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Doubling diversity: a cautionary tale of previously unsuspected mammalian diversity on a tropical oceanic island

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Abstract. The development of meaningful models of species richness dynamics in island ecosystems requires accurate measurement of existing biodiversity. To test the assumption that mammalian diversity on tropical oceanic islands is well documented, we conducted a 12-year intensive survey of the native mammal fauna on Luzon Island, a large (ca. 103,000 km²), mostly volcanic island in the Philippines, which was thought to be well known. Prior to the start of our study in 2000, 28 native, non-flying mammals had been documented, and extrapolation from prior discoveries indicated that the rate of discovery of new species was steady but low. From 2000 to 2012, we surveyed non-flying mammals at 17 locations and discovered at least 28 additional species, doubling the number known. Nearly all of the new species are restricted to a single mountain or mountain range, most of which had not been sampled previously, thus also doubling the number of local centers of endemism within Luzon from four to eight. The number of species on a mountain is strongly correlated with the elevation of the peak, and the number of endemic species on a mountain range is strongly correlated with the maximum elevation of the range. All 28 of the new species, and 20 of the species discovered prior to 2000, are members of two morphologically and ecologically diverse endemic clades (“cloud rats” and “earthworm mice”), which strongly implies that species richness has primarily been the product of speciation within the island. We reject the general assumption that mammals on tropical oceanic islands are sufficiently well known that analysis and modeling of the dynamics of species richness may be conducted with precision. In the development of conceptual biogeographic models and implementation of effective conservation strategies, existing estimates of species richness, levels of endemism, and the number of subcenters of endemism should be actively reassessed and verified through robust field, museum, and laboratory studies.

Keywords. Biogeography, conservation, diversification, elevation, endemism, extrapolation, new species, oceanic islands, Philippines, single-area endemics, single-island endemics, speciation, verification of data.

Introduction

Species richness is the most fundamental measure of biodiversity. From this starting point, pattern and process in evolution and ecology are inferred, and often conservation priorities are strongly influenced (e.g., Brooks 2014, Pouzols et al. 2014). Clearly, the extent to which our assessment of species richness is accurate and precise will have a pervasive influence on our analyses and conclusions.

It is often assumed that mammalian species richness is sufficiently well known that meaningful analysis and modeling of both global and local biodiversity patterns and processes may be conducted (e.g., Scheffers et al. 2012). While this assumption may be true for some parts of the world where field surveys have been conducted methodically and extensively for many decades, in other regions the assumption of complete or nearly complete sampling of mammals may not be jus-

tified (e.g., Demos et al. 2013). Previously unknown species are discovered frequently, some of which represent novel evolutionary lineages (e.g., previously unknown genera from Luzon: *Musseromys* [Heaney et al. 2009] and *Soricomys* [Balet et al. 2012]; from Sulawesi: *Pacidentomys* [Esselstyn et al. 2012], *Hyorhinomys* [Esselstyn et al. 2015], *Waiomys* [Rowe et al. 2014], and *Gracilimus* [Rowe et al. 2016]; and from Halmahera: *Halmaheramys* [Fabre et al. 2013]). Moreover, in the wet tropics—the regions where species richness is generally regarded to be highest but knowledge most incomplete—there are few cases where inferred measures of biodiversity over large areas have been verified with comprehensive field surveys to a degree that allows us to test the extent of our knowledge of mammalian richness.

As part of a study of the dynamics of mammalian species richness in the Philippine Islands, a

geologically old and complex tropical oceanic archipelago (Hall 2013), we recently completed a 12-year project to comprehensively survey the mammals of Luzon Island (Heaney et al. 2016). Luzon (Fig. 1) is one of the largest oceanic islands (ca. 103,000 km²), lying entirely within the tropics, with a mammal fauna that has been actively studied since the 1890s. Luzon is a natural biogeographic unit; aside from a few, much smaller islands (e.g., Catanduanes and Marinduque) that were connected to Luzon by land-bridges during much of the Pleistocene, the current island of Luzon is surrounded by deep water and has not been connected to any other land area throughout its existence (Heaney 1985, 1986, Heaney et al. 2016, Voris 2000). The adjacent small, shallow-water islands support a few of the widespread Luzon endemics, but none of them have their own locally endemic species (e.g., Heaney et al. 1991,

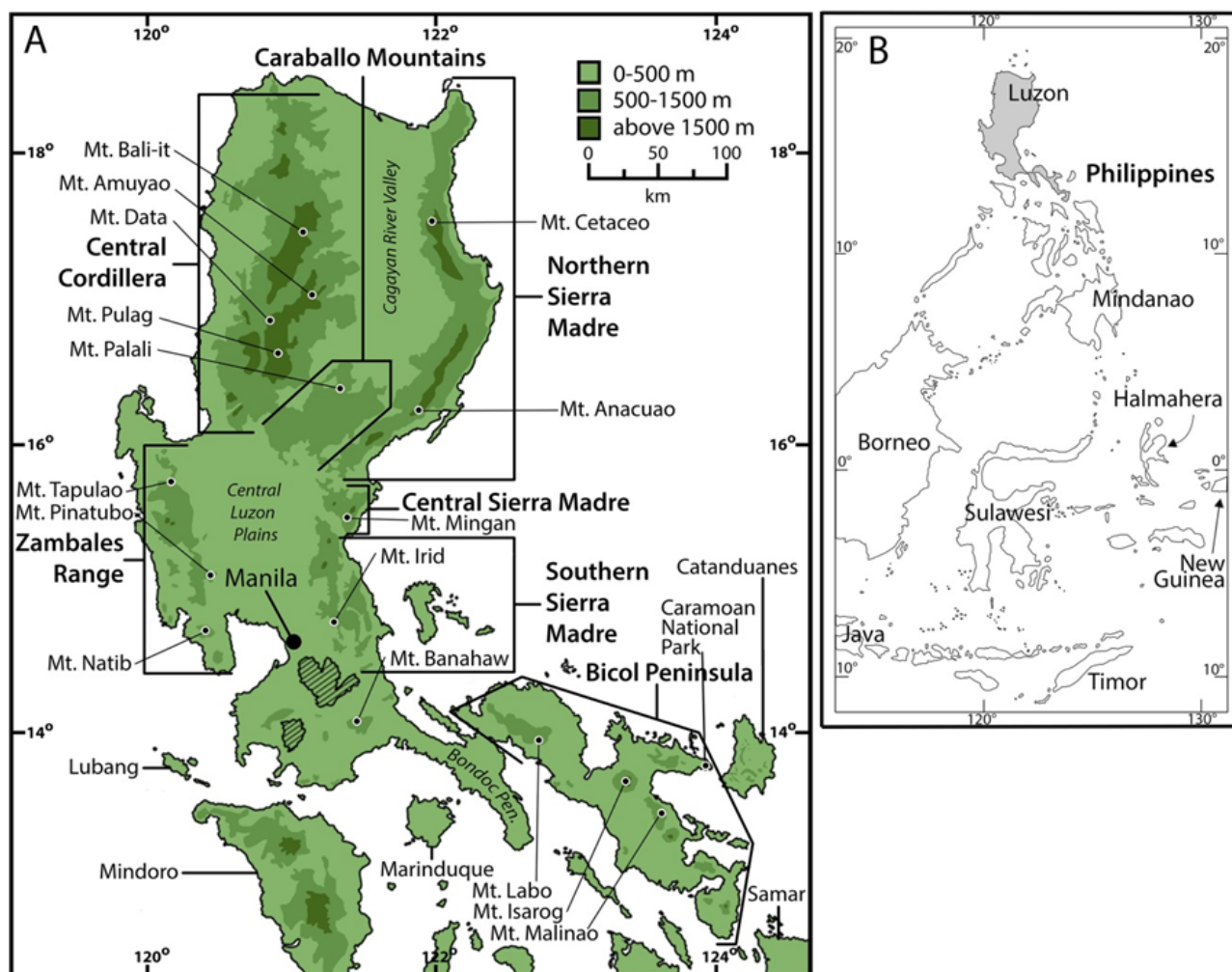


Figure 1. (A) Map of Luzon and adjacent islands, showing the locations of mountain ranges and mountains referred to in the text, and the locations of our intensive study areas. Hatched areas are large lakes. (B) Southeast Asia, showing the location of Luzon and other islands referred to in the text.

2010, 2016). The current island is an amalgamation of about ten islands that originated through tectonically-based volcanic processes and uplift; the oldest current and continuously dry land area (the Central Cordillera) emerging about 27 MYA, but with major steps in the amalgamation process continuing to about 0.5 MYA (Heaney et al. 2016).

Luzon's fauna had been thought to be well-known (Hollister 1913, Taylor 1934, Sanborn 1952, Heaney 1986), and had been included in several analyses of patterns of island biogeography (e.g., Heaney 1986, 2000, 2001, 2004, Heaney and Rickart 1990). However, our biogeographic, phylogenetic, and taxonomic studies of the Luzon fauna (see Heaney et al. 2016, and citations below) refute the assumption that the mammalian fauna was well-documented: only half of the currently recognized species of non-volant mammals on Luzon were known to science as recently as 2000. Here, we summarize our results and discuss the importance for inferences in island biogeography of conducting intensive field-based biodiversity surveys of species richness combined with taxonomic and phylogenetic studies of the specimens obtained.

The studies that we initiated in 2000 were driven by three observations. First, it was evident that 23 of the 28 native species (82%) of non-flying mammals then known were endemic to Luzon (i.e., they were Single Island Endemics [SIEs]). Second, 16 of the 28 species (57%) were endemic to one of four subcenters of endemism within Luzon. Third, nearly all of these single-area endemics (SAEs) were known only from places above about 1200 m elevation, and our initial surveys along elevational gradients on Luzon and elsewhere in the Philippines showed that species richness for native non-flying mammals increased with increasing elevation, often with a four or five-fold increase at high elevation over that at low elevation (Heaney et al. 1989, Heaney and Rickart 1990, Rickart et al. 1991a, Heaney 2001). This pattern of increasing species richness of small mammals from sea level up to ca. 2200–2500 m was novel at the time, but is now recognized as a general global phenomenon (McCain 2005).

At the time we began this study, most of the

known SAEs occurred in one specific region, the Central Cordillera of northern Luzon, and only a few in three other subcenters of endemism on the island. Surprisingly, the geographically smallest and most isolated of these subcenters (Mt. Isarog; Fig. 1), had more SAEs (three) than two of the much larger subcenters (the Zambales Mountains with one species, and the Northern Sierra Madre Mountains with two). Even more perplexing, other mountains on Luzon with areas that are substantially above 1200 m had no recorded SAEs. While our limited data appeared to show the pattern of increasing species richness with increasing elevation on a few mountains, we lacked sufficient data to determine if the pattern was consistent. Finally, we could not determine if the number of SAEs in a given mountain range (or individual isolated mountain) was correlated with the height of the range, as might be expected when species richness increases with elevation and many species occur only in isolated areas at high elevation.

A search of published literature and information from museum research collections immediately yielded a tantalizing result: other than the four known subcenters of endemism, none of the other isolated highland areas on Luzon had been the subject of *any* substantial mammal surveys. Furthermore, only on one of the four previously studied mountains (Mt. Isarog) had there been a thorough, methodical survey along an elevational gradient, followed by detailed analyses of species-level taxonomy (Rickart et al. 1991a,b, Heaney et al. 1999). We therefore began field surveys of all likely mountainous areas on Luzon, combined with intensive morphological and molecular phylogenetic studies of the resulting voucher specimens to determine the actual level of species richness, including the presence and distribution of the previously documented and any previously unknown species. Specifically, we asked (1) were all of the native non-volant mammals known; (2) were all local subcenters of endemism known; (3) is there a consistent relationship between the number of species and the elevation of a given mountain; and (4) is there a consistent relationship between the number of SAEs and the maximum elevation of a given mountain range?

Methods

We summarized existing information about the mammals of Luzon from published literature and specimens in museum research collections (Heaney et al. 2010, 2016). Non-volant species were designated as native and non-native based on a combination of fossil, archeological, and genetic data. We regard long-tailed macaques (*Macaca fascicularis*), palm civets (*Paradoxurus philippinensis*), and Malay civets (*Viverra zibetha*) as having been introduced to Luzon by humans, as they have been over wide parts of Wallacea (Heaney et al. 2016, Patou et al. 2008, 2010, van der Geer et al. 2010, Veron et al. 2014), and therefore exclude them from our calculations of numbers of native and endemic species. We do not include bats in this study because most are difficult to capture, their taxonomy and distribution are poorly known in many cases, and they have different patterns of distribution and diversity from non-volant mammals because of their ability to fly (but see Heaney and Rickart 1990, Heaney 1991, and Heaney and Roberts 2009 for studies of the diverse Philippine fruit bats, Pteropodidae). We did not include large mammals because only two native species (one deer, *Cervus mariannus*, and one warty pig, *Sus philippensis*) are present, both are heavily over-hunted (thus generally unavailable for study), and few specimens are available in museums.

From 2000 to 2012, we conducted detailed, standardized trapping surveys of small non-flying mammals along elevational transects at 17 intensively sampled sites on Luzon (e.g., Balete et al. 2009, 2011, 2013a,b, Heaney 2011, 2013, Heaney et al. 2013a,b, Rickart et al. 2011a,b, 2013, 2016). These surveys involved approximately 37 months of field work by teams of six to eight people, all undertaken during the relatively dry months of January–May. Survey transects extended from the lowest elevation with remaining forest, usually beginning in patchwork matrices of mixed agriculture and regenerating lowland forest at 400 to 800 m elevation, and proceeding to near the tops of the highest peaks. Individual sampling areas were spaced at elevational intervals of 200–300 m, depending on local circumstances, with at least

ca. 600 trap-nights at each elevation. We used a standardized trapping protocol that targeted species with different dietary preferences and habitat utilization patterns. This involved using traps of several designs, use of two primary types of bait (fried coconut coated with peanut butter, or live earthworms), and placement of traps both on the ground and arboreally (on branches and vines). Voucher specimens from these surveys have been deposited at the Field Museum of Natural History; half (including all holotypes) are being sent to the National Museum of the Philippines as taxonomic studies are completed. Our surveys were conducted in accordance with all Philippine laws and regulations regarding field research on wild mammals.

Current taxonomic designations are used throughout our analysis (see Musser and Carleton 2005, and more recent publications cited here). Most species we have discovered since 2000 have been formally described and named, as cited herein. However, we also include nine newly discovered species that are morphologically or genetically distinct but have yet to be formally described. Our current estimate of the number of species yet to be described may be conservative, given that our ongoing taxonomic studies of several genera are not yet complete.

We use the term “cloud rats” to refer to all members of the *Phloeomys* Division of Musser and Carleton (2005; = tribe Phloeomyini of LeCompte et al. 2008), including both small and “giant” species. We use “earthworm mice” to refer to all members of the *Chrotomys* Division of Musser and Carleton (2005; a clade within the tribe Hydromyini of LeCompte et al. 2008), rather than “shrew rats” because many are small (“mouse-sized”), many have little external resemblance to the popular conception of “rats”, and the name refers to their distinctive preference for earthworms as food. This also avoids confusion with the “shrew rats” of Sulawesi (Rowe et al. 2016).

We compiled the number of native non-volant mammals known by 20-year increments from 1880 to the present to determine the temporal pattern of species discovery. We also compiled the number of species known for each of

four crucial periods (up to 1900, 1901 to 1952, 1953 to 2000, and 2001 to 2014, as described below), and for each period tallied the number that are multi-island species, single-island endemics (SIEs), widespread endemics on Luzon, and single area endemics (SAEs). Analyses of correlations were conducted using a non-parametric test, Spearman's rank correlation (r_s).

Results

Assessments of small mammal diversity, 1880-2012

When Alfred Russel Wallace published his grand synthesis, "Island Life" (1880), three native species of non-volant mammals were known from Luzon (Fig. 2, Table 1). Two of these were widespread in the Philippines (*Cervus mariannus* and *Rattus everetti*), and one was widespread in central and southern Luzon (*Phloeomys cumingi*); the other 18 Philippine species he knew of occurred on other islands. No areas of local endemism were known on Luzon, and only one genus (*Phloeomys*, a giant cloud rat) was endemic to Luzon (plus adjacent small islands), leading Wallace to view the Philippines overall as having a mammal fauna high in endemic species but rather depauperate, and with a "comparative poverty in [endemic] genera" (Wallace 1880:361).

By 1900, this perception had changed abruptly, with the number of native, non-volant species increasing to 16, largely as a result of the field research conducted by John Whitehead at two locations on Luzon, the primary one on Mt. Data in the Central Cordillera of northern Luzon and the other in Isabela Province in the northern Sierra Madre, followed by systematic studies at the British Museum (Thomas 1895, 1898; Fig. 2). Seven of these species are endemic to the Central Cordillera and one to the northern Sierra Madre, establishing the existence of two subcenters of endemism within the island (Fig. 3). Moreover, the new species represented seven new genera endemic to Luzon, suggesting a richness of diversity that implied a far deeper history of the fauna than anticipated by Wallace, and three of the Luzon endemic genera included two species each, implying the existence of diversification within the island (Table 1).

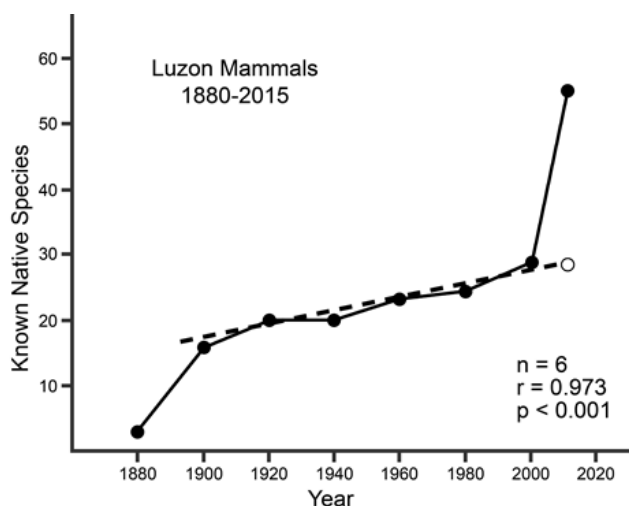


Figure 2. Species accumulation curve for native non-volant mammals on Luzon Island at 20-year intervals from 1880 to 2000, and from 2000 to 2014, based on data in Tables 1 and 2. Regression line for 1900-2000 ($N = 6$, $r_s = 0.973$, $P < 0.001$) predicts 28.4 species in 2012 (shown as open circle).

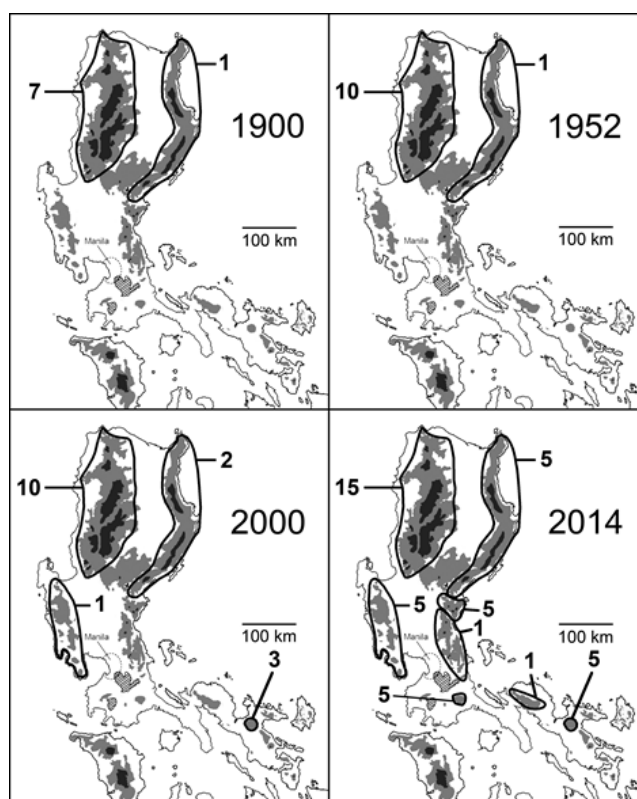


Figure 3. Maps of Luzon showing the number of species endemic to subcenters of endemism on Luzon in 1900, 1952, 2000, and 2014, based on data in Tables 1 and 2.

Table 1. List of non-volant native mammals known to occur on Luzon Island up to 2000, using current taxonomy and assessment of distribution (see text).

Species	Group	Year described	Single Island Endemic?	Subcenter Endemic?
1. <i>Cervus mariannus</i>	deer	1822	no	no
2. <i>Phloeomys cumingi</i>	cloud rat	1839	yes	no
3. <i>Rattus everetti</i>	“new endemic” murid	1879	no	no
4. <i>Sus philippensis</i>	pig	1886	no	no
5. <i>Crocidura grayi</i>	shrew	1890	no	no
6. <i>Phloeomys pallidus</i>	cloud rat	1890	yes	no
7. <i>Batomys granti</i>	cloud rat	1895	yes	yes - Cordillera
8. <i>Bullimus luzonicus</i>	“new endemic” murid	1895	yes	no
9. <i>Carpomys melanurus</i>	cloud rat	1895	yes	yes - Cordillera
10. <i>Carpomys phaeurus</i>	cloud rat	1895	yes	yes - Cordillera
11. <i>Chrotomys silaceus</i>	earthworm mouse	1895	yes	yes - Cordillera
12. <i>Chrotomys whiteheadi</i>	earthworm mouse	1895	yes	no
13. <i>Crateromys schadenbergi</i>	cloud rat	1895	yes	yes - Cordillera
14. <i>Rhynchomys soricoides</i>	earthworm mouse	1895	yes	yes - Cordillera
15. <i>Crunomys fallax</i>	“new endemic” murid	1897	yes	yes - N Sierra Madre
16. <i>Apomys datae</i>	earthworm mouse	1899	yes	yes - Cordillera
17. <i>Batomys dentatus</i>	cloud rat	1910	yes	yes - Cordillera
18. <i>Tryphomys adustus</i>	“new endemic” murid	1910	yes	no
19. <i>Apomys musculus</i>	earthworm mouse	1911	yes	yes - Cordillera
20. <i>Apomys microdon</i>	earthworm mouse	1913	yes	no
21. <i>Chrotomys mindorensis</i>	earthworm mouse	1945	no	no
22. <i>Abditomys latidens</i>	“new endemic” murid	1952	yes	no
23. <i>Apomys abrae</i>	earthworm mouse	1952	yes	yes - Cordillera
24. <i>Apomys sacobianus</i>	earthworm mouse	1962	yes	yes - Zambales
25. <i>Rhynchomys isarogensis</i>	earthworm mouse	1981	yes	yes - Isarog
26. <i>Archboldomys luzonensis</i>	earthworm mouse	1982	yes	yes - Isarog
27. <i>Chrotomys gonzalesi</i>	earthworm mouse	1991	yes	yes - Isarog
28. <i>Soricomys musseri</i>	earthworm mouse	1998	yes	yes - N Sierra Madre

Field studies conducted from 1900 through 1940 during the period when the Philippines was an American colony added only four species to the fauna of Luzon (Table 1). Immediately following World War II, a major effort to survey the mammals of the Philippines (Hoogstraal 1951, Sanborn 1952) included additional collecting on Mt. Data and a few other areas; the net result was an in-

crease in the number of endemic mammals in the Central Cordillera from seven in 1900 to ten in 1952 (Table 1, Figs. 2, 3).

Only one species was added to the Luzon mammal fauna from 1953 to 1980, and four from 1981 to 2000. These included one from the northern Sierra Madre, one from the Zambales Mountains, and three from Mt. Isarog, an isolated

Table 2. List of non-volant native mammals that occur on Luzon Island discovered since 2000, using current taxonomy and assessment of distribution (see text).

Species	Group	Year described	Single Island Endemic?	Subcenter Endemic?
1. <i>Soricomys kalinga</i>	earthworm mouse	2006	yes	yes - Cordillera
2. <i>Rhynchomys banahao</i>	earthworm mouse	2007	yes	yes - Banahaw
3. <i>Rhynchomys tapulao</i>	earthworm mouse	2007	yes	yes - Zambales
4. <i>Musseromys gulantang</i>	cloud rat	2009	yes	yes - Banahaw
5. <i>Apomys aurorae</i>	earthworm mouse	2011	yes	yes - Mingan
6. <i>Apomys banahao</i>	earthworm mouse	2011	yes	yes - Banahaw
7. <i>Apomys brownorum</i>	earthworm mouse	2011	yes	yes - Zambales
8. <i>Apomys magnus</i>	earthworm mouse	2011	yes	yes - Banahaw
9. <i>Apomys minganensis</i>	earthworm mouse	2011	yes	yes - Mingan
10. <i>Apomys sierrae</i>	earthworm mouse	2011	yes	no
11. <i>Apomys zambalensis</i>	earthworm mouse	2011	yes	yes - Zambales
12. <i>Archboldomys maximus</i>	earthworm mouse	2012	yes	yes - Cordillera
13. <i>Soricomys leonardocoi</i>	earthworm mouse	2012	yes	yes - Mingan
14. <i>Soricomys montanus</i>	earthworm mouse	2012	yes	yes - Cordillera
15. <i>Apomys iridensis</i>	earthworm mouse	2014	yes	yes - S Sierra Madre
16. <i>Musseromys anacuaao</i>	cloud rat	2014	yes	yes - N Sierra Madre
17. <i>Musseromys beneficus</i>	cloud rat	2014	yes	yes - Cordillera
18. <i>Musseromys inopinatus</i>	cloud rat	2014	yes	yes - Cordillera
19. <i>Batomys uragon</i>	cloud rat	2015	yes	yes - Isarog
20. <i>Apomys</i> "karst"	earthworm mouse	In prep	yes	yes - N Sierra Madre
21. <i>Apomys</i> "microdon 2"	earthworm mouse	"	yes	no
22. <i>Apomys</i> "musculus 2"	earthworm mouse	"	yes	yes - N Sierra Madre
23. <i>Apomys</i> "musculus 3"	earthworm mouse	"	yes	yes - Mingan
24. <i>Apomys</i> "musculus 4"	earthworm mouse	"	yes	yes - Zambales
25. <i>Apomys</i> "musculus 5"	earthworm mouse	"	yes	yes - Banahaw
26. <i>Apomys</i> "musculus 6"	earthworm mouse	"	yes	yes - Isarog
27. <i>Rhynchomys</i> sp.	earthworm mouse	"	yes	yes - Mingan
28. <i>Rhynchomys</i> sp.	earthworm mouse	"	yes	Yes - Labo

mountain peak in southern Luzon (Figs. 1 and 3), which increased the number of local centers of endemism from two to four. Among the five species were two new endemic genera (*Abditomys* and *Archboldomys*), which again emphasized the distinctiveness of the mammal fauna of Luzon. The first morphologically-based phylogenetic studies were conducted during the latter period and

indicated that some of the endemic genera were members of higher-level endemic clades, suggesting even deeper histories for the mammal fauna, and greater importance for speciation within the island (e.g., Heaney and Rickart 1990, Musser and Heaney 1992). It should be noted that, with only one exception, all native small mammals described prior to 2000 are currently

Table 3. Numbers of native Luzon mammal species (excluding bats) recognized in 1900, 1952, 2000, and 2014, based on current taxonomy.

Year	Total species	Multi-Island Species	Single Island Endemics	Endemic, Widespread on Luzon	Local Area Endemics	Number of Endemic Subcenters
1900	16	4 (25%)	12 (75%)	4 (25%)	8 (50%)	2
1952	23	5 (22%)	18 (78%)	7 (30%)	11 (48%)	2
2000	28	5 (18%)	23 (82%)	7 (25%)	16 (57%)	4
2014	56	5 (9%)	51 (93%)	9 (16%)	42 (76%)	8

considered to be valid species (*Apomys major* is now treated as a junior synonym of *A. datae*; Musser 1982, Heaney et al. 2011).

Extrapolation from the steady but slow growth in the number of recorded species, evident in Fig. 2 from 1900 to 2000, would lead one to expect the discovery by 2015 of few new species. A linear regression of the counts for the two-decade intervals from 1900 to 2000 (Fig. 2) predicted the total for Luzon in 2015 to be about 28 (which was the number known in 2000). We tested the accuracy of extrapolation as a method of prediction by conducting surveys of non-volant mammals at 17 primary locations that include both the five major mountain ranges on Luzon and four single isolated mountains that rise above 1200 m (Fig. 1). As of mid-2015, we had discovered two new genera and at least 28 previously unknown species, all of which are SIEs (i.e., endemic to Luzon), bringing the total of all native species to 56 (an increase of 100%). Of these 28 new species, 26 (93%) are SAEs (i.e., endemic to a single subcenter of endemism on Luzon; Tables 2 and 3). The number of multi-island Philippine endemic species increased from four in 1900 to five by 1952, and has not increased since then, while the number of SIEs increased from 12 in 1900 to 23 in 2000 and 51 in 2015. Among the SIEs, the number widespread on Luzon increased from four in 1900 to nine in 2015, while the number of SAEs rose from 8 in 1900 to 16 in 2000 and 42 in 2014 (a 263% increase from 2000 to 2014; Table 3). These discoveries have also doubled the number of subcenters of endemism, from 4 to 8 (Tables 2 and 3). Sampling intensity probably varied during the 1900–2000 period, and cannot be quantified, but it certainly was much lower than during the 12 years of our intensive, geographically structured surveys.

Elevational patterns in diversity

The increase in diversity of native small mammals documented in the preceding section was intimately related to the distribution of small mammals on a local scale, specifically along elevational gradients. For example, on small mountain ranges such as Mt. Isarog and Mt. Mingan that are isolated by extensive lowlands from other high-elevation areas, only three or four native species were known below about 1000 m, and only rarely was more than one of these a local endemic species (Fig. 4). With increasing elevation up to about 1600 m on these mountains, the total number of native species, the number of local endemics, and the percentage of local endemics increased steadily, reaching five species of local endemics that accounted for 60% or more of the total small mammal fauna. Above this elevation, where the terrain became increasingly steep and rocky, total species richness and representation of local endemics decreased slightly (Fig. 4).

We also sampled small mammals on three mountains in the Central Cordillera, the largest and highest of the Luzon mountain ranges (Fig. 1); taken together, they provide an approximation of variation along the mountain range in general. As with the smaller mountains, species richness and levels of endemism are low at the low elevations, but increase greatly by ca. 1600 m. Up to eight species that are endemic to the Central Cordillera are present at many high-elevation localities (Fig. 4), and the endemics make up 50% to 70% of the high-elevation fauna. Above about 2500 m, a decline in species richness becomes apparent, including a decline in the number of local endemics, but the percentage of endemics remains high (Fig. 4). Taken together, these data suggest that (1) species richness typically increases with increasing

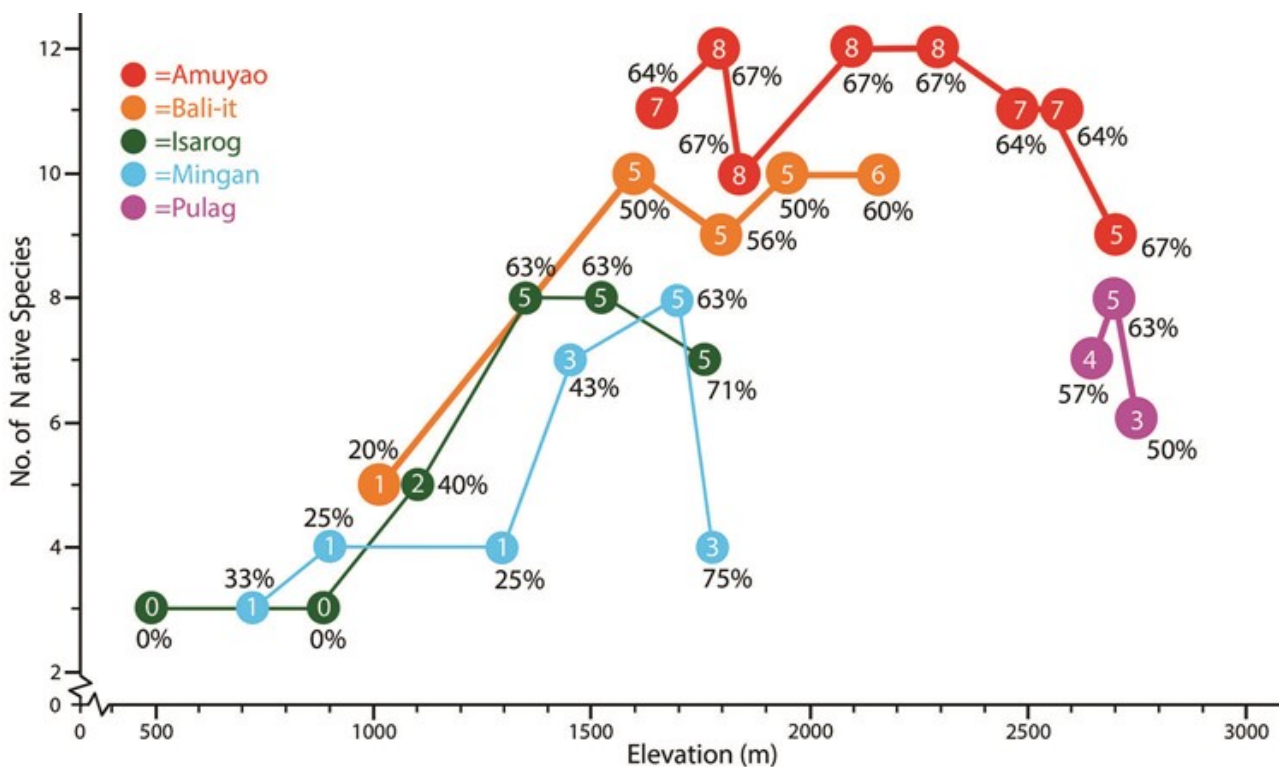


Figure 4. The number of species of native small mammals present at sampling localities along five elevational transects on Luzon. The position of circles shows the total number of species present, read from the left axis; the number within the circle is the number of local endemics, and the percentages are the number of local endemics divided by the total native species. Mts. Amuyao, Bali-it, and Pulog are all in the Central Cordillera; Mts. Isarog and Mingan are small, isolated mountain ranges. Modified from Heaney et al. (2016).

elevation up to a point near the mountain peak, and (2) the number of locally endemic species shows an especially dramatic increase with increasing elevation, and appears to reach the highest levels on the highest mountains.

To further investigate these patterns, we compiled data on eleven mountains that we surveyed (including more than one mountain in several large mountain ranges; Fig. 1). The cumulative number of species documented along the entire elevational gradient ranged from 3 to 13 (Table 4, Fig. 5), with a significant correlation ($r_s = 0.924$, $P = 0.001$) between the elevation of the peak of the mountain and the number of native small mammal species. In eight mountain ranges (or isolated individual mountains), the number of SAEs varied from 1 to 15 (Table 5, Fig. 6), with a significant correlation between the maximum elevation of the mountain range and the number of SAEs ($r_s = 0.912$, $P = 0.004$).

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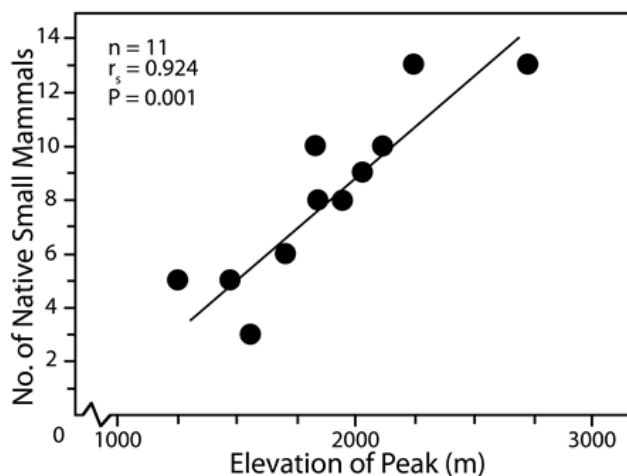


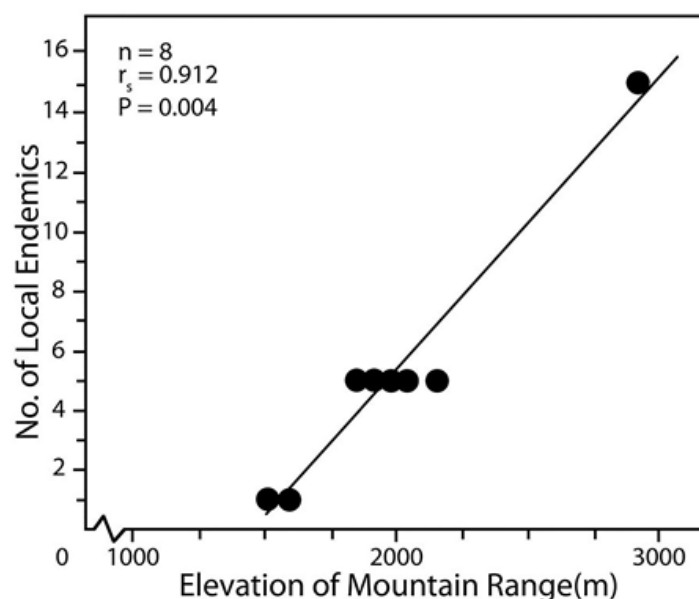
Figure 5. Plot of the relationship between the peak elevation of a given mountain on Luzon and the number of native non-volant small mammal species on the mountain, based on data in Table 4.

Table 4. Luzon mountains that have had extensive surveys of small mammals, with number of native species recorded and maximum elevation. Data from Heaney et al., 2013a.

Name and Province	Elevation (m)	No. of species	Source
Mt. Natib, Bataan	1253	5	Rickart et al. 2013
Mt. Irid, Rizal	1469	5	Balete et al. 2013
Mt. Labo, Camarines Norte	1544	3	Rickart et al. 2011a
Mt. Palali, Nueva Vizcaya	1707	6	Alviola et al. 2011
Mt. Anacuaao, Aurora	1850	8	Heaney et al. 2013a
Mt. Mingan, Aurora	1901	10	Balete et al. 2011
Mt. Isarog, Camarines Sur	1966	8	Rickart et al. 1991
Mt. Tapulao, Zambales	2037	9	Balete et al. 2009
Mt. Banahao, Quezon	2158	10	Heaney et al. 2013b
Mt. Bali-it, Kalinga	2239	13	Rickart et al. 2011a
Mt. Amuyao, Mountain Province	2710	13	Rickart et al. 2011b

Table 5. Mountain ranges (and isolated mountains) on Luzon, with maximum elevation and number of local endemic non-volant mammal species.

Mountain Range	Elevation	No. Local Endemics	Source
S. Sierra Madre	1530	1	Balete et. al. 2013a
Mt. Labo	1544	1	Balete et al. 2013b
N. Sierra Madre	1850	5	Heaney et. al. 2013b
Mingan Mts.	1901	5	Balete et. al. 2011
Mt. Isarog	1966	5	Rickart et. al. 1991a, b, Balete et al. 2015
Zambales Mts.	2037	5	Balete et. al. 2009
Mt. Banahaw	2158	5	Heaney et. al. 2013a
Central Cordillera	2930	15	Rickart et. al. 2011b

**Figure 6.** Plot of the relationship between the peak elevation of a given mountain range (or individual isolated mountain) on Luzon and the number of locally endemic species of native small mammals, based on data in Table 5.

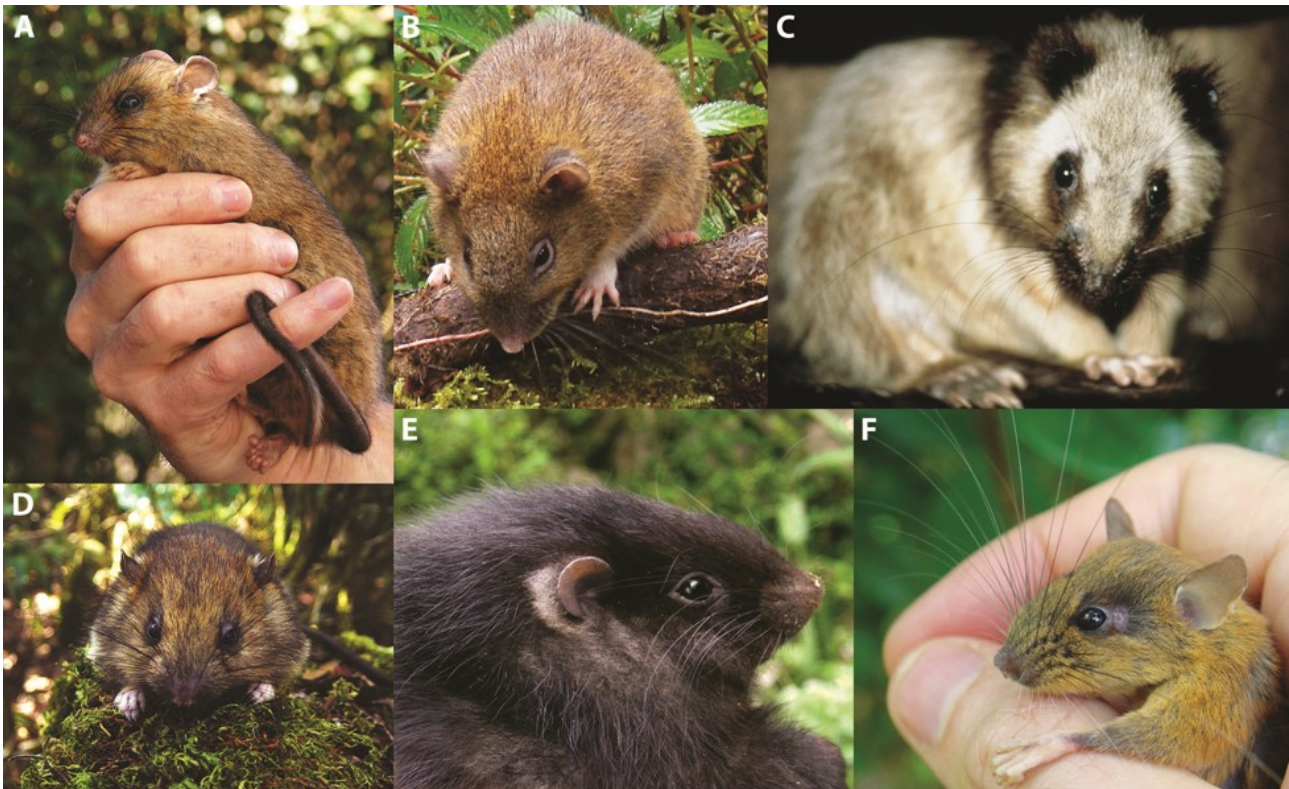


Figure 7. Photographs of (A) *Carpomys melanurus*, (B) *Batomys granti*, (C) *Phloeomys pallidus*, (D) *Carpomys phaeurus*, (E) *Crateromys schadenbergi*, and (F) *Musseromys gulantang*. All photos by the authors; from Heaney et al. (2016).

veyed (including more than one mountain in several large mountain ranges; Fig. 1). The cumulative number of species documented along the entire elevational gradient ranged from 3 to 13 (Table 4, Fig. 5), with a significant correlation ($r_s = 0.924$, $P = 0.001$) between the elevation of the peak of the mountain and the number of native small mammal species. In eight mountain ranges (or isolated individual mountains), the number of SAEs varied from 1 to 15 (Table 5, Fig. 6), with a significant correlation between the maximum elevation of the mountain range and the number of SAEs ($r_s = 0.912$, $P = 0.004$).

Phylogenetic perspectives

Concurrently, our molecular phylogenetic studies (e.g., Steppan et al. 2003, Jansa et al. 2006, Heaney et al. 2009, 2011, 2014, Balete et al. 2012, 2015, Justiniano et al. 2015) have shown that most native non-volant mammal species present on Luzon are members of just two endemic clades: the cloud rats (arboreal, herbivorous rodents, so called because most species live in cloud forest; Fig. 7) and the earthworm mice (so called

because most of them are small animals that primarily consume earthworms; Fig. 8).

All of the new species discovered since 2000 are members of these two clades; based on calibrated molecular phylogenies, the cloud rats are estimated to have arrived on Luzon about 10–14 million years ago, and the earthworm mice about 6–8 million years ago (Fig. 9; Schenk et al. 2013, Heaney et al. 2016, Rowe et al. 2016). Each of these clades contains five genera, the cloud rats with 18 species now known (12 on Luzon) and the earthworm mice with 36 species formally described (28 on Luzon, with others as listed in Table 2); together, these “old endemic” clades account for 84% of the native non-volant mammal species on Luzon (Tables 1, 2). The great majority of these species occur only above 1000 m elevation, and only a few occur as low as 600 m (Heaney 2011, 2013, Heaney et al. 2010, 2016).

Lineages of murid rodents that have arrived recently (i.e., during the last ca. 3–4 million years) are collectively referred to here as “new endemic” murids (Fig. 9; these include the genera *Abditomys*, *Bullimus*, *Crunomys*, *Tryphomys*, and the na-

tive species *Rattus everetti*); four of these occur widely on Luzon, all occur entirely in or including the lowlands, and all had been discovered by 1952.

Discussion

Our studies of mammalian diversity on Luzon were prompted in part by the crucial realization that began in the early 1990s that biological diversity is not always highest in tropical lowlands; rather, for many groups of organisms, diversity increases with increasing elevation up to some point along the elevational gradient, with many species absent from the lowlands (e.g., Rickart et al. 1991a, Rahbeck 1995, Heaney 2001, Lomolino 2001, Cadena et al. 2012). This carried implications for patterns of endemism and speciation, since populations restricted to highland areas in the wet tropics are, by definition, likely to experience no current gene flow with relatives that are isolated in non-contiguous highland areas (Janzen 1967, Ghalambor et al. 2006, Kier et al. 2009, Cadena et al. 2012, Fjeldsa et al. 2012, Steinbauer et al. 2012). The doubling of mammalian diversity described here was the outcome of our efforts to understand the interactions of elevational diversity patterns, geographical distribution and isolation, and speciation processes, in the context of



Figure 8. Photographs of (A) *Apomys musculus*, (B) *Rhynchomys soricoides*, (C) *Soricomys montanus*, (D) *Chrotomys whiteheadi*, (E) *Archboldomys maximus*, and (F) *Chrotomys silaceus*. All photos by the authors; from Heaney et al. (2016).

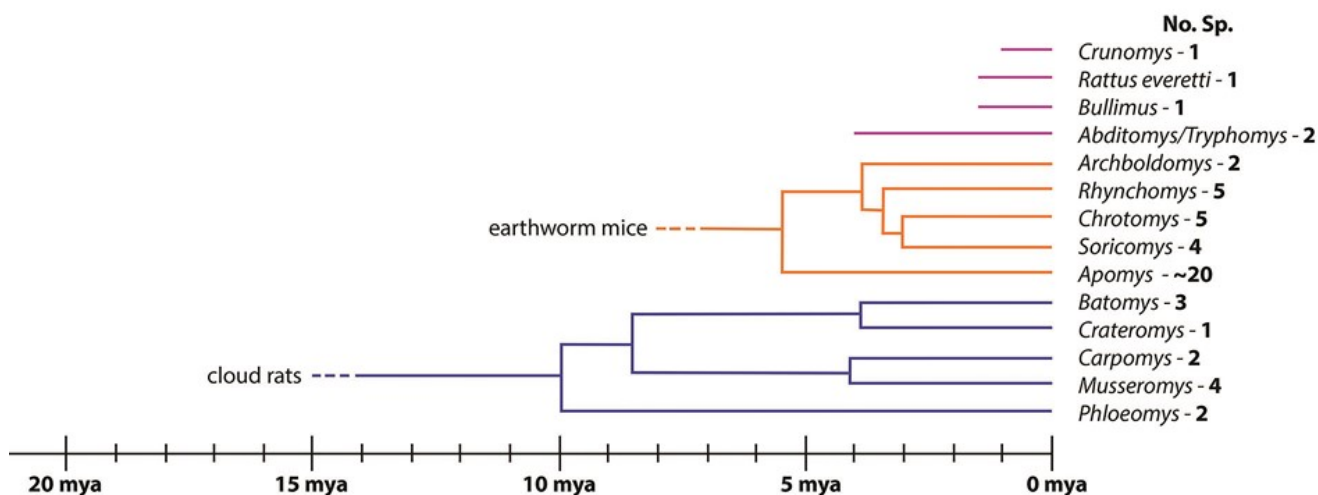


Figure 9. Phylogenies for the cloud rats, earthworm mice, and “New Endemics” for clades that are present on Luzon, with the estimated temporal calibration for arrival and diversification events; each of these events has confidence limits of approximately $\pm 25\%$. The number of species in each genus on Luzon is shown in boldfaced numbers to the right of the phylogenies. Based on Heaney et al. (2014) and Schenk et al. (2013), and modified from Heaney et al. (2016) based on Kyriazis et al. (submitted) for *Bullimus*.

geological evolution within a dynamic volcanic archipelago (Steppan et al. 2003, Jansa et al. 2006, Justiniano et al. 2015, Heaney et al. 2016).

This doubling of species richness was not predicted by extrapolating from prior rates of discovery (Fig. 2), and certainly not the 28 new species as currently estimated. Similarly, documentation of the number of endemic species, and especially doubling the number of local areas of endemism (Fig. 3), could not have been anticipated by extrapolation.

Although the pattern of increasing species richness of small mammals with increasing elevation from sea level up to ca. 2200–2500 m (Fig. 4) is now recognized as a global phenomenon (e.g., McCain 2005, Cadena et al. 2012), we know of no prior finding of a significant correlation between the peak elevation of a set of mountains and the number of native small mammal species on each mountain (Fig. 5), but it is that correlation that sets the stage for our final result, that the number of species endemic to a given range is correlated with the elevation of that mountain range (Fig. 6). Clearly, the distribution of species along elevational gradients within an island (or presumably other region) is a key component of the generation of patterns of endemism.

Although our studies of mammalian diversity on Luzon have not been completed, and some additional new species may yet be discovered, the impact of our analyses thus far yields some clear conclusions. These have implications specifically for studies of mammals on Luzon and in the Philippines, but also more broadly for studies of island biogeography and other assessments of pattern and process in biodiversity.

First, we have no reason to believe that our results are unique for Luzon. Our preliminary studies of mammals on Mindanao, an island in the southern Philippines of similar area (ca. 98,000 km²) and geological and topographic complexity (Hall 2013, Yumul et al. 2003, 2009), lead us to expect similar levels of currently undetected diversity there (Rickart et al. 1998, 2003, Balete et al. 2008). Studies of amphibians and reptiles throughout the Philippines show similar levels of discovery (e.g., Brown et al. 2009, Siler et al. 2011,

2012), and the same is true even for such distinctive organisms as *Rafflesia*, a group of parasitic plants with large, odoriferous flowers, which increased in documented number of species in the Philippines from 4 in 2000 to 11 in 2011 (Balete et al. 2010, Barcelona et al. 2011). Recent studies of earthworms have produced several dozen previously unknown, locally endemic species that appear to be members of several diverse endemic clades (see Aspe and James 2015 and references cited therein), and studies of ant diversity, though unusually high in the Philippines, is considered to be “in its infancy” (General and Alpert 2012). We think it is likely that most groups of organisms in the Philippines remain inadequately documented, as were mammals on Luzon in 2000.

Second, we have no reason to believe that these results are unique to the islands of the Philippines. For example, Sulawesi (formerly known as Celebes) is a large tropical oceanic island in the Wallacean region of Indonesia where earlier, highly productive surveys and systematic studies (e.g., Musser 1987, 1991, Musser and Durden 2002) revealed a rich endemic mammal fauna. However, newly initiated studies that focus on previously unsurveyed mountains have resulted in the discovery of a steadily increasing number of new species of mammals (Achmadi et al. 2012), including four new genera (Esselstyn et al. 2012, 2015, Rowe et al. 2014, 2016). Given the current topographic and historical geological complexity of Sulawesi and the yet incomplete surveys of the many isolated mountain regions, future discovery of many more species seems certain. Other islands in Wallacea are smaller but have high topographic complexity, and may yield similar results (e.g., Halmahera: Fabre et al. 2013). Recent field surveys and taxonomic studies on the island-continent of Madagascar have yielded a substantial number of new tenrecs, lemurs, and rodents (e.g., Goodman 2009, Soarimalala and Goodman 2011). Moreover, many continental areas, such as the Eastern Arc Mountains of tropical East Africa, are yielding similar results (e.g., Demos et al. 2013, Taylor et al. 2009, Stanley et al. 2005). Given the especially high concentration of local endemism on Luzon, we suspect that tropical oceanic

islands, particularly those of Indo-Australia, may be especially rich sources of new discoveries (and current serious under-estimates) of mammalian diversity.

Thorough documentation of species richness of mammals (and other organisms) on islands could have a profound impact on our understanding of many key aspects of the dynamics of biodiversity. For example, a previous study (Heaney 1986) compared islands on the Sunda Shelf of SE Asia that had been connected to the Asian mainland during the last glacial maximum (ca. 20,000 to 12,000 bp; Voris 2000) with islands in the Palawan chain that may have been connected to Borneo during an earlier Pleistocene period of low sea level (see Esselstyn et al. 2010, Piper et al. 2011). That study concluded that Luzon, along with other Philippine oceanic islands, was substantially depauperate in its non-volant mammal fauna. Our new data that have doubled the number of species lead us to overturn that conclusion: the number of species now known on Luzon (a purely oceanic island) falls near the number that would be expected for an island on the continental shelf, and Luzon cannot be considered depauperate in terms of its species richness, and especially in its level of endemism. The previous conclusion was an artifact of insufficient sampling effort.

Further, given the evidence cited above that speciation within Luzon during the last ca. 14 million years has generated most of the mammalian diversity now present, the role of colonization in determining species richness must be re-evaluated. The number of unique colonization events that have given rise to the non-volant mammal fauna on Luzon (Heaney and Rickart 1990) has been greatly reduced by our phylogenetic studies, which group most species into a few endemic clades (Jansa et al. 2006, Schenk et al. 2013, Heaney et al. 2016). These findings have shifted the relative importance away from direct colonization to a greater role for speciation within the island, while simultaneously increasing the time-scale over which the diversity has evolved (Steppan et al. 2003, Justiniano et al. 2015). These changes have direct impact on our view of the

appropriate models for interpreting the available evidence, away from the equilibrium model of MacArthur and Wilson (1963, 1967; see also Losos and Ricklefs 2010) to the general dynamic model of Whittaker and colleagues (Whittaker et al. 2007, 2008), with the attendant shift in emphasis from “ecological time” to “evolutionary time”, and from treatment of islands as effectively static entities to the recognition that islands and archipelagos are dynamic entities, with complex geological histories that directly influence biodiversity processes (Borregaard et al. 2016, Heaney et al. 2013c, 2016).

These new data and the shift in understanding of pattern and process that accompanies them have important implications for conservation as well. Efforts to protect areas of endemism (“Key Biodiversity Areas”), which underpins many national conservation programs (such as in the Philippines; Mittermeier et al. 1990, Heaney and Mallari 2000, Ong et al. 2002, Wikramanayake et al. 2002, Schipper et al. 2008, Mallari et al. 2015), are deeply influenced by the discovery of new areas of local endemism. Other conservation efforts target “restricted area species” that we discovered in abundance and we predict will be found by any future projects like the one described here. And more fundamentally, concern about individual species that suffer from any source of threat can result in active management only when those species are known to exist and their distribution and basic ecology is documented.

We conclude with a point that is perhaps obvious, but frequently disregarded in practice: any study of geographic patterns of biodiversity, whether for conceptual or practical conservation purposes, must be viewed with skepticism unless it is solidly grounded in thorough, intensive field surveys that are coupled with equally intensive studies of morphology and genetics that produce reliable information about the extent and distribution of biodiversity (Ferreira et al. 2016). As our study demonstrates, even information on the diversity of mammals, which are often regarded as well known (second only to birds), requires substantial “ground-truthed” verification to avoid major factual and conceptual errors.

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Author contributions

This project was initially conceived by Heaney and Rickart, and field surveys conducted by Balete, MR Duya, MV Duya, Heaney, and Rickart. Phylogenetic analyses were conducted by Jansa and Steppan. Heaney served as lead author of the manuscript; all authors contributed to writing the manuscript and approved its content.

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