RESEARCH PAPER

How small an island? Speciation by endemic mammals (*Apomys*, Muridae) on an oceanic Philippine island

Lawrence R. Heaney[1] | Christopher C. Kyriazis[1] | Danilo S. Balete[1] | Scott J. Steppan[2] | Eric A. Rickart[3]

[1]Field Museum of Natural History, Chicago, Illinois

[2]Department of Biological Sciences, Florida State University, Tallahassee, Florida

[3]Natural History Museum of Utah, Salt Lake City, Utah

Correspondence
Lawrence Heaney, Field Museum of Natural History, Chicago, IL 60505-2496.
Email: lheaney@fieldmuseum.org

Heaney and Kyriazis co-first authors

ABSTRACT

Aim: To investigate the influence of oceanic island area on speciation by small mammals, in the context of other land vertebrates.

Location: Mindoro Island ($9{,}735$ km^2), an oceanic island in the Philippines.

Methods: Extensive field surveys on Mindoro, followed by sequencing one mitochondrial and three nuclear genes for use in phylogenetic, population genetic and coalescent-based analyses, and by morphometric analysis of craniodental data.

Results: Our analyses documented the presence on Mindoro of an endemic clade of probably four species of *Apomys*, subgenus *Megapomys*. The common ancestor likely arrived from Luzon Island across a narrow sea channel between 2.4 and 1.5 Ma; the four probable species occur allopatrically, with variation in their ranges along elevational gradients. Mindoro thus becomes the smallest oceanic island on which speciation by small mammals has been documented.

Main conclusions: A review of land-living vertebrates suggests that bats and large mammals have the greatest area requirements for speciation, whereas frogs, lizards, birds and small mammals have lower and similar minimum area requirements. However, with the exception of *Anolis* lizards, data are scattered and limited; much research is needed to document the impact of island area on speciation. The existence of a lower limit implies that the biological processes that influence species richness do not operate equivalently along a gradient of island areas: speciation within islands may not contribute to changes in species richness below some limit, unlike colonization and extinction, which operate at all island sizes.

KEYWORDS
diversification, island area, *Megapomys*, minimum area, multi-locus, oceanic island biogeography, phylogeny, species richness, species tree, vertebrates

1 | INTRODUCTION

Species richness in any given place is determined by three primary biological processes: colonization, extinction and speciation. Studies of these processes have often focused on islands, especially on oceanic islands, because they represent places where these processes can be investigated most readily. While all three processes were explicitly considered in early discussions about island biodiversity (e.g. Wallace, 1880), attempts to quantify them generally began after the publication of MacArthur and Wilson's (1963) seminal paper and monograph (MacArthur & Wilson, 1967), in response to their mathematical and graphical models.

Although MacArthur and Wilson mentioned speciation within some isolated islands and archipelagos under the rubric of a "radiation zone" (MacArthur & Wilson, 1963, 1967, p. 175), they and many who followed them did little to incorporate this process, and

instead focused on colonization and extinction. As a result, in situ speciation remained peripheral to most studies of island biogeography for about three decades (Rosindell & Phillimore, 2011), in spite of some studies that highlighted the importance of speciation (e.g. Grant, 1981, 1998; Heaney, 1986; Ricklefs & Cox, 1972). By the late 1990s, accumulating genetic evidence had increasingly shown the importance of speciation on oceanic islands (e.g. Losos, 1998; Roughgarden, 1995; Wagner & Funk, 1995), and some graphic models incorporating speciation began to appear (e.g. Heaney, 2000; Lomolino, 2000a, 2000b). The recent formulation of the General Dynamic Model of oceanic island biodiversity (Whittaker, Fernandez-Palacios, Matthews, Borregaard, & Triantis, 2017; Whittaker, Triantis, & Ladle, 2008 see also Stuessy, 2007), which places speciation on an equal conceptual footing with colonization and extinction, has engendered many studies of the impacts and interactions of these processes within the context of geological changes in the age, area and topographic diversity of the islands themselves (e.g. Borregaard et al., 2017; Warren et al., 2015).

This increased emphasis on speciation has made it apparent that many gaps remain in our empirical knowledge of speciation on oceanic islands. One aspect that is especially important in developing accurate models pertains to a fundamental difference between colonization and extinction compared to speciation. Both colonization and extinction can take place to/on an island of any size, but because speciation is predominantly (and for some taxa, nearly exclusively) allopatric, it requires some minimum island size for the factors that promote geographical isolation to operate (Coyne & Price, 2000; Losos & Schluter, 2000; Kisel & Barraclough, 2010; Rabosky & Glor, 2010; Sly et al., 2011; Steinbauer et al., 2016). The few reviews that include multiple examples have found great variation among taxa in the minimum area that is required, and have noted a general or quantitative association of the minimum area requirement with the vagility of the taxa, with less vagile taxa able to speciate within smaller areas (e.g. Gillespie, 2004; Gillespie & Roderick, 2014; Kisel & Barraclough, 2010; Losos & Parent, 2010; Rosindell & Phillimore, 2011; Triantis, Economo, Guilhaumon, & Rickleffs, 2015). Many of these studies have shown that much speciation in archipelagos takes place in isolation on different islands, and that speciation within a single island operates largely independently of the speciation among islands (e.g. Coyne & Price, 2000; Gillespie & Roderick, 2014; Rosindell & Phillimore, 2011; Triantis, Mylonas, & Whittaker, 2008; Triantis et al., 2015). In the remainder of this paper, we focus on speciation by vertebrates within a single island.

1.1 | Minimum area estimates for speciation among land vertebrates: A brief overview

The earliest consideration of the role of taxonomic variation in minimum area requirements that we are aware of appeared in the context of conservation biology. Soulé (1980) posed the question, are there any national parks large enough to permit speciation by vertebrates and higher plants? Without citing sources, he listed the smallest island where each taxon had undergone within-island speciation. For birds and large mammals, he listed Madagascar as the smallest; for higher plants, New Caledonia; for small mammals, Luzon and Cuba; for riverine fish, Ceylon; for both reptiles and amphibians, Jamaica, and for lake-dwelling fish, Lake Lanao. He concluded that no national park was large enough to support speciation by mammals or birds, and that very few could support speciation by reptiles and amphibians. This information was subsequently cited in conservation biology textbooks (e.g. six editions of Primack, 2014), but not in the biogeography literature.

To provide context for our own study, presented below, we briefly reviewed the available literature to (1) determine if Soulé's (1980) assertions about speciation on specific islands are supported, and (2) seek examples of additional islands within which speciation has been demonstrated. We restricted our search to tropical oceanic islands, because they are likely to be less influenced by multiple colonizations than are land bridge islands, and because diversity of these vertebrates is highest in the tropics. We focused on finding examples from the low end of the area range for each taxon, as these are most relevant to our question (see Section 2).

Most subsequent estimates have hewn remarkably closely to Soulé's examples (Figure 1; see also Table S1.1). Among birds, which are arguably the best-known vertebrates, Coyne and Price (2000) noted a likely case of speciation within Jamaica (11,400 km^2), but knew of no other examples on islands smaller than Madagascar (c. 588,000 km^2). Intra-island diversification by *Robsonius* ground-warblers within Luzon (103,000 km^2) and by *Aethopyga* sunbirds on Mindanao (99,078 km^2) adds examples from islands between Jamaica and Madagascar in area (Figure 1). The presence of endemic species-pairs on Hispaniola has been shown, but is thought to have involved divergence by the birds prior to merging of palaeo-island blocks and therefore may not represent within-island speciation (Sly et al., 2011). Finally, studies of endemic Hawaiian avian radiations have explicitly not found evidence of within-island speciation (e.g. VanderWerf, Young, Yeung, & Carlon, 2009). Kisel and Barraclough (2010) noted a possible speciation event on Norfolk Island (64 km^2), but this was regarded by Coyne and Price (2000) as more likely the result of two colonization events, and another in the Tristan da Cunha archipelago (705 km^2) that may have involved inter-island speciation (but see also Ryan, Bloomer, Moloney, Grant, & Delport, 2007); this leaves the example from Jamaica as the smallest that is reasonably certain.

Among reptiles, intensive study of *Anolis* lizards in the Caribbean has shown within-island speciation on Puerto Rico (9,100 km^2) as well as on Jamaica, Hispaniola and Cuba (11,190–105,806 km^2), but not on any smaller islands. Speciation within Luzon by monitor lizards provides an example from a larger island.

Speciation by anurans has been documented within Mindanao and Cuba, and extensive speciation within Jamaica, as noted by Soulé (1980) has been confirmed, but a likely case of speciation by frogs on Puerto Rico appears to now leave that island as the smallest showing within-island speciation among amphibians (Figure 1, Table S1.1).

FIGURE 1 Documented cases of speciation within a given island by six groups of terrestrial vertebrates. Solid circles based on sources cited in Table S1.1; asterisk is based on this study
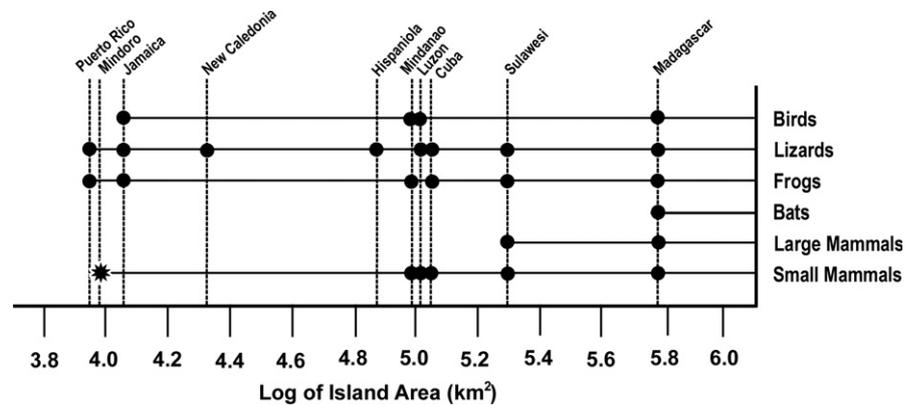
Surprisingly, little has been written about the minimum area requirements for speciation by mammals. Kisel and Barraclough (2010) noted speciation by both bats and large mammals on Madagascar, which were subsequently well documented. Bats in the Philippines and the Caribbean show much inter-island speciation, but none intra-island (Davalos, 2009; Heaney & Roberts, 2009), leaving Madagascar as the current smallest single island showing speciation by bats. However, several groups of large mammals (operationally defined here as >4 kg) show speciation on Sulawesi (180,681 km^2), including primates and water buffalo, substantially lowering the threshold defined by Soulé (1980) and Kisel and Barraclough (2010; Figure 1, Table S1.1).

MacArthur and Wilson's (1967) reference to speciation among small mammals on Luzon, as also stated by Soulé (1980), has been well documented; more than 80% of the 56 species of non-volant native mammals that are present on Luzon are the result of two colonization events by murid rodents followed by extensive diversification (Heaney, Balete, & Rickart, 2016; Jansa, Barker, & Heaney, 2006). Evidence of speciation by small, non-volant mammals on larger islands is abundant, including Cuba (105,806 km^2), and Sulawesi (180,681 km^2). The only island smaller than Luzon to show evidence of within-island speciation is Mindanao. These values (Figure 1, Table S1.1) leave the impression that speciation by small mammals on islands below about 100,000 km^2 may be absent, a finding that seems incongruous given the much lower limits for birds (Jamaica, 11,400 km^2) and reptiles and amphibians (Puerto Rico, 9,100 km^2). Here, we document a new lower limit for island size and speciation in mammals, on Mindoro Island, Philippines, and place that finding into the broader context of the process of speciation by vertebrates on oceanic islands.

1.2 | The Philippines and *Apomys* study system

The Philippine archipelago is ideal for studies of island biogeography. About 7,000 islands are present, ranging in area up to 103,000 km^2. All are oceanic in origin with the probable exception of Palawan and adjacent small islands (Piper, Ochoa, Robles, Lewis, & Paz, 2011). Islands began to emerge by 35 Ma (Hall, 2013), and the oldest modern island (Luzon) has had subaerial portions continuously emergent for about 27 Myr (Heaney et al., 2016). Some islands merged during

Pleistocene periods of low sea level, but many remained isolated by sea channels (Heaney, 1986). The presence of both between and within-island speciation has long been recognized (Heaney, 1986; Heaney & Rickart, 1990); much of the within-island speciation has been associated with the rugged topography of the larger islands, with many locally endemic species at high elevation (Brown et al., 2013; Justiniano et al., 2015).

Following extensive studies of mammalian diversification on Luzon (Heaney et al., 2016), we began studies in 2013 on Mindoro (Figure 2a) to determine the extent of mammalian diversity, the geographic origins of each species, and the timing of the colonization and any speciation events that produced the extant fauna. With an area of 9,735 km^2, Mindoro is an oceanic island about one-tenth the size of Luzon from which it is isolated by surrounding waters at least 250 m deep (Heaney, 1986; Voris, 2000). Most of the island consists of uplifted continental rock that rifted off the southern edge of what is now China beginning about 30 Ma, probably under water at the time (Hall, 1998, 2013). The time of emergence of Mindoro is uncertain, but was at least partially emergent by 8 Ma, and possibly as early as 15 Ma (Hall, 2013). With a maximum elevation of 2,446 m, Mindoro supports lowland (0–900 m), montane (900–1,500 m) and mossy (1,500–2,440 m) forest, with continuously moist lowland forest on the east side and seasonally dry forest on the west side (Fernando, Suh, Lee, & Lee, 2008). Three montane areas separated by lowlands are present, forming a long arc of upland terrain that runs roughly from the north-west corner to the south-central edge (Figure 2).

Apomys is a species-rich genus of forest mice endemic to the oceanic portions of the Philippines. These are small (*c.* 20–120 g), often abundant mice that feed on invertebrates, seeds and fruit (Heaney et al., 2010, 2016). They are members of an extensive endemic radiation of five genera and over 50 species that is centred on Luzon (Jansa et al., 2006; Justiniano et al., 2015; Steppan, Zawadski, & Heaney, 2003). On Luzon, the subgenus *Megapomys* has produced at least eleven species during the last *c.* 2 Myr; most occur at middle to high elevations. A single Mindoro endemic species *Apomys gracilirostris* (Ruedas, 1995) had been described previously, but despite the topographic diversity of the island, nearly all field surveys of mammals had taken place on a single mountain, Mt. Halcon.
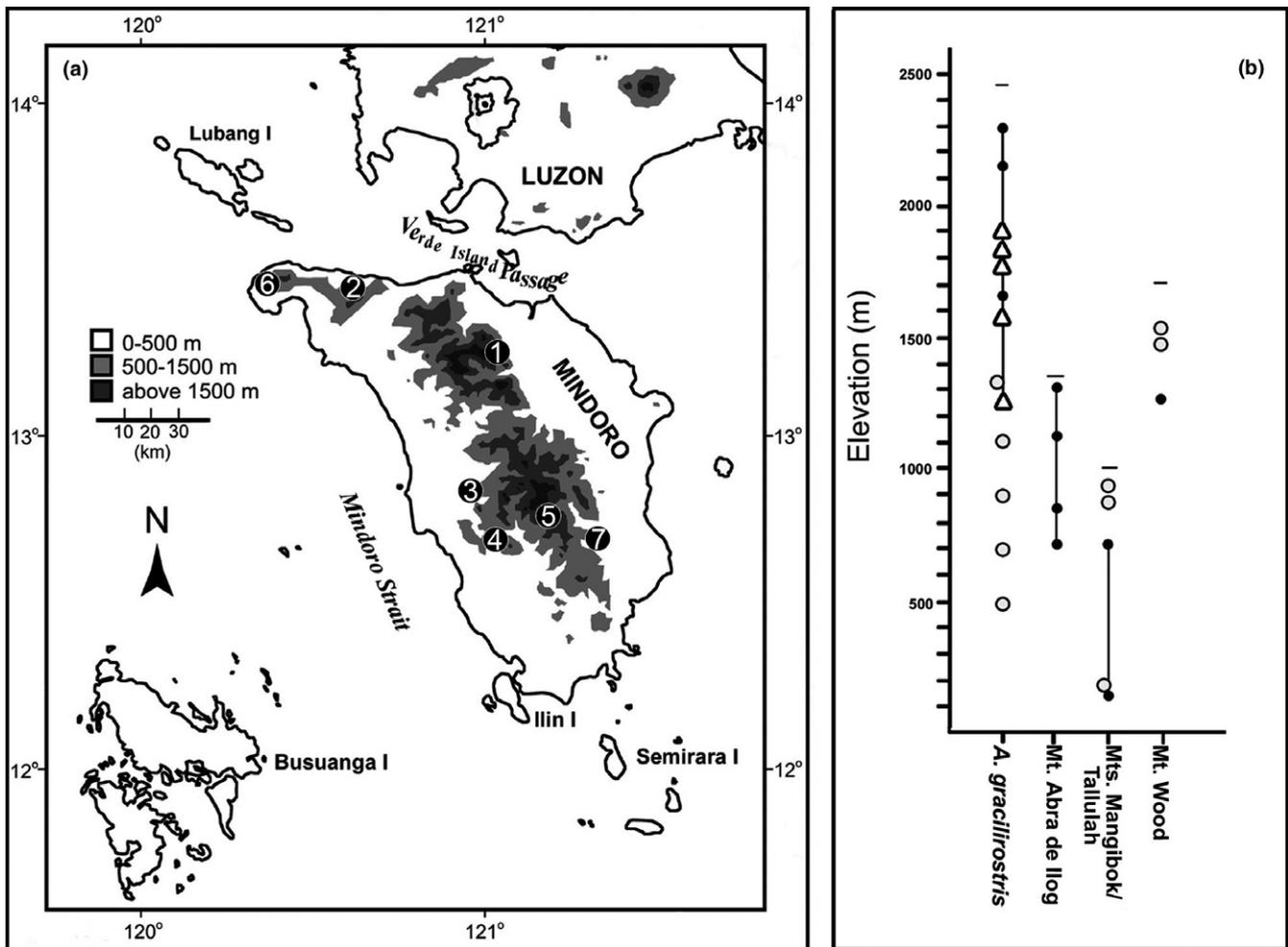
FIGURE 2 (a) Map of Mindoro Island showing topographic features and the locations of elevational transects surveyed. 1 = Mt. Halcon, 2 = Mt. Abra de Ilog, 3 = Mt. Tallulah, 4 = Mt. Mangibok, 5 = Mt. Wood, 6 = Mt. Calavite, 7 = Mt. Hinunduang. (b) Elevational ranges for *Apomys* (*Megapomys*) documented during this study (solid circles), and previous studies (triangles); open circles indicate elevations that were surveyed where *Megapomys* was not found

2 | MATERIALS AND METHODS

2.1 | Literature review

In our search for information about speciation by land-living vertebrates on tropical oceanic islands, we included old continental fragments such as Cuba, Hispaniola, Jamaica, Madagascar and Puerto Rico because the studies cited generally showed that the example of speciation occurred as a result of over-water colonization long after the island became isolated (see references in Appendix S1), and because these islands figured prominently in Soulé's (1980) original summary. We did not include examples from Pleistocene land bridge islands because they, by definition, have a history of frequent massive colonization by continental faunas that are likely to affect the occurrence of speciation. We focused our search for speciation on islands near or below the limits cited by Soulé (1980). We sought information by searching in Google Scholar with the subjects "oceanic island AND speciation AND name of taxon", and "oceanic island AND diversification AND name of taxon". Once the names of likely islands had been

identified, we also searched using ("name of island" AND speciation AND "name of taxon"). We also consulted knowledgeable colleagues for possible gaps in our search. Many of the examples that we found came from the phylogenetic and taxonomic literature, and did not highlight the connection between island area and speciation.

2.2 | Species sampling

We conducted sampling of small mammals, including members of the subgenus *Megapomys*, along seven elevational transects on Mindoro from 2012 to 2016, following procedures used extensively on Luzon (Figure 2; Heaney et al., 2016; Rickart, Heaney, Balete, & Tabaranza, 2011) and all Philippine laws and regulations for the conduct of research. We documented *Megapomys* along five transects (Figure 2: Mt. Halcon, Mt. Abra de Ilog, Mt. Wood, and the adjacent Mts. Mangibok and Tallulah), and sampled tissues from 21 individuals from these transects (Table S2.2). As reference samples, we used tissues of *Apomys lubangensis*, geographically the nearest species of *Megapomys*, plus four species of *Megapomys* from Luzon, and three

species of the subgenus *Apomys* as an outgroup (Table S2.2). We included sequences from six additional *Megapomys* species from our previous studies.

2.3 | Laboratory methods

We extracted genomic DNA from 40 tissue samples using Qiagen DNeasy kits (Qiagen, Valencia, CA, USA) following the manufacturer's protocol. We used standard PCR protocols to amplify four genetic markers, including the mitochondrial cytochrome *b* (cyt *b*), intron 3 of the X-linked locus opn1mw (OPN), exon 1 of growth hormone receptor (GHR) and intron 7 of the autosomal beta fibrinogen gene (BFIBR; see Table S2.3 for primer sequences and annealing temperatures); all of the nuclear genes are single-copy. We sequenced each PCR product using an ABI 3730 DNA analyser (Life Technologies, Carlsbad, CA, USA).

2.4 | Sequence assembly and alignments

We used GENEIOUS 6.1.2 (Kearse et al., 2012) to assemble sequence reads, inspect sequences for errors, and assign IUPAC ambiguity codes for heterozygous sites. We aligned consensus sequences for each gene using MUSCLE (Edgar, 2004). We estimated haplotype phases for each nuclear locus using PHASE (Stephens, Smith, & Donnelly, 2001) implemented by DNASP 5.10.1 (Librado & Rozas, 2009). Prior to phasing, we trimmed our nuclear alignments to minimize missing data and facilitate more reliable estimation of haplotypes. Hereafter, we refer to these alignments, together with the cyt *b* alignment, as our "trimmed/phased alignments."

2.5 | Haplotype networks and gene trees

We used POPART (Leigh & Bryant, 2015) to create median joining networks for each gene (Bandelt, Forster, & Röhl, 1999) using our trimmed/phased alignments for the nuclear loci. We also used our trimmed/phased alignments to estimate gene trees for each locus using RAXML 8.2.3 (Stamatakis, 2014). We used the GTRCAT substitution model for each gene and conducted bootstrapping until automatically halted.

2.6 | Concatenated analyses, species tree and molecular dating

We used RAXML 8.2.3 (Stamatakis, 2014) to estimate a phylogenetic tree from a concatenated data matrix. We used PARTITIONFINDER2 (Lanfear, Calcott, Ho, & Guindon, 2012; Lanfear, Frandsen, Wright, Senfeld, & Calcott, 2016) to determine the optimal partitioning scheme from a total of eight partitions (three codon positions each for cyt *b* and GHR and one partition each for OPN and BFIBR) using AICc and a greedy search algorithm. We applied the GTR+G substitution model to each of the resulting partitions (cytb_pos1, cytb_pos2, cytb_pos3, GHR_-pos3+BFIBR, GHR_pos1, GHR_pos2, OPN) and conducted bootstrap replicates using the GTRCAT until automatically halted. We used the same concatenated data matrix to estimate a time-calibrated phylogeny using BEAST2 (Bouckaert et al., 2014). We treated each gene as a

different partition, and selected appropriate substitution models with JMODELTEST 2.1.7 (Darriba, Taboada, Doallo, & Posada, 2012; Guindon & Gascuel, 2003) using AICc (Table S1.2). To date the tree, we constrained the node representing the split between the subgenera *Apomys* and *Megapomys* using a lognormal distribution with mean 2.76 Ma and 95% range (2.351–3.269), reflecting the estimates of a fossil-calibrated analysis of muroid rodent evolution (Steppan & Schenk, 2017). We used a calibrated Yule tree model, a relaxed lognormal clock model, and left all other settings as default. We ran the analysis for 100 million generations sampling every 10,000, repeating runs to confirm consistency. We used our trimmed/phased alignments to estimate a time-calibrated species tree using *BEAST (Heled & Drummond, 2010). We included species that were sequenced for all four loci (Table S2.1). Due to lack of reciprocal monophyly (Figures 2 and 3) and moderate support for delimitation (Table 1), we treated Mt. Mangibok and Mt. Tallulah populations as one population/species. We used the same partitioning scheme, substitution models, tree model, clock model and divergence dating scheme described for the BEAST2 analysis above. We ran the analysis for 200 million generations sampling every 10,000. For both the *BEAST and BEAST2 analyses, we used TRACER 1.6 (Rambaut & Drummond, 2007) to examine log files for convergence and used TREEANNOTATOR 2.2.1 (Bouckaert et al., 2014) to construct maximum clade credibility trees with a 20% burn-in. All phylogenetic analyses described above were run using the Cipres Science Gateway (Miller, Pfeiffer, & Schwartz, 2010) and viewed using used FIGTREE 1.4.3 (Rambaut, 2009).

2.7 | Coalescent-based species delimitation

We used BPP 3.3 (Yang & Rannala, 2010, 2014) to test alternative models of species delimitation among Mindoro *Megapomys* populations. Given evidence for genetic distinctiveness, we treated each sampling locality on Mindoro as a different population. We used our trimmed/phased nuclear alignments and assigned heredity scalars for each locus. To examine the impacts of varying population size and divergence time priors, we tested three different schemes following Leache and Fujita (2010). In the first scheme, we assumed relatively large ancestral population sizes and deep divergences with $\theta{\sim}G(1,10)$ and $\tau_0{\sim}G(1, 10)$; in the second, we assumed relatively small ancestral population sizes and shallow divergences among with $\theta{\sim}G(2, 2,000)$ and $\tau_0{\sim}G(2, 2,000)$; in the third, we assumed large ancestral populations sizes with $\theta{\sim}G(1, 10)$ and shallow divergences among species with $\tau_0{\sim}G(2, 2,000)$. We ran each analysis for 500,000 generations with a sampling interval of 50 and a burn-in of 2,000, repeating runs using both rjMCMC algorithms 0 and 1 to check for consistency.

2.8 | Morphometric analyses

To examine the extent of morphological differentiation among Mindoro *Megapomys*, we used SYSTAT 10 for Windows (SPSS Inc. 2000) to assess quantitative phenetic variation through principal components analysis of 18 cranial and dental measurements from 29 adult specimens, using the correlation matrix of $\log_{10}$-transformed measurements (Appendix S4).
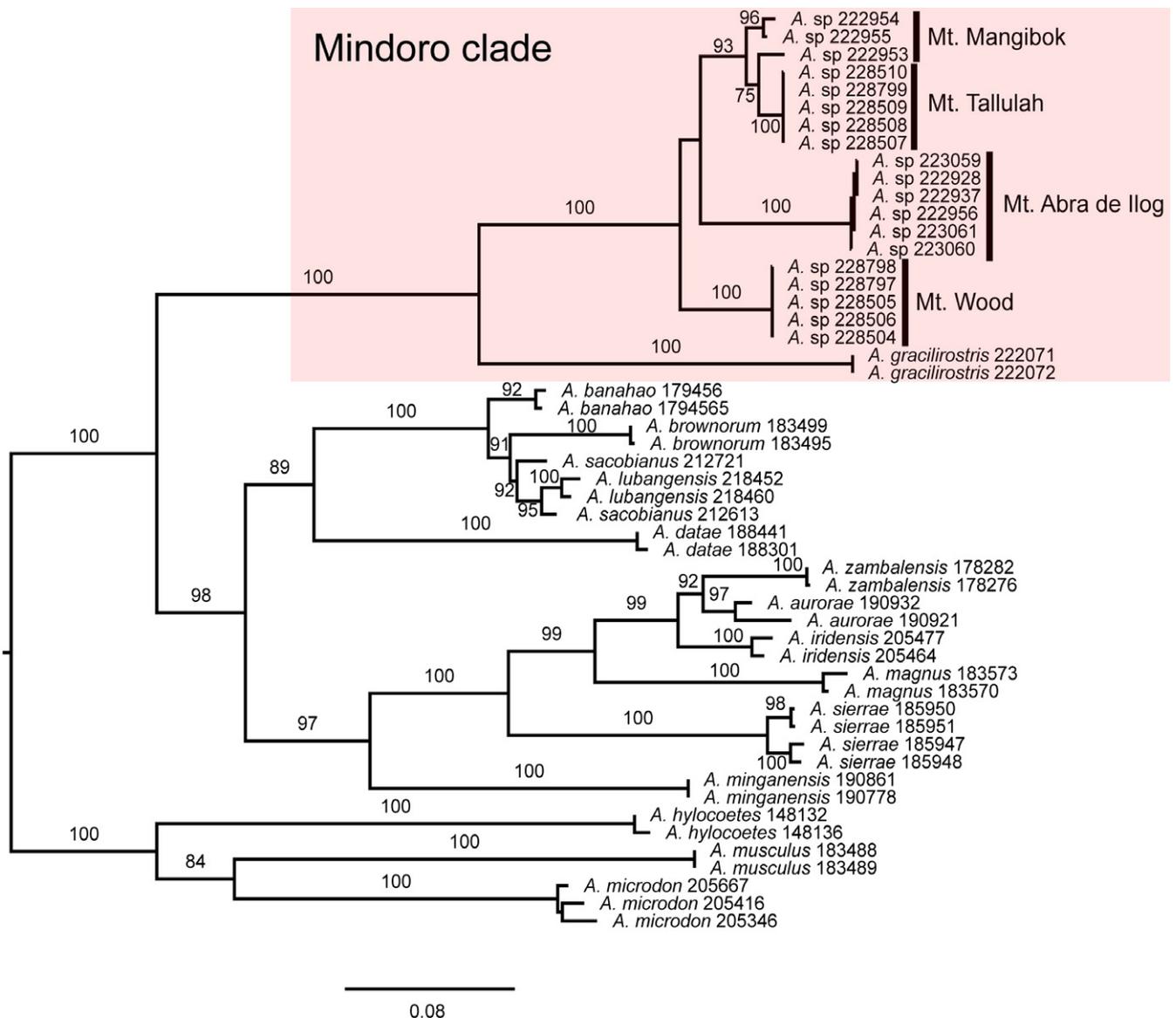
FIGURE 3 Concatenated maximum likelihood phylogeny of *Apomys* sequences estimated using RAxML. Bootstrap support shown for nodes with BS>70. Branch length units are mean number of substitutions per site. All voucher numbers are FMNH [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 1 Results of coalescent-based species delimitation analysis using BPP across three prior schemes. For each population, Bayesian posterior probability of delimitation is shown, with significant values >.95 in bold

Ancestral pop. size prior	Divergence depth prior	*Apomys gracilirostris*	Mt. Abra de Ilog	Mt. Wood	Mt. Mangibok	Mt. Tallulah
Large	Deep	**1.0**	**1.0**	.99	.85	.85
Large	Shallow	**1.0**	**1.0**	.99	.91	.91
Small	Shallow	**1.0**	**1.0**	**1.0**	**.97**	**.98**

3 | RESULTS

3.1 | Distribution and diversity of *Apomys* on Mindoro

Our surveys obtained specimens of three species groups of *Apomys* on Mindoro. Two were members of the *Apomys microdon* and *A. musculus* species groups in subgenus *Apomys*; these are currently

under study and will be reported elsewhere. The remainder belonged to the subgenus *Megapomys* and are the subject of this paper. In addition to confirming the presence of *Apomys* (*Megapomys*) *gracilirostris* on Mt. Halcon, we obtained specimens not assignable to a known species along the four additional transects on Mts. Abra de Ilog, Mangibok, Tallulah and Wood (Figure 2a). We did not detect *Megapomys* on Mt. Calavite or Mt. Hinunduang; Figure 2a). *Apomys gracilirostris* was present from about 1,250 m to near the peak of

Mt. Halcon, but was not detected at four lower sampling sites (unpubl. field notes and specimens in FMNH). Specimens from Mt. Abra de Ilog were documented from 710 m to 1,325 m (near the peak), from Mt. Wood at 1,280 m but not at two higher sampling areas, from Mt. Mangibok at 700 m but not at 1,480 or 1,520 m, and from Mt. Tallulah at 140 m but not at 160 or 180 m (Figure 2b).

3.2 | Sequence and alignment characteristics

We obtained 40 cyt *b* sequences (1,101 bp), 37 BFIBR sequences (692 bp), 30 OPN sequences (1,224 bp) and 36 GHR sequences (779 bp; Table S2.2). The trimmed/phased nuclear alignment lengths were 579, 684 and 738 bp, respectively. New sequences are archived on GenBank under accession numbers MH092661–MH092803 (Table S2.2).

3.2.1 | Phylogenetic analyses and haplotype networks

Our phylogenetic analyses found strong support for the monophyly of all *Megapomys* from Mindoro (Figures 3 and 4, Figure S3.1). Three of the four individual gene trees recovered all Mindoro samples as monophyletic with bootstrap support (BS) >90; this was reflected in BS of 100 in the concatenated maximum likelihood analysis (Figure 3) and Bayesian posterior probability (PP) of 1.0 in the concatenated Bayesian analysis (Figure S3.1) and species tree analysis (Figure 4).

Within Mindoro, our gene trees, haplotype networks, and concatenated analyses depicted substantial genetic structure. For cyt *b*, we found that no haplotypes were shared among sampling transects (Figure S3.6), and that Mindoro samples fell into four divergent and strongly supported (BS = 100) reciprocally monophyletic groups (Figure S3.2). These included: (1) *A. gracilirostris*, which was sister to all other Mindoro populations and highly divergent with minimum uncorrected pairwise cyt *b* distance (p-distance) of 9.3%, (2) Mt. Abra de Ilog, which was moderately divergent with minimum p-distance = 4.1%, (3) Mt. Wood, with minimum p-distance = 3.8%, and (4) Mts. Tallulah and Mangibok, also with minimum p-distance = 3.8%. Additionally, we found that Mts. Mangibok and Tallulah were each shallowly divergent, and that Mt. Tallulah was strongly supported as monophyletic, though Mt. Mangibok was recovered as paraphyletic (Figure S3.2). In our nuclear gene trees (Figures S3.3–S3.5) and haplotype networks (Figures S3.7–S3.9), we recovered genetic structure for the introns BFIBR and OPN that generally reflected the above mtDNA clades, although we found little evidence of genetic structure for the exon GHR. Our concatenated analyses (Figure 3 and Figure S3.1) largely mirrored the cyt *b* results, recovering the same four well-supported and reciprocally monophyletic groups. Additionally, we found strong support (PP = 0.99) for Mt. Abra de Ilog as sister to Mts. Wood, Tallulah and Mangibok in our concatenated BEAST2 analysis (Figure S3.1); this was reflected in our *BEAST species tree analysis (Figure 4), which found moderate support (PP = 0.83) for this grouping.

3.2.2 | Coalescent-based species delimitation

Coalescent-based species delimitation analyses conducted using BPP found strong support for delimiting *A. gracilirostris*, populations from Mt. Wood and Mt. Abra de Ilog (PP > 0.99 across three prior schemes), and moderate to strong support for delimiting Mt. Mangibok and Mt. Tallulah (PP range from 0.85 to 0.98; Table 1). Overall, BPP favoured a model including five distinct populations on Mindoro, though the support for distinguishing between samples from Mts. Mangibok and Tallulah was usually not above a 0.95 PP threshold (range 0.84–0.97; Table 1).

3.2.3 | Timing of diversification

Divergence dating using a *BEAST species tree approach (Figure 4) placed the split between Mindoro *Megapomys* lineages and the rest of *Apomys* at 2.29 Ma (95% HPD: 1.79–2.85), with *A. gracilirostris* diverging from other Mindoro lineages 1.46 Ma (95% HPD: 0.96–1.97), Mt. Abra de Ilog diverging 208 ka (95% HPD: 79–395), and Mt. Mangibok/Tallulah populations diverging from Mt. Wood 88.1 ka (95% HPD: 23–187). Using a concatenated BEAST2 approach (Figure S3.1), those splits were estimated at 2.30 Ma (95% HPD: 1.82–2.81), 1.57 Ma (95% HPD: 1.15–2.08), 692 ka (95% HPD: 476–926) and 545 ka (95% HPD: 368–751), respectively.

3.2.4 | Morphometric results

A principal components analysis of 18 craniodental measurements from 29 individuals including adults from all five transects found interpretable variation (eigenvalues >1.2) on the first three components, which collectively accounted for 79.4% of the total variance (Table S4.5). All but one variable had moderate to high magnitude loadings on the first axis (which accounted for 63.5% of the total variance), with highest loading for basioccipital length (which presents the greatest length of skull). We interpret this axis as primarily representing overall size. One of these variables, breadth of the incisors at the tip had a high negative value, showing that relative incisor width is inversely related to overall size. The second component accounted for 8.9% of the total variation (Table S4.5); length of incisive foramen was the variable with the highest positive value on this component, while rostral depth and orbital length had moderately high loadings. Component 3 accounted for only 7.0% of the total variation, had an eigenvalue of 1.3, which is near the lower limit for interpretablility, and none of the variables had high magnitude loadings; we therefore disregard this axis.

A plot of the scores of individual mice on axes 1 and 2 (Figure 5) shows a clear separation between *A. gracilirostris* and the other populations along axis 1. On axis 2, specimens of *A. gracilirostris* span most of the range of variation, but specimens from Abra de Ilog have moderate to low scores, specimens from Mts. Mangibok and Tallulah have high scores, and two specimens from Mt. Wood are intermediate. In other words, *A. gracilirostris* is consistently larger than the other populations, and have narrow incisors; specimens from the other localities
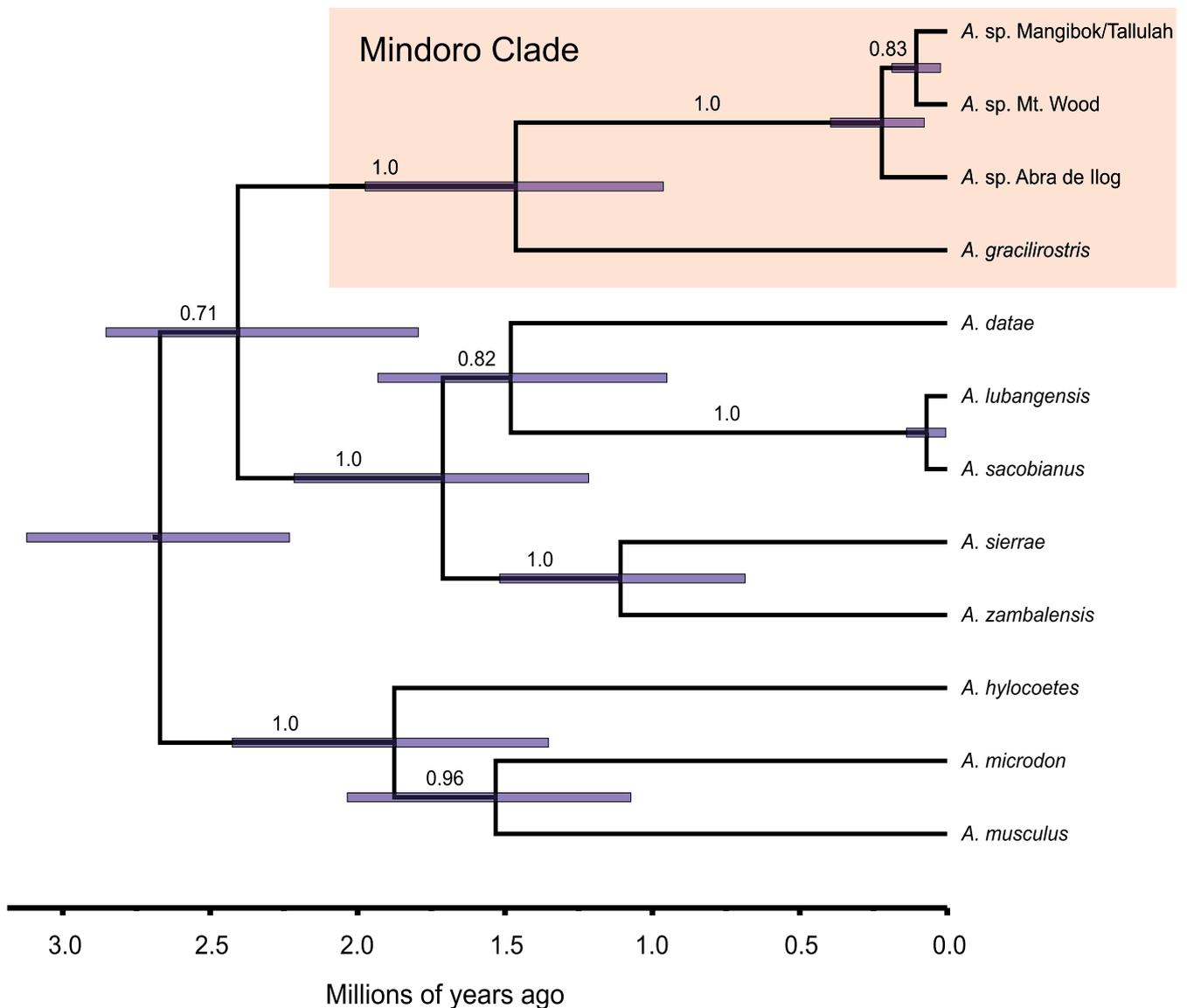
FIGURE 4 Multi-locus species tree for Mindoro *Megapomys* and seven outgroup species estimated using *BEAST. Tree dated using secondary calibration from Steppan and Schenk (2017). Node bars represent 95% HPD intervals for divergence date estimates [Colour figure can be viewed at wileyonlinelibrary.com]

are similar to each other in overall size and have proportionately broader incisors, but specimens from Abra de Ilog and Mts Mangibok and Tallulah have incisive foramina that differ substantially in length; a few specimens from Mt. Wood are intermediate.

4 | DISCUSSION

4.1 | Distribution and species limits in Mindoro *Megapomys*

Our field surveys showed that mice of the genus *Apomys*, subgenus *Megapomys* are more widespread than the single mountain, Mt. Halcon, where the only known Mindoro endemic species (*A. gracilirostris*) had been recognized previously (Ruedas, 1995). We obtained specimens along four transects, all along the seasonally dry

western side of Mindoro, but not on Mt. Calavite or on Mt. Hinunduang (Figure 2a; unpubl. data and specimens in FMNH).

All of our analyses of genetic data (Figures 3 and 4; Appendix S3) show all *Megapomys* from Mindoro as members of an endemic clade with high support. Within this endemic clade, we recovered four main groupings: (1) *A. gracilirostris*, (2) Mt. Abra de Ilog, (3) Mt. Wood and (4) Mts. Mangibok and Tallulah. Our coalescent-based species delimitation analyses corroborated these results, finding strong support (PP ≥ 0.99) across all prior schemes for delimiting *A. gracilirostris*, Mt. Abra de Ilog and Mt. Wood, and mixed support for splitting the more shallowly divergent and not reciprocally monophyletic Mts. Mangibok and Tallulah populations (PP range 0.85–0.98; Table 1). In light of research suggesting that BPP delimits genetic structure, and not necessarily species (Sukumaran & Knowles, 2017), we conservatively interpret the moderate and often
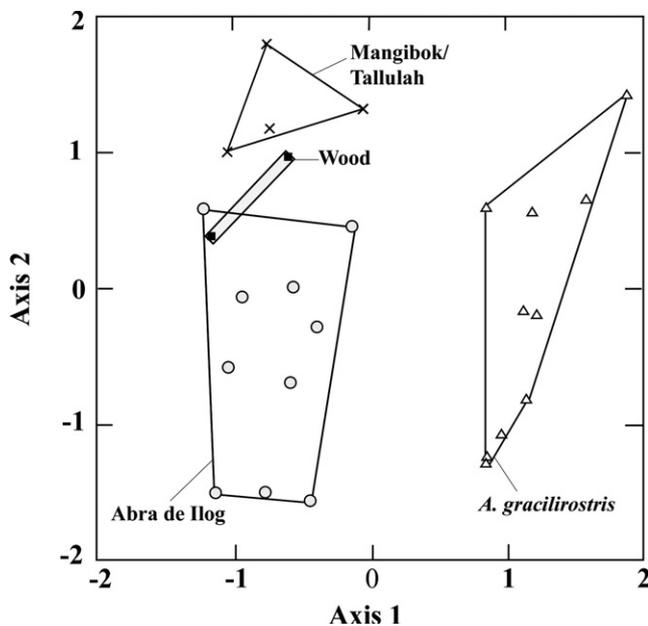
FIGURE 5 Results of principal components analysis of 18 craniodental measurements (Table S4.4) of adult *Megapomys* from Mindoro; loadings are shown in Table S4.5

non-significant (PP < 0.95) support for separating Mts. Mangibok and Tallulah as evidence against these populations being distinct from each other, and consider the support for three new distinct species as strong but subject to additional testing. Overall, these genetic results are consistent with our morphometric results, which show *A. gracilirostris* and Mt. Abra de Ilog as distinct, and fail to show a difference between specimens from Mts. Mangibok and Tallulah but show them collectively to be distinct (Figure 5). Our limited cranial samples from Mt. Wood (*n* = 2) were found to be intermediate between Mt. Abra de Ilog and Mts. Mangibok/Tallulah samples, and not entirely distinct from Mt. Abra de Ilog (Figure 5). Taking the genetic and morphometric results together, we conclude that at least three and probably four species are present on Mindoro, one from Mt. Halcon (*A. gracilirostris*), and one each from Mt. Abra de Ilog, Mt. Wood and Mts. Mangibok/Tallulah.

4.2 | Timing and mechanisms of diversification

Our results indicate that the common ancestor of Mindoro *Megapomys* arrived between about 2.4 Ma and about 1.5 Ma (Figure 4 and Figure S3.1). The occurrence on Luzon of all but one other species of *Megapomys*, along with several members of the subgenus *Apomys* and nearly all of the species in genera closely related to *Apomys* (Heaney et al., 2016) makes it likely that the colonization occurred from Luzon to Mindoro. The one *Megapomys* that occurs on neither Luzon nor Mindoro is *A. lubangensis*, from Lubang Island, which lies just to the north of Mindoro (Figure 2a). Our analyses show *A. lubangensis* as embedded deeply within the Luzon clade of *Megapomys* and not closely related to the Mindoro clade (Figures 3–5).

The timing of speciation within Mindoro *Megapomys* is estimated differently in our concatenated gene tree generated with BEAST2

(Figure S3.1) and our species tree generated with *BEAST (Figure 4). Both estimate the split between *A. gracilirostris* and the others at about 1.5 Ma, but the split of the other three beginning at either about 690 or 230 ka. Such differences may be the result of moderate levels of nuclear haplotype sharing among these populations (Figure S3.7–S3.9), which is explicitly treated in a species tree approach though not in a concatenated analysis (Heled & Drummond, 2010; McCormack, Heled, Delaney, Peterson, & Knowles, 2011). Given the more explicit coalescent-based models of lineage divergence employed by the species tree approach, we place greater confidence in the dates estimated by our *BEAST tree, though acknowledge considerable uncertainty in either set of estimates. Overall, we conclude that diversification began during the middle Pleistocene, and has continued into the terminal Pleistocene to produce four species on Mindoro. Additionally, we note that the branch lengths among the Mindoro *Megapomys* are similar to those among Luzon *Megapomys*, implying that the diversification rate on the two islands was comparable.

Our ability to determine the mechanism of speciation among these species is limited both by the limited number of species and by the limited number of transects we sampled, but some general patterns seem evident. We found no evidence of sympatry among the four putative species; the putative species from Mt. Abra de Ilog occurs only at moderately high elevations in the isolated NW montane region, *A. gracilirostris* occurs only at high elevations in the north-central mountains (including Mt. Halcon), and the putative species from Mt. Wood at high elevations in the south-central mountain mass. The Mts. Mangibok/Tallulah species is also in the south-central mountain mass but has a much lower elevational range (Figure 2). These observations imply allopatric speciation that may also have involved some shifts in habitat use along elevational gradients.

4.3 | Minimum island area for the speciation of land vertebrates

Our brief review of current information regarding the minimum sizes of oceanic islands that have been documented to support speciation by land vertebrates (Figure 1, Appendix S1) reveals several patterns. Substantial variation exists among the taxa; speciation by bats is not known within islands smaller than Madagascar (*c.* 588,000 km^2), nor by large mammals on islands smaller than Sulawesi (180,681 km^2). In contrast, birds have undergone speciation on islands as small as Jamaica (11,400 km^2), small mammals on islands as small as Mindoro (9,735 km^2), and lizards and frogs on islands as small as Puerto Rico (9,100 km^2).

These data imply that species with high vagility (as among bats) and large body size (as among large mammals) only speciate on the largest islands; species with lower vagility and smaller body size (frogs, lizards and small mammals) may undergo speciation on smaller (but still large) islands, over about 9,000 km^2. These observations are consistent with a correlation between likelihood of speciation with rates of gene flow (Kisel & Barraclough, 2010). These observations

may also point to a correlation between small population size and likelihood of extinction among large mammals on islands of decreasing area, and perhaps among other taxa that maintain low population densities.

The apparent relationship between island size and presence of speciation within a given taxon is strong. However, we acknowledge several limitations that are implicit in Figure 1. First, for most of these data, we must rely on scattered reports; for most taxa, there has been no attempt to examine the impact of speciation along a gradient of island sizes in a systematic fashion. Thus, we can expect that the patterns that seem apparent are crude and require extensive investigation to verify the overall pattern and detect important features. The sole exception to this deficiency is the premier example of the role of island area on speciation involving *Anolis* lizards on the Caribbean islands. In this case, it has been shown that extensive speciation is exhibited on *all* islands down to the size of Puerto Rico, but it is probably absent on the many smaller islands (Losos & Parent, 2010; Losos & Schluter, 2000). In no other group are there comparable data; we suggest that development of such data may provide a perspective on likelihood of speciation that is comparable to the incidence functions that provide insight into the likelihood of population-level extinction within individual species, and that, when aggregated among species, provide a broad perspective on the role of the relevant process along an area gradient (Whittaker & Fernandez-Palacios, 2007, pp. 257–259).

Second, few islands are represented in Figure 1. Much of the relevant data come from large islands in the Caribbean, which have been relatively intensively studied. Far fewer studies are cited from the greater number of islands in Indo-Australia; in addition to Luzon, Mindanao and Mindoro in the Philippines, Timor (28,418 km^2), Halmahera (17,943 km^2), Seram (17,148 km^2), Sumbawa (15,522 km^2), Sumba (11,153 km^2), Buru (8,806 km^2), Wetar (3,626 km^2) and Obi (951 km^2) form a graded series of oceanic islands of relevant area that deserve investigation (e.g. Fabre, Reeve, Fitriana, Aplin, & Helgen, 2018). Smaller oceanic islands exist in many parts of the globe; we should not assume that speciation by land vertebrates has not taken place on them.

Third, we have restricted our brief review to tropical oceanic islands. However, we note that there is likely a strong latitudinal component, analogous to or perhaps a consequence of the latitudinal diversity gradient. Most very large islands in the polar regions (e.g. Greenland, Ellesmere, Baffin) or large, land bridge islands in temperate regions (e.g. Great Britain, Tasmania, Hokkaido) do not show evidence for in situ speciation for small mammals, in contrast to many much smaller tropical islands that do; these observations suggest additional variables that should be included in the development of a broad model.

Finally, we note that Mindoro is a geologically old, topographically diverse island. The rationale that underlies the General Dynamic Model of Whittaker et al. (2008) and Borregaard et al. (2017) leads us to expect that speciation will generally be found far more commonly on such islands than on islands that are geologically young or topographically homogeneous. This aspect of factors that influence diversification within islands deserves careful study as well as the others discussed above. But most importantly, the data presented here show that there is a lower limit on island area below which speciation for any group of organisms, regardless of other features of the island, does not take place. This has important implications for future modelling of island biodiversity dynamics, and for empirical study of any given island or taxon.

5 | CONCLUSIONS

Speciation differs from colonization and extinction in that it is typically area-limited: for any given taxon, there appears to be a lower limit below which speciation may not take place. Among land vertebrates, that lower limit ranges from the size of Madagascar (for bats) and Sulawesi (for large mammals) down to about 9,000 km^2, the size of Puerto Rico, Mindoro and Jamaica (for frogs, lizards, small mammals and birds). While much research is needed to determine the precision and heterogeneity of this lower limit for each taxon, the existence of a lower limit implies that the biological processes that influence species richness do not operate equivalently along a gradient of island areas: speciation within islands may not contribute to changes in species richness below some area limit, unlike colonization and extinction, which operate at all island sizes. Further development of island biogeography theory should explicitly include this factor as it moves towards increased realism and comprehensiveness.

ORCID

Lawrence R. Heaney (iD) http://orcid.org/0000-0003-3334-4400

Christopher C. Kyriazis (iD) http://orcid.org/0000-0002-8771-3681

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BIOSKETCH

Lawrence Heaney's primary research interest is in the long-term dynamics of biodiversity on islands, especially mammals in the Philippines.

Chris Kyriazis is interested in the evolution and conservation of vertebrates.

Author contributions: LH, DB and ER conceived the project and designed field aspects; DB led the field team; CK generated, analysed, and wrote all portions of the manuscript that deal with genetic data; ER conducted and wrote about morphometric analyses; LH wrote all other portions of the manuscript; SS advised on genetic analyses and contributed to development of the manuscript.

SUPPORTING INFORMATION

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