

LETTER

Phylogenetic and functional clustering illustrate the roles of adaptive radiation and dispersal filtering in jointly shaping late-Quaternary mammal assemblages on oceanic islands

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Funding information

Villum Fonden, Grant/Award Number: 16549; Royal Botanic Gardens; Shanghai Rising-Star Program, Grant/Award Number: 19QA1403300; Stiftelsen för Strategisk Forskning; Swedish Research Council, Grant/Award Number: 2017-03862; Program for Professor of Special Appointment (Eastern Scholar), Grant/Award Number: P2020016; National Natural Science Foundation of China, Grant/Award Number: 31872210, 32030066 and 32071545; Carlsbergfondet, Grant/Award Number: CF16-0005

Editor: Timothée Poisot

Abstract

Islands frequently harbour unique assemblages of species, yet their ecological roles and differences are largely ignored in island biogeography studies. Here, we examine eco-evolutionary processes structuring mammal assemblages on oceanic islands worldwide, including all extant and extinct late-Quaternary mammal species. We find island mammal assemblages tend to be phylogenetically clustered (share more recent evolutionary histories), with clustering increasing with island area and isolation. We also observe that mammal assemblages often tend to be functionally clustered (share similar traits), but the strength of clustering is weak and generally independent from island area or isolation. These findings indicate the important roles of in situ speciation and dispersal filtering in shaping island mammal assemblages under pre-anthropogenic conditions, notably through adaptive radiation of a few clades (e.g. bats, with generally high dispersal abilities). Our study demonstrates that considering the functional and phylogenetic axes of diversity can better reveal the eco-evolutionary processes of island community assembly.

KEYWORDS

community assembly, dispersal, eco-evolutionary dynamic, island biogeography, mammal, speciation, species coexistence, species pool

INTRODUCTION

Species diversity on oceanic islands has been explored throughout the history of island biogeography (Palmgren, 1921; Rosenzweig, 1995; Whittaker & Fernández-Palacios, 2007), and the mechanisms of species coexistence on island systems have attracted considerable attention and debate (Diamond, 1975; Simberloff, 1978). However, the ecological roles of species in assemblages are largely ignored in island biogeography studies (Warren et al., 2015). Functional and phylogenetic methods that incorporate species differences are being increasingly integrated into ecology (Cavender-Bares et al., 2009; McGill et al., 2006), including in studies examining oceanic islands (Emerson & Gillespie, 2008; Gillespie, 2004; Ottaviani et al., 2020; Sobral et al., 2016; Whittaker et al., 2014), and provide a powerful approach to assess community assembly mechanisms. Here, we explore the functional and phylogenetic structure of island mammal assemblages worldwide, and how this relates to island area and isolation at the global scale (Patiño et al., 2017; Santos et al., 2016).

In contrast to assumptions of species neutrality implicit in the theory of island biogeography (MacArthur & Wilson, 1963, 1967), ecological (e.g. competition and filtering) and evolutionary processes (e.g. in situ speciation) are frequently inferred to have been important in structuring species assemblages on islands (HilleRisLambers et al., 2012; Mittelbach & Schemske, 2015). On oceanic islands, closely related species with similar ecological requirements or resource utilisation might be excluded by competitive interactions (Emerson & Gillespie, 2008). The resulting community structure would then comprise species more dissimilar in traits (the scaled Euclidean distance) or evolutionary histories (the amount of time separating species) than expected by chance sampling from the regional species pool (overdispersed). Alternatively, it is possible that only species with specific traits, such as the strong dispersal abilities that bats generally have compared to non-volant mammals, can successfully colonise islands (i.e. dispersal filtering) (Cardillo et al., 2008), or that island environments filter based on habitat affinities (i.e. environmental filtering) (Carvajal-Endara et al., 2017). These again suggest non-random associations of species in traits or evolutionary histories, and here the expected assemblages are more functionally or phylogenetically clustered (species in an assemblage are more functionally or phylogenetically similar relative to null expectations). Phylogenetic clustering of island faunas could be further generated endogenously through evolutionary processes (e.g. in situ speciation) (Vamosi et al., 2009), adding new species that have closely related sister taxa into the regional pool (Grant & Grant, 2006; Mittelbach & Schemske, 2015). However, during island adaptive radiations, species coexistence is often enhanced through character displacement, either

early in a radiation followed by subsequent filtering, or through repeated events (Grant & Grant, 2006; Schluter, 2000b). Such a process might lead to phylogenetic clustering and functional overdispersion (Cadotte et al., 2019), within the genetic and morphological constraints of the clade undergoing diversification (Davies et al., 2012) (Figure 1).

Island area and isolation might also influence particular ecological and evolutionary processes, leading to predictable functional and phylogenetic structures on different islands. For example, environmental filtering might be stronger on smaller islands because they likely contain fewer habitat or topographic types (Matthews et al., 2020; Si et al., 2017). Island isolation is also likely to result in greater functional clustering, by biasing colonisation towards those species possessing long-distance dispersal capabilities (e.g. bats or migratory birds) (Si et al., 2017), which would also be reflected in greater phylogenetic clustering if the traits related to dispersal are phylogenetically conserved. Thus, where ecological processes (environmental and dispersal filtering) dominate mechanisms structuring island assemblages, we predict greater functional or phylogenetic clustering on smaller (high habitat filtering) and more remote islands (selecting for good dispersers).

Similarly, island attributes could also shape evolutionary processes. Larger and more remote islands should more often support in situ speciation (Rosindell & Phillimore, 2011). Large islands can sustain larger population sizes and environmental heterogeneity, both of which promote in situ speciation and diversification (Schluter & Pennell, 2017; Stuessy et al., 2006). Remote islands will also favour speciation via reproductive isolation, where long-distance dispersal events are rare (Gillespie, 2004; Valente et al., 2020; Whittaker et al., 2017). If in situ evolutionary dynamics dominate mechanisms structuring island assemblages, we would predict that large and remote islands would show greater phylogenetic clustering. However, a strong divergent selection of closely related sister taxa should result in the rapid accumulation of niche and trait differences (Davies et al., 2007). We thus expect phylogenetic clustering to be stronger than functional clustering if adaptive radiation has been important in shaping mammal assemblages, as a single or few clades might expand to fill the available niches (Figure 1).

Here, we conduct a global analysis of terrestrial mammals on oceanic islands to evaluate the relative role of ecological and evolutionary processes in structuring mammal assemblages. Mammals are one of the best-known groups with readily available data on traits, phylogenies, and species distributions, and have high-quality historical range data due to better fossilisation than other vertebrate groups (Benton, 2009). Island biotas have experienced dramatic human-linked global extinctions (Alcover et al., 1998; Blackburn et al., 2004; Dirzo et al., 2014), that might be of a magnitude large enough to

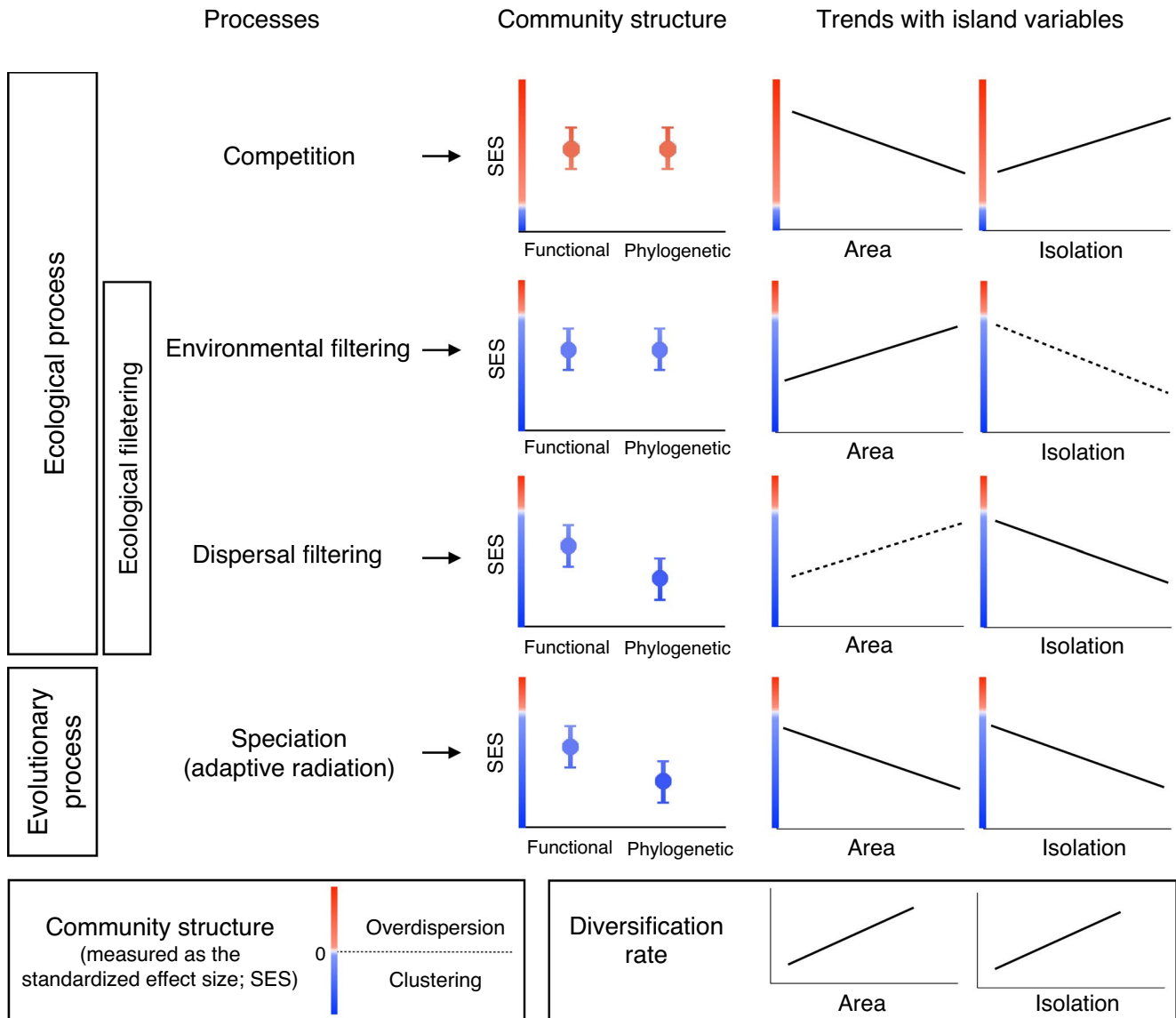


FIGURE 1 Hypothesised effect of island area and isolation on terrestrial mammal community structure. Community structure is measured as the normalised deviation from null expectations randomly drawn from regional species pools (standardised effect size, SES) and deviations identified as more overdispersed ($SES > 0$) or more clustered ($SES < 0$) than null expectations. This framework is an extension of that presented in Si et al. (2017), and considers the importance of ecological and evolutionary processes in structuring mammal assemblages on global oceanic islands. We expect island assemblages to be more clustered on smaller (high habitat filtering) and more remote islands (selecting for good dispersers) if ecological filtering is dominant. Island assemblages will be more clustered on larger and more remote islands if in situ speciation through adaptive radiations is a dominant process. Under adaptive radiations on oceanic islands, we further expect stronger phylogenetic, but weaker functional clustering in island mammals, as a single or few clades might expand to fill the available niches. We also expect diversification rates to increase with island area and isolation. Hypothesised relationships indicated by dashed lines are uncertain

alter inferences from macro-ecological analyses (Russell & Kueffer, 2019). In this study, we include extant native species as well as extinct native species known to have inhabited an island within the late Quaternary (the last ~130,000 years). The exact extinction dates of many of these species are not known with certainty, but nearly all extinctions of mammals on oceanic islands took place in the Holocene (the last 11,650 years) (Turvey, 2009). By including these historical distributions, we avoid being misled by the massive anthropogenic extinctions and introductions that occurred on islands worldwide (Davis

et al., 2018; McCreless et al., 2016; Russell & Kueffer, 2019).

We examine the global functional and phylogenetic structure of mammal assemblages on oceanic islands. Given the difference in life forms, we separate island mammals into bats and non-volant mammals, as bats generally have high dispersal abilities. By doing so, we can better explore unique mechanisms of community assembly that might characterise volant versus non-volant mammals. We here address the following questions: (1) How does mammal community structure

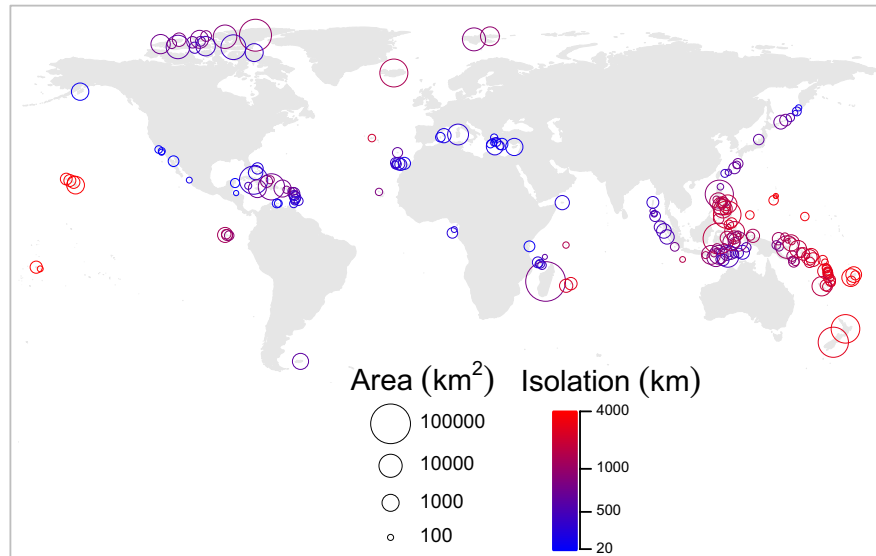


FIGURE 2 The distribution of 212 oceanic islands included in this study. Isolation is measured as the distance from the centroid of an island to the nearest mainland coast

on oceanic islands vary with area and isolation? (2) What are the relative contributions of ecological and evolutionary processes in shaping island mammal assemblages?

MATERIAL AND METHODS

Island data

We obtained island variables from a standardised dataset of the world's islands (Weigelt et al., 2013), including area, isolation and climatic factors (temperature and precipitation). Island area (km²) was measured as the polygon area of landmass surrounded by ocean using a cylindrical equal-area projection (Weigelt et al., 2013). Isolation (km) was calculated as the distance from an island's mass centroid to the nearest mainland coast (excluding Antarctica, which is covered by ice permanently) (Weigelt et al., 2013). We included maximum values per island polygon of mean annual temperature (°C) and mean annual precipitation (mm) (Weigelt et al., 2013) as additional independent variables to adjust for potential confounding effects of climate on community structure (see more details about island variables in Appendix S1). To increase model fit, we log₁₀-transformed island area, isolation and temperature. Specifically, temperature was transformed as: $-1 \times \log_{10}(\max(x) + 1 - x)$, where $\max(x)$ is the maximum value of temperature (in °C) for included islands, to avoid non-positive values in log₁₀-transformation. Precipitation was rescaled as $x/1000$, where x is the original value of precipitation in millimetres. Although island variables were correlated (absolute values of Pearson's $r < 0.60$, $p < 0.05$; Table S1), they contribute to explaining unique variations in our statistical models.

We focus on oceanic islands, defined here as volcanic islands that emerged from the oceanic floor or continental islands that occur in the world's oceans, *and* which were not connected to larger islands or nearby continental landmasses during the Last Glacial Maximum (LGM) (Whittaker & Fernández-Palacios, 2007). Thus, all continental fragments (e.g. New Guinea, Borneo, Great Britain, and Hainan Island) and volcanic islands (e.g. Honshu and Kyushu Islands of Japan, Kefallinia and Ikaria Islands of Greece) that were attached to larger islands or continental landmasses during the LGM were excluded, whereas islands containing continental plate fragments which have been isolated during the LGM (e.g. New Caledonia) were included. We examined the potential for island type (oceanic or continental) to have an effect on mammal diversity and community structure, and found that it did not influence the general patterns (see more details in Appendix S1: Island types).

Last, we excluded islands with area < 100 km² because it was not possible to obtain reliable data of species occurrence: mammal ranges in PHYLACINE 1.2 (see below) are rastered at a scale of 100 km, and for small islands adjacent to large islands (e.g., many islands in Indonesia), there is a lack of data on how humans may have modified mammal ranges.

Mammal data

Mammal occurrence data, mainly from Faurby and Svenning (2015a) and IUCN version 2016–3, were extracted from the PHYLACINE 1.2 database (Faurby et al., 2018). These data contain the map of present-natural ranges (i.e. where species would live without anthropogenic pressures) (*sensu* Peterken, 1977) of all extant and extinct late-Quaternary mammal species in

the last ~130,000 years (we note, however, that the vast majority of island extinctions occurred in the Holocene, i.e. the last 11,650 years). Occurrences of extinct species on islands were based on fossil evidence. Our data thus represent estimated island occurrences in the absence of human modification (Faurby et al., 2018). We focus on terrestrial (non-marine) mammals, and thus excluded sirenians, pinnipeds, cetaceans, and marine non-pinniped carnivores. Our study includes all oceanic islands worldwide with areas ≥ 100 km², ranging from 100.65 km² (Montserrat) to 5.91×10^5 km² (Madagascar), and with at least two terrestrial mammal species (note that 39 islands that exceeded our size threshold had only one species), resulting in a total of 212 islands (Figure 2, Table S2). More details about the mammal occurrence data are provided in Appendix S1: Mammal data.

We obtained data on body mass (grams, \log_{10} -transformed), diet, foraging strata, and daily timing of foraging activity for all extant mammal species, and data on body mass and diet for extinct late-Quaternary mammal species. Foraging stratum and daily timing of foraging activity of extinct species were recorded as NA (189 of 1,050 species). We selected species traits primarily based on ecological relevance (Oliveira et al., 2016; Safi et al., 2011) and data availability, which was limited given the global scale of analyses, and the inclusion of recently extinct mammal species in this study. For example, body mass can reflect species' dispersal abilities, which is also one of the most important traits defining the ecological niche in mammals. Specifically, body mass and diet were extracted from PHYLACINE 1.2 (Faurby et al., 2018), which was compiled from multiple resources (Faurby & Svenning, 2016; Kissling et al., 2014; Smith et al., 2003; Wilman et al., 2014). Body mass was recorded as a continuous variable, ranging from 1.8 g (*Crocidura levicula*) to 2,000,000 g (*Stegodon florensis*). Diet was recorded as the percentage of three categories (i.e. vertebrate prey, invertebrate prey and plants). Foraging stratum and the time of foraging activity were compiled from EltonTraits v1.0 (Wilman et al., 2014). Foraging stratum was coded as aerial, arboreal, ground-level or fossorial. We defined fossorial species as those that live in burrows and are capable of excavating burrows (Healy et al., 2014). The timing of daily foraging activity was coded as diurnal, nocturnal, crepuscular (active at dusk and dawn), or cathemeral (active at any time of day).

The PHYLACINE 1.2 database has a posterior distribution of 1,000 trees of all known extant and extinct late-Quaternary mammals (a total of 5,831 species) constructed using Bayesian methods (Faurby & Svenning, 2015b). To derive phylogenetic structure metrics, we arbitrarily selected the first tree of 1,000 posterior phylogenies (Alroy, 2019; Faurby et al., 2018). We then pruned the selected tree (5,831 species) to the set of terrestrial mammals on oceanic islands included in this study (1,050 species), including 424 bat species and 626 non-volant mammals. We additionally examined 100 alternative

tree topologies from the same pool of 1,000 posterior phylogenies (Faurby & Svenning, 2015b) to examine the robustness of phylogenetic summary metrics, and found results were qualitatively indistinguishable (Appendix S1: phylogenetic uncertainty). For simplicity, we present results here using the initial tree selected above (Figure S1).

To estimate functional metrics of each island, we used tree-based approaches that are easier to compare with phylogenetic metrics (e.g., Cadotte et al., 2009). We first computed functional distances between all species pairs using Gower's distance, which can handle quantitative and qualitative variables (Gower, 1966), and constructed a functional dendrogram using hierarchical clustering and the Unweighted Pair Group Method with Arithmetic Mean (UPGMA) algorithm.

Standardised effect size of functional and phylogenetic metrics

We quantified community structure of each island as the departure of functional or phylogenetic distances of co-occurring species within an assemblage relative to a random sampling of species from a regional species pool (Webb et al., 2002). The analysis of functional or phylogenetic community structure can link community ecology with biogeography, which may help infer mechanisms of contemporary coexistence (Webb et al., 2002) and character evolution (Vamosi et al., 2009).

We calculated the metrics of functional community structure as the standardised effect size (SES) of the mean functional pairwise distances (SES.MFD), and the mean nearest functional taxon distance (SES.MNFD), for each mammal assemblage relative to simulated communities randomly drawn from the species pool. Standardised effect sizes were calculated as: (observed – mean expected)/SD(expected), which is analogous to normalised Z-values. Expected values were calculated from 1,000 random communities (Gotelli & Graves, 1996), using the tip-shuffling null model (Kembel, 2009) that allows us to randomise species identity (i.e. the names of taxa on the phylogeny) while maintaining the community data matrix that captures the distribution of species richness and occurrence on individual islands (Swenson, 2014), which might be determined more by ecological constraints of individual islands. Negative SES values indicate functional or phylogenetic clustering—species are more similar to each other than null expectations, and positive SES values indicate functional or phylogenetic overdispersion—species less similar to each other than null expectations (Webb et al., 2002). Phylogenetic community structure was calculated similarly as the SES of mean phylogenetic pairwise distances (SES.MPD), and the mean nearest phylogenetic taxon distance (SES.MNPD). We defined the mean of the pairwise distances (SES.MFD

and SES.MPD) as the index of the root-level community structure, which is more sensitive to splits deeper in the phylogeny, closer to the root of the tree, reflecting processes acting across the deeper structure of the functional and phylogenetic trees. In contrast, we defined the mean of the nearest neighbour distances (SES.MNFD and SES.MNPD) as the index of tip-level community structure, which is more sensitive to the terminal structure near the tips of the tree (Mazel et al., 2016; Swenson, 2014).

The definition of species pools can strongly influence the estimations of community structure and the interpretation of the patterns (Carstensen et al., 2013; Graves & Rahbek, 2005). It is common to consider all species in a given region as potential colonisers, although this is not always well justified nor properly defined (Borregaard et al., 2020). We therefore used a more evolutionarily realistic delineation of the regional species pool to reflect the variations in dispersal ability between species, defined as the dispersion field (*sensu* Lessard et al., 2012). The dispersion field represents the pool of genera with geographic extents overlapping the focal assemblage. We used the genus level to better capture lineages with the potential to colonize a given island and the potential for evolutionary diversification within genera. Island colonisations often result in the colonisers becoming differentiated from the mainland source species, so defining species pools at the species level will therefore fail to effectively capture the potential source biota for a given island. Our dispersion-field species pool thus includes all species within the genera that occur at least once within the dispersion field (see R code for dispersion-field species pools in Appendix S2).

Statistical analyses

We examined the functional and phylogenetic structure of island mammals using spatial error-type autoregressive models (SARerr) (Kissling & Carl, 2008), regressing each metric of mammal community structure against island variables, using the R function `'errorsarlm'` in the `'spatialreg'` package (Bivand & Piras, 2015). Within each of the SARerr models, we varied the distances from the lower to upper distance bounds (e.g. minimum neighbour distance $\times 1.1 = 25.83$ km and maximum neighbour distance: 6330.18 km for all terrestrial mammals on 212 islands) at 20 intervals using the row standardised weighting scheme to identify the most appropriate neighbour distance. We used AICc (corrected Akaike's information criterion) and minRSA (minimum residual spatial autocorrelation) jointly in SARerr models to determine the most appropriate neighbour distance (Kissling & Carl, 2008). Moran's I was used to measure the spatial autocorrelation in model residuals. Pseudo- R^2 values (hereafter referred to R^2) were calculated as the squared

Pearson's correlation between predicted and observed values (Kissling & Carl, 2008).

Finally, we ran an additional analysis to examine the relationships between diversification rates and island variables, which could shed additional light on the relationship between island area, isolation, and the likelihood of in situ speciation. We estimated a species-level metric of diversification rates—species tip DR (Redding & Mooers, 2006)—on the full 5,831 species trees, as the reciprocal of the equal splits metric of evolutionary distinctiveness. Species tip DR has been shown to correlate highly with model-based estimators of speciation rates (Quintero & Jetz, 2018; Title & Rabosky, 2019), and can be readily calculated across a large set of phylogenetic trees (Upham et al., 2019), such as across the 1,000 posterior trees from the PHYLACINE database we used here. For each island, we calculated the average of species tip DR, providing a measure of the *assemblage tip DR*. Because we were most interested in the maximum diversification rates, as these reflect more recent speciation events and better capture island limits to diversification, we took the average of the top 10% and 20% species tip DR on each island to represent the assemblage tip DR. This is qualitatively similar to conducting quantile regression (Cade & Noon, 2003), but allows us to model assemblage tip DR in our spatial regression framework. We then regressed the \log_{10} -transformed assemblage tip DR against island variables using SARerr models, as above. We also generated models separately for bats and non-volant mammals.

RESULTS

We recorded a total of 1,050 late-Quaternary native terrestrial mammals on 212 oceanic islands, with a mean of just under 13 species per island, representing 424 bats on 169 islands and 626 non-volant mammals on 107 islands (Table S2). Our dataset included 17 bats and 116 non-volant mammals that are now globally extinct (Appendix S1: current species). Diversification rates (i.e. top 10% quantile of tip DR estimates) were higher on larger islands for all mammals as well as for non-volant mammals separately, while there was no significant relationship between area and diversification rate for bats (Table S4). Diversification was independent of island isolation across all groups (Table S4).

Mammal assemblages on islands generally tended to be functionally and phylogenetically clustered (i.e. SES values <0), with a higher strength of phylogenetic clustering than functional clustering (Wilcoxon signed-rank test, $p = 0.03$) (Figure 3). However, non-volant mammal assemblages demonstrated a tendency for functional overdispersion (i.e. SES values >0) (Figure 3). The strength of functional and phylogenetic clustering for all mammals was stronger than for bats and non-volant

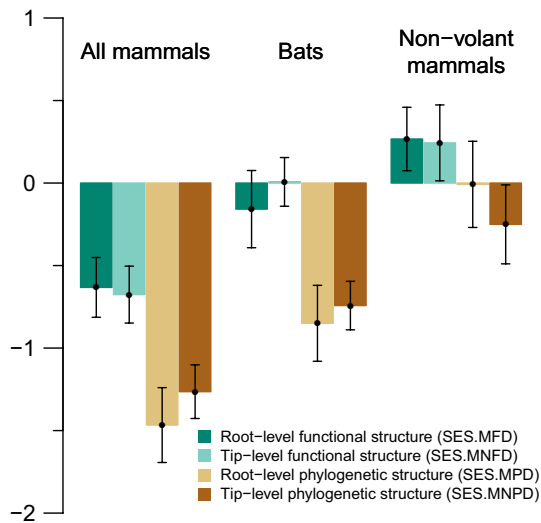


FIGURE 3 The means and standard errors of the functional and phylogenetic community structure of all terrestrial mammals, bats, and non-volant mammals. We calculated root-level community structure as the standardised effect size of the mean functional and phylogenetic pairwise distances (SES.MFD and SES.MPD), and tip-level community structure as the standardised effect size of the mean nearest functional and phylogenetic taxon distances (SES.MNFD and SES.MNPD). Island mammal assemblages generally tend to be functionally and phylogenetically clustered, with a higher strength of phylogenetic clustering than functional clustering. The stronger clustering for all mammals relative to the sub-clades likely reflects overrepresentation of bats on islands, with strong functional and phylogenetic clustering of this species-rich group relative to other mammals

mammals separately, with more than 18% of islands being significantly clustered (Figure 4 and Table S5).

Phylogenetic clustering (SES.MPD and SES.MNPD) for all mammals and non-volant mammals, and clustering of root-level functional (SES.MFD) and tip-level phylogenetic structure (SES.MNPD) for bats, increased with island area (Figures 5 and 6, Table S3). Trends with island isolation were less clear; however, clustering of tip-level phylogenetic structure (SES.MNPD) increased with island isolation for all mammals and bats (Figures 5 and 6, Table S3). Thus, there was a general, but not a universal trend for species on more remote islands to show greater phylogenetic clustering.

DISCUSSION

Island assemblages frequently have unique functional and phylogenetic community structure; however, traditional island biogeography studies incorporating ecological differences among species in communities indexed via species traits and phylogenetic distances are still limited due to the unavailability of large-scale datasets. We explored the functional and phylogenetic structure of island mammal assemblages worldwide, focusing on all extant and extinct late-Quaternary island faunas, thus we accounted for the potential influences of anthropogenic

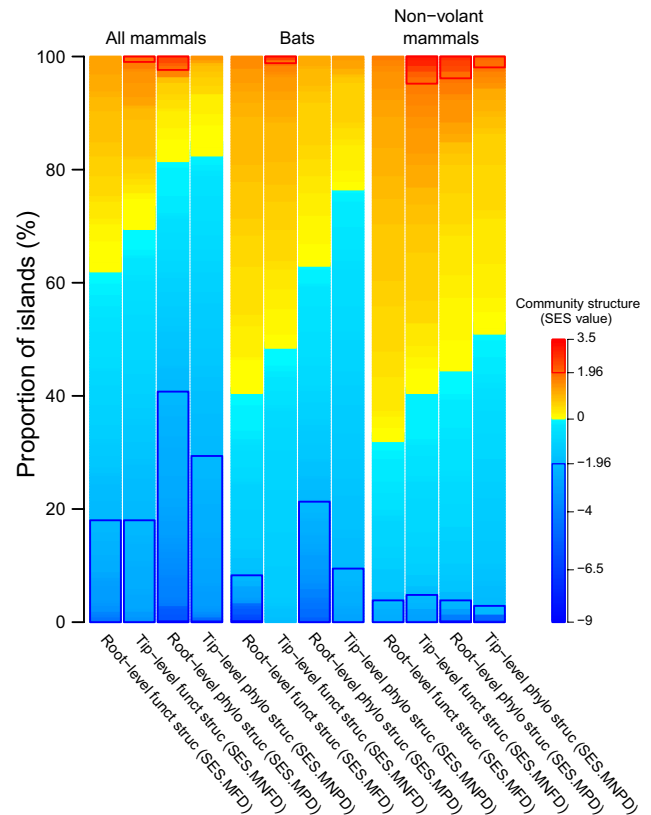


FIGURE 4 Proportion of islands on which the community structure of mammals is clustered (SES < 0) in blue, and overdispersed (SES \geq 0) in red. Rectangles indicate statistical significance (SES \leq -1.96 or \geq 1.96). The gradient of colours indicates the range of SES values for each island. We calculated root-level community structure as the standardised effect size of the mean functional and phylogenetic pairwise distances (SES.MFD and SES.MPD), and tip-level community structure as the standardised effect size of the mean nearest functional and phylogenetic taxon distances (SES.MNFD and SES.MNPD). While the community structure of individual island mammal assemblages is generally not significantly different from null expectations, island mammal assemblages tend to be on average more functionally and phylogenetically clustered, with a higher frequency of significant values for clustering than for overdispersion

extinctions and introductions. We found diversification rates (i.e. assemblage tip DR) increased with area, consistent with expectations (Losos & Schluter, 2000). Island mammal assemblages generally tended to be functionally and phylogenetically clustered, which we suggest these patterns reflect the importance of in situ speciation and dispersal filtering in shaping mammal assemblages on oceanic islands across the globe.

Clustering of island mammal structure

Island mammal assemblages generally showed functional and phylogenetic clustering, with effect sizes stronger for phylogenetic than functional indices (Figure 3). The stronger clustering for all mammals relative to bats and non-volant mammals separately likely reflected the

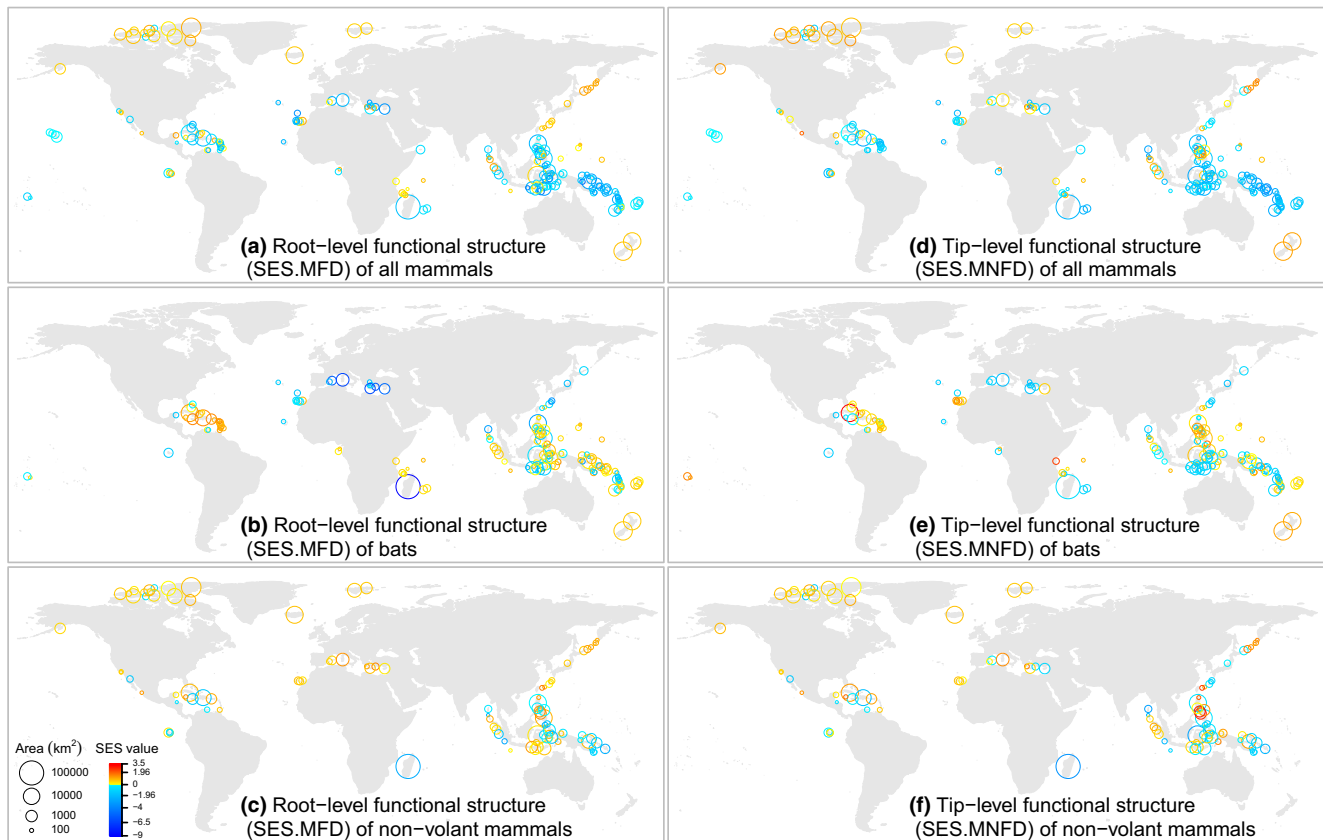


FIGURE 5 The functional community structure of all mammals, bats, and non-volant mammals on oceanic islands. Root-level functional structure is measured as the standardised effect size of the mean functional pairwise distances (SES.MFD), and tip-level functional structure is measured as the standardised effect size of the mean nearest functional taxon distances (SES.MNFD). Mammal assemblages often tend to be functionally clustered, but the strength of the clustering is weak, not ubiquitous, and generally independent from island area or isolation

overrepresentation of bats on islands (i.e. bats dominate the species pool of all mammals), with strong functional and phylogenetic clustering of this species-rich group relative to other mammals (see below). The large functional and phylogenetic distance between bats and other mammals may have further contributed to the stronger clustering observed for all mammals— islands provide an environment that filters for bats.

The clustering of mammal assemblages may arise from both ecological processes (dispersal and environmental filtering) and evolutionary processes (in situ speciation, such as intra-island or intra-archipelago cladogenesis). Dispersal ability and environment act as ecological filters, selecting for species with particular traits. For example, bat species with long-distance dispersal capacities are more likely to colonise remote islands, and their fit to local habitats determines the probability of successful establishment. If these dispersal and niche traits are phylogenetically conserved, there is indirect filtering for phylogenetic affinities, resulting in functional and phylogenetic clustering, especially for bat assemblages. Because filtering acts directly on traits, and only indirectly on phylogeny, we would expect filtered assemblages to demonstrate greater functional clustering than phylogenetic clustering. However, it is

possible that the traits on which filtering operated were not included in analyses, potentially weakening the link with functional clustering (Cadotte et al., 2019). In contrast, in situ speciation would drive strong phylogenetic clustering as newly emerged species are, by definition, most closely related to extant community members. However, if species radiate adaptively, we might not necessarily observe strong functional clustering, as species may have diverged in their phenotypes. Under a scenario of adaptive radiation, we might then predict strong phylogenetic clustering (many young, closely related species) but little or weak clustering of traits.

The structure of mammal assemblages across island area and isolation

Phylogenetic clustering of all three groups (all mammals, bats, and non-volant mammals alone) typically increased with island area. The strong links between island area and clustering supported in situ speciation rather than environmental or dispersal filtering as the dominant structuring process—large islands are likely to promote in situ speciation through intra-island cladogenesis (Emerson & Patiño, 2018), and this would be expected to

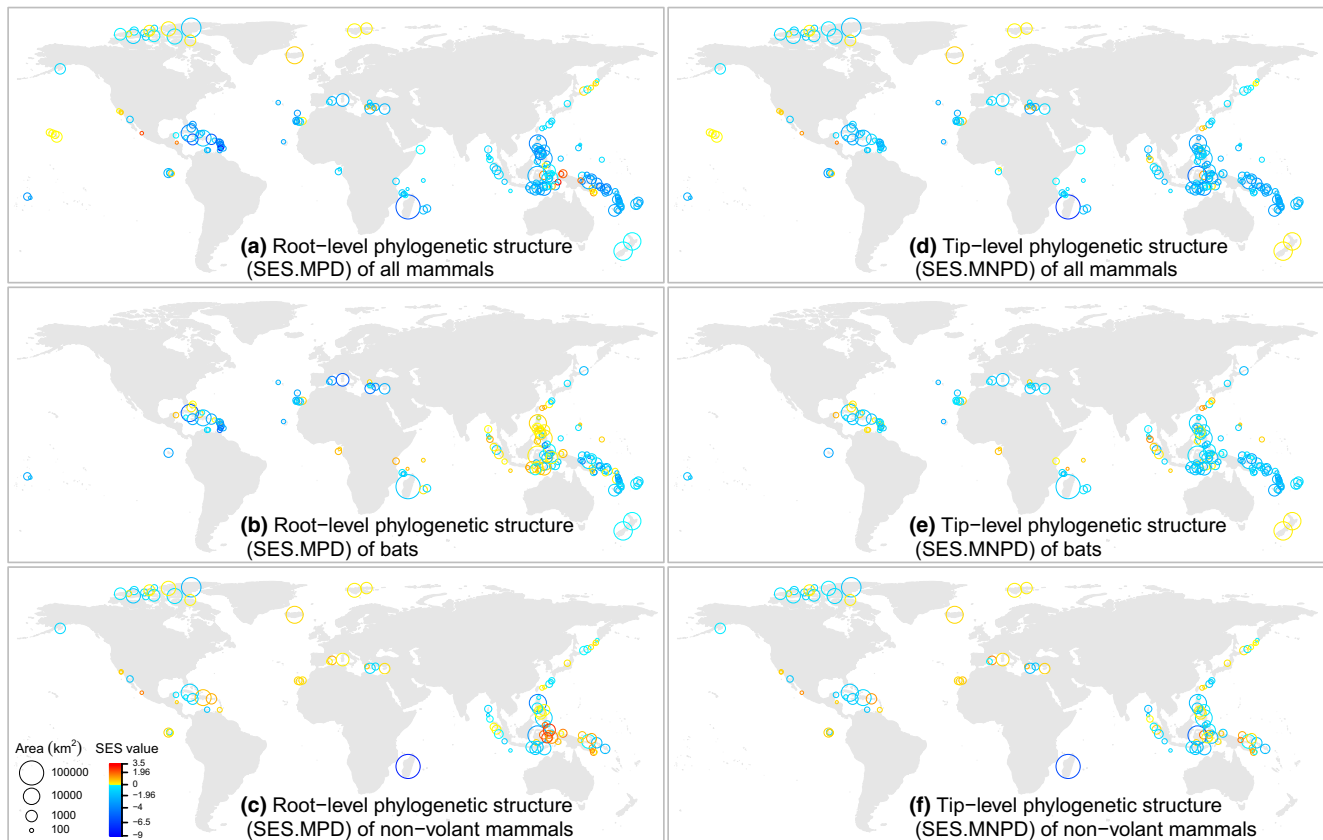


FIGURE 6 The phylogenetic community structure of all mammals, bats, and non-volant mammals on oceanic islands. Root-level phylogenetic community structure is measured as the standardised effect size of the mean phylogenetic pairwise distances (SES.MPD), and tip-level phylogenetic structure as the standard effect size of the mean nearest phylogenetic taxon distances (SES.MNPD). Phylogenetic structure of island mammal assemblages generally tends to be clustered, with clustering increasing with island area and isolation

drive phylogenetic clustering. In contrast, if environmental or dispersal filtering was the primary process driving clustering, we would expect stronger filtering on small islands. For example, small islands would have, on average, more restricted or smaller numbers of habitat types (Matthews et al., 2020). However, patterns among bats were more nuanced than those for non-volant mammals. It is possible that bats are structured by both speciation and dispersal filtering because they tend to be relatively good dispersers. We found some direct evidence supporting more rapid speciation on larger islands using a species-level metric of diversification rates, and this correlation was stronger for non-volant mammals, consistent with diversification contributing more strongly to structuring non-volant mammal assemblages. The weaker relationship between area and diversification in bats could also help explain why this group showed a more variable relationship between area and strength of phylogenetic clustering. Larger islands also tended to have more narrowly distributed or endemic mammal species (Appendix S1: Species ranges), again likely suggesting significant intra-island cladogenesis (Rosindell & Phillimore, 2011). The more mixed patterns of functional dispersion observed for non-volant mammals, which showed some signal of overdispersion (Figure 3),

might provide evidence for species coexistence through evolutionary character displacements (Schluter, 2000a) or adaptive radiation, in which island species rapidly diverge to fill available niches (Mittelbach & Schemske, 2015), as documented in other studies of island biotas (Grant & Grant, 2006).

We were surprised that we did not observe a consistent trend in mammal community structure with island isolation. Given the relatively low dispersal abilities of non-volant mammals, it is possible that they are more sensitive to the remoteness of islands – dispersal events to islands are highly unlikely for non-volant mammals unless islands are extremely close to the source species pool. The complexity of isolation measures (Weigelt & Krefl, 2013) and the potential influence of the paleo-configuration of islands (Norder et al., 2019) could further obscure the detection of isolation effects (see more discussions in Appendix S1: Isolation variables). However, there was some evidence for greater tip-level clustering on more remote islands, especially for bats. Increased phylogenetic clustering in the absence of functional clustering could suggest a strong dispersal filter, leading to a species-poor community and subsequent speciation, followed by niche-filling in the community. Although we did not find evidence in our data for speciation rates increasing with

isolation, this result may be explained by the fact that mammals, especially non-volant mammals, generally have low speciation rates such that trends are difficult to detect. However, a positive relationship between speciation rate and isolation has been reported in other taxa, such as in birds (Rosindell & Phillimore, 2011; Valente et al., 2020).

Anthropogenic effects on island faunas

Because of the widespread effects of human disturbances on islands (Nogué et al., 2021), we suggest that it is preferable to include recently extinct and extirpated species and exclude non-native species when searching for natural macroecological patterns in island biogeography (see also discussions in Cardillo et al., 2008; Pyron & Burbrink, 2014). To further explore this concept, we conducted *post hoc* analyses on the current ranges of extant native species on oceanic islands (Appendix S1: current species). Around 12.7% of terrestrial mammals (133 species) on oceanic islands became globally extinct during the Holocene or Late Pleistocene, and community structure solely based on extant native mammals was more clustered relative to the intact fauna (Figures. S2 and S3; Appendix S1: current species). It is possible, therefore, that using current species distributions would not only underestimate natural island diversity, but also overestimate the pre-anthropogenic strength of clustering of community structure. However, we did not find that human activities were sufficient to significantly alter the rules of island biogeography explored here (Tables S6 and S7). An important challenge for the future is to evaluate how anthropogenic pressures on island community structure (Helmus et al., 2014; Valente et al., 2017) might impact the integrity and functioning of island systems (Bellard et al., 2017; Faurby & Svenning, 2015a).

Limitations and future directions

Competition is often considered a key process driving functional overdispersion, through competitive exclusion of functionally similar species. We did not commonly observe overdispersion at the scale of our analysis, possibly because we lacked a fine-grained dataset of global mammal traits that could be used to infer competition among species (e.g. Cadotte et al., 2009). However, it is possible that competition might mediate the effects of ecological filtering. Inferring competition from community dispersion metrics is fraught with challenges, because numerous processes can result in similar patterns (Davies, 2021; Münkemüller et al., 2020). It remains possible that larger islands provide an opportunity for spatial separation of functionally similar species, and thus greater clustering at the island level and a

positive clustering–area relationship. Therefore, we cannot exclude competition as a minor structuring process on islands.

The fossil record used to infer the distribution of extinct mammals on islands is incomplete – new fossils will be discovered in the future, meaning that we may thus underestimate total island diversity. However, missing species would not necessarily bias estimates of clustering, which is more sensitive to the phylogenetic placement of species (Si et al., 2018). In addition, we note that the inclusion of islands with area <100 km² may increase the role of environmental filtering and decrease the role of in situ speciation (which is less likely on small islands), although we currently lack reliable data on mammal occurrences on small islands to explore this further.

CONCLUSION

We found that late-Quaternary native island mammal assemblages tend to be phylogenetically clustered, although individually, they are often not significantly different from null communities randomly drawn from the species pools. The clustering of phylogenetic structure increases with island area, suggesting the structure of mammal assemblages is influenced by an increasing predominance of in situ speciation. Evidence for phylogenetic clustering is stronger than that for functional clustering, further supporting the predominant role of evolution, notably through adaptive radiation of a few clades (such as the generally well-dispersing bats). Our results demonstrate the joint effects of adaptive radiation and dispersal filtering in shaping island mammal assemblages. By incorporating species' traits and evolutionary histories, our study provides a novel conceptual framework for disentangling the complex interplay between ecological and evolutionary processes structuring community assembly.

ACKNOWLEDGEMENTS

This study was supported by National Natural Science Foundation of China (#31872210, #32071545, and #32030066), Program for Professor of Special Appointment (Eastern Scholar) (#TP2020016), Shanghai Rising-Star Program (#19QA1403300), and the Fundamental Research Funds for the Central Universities. S.F. is supported by the Swedish Research Council (#2017-03862). J.-C.S. considers this work a contribution to his Carlsberg Foundation Semper Ardens project MegaPast2Future (#CF16-0005) and to his VILLUM Investigator project “Biodiversity Dynamics in a Changing World” funded by VILLUM FONDEN (#16549). A.A. is supported by the Swedish Research Council, the Swedish Foundation for Strategic Research and the Royal Botanic Gardens, Kew. We thank Kostas Triantis and two anonymous reviewers for their constructive comments, and Dr.

Rhian Smith for language editing of the revised manuscript. Finally, we would like to dedicate our paper to Edward O. Wilson for his pioneering studies in island biogeography.

AUTHOR CONTRIBUTIONS

X.S. designed the study. X.S., M.W.C., T.J.D. and P.D. conceived the ideas. X.S., J.-C.S. and S.F. collected the data. X.S. analysed the data and wrote the first draft. All authors contributed to the writing, edited, and commented on the manuscript.

PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/ele.13997>.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available at <https://doi.org/10.6084/m9.figshare.19193393>

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REFERENCES

- Alcover, J.A., Sans, A. & Palmer, M. (1998) The extent of extinctions of mammals on islands. *Journal of Biogeography*, 25, 913–918.
- Alroy, J. (2019) Small mammals have big tails in the tropics. *Global Ecology and Biogeography*, 28, 1042–1050.
- Bellard, C., Rysman, J.-F., Leroy, B., Claud, C. & Mace, G.M. (2017) A global picture of biological invasion threat on islands. *Nature Ecology & Evolution*, 1, 1862–1869.
- Benton, M.J. (2009) *Vertebrate palaeontology*, 4th edn. Oxford, UK: BlackWell.
- Bivand, R. & Piras, G. (2015) Comparing implementations of estimation methods for spatial econometrics. *Journal of Statistical Software*, 63, 1–36.
- Blackburn, T.M., Cassey, P., Duncan, R.P., Evans, K.L. & Gaston, K.J. (2004) Avian extinction and mammalian introductions on oceanic islands. *Science*, 305, 1955–1958.
- Borregaard, M.K., Graves, G.R. & Rahbek, C. (2020) Dispersion fields reveal the compositional structure of South American vertebrate assemblages. *Nature Communications*, 11, 491.
- Cade, B.S. & Noon, B.R. (2003) A gentle introduction to quantile regression for ecologists. *Frontiers in Ecology and the Environment*, 1, 412–420.
- Cadotte, M.W., Carboni, M., Si, X. & Tatsumi, S. (2019) Do traits and phylogeny support congruent community diversity patterns and assembly inferences? *Journal of Ecology*, 107, 2065–2077.
- Cadotte, M.W., Cavender-Bares, J., Tilman, D. & Oakley, T.H. (2009) Using phylogenetic, functional and trait diversity to understand patterns of plant community productivity. *PLoS One*, 4, e5695.
- Cardillo, M., Gittleman, J.L. & Purvis, A. (2008) Global patterns in the phylogenetic structure of island mammal assemblages. *Proceedings of the Royal Society B*, 275, 1549–1556.
- Carstensen, D.W., Lessard, J.P., Holt, B.G., Borregaard, M.K. & Rahbek, C. (2013) Introducing the biogeographic species pool. *Ecography*, 36, 1310–1318.
- Carvajal-Endara, S., Hendry, A.P., Emery, N.C. & Davies, T.J. (2017) Habitat filtering not dispersal limitation shapes oceanic island floras: species assembly of the Galápagos archipelago. *Ecology Letters*, 20, 495–504.
- Cavender-Bares, J., Kozak, K.H., Fine, P.V.A. & Kembel, S.W. (2009) The merging of community ecology and phylogenetic biology. *Ecology Letters*, 12, 693–715.
- Davies, T.J. (2021) Ecophylogenetics redux. *Ecology Letters*, 24, 1073–1088.
- Davies, T.J., Cooper, N., Diniz-Filho, J.A.F., Thomas, G.H. & Meiri, S. (2012) Using phylogenetic trees to test for character displacement: a model and an example from a desert mammal community. *Ecology*, 93, S44–S51.
- Davies, T.J., Meiri, S., Barraclough, T.G. & Gittleman, J.L. (2007) Species co-existence and character divergence across carnivores. *Ecology Letters*, 10, 146–152.
- Davis, M., Faurby, S. & Svenning, J.-C. (2018) Mammal diversity will take millions of years to recover from the current biodiversity crisis. *Proceedings of the National Academy of Sciences of the United States of America*, 115, 11262–11267.
- Diamond, J.M. (1975) Assembly of species communities. In: Cody, M.L. & Diamond, J.M. (Eds.) *Ecology and evolution of communities*. Cambridge, MA: Harvard University Press, pp. 342–444.
- Dirzo, R., Young, H.S., Galetti, M., Ceballos, G., Isaac, N.J. & Collen, B. (2014) Defaunation in the anthropocene. *Science*, 345, 401–406.
- Emerson, B.C. & Gillespie, R.G. (2008) Phylogenetic analysis of community assembly and structure over space and time. *Trends in Ecology & Evolution*, 23, 619–630.
- Emerson, B.C. & Patiño, J. (2018) Anagenesis, cladogenesis, and speciation on islands. *Trends in Ecology & Evolution*, 33, 488–491.
- Faurby, S., Davis, M., Pedersen, R.Ø., Schowaneck, S.D., Antonelli, A. & Svenning, J.-C. (2018) PHYLACINE 1.2: the phylogenetic atlas of mammal macroecology. *Ecology*, 99, 2626.
- Faurby, S. & Svenning, J.-C. (2015a) Historic and prehistoric human-driven extinctions have reshaped global mammal diversity patterns. *Diversity and Distributions*, 21, 1155–1166.
- Faurby, S. & Svenning, J.-C. (2015b) A species-level phylogeny of all extant and late quaternary extinct mammals using a novel heuristic-hierarchical Bayesian approach. *Molecular Phylogenetics and Evolution*, 84, 14–26.
- Faurby, S. & Svenning, J.-C. (2016) Resurrection of the island rule: human-driven extinctions have obscured a basic evolutionary pattern. *American Naturalist*, 187, 812–820.
- Gillespie, R. (2004) Community assembly through adaptive radiation in Hawaiian spiders. *Science*, 303, 356–359.
- Gotelli, N.J. & Graves, G.R. (1996) *Null models in ecology*. Washington, DC: Smithsonian Institution Press.
- Gower, J.C. (1966) Some distance properties of latent root and vector methods used in multivariate analysis. *Biometrika*, 53, 325–338.
- Grant, P.R. & Grant, B.R. (2006) Evolution of character displacement in Darwin's finches. *Science*, 313, 224–226.
- Graves, G.R. & Rahbek, C. (2005) Source pool geometry and the assembly of continental avifaunas. *Proceedings of the National Academy of Sciences of the United States of America*, 102, 7871–7876.
- Healy, K., Guillaume, T., Finlay, S., Kane, A., Kelly, S.B.A., McClean, D. et al. (2014) Ecology and mode-of-life explain lifespan variation in birds and mammals. *Proceedings of the Royal Society B*, 281, 20140298.
- Helmus, M.R., Mahler, D.L. & Losos, J.B. (2014) Island biogeography of the anthropocene. *Nature*, 513, 543–546.

- HilleRisLambers, J., Adler, P., Harpole, W., Levine, J. & Mayfield, M. (2012) Rethinking community assembly through the lens of coexistence theory. *Annual Review of Ecology Evolution and Systematics*, 43, 227–248.
- Kembel, S.W. (2009) Disentangling niche and neutral influences on community assembly: assessing the performance of community phylogenetic structure tests. *Ecology Letters*, 12, 949–960.
- Kissling, W.D. & Carl, G. (2008) Spatial autocorrelation and the selection of simultaneous autoregressive models. *Global Ecology and Biogeography*, 17, 59–71.
- Kissling, W.D., Dalby, L., Fløjgaard, C., Lenoir, J., Sandel, B., Sandom, C. et al. (2014) Establishing macroecological trait datasets: digitalization, extrapolation, and validation of diet preferences in terrestrial mammals worldwide. *Ecology and Evolution*, 4, 2913–2930.
- Lessard, J.-P., Borregaard, M.K., Fordyce, J.A., Rahbek, C., Weiser, M.D., Dunn, R.R. et al. (2012) Strong influence of regional species pools on continent-wide structuring of local communities. *Proceedings of the Royal Society B*, 279, 266–274.
- Losos, J.B. & Schluter, D. (2000) Analysis of an evolutionary species–area relationship. *Nature*, 408, 847–850.
- MacArthur, R.H. & Wilson, E.O. (1963) An equilibrium theory of insular zoogeography. *Evolution*, 17, 373–387.
- MacArthur, R.H. & Wilson, E.O. (1967) *The theory of island biogeography*. Princeton, NJ: Princeton University Press.
- Matthews, T.J., Rigal, F., Kougioumoutzis, K., Trigas, P. & Triantis, K.A. (2020) Unravelling the small-island effect through phylogenetic community ecology. *Journal of Biogeography*, 47, 2341–2352.
- Mazel, F., Davies, T.J., Gallien, L., Renaud, J., Groussin, M., Münkemüller, T. et al. (2016) Influence of tree shape and evolutionary time-scale on phylogenetic diversity metrics. *Ecography*, 39, 913–920.
- McCrealess, E.E., Huff, D.D., Croll, D.A., Tershy, B.R., Spatz, D.R., Holmes, N.D. et al. (2016) Past and estimated future impact of invasive alien mammals on insular threatened vertebrate populations. *Nature Communications*, 7, 12488.
- McGill, B.J., Enquist, B.J., Weiher, E. & Westoby, M. (2006) Rebuilding community ecology from functional traits. *Trends in Ecology & Evolution*, 21, 178–185.
- Mittelbach, G.G. & Schemske, D.W. (2015) Ecological and evolutionary perspectives on community assembly. *Trends in Ecology & Evolution*, 30, 241–247.
- Münkemüller, T., Gallien, L., Pollock, L.J., Barros, C., Carboni, M., Chalmandrier, L. et al. (2020) Dos and don'ts when inferring assembly rules from diversity patterns. *Global Ecology and Biogeography*, 29, 1212–1229.
- Nogué, S., Santos, A.M.C., Birks, H.J.B., Björck, S., Castilla-Beltrán, A., Connor, S. et al. (2021) The human dimension of biodiversity changes on islands. *Science*, 372, 488–491.
- Norder, S.J., Proios, K., Whittaker, R.J., Alonso, M.R., Borges, P.A.V., Borregaard, M.K. et al. (2019) Beyond the Last Glacial Maximum: Island endemism is best explained by long-lasting archipelago configurations. *Global Ecology and Biogeography*, 28, 184–197.
- Oliveira, B.F., Machac, A., Costa, G.C., Brooks, T.M., Davidson, A.D., Rondinini, C. et al. (2016) Species and functional diversity accumulate differently in mammals. *Global Ecology and Biogeography*, 25, 1119–1130.
- Ottaviani, G., Keppel, G., Götzenberger, L., Harrison, S., Opedal, Ø.H., Conti, L. et al. (2020) Linking plant functional ecology to island biogeography. *Trends in Plant Science*, 25, 329–339.
- Palmgren, A. (1921) Die Entfernung als pflanzengeographischer Faktor. *Acta Societatis pro Fauna Et Flora Fennica*, 49, 1–113.
- Patiño, J., Whittaker, R.J., Borges, P.A.V., Fernández-Palacios, J.M., Ah-Peng, C., Araújo, M.B. et al. (2017) A roadmap for island biology: 50 fundamental questions after 50 years of The Theory of Island Biogeography. *Journal of Biogeography*, 44, 963–983.
- Peterken, G. (1977) Habitat conservation priorities in British and European woodlands. *Biological Conservation*, 11, 223–236.
- Pyron, R.A. & Burbrink, F.T. (2014) Ecological and evolutionary determinants of species richness and phylogenetic diversity for island snakes. *Global Ecology and Biogeography*, 23, 848–856.
- Quintero, I. & Jetz, W. (2018) Global elevational diversity and diversification of birds. *Nature*, 555, 246–250.
- Redding, D.W. & Mooers, A.Ø. (2006) Incorporating evolutionary measures into conservation prioritization. *Conservation Biology*, 20, 1670–1678.
- Rosenzweig, M.L. (1995) *Species diversity in space and time*. Cambridge, UK: Cambridge University Press.
- Rosindell, J. & Phillimore, A.B. (2011) A unified model of island biogeography sheds light on the zone of radiation. *Ecology Letters*, 14, 552–560.
- Russell, J.C. & Kueffer, C. (2019) Island biodiversity in the Anthropocene. *Annual Review of Environment and Resources*, 44, 31–60.
- Safi, K., Cianciaruso, M.V., Loyola, R.D., Brito, D., Armour-Marshall, K. & Diniz-Filho, J.A.F. (2011) Understanding global patterns of mammalian functional and phylogenetic diversity. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 366, 2536–2544.
- Santos, A.M.C., Field, R., Ricklefs, R.E. & Borregaard, M. (2016) New directions in island biogeography. *Global Ecology and Biogeography*, 25, 751–768.
- Schluter, D. (2000a) Ecological character displacement in adaptive radiation. *American Naturalist*, 156, S4–S16.
- Schluter, D. (2000b) *The ecology of adaptive radiation*. Oxford, UK: Oxford University Press.
- Schluter, D. & Pennell, M.W. (2017) Speciation gradients and the distribution of biodiversity. *Nature*, 546, 48–55.
- Si, X., Cadotte, M.W., Zeng, D., Baselga, A., Zhao, Y., Li, J. et al. (2017) Functional and phylogenetic structure of island bird communities. *Journal of Animal Ecology*, 86, 532–542.
- Si, X., Cadotte, M.W., Zhao, Y., Zhou, H., Zeng, D., Li, J. et al. (2018) The importance of accounting for imperfect detection when estimating functional and phylogenetic community structure. *Ecology*, 99, 2103–2112.
- Simberloff, D. (1978) Using island biogeographic distributions to determine if colonization is stochastic. *American Naturalist*, 112, 713–726.
- Smith, F.A., Lyons, S.K., Ernest, S.K.M., Jones, K.E., Kaufman, D.M., Dayan, T. et al. (2003) Body mass of late Quaternary mammals. *Ecology*, 84, 3403.
- Sobral, F.L., Lees, A.C. & Cianciaruso, M.V. (2016) Introductions do not compensate for functional and phylogenetic losses following extinctions in insular bird assemblages. *Ecology Letters*, 19, 1091–1100.
- Stuessy, T.F., Jakubowsky, G., Gomez, R.S., Pfosser, M., Schluter, P.M., Fer, T. et al. (2006) Anagenetic evolution in island plants. *Journal of Biogeography*, 33, 1259–1265.
- Swenson, N.G. (2014) *Functional and phylogenetic ecology in R*. New York, NY: Springer.
- Title, P.O. & Rabosky, D.L. (2019) Tip rates, phylogenies and diversification: what are we estimating, and how good are the estimates? *Methods in Ecology and Evolution*, 10, 821–834.
- Turvey, S.T. (2009) *Holocene extinctions*. Oxford, UK: Oxford University Press.
- Upham, N.S., Esselstyn, J.A. & Jetz, W. (2019) Inferring the mammal tree: species-level sets of phylogenies for questions in ecology, evolution, and conservation. *PLoS Biology*, 17, e3000494.
- Valente, L., Etienne, R.S. & Dávalos, L.M. (2017) Recent extinctions disturb path to equilibrium diversity in Caribbean bats. *Nature Ecology & Evolution*, 1, 0026.

- Valente, L., Phillimore, A.B., Melo, M., Warren, B.H., Clegg, S.M., Havenstein, K. et al. (2020) A simple dynamic model explains the diversity of island birds worldwide. *Nature*, 579, 92–96.
- Vamosi, S.M., Heard, S.B., Vamosi, J.C. & Webb, C.O. (2009) Emerging patterns in the comparative analysis of phylogenetic community structure. *Molecular Ecology*, 18, 572–592.
- Warren, B.H., Simberloff, D., Ricklefs, R.E., Aguilée, R., Condamine, F.L., Gravel, D. et al. (2015) Islands as model systems in ecology and evolution: prospects fifty years after MacArthur-Wilson. *Ecology Letters*, 18, 200–217.
- Webb, C.O., Ackerly, D.D., McPeck, M.A. & Donoghue, M.J. (2002) Phylogenies and community ecology. *Annual Review of Ecology and Systematics*, 33, 475–505.
- Weigelt, P., Jetz, W. & Krefl, H. (2013) Bioclimatic and physical characterization of the world's islands. *Proceedings of the National Academy of Sciences of the United States of America*, 110, 15307–15312.
- Weigelt, P. & Krefl, H. (2013) Quantifying island isolation—insights from global patterns of insular plant species richness. *Ecography*, 36, 417–429.
- Whittaker, R.J., Fernández-Palacios, J.M., Matthews, T.J., Borregaard, M.K. & Triantis, K.A. (2017) Island biogeography: taking the long view of nature's laboratories. *Science*, 357, eaam8326.
- Whittaker, R.J. & Fernández-Palacios, J.M. (2007) *Island biogeography: ecology, evolution, and conservation*, 2nd edn. Oxford, UK: Oxford University Press.
- Whittaker, R.J., Rigal, F., Borges, P.A.V., Cardoso, P., Terzopoulou, S., Casanoves, F. et al. (2014) Functional biogeography of oceanic islands and the scaling of functional diversity in the Azores. *Proceedings of the National Academy of Sciences of the United States of America*, 111, 13709–13714.
- Wilman, H., Belmaker, J., Simpson, J., de la Rosa, C., Rivadeneira, M.M. & Jetz, W. (2014) EltonTraits 1.0: Species-level foraging attributes of the world's birds and mammals. *Ecology*, 95, 2027.

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How to cite this article: Si, X., Cadotte, M.W., Davies, T.J., Antonelli, A., Ding, P., Svenning, J.-C. & et al. (2022) Phylogenetic and functional clustering illustrate the roles of adaptive radiation and dispersal filtering in jointly shaping late-Quaternary mammal assemblages on oceanic islands. *Ecology Letters*, 00, 1–13. Available from: <https://doi.org/10.1111/ele.13997>