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A new biogeographical classic

The Mammals of Luzon Island: Biogeography and Natural History of a Philippine Fauna by Lawrence R. Heaney, Danilo S. Balete and Eric A. Rickart, 2016, John Hopkins University Press, 304 pp. \$75.00 (Hardback) ISBN: 978-1-4214-1837-7; <https://jhupbooks.press.jhu.edu>

With the publication of this book, the mammals of Luzon Island deserve to take their place among the classic case studies in the biogeographical canon. The depth of information presented is impressive, condensing the contents of numerous papers, alongside natural history observations accumulated over the course of decades of grueling and dedicated fieldwork. As an exemplar of how to construct a cohesive, integrated, biogeographical research program I cannot think of its equal. In my own undergraduate lectures I have spent many years teaching students about New Zealand and Madagascar; this time they will learn about Luzon instead.

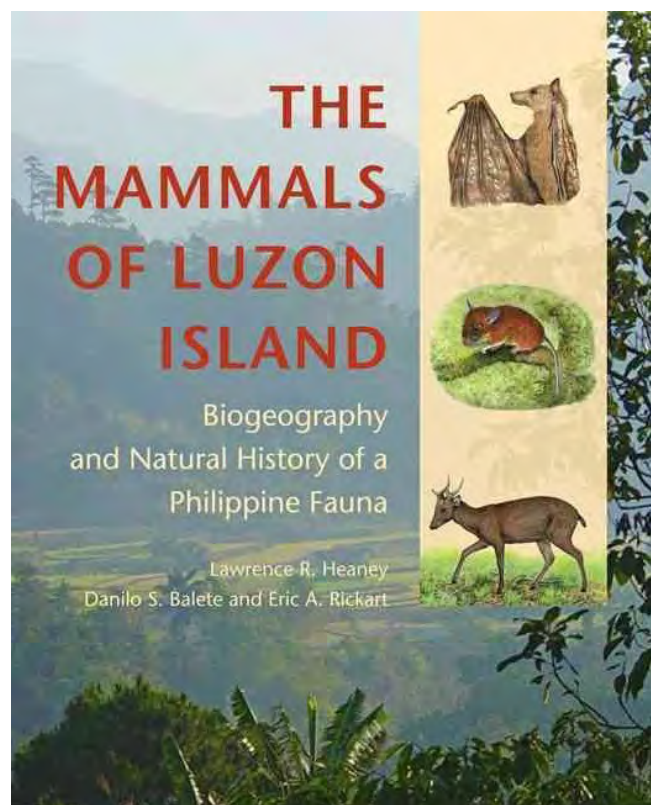
Luzon has long been recognised as an exceptional region. I began with an ignorance shared by Wallace, who believed the Philippines to contain few endemic mammals. This casual assumption was overturned by Whitehead, who reached the summit of the aptly-named Mount Danao on a collection trip in 1895, and stumbled upon a rich mammal assemblage. He discovered that their species richness increases with altitude, a pattern replicated elsewhere on the archipelago. That the giant cloud rats had remained undiscovered by Western science was at least in part because no-one had imagined that such creatures might dwell in the mountains.

In total the island contains 47 native species of murid rodent, 96% of which are endemic. Even among tropical mountain regions, can there be another region with as many endemic mammals in such a small area, and with as many centres of endemism? The key to the generation and maintenance of such richness has been the isolated mountain chains, which are themselves highly variable in their edaphics. Hence the discovery that 79% of the species are locally endemic to restricted areas.

Luzon originated 26–30 million years ago (Mya) as a merging of small islands, with its cur-

rent form developing in the last million years. Despite being separated by only 15 km from greater Mindanao, sea levels at the last glacial maximum have maintained a striking faunal barrier across the San Bernardino Strait. Luzon's formation included both volcanism and continental uplift, generating an ever-increasing degree of topographic complexity as the island grew in size. The wet and foggy conditions in the high mountains preserve unique communities, at altitudes which receive occasional frost, with climatic barriers revealed daily by patterns of cloud cover.

The endemic small mammals form two distinct groups. One set arises from two ancient radiations, whose species are diverse and specialised. Cloud rats arrived 14 Mya and now comprise 12 species on Luzon (with six elsewhere on the archipelago). Earthworm mice were present from 7 Mya and now make up at least 36 species, in addition to 16 on neighbouring islands. These



reach remarkable degrees of alpha richness, with up to 6 cloud rat and 7 earthworm mice living in the same habitat patches, all at medium to high elevations in mature montane and mossy forest. More recent endemics (less than 4 Mya) are typically habitat generalists and related to Greater Mindanao species with limited differentiation.

Based on painstaking accumulation of evidence, a picture emerges of how the assemblage of mammals was formed. Among small mammals, local speciation accounts for seven times as many species as colonisation. This clearly contravenes traditional island biogeographical theory, though here MacArthur and Wilson were prescient; Luzon's mammals are recognised in their original text as a potential exception to the general model (1967:173–175). Unsurprisingly the converse is true of bats, with colonisation overwhelmingly exceeding speciation in generating the assemblage, although there may be cryptic endemism. The island does not, however, present a clear fit to the General Dynamic Model, as plate margin islands develop in a different fashion to volcanoes. Their long lifespan provides time for specialist endemics to evolve, potentially making them more resistant to invasion.

The mountain redoubts provide one of the keys to the remarkable persistence of Luzon's mammals. It is not known when humans first arrived in Luzon, but a major influx from Taiwan occurred 4,000 years ago, associated with the arrival of crops and invasive species. Now an island of a little over 100,000 km² contains 42 million people, making it one of the densest-populated globally. By 1875 there are records of extensive forest clearance in the lowlands, in addition to shifting agriculture, rice paddies and fires in the uplands. Since then Luzon's forests have declined from 70% of the island in 1900 to around 20% today, all of which are degraded to some extent.

If there is a reason for optimism, it is that it can't get much worse, if only because there is little commercial-grade timber left to fell. Only 4% of the lowland forest remains in any recognisable state. This was probably catastrophic for bats, but the upland rats have persisted. It is possible that frequent disturbance from volcanoes and hurri-

canes have pre-adapted the fauna to cope with human impacts. Meanwhile, despite the presence of invasives in transformed and disturbed habitats, the specialised endemics appear capable of resisting their incursions into the native forests.

There are reasons to be wary, however. The once remote forests of Mount Data which Whitehead surveyed have been reduced to a National Park containing only 80 ha from an original 5512 ha. Many of the parks exist only on paper, with no meaningful protection. Increasing mining impacts are concentrated on the rare ophiolite outcrops, which host the most distinctive forests (and mammals).

The book divides into two parts. The first could double as an introductory textbook of island biogeography as it covers most key processes in the specific context of Luzon. Although becoming repetitive by the final discussion chapter, it succeeds in bringing the reader to the forefront of current theory, and shows how further research on Luzon might reveal yet more. The remainder of the book documents the natural history, distribution and taxonomy of over 110 mammal species.

In short, I cannot recommend this book highly enough. It is an insightful, thorough and fascinating text based upon a lifetime of thought and hard-won data. The text is engagingly written throughout, the volume wonderfully produced and illustrated, and overall well worth the cover price. It could be set as a discussion text for students, used to generate examples for lectures, or simply read for pleasure alone.

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