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Source pool diversity and proximity shape the compositional uniqueness of insular mammal assemblages worldwide

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Handling Editor: Judith Masters**Abstract**

Aim: Islands have been the test bed of several theories in community ecology, biogeography, and evolutionary biology. Progress within these disciplines has given a more comprehensive and mechanistic understanding of the processes governing variation in species richness among islands. However, it remains unclear whether these same processes also explain variation in species and phylogenetic composition among islands. Integrating theory from ecology and biogeography, we infer the roles of dispersal, selection, and stochasticity on the composition of insular assemblages within archipelagos. We further assess the influence of source pool diversity and connectivity on the compositional uniqueness of insular assemblages.

Location: Island systems worldwide.

Taxon: Mammals.

Methods: We compiled data on species composition of nonvolant mammals on ~200 islands in nine archipelagos distributed worldwide from the literature. We used variation partitioning to quantify the relative influence of the environment (selection) and geographic distance (dispersal) relative to a null model (stochasticity, randomness) on taxonomic and phylogenetic compositional turnover within archipelagos. We then used a linear mixed model to gain further insight into the underlying mechanisms shaping variation in assemblage composition among islands at a global scale. Specifically, we assessed the influence of source pool diversity, isolation from the source pool, and island characteristics on compositional uniqueness.

Results: Our results suggest that within-archipelago variation in the composition of insular mammal assemblages is associated with stochastic or unmeasured processes rather than abiotic selection or dispersal limitation. The diversity and proximity of the source pool, as well as some island characteristics, explained variation in phylogenetic, but not taxonomic, compositional uniqueness globally. Globally, isolated islands associated with phylogenetically diverse source pools exhibit high phylogenetic uniqueness whereas well-connected islands associated with phylogenetically clustered source pools show the opposite trend. Phylogenetically unique assemblages also tend to occur on islands with a small elevational span and low annual temperature variation.

Main conclusions: Taken together, our results suggest that source pool diversity, along with the potential for colonization from those pools, has a strong influence on the composition of insular mammal assemblages worldwide.

KEYWORDS

community dissimilarity, deterministic, environmental filtering, island biogeography, regional species pool, source-sink dynamics, species sorting

1 | INTRODUCTION

Islands have been the cornerstone of theoretical developments in ecology (Connor & Simberloff, 1979; Diamond, 1977), biogeography (MacArthur & Wilson, 1967; Simberloff, 1976), and evolutionary biology (Grant & Grant, 2002; Schluter, 2000). In particular, islands are regularly used to investigate ecological and evolutionary processes underpinning community assembly (Gillespie, 2004; Losos et al., 1997; Simberloff & Wilson, 1969). Progress within these disciplines and integration of concepts between them resulted in a mechanistic understanding of processes by which species originate and diversity is maintained through time (Losos & Ricklefs, 2009). This accumulated knowledge has further coalesced into mechanistic models accurately predicting geographic variation in species richness among islands (Valente et al., 2020; Whittaker et al., 2008). The basic premise of most if not all models of island biogeography is that species richness increases with island size and decreases with isolation, owing to colonization and extinction (MacArthur & Wilson, 1967; Simberloff, 1976). More recent models further incorporate rates of speciation (Valente et al., 2020) and island ontogeny (Valente et al., 2014; Whittaker et al., 2008). Whereas much of the focus in island biogeography has been on the number of species inhabiting islands (MacArthur & Wilson, 1967; Matthews et al., 2016; Simberloff, 1976; Simberloff & Wilson, 1969; Triantis et al., 2012; Valente et al., 2020), there has been less investigation of whether the fundamental processes involved in those theories could also explain other aspects of assemblage structure, such as species composition (but see Cardillo et al., 2008; Lu et al., 2019; Millien & Gonzalez, 2011; Si et al., 2017; Whittaker et al., 2014). Questions regarding the processes that underlie the assembly of island communities and determine their species composition remain a persistent line of inquiry in modern biogeography (Patiño et al., 2017).

Whereas evolutionary and historical processes such as speciation, extinction, and colonization ultimately determine the number and “kinds” of species on an island, ecological processes fuel these long-term temporal dynamics. Hence, the signature of predominant ecological processes should persist through time, despite the unequivocal fact that historical and evolutionary processes are the engine of community assembly. Most ecological processes driving the assembly and the composition of species assemblages can be summarized under at least three broad categories: dispersal, selection, and ecological drift (Vellend, 2010). In the context of island biogeography, dispersal involves the movement of individuals through space and therefore determines the pattern of colonization of islands by new species. Selection relates to deterministic differences in the fitness of individuals, which can lead to the persistence and overrepresentation of particular species

when conditions are suitable, and their extinction when conditions are not suitable. Ecological drift involves the stochastic (i.e., unpredictable) fluctuations in the number of individuals through time and can therefore lead to stochastic extinctions of species on islands when populations are small, whereas larger populations are more likely to persist (König et al., 2017). To our knowledge, no study to date has explicitly assessed the relative influence of these ecological processes on the composition of insular species assemblages at a global scale.

Geographic variation in insular assemblage compositions can be partitioned into spatial (dispersal), environmental (selection), and stochastic (ecological drift) or unexplained components. Specifically, a correlation between compositional turnover, which represents species replacement between sites (Baselga, 2010), and turnover in relevant environmental variables between (Legendre et al., 2005; Myers et al., 2013) can be assumed to indicate the strength of abiotic selection. Similarly, the association between compositional turnover and the spatial distances between communities can be used as a proxy for the strength of dispersal, under the assumption that dispersal is a stronger limitation between sites that are further apart in a given region, which drives communities to become more dissimilar at larger distances. Finally, the remaining unexplained portion of compositional turnover might arise from other stochastic processes, such as ecological drift (Chesson, 2000), long-distance dispersal events (Gillespie et al., 2012), historical priority effects (Fukami, 2015), and/or a suite of unmeasured processes. While these approaches are increasingly used to tease apart the relative influence of multiple assembly processes, they have seldom been applied in the context of island biogeography.

Although most ecological processes underpinning assemblage composition on islands fall under the umbrella of dispersal, selection, and ecological drift, these processes can operate in various ways and at various spatiotemporal scales. As an example, dispersal at the scale of archipelagos relates to island connectivity, while at a broader spatiotemporal scale, dispersal also relates to isolation from the mainland. In both cases, dispersal depends on current and historical geology. Oceanic islands, which emerged as a result of volcanic activity, have a pervasive history of isolation compared to land-bridge islands, which emerged by separation from another landmass through seismic activity or sea-level rises (Warren et al., 2015). While land-bridge islands inherit species from a previous landmass and benefited from higher dispersal rates during the Quaternary, oceanic islands depend on long-distance overwater dispersal, which is a strong dispersal barrier for terrestrial organisms like mammals (Cardillo et al., 2008; Heaney, 1984).

Isolation from the mainland or source pool (a.k.a. species pool) could also exert a strong influence on dispersal rates and therefore on island community composition (Graves & Gotelli, 1983). Defining the

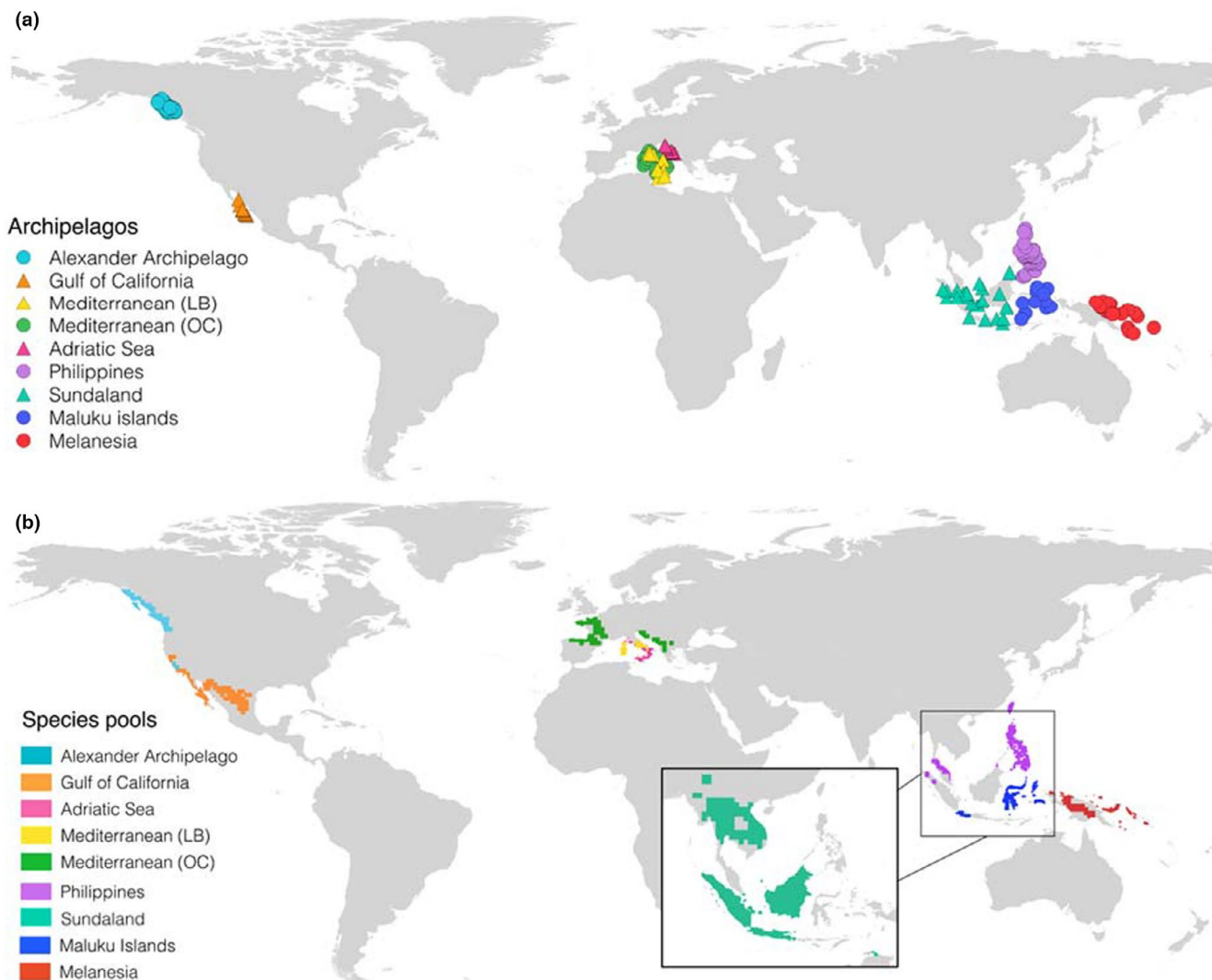


FIGURE 1 The geographic location of the nine island archipelagos, and spatial extent of the nine associated source pools. Each point in (a) represents a terrestrial nonvolant mammal community on an island. Triangles represent land-bridge systems, and circles represent oceanic systems. Source pools in (b) include all terrestrial, extant, non-volant mammal species whose distributional ranges overlap within the 25% most climatically similar grid cells, along with all species within the island system. LB, land-bridge; OC, oceanic.

source pool in itself is not trivial and requires careful consideration of colonization probability and environmental matching between colonizing species and ambient conditions on the island (Graves & Gotelli, 1983). Source pools are a combination of species present at the margins of the nearest continental landmass and species present on “nearby” islands (Figure 1). High dispersal rates are expected to homogenize assemblages and reduce compositional turnover among islands while decreasing their compositional uniqueness (Lu et al., 2019). Isolation can further interact with the size (i.e., diversity) of the source pool, which alone can influence assemblage composition (Karger et al., 2015; Lessard, Belmaker, et al., 2012; Lessard, Borregaard, et al., 2012). For instance, assuming similar isolation and ecologically equivalent species between pools, a highly speciose source pool would contribute proportionally more species propagules to a given island than would a species-poor source pool, simply

because it is more diverse. Larger source pools can even possibly buffer the effect of moderate isolation on dispersal rates due to this proportionally larger potential for contributing propagules. Finally, source pool diversity could also interact with ecological processes such as abiotic selection to increase the amount of compositional turnover explained by the environmental turnover between islands (Questad & Foster, 2008; Spasojevic et al., 2018).

Mammals are one of the most studied taxa worldwide, making them a convenient study group to explore global trends in insular assembly processes. Mammal distributions are well-documented even in island systems (Cardillo et al., 2008; Schipper et al., 2008; Van der Geer et al., 2011), owing to the extensive use of insular mammal assemblages to investigate species-area relationships (Lawlor, 1986), the evolution of body size (Millien, 2006, 2011; Van Valen, 1973), nestedness patterns (Patterson & Atmar, 1986), and island

biogeography theory (Connor & Simberloff, 1979). Our knowledge of mammal distributions on islands thus offers an important opportunity to explore ecological processes in several regions, shedding light on the drivers of insular mammal distributions.

Here, we first used taxonomic and phylogenetic turnover to assess the relative influence of ecological processes such as dispersal, selection, and stochasticity in insular mammal faunas of 9 island systems distributed worldwide. These island systems include 4 land-bridge and 5 oceanic archipelagos, distributed in 6 biogeographic regions and comprising ~200 islands. We then conducted a global analysis to assess the influence of geological history, isolation, source pool diversity, and island characteristics such as climate and topography on the compositional uniqueness of insular mammal assemblages. Using these analyses, we tested three hypotheses: (1) the geological history (i.e., land-bridge or oceanic island systems) affects the relative amount of compositional turnover explained by abiotic selection, dispersal limitation, and stochastic processes within archipelagos. Dispersal limitation and stochastic extinctions should leave a marked signature on compositional turnover in oceanic systems due to consistent dispersal barriers, while higher levels of connectivity in land-bridge systems during the quaternary should have enabled species and lineages to track their abiotic niches, leaving a marked signature of abiotic selection. We also tested the hypothesis that (2) highly diverse source pools are associated with a stronger correlation between compositional and environmental turnover because more diverse pools supply a diversity of potential colonizers that are capable of saturating a wider spectrum of insular niches. As such, we expected archipelagos drawing species from more diverse source pools to exhibit a stronger signature of abiotic selection. Finally, we examined the relative influence of geological history, isolation, source pool diversity, and island characteristics on geographic variation in the compositional uniqueness of insular assemblages. Here, based on classical island biogeography theory, we hypothesized (3) that isolation and island area would explain more variation in compositional uniqueness of island mammal assemblages than

would geological history, source pool diversity, and climatic conditions on the islands.

2 | MATERIALS AND METHODS

2.1 | Island mammal archipelagos

We compared the relative influence of dispersal, ecological drift, and selection on mammal assemblage composition in 9 island systems, or archipelagos, distributed globally (Table 1). We classified archipelagos as land-bridge or oceanic according to the presence of a connection to the mainland during the Last Glacial Maximum (LGM) following Weigelt et al. (2013), except for the Alexander Archipelago. We considered the Alexander Archipelago as oceanic because the islands were colonized via dispersal after emerging as a “blank slate” when deglaciation occurred approximately 15,000 years ago (Conroy et al., 1999). However, the archipelago is geologically a land-bridge and is closer to the mainland relative to typical oceanic islands (Conroy et al., 1999). See Table 1 for further description of the archipelagos.

We compiled data on the occurrence of non-volant terrestrial mammals on each of the 204 islands included in this study using published records in the primary literature, archipelago-wide checklists, and atlases, and cross-referenced community composition among multiple sources (Table S1). Species lists for the Gulf of California, Sundaland, Philippines, and the Mediterranean are based on datasets compiled by Millien and Gonzalez (2011) and were updated, validated, and expanded using additional sources (Table S1). Domesticated and introduced species were omitted when indicated as non-native in the source data or the IUCN Red List because their occurrence results from anthropogenic intervention rather than ecological and evolutionary drivers of community composition. Access to complete species-level occurrence data for the entire mammal fauna of individual islands limited our selection of island systems.

TABLE 1 Biogeographical description of the nine island archipelagos

Archipelago	Abb.	Type	Age	Islands	Species	Endemic	Pool
Alexander Archipelago	Alx	Oceanic ^a	15,000 years	51	34	0	130
Gulf of California	Clf	Land-bridge	Pliocene to early Holocene	10	24	4	293
Mediterranean	MdtLB	Land-bridge	Quaternary	22	17	1	70
Mediterranean	MdtOC	Oceanic	Plio-Pleistocene	11	17	1	71
Adriatic Sea	Adr	Land-bridge	10,000 years	13	15	0	112
Philippines	Phl	Oceanic	Miocene	34	76	42	440
Sundaland	Snd	Land-bridge	Pleistocene	29	83	45	477
Maluku islands	Mlk	Oceanic	Pliocene	11	83	67	247
Melanesia	Mln	Oceanic	Paleocene	23	24	19	215

Note.: Type, geological history as in Weigelt et al. (2013) (Land-bridge, i.e., connected to the mainland during Last Glacial Maximum (LGM); Oceanic, i.e., not connected to the mainland during LGM); Islands, number of islands included; Age, estimated isolation or emergence time of the archipelago (see Table S2 for sources of estimated age); Species, number of native terrestrial nonvolant mammals in the archipelago; Endemic, number of species classified as endemic by Faurby et al. (2016); Pool, taxonomic richness of the source pool.

^aAlexander Archipelago is considered “oceanic” because its post-deglaciation colonization mimics the emergence of oceanic islands.



2.2 | Taxonomic and phylogenetic turnover

We measured taxonomic turnover as Simpson pairwise dissimilarities ($T\beta_{sim}$) between islands, which measures species replacement between sites independently of species richness (Baselga, 2010). We calculated phylogenetic turnover ($P\beta_{sim}$) following Leprieur et al. (2012), which describes the replacement of unique lineages between paired communities independently of differences in phylogenetic diversity. To compute $P\beta_{sim}$, we pruned the Fritz et al. (2009) mammalian phylogeny to each archipelago. Species that were not available in the tree were each added at random to any internal node within their genus (Table S3), following Rangel et al. (2015). Because differences in source pool diversity between archipelagos can cause sampling effects and bias our estimation of turnover, we computed standardized effect sizes of turnover (Kraft et al., 2011). Since our conclusions were not affected by the standardization, we present results based only on observed turnover (but see Data S1 for results with SES).

2.3 | Ecological processes within archipelagos

We used a distance-based redundancy analysis (dbRDA) to assess the relative effect of dispersal and selection on the taxonomic and phylogenetic turnovers within each archipelago. To estimate spatial distances between islands, we computed positive distance-based Moran's eigenvector maps (dbMEMs) using the coordinates of each island's centroid, collected from Weigelt et al. (2013) and Borcard et al. (1992). Because climate and topography are important drivers of mammalian community structure (Cardillo et al., 2008; Peixoto et al., 2017), we characterized the local abiotic environment using topographic variables (island area, maximum elevation) and climatic variables (annual mean temperature, temperature seasonality, annual precipitation, and precipitation seasonality) for each island. These environmental variables generally vary among islands within an archipelago (Figure S1), though there are some environmental similarities between archipelagos in close geographic proximity (Figure S2). The chosen variables are often correlated within a region, resulting in collinearity that can inflate or obscure the importance of selection (Zuur et al., 2010). To account for this collinearity, we sequentially removed correlated variables according to variance inflation factors ($VIF \geq 3$; Zuur et al., 2010). See Table S4 for a list of the environmental variables included in each archipelago (see Table S5 for an equivalent table when controlling turnover for random sampling effects).

We decomposed the taxonomic and phylogenetic turnover within each archipelago into fractions of variation explained [a] purely by spatial variables (i.e., dispersal), [b] jointly by spatial and environmental variables (i.e., spatially structured selection), [c] purely by abiotic environmental variables (i.e., selection), and [d] unexplained variation (Legendre et al., 2005). We assessed the statistical significance of each fraction using permutation tests with 999 iterations, except for fraction [b], the significance of which cannot be tested because it is an indirect measure of variance (Legendre & Legendre, 2012). Negative values obtained for fractions [a] and [c] were interpreted

and plotted as 0, meaning the selected variables could not meaningfully explain turnover (Legendre & Legendre, 2012).

To ensure that the results of variation partitioning were not sampling artefacts, we assessed whether the detected strength of selection and dispersal within a given archipelago were related to mean environmental and geographic distances computed for that particular archipelago, respectively. However, we did not find any significant correlation between the signal of these processes and the environmental and spatial turnover within the archipelagos (Data S2, Table S9).

2.4 | Influence of source pools on ecological processes

The source pool includes all species that could potentially disperse and persist in a given location or area (Graves & Gotelli, 1983; Graves & Rahbek, 2005; Zobel, 1997). Note that we use the term "source pool" as opposed to "species pool" in the context of isolation from large landmasses. The "source pool" implies the unidirectional and disproportionate influence of one or few large sources of colonist species (Graves & Gotelli, 1983; MacArthur & Wilson, 1967), and the "species pool" implies that the focal island is nested within the pool and dispersal can come from any direction or source with more equal probabilities (Carstensen et al., 2013; Lessard, Belmaker, et al., 2012). To assess the interdependence of ecological processes and source pool diversity (Spasojevic et al., 2018), we defined the source pool individually for each archipelago (Figure 1; Data S3), using dispersion fields to delineate the maximum extent of each pool (Borregaard et al., 2020; Carstensen et al., 2013; Lessard, Belmaker, et al., 2012; Lessard, Borregaard, et al., 2012). Such source pools included large swaths of adjacent continental landmass. We then refined these pools by applying an environmental filter, which excluded species that lack the environmental affinities to tolerate conditions within each archipelago (Lessard, Belmaker, et al., 2012; Lessard et al., 2016). We explored the effect of varying the environmental similarity cut-off points on the diversity and climatic space covered by these source pools and found strong correlations between pools defined with different cut-off points (Table S10; Figures S7 and S8).

We then calculated the taxonomic and phylogenetic diversity of each source pool. Taxonomic diversity is measured as the total number of species in the pool (TR). Phylogenetic diversity of the pool is measured as the standardized effect size of pairwise (phylogenetic) distances between species (sesMPD), which is a standardized measure of mean phylogenetic distances (Webb et al., 2002). Phylogenetic diversity was calculated as $sesMPD = [MPD_{obs} - \text{mean}(MPD_{null})] / \text{sd}(MPD_{null})$, where MPD_{obs} is the observed mean phylogenetic distance (MPD) among species in the source pool, and MPD_{null} is the MPD among species in 999 randomly sampled regional pools, which represent a null expectation of the regional pool's phylogenetic structure. Null pools were generated by randomly sampling species from the entire mammalian phylogeny, excluding bats (Fritz

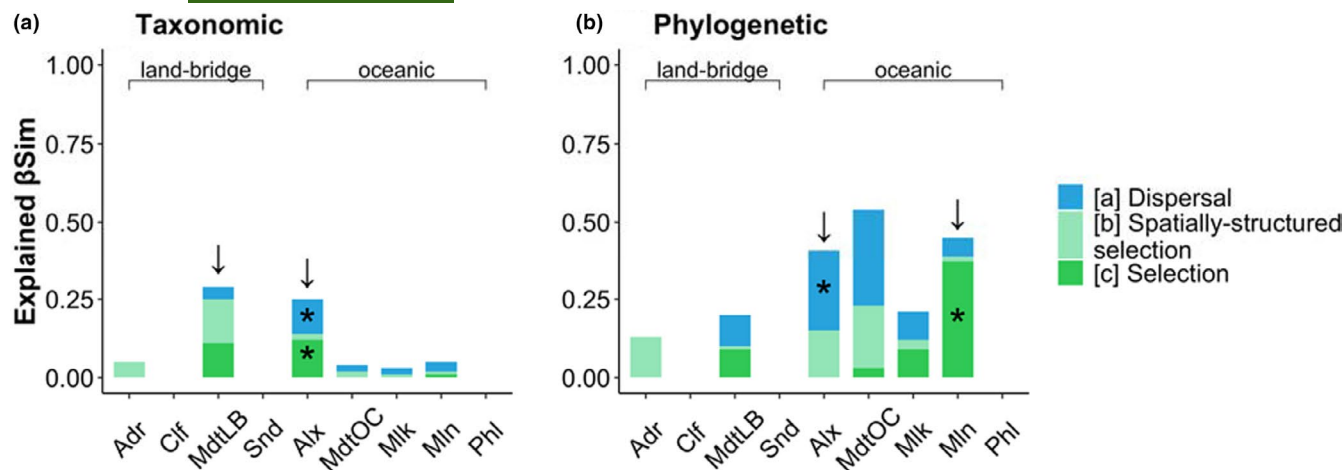


FIGURE 2 Disentangling the influence of dispersal and selection on the (a) taxonomic and (b) phylogenetic turnover of insular mammal assemblages across archipelagos. Arrows indicate that the included spatial and environmental variables significantly explain total compositional turnover. Asterisks indicate each testable fraction's significance ($p < 0.05$). Fraction [b] cannot be tested for significance, as it is not a true measure of variation. Archipelago names are abbreviated as follows: Alexander Archipelago (Alx), Gulf of California (Clf), Mediterranean Land-bridge (MdtLB), Mediterranean Oceanic (MdtOC), Adriatic Sea (Adr), Philippines (Phl), Sundaland (Snd), Maluku islands (Mlk), Melanesia (Mln)

et al., 2009). Negative sesMPD indicates that the regional pool is phylogenetically clustered, while positive sesMPD indicates that the source pool contains higher phylogenetic diversity than expected by chance.

2.5 | Global patterns of compositional uniqueness

To gain deeper insights into the processes shaping species composition on islands at a global scale, we assessed the influence of geological history, isolation, source pool diversity, and island characteristics on compositional uniqueness (Cardillo et al., 2008; Holt et al., 2013). Compositional uniqueness was calculated by comparing the mean turnover of each island with all other islands within its archipelago. Predictors relating to isolation were distance from the mainland and surrounding landmass proportion (SLMP), which relate to the connectivity of the focal island to its source pool, and geological history, which relates to historical connectivity. Predictors relating to island characteristics were climatic variables (annual mean temperature, annual precipitation, temperature seasonality, precipitation seasonality) and topography (area, maximum elevation). To estimate pool richness, taxonomic richness and standardized effect size of mean pairwise phylogenetic distances (sesMPD) were calculated for each island-specific pool (Figure S9). For this analysis, source pools were defined separately for each island rather than each archipelago but using the same approach as for the within-archipelago analyses (Data S3).

To avoid collinearity between climatic and topographic predictors (Figure S10), we used a principal components analysis to transform quantitative variables (island area, maximum elevation, annual mean temperature, annual precipitation, temperature seasonality, precipitation seasonality, area, maximum elevation,

distance from the mainland and surrounding landmass proportion) into principal component axes. Axes were retained based on inspection of a scree plot using the elbow method (Figure S11) and used as fixed effects in a global linear model. As such, we built a linear mixed model to determine the influence of island characteristics (PC1, PC2, PC3), geological history (GMMC), and each island's source pool diversity (either taxonomic richness or sesMPD) on taxonomic or phylogenetic compositional uniqueness, with archipelago as a random effect on the intercept. PC1 was positively related to surrounding landmass proportion and temperature seasonality and was negatively related to distance from the mainland and annual mean temperature (Figure S12). PC2 most strongly represented maximum elevation (Figure S12). PC3 was positively related to annual precipitation and was negatively related to maximum elevation and precipitation seasonality (Figure S12). See Data S4 for more details on model construction, and Figures S13 and S14 for taxonomic and phylogenetic model validation. The linear mixed model was built using the R package *nlme* and island characteristic variables were from Weigelt et al. (2013).

3 | RESULTS

3.1 | Ecological processes within archipelagos

We detected the signature of dispersal limitations on community composition in one of the five oceanic island systems. In the Alexander Archipelago, geographic distance alone ([a]) accounted for 11% of $T\beta_{Sim}$ (Figure 2a; $R_{adj} = 0.11$, $p = 0.001$) and 26% of $P\beta_{Sim}$ (Figure 2c; $R_{adj} = 0.26$, $p = 0.001$). The four remaining true oceanic archipelagos (i.e., Mediterranean, Philippines, Maluku islands, and



Melanesia) did not show a pattern consistent with dispersal limitation (Figure 2).

Contrary to our expectation of stronger selection in land-bridge archipelagos, none of the four focal land-bridge archipelagos showed a pattern consistent with the effects of abiotic selection (Figure 2). Spatially structured selection ([b]) accounted for 14% of the $T\beta_{Sim}$ in the land-bridge subset of the Mediterranean archipelago (Figure 2a; $R_{adj} = 0.14$, $p = NA$), though this was not found in any other measure of turnover. Instead, we found a pattern consistent with abiotic selection ([c]) on compositional turnover in two oceanic archipelagos. In the Alexander Archipelago, variation in the abiotic environment ([c]) accounted for 12% of $T\beta_{Sim}$ (Figure 2a; $R_{adj} = 0.12$, $p = 0.001$), although it did not explain a significant amount of variation in $P\beta_{Sim}$. In Melanesia, variation in the abiotic environment ([c]) accounted for 39% of $P\beta_{Sim}$ within the archipelago (Figure 2b; $R_{adj} = 0.39$, $p = 0.01$).

Taxonomic and phylogenetic turnover did not relate to variation in the abiotic environment or geographic distances between islands in the remaining archipelagos regardless of their geological history (Figure 2). However, average phylogenetic turnover at the scale of the archipelago significantly deviated from a stochastic (null) model, except for Melanesia (Table S6; Figure S5). Average taxonomic turnover in the oceanic portion of the Mediterranean archipelago also deviated significantly from the stochastic expectation (Table S6; Figure S5). See Table S7 for full variation partitioning results, and Figure S3 and Table S8 for results accounting for random sampling effects.

3.2 | Influence of source pools on ecological processes

Biogeographic source pools varied widely in taxonomic and phylogenetic diversity across the nine archipelagos (Figure 1), generally peaking in Southeast Asia (i.e., Sundaland, the Philippines, and Melanesia; Figure S6; Table S10). Taxonomic richness (TR) ranged from 70 species in the land-bridge Mediterranean source pool to 477 species in the Sundaland pool. Source pools ranged in phylogenetic diversity from the least diverse in the Gulf of California ($sesMPD = -5.65$) to the most diverse in Melanesia ($sesMPD = 1.09$).

3.3 | Global patterns of compositional uniqueness

Island pool diversity was positively related to phylogenetic compositional uniqueness ($sesMPD = 0.05$, $p = 0.038$), though this relationship was not significant in the taxonomic model ($TR = 0.04$, $p > 0.05$). Island distance from the mainland and surrounding landmass proportion (PC1) were both related to phylogenetic compositional uniqueness, where less isolated islands tended to be less unique. Higher annual mean temperature (PC1 and PC2), lower temperature seasonality (PC1), and higher precipitation seasonality (PC2) were associated with higher phylogenetic compositional uniqueness. Higher maximum elevation (PC2) was also associated with lower phylogenetic uniqueness. Geological history did not influence taxonomic or

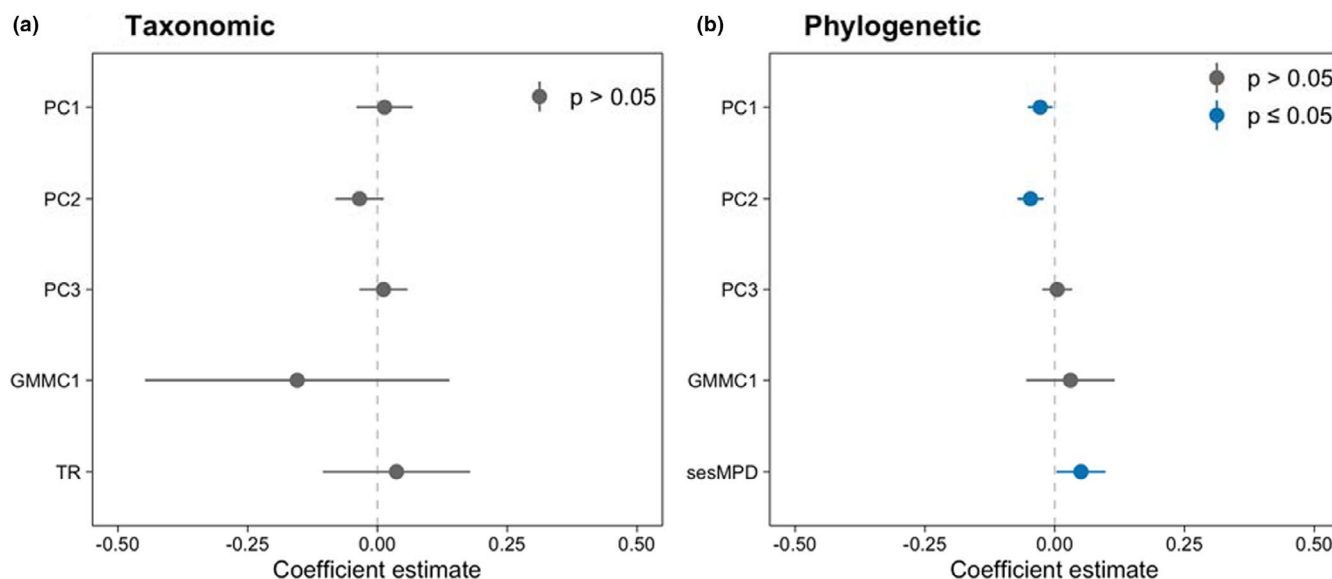


FIGURE 3 Influence of geological history (GMMC), source pool diversity (TR or sesMPD), and island characteristics on (a) taxonomic and (b) phylogenetic compositional uniqueness across the nine archipelagos. Archipelago was included as a random effect on the intercept. The influence of each variable on mean turnover is shown as the coefficient estimate from a linear mixed model where fixed effects are principal component axes representing island characteristics (PC1, PC2, PC3), geological history [GMMC1 = connection to the mainland during Last Glacial Maximum (i.e., 1 = land-bridge or 0 = oceanic)], and the diversity of each island's pool, where TR = taxonomic richness and sesMPD = standardized effect size of mean pairwise (phylogenetic) dissimilarity of the source pool. PC1 was positively related to surrounding landmass proportion and temperature seasonality and was negatively related to distance from the mainland and annual mean temperature (Figure S12). PC2 most strongly and positively correlated with maximum elevation (Figure S12). PC3 was positively related to annual precipitation and was negatively related to maximum elevation and precipitation seasonality (Figure S12)

phylogenetic compositional uniqueness. Taxonomic uniqueness was not related to island characteristics, geological history, or island pool diversity at a global scale (Figure 3a; Table S11).

4 | DISCUSSION

Contrary to our expectations, our results suggest that the relative influence of dispersal and selection does not vary with geological history or source pool diversity in a generalizable way across the nine archipelagos. In fact, we did not find a strong or consistent signature of these processes on taxonomic or phylogenetic turnover in a majority of the focal archipelagos. As such, it appears that stochastic processes, relating perhaps to ecological drift, colonization history, evolutionary processes, or human intervention, may play an important role in shaping the compositional differences between insular mammal communities at the scale of archipelagos. Globally, isolated islands associated with highly diverse source pools exhibit high phylogenetic uniqueness whereas well-connected islands associated with small source pools show the opposite trend. Phylogenetically unique assemblages also tend to occur on islands with a small elevational span and low annual temperature variation. Taken together, our results suggest that patterns of compositional turnover within archipelagos are highly idiosyncratic whereas, on a global scale, the compositional uniqueness of insular mammals relates to isolation from the source pool and processes that relate to climate.

4.1 | Ecological processes within archipelagos

We found some support for the hypothesis that dispersal influences compositional turnover in only two of the five oceanic island systems: the Alexander Archipelago and Melanesia. In the Alexander Archipelago, geographic distances explained taxonomic and phylogenetic turnover, suggesting that successful dispersal within the archipelago strongly depends on spatial proximity between islands (Conroy et al., 1999). Mammal assemblages in the Alexander Archipelago are relatively young, having undergone colonization within the last 15,000 years (Conroy et al., 1999). As such, there has been less time for stochastic extinction to occur, and mammal assemblages may therefore be particularly affected by relatively recent colonization and dispersal dynamics. In support of this hypothesis, the Alexander Archipelago is also one of the few island systems where we detected the signature of abiotic selection on assemblage composition.

We expected a strong selection signature on the composition of mammal assemblages in land-bridge island archipelagos, where high dispersal rates during the Quaternary enabled species to track suitable environmental conditions within the archipelago. Given that compositional and environmental turnover are correlated among mainland mammal assemblages at a global scale (Holt et al., 2018), the lack of such patterns in most oceanic

systems is intriguing. A pattern consistent with abiotic selection was observed in only two oceanic archipelagos: Melanesia and the Alexander Archipelago. In Melanesia, the relationship between phylogenetic and environmental turnover suggests that abiotic selection operates on entire phylogenetic lineages owing to environmental niche conservatism. Moreover, high levels of endemism could distort the signature of abiotic selection on taxonomic turnover by creating extreme compositional turnover between many island pairs. The correlation between phylogenetic and environmental turnover could be indicative of diversification mediated by the colonization of new islands followed by selection-driven adaptation to local abiotic conditions (Emerson & Gillespie, 2008; Gillespie, 2004). These results are particularly interesting given that Melanesia, which includes the Bismarck Archipelago, was the center of heated debate on the influence of competitive exclusion on the composition of island avifaunas (Connor & Simberloff, 1979; Diamond, 1977). Clearly, if competition is important for mammals, its signature is hidden under that of abiotic selection in this insular system (Lessard et al., 2016).

Although dispersal dynamics and environmental gradients did not appear to influence compositional turnover in most archipelagos, the spatial organization of phylogenetic turnover was nevertheless nonrandom in almost all archipelagos, except the land-bridge Mediterranean islands and the Philippines (Table S6; Figure S5). Phylogenetic turnover was either greater or lower than expected under a stochastic model in most archipelagos, which is surprising given the prevalence of random phylogenetic structure in insular mammal communities found in Cardillo et al. (2008). High phylogenetic turnover implies that islands within the archipelago differ in the composition of lineages present, but that neither dispersal dynamics nor selection-driven abiotic filtering explains such spatial segregation. However, based on our global analyses, it appears that isolation from phylogenetically rich source pools, whether the mainland or a large island, could explain the nonrandom phylogenetic turnover in the focal archipelagos (Figure 3b). Multiple stochastic waves of colonization from a large source pool to particular islands, combined with the inability to disperse easily within the archipelago, could produce such patterns by creating high levels of taxonomic and phylogenetic endemism (Emerson & Gillespie, 2008; Jönsson et al., 2008, 2011).

4.2 | Influence of source pools on ecological processes

The structure of the species or source pool can interact with ecological processes to shape species composition (Spasojevic et al., 2018). Theoretical views on community assembly often posit that species present in the pool must pass through a dispersal filter and abiotic and biotic environmental filters to establish locally (Mittelbach & Schemske, 2015). As such, species with adaptations matching the local conditions are more likely to establish and fill available niches (Keddy, 1992). If this is true, the number of



niches being “filled” on any particular island may be higher when the pool of species and lineages is highly diverse. Our results corroborate this hypothesis to some degree as, when comparing the nine archipelagos around the world, the strength of correlation between phylogenetic and environmental turnover was related to the phylogenetic diversity of the species pool, though our low sample size ($n = 9$) limits our interpretation of this correlation (Figure S4). This relationship was also highly influenced by the hyper-diverse source pool of Melanesia, which is connected to Papua New Guinea—a major evolutionary “species pump”, at least for birds (Jønsson et al., 2011). The inclusion of more archipelagos with high phylogenetic diversity would be required for a robust test of this hypothesis.

4.3 | Global patterns of compositional uniqueness

Although stochastic or unmeasured processes appear to be overwhelmingly influential in shaping compositional turnover among mammal assemblages, our initial assessment was limited to processes that would operate within the archipelago. Further investigations into external factors that could also influence species composition suggest that isolation from large landmasses, which serve as source pools, plays an important role in the global distribution of phylogenetic uniqueness (Figure 3). Indeed, isolation from source pools of mammalian species and lineages is associated with phylogenetically differentiated and unique assemblages. Compositional uniqueness is expected to increase with island isolation as a result of limited dispersal, which would prevent the replacement of extinct species, and promote in situ speciation (Rosindell & Phillimore, 2011). Alternatively, islands that are close to several landmasses harbor more cosmopolitan species assemblages. Dispersal from nearby source pools thus appears to play an important role in shaping island assemblage composition, which is consistent with previous work identifying isolated islands as radiation zones (Heaney, 2000; Rosindell & Phillimore, 2011).

Source pool diversity also explained some of the variation in compositional uniqueness (Santos et al., 2011), which suggests that dispersal dynamics involving source pools external to the archipelago act in concert with long-term historical and evolutionary processes in building biodiversity within biogeographic regions (Losos & Ricklefs, 2009; Ricklefs, 1987; Warren et al., 2015). Indeed, islands associated with phylogenetically diverse source pools tended to be more phylogenetically unique than those associated with smaller pools. The influence of source pool diversity and connectivity may appear to contradict the results of the variation partitioning analyses, which showed little influence of dispersal limitations when focusing on pairwise geographical distances between islands at the scale of archipelagos. However, the influence of isolation on assemblage composition at a global scale may simply indicate the particular mechanism by which dispersal mediates assembly and shape composition, as well as the spatiotemporal scale at which it operates (Lessard et al., 2016).

Moreover, isolation may not only relate to historical colonization history and source pool evolutionary history but also to the impact it might have on in situ speciation, and on evolutionary processes more generally (Millien, 2006, 2011). Clearly, long-distance and long-term isolation play an important role in shaping island diversity, not only by affecting rates of colonization, but also by influencing the predominant mode of speciation (Rosindell & Phillimore, 2011).

Island characteristics also explain some of the global variation in compositional uniqueness (Figure 3). In particular, islands where temperature is stable throughout the year harbor more unique communities, which may reflect the higher specialization and/or lower rates of extinction in these regions, and a consequent increase in the degree of phylogenetic endemism. Historically, climatic stability is associated with lower rates of extinction and the persistence of species with small populations and geographic ranges (i.e., endemics; Sandel et al., 2011). Similarly, endemic phylogenetic lineages comprising only a few small-ranged species might result in a high degree of phylogenetic uniqueness (Holt et al., 2013). Interestingly, maximum elevation is negatively related to phylogenetic uniqueness on a global scale. Maximum elevation is often associated with island size, and small islands (low elevation) may be more prone to stochastic extinction owing to the typically small populations inhabiting these islands (Alzate et al., 2019; Cardillo et al., 2008; Valente et al., 2020). Thus, ecological drift, rather than selective forces, could push species to extinction, which would lead to a disequilibrium or mismatch between current abiotic conditions and the composition of island assemblages, and explain why abiotic selection generally appears to play a minor role (MacArthur & Wilson, 1967; Valente et al., 2020). The lower phylogenetic uniqueness on islands with large elevational spans is somewhat surprising given that one might expect islands with broad abiotic gradients to offer more opportunity for in situ speciation (Cardillo et al., 2008; Steinbauer et al., 2016). Taken together, our results corroborate claims from a recent study that was more limited in geographic and taxonomic scope, which concluded that high turnover is associated with small, isolated islands (Lu et al., 2019). However, Lu et al. (2019) found no evidence that source pool diversity and proximity could interact with island topography to shape richness.

4.4 | Caveats

Unexplained compositional turnover could be attributed to a suite of ecological, evolutionary, and historical processes. Colonization history can create unpredictability in the composition of insular assemblages in the presence of strong priority effects (Fukami, 2015). In this scenario, the order of arrival of species or lineages on an island dictates the trajectory of assembly via competitive interactions. As an example, the arrival of a particularly dominant and generalist species can prevent the establishment of future colonizers (Cole, 1983). This phenomenon could be particularly influential on small islands where species are forced to interact, which aligns with our

results. Competition appears to have influenced community assembly on islands worldwide (Cardillo et al., 2008; Millien & Gonzalez, 2011), and admittedly, our analytical approach does not allow the detection of processes occurring within islands such as niche differentiation (Hortal et al., 2009) or character displacement (Dayan & Simberloff, 1994). The ocean is also a relatively impenetrable dispersal barrier between islands for many vertebrates, and particularly non-volant mammals, which could result in dispersal rates that are too low to realistically link islands within an archipelago (Diamond et al., 1976). For example, Heaney (1986) estimated that successful colonization events by non-volant mammals take place only once every 500,000 years in Southeast Asia, pointing to the remarkably low dispersal rates between these islands. It is also possible that spatial distances between island centroids are not accurate proxies for dispersal in these systems. Wind and ocean currents might be more appropriate indicators of dispersal between islands, as rafting can be an important mode of oceanic dispersal (Gillespie et al., 2012).

Anthropogenic modifications of the insular mammal assemblages under study might also account for much of this unexplained turnover. Insular mammal communities have become homogenized since the human occupation of island systems worldwide, as a result of species introductions and human-driven local extinctions (Longman et al., 2018). Such extinctions have also severely distorted mammalian body mass distributions on islands globally (Faurby et al., 2016), as extinction risk is associated with body size in mammals (Fritz et al., 2009). These extinctions modify community composition very differently from the selective extinctions during the relaxation period following the isolation of land-bridge islands or during the colonization process of newly uncovered oceanic islands (Diamond, 1972). Rather than selectively removing species that cannot survive in the emergent habitat due to mismatched traits or interrupted “source-sink” dispersal, human-driven extinctions eliminate species based on traits that are not necessarily related to the island environment or dispersal abilities (Whittaker et al., 2017). As such, these extinctions, in addition to other stochastic processes, could “blur” the signature of ecologically-driven assembly processes (Cardillo et al., 2008).

The particulars of our analytical approach could also be partially responsible for some of our negative results. Although variation partitioning has previously been used to quantify the relative influence of dispersal limitations and abiotic selection on compositional turnover, it has never been used at the scale of the present study. Variation partitioning assumes a linear relationship between the response and explanatory variables and may fail to detect non-linear relationships such as those describing distance-decay relationships in many groups of organisms (Soininen et al., 2007). Moreover, we used a beta diversity metric that is not sensitive to the nestedness component of compositional dissimilarity, which has been recommended for the quantification of compositional dissimilarity at large spatial scales (Kreft & Jetz, 2010), but other metrics could yield different results. We used well-established protocols to define our source pools (Borregaard et al., 2020; Carstensen et al., 2013; Graves & Gotelli, 1983; Graves & Rahbek, 2005; Lessard, Belmaker, et al., 2012; Lessard, Borregaard, et al., 2012; Lessard et al., 2016),

but a more historical approach considering the biogeographic origins of lineages (e.g., ancestral area reconstruction) would help refine our pool definitions and perhaps yield different results.

4.5 | Conclusions

Half a century after the publication of the *Theory of Island Biogeography*, we show that the diversity and proximity of the source pool, but not island size, exert a predominant influence on the composition of island fauna. In addition, we show that source pool diversity and climate interact with source pool connectivity to influence compositional uniqueness. The effect of source pool proximity is likely mediated by long-term dispersal dynamics by which islands are regularly and continuously replenished leading to cosmopolitan assemblages, which can nevertheless be speciose (Fabre et al., 2014; Jönsson et al., 2008). On the other hand, islands that are disconnected from these major “species pumps”, may receive fewer colonization waves, and result in phylogenetically unique sets of species, whose composition is determined by stochastic dispersal events. This phenomenon appears to be even stronger in regions harboring phylogenetically diverse source pools, which may relate to the phylogenetic endemism in the pool, and colonization of islands by small, regionally endemic lineages. Finally, islands with limited elevation spans tend to harbor more unique assemblages as well, which might relate to the generally small size of such islands, in line with the findings of Cardillo et al. (2008). The effect of isolation could be exacerbated in the case of small islands, which are more prone to stochastic extinctions owing to unpredictable demographic crashes, and to historical priority effects, which can hamper future colonization attempts. Small, isolated islands may thus comprise unusual combinations of species and lineages. In sum, while a complex suite of ecological, evolutionary, and historical process interacts to shape island biodiversity (Connor & Simberloff, 1979; Dayan & Simberloff, 1994; Losos & Ricklefs, 2009; MacArthur & Wilson, 1967; Valente et al., 2014, 2020; Whittaker et al., 2017), the present study demonstrates that the processes involved in the generation of source pool diversity interact with source pool connectivity to influence insular assemblage composition worldwide.

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DATA AVAILABILITY STATEMENT

All data supporting the results are archived on Dryad (<https://doi.org/10.5061/dryad.rfj6q579r>). R scripts to produce some figures and some analyses are available on GitHub (<https://github.com/katherinehebert/insular-mammals>).

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BIOSKETCHES

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Author contributions: All authors designed the study. KH and VM collected data. KH performed data analyses. KH and JPL wrote the first draft of the manuscript. VM and JPL contributed substantially to revisions.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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