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SYNTHESIS

Integrating phylogenetic and taxonomic evidence illuminates complex biogeographic patterns along Huxley's modification of Wallace's Line

Jacob A. Esselstyn[1]*, Carl H. Oliveros[1], Robert G. Moyle[1], A. Townsend Peterson[1], Jimmy A. McGuire[2] and Rafe M. Brown[1]

[1]Biodiversity Institute and Department of Ecology and Evolutionary Biology, University of Kansas, Lawrence, KS 66045, USA, [2]Museum of Vertebrate Zoology, University of California, Berkeley, CA 94720, USA

*Correspondence: Jacob A. Esselstyn, Biodiversity Institute, 1345 Jayhawk Blvd, Lawrence, KS 66045, USA.
E-mail: esselsty@ku.edu

ABSTRACT

Aim Nearly 150 years ago, T. H. Huxley modified Wallace's Line, including the island of Palawan as a component of the Asian biogeographic realm and separating it from the oceanic Philippines. Although Huxley recognized some characteristics of a transition between the regions, Palawan has since been regarded primarily as a peripheral component of the Sunda Shelf. However, several recent phylogenetic studies of Southeast Asian lineages document populations on Palawan to be closely related to taxa from the oceanic Philippines, apparently contradicting the biogeographic association of Palawan with the Sunda Shelf. In the light of recent evidence, we evaluate taxonomic and phylogenetic data in an attempt to identify the origin(s) of Palawan's terrestrial vertebrate fauna.

Location The Sunda Shelf and the Philippines.

Methods We review distributional and phylogenetic data for populations of terrestrial vertebrates from Palawan. Using taxonomic data, we compare the number of Palawan taxa (species and genera) shared with the Sunda Shelf and oceanic Philippines. Among widespread lineages, we use phylogenetic data to identify the number of Palawan taxa with sister relationships to populations or species from the Sunda Shelf or oceanic Philippines.

Results Although many terrestrial vertebrate taxa are shared between Palawan and the Sunda Shelf, an increasing number of species and populations are now recognized as close relatives of lineages from the oceanic Philippines. Among the 39 putative lineages included in molecular phylogenetic studies with sampling from the Sunda Shelf, Palawan and the oceanic Philippines, 17 of them reveal sister relationships between lineages from Palawan and the oceanic Philippines.

Main conclusions Rather than a simple nested subset of Sunda Shelf populations, Palawan is best viewed as having played multiple biogeographic roles, including a young *and* old extension of the Sunda Shelf, a springboard to diversification in the oceanic Philippines, and a biogeographic component of the Philippine archipelago. Palawan has a long, complex geological history, which may explain this variation in pattern. Huxley originally noted transitional elements in Palawan's fauna; we therefore suggest that his modification of Wallace's Line should be recognized as a filter zone, reflecting both his original intent and available taxonomic and molecular evidence.

Keywords

Amphibians, birds, Borneo, island biogeography, mammals, Palawan, Philippines, phylogeny, reptiles, Sunda Shelf.

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INTRODUCTION

> A zoogeographic border *is not a line without width* [our emphasis] … by necessity there is a mixture of faunal elements along the border of two zoogeographic regions, caused by reciprocal penetration.
>
> Pelseneer (1904), translated and quoted by Mayr (1944, p. 9)

Biogeographers have long investigated the similarities and differences among floras and faunas on adjacent landmasses, illuminating the processes of speciation, extinction and community assembly (Simpson, 1940; Wegener, 1966; Brown, 1971; Heaney, 1986). Continental islands, and the biological communities that reside on them, have proven especially crucial to the maturation of biogeographic principles, being pivotal in the development of theories of community assembly, island area–diversity relationships and the processes by which faunas on recently isolated islands may relax to long-term equilibria (Simpson, 1940; MacArthur & Wilson, 1963; Heaney, 1984; Patterson, 1990).

The Palawan island group (including Balabac, Bugsuk, Busuanga, Culion, Palawan and many small islands), which is politically part of the Philippines, lies at the periphery of the continental shelf (= Sunda Shelf) in Southeast Asia (Fig. 1), and has long served as an integral component of biogeographic investigations (e.g. Huxley, 1868; Holloway, 1982). Palawan's fauna has generally been treated as most similar to that of Borneo (e.g. Dickerson, 1928; Inger, 1954; Heaney, 1985; Esselstyn *et al.*, 2004), but other authors have found equal or greater similarity to the oceanic Philippines (e.g. McGuire & Alcala, 2000; McGuire & Kiew, 2001; Brown & Guttman, 2002; Evans *et al.*, 2003; Beck *et al.*, 2006).

Wallace (1860), with a very imperfect knowledge of the Philippine fauna, originally grouped the entire country with the Asian region, while simultaneously noting the Philippines' deficiency in several Asian groups. By 1876, Wallace (1876) knew of only 14 non-volant mammals and 159 land birds from the Philippines, roughly 15% and 40% of current estimates for diversity, respectively (Heaney *et al.*, 1998, 2009; Kennedy *et al.*, 2000; Hutterer, 2007; Esselstyn & Goodman, in press). Among the Philippine mammals of which Wallace had knowledge at that time, nearly all are widespread Asian genera. By the time he wrote *Island life*, Wallace (1881) knew of 21 species of Philippine mammals, most of which are either widespread species or Palawan endemics. Thus, he had virtually no knowledge of the highly endemic mammal communities in the oceanic Philippines. At the time, even less was known of amphibian and reptile diversity (Boulenger, 1894). Thus, Wallace's impression of the Philippine fauna, and his biogeographic delineations of it, were taken from a very small, biased sample of the diversity.

Huxley (1868), also relying primarily on bird and mammal distributions, was the first to note that Palawan's fauna is Asian, but the remaining Philippine islands possess a community of peculiar animals. Huxley (1868, p. 317) commented, 'It is extremely remarkable; why Borneo [including Palawan] and the Philippines should have…so much and so little in common with Asia [respectively]…'. Hence, while hinting at sea depth as a possible explanation, Huxley (1868) simultaneously named and modified Wallace's Line (Fig. 1). However, it should be noted that Huxley (1868) recognized that biogeographic boundaries are places where faunas grade into one another, as indicated on p. 317: 'The eastern boundary between Arctogaea and Australasia is formed, not by a line, but by a broad zone of border islands…'. Following

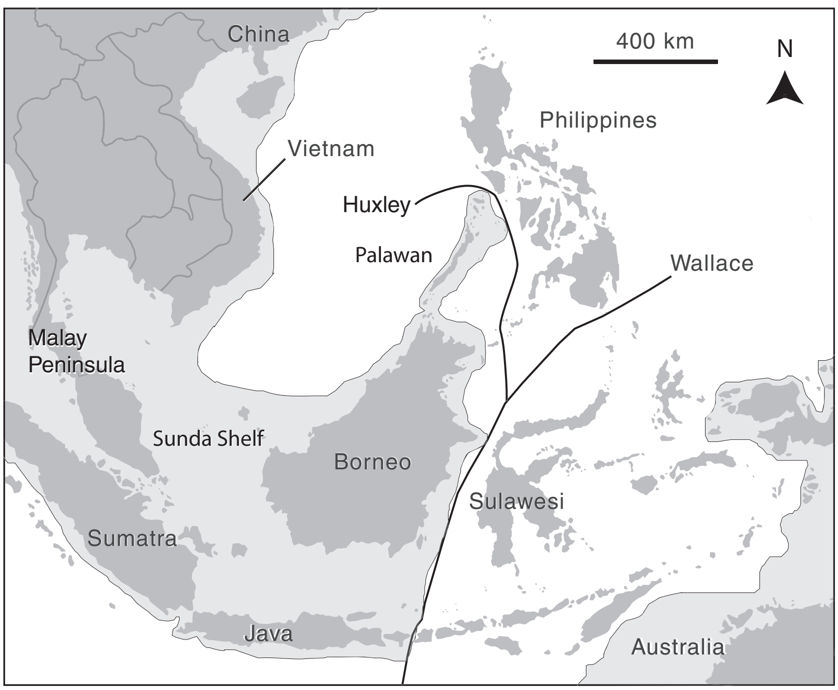

Figure 1 Map of Southeast Asia showing the traditional view of the Sunda Shelf, which includes Palawan. Modern islands are shown in medium grey and the continental shelf is indicated by light grey. Delineation of the shelf approximates the 120 m isobath. However, the narrow, slightly deeper channel (*c.* 140 m) between Palawan and Borneo is included as part of the shelf in this depiction. Modified from Voris (2000). East of the Sunda Shelf lie the oceanic islands of Wallacea and the Sahul Shelf (Australia and New Guinea). Huxley's modification of Wallace's Line delineates the extent of Sundaland.

Huxley's observations, others drew similar conclusions and grouped Palawan with Borneo (Everett, 1889; Boulenger, 1894).

With the publication of Dickerson's (1928) extensive volume on Philippine biodiversity, knowledge of the Philippine fauna had greatly improved, and the grouping of Palawan with Borneo, and concurrent recognition of the oceanic Philippines as a unique centre of endemism, were well established. Most authors recognized exceptions to these general patterns, but considered the evidence in support of Huxley's Line to be convincing (e.g. Mayr, 1944). More recent distributional data have supported these conclusions, again with occasional exceptions noted (e.g. Holloway, 1982; Kennedy *et al.*, 2000; Esselstyn *et al.*, 2004).

Although biogeographers occasionally overemphasize the significance of the precise placement of faunal boundaries (Simpson, 1977), assignment of any particular island to a biogeographic region has important implications for both conservation and evolutionary biology. For instance, thorough knowledge of the distribution of biodiversity facilitates the appropriate allocation of scarce resources for conservation efforts and, in the context of evolutionary biology, summary data characterizing distributions and relationships of organisms provide insights into: (1) the events that may have triggered speciation, (2) the directions and timing of colonization events, and (3) the degree of congruence of particular processes among disparate lineages.

Geology, sea levels and geography

The geological history of Palawan is complex and involves extensive movement across the South China Sea (Hall, 1996, 1998; Zamoras & Matsuoka, 2004; Yumul *et al.*, 2009a,b). Northern Palawan was initially part of the Asian mainland near modern Taiwan, but rifted from the continent during the Oligocene and travelled south for *c.* 30 Myr (Hall, 2002). After separating from the Asian mainland, the continental fragment was probably mostly submerged, as evidenced by Eocene to early Miocene carbonate deposits layered on top of older rocks (Yumul *et al.*, 2009a). As the Palawan microcontinental block (includes Palawan and parts of Mindoro, Panay and Romblon) continued to travel south, it collided with the Philippine mobile belt *c.* 20–16 Ma (Hall, 2002; Yumul *et al.*, 2009b), probably resulting in uplift and perhaps the production of islands. Evidence for erosion in the area (Bird *et al.*, 1993) suggests islands were present by *c.* 20–16 Ma, as does the existence of 15–13 Myr old granite in north Palawan (Encarnación & Mukasa, 1997), the formation of which requires a thick crust. Palawan came into close proximity with Borneo *c.* 10 Ma (Hall, 2002), and southern Palawan may have been uplifted around this time. Most depictions of the geological history of Palawan distinguish the northern half of the island (marine-capped continental fragments) from the southern (uplifted marine sediments and volcanics), but Durkee (1993) provides an alternative perspective, in which the apparent fault between the northern and southern parts of the island does not exist. Rather, Durkee (1993) refers to southern Palawan as a thrust-pile from northward movement of crust over the south-moving microcontinental block. Although many questions regarding the geological history of Palawan remain unanswered, it is significant that we know that some portion of the island broke away from the Asian mainland and drifted south and that most, but perhaps not all, of this continental fragment was submerged at one time or another, and that islands were possibly emerging as early as 20 Ma.

By the Pleistocene, climatic oscillations were generating major fluctuations in global sea levels (Bintanja *et al.*, 2005; Thomas *et al.*, 2009). The Sunda Shelf, of which Palawan is now a part, is the largest continental shelf in the world and consists of many islands (= Sundaland) and a shallow sea extending south and east from the Malay Peninsula (Fig. 1). During periods of low sea level, the shelf was exposed repeatedly as dry land, and the large islands of Borneo, Java and Sumatra were united into a single contiguous, continental landmass (Kloss, 1929; Inger, 1954; Heaney, 1985; Voris, 2000; Woodruff & Turner, 2009). The terrestrial fauna of Sundaland is thus Asian, with moderate levels of endemism (Inger, 1954, 1966, 1999; Heaney, 1984; Cracraft, 1988; Corbet & Hill, 1992; MacKinnon & Phillipps, 1993; Inger & Tan, 1996). Sundaic endemism is generally attributed to isolation caused by rising sea levels (Heaney, 1985; Inger & Voris, 2001; Woodruff & Turner, 2009) or altered distributions of forest and savanna habitats during the Pleistocene (Heaney, 1991; Meijaard, 2003; Gorog *et al.*, 2004; Bird *et al.*, 2005). However, some studies have inferred or implied invasions of the shelf much earlier than the Pleistocene (e.g. Jansa *et al.*, 2006; Outlaw & Voelker, 2008; Matsui *et al.*, 2010).

Palawan Island is currently isolated from Borneo by a *c.* 140 m deep channel (Heaney, 1985, 1986). Until very recently, most sea-level reconstructions suggested that Palawan and Borneo were united, or nearly so, with an inferred sea-level minimum of *c.* −140 m during the penultimate glacial maximum *c.* 140 ka (Gascoyne *et al.*, 1979; Rohling *et al.*, 1998). However, the most recent sea-level estimates for the penultimate glacial period suggest that Palawan and Borneo were not united at that time, with reconstructed sea-level minima nearer the −120 m typically inferred for the most recent glacial maximum (e.g. Siddall *et al.*, 2003, 2006; Bintanja *et al.*, 2005; Thomas *et al.*, 2009). Earlier glacial periods reduced sea levels to *c.* −130 m, *c.* 430 and 630 ka (Miller *et al.*, 2005; Bintanja *et al.*, 2005), suggesting that Palawan has remained isolated by a narrow sea channel for the last million years. However, we note that rates of tectonic change around Palawan have been rapid, and current bathymetry may only be useful for understanding relatively recent (*c.* $<$ 1 Ma) patterns of inter-island connectedness. Additionally, we note that the breadth of any land bridges or sea channels would be an important factor in determining which organisms would represent potential colonists.

Patterns of faunal similarity, data availability and putative biogeographic histories

Palawan's vertebrate fauna has been considered similar to that of Borneo, but with moderate levels of endemism (Everett, 1889; Dickerson, 1928; Esselstyn *et al.*, 2004). However, early studies were dominated by investigations of bird and mammal distributions (Huxley, 1868; Everett, 1889), with other terrestrial organisms (e.g. amphibians, reptiles, invertebrates, plants) receiving far less attention (but see Günther, 1872; Boulenger, 1894). More recently, several phylogenetic studies have shown Palawan taxa to be more closely related to species from the oceanic Philippines or Sulawesi than to Sundaic populations (e.g. McGuire & Kiew, 2001; Brown & Guttman, 2002; Evans *et al.*, 2003; Esselstyn *et al.*, 2009). Other researchers have noted that in some groups, diverse Bornean communities are absent from Palawan (e.g. none of the nine Bornean species of flying lizards are found on Palawan: McGuire & Alcala, 2000). Given the early biases in available distributional data and the results of recent phylogenetic inferences, some have questioned the characterization of Palawan as a simple extension of the Sunda Shelf (e.g. McGuire & Alcala, 2000; Atkins *et al.*, 2001; Brown & Guttman, 2002; Beck *et al.*, 2006; Brown & Diesmos, 2009). Furthermore, recent collections of terrestrial vertebrates from the island have provided new distributional records and facilitated taxonomic revisions that potentially shed light on the biogeographic relationships of these areas (Kennedy *et al.*, 2000; Esselstyn *et al.*, 2004; Hutterer, 2007; Brown *et al.*, 2009; Welton *et al.*, 2009).

In this paper we review the distributions and phylogenetic relationships of the terrestrial vertebrates of Palawan, taking into account recent taxonomic changes and new distributional records of extant and fossil taxa. In effect, we consider the universality of Huxley's Line by exploring the possible origins of Palawan's terrestrial vertebrate fauna, including whether it is a subset of Borneo's with a Pleistocene origin, whether a substantial proportion of Palawan's fauna might originate from the oceanic Philippines or elsewhere, whether Palawan might have served as a colonization route into the oceanic Philippines and whether the island's fauna has a complex of lineage-specific relationships.

MATERIALS AND METHODS

Distribution of terrestrial vertebrates

We gathered distributional information from published sources, as well as unpublished records of recently documented species. Mammal records for Palawan and associated small islands were taken from Esselstyn *et al.* (2004) and Heaney *et al.* (1998) and updated with recent discoveries and taxonomic changes (Gaubert & Antunes, 2005; Helgen, 2005; Lucchini *et al.*, 2005; Hutterer, 2007; Piper *et al.*, 2008). We also include unpublished records of an endemic shrew (*Suncus*) and the widespread hairy-winged bat (*Harpiocephalus harpia*), each first collected on Palawan in 2007 (D.S. Balete & J.A. Esselstyn, unpublished). Mammal records for the Sunda Shelf and oceanic Philippines were drawn from several sources (Payne *et al.*, 1985; Corbet & Hill, 1992; Heaney *et al.*, 1998). Records of breeding land birds were taken from Kennedy *et al.* (2000) and MacKinnon & Phillipps (1993), but taxonomy follows Dickinson (2003). Distributional records of reptiles and amphibians were taken from Taylor (1922a,b,c,d,e, 1923, 1925, 1928), Inger (1954) and Brown & Alcala (1970, 1978, 1980), with recent records summarized by Diesmos *et al.* (2002) and Brown (2007). The most recent discoveries and taxonomic updates are included (e.g. Brown *et al.*, 2009, 2010; Welton *et al.*, 2009; Koch *et al.*, 2010; Linkem *et al.*, 2010).

We tallied the total numbers of species and genera of birds, mammals, amphibians and reptiles occurring on Palawan. Of those species and genera, we counted how many are shared with the oceanic Philippines versus the Sunda Shelf.

Phylogenetic evidence

We sought phylogenetic studies that used molecular evidence to infer relationships among widespread taxa found on the Sunda Shelf, Palawan and oceanic Philippines. We limited our sources of data to studies that sampled populations of a putative lineage (genus or species) from all three areas, because these studies provide evidence beyond that available from summaries based on taxonomy. Studies that sampled taxa from only two of the three areas are not included because these would be uninformative with regard to the question of whether the Palawan population is more closely related to Sunda Shelf or Philippine populations. We consider the included phylogenies to provide the same information as taxonomic studies, but at a finer level of resolution and with more explicit statements of shared ancestry.

RESULTS

Distribution of terrestrial vertebrates

Most terrestrial vertebrate species documented from Palawan are widespread across the region, are Palawan endemics or are shared with the Sunda Shelf (Fig. 2). However, several species (especially reptiles and birds) occur on Palawan and the oceanic Philippines only, and not on the Sunda Shelf (Fig. 2). When distributional data for genera are examined, Palawan's fauna is more similar to that of the Sunda Shelf for all groups, but the differences are not great (Fig. 3a). However, this pattern is driven by widespread genera, and stronger similarity is noted between Palawan and the Sunda Shelf when the comparison is limited to genera that occur in only two of the three areas (Palawan, Sunda Shelf, oceanic Philippines: Fig. 3b). Generic distributions reveal that the similarity between the faunas of Palawan and the Sunda Shelf is much stronger in mammals than in other taxa. All distributional data are provided in Appendix S1 in the Supporting Information.

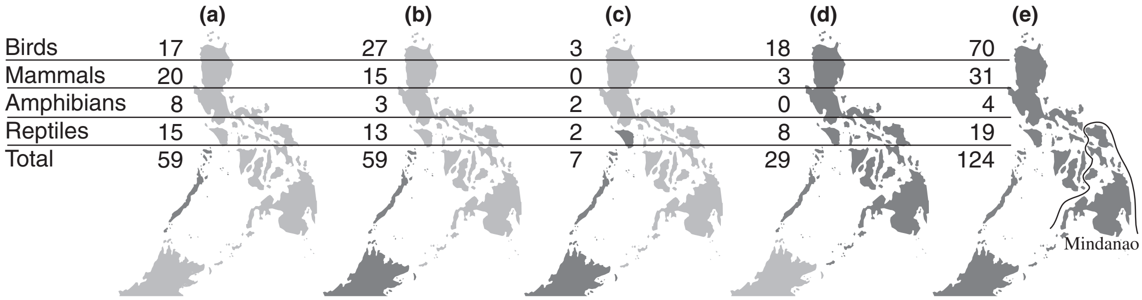

Figure 2 Terrestrial vertebrates from Palawan reveal five common distributional patterns: (a) endemic to Palawan; (b) present on Palawan and the Sunda Shelf; (c) as (b), but also present on Mindoro Island; (d) widespread within the Philippines, including Palawan; and (e) widespread throughout the region occurring on the Sunda Shelf, Palawan and in the oceanic Philippines. The number of species of each higher taxon, and the total, are listed next to each map. Among the species in category (e), several taxa only marginally enter the oceanic Philippines and are restricted to the Mindanao faunal region south of the curved line (two birds, one mammal, four amphibians and two reptiles).

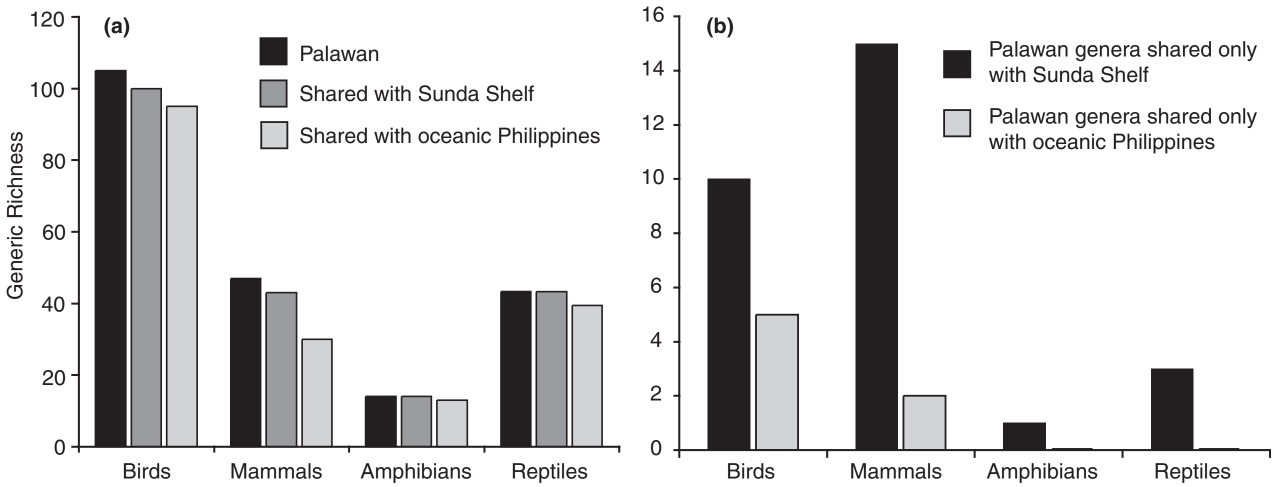

Figure 3 Numbers of genera of terrestrial vertebrates from Palawan and their regional distributions. Panel (a) shows the numbers of genera shared with the Sunda Shelf and oceanic Philippines while panel (b) considers only genera that occur on Palawan and either the Sunda Shelf or oceanic Philippines, but excludes genera that occur in all three areas.

Phylogenetic evidence

We identified 39 Palawan species or populations that have been included in phylogenetic studies (some of which are in progress), with representatives also sampled from both the Sunda Shelf and oceanic Philippines (Table 1). Among these taxa, 17 Palawan populations are sister to Philippine lineages, 10 have sister relationships to Sunda Shelf populations, eight are sister to populations from the oceanic Philippines and Sunda Shelf, two are sister to Sulawesi taxa, and one is sister to populations from the Philippines and Sulawesi. One lineage is genetically homogeneous across the Borneo–Palawan–Philippines arc (Fig. 4, Table 1).

DISCUSSION

Our results reveal that a substantial component of Palawan's terrestrial vertebrate diversity is indeed closely related to populations from the Sunda Shelf, especially among mammals and birds. However, numerous taxa occur in all three areas (Fig. 2), and many Palawan populations are most closely related to taxa from the oceanic Philippines or Sulawesi (Fig. 4, Table 1), especially among reptiles. We must note that differing taxonomic philosophies may contribute to the distinct patterns observed among groups of vertebrates. For instance, more Palawan endemic genera and species are found among birds and mammals than among reptiles or amphibians (Fig. 2). This may be due to: (1) Palawan's bird and mammal groups representing older clades, (2) birds and mammals exhibiting faster rates of morphological evolution, or (3) differing taxonomic philosophies among the systematists that focus on these groups. Despite these possibilities, the similarity of the Palawan fauna to that of the Sunda Shelf is apparent from taxonomy, and is supported by some phylogenetic evidence (e.g. bulbuls: Oliveros & Moyle, 2010; flowerpeckers: Nyári *et al.*, 2009; and flycatchers: Outlaw & Voelker, 2008),

Table 1 Summary of phylogenetic/phylogeographic evidence showing the distributions of populations that are sister to taxa from Palawan Island.

Species from Palawan	Sister population	Reference
Birds		
Ficedula platenae	Sunda Shelf	Outlaw & Voelker (2008)
Iole palawanensis[1]	Sunda Shelf	Oliveros & Moyle (2010)
Pernis ptilorhyncus	Sunda Shelf	Gamauf & Haring (2004)
Phylloscopus trivirgatus	Philippines	Jones & Kennedy (2008)
Prionochilus plateni	Sunda Shelf	Nyári *et al.* (2009)
Pycnonotus atriceps	Sunda Shelf	Oliveros & Moyle (2010)
Pycnonotus plumosus	Sunda Shelf	Oliveros & Moyle (2010)
Stachyris hypogrammica	Philippines	Moyle *et al.* (2009)
Mammals		
Crocidura batakorum	Sulawesi	Esselstyn *et al.* (2009)
Crocidura palawanensis[2]	Philippines	Esselstyn *et al.* (2009)
Cynopterus brachyotis[3]	Philippines & Sunda Shelf	Campbell (2004)
Paradoxurus hermaphroditus[4]	Philippines & Sunda Shelf	Patou *et al.* (2010)
Sundasciurus hoogstraali[5]	Philippines & Sunda Shelf	den Tex *et al.* (2010)
Sundasciurus juvencus[5]	Philippines & Sunda Shelf	den Tex *et al.* (2010)
Sundasciurus moellendorffi[5]	Philippines & Sunda Shelf	den Tex *et al.* (2010)
Sundasciurus rabori[5]	Philippines & Sunda Shelf	den Tex *et al.* (2010)
Sundasciurus steerii[5]	Philippines & Sunda Shelf	den Tex *et al.* (2010)
Sus ahoenbarbus	Philippines	Lucchini *et al.* (2005)
Tupaia palawanensis[6]	Sunda Shelf	Roberts *et al.* (2009)
Amphibians		
Kaloula baleata	Sulawesi	R.M. Brown *et al.* (in prep.)
Leptobrachium tagbanorum[2]	Philippines	Brown *et al.* (2009)
Limnonectes palavanensis	Sunda Shelf	Evans *et al.* (2003)
Limnonectes acanthi	Philippines	Evans *et al.* (2003)
Megophrys ligayae	Sunda Shelf	R.M. Brown (unpubl.)
Occidozyga laevis	Philippines	C.D. Siler *et al.* (unpubl.)
Polypedates leucomystax[7]	Philippines	Brown *et al.* (in press)
Polypedates macrotis	Sunda Shelf	Brown *et al.* (in press)
Rana sanguinea	Philippines	Bossuyt *et al.* (2006)
Rana moellendorffi[2]	Philippines	Brown & Guttman (2002)
Lizards, snakes, turtles		
Bronchocela cristatella	Philippines & Sulawesi	J.A. McGuire *et al.* (in prep.)
Cuora amboinensis	Philippines	R.M. Brown *et al.* (unpubl.)
Cyrtodactylus redimiculus[8]	Philippines & Sunda Shelf	Siler *et al.* (2010)
Cyrtodactylus tautbatorum	Philippines	Welton *et al.* (2009); Siler *et al.* (2010)
Draco palawanensis	Philippines	McGuire & Kiew (2001)
Parias schultzei	Sunda Shelf	Sanders *et al.* (2004)
Sphenomorphus victoria[9]	Philippines	C.W. Linkem *et al.* (unpubl.)
Sphenomorphus traanorum[9]	Philippines	C.W. Linkem *et al.* (unpubl.)
Sphenomorphus wrighti[9]	Philippines	C.W. Linkem *et al.* (unpubl.)
Varanus palawanensis	Philippines	L.J. Welton *et al.* (unpubl.)

[1]We include *Iole* because some authors synonymize it with *Hypsipetes*, which is present on the Sunda Shelf and in the oceanic Philippines.
[2]Denotes Sunda Shelf taxa sister to Palawan + oceanic Philippines clades.
[3]Mitochondrial gene trees reveal two clades from Palawan, one closely related to populations from the oceanic Philippines and one to Sunda Shelf populations.
[4]Haplotypes are shared among Philippine, Bornean and Palawan individuals.
[5]These five Palawan endemics of *Sundasciurus* form a clade that is sister to a clade found from the oceanic Philippines and Sunda Shelf.
[6]We include *Tupaia* here because some authors include *Urogale*, which is present in the oceanic Philippines, within *Tupaia*, and because molecular evidence supports this arrangement.
[7]*Polypedates leucomystax* may be an introduced species on Palawan (Brown *et al.*, in press).
[8]Mitochondrial gene trees show a close relationship between Palawan and oceanic Philippine populations, whereas nuclear gene trees suggest a close relationship between populations from Palawan and Borneo. Siler *et al.* (2010) hypothesize that the discordance is due to ancestral polymorphism and the Palawan + oceanic Philippines hypothesis is the favoured species tree topology.
[9]These three Palawan endemics of *Sphenomorphus* form a clade that is nested within a clade from the oceanic Philippines.

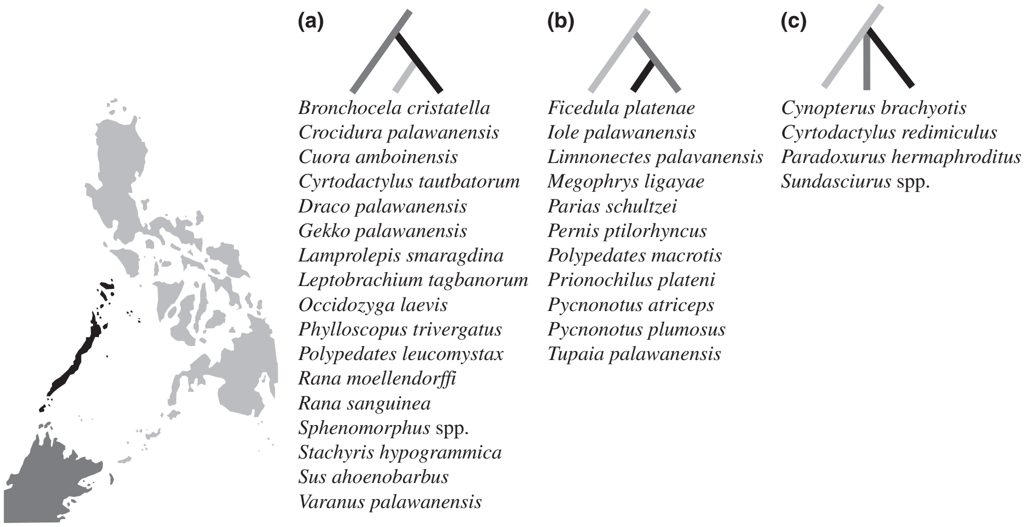

Figure 4 Map of the Philippines and northern Borneo alongside three common phylogenetic patterns where Palawan species are (a) sister to taxa from the oceanic Philippines, (b) sister to taxa from the Sunda Shelf or (c) have either ambiguous or undifferentiated relationships. Taxa fitting each pattern are listed below the schematic phylogeny. Species revealing other relationships (e.g. sister to Sulawesi populations) are not included. References are listed in Table 1.

but apparently is contradicted by the commonness of close phylogenetic relationships with taxa from the oceanic Philippines or Sulawesi (e.g. flying lizards: McGuire & Kiew, 2001; frogs: Brown & Guttman, 2002; Evans *et al.*, 2003; and shrews: Esselstyn *et al.*, 2009).

We note that sister relationships between Palawan and oceanic Philippine populations do not necessarily contradict the view of Palawan as a Sundaic peninsula, but expand it beyond the simplicity of a 'nested subset' prediction. Rather, this pattern is precisely what would be expected if Palawan served as a colonization route into the oceanic Philippines. In cases where taxa colonized the oceanic Philippines via Palawan, we expect to see Bornean populations inferred as sister to clades composed of Palawan + oceanic Philippines populations. Among the 17 groups that show a Palawan + oceanic Philippines relationship, this pattern is evident in a shrew (*Crocidura palawanensis*: Esselstyn *et al.*, 2009) and three frogs (*Leptobrachium tagbanorum*: Brown *et al.*, 2009; *Limnonectes acanthi*: Evans *et al.*, 2003; *Rana moellendorffi*: Brown & Guttman, 2002). A similar pattern is noted in a gecko lineage (*Cyrtodactylus*), where two species from Palawan are each sister to small radiations from the oceanic Philippines (Siler *et al.*, 2010). These two clades (including the Palawan species), are sister groups, and taxa from the Sunda Shelf are sister to the entire clade (Siler *et al.*, 2010). These cases suggest that Palawan may indeed have served as an important point of entry to the oceanic Philippines (e.g. Myers, 1949; Diamond & Gilpin, 1983; de Jong, 1996).

If Palawan were a peninsula of Borneo, with frequent connections emerging during periods of low sea level, then many Palawan populations should be *closely* related to Bornean taxa, having been isolated since the Pleistocene. However, when Palawan taxa are sister to Sunda Shelf populations, these relationships often appear to be old divergences that pre-date Pleistocene, and in some cases Pliocene, sea-level fluctuations. For instance, Oliveros & Moyle (2010) found that all four species of bulbul from Palawan are sister to Bornean taxa, but three of the four are old lineages long isolated from their Bornean sisters. To obtain divergence time estimates, we inferred maximum likelihood (ML) divergences between the three highly divergent Palawan–Borneo pairs of bulbuls using the data and models of sequence evolution reported by Oliveros & Moyle (2010). We optimized branch lengths on their ML topology in PAUP* 4.0b (Swofford, 1999), resulting in ML divergences of 0.45 in *Iole*, 0.24 in *Pycnonotus plumosus* and 0.20 in *Alophioxus bres*. If one were willing to assume a molecular clock, even with a fast rate of divergence (0.054 Myr^{-1}: Drovetski *et al.*, 2004), these lineages would have been isolated for *c.* 4–8 Myr. Given the deep isolation of Palawan populations and the apparent lack of successful invasion of the oceanic Philippines via Palawan, Oliveros & Moyle (2010) characterized Palawan as an evolutionary dead end for bulbuls, rather than a biogeographic umbilicus (*sensu* Diamond & Gilpin, 1983). Similarly, den Tex *et al.* (2010) estimated the divergence of Palawan tree squirrels (*Sundasciurus*) from their Sundaic relatives to have occurred more than 6 million years ago. Thus, although the results of Oliveros & Moyle (2010) and den Tex *et al.* (2010) are consistent with the topological expectation of Palawan representing a recently isolated peninsula of Borneo, they qualitatively reject the temporal expectation of recent divergence.

Diversification within Palawan has probably not made major contributions to extant diversity. Most genera on the island are represented by a single species, but where multiple species within deeper lineages are present on Palawan most studies found that they are distant relatives derived from independent colonization events (e.g. Evans *et al.*, 2003; Brown *et al.*, 2009; Esselstyn *et al.*, 2009; Oliveros & Moyle, 2010). However, a few remaining potential cases of *in situ* diversification exist, including the five allopatric species of tree squirrels (*Sundasciurus*), two allopatric species of tree shrews (*Tupaia*) and several sympatric species of *Sphenomorphus* (Brown & Alcala, 1980; Heaney, 1979; Heaney *et al.*, 1998; Esselstyn *et al.*, 2004; Helgen, 2005). Preliminary evidence from *Sphenomorphus* suggests that three species from Palawan form a clade most closely related to taxa from the oceanic Philippines (Linkem *et al.*, 2010; C. W. Linkem & R. M. Brown, unpublished). Similarly, den Tex *et al.* (2010) found that several species of tree squirrel (*Sundasciurus*) from Palawan form a clade, but the divergences among them are limited.

Although there is little evidence for *in situ* diversification as a *significant* generator of diversity on Palawan, potential mechanisms do exist. Bird *et al.* (2007) suggested that plant communities on the island shifted between forest and savanna during the Pleistocene, perhaps providing opportunities for isolation of populations of forest-dependent animals. Hutterer (2007) hinted that the population of shrews (*Crocidura palawanensis*) on Balabac Island at the southern end of the Palawan group may represent a species distinct from populations on the main Palawan Island, and we suspect that this could be a common pattern. The long, narrow shape of Palawan (Fig. 1) has the potential to promote diversification along its long axis, by allowing relatively small areas of unsuitable habitat to represent substantial barriers to dispersal, or simply by generating strong isolation-by-distance over contiguous habitats.

The shape of Palawan may explain another pattern noted by McGuire & Alcala (2000), in which none of the nine Bornean species of flying lizards (*Draco*) are found on Palawan. This may be an isolated phenomenon, or a general pattern. Numerous Bornean genera are absent from Palawan, but this is expected because Palawan is so small relative to Borneo. Future research may demonstrate that the Palawan fauna includes fewer Bornean taxa than are present on other, demonstrably land-bridge, islands. If Palawan does indeed hold fewer Bornean species than other land-bridge islands, it may be that the island's long narrow shape and northerly orientation (Fig. 1) simply presents a small 'target' for potential colonists originating from northern Borneo (e.g. Lomolino, 1990).

Finally, the possible existence of Palawan as an oceanic island prior to its approach to Borneo would explain many of the patterns we note. In particular, the ancient divergences between Palawan and Bornean taxa would make sense if Palawan were colonized over water several million years ago. Similarly, faunal exchange with the oceanic Philippines might have occurred frequently when a proto-Palawan was nearest the oceanic parts of the Philippines, perhaps explaining the close relationships between some taxa in these areas.

CONCLUSIONS

We conclude that attempting to assign a single historical process to Palawan's vertebrate biodiversity is overly simplistic. It is unreasonable to expect all organisms living on an island to have experienced identical evolutionary processes, especially when the island in question has such a long, complex geographic history. Distributional and phylogenetic data on Palawan vertebrates contain signals consistent with a variety of evolutionary histories. Many species and genera are shared with Borneo, including some recently diverged taxa, but other populations have been isolated on Palawan for millions of years (e.g. Oliveros & Moyle, 2010). Several other Palawan lineages have close relationships with populations from the oceanic Philippines. Some of these relationships are probably due to invasion of the oceanic Philippines via Palawan (e.g. Esselstyn *et al.*, 2009; Siler *et al.*, 2010), but in other cases Palawan populations are nested within clades otherwise restricted to the oceanic Philippines (e.g. McGuire & Kiew, 2001), suggesting invasion of Palawan from the oceanic Philippines. Given the prevalence of deep divergences between Bornean and Palawan populations and close relationships between Palawan and oceanic Philippine populations, along with evidence for thickened crust and erosion in the area *c.* 20–13 Ma (Bird *et al.*, 1993; Encarnación & Mukasa, 1997; Yumul *et al.*, 2009b), we consider it likely that Palawan existed as an oceanic island prior to its approach to Borneo. If this is the case, it might explain the complex set of relationships exhibited by Palawan's terrestrial vertebrates.

Available evidence suggests that Palawan represents both a *young and old* extension of the Sunda Shelf (Oliveros & Moyle, 2010), a springboard to diversification in the oceanic Philippines (Esselstyn *et al.*, 2009; Siler *et al.*, 2010), a biogeographic component of the Philippine archipelago (McGuire & Alcala, 2000; Brown & Diesmos, 2009) and, in some cases, a 'dead end' for faunal elements that dispersed from the oceanic Philippines but never made it as far as Borneo (e.g. emerald green tree skinks, *Lamprolepis smaragdina*). It remains possible that Palawan played these various roles at different times in its history. However, given the extensive variation in dispersal capacity among Southeast Asian vertebrates, it seems reasonable that when Palawan was in a particular geographic position it may have served, for example, as a springboard to the oceanic Philippines for some organisms, while simultaneously representing a dead-end Sundaic peninsula for others.

Thoroughly testing these hypotheses will require improved geological and sea-level reconstructions and many more phylogenies than are currently available, each with precise and accurate time-scales alongside dense geographic sampling. Future taxonomic updates will probably lead to the increased recognition of Palawan populations as endemic species (Peterson, 2006; Brown & Diesmos, 2009). However, we anticipate that the complex pattern of biogeographic relationships we summarize here will remain, even as new data are collected and gradually refine our knowledge of the relationships among organisms in the region.

Given the evidence presented here, Huxley's Line, which has long 'divided' the oceanic Philippines from Palawan, is best viewed as a filter barrier that strongly impacts some lineages, others moderately so, and some not at all. Perhaps, when discussing the importance of biogeographic boundaries such as Huxley's Line, biogeographers would be advised to acknowledge the combined effect of geographic history, lineage-specific dispersal characteristics and historical contingencies, which gives rise to everything from strict adherence to complete defiance of the line (Evans *et al.*, 2003). We therefore suggest adoption of the more accurate terminology 'Huxley's Filter Zone'. This terminology recognizes Huxley's significant contributions and original intent, and imparts a biologically meaningful characterization of this classic biogeographical theme.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 List of the species of terrestrial vertebrates recorded from Palawan Island and its satellites, with details of their occurrence on the Sunda Shelf and in the oceanic Philippines.

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BIOSKETCH

The authors share a general interest in historical biogeography, especially in Southeast Asia. All are involved in research programmes investigating the evolutionary history of various Southeast Asian vertebrate lineages. By combining active field programmes with modern molecular and bioinformatic techniques, we hope to contribute to a synthetic understanding of why there are so many species in Southeast Asia.

Author contributions: J.A.E., J.M.G. and R.M.B. conceived the project; J.A.E. compiled the mammal data, C.H.O. and R.G.M. the bird data, and R.M.B the reptile and amphibian data; all authors contributed to the interpretation of data and writing.

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