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

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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 endemicity 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; Esseslstyn 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 Guttman 2002; Esselstyn et al. 2009, 2010). More recent reconsiderations, 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 Guttman 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 Guttman 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 foxworthyi*, *Xanthostemon speciosus*, *Gymnostoma* sp. and *Tristaniopsis* sp., *Diospyros* sp., *Ilex* sp. and in high elevations (> 550m) 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

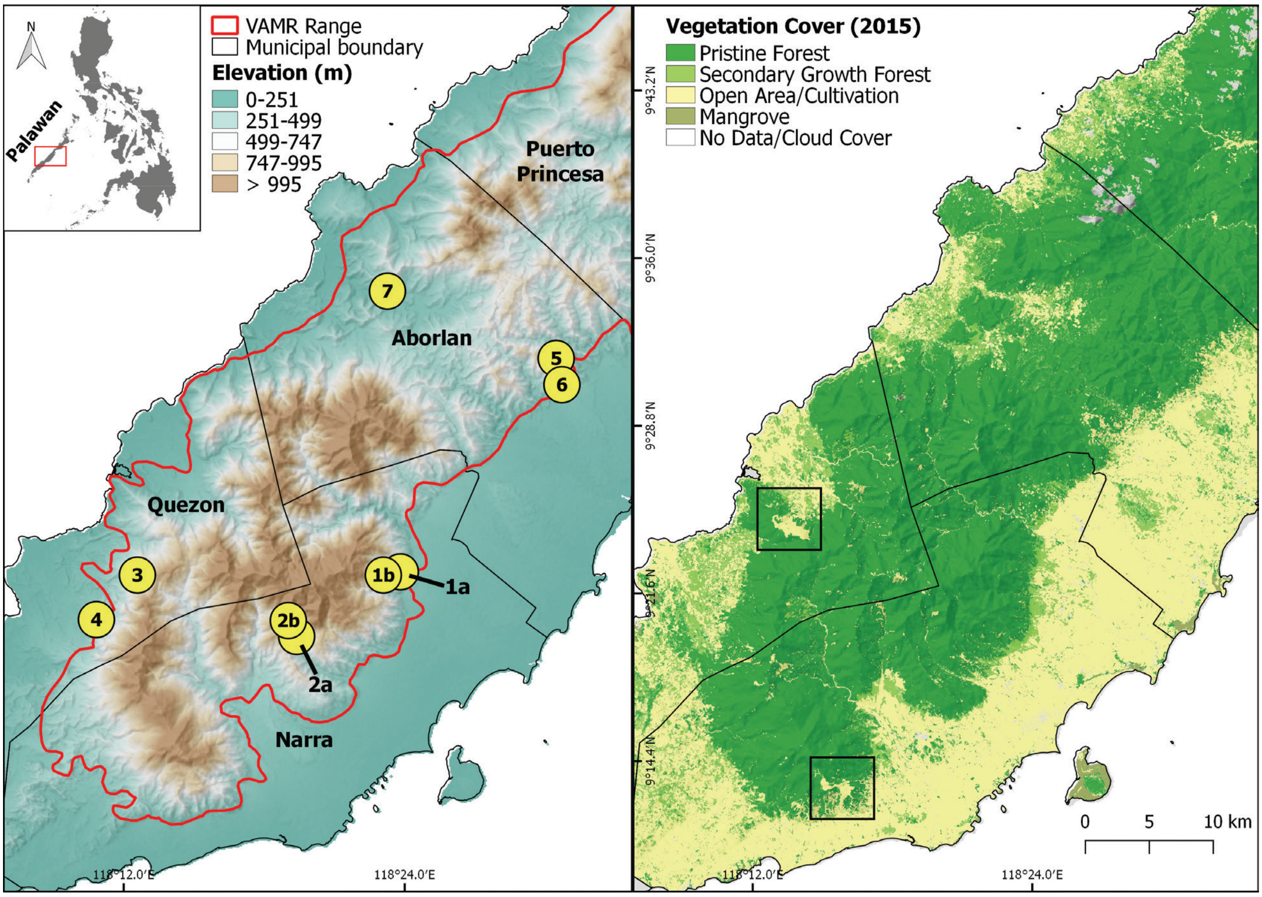

Figure 1. Map of Victoria-Anepahan Mountain Range (VAMR), of central Palawan Island, Philippines (inset map). The right panel includes sampling sites, indicated by numbered circles. The extent of the VAMR is indicated (red polygon) and the elevation represented by incremental coloured shading. The left 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	Muncipality 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°31'33.96"N, 118°30'28.116"E
6	Muncipality of Aborlan	Barangay Iraan	IT1-3 – ESG*; IT4-5 – ASG**	9°30'26.64"N, 118°30'42.84"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

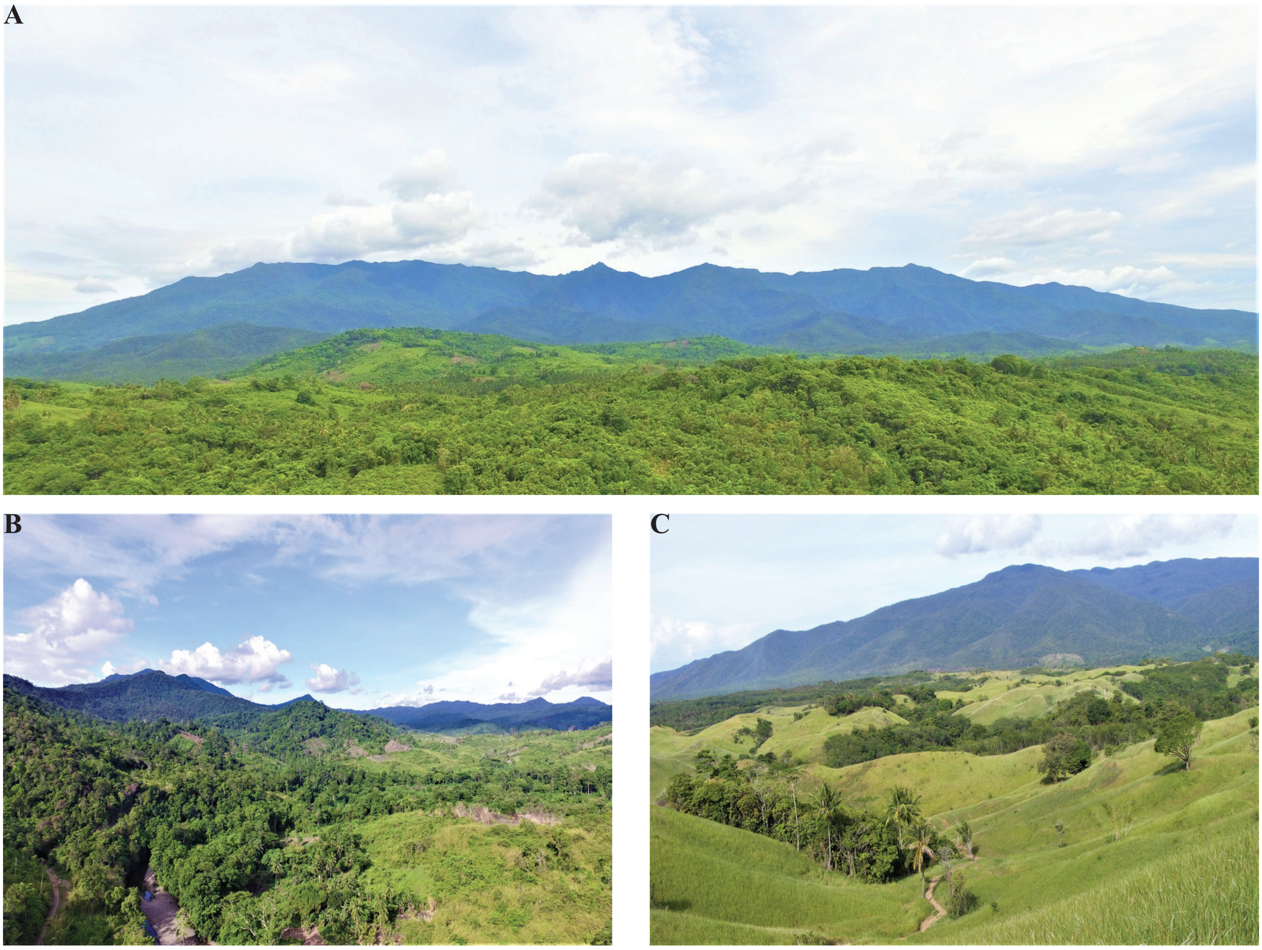

Figure 2. The Victoria-Anepahan Mountain Range (VAMR). **A** – the VAMR massif viewed from Site 7, showing the extent of pristine forest at higher elevation and degraded secondary growth forest at lower elevation; **B** – sampling in Site 7, with recently cleared patches of forest; **C** – the VAMR massif, as viewed from site 2, with emerging grasses characterising previously-cleared forests in relatively flat areas at the base of the massif. Photos by C. Supsup and A. Asis

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 endemicity (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 analyis findings: two distinct parterns of assemblage (Fig. 11). Species situated in secondary forest (Group 1) included 11 frogs (*Pulchrana moellendorffi*, *Ingerophryrnus philippinicus*, *Leptobrachium tagbanorum*, *Limonectes acanthi*, *Megophrys ligayae*, *Occidozyga laevis*, *Philautus everetti*, *Polypedates leucomystax*, *Polypedates macrotis*, *Staurois nubilus*, *Sanguirana sanguinea*), three lizards (*Eutropis multifasciata*, *Gekko gecko*, *Hemiphyllodactylus typus*) and three snakes (*Dendrelaphis marenae*, *Dryophiops rubescens*, *Boiga schultzei*); and species positioned in pristine forests (Group 2) included four frogs (*Barbourula busuangensis*, *Chaperina fusca*, *Limnonectes palavanensis*, *Philautus longicrus*), four lizards (*Bronchocela cirstatella*, *Cyrtodactylus redimiculus*, *Gekko athymus*, *Gekko monarchus*) 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-Anephan 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 busuangensis 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, 4, 7	VU	ACD 8589, 8599
Limnonectes palavanensis (Boulenger 1894)	2a, 3, 4	LC	ACD 8573, 8581, 8596–98
Occidozyga laevis (Günther 1858)	1a, 5	LC	ACD 8529
Megophryidae			
Leptobrachium 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	2a, 4	LC	ACD 8566–68, 8590
Kaloula pulchra Gray 1831	1a	LC	no specimens
Ranidae			
Pulchrana moellendorffi (Boettger 1893) *	1a, 7	LC	ACD 8518, 8528
Sanguirana sanguinea (Boettger 1893) *	1a, 2ab, 4, 5, 6, 7	LC	ACD 8522, 8527, 8545, 8554, 8561, 8588
Staurois nubilus (Mocquard 1890) *	1a, 4, 7	NT	ACD 8524, 8586, 8592–93
Rhacophoridae			
Philautus everetti (Boulenger 1894) *	5	EN	no specimens
Philautus longicrus (Boulenger 1894)	1ab, 2ab, 3, 4, 6	NT	ACD 8520, 8537–38, 8550–51, 8553, 8555–56, 8565
Polypedates leucomystax (Gravenhorst 1829)	6	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 McGuire and Alcala 2000*	4	NE	ACD 8602
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 gecko Linnaeus 1758	4, 7	NE	ACD 8600
Gekko monarchus (Schlegel 1836)	1a, 2a, 4, 6	LC	ACD 8525, 8564, 8572, 8591
Hemidactylus frenatus Schlegel 1836	7	LC	no specimens
Hemiphyllodactylus typus Bleeker 1860	6	NE	no specimens
Scincidae			
Eutropis multifaciata (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, 7	NE	no specimens
REPTILIA (SNAKES)			
Colubridae			
Boiga schultzei Taylor 1923 *	6	LC	no specimens
Dendrelaphis marenae Vogel and Van Rooijen 2008	1a, 4	NE	ACD 8583
Dryophiops rubescens (Gray 1834)	5	NE	no specimens
Lycodon sealei Leviton 1955 *	5	LC	no specimens
Ptyas carinata (Günther 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 8601
Lamprophiidae			
Psammodynastes pulverulentus (Boie 1827)	2a	NE	ACD 8543, 8549
Natricidae			
Rhabdophis chrysargos (Schlegel 1837)	2a, 4	LC	ACD 8544, 8584
Pareidae			
Aplopeltura boa (Boie 1828)	1a, 2a, 3, 4, 6	LC	ACD 8516, 8558, 8571, 8594
Viperidae			
Trimeresurus schultzei Griffin 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** – *Pulchrana 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 boa*; **I** – *Boiga schultzei*; **J** – *Calliophis 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.

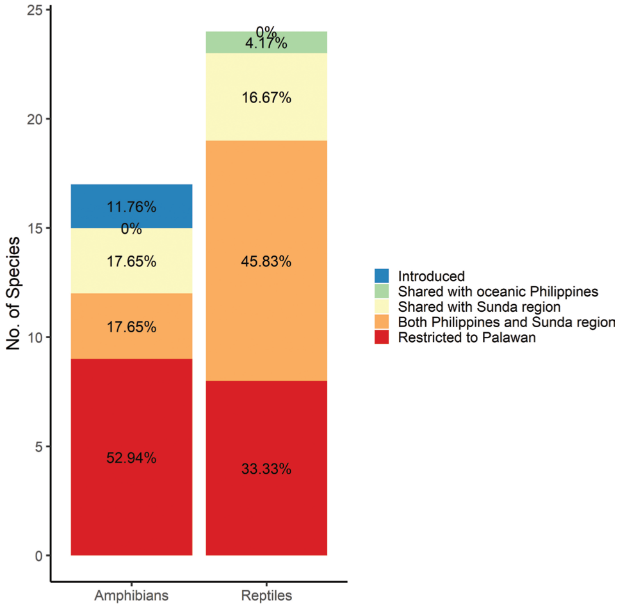

Figure 5. Totals of amphibians and reptiles recorded from the Victoria-Anepahan Mountain Range (VAMR) and species residency status proportions (by percentage), based on current understanding of their distributional range.

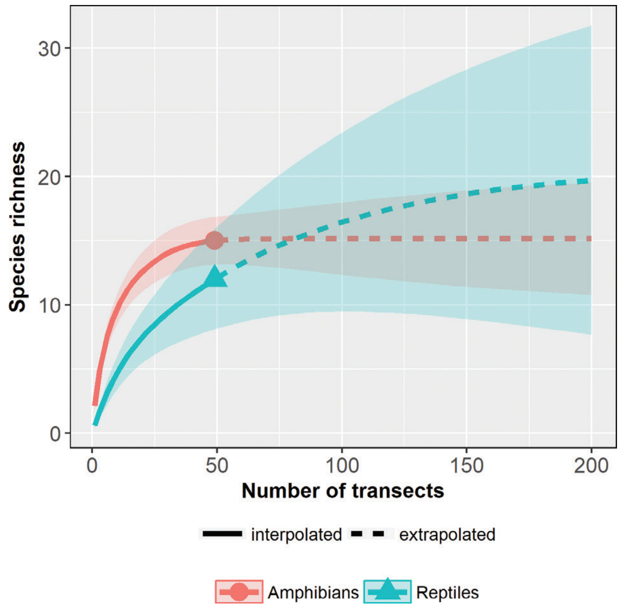

Figure 7. Sample-sized-based rarefaction (solid lines) and extrapolation curves (dashed lines) of amphibian and reptile richness in sampling sites, with 95% confidence interval (shaded areas).

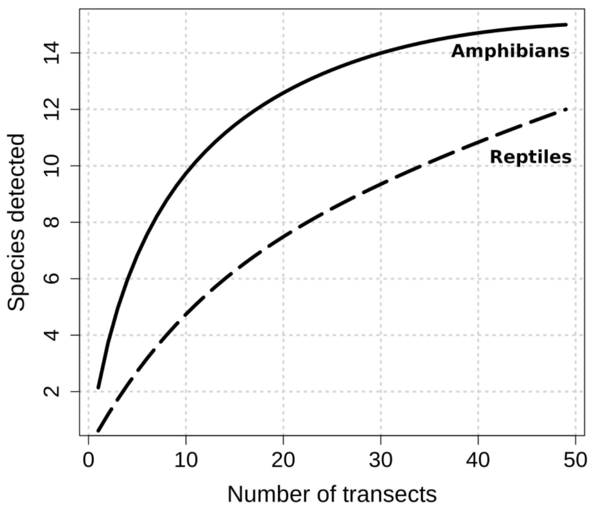

Figure 6. A species accumulation curve, depicting the cumulative number of amphibian and reptile species detected in the Victoria-Anepahan Mountain Range (VAMR).

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

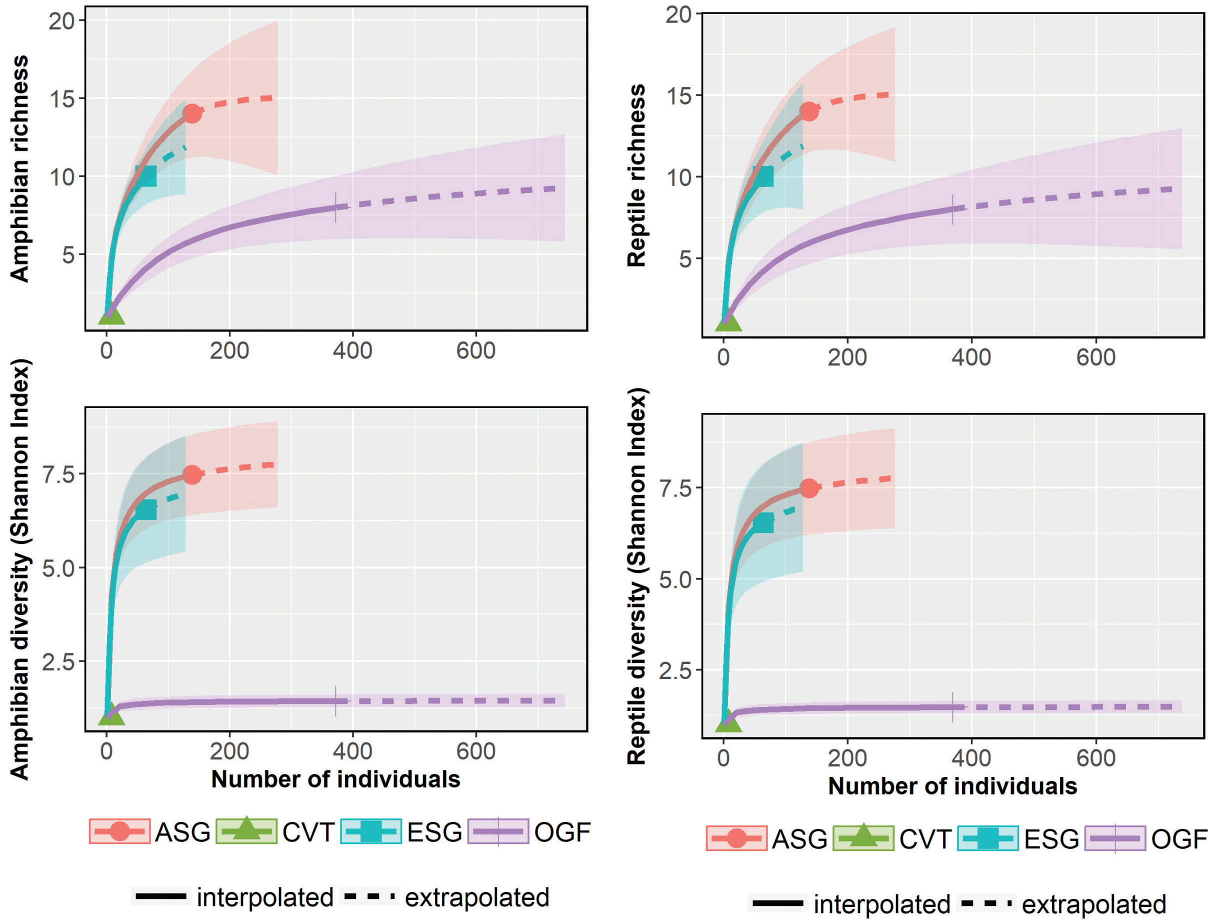

Figure 8. Individual-based rarefaction (solid lines) and extrapolation (dashed lines) curves of herpetofaunal richness (upper panel) and diversity (lower panel) across primary habitat types in VAMR, with 95% confidence interval (shaded areas). Habitat types were Cultivation (CVT); Early Secondary Growth (ESG); Advanced Secondary Growth (ASG); and Old Growth Forest (OGF).

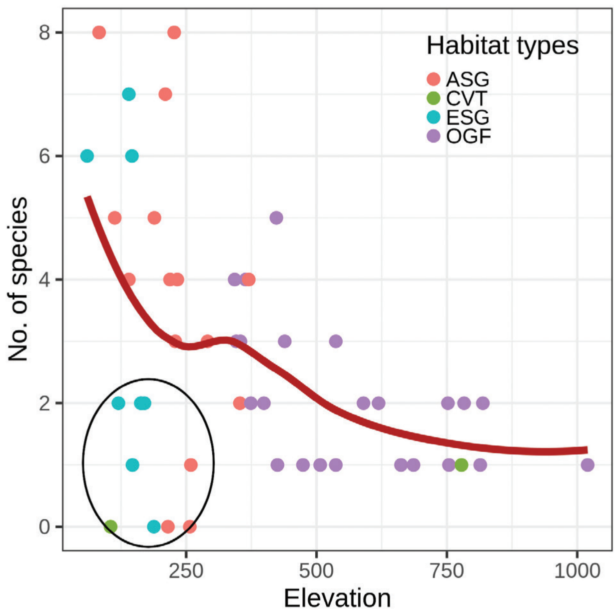

Figure 9. Variation of species richness along habitat and elevational gradient in the VAMR. The ellipse indicates habitat sampled in lower elevations, found along forest edges and disturbed areas, which yielded the least number of species during surveys including some samples of old growth forest from high elevations.

and Guttman 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).

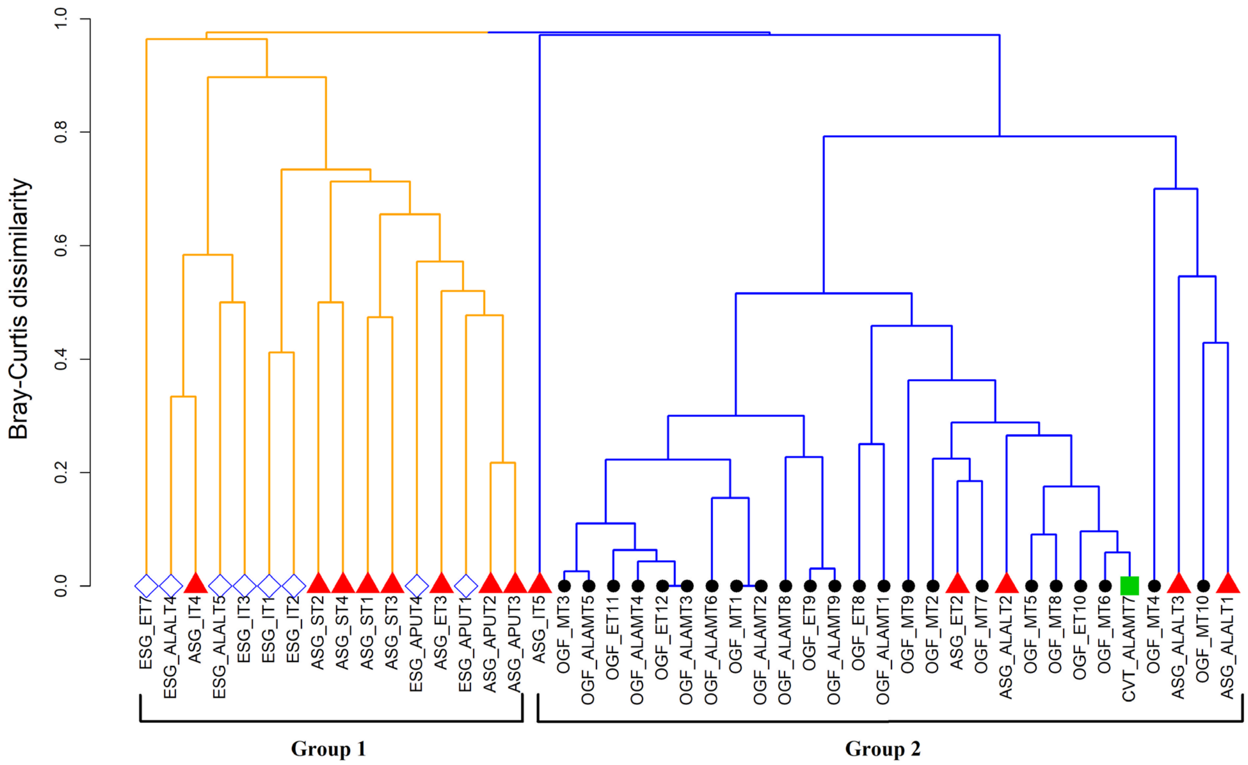

Figure 10. A cluster dendrogram of survey sites (habitat types) dissimilarities, based on species composition of amphibians and reptiles observed in the VAMR. Habitat types are represented by leaf point shapes (solid square – cultivation, open diamond – early secondary growth forest, solid triangle – 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.

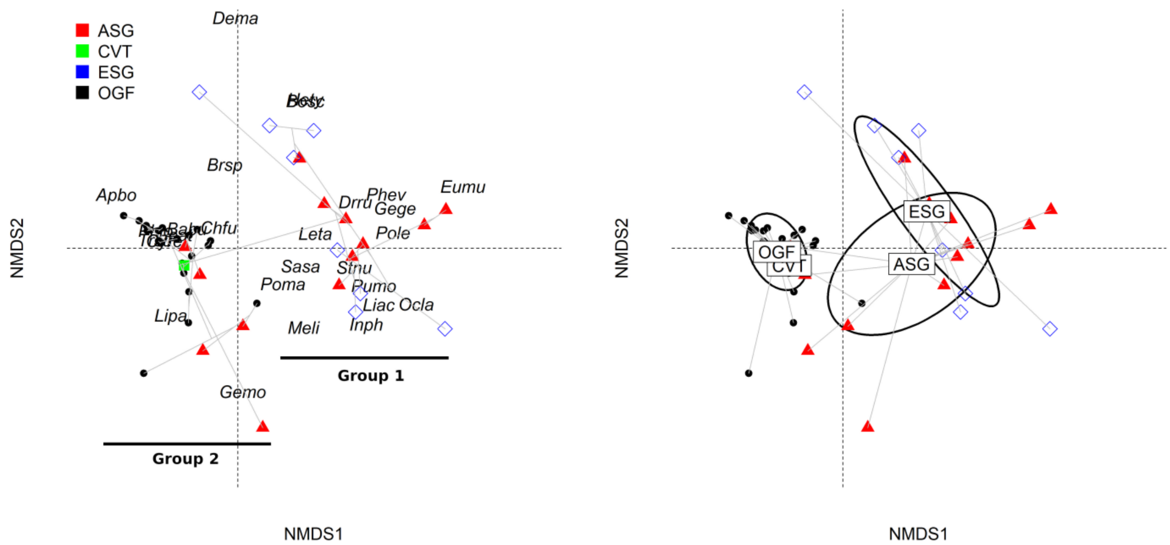

Figure 11. Non-metric Multidimensional Scaling plot of sites and species. **Left** – showing the position of species (coded as follows: Babu = *B. busuangensis*, Chfu = *C. fusca*, Poma = *P. moellendorffi*, Inph = *I. philippinicus*, Leta = *L. tagbanorum*, Liac = *L. acanthi*, Lipa = *L. palavanensis*, Meli = *M. ligayae*, Ocla = *O. laevis*, Phev = *P. everetti*, Phlo = *P. longicrus*, Pole = *P. leucomystax*, Poma = *P. macrotis*, Sasa = *S. sanguinea*, Stnu = *S. nubilus*, Brsp = *B. cristatella*, Cyre = *C. redimiculus*, Geat = *G. athymus*, Gege = *G. gecko*, Gemo = *G. monarchus*, Eumu = *E. multifasciata*, Hety = *H. typus*, Apbo = *A. boa*, Bosc = *B. schultzei*, Dema = *D. marenae*, Drru = *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. leucomystax*, *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. moellendorffi*, *P. everetti*, *B. schultzei* 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. schultzei*) and non-endemic (*C. fusca*, *L. palavanensis*, *P. longicrus*, *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 microhabitat 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 km^2, 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. moellendorffi*. The status of *P. everetti* should be downgraded to "Vulnerable," given that its EOO is > 5,000 km^2, 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 *Bronchocela* 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.

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Supplementary material 1

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

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Data type: Occurrence records

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

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