

Evolutionary Processes of Diversification in a Model Island Archipelago

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adaptive radiation, comparative phylogeography, conservation hot spots, Huxley's filter zone, nonadaptive radiation, oceanic islands, Southeast Asia, Sunda Shelf, underestimated biodiversity, Wallace's Line, Wallacea

Abstract

Long celebrated for its spectacular landscapes and strikingly high levels of endemic biodiversity, the Philippines has been studied intensively by biogeographers for two centuries. Concentration of so many endemic land vertebrates into a small area and shared patterns of distribution in many unrelated forms has inspired a search for common mechanisms of production, partitioning, and maintenance of life in the archipelago. In this review, we (a) characterize an ongoing renaissance of species discovery, (b) discuss the changing way biogeographers conceive of the archipelago, (c) review the role molecular phylogenetic studies play in understanding the evolutionary history of Philippine vertebrates, and (d) describe how a 25-year Pleistocene island connectivity paradigm continues to provide some explanatory power, but has been augmented by increased understanding of the archipelago's geological history and ecological gradients. Finally, we (e) review new insights provided by studies of adaptive versus nonadaptive radiation and phylogenetic perspectives on community ecology.

INTRODUCTION

This complex history, along with the high isolation, high precipitation, and relatively rich, volcanic soils, created a productive and dynamic evolutionary arena that allowed the archipelago's biota to diversify to the point that the Philippines ranks among the world's richest hotspots of biological diversity. —Lomolino et al. (2010, p. 756)

Island archipelagos that support taxonomically diverse and species-rich, codistributed lineages provide important models for understanding processes of diversification because individual lineages provide experimental replicates with shared geological, evolutionary, and/or climatic histories (Gillespie 2007, Losos & Ricklefs 2009, Vences et al. 2009). The terrestrial fauna of the Philippine archipelago is extremely diverse and provides numerous opportunities for illuminating evolutionary and ecological processes. The archipelago is located at the interface of the Asian and Australasian faunal zones, abutting the sharpest faunal demarcation on the planet (see Wallace's Line in **Figure 1**) (Lomolino et al. 2010). As such, the Philippines has emerged as a natural laboratory in which to study the impacts of the geographic template on the production, partitioning, and maintenance of biodiversity (Heaney 2007, Brown & Diesmos 2009). In particular, over the past few decades, the archipelago has attracted the attention of biogeographers around the world. The country shares only with Madagascar the distinction of being designated as both a megadiverse nation and a global biodiversity conservation hot spot (Mittermeier et al. 1999). A growing community of biogeographers, population geneticists, conservation biologists, and phylogeneticists has begun to focus on the archipelago and its diverse, endemic forms of life as a model system for addressing a variety of conceptual questions related to evolutionary diversification (Heaney et al. 2005, Brown & Diesmos 2009, Oaks et al. 2013).

Although still far from complete, a 200-year tradition of study has provided a rich source of species distributional data (Everett 1889, Steere 1894, McGregor 1909, Dickerson 1928, Inger 1954, Dickinson et al. 1991, Kennedy et al. 2000, Heaney et al. 2010). As part of this historical legacy, detailed faunistic, ecological, and evolutionary studies have given rise to a paradigm shift for understanding the evolution and ecological assembly of the archipelago's strikingly high levels of

Ecological assembly:

process of species accumulation and persistence across habitat gradients, habitat heterogeneity, or environmental variation

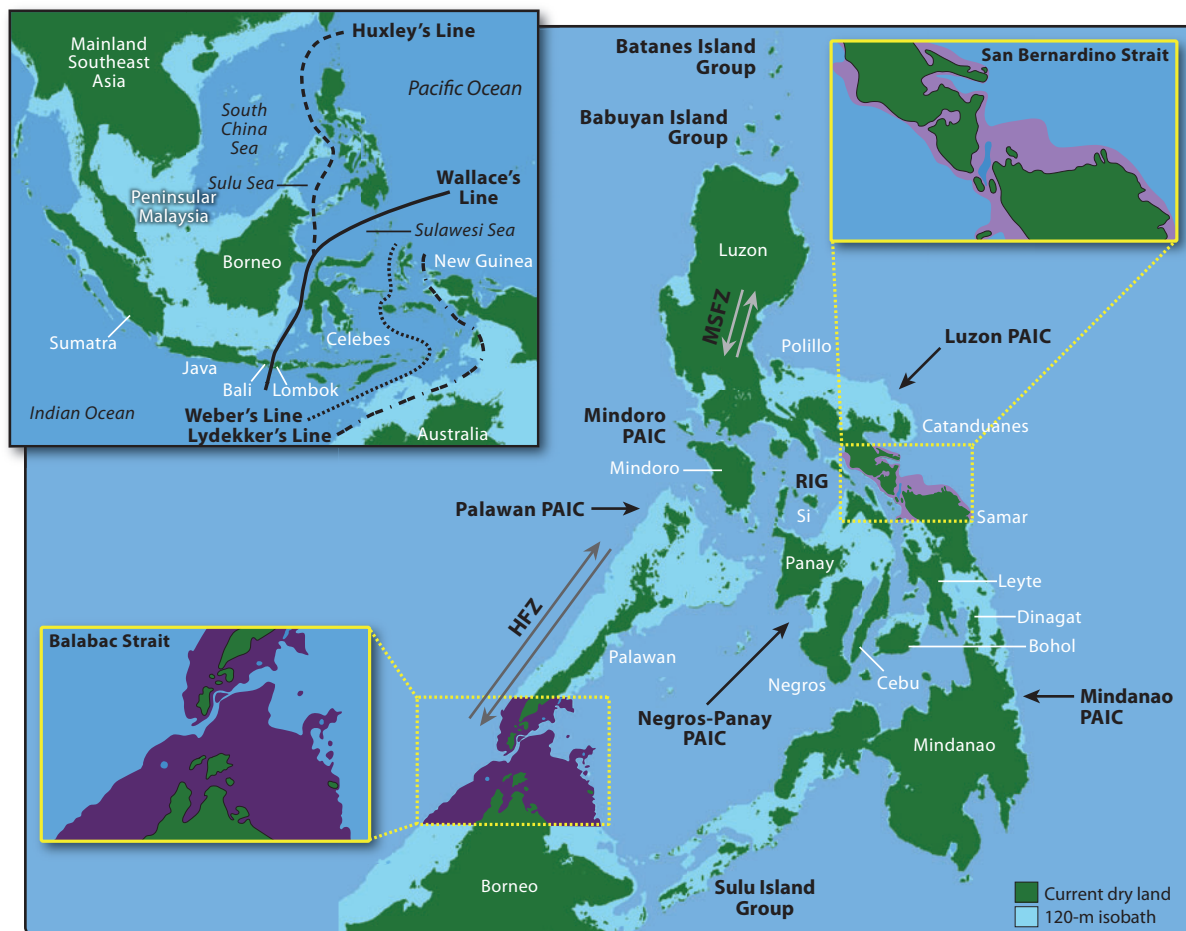


Figure 1

The Philippine island archipelago in relation to other southeast Asian and southwestern Pacific landmasses (*top left inset*) with indication of current dry land (*green*), surrounded by 120-m submarine bathymetric contour (isobath in *light blue shading*, indicating late Pleistocene sea shores), reconstructed from ETOPO1 1-Arc Minute Global Relief Model (Christopher & Eakins 2009). Areas where new estimates of land connectivity are different than previous studies (Inger 1954, Heaney 1985, Voris 2000) are enlarged for emphasis (*light and dark purple shading*). Abbreviations: HFZ, Huxley's Filter Zone (Esselstyn et al. 2010); MSFZ, Mid-Sierra Filter Zone (Welton et al. 2010a); PAIC, Pleistocene Aggregate Island Complex (Brown & Diesmos 2002, 2009); RIG, Romblon Island Group.

endemic (found only in this archipelago) land vertebrate biodiversity (Heaney 2000, 2007; Brown & Diesmos 2009). Now recognized as likely supporting the highest concentration of endemic terrestrial vertebrates per unit land area on Earth (Catibog-Sinha & Heaney 2006, Brown & Diesmos 2009), the archipelago has become an often-cited model for producing, partitioning, and maintaining biodiversity by four primary processes: (*a*) isolation of ancient colonists that diversified on precursor paleoislands over the past 5–30 Ma (Jansa et al. 2006, Blackburn et al. 2010, Siler et al. 2012); (*b*) relatively recent arrival of mainland-derived colonists through biogeographic colonization routes such as Pleistocene land bridges and linear island chains (Inger 1954, Diamond & Gilpin 1983, Heaney 1985, Brown & Guttman 2002, Jones & Kennedy 2008, Brown & Siler 2013); (*c*) stratification and fine-scale in situ diversification (including possible ecological and

AN EMERGING PHILIPPINE CONSERVATION MOVEMENT

The incredible biological wealth of the Philippines has been severely degraded (Brown & Diesmos 2009). Centuries of unchecked colonial rule, political conflict, hegemony, and political corruption have fostered systematic exploitation of Philippine natural resources, resulting in rates of environmental destruction exceeding that of anywhere else on the planet (Sodhi et al. 2004). Originally >85% forested, the archipelago now retains only 4–8% of original forest cover (Catibog-Sinha & Heaney 2006). As a result, international conservation communities have considered the country one of the hottest of the global conservation hot spots (Mittermeier et al. 1999). Despite a greater understanding of biodiversity gained during the past 20 years, knowledge is accumulating too slowly, and political and societal change is too gradual, to stem the loss of the archipelago's biodiversity. In short, the Philippines is one of the planet's highest conservation priorities. Previously considered an ecological disaster and a lost cause, new hope is emerging from an expanding environmentally aware civil society in the Philippines. In a recent comprehensive review of conservation in the country, Posa et al. (2008) suggested that this movement, against many odds, shows marked signs of success, and thus is deserving of even increased investment from the international community.

geographical speciation) and species accumulation along replicated elevational gradients (Heaney et al. 2011, Linkem et al. 2011); and (*d*) the “species pump” action of oscillating sea levels that resulted in the repeated formation and fragmentation of Pleistocene Aggregate Island Complexes (the PAIC Diversification Model) (Heaney 1985; Brown & Diesmos 2002, 2009; Esselstyn & Brown 2009; Lomolino et al. 2010; Siler et al. 2010). The PAIC model has dominated discussions of vertebrate evolution in the archipelago for the past 25 years (Heaney 1985; Brown & Guttman 2002; Evans et al. 2003; Heaney et al. 2005; Roberts 2006; Linkem et al. 2010; Siler et al. 2010, 2011a, 2012). Recent studies have departed from past reliance on species distributions and instead have used genetic data to test well-developed predictions in an evolutionary and historical context (Steppan et al. 2003; Roberts 2006; Esselstyn & Brown 2009; Esselstyn et al. 2009; Linkem et al. 2011; Siler et al. 2011a, 2012).

Here, we review the rich tradition of biogeography in the Philippines and provide a synthesis of recent studies shedding new light on classic questions related to evolutionary radiations in archipelagos. Already recognized as a global conservation priority, the Philippines is also emerging as an important theater for study of evolutionary diversification in archipelagos (see the sidebar, An Emerging Philippine Conservation Movement).

THE HISTORICAL SETTING FOR BIOGEOGRAPHY IN THE PHILIPPINES

Early Biogeographers' Perspectives of the Archipelago

It is worthy of notice that its staunchest defenders were those naturalists who actually studied and collected animal life on both sides of [Wallace's] line, like Dickerson and his associates in the Philippines. —Mayr (1944, p. 4).

With the inception of the field of biogeography (Wallace 1860, 1863), the Philippine archipelago took on an important role in the development of early biogeographic thought (Wallace 1869). Wallace used geological explanations (Wallace 1860) to support his discovery of an abrupt faunal transition along a north-south line following the Makassar (Borneo–Sulawesi) and Lombok straits (Bali–Lombok; **Figure 1**). He later formalized its position (Wallace 1863)

Pleistocene Aggregate Island Complex (PAIC):

a suite of islands that joined together by land bridges during periods of low sea level in the Pleistocene

and explained its significance (Wallace 1869). In these works, Wallace considered the Philippines to be part of the Asian realm.

In an insightful paper with lasting impacts on Philippine biogeography, Huxley (1868) modified the northern portions of Wallace's Line to wrap around the Palawan island group, effectively dividing the Philippines between the Asian region and what would later be known as Wallacea (the islands between Wallace's and Lydekker's lines; **Figure 1**). This rearrangement had two major implications for subsequent biogeographic studies in the Philippines. First, the western Philippines (the Palawan island group) were allied faunistically with the Sunda Shelf islands (Huxley 1868, Everett 1889, Boulenger 1894, Brown & Alcala 1970, Heaney 1985, Esselstyn et al. 2004). Second, the eastern Philippines was either grouped loosely with transitional landmasses of Wallacea or considered a separate subregion (Dickerson 1928, Kloss 1929, Mayr 1944, Lohman et al. 2011).

The debate over Wallace's observations spurred intense interest in species distributions across the region (Allen 1910, Hollister 1913, Dickerson 1928, Mayr 1944, Sanborn 1952, Inger 1954). In a timely summary of distributions of plant and animal groups north of the widely accepted Bali–Lombok split, Dickerson (1928) and colleagues called attention to a transition zone between the Asian and Australian biotas and coined the term Wallacea for this area. However, the formal association of the archipelago east of Huxley's line with one faunal region or another was de-emphasized in response to Simpson's (1977) expressed frustration with the focus on naming and debating biogeographic lines. Numerous empirical studies chronicling the uniqueness of the Philippine fauna emerged (Taylor 1920, Inger 1954, Leviton 1963, Brown & Alcala 1970, Musser & Heaney 1992), and as a result, most recent efforts treat the Philippines as a unique biogeographic entity (Lohman et al. 2011, but see Michaux 2010). Just as the shifting perspective on the meaning and position of biogeographic boundaries illuminated evolutionary history (Lohman et al. 2011), changing perceptions of biodiversity in the Philippines have shaped refined views of diversification processes as we try to understand the “zoogeographic puzzle” (Diamond & Gilpin 1983) represented by the archipelago.

Immigrant Patterns, Depauperate Faunas, and the Fringing Archipelago

... *The Philippines [has] presented a zoogeographic puzzle ever since the time of Wallace...* —Diamond & Gilpin (1983, p. 313)

Early perceptions of biogeographic patterns in the Philippines led authors to conceive of the country as a “fringing” archipelago (Dickerson 1928, Delacour & Mayr 1946, Darlington 1957, Leviton 1963, Brown & Alcala 1970), characterized by a suite of “immigrant patterns” (Lomolino et al. 2010) or nested species distributions (Patterson & Atmar 1986). According to this perception, species are expected to be distributed along colonization routes into the archipelago (Dickerson 1928, Leviton 1963, Brown & Alcala 1970, Diamond & Gilpin 1983), and various faunal groups should reach geographic points along these corridors for immigration in accordance with their relative dispersal abilities (Darlington 1957, Carlquist 1965, Diamond & Gilpin 1983). Under this perspective, most evidence suggested that primary conduits for colonization (see the section titled Recent Arrivals via Biogeographic Colonization Routes, below) were along the eastern and western island arcs (**Figure 2c**) (Dickerson 1928, Inger 1954, Myers 1962, Leviton 1963, Diamond & Gilpin 1983). Northern islands, perceived as the ends of colonization routes (Diamond & Gilpin 1983, Brown & Guttman 2002, Jones & Kennedy 2008), were viewed as the last, most extreme endpoints of dispersal for Sundaic faunal elements (Huxley 1868; Dickerson 1928; Inger 1954, 1999; Myers 1962). As a consequence, various workers considered the biodiversity of the northern

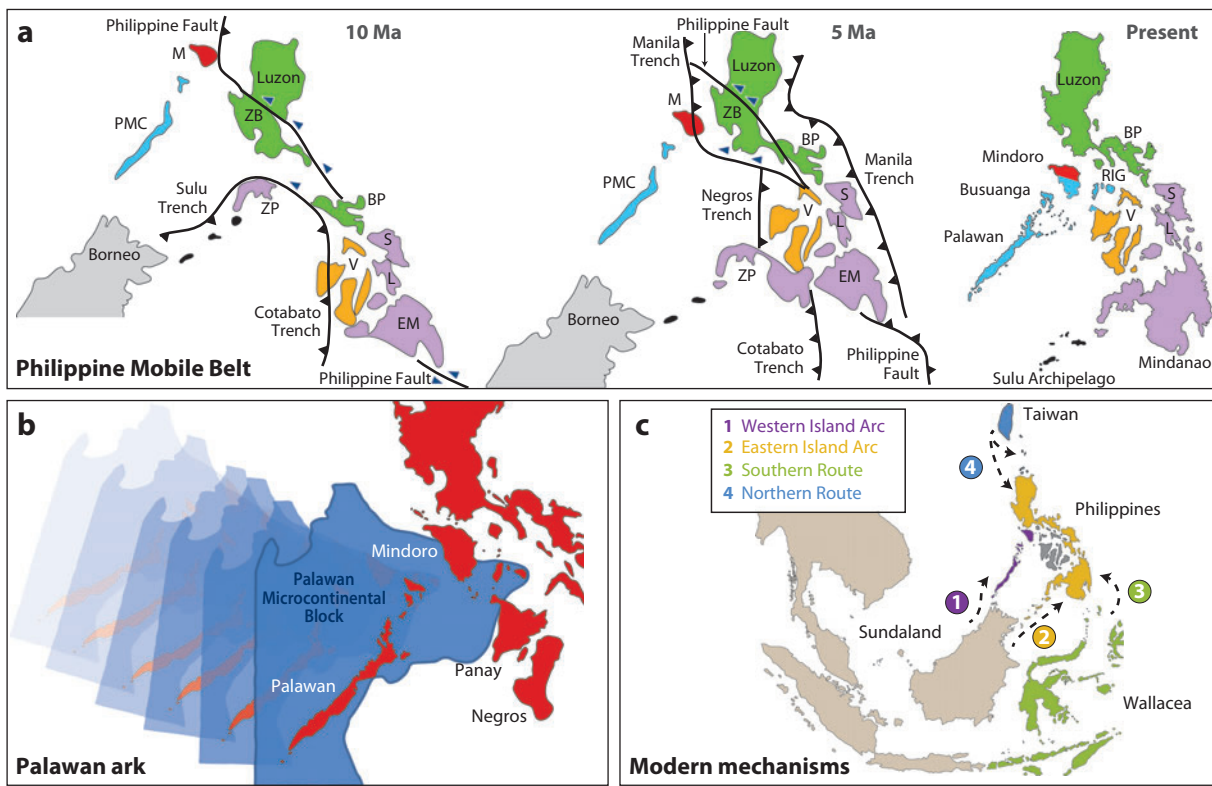


Figure 2

Major geological features and approximate tectonic evolution of the archipelago (Hall 1996, 1998; Yumul et al. 2003, 2009): (a) The Philippine Mobile Belt [BP, Bicol Peninsula; EM, Eastern Mindanao; L, Leyte; M, Mindoro (*red*); PMC, Palawan Microcontinent (*light blue*); RIG, Romblon Island Group; S, Samar; V, Visayan PAIC [Pleistocene Aggregate Island Complex (*orange*)]; ZB, Zambales Block of Luzon (*green*); ZP, Zamboanga Peninsula of Mindanao (*purple*)], (b) the Palawan Microcontinental Block, and (c) the hypothesized modern colonization routes into the archipelago.

Philippines as “depauperate,” in the sense that it was expected to hold a reduced subset of species derived from mainland sources (Dickerson 1928, Inger 1954, Brown & Alcala 1970, Lomolino et al. 2010); this view persisted late into the twentieth century (Inger 1954, Leviton 1963, Brown & Alcala 1970). Recent field inventories and densely sampled systematic studies (Brown et al. 2013, Linkem et al. 2010, Heaney et al. 2011), however, have drawn attention to high species diversity and endemism and a long history of in situ speciation (Jansa et al. 2006; Brown & Diesmos 2009; Heaney et al. 2011; Siler et al. 2011a; Brown et al. 2013; Hosner et al. 2013a,b). Hence, the northern portions of the archipelago may be substantially more diverse than generally appreciated (Heaney et al. 2010, 2011; Balete et al. 2011; Duya et al. 2011; Siler et al. 2011b; Brown et al. 2013).

NEW ESTIMATES OF PHILIPPINE LAND VERTEBRATE BIODIVERSITY

For an archipelago of its size (collective landmass of just 300,000 km²; for comparison, Borneo is 740,000 km²), resident species diversity is startlingly high. Until recently, Philippine land

vertebrate biodiversity was considered to be reasonably understood. Well-developed taxonomies, stemming from more than a century of study by specialists (McGregor 1909, Hollister 1913, Taylor 1920, Dickerson 1928) resulted in reasonably stable diversity estimates, checklists, faunal synopses, and field guides (Inger 1954, duPont 1971, Alcalá 1986, Dickinson et al. 1991, Heaney et al. 1998, Kennedy et al. 2000). Compared with other countries in the region (e.g., Indonesia, Vietnam, Thailand), Philippine diversity appeared moderately high and distinctly characterized by high proportions of vertebrate species that occur nowhere else in the world.

Starting in the early 1990s, a flurry of discoveries prompted comprehensive systematic reconsiderations, in many cases using new techniques, genetic data, and new diagnostic tools for species delimitation (e.g., Brown et al. 1997; Brown et al. 2009; Siler et al. 2010, 2011a; Welton et al. 2010a,b; Baleté et al. 2011; Brown & Stuart 2012; Esselstyn et al. 2012). The swift accumulation of many discoveries encouraged field biologists to revisit numerous islands, mountain ranges, and inaccessible regions of the archipelago (Siler et al. 2010, 2011a; Brown et al. 2011, 2013). The result has been a steady pace of species discovery, with continued diversity accumulation beyond the asymptotes seen in accumulation curves from some surrounding regions (Brown et al. 2002, 2008; Catibog-Sinha & Heaney 2006; Posa et al. 2008; Heaney et al. 2010), and many detailed reevaluations of earlier taxonomic classifications (Brown & Diesmos 2002, Peterson 2006, Oliveros & Moyle 2010, Hosner et al. 2013b).

Current land vertebrate summaries (Heaney et al. 2010) (*Biodiversity Research and Education Outreach—Philippines*: <http://philbreo.lifedesks.org>; *IOC World Bird List (Version 3.4)*: <http://www.worldbirdnames.org>; *Synopsis of Philippine Mammals*: <http://fieldmuseum.org/explore/synopsis-philippine-mammals>) recognize approximately 440 native resident bird species (56% endemic to the Philippines), 215 native mammals (70% endemic), 111 amphibians (80% endemic), and 270 reptiles (74% endemic). Amphibian, reptile, and mammal species accumulation curves all exhibit continued *de novo* species discoveries over the past three to four decades (**Figure 3a**). In birds, 69 new endemic bird species, an increase of 39% in country endemics, have been recognized since the guide by Kennedy et al. (2000) was published. However, 65 of these represent subspecies that were elevated to full species or taxa resurrected from synonymy (e.g., Oliveros & Moyle 2010; Collar 2011; Hosner et al. 2013a,b), and only four are newly discovered species. This recent tremendous increase in bird diversity is not reflected in the species accumulation curve (**Figure 3a**) because most of these taxa were described several decades, if not more than a century, ago (but have been treated as unrecognized synonyms or subspecies in modern studies). The Philippines may have as many as 15,000 species of native plants and 38,000 species of animals (vertebrates + invertebrates), for a possible total of 53,000 species (Catibog-Sinha & Heaney 2006, Brown & Diesmos 2009, Heaney et al. 2010). Armed with new estimates of resident biodiversity, it has become more important than ever for biogeographers to ask, Can we find support for common mechanisms of diversification across lineages?

Subduction:

the tectonic process wherein one crustal fragment moves under another

ORIGIN OF LAND VERTEBRATE DIVERSITY AND MECHANISMS OF DIVERSIFICATION

Geological Setting

Discussions of diversification of land vertebrates in the Philippines rely on an understanding of the major geologic features of the archipelago (Yumul et al. 2008) and a changing appreciation for the temporal series of events underlying the formation of the archipelago (Yumul et al. 2009; Hall 1996, 1998, 2002). Bound by a pair of subduction zones (the Manila Trench to the west and the proto-East Luzon Trough to the east; Yumul et al. 2009), the NW-SE oriented Philippine Mobile

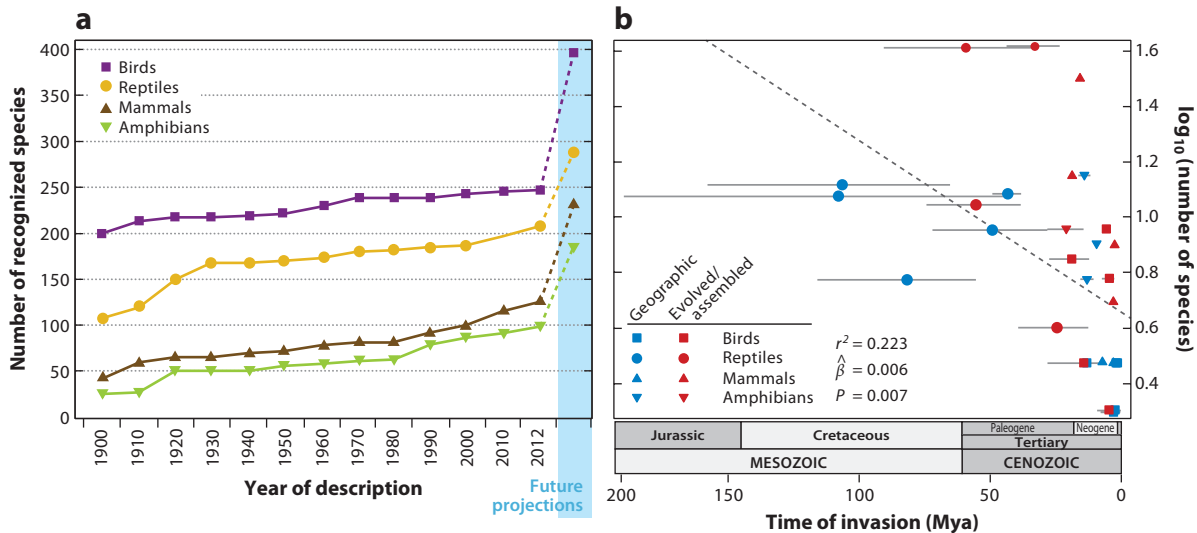


Figure 3

(a) Species accumulation plot for Philippine endemic birds, reptiles, mammals, and amphibians; projected unrecognized species diversity is indicated with dashed lines (*blue area*). For unrecognized species diversity, estimates are as follows: for amphibians and reptiles, new species, in collections, currently awaiting taxonomic description (R.M. Brown, A.C. Diesmos, C.D. Siler, and A.C. Alcala, unpublished data); for birds, results of revisionary subspecies taxonomic studies currently underway (C.H. Oliveros, R.G. Moyle, and P.A. Hosner, unpublished data); for mammals, from current species diversity (125) plus a percentage of unrecognized species of bats (*Hipposideros*), inferred by mixed Yule-coalescent analyses and echolocation call frequencies (Esselstyn et al. 2012), and extrapolated to other mammal groups. (b) Time for diversification effect: bivariate plot of estimates of clade ages (from Bayesian molecular phylogenetic analyses) against recognized species diversity for each clade. All analyses were conducted in BEAST under strict clock models with constrained rates from the literature and an exponential prior on the rate equivalent to the midpoint between the estimated age of crown and stem node of the group. For all data analyzed and for publications that provided credibility intervals on ages: The illustrated 95% highest posterior density (HPD) interval includes a low end of the crown node to an upper end of 95% HPD of stem node (for publications that did not provide confidence intervals, HPDs span the crown node age up to stem node age). “Geographic” refers to radiations with single species per island or Pleistocene Aggregate Island Complex (PAIC); “evolved/assembled” refers to radiations characterized by instances of sympatric species, with 2–5 co-occurring taxa per island or PAIC.

Belt (Yumul et al. 2003; Hall 1996, 1998) (**Figure 2a**) is a series of tectonically and volcanically active island arcs, ophiolite suites (uplifted exposed sections of crust and underlying mantle), and exposed terranes of continental origin (Hall 1996, Yumul et al. 2009). The archipelago is roughly bisected along its NW-SE axis by the Philippine fault (Hall 2002, Yumul et al. 2009). In one recent model, Yumul et al. (2008) described the mobile belt landmasses moving great distances as they were pushed up and exposed above sea level by collision between the Philippine Sea Plate and Sundaic or Eurasian continental fragments (the Palawan Microcontinent Block, the Zambales Block, the Zamboanga Peninsula and the southern Mindanao Daguma Range Block).

Paleoendemic Lineages on Old Landmasses

Geologic events (island emergence, migration, and collision) likely have played several roles in transporting land vertebrates to the Philippines via a variety of mechanisms at different times (**Figure 2a,b**). Although inferences remain speculative (based on geologic reconstructions and gross temporal correlations), notable cases of highly diverse and/or ancient, paleoendemic clades

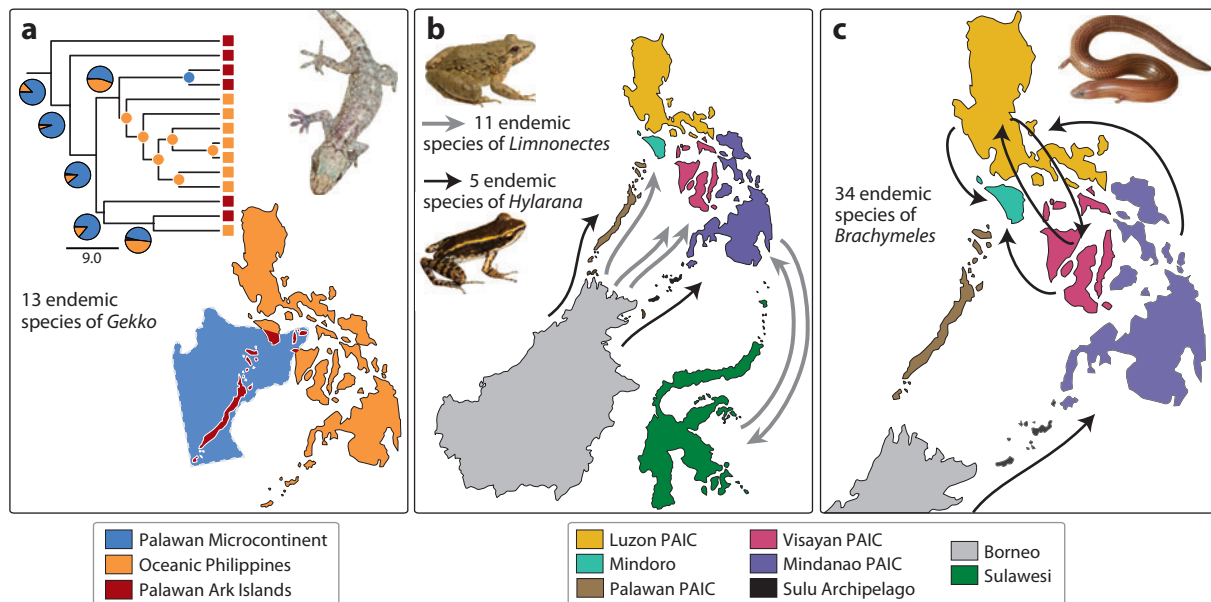


Figure 4

Comparative biogeographic reconstructions derived from ancestral state reconstructions. (a) Geckos and the Palawan Ark hypothesis (Blackburn et al. 2010, Siler et al. 2012); (b) the Dual Invasion pattern in stream frogs (genus *Hylarana*; Brown & Guttman 2002, Brown & Siler 2013) versus multiple faunal exchanges between Mindanao and Sulawesi (Indonesia) in fanged frogs (genus *Limnonectes*; Evans et al. 2003, Setiadi et al. 2011); (c) complex back-and-forth dispersal between Luzon and the Visayas in Philippine slender skinks (Siler et al. 2011a). Abbreviation: PAIC, Pleistocene Aggregate Island Complex.

originating in the archipelago via geologic mechanisms have been inferred (e.g., Blackburn et al. 2010, Siler et al. 2012) (**Figures 2b** and **4a**). For example, Australasian faunal elements form conspicuous components of the archipelago's fauna that may have been tectonically transported into the oceanic portions of the Philippines via geological activity associated with the north-west movements of the Mobile Belt (Jansa et al. 2006, Michaux 2010) (**Figure 2a**). In some cases, these events are assumed to have given rise to highly diverse clades (Inger 1954, Leviton 1963, Brown & Alcalá 1970, Jansa et al. 2006). Palawan Microcontinent Block paleoendemism (**Figure 2b**) may represent cases of tectonically transported lineages that subsequently diversified in situ (Siler et al. 2012) (**Figure 4a**) or exhibited limited species diversity that evolved in isolation and may have dispersed out of the Philippines (Blackburn et al. 2010). The remaining continental fragments (the Zamboanga Peninsula, Daguma Range Block, and Zambales Block; Yumul et al. 2009) may, likewise, be associated with ancient endemics in some of the archipelago's most diverse clades (Steppan et al. 2003; Jansa et al. 2006; Esselstyn et al. 2009; Michaux 2010; Linkem et al. 2011; Siler et al. 2011a, 2012). The Philippines also contains old endemic taxa that do not show strong associations with mobile terranes and likely resulted from ancient dispersal events (e.g., Jansa et al. 2006, Oliveros et al. 2012). Other than the possibility of selected paleoendemic faunal element transport to the archipelago on rifted continental microterranes or rising sea-level landmass fragmentation (and associated vicariance) associated with the end of the Pleistocene (see below), hypotheses of diversification involving oceanic island endemics in the Philippines necessarily invoke some form of dispersal-related explanations, especially for recently-derived groups (Heaney 2001, Evans et al. 2003, Esselstyn et al. 2011, Linkem et al. 2012, Brown & Siler 2013).

Oceanic islands: islands that have never or not recently been connected to the adjacent mainland

Land-bridge islands: islands that have been connected to other landmasses by exposed land bridges during Pleistocene reductions in sea levels

Recent Arrivals via Biogeographic Colonization Routes

Given the relatively stable configuration of the archipelago over the past 5 Ma (**Figure 2**), several dispersal routes have been posited to explain more recent colonization of the archipelago. Four major colonization routes, or biogeographic umbilici (Diamond & Gilpin 1983), have been identified (**Figure 2c**) as entryways to portions of the archipelago that have never been connected to a mainland (Dickerson 1928, Inger 1954, Diamond & Gilpin 1983, Brown & Guttman 2002, Brown & Diesmos 2009). These passageways include two 800-km-long island chains that may have allowed “stepping stone” dispersal into the archipelago from Borneo, which constitutes the edge of the Sunda Shelf (Inger 1954, Heaney 1985, Voris 2000) (**Figures 1** and **2c**). These two most widely evoked colonization routes include western (Borneo–Palawan–Mindoro–Luzon; Huxley 1868, Everett 1889) and eastern island arcs (Sulu Archipelago–Mindanao–Leyte–Samar–Luzon; Dickerson 1928, Mayr 1944) (**Figures 1** and **2c**). However, Inger (1954), Diamond & Gilpin (1983), and Dickinson et al. (1991) also emphasized Australo–Papuan groups in the Philippines, suggesting that the Sangihe–Talaud–Sarangani island chain of eastern Indonesia may have permitted some colonization from the south (Evans et al. 2003). Finally, early biogeographers considered a possible northern route (**Figures 1** and **2c**) via the Taiwan–Batanes–Babuyans island chain (Dickerson 1928).

Although phylogenetic evidence in favor of northern and southern dispersal routes is limited (Jones & Kennedy 2008, Esselstyn & Oliveros 2010, Oliveros & Moyle 2010, Oliveros et al. 2011), numerous recent analyses have found phylogenetic patterns consistent with island chain–facilitated dispersal along both the western and eastern island arcs, resulting in Philippine populations clearly derived from Sunda Shelf vertebrate groups and often still inhabiting land-bridge islands (Brown & Guttman 2002; Evans et al. 2003; Esselstyn et al. 2004, 2009, 2010; Jones & Kennedy 2008; Brown et al. 2009; Esselstyn & Brown 2009; Oliveros & Moyle 2010; Moyle et al. 2011, 2012; Blackburn et al. 2013; Brown & Siler 2013) (**Figure 4b**). Phylogenetic relationships in fanged frogs (genus *Limnonectes*; Evans et al. 2003) supported the southern colonization route and indicated multiple faunal exchanges, in both directions, between Mindanao and the Indonesian island of Sulawesi (see also Esselstyn et al. 2009, Setiadi et al. 2011) (**Figure 4b**). Although most studies have focused on faunal colonization of the archipelago or within archipelago dispersal (**Figure 4c**), out-of-the-Philippines dispersal (Linkem et al. 2012, Andersen et al. 2013, Barley et al. 2013) and dispersal to the mainland or to continental, land-bridge islands have been inferred in a few studies (Evans et al. 2003, Blackburn et al. 2010, Welton et al. 2013b; C.H. Oliveros and R.G. Moyle, unpublished data). Finally, diversification may be related to colonization route. In birds, for example, a few studies have documented dispersal along the western island arc, through Huxley’s Filter Zone (the northern portions of the island of Palawan; Esselstyn et al. 2010) (**Figure 1**), resulting in a species or two on Mindoro or Luzon but with limited subsequent radiation (e.g., Brown et al. 2009, Lim et al. 2010, Oliveros & Moyle 2010, Brown & Siler 2013). In contrast, colonists traced to the eastern arc colonization route (Borneo–Sulu–Mindanao) tend to colonize the whole archipelago and diversify substantially (Evans et al. 2003, Oliveros & Moyle 2010, Barley et al. 2013, Blackburn et al. 2013, Hosner et al. 2013a).

The Pleistocene Aggregate Island Complex (PAIC) Diversification Model

Every Ice-Age island in the Philippines is a unique center of diversity, even those only 250 square kilometers in area. —Heaney & Regalado (1998, p. 42)

Within the archipelago, a hierarchical temporal structure of landmass connectivity during the Pleistocene gave rise to a simple model of diversification. This model was based on the initial

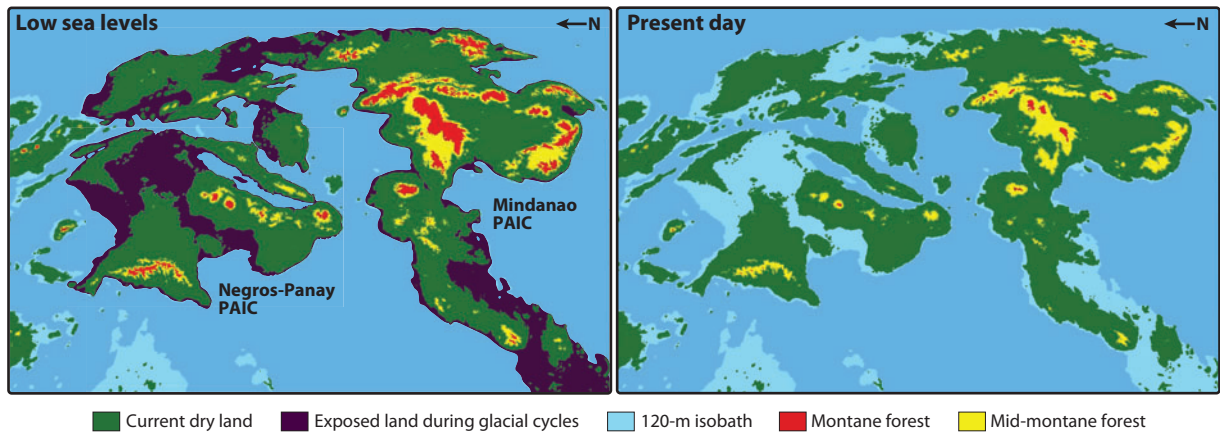


Figure 5

Fundamentals of the Pleistocene Aggregate Island Complex (PAIC) diversification model and estimates of the extremes of land connectivity and habitat connectivity during glacial-interglacial cycles (Heaney 1985, Brown & Diesmos 2009). A view of western Mindanao and the Visayan PAIC from the west, emphasizing increased land exposure and connectivity estimated from the 120-m reduction in sea levels at the last glacial maxima (*left*) and depressed (extending to lower elevation) montane (*red*) and mid-montane (*yellow*) forest estimates (Heaney 1991), versus contracted and reduced land and forest areas during interglacials (present day, *right*). Reconstructed with ETOPO data (Christopher & Eakins 2009).

observations that species distributions were organized into biogeographic subprovinces (Steere 1894; Inger 1954; Leviton 1963; Brown & Alcala 1970; Heaney 1985; Brown & Diesmos 2002, 2009), which corresponded to Pleistocene land connections estimated by tracing underwater 120-m bathymetric contours (Kloss 1929, Inger 1954, Heaney 1985, Voris 2000). These observations produced a 25-year paradigm of diversification representing an elegant, heuristic model for hypothesis testing (Brown & Diesmos 2009, Lomolino et al. 2010).

Alluded to by Dickerson (1928) and Kloss (1929), and formally defined later by Inger (1954) and Heaney (1985), the seven PAICs (Brown & Diesmos 2002, 2009) (**Figure 1**) formed repeatedly (perhaps ten times during the late Pleistocene) (**Figure 5**) as a result of oscillating sea levels (Voris 2000) associated with Pleistocene glacial cycling (Siddal et al. 2003). Five large PAICs are recognized as primary biogeographic regions: the Luzon, Mindanao, Mindoro, Negros-Panay (or West Visayan), and Palawan faunal regions (Inger 1954, Heaney 1985, Brown & Diesmos 2009) (**Figure 1**); smaller PAICs include the Romblon and Sulu centers of endemism. Many additional isolated islands (e.g., Siquijor, Lubang, Camiguin Sur, and Maestre de Campo, among others) and small island groups (e.g., Babuyan and Batanes) surrounded by deep ocean channels never shared land-bridge connections to other major islands (**Figures 1** and **5**). Despite their close proximity to larger islands, many of these peripheral deep-water islands hold restricted-range endemics (e.g., the Romblon Island Group, with endemic birds, mammals, amphibians, and reptiles; Goodman et al. 1995, Esselstyn & Goodman 2010, Brown et al. 2011).

The PAIC diversification model articulates clear and testable predictions derived from over-land gene flow during periods of low sea level. These predictions have been used with species distribution data (Heaney 1985), population-genetics results (Brown & Guttman 2002, Heaney et al. 2005, Roberts 2006, Esselstyn & Brown 2009, Siler et al. 2010), coalescent-based simulation studies (Oaks et al. 2013), and topology-based phylogenetic tests (Esselstyn & Brown 2009; Siler et al. 2010, 2011a, 2012; Linkem et al. 2010). Philippine PAICs are characterized by high levels of vertebrate endemism (Heaney 1985; Dickinson et al. 1991; Brown et al. 2002, 2009), seemingly

confirming a dominant role in partitioning and maintaining diversity, possibly associated with processes of speciation.

Testable PAIC-derived predictions include expectations of (a) coincident species distributions that match PAIC geographic boundaries, (b) widespread species that may exhibit greater among-PAIC than within-PAIC genetic variation, (c) repeated fragmentation of populations within PAICs that may result in greater genetic variation within PAICs, (d) monophyly of lineages within a PAIC, and (e) within-PAIC population divergences temporally clustered at interglacial island fragmentations.

Virtually all explicit tests of these hypotheses have found consistencies with the model and, simultaneously, marked deviations from purely PAIC-derived predictions (Evans et al. 2003; Heaney et al. 2005; Roberts 2006; Esselstyn & Brown 2009; Linkem et al. 2010; Siler et al. 2010, 2011a, 2012; Welton et al. 2010b); until recently, however, only Esselstyn et al. (2009) and Oaks et al. (2013) have tested explicitly whether sea-level oscillations have driven diversification within PAICs. However, neither study was able to identify clear evidence of diversification being temporally associated with sea-level fluctuations. Regardless of the idiosyncratic way in which lineages may deviate from strict PAIC expectations, the PAIC paradigm continues to provide viable explanations for many observations, including species distributions and patterns of relatedness (much like the Hardy-Weinberg equation or equilibrium model of island biogeography). The model has provided a valuable suite of testable predictions that have stimulated inquiry and inspired new ways of testing hypotheses concerning evolutionary diversification in the archipelago.

Beyond the PAIC Paradigm

Despite the elegant simplicity and heuristic value of the PAIC paradigm and support for many predictions of the model, recent empirical studies have identified patterns of diversification that suggest processes beyond the dry land connections between modern islands. First, substantial diversification of land vertebrates prior to the Pleistocene has been inferred in most recent phylogenetic studies (Jansa et al. 2006; Esselstyn & Brown 2009; Esselstyn et al. 2009; Siler & Brown 2011; Siler et al. 2011a, 2012; Hosner et al. 2013a). A simple bivariate ordination of inferred clade age (based on time-calibrated molecular phylogenetic analyses) and size (number of species) indicates a relationship between a clade's age and its diversity (**Figure 3b**), suggesting that older clades (e.g., skinks and geckos; Linkem et al. 2011, 2012; Siler et al. 2012; Barley et al. 2013) and the first colonists of the archipelago diversified more substantially than younger groups that arrived in the archipelago more recently. A multitaxon, comparative, time-calibrated phylogenetic framework for vertebrate diversification is one of the obvious, sorely-needed next steps for understanding diversification across the archipelago (Oaks et al. 2013).

Several studies have used phylogenies to demonstrate another fundamental deviation from the expectation of purely PAIC-derived structuring of biodiversity. By documenting substantial within-PAIC diversification and fine-scale differentiation within islands, new studies have demonstrated that adherence to PAIC-level explanations can provide only partial explanations for high species diversity in the archipelago (Welton et al. 2010a,b; Balet et al. 2011; Heaney et al. 2011; Linkem et al. 2011; Siler et al. 2011a; Blackburn et al. 2013; Hosner et al. 2013a). Analyses of vegetation and forest change in southeast Asia derived from fossil pollen, bat guano deposits, and stable isotopes suggest that, at alternating times, montane forests and savannahs alternately expanded in some parts of the archipelago (Heaney 1991; Bird et al. 2007; Wurster et al. 2010), providing another mechanism of isolation and diversification for species with narrow habitat requirements (**Figure 5**). These habitat oscillations are analogous to the sea-level oscillations and produce similar predictions, but at a smaller geographic scale. They may have contributed to

isolation in several conspicuous montane endemic clades (Brown et al. 2010, Linkem et al. 2011, Hosner et al. 2013a) and may have produced important ecological barriers that have structured and isolated species distributions as much as island shorelines (e.g., Welton et al. 2010a,b; Balete et al. 2011; Hosner et al. 2013b).

Whereas species turnover was previously expected and commonly inferred between PAICs, the presence of within-PAIC species diversity has been highlighted in recent studies. For example, several phylogenetic studies found deep phylogenetic splits between taxa endemic to Samar, Leyte, and Bohol islands and their sister groups endemic to Mindanao Island, all of which are within the Mindanao PAIC (Steppan et al. 2003; Esselstyn et al. 2009, 2012; Welton et al. 2010b; Siler et al. 2012). Despite broad Pleistocene land bridges connecting these islands (Heaney 1985, Voris 2000) (**Figures 1 and 5**) that should have allowed gene flow, ecological barriers unrelated to coastlines (climate, forest type differences) facilitated divergence and promoted lineage diversification. Paleodistribution models for multiple codistributed bird lineages confirm broad disjunctions of suitable areas on Pleistocene landmasses corresponding to deep splits in some lineages (**Figure 6**). This suggests a nested PAIC model might be worthy of consideration, with an outer level (fluctuating sea levels) causing land connection-isolation cycles and the inner level (fluctuating habitats) creating terrestrial habitat connection-isolation cycles.

Ecological Processes: Elevational Gradients and Within-Island Diversification

The predominance of the PAIC paradigm has focused attention on among-island mechanisms as drivers of speciation, leaving within-island diversification less emphasized. However, elevationally structured ecological gradients are often cited as key promoters of diversification (**Figure 5**), and their study is a classic theme in studies of Philippine biodiversity (Heaney & Regalado 1998, Catibog-Sinha & Heaney 2006). A long series of elevational transect studies focusing on mammals (Heaney 2001; Heaney et al. 1989, 1999; Heaney & Rickart 1990), birds (Goodman et al. 1995, Peterson et al. 2008), and amphibians and reptiles (Brown & Alcalá 1961, Siler et al. 2010, Brown et al. 2013) has produced ample literature detailing associations of elevational, habitat, temperature, and precipitation gradients throughout the country (Heaney 2001, Catibog-Sinha & Heaney 2006). Pronounced differences are apparent among taxa: Mammals exhibit an upper-mid-elevation (1,500–2,000 m) peak in species diversity and abundance, but amphibian and reptile diversity peaks at lower elevations (700–900 m; Siler et al. 2010, Brown et al. 2013). Mammals exhibit curvilinear or positive relationships between both species richness and abundance and elevation (Heaney & Rickart 1990, Heaney 2001, Heaney et al. 2011), whereas amphibians and reptiles exhibit inverse relationships between these variables and elevation (Brown & Alcalá 1961, Brown et al. 2013). Comparing multiple taxa and multiple causal hypotheses, Heaney (2001) found support for the hypothesis that diversity correlates with productivity gradients, rainfall patterns, habitat heterogeneity, and areas of community overlap or habitat-type interdigitization. Recent studies have borne out these findings (Balete et al. 2011, Duya et al. 2011) and extended them to disturbance gradients (Rickart et al. 2007, 2011a,b).

Although species ranges are clearly partitioned by elevational gradients, it remains unclear whether these gradients have played a significant role in promoting divergence and generating vertebrate biodiversity. If so, which of the many habitat and atmospheric factors that covary with elevation influence differentiation? Across >40 detailed molecular studies of Philippine species complexes, only a few cases of recently diverged sister species with distributions structured by elevation have been identified (Steppan et al. 2003, Heaney et al. 2011; R.M. Brown, J.A. Esselstyn, C.D. Siler, P.A. Hosner, and R.G. Moyle, unpublished data).

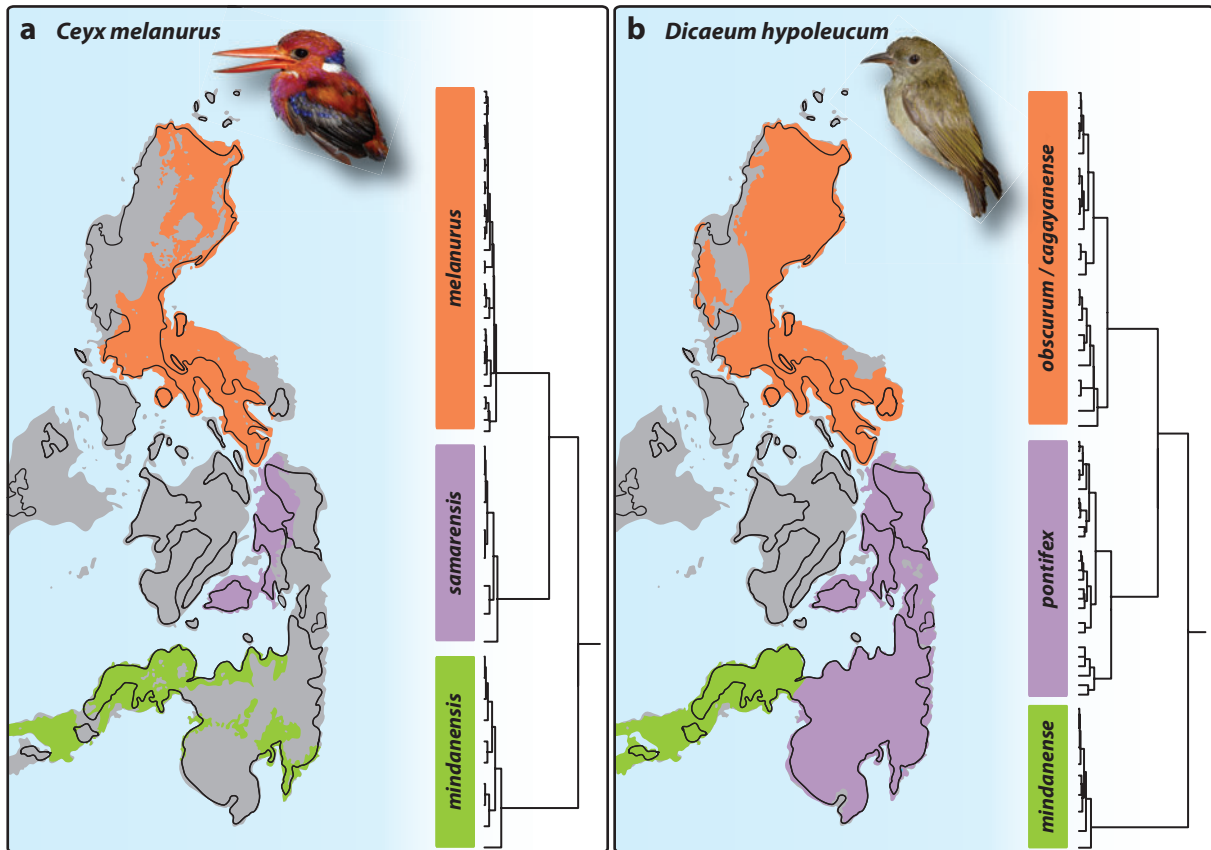


Figure 6

Avian comparative phylogeography and paleo projections of ecological niche models. Niche models estimate climatic requirements of bird species (subspecies names in *colored boxes*); models are projected to the last glacial maximum paleoclimate scenarios (current coastlines depicted with *black outlines*) that correctly anticipated phylogeographic breaks within the Mindanao Pleistocene Aggregate Island Complexes (PAICs) in seven of eight codistributed polytypic bird species restricted to the Mindanao and Luzon PAICs. Model projections followed two contrasting patterns (P.A. Hosner, C.H. Oliveros, and R.G. Moyle, unpublished data): (a) In *Ceyx melanurus* and four other species, unsuitable environmental (*gray*) conditions isolated populations into two refugia within the Mindanao PAIC. (b) In *Dicaeum hypoleucum* and one other species, models supported broad environmental suitability (without refugia) across the Mindanao PAIC.

Despite the lack of evidence for speciation along elevational gradients, it is clear that topographic complexity interacts with species' autecology and contributes to speciation, particularly on large islands (i.e., Luzon and Mindanao; Heaney 2007, Esselstyn & Brown 2009, Welton et al. 2010b, Linkem et al. 2011, Sanguila et al. 2011, Siler et al. 2011b, Hosner et al. 2013a). Although not likely to be the dominant diversification mechanism in the archipelago, fine-scale differentiation may be important in taxa with specialized ecological requirements or limited dispersal abilities. In these cases, isolation of populations among mountain ranges, valleys, rivers, or habitat types may be common on islands with heterogeneous geographic templates, allowing further accumulation of vertebrate diversity at replicated sites across large islands (Welton et al. 2010a,b; Balet et al. 2011). Our understanding of these processes is still in its infancy but derives predominantly from recent field work and molecular phylogeographic studies (Heaney 2001, 2007;

Brown & Diesmos 2009). Integration of these ecological and geographic considerations, and determination of conditions under which each is important, remains a challenge for the future (Heaney 2001, Heaney et al. 2011). Recent developments in statistical phylogeography and landscape genetics (Manel et al. 2003, Knowles 2009, Lemey et al. 2010) provide ample opportunities for new insights into these questions.

FAUNAL ASSEMBLY AND IN SITU DIVERSIFICATION

A major advance over the past two decades has been the impact of robust well-sampled phylogenetic analyses toward understanding of evolutionary radiations, complex biogeographic histories, and community assembly (Brown & Diesmos 2009; Esselstyn et al. 2009, 2011; Siler & Brown 2011; Heaney et al. 2011). These studies provide new insight into the temporal framework for vertebrate diversification in the archipelago, ecological factors impacting species distributions, and species interactions.

Community Evolution and Assembly

Several well-sampled phylogenetic studies demonstrate distinctions between islands with faunas that are phylogenetically clustered (e.g., an island with species stemming from a single common ancestor, or few ancestors) versus islands with faunas that are randomly assembled or phylogenetically overdispersed (species on an island are more closely related to species on other islands than would be expected by chance alone, suggesting ecological processes, environmental filtering, colonization/dispersal, and/or competitive species interactions; Webb et al. 2008). Many simple geographic radiations are known, with a single species per island or per PAIC (McGuire & Alcala 2000; Brown & Guttman 2002; Moyle et al. 2009, 2011, 2013; Siler et al. 2010; Esselstyn et al. 2011; Brown & Siler 2013; Welton et al. 2013a,b). Many additional complex assemblages are also represented, consisting of multiple distantly related and phenotypically divergent species, consistently observed paired together in a seemingly repeated, deterministic pattern. Examples of this latter pattern include distantly related pairs of large- and small-bodied fanged frogs of the genus *Limnonectes* (Evans et al. 2003, Setiadi et al. 2011), slender skinks of the genus *Brachymeles* (Siler & Brown 2011), and sun skinks of the genus *Eutropis* (Barley et al. 2013).

For highly diverse clades, opportunities exist for studies employing statistical and phylogenetic approaches to community structure (Esselstyn et al. 2011). *Sphenomorphus*-Group forest skinks (genera *Pinoyoscincus*, *Parvosincus*, *Otosaurus*, *Insulasaurus*, and *Tyttboscincus*) are predominantly found in faunal communities that have assembled on the southern island of Mindanao, but this group also includes some phylogenetically clustered (Webb et al. 2008) communities in the northern island of Luzon (Linkem et al. 2011) (**Figure 7**). In the latter case, clades of endemic species (minor radiations) have evolved in situ in the mountains of Luzon (Brown et al. 2010, Linkem et al. 2011); that is, any one species is more likely related to other Luzon endemic species than expected by chance alone. In contrast, on Mindanao, with its close proximity to the Sunda Shelf (**Figure 1**), frequent colonization from outside the Philippines and from other islands in the Philippines results in a random assemblage of species (Linkem et al. 2011). However, minor endemic radiations of birds and putative toad species have been identified in the mountains of Mindanao (Sanguila et al. 2011, Hosner et al. 2013a), suggesting that Mindanao may also hold phylogenetically clustered communities.

Many clades fall in between the extremes of phylogenetically clustered versus overdispersed faunas (Webb et al. 2008); we suspect this pattern will prove dominant for many groups with lengthy evolutionary histories in the archipelago. The phylogeny of several bird and reptile groups

Phylogenetically overdispersed:

when members of a community (or species on an island) are more distantly related than expected by chance

Geographic radiation:

the product of nonadaptive diversification resulting in archipelago-wide groups of ecologically similar species with few cases of sympatry

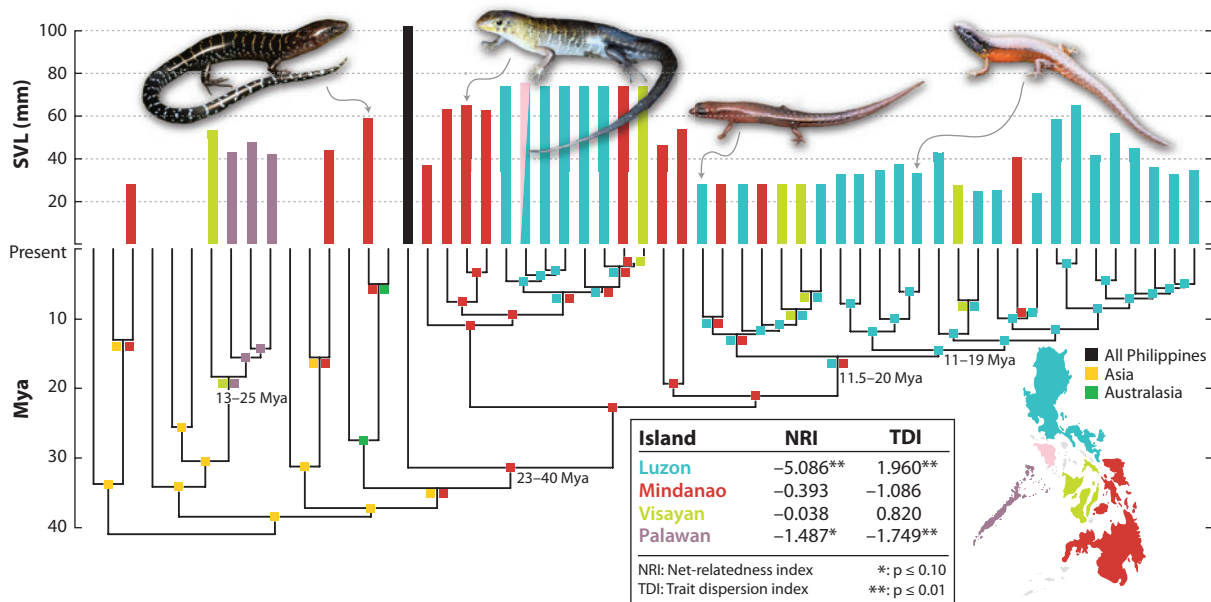


Figure 7

Evolution of island communities versus assembly of island communities in Philippine forest skinks (Linkem et al. 2011, Siler et al. 2011a). A combination of ancestral range reconstruction on a fossil-calibrated phylogeny (Lagrange: Ree & Smith 2008) and analyses of community structure (Webb et al. 2008) show that communities on Mindanao Island and in the Visayan faunal region are not phylogenetically clustered but instead randomly assembled from other source populations (NRI near zero), whereas communities on Luzon and Palawan have evolved in situ multiple times (phylogenetically clustered, significantly negative NRI). Species on Luzon are convergent in body size (significantly negative TDI), which is in contrast to communities characterized by random body size on the Mindanao and Visayan islands. The Palawan community has a conserved body size. Images left to right: *Sphenomorphus fasciatus*, *Pinoyscincus jagori*, *Parvosincincus steerei*, and *Parvosincincus abstrusus*. Abbreviations: Mya, million years ago; SVL, snout-vent length.

contains at least one endemic radiation of multiple species and additional independent colonizations involving single species (Oliveros & Moyle 2010; Sánchez-González & Moyle 2011; Sheldon et al. 2012; Siler et al. 2011a, 2012; Barley et al. 2013), resulting in sympatry of both closely related and unrelated pairs of taxa.

Adaptive Radiation in the Philippines?

Strikingly high estimates of Philippine endemic land vertebrate diversity necessarily beg the question of the fundamental processes that have fueled diversification within the archipelago. Although the Philippines has not historically been identified as home to major adaptive radiations, several conspicuous clades bear hallmarks of adaptive radiation (Schluter 2000, Glor 2010) and are worthy of note.

Setiadi et al. (2011) concluded that Philippine fanged frogs (genus *Limnonectes*) did not radiate adaptively into the same wide array of body size classes found on Sulawesi Island, most likely as a consequence of other Philippine lineages (ceratobatrachid frogs; Brown et al. 2008, Brown 2009) filling those ecological niches. In contrast, other well-studied groups possess the conspicuous characteristics heralded as evidence of adaptive radiation (Schluter 2000). Phylogenetic studies of several vertebrate clades have demonstrated monophyly of highly diverse Philippine

Adaptive radiation:

the product of accelerated species diversification in response to ecological opportunity and natural selection operating on a phenotype-environment correlation

groups, with strong phenotype–environment correlations, and replicated evolution of apparently functional traits. Examples include murid rodents (Heaney & Rickart 1990, Jansa et al. 2006, Brown & Diesmos 2009, Heaney et al. 2011), some clades of scincid lizards (Siler & Brown 2011, Linkem et al. 2011), ceratobatrachid frogs (Brown et al. 2008, Brown 2009), and microhylid frogs (Blackburn et al. 2013). Full characterization of Philippine adaptive radiations provides compelling opportunities for future research.

CONCLUSIONS

Long understood as an important regional center of biodiversity presenting unique biogeographical problems, the Philippine archipelago has emerged as a globally significant model island archipelago for studies of evolutionary processes of diversification. The archipelago has served as a key backdrop for tests of predictive models (e.g., species/area relationship, equilibrium theory, species pump mechanisms), and continues to reveal biogeographic patterns and novelties of process that prompt new integrative approaches and inspire the search for common mechanisms of diversification. Future work will be enabled greatly by comprehensive estimates of species diversity, sustained biodiversity field surveys, improved understanding of the geological history of the islands, and application of new and powerful statistical phylogeographic tools.

SUMMARY POINTS

1. With over 7,100 islands, a land mass of only 300,000 km² (roughly the size of the US state of Arizona), very high species diversity per unit land, and a soaring human population, the Philippines is a global conservation priority.
2. Strikingly high new estimates of resident land vertebrate biodiversity have resulted from the past two decades of taxonomic revisions; *de novo* species discoveries; new biodiversity surveys; and recent, increasingly sophisticated comprehensive reviews of major vertebrate groups. Numerous recent molecular phylogenetic analyses have provided new insights into species boundaries, existence of morphologically cryptic species, and tests of traditional taxonomies.
3. Explicit phylogeny-based and population-genetic tests of predictions derived from the PAIC diversification model have documented many likely coincident processes, but also numerous deviations from predictions of the model.
4. A consensus among biogeographers suggests that the PAIC model only partially explains the high levels of endemic biodiversity of the archipelago. Rather, a multifaceted model incorporating Pleistocene sea-level oscillations, deep-time phylogenetic patterns of diversification, ancient geological mechanisms, and ecological features of the archipelago that promote diversification within islands will be necessary.
5. Although the number of well-sampled phylogenies incorporating endemic Philippine species has improved vastly, a full understanding of processes producing Philippine land vertebrate biodiversity is limited not by technology but by the availability of archipelago-wide genetic sampling available in biodiversity repositories; thus, continued, sustained, biodiversity surveys, combined with training and educational opportunities, are urgently needed in many of the country's poorly explored and biologically understudied areas.

FUTURE ISSUES

Although many avenues of research are interesting, such as more work on conservation, species discovery, ecological speciation, adaptive radiation, and comparative phylogeography, the following are several areas where integrative new research programs could generate ideas of general interest to the global community of biodiversity specialists, biogeographers, and evolutionary biologists.

1. Seldom studied, because of PAIC-paradigm-generated expectations that land-bridge islands will not support endemics, some small islands recently have been shown to support some phylogenetically distinct, genetically divergent, and morphologically unique microendemic vertebrates. Do these often neglected small islands support more endemic resident biodiversity than presently appreciated? Have small islands contributed to archipelago-wide processes of diversification?
2. Have adaptive processes or nonadaptive geographic radiations contributed disproportionately to the generation and accumulation of species diversity in the archipelago? Will direct evidence emerge of elevational gradients contributing directly to diversification, or do elevational gradients serve as ecological filters in areas of habitat heterogeneity? Do adaptive radiations tend to occur in more isolated portions of the archipelago, and can they be shown to be associated with ecological gradients and habitat heterogeneity?
3. Can we identify periods of increased diversification in the Philippines or has speciation been a gradual, more constant process? Are sizes of clades simply a function of time? A multilineage, time-calibrated temporal framework for diversification is an important goal for future studies.
4. We have identified cases of geographically coincident species splits, seemingly associated with apparent terrestrial habitat barriers but not marine barriers. Increased study of these species contact and filter zones is needed to understand their role in generating and maintaining diversity.

DISCLOSURE STATEMENT

The authors are unaware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

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Map of Life Project: <http://www.mappinglife.org/>

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