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Diversification rates of the "Old Endemic" murine rodents of Luzon Island, Philippines are inconsistent with incumbency effects and ecological opportunity

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Diversity-dependent cladogenesis occurs when a colonizing lineage exhibits increasing interspecific competition as it ecologically diversifies. Repeated colonization of a region by closely related taxa may cause similar effects as species within each lineage compete with one another. This may be particularly relevant for secondary colonists, which could experience limited diversification due to competition with earlier, incumbent colonists over evolutionary time. We tested the hypothesis that an incumbent lineage may diminish the diversification of secondary colonists in two speciose clades of Philippine "Old Endemic" murine rodents—Phloeomyini and Chrotomyini—on the relatively old oceanic island of Luzon. Although phylogenetic analyses confirm the independent, noncontemporaneous colonization of Luzon by the ancestors of these two clades, we found no support for arrested diversification in either. Rather, it appears that diversification of both clades resulted from constant-rate processes that were either uniform or favored the secondary colonists (Chrotomyini), depending on the method used. Our results suggest that ecological incumbency has not played an important role in determining lineage diversification among Luzon murines, despite sympatric occurrence by constituent species within each lineage, and a substantial head start for the primary colonists.

KEY WORDS: adaptive radiation, Phloeomyini, Chrotomyini, Murinae, oceanic island, systematics.

The factors that contribute to species and ecological diversity are of central concern in evolutionary biology. One of the key triggers shown to contribute to cladogenesis and morphological evolution is ecological opportunity, or the availability of unoccupied niches for a lineage to diversify into (Schluter 2000a; Yoder et al. 2010). This opportunity can be generated by several factors, including dispersal to a depauperate ecosystem, such as an oceanic island (Baldwin and Sanderson 1998, Reddy et al. 2012; Borregaard et al. 2017) or an evolutionary innovation that provides relief from existing competition (Wainwright et al. 2012). Ecological opportunity can facilitate adaptive radiation, rapidly producing a variety of ecologically and morphologically diverse species (Lack 1947; Gillespie 2004; Losos 2011). When examined in a phylogenetic context, ecological opportunity may manifest as a pattern of diversity-dependent cladogenesis, in which lineage diversification rates decrease as competition for available niches increases during a radiation (Nee et al. 1992; Rabosky and Lovette 2008; Skipwith et al. 2016). The phylogenetic signature left by this process can be detected by analyzing the branching patterns of the focal clade using standard diversification rate analyses (Rabosky 2006; Rabosky 2014).

The influence of competition in shaping diversity has been explored for unfolding adaptive radiations in a variety of natural systems, especially islands, and previous studies have provided support for its effects on the rate of species accumulation (which we refer to as diversification rates) and morphological change over

time (which we refer to more broadly as phenotypic evolutionary rates) (Whittaker and Fernandez-Palacios 2007). For example, Schluter and Grant (1983) showed that community assembly of *Geospiza* finches is functionally overdispersed, which minimizes interspecific competition for limited food resources. In a taxonomically broad study, Schluter (2000b) used a meta-analysis approach to examine the prevalence of ecological character displacement, or the divergence in phenotype associated with niche differentiation in closely related species, in natural systems. His results indicated this phenomenon is common and strongly supported in taxa such as *Gasterosteus* sticklebacks, *Geospiza* finches, and heteromyid rodents of the North American desert southwest, although direct causal links between interspecific competition and phenotypic change were often lacking (Schluter 2000b). In this regard, Parent and Crespi (2009) determined intraspecific variation in Galápagos *Bulimulus* land-snail shell shape was negatively correlated with the number of congeners occurring in the same habitat type and positively correlated with food resource heterogeneity. Finally, several recent studies of lineages on oceanic islands have detected patterns of lineage diversification consistent with declining ecological opportunity, including Hawaiian leafhoppers (Bennett and O'Grady 2013), New Caledonian geckos (Skipwith et al. 2016), and Philippine frogs (Blackburn et al. 2013). In sum, these studies provide evidence that resource availability in the absence of competition can expand the intraspecific variation that may promote the evolution of ecologically distinct species and thus result in increased lineage diversification as well as morphological evolution.

Nevertheless, most studies to date have focused on the evolution of a single lineage and have not addressed how diversification is affected when a system contains multiple, ecologically similar, radiating lineages. Just as density dependence can slow diversification within a single radiating lineage, we can predict that the presence of an ecologically similar lineage may reduce the rate of diversification of a second lineage that disperses to the system. If the colonizing events were asynchronous, the later-dispersing clade may experience a lower diversification rate proportional to the extent of diversification of the primary lineage at the time of secondary colonization. The macroevolutionary advantage held by this primary colonizing lineage is an example of an incumbency effect, whereby a lineage gains an advantage simply by being present in an area first (Case 1991; Alroy 1996).

Whereas our study focuses on the role of incumbency at the macroevolutionary scale, historically, incumbency (or priority) effects were hypothesized as a mechanism to explain alternative stable states in community assembly. In this context, the presence of certain species can alter, whether positively or negatively, the ability of other species to become established (Sutherland 1974). This theory has been extended to suggest that community assembly can be altered simply by the order of colonization of the constituent species (Drake 1991). The ability of a lineage to colonize given the existence of a competitor is dependent on several factors, including habitat availability, presence of predators, and relatedness of invading species to incumbent species (Fukami 2007; Louette and De Meester 2007; Tan et al. 2012). These short-term ecological effects on community composition, when extended over large temporal scales, may result in differences in evolutionary process between primary and secondary colonizing lineages.

From this macroevolutionary perspective, incumbency effects can be examined in two different types of systems: those that have been released from incumbency effects through extinction of competitors or dispersal to a novel environment, and those in which lineages come into competition due to secondary colonization. A popular example of diversification after extinction of a competing lineage is the Cretaceous-Paleogene (K-Pg) extinction and subsequent ecological release of mammals during the Cenozoic (O'Leary et al. 2013, but see dos Reis et al. 2014). Similarly, Darwin's finches provide a classic example of diversification after dispersal to a competitor-deficient system (Burns et al. 2014). In both cases, the focal lineage undergoes rapid diversification after existing incumbency effects—in the form of competing lineages—have been removed. Detecting such examples requires analysis of diversification rates either in the context of a densely sampled fossil record or with a phylogenetic perspective that includes both dispersing lineages as well as source taxa. Alternatively, incumbency effects on diversification may occur when two lineages come into contact through independent colonizations of a system. In this case, we might expect secondary colonists to experience reduced ecological opportunity—and resulting lower diversification rates—compared to primary colonists. Detecting incumbency effects in this case requires a robust phylogenetic framework for the two interacting clades, along with analyses of diversification patterns and rates. In addition, researchers must also make *prima facie* arguments that the two lineages are ecologically similar enough to potentially compete over limited resources. Systems that satisfy these biological and methodological requirements for either approach are relatively rare, meaning there is much to learn about how incumbency and ecological release affect diversification.

Despite the relative scarcity of studies in which multiple ecologically similar clades have colonized a system, several authors have used this approach to test for incumbency effects at continental scales in birds, fishes, and mammals, examining both rates of lineage diversification (Betancur-R. et al. 2012; Schenk et al. 2013) and morphological evolution (Jønsson et al. 2015; Alhajeri et al. 2016), with mixed support for incumbency affecting diversification. However, the geographic scale at which incumbency may be important in diversification remains an open question. For example, in a study of muroid rodents, Schenk et al.

(2013) found some evidence for ecological opportunity affecting diversification at the continental scale for South American muroids, but little evidence for ecological opportunity or incumbency effects in other geographic regions. This study did not examine these processes at the scale of individual islands, and in some cases aggregated archipelagic and continental regions with endemic rodent assemblages (e.g., Southeast Asia), potentially masking more localized patterns of diversification. Furthermore, the analysis of continent-sized landmasses, rather than more spatially limited systems, may be too broad for the detection of adaptive radiation and/or incumbency effects at relatively short timescales. If the breadth of land area and niches available to a clade are sufficiently large or temporally dynamic, interspecific competition may be outweighed by other factors affecting diversification, such as phylogenetically conserved range limits and climatic or geological vicariant events (Goldberg and Lande 2007; Ribas et al. 2007; Derryberry et al. 2011). As a result, the hypothesis that incumbency limits ecological opportunity and slows diversification may best be tested at finer geographic scales, with clades that are more likely to be competing for niches, to measure its importance in determining the species diversity of natural systems.

The endemic rodents of Luzon Island, Philippines afford the opportunity to test hypotheses regarding incumbency and diversification rates at a spatially limited scale. The endemic murine rodents of Luzon have been the subject of extensive field and museum studies in recent decades (reviewed in Heaney et al. 2016a,b) and are an exceptional instance of endemism and diversification following repeated colonization, with up to six colonization events since the middle Miocene (Jansa et al. 2006). The two oldest colonizing lineages, Phloeomyini and Chrotomyini, are referred to as the Luzon "Old Endemic" radiations and comprise the majority (nearly 90%) of native non-volant mammalian diversity on Luzon. These two clades exhibit substantial variation in body size, diet, and other traits, both within and between each clade, yet species in each clade typically occur sympatrically in high-elevation montane and mossy forest (Heaney et al. 2016a). Importantly, the Luzon Old Endemic (LOE) rodents are not sister clades within Murinae and appear to have colonized Luzon several million years apart during the middle Miocene (Jansa et al. 2006; Schenk et al. 2013; Rowe et al. 2016). An estimated four additional rodent colonizations of Luzon have occurred within the last 5 million years; these four independent colonization events resulted in less diverse, primarily low-elevation clades that are collectively referred to as the "New Endemic" murine rodents (Jansa et al. 2006; Kyriazis et al. 2017). Despite extensive surveys cataloging Luzon's mammalian biodiversity, the LOE rodents lack a comprehensive species-level phylogeny. The absence of this phylogeny obscures the relationships within each clade, the history of island colonization and intra-island diversification, as well as estimates of lineage diversification and phenotypic evolutionary rates.

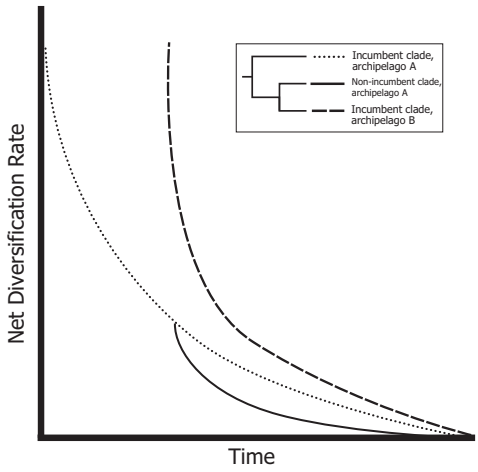

Figure 1. Diversification rates-through-time for a three-clade scenario supporting ecological opportunity and incumbency driving diversification. A phylogenetic tree illustrates the relationships among two incumbent clades and a secondary-colonizing clade. The dotted line represents the incumbent clade in the focal system, the solid line represents the second colonizing clade in the focal system, and the dashed line represents an incumbent clade of a different system which is sister to the secondary-colonizing clade of the focal system. All clades follow a model of diversity-dependent cladogenesis, suggesting ecological opportunity is the driving diversification process, but the secondary colonist has a lower diversification rate than both the incumbent lineage and its sister lineage.

In addition to generating the first species-level phylogeny of these two clades, we use the LOE rodents to test several predictions of how incumbency and ecological opportunity impact lineage diversification using finely sampled molecular phylogenies and macroevolutionary inference. If ecological opportunity and incumbency have played an important role in the diversification of LOE rodents, we first expect to recover temporally decelerating diversification rates in both clades consistent with clade-specific, diversity-dependent cladogenesis. Second, if the two clades share a background diversification rate, we expect the secondary colonizing clade (i.e., Chrotomyini) to experience a decrease in that rate. Third, since the two potentially competing clades are not sister clades, we expect to find a lower diversification rate in the secondary colonizing clade relative to its sister clade (Fig. 1). This is because the secondary colonizing lineage must compete with the primary colonizing clade as well as with other descendant species of its own lineage. Recovering support for this prediction would implicate colonization of Luzon in the decreased diversification rate of Chrotomyini, rather than a decreased diversification rate inherited prior to colonization. The disparity in diversification rate is most easily testable if the secondary-colonizing clade's sister

lineage is a primary colonist of another system. In this case, Chrotomyini are sister to the Sahul Old Endemic (SOE) rodents, so named for their range which includes New Guinea and Australia (Rowe et al. 2008). This clade does not overlap in distribution with either focal clade and may exhibit ecological opportunity consistent with an absence of potential competitors.

Materials and Methods

TAXON SAMPLING

We sampled 204 murid rodent species, including 39 species of Luzon Old Endemic (LOE) rodents, nine species of Old Endemic rodents from elsewhere in the Philippine archipelago, and three species of Luzon "New Endemic" rodents to generate a comprehensive phylogeny of LOE species in the context of broader Murinae. We included all species of murids currently known from Luzon except *Batomys dentatus*, *Crunomys fallax*, *and Tryphomys adustus*. The first and second of these are known only from the holotypes, and the third from a small number of specimens without easily sampleable genetic material (Heaney et al. 2016a).

Sequences from additional murid species were chosen primarily from publicly available sources obtained from previous studies (Steppan et al. 2005; Rowe et al. 2008; Benson et al. 2013; Schenk et al. 2013; Pagès et al. 2016; Rowe et al. 2016; P.-H. Fabre, Université Montpellier II, personal communication, August 2017) and were included to place the Philippine murine radiations in the context of murid phylogeny and to provide the best possible divergence date estimates given available fossil data. We selected taxa from subfamilies Gerbillinae, Deomyinae, and Lophiomyinae as outgroups based on their close phylogenetic proximity to Murinae (Schenk et al. 2013; Pagès et al. 2016; Steppan and Schenk 2017).

DNA EXTRACTION AND SEQUENCING

We sampled seven loci at varying coverage for the species in this dataset: the entire mitochondrial gene cytochrome *b* (CYTB, 1144 bp), exon 11 of breast cancer activating gene 1 (BRCA1, 2784 bp), exon 10 of growth hormone receptor (GHR, 937 bp), exon 1 of interphotoreceptor retinoid-binding protein (IRBP, 1300 bp), recombination activating gene 1 (RAG1, 3040 bp), parts of exons 2 and 3 and the intervening intron of acid phosphatase 5 (ACP5, 450 bp), and intron 7 of β-Fibrinogen (FGB7, 794 bp).

For newly generated sequences, tissues were obtained from vouchered specimens held at the Field Museum of Natural History (FMNH) and the Smithsonian National Museum of Natural History (USNM). DNA was extracted using a DNeasy Blood and Tissue Kit (Qiagen, Germantown, MD). We amplified genes using PCR with the following primers for each locus: CYTB: MVZ05a and UMMZ04 (Smith and Patton 1991; Jansa et al. 1999); GHR: GHRF1 (GHREXON10 in Adkins et al. 2001) and GHREND (Adkins et al. 2001); IRBP: IRBPA and IRBPB (Stanhope et al. 1996); FGB7: FGB7F1 (5' ACGGCATGTTCTTCAGCACG 3'); and FGB7R1 (5' ATCCCTTCCAGTTCATCCACAC 3'). These sequence data have been submitted to the GenBank database under accession numbers MH330617-MH330660. All BRCA1, RAG1, and ACP5 sequences were obtained from previous studies. The concatenated sequence matrix was deposited in TreeBase under accession number 22736; GenBank numbers of sequences used in our phylogenetic analyses can be found in Supporting Information Table S1.

All genes were amplified by PCR with a touchdown protocol optimized for each locus (Jansa and Weksler 2004). Amplicons were sequenced using Sanger sequencing from both template strands. Sequencing was performed by GENEWIZ (South Plainfield, NJ) and the resultant reads were assembled in Geneious R10 (Biomatters Ltd., Auckland, New Zealand). Consensus DNA sequences were aligned using MUSCLE (Edgar 2004) and concatenated for phylogenetic analysis.

PHYLOGENETIC INFERENCE

We used PartitionFinder version 1.1.1 (Lanfear et al. 2012) to determine the best-fitting scheme of nucleotide partitioning and corresponding substitution models. Our partitioning scheme varied depending on the analytical approach. For maximum likelihood analyses, we specified candidate partitions for each codon position within each exon and one partition for each intron for a total of 20 potential partitions. For the Bayesian estimation of phylogeny, multiple partitions for each locus produced schemes that prevented Markov-Chain Monte Carlo (MCMC) convergence. Because of this, we used a simpler model allowing one partition for each locus, other than ACP5, for which we proposed one partition for the exons and one for the internal intron. Candidate substitution models were selected based on those implemented in RAxML (Stamatakis et al. 2008) and BEAST 2 (Bouckaert et al. 2014), and compared using the Bayesian Information Criterion (BIC; Schwarz 1978).

We inferred murine phylogeny using maximum likelihood in RAxML v8.2.9, using resources of the CIPRES Science Gateway (Stamatakis et al. 2008; Miller et al. 2010). Variants of the general time reversible model allowing for among-site rate heterogeneity were applied to each partition (GTR with invariant sites and gamma-distributed rates; Gu et al. 1995). We specified 10 independent searches from randomly-generated starting trees, and nodal support was assessed using 1000 bootstrap permutations conducted using each of 10 starting trees.

Bayesian estimation of phylogeny was conducted using BEAST version 2.4.2 (Bouckaert et al. 2014) on the concatenated data partitioned by locus using the best scheme selected

by PartitionFinder. We linked tree models across all partitions, allowed site models to vary among partitions, and estimated separate log-normally-distributed relaxed uncorrelated clock models for CYTB and the nuclear loci (Drummond et al. 2006). To provide divergence date estimates in absolute time, we specified uniform age priors on specific taxa as follows, based on fossil age estimates provided in Kimura et al. (2015): The "*Mus-Arvicanthis*" split: 11.1-12.3 million years ago (Ma); the most recent common ancestor (MRCA) of the *Arvicanthis*, *Otomys,* and *Millardia* divisions: 8.7-10.1 Ma; the MRCA of Murini: 7.3–8.3 Ma. We additionally applied a log-normally-distributed prior on the age of Gerbillinae + Deomyinae with 95% quantiles of 16.0–23.0 Ma (Thomas et al. 1982; Schenk et al. 2013). We specified a Yule tree prior with an estimated birth rate given an exponential prior with the initial mean set to 10. All other priors were left with default values. The BEAST analysis was conducted on the CIPRES Science Gateway (Miller et al. 2010) using four independent runs: one run for 3.1×10^8 generations and three additional runs for 1.7×10^8 generations, with trees sampled every 50,000 generations. Parameter convergence was analyzed using Tracer v1.6, with the first 10% of trees discarded as burn-in from each run before combining. The first 2.2×10^8 of the resulting 7.4×10^8 sample generations was subsequently discarded. In total, 1.0×10^5 trees were generated from this remaining distribution. A maximum clade credibility (MCC) tree was generated from this posterior tree distribution using TreeAnnotator version 2.4.0 (Bouckaert et al. 2014). In addition to generating concatenated trees, we generated gene trees for each locus in BEAST, the MCC trees for which are reported in Supporting Information Fig. S2.

ESTIMATES OF LUZON COLONIZATION TIMES

We used the Bayesian posterior tree distribution to estimate colonization times for each of the five Luzon rodent groups we sampled. For the LOE rodents, we calculated the interval of colonization as the time between the stem and crown ages of the clade, corresponding to the maximum and minimum colonization times for each clade. These times were calculated across the 95% highest posterior density (HPD) of divergence times for each clade. We generated probability distributions by populating 0.2 My bins between the maximum and minimum age for each estimate with the normalized proportion of trees in which the given date fell between the stem and crown ages of a clade. Because intra-island speciation events were unavailable to sample for the three New Endemic rodent colonization events, we calculated the maximum colonization ages for these species as the divergence date between each Luzon species and their non-Luzon sister lineage. The distribution of times for each clade was plotted to visualize the probability of independent colonization.

TESTING FOR DIVERSITY-DEPENDENT CLADOGENESIS AND DIMINISHED ECOLOGICAL OPPORTUNITY

To assess the role of ecological opportunity in diversification, we first assessed whether the pattern of diversification was consistent with expectations of diversity-dependent cladogenesis for each LOE rodent clade. This model predicts initially rapid speciation that diminishes toward the present as ecological opportunity declines. We visualized lineages-through-time (LTT; Nee et al. 1992) of the two Philippine Old Endemic clades after non-Luzon species were pruned from the MCC tree to determine whether the rate of speciation was approximately constant on a logarithmic scale. Under diversity-dependent cladogenesis, lineages are expected to accumulate nonlinearly on a logarithmic scale, with a decrease in slope over time. This change in branching times was quantified using the gamma (γ) statistic applied to each LOE clade, which tests the null hypothesis that the rate of speciation is constant through time. Estimating a γ value less than the critical value of –1.645 (at $\alpha = 0.05$) indicates that speciation events are closer to the root of the reconstructed phylogeny, and thus that the majority of diversification took place earlier in the clade's history, than would be expected under a pure birth diversification process (Pybus and Harvey 2000). This method assumes complete species-level sampling of the clades of interest. While we are reasonably confident that our sampling of LOE species is near completion, our sampling of SOE rodents is far from complete. As such, we could not meaningfully perform this analysis on the SOE rodents. We performed these analyses using the *ape* and *phytools* packages in *R* (Paradis et al. 2004; Revell 2012; R Core Team 2015).

We also tested for temporally decelerating diversification rates using a model-fitting approach. We compared the fit of five evolutionary models, including a Yule diversification model, a constant-rate birth-death model, and time-dependent rate models with decreasing speciation rates (SPVAR), increasing extinction rates (EXVAR), or both (BOTHVAR; Yule 1924; Nee et al. 1994; Rabosky 2006). The fit of these models was compared using the Akaike information criterion corrected for small sample sizes (AICc; Akaike 1974; Hurvich and Tsai 1989), with the model with the highest Akaike weight (w) accepted as the best. Model fitting was conducted using the *laser* package of *R* using default parameter settings for each function (Rabosky 2006). To ensure that model selection was not driven by the choice of a Yule tree prior in our BEAST analysis, we performed an additional model selection analysis using a distribution of trees sampled under a birth–death prior with the topology constrained to that of the original tree (samples generated: 2.9×10^8, trees generated: 2.9×10^5). As with the LTT analysis, we did not perform diversification model fitting using on the SOE rodents, for which we lack species-level sampling.

To test for incumbency effects, we assessed whether the secondary colonizing clade (Chrotomyini) has a lower diversification rate than either (1) the incumbent clade that occupies the same system (Phloeomyini) as well as (2) its sister clade (the SOE), which diversified across Sahul in the absence of an earlier-arriving clade of murine competitors. We estimated diversification rate parameters for these three, independent radiations using a likelihood-based framework that accounts for lineage-specific sampling probabilities (Alfaro et al. 2009; estimated using modified MEDUSA code from Jansa et al. 2014). For this analysis, we pruned our MCC tree to include the two focal groups in each test. Furthermore, we pruned the SOE clade to genus level (i.e., by removing *Pogonomys macrourus* and *P. sylvestris*) and enumerated the species represented by each genus according to Musser and Carleton (2005) supplemented by Rowe et al. (2008) and Rowe et al. (2016). Pruning two of the three species of *Pogonomys* was necessary due to incomplete phylogenetic sampling of this genus and uncertainty associated with relationships of these unsampled species to the three species that were sampled. We then estimated the maximum likelihood parameter values and 95% confidence interval on the net diversification rate ($r = \lambda - \mu$, where λ represents speciation rate and μ represents extinction rate) and extinction fraction ($\varepsilon = \mu/\lambda$) for each clade. This confidence interval was approximated by generating the likelihood surface up to 3 log-likelihood units from the maximum likelihood estimate of these parameters. If incumbency has affected diversification of Chrotomyini, we would expect this clade to exhibit a lower net diversification rate than both Phloeomyini (the competing clade) and the SOE rodents (its sister clade, which radiated elsewhere without other murine competitors). Statistical significance for the difference in rates is inferred if the maximum likelihood estimate (MLE) of diversification rate for one clade falls outside an interval described by 3 log-likelihood units around the MLE for the other.

Finally, as an additional approach to testing these three diversification rate hypotheses, we examined rate heterogeneity using Bayesian Analysis of Macroevolutionary Mixtures v2.5.0 (BAMM; Rabosky 2014) to test differences in diversification rate for each clade of LOE rodents, while allowing for time-dependent diversification rates and clade-specific sampling probabilities. We used a backbone species sampling probability of 0.89. This value was calculated as the ratio of the estimated number of species within murine genera sampled in our phylogenetic analysis out of the total number of murine species, effectively accounting for the proportion of murine rodents in genera unsampled in our phylogenetic analysis. We also determined genus-specific sampling probabilities to account for unsampled species within sampled genera. In both cases, murid species richness was determined using Musser and Carleton (2005), supplemented by additional sources for many genera (Supporting Information Table S2).

Table 1. Partitions best supported by model comparison using PartitionFinder version 1.1.1 (Lanfear et al. 2012).

Partition	Model	Coding positions
RAxML 1	GTR+I+Γ	CYTB pos 1
RAxML 2	GTR+I+Γ	CYTB pos 2
RAxML 3	GTR+I+Γ	CYTB pos 3
RAxML 4	GTR+I+Γ	GHR pos 1, IRBP pos 2, RAG1 pos 1, ACP5 exon pos 2
RAxML 5	GTR+I+Γ	GHR pos 2, IRBP pos 3, RAG1 pos 2, ACP5 exon pos 3
RAxML 6	GTR+Γ	GHR pos 3, BRCA1 pos 3, FGB7
RAxML 7	GTR+Γ	IRBP pos 1, RAG1 pos 3
RAxML 8	GTR+Γ	BRCA1 pos 1, BRCA1 pos 2, ACP5 exon pos 1
RAxML 9	GTR+I+Γ	ACP5 intron
BEAST 1	GTR+I+Γ	CYTB
BEAST 2	K80+I+Γ	GHR
BEAST 3	SYM+I+Γ	IRBP
BEAST 4	GTR+Γ	BRCA1
BEAST 5	SYM+I+Γ	RAG1
BEAST 6	SYM+I+Γ	ACP5 exon
BEAST 7	HKY+I+Γ	ACP5 intron
BEAST 8	GTR+Γ	FGB7

We used initial parameters suggested by the setBAMMPriors function of the *R* package *BAMMtools* (Rabosky et al. 2014) and conducted an MCMC analysis for 10^8 generations, saving one in every 1000 states. We discarded 10% of samples of the resultant distribution as burn-in and subsampled the remaining samples to 5000. We then examined the 95% credible shift set of this distribution to determine support for rate shifts on branches leading to the clades containing LOE rodents. We interpreted support for diversification driven by ecological opportunity as recovering diversity-dependent cladogenesis with a higher initial diversification rate in the LOE rodent clades compared to the background diversification rate. Conversely, we interpreted support for diminished ecological opportunity as recovering a rate shift followed by decreasing diversification rates along the branch leading to Chrotomyini.

Results

PHYLOGENETIC RELATIONSHIPS AMONG MURINES

The PartitionFinder analysis identified nine nucleotide partitions for maximum likelihood (ML) analysis and eight for the Bayesian analysis as the best fit models given the candidate partitions (Table 1). Among the OE rodents, bootstrap support values in ML analysis were comparatively weakest within the genus *Apomys*,

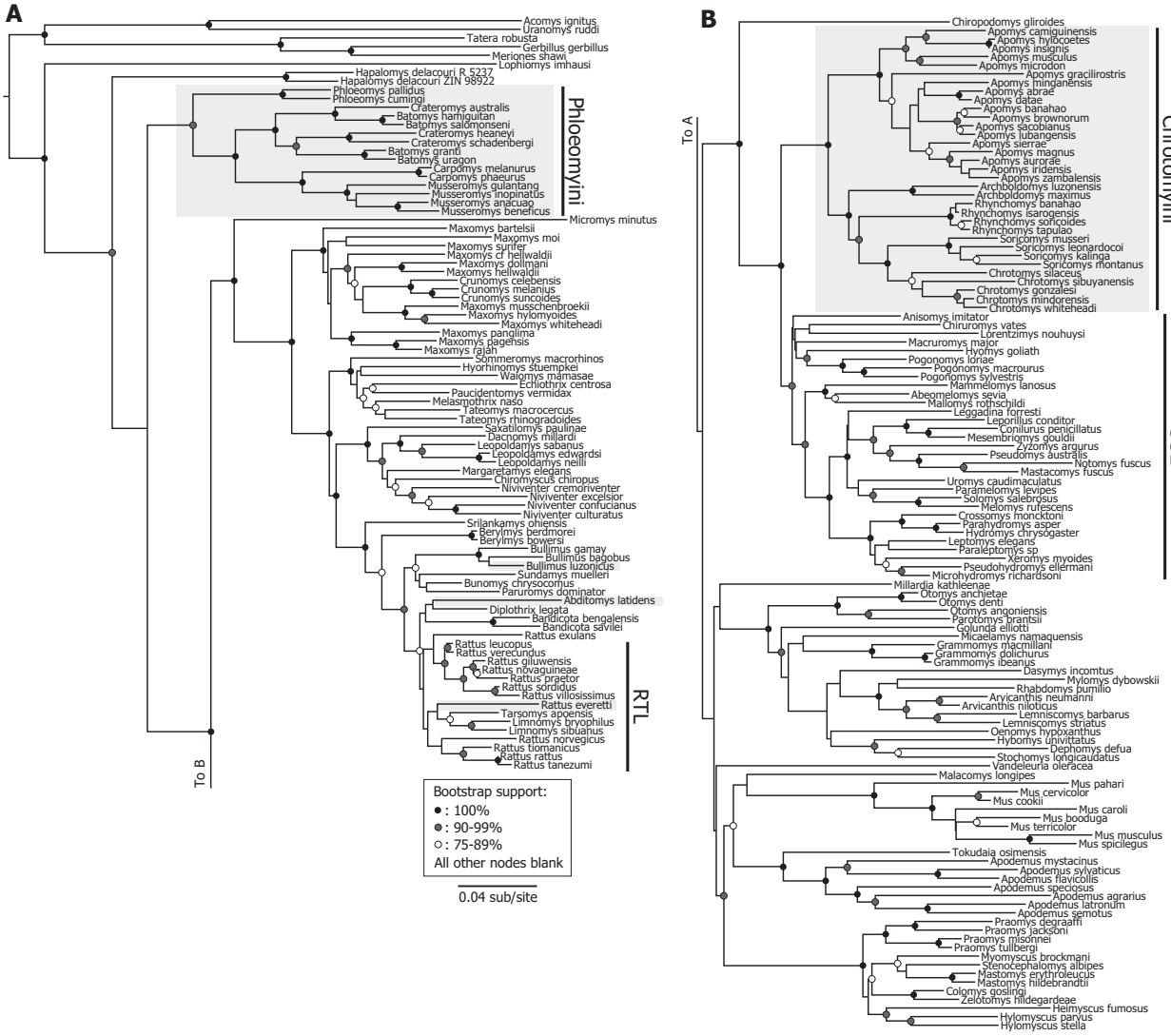

Figure 2. Maximum likelihood tree topology generated from concatenated sequence data. Branches are proportional to number of nucleotide substitutions. Dots at nodes correspond to bootstrap support (BS): BS = 100%: black, 90% ≤ BS < 100%: gray, 75% ≤ BS < 90%: white, BS < 75%: blank. Clades containing Luzon-endemic murines are enclosed in gray boxes. Sahul Old Endemics (SOE) and *Rattus-Tarsomys-Limnomys* (RTL) are abbreviated for clarity.

with other areas of weak support including divergences within *Chrotomys*, *Musseromys*, and *Soricomys* (Fig. 2). Bayesian nodal support values were generally stronger than their ML counterparts (>0.95) apart from some areas of weak support within *Chrotomys*, *Musseromys*, and *Soricomys* (Fig. 3).

The phylogenetic relationships we recovered among OE rodents were generally consistent with previous studies (Jansa et al. 2006; Schenk et al. 2013; Justiniano et al. 2015; Rowe et al. 2016). A single exception occurred in the placement of *Apomys minganensis*, which we recovered as sister to *Apomys abrae* and *Apomys datae* compared to the placement as sister to the clade containing *A. brownorum* and *A. sacobianus* as estimated in previous work (Justiniano et al. 2015). Interestingly, the phloeomyine genera *Crateromys* and *Batomys* were not reciprocally monophyletic. *Crateromys australis*, a species endemic to Dinagat Island and represented only by the species holotype, was placed in a well-supported clade containing the other two species of Greater Mindanao phloeomyines, *Batomys salomonseni* and *Batomys hamiguitan*. The remaining *Batomys* and *Crateromys* species found on Luzon and Panay have a robust sister relationship (Figs. 2 and 3).

Among relevant non-Philippine Asian murines, the phylogenetic placement of *Vandeleuria* and *Millardia* remains uncertain. Our study corroborates previous molecular studies that fail to find the suggested alliance of *Vandeleuria oleracea* with *Chiropodomys* that has been postulated based on dental characters (Musser and Carleton 2005) and instead strongly supports a sister-taxon relationship between *Chiropodomys* and the clade containing Chrotomyini + SOE murines (Schenk et al. 2013;

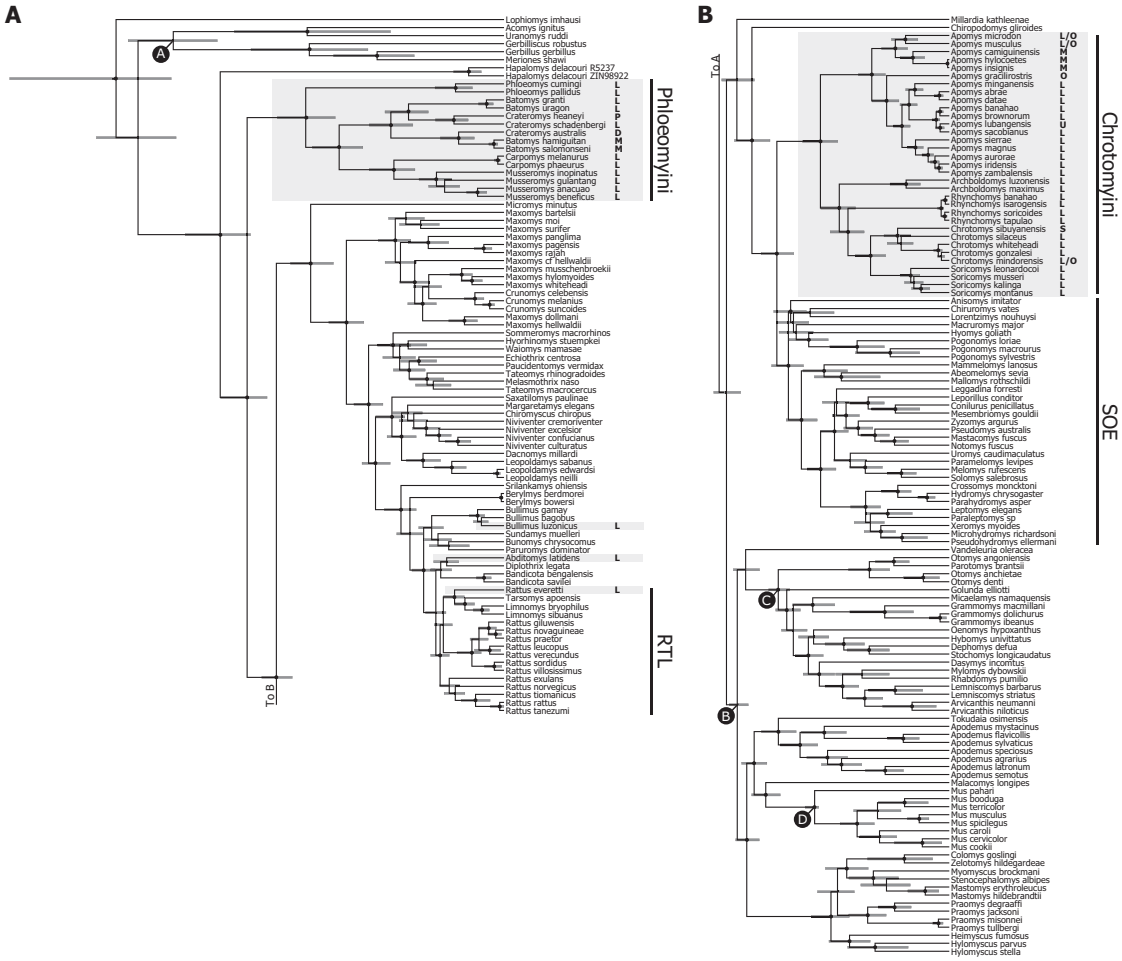

Figure 3. Time-calibrated maximum clade credibility (MCC) tree generated from concatenated sequence data. Nodes with ≥0.95 PP are indicated with a dot. Bars at nodes represent 95% highest posterior density (HPD) intervals for node ages. Nodes constrained with fossil data (Thomas et al. 1982; Kimura et al. 2015) are indicated with letters circumscribed by black circles. Clades containing Luzon-endemic murines are enclosed in gray boxes. Letters adjacent to taxon names correspond to the endemic faunal region of the species. L: Luzon Island, P: Panay I., D: Dinagat I., M: Mindanao I., O: Mindoro I., S: Sibuyan I., U: Lubang I. Sahul Old Endemics (SOE) and *Rattus-Tarsomys-Limnomys* (RTL) are abbreviated for clarity.

Steppan and Schenk 2017). Otherwise, the phylogenetic position of *Vandeleuria* is not secure in any molecular analysis to date (Schenk et al. 2013; Pagès et al. 2016; this study). Likewise, the placement of *Millardia* (represented here by *M. kathleenae*) varies depending on analytical approach (Fig. 3; see also Schenk et al. 2013), and is also not well supported by any analysis of any molecular dataset to date.

ESTIMATES OF LUZON COLONIZATION TIMES

Median estimates of colonization time for the LOE rodents were 12.8 ± 1.2 and 8.4 ± 0.9 Ma for Phloeomyini and Chrotomyini, respectively, with a median difference in crown clade age of 3.9 ± 0.9 My, suggesting Phloeomyini were present on Luzon at least 3 My prior to Chrotomyini. We obtained mean maximum colonization age estimates of Luzon for the New Endemic rodents of 3.6 ± 0.4, 2.8 ± 0.3, and 1.4 ± 0.2 Ma for the lineages *Abditomys latidens*, *Rattus everetti*, and *Bullimus luzonicus,* respectively. No overlap in distribution of colonization times occurred between the Old Endemic and New Endemic groups (Fig. 4). The colonization ages between Phloeomyini and Chrotomyini exhibited only slight overlap: 3.6% of the phloeomyine 95% HPD overlappped with 7.4% of the chrotomyine density, for a pooled probability density of 5.2%, suggesting time-staggered colonization between the two Old Endemic clades was likely (Fig. 4).

DIVERSITY-DEPENDENT CLADOGENESIS AND DIMINISHED ECOLOGICAL OPPORTUNITY

LTT plots and γ−statistics for the Luzon representatives of each Old Endemic clade (i.e., excluding taxa occurring on other Philippine islands) failed to show any signal of temporally

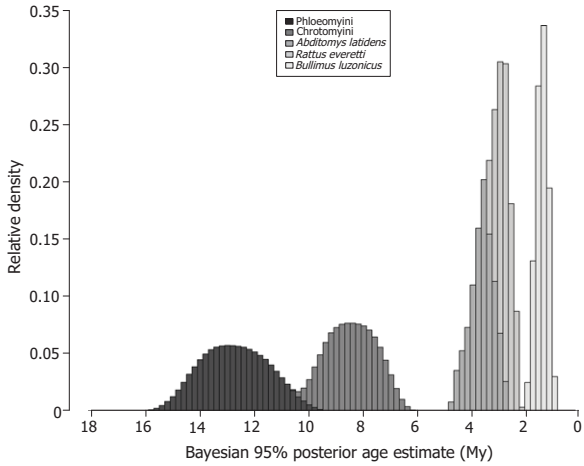

Figure 4. Histogram of inferred colonization ages for each clade of murine colonists on Luzon Island. Bars represent cladewise probability of colonization during 0.2 My intervals. Intervals for Phloeomyini and Chrotomyini represent 95% HPD of minimum and maximum age estimates inferred from crown and stem clade ages respectively. Intervals for *Abditomys latidens*, *Rattus everetti*, and *Bullimus luzonicus* are inferred from ages of divergence from their non-Luzon sister taxa and thus represent maximum colonization ages.

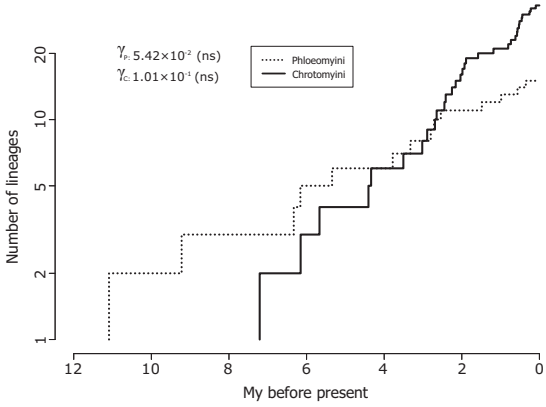

Figure 5. Lineage-through-time plots for Luzon Phloeomyini and Chrotomyini. The branching times for each clade could not be distinguished from that of a constant-rate process.

dynamic diversification rates (Phloeomyini: $\gamma_P = 5.42\times10^{-2}$, $P = 0.96$; Chrotomyini: $\gamma_C = 1.01\times10^{-1}$, $P = 0.91$; Fig. 5). Furthermore, we recovered a Yule diversification process, rather than time-variable processes, as the best-fit model of lineage diversification for each LOE group (Phloeomyini: $\ln(L)_P = -10.27$, $AICc_P = 22.99$, $w_P = 0.78$; Chrotomyini: $\ln(L)_C = 15.20$, $AICc_C = -27.96$, $w_C = 0.77$). Also contrary to our predictions, we recovered a net diversification rate (r) of Luzon Chrotomyini more than double that of Luzon Phloeomyini using this model selection approach ($r_P = 0.16$, $r_C = 0.41$). The best-fit model did not differ when conducted using an MCC tree generated under a birth–death tree prior ($\ln(L)_P = -10.33$, $AICc_P = 23.10$, $w_P = 0.78$; $\ln(L)_C = 12.83$, $AICc_C = -23.21$, $w_C = 0.78$).

Likelihood estimation of diversification rate parameters for the two LOE clades corroborated the differences in rate parameters obtained using our model selection approach, with a difference in maximum likelihood estimates (MLE) >3 log-likelihood units for each clade (Fig. 6A, Table 2). Rate parameter comparisons for Chrotomyini and SOE rodents, by contrast, suggested the two clades evolved under processes with comparable diversification rates and similarly low extinction fractions (Fig. 6B, Table 2). The MLE for all clades under a birth–death process was not significantly different from the maximum likelihood assuming a Yule process ($D_P = 0.88$, $P = 0.35$, df = 1; $D_C = 0.036$, $p = 0.85$, df = 1; $D_S = 0.050$, $P = 0.82$, df = 1). Both comparisons failed to support the hypotheses that diversification of Chrotomyini was depressed with respect to either Phloeomyini or the SOE rodents.

Analysis of diversification rates using BAMM suggests nearly constant diversification rates for the majority of Murinae (Fig. 7). We recovered strong support for a model allowing rate heterogeneity in the murine tree, with the largest posterior-to-prior ratio supporting three rate shifts (Bayes factor: 108.8, but such models were rarely sampled). Instead, both the maximum a posteriori (MAP) rate-shift configuration and modal number of shifts inferred in our BAMM analysis suggest two diversification rate shifts. These rate shifts were proposed in similar locations across the 95% credible-shift set. First, we recovered an increasing extinction rate along the branch leading to *Lophiomys imhausi* (the sole representative of Lophiomyinae), yielding a lower net diversification rate compared to the rest of Muridae. Second, an additional shift with increased speciation and extinction rates occurred along the branch leading to the *Rattus-Tarsomys-Limnomys* (RTL) division, yielding an increased net diversification rate (Supporting Information Fig. S2). The remainder of the tree exhibits a slowly declining net diversification rate with near-zero extinction, with an average time-integrated diversification rate of 0.30 lineages/My across the posterior distribution. In contrast to the nearly twofold difference in rates inferred from the ML analyses reported above, this analysis recovers nearly identical average diversification rates for Phloeomyini and Chrotomyini ($r_P = 0.29$, $r_C = 0.28$; Table 2). The 95% credible-shift set included 38 distinct rate shift configurations, but were largely similar to one another and the MAP configuration. Rate shifts were frequently sampled along the split between *Lophiomys* and remaining Muridae, with a lower net diversification rate than the remaining Muridae, and in the core *Rattus* division, with higher diversification rates than the background diversification process (Supporting Information Fig. S3). Consistent with our maximum likelihood analyses of diversification rates (Fig. 6), we failed to recover support for

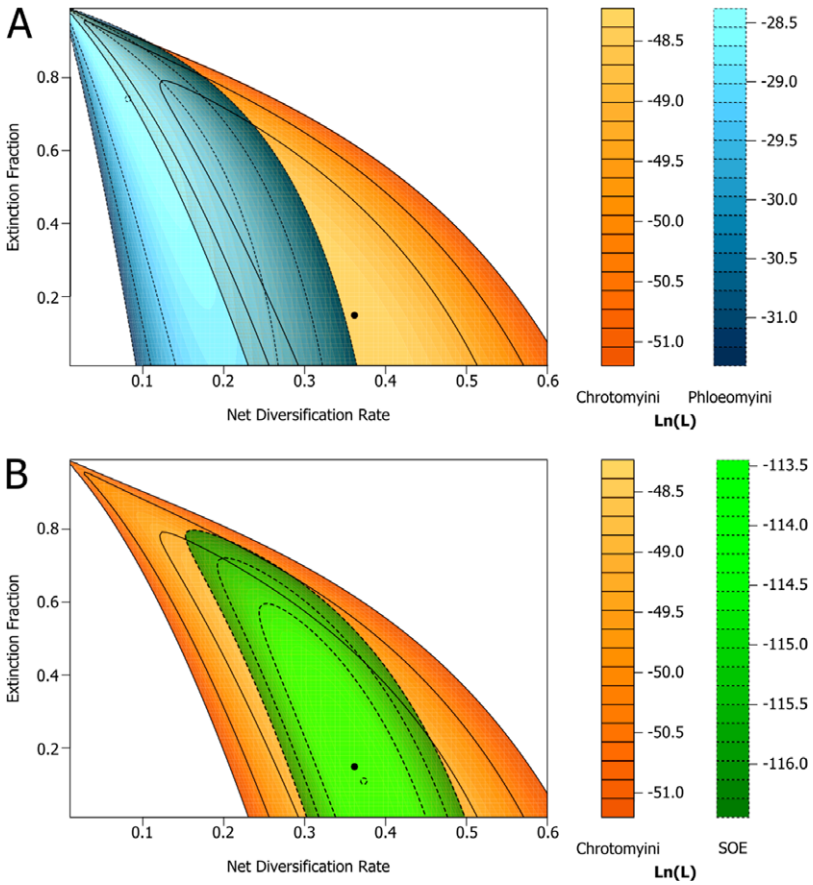

Figure 6. Comparison of the net diversification rate ($r = \lambda - \mu$) and extinction fraction ($\varepsilon = \mu/\lambda$) parameters inferred using MEDUSA for each of three murine clades. Panel (A) compares the Luzon Chrotomyini (orange, solid lines, filled point) and Phloeomyini (blue, dashed lines, empty circle), whereas 6B compares the Luzon Chrotomyini with the Sahul Old Endemic (SOE) rodents (green, dashed lines, empty circle). Higher likelihood values are represented with brighter colors. The variation in the size of the likelihood surface stems from variation in uncertainty of parameter estimates for each clade. The maximum likelihood estimate (MLE) for each clade is shown with a point and –1, –2, and –3 log-likelihood unit contours are shown with lines. The parameter area within three log-likelihood units approximates a 95% confidence interval of each clade's MLE, and recovering a MLE outside of the interval of the other clade suggests that the two exhibit distinct evolutionary processes.

Table 2. Diversification rate parameters inferred for Phloeomyini, Chrotomyini, and Sahul Old Endemic (SOE) rodents using MEDUSA and BAMM.

	MEDUSA			BAMM		
Lineages/My	Phloeomyini	Chrotomyini	SOE	Phloeomyini	Chrotomyini	SOE
Speciation rate (λ)	3.2×10^{-1}	4.2×10^{-1}	4.2×10^{-1}	3.0×10^{-1}	2.9×10^{-1}	3.0×10^{-1}
Extinction rate (μ)	2.3×10^{-1}	6.3×10^{-2}	4.6×10^{-2}	1.0×10^{-2}	1.0×10^{-2}	8.8×10^{-3}
Diversification rate (r)	8.1×10^{-2}	3.6×10^{-1}	3.7×10^{-1}	2.9×10^{-1}	2.8×10^{-1}	2.9×10^{-1}
Extinction fraction (ε)	0.74	0.14	0.11	3.4×10^{-2}	3.5×10^{-2}	3.0×10^{-2}

our hypotheses of lowered diversification rates in Chrotomyini compared to either Phloeomyini or the SOE rodents. Although we recovered slowly declining diversification rates for both LOE clades, the generating process is identical for most of the remainder of the murine tree.

Discussion

ESTIMATES OF LUZON COLONIZATION TIMES

In reconstructing the first species-level phylogeny of LOE rodents, we provide evidence that colonization of Luzon by these two major rodent groups was temporally staggered. Previously,

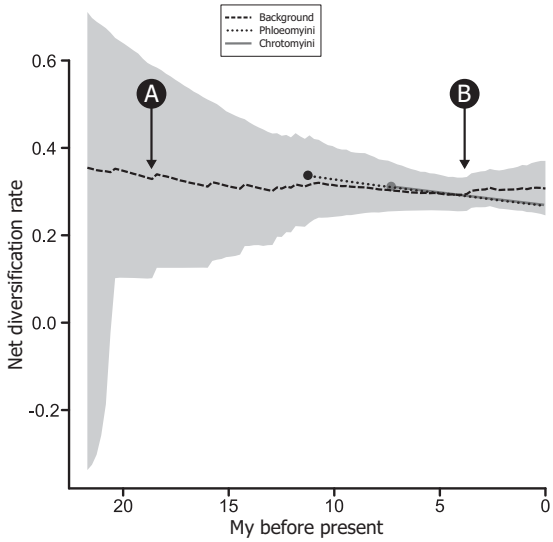

Figure 7. Diversification rate-through-time of Murinae and outgroups inferred from the distribution of BAMM rate configurations. Dashed line represents net diversification rate for the entire tree inferred from the average of the posterior (time-integrated rate: 0.30 lineages/My); gray envelope indicates the 95% confidence interval of the estimate. The dotted gray line indicates average diversification rate inferred for Phloeomyini (0.29 lineages/My) and the solid gray line indicates the inferred rate of Chrotomyini (0.28 lineages/My), with circles at the clade origin for clarity. Lettered circles indicate inferred rate shift positions based on the maximum a posteriori (MAP) rate shift configuration: (A) extinction rate increase along branch leading to *Lophiomys imhausi*; (B) speciation and extinction rate increase along branch leading to the *Rattus-Tarsomys-Limnomys* (RTL) division.

a two-phase model for colonization of Philippine Old Endemic versus New Endemic rodents was supported, but individual clades within each of these groups could not be temporally differentiated (Jansa et al. 2006). Our study refines this estimate by temporally separating the invasion of Luzon by Phloeomyini from that of Chrotomyini, and provides the first step in differentiating the timing of colonization of the Luzon New Endemics, suggesting independent colonization of *Bullimus luzonicus* from *Abditomys latidens* and *Rattus everetti* (based on maximum clade ages; Fig. 4). Recovering Phloeomyini and Chrotomyini as colonizing millions of years apart provides the basis for the prediction that competition for niches was potentially weaker for the phloeomyines compared to the chrotomyines.

DIVERSITY-DEPENDENT CLADOGENESIS AND DIMINISHED ECOLOGICAL OPPORTUNITY

For this study, we sought to test three predictions regarding how ecological opportunity, diminished in secondary colonists by incumbency of another clade, alters lineage diversification. First, we tested whether diversity-dependent cladogenesis provided a good fit for the diversification of the two clades of LOE rodents, but failed to recover any evidence of temporally decelerating cladogenesis. Our BAMM analysis recovered slightly decreasing diversification rates through time for both Chrotomyini and Phloeomyini, but this process appears to be no different from the remainder of Murinae (excluding *Rattus-Tarsomys-Limnomys*, which show accelerated rates of diversification). Based on these results, we conclude that species diversification of LOE rodents is not consistent with expectations of ecological opportunity presented by colonizing a new landmass.

The second prediction we tested was that Chrotomyini should exhibit lower diversification rates than Phloeomyini, due to incumbency effects. Two lines of evidence suggest that this was not the case. First, we did not detect a change in diversification rate in the murine phylogeny between these two clades in our BAMM analysis (Fig. 7). Second, although we did recover a significant difference in diversification rate using maximum-likelihood analysis, this difference was not in the expected direction: the estimated diversification rate of Chrotomyini in these analyses was up to fourfold faster than that of Phloeomyini (Fig. 6, Table 2). Recovering, at minimum, similar diversification rates, or as we found, a much higher diversification rate in Chrotomyini, directly contradicts the expectation that a colonizing clade is prevented from achieving comparable diversity to an incumbent lineage.

Our final prediction was that Chrotomyini should exhibit a lower diversification rate than their sister clade, the Sahul Old Endemics, which constitutes the earliest rodent colonists of the Sahul region. Comparing these two clades allowed us to explore how chrotomyine diversification may have unfolded in the absence of primary colonists on Luzon. Again, in contrast to our predictions, the two clades had diversification rates consistent with evolution under a single macroevolutionary process. The uniformity we recovered provides an additional line of evidence that Chrotomyini were not limited in their diversification by colonizing Luzon after Phloeomyini. Our failure to recover support for any of the three predictions that formed the basis of this study point to the conclusion that the diversification history of the Luzon Old Endemic rodents is more prominently influenced by factors other than incumbency effects. The dominant pattern for the LOE rodents, and the majority of Murinae, is a constant or slowly decelerating diversification rate with a relatively low apparent extinction rate.

The patterns illustrated in these two clades of island rodents corroborate the patterns found for rodents in continental systems (Schenk et al. 2013). These authors found that incumbency effects, whereby secondary colonists exhibit diminished diversification rates compared to primary colonists, were the exception rather than the rule among muroid rodents. The authors recovered diversity-dependent cladogenesis among South American muroid rodents with strong support, and among the SOE rodents with weak support, but found no support for secondary colonists

having decreased diversification rates in any of their biogeographic categories. In aggregate, these findings suggest that incumbency's influence on lineage diversification may be easily overshadowed by other phenomena (Derryberry et al. 2011; Schenk et al. 2013). With this context in mind, there are several mutually compatible scenarios that could be responsible for the observed diversification history of the LOE. We outline three below.

First, Phloeomyini may have not had enough time for sufficient speciation to occur to impose incumbency effects on Chrotomyini. To assess how much diversification could have occurred within Phloeomyini before Chrotomyini arrived on Luzon, we simulated the number of phloeomyine lineages present at the inferred median colonization age of Chrotomyini. Based on the diversification rates inferred using MEDUSA and BAMM, we performed 100 constant-rate birth–death simulations, which yielded an average of three species present for each set of assumed rates (simulations performed using *TESS* in R; Hoehna 2013). The relatively low rate of early cladogenesis among Phloeomyini is further supported by our failure to recover diversity-dependent cladogenesis as the best-supported diversification model for this clade. Additionally, if density-independent time-for-speciation processes were the dominant mechanism of early diversification in this clade, as suggested by our analyses, then we would not expect the rapid early cladogenesis predicted under a model of ecological opportunity (Stephens and Wiens 2003; Rabosky 2012). As a result, the relatively low early diversity of phloeomyine species may not have exhibited a strong enough competitive pressure on the secondary colonists to depress their diversification.

Second, the extent of geographic dynamism may be too great to impose realistic ecological limits on species diversity, even at the scale of a single island. Numerous studies encompassing a variety of clades illustrate that allopatric speciation is a prevalent mode of diversification on continental landmasses (Ribas et al. 2007; Derryberry et al. 2011; Giarla and Jansa 2014). At large, geographically complex spatial scales, vicariance or dispersal events facilitate diversification without increasing interspecific competition (Esselstyn et al. 2009; Maestri et al. 2016; Pavan et al. 2016). Thus, geographic scale and isolation likely influence the mechanism by which diversification occurs, as has been suggested in the tropical Andes (Hutter et al. 2017). Despite the limited space afforded to colonists of Luzon compared to continental radiations, the patterns of LOE diversification were more consistent with a mechanism of allopatric speciation, where species diversity is able to accumulate nearly constantly, offset slightly by background extinction rates. This conclusion is consistent with the observation that Luzon, as a volcanic oceanic island, has had a markedly dynamic history: tectonic uplift, sea level fluctuations, and volcanism have all contributed to substantial changes in available land area and suitable habitat (Hall 2013; Heaney et al. 2016a). This temporal dynamism may mean speciation is driven less by competition for niches and more by dispersal to newly available habitat generated by geological processes, specifically, the montane "islands" formed by volcanism and tectonic uplift over the past 15 million years. Importantly, these montane islands, while originally isolated from one another in the form of individual oceanic islets, probably coalesced into their contemporary configuration only within the last 5 million years (Heaney et al. 2016a). Considering many of the species-level divergences in both LOE clades began after Luzon's coalescence, and that sister species within either clade often occupy nonadjacent ranges (Heaney et al. 2016b), we suggest that a mixture of over-land and over-water dispersal to other mountain ranges on Luzon has been at least as important in LOE evolutionary history as processes of ecological specialization and differentiation, and that lowland habitat presents a prominent, but not insurmountable, dispersal barrier to most LOE species. The patterns of allopatric speciation we propose are supported in several clades of Southeast Asian mammals (Esselstyn et al. 2009; Achmadi et al. 2013; Justiniano et al. 2015), suggesting that the climatic and geological dynamism of this region may be paramount in explaining its biodiversity.

Third, the effects of incumbency may still be apparent in this system, but they are acting not on diversification history, but rather on patterns of phenotypic diversity. If true, we may still recover diversity-dependent trait evolution with decreased rates of phenotypic evolution among secondary colonists. This hypothesis seems intuitive, considering phenotypic evolution driven by ecological opportunity forms the basis for adaptive radiation theory (Parent and Crespi 2009; Mahler et al. 2010), but it remains to be tested in this system. In the context of incumbency, the rate of morphological evolution may be suppressed in secondary colonists, although lineage diversification (via allopatric speciation) is unaffected, yielding many ecologically similar species. Alternatively, incumbent clades may filter secondary colonists in favor of those lineages occupying distinct regions of ecomorphospace. The resulting morphological variation may be such that cladewise overlap is minimized (Jønsson et al. 2015). In the context of the LOE rodents, the colonizing ancestor of Chrotomyini may have been ecologically distinct enough to facilitate coexistence through divergent evolutionary trajectories. For example, comparative analysis of Floridian *Quercus* oaks suggests that, within ecological communities, individual species are less ecologically similar and more phylogenetically distant than would be expected by chance (Cavender-Bares et al. 2004). The phylogenetic and ecological overdispersion reported by these authors may extend more broadly to the island scale such that, for a lineage to successfully invade, it must be phenotypically distinct enough from other lineages to minimize competition. Preliminary evidence to support this prediction stems from field observations suggesting the LOE rodent clades differ in their modal dietary and

habitat preferences: members of Phloeomyini are primarily arboreal herbivores whereas chrotomyine species are predominantly terrestrial animalivores (Heaney et al. 2016a).

One additional aspect that is also worth considering is the potential impact the two Old Endemic clades have had on the diversification of the Luzon New Endemics. We did not include these more recent colonists in our analyses, because they lack species diversity due to their relatively recent origin on Luzon. Nevertheless, these recently colonizing species do exhibit substantial ecological differences from the LOE rodents. As an example, the New Endemics are typically found either in low elevation or disturbed habitats. Their distribution may be the result of competitive exclusion by the Luzon Old Endemics, which are concentrated in high elevation, primary montane forest habitats (Heaney et al. 2016a). The ecological disparity may otherwise stem from an ongoing taxon cycle in which the two colonization regimes are in different stages: the Old Endemics may have achieved relative stasis due to their comparatively ancient colonization and subsequent ecological specialization; in contrast, the New Endemics, due to recent colonization, represent an incipient taxon expansion (Ricklefs and Bermingham 2002). Whether the differences in habitat use is the result of active exclusion by the LOE rodents or habitat preferences among the Luzon New Endemics remains to be discovered, but could shed additional light on how incumbency alters macroevolutionary processes and community assembly.

Conclusions

The extent to which ecological interactions among species and clades influence macroevolutionary processes is an important question for understanding the origination and maintenance of biodiversity. Our study examined whether incumbency of another clade diminishes the rate at which secondary colonists diversify while also providing the most complete record of Luzon Old Endemic rodent phylogenetic diversity. We did not recover a signal of incumbency-mediated diversification, but there is still the potential for inter-clade interactions to have shaped the diversification of both. Given the complexity of natural systems, many processes have likely contributed to the evolution of species diversity to varying degrees over the history of Luzon Island, including incumbency effects, within-clade interspecific competition, and allopatric speciation through island and/or montane habitat hopping (Heaney et al. 2016b). Nevertheless, we argue that ecological opportunity does not appear to be the primary mechanism determining the generation of species among these mammals and propose that incumbency effects may only be detectable in spatially limited scales that have remained geologically and climatically static over evolutionary time.

AUTHOR CONTRIBUTIONS

DMR and *SAJ* designed the research; *DMR*, *LRH*, and *SAJ* collected the data; *DMR* analyzed the data; and *DMR*, *LRH*, and *SAJ* wrote the manuscript.

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DATA ARCHIVING

Sequence data are deposited in GenBank using accession numbers MH330617-MH330660. Nucleotide alignments and tree files are deposited in TreeBase using accession number 22736.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

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Supporting Information

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

Figure S1. Gene MCC trees generated for BRCA1, CYTB, FGB7, GHR, IRBP, and RAG1.
Figure S2. BAMM maximum a posteriori (MAP) rate configuration based on MCC tree.
Figure S3. BAMM 66.3% credible shift set of different rate configurations ordered by their sampling probabilities (*f*).
Table S1. Full specimen matrix for phylogenetic analyses. Cells indicate GenBank numbers when available.
Table S2. Clade-specific sampling probabilities used in our BAMM analysis accompanied by source(s) used for justifying the number of species in the clade.