Variation in species richness, composition and herpetological community structure across a tropical habitat gradient of Palawan Island, Philippines

Christian E. Supsup¹, Augusto A. Asis², Uldarico V. Carestia Jr.³, Arvin C. Diesmos⁴, Neil Aldrin D. Mallari¹,⁵, Rafe M. Brown⁶

¹ Biology Department, De La Salle University, 2401 Taft Avenue, Manila, 1004, Philippines
² Puerto Princesa Subterranean River National Park, Puerto Princesa City, 5300, Philippines
³ Yapang, Barangay Batong-Buhay, Sablayan, Occidental Mindoro, 5104, Philippines
⁴ Philippine Museum of Natural History, Zoology Division, Herpetology Section, Rizal Park, Burgos Street, Manila, 1000, Philippines
⁵ Center for Conservation Innovations, 208 Civic Prime Building, Civic Drive Alabang, Muntinlupa, 1781, Philippines
⁶ Department of Ecology and Evolutionary Biology and KU Biodiversity Institute, University of Kansas, Lawrence, Kansas 66045, USA

http://zoobank.org/A383288C-1E42-4EA7-9D3A-52AA904AA5EF
Corresponding author: Christian E. Supsup (supsupchristian@gmail.com)

Abstract

Information on species richness and community structure is invaluable for guiding conservation and management of biodiversity, but is rarely available in the megadiverse biodiversity conservation hotspot of Philippines – particularly for amphibians and reptiles. This study provides the first report and characterisation of amphibians and reptile communities across primary habitat types of the Victoria-Anepahan Mountain Range on Palawan Island along the western edge of the archipelago. A total of 41 amphibian and reptile species were recorded throughout our sampling sites (n = 27 species) or in targeted habitat searches (14 species). A species richness estimator predicted that 35 species may be present in our sampling sites, suggesting that a significant proportion of secretive species may continue to be unrecorded, especially for reptiles. Higher species richness was found in secondary growth than in mixed-use agricultural areas or even pristine forest. The low species richness recorded from pristine forest types may be due to these forests now being restricted to higher elevations where species diversity has been documented to decrease. Our results also show that complex community structures (species assemblages) are to be equally expected in both secondary growth and pristine forests. Together, our results show how species richness and community assemblages may vary across habitats, highlighting that old growth forest does not always support higher species richness, particularly in high elevations.

Key Words

amphibians, biogeography, conservation, iNEXT, reptiles, Victoria-Anepahan Mountain Range

Introduction

Patterns of community assembly of amphibians and reptiles across habitat types are rarely examined in the Philippines (Brown et al. 2001). Generally, amphibians and reptiles are known to occupy moist habitats (Alcala and Brown 1998; Brown et al. 2001), but their overall community structure (composition of assemblages at any one site) is expected to vary significantly along elevational gradients (Auffenberg and Auffenberg 1988; Brown et al. 2001). Early works suggest that species richness and diversity decreases and that endemism increases in high elevation (Brown and Alcala 1961; Brown et al. 1995; Diesmos 1998; Ferner et al. 2000). This pattern has also
been observed in other vertebrates (Heaney et al. 1989; Goodman et al. 1995; Heaney 2001), but fine scale information is still lacking for Philippine amphibians and reptiles (Brown et al. 2001; Sanguila et al. 2016). As an archipelago with varying terrains, climatic conditions and habitat types, there is little information available about how species richness and community composition changes with elevation, atmospheric gradients and related forest type. Some studies have called attention to a possible mid-elevation swell in species richness and diversity (Brown and Alcala 1961; Auffenberg and Auffenberg 1988; McCain and Grytnes 2010). How other environmental conditions (e.g. climate, temperature, precipitation, habitat types) shape community assembly have not been rigorously characterised in the Philippines (but see Auffenberg and Auffenberg 1988; Diesmos et al. 2004a), although limited recent work suggests community assembly is influenced by habitat complexity and extent of the remaining natural forest (Alcala et al. 2004; Diesmos 2008; Causaren 2012).

The Palawan Island group is situated between the South China Sea (West Philippine Sea) and Sulu Sea and was considered an extension of Sunda Shelf landmasses because of the presence of conspicuous vertebrates shared with Borneo (Everett 1889; Boulenger 1894) and the assumption that Palawan was connected previously to it (Dickerson 1928; Inger 1954; Heaney 1985, 1991; Esselstyn et al. 2004, 2010). However, the biogeographic significance of any ephemeral dry land connection has been questioned by biogeographers who have pointed out that such biogeographical affinities were derived historically from faunal similarity exercises involving birds and mammals (McGuire and Kiew 2001; Brown and Gutman 2002; Esselstyn et al. 2009, 2010). More recent considerations, based on phylogenetic analyses, suggest that much of Palawan’s fauna is actually closely-related to lineages endemic to the oceanic regions of the Philippines (McGuire and Kiew 2001; Brown and Gutman 2002; Esselstyn et al. 2009, Welton et al. 2009) or even Eurasia (Blackburn et al. 2010; Siler et al. 2012; Lim et al. 2014; Brown et al. 2016; Chan and Brown 2017) which prompted Esselstyn et al. (2010) to suggest that Palawan may best be viewed as a biogeographic filter zone and not a sharp faunal demarcation as suggested by Huxley’s modification of Wallace’s Line (see also Oliveros and Moyle 2010; Sheldon et al. 2015; Hutterer et al. 2018).

The herpetofauna of Palawan has been documented for more than a century now (Everett 1889; Boulenger 1894; Griffin 1909; Taylor 1928; Inger 1954; Brown and Alcala 1970), but most of these earlier works constitute species lists, dependent on unverified or outdated taxonomy and with limited information on distributions or habitat requirements. Analysis of phylogenetic relationships has only recently been integrated into consideration of Palawan’s amphibian and reptile diversity (Siler et al. 2012; Brown et al. 2016; Chan and Brown 2017), via taxonomic revisions and descriptions of new species (Brown and Gutman 2002; Welton et al. 2009; Linkem et al. 2010; Brown et al. 2010; Siler et al. 2012; Welton et al. 2013; Brown et al. 2016). As emphasised by Brown et al. (2010) and Esselstyn et al. (2010), these findings indicate that Palawan’s herpetofauna remains underestimated; this misunderstanding of its fauna calls for immediate and comprehensive herpetological inventory work. At present, there are 96 species (26 amphibians, 70 reptiles) reported from Palawan (Diesmos and Palomar 2004; ACD, unpublished data), but this estimate will likely change with ongoing inventories and taxonomic assessments.

In this paper, we contribute an amelioration of some information gaps in our understanding of herpetological diversity of Palawan. Here, we present a new assessment of herpetofauna for the geographical centre of Palawan, the Victoria-Anepahan Mountain Range (VAMR). We analyse species richness and community composition across a tropical habitat and atmospheric gradient associated with the island’s steep topography and empirically characterise, for the first time, elevational variation in species assemblages. Finally, we discuss patterns of community structure which can provide information about management practices of Palawan’s forested resources.

Methods

Study area

The VAMR, a key biodiversity area at the centre of Palawan (Fig. 1; Mallari et al. 2001), has an area of ca. 210,000 ha, spanning from Puerto Princesa City to municipalities of Aborlan, Quezon and Narra and includes the largest ultramafic forest in Palawan (Mallari et al. 2001; Fernando et al. 2008). Other forest types include lowland dipterocarp and upper montane forests. Native trees at lower elevations (< 550 m) are dominated by Ormosia bancana, Swintonia foxtworthyi, Xanthostemon speciosus, Gymnostoma sp. and Tristaniopsis sp., Diospyros sp., Ilex sp. and in high elevations (> 550 m) include Cinnamomum rupestre, Syzygium punctilimbum, Planchonella firma, Gymnostoma sp. and Tristaniopsis sp. (Fernando et al. 2008). There are two major climatic conditions on mainland Palawan, the south-eastern side including a region lacking pronounced rainy season (south-eastern VMAR: maximum annual precipitation ≤ 2,000 mm) and another, characterised by a more pronounced rainy season (north-western VMAR: maximum annual precipitation ≥ 3,000 mm; DOST-PAGASA 2019); both have mean annual temperatures of 27.3–28.0 °C.

Our surveys were conducted on three separate visits, study Sites 1–4 were surveyed 05 July–22 August (2013), Sites 5 and 6 from 4–10 February (2016) and Site 7 was surveyed 24 May–01 June (2018; Table 1; Figs 1, 2). We visited Sites 1–5 at the onset of the wet season (mean temperatures from 26.5–27 °C) and anthropogenic disturbances included upland rice cultivation, charcoal production, coconut plantation and large scale mining (Fig. 1). Timber extraction was evident in all forests, particularly at Site
Figure 1. Map of Victoria-Anepahan Mountain Range (VAMR), of central Palawan Island, Philippines (inset map). The right panel includes sampling sites, indicated by numbered circles. The extent of the VAMR is indicated (red polygon) and the elevation represented by incremental coloured shading. The left panel shows the vegetation cover of VAMR based on 2015 Land Satellite Image, reproduced from Supsup and Asis (2018). Boxes indicate locations of two mining areas in close proximity to the VAMR massif.

Table 1. The general and specific locality of survey sites in the Victoria-Anepahan Mountain (VAMR). Shown also are the transect and habitat type codes used for cluster analysis. Geographic coordinates are in decimal degree. The asterisks denote sampling which involved stream (*) or near water bodies (**).

| Site No. | General Locality | Specific Locality | Transect Code & Habitat Type | Latitude / Longitude |
|----------|------------------|-------------------|-----------------------------|----------------------|
| 1a       | Municipality of Narra | Barangay Estrella – Sitio Elmogon, Camp 1 | ET1-2 – ASG*, ET5, ET7 – ESG; ET6 – CVT | 9°22’26.9868”N, 118°23’48.876”E |
| 1b       | Municipality of Narra | Barangay Estrella – Sitio Elmogon, Camp 2 | ET8-12 – OGF | 9°22’18.6132”N, 118°23’5.2188”E |
| 2a       | Municipality of Narra | Barangay Malinao – Sitio Carañogan, Camp 1 | MT7-10 – OGF** | 9°19’41.4804”N, 118°19’23.1852”E |
| 2b       | Municipality of Narra | Barangay Malinao – Sitio Carañogan, Camp 2 | MT1-6 – OGF | 9°20’22.1928”N, 118°19’1.7904”E |
| 3        | Municipality of Quezon | Barangay Aramaywan – Sitio Lamane | ALAMT1-6, ALAMT8-9 – OGF**; ALAMT7 – CVT | 9°22’18.6384”N, 118°12’35.0856”E |
| 4        | Municipality of Quezon | Barangay Aramaywan – Sitio Lalid | ALALT1-3 – ASG; ALAT4-5 – ESG | 9°20’24.594”N, 118°10’50.1276”E |
| 5        | Municipality of Aborlan | Barangay Sagpangan | ST1-4 – ASG | 9°31’33.960”N, 118°30’28.116”E |
| 6        | Municipality of Aborlan | Barangay Iraan | IT1-3 – ESG*, IT4-5 – ASG** | 9°30’26.644”N, 118°30’42.842”E |
| 7        | Municipality of Aborlan | Barangay Apurawan – Sitio Daan | APUT1,4 – ESG; APUT2,3 – ASG | 9°34’26.3496”N, 118°23’15.8208”E |

2. Sites 5 and 6 were surveyed in dry season months, but were unusually rainy during our survey: daily intermittent rain characterised the afternoon between 14:00 and 16:00 h and evening 18:00 and 21:00 h. Temperature at Sites 5 and 6 varied from 27–28 °C and anthropogenic disturbances included shifting cultivation, palm oil cultivation and timber extraction. Site 7 was visited at the end of the dry season and daytime mean temperature was 28 °C; shifting cultivation and sand quarrying were evident.

Herpetofaunal surveys
We surveyed amphibians and reptiles with 49 randomly-established 10 × 100 m strip transects (Heyer et al. 1994; Diesmos 2008; Supsup et al. 2016) across habitat types, positioned ca. 100–200 m apart. Habitat types, based on relative successional stages, were determined during the survey following the classification of Mallari et al. (2011) as: Cultivation (CVT); Early Secondary...
Growth (ESG); Advanced Secondary Growth (ASG); and Old Growth Forest (OGF). Transects were surveyed by three persons during daytime (07:00–11:00 h) and nighttime (18:00–23:00 h). To avoid disturbance, transects surveyed during the day were not traversed on the same night and vice versa. We employed time-constrained visual and acoustic searches and exhaustively searched all microhabitats (logs, rocks, tree holes, bark crevices, tree buttresses, forest floor litter etc.). To avoid pseudo-replication, we restricted our search to 1 hr per transect, with three to four transects being sampled per night/day. Individuals seen or heard already from the same location while traversing the transect were not recorded again. Transects were repeated on different days in reverse direction to minimise bias attributed to route direction and temporal influences on animal activity. We counted the number of individuals within each transect and recorded the activity of each subject upon first encounter (e.g. calling, foraging). Searches were also conducted along roads, forest trails and clearings. A total of 294 man-hours (98 hours/person) were spent during surveys. Despite efforts geared towards standardisation of sampling effort, our sampling across habitat types was uneven because of logistical constraints; accordingly, we selected methods of analysis to allow for comparisons amongst sites with non-equivalent sampling effort (see below). To facilitate identification, voucher specimens were humanely euthanised with aqueous chloratone, fixed in 10% buffered formalin and subsequently transferred to 70% ethanol. Our Wildlife Gratuitous Permit (No. 2013-02) was issued by the Palawan Council for Sustainable Development (PCSD) and all specimens were deposited at the Philippine Museum of Natural History. In this study, we followed the taxonomic arrangements of AmphibiaWeb (2019), Amphibian Species of the World (Frost 2016) and Reptile Database (Uetz et al. 2016).

Analyses

We performed all statistical analyses in R version 3.4.4 (R Development Core Team 2018). Sampling effort was evaluated with a species accumulation curve using the vegan package (specaccum function; method = exact;
Orksanen 2019). Species richness was estimated using Hill numbers developed by Chao et al. (2014). We chose this approach over traditional estimators (e.g. Chao 2, Jackknife) because it allows comparison of species richness despite differences in sampling effort and, most importantly, its ability to extrapolate and compare species richness at equal sample coverage even with smallest samples (Chao et al. 2014). We generated rarefaction curves using the iNEXT package (Hsieh et al. 2016), with 200 bootstraps to estimate 95% confidence limits (CL) and using only records from transects (species observed = 15 amphibians, 12 reptiles); general search records were excluded from these analyses. We arbitrarily set the end point of extrapolation to 200 transects. Only pooled presence-absence (incidence) data were used for estimating the overall amphibian and reptile richness. Variation in species richness and diversity (Shannon Index) across habitat types were calculated from abundance data (Suppl. material 1). For simplicity and ease of interpretation, species richness patterns along our elevational gradient were initially examined using a simple scatter plot with a local regression curve. To determine the community structure across sites (= habitats), we performed cluster analysis using vegdist and hclust functions; transects lacking observations were excluded. We used the Bray-Curtis Dissimilarity Index (BCDI) to measure similarities of sites based on overall species composition, weighted by abundance (Bray and Curtis 1957). Sites were clustered using the agglomerative hierarchical clustering algorithm (method = average) and we further examined community structure with Non-metric Multidimensional Scaling (NMDS), based on BCDI using the metaMDS function (Faith et al. 1987; Minchin 1987). NMDS ordination was overlaid on our cluster analysis to represent community structure.

Results

Species richness, diversity and composition

We recorded 41 species, including 17 frogs, 11 lizards, 12 snakes and one turtle (Table 2; Figs 3, 4). Of these, 27 were observed within transects; 14 were observed during general searches. More than 50% of anurans and 33.3% of reptile species observed are known to be restricted to Palawan, indicating high levels of proportional endemism (Fig. 5). The remaining non-endemic species are taxa shared with the oceanic Philippines and/or Sundaland. Only two reptiles (Lamprolepis smaragdina philippinica and Dendrelaphis marenae) are exclusively shared with the oceanic portion of the archipelago. We also recorded two introduced frog species in our study areas (Hoplobatrachus rugulosus and Kaloula pulchra), amongst several additional invasive species now documented on the island; Diesmos et al (2015) which are present in cultivation and developed coastal areas. Despite an intensive transect search with 294 observation hours and unaccounted general searches spent in VAMR, our species accumulation curve suggests that many species were overlooked during the surveys (Fig. 6). Our species richness estimates from transect data suggest that 35 species may be present and our extrapolation curve suggests that additional species are expected with increased sampling, especially for reptiles (Fig. 7). Significant differences in species richness and diversity were found across habitat types, as indicated by non-overlapping confidence intervals (Fig. 8). The highest richness and diversity for both amphibians and reptiles were recorded in advanced secondary growth (ASG), followed by early secondary growth (ESG) and old growth forest (OGF); our lowest estimates were derived from cultivated areas. Finally, our data revealed that species richness exhibited a declining trend with increasing elevation and that samples of old growth forests found in high elevation had the lowest number of species observed including some secondary growth forests found near disturbances (Figure 9).

Community structure

The cluster analysis of species composition resulted in two primary groupings (Fig. 10). Group 1 is formed primarily by Sites 5–7 transects (Aborlan). These habitats are dominated by secondary forests (ESG, ASG) and species recorded are typical secondary forest residents. Group 2 is a cluster of Sites 1–4 transects (Narra and Quezon). Their habitats are mainly OGF, ASG and CVT and species recorded include several pristine forest habitat specialists. The presence of CVT from Site 3 represents an exemption: a small patch inside old growth, with one species recorded (Philautus longicrus).

The two-dimensional NMDS has a stressplot value of 0.074, indicating acceptable ordination and representation (Clarke and Warwick 1994). Our NMDS confirmed cluster analysis findings: two distinct patterns of assemblage (Fig. 11). Species situated in secondary forest (Group 1) included 11 frogs (Pulchrana moellendorffi, Ingerophrynus philippinicus, Leptobrachium tagbanorum, Limnonectes acanthi, Megophrys ligayae, Occidozyga laevis, Philautus everetti, Polypedates leucomystax, Polypedates macrotis, Staurus nubilus, Sanguirana sanguinea), three lizards (Eutropis multifasciata, Gekko gecko, Hemiophyllodactylus typus) and three snakes (Dendrelaphis marenae, Dryophiops rubescens, Boiga schultzei); and species positioned in pristine forests (Group 2) included four frogs (Barbourula bussuangensis, Chaperina fusca, Limnonectes palavanensis, Philautus longicrus), four lizards (Bromochorea cirratateula, Cyrtodactylus redimiculus, Gekko athymus, Gekko monachus) and two snakes (Aplopeltura boa, Tropidolaemus subannulatus). Both the cluster analysis and NMDS ordination consistently identified a separation of assemblages, both geographically and by habitat types. Sites 5–7 have assemblages often found in secondary forest, particularly common frogs, distributed widely in Palawan. Sites 1–4, contain species that are rarely observed and typically restricted to pristine forests.
Table 2. Amphibians (frogs) and reptiles (lizards, snakes and turtle) recorded from Victoria-Anepahan Mountain Range. Numbers in sites column indicate specific location of species observation (see Table 1). Shown also are the species current IUCN (2019) conservation status (LC = Least Concern, NT = Near Threatened, VU = Vulnerable, EN = Endangered; NE = Not Evaluated) and voucher number of collected specimen, deposited at the Philippine Museum of Natural History. Asterisk (*) denotes species restricted to Palawan faunal region.

| Taxa | Sites | IUCN status | Voucher number |
|------|-------|--------------|----------------|
| **AMPHIBIA (FROGS)** | | | |
| Bombinatoridae | | | |
| Barbourula bussaungensis Taylor and Noble 1924 * | 1a, 4, 7 | NT | ACD 8513–15, 8521, 8585 |
| Bufonidae | | | |
| Ingerophrynus philippinicus (Boulenger 1887) * | 1a, 2a, 3, 7 | LC | ACD 8541 |
| Dicroglossidae | | | |
| Hoplobatrachus rugulosus (Wiegmann 1834) | 1a | LC | ACD 8532 |
| Limnonectes acanthi (Taylor 1923) * | 1a, 2a, 3, 4 | LC | ACD 8573, 8581, 8596–98 |
| Limnonectes palavanensis (Boulenger 1894) | 1a, 2a, 3, 4, 7 | LC | ACD 8529 |
| Megophryidae | | | |
| Leptodactylus tagbanorum Brown, Siler Diesmos and Alcala 2009 * | 1a, 2a, 3, 4, 7 | NE | ACD 8540 |
| Megophrys ligayae Taylor 1920 * | 1a, 2a, 3, 5, 6, 7 | NT | ACD 8530, 8552, 8559–60, 8560, 8563, 8569 |
| Microhylidae | | | |
| Chaperina fusca Mocquard 1892 | 1a, 4, 7 | LC | ACD 8566–68, 8590 |
| Kaloula pulchra Gray 1831 | 1a | LC | no specimens |
| Ranidae | | | |
| Pulchrana moellendorffi (Boettger 1893) * | 1a, 2a, 3, 4, 7 | LC | ACD 8518, 8528 |
| Sanguirana sanguinea (Boettger 1893) * | 1a, 2a, 3, 4, 5, 6, 7 | LC | ACD 8522, 8527, 8545, 8554, 8555, 8588 |
| Staurois nubilus (Mocquard 1890) * | 1a, 4, 7 | NT | ACD 8524, 8586, 8592–93 |
| Rhacophoridae | | | |
| Philautus everetti (Boulenger 1894) * | 1a, 4, 7 | LC | ACD 8517, 8536, 8547, 8562, 8570, 8587 |
| Philautus longicrus (Boulenger 1894) | 1a, 2a, 3, 4, 6 | NT | ACD 8520, 8537–38, 8550–51, 8553, 8555–56, 8565 |
| Polypedates leucomystax (Gravenhorst 1829) | 5 | LC | no specimens |
| Polypedates macrotis (Boulenger 1891) | 1a, 3, 7 | LC | ACD 8526, 8577 |
| **REPTILIA (LIZARDS)** | | | |
| Agamidae | | | |
| Bronchocela cristatella (Kuhl 1820) | 1b, 2ab, 4, 5 | NE | ACD 8531, 8548, 8582 |
| Draco palawanensis McCruig and Alcala 2000 * | 1a, 4 | NE | ACD 8562 |
| Gekkonidae | | | |
| Cyrtodactylus redimiculus King 1962 * | 1b, 2ab, 3 | NT | ACD 8533, 8539, 8557, 8578 |
| Gekko athymus Brown and Alcala 1962 * | 3 | NT | ACD 8579 |
| Gekko dieguensis Linnaeus 1758 | 4, 7 | NE | ACD 8560 |
| Gekko monarchus (Schlegel 1836) | 1a, 2a, 4, 6 | LC | ACD 8525, 8564, 8591 |
| Hemidactylus frenatus Schlegel 1836 | 7 | LC | no specimens |
| Hemiphysodiactylus zephyr Bleeker 1860 | 6 | NE | no specimens |
| Scincidae | | | |
| Eutropis multifasciata (Kuhl 1820) | 1a, 5 | NE | ACD 8519, 8523 |
| Lamprolepis smaragdina philippinica (Mertens 1928) | 4 | NE | ACD 8595 |
| Varanidae | | | |
| Varanus palawanensis Koch et al. 2010 * | 1a, 3, 5, 6 | NE | no specimens |
| **REPTILIA (SNAKES)** | | | |
| Colubridae | | | |
| Boiga schultzei Taylor 1923 * | 6 | LC | no specimens |
| Dryophis maculatus Vogel and Van Rooijen 2008 | 1a, 4 | NE | ACD 8531 |
| Dryophis rubescens (Gray 1834) | 5 | NE | no specimens |
| Lycodon sanctus Leviton 1955 * | 5 | NE | no specimens |
| Ptyas carinata (Günter 1858) | 6 | LC | no specimens |
| Elapidae | | | |
| Calliophis bilineata (Peters 1881) * | 1a, 2a, 4 | LC | ACD 8517, 8536, 8547, 8562, 8570, 8587 |
| Naja sumatrana Müller 1890 | 4 | LC | ACD 8561 |
| Lampropholidae | | | |
| Psammodyastes palustris (Boie 1827) | 2a | NE | ACD 8543, 8549 |
| Natricidae | | | |
| Rhabdophis chrysargus (Schlegel 1837) | 2a, 4 | LC | ACD 8554, 8584 |
| Viperidae | | | |
| Trimeresurus schultzei Grün 1909 * | 2a, 3 | LC | ACD 8574, 8580 |
| Tropidolaemus subannulatus (Gray 1842) | 1b, 2a, 3 | LC | ACD 8534–35, 8542, 8546, 8576 |
| **REPTILIA (TURTLES)** | | | |
| Cyclemys dentata (Gray 1831) | 1a | NT | no specimens |
Figure 3. Fifteen of 17 amphibian species (frogs) observed in the vicinity of Victoria-Anepahan Mountain Range (VAMR). A – Barbourula busuangensis; B – Chaperina fusca; C – Ingerophrynus philippinicus; D – Kaloula pulchra; E – Leptobrachium tagbanorum; F – Limnonectes acanthi; G – Limnonectes palavanensis; H – Megophyrs ligayae; I – Occidozyga laevis; J – Philautus everetti; K – Philautus longicrus; L – Polypedates macrotis; M – Pulchranana moellendorffi; N – Sanguirana sanguinea; O – Staurois nubilus. Photos by C. Supsup.
Figure 4. Eighteen of 24 reptile species (lizards, snakes, turtle) observed in the vicinity of Victoria-Anepahan Mountain Range (VAMR).

A – Bronchocela cristatella; B – Cyrtodactylus redimiculus; C – Eutropis multifasciata; D – Gekko athymus; E – Gekko monarchus; F – Hemiphyllodactylus typus; G – Lamprolepis smaragdina philippinica; H – Aplopeltura boor; I – Boiga schultzei; J – Caliophis bilineata; K – Dryophiops rubescens; L – Lycodon sealei; M – Naja sumatrana; N – Psammodynastes pulverulentus; O – Rhabdophis chrysargos; P – Tropidolaemus subannulatus; Q – Trimeresurus schultzei; R – Cyclemys dentata. Photos by C. Supsup.
Figure 5. Totals of amphibians and reptiles recorded from the Victoria-Anepahan Mountain Range (VAMR) and species residency status proportions (by percentage), based on current understanding of their distributional range.

Figure 6. A species accumulation curve, depicting the cumulative number of amphibian and reptile species detected in the Victoria-Anepahan Mountain Range (VAMR).

Figure 7. Sample-sized-based rarefaction (solid lines) and extrapolation curves (dashed lines) of amphibian and reptile richness in sampling sites, with 95% confidence interval (shaded areas).

Discussion

The foundational knowledge of Palawan herpetofauna has been established from 1889–1970. A handful of recent studies have provided accounts of species recorded in Palawan protected areas, for example, Diesmos et al. (2004b), Schoppe and Cervancia (2009), Esselstyn et al. (2010), Siler et al. (2012), Brown et al. (2013, 2016), Jose and van Beijnen (2017) and CCI (2018). Recently, Diesmos et al. (2015) and Leviton et al. (2018) presented updated checklists of Philippine amphibians and snakes, respectively, in an effort to provide comprehensive summaries of the archipelago’s herpetological species diversity. Here, we contribute to this effort with new data summarising species richness from herpetological communities across habitat variation in a largely unknown, but central mountain range of Palawan.

Despite seemingly intensive sampling effort in this survey, our analysis suggests incomplete detection, especially of the more secretive/skulking species. This outcome reinforces findings from similar studies involving sites repeatedly surveyed, emphasising the importance of repeated survey-and-resurvey protocols for estimation of total biodiversity (Brown et al. 2000, 2017; Siler et al. 2011b; Supsup et al. 2017). Taxa with secretive behaviour and/or low detection probability (e.g. fossorial lizards of genus Brachymeles and Lygosoma; Siler et al. 2011a; Davis et al. 2014; Supsup et al. 2016) are obvious concerns, but species detection additionally could be hindered by variability of environmental conditions. As previously noted, many amphibians and reptiles are more active and detectable during the rainy season (Alcala and Brown 1998; Brown et al. 2001, 2012; Alcala et al. 2012); therefore, surveys conducted during the dry season may fail to detect species that are active in cooler habitats (Siler et al. 2007; McLeod et al. 2011; Supsup et al. 2016). Both variable detection probability and seasonal variation in atmospheric conditions are strong justifications for the critical importance of repeated, survey-and-resurvey biodiversity estimation methods (Alcala et al. 2012; Brown et al. 2012, 2013).

Simultaneous examination of morphology and genetic data often reveal the underestimated nature of species diversity, even in taxonomic groups with recent, well-developed taxonomies. In recent years, studies that rigorously examined these data have uncovered high levels of unrecognised diversity amongst Philippine frogs (Brown
Figure 8. Individual-based rarefaction (solid lines) and extrapolation (dashed lines) curves of herpetofaunal richness (upper panel) and diversity (lower panel) across primary habitat types in VAMR, with 95% confidence interval (shaded areas). Habitat types were Cultivation (CVT); Early Secondary Growth (ESG); Advanced Secondary Growth (ASG); and Old Growth Forest (OGF).

Figure 9. Variation of species richness along habitat and elevational gradient in the VAMR. The ellipse indicates habitat sampled in lower elevations, found along forest edges and disturbed areas, which yielded the least number of species during surveys including some samples of old growth forest from high elevations. and Guttmann 2002; Brown et al. 2009, 2017), lizards (Linkem et al. 2010; Siler et al. 2010, 2011a; Welton et al. 2013; Davis et al. 2014) and snakes (Van Rooijen and Vogel 2012; Weinell and Brown 2018). Species from the VAMR, urgently requiring taxonomic revision (Esselstyn et al. 2010), include *Hemiphyllodactylus typus* (Grismer et al. 2013), *Bronchocela cristatella*, *Lamprolepis smaragdina* (Linkem et al. 2013), *Eutropis indeprensus* (Barley et al. 2013, in press) and frogs of the genera *Kaloula* (Blackburn et al. 2013) and *Philautus* (Hertwig et al. 2011).

Our surveys identified a relatively high proportion of Palawan endemics, indicating that the VAMR is an important area for conservation of species restricted to this faunal region. The high concentration of endemic species on Palawan is attributed to the island’s complex geological history and biogeographical affinities, which have contributed to the generation of evolutionarily distinct taxa (Blackburn et al. 2010; Brown et al. 2013, 2016; Heitz et al. 2016; Oliver et al. 2018; Wood et al. 2020) along with the substantial extent of natural vegetation remaining on Palawan, particularly in montane forests, providing suitable microhabitats and resources for specialised, interior forest endemic species (Supsup and Asis 2018).
Figure 10. A cluster dendrogram of survey sites (habitat types) dissimilarities, based on species composition of amphibians and reptiles observed in the VAMR. Habitat types are represented by leaf point shapes (solid square – cultivation, open diamond – early secondary growth forest, solid triangle – advanced secondary growth forest, solid circle – old growth forest). Brackets indicate the two major groups of sites inferred here. Site codes are presented in Table 1.

Figure 11. Non-metric Multidimensional Scaling plot of sites and species. Left – showing the position of species (coded as follows: Babu = B. busuangensis, Chfu = C. fusca, Poma = P. moellendorffi, Inph = I. philippinicus, Leta = L. tagbanorum, Liac = L. acanthi, Lipa = L. palawanensis, Meli = M. ligayae, Ocla = O. laevis, Phev = P. everetti, Phil = P. longicrus, Pole = P. leucomystax, Poma = P. macrotis, Sasa = S. sanguinea, Stmu = S. nubilus, Brsp = B. cristatella, Cyre = C. redimiculas, Geat = G. athymus, Gege = G. gecko, Gemo = G. monarchus, Eumu = E. multifasciata, Hety = H. typlus, Apbo = A. boa, Bosc = B. schultzei, Dema = D. marenas, Dru = D. rubescens, Trsu = T. subannulatus) and sites (point shapes) along the NDMS axes. The grey line represents the overlaid branches of dendrogram from cluster analysis and groups are indicated by solid lines. Right – A bivariate plot depicting the standard deviation of sites scores per habitat type, represented by ellipses; grey lines indicate sites connected and associated with a particular habitat type.
The observed herpetofaunal richness in the VAMR is moderately high for the Palawan faunal region, comparable to records recently compiled for amphibians from Cleopatra’s Needle Mountain Range in Puerto Princesa (11 species; Jose and van Beijnen 2017), the Pagdanan Mountain Range and Dumaran Island (12 amphibians, 31 reptiles; Schoppe and Cervancia 2009) and Mount Bulanjao in southern Palawan (11 amphibians, 11 reptiles; CCI 2018). Despite slight differences in species richness amongst these sites, we suspect species richness is comparable amongst these areas. As discussed above, empirical information of species diversity is affected by detection probability, intensity of sampling and differences amongst sampling methods. Comparison of species richness amongst sites/studies is only possible if systematic and intensive surveys have been completed, accounting for potential effects of variable environmental conditions. Therefore, these records only indicate that a large portion of Palawan remains understudied, re-affirming the need for more comprehensive biodiversity surveys and re-surveys in Palawan’s forests (Brown et al. 2010, 2012, 2013; Sanguila et al. 2016).

Our species richness analysis, based on transect data, shows that our sampling sites in VAMR is estimated to have up to 35 species. The addition of 14 species from general searches supports this estimate. Recent studies on Philippine amphibian geographic ranges, based on species distribution modelling, may be partially consistent with this estimate, revealing that central Palawan, especially the VAMR, is predicted to have an intermediate to high proportion of amphibians (25–30 species; Anamza 2016). However, our estimates cannot be fully realised until follow-up surveys are conducted. High species richness observed in secondary growth forests can be attributed to the structural complexity of this habitat, particularly its understorey vegetation. Numerous studies have documented how structurally complex habitats are expected to provide high levels of species richness and diversity (Kerr and Packer 1997; Tews et al. 2004; Loehle et al. 2005; Gingold et al. 2010). Auffenberg and Auffenberg (1988) noted in their study of Philippine scincid lizards of southern Luzon that vegetation density and structural complexity are amongst the highest correlates of diverse lizard communities. Additionally, the presence of highly disturbance-tolerant species, observed along with persisting forest-obligates, might also have contributed to high richness in secondary growth forest. The relatively low species richness recorded in old growth forests is maybe due to the position of some samples in high elevations where it was expected to decrease (Figure 9). It is widely recognised that high elevations generally have low species richness because of reduced productivity caused by varying environmental conditions and that low elevations with appropriate conditions (climate, habitats) support more species than in cold high regions (O’Brien 1993; Rahbek 1995, 1997; McCain and Grytnes 2010). Amphibian and reptile richness has been documented to be positively influenced by warmer temperatures and presence of water bodies, which has often been observed in low elevations (Owen 1989; Qian et al. 2007; da Silveira Vasconcelos et al. 2010). Therefore, species, not adapted to the cold environment of high elevations, are expected to become less prevalent, particularly reptiles (Fu et al. 2007; McCain and Grytnes 2010). Cultivation or highly disturbed habitat supported the lowest species richness and diversity, emphasising how complete alteration or conversion of natural forests can negatively impact communities.

Our analysis revealed that herpetofaunal communities of the VAMR have two distinct assemblage patterns. Disturbance tolerant-species with broad geographical distributions characterised sites with secondary growth forests, whereas forest-dependent and rarely-detected species were recorded in sites with pristine forests. For instance, the commonly-detected species *P. leucomyxstax*, *O. laevis*, *E. multifasciata*, *G. gecko* and *D. marenae* are distributed almost throughout the Philippines and occupy a variety of habitats, from cultivated areas to pristine forests (Gaulke 2011; Diesmos et al. 2015; Leviton et al. 2018). A number of Palawan endemics are distributed throughout Palawan; these are broadly distributed habitat generalists (*I. philippinicus*, *S. nubilus*, *L. tagbanorum*, *M. ligayae*, *P. moellendorfii*, *P. everetti*, *B. Schulzei* and *D. rubescens*). Although, these species are often encountered in forested areas, they can be considered forest generalists and are frequently observed in different forest habitat types, including degraded forests. Forest-dependent species include endemic (*B. busuangensis*, *C. redimiculus*, *G. athymus* and *T. Schulzei*) and non-endemic (*C. fusca*, *L. palavansensis*, *P. longicus*, *B. cristatella* and *A. boa*). These species are distributed widely in Palawan forests, but are not commonly observed/encountered because of secretive behaviour and/or specialised micro-habitat preferences (e.g. the fully aquatic frog *B. busuangensis*; Diesmos et al. 2004c, 2015; Schoppe and Cervancia 2009) and the primary forest, mature tree-trunk obligate, crepuscular gekkonid lizard *G. athymus* (CES & RMB, personal observations). Our results demonstrate that species’ positions in our cluster dendrogram and NMDS plots are consistent with empirically-observed, field-based assessments of species microhabitats. These results also suggest that secondary growth and pristine forest habitats may be equally important in terms of supporting unique species assemblages.

In 2017, the conservation status of several Palawan amphibian species was re-assessed (IUCN SSC Amphibian Specialist Group 2018). Previously categorised “Threatened” endemic species (*B. busuangensis*, *M. ligayae*) were downgraded to “Near Threatened.” We support this assessment because these species remain abundant in documented areas of occurrence. In the VAMR, *M. ligayae* can be encountered regularly along rivers and streams and *B. busuangensis* which may be difficult to observe (because they spend most of their time in water under rocks), are ubiquitously present. Two endemic species were elevated, *S. nubilus* and *P. everetti*, from “Near
Threatened” to “Endangered”. However, we recommend to revert the status of *S. nubilus* to “Least Concern” because its extent of occurrence (EOO) is > 20,000 km², occurring throughout mainland Palawan and possibly neighbouring small islands (Diesmos et al. 2015). The population from the VAMR is abundant and this species undoubtedly is the most common stream frog along with *P. moellendorfii*. The status of *P. everetti* should be downgraded to “Vulnerable,” given that its EOO is > 5,000 km², above the threshold of the “Endangered” criterion. Although we only recorded a few individuals from the VAMR, its inconspicuous (quiet) behaviour, combined with the relatively dry condition of some sites during our surveys, might have hindered its detection. In our recent survey in Mount Bulanjao (CES unpublished data; see also CCI 2018) and during past survey work on Mt. Mantalingajan and Cleopatra’s Needle (RMB, personal observations), it was fairly common along undisturbed rivers, often encountered on sapling and understorey tree leaves near streams. Finally, we suggest the non-assessed endemic frog *L. tagbanorum* should be considered as “Least Concern” because it has a large EOO and is commonly encountered in riparian habitats, even in the absence of intact forest.

The majority of reptile species are non-assessed and we recommend to consider all non-assessed species (including Palawan endemics) listed here as “Least Concern” because they are common and widely distributed, with the exception of *B. cristatella* and *H. typus*. There are two recognised species of Bronchocele in the Philippines, *B. marmorata* (Luzon) and *B. cristatella* (remainder of the Philippines), but taxonomic issues plague this group, which needs to be re-evaluated with genomic data (see Brown et al. 2012, 2013; Siler et al. 2012; Supsup et al. 2017). We suggest the species status should be assessed once the taxonomic problem has been resolved. The rarely-seen lizard *H. typus* should be considered as “Data Deficient” due to taxonomic uncertainty and insufficient information on species distribution and population. The overall species conservation status indicates that no immediate conservation action is required for most species recorded from the VAMR. However, this may change in the near future if ongoing habitat destructions and other anthropogenic pressures (e.g. direct persecution) are not properly managed or minimised. In fact, between 1992 and 2010, Palawan’s original forest cover was reduced from 55 to 48 percent, with annual forest loss of ca. 5,500 hectares/year (PCSD 2015). The loss is due mainly to the increasing rate of forest conversion to agricultural plots (slash and burn), infrastructure development and large scale mining and quarrying, especially in lowland forests (PCSD 2015; Schoppe and Cervancia 2009).

Our study provides the first empirically habitat-based summary of amphibians and reptiles from the central Palawan mountains. Our results demonstrate that forests of the VAMR support a number of endemic amphibian and reptile species, several of which require conservation attention, despite the fact that the IUCN provides no justification for immediate conservation actions for most species. We believe that providing data-based justification for conservation initiatives will prevent further loss of remaining forest habitats and species, particularly for threatened taxa (e.g. sensitive amphibians such as the endemic species *L. acanthi*). However, prior to any conservation initiatives in the VAMR or other parts of Palawan, we encourage authorities to establish ecological baselines (considering both fauna and flora) to provide information about the process of conservation and, most importantly, to avoid potential information mismatch when prioritising areas or habitats for formal protection. Recently, review of protected areas in the country revealed that many have failed to assign the appropriate management zonation in critical habitats, creating a problematic mismatch between protected area boundaries and known key biodiversity areas (Mallari et al. 2001, 2015).

In this paper, we demonstrated a simple and straightforward approach, which may help decision-makers understand species assemblages in different habitat types. Our analysis showed that both pristine and secondary growth forests are perhaps equally important in supporting populations of different endemic species. This indicates that these-and likely other-habitat types should be considered when designing management zones. In the Philippines, currently-implemented management zonation is typically based on topographic data (elevation, slope) and forest cover; thus, species microhabitat requirements and biodiversity conservation value are barely considered (Mallari 2009; Mallari et al. 2015; Supsup and Asis 2018). In summary, we anticipate that this study may encourage wildlife researchers, managers and conservationists to thoroughly examine the ecological patterns of herpetofaunal communities across islands, habitats and biogeographic regions, in order to provide valuable and relevant information to guide conservation and management programmes.

Acknowledgements

We are grateful to the following organisations who provided technical and financial support for the study: Fauna and Flora International Philippines, Non-timber Forest Products – Exchange Program (NTFP), Nagkakaisang mga Tribu ng Palawan, Institution for the Development of Educational and Ecological Alternatives (IDEAS), Environmental Legal Assistance Center (ELAC) and the Palawan Council for Sustainable Development (PCSD); RMB’s work on Palawan has been supported by grants from the U.S. National Science Foundation (DEB 0073199, 0743491 and 1654388). We thank the authorities and local communities of the municipalities of Narra, Quezon and Aborlan for providing logistical support. We also thank the Palawan and Tagbanua Tribes and to the following colleagues who joined and provided their full support during our surveys: E. Rico, J. de Alban, R. Alamirano, N. Puna, J. Avanceña, D. Tablazon, A. Monzon, and the authors who provided support during our surveys: E. Rico, J. de Alban, R. Alamirano, N. Puna, J. Avanceña, D. Tablazon, A. Monzon.
References

Alcala AC, Brown WC (1998) Philippine Amphibians: An Illustrated Field Guide. Bookmark, Manila, 116 pp.
Alcala EL, Alcala AC, Dolino CN (2004) Amphibians and reptiles in tropical rainforest fragments on Negros Island, Philippines. Environmental Conservation 31: 254–261. https://doi.org/10.1017/S0376892904001407
Alcala AC, Bucol AA, Diesmos AC, Brown RM (2012) Vulnerability of Philippine amphibians to climate change. Philippine Journal of Science 141: 77–87.
AmphibiaWeb (2019) Information on amphibian biology and conservation. http://amphibiaweb.org/
Anamza T (2016) Analysis of stacked species distribution models provides a new perspective on biogeography and conservation of Philippine amphibians. MSc Thesis. University of Kansas.
Auffenberg W, Auffenberg T (1988) Resource partitioning in a community of Philippine skinks: (Sauria; Scincidae). Bulletin of the Florida State Museum of Biological Sciences, 201–247 pp.
Barley AJ, Diesmos AC, Siler CD, Martinez CM, Brown RM (in press) Taxonomic revision of Philippine Sun Skinks (Reptilia: Squamata; Scincidae: Eutropis), and descriptions of eight new species. Herpetological Monographs.
Blackburn DC, Bickford DP, Diesmos AC, Iskandar DT, Brown RM (2010) An ancient origin for the enigmatic Flat-Headed Frogs (Bombinatoridae: Barbourula) from the Islands of Southeast Asia. PLoS ONE 5: e12090. https://doi.org/10.1371/journal.pone.0012090
Boulenger GA (1894) On the herpetological fauna of Palawan and Balabac. Annals and Magazine of Natural History 14: 81–90. https://doi.org/10.1080/00222939408677772
Bray JR, Curtis JT (1957) An ordination of the upland forest communities of Southern Wisconsin. Ecological Monographs 27: 325–349. https://doi.org/10.1890/13-0133.1
Brown RM, Diesmos AC, Alcala AC (2001) The state of Philippine herpetology and the challenges for the next decade. Siliman Journal 42: 18–87.
Brown RM, McGuire JA, Ferner JW, Icarangal N, Kennedy RS (2000) Amphibians and reptiles of Luzon Island, II: preliminary report on the herpetofauna of Aurora Memorial National Park, Philippines. Hamadryad-Madras 25: 175–195.
Brown RM, Diesmos AC, Duya MV, Garcia HJ, Rico ELB (2010) New Forest Gecko (Squamata; Gekkonidae; Genus Luperosaurus) from Mt. Mantalingajan, Southern Palawan Island, Philippines. Journal of Herpetology 44: 37–48. https://doi.org/10.1670/08-316.1
Brown RM, Prue A, Ong CK, Gaukule M, Sanguila MB, Siler CD (2017) Taxonomic reappraisal of the Northeast Mindanao Stream Frog, Sanguirana albotuberculata (Inger 1954), Validation of Rana mearsii, Stejneger 1905, and description of a new species from the Central Philippines. Herpetological Monographs: 182–203. https://doi.org/10.1655/HERPMONOGRAPHS-D-16-00009.1
Brown RM, Su Y-C, Barger B, Siler CD, Sanguila MB, Diesmos AC, Blackburn DC (2016) Phylogeny of the island archipelago frog genus Sanguirana: Another endemic Philippine radiation that diversified “Out-of-Palawan.” Molecular Phylogenetics and Evolution 94: 531–536. https://doi.org/10.1016/j.ympev.2015.10.010
Brown RM, Oliveros CH, Siler CD, Fernandez JB, Welton LJ, Buenavente PAC, Diesmos MLL, Diesmos AC (2012) Amphibians and reptiles of Luzon Island (Philippines), VII: Herpetofauna of Ilocos Norte Province, Northern Cordillera Mountain Range. Check List 8: 469–490. https://doi.org/10.15560/8.3.469
Brown RM, Siler CD, Oliveros CH, Esselstyn JG, Diesmos AC, Hosner PA, Linkem CW, Barley AJ, Oaks JR, Sanguila MB, Welton LJ, Blackburn DC, Moyle RG, Townsend Peterson A, Alcala AC (2013) Evolutionary processes of diversification in a Model Island Archipelago. Annual Review of Ecology, Evolution, and Systematics 44: 411–435. https://doi.org/10.1146/annurev-ecolsys-110411-160323
Brown WC, Alcala AC (1970) The zoogeography of the herpetofauna of the Philippine Islands, a fringing archipelago. California Academy of Sciences 38: 105–130.
Caussanet RM (2012) Determinant of species diversity, abundance and habitat associations of the anuran fauna from forest fragments in Cavite, Luzon Island, Philippines. PhD Thesis. De La Salle University-Manila.
CCI (2018) High conservation value areas assessment in West Mt. Baluajan, Southern Palawan. Center for Conservation Innovations Philippines, Tagaytay City, 100 pp.
Chan KO, Brown RM (2017) Did true frogs “dispersify”? Biology Letters 13: 20170299. https://doi.org/10.1098/rsbl.2017.0299
Chao A, Gotelli NJ, Hsieh TC, Sander EL, Ma KH, Colwell RK, Ellison AM (2014) Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. Ecological Monographs 84: 45–67. https://doi.org/10.1890/13-0133.1
Clarke KR, Warwick RM (1994) Similarity-based testing for community pattern: the two-way layout with no replication. Marine Ecology 118: 167–176. https://doi.org/10.1007/BF0069231
Davis DR, Feller KD, Brown RM, Siler CD (2014) Evaluating the diversity of Philippine Slimy Skinks of the Brachymeles bonitae Complex (Reptilia: Squamata: Scincidae): redescription of B. triactyla and descriptions of two new species. Journal of Herpetology 48: 480–494. https://doi.org/10.1670/13-173
Dickerson RE, Merrill ED, McGregor RC, Schultz W, Taylor EH, Herre AW (1928) Distribution of life in the Philippines. Monograph. Bureau of Printing, Manila, Philippines 2: 1–322.
Diesmos AC (1998) The amphibian faunas of Mt. Banahao, Mt. San Cristobal, and Mt. Maquiling, Luzon Island, Philippines. MSc Thesis. University of the Philippines Los Baños.

Diesmos AC, Brown RM, Gee GVA (2004a) Preliminary report on the amphibians and reptiles of Balbalasang-Balbalan National Park, Luzon Island, Philippines. Syltavrop, Technical Journal of Philippine Ecosystems and Natural Resources 13: 63–80.

Diesmos AC (2008) Ecology and diversity of herpetofaunal communities in fragmented lowland rainforests in the Philippines. PhD Thesis. National University of Singapore.

Diesmos AC, Palomar N (2004) On the role of biological diversity in the Palawan Corridor. In: Anda RD, Tabangay-Baldero JG (Eds) Surubien: Strategies to Conserve Palawan’s Biodiversity. Provincial Government of Palawan, Palawan Council for Sustainable Development Staff, Department of Environment and Natural Resources-MIMAROPA Region IV, Palawan NGO Network Inc., and Conservation International, Puerto Princesa City, Philippines.

Diesmos AC, Gee GV, Diesmos ML, Brown RM, Widmann PJ, Dimalibot JC (2004b) Rediscovery of the Philippine forest turtle, Heosemys leytensis (Chelonia: Bataguridae), from Palawan Island, Philippines. Asian Herpetological Research 10: 22–27.

Diesmos AC, Diesmos ML, Gee GV (2004c) Lost frogs and reptiles rediscovered on Palawan Island, Philippines. Oryx 38: 1–255.

Diesmos AC, Watters JL, Huron NA, Davis DR, Alcala AC, Cymbrie RI, Afaung LE, Gee-Das G, Sison RV, Sangiula MB, Penrod ML, Labonte MJ, Davey CS, Levine EA, Diesmos ML, Sy EY, Welton LJ, Brown RM, Siler CD (2015) Amphibians of the Philippines, Part I: Checklist of the Species. Proceedings of the California Academy of Sciences 62: 457–539.

DOST-PAGASA (2019) Department of Science and Technology – Philippine Atmospheric, Geophysical and Astronomical Services Administration (DOST-PAGASA) Climate Data. http://bagong.pagasa.dost.gov.ph/climate/

Esselstyn JA, Widmann P, Heaney LR (2004) The mammals of Palawan Island, Philippines. Proceedings of the Biological Society of Washington 117: 271–302.

Esselstyn JA, Timm RM, Brown RM (2009) Do geological or climatic processes drive speciation in dynamic archipelagos? The tempo and mode of diversification in Southeast Asian shrews. Evolution 63: 2595–2610. https://doi.org/10.1111/j.1558-5646.2009.00743.x

Esselstyn JA, Oliveros CH, Peterson AT, McGuire JA, Brown RM (2010) Integrating phylogenetic and taxonomic evidence illuminates complex biogeographic patterns along Huxley’s modification of Wallace’s Line: Phylogenetic patterns along Wallace’s Line. Journal of Biogeography 37: 2054–2066. https://doi.org/10.1111/j.1365-2699.2010.02378.x

Everett AH (1889) Remarks on the zoological relationships of the Island of Palawan and some adjacent Islands. Proceedings of the Zoological Society of London 57: 220–228. https://doi.org/10.1111/j.1469-7998.1889.tb06766.x

Faith DP, Minchin PR, Belbin L (1987) Composition dissimilarity as a robust measure of ecological distance. Vegetation 69: 57–68. https://doi.org/10.1007/BF00386878

Fernando ES, Suh MH, Lee J, Lee DK (2008) Forest formations of the Philippines. ASEAN-Korea Environmental Cooperation Unit, 232 pp.

Ferner JW, Brown RM, Sison RV, Kennedy RS (2000) The amphibians and reptiles of Panay Island, Philippines. Asiatic Herpetological Research 9: 34–70. https://doi.org/10.5962/bhl.part.15561

Frost DR (2019) Amphibian Species of the World: an Online Reference. Version 6.0. https://amphibiaweb.org/

Fu C, Wang J, Pu Z, Zhang S, Chen H, Zhao B, Chen J, Wu J (2007) Elevational gradients of diversity for lizards and snakes in the Hengduan Mountains, China. Biodiversity and Conservation 16: 707–726. https://doi.org/10.1007/s10531-005-4382-4

Gaulke M (2011) Herpetofauna of Panay Island, Philippines. Edition Chimaira, 390 pp.

Gingold R, Mundo-Ocampo M, Holovachov O, Rocha-Olivares A (2010) The role of habitat heterogeneity in structuring the community of intertidal free-living marine nematodes. Marine Biology 157: 1741–1753. https://doi.org/10.1007/s00227-010-1447-z

Goodman SM, Willard DE, Gonzales PC (1995) The birds of Sibuyan Island, Romblon Province, Philippines: with particular reference to elevational distribution and biogeographic affinities. Fieldiana Zoology 82: 1–57. https://doi.org/10.5962/bhl.title.3526

Griffin LE (1909) A list of snakes found in Palawan. Philippine Journal of Science 4: 595–601.

Grissmer LL, Wood Jr. PL, Anuar S, Muin MA, Quah ESH, McGuire JA, Brown RM, Tri JV (2013) Integrative taxonomy uncovers high levels of cryptic species diversity in Hemiphlodactylus Bleeker, 1860 (Squamata: Gekkonidae) and the description of a new species from Peninsular Malaysia. Zoological Journal of the Linnean Society 169: 849–880. https://doi.org/10.1111/zol.12064

Heaney LR (1985) Zoogeographic evidence for middle and late Pleistocene land bridges to the Philippine Islands. Modern Quaternary Research in Southeast Asia 9: 127–144.

Heaney LR, Heideman PD, Rickart EA, Uzturrun RB, Klompen JSH (1989) Elevational zonation of mammals in the central Philippines. Journal of Tropical Ecology 5: 259–280. https://doi.org/10.1017/S026647440003643

Heaney LR (1991) A synopsis of climatic and vegetational change in Southeast Asia. Climatic Change 19: 53–61. https://doi.org/10.1007/BF00142213

Heaney LR (2001) Small mammal diversity along elevational gradients in the Philippines: an assessment of patterns and hypotheses. Global Ecology and Biogeography 10: 15–39. https://doi.org/10.1046/j.1466-822X.2001.00227.x

Heitz BB, Diesmos AC, Freitas ES, Ellsworth ED, Grismer LL, Aow Cristobal, and Mt. Maquiling, Luzon Island, Philippines. MSc Thesis, University of the Philippines Los Baños.

Hengduan Mountains, China. Biodiversity and Conservation 16: 707–726. https://doi.org/10.1007/s10531-005-4382-4

Hidayatullah MA, Minta MD, Anees M, Sheik MMT, Quah ESH, McGuire JA, Brown RM, Siler CD (2014) A new Supple Skink, Genus Lysomogarma (Reptilia: Squamata: Scincidae), from the Western Philippines. Herpetologica 72: 352–361. https://doi.org/10.1655/Herpetologica-D-16-0023.1

Hertwig ST, Das I, Schweizer M, Brown R, Haas A (2011) Phylogenetic relationships of the Rhacophorus everetti-group and implications for the evolution of reproductive modes in Philautus (Amphibia: Anura: Rhacophoridae): Evolution of Sundaland Bush Frogs. Zoologica Scripta 41: 29–46. https://doi.org/10.1111/j.1463-6409.2011.00499.x

Heyer WR, Downey LA, McDermid RW, Hayek LC, Foster MS [Eds] (1994) Measuring and monitoring biological diversity: standard methods for amphibians. Smithsonian Institution Press, Washington, 364 pp.

Hsieh TC, Ma KH, Chao A (2016) iNEXT: an R package for rarefaction and extrapolation of species diversity (Hill numbers). Methods in Ecology and Evolution 7: 1451–1456. https://doi.org/10.1111/2041-210X.12613

Hutterer R, Balete DS, Giarla TC, Heaney LR, Esselstyn JA (2018) A new genus and species of shrew (Mammalia: Soricidae) from Hengduan Mountains, China. Biodiversity and Conservation 16: 707–726. https://doi.org/10.1007/s10531-005-4382-4

Hutterer R, Balete DS, Giarla TC, Heaney LR, Esselstyn JA (2018) A new genus and species of shrew (Mammalia: Soricidae) from Herpetozoa 33: 95–111 (2020)
Christian E. Supsup et al.: Amphibians and Reptiles from Victoria-Anepahan Mountain Range

Palawan Island, Philippines. Journal of Mammalogy. https://doi.org/10.1093/jmammal/gyy041

Inger RF (1954) Systematics and zoogeography of Philippine amphibians. Chicago Natural History Museum, Chicago, 364 pp. https://doi.org/10.5962/bhl.title.5571

IUCN (2019) IUCN Red List of Threatened Species. Version 2018.2. http://www.iucnredlist.org/

IUCN SSC Amphibian Specialist Group (2018) The IUCN Red List of Threatened Species. https://www.iucnredlist.org/

José ED, van Beijnen J (2017) Notes on the forest frogs of Cleopatra’s Needle Mountain Range, with special reference to the newly defined and expanded geographical range of Pelophryne albotaeniata (Barbour, 1938): for the conservation of the forests of northern Palawan Island, Philippines. Journal of Natural History – National Museum of the Philippines 2: 33–37.

Kerr JT, Packer L (1997) Habitat heterogeneity as a determinant of mammal species richness in high-energy regions. Nature 385: 252–254. https://doi.org/10.1038/385252a0

Levтон AE, Siler CD, Weinell JL, Brown RM (2018) Synopsis of the Snakes of the Philippines: A Synthesis of Data from Biodiversity Repositories, Field Studies, and the Literature. Proceeding of the California Academy of Sciences, 66 pp.

Lim H, Chua V, Benham P, Oliveros C, Abdul Rahman M, Moyle R, Leviton AE, Siler CD, Weinell JL, Brown RM (2018) Synopsis of the herpetological Directory of Important Bird Areas. Bookmark, 490 pp.

Linkern CW, Diesmos AC, Brown RM (2010) A new species of Scincid Lizard (Genus Sphenomorphus) from Palawan Island, Philippines. Herpetologica 66: 67–79. https://doi.org/10.1655/08-074.1

Linkern CW, Brown RM, Siler CD, Evans BJ, Austin CC, Iskandar DT, Diesmos AC, Supratna J, Andayani N, McGuire JA (2013) Stochastic faunal exchanges drive diversification in widespread Wallacean and Pacific island lizards (Squamata: Scincidae: Lamprolepis smaragdina). Journal of Biogeography 40: 507–520. https://doi.org/10.1111/jbi.12022

Loehle C, Wigley TB, Shipman PA, Fox SF, Rutzmoser S, Thill RE, Melchior MA (2005) Herpetofaunal species richness responses to forest landscape structure in Arkansas. Forest Ecology and Management 209: 293–308. https://doi.org/10.1016/j.foreco.2005.02.007

Mallari NAD (2009) Maximising the value of ecological and socio-economic data in support of conservation planning for key understorey bird species in Palawan, Philippines. PhD Thesis. Manchester Metropolitan University.

Mallari NAD, Tabaranza BR, Crosby MJ (2001) Key Conservation Sites in the Philippines: a Harbison Foundation & Birdlife International Directory of Important Bird Areas. Bookmark, 490 pp.

Mallari NAD, Collard NJ, Lee DC, McGowan PJK, Wilkinson R, Marsden SJ (2011) Population densities of understory birds across a habitat gradient in Palawan, Philippines: implications for conservation. Oryx 45: 234–242. https://doi.org/10.1017/S0030605310010313

Mallari NAD, Collard NJ, McGowan PJK, Marsden SJ (2015) Philippine protected areas are not meeting the biodiversity coverage and management effectiveness requirements of Aichi Target 11. Ambio 45: 313–322. https://doi.org/10.1007/s13280-015-0740-y

McCain CM, Geytanes JA (2010) Elevational gradients in species richness. In Encyclopedia of Life (ELS). John Wiley & Sons, Ltd, Chichester, 10 pp. https://doi.org/10.1002/9780470015902.a0022548

McGuire JA, Kiew HB (2001) Phylogenetic systematics of Southeast Asian flying lizards (Iguania: Agamidae: Draco) as inferred from mitochondrial DNA sequence data. Biological Journal of the Linnean Society 72: 203–229. https://doi.org/10.1006/bijl.2000.0487

Meleod DS, Siler CD, Diesmos AC, Diesmos ML, Garcia VS, ArkenCEO AO, Balaquit KL, Uy CC, Villasearan MM, Yarra EC (2011) Amphibians and reptiles of Luzon Island, V: the herpetofauna of Angat Dam Watershed, Bulacan Province, Luzon Island, Philippines. Asian Herpetological Research 2: 177–198. https://doi.org/10.3724/SP.J.1245.2011.00177

Minchin PR (1987) An evaluation of the relative robustness of techniques for ecological ordination. Vegetatio 69: 89–107. https://doi.org/10.1007/BF0038690

O’Brien EM (1993) Climatic gradients in woody plant species richness: towards an explanation based on an analysis of southern Africa’s woody flora. Journal of Biogeography 20: 181–198. https://doi.org/10.2307/2845670

Oksanen J (2013) Vegan: an introduction to ordination. CRAN.

Oliver PM, Brown RM, Kraus F, Rittmeyer E, Travers SL, Siler CD (2018) Lizards of the lost arcs: mid-Cenozoic diversification, persistence and ecological marginalization in the West Pacific. Proceedings of the Royal Society B 285: 20171760. https://doi.org/10.1098/rspb.2017.1760

Oliveros CH, Moyle RG (2010) Origin and diversification of Philippine bulbuls. Molecular Phylogenetics and Evolution 54: 822–832. https://doi.org/10.1016/j.ympev.2009.12.001

Owen JG (1989) Patterns of herpetofaunal species richness: relation to temperature, precipitation, and variance in elevation. Journal of Biogeography 16: 141–150. https://doi.org/10.2307/2845088

PCSD (2015) State of the environment of Palawan: 2015 updates. Palawan Council for Sustainable Development, Puerto Princesa, 76 pp.

Qian H, Wang X, Wang S, Li Y (2007) Environmental determinants of amphibian and reptile species richness in China. Ecography 30: 471–482. https://doi.org/10.1111/j.0906-7590.2007.05025.x

Rahbek C (1995) The elevational gradient of species richness: a uniform pattern? Ecography 18: 200–205. https://doi.org/10.1111/j.1600-0587.1995.tb00341.x

Rahbek C (1997) The relationship among area, elevation, and regional species richness in neotropical birds. The American Naturalist 149: 875–902. https://doi.org/10.1086/286028

R Development Core Team (2018) R: A language and environment for statistical computing. https://www.R-project.org/

Sangguia MB, Cobb KA, Siler CD, Diesmos AC, Alcala AC, Brown RM (2016) The amphibians and reptiles of Mindanao Island, southern Philippines, II: the herpetofauna of northeast Mindanao and adjacent islands. ZooKeys 624: 1–132. https://doi.org/10.3897/zookeys.624.9814

Schoppe S, Cervancia M (2009) Herpetological surveys along Pagdanan Range and Dumaran Island, Northern Palawan, Philippines. Hamadryad 34: 95–106.

Sheldon FH, Lim HC, Moyle RG (2015) Return to the Malay Archipelago: How and why biogeographical patterns evolved. Science 349: 1456–1459. https://doi.org/10.1126/science.aab4837

Siler CD, Linkern CW, Diesmos AC, Alcala AC (2007) A new species of Platymantis (Amphibia: Anura: Ranidae) from Panay Island, Philippines. Hamadryad 34: 95–106. https://doi.org/10.3897/zookeys.624.9814

Siler CD, Jones RM, Welton LJ, Brown RM (2011a) Redescription of Brachymeles mcdonaldi (Brachymeles: Tetradactyl Philippine Slender Skinks (Genus Brachymeles). Herpetological Journal 156: 91–113. https://doi.org/10.1655/08-074.1

Thompson SD, Hedges SP, Siler CD, Jones RM (2011b) A new species of Platymantis (Amphibia: Anura: Ranidae) from Panay Island, Philippines. Herpetological Journal 156: 91–113. https://doi.org/10.1655/08-074.1
Supplementary material 1

Occurrence records of amphibians and reptiles from Victoria-Anepahan Mountain Range of Palawan Island, Philippines

Authors: Christian Supsup, Augusto Asis, Uldarico Carestia Jr, Arvin Diesmos, Neil Aldrin Mallari, Rafe Brown

Data type: Occurrence records

Explanation note: The file contains data on habitat types, geographic coordinates and species abundance.

Copyright notice: This dataset is made available under the Open Database License (http://opendatacommons.org/licenses/odbl/1.0/). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: https://doi.org/10.3897/herpetozoa.33.47293.suppl1