

RESEARCH PAPER



Oceanic islands of Wallacea as a source for dispersal and diversification of murine rodents

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Abstract

Aim: To determine the historical dynamics of colonization and whether the relative timing of colonization predicts diversification rate in the species-rich, murine rodent communities of Indo-Australia.

Location: Indo-Australian Archipelago including the Sunda shelf of continental Asia, Sahul shelf of continental Australia, the Philippines and Wallacea of Indonesia.

Taxon: Order Rodentia, Family Muridae.

Methods: We used a fossil-calibrated molecular phylogeny and Bayesian biogeographical modelling to infer the frequency and temporal sequence of biogeographical transitions among Sunda, Sahul, the Philippines and Wallacea. We estimated diversification rates for each colonizing lineage using a method-of-moments estimator of net diversification and Bayesian mixture model estimates of diversification rate shifts.

Results: We identified 17 biogeographical transitions, including nine originating from Sunda, seven originating from Sulawesi and broader Wallacea and one originating from Sahul. Wallacea was colonized eight times, the Philippines five times, Sunda twice and Sahul twice. Net diversification rates ranged from 0.2 to 2.12 species/lineage/My with higher rates in secondary and later colonizers than primary colonizers. The highest rates were in the genus *Rattus* and their closest relatives, irrespective of colonization history.

Main Conclusions: Our inferences from murines demonstrate once again the substantial role of islands as sources of species diversity in terrestrial vertebrates of the IAA with most speciation events occurring on islands. Sulawesi and broader Wallacea have been a major source of colonists for both island and continental systems. Crossings of Wallace's Line were more common than subsequent transitions across Lydekker's Line to the east. While speciation following colonization of oceanic archipelagos and large islands is consistent with adaptive radiation theory and ideas regarding ecological opportunity, we did not observe a strong signal of incumbency effects. Rather, subsequent colonists of landmasses radiated unhindered by previous radiations.

KEYWORDS

community assembly, diversification, island biogeography, Muridae, phylogenetics, Sulawesi, upstream colonization



1 | INTRODUCTION

Island systems, because of their discrete boundaries in time and space, provide a clear framework for understanding how biological communities are assembled (Wallace, 1880; Whittaker, Fernández-Palacios, Matthews, Borregaard, & Triantis, 2017). For islands that are oceanic in origin or have been isolated from relevant source areas throughout the history of a particular clade, colonization is a necessary, but often not sufficient historical explanation of current diversity. The last two decades of phylogenetic research have made clear that speciation plays an important role in building many local communities even when overwater colonization by terrestrial animals is relatively common (Heaney, 2007; Warren et al., 2015; Whittaker et al., 2017; Whittaker, Triantis, & Ladle, 2008). The frequency of colonization and the net diversification rate together assemble island communities, but their magnitudes are highly variable, each depending on a multitude of geographic, geological and biological factors (MacArthur, 1984; MacArthur & Wilson, 1963, 1967; Price, 2008; Rabosky & Glor, 2010; Schluter, 2000). At one end of the spectrum, diverse island communities may be assembled entirely through colonization. Successful establishment requires that arriving organisms either fit existing community circumstances or displace a previous arrival, processes referred to as habitat filtering (Diamond, 1975; Webb, Ackerly, McPeck, & Donoghue, 2002; Weiher & Keddy, 1995, 1999) and taxon cycling (Economato & Sarnat, 2012; Ricklefs & Bermingham, 2002; Wilson, 1961) respectively. At the opposite extreme, a single colonizing lineage may diversify in place, filling available ecological space through adaptive radiation (Glor, 2010; Losos, 2010). Under this model, colonization of new areas should yield an early burst in the diversification rate (i.e. diversity-dependent diversification). Furthermore, when multiple colonists arrive sequentially in an area, primary colonizers should have the highest diversification rates (i.e. incumbency effects; Gavrilits & Losos, 2009; Mahler, Revell, Glor, & Losos, 2010; Rabosky, 2013; Rabosky & Lovette, 2008; Rowsey, Heaney, & Jansa, 2018; Schenk, Rowe, & Steppan, 2013; Schluter, 2000). Thus, quantifying both the frequency and temporal sequence of colonization is a critical initial step in understanding how insular communities are assembled.

The Indo-Australian Archipelago (IAA), the insular region spanning western Indonesia to Australia, is an exceptional arena for evolutionary biologists to quantify colonization and diversification in the assembly of communities (Figure 1; Brown et al., 2013; Lohman et al., 2011; Sheldon, Lim, & Moyle, 2015). With more than 20,000 islands distributed among closely packed island systems, including adjacent continental and oceanic archipelagos, the region offers enormous opportunities for studying the diversification of terrestrial species following overwater colonization. Several studies have demonstrated that island systems of the IAA are both recipients and sources of colonizations with most, but not all, taxa colonizing from east (continental Asia) to west (Wallacea, Philippines, Australia; Balke et al., 2009; Bocek & Bocak, 2019; de Bruyn et al., 2014; Crayn, Costion, & Harrington, 2015; Jønsson, Fabre, Ricklefs, & Fjeldså, 2011; Tänzler, Toussaint, Suhardjono, Balke, & Riedel, 2014;

Tänzler et al., 2016; Wood, Heinicke, Jackman, & Bauer, 2012). In some taxa, repeated colonization of and diversification on islands of the IAA have led to replicated evolutionary “experiments” (Fabre et al., 2013; Jansa, Barker, & Heaney, 2006; Rowe, Aplin, Baverstock, & Moritz, 2011; Rowsey et al., 2018; Tänzler et al., 2014; Tänzler et al., 2016; Toussaint, 2015).

Rodents of the family Muridae are diverse, ubiquitous members of terrestrial mammal communities across the IAA. With 891 species, Muridae is the most diverse mammalian family and most murids are members of the subfamily Murinae (704 species; Burgin, Colella, Kahn, & Upham, 2018; Mammal Diversity Database, 2018). Nearly two-thirds of murine species are endemic to Southeast Asia and the IAA, an area where no other murid subfamily is represented (Musser & Carleton, 2005). Among IAA mammal clades, murines are unusual in that they are widespread in the region, having crossed Wallace's, Huxley's and Lydekker's lines (Figure 1), which represent some of Earth's sharpest biogeographical boundaries (Fabre et al., 2013; Holt et al., 2012; Jansa et al., 2006; Rowe, Reno, Richmond, Adkins, & Steppan, 2008; Schenk et al., 2013). Despite the boundary-crossing distribution of the subfamily, species and genera of murines are almost entirely endemic to only one of the four primary biogeographical units that comprise the IAA, that is (a) Sundaland (Borneo, Java, Sumatra, Malay Peninsula, Palawan and neighbouring islands), (b) oceanic portions of the Philippines (Luzon, Mindanao, Mindoro and neighbouring islands), (c) Wallacea (Sulawesi and neighbouring islands, Lesser Sundas, Maluku Islands) and (d) Sahul (New Guinea, Australia and neighbouring islands) (Figure 1). The notable exceptions are a handful of species in three primarily Sahulian genera that are also found on the other side of Lydekker's Line in the Maluku Islands of eastern Wallacea (*Hydromys chrysogaster*, *Melomys* spp., *Uromys* sp.; Fabre, Reeve, Fitriana, Aplin, & Helgen, 2018; Helgen, 2003). Indeed, many species are endemic to individual islands or mountain ranges within islands (Flannery, 1995; Heaney, Balete, & Rickart, 2016; Justiniano et al., 2015; Musser, 2014). In addition to their fine-scale endemism, IAA murines encapsulate extensive ecological diversity on large oceanic and continental islands, with a variety of roles played by individual species occurring in sympatry. For example on Mt. Gandang Dewata, Sulawesi Island, a murine community consisting of at least 24 species includes, among others, an amphibious rat that feeds on aquatic insects (*Waiomys mamasae*), a vermivorous rat that is unique among rodents in its lack of molars (*Paucidentomys vermidax*), a diurnal rat that feeds on invertebrates (*Melasmothrix naso*), an endemic species of arboreal *Rattus* (*Rattus facetus*), a large, montane, arboreal and woolly rat (*Eropeplus canus*), a small arboreal mouse that feeds on fruit and seeds (*Haeromys minahassae*), and a large, terrestrial frugivore (*Paruromys dominator*; Achmadi, Rowe, & Esselstyn, 2014; Esselstyn, Achmadi, & Rowe, 2012; Musser, 2014; Rowe, Achmadi, & Esselstyn, 2014, 2016a). Murine communities with comparable ecological diversity are endemic to Luzon and Mindanao islands in the Philippines, and to New Guinea (Flannery, 1995; Heaney, Balete, Duya, et al., 2016; Musser & Lunde, 2009). Previous research demonstrated that the

murine faunas of the Philippines and Sahul are derived from five and two independent colonizations respectively (Fabre et al., 2013; Jansa et al., 2006; Rowe et al., 2011). These colonists differ dramatically in their arrival times (c. 15–3 Ma in the Philippines and c. 6 and 1 Ma in Sahul) and the extent to which they diversified after arrival (3–32 descendent species per colonist in the Philippines and 159 and 24 species in Sahul; Jansa et al., 2006; Rowe et al., 2011; Rowe et al., 2008; Rowsey et al., 2018). However, while the murine faunas of the Philippines and Sahul have been subject to phylogenetic and biogeographical investigations, the number of dispersal events and the extent of in situ diversification in the centrally located Wallacean region remains unknown. High levels of subduction and volcanic arcs along the abundant Wallacean geological faults have resulted in the formation of numerous oceanic islands (Hall, 2002, 2009, 2013) that are likely stepping stone areas for murine dispersals. Among Wallacean Islands, Sulawesi is the largest, and although modern Sulawesi has resulted from collisions of oceanic and continental fragments from the Miocene to the present, it has remained an available and isolated landmass throughout murine history in the region (i.e. <15 Ma; Nugraha & Hall, 2018). In other parts of Wallacea, such as the Maluku Islands, some islands have formed more recently in the Late Miocene to Pliocene

(e.g. Seram, Buru), but others are older (e.g. Halmahera) providing sub-aerial land while remaining isolated by marine channels from other biogeographical units of the IAA throughout murine history. The importance of Sulawesi and the rest of Wallacea as a potential stepping stone for access to the Philippines or Sahul remains largely untested, with the exception that at least one genus, *Crunomys*, probably colonized the Philippines from Sulawesi (Rowe, Achmadi, & Esselstyn, 2016b).

Herein, we conduct the most comprehensive phylogenetic analyses to date of IAA murines, with an emphasis on new information from the fauna of Sulawesi, a large, geomorphologically complex island containing an ecologically diverse assemblage of rats (Esselstyn, Achmadi, Handika, & Rowe, 2015; Esselstyn et al., 2012; Musser, 2014; Musser & Durden, 2002; Nugraha & Hall, 2018; Rowe, Achmadi, & Esselstyn, 2014, 2016a). We use the resulting phylogeny to infer the history of dispersal events across the IAA, thereby testing the importance of Wallacea as either a source or sink for colonization. Lastly, we estimate the tempo of diversification subsequent to each dispersal event, with the expectation that diversification rates were highest soon after colonization and that the earliest colonists of each area diversified most rapidly, as predicted by theories of ecological opportunity and adaptive radiation (Schluter, 2000; Simpson, 1953).

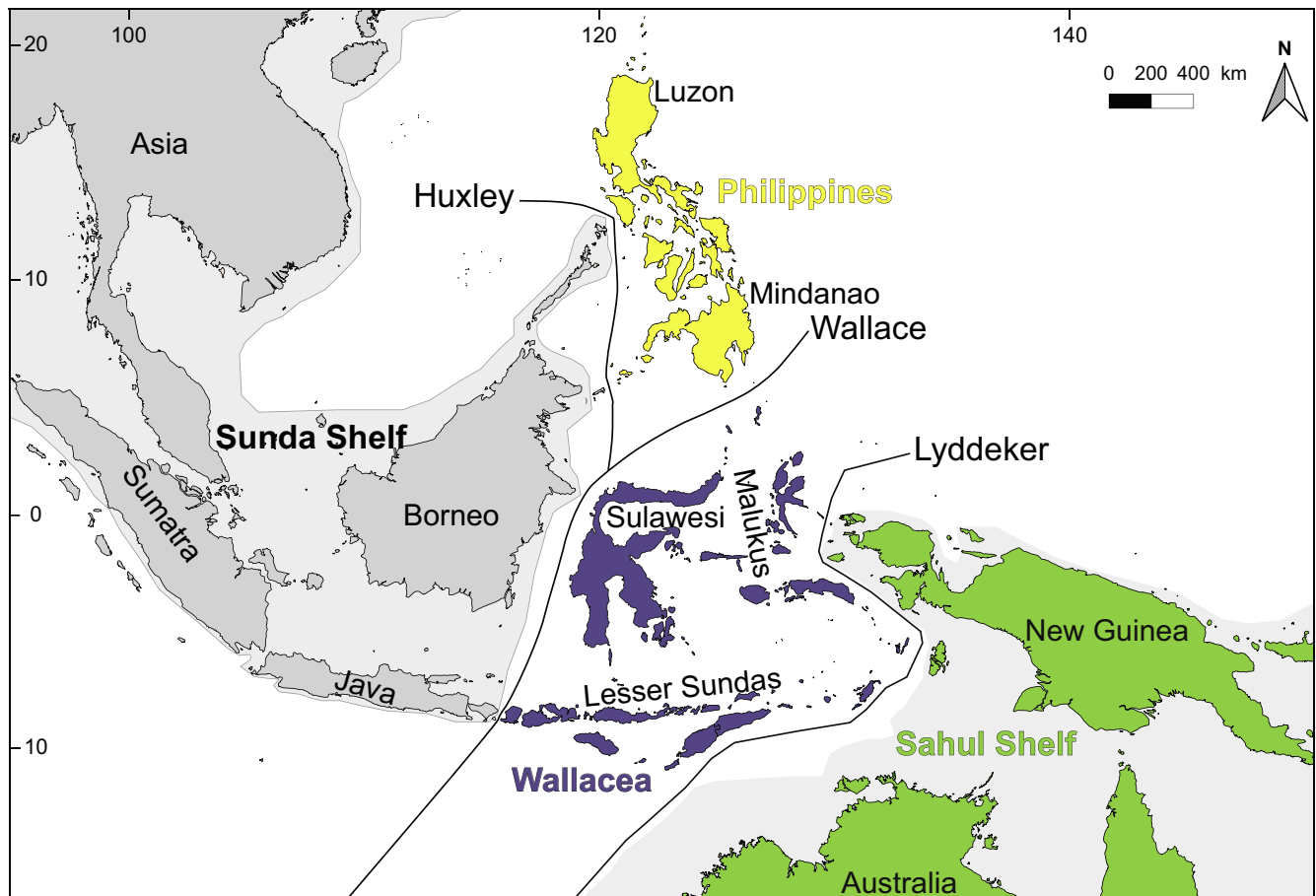


FIGURE 1 Map of the Indo-Australian Archipelago with the four biogeographical units, Sunda (grey), Philippines (yellow), Wallacea (blue) and Sahul (green), identified. Huxley's, Wallace's and Lydekker's lines are indicated and show the separation among units



2 | MATERIALS AND METHODS

2.1 | Taxon sampling and DNA sequencing

We compiled DNA sequences from five commonly sequenced genes, including a mitochondrial protein coding locus (cytochrome b) and four nuclear exons (exon 11 of breast cancer 1 [BRCA1], exon 1 of retinol-binding protein 3 [IRBP], the single exon of recombination activating gene 1 [RAG1] and exon 10 of growth hormone receptor [GHR]), using the alignments of Rowe, Achmadi, and Esselstyn (2016a), and Rowe et al. (2016b) as our starting point (138 species in the Muridae). To these alignments, we added sequences from 132 additional species of Muridae, including new sequences from 32 previously unavailable species. All new sequences are available on GenBank www.ncbi.nlm.nih.gov/genbank with accession numbers MN272952–MN273051. GenBank accession numbers for all sequences used in this study are available in Table S1. For most species, we extracted DNA from frozen tissues and generated new sequences using standard polymerase chain reaction and Sanger sequencing methods that follow Rowe et al. (2016b). For two species, we obtained sequences from historical museum skins (*Baiyankamys habbema* and *Hydromys neobrittanicus*). DNA extraction and nuclear loci sequencing approaches for these two skin samples followed Pagès et al. (2016). Mitochondrial cytochrome b sequences were obtained from skins with the same extractions but using Illumina sequencing to recover whole mitogenomes following Tilak et al. (2015). Geographically, our new sequences are primarily from samples representing Wallacean endemics (26 species), but also include previously unavailable taxa from the Sunda (3 species) and Sahul (3 species) regions. Our taxon sampling covers 56% of named species native to the IAA (164 of 294), representing 91% of genera (69 of 76) from the Philippines, Sahul and Wallacea. Across Murinae our sampling includes c. 80% of genera and c. 40% of species and representatives of all murine divisions (reflecting major clades) except the Hadromys division, which comprises only two species endemic to northeast India and southern China. We excluded from our analyses available sequence data from some African species and genera, which previous studies show are closely related to other African taxa in our study and are not relevant to the biogeographical history of Indo-Australian taxa (Aghova et al., 2018; Bryja et al., 2017).

2.2 | Phylogenetic analyses

We aligned sequences in CodonCode ver. 8.0.1 (CodonCode Corporation) and manually inspected alignments in ALVIEW 1.20 (Larsson, 2014). We determined appropriate DNA sequence partitions and substitution models using PARTITIONFINDER 1.1.1 (Lanfear, Calcott, Ho, & Guindon, 2012) and estimated phylogenetic relationships using RAXML 8.2.12 (Stamatakis, 2006). We conducted RAXML analyses with 1,000 bootstrap pseudoreplicates using the partitions selected by PARTITIONFINDER.

To estimate the ages of colonizations, we used a relaxed molecular clock approach in BEAST 2.5.0 (Bouckaert et al., 2014). We defined data partitions based on the results of PARTITIONFINDER, with the maximum number of partitions defined by the three codon positions of each locus. Among partitions, we unlinked clock and substitution models but linked the trees. We set the priors on substitution models based on the best models obtained from PARTITIONFINDER. We rejected a strict molecular clock for the concatenated data (likelihood ratio test: $p < .01$) and therefore used the uncorrelated lognormal relaxed-clock model for each partition. We applied a Yule speciation prior, set the birthrate prior to exponential with a mean of 1 and left other priors at default settings. We initiated the BEAST analysis using the topology from RAXML, but allowed tree space to be fully explored. We set four calibration priors combining three fossils from the Siwalik formation (Aghova et al., 2018; Kimura, Hawkins, McDonough, Jacobs, & Flynn, 2015) with a calibration for the origin of Australian murines (described in Aplin & Ford, 2014 and specified in Smitsen & Rowe, 2018). These previous studies provide extensive detail on ages and phylogenetic placement of fossils as well as evaluation of their utility as fossil constraints for dating the phylogeny of Murinae. In our phylogeny, these fossils refer to the shared ancestors of (a) *Mus* and *Arvicanthis* (11.1–12.3 Ma), (b) *Arvicanthis* and *Otomys* (8.7–10.1 Ma), (c) species of the genus *Mus* (7.3–8.3 Ma) and (d) *Pseudomys* and *Zyomys* (4.0–4.5 Ma). All fossil calibrations were set in BEAST as lognormal distributions with means and offsets following guidelines in Aghova et al. (2018): (a) offset = 10.47, $\log(SD) = 1.0$, $\log(\text{mean}) = 4.0$; (2) offset = 8.52, $\log(SD) = 1.0$, $\log(\text{mean}) = 4.6$; (3) offset = 7.29, $\log(SD) = 1.0$, $\log(\text{mean}) = 4.9$; (4) offset = 4.0, $\log(SD) = 1.0$, $\log(\text{mean}) = 1.0$. We used initial runs to optimize operators and conducted a final MCMC run with 2×10^8 generations, sampling trees and other parameters every 2,000 generations. We evaluated convergence and assessed sampling adequacy in TRACER 1.4. We used TREEANNOTATOR to discard the first 20% of trees as burn-in and pool the remaining samples to form the posterior distribution and generate a maximum clade credibility tree.

2.3 | Biogeography and diversification rates

To reconstruct biogeographical transitions on the phylogeny, we first coded all terminal taxa to one of four biogeographical units (Figure 1, following Rowe et al., 2016b): continental, including Africa and Eurasia to the eastern limit of the Sunda shelf (C), Wallacea, including Sulawesi, the Lesser Sundas and Maluku Islands (W), the oceanic Philippines, excluding Palawan and other continental islands, which we included in 'continental' (P), or Sahul, including Australia, New Guinea, the Solomons, and adjacent Islands (S). Except for the amphibious *H. chrysogaster*, which are found on the Maluku Islands of Wallacea and across Sahul, all extant murine species are endemic to one of these four biogeographical units with no species shared among them. These four biogeographical units represent a necessary simplification of more complex continental and oceanic archipelagos that masks overwater dispersal

within units. They also mask ecological and biotic differences within units. For instance in the oceanic Philippines, distinct mammalian communities including tarsiers, colugos, gymnures, squirrels and other mammals are present on Mindanao but absent on Luzon, where murine rodents are the dominant terrestrial mammals (Heaney, Balete, & Rickart, 2016). We used the R package BioGeoBEARS (Matzke, 2013) to infer ancestral areas. We allowed ranges at ancestral nodes to occupy a maximum of two states because, as noted above, extant murine species are almost entirely endemic to a single biogeographical unit of the IAA, and we assume that the typical sizes of species' ranges have remained relatively constant over evolutionary time scales. We estimated biogeographical transitions and compared dispersal rate models using the DEC (Dispersal Extinction Cladogenesis) and DEC + J models in BioGeoBEARS (Matzke, 2013; Ree, 2005). Both models include dispersal and extinction parameters, whereas the DEC + J model also includes a founder event speciation parameter, which is suited to island systems. To examine the significance of continents and islands as sources and destinations we tested six dispersal rate models by varying dispersal rates among biogeographical units. Our six dispersal rate models comprised (a) an equal-rates model where we set all dispersal rates to 1; (b) a nearest-neighbour model where we set dispersal rates among adjacent biogeographical units to 1 and among non-adjacent units to 0.1; (c) a continental-source model where we set dispersal rates from continental to other biogeographical units to 1 and all other dispersal rates to 0.1; (d) a Wallacea nexus model where we set dispersal rates from continental to Wallacea and from Wallacea to all other units to 1 with all other dispersal rates set to 0.1; (e) a Philippines nexus model, identical to model 4 but with the Philippines substituted for Wallacea; and finally (f) a Sahul nexus model, which is identical to model 4 but with Sahul substituted for Wallacea. Based on the model with the highest likelihood, we computed the ancestral area probabilities for each node, and hence inferred the ancestral lineages that colonized each area. We plotted these ancestral area probabilities on the majority-rule chronogram from our BEAST analysis using R scripts.

We estimated diversification rates for each colonization of Wallacea, the Philippines and Sahul that resulted in >2 species in our phylogeny. To facilitate comparison with previous studies, we first estimated net diversification using the method-of-moments estimate described in Magallon and Sanderson (2001) and implemented in the R package GEIGER 2.0.6. (Harmon, Weir, Brock, Glor, & Challenger, 2007). We estimated a range of rates by considering the 95% highest posterior densities of both median crown and median stem ages sampled from the post-burnin posterior of the BEAST trees. We also used BAMM via the BAMMtools R package to infer diversification rates across our phylogeny and compared diversification among colonizing clades (Rabosky, 2014; Rabosky et al., 2014). We ran four MCMC chains for 25 million generations and sampled every 2,000 generations. Other parameters were set to default values except for the Poisson process prior that was set to 1.0 (Rabosky et al., 2014). We launched four independent runs (with a burn-in of

15%) using different initial seeds. We considered effective sample sizes >200 as indicating parameter convergence. We used the posterior distribution to estimate mean rates of diversification and diversification rates through time for each colonization of Wallacea, the Philippines and Sahul. In addition, we inferred the number of diversification rate shifts on the phylogeny using Bayes factors to compare alternative diversification models with different numbers of diversification rates (M_0 being the null model without shift and M_i the alternative models with i shifts). The best selected model is usually the one with the highest Bayes factor as compared to the null model M_0 . We tested three different priors for the number of diversification rate shifts ($i = 1, 10$ or 50). As these priors had no impact on the inferred shift of diversification rate we present the analysis with $i = 1$.

3 | RESULTS

Our concatenated alignment of one mitochondrial gene and four nuclear exons is 6,059 bp long, with 268 species represented. Each locus-specific alignment contains 144–245 taxa (Table S1) and the entire matrix is 60% complete at the nucleotide level. Our phylogenetic estimate consisted of well supported nodes, three-quarters of which had a bootstrap or a posterior probability >0.95 (Figure 2, RAXML and BEAST trees available in Supporting information). The topology is consistent with previous inferences, but our expanded taxon sampling shows the repeated invasion of each biogeographical unit by murines, including dispersal events from islands to continents (Figure 2). We identified five clades in the Philippines, eight in Wallacea, two in Sahul and many residing in the continental regions of Sunda, Asia and Africa (Figure 2). As inferred by Pagès et al. (2016) and Steppan and Schenk (2017), we placed the marmoset rat *Hapalomys* (*Hapalomyini*) as the sister to all other Murinae, with a murine crown age of c. 15 Ma (13.7–16.7 Ma). At c. 13.5 Ma (12.8–14.5 Ma), the largely arboreal Philippine cloud rats (*Phloeomyini*) diverged from the remaining taxa. Subtending this node are three large clades containing (a) the Rattini (including *Micromys*), (b) the Hydromyini (including *Chiropodomys*, *Haeromys* and the *Chrotomyini sensu* Rowsey et al., 2018) and (c) the “Other Murinae,” consisting of the Apodemurini, Arvicanthini, Malacomyini, Millardini, Murini, Praomyini and Vandeleurini, that diverged c. 11.4 Ma (11.2–11.6 Ma). The first two of these three clades contain lineages distributed in each of the biogeographical units east of Wallace's Line, whereas the third does not and is largely African (see also Fabre et al., 2013; Schenk et al., 2013). Within the Rattini and Hydromyini, we infer that several murine divisions (*sensu* Musser & Carleton, 2005) are unnatural groupings, including the Echiothrix, Melasmothrix, Crunomys, Maxomys, *Micromys* and *Pithecheir* divisions, as previously noted (e.g. Achmadi, Esselstyn, Rowe, Maryanto, & Abdullah, 2013; Pagès et al., 2016; Rowe et al., 2016b; Steppan & Schenk, 2017). As such, we propose redefining divisions within

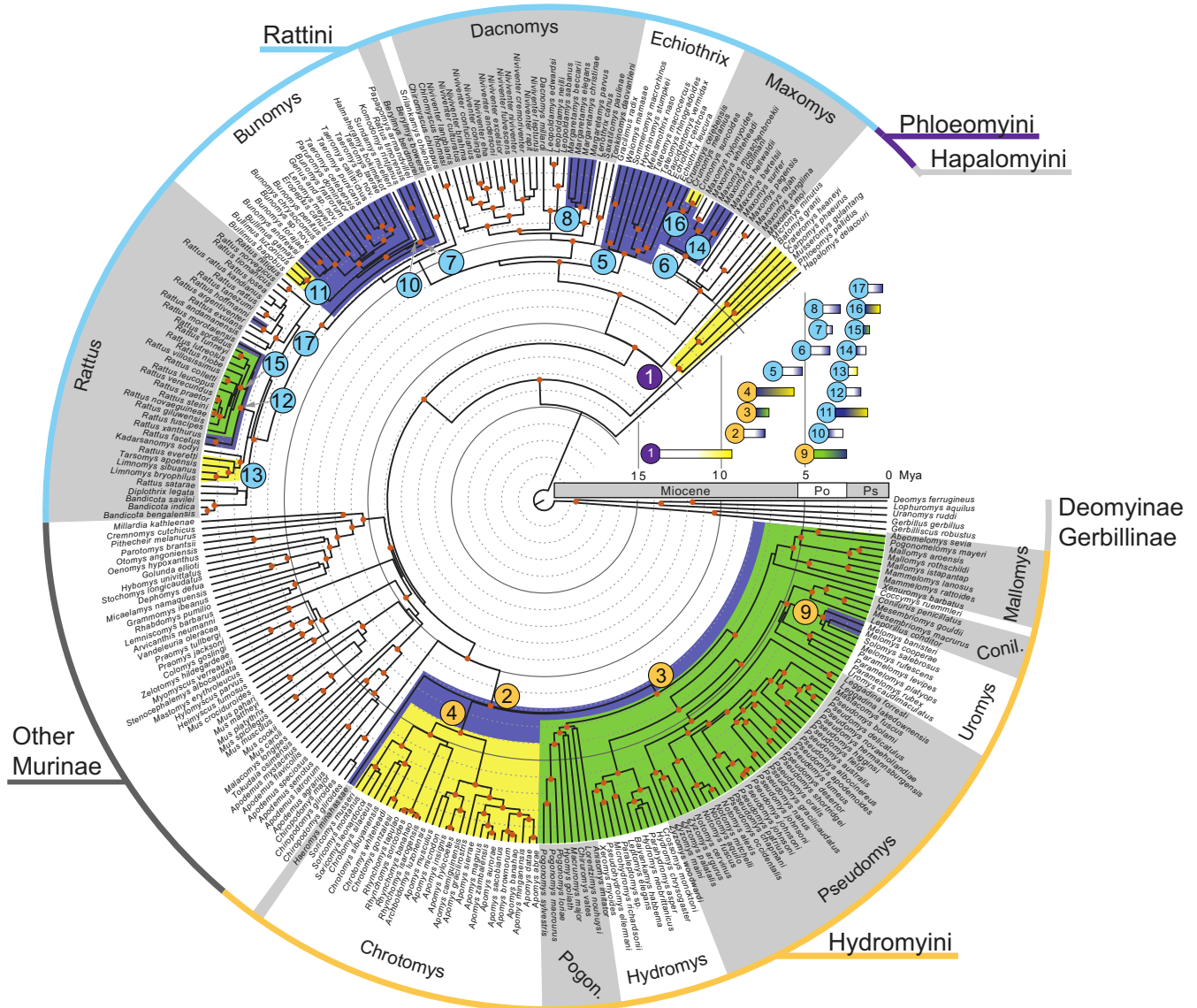


FIGURE 2 Time-calibrated phylogeny of Murinae resulting from our BEAST analyses. Murid subfamilies and murine tribes identified by outer bands. Divisions within the tribes Rattini and Hydromyini are labelled and indicated by alternating white and grey shading. Monogeneric divisions are not labelled (see Table 1). The 17 colonizations by murine rodents across the Indo-Australian Archipelago, inferred using BioGEOBEARS, are indicated with numbers in circles. Circles are coloured to indicate murine tribes. Clades are coloured to indicate taxa endemic to Wallacea (blue), the oceanic Philippines (yellow), Sahul (green) and Continental (white; including Sunda). Orange circles identify nodes supported by >0.95 posterior probabilities. For inset time scale, bars denote the age ranges of colonizations from median stem age to median crown age. Colours of bars represent the source (left side) and destination (right side) of each colonization. The ranges of ages for colonizations 2, 10 and 17 are based on minimum and maximum stem ages as these clades lack crown ages

these tribes to reflect monophyletic groups (Table 1). In addition to our study, these revisions incorporate newly described genera from the recent subfossil record and recent revisions of African divisions (Bryja et al., 2017; Louys, O'Connor, Higgins, Hawkins, & Maloney, 2018; Turvey et al., 2017). We resolved a single radiation of Sulawesi shrew-rats, which we label the Echiothrix division (following Rowe et al., 2016b). We show that *Eropeplus* and *Lenomys* are part of an endemic Sulawesi radiation including *Bunomys*, *Paruromys*, *Taeromys* and an undescribed taxon, which we refer to as the Bunomys division. Following Pagès et al. (2016), our phylogeny placed *Margaretamys* as sister

to *Lenothrix* in the Dacnomys division. We also placed the Sunda endemic, *Pithecheir*, close to African and Indian taxa in the Otomyini and Millardini. As in Achmadi et al. (2013), we placed *Crunomys* within *Maxomys*, and we label this group the Maxomys division (Table 1).

3.1 | Biogeographical inferences

For both the DEC and DEC + J biogeographical models, the best-fitting dispersal model was the Wallacean nexus, where the dispersal rate is maximal ($d = 1$) from continental to Wallacea and from

**TABLE 1** Proposed assignment of murine genera to monophyletic tribes and divisions within Murinae based on this study and Bryja et al. (2017); Turvey et al. (2017); Louys et al. (2018)

Tribe	Division	Genera
Apodemini	Apodemus	<i>Apodemus</i> , <i>Rhagamys</i> ^E , <i>Tokudaia</i>
Arvicanthini	Aethomys	<i>Aethomys</i> , <i>Micaelamys</i>
Arvicanthini	Arvicanthis	<i>Arvicanthis</i> , <i>Desmomys</i> , <i>Lamottemys</i> , <i>Lemniscomys</i> , <i>Mylomys</i> , <i>Pelomys</i> , <i>Rhabdomys</i>
Arvicanthini	Dasymys	<i>Dasymys</i>
Arvicanthini	Golunda	<i>Golunda</i>
Arvicanthini	Hybomys	<i>Hybomys</i> , <i>Dephomys</i> , <i>Stochomys</i>
Arvicanthini	Oenomys	<i>Oenomys</i> , <i>Thamnomyms</i> , <i>Grammomys</i> , <i>Thallomys</i>
Hapalomyini	Hapalomys	<i>Hapalomys</i>
Hydromyini	Chiropodomys	Chiropodomys
Hydromyini	Chrotomys	<i>Apomys</i> , <i>Archboldomys</i> , <i>Chrotomys</i> , <i>Rhynchomys</i> , <i>Soricomys</i>
Hydromyini	Conilurus	<i>Conilurus</i> , <i>Leporillus</i> , <i>Mesembriomys</i>
Hydromyini	Hydromys	<i>Baiyankamys</i> , <i>Crossomys</i> , <i>Hydromys</i> , Leptomys , <i>Microhydromys</i> , <i>Parahydromys</i> , <i>Paraleptomys</i> , Pseudohydromys , Xeromys
Hydromyini	Mallomys	<i>Abeomelomys</i> , <i>Mallomys</i> , <i>Mammelomys</i> , <i>Pogonomelomys</i> , <i>Xenuromys</i>
Hydromyini	Pogonomys	<i>Anisomys</i> , <i>Chiruromys</i> , <i>Hyomys</i> , Lorentzimys , <i>Macruromys</i> , <i>Pogonomys</i>
Hydromyini	Pseudomys	<i>Leggadina</i> , <i>Mastacomys</i> , <i>Notomys</i> , <i>Pseudomys</i> , <i>Zyzomys</i>
Hydromyini	Uromys	<i>Melomys</i> , <i>Paramelomys</i> , <i>Protochromys</i> , <i>Solomys</i> , <i>Uromys</i>
Hydromyini	Haeromys	Haeromys
Hydromyini	<i>Incertae sedis</i>	<i>Brassomys</i> , <i>Coccymys</i>
Malacomyini	Malacomys	<i>Malacomys</i>
Millardini	Millardia	<i>Cremnomys</i> , <i>Diomys</i> , <i>Madromys</i> , <i>Millardia</i>
Murini	Mus	<i>Mus</i> , <i>Muriculus</i> , <i>Malpaisomys</i> ^E
Otomyini	Otomys	<i>Myotomys</i> , <i>Otomys</i> , <i>Parotomys</i>
Phloeomyini	Phloeomys	<i>Batomys</i> , <i>Carpomys</i> , <i>Crateromys</i> , <i>Musseromys</i> , <i>Phloeomys</i>
Praomyini	Colomys	<i>Colomys</i> , <i>Nilopegamys</i> , <i>Zelotomys</i>
Praomyini	Stenocephalemys	<i>Heimyscus</i> , <i>Hylomyscus</i> , <i>Mastomys</i> , <i>Myomyscus</i> , <i>Praomys</i> , <i>Stenocephalemys</i>
Rattini	Berylmys	<i>Berylmys</i>
Rattini	Bunomys	<i>Bullimus</i> , <i>Bunomys</i> , <i>Halmaheramys</i> , <i>Komodomys</i> , <i>Papagomys</i> , <i>Paulamys</i> , <i>Paruromys</i> , <i>Rattus timorensis</i> , <i>Sundamys</i> , <i>Taeromys</i>
Rattini	Dacnomys	<i>Chiromyscus</i> , <i>Dacnomys</i> , Lenothrix , <i>Leopoldamys</i> , Margaretamys , <i>Niviventer</i> , <i>Saxatilomys</i> , <i>Tonkinomys</i>
Rattini	Echiothrix	<i>Echiothrix</i> , Gracilimus , Hyorhinomys , Melasmothrix , Paucidentomys , Sommeromys , Tateomys , Waiomys
Rattini	Maxomys	Crunomys , <i>Maxomys</i>
Rattini	Micromys	<i>Micromys</i>
Rattini	Rattus	<i>Abditomys</i> , <i>Bandicota</i> , <i>Diplothrix</i> , <i>Kadarsanomys</i> , <i>Limnomys</i> , <i>Nesokia</i> , <i>Nesoromys</i> , <i>Palawanomys</i> , <i>Rattus</i> , <i>Tarsomys</i> , <i>Tryphomys</i>
Rattini	Srilankamys	<i>Srilankamys</i>
Rattini	<i>Incertae sedis</i>	<i>Anonymomys</i>
<i>Incertae sedis</i>	Pithecheir	<i>Pithecheir</i> , <i>Pithecheirops</i>
<i>Incertae sedis</i>	<i>Incertae sedis</i>	<i>Alormys</i> ^E , <i>Coryphomys</i> ^E , <i>Hadromys</i> , <i>Hooijeromys</i> ^E , <i>Milimonggamys</i> ^E , <i>Rakasamys</i> ^E , <i>Spelaeomys</i> ^E , <i>Vandeleuria</i> , <i>Vernaya</i>

Note: New tribes since Lecompte et al. (2008) and new divisions since Musser and Carleton (2005) are indicated in bold. Genera that are newly placed into existing divisions or tribes are in bold. Extinct taxa are indicated with a superscript 'E'.



Wallacea to the Philippines and Sahul, and minimal ($d = 0.01$) between all other regions (Table 2). The second-best model in terms of likelihood was the nearest-neighbour model, which because of Wallacea's central location, is more similar to the Wallacean nexus model than are the other models. Regardless of model fit, all models inferred 17 colonization events to Wallacea ($n = 8$), the Philippines ($n = 5$), Sahul ($n = 2$) and Sunda ($n = 2$; Figures S1–S24). The Wallacea nexus, nearest neighbour, continental source and all equal dispersal models inferred nine colonizations from Sunda to Wallacea ($n = 7$) and the Philippines ($n = 2$) and seven colonizations from Wallacea to Sunda ($n = 2$), Sahul ($n = 2$) and the Philippines ($n = 3$; Figure 3). All models inferred a single colonization event from Sahul to Wallacea. Despite the antiquity of some Philippine taxa, there is no evidence of a colonization originating from there. As such, most of the colonization occurred from West to East and Wallacea was a nexus that facilitated access to other parts of the archipelago (Table 3).

3.2 | Diversification rates

All but one (the Sulawesi *Haeromys*) of the 17 colonizations across the IAA led to subsequent in situ speciation (Table 4; Figure 3). However, an undescribed species of *Haeromys* has been reported from Sulawesi (Musser, 2014), suggesting at least limited speciation following colonization for all clades. For the 14 colonizations resulting in three or more species, net diversification (ND) rates from crown ages ranged from 0.2 to 2.12 species/lineage/My and

rates from stem ages ranged from 0.13 to 1.64 species/lineage/My (Table 3; Figure 3). For the Philippines, Wallacea and Sahul, the primary colonizers always had lower ND than one or more of the clades descendant from subsequent colonists. Back colonization of the Sunda shelf by *Maxomys* from Sulawesi led to only two species in our sampling and thus we could not calculate net diversification for this clade. For the colonization of the Maluku Islands by *Melomys*, we could not calculate net diversification because the number of species assignable to this radiation remains unknown from our sampling, which included only two *Melomys* from the Malukus and failed to resolve relationships among the few *Melomys* in our analyses (Figure 2).

Average rates of speciation estimated from BAMM were largely concordant with our ND estimates from crown ages and primary colonizers had lower speciation rates than one or more subsequent colonists (Table 4). We recovered a significant instantaneous increase in the diversification rate at the base of the core Murinae excluding *Hapalomys* and *Phloeomyini* and at the base of the *Rattus* division (as defined here in Table 1; not sensu Musser & Carleton, 2005). In the first case, this rate shift is supported by previous studies with more complete outgroup sampling (Schenk et al., 2013; Stepan & Schenk, 2017). We did not detect significant shifts in diversification rates associated with any of the 17 colonization events across the IAA. However, for nine of the 10 most diverse radiations where we estimated speciation rates through time, we found a declining trend in speciation rates from colonization to the present (Figure 4). The decline in speciation towards the present

TABLE 2 Colonization events by Murinae of the four biogeographical units of the IAA. Nodes correspond with Figure 2

Node	Clade	Tribe	Division	Biogeographical Unit	Colonized from	Subsequently colonized to
1	Phloeomyini	Phloeomyini	Phloeomys	Philippines	Continental	None
2	Sulawesi <i>Haeromys</i>	Hydromyini	Haeromys	Wallacea	Continental	Sahul, Philippines
3	Sahul Hydromyini	Hydromyini	Various	Sahul	Wallacea	Wallacea
4	Philippines Hydromyini	Hydromyini	Chrotomys	Philippines	Wallacea	None
5	Echiothrix division	Rattini	Echiothrix	Wallacea	Continental	None
6	Sulawesi <i>Maxomys</i> division	Rattini	Maxomys	Wallacea	Continental	Continental, Philippines
7	Wallacea <i>Bunomys</i> division	Rattini	Bunomys	Wallacea	Continental	Continental, Philippines
8	<i>Margaretamys</i>	Rattini	Dacnomys	Wallacea	Continental	None
9	Maluku <i>Melomys</i>	Hydromyini	Uromys	Wallacea	Sahul	None
10	<i>Sundamys</i>	Rattini	Bunomys	Sunda	Wallacea	None
11	<i>Bullimus</i>	Rattini	Bunomys	Philippines	Wallacea	None
12	<i>R. xanthurus</i> group	Rattini	<i>Rattus</i>	Wallacea	Continental	Sahul
13	Limnomys clade	Rattini	<i>Rattus</i>	Philippines	Continental	None
14	Sunda <i>Maxomys</i>	Rattini	Maxomys	Sunda	Wallacea	None
15	Sahul <i>Rattus</i>	Rattini	<i>Rattus</i>	Sahul	Wallacea	None
16	Philippines <i>Crunomys</i>	Rattini	Maxomys	Philippines	Wallacea	None
17	<i>R. hoffmanni</i> group	Rattini	<i>Rattus</i>	Wallacea	Continental	None

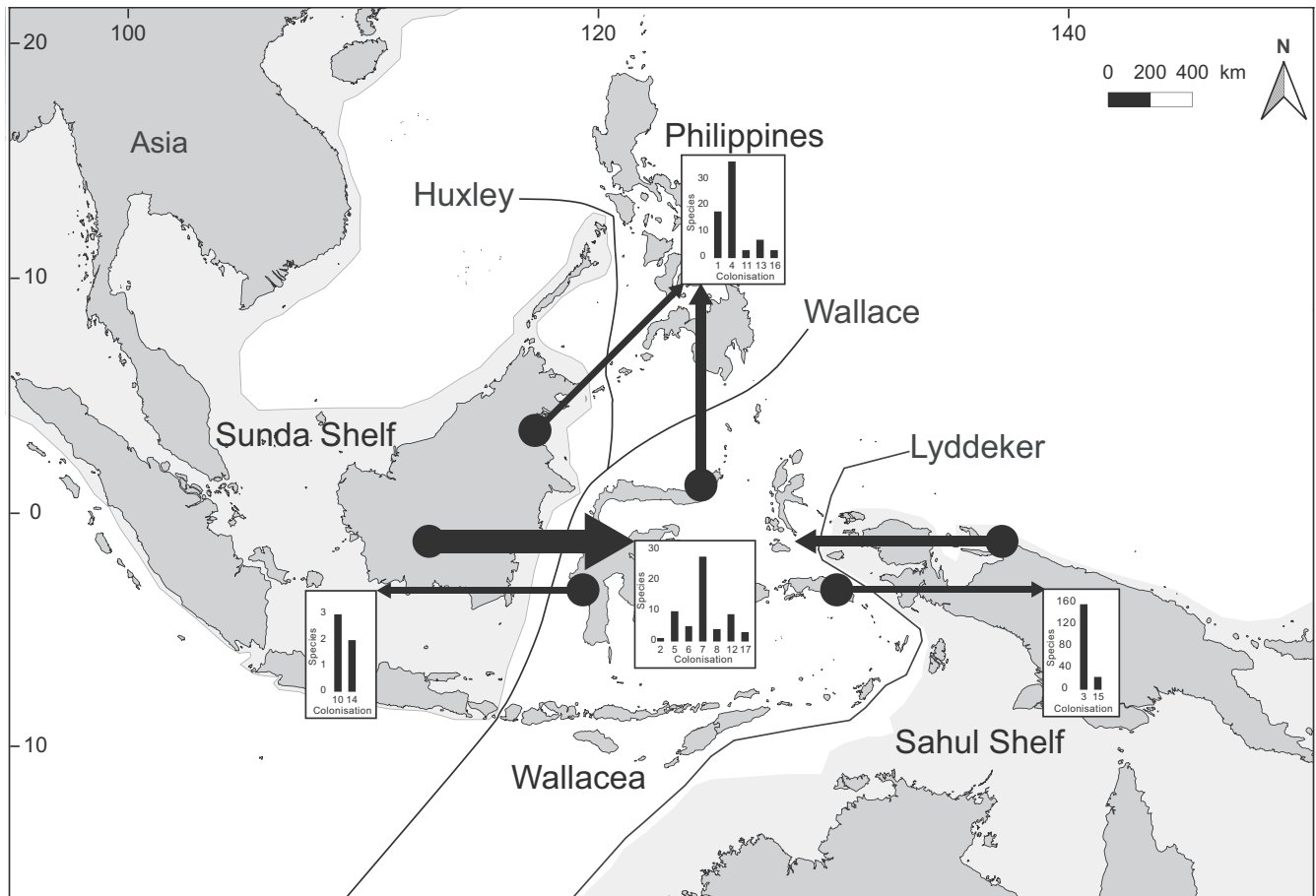


FIGURE 3 Summary of colonizations among four biogeographical units of the IAA. Arrows are drawn from source to destination and scaled to the number of colonization events ranging from two to seven. Bar plots connected to the end of arrows represent the number of extant species resulting from each colonization event. Numbers below each bar correspond to nodes in Figure 2. From our phylogeny we inferred a single colonization event from Sahul to the Maluku Islands of Wallacea, but here we include two additional events from Sahul to the Malukus reflecting unsampled *Uromys* spp. and *Hydromys chysogaster* which have an origin on Sahul but are distributed on the Malukus

was weakest in the Phloeomyini, in which speciation rates were generally low.

4 | DISCUSSION

Previous investigations of the phylogeny and historical biogeography of IAA murines resolved many of the relationships among Philippine, Sunda and Sahul lineages, but left the centrally located and substantial Wallacean diversity largely unsampled (Fabre et al., 2013; Jansa et al., 2006; Rowe et al., 2016b, 2008; Schenk et al., 2013; Stepan & Schenk, 2017). Here, we added 32 species to the existing phylogenetic framework, placing for the first time the majority of Wallacean endemic taxa. Our comprehensive phylogenetic sampling of endemic murine genera from Sulawesi, while consistent with many previous inferences, provides the first demonstration that the ancestors of at least seven clades of murines colonized and diversified in situ on Sulawesi. These clades are: (a) the endemic Echiothrix division (Table 1; *Echiothrix*, *Gracilimus*, *Hyorhinomys*, *Melasmothrix*,

Paucidentomys, *Sommeromys*, *Tateomys* and *Waiomys*); (b) a radiation of the Bunomys division (Table 1; *Bunomys*, *Eropeplus*, *Lenomys*, *Paruromys*, *Taeromys* and an undescribed genus); (c) *Haeromys* of Sulawesi; (d) the endemic genus *Margaretamys*; (e) a small radiation of *Maxomys* and *Crunomys*; (f) the endemic *Rattus xanthurus* group and (g) the endemic *Rattus hoffmanni* group. The Bunomys division also includes other Wallacean endemics from the Lesser Sundas (*Papagomys*, *Komodomys* and *Rattus timorensis*) and Maluku Islands (*Halmarehamys*) implying at least two inter-island colonizations within Wallacea. Previous systematic hypotheses, based on morphological characters, did not predict these clades (Musser & Carleton, 2005). Members of our Echiothrix division were split among three murine divisions (Echiothrix, Melasmothrix and Crunomys) by Musser and Carleton (2005) or undescribed (Esselstyn et al., 2015, 2012; Rowe, Achmadi, & Esselstyn, 2014; Rowe et al., 2016a). *Eropeplus* and *Lenomys*, which we placed in the Bunomys division, were previously placed in the Pithecheir division, along with *Margaretamys* and *Lenothrix*. Finally, the genera *Maxomys* and *Crunomys* were each assigned previously to separate divisions, the latter allied with *Sommeromys*, now a member

**TABLE 3** Comparison of biogeographical models tested in BioGeoBEARS

Dispersal model	Model	ln L	<i>d</i>	<i>e</i>	<i>j</i>	AIC	ΔAIC
Wallacea Nexus	DEC + J	-89.15192	1.00E-12	1.00E-12	0.036	184.30	0.00
Nearest Neighbour	DEC + J	-92.44433	1.00E-12	1.00E-12	0.015	190.89	6.58
All Equal	DEC + J	-96.54741	1.00E-12	1.00E-12	0.012	199.09	14.79
Continental Source	DEC + J	-102.23089	1.00E-12	1.00E-12	0.028	210.46	26.16
Philippine Nexus	DEC + J	-107.15584	1.00E-12	1.00E-12	0.038	220.31	36.01
Sahul Nexus	DEC + J	-114.06278	1.00E-12	1.00E-12	0.025	234.13	49.82
Wallacea Nexus	DEC	-130.24733	1.29E-02	1.00E-12	na	264.49	80.19
Nearest Neighbour	DEC	-131.19557	6.06E-03	4.38E-04	na	266.39	82.09
All Equal	DEC	-134.24981	4.64E-03	4.93E-04	na	272.50	88.20
Continental Source	DEC	-140.29739	8.38E-03	1.35E-03	na	284.59	100.29
Philippine Nexus	DEC	-142.37829	1.27E-02	3.80E-04	na	288.76	104.45
Sahul Nexus	DEC	-145.14131	9.72E-03	4.66E-04	na	294.28	109.98

of the Echiothrix division. Our phylogenetic hypothesis, which groups morphologically disparate taxa into monophyletic radiations that are largely endemic to Sulawesi, highlights the extent of morphological evolution that occurred on this oceanic island.

Our biogeographical analyses suggest that crossings of Wallace's Line were more common than subsequent transitions across Lydekker's Line to the east (Figure 3). Recent studies across diverse terrestrial taxa also recovered repeated transitions across Wallace's line, suggesting that the boundary is more permeable than traditionally recognized (Balke et al., 2009; Bocek & Bocak, 2019; Evans et al., 2017; Hausdorf, 2018; Tänzler et al., 2014, 2016; Toussaint, Tänzler, Rahmadi, Balke, & Riedel, 2015). Murines crossed Huxley's modification of Wallace's line 11 times, including two back transitions from east to west. In contrast, only three transitions across Lydekker's line are evident in our data (one from the east). The *Bunomys* division reached the eastern limits of the Maluku Islands and the Philippines but did not cross Lydekker's Line to New Guinea. Four other clades reached Sulawesi but did not cross to the Malukus or Sahul. Our sampling included two species of *Melomys* from the Maluku Islands but lacked other Sahulian Hydromyini that are known from the islands (i.e. *H. chrysogaster*, *Melomys* spp., *Uromys* sp.), which suggests that at least two additional transitions from New Guinea to eastern Wallacea would be evident if these co-distributed taxa were included (Figure 3). Thus, murine rodent communities of the Maluku Islands are derived from multiple transitions from Sahul (at least three) and three transitions from Sunda, whereas in other areas of Wallacea the murine rodents are derived only from Sunda. The Maluku Islands are oceanic in origin and have not been connected by land to either continental Sahul or other islands of Wallacea during the history of Murinae (Hall, 2013). Murine colonization from adjacent Sulawesi and Sahul, indicates that the Malukus represent a transition zone between Sulawesi and Sahul, consistent with the placement of Weber's Line west of the Maluku Islands (Fabre et al., 2018; Weber, 1902). The biogeographical distinction of the Maluku Islands apart from other areas of Wallacea is supported by other endemic fauna (Carstensen et al., 2012). Our grouping of many

permanently isolated islands into single biogeographical units (e.g. Wallacea) means that many of the individual colonization events we inferred were more likely stepping stone processes involving multiple over-water dispersal events. The probable necessity of stepping stone processes between some of the major IAA landmasses may explain some of the apparent differences in the frequency of colonization events. For instance while colonization of Sulawesi from Sunda requires a single overwater transition, dispersal from Sulawesi to Sahul probably involved multiple overwater dispersal events between relatively small islands, perhaps making the latter more difficult and explaining the higher number of events across Wallace's Line compared to Lydekker's Line (see also Carstensen et al., 2012; Evans et al., 2017; Hausdorf, 2018).

Although islands are often thought of as destinations for colonizing lineages, our inferences on murines demonstrate once again the substantial role of islands as sources of species diversity in terrestrial vertebrates of the IAA (Bellemain & Ricklefs, 2008; Heaney, 2007; Mayr & Diamond, 2001; Whittaker et al., 2017). First, islands of the IAA provide a pool of potential colonists capable of dispersing to other landmasses, including continents, as documented in recent phylogenetic studies (Balke et al., 2009; Bocek & Bocak, 2019; Condamine et al., 2015; Filardi & Moyle, 2005; Jönsson et al., 2011; Tänzler et al., 2014, Tänzler et al., 2016). Our biogeographical analyses demonstrate, in particular, the central importance of Wallacea and the island of Sulawesi as a source of colonists in the spread of murine rodents across the IAA (Table 1; Figure 3). Previous meta-analyses identified relatively few cases of colonization events originating from Wallacea or Sulawesi (de Bruyn et al., 2014; Stelbrink, Albrecht, Hall, & Rintelen, 2012), but exceptions are emerging (Bocek & Bocak, 2019; Condamine et al., 2015; Tänzler et al., 2016). While we also inferred that a majority of colonizations originated from the continental sources of Sunda (9) and Sahul (1), all but two of these were to the oceanic archipelago of Wallacea (five to Sulawesi only) and the remaining seven colonizations originated from Wallacea (primarily Sulawesi). Two Philippine clades, two Sunda clades and one Sahul clade are clearly derived from Wallacean origins. The genus



TABLE 4 Median and lower and upper bounds of the 95% highest posterior distribution (HPD) for crown ages of colonizing clades and their stem divergence from sister clades in millions of years. Net diversification estimates using Magallon and Sanderson (ND) for median crown and stem ages, mean and HPD speciation rates from BAMM for each colonizing clade in species per lineage per million years. Nodes correspond with Figure 2

Node	Clade	Crown median	Crown HPD	Stem median	Stem HPD	Species sampled	Species total	M&S ND crown median	M&S ND stem median	BAMM mean	BAMM HPD
	Murinae	15.10	13.66–16.67	20.33	18.11–22.07	270	704	0.38	0.29	0.42	0.40–0.48
1	Phloeomyini	9.42	8.17–10.68	13.59	12.78–14.46	5	18	0.23	0.16	0.29	0.16–0.46
2	Sulawesi <i>Haeromys</i>	na	na	7.96	7.41–8.58	1	1	0	0	na	na
3	Sahul <i>Hydromyini</i>	7.26	6.72–7.74	7.91	7.37–8.39	72	159	0.60	0.55	0.38	0.34–0.43
4	Philippines <i>Hydromyini</i>	5.85	5.23–6.45	7.91	7.37–8.39	28	34	0.48	0.36	0.41	0.34–0.62
5	Echiothrix division	5.11	4.49–5.69	6.37	5.86–6.92	10	10	0.31	0.25	0.38	0.34–0.42
6	Sulawesi <i>Maxomys</i> division	3.72	3.21–4.29	4.83	4.07–5.15	4	5	0.25	0.19	0.36	0.32–0.41
7	Wallacea <i>Bunomys</i> division	3.45	3.09–3.81	3.67	3.29–4.03	19	28	0.76	0.72	0.39	0.31–0.79
8	<i>Margaretomys</i>	2.92	2.29–3.51	3.84	3.19–4.49	4	4	0.24	0.18	0.36	0.32–0.41
9	Maluku <i>Melomys</i>	2.48	1.99–2.95	4.60	4.11–5.07	2	na	na	na	0.38	0.32–0.42
10	<i>Sundamys</i>	na	na	3.23	2.88–3.57	1	3	na	0.13	na	na
11	<i>Bullimus</i>	1.20	0.90–1.49	3.08	2.72–3.40	3	3	0.34	0.13	0.39	0.31–0.79
12	<i>R. xanthurus</i> group	1.57	1.22–1.95	2.44	2.11–2.75	3	9	0.96	0.62	1.27	0.85–1.71
13	Limnomys clade	1.90	1.54–2.22	2.24	1.91–2.61	4	7	0.66	0.56	1.25	0.82–1.65
14	Sunda <i>Maxomys</i>	1.35	0.96–1.82	1.99	1.54–2.47	2	2	0	0	0.38	0.34–0.42
15	Sahul <i>Rattus</i>	1.17	0.87–1.53	1.49	1.19–1.85	8	24	2.12	1.67	1.27	0.85–1.72
16	Philippines <i>Crunomys</i>	0.67	0.39–0.97	1.34	0.92–1.80	2	3	0.61	0.30	0.34	0.29–0.39
17	<i>R. hoffmanni</i> group	na	na	0.88	0.60–1.16	1	3	na	0.46	1.25	0.83–1.65

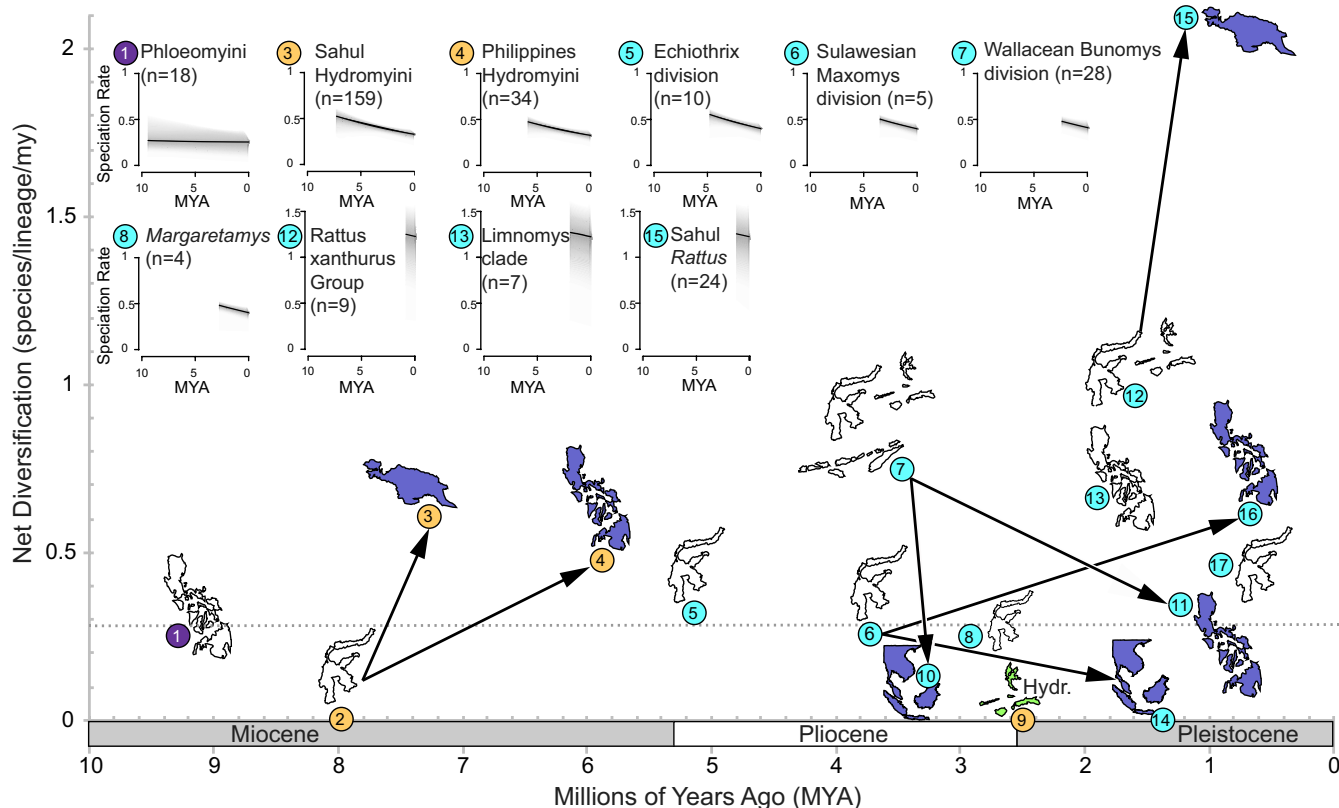


FIGURE 4 Diversification rate estimates for the 17 colonizations inferred from our phylogeny for murine rodents across the Indo-Australian Archipelago. Areas of colonization are indicated by shapes representing the oceanic Philippines, Sahul (depicted as New Guinea) and Wallacea (see Figure 1 for reference). For Wallacean colonizations, shapes include Sulawesi, the Lesser Sundas, and/or the Malukus depending on the areas occupied by that colonization. Shapes are coloured to reflect the source of colonizations from Sunda (white), Wallacea (blue) or Sahul (green). Arrows indicate colonizations leading to subsequent colonizations of other biogeographical units. Numbers in circles beside shapes are centred on the median crown estimates for the age of the colonizations and their net diversification rates following colonization (numbers follow Figure 2). Circles are coloured to indicate murine tribes as in Figure 2. Colonizations 2, 10, and 17 are centred on median stem estimates. Net diversification for crown Murinae is indicated with a dashed line. Bamm estimates of speciation rates through time for the 10 most species-rich clades resulting from colonization are presented as inset figures. Black lines represent the median estimate and gray shading the 95% highest posterior density of speciation rate estimates

Crnomys includes three Philippine and one Sulawesian endemic species that are nested within a group of *Maxomys* endemic to Sulawesi (Achmadi et al., 2013). Two Sunda shelf *Maxomys* are also nested within this group, and we infer a Wallacean (Sulawesi) ancestor for these Sunda endemics, indicating a colonization from oceanic island to continent (Node 16: Figures 2 and 4). The endemic Philippine genus *Bullimus* is nested within taxa from Wallacea (Lesser Sundas, Sulawesi and Maluku) in the Bunomys division (Table 1; Figure 4). The Sunda shelf endemic *Sundamys* also is nested within this primarily Wallacean radiation, suggesting a Wallacean origin for the genus and a second island-to-continent colonization. The substantial continental radiation of Sahul *Rattus* (Rowe et al., 2011) also appears to result from an island-to-continent colonization with a Wallacean origin. It is phylogenetically nested among species endemic to Sulawesi (*R. xanthurus* group) and the Maluku Islands (*Rattus morotaiensis*). Finally, our biogeographical model suggests that the Hydromyini of the Philippines and Sahul are potentially derived from a Wallacean (Sulawesi) ancestor. This is based on the placement of *Haeromys minahassae* from Sulawesi as sister to the remaining Hydromyini.

However, this inference is less certain than our other findings, largely because three species of Sundaic *Haeromys* were not available. The presumed monophyly of *Haeromys*, and the relationships of species from Sunda and Sulawesi remain to be tested. Moreover, the long branch leading to Sulawesian *Haeromys* and other Hydromyini, suggest that extinction may mask the biogeographical origins for this group, as hypothesized for the Phloeomyini of the Philippines (Fabre et al., 2013; Rowsey et al., 2018; see also Meijer, van den Hoek Ostende, van den Bergh, & de Vos, 2010; Musser, 1981; Turvey et al., 2017).

Islands, particularly the large and geomorphologically complex ones, also serve as centres of in situ diversification (Heaney, Kyriazis, Balete, Stepan, & Rickart, 2018; Losos & Ricklefs, 2009; Whittaker et al., 2017). Here, we simplified our biogeographical framework to model transitions among four isolated archipelagos containing numerous islands. In some cases, the islands across these archipelagos are oceanic and have been isolated by marine barriers continuously (e.g. Wallacea and the Philippines), whereas in other cases the islands are continental and have been connected by land during periods of

low sea level (e.g. Sunda and Sahul Shelf; Baldwin, Fitzgerald, & Webb, 2012; Hall, 2002, 2009, 2013; Heaney, Balete, Duya, et al., 2016; Lohman et al., 2011; Nugraha & Hall, 2018). In addition, our phylogenetic sampling does not include some island endemic species, particularly in the Philippines, Maluku and smaller islands off New Guinea, precluding an analysis at the island level. Regardless, with more than 20,000 islands across the IAA, some simplification was required.

Despite our simplified biogeographical framework, most speciation in murines of the IAA occurred on the largest islands within archipelagos (i.e. Sulawesi, New Guinea and Luzon). Thus, our simplification to archipelagos as biogeographical units, is not likely to have biased our results dramatically (but see *Bunomys* division of Wallacea, and *Hydromyini* of the Maluku as mentioned above). The clades that arrived on isolated landmasses of the IAA vary dramatically in their extant diversity (Figure 3), from just one (e.g. *Haeromys* on Sulawesi; possibly two, see Musser, 2014) to 159 species (*Hydromyini* of Sahul). While Sahul is both continental and large, most of the species (84) and in situ diversification is centred on the island of New Guinea, with smaller radiations on Australia and other islands of the Sahul region (Rowe et al., 2008; Smitsen & Rowe, 2018). Across Wallacea, Sulawesi Island is the major centre of diversification and greater than two-thirds of murine species native to Wallacea are endemic to this one island. On Sulawesi, seven colonization events account for <15% of species diversity, whereas >85% of species are the outcome of in situ speciation following colonization. Indeed, in situ diversification resulting from just two colonizations of Sulawesi (*Echiothrix* and *Bunomys* divisions) accounts for >60% of murine species on the island. On Luzon, in the Philippines, colonization and subsequent diversification by the *Phloeomyini* and *Hydromyini*, produced >90% of murine species (Heaney, Balete, Duya, et al., 2016; Rowsey et al., 2018). The two colonizations of Sahul via the island of New Guinea produced far more species than the combined 12 colonizations of Wallacea and the Philippines, again indicating the importance of in situ speciation, but also the effect of land area (New Guinea is the largest island in the IAA) in generating species richness. In total, 296 species (>40% of murines globally) are the descendants of the 17 colonization events across the IAA, demonstrating that dispersal is the seed, but in situ speciation on large islands (Sulawesi, New Guinea, Luzon) or within our biogeographical units (i.e. across archipelagos) is the dominant source of alpha diversity.

While in situ speciation of IAA murines following colonization of islands is consistent with adaptive radiation theory and ideas regarding ecological opportunity (Gavrilets & Losos, 2009; Mahler et al., 2010; Schluter, 2000), we did not observe a strong signal of incumbency effects or diversity-dependent diversification. The first colonists of Wallacea (primarily Sulawesi), the oceanic Philippines (primarily Luzon) and Sahul (primarily New Guinea) did not exhibit the fastest diversification rates, and their descendant clades (at least in Wallacea and the Philippines) do not contain exceptional species numbers (Figures 3 and 4; Table 4). Rather, the highest rate of diversification occurred following one of the most recent colonizations; the Sahulian *Rattus*, which arrived more than 6 Myr after

the Sahulian *Hydromyini* (Rowe et al., 2011). On the Philippines, all ($n = 4$) subsequent colonizations resulted in higher diversification rates than the earliest colonists, the *Phloeomyini* (see also Rowsey et al., 2018). We also did not observe a significant increase in diversification rates associated with any colonization event. Instead we identified a shift in the diversification rate within the *Rattus* division (as defined here in Table 1). These findings are consistent with the limited evidence for diversification rate shifts associated with the >30 continental colonizations by muroid rodents globally (Schenk et al., 2013). However, virtually all the diversity in IAA murines has evolved following colonizations, making it difficult (or inappropriate) to disentangle post-colonization rates from background rates. Nevertheless, following colonizations, we observed a consistent trend of temporally decreasing speciation rates, suggesting that colonizing lineages have more opportunities for diversification early in their tenure, even if not exceptional compared to the subfamily as a whole (Figure 4). Although our biogeographical framework grouping many islands into biogeographical units masks some allopatric speciation, most alpha diversity resides on the large islands where our taxon sampling was good. Therefore, we do not expect improved sampling of small-island taxa to substantially alter our conclusion that diversification on large islands is an important process that contributed substantially to extant murine diversity.

Competition among closely related taxa is one mechanism expected to result in limited diversification by secondary colonizers and diversity-dependent diversification (Moen & Morlon, 2014; Rabosky, 2013). Discrete ecological differences among many of the colonizing clades of IAA murines suggest that competition among some clades is limited and that incumbency effects, at most, have limited colonization by lineages that are ecologically similar to incumbent radiations. For example the *Phloeomyini* of the Philippines are herbivorous and almost wholly arboreal, whereas the second colonists, the Philippine *Hydromyini* (*Chrotomys* division), are terrestrial or scansorial carnivores and omnivores with almost no morphological overlap with the extant *Phloeomyini* (Rowsey et al., 2018; Rowsey, Heaney, & Jansa, 2019). On Sulawesi, the oldest radiation, the *Echiothrix* division, comprises largely carnivorous taxa that are ecomorphological outliers among murines of Sulawesi (Musser & Durden, 2014; Rowe et al., 2016a). Similar arguments could be made for most of the subsequent murine lineages that colonized Sulawesi. However, exceptions to this pattern suggest that incumbent radiations do not always limit ecological diversification of subsequent colonizers. For example while the *phloeomyines* are almost wholly arboreal, one genus, *Batomys*, is also active on the ground, an ecological trait that evolved only after the diverse clade of wholly terrestrial murines, the *Chrotomys* division, had colonized and radiated on the islands (Rowsey et al., 2018). A second example is *Crunomys*, a small, diurnal and carnivorous murine that evolved on Sulawesi from medium-sized, nocturnal and omnivorous *Maxomys* despite the presence of small, carnivorous and diurnal rats (e.g. *Melasmothrix*) in the *Echiothrix* division (Rowe et al., 2016b). From Sulawesi, *Crunomys* also colonized and diversified on the Philippines amidst similar species in the *Hydromyini*



(e.g. *Archboldomys*). On Sulawesi, arboreal and tufted-tailed species of the *Rattus xanthurus* group colonized and diversified in the presence of resident arboreal and tufted-tailed species in the genus *Margaretamys*. The Sulawesi members of the *Bunomys* division, which we estimate to be the third colonizer of Sulawesi, have perhaps the widest ecomorphological range of any radiation on the island including terrestrial to arboreal locomotion, small to large body size and herbivorous to carnivorous diets (Musser, 2014) that overlap ecologically with species from incumbent radiations. More work is needed to quantify ecomorphological overlap and convergence among the sympatric radiations of murines of large islands from the IAA, particularly for species with derived traits that evolved in situ with incumbent lineages (Rowsey et al., 2019).

From the Pliocene through the Pleistocene, transitions of murines across the IAA remained fairly continuous (Figure 4), further suggesting that incumbent lineages do not preclude subsequent colonizations, even on Sulawesi where descendants of seven colonists have become established or on Sunda where IAA murines originated. However, some filtering of colonizing lineages is evident in the temporal segregation of murine tribes with Miocene transitions by the *Phloeomyini* and *Hydromyini* followed by Pliocene expansion of the *Rattini*. The most recent colonizations are primarily by species in the genus *Rattus* or their closest relatives in the *Rattus* division, and preceded largely by their sister clade the *Bunomys* division (Figure 2). The base of the *Rattus* division is the only node within Murinae where we detected a significant increase in diversification rate; this may have aided *Rattus* and their relatives in their ability to colonize and diversify on islands with already diverse murine communities (Wiens, 2018).

Overall, our new phylogenetic and biogeographical framework for IAA murines demonstrates the crucial role of dispersal, both to and from archipelagos, as a source of biodiversity. In situ diversification across archipelagos and on large islands may generate most of the species that make up modern murine communities, but colonizations have repeatedly contributed new diversity and spawned substantial secondary radiations in each biogeographical region. Thus, millions of years of speciation and ecological diversification on Sunda, Sahul, the Philippines and across Wallacea, has not precluded colonization and diversification by subsequent murine lineages. The outcome of these evolutionary “experiments” is a series of ecologically rich communities containing many species that we are still discovering (Esselstyn et al., 2015; Fabre et al., 2018; Heaney, Balete, Duya, et al., 2016; Louys et al., 2018; Rickart et al., 2019; Rowe et al., 2016a).

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DATA AVAILABILITY STATEMENT

All new sequences generated for this study are available on GenBank www.ncbi.nlm.nih.gov/genbank with accession numbers MN272952–MN273051. GenBank accession numbers for all sequences used in this study are available in Table S1. Phylogenetic trees used in this study (RAxML and BEAST) are available in Supporting information.

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SUPPORTING INFORMATION

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