is more resistant than species richness to disturbance (Mazel et al., 2014; White et al., 2017). Our finding that trophic levels were governed by different assembly mechanisms in the Ryūkyū archipelago suggests that we should consider differences in disassembly rules for these groups to best manage biodiversity of these islands in future.

5 | CONCLUSIONS

Island biogeography theory now reaches beyond the taxonomic dimension of biodiversity (Smith et al., 2013; Wang et al., 2013). Here, we found utility for extensions of island biogeography theory as a framework for analysing multiple dimensions of avian diversity in the Ryūkyū archipelago of Japan. In contrast to predictions of the trophic TIB (Gravel et al., 2011; Massol et al., 2017), we found that trophic rank did not predict the scaling of species richness with island area. However, the fact that avian trophic guilds differed in their diversity–area relationships indicates that functional aspects do matter for island community assembly, they just may not be a simple function of trophic rank. Moreover, functional and phylogenetic diversity scaling was not on the whole consistent with theoretical predictions, although non-random patterns do emerge, including limited evidence of trait-based community assembly of body-size (Jacquet et al., 2017). Since this is one of the first studies to test multiple extensions of island biogeography theory and the first to test for differences in diversity–area scaling and community assembly processes among trophic groups, there is still a clear need for further empirical studies testing predictions and providing feedback for theory development, particularly in a multitrophic context (Seibold et al., 2018). A critical, but open question is the extent to which general theories will be able to capture the scaling of multiple components of diversity across regions and taxonomic groups, or if each group will need their own theory. Unravelling the degree to which our observed patterns are generalizable or idiosyncratic will be an important next step in developing further extensions to island biogeography theory.

AUTHORS' CONTRIBUTIONS

All authors conceived and designed the study; N.R.F. and J.J. compiled the data; S.R.P-J.R. ran the simulations with guidance from E.P.E.; S.R.P-J.R., N.R.F. and E.P.E. analysed the data; E.P.E. supervised the research; S.R.P-J.R. led the writing of the manuscript; J.J. and S.R.P-J.R. prepared the figures with input from all authors. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

All global databases used in the study are listed in the Materials and Methods section under the "*Biodiversity indices*" subheading (see Jetz et al., 2012, Wilman et al., 2014, Del Hoyo et al., 2017). Checklist data are publicly available on Avibase (https://avibase.bsc-eoc.org/, see LePage et al., 2014), and all diversity metrics calculated in this study are archived in the Dryad Digital Repository: https://doi.org/10.5061/dryad.54tm887 (Ross, Friedman, Janicki, & Economo, 2019).

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SUPPORTING INFORMATION

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