

ECOLOGY AND DIVERSITY OF HERPETOFAUNAL  
COMMUNITIES IN FRAGMENTED LOWLAND  
RAINFORESTS IN THE PHILIPPINES

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FRAGMENTED LOWLAND RAINFORESTS IN THE PHILIPPINES

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## **Dedication**

To Mae, Aeja, and Pangaea Aena: for making my heart leap.

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## Summary

*Diesmos, A. C. 2008. Ecology and Diversity of Herpetofaunal Communities in Fragmented Lowland Rainforests in the Philippines. Ph.D. Dissertation. National University of Singapore.*

Using the species-area relationship, I estimated the numbers of amphibian and reptilian species that are predicted to become extinct with massive deforestation of the Philippine lowland forest. This study reveals a looming extinction crisis in Philippine herpetofauna, with up to 42 species predicted to become extinct. More species of reptiles than amphibians are expected to vanish and the levels of extinction would be most severe in highly deforested regions and small island ecosystems. The disparity between the number of predicted species extinctions and the actual number of globally threatened species (based on The World Conservation Union [IUCN] Red List) clearly demonstrates the lack of basic autecological knowledge of many Philippine amphibians and reptiles, which undermines accurate assessments of the conservation status of species. Immediate and effective conservation programs are needed for the West Visayas, Mindoro, Batanes, and Gigante—the hotspots of herpetofaunal conservation in the Philippines. These regions have likely reached a threshold of deforestation; further loss of habitat guarantees the extinction of at least half of their herpetofaunas.

I investigated the effects of habitat fragmentation on herpetofaunal communities that inhabit forest patches along spatial and disturbance gradients. I characterized the patterns of diversity, distribution, and ecological guild membership in amphibians and reptiles from contiguous forest and 10 forest fragments. The ecological correlates of species vulnerability to local extinction were identified through an information theoretic approach. Fragmentation resulted in a cascading loss of species with 15–

94% of the total species pool disappearing in forest fragments. Snakes manifested the sharpest decline in both richness and abundance and are most vulnerable to the effects of fragmentation. Species whose mode of reproduction is either through direct development or ovoviviparity are most especially susceptible to extirpation. Although the preservation of large forest areas is the best strategy to maintain herpetofaunal diversity, fragments may serve as important refuges for some species, including rare endemics and threatened species. The restoration of these altered habitats should be included as part of current conservation strategy in the Sierra Madre Mountains.

I sought evidence for competition between invasive alien frogs (cane toad *Bufo marinus* and Chinese tiger frog *Hoplobatrachus rugulosus*) and native frogs (*Limnonectes macrocephalus*, *L. woodworthi*, *Occidozyga laevis*, *Rana luzonensis*, *R. similis*, *Fejervarya vittigera*, *Kaloula picta*, and *Polypedates leucomystax*) that co-occur in forests and non-forested habitats by examining ecological overlap in food and habitat niche dimensions. Diet analysis showed that both groups of species consumed similar types and abundances of prey items, although introduced frogs preyed on more types and consumed larger volumes of vertebrates that included endemic species of frogs, snakes, and rodents. The high degree of dietary and spatial overlap between alien and native frogs reveals the potential for intense competition. The contrasting food and habitat niche widths, however, appear to reduce the overall ecological overlap in *B. marinus* and *H. rugulosus* and allow these aggressive consumers to co-exist. These two alien species appear to exert a more severe competitive pressure on non-forest frogs as indicated by a high degree of niche overlap.

The detection of rapid morphological change in introduced *B. marinus* populations in continental Australia presented another level of complexity in the management and

control of harmful invasive species. I found similar rapid morphological divergence in *B. marinus* populations in the Philippines. Toads in large islands had longer legs, but body size was generally larger in small islands. Younger toad populations also possessed shorter legs than older populations. The observed morphological shift appears to be the effect of evolutionary forces intrinsic to island ecosystems with possible synergistic interactions with conditions that render islands invulnerable, such as the lower levels of competitors and availability of resources. Destruction of native habitats plays a vital role in invulnerability of islands by providing appropriate habitats for introduced species to exploit. These results suggest that strategies to manage and control invasive species must also integrate biogeographic variables. Management approaches that were designed in continental regions may not be wholly applicable to island archipelagoes.

## **Chapter 1: General Introduction**

### **1.1 Relevance**

The Philippine Archipelago (Fig. 1) is comprised of 7,107 islands and is located on the western edge of the Pacific Ocean and northeast of Sundaland in Southeast Asia. It occupies a land area of about 300,000 km<sup>2</sup> with a coastline (36,289 km<sup>2</sup>) that is nearly twice that of the continental United States. The islands are mountainous and receive heavy rainfall half of the year and typically in the form of tropical cyclones (Inger 1954; Salita 1974; Auffenberg 1988; Hall 1996). Unlike most regions of Southeast Asia, the Philippines is generally lacking in (extant) large-bodied mammalian fauna, a characteristic typical to many oceanic islands (Heaney 1985; Lomolino et al. 2006). Its biodiversity, however, is unusually rich and includes the highest concentration of endemic species in the world (Heaney & Mittermeier 1997; Heaney & Regalado 1998; Myers et al. 2000). Some of the processes that were crucial to the evolution of this unique biodiversity are the islands' complex geological history with long periods of isolation, a dynamic sequence of fragmentation and coalescence of landmasses during the Pleistocene brought about by sea-level changes, autochthonous diversification of ancestral species stocks within the archipelago, and a biota that originated from two distinct biogeographic regions (Heaney & Mittermeier 1997; Brown & Diesmos 2002; Evans et al. 2003; Stepan et al. 2003).

Information amassed from biodiversity inventories in recent decades have enhanced ongoing conservation efforts and provided the foci for identifying key biodiversity areas across the islands (Mallari et al. 2001; Ong et al. 2002). Among the most astonishing results of these field surveys was the persistent discovery of undescribed



species not only of poorly known (e.g., earthworms: James 2005) or uncharismatic groups (e.g., rats and bats: Balete et al. 2006; Esselstyn 2007), but even of well-studied taxa such as birds (Kennedy et al. 2001; Allen et al. 2004) and conspicuous species like *Rafflesia* (Barcelona et al. 2007). Of terrestrial vertebrates, the amphibians and reptiles show the highest rates of discoveries with well over 60 new species discovered only in the last two decades (Brown et al. 2002; Diesmos et al. 2002; Brown 2004). Still, scientists believe that large numbers of species remains to be discovered; these estimates include both closely-related sibling species and new, phylogenetically divergent “spectacular” discoveries (Brown & Diesmos 2002; Steppan et al. 2003; Brown & Gonzalez 2007; Wallach et al. 2007).

Philippine biodiversity is severely threatened by habitat loss, pollution, over-exploitation (e.g., over-harvesting for commercial purposes, illegal wildlife trade), and introduction of invasive species (Heaney & Regalado 1998; Mallari et al. 2001; Ong et al. 2002; Diesmos et al. 2006). The large-scale destruction and fragmentation of the country’s lowland dipterocarp forest (Kummer 1992) have already had adverse impacts on flora and fauna. This is clearly manifested by the high proportions of endemic species that are now on the verge of extinction (IUCN 2007) and especially the documented extinction of some well studied taxa (Dickinson et al. 1991; WCSP 1997). But since most Philippine endemic species are poorly known (WCSP 1997; Brown et al. 2002; Heaney 2002), the proportions of species that may have been adversely affected by deforestation may be higher than are currently known. The lack of basic ecological information on many species seriously undermines the effective conservation of currently established protected areas (Mallari et al. 2001; MacKinnon 2002; Posa et al. 2008). A sustained biodiversity research agenda is important to set

priorities for conservation actions and policy-making, and should complement ongoing management and habitat protection efforts.

## **1.2 Objectives**

The main objective of this dissertation was to measure the impact of deforestation and fragmentation of the lowland forest on Philippine amphibians and (non-marine) reptiles. This problem was approached at two spatial scales. At the macro-ecological scale, I compiled and analyzed data on historical changes of lowland forest cover across the Philippines. Using the species-area relationship, I measured the consequence of habitat loss to the whole herpetofauna. At the micro-ecological scale, I examined fragmentation effects on herpetofaunal communities that inhabit forest patches along spatial and disturbance gradients. I compared herpetofaunal communities found in forest fragments to those from contiguous forest to determine the effects of habitat loss. And also at the community level, I determined the adverse ecological impacts of invasive alien frogs on native frogs from both degraded habitats and forest fragments. I performed diet analysis and field observations to find evidence for competition by measuring ecological overlap in food and habitat niches between these groups of species.

## **1.3 Outline**

In the Philippines, very little research has been done to investigate the dynamics of forest fragmentation, which is somewhat paradoxical considering that much of the remaining lowland forests in the country are now highly fragmented, and perhaps most importantly, are the only habitats that remain for many unique and highly threatened species (Magsalay et al. 1995; Alcala et al. 2004; Paguntalan et al. 2004).

The broad implications of understanding this process to biodiversity conservation cannot be over-emphasized. This dissertation is only the third study to be conducted on the Philippines that investigated fragmentation effects on amphibians and reptiles (see Alcala et al. 2004; K. Hampson, unpublished data available in the website <http://polillo.mampam.com/>), and is the first on the island of Luzon. Chapter 2 provides the results of what is likely to be the first of its kind on the analysis of species extinctions of Philippine herpetofauna. This study also identified the priority areas (or “hotspots”) for herpetofaunal conservation. Chapter 3 describes the effects of fragmentation on herpetofaunal communities in the lowland forests of the Sierra Madre Mountains, Luzon. This chapter provides insights on critical size of habitat patches that would likely hold optimum levels of herpetofaunal diversity. The final chapter, Chapter 4, essentially integrates two studies. The first examined evidence for competition between invasive alien species of frogs (specifically *Bufo marinus* and *Hoplobatrachus rugulosus*) and native anurans that inhabit forest and non-forested habitats. The other examined various island populations of *B. marinus* to look for the presence of morphological divergence among these populations. The chapter provides important ecological information that can be utilized in formulating strategies for the control and management of invasive alien species in the Philippines.

## **Chapter 2: Loss of Lowland Forests Predicts Extinctions in Philippine Amphibians and Reptiles**

### **2.1 Abstract**

Despite having lost over 80% of its original forest, particularly of the lowland dipterocarp community, not a single amphibian or reptilian species has been documented to have become extinct in the Philippines. The reason for this is more likely due to an absence of critical analysis of this subject. Using the species-area relationship, I estimated the numbers of herpetofaunal species that are predicted to become extinct with massive losses of the lowland forest to date. I compiled a database of known and undescribed native species of frogs, caecilians, lizards, snakes, and freshwater turtles that inhabit lowland forests (297 species) and identified the number of species that are currently recognized as threatened by The World Conservation Union (IUCN). The analyses centered on 11 distinct herpetofaunal sub-provinces (i.e., Pleistocene Aggregate Island Complexes, PAICs), which are regions of diversity and endemism, in order to gain a better understanding of the extent of potential extinctions of Philippine endemic species. The Philippines could lose 19–55% of its total herpetofaunal species to extinction with more reptiles predicted to become extinct than amphibians. Severely deforested regions and island PAICs would likely lose half of their herpetofaunas. Incremental losses of habitat (at 2.1% in the next five years, according to recent estimates) would likewise result to high levels of extinctions, with some PAICs losing additional species. The disparity between the numbers of predicted extinctions and currently identified globally threatened species is a manifestation of the dire insufficiency of basic autecological knowledge of many Philippine amphibians and reptiles, which undermines accurate conservation

assessments of species. Immediate and effective conservation programs are needed for West Visayas, Mindoro, Batanes, and Gigante—the PAICs of utmost priority for herpetofaunal conservation. These regions have likely reached a threshold in habitat loss; further deforestation will guarantee the extinction of at least half of their herpetofaunas.

## **2.2 Introduction**

Once covered in tropical moist forest from the coasts up to the mountains, the Philippines represents a case study of a country that has undergone massive deforestation in modern times (Kummer 1992; Heaney & Regalado 1998; Roque et al. 2000; Posa et al. 2008). Estimates of annual forest clearance between 1950 and 1995 ranged from 1.6 to 3.6% (1,570 to 3,048 km<sup>2</sup>)—a rate that is among the highest in the world (Kummer 1992; Myers 1988; Myers et al. 2000). This deforestation rate has apparently declined beginning in the 1990s (DENR 1994) due largely to the already reduced extent of commercially valuable timber resources (i.e., dipterocarp forest) and partly because of a logging moratorium that was imposed by the Philippine government in the early 1990s (Vitug 1993; DENR 1996; Malayang 2000). Nonetheless, the current deforestation rate at 2.1% (from the year 2000 to 2005) remains the highest in Southeast Asia (FAO 2007) and is caused by an expanding monoculture agriculture, *kaingin* (shifting agriculture), and most especially illegal logging; these activities are even occurring within protected areas (Mallari et al. 2001; MacKinnon 2002).

For decades, ecologists have warned of catastrophic species extinctions resulting from the large-scale destruction and disappearance of the country's forests (Rabor 1959, 1979; Brown & Alcala 1986; Hauge et al. 1986; Myers 1988). Indeed, a number of

species and endemic races of birds are known to have disappeared (Rabor 1959; Dickinson et al. 1991) including several populations of mammals, plants, and invertebrates (WCSP 1997). The fossil record also provides evidence of species that became extinct from some parts of the islands (Reis & Garong 2001; Croft et al. 2006). Yet the body of literature on this subject remains sparse. Modern extinction events are poorly documented and very little information is available on how many species have disappeared, especially for poorly studied fauna and flora. For amphibians and reptiles, not a single forest species is known to have gone extinct although herpetologists recognize several “lost” species—those that occur in localities where either the habitat has been completely removed or field surveys are generally lacking (Brown et al. 2002; Diesmos et al. 2002a). This is not, by all means, an indication that extinction has not occurred in this group. Species extinction is notoriously difficult to measure (Diamond 1987) and there exists a time lag between habitat loss and species extinction (Simberloff 1986; Brooks et al. 1999). But perhaps a more plausible and relevant rationale is the lack of critical analysis of this subject to date (Brown et al. 2002; Diesmos et al. 2002a).

In this chapter, I estimated the number of amphibian and reptilian species that are expected to become extinct based on the extent of remaining lowland forest. I also identified which regions and islands are extinction hotspots for Philippine herpetofauna—those areas that stand to lose the most number of species with sustained deforestation. This study centered on species in lowland dipterocarp forests (*sensu* Whitmore 1998) for two important reasons: (1) this forest community is the most threatened habitat in the Philippines (Kummer 1992; Heaney & Regalado 1998) and with very little remaining in spatial coverage, and (2) a high proportion (over

80%) of the herpetofauna are dependent on this habitat (Brown et al. 2002; Diesmos et al. 2002a), making them the most vulnerable to extinction.

### **2.2.1 Brief history of deforestation in the Philippines**

Except for populated areas and cultivated land, over 90% of the land area of the Philippine islands were covered with forest prior to European contact in the 16<sup>th</sup> century (Kummer 1992; Roque et al. 2000; Bankoff 2007). Deforestation essentially began under the Spanish colonial period (1565–1898) and intensified during the American rule (1898–1941). Forests were cleared to build settlements and to establish mono-crop plantations; timber was felled to supply materials for shipbuilding industries, to fuel processing plants, and exported to international markets. Commercial logging and the mining industry were introduced and burgeoned during the American period, which accelerated further clearing of forests. The brief Japanese occupation of the Philippines between 1941 and 1945 similarly led to considerable forest removal through timber exports. From the colonial era to World War II, Philippine forest cover has declined to under 60% (Myers 1988; Kummer 1992; Roque et al. 2000). After gaining independence in 1946, the Philippine government perpetuated the same macropolicies that promoted heavy cutting of forests. The roads opened by logging and mining (both legal and illegal) also became channels where impoverished migrants streamed through to convert residual forests into agriculture areas and settlements. The pace of deforestation peaked between 1950 and mid-1980s chiefly from over-exploitation, and was fueled by illegal practices from sectors of the government and a political atmosphere that guaranteed the systemic plunder of the country's natural resources (Myers 1988; Porter & Ganapin 1988; Vitug 1993). By

the 1980s, forests have dwindled to a startling 20% of land area (Myers 1988; Kummer 1992; Heaney & Regalado 1998).

## **2.3 Methodology**

### **2.3.1 Lowland forest estimates**

The most recent estimate of the remaining tropical moist forest in the Philippines is by the Food and Agriculture Organization of the United Nations, which gives a figure of 71,620 km<sup>2</sup> or 23.9% of the land area (FAO 2007). Estimates of the extent of lowland dipterocarp forest, on the other hand, remain contentious, and for the most part, reflect the vagaries of the definition of “forest” and forest types (Kummer 1992). Whitford (1911) estimated 77,700 km<sup>2</sup> of dipterocarp forest remaining in the early 1900s. In the mid-1970s, at the height of commercial exploitation of forests, the Philippine government estimated dipterocarp forests to cover 67,690 km<sup>2</sup> (NEDA 1978), which Kummer (1992) found highly suspect in his in-depth analysis of deforestation in the Philippines. The Forest Management Bureau of the Philippine Department of Environment and Natural Resources in 1997 provided a figure of 8,000 km<sup>2</sup> or < 3% of total land area (DENR 1998), but several years later, came up with a new estimate of 12–20% lowland forest cover (includes old-growth, logged over, and secondary) based on satellite data and refined definitions of habitat types (DENR 1997, 2003; Catibog-Sinha & Heaney 2006). The latest forest data was adopted by FAO (2007); I used this data in all analysis. We calculated the proportions of lowland forest cover for each island or island groups using ArcView GIS version 3.1 (ESRI, California, U.S.A.). (GIS data are available upon request to O. Coroza, Conservation International Philippines.) Habitat loss was not uniform with some islands retaining sizable portions of area in forest (e.g., Sibuyan, Palawan, Samar) and several that are



nearly completely deforested (e.g., Cebu, Masbate, Negros). Data are summarized in Fig. 1 and Appendix 1.

### **2.3.2 Database of Philippine amphibians and reptiles**

I compiled a database of Philippine amphibians (frogs, caecilians) and reptiles (lizards, snakes, freshwater turtles, crocodiles) and assembled available information on habitat, elevation, and distributions of species from monographs, journal articles, field guides, and online databases and websites (e.g., HerpWatch Philippines: <http://www.herpwatch.org/>). I also drew upon my own unpublished field data and those of other workers. Taxonomy and nomenclature follow Brown and Alcala (1978, 1980), Frost (2007), and the Reptile Database (<http://reptile-database.org/>). Conservation status of species is based on The World Conservation Union (IUCN) Red List of Threatened Animals (IUCN 2007) and from the recently completed (December 2007) but still unpublicized Global Reptile Assessment of Philippine reptilian species. A total of 54 species are threatened (30 amphibians, 24 reptiles) with 48 (~16% of fauna) that are too inadequately known to be assessed in detail, thus, were considered Data Deficient (10 amphibians, 38 reptiles). Nonetheless, a high proportion of species in the latter category could eventually be proven to be globally at risk (Stuart et al. 2004).

I classified a total of 297 species (94 amphibians and 203 reptiles) as lowland forest species, those whose main altitudinal distribution range generally falls below 800–1,000 m (Table 1). The list included species that were occasionally recorded above 1,000 m (83 species) but were essentially distributed in the lowlands. Included in the analysis were newly-discovered species (31 frogs, two lizards, one snake) that are in

the process of being described (see Appendix 2), with the intention of obtaining an estimate of the true extent of potential species extinctions with habitat loss to date. These species have yet to be assessed of their conservation status (i.e., IUCN Red List). I excluded from the analysis introduced species (five frogs, three freshwater turtles) (Diesmos et al. 2006; Brown 2007; Diesmos et al., in press) and those species that are not exclusively found in dipterocarp forest (59 species) and/or other forest habitats (63 species).

Analysis centered on distinct regions of herpetofaunal diversity and endemism (Table 1). These biogeographic sub-provinces, or Pleistocene Aggregate Island Complexes (PAIC; Brown & Diesmos 2002), harbor unique and often non-overlapping flora and fauna and correspond to paleo-islands that existed during periods of low sea level during the mid- to late-Pleistocene (Inger 1954; Heaney 1985) (Fig. 1). These faunal sub-provinces are either an amalgamation of large to small offshore islands or tiny isolated islands that, on their own, are centers of endemism. In addition, these are further partitioned into sub-regions of endemism (Brown & Diesmos 2002). I considered 11 PAICs and excluded three (Lubang, Burias, and Siquijor) that lack PAIC-level endemic herpetofauna (Appendix 1). It is, however, anticipated that current progress in phylogeographic studies and ongoing field surveys of other deep-channel island systems may result in the recognition and discovery of significant numbers of single-PAIC endemics (Brown & Diesmos 2002; Brown 2004).

### **2.3.3 Predicting extinctions using the species-area relationship**

The species-area relationship, considered the most universally recognized diversity pattern in modern ecology (Rosenzweig 1995), describes that large areas contain

more species than smaller ones. I used the species-area curve to predict species extinctions following habitat loss. The relationship between area and species number is expressed in the equation  $S = cA^z$ , where  $S$  is species number,  $A$  is area, and both  $c$  and  $z$  are constants (Preston 1948; MacArthur & Wilson 1967). I initially calculated the extent of remaining lowland forest ( $A_{\text{new}}/A_{\text{original}}$ ) to predict the proportion of forest species that is expected to persist ( $S_{\text{new}}/S_{\text{original}}$ ). Deriving from the species-area curve, I arrive at the equation  $S_{\text{new}}/S_{\text{original}} = (A_{\text{new}}/A_{\text{original}})^z$ . The proportion of species that is *not* likely to become extinct is  $S_{\text{new}} = S_{\text{original}} (A_{\text{new}}/A_{\text{original}})^z$ , and that predicted to become extinct is  $S_{\text{extinct}} = S_{\text{original}} - S_{\text{new}}$  (Simberloff 1992). This expression is independent of the constant  $c$  and the value of  $z$  is widely shown to approximate 0.25 in fragmented ecosystems (Simberloff 1986; Rosenzweig 1995), which has repeatedly been used in previous studies (Pimm & Askins 1995; Brooks et al. 1997; Brooks et al. 2002). And because much of the remaining lowland forest of the Philippine archipelago is highly fragmented, the choice of this  $z$ -value is applicable to all faunal groups. The predicted extinctions of lowland forest species were limited to Philippine-endemic species.

## **2.4 Results**

### **2.4.1 Predicted species extinctions**

The Philippine herpetofauna stands to lose from three to 42 species with current losses of lowland forest (Fig. 2A). Comparing between groups, one to 13 species of amphibians and two to 35 reptiles were expected to become extinct. More species of reptiles (mean = 13) were apparently bound for extinction than amphibians (mean = 4;  $t = -2.72$ ,  $df = 20$ ,  $p = 0.013$ )(Fig. 2B). Projected extinctions in the herpetofaunal regions ranged from 19% (7 species) for Jolo–Tawitawi to as high as 55% (42

species) for the West Visayas (Table 1). Five PAICs (Luzon, Mindoro, Palawan, Mindanao, and the West Visayas) were expected to lose >10 species or 20–55% of their faunas. Regions with the most number of predicted species extinctions were the West Visayas, Luzon, and Mindanao (the latter two PAICs each with 38 species). On the other hand, those with the highest proportions of extinctions were West Visayas and Mindoro. Not surprisingly, the extent of habitat loss in a region was inversely associated with the proportions of species becoming extinct ( $r = -0.942$ ,  $df = 9$ ,  $p = <0.0001$ ), such that regions with the least remaining forest, such as the West Visayas and Mindoro, would suffer the highest number of extinctions.

I also estimated potential extinctions of single-PAIC endemic species (Table 2). With the exception of Camiguin (zero predicted extinction), all PAICs were similarly expected to lose significant proportions of their endemic herpetofauna. Predicted extinctions ranged from 0 to 17 species (0–54.5% of faunas), for a total of 54 Philippine species. Again, the West Visayas registered the highest proportion of predicted extinctions (54.5% of its known fauna), followed closely by the tiny PAICs of Batanes and Gigante (both of which would lose half of their PAIC-level endemics), and Mindoro (40%). Of the two largest PAICs, Luzon was expected to lose a slightly higher proportion of species than Mindanao. There is no statistical difference in the proportions of expected extinctions between single-PAIC endemics and the total forest fauna ( $F_{1,20} = 0.114$ ,  $p = 0.740$ ).

#### **2.4.2 Comparison of predicted extinctions with threatened species**

I compared the predicted number of extinctions with the actual number of currently recognized threatened species (IUCN 2007; Global Reptile Assessment, unpublished

data) to assess if these sets of numbers complement each other (Fig. 3). They do not. There were more species predicted to become extinct with habitat loss to date than the number of species that are currently recognized as threatened. These two variables were also positively and strongly correlated ( $r = 0.872$ ,  $df = 9$ ,  $p = 0.0001$ ). The same pattern holds if amphibians and reptiles were assessed separately (amphibians:  $r = 0.952$ ,  $df = 9$ ,  $p < 0.0001$ ; reptiles:  $r = 0.691$ ,  $df = 9$ ,  $p = 0.018$ ). These findings suggest that the numbers of extinctions predicted by deforestation markedly overestimated the number of threatened species, that is, there should have been more species considered as threatened than are presently recognized in the IUCN Red List.

The proportions of threatened lowland forest species ( $S_{\text{threatened}}/S_{\text{original}}$ ) and those that are predicted to become extinct were significantly different (Mann–Whitney Test = 71.0,  $p = 0.0003$ ), which suggests that habitat loss did not accurately predict the number of threatened species. In contrast, deforestation accurately predicts threat to single-PAIC endemic species since both these variables were comparable (Mann–Whitney Test = 144.0,  $p = 0.26$ ).

### **2.4.3 Future habitat loss and extinctions**

If deforestation continues at a rate of 2.1% in the next 5 years (FAO 2007), the regions of Batanes, the West Visayas, and Mindanao PAICs were anticipated to lose one additional species. But the overall species loss resulting from deforestation to date and from future habitat loss was comparable ( $p > 0.05$ ; Table 3). For single-PAIC endemics, only the region of Mindanao will lose an extra species with continued deforestation.

## 2.5 Discussion

There were high levels of predicted species extinctions coincident with the current level of habitat loss. This is true for both the total lowland forest herpetofauna and PAIC-level endemics. Predicted extinctions were likewise high if future habitat loss is considered, with some regions expected to lose additional species through time. As expected, the highest proportions of expected extinctions were in areas where deforestation was most severe, specifically in the West Visayas and Mindoro regions. Thus, these are the critical areas for herpetofaunal conservation in the Philippines. Species that are restricted to a single PAIC are highly susceptible to extinction; this is especially true for those that occur on tiny islands or island groups, such as Batanes, Babuyan, and Gigante. The absence of extinction-prone single-PAIC endemics on the island of Camiguin, on the other hand, may be artifactual; a re-assessment of the herpetofauna along the lines of this study following the completion of ongoing herpetological studies on the island would likely lead to contrasting conclusions. It is noteworthy that a considerable number of single-PAIC species are limestone karst specialists, which is a severely threatened habitat in Southeast Asia (Clements et al. 2006). Threatened limestone herpetofauna (Alcala et al. 2004; Brown 2004; Rösler et al. 2006; Siler et al. 2007) includes *Gekko gigante*, *G. ernstkelleri*, *Platymantis spelaeus*, *P. insulatus*, *P. paengi*, and three newly discovered limestone frogs (IUCN 2007; Global Reptile Assessment, unpublished data; Rafe Brown and Cam Siler, personal communication).

Deforestation generally overestimated the number of threatened forest herpetofauna. These findings revealed that the number of forest species predicted to become extinct (thus, “threatened”) were not congruent with the number of species that are currently

in the IUCN Red List, with a deficit of 4–31 species. I offer several explanations for this. One of the most parsimonious is that the species-area calculations may be incorrect owing to errors associated with estimation of forest cover. If the percentages of forest cover were decreased by, for example, one-half of the figures used in the study, this would result in higher numbers of species extinctions. Conversely, increasing the forest cover by one-half would significantly reduce the numbers of predicted extinctions to the level of current number of threatened species. However, it is highly doubtful (even implausible) that the “true” extent of remaining lowland forest in the Philippines is higher than the figures used in this study (and certainly not by an additional one-half) especially in light of past treatises on the subject, all of which evidentially revealed the dismal state of lowland forest in the country. Hence the forest cover data I used in the study may well approach the current extent of lowland forest, or even tend to be conservative. A closely related possible explanation is that the  $z$ -value I used may be inapplicable to the system I studied. One might argue that higher  $z$ -values should be used instead, such as 0.6–1.0, which are typical to tiny, isolated habitat fragments (Rosenzweig 1995). However, using higher  $z$ -values to calculate the species-area curve results in much higher numbers of predicted species extinctions (data not shown).

Perhaps the most plausible explanation for the observed pattern is that there simply is a lack of knowledge on the conservation status of many species of amphibians and reptiles in the Philippines, as reflected in the assessment of threatened species (i.e., IUCN Red List). If this is true, and numerous Philippine species are in fact complexes of many independent evolutionary lineages (Brown and Diesmos 2002; Evans et al. 2003), it is to be expected that the current underdeveloped state of taxonomy of

Philippine amphibians exacerbates this issue and compounds error in biodiversity estimates. Threatened species are assessed bottom-up. Species are evaluated on the basis of knowledge of their ecology, taxonomy, distribution, and prevailing threats (Brooks et al. 1997; IUCN 2001). To illustrate this with an example, the Philippine monitor lizards *Varanus olivaceus* and *V. marmoratus* are both heavily hunted for their meat but were red-listed differently (the former species is threatened and the latter is not; Global Reptile Assessment, unpublished data). *Varanus olivaceus* has restricted distribution (confined to eastern Luzon and the land-bridge islands of Polillo and Catanduanes) and its forest habitat is under severe human pressure, whereas *V. marmoratus* is wide-ranging (found in six PAICs) and can thrive in non-forested habitats (Alcala 1986; Auffenberg 1988). Further support for the assertion that species are assessed on the merits of autecological information is the fact that the total number of currently recognized threatened Philippine herpetofaunal species does not correlate with the extent of remaining forest habitat ( $p > 0.05$ ), which demonstrates that assessments were not chiefly based on a species' remaining habitat. The high numbers of species in the Data Deficient category (48 species or ~16% of the fauna assessed in this study) attests to the inadequacy of knowledge of many species. In particular, basic information on the ecology and systematics of approximately 70% of all known Philippine species is lacking (Brown et al. 2002; Diesmos et al. 2002a). Data Deficient species could eventually be proven to be threatened species, and thus warrant increased research attention and be allocated with the same amount of resources as threatened species (Stuart et al. 2004; Pimenta et al. 2005). Additionally, if many current species are in fact complexes of numerous unrecognized species, future recognition of true diversity may result in additional range-restricted species.



In addition to the preceding argument, the inclusion of species new to science (34 species) may have led to a bias toward predicted extinctions in the species-area calculations, simply because the conservation (or threat) statuses of these undescribed taxa have not been assessed yet. Nonetheless, this explanation may be true for amphibians because of the high numbers of new taxa (with 31 undescribed species) but is not likely to be the case for reptiles (with only three new species). Finally, this disparity may also be due to the continued persistence of some forest species in marginal, secondary, or otherwise degraded forest habitat.

## **2.6 Conclusions**

These results of the study hinge on the premise that extinction in Philippine amphibians and reptiles have not yet occurred, an assumption that is chiefly based on the absence of documented evidence. Yet the high numbers of species projected to become extinct with deforestation that has already been carried out, plus the fact that human activities in the past four centuries have already destroyed or completely removed lowland forest habitats in many parts of the Philippines, provide compelling evidence that species extinctions could have occurred undetected. These observations underscore the potential for a looming extinction crisis in Philippine herpetofauna. The Philippines simply cannot afford to lose more forest habitat through continued deforestation, arguably the most fundamental threat to the herpetofauna (and to Philippine biodiversity in general). In addition, the results of the study clearly demonstrate that further incurred habitat loss will commit more species to extinction. Especially vulnerable are those species that are range-restricted or are confined to tiny PAICs; it is predicted that at least half of the faunas from these regions may disappear

with habitat losses to date. It is also emphasized that the inadequacy of basic ecological information of species and the status of their habitat hinders an accurate assessment of their conservation status, which can be remedied by supplementing ongoing habitat protection efforts with active field studies of species. And such efforts should focus on the West Visayas, Mindoro, Batanes, and Gigante—the regions that are considered high priority for herpetofaunal conservation. In other regions of Southeast Asia, ongoing massive deforestation would likely lead to similar high levels of species extinctions, especially in species-rich areas such as Borneo and many parts of Indonesia, where current rates of forest loss are similarly high (Sodhi & Brook 2006; FAO 2007).

## **Chapter 3: Ecological Correlates of Herpetofaunal Communities in a Fragmented Lowland Rainforest in the Sierra Madre Mountains of the Philippines**

### **3.1 Abstract**

I investigated the effects of habitat fragmentation on herpetofaunal communities in disturbed lowland forests of the Sierra Madre Mountains, a key biodiversity area in the Philippines. Using strip transect sampling protocols, I characterized the patterns of richness, endemism, abundance, distribution, and ecological guild membership in amphibians and reptiles from contiguous forest and 10 forest fragments. The ecological correlates of species vulnerability to local extinction were identified through an information theoretic approach. Microclimate and habitat structure influenced the observed patterns of distribution. Frogs, lizards, and snakes responded variedly to fragmentation, which is attributed to differences in their guilds and life history traits. Fragments tended to support higher densities of lizards. This study indicates that body size is not an important correlate of extinction risk in the herpetofauna, in contrast to studies of other vertebrate species. Fragmentation resulted in a cascading loss of species and had profound effects on community structure. Extirpations ranged from 15% to as high as 94% with snakes manifesting the sharpest declines and were most sensitive to fragmentation. Over 61% of species were vulnerable to extirpation, with reproductive mode as the most important trait to predict extinction proneness. Although preservation of large forest areas is the best strategy to maintain herpetofaunal diversity, fragments may serve as important refuges for some species, including rare endemics and threatened species. The restoration of these altered habitats is a viable conservation strategy.

### **3.2 Introduction**

Habitat fragmentation is among the greatest threats to global biodiversity. Its impacts are thought to be most severe in the humid tropics—the world’s most biologically diverse region (Whitmore & Sayer 1992; Wilson 1992). The scientific studies of habitat fragmentation have steadily infused critical information and practical knowledge in the conservation of biotic populations and habitats in anthropogenic landscapes (see reviews by Saunders et al. 1991; Schelhas & Greenberg 1996; Laurance & Bierregaard 1997; Bierregaard et al. 2001).

Most countries in Southeast Asia had already lost extensive tracts of forest cover, particularly of the lowland dipterocarp community. Those that remain are scarcely pristine, are continually being felled, or are highly fragmented (Laurance & Peres 2006; Sodhi & Brook 2006). The ecological impact of forest fragmentation has been poorly investigated in this region where, ironically, the highest rates of deforestation are occurring and where the biodiversity is extremely imperiled (Myers et al. 2000; Brooks et al. 2002; Sodhi et al. 2004). Further, available studies on the ecological effects of tropical rainforest fragmentation are restricted to a few taxonomic groups (e.g., Turner et al. 1996; Turner & Corlett 1996; Lynam & Billick 1999; Castelletta et al. 2000; Liow et al. 2001; Sodhi 2002; Alcalá et al. 2004).

Of the countries in the region, the Philippines has likely suffered the most devastating consequences of large-scale deforestation (Heaney & Regalado; Posa et al. 2008). Apart from severe economic repercussions and great losses of human lives from frequent episodes of flooding, landslides, and drought (Myers 1988; Vitug 1993; Goldoftas 2006), a high proportion of its known terrestrial biodiversity is threatened

with extinction due to the almost complete clearance of its lowland rainforest (Heaney & Regalado 1998; Mallari et al. 2001; Ong et al. 2002). With an exceptionally rich endemic fauna coupled with alarming rates of forest loss and continued destruction of important natural habitats, the Philippines is currently recognized as one of the hottest of global biodiversity hotspots (Heaney & Mittermeier 1997; Myers et al. 2000; Brooks et al. 2004). More than 80% of its known amphibian and reptilian species are confined to the archipelago, making the Philippines one of the world's most important centers of herpetofaunal endemism. And because over 80% of species are dependent on forest, this group is also among the most threatened (Alcala 1986; Brown et al. 2002; Diesmos et al. 2002a). The Global Amphibian Assessment (<http://www.globalamphibians.org/>) ranks the Philippines among the top countries worldwide with the greatest concentrations of threatened amphibians; nearly 50% of Philippine amphibians are currently facing a high risk of extinction (Stuart et al. 2004). But the poor knowledge on the ecology and distribution of this threatened fauna impedes the formulation of informed strategies for their conservation and management (Alcala 1986; Brown et al. 2002; Diesmos et al. 2002a; Alcala et al. 2004).

Amphibians represent the more ecologically sensitive taxa and are excellent indicators of global environmental health and contamination (Hero et al. 2005; Blaustein et al. 2007). Over 160 species are considered to have become extinct while 43% of the over 5900 species are in decline, including those whose populations are found in relatively undisturbed, well-protected forest habitats (Stuart et al. 2002; IUCN, Conservation International, and NatureServe 2006). Reptiles are similarly

facing large-scale population declines and species loss and may even be in greater threat of extinction than amphibians (Gibbons et al. 2000).

The objectives of this study were to investigate the effects of habitat fragmentation on herpetofaunal communities in the lowland rainforest of the Sierra Madre Mountains on Luzon Island, the Philippines. I compared patterns of species richness and endemism, abundance, spatial distribution, and ecological guilds of amphibians and reptiles between contiguous forest and forest fragments. I also determined the ecological correlates of extinction proneness of species by examining their unique life history and ecological attributes. Finally, I provide recommendations to help conserve both species and habitat in an anthropogenic landscape in the critically important Sierra Madre Mountains.

### **3.3 Methodology**

#### **3.3.1 Sierra Madre Mountains**

The Sierra Madre Mountains is an elongate chain of mountains at the northeast coast of Luzon Island, Republic of the Philippines (Fig. 4). This vast and rugged mountain range spans nearly 500 km from north to south and is roughly 40 km at its widest point. More than a dozen peaks reach heights of over 1,000 m and numerous drainage systems and deep valleys bisect mountain massifs. This and other major mountains (Central Cordilleras, Zambales Mountains, and Bicol Peninsula) were paleo-islands that accreted into the landmass of Luzon during the Pleistocene (Hashimoto 1981; Auffenberg 1988; Hall 1996). Climate varies markedly on either side of the range. The east slope is predominantly wet throughout the year with annual rainfall of 2,500–5,000 mm. The west slope has a pronounced dry season (December to May)

and an average annual rainfall of 2,000 mm. It lies in a major typhoon track of the Asia-Pacific region, receiving an average of 20 typhoon landfalls a year (Flores & Balagot 1969; Salita 1974). The Sierra Madres is a priority site for biodiversity conservation, harboring a rich biodiversity with high numbers of endemic and threatened species and diverse ecosystems (Mallari & Jensen 1993; Danielsen et al. 1994; Tan 2000; Mallari et al. 2001).

Prior to commercial logging operations that began in the 1960s, the Sierra Madre lowlands were blanketed with dipterocarp forest. Large-scale timber extraction (which supplied international markets) from 1969 to 1992 cleared 220 km<sup>2</sup> of forest annually. By 1981 over 80% of its lowland forest has been logged (Tan 2000; van den Top 2003). The Philippine government instituted a countrywide ban on logging in 1992 but its enforcement was ineffective in many areas (Vitug 1993; Goldoftas 2006). Toward the end of logging operations, poor migrant settlers streamed into remote deforested areas and established small villages. A majority of these communities rely heavily on an agricultural system that is unsustainable (i.e., wanton expansion of cultivated area, debt bondage) and environmentally destructive (soil degradation, intensive use of agrochemicals) (Hobbes & de Groot 2003; van den Top 2003; Overmars 2006). The remaining lowland forest of the Sierra Madres, ravaged in the past by high-intensity commercial logging, continues to be felled by illegal logging and agricultural expansion (Tan 2000; Mallari et al. 2001; van den Top 2005; Overmars 2006).

### 3.3.2 Forest sites

The study encompassed 11 sites in lowland dipterocarp forest (Whitmore 1998) on the west slope of the Sierra Madres (Fig. 4, Table 4). Fieldwork was conducted from January to May 2005 and April to July 2006. Two plots were established within the west boundary of the Northern Sierra Madre National Park (NSMNP) in contiguous, selectively logged old growth forest; this area served as the reference site. A patchwork mosaic of agricultural land, pastureland, scrub, grassland, roads, and human population centers surrounds the ten study fragments. Forest regrowth in the matrix is suppressed by sustained clearing and burning (van Weerd et al. 2004; Overmars 2006). The study fragments ranged in size from 0.5 to 700 ha and became isolated habitats 20 to 40 years ago. Elevation varied between 10 and 350 m above sea level. All sites are subjected to enormous anthropogenic pressures. Illegal logging is rife in NSMNP and in the larger fragments, while intensive slash-and-burn *kaingin* (shifting agriculture) and forest clearing for mono-crop plantations and pastureland encroach the other patches. All sites are open-access to bushmeat hunting, firewood gathering, and harvesting of non-timber forest products. One of the larger fragments (Site 2) was recently established as a sanctuary for the threatened Philippine crocodile (*Crocodylus mindorensis*), considerably reducing human disturbance on the site (van Weerd & van der Ploeg 2004).

### 3.3.3 Herpetofaunal surveys

Surveys of amphibians and reptiles were conducted in 77 standardized 10 X 100 m strip transects, the number of which varied depending on patch size (Table 4). The transect line (mid-point) was marked at 10-m intervals with numbered fluorescent flagging tapes and served as focal points for habitat analysis. Transects were placed



over 100 m apart in all representative habitats in each forest site. I performed visual and aural searches (Crump & Scott 1994; Zimmerman 1994) for individuals of species and recorded data on richness and abundance, vertical distribution (perch height above ground), distance from nearest water body, microhabitat type, perpendicular distance from the transect line, time of observation, and behavior of the animal when observed (e.g., calling, foraging, basking, etc.). Up to two transects were sampled daily by the same three observers throughout the course of this study for an average of 90 min (range 60–120 min) per observer. All accessible microhabitats confined within the transect where animals may be ensconced were searched by raking the forest floor litter, probing epiphytes and tree hollows, upturning rocks and logs, and splitting-open decayed logs. Each transect was sampled during the day and at night. Diurnal censuses took place between 0800 and 1100 h while nocturnal searches were between 1800 and 2200 h. To minimize disturbance on herpetofaunal assemblages, transects that were surveyed during the day were revisited for nocturnal sampling only after two subsequent nights. I also installed dry-type pitfall traps with drift fences and used a combination of straight-line fence and three-fence array design (Corn 1994). A pitfall station comprised of four pits (plastic buckets 27 cm diameter, 40 cm depth) inter-connected by a durable plastic sheet 3 m long and 30 cm high, the bottom edge of which was embedded into the ground. Pits were buried in the ground and the brim flush with the surface. Each pit was fitted with a plastic funnel to prevent captured animals from escaping. Each station was assigned a unique number for data recording purposes. Traps were installed in representative habitats in each site on level ground and checked daily in the morning (0700–0900 h), midday (1100–1300 h), and early evening (1700–1900 h). Non-random searches (general collecting sorties) were also carried out in all forest sites and matrix habitat. All captured

animals were identified to species, weighed, measured (in mm, snout-vent length, SVL, and total length; size classes based on SVL are, frogs: 1 = < 40, 2 = 40–80, 3 = > 80; lizards: 1 = 40, 2 = 40–130, 3 = > 130; snakes: 1 = < 400; 2 = 400–1,000; 3 = > 1,000), classified according to sex and age, and released at sites of capture. Frog advertisement calls were recorded to aid in species identification. Nomenclature follows Alcalá (1986), Frost (2007), and the Reptile Database (<http://reptile-database.org/>).

Transect sampling detected 95% (81 of 85 species) of the total herpetofaunal richness and 75% (1808 of 2410) of the total number of individuals recorded; hence I limited the analyses to data gathered from this method alone. Data from pitfall traps and non-random searches were nonetheless valuable in understanding the area's overall herpetofaunal diversity; for instance, seldom-observed and poorly studied taxa (crocodiles, worm skinks, subterranean snakes) were detected only through these methods. Data from all methods were pooled to produce a species presence by site matrix.

Because the species composition and richness of the herpetofauna of the Sierra Madre Mountains is poorly known (Brown et al. 2007), voucher specimens were collected (as per stipulated protocols detailed in research and collecting permits granted by the Philippine wildlife authority) that represented undescribed taxa and those that were not confidently identified in the field, using standard preservation techniques and storage (Heyer et al. 1994; Simmons 2002). The specimens are deposited in the Herpetology Section of the National Museum of the Philippines, Manila.

### 3.3.4 Environmental variables and habitat characterization

At each strip transect I documented the forest structure (number and height of trees with > 5 cm diameter-at-breast-height, DBH), percent canopy cover, leaf-litter depth, litter mass (wet and dry weights), temperature, relative humidity (RH), understorey density (number of trees, palms, saplings), number of decayed logs, and elevation. The number of trees was counted within a 5-m radius at three different points of the transect. Measurement of litter depth and mass were taken from 1-m<sup>2</sup> plots that were randomly placed within the same points. Understorey density was estimated by recording the number of contacts between a 5-m vertical pole and understorey plants at each 10-m interval of the transect. Temperature and RH (ambient and ground) were recorded before and after each sampling event. Temperature, RH, and rainfall were registered daily from each site.

I distinguished a total of seven habitat types from the study area: selectively logged old growth forest, secondary forest, limestone forest, riverine forest, marshes, forest plantation, and agricultural areas. I estimated the area of each habitat type based on available data in the literature, vegetation cover, and land use maps and used the estimates to compute for an index of habitat diversity following the Shannon index  $H'$  (Magurran 2004). I calculated a disturbance index to quantify the extent of human disturbance at each site. I considered five disturbance components (proportion of agriculture/pasture area, frequency of logging activity, frequency of bush meat hunting/harvesting of forest products, number of felled timber, and extent of clearing/burning for agriculture/pasture), each of which was given a score. Possible index scores ranged from 0 to 1 (Table 4).

### 3.3.5 Ecological correlates of extinction-prone species

I determined the correlates of extinction proneness of species by examining life history and ecological traits. I classified a species as extinction-prone if it exhibited combinations of the following attributes: (1) found exclusively in contiguous forest during the surveys; (2) occurred in low abundance (see Appendix 3); (3) were rare based on an index of rarity (Watling & Donnelly 2007); (3) fragmentation-sensitive (Fig. 5); and (4) were extirpated in  $\geq 50\%$  of the fragments (Appendix 3). I excluded crocodiles and freshwater turtles from the analysis as these were encountered exclusively in riparian habitats that transcend both forest and matrix habitat; all are highly threatened species (IUCN 2007). Overall, I assessed 78 species (48 were classified as extinction-prone) and considered their vertical stratum distribution, level of endemism, adult habit, body size, larval development site, and reproductive development mode (Table 5). Some of these traits are important correlates of extinction risk in species from altered landscapes elsewhere (e.g., Pimm et al. 1988; Davies et al. 2000; Lips et al. 2002; Henle et al. 2004; Hero et al. 2005; Watling & Donnelly 2007).

For this analysis, I fitted generalized linear mixed-effects models (GLMM) to data using the *lmer* function in the *R* Package (R Development Core Team, Vienna, Austria). Extinction proneness was coded as a binomial response variable (0 = not prone, 1 = extinction-prone) and each trait as a linear predictor (fixed effects), assigning each model a binomial error distribution and a *logit link* function, with phylogenetic co-variance modeled as a hierarchical taxonomic (Order/Family) random effect (Burnham & Anderson 1998). Body size effects were likewise controlled in the models. Given the small sample size, the a priori model was

restricted set to include seven models that best represented thematic hypothesis to test (Table 6). An index of Kullback–Leibler information loss was used to assign relative strengths of evidence to different competing models and Akaike’s Information Criterion (AIC<sub>c</sub>) was used to compare relative model support for small sample sizes (Burnham & Anderson 2004). The amount of variance in the response variable from the various models was assessed as the percent deviance explained (%DE).

### **3.3.6 Data analysis**

Estimates of species richness and accumulation curves (sample-based rarefaction curves) based on both sampling effort and number of individuals of species detected were calculated (500 randomizations without replacement) using EstimateS version 8.0.0 (Robert K. Colwell, University of Connecticut, USA). An average of the species richness values ( $\pm$  SE) generated from various non-parametric estimators was used as a measure of the overall herpetofaunal richness of each forest site (Table 7). I used the *T* metric calculated from the Nestedness Temperature Calculator (Atmar & Patterson 1995) to evaluate the nested subset distribution of the herpetofauna. Values of *T* range from 0° for perfect nestedness (maximum order) to 100° for completely random (maximum disorder) species assemblages. I performed 1,000 Monte Carlo simulations to assess the statistical significance of the *T* value.

Habitat and environmental variables (counts, mean percentages, and measurements) were initially tested for normality and adequately log-transformed prior to analyses (Zar 1999). The correlation between these variables and species composition (using a presence/absence data matrix) was determined through non-metric multidimensional scaling (NMDS), which is considered the most effective ordination analysis for

community data as it does not assume linear relationships and reveals the environment in a way that it is interpreted by the biotic community (McCune & Grace 2002). NMDS was run in “autopilot (slow and thorough)” setting with random starting configurations and Sorensen (Bray–Curtis) distance as the dissimilarity measure. Introduced species were excluded and an outlier analysis was performed prior to ordination procedure. Environmental and habitat variables that were strongly correlated ( $r > 0.5$ ) were plotted as vectors with the length representing the magnitude of the correlation. Multi-response permutation procedures (MRPP) provided a non-parametric test of differences between the resulting clusters (localities and species) from the ordination (McCune & Grace 2002). Both NMDS and MRPP were performed on PC-ORD version 4.14 (MjM Software, Oregon, USA). All other statistical analyses were performed using JMP version 5.1 (SAS Institute, North Carolina, USA).

### **3.4 Results**

#### **3.4.1 Patterns of species richness and abundance**

Field surveys recorded a total of 85 species (25 frogs, 30 lizards, 27 snakes, two freshwater turtles, and a crocodile) and 2410 individuals from the forest sites and matrix habitat. The herpetofauna includes eight putative new taxa (see Brown 2004) and populations of five species that are either newly discovered (Brown et al. 2007) or were last encountered by herpetologists 80 to 140 years ago (Taylor 1921; Brown & Alcalá 1980). Sixty-two species (ca. 73% of the fauna) are endemics of which 29 are restricted to Luzon biogeographic region. Thirteen species are included in global lists of threatened and trade-regulated fauna (IUCN 2007; CITES 2005), some of which occurs in the forest fragments (Appendix 3). Fifty-eight species are restricted to forest

habitats and 24 were also found in the matrix. The matrix herpetofauna is composed largely of synanthropic and disturbance-tolerant species dominated by *Bufo marinus* and *Hoplobatrachus rugulosus*; both are invasive alien species in the Philippines (Diesmos et al. 2006; Brown 2007).

I recorded 56 species at the reference site in NSMNP and 64 in the study fragments. This difference in richness may be partly explained by the greater sampling effort in the latter site (25 strip transects in the reference site vs. 52 in all fragments). But since the entire area was once forested, it is reasonable to assume that species that were found exclusively in the fragments also exist in contiguous forest. Sampling completeness ratio was highest in frogs (0.58–0.95), followed by lizards (0.51–0.93), and snakes (0.36–0.91). At NSMNP, 74 to 95% of the predicted species richness (all groups combined) was detected compared with 36 to 94% in the fragments. The ranges of observed and mean estimated species richness at NSMNP were 17 to 20 and 20 to 25 species, respectively, and that for fragments were 1 to 17 and 1 to 25 species (Table 7). Non-parametric tests did not detect differences in the estimates of species richness across all sites and between contiguous and fragmented forests. Species accumulation curves for both lizards and snakes at the reference site did not reach an asymptote. Frogs and lizards are adequately sampled particularly in the smaller fragments. The sampling effort for snakes was generally insufficient across all sites (Fig. 6A, B).

Species richness and faunal abundance declined en masse in the forest fragments. Richness was strongly influenced by patch size as indicated by a double log scale plot (Fig. 7A). Simple regression analysis revealed that area is the most important

determinant of variation in species richness across all sites, for frogs ( $R^2 = 0.63$ ,  $p = 0.003$ ), lizards ( $R^2 = 0.69$ ,  $p = 0.002$ ), and snakes ( $R^2 = 0.69$ ,  $p = 0.002$ ). Habitat area and species richness are likewise strongly and positively correlated; a reduction in forest area results in declines of richness in frogs (Spearman:  $r_s = 0.78$ ,  $p = 0.001$ ), lizards ( $r_s = 0.87$ ,  $p = 0.001$ , and snakes ( $r_s = 0.72$ ,  $p = 0.02$ ). The two largest forest fragments (Sites 1 and 2) collectively lost 37–58% frog species, 15–30% lizards, and 47–76% snakes. In contrast the smaller fragments (Sites 3–10) lost 53–79% frogs, 35–80% lizards, and 76–94% snakes. Overall, the percentages of species loss with decreasing forest size ranged from 15–94% for all groups combined (Table 7). The proportion of endemic species and abundance similarly showed a linear relationship with area (Fig. 7B, C). Compared with other groups, snakes consistently exhibited a steeper slope (higher  $z$ -values: 0.22–0.29) in all species-area regression equations.

Frogs comprised the five most abundant forest-obligate species (35.6% of the individuals of all groups combined) and were dominated by fanged river frogs (*Limnonectes woodworthi* and *Limnonectes* sp.) and rain frogs (*Platymantis pygmaeus*, *P. taylori*, and *Platymantis* “sp. C”). The litter-dwelling skinks (*Sphenomorphus decipiens*, *S. jagori*, and *S. steerei*) were the most abundant lizards. Snakes were relatively rare from all sites. Only lizard abundance varied significantly across the sites (Kruskal–Wallis ANOVA = 32.93,  $df = 10$ ,  $p = 0.001$ ). Positive correlations exist between lizard richness and habitat diversity (Pearson:  $r = 0.63$ ,  $p = 0.006$ ) and between faunal abundance and forest area ( $r = 0.62$ ,  $p = 0.41$  in frogs;  $r = 0.73$ ,  $p = 0.01$  in lizards;  $r = 0.84$ ,  $p = 0.001$  in snakes). None of the other biogeographic variables (distance to contiguous forest and isolation period) were correlated with species richness and faunal abundance.



### 3.4.2 Community structure

Total herpetofaunal density in the reference site is estimated at 4400 animals/ha (3050 frogs, 870 lizards, and 480 snakes) and 13,190 animals/ha in forest fragments (7580 frogs, 5120 lizards, and 490 snakes). The estimates of frog and lizard density in NSMNP is 25-fold of that recorded from a comparable site in the Bornean lowlands (156 animals/ha) and 34-fold of that from Thailand (115 animals/ha) (Inger 1980). Frogs registered the highest population densities in all forest sites, and the snakes, the lowest. The mean total density of lizards (Wilcoxon:  $\chi^2 = 15.93$ ,  $p < 0.0001$ ) and of snakes ( $\chi^2 = 6.60$ ,  $p = 0.01$ ) differed significantly between contiguous forest and fragments, with lizards having a higher concentration in the fragments and the opposite trend for snakes, which were more abundant in contiguous forest (Fig. 6C, Fig. 8A). The aggregate fresh biomass is 8.1 kg/ha in contiguous forest (frogs = 2.4 kg/ha, lizards = 0.9 kg/ha, snakes = 4.8 kg/ha) and 54.2 kg/ha in forest patches (frogs = 8.1 kg/ha, lizards = 30.9 kg/ha, snakes = 15.2 kg/ha), with lizards accounting for 57% of the total herpetofaunal biomass in the latter site ( $\chi^2 = 19.46$ ,  $p < 0.001$ ). Biomass densities (Fig. 8B) varied across all sites for frogs ( $F_{10, 66} = 4.35$ ,  $p < 0.001$ ), lizards ( $F_{10, 66} = 6.41$ ,  $p < 0.001$ ), and snakes ( $F_{10, 66} = 7.33$ ,  $p < 0.001$ ).

Small- ( $\chi^2 = 10.21$ ,  $p < 0.001$ ) and medium-bodied lizards ( $\chi^2 = 9.97$ ,  $p = 0.002$ ), comprising 87% of all species in this group, were more abundant in the fragments. Medium-sized snakes (44% of species) abound in contiguous forest ( $\chi^2 = 7.00$ ,  $p = 0.008$ ). Size class distribution in frogs did not differ in both sites. There was no statistically detectable difference in the distribution of large-bodied species between contiguous and fragmented forests (Fig. 8C). Vertical stratum distributions shifted between forest sites for some groups (Fig. 8D). The proportions of ground-dwelling

lizards ( $\chi^2 = 14.93$ ,  $p < 0.001$ ) and those that occupy a wide stratum (i.e., from forest floor to arboreal microhabitats;  $\chi^2 = 4.34$ ,  $p = 0.037$ ) are higher in forest patches than in contiguous forest. Arboreal frogs ( $\chi^2 = 3.93$ ,  $p = 0.047$ ) and ground-dwelling (fossorial) snakes ( $\chi^2 = 4.93$ ,  $p = 0.026$ ) both declined in the fragments. All herpetofaunal guilds were present in both sites. Herpetofaunal biomass did not show any relationship with area as opposed to variations in population density of all indicator groups, which were related with area ( $r = 0.75$ ,  $p = 0.007$  for frogs;  $r = 0.72$ ,  $p = 0.011$  for lizards;  $r = 0.79$ ,  $p = 0.004$  for snakes).

Species occurrence across all sites is significantly nested than expected by chance alone ( $T = 16.8^\circ$ ,  $p = 7.17 \times 10^{-6}$  for frogs;  $T = 23.2^\circ$ ,  $p = 6.13 \times 10^{-8}$  for lizards;  $T = 13.5^\circ$ ,  $p = 2.30 \times 10^{-4}$  for snakes), confirming that the faunas in the fragments are subsets of that found in contiguous forest. Matrix fill percentage (f) is lowest in snakes (frogs = 32%, lizards = 37.2%, snakes = 19.5%) and could signify an idiosyncratic distribution in this group (Atmar & Patterson 1993).

Six of 11 habitat and environmental variables varied significantly between contiguous and fragmented forests. Percent canopy cover ( $\chi^2 = 5.37$ ,  $p = 0.02$ ), RH ( $\chi^2 = 28.24$ ,  $p < 0.001$ ), mean DBH of trees ( $\chi^2 = 20.98$ ,  $p < 0.001$ ), and mean number of decayed logs ( $\chi^2 = 25.31$ ,  $p < 0.001$ ) all had higher mean values in contiguous forest than in the fragments. In contrast, basal area ( $\chi^2 = 9.64$ ,  $p = 0.002$ ) and temperature ( $\chi^2 = 37.38$ ,  $p < 0.001$ ) were higher in forest fragments than in contiguous forest. NMDS analysis yielded an optimum three-dimensional ordination space that collectively explained 62.8% of the variance with a satisfactory stress value of 16.4 (McCune & Grace 2002) in 400 iterations. Two axes that represented high variance (24% and 20.5%)

were used in the final ordination plots and showed a distinct clustering of scores for contiguous forest and fragments (Fig. 9A; MRPP pairwise comparison tests,  $p < 0.001$ ). The herpetofauna (Fig. 9B) is well distributed among the sites, albeit the preponderance of frogs in contiguous forest (14 of 22 species). Gradient analysis further identified four variables (i.e., temperature, RH, mean DBH of trees, and mean number of decayed logs) that exhibited high correlation values ( $r > 0.5$ ) and were significantly associated with species distributions and sites. Temperature is the only variable that was positively associated with forest fragments including 28% of the fauna (six frogs, eight lizards, and eight snakes). Species in this cluster are matrix-tolerant and are relatively abundant. Vector plots of RH, mean DBH of trees, and mean number of decayed logs, showed a positive association with contiguous forest and with 44% of the fauna (14 frogs, eight lizards, 12 snakes). This cluster (lower right quadrant) includes species that are fragmentation-sensitive, most of which were classified as extinction-prone (Table 5). Two-thirds of the species are arboreal (e.g., *Platymantis luzonensis*, *Luperosaurus kubli*, *Lipinia vulcania*) or fossorial, litter-dwellers (e.g., *Platymantis pygmaeus*, *Brachymeles bicolor*, *Calamaria bitorques*). The rest are aquatic and semi-aquatic frogs (*Limnonectes* spp., *Rana luzonensis*, *R. similis*). The presence of water as a variable, however, did not correlate strongly in the ordination analysis.

### **3.4.3 Extinction-proneness of species**

Reproductive development mode was identified as the most significant predictor of extinction proneness of the herpetofauna (Table 8). The most parsimonious model exhibited a remarkable  $wAICc$  of 57.4%, which explained 7.3% of the variation in the probability of extinction. The next highest-ranked model ( $wAICc = 16.5\%$ ) included

the effect of body size alone but contributed only 0.3% of the deviance (the lowest contribution among all models), hence is a weak predictor of extinction risk. All other models had weak support ( $wAICc < 9\%$ ) although one of these (a combination of reproductive mode and adult habit) accounted for the highest %DE (8.1%) in explaining for herpetofaunal extinction proneness. Over 90% of extinction-prone species from the study sites are rare endemics (Table 5). Both range-restriction and rarity are often identified as important correlates of species vulnerability (see Davies et al. 2000; Lips et al. 2002; Henle et al. 2004; Hero et al. 2005; Watling & Donnelly 2007) and are the primary predictors of endangerment for a majority of globally threatened species of birds, mammals, and amphibians (IUCN 2007; Stuart et al. 2004). I excluded these traits from the analysis to avoid potential circularity in explaining for extinction proneness.

### **3.5 Discussion**

#### **3.5.1 Fragmentation effects on herpetofaunal diversity and community structure**

Consistent with the predictions of the species-area relationship (MacArthur & Wilson 1967; Rosenzweig 1995), richness declined logarithmically with decreasing forest area. Nearly half (48%) of the species found in the reference site at NSMNP disappeared in the two larger fragments ( $> 500$  ha) while up to 77% were lost in the smaller fragments ( $\leq 10$  ha). In turn, forest patches 5–10 ha in area lost nearly half (46%) of the fauna occurring in the larger fragments; the smallest patches ( $< 5$  ha) lost up to 63% of the species. Abundance also declined 39–79% of that recorded from NSMNP. With few exceptions, species that occur in low abundance in contiguous forest are the first ones to disappear in the fragments. These observations underscore the significance of area as predictor of herpetofaunal diversity. Large forest areas tend

to encompass a richer variety of habitats, which consequently promotes species diversity because of greater availability of resources, niches, and a suite of other ecological variables (MacArthur & Wilson 1967; Rosenzweig 1995). The observed pattern of richness and abundance in the sites, however, was only partly explained by habitat variety per se. Microclimatic conditions and the presence of key microhabitats are the prime ecological correlates of the herpetofaunal community (Fig. 9). The removal of large trees not only alters the structure of forests but also has profound effects on the microclimate of this ecosystem (Whitmore 1998). The study fragments are characterized by a scarcity of large trees and reduced canopy cover, among the consequences of which include significantly higher ambient and substrate temperatures and lower relative humidity. These conditions may be hostile to amphibians and reptiles since their reproductive biology and physiology (e.g., water balance and thermoregulation) are intricately linked with the environment (Crump 1982; Duellman & Trueb 1994; Zug et al. 2001). Critical microhabitats were generally diminished in forest patches specifically those that are utilized as sites for breeding or egg deposition, nocturnal/diurnal shelter, or as cover to escape predation (e.g., water-filled tree hollows, epiphytes, decayed logs). Species with highly specific microhabitat requirements are particularly susceptible to this form of disturbance. Indeed, the marked decline in arboreal frogs and lizards and fossorial/litter-dwelling species in the fragments (Fig. 8D) could be attributed to the absence of appropriate microhabitats, apart from the adverse trend in the microclimate in those sites. This finding mirrors that from La Selva in South America (Whitfield et al. 2007) wherein the observed declines in forest frogs and lizards is attributed to climate change-induced reduction of key herpetofaunal microhabitats. As with richness and abundance, larger forest sites invariably harbored greater numbers of endemic

species. But quite remarkable is the fact that the proportion of endemic species in the patches remained considerably high (40–79%), suggesting that some endemic species may be resilient to some forms of disturbance. It also demonstrates that fragments serve as important habitats for this subset of the herpetofauna. These conjectures warrant comprehensive investigations because of their broad implications to Philippine biodiversity conservation, in light of the continuing destruction of lowland forests across the archipelago (FAO 2007), which in turn is driving the exponential increase in the extent of disturbed and fragmented habitats. Relevant to this pressing issue is the tendency of local environment authorities to overlook the conservation potential of degraded habitats.

The high density and biomass of lizards in the fragments (Fig. 8A, B) exhibit a case of “density overcompensation” (MacArthur et al. 1972; Rodda & Dean-Bradley 2002). This phenomenon describes the condition wherein a species, which has been ecologically released from predation or inter-specific competition, is able to expand its niche and undergoes an elevated increase in density (MacArthur et al. 1972; Lomolino et al. 2006). This scenario may apply to the prevailing community structure of the herpetofauna in the study fragments where diversity is generally depauperate and where snakes, which are chief predators of lizards (Brown & Alcala 1980; Alcala 1986), are sparse. Although this phenomenon is more peculiar to species-poor (true) island faunas, it has also been detected from anthropogenic islands and in a fragmented landscape in Central America (Lambert et al. 2003; Bell & Donnelly 2006). This is the first study to document this ecological pattern in Southeast Asia. Whether it is pervasive among other faunal groups occurring in anthropogenic fragments, and from various localities of the region, invites further studies.

Species extirpation did not show a consistent pattern with respect to body size distribution. The smallest (12–16 mm SVL, *Platymantis pygmaeus*) and largest frogs (100–150 mm SVL, *Limnonectes macrocephalus*) went extinct in most patches. There is no statistical difference in the density of large frogs between contiguous and fragmented forests. Although there were more small- and medium-sized lizards in the fragments, large ones (e.g., monitor lizards) were found there as well. Small- and medium-bodied snakes did not survive in the smaller fragments, but large snakes did; for example, I recorded three large species ( $\geq 1$  m total length, *Coelognathus erythrurus manillensis*, *Naja philippinensis*, and *Ptyas luzonensis*) from 2-ha patches. These observations suggest that large body size may not be an important correlate of extinction risk for the herpetofauna. This premise is inconsistent with studies that found higher incidences of extinction in larger-bodied (or heavier) vertebrates over smaller-bodied ones (Pimm et al. 1988; Cardillo & Bromham 2001), which I note, as did Davies et al. (2000), were largely based on observations of birds and mammals. Future fragmentation studies of the herpetofauna involving a larger sample size and with a wider spatial scale (Davies et al. 2000) could help uncover a more compelling pattern on this subject.

I observed that large-bodied forest obligate herpetofauna are more likely to cross the inhospitable matrix than small-bodied ones. This could partly explain the presence of large species of lizards and snakes in the smallest patches (Fig. 8C), which may have emigrated there from “source” areas (MacArthur & Wilson 1967; Hanski 1999). But ongoing human pressures on the fragments (i.e., persecution, bushmeat hunting) are anticipated to seriously impact the already small populations of these conspicuous fauna. By contrast, the populations of small forest frogs and lizards in the fragments

may be relictual, as evidenced by their matrix-aversion. If these populations are indeed effectively isolated from others, it is doubtful whether they could continue to persist in the fragments in the face of human disturbance, environmental stochasticity, and metapopulation effects (Hanski 1999). This presents an opportunity for a suite of ecological investigations on the metapopulation dynamics of insular populations in order to have a better understanding of the extinction process—and conservation prospects—in the herpetofauna.

The high  $z$ -values registered for snakes (Fig. 7) could either reflect their overall vulnerability to extinction with decreasing habitat size (*sensu* Pimm & Askins 1995) or a low immigration rate (Rosenzweig 1995) particularly of small-bodied species, which might explain their general absence in habitat patches. And because snakes suffered the highest decline in richness (94%), abundance (98%), and comprised 40% of all extinction-prone species, these observations portend that they are the most susceptible to extinction among all indicator groups.

### **3.5.2 Correlates of extinction-prone amphibians and reptiles**

Oviparity is considered a more generalized reproductive mode whereas both direct development and ovoviviparity are specialized strategies that typically involve various forms of parental care (Crump 1982). Direct development is an adaptive strategy to natural environmental stochasticity and fluctuations in tropical areas and has allowed species to occupy a variety of ecological niches and a wide geographic distribution (Crump 1982; Alcalá 1986; Duellman & Trueb 1994; Zug et al. 2001).



Nearly all of the direct developers (9 of 10 species) and ovoviviparous species (5 of 6 species) in the study sites are extinction-prone compared with about half (34 of 69 species) of oviparous species. Frogs of the genus *Platymantis* breed out of water and lay eggs that undergo direct development in both terrestrial and arboreal situations (Alcala 1986; Brown 2004). *Brachymeles* lizards are live-bearers and breed in moist forest litter, decayed logs, and other microhabitats on the forest floor stratum (Brown & Alcala 1980). The vulnerability of these species to habitat fragmentation is likely due to the lack of appropriate egg deposition or breeding sites and the susceptibility of *Platymantis* eggs to desiccation in the relatively drier environments of forest fragments. Similar declines in species belonging to these taxa have recently been documented from Negros Island (Alcala et al. 2004). My observations on Philippine frogs are in contrast with those of Hero et al. (2005) in Australia wherein they found oviparous species to be more vulnerable to decline and extinction than direct developers.

Reproduction mode is not traditionally associated with extinction risk in most vertebrate groups (see Pimm et al. 1988; Davies et al. 2000; Lips et al. 2002; Henle et al. 2004; Watling & Donnelly 2007). It may be an underlying mechanism in extinction proneness because the reproductive success of a species is inherently dependent on environmental and habitat conditions (Crump 1982; Duellman & Trueb 1994; Zug et al. 2001). Investigations of this trait are encouraged to further understand its significance in the extinction process of amphibians and reptiles.

### 3.5.3 A caveat on herpetofaunal richness

The discovery of possible new taxa from the Sierra Madres is not surprising (Brown et al. 1999; Brown et al. 2007) and highlights the poor knowledge of the herpetofauna of Luzon (Diesmos et al. 2002b; Brown & Gonzalez 2007). Because an accurate appraisal of species diversity is fundamental to conservation biology (Wilson 1992; Savage 1995), I discuss factors that may have important implications on the analysis of the herpetofaunal diversity from the study sites. (1) The Philippine clades of genera *Platymantis*, *Limnonectes*, and *Sphenomorphus* exhibit a marked prevalence for cryptic speciation (Brown & Diesmos 2002; Evans et al. 2003; Brown 2004). Hence I suspect that detailed taxonomic examination (incorporating morphological, acoustic, and genetic analyses) of voucher materials of these taxa may yet uncover additional unrecognized diversity (Brown & Diesmos 2002); (2) The field methods used in the herpetofaunal inventories permitted the sampling of only a limited dimension of the forest stratum (< 5 m). Canopy-associated herpetofauna (Brown et al. 2007) are underrepresented in this study. Surveys directed at the canopy zone could result in startling new discoveries; (3) Surveys were conducted during the transition period from wet to dry season. And because high levels of reproductive activity and movement in tropical herpetofaunal species (especially amphibians) are associated with periods of high rainfall (Duellman & Trueb 1994; Zug et al. 2001), I anticipate that additional species will be detected from the study sites if surveys are undertaken during the wetter months of the year. These three factors importantly point out that the appraisal of species richness, and of species loss from forest fragmentation, are underestimated and conservative, at best. I recommend that comprehensive herpetofaunal studies be undertaken in the Sierra Madres with increased attention to

lowland forest remnants, which is anticipated to enhance knowledge on the biodiversity and the conservation of this critical biodiversity area.

### **3.6 Conclusions**

The preservation of the remaining block of lowland forest in the Sierra Madres is the key conservation strategy that will maintain optimum levels of herpetofaunal diversity. Efforts at curbing timber poaching must be intensified. It is believed that the scale of destruction wrought by illegal logging matches that of past commercial logging operations in the Sierra Madres in terms of forest cover reduction and the consequential human migration into logged-over areas, further exacerbating deforestation (Mallari & Jensen 1993; Danielsen et al. 1994; Tan 2000; van den Top 2003). Agricultural expansion, another serious threat, must be deflected away from forests into vast open areas and grasslands. This can be achieved by establishing a sustainable agricultural system (Hobbes & de Groot 2003; van den Top 2005; Overmars 2006), which was instrumental in slowing down deforestation in other regions of the country and providing for the basic needs of upland communities (Coxhead & Buenavista 2001). The growing involvement of upland communities and other stakeholders for sustained management of natural resources in return for environmental services, as opposed to wanton exploitation, is a positive direction for biodiversity conservation in the Philippines (Coxhead & Buenavista 2001; Boquiren 2004). This approach needs to be enhanced and applied in regions where impoverished immigrants exist within important biodiversity areas.

Forest fragments (as long as they retain original vegetation) can serve as functional refuges to subsets of herpetofaunal diversity including rare endemics and threatened

species. This study attests to the biodiversity value of fragments, and complements the findings of others; for example, the rediscovery from patches of degraded habitats of birds, lizards, and mammals that have not been seen for decades (Brown et al. 1997; van Weerd & Hutchinson 2004) and those that were previously thought to be extinct (Magsalay et al. 1995; Paguntalan et al. 2004; ). As such, the restoration and rehabilitation of important habitat fragments is a viable conservation option (see Turner & Corlett 1996). The management of these “miniature conservation areas” may be done at the local scale, whether through an alliance among local governments, civil society groups, and communities. Some successful conservation programs of both critically endangered species (e.g., the Philippine crocodile and Philippine cockatoo) and their dwindling habitats, have drawn upon such bottom-up management approach (van der Ploeg & van Weerd 2004; Widmann et al. 2006). Because forest fragments still provide environmental services that benefit marginalized communities (Coxhead & Buenavista 2001; van Weerd et al. 2004; Overmars 2006), management schemes must consider this aspect to bolster conservation efforts. Habitat patches that exist on private lands necessitate a management approach that prevents clear-cutting of remnant vegetation. Relevant to this subject is a Brazilian law on forestland development that requires landowners to leave parcel of their property in forest (Bierregaard et al. 2001). This Brazilian model may be worthy of emulation in formulating national biodiversity management plans.

This study has shown that localized extinctions of herpetofaunal species are an inevitable consequence of forest fragmentation. Patches below 1,000 ha will initially lose about 10% of the original species pool following isolation, and with continued reduction of habitat, the rate of species loss is amplified to over 90%. Among all groups, snakes are the most vulnerable to fragmentation effects. This study carries

important insights into the conservation of the herpetofauna of the Philippines and Southeast Asia, as the last vestiges of lowland forest in this biodiversity-rich region succumbs to deforestation (Laurance & Peres 2006; Sodhi & Brook 2006; FAO 2007).

## **Chapter 4. Niche Overlap and Rapid Morphological Change in Invasive Alien Frogs in the Philippines: a Comparative Study Involving Cane Toads (*Bufo marinus*) and the Taiwanese Tiger Frog (*Hoplobatrachus rugulosus*)**

### **4.1 Abstract**

There are currently five alien frogs in the Philippines, most of which were deliberately introduced either as a biological control agent of agricultural pests or for food and commercial purposes. Of these species, the cane toad *Bufo marinus* and Taiwanese tiger frog *Hoplobatrachus rugulosus* have been suspected as harmful invasives because of their ubiquitous distributions, high population densities, and the potential to displace native frogs through competition in food and habitat resources or as predators of local fauna. I sought evidence for this hypothesis by examining ecological overlap in food and habitat niche dimensions between populations of these two alien species (*B. marinus* and *H. rugulosus*) and eight native species (*Limnonectes macrocephalus*, *L. woodworthi*, *Occidozyga laevis*, *Rana luzonensis*, *R. similis*, *Fejervarya vittigera*, *Kaloula picta*, and *Polypedates leucomystax*) that co-occur in forests and non-forested habitats. Diet analysis showed that both groups of species consumed similar types and abundances of prey items, although introduced frogs (especially *H. rugulosus*) preyed on more types and consumed larger volumes of vertebrates that included endemic species of frogs, snakes, and murid rodents. The high degree of dietary and spatial overlap between alien and native frogs reveals the potential for intense competition. However, the contrasting niche widths in food and habitat appear to reduce the overall niche overlap in *B. marinus* and *H. rugulosus*, allowing these aggressive consumers to co-exist. A similar pattern of resource partitioning was also exhibited by native species that were occupying similar habitats.

Overall, the two alien species appear to exert a more severe competitive pressure on non-forest frogs as indicated by a high degree of food and habitat niche overlap with this group of species.

A recent study that detected rapid shift in leg length morphology of introduced *B. marinus* populations in continental Australia presented another level of complication in the management and control of harmful invasive species in that region. I found similar rapid morphological change in body size and relative leg lengths of *B. marinus* in seven island populations in the Philippines. Toads in large islands had longer legs, but body size was generally larger in small islands. Younger toad populations also possessed longer legs than older populations. The morphological divergence observed in *B. marinus* appears to be the effect of evolutionary forces intrinsic to island ecosystems with possible synergistic interactions with conditions that render islands invisable, such as the lower levels of competitors and availability of resources. Destruction of native habitats plays a vital role in invasibility of islands by providing appropriate habitats for introduced species to exploit. These results suggest that strategies to manage and control invasive species must also integrate biogeographic variables. Management approaches that were designed in continental regions may not be wholly applicable to island archipelagoes.

## **4.2 Introduction**

Biological invasions are currently recognized as one of the major threats to global biodiversity and have caused the decline and extinction of native species, especially on oceanic islands (e.g., Simberloff 1981; Savidge 1987; Coblentz 1990; Lodge 1993; Clavero & Garcia-Berthou 2005). Yet the rate of introduction of exotic species into

new environments continues to accelerate with intensification of human travel and international transport of trade (Perrings et al. 2001; Levine & D'Antonio 2003; Ehrenfeld 2005; Lin et al. 2007), and the greater availability of invasible habitats because of disturbance of native habitats (Lonsdale 1999; Alpert et al. 2000). Although not all exotic organisms are harmful to native biodiversity, identifying those that are potentially noxious and predicting the localities and ecosystems where they can inflict the most damage, has been the subject of rigorous scientific studies in recent years (Kolar & Lodge 2001; Peterson & Vieglais 2001; Levine & D'Antonio 2003).

The Global Invasive Species Database (<http://www.issg.org/database/>) lists two species of frogs as among the world's worst invasives. These are the American bullfrog *Rana catesbeiana* and cane toad *Bufo marinus*. The bullfrog has been introduced in 25 countries through the pet trade and for commercial farming. The species is a known carrier of chytrid fungus (Hanselmann et al. 2004), an emerging amphibian disease that has caused amphibian population declines and extinction in many regions of the world (Stuart et al. 2004). The cane toad, a native of South and Central America, was introduced into 22 countries as a biological control agent. Largely unsuccessful in controlling crop pests, instead it became a serious threat to the native fauna in many countries (Zug & Zug 1979). For example, *B. marinus* has been implicated in declines of Australian fauna (Phillips et al. 2003; Aldhous 2004; Boland 2004). The situation is made even more alarming with results of a recent study that found evidence for rapid change in its morphology (Phillips et al. 2006). Toads at the invasion front were found to possess longer legs compared to older (founder) toad populations, which enables them to expand their range rapidly and to invade



previously unoccupied territories including sensitive areas of native biodiversity (Phillips et al. 2006).

The Philippine amphibian fauna includes five introduced species: *B. marinus*, *R. catesbeiana*, *Hoplobatrachus rugulosus*, *Rana erythraea*, and *Kaloula pulchra* (Brown et al. 2002; Diesmos et al. 2006; Brown 2007). *Bufo marinus* and *R. erythraea* are the most widely distributed and relatively better studied among the species (Diesmos et al. 2006). Both *H. rugulosus* and *R. catesbeiana* were intentionally introduced for commercial farming but *R. catesbeiana* appears to have failed to establish breeding populations, and its overall status and distribution remains uncertain (Diesmos et al. 2006). A recent invader is *K. pulchra*, known thus far from a few localities. Unlike past introductions that are presumably related to farming and agriculture, this species was likely introduced through the pet trade (Diesmos et al. 2006). The impacts these introduced species might have on native biota of the Philippines are poorly known (Brown et al. 2002; Diesmos et al. 2006) because ecological studies are inadequate and far between. Although the handful of studies point out the possible adverse impacts of introduced frogs through competition in food resource, they suffer from a lack of comparative data from native species because most observations were based upon examinations of prey that were consumed by introduced species (see Rabor 1952; Alcalá 1955, 1957; Espiritu 1985; Adraneda et al. 2005). A recent review (Diesmos et al. 2006) suggested that among the introduced frogs, *B. marinus* and *H. rugulosus* are potentially harmful invasives as both are capable of invading forest habitats and breeding there as well. This finding carries serious implications to amphibian conservation in the Philippines because over

80% of the fauna, most of which are endemics, are forest obligates (Alcala & Brown 1998; Brown et al. 2002; Diesmos et al. 2002).

The main goal of this study was to determine the ecological impact of invasive alien frogs on native species. I investigated this by looking for evidence of competitive interactions between the invasives *B. marinus*, *H. rugulosus* and native frogs from both forest and non-forested habitats. I measured ecological niche widths and niche overlap in sympatrically occurring populations with respect to spatial and dietary dimensions. Finally, I investigated the presence of rapid morphological change in *B. marinus* from several island populations to assess whether local cane toad populations may be capable of rapid expansion, and thus, pose a similar threat in the Philippines as those seen of introduced toads in continental Australia. It is hoped that this approach will provide critical information to help fill the large gap in knowledge on the ecology of invasive species in the Philippines.

#### **4.2.1 History of introduction of *Bufo marinus* and *Hoplobatrachus rugulosus* in the Philippines**

The study centered on *B. marinus* and *H. rugulosus*. The Philippine Bureau of Plant Industry introduced *B. marinus* into the Philippines in 1934 in an attempt to control explosive populations of sugarcane pests (Rabor 1952). A founder population was initially maintained and captive-bred in Manila and Los Baños, Luzon Island and soon thereafter were released in rice and sugarcane fields in the central regions of the island. A year later, stocks from this population were shipped to the island of Negros and released in sugarcane plantations across the island (Fig. 10). By 1941—less than a decade of its introduction—large numbers of cane toads were observed to have established breeding populations in several regions of these two islands (Rabor 1952;

Alcala 1957). Originally found from just four islands in the late 1940s (Inger 1954), *B. marinus* now occurs on 24 islands throughout the Philippines through successive human-mediated introductions and now occupies an estimated range of 100,000 km<sup>2</sup> (Diesmos et al. 2006). *Hoplobatrachus rugulosus* is native to the western regions of mainland Asia, Taiwan, and Indochina. The history of its introduction in the Philippines is ambiguous and undocumented. It was apparently introduced in the early 1960s alongside *R. catesbeiana* under the rubric of a bullfrog-breeding program that was instituted by the Philippine government (Ministry of Natural Resources 1981). Breeding populations of tiger frogs can now be found on at least five major islands following deliberate and accidental releases in the wild. Density estimates of frogs during the rainy season in flooded rice fields of Isabela Province, northern Luzon place *H. rugulosus* at 2,440 frogs/ha and *B. marinus* at 1,984 frogs/ha (Diesmos et al. 2006).

### **4.3 Methodology**

#### **4.3.1 Niche overlap and niche width**

I studied populations of *B. marinus* and *H. rugulosus* that co-occur with eight native anuran species in forest and matrix habitats (altitudinal range 10–200 m) from two sampling plots (~500 ha each) on northern Luzon, Philippines (Fig. 10). Forest species were *Limnonectes macrocephalus*, *L. woodworthi*, *Occidozyga laevis*, *Rana luzonensis*, and *R. similis*. Non-forest species were *Fejervarya vittigera*, *Kaloula picta*, and *Polypedates leucomystax*; these are synanthropic frogs and are typically found in human modified environments and degraded habitats. I excluded other frog species that occur particularly in forest sites (i.e., forest frogs of the genus *Platymantis*) as these species were rarely found in the same microhabitats as *B.*

*marinus* and *H. rugulosus* (rivers, streams, and ponds in degraded forest) during the period of this study. *Platymantis* frogs inhabit terrestrial microhabitats that are typically far from water bodies (Inger 1954; Alcalá & Brown 1998). The 10 study species are nocturnal and are either partly or wholly dependent on aquatic microhabitats. Frogs were recorded and collected from rivers, streams, ponds, flooded rice fields, irrigation ditches, and reservoirs. I surveyed frogs in 10 x 100 m strip transects that were established in forests and anthropogenic habitats; a total of 20 were sampled within the sampling plots. Fieldwork was conducted from January to May 2005 and April to July 2006, which coincided with the dry season in the study area. Detailed descriptions of habitat and other environmental features of the study area in the Sierra Madres are found in van Weerd et al. (2002) and Diesmos et al. (unpublished data).

I analyzed stomach contents of 495 post-metamorphic frogs with identifiable food materials. Gut contents were examined and sorted under a stereomicroscope. I identified a total of 2,774 prey items and scored them in 28 general food types belonging to five broad taxonomic categories (Table 9). I distinguished 10 natural and anthropogenic habitats from the study sites where *B. marinus* and *H. rugulosus* occurred in sympatry with native anurans. I recorded a total of 1,186 individual (post-metamorphic) frogs and scored them according to habitat type where they were observed (Table 10). Specimens of frogs were preserved using standard techniques (Heyer et al. 1994) and were deposited in the Herpetology Section of the National Museum of the Philippines, Manila.

I calculated niche overlap along two niche dimensions, food type and habitat use, with the formula:

$$O_{jk} = \frac{\sum_i^n p_{ij} p_{ik}}{\sqrt{\sum_i^n p_{ij}^2 \sum_i^n p_{ik}^2}}$$

where  $P_{ij}$  and  $P_{ik}$  represent the proportions of the  $i^{\text{th}}$  resource used by consumer species  $j$  and species  $k$ , and  $n$  is the total number of resources. This equation measures the shared niche space or resource utilization between two species and is also used to estimate inter-specific competition coefficients (Pianka 1974; Case 1983). The possible niche overlap scores range from 0 (no overlap) to 1 (complete overlap). Next, I measured the niche width of each species to compare their utilization of habitat and prey items using the inverse of Simpson's index (Pianka 1974; Case 1983):

$$NW = \frac{1}{\sum_i^n p_i^2}$$

where  $P_i$  is the proportion of the  $i^{\text{th}}$  resource used by consumer species  $j$  and  $n$  is the number of resources. A high index score signifies wide spatial use or utilization of a diverse dietary resource. I interpreted the results from each niche dimension separately. Differences in mean numbers and densities of dietary and spatial data were examined through non-parametric  $\chi^2$  tests, Kruskal–Wallis ANOVA, and multiple comparison post hoc test (Tukey's HSD). Relationships between variables were evaluated with a Pearson correlation of coefficient (Zar 1999).

#### **4.3.2 Rapid morphological change in *Bufo marinus***

I investigated the occurrence of rapid morphological change in *B. marinus* (Phillips et al. 2006) by comparing relative leg length of toads among various populations in the

Philippines. Relative leg length is the residual score from the general linear regression of log-transformed snout-vent length versus log-transformed tibia length (Phillips et al. 2006). Measurements were based on 309 live adult individuals from seven island populations. Data were compiled from separate herpetofaunal surveys conducted between 2005 and 2007. Toads were captured from anthropogenic habitats (scrub land, grassland, rice fields, farm ponds, home gardens) at elevations < 100 m. Data is summarized in Appendix 4.

I used one-way ANOVA to inspect differences in leg lengths among various populations. I tested relationships of the response variable (relative leg length) with log-transformed data on population age and island area through simple linear regression procedures. Population age is the number of years elapsed since time of introduction in a locality/island based on available information in the literature (Rabor 1952; Alcala 1957; Espiritu 1985) and from herpetological registries of the following institutions: National Museum of the Philippines, Field Museum of Natural History, California Academy of Sciences, and United States National Museum of Natural History. Estimates of population age were limited to the year 2004 for data uniformity. All statistical analysis was performed using JMP version 5.1 (SAS Institute, North Carolina, USA).

## **4.4 Results**

### **4.4.1 Prey diversity and volume**

The anuran community consumed a wide range of food types. The most important were insects (46.4%), followed by crustaceans (21.4%), and vertebrates (17.9%). Annelids and mollusks each accounted for 7.1% of all prey types (Table 9). Ants

comprised 48.7% by volume and were the most important food item of *B. marinus*, *K. picta*, *L. macrocephalus*, *L. woodworthi*, and *O. laevis*. Both alien and native frogs included vertebrates in their diet with *H. rugulosus* consuming the most in terms of type and number. Tiger frogs (*H. rugulosus*) preyed on juvenile and adult frogs (*F. vittigera*, *K. picta*, and *H. rugulosus*), snakes (*Calamaria gervaisii* and *Rhabdophis spilogaster*), and unidentified murid rodents (Table 9, Fig. 11). There were wide variations among species in dietary diversity ( $F_{1, 18} = 22.39$ ,  $p < 0.0001$ ) and prey volume ( $F_{1, 18} = 12.80$ ,  $p = 0.002$ ). Prey type selection was either broad (e.g., most non-forest frogs preyed on 80% of all food types) or was specialized to certain food categories (e.g., *K. picta* fed only on insects). Increasing sample size of specimens particularly of forest frogs and undertaking fine-scale taxonomic identifications of prey items may uncover additional and more remarkable patterns. In spite of interspecific differences in prey type selection and prey volume consumption, there were no significant differences on these variables when comparing between native and invasive frogs. The major difference I found was that invasive frogs consumed more gastropods ( $\chi^2 = 4.97$ ,  $p = 0.026$ ) and vertebrates ( $\chi^2 = 5.11$ ,  $p = 0.024$ ) than native frogs. Specimens of *B. marinus* and *H. rugulosus* collected from both forest and matrix habitats preyed on comparable prey types and volume.

#### 4.4.2 Dietary overlap

Cane toads exhibited a high degree of dietary niche overlap ( $O_{ij} = 0.015$ – $0.964$ ) with half of the native species in degraded forest and matrix habitats. Niche overlap between *H. rugulosus* and *B. marinus* was remarkably lower ( $O_{ij} = 0.132$ ) compared with *H. rugulosus* and native species ( $O_{ij} = 0.095$ – $0.319$ ; Table 12). I found a slight

difference in overlap indices between *H. rugulosus* and *B. marinus* (Mann–Whitney Test = 87.0,  $p = 0.052$ ), with *H. rugulosus* having a lower mean index.

Tiger frogs had the widest dietary niche width among all species whereas the forest-dwelling fanged frogs (*Limnonectes*) had the narrowest (Table 11). Except for *L. macrocephalus* and *L. woodworthi*, native species from forest and matrix habitats tended to have wide niches. *Bufo marinus* and *H. rugulosus* showed highly contrasting niche size. Food niche of tiger frogs was over three times wider than that of cane toads (Table 12). I found a significant negative association between food niche width and overlap in habitat ( $r = -0.67$ ,  $df = 8$ ,  $p = 0.035$ ) and between food niche and dietary overlap ( $r = -0.73$ ,  $df = 8$ ,  $p = 0.016$ ).

#### **4.4.3 Spatial overlap**

The resulting overlap indices essentially reflected the innate habitat distribution of species. As expected, I found very high to complete niche overlap among species that shared the same habitat and minimal to non-overlapping niches in species that occupied different habitats (Table 12). There were no difference in spatial overlap between *B. marinus* and *H. rugulosus*. But both *B. marinus* and *H. rugulosus* had significantly high degree of overlap with frogs occupying matrix (non-forested) habitats (*B. marinus* and *H. rugulosus*:  $\chi^2 = 6.05$ ,  $p = 0.014$ ) compared with the forest frogs. Among native species, forest frogs showed a higher degree of inter-specific overlap ( $\chi^2 = 6.39$ ,  $p = 0.012$ ).

Species that were recorded from both degraded forest and non-forested habitats (i.e., *B. marinus*, *H. rugulosus*, *L. woodworthi*, and *P. leucomystax*) showed wider spatial



niches (Table 12). The two species with the narrowest niche widths (*R. luzonensis* and *R. similis*) were observed only from rivers and streams in remnant and contiguous old growth forest. Except for *L. woodworthi*, forest obligate species were rarely found in degraded non-forested habitats (Table 10). Of the 10 species, *P. leucomystax* appeared in all habitat types at varying densities, which was reflected in its overlap index with other species. I recorded *B. marinus* and *H. rugulosus* from mixed artificial and natural forest, second growth, and fragments of original forest below 10 ha in size, but found these species in fairly low densities in such habitats (Table 10). Unlike in degraded forests, I did not detect them in contiguous old growth forest during the surveys nor found evidence of breeding. It is likely that surveys conducted during the rainy months may provide alternative observations. To illustrate this point, dry-season estimates of the population densities of *B. marinus* and *H. rugulosus* from flooded rice fields (Table 10) were 64–87% lower than the wet-season estimates (see Section 4.2.1; Diesmos et al. 2006).

#### **4.4.4 Rapid morphological change in *Bufo marinus***

I found highly significant differences in relative leg length of *B. marinus* populations from seven islands ( $F_{6, 302} = 6.498, p < 0.0001$ ) and from nine localities ( $F_{8, 300} = 15.373, p < 0.0001$ ) within these islands (Fig. 10, Table 13). Non-parametric tests also revealed within-island variations in leg lengths: there are marked differences between northern and southern populations of *B. marinus* on Luzon ( $\chi^2 = 41.49, p < 0.0001$ ) and on Negros ( $\chi^2 = 14.46, p = 0.0001$ ). The population on Leyte was unusual in that it did not exhibit statistical differences with other populations (Table 13).

There is a weak yet significant positive relationship between island size and relative leg length ( $r = 0.129$ ,  $df = 307$ ,  $p = 0.024$ ) such that toads from larger islands possessed longer legs ( $R^2 = 0.017$ ,  $p = 0.024$ ) (Fig. 12A). Nevertheless, body size alone (SVL) showed a strong negative correlation with island size ( $r = -0.299$ ,  $df = 307$ ,  $p < 0.001$ ) (Fig. 12B), indicating that toads were larger in smaller islands ( $R^2 = 0.089$ ,  $p = 0.0001$ ). I found further evidence of a positive correlation between leg length and population age ( $r = 0.182$ ,  $df = 209$ ,  $p = 0.008$ ). This suggests that relative leg length declined with time in more recent (or younger) toad populations ( $R^2 = 0.033$ ,  $p = 0.009$ ) (Fig. 12C).

## 4.5 Discussion

### 4.5.1 Competition between native and invasive frogs

Analyses of dietary niche overlap revealed the potential evidence for competition between native frogs and the invasive alien species *B. marinus* and *H. rugulosus*. For the most part, invasive frogs consumed similar types and volume of prey as native frogs did, especially in species that occupy non-forested habitats. The former, however, preyed on more vertebrates, which included endemic forms. Data indicate that *B. marinus* and *H. rugulosus* are aggressive competitors that may significantly threaten native frogs including other (smaller-bodied) vertebrate fauna, through competition and direct predation. The high ecological niche overlap (in both food and habitat) between *B. marinus*–*H. rugulosus* and non-forest native frogs suggest a possible competitive pressure on the latter group of species. Because of a lack of comparable baseline data, it is not known whether native species have already been displaced through competition with *B. marinus* and *H. rugulosus* ever since these alien species were introduced in the Philippines. Moreover, data is not available to

suggest if population declines in native amphibians have occurred because of competition with alien invasives. This critical subject needs to be investigated in future studies. Competitive pressure from alien frogs appeared to be more prevalent on non-forest species than on forest frogs chiefly because *B. marinus* and *H. rugulosus* were ubiquitous in degraded, non-forested habitats. These two species were more restricted to degraded and artificial forest habitats such as plantations (of non-native trees), second growth, and small forest fragments (< 10 ha) and occurred there in low densities. Both species were not encountered in contiguous old growth, suggesting that these species may have failed to expand their range to include relatively undisturbed forests. One possible explanation for this observation is that (native) anuran species diversity is much higher in intact forest (Alcala & Brown 1998; Brown et al. 2002), which could serve as potential competitors to resist the influx of invasives (Green et al. 2004). The intense niche overlap that was seen among native forest frogs could imply that these species can outcompete potential invaders (see Alpert et al. 2000). Additionally, appropriate habitats and microclimatic conditions may be lacking in intact forest for invasive frogs to exploit; the failure of this study to find evidence of breeding by *B. marinus* and *H. rugulosus* in large forest fragments and contiguous forest lends support to these observations. Yet as already discussed, undertaking field surveys during the rainy months may lead to quite different conclusions.

Although data provided strong empirical evidence for potential competition between native and invasive frogs, the contrasting levels of niche overlap in habitat and food dimensions also suggest that species may be avoiding intense competition via resource partitioning (Pianka 1981). Competition theory predicts that sympatric

competitors tend to differ in their use of a common resource to reduce competition (Pianka 1981). Moreover, co-existing species with high overlap in one resource dimension often exhibit narrow overlap in another, which tends to minimize the effective niche overlap (Pianka 1974; Case 1983). Data suggest similar patterns prevail in this anuran community. Additionally, the observed inverse relationship of food niche width with both habitat and food niche overlap may help to minimize inter-specific competition. To illustrate briefly, I found that species with narrow food niche breadths overlapped broadly in food and/or habitat niche with other species, and vice versa. This suggests that species may be maximizing food resource-use by becoming specialists (or generalists, if the converse) in the presence of high competition over space or food niche, hence reducing competition. This pattern may be one of the underlying mechanisms that could explain why *B. marinus* and *H. rugulosus* have become successful invaders in the Philippines.

#### **4.5.2 *Bufo marinus* and *Hoplobatrachus rugulosus* as successful invaders**

Data indicate that *B. marinus* and *H. rugulosus* have not invaded “empty” (or available) ecological niches in the Philippines, in contrast to conclusions made by earlier studies (on *B. marinus*: Alcala 1957; Espiritu 1985). Also, both species appear to co-exist through resource partitioning and the contrasting ecological niche dimensions they exhibited. Tiger frogs exploit food resources that were not fully utilized by *B. marinus* (and by non-forest native frogs). On the other hand, *B. marinus* exhibits selectivity in its foraging habit; toads from the study sites disproportionately ate more ants and termites than any other prey, a behavior that is strikingly similar to observations of toads from within their native range in Central America (Evans & Lampo 1996). Niche partitioning is possibly just one of several mechanisms that

promote the successful establishment of both *B. marinus* and *H. rugulosus* in the Philippines. Another such mechanism is the high reproductive success rates of these species (e.g., Lampo & de Leo 1998) as evidenced by their high population densities in non-forested habitats (see also Diesmos et al. 2006). Another important mechanism is their possession of life history traits that favor the survival of their progenies over sympatric native species. To illustrate, tadpoles of *Hoplobatrachus* are carnivorous and prey upon larvae of other species (Chou & Lin 1997; Grosjean et al. 2004). The eggs and larvae of *B. marinus* are toxic to aquatic predators and other anuran larval species (Punzo & Lindstrom 2001). The possession of toxins is possibly among the most important factor that is driving the success of *B. marinus* as an invasive. Adult cane toads possess skin toxins that when ingested are fatal to other wild vertebrates and domesticates—including humans (Rabor 1952; Allen & Neill 1956). As a result, the species has no immediate predators in the Philippines (Alcala 1957). One evolutionary consequence of decreased predation is that it could select for increased competitive ability on the part of the invasive (Mitchell et al. 2006), which undoubtedly has grave implications to native fauna.

#### **4.5.3 Rapid morphological change in *Bufo marinus***

Phillips et al. (2006) were the first to document rapid morphological change in *B. marinus* from introduced populations in the Australian continent. This study also detected the presence of rapid morphological shift in *B. marinus* populations in the Philippines. The results of this study, however, were remarkable in three respects: (1) leg length was positively associated with island area; (2) toads from small islands have larger body sizes than on larger islands; and (3) older populations of *B. marinus* had *longer* leg lengths, in complete contrast to the findings of Phillips et al. (2006)

wherein they found older populations of *B. marinus* in Australia possessed *shorter* legs.

Islands, with their suite of unique environmental and geological attributes, are well known to profoundly influence the ecology and evolution of the biota they harbor. Studies of islands have led to some of the most astonishing discoveries of natural and ecological patterns that shape the natural world (Lomolino et al. 2006). Two of the most fundamental patterns in island biogeography include the intrinsic relationship of islands with species diversity and body size of insular organisms. Large islands contain more species than smaller islands (MacArthur & Wilson 1967). Insular forms of plants and animals often trend toward either gigantism or dwarfism in comparison with their mainland forms ("island rule"; Van Valen 1973). Keeping these principles in mind, I deduce that smaller Philippine islands (because of their lower number of species) have few potential competitors to *B. marinus*. And, as relevant to the foregoing observation is the scarcity or absence of predators on *B. marinus* in the Philippines due to the toad's highly toxic properties. Among the well-documented evolutionary trends in organisms from insular systems is that in the absence of predators and low competitive pressure (among others factors), selective pressures promote increases in body size (Van Valen 1973; Heaney 1978; Lomolino 2005). An increase in body size is also associated with a decrease in dispersal abilities (Lomolino et al. 2006) and allows an organism to exploit a wider variety of ecological resources (Grant 1965). These selective forces—which were likely interacting with one another—may be behind the observed divergence of body size and relative leg length in *B. marinus* in the Philippines. The apparent decrease in relative leg length of toads from younger (newly-established) populations seems to be the effect of the

proportionate increase in both morphological components (i.e., SVL and tibia length) in younger toad populations. This also suggests that the mean body size of toads in the founder population (cane toads in the 1930s) were smaller than that of present populations.

#### **4.6 Conclusions**

This study provided evidence of the potential for intense competition particularly on food resource between native frogs and *B. marinus* and with *H. rugulosus*. The absence of baseline data hinders any meaningful analysis on the possibility that native species are being displaced (or are declining) because of competitive interactions with the two invasives. This subject should be considered a priority for future research. *Bufo marinus* and *H. rugulosus* appear to co-exist by partitioning food and habitat resources in areas they co-inhabit, but exert severe competitive pressure over native frogs that occupy the same habitats, most especially in non-forested habitats.

To the best of my knowledge, this study is the first to detect the effect of area on morphological change in a globally widespread invasive vertebrate. Island effects and favorable community interactions (especially low predation pressures and little inter-specific competition) likely influenced the observed morphological divergence of *B. marinus* in the Philippines. Also, these mechanisms are likely to be interacting synergistically. Adaptive change in species is known to vary by geography and species that exhibit high phenotypic plasticity are more predisposed to rapid divergence. *Bufo marinus* is known to exhibit such plasticity (Doyungan & Barrion 1995; Lampo & de Leo 1998; Phillips et al. 2006). These findings may represent the adaptive response of an invasive vertebrate found in island archipelagoes. Hence, the

design of strategies to control and manage invasive species must also consider biogeographic variables.

Artificial and degraded forests and small fragments were prone to invasion by *B. marinus* and *H. rugulosus* whereas contiguous and larger fragments (> 500 ha) of relatively intact natural forests were not invasible. This assertion needs further scrutiny through field studies that incorporate temporal variations in seasonality and a larger sample size. What is certain, however, is that the ongoing rapid and extensive conversion of natural habitats in the Philippines, particularly of the lowland forest, into degraded anthropogenic environments and cultivated fields, will accelerate the geographic expansion of these and other invasive frogs simply because of the greater availability of invasible habitats (Lonsdale 1999; Alpert et al. 2000). Upon consideration of the role of habitat disturbance—and other factors previously described—in the successful invasion by alien frogs, it is doubtful whether eradication could be an effective strategy in the control of these invasives. Perhaps the most meaningful and important conservation option is to prevent their spread into areas that are free of invasive species, especially on isolated islands that harbor unique (island) endemics. Islands are some of the best-studied systems in invasion ecology and are also known to be the most sensitive to invasion—often with disastrous results (Savidge 1987; Simberloff 2001). Among the “ecologically sensitive” Philippine islands include Gigante (where the single-island endemic limestone frog, *Platymantis insulatus*, exists) and Palawan (where numerous endemic amphibians and reptiles are found) (Inger 1954; Alcala & Brown 1998).



Invasion ecology is possibly the most neglected field of biodiversity research in the Philippines, but one that is anticipated to be most fruitful through a sustained research and conservation program. Therefore, studies are encouraged to accumulate important empirical data that could provide answers to the most pressing issues in the invasive species problem and those that can be used for effective control and management of invasives. Future studies should determine the impacts of competition with and predation by invasive frogs, focusing on displacement or declines that might have transpired on the part of native species. Natural experiments, especially those that compare biotas with and without the presence of invasive species, and ecological experiments, such as the removal of invasives from occupied habitats, may provide valuable insights on how invasive species could affect community structure of native biota and ecosystem functioning in island archipelagoes.

## **Chapter 5: General Discussion and Conclusions**

The Philippines represents a case study of a country that has undergone massive deforestation in modern times. Although the exploitation of the country's forest resources essentially began with European contact in the 16<sup>th</sup> century, it is remarkable that the rate of deforestation peaked only in the last 50 years of the 20<sup>th</sup> century (Kummer 1992; Vitug 1993; Roque et al. 2000; Bankoff 2007). As in the past, the direct causes of forest decline (illegal and legal logging, destructive mining practices, agricultural expansion, shifting agriculture, and dubious schemes by interest groups that take advantage of forestry programs) remain prevalent today. The root causes of destruction and degradation of the Philippine rainforest and other natural habitats are: (1) the high human population density and growth rates, (2) perpetuation by the national government of the same land use system and policies that were implemented by past colonial governments (export-driven economy that promotes unsustainable use of natural resources), (3) widespread poverty, and (4) corrupt bureaucracy (see Hauge et al. 1986; Myers 1988; Roque et al. 2000; Vitug 1993).

The impacts of forest destruction have been directly observed by Filipinos in times of ecological disasters, such as catastrophic floods and massive landslides, which have already claimed the lives of thousands of people (Broad & Cavanagh 1993; Heaney & Regalado 1998; Goldoftas 2006; see Chapter 1). The implication of forest loss to Philippine biodiversity is equally severe (Heaney & Regalado 1998; Myers et al. 2000; Posa et al. 2008) but the significance of which is generally under-appreciated by the public, including policy makers. Through an extrapolation of the findings of this dissertation, deforestation may have a more severe impact on Philippine

biodiversity than is presently known. Furthermore, key results of this study suggest a looming extinction crisis in Philippine amphibians and reptiles.

The projected extinctions in 11 centers of endemism (PAICs) with loss of lowland forests to date ranged from 19% to as high as 55% of the total known herpetofauna. In terms of PAIC-level endemic species, a total of 54 species are predicted to become extinct. Extinction levels are much higher in regions that have been severely deforested. Thus, in the West Visayas PAIC where original lowland forest cover has fallen way below 4% of total land area, the analyses predicted over half of its endemic species may be committed to future extinction. This region is undeniably where immediate and decisive conservation actions should be directed. In fragmented landscapes, a 10% decline in species richness from the original species pool was observed in forest patches < 1,000 ha in area. In smaller ( $\leq 10$ -ha) and isolated forest fragments, species loss reached to over 90% of the original species pool.

How long will these species last before they become extinct? The best source of available data to estimate this is the IUCN Red List Categories (IUCN 2001). By definition, the probabilities of extinction for “Critical” species, “Endangered” species, and “Vulnerable” species are, respectively, 50% within 10 years, 20% within 20 years, and 10% within 100 years. By applying these extinction probabilities to the herpetofauna, a total of 54 Philippine endemic species are likely to become extinct within 100 years, and nearly a third of this number will be extinct within 20 years. Which species are particularly at high risk of extinction? Results of Chapter 3 could provide some insights. Forest snakes were found to be more vulnerable to fragmentation effects and suffered high levels of extirpation and decline in abundance

compared with frogs and lizards. Frogs with direct development mode of reproduction and ovoviviparous lizards and snakes were also more susceptible to local extinction as a result of habitat loss and fragmentation.

Results of the study demonstrated that habitat fragmentation had profound effects on herpetofaunal richness and distribution and resulted in shifts in population and community structure. Habitat fragmentation precipitated dramatic changes in microclimate and habitat structure, a significant second-order effect was the reduction or disappearance of important microhabitats of amphibians and reptiles. Forest fragmentation and degradation also rendered natural habitats to become more invisable to alien species (Chapter 4), with serious ramifications to some native fauna.

This dissertation investigated the ecological impacts of deforestation and fragmentation of the lowland forest on the herpetofauna at the macro-ecological scale (Chapter 2) and at the community level (Chapter 3). While the methodology and data analyses differed, the conclusions reached in both approaches were identical and unequivocal: (1) that amphibians and reptiles are adversely affected by deforestation and fragmentation, (2) reptiles, particularly snakes, appear to be more vulnerable to fragmentation effects, and (3) those areas where forest habitats have been severely reduced tend to be the ones that are predicted to suffer high levels of global extinction events. Without stopping the continued habitat loss across the Philippines (Goldoftas 2006; FAO 2007; Posa et al. 2008), a concomitant increase in the level of predicted extinctions in amphibians and reptiles is to be expected.

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## Tables

Table 1. Total number of lowland forest amphibians and reptiles from each herpetofaunal region (Pleistocene Aggregate Island Complex, PAIC) in the Philippines and the numbers and proportions of species that are predicted to become extinct.

PAIC	Forest cover (%)	Total species	Threatened species	Data Deficient	Not Assessed	Predicted extinctions (%)
Batanes	19.3	15	0	2	0	5 (33.7)
Babuyan	24.9	22	2	2	1	6 (29.4)
Luzon	19.5	113	14	29	17	38 (33.5)
Mindoro	12.0	39	6	10	3	16 (41.2)
Romblon–Sibuyan	21.0	25	4	8	2	8 (32.3)
Palawan	40.6	63	8	18	2	13 (20.2)
West Visayas	4.1	77	11	29	4	42 (55.1)
Gigante	16.7	7	2	2	0	3 (36.1)
Camiguin	26.3	35	2	6	0	10 (28.4)
Mindanao	23.4	126	18	39	6	38 (30.5)
Jolo–Tawitawi	43.1	37	8	5	0	7 (19.0)

Table 2. Single-PAIC endemics and the numbers and proportions of species expected to become extinct. “Threatened species” refer only to the number of PAIC-level endemics that are identified as threatened by IUCN (2007) and the Global Reptile Assessment (unpublished data; assessed in 2007).

PAIC	Total species	Threatened species	Species extinctions (%)
Batanes	2	0	1 (50.0)
Babuyan	5	2	1 (20.0)
Luzon	51	10	17 (33.3)
Mindoro	5	2	2 (40.0)
Romblon–Sibuyan	4	1	1 (25.0)
Palawan	26	5	5 (19.2)
West Visayas	22	6	12 (54.5)
Gigante	2	2	1 (50.0)
Camiguin	1	0	0 (0)
Mindanao	44	10	13 (29.5)
Jolo–Tawitawi	6	2	1 (16.7)

Table 3. Numbers of predicted extinctions of total fauna in lowland forest and species that are endemic to a single PAIC. Expected extinctions are based on habitat loss to date (predicted extinctions), in five more years of deforestation (future extinctions), and the additional number predicted to become extinct in another five years.

PAIC	Forest cover (%)		Total fauna			Single-PAIC endemics		
	Now	5 years	Predicted	Future	Extra	Predicted	Future	Extra
			extinct	extinct	extinct	extinct	extinct	extinct
Batanes	19.3	18.9	5	5	0	1	1	0
Babuyan	24.9	24.4	6	7	1	1	1	0
Luzon	19.5	19.1	38	38	0	17	17	0
Mindoro	12.0	11.7	16	16	0	2	2	0
Romblon–Sibuyan	21.0	20.6	8	8	0	1	1	0
Palawan	40.6	39.7	13	13	0	5	5	0
West Visayas	4.1	4.0	42	43	1	12	12	0
Gigante	16.7	16.3	3	3	0	1	1	0
Camiguin	26.3	25.7	10	10	0	0	0	0
Mindanao	23.4	22.9	38	39	1	13	14	1
Jolo–Tawitawi	43.1	42.2	7	7	0	1	1	0

Table 4. Description of the study sites on Luzon Island with ecological and biogeographical variables. Data for area, years of isolation, and distance to continuous forest are estimates.

Sites	Locality	Coordinates	Area (ha)	Elevation (m)	Year isolated	Distance to continuous forest (km)	No. of strip transects (area in ha)	Habitat diversity index ( $H'$ )	Disturbance index
Control	Apaya - Dibanti	17°01'43" N, 122°11'37" E; 17°00'55" N, 122°12'13" E	5000 plots	150–350	–	–	25 (2.5)	1.17	0.07
1	Nassiping	17°58'12" N, 122°39'12" E	700	10–60	1970	37	11 (1.1)	1.47	0.15
2	Dunoy	16°59'34" N, 122°09'24" E	650	150–300	1990	4	11 (1.1)	1.13	0.05
3	Binatug	16°57'15" N, 122°04'01" E	10	100–160	1980	14.9	6 (0.6)	1.33	0.07
4	Del Pilar	16°51'33" N, 122°06'19" E	9	150–260	1980	3.2	6 (0.6)	1.11	0.67
5	Maldam	16°56'18" N, 122°03'20" E	5	100–150	1990	13	5 (0.5)	1.08	0.11
6	Puerta	17°25'34" N, 121°55'04" E	4	150–200	1990	2	4 (0.4)	0.33	0.15
7	San Jose 2	16°56'12" N, 122°07'45" E	2.5	150–190	1990	4.1	3 (0.3)	1.15	0.30
8	Garita	17°24'25" N, 121°49'11" E	2	40–70	1970	15	3 (0.3)	0.75	0.44
9	San Jose 1	16°56'03" N, 122°07'39" E	1.5	150–190	1990	4.1	2 (0.2)	1.07	0.22
10	Alibadabad	16°57'48" N, 122°02'46" E	0.5	85–100	1980	14.2	1 (0.1)	1.02	0.10

Table 5. Summary information on life history and ecological traits of 78 species evaluated for extinction proneness. Other terms include: level of endemism, EN (0 = non-endemic, 1 = endemic to the Philippines, 2 = endemic to Luzon biogeographic region); body size, BS (log-transformed snout-vent lengths); reproductive mode, RM (1 = oviparous, 2 = ovoviviparous, 3 = direct development); RI = rarity index; development site, DS (1 = aquatic, 2 = terrestrial, 3 = arboreal); vertical stratum, VS (1 = ground level, 2 = arboreal, 3 = ground level and arboreal); and habit, HA (1 = terrestrial, 2 = aquatic and terrestrial, 3 = arboreal).

Code	Species	EN	BS	RM	RI	DS	VS	HA	Extinction-prone
F1	<i>Kaloula kalingensis</i>	2	1.52	1	0.06	3	2	3	1
F2	<i>Kaloula picta</i>	1	1.63	1	0.10	1	1	1	0
F3	<i>Kaloula rigida</i>	2	1.64	1	0.05	1	1	1	1
F4	<i>Fejervarya vittigera</i>	1	1.88	1	0.04	1	1	2	0
F5	<i>Limnonectes macrocephalus</i>	2	1.98	1	0.04	1	1	2	1
F6	<i>Limnonectes woodworthi</i>	2	1.81	1	0.19	1	1	2	0
F7	<i>Limnonectes</i> sp.	2	1.88	1	0.16	1	1	2	0
F8	<i>Occidozyga</i> cf. <i>laevis</i>	0	1.61	1	0.19	1	1	2	0
F9	<i>Platymantis cornutus</i>	2	1.48	3	0.05	3	2	3	1
F10	<i>Platymantis corrugatus</i>	1	1.57	3	0.08	2	1	1	1
F11	<i>Platymantis luzonensis</i>	2	1.54	3	0.06	3	2	3	1
F12	<i>Platymantis pygmaeus</i>	2	1.11	3	0.26	2	1	1	1
F13	<i>Platymantis taylori</i>	2	1.46	3	0.27	2	1	1	1
F14	<i>Platymantis</i> sp. A	2	1.45	3	0.19	2	1	1	1
F15	<i>Platymantis</i> sp. B	2	1.28	3	0.18	2	1	1	1
F16	<i>Platymantis</i> sp. C	2	1.43	3	0.65	2	1	1	0
F17	<i>Platymantis</i> sp. D	2	1.57	3	0.22	2	1	1	1
F18	<i>Platymantis</i> sp. E	2	1.45	3	0.22	2	1	1	1
F19	<i>Rana luzonensis</i>	2	1.64	1	0.04	1	3	2	1
F20	<i>Rana similis</i>	2	1.69	1	0.13	1	1	2	1
F21	<i>Polypedates leucomystax</i>	0	1.79	1	0.36	1	3	3	0
F22	<i>Rhacophorus pardalis</i>	0	1.64	1	0.06	1	3	3	1
L1	<i>Bronchocela cristatella</i>	0	2.01	1	0.01	2	3	3	0
L2	<i>Draco spilopterus</i>	1	1.82	1	0.19	2	2	3	0
L3	<i>Cyrtodactylus philippinicus</i>	1	1.93	1	0.09	2	3	3	1
L4	<i>Gehyra mutilata</i>	0	1.74	1	0.03	2	3	3	0
L5	<i>Gekko gecko</i>	0	2.13	1	0.03	3	3	3	0
L6	<i>Gekko monarchus</i>	0	1.89	1	0.05	3	3	3	0
L7	<i>Hemidactylus frenatus</i>	0	1.70	1	0.06	3	3	3	0
L8	<i>Hemidactylus stejnegeri</i>	0	1.74	1	0.01	3	3	3	0
L9	<i>Lepidodactylus</i> cf. <i>planicaudus</i>	1	1.57	1	0.05	3	3	3	1
L10	<i>Luperosaurus kubli</i>	2	2.02	1	0.03	3	2	3	1
L11	<i>Brachymeles bicolor</i>	2	2.13	2	0.08	2	1	1	1
L12	<i>Brachymeles bonita</i>	1	1.86	2	0.08	2	1	1	1
L13	<i>Brachymeles b. boulengeri</i>	2	2.00	2	0.18	2	1	1	0



L14	<i>Brachymeles talinis</i>	1	1.75	2	0.06	2	1	1	1
L15	<i>Brachymeles</i> sp.	2	1.58	2	0.04	2	1	1	1
L16	<i>Eutropis cumingi</i>	0	1.72	1	0.18	2	1	1	1
L17	<i>Eutropis m. borealis</i>	1	1.83	1	0.68	2	1	1	0
L18	<i>Eutropis multifasciata</i>	0	2.03	1	0.23	2	1	1	0
L19	<i>Lamprolepis s. philippinica</i>	1	2.00	1	0.10	3	3	3	0
L20	<i>Lipinia</i> cf. <i>vulcania</i>	1	1.58	1	0.01	3	2	3	1
L21	<i>Sphenomorphus cumingi</i>	1	2.08	1	0.04	2	1	1	1
L22	<i>Sphenomorphus decipiens</i>	1	1.58	1	0.21	2	1	1	0
L23	<i>Sphenomorphus jagori</i>	1	1.91	1	0.30	2	1	1	0
L24	<i>Sphenomorphus leucospilos</i>	2	1.66	1	0.08	2	1	2	1
L25	<i>Sphenomorphus steerei</i>	1	1.58	1	0.42	2	1	1	0
L26	<i>Sphenomorphus</i> sp.	2	1.43	1	0.13	2	1	1	1
L27	<i>Tropidophorus grayi</i>	1	2.01	2	0.01	2	1	2	1
L28	<i>Varanus olivaceus</i>	2	2.71	1	0.01	3	3	3	1
L29	<i>Varanus s. marmoratus</i>	1	2.70	1	0.14	2	3	1	0
S1	<i>Ramphotyphlops braminus</i>	0	2.13	1	0.04	2	1	1	0
S2	<i>Typhlops</i> cf. <i>luzonensis</i>	1	2.33	1	0.05	2	1	1	1
S3	<i>Python reticulatus</i>	0	3.60	1	0.03	2	3	1	0
S4	<i>Ahaetulla p. preocularis</i>	1	2.85	1	0.05	3	2	3	0
S5	<i>Boiga angulata</i>	1	3.10	1	0.01	3	3	3	1
S6	<i>Boiga d. divergens</i>	2	3.00	1	0.01	2	3	1	1
S7	<i>Boiga philippina</i>	1	3.04	1	0.03	3	3	3	1
S8	<i>Calamaria bitorques</i>	1	2.33	1	0.04	2	1	1	1
S9	<i>Calamaria gervaisii</i>	1	2.15	1	0.03	2	1	1	1
S10	<i>Coelognathus e. manillensis</i>	1	3.07	1	0.03	2	1	1	0
S11	<i>Cyclocorus lineatus</i>	1	2.55	1	0.08	2	1	1	1
S12	<i>Dendrelaphis c. luzonensis</i>	1	2.81	1	0.05	3	3	1	0
S13	<i>Dendrelaphis p. pictus</i>	1	2.74	1	0.03	3	1	1	1
S14	<i>Dryophiops philippina</i>	1	2.74	1	0.01	2	1	1	1
S15	<i>Gonyosoma oxycephalum</i>	0	2.90	1	0.01	3	3	3	0
S16	<i>Lycodon aulicus</i>	0	2.71	1	0.01	2	1	1	0
S17	<i>Lycodon muelleri</i>	2	2.61	1	0.04	2	3	2	1
S18	<i>Oligodon modestum</i>	1	2.43	1	0.01	2	1	1	1
S19	<i>Psammodynastes pulverulentus</i>	0	2.60	1	0.03	3	3	3	1
S20	<i>Pseudorabion oxycephalum</i>	1	2.36	1	0.13	2	1	1	1
S21	<i>Ptyas luzonensis</i>	1	3.03	1	0.04	3	3	1	1
S22	<i>Rhabdophis spilogaster</i>	2	2.67	1	0.12	2	1	2	1
S23	<i>Tropidonophis dendrophiops</i>	1	2.75	1	0.03	2	1	2	1
S24	<i>Hemibungarus calligaster</i>	2	2.70	1	0.01	2	1	1	1
S25	<i>Naja philippinensis</i>	2	3.00	1	0.01	2	1	1	0
S26	<i>Ophiophagus hannah</i>	0	3.40	1	0.01	2	1	1	1
S27	<i>Trimeresurus flavomaculatus</i>	1	2.82	1	0.08	3	3	3	1

Table 6. Generalized linear mixed-effects models (GLMM) used to examine correlation between extinction proneness and ecological and life history attributes of the herpetofauna. These models and their combinations were derived a priori and represent specific analytical themes. Abbreviations: PR = Extinction proneness, BS = body size, RM = reproductive mode, DS = development site, VS = vertical stratification, and HA = habit.

No.	Model	Analytical theme
1	PR~BS	allometry
2	PR~BS+RM	allometry + reproductive mode
3	PR~BS+DS	allometry + development site
4	PR~BS+VS	allometry + vertical stratification
5	PR~BS+HA	allometry + habit
6	PR~BS+RM+HA	allometry + reproductive mode + habit
7	PR~BS+ RM+DS	allometry + reproductive mode + development site

Table 7. Species richness estimates ( $\pm$  SE) in each study site based on non-parametric estimators in EstimateS. Data are based on strip transects.

Site	Group	Species observed	Individuals observed	ACE	ICE	Chao1	Chao2	Jack1	Jack2	Bootstrap	MMRuns	MMMeans	Mean species richness	Proportion detected
Control	Frogs	19	305	19.2	19.3	19.0	19.0	20.0	20.0	19.7	22.4	22.2	20.0 $\pm$ 0.41	0.95
	Lizards	20	87	22.5	25.8	21.4	23.4	26.7	28.8	23.3	33.2	28.8	25.4 $\pm$ 1.28	0.79
	Snakes	17	48	22.0	21.7	18.9	18.8	22.8	22.1	20.1	37.3	30.0	23.1 $\pm$ 1.93	0.74
1	Frogs	8	121	8.0	8.6	8.0	8.0	8.9	8.3	8.6	11.0	10.3	8.8 $\pm$ 0.33	0.91
	Lizards	17	140	17.3	18.2	17.0	17.2	18.8	16.8	18.4	25.7	22.0	18.8 $\pm$ 0.91	0.90
	Snakes	4	7	5.8	9.5	4.5	9.5	7.6	10.9	5.4	22.7	0.0	8.0 $\pm$ 1.92	0.50
2	Frogs	12	120	13.3	20.6	13.0	30.0	17.5	21.6	14.3	33.1	15.8	19.1 $\pm$ 2.31	0.63
	Lizards	14	46	26.4	22.7	38.5	26.3	20.4	24.6	16.8	39.8	22.8	25.2 $\pm$ 2.64	0.56
	Snakes	9	16	30.1	30.5	30.0	28.1	15.4	21.1	11.5	49.7	22.0	25.0 $\pm$ 3.74	0.36
3	Frogs	7	59	8.4	13.9	9.0	15.0	10.3	12.5	8.4	11.0	10.5	10.6 $\pm$ 0.81	0.66
	Lizards	13	72	27.2	28.9	25.3	45.0	19.7	24.5	15.8	34.8	19.2	25.3 $\pm$ 2.99	0.51
	Snakes	4	4	10.0	9.0	10.0	9.0	7.3	10.0	5.3	9.9	0.0	7.5 $\pm$ 1.10	0.53
4	Frogs	9	143	9.0	9.6	9.0	9.0	9.8	7.8	9.8	23.9	11.8	10.9 $\pm$ 1.48	0.83
	Lizards	8	56	11.9	9.9	12.5	10.3	10.5	11.4	9.2	36.1	13.6	13.3 $\pm$ 2.58	0.60
	Snakes	3	3	6.0	5.5	6.0	5.5	5.5	7.5	4.0	9.3	0.0	5.2 $\pm$ 0.80	0.58
5	Frogs	9	58	9.0	11.4	9.0	9.8	11.4	12.3	10.2	16.4	12.6	11.1 $\pm$ 0.73	0.81
	Lizards	9	64	9.0	9.5	9.0	9.0	9.8	9.1	9.6	12.0	11.0	9.7 $\pm$ 0.32	0.93
	Snakes	1	1	1.0	1.0	1.0	1.0	1.8	2.4	1.3	0.7	0.0	1.1 $\pm$ 0.20	0.91
6	Frogs	5	38	5.6	5.6	5.0	5.0	5.2	5.3	5.5	7.8	7.1	5.7 $\pm$ 0.30	0.88
	Lizards	4	40	4.0	4.6	4.0	4.0	4.8	5.3	4.3	4.4	4.4	4.4 $\pm$ 0.13	0.91
	Snakes	4	5	10.0	11.5	5.5	5.1	6.3	7.4	5.0	14.6	15.2	8.5 $\pm$ 1.30	0.47
7	Frogs	5	72	6.0	7.3	5.0	5.2	6.3	6.5	5.7	5.6	9.2	6.2 $\pm$ 0.41	0.81
	Lizards	7	23	8.8	8.3	7.5	7.1	8.3	8.3	7.8	14.7	10.4	8.8 $\pm$ 0.72	0.80
	Snakes	2	3	3.0	2.7	2.0	2.7	3.3	4.0	2.6	4.1	0.0	2.6 $\pm$ 0.37	0.77
8	Frogs	8	113	9.1	8.5	8.0	8.0	8.7	8.8	8.3	8.6	8.6	8.5 $\pm$ 0.12	0.94
	Lizards	8	38	8.5	12.9	8.0	9.0	10.7	11.5	9.3	9.4	14.0	10.1 $\pm$ 0.65	0.79
	Snakes	3	3	6.0	5.0	6.0	5.0	5.0	6.0	3.9	0.0	0.0	4.0 $\pm$ 0.73	0.75

9	Frogs	4	10	5.0	14.5	5.0	8.5	5.5	5.5	4.8	6.0	10.0	6.9 ± 1.02	0.58
	Lizards	7	16	10.0	17.5	7.8	17.5	10.5	10.5	8.8	8.4	0.0	9.8 ± 1.60	0.71
	Snakes	2	3	3.0	2.5	2.5	2.5	3.0	3.0	2.5	2.0	0.0	2.3 ± 0.28	0.87
10	Frogs	6	74	6.0	6.0	6.0	6.0	6.0	0.0	6.0	0.0	0.0	4.2 ± 0.92	*
	Lizards	7	17	7.3	7.0	7.3	7.0	7.0	0.0	7.0	0.0	0.0	5.0 ± 1.08	*
	Snakes	3	3	*	*	*	*	*	*	*	*	*	*	*

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\* Species estimates not calculated because of low sample size ( $n = 1$ ).

Table 8. Information-theoretic ranking of seven GLMM models investigating the correlates of extinction proneness (PR) of 78 species of amphibians and reptiles from the lowland forest of the Sierra Madre Mountains. The models are in accordance with Akaike's Information Criterion corrected for small sample size ( $AIC_c$ ). Shown are the number of parameters ( $k$ ), the negative log-likelihood ( $-LL$ ), the difference in  $AIC_c$  for each model from the most parsimonious model ( $\Delta AIC_c$ ),  $AIC_c$  weight ( $wAIC_c$ ), and the percent deviance (%DE) explained in the response variable by the model under consideration.

Models	$k$	$-LL$	$\Delta AIC_c$	$wAIC_c$	%DE	$\Delta\%DE$
PR~BS+RM	7	-48.165	0.000	0.574	7.3	7.0
PR~BS	5	-51.795	2.493	0.165	0.3	–
PR~BS+DS	7	-50.086	3.842	0.084	3.6	3.3
PR~BS+RM+HA	9	-47.732	4.181	0.071	8.1	7.8
PR~BS+ RM+DS	9	-48.092	4.902	0.049	7.4	7.1
PR~BS+VS	7	-50.944	5.559	0.036	1.9	1.6
PR~BS+HA	7	-51.513	6.697	0.020	0.8	0.5

Table 9. Volumetric percentage of prey items in 28 food types. Species abbreviations: Bm = *Bufo marinus*, Fv = *Fejervarya vittigera*, Hr = *Hoplobatrachus rugulosus*, Kp = *Kaloula picta*, Lm = *Limnonectes macrocephalus*, Lw = *L. woodworthi*, Ol = *Occidozyga laevis*, Pl = *Polypedates leucomystax*, Rl = *Rana luzonensis*, and Rs = *R. similis*. Sample sizes are in parentheses.

Food type	Bm (84)	Fv (57)	Hr (32)	Kp (74)	Lm (43)	Lw (104)	Ol (23)	Pl (36)	Rl (10)	Rs (32)
<b>Insecta</b>										
Hymenoptera (ants)	62.2	16.2	3.0	39.9	70.9	77.1	52.0	0	19.2	0
Lepidoptera (adult)	0	0	0	0.6	0	0	0	0	0	0
Lepidoptera (larvae)	0	1.9	0	0.1	0	0	0	0	0	0
Dermaptera	0	4.9	0	19.5	0	0	0	0	0	0
Orthoptera	0	39.3	0	1.5	0	0	0	0	30.8	0
Odonata	0	0.5	0	0.1	0	0	0	0	0	20.0
Coleoptera (adult)	6.3	12.5	18.2	11.5	6.8	7.6	16.0	26.7	23.1	6.7
Coleoptera (larvae)	16.3	0	0	0	1.0	1.7	0	13.3	0	0
Blattodea	0.1	0	6.1	0	0	0	0	0	0	6.7
Diptera	0.8	1.2	3.0	2.0	0	0	0	0	0	0
Isoptera (adult)	11.1	8.9	0	24.6	1.9	3.7	12.0	0	0	0
Isoptera (larvae)	0	0	0	0	0	0.8	0	0	0	0
Hemiptera	0	1.4	0	0.1	0	1.7	8.0	13.3	0	0
<b>Non-insect arthropods</b>										
Scorpiones	0.5	0	0	0	0	0.3	0	0	0	0
Araneae	0.4	3.5	0	0	0	2.0	0	13.3	15.4	33.3
Diplopoda	0.4	0	9.1	0	0	0	0	0	0	0
Chilopoda	0	3.5	0	0	0	0.6	0	0	0	0
Caridea	0.1	0.7	3.0	0	0	0.3	4.0	0	0	0
Brachyura	0.1	0.5	18.2	0	1.0	0	0	0	0	0
<b>Annelida</b>										
Oligochaeta	0.2	3.5	0	0	10.7	3.4	8.0	6.7	0	20.0
Nematoda	0	0	0	0	5.8	0.8	0	0	11.5	13.3
<b>Mollusca</b>										
Gastropoda (snails)	0.2	0.7	18.2	0	0	0	0	0	0	0
Gastropoda (slugs)	1.1	0.5	0	0	1.0	0	0	20.0	0	0
<b>Chordata</b>										
Teleostei	0.1	0.2	0	0	0	0	0	0	0	0
Anura	0	0	12.1	0	1.0	0	0	0	0	0
Sauria (gekkonid)	0	0	0	0	0	0	0	6.7	0	0
Serpentes	0	0	6.1	0	0	0	0	0	0	0
Muridae (mice)	0.1	0	3.0	0	0	0	0	0	0	0
Total prey items ( <i>n</i> )	928	425	33	850	103	354	25	15	26	15
Food types/species	16	17	11	10	9	12	6	7	5	6

Table 10. Density estimates of species (frogs/ha) in 10 habitat types in the Sierra Madre Mountains. See Table 9 for species abbreviations.

Habitat type	Bm	Fv	Hr	Kp	Lm	Lw	Ol	Pl	Rl	Rs
Home lots, villages	125	10	40	35	0	0	0	30	0	0
Scrub, grassland	545	25	80	145	0	0	0	35	0	0
Flooded rice fields	720	290	315	425	0	40	0	75	0	0
Orchards	40	15	20	55	0	30	0	35	0	0
Reservoir, farm ponds	50	15	60	30	0	10	0	20	0	0
Artificial forest (exotic trees)	55	10	45	15	0	20	0	15	0	0
Mixed artificial and natural forest	40	0	15	10	15	45	10	15	0	0
Second growth	75	0	30	15	210	295	135	325	5	10
Remnant forest*	10	0	0	5	0	40	0	30	0	0
Contiguous old growth forest	0	0	0	0	260	275	160	5	160	260
Habitat types occupied	9	6	8	9	3	8	3	10	2	2

\* We sampled three forest fragments of varying sizes (0.5, 10, and 650 ha).

Table 11. Dietary niche overlap and niche width of species. Species abbreviations as in Table 9.

Species	Bm	Fv	Hr	Kp	Lm	Lw	Ol	Pl	Rl	Rs
<i>Bufo marinus</i>	1.0	0.395	0.132	0.827	0.948	0.964	0.929	0.149	0.434	0.015
<i>Fejervarya vittigera</i>		1.0	0.181	0.489	0.389	0.393	0.455	0.225	0.860	0.131
<i>Hoplobatrachus rugulosus</i>			1.0	0.177	0.139	0.132	0.221	0.319	0.278	0.095
<i>Kaloula picta</i>				1.0	0.784	0.803	0.860	0.142	0.440	0.033
<i>Limnonectes macrocephalus</i>					1.0	0.991	0.947	0.095	0.466	0.100
<i>Limnonectes woodworthi</i>						1.0	0.952	0.092	0.464	0.054
<i>Occidozyga laevis</i>							1.0	0.247	0.510	0.100
<i>Polypedates leucomystax</i>								1.0	0.418	0.344
<i>Rana luzonensis</i>									1.0	0.373
<i>Rana similis</i>										1.0
Niche width	2.308	4.731	7.510	3.682	1.914	1.655	3.079	5.769	4.507	4.592



Table 12. Spatial niche overlap and niche width of species. Species abbreviations as in Table 9.

Species	Bm	Fv	Hr	Kp	Lm	Lw	Ol	Pl	Rl	Rs
<i>Bufo marinus</i>	1.0	0.840	0.915	0.945	0.053	0.148	0.055	0.336	0.003	0.003
<i>Fejervarya vittigera</i>		1.0	0.965	0.967	0	0.103	0	0.240	0	0
<i>Hoplobatrachus rugulosus</i>			1.0	0.981	0.058	0.174	0.059	0.348	0.003	0.003
<i>Kaloula picta</i>				1.0	0.022	0.130	0.022	0.296	0.001	0.001
<i>Limnonectes macrocephalus</i>					1.0	0.974	1	0.611	0.796	0.801
<i>Limnonectes woodworthi</i>						1.0	0.977	0.739	0.690	0.695
<i>Occidozyga laevis</i>							1.0	0.627	0.783	0.788
<i>Polypedates leucomystax</i>								1.0	0.044	0.051
<i>Rana luzonensis</i>									1.0	1
<i>Rana similis</i>										1.0
Niche width	3.259	1.560	3.200	2.605	2.102	3.367	2.118	2.941	1.062	1.077

Table 13. Summary of multiple comparison Tukey's HSD test ( $q = 3.125$ ,  $df = 308$ ) of relative leg length of *Bufo marinus* from populations in seven Philippine islands. Positive values represent significant differences ( $p < 0.05$ ) between paired means.

Island (population)	<i>n</i>	<i>1</i>	<i>2</i>	<i>3</i>	<i>4</i>	<i>5</i>	<i>6</i>	<i>7</i>	<i>8</i>	<i>9</i>
<i>1</i> Luzon (northern)	45	-0.022	0.027	-0.018	0.023	-0.009	0.004	0.009	-0.012	0.023
<i>2</i> Luzon (southern)	90		-0.015	0.031	-0.021	0.013	-0.012	-0.017	-0.020	-0.019
<i>3</i> Panay	31			-0.026	0.028	0.010	0.009	0.014	-0.006	0.027
<i>4</i> Negros (northern)	15				-0.038	-0.005	-0.014	-0.018	-0.019	-0.023
<i>5</i> Negros (southern)	41					-0.023	-0.010	-0.005	-0.026	0.009
<i>6</i> Cebu	19						-0.034	-0.028	-0.040	-0.015
<i>7</i> Bohol	20							-0.033	-0.034	-0.020
<i>8</i> Leyte	8								-0.052	-0.023
<i>9</i> Mindanao	40									-0.023

## Figures

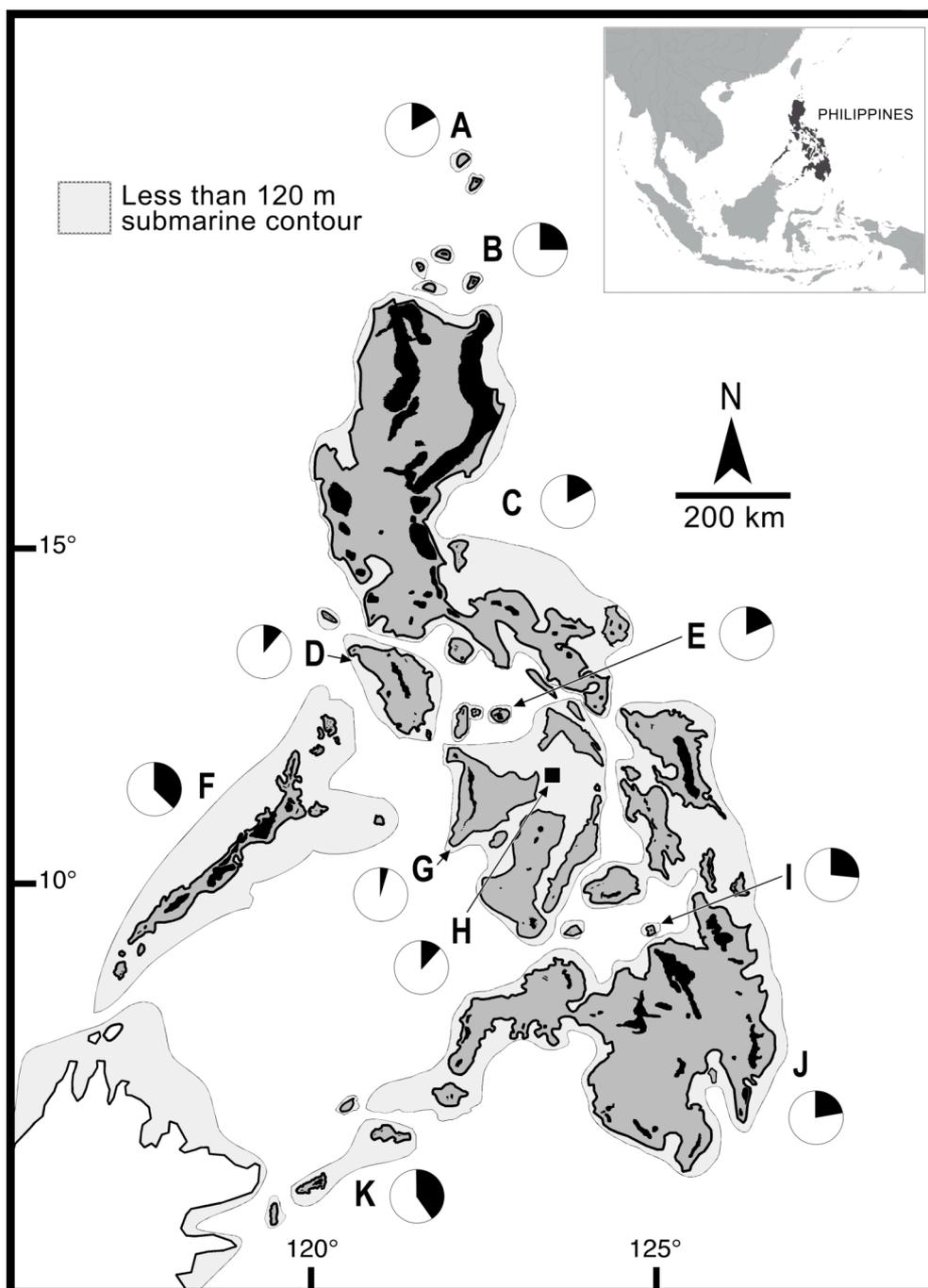


Figure 1. The Philippines, showing the estimated extent (black-shaded areas) and proportions (pie charts) of old growth forest. Evaluated were the herpetofauna of 11 Pleistocene Aggregate Island Complexes (PAICs) that correspond to sub-centers of herpetofaunal diversity and endemism (A to K). These PAICs trace the 120 m bathymetric contours of landmass exposure during the mid- to late-Pleistocene (Heaney 1985, Brown and Diesmos 2002). Abbreviations: A = Batanes, B = Babuyan, C = Luzon, D = Mindoro, E = Romblon-Sibuyan, F = Palawan, G = West Visayas, H = Gigante, I = Camiguin, J = Mindanao, and K = Jolo-Tawitawi. Inset map shows the location of the Philippines in Southeast Asia.

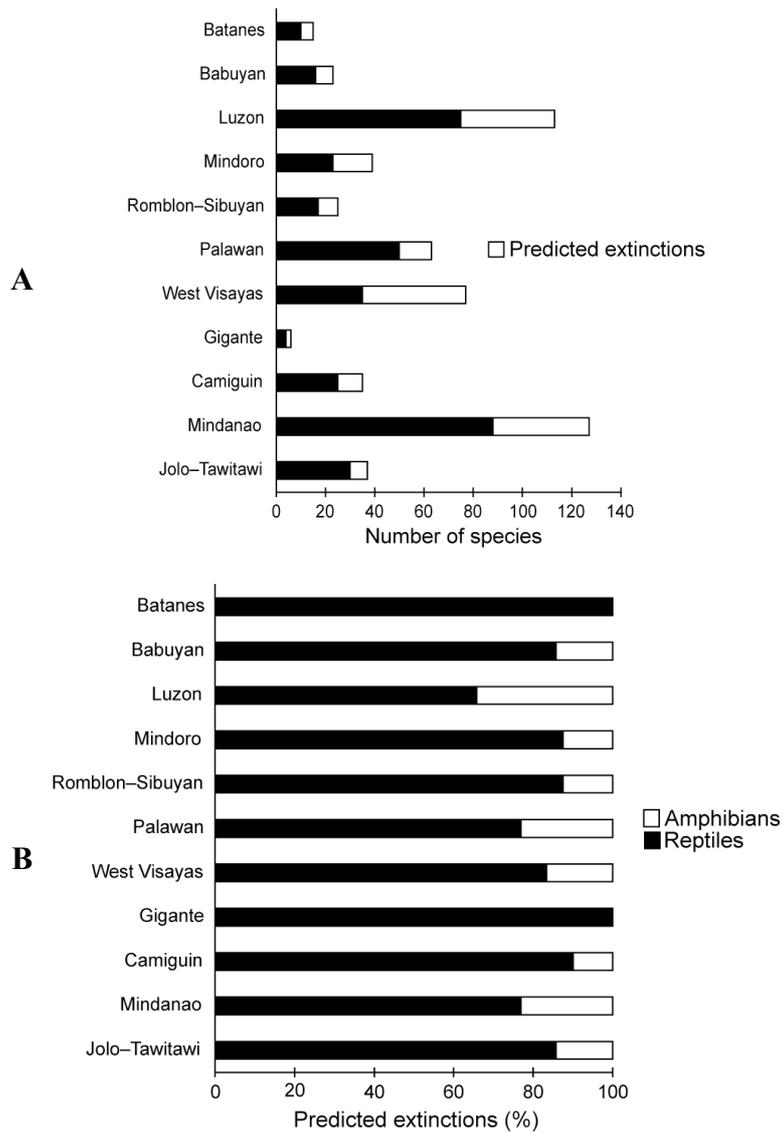


Figure 2. Total numbers of species of amphibians and reptiles predicted to become extinct from 11 herpetofaunal regions (Pleistocene Aggregate Island Complexes, PAICs) (A). Reptiles account for over 60% of the predicted extinctions (B).

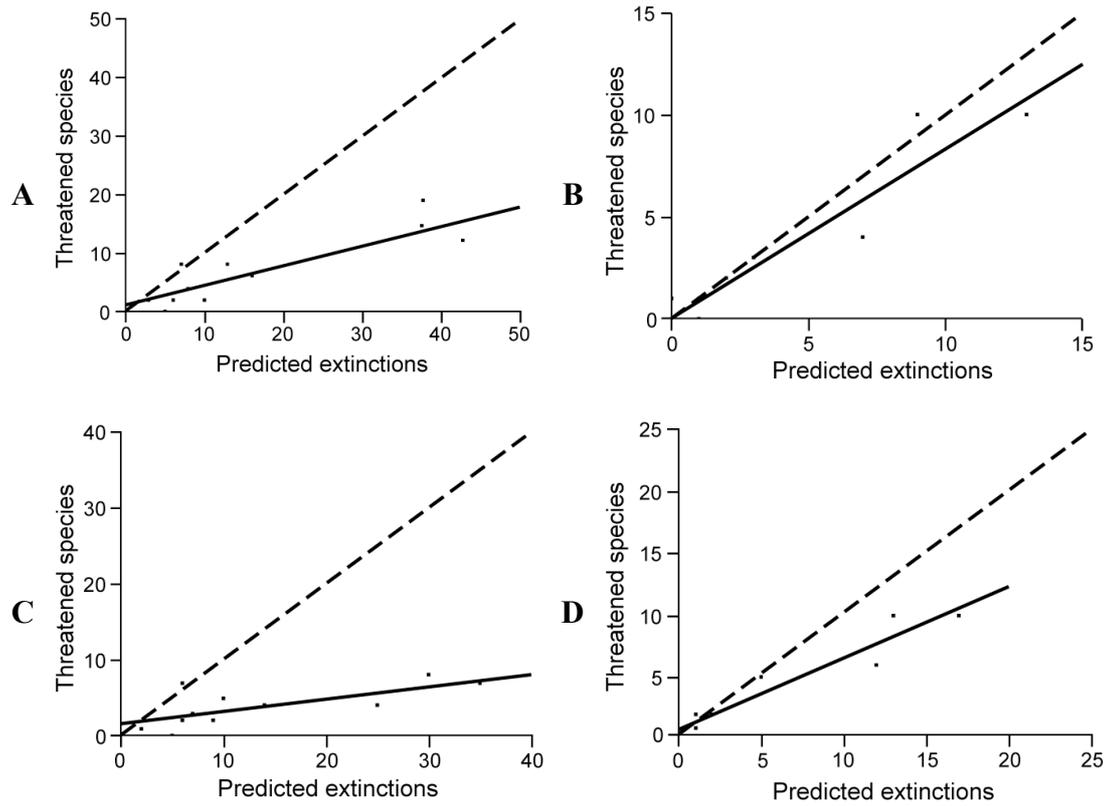


Figure 3. The total number of species that were predicted to become extinct is more than the currently recognized threatened species (A). There are fewer numbers of threatened amphibians (B) and reptiles (C) than predicted. In contrast, threatened species and predicted extinctions in the PAICs were not significantly different (D). (Regression line = solid lines, line of equality = dashed lines.)

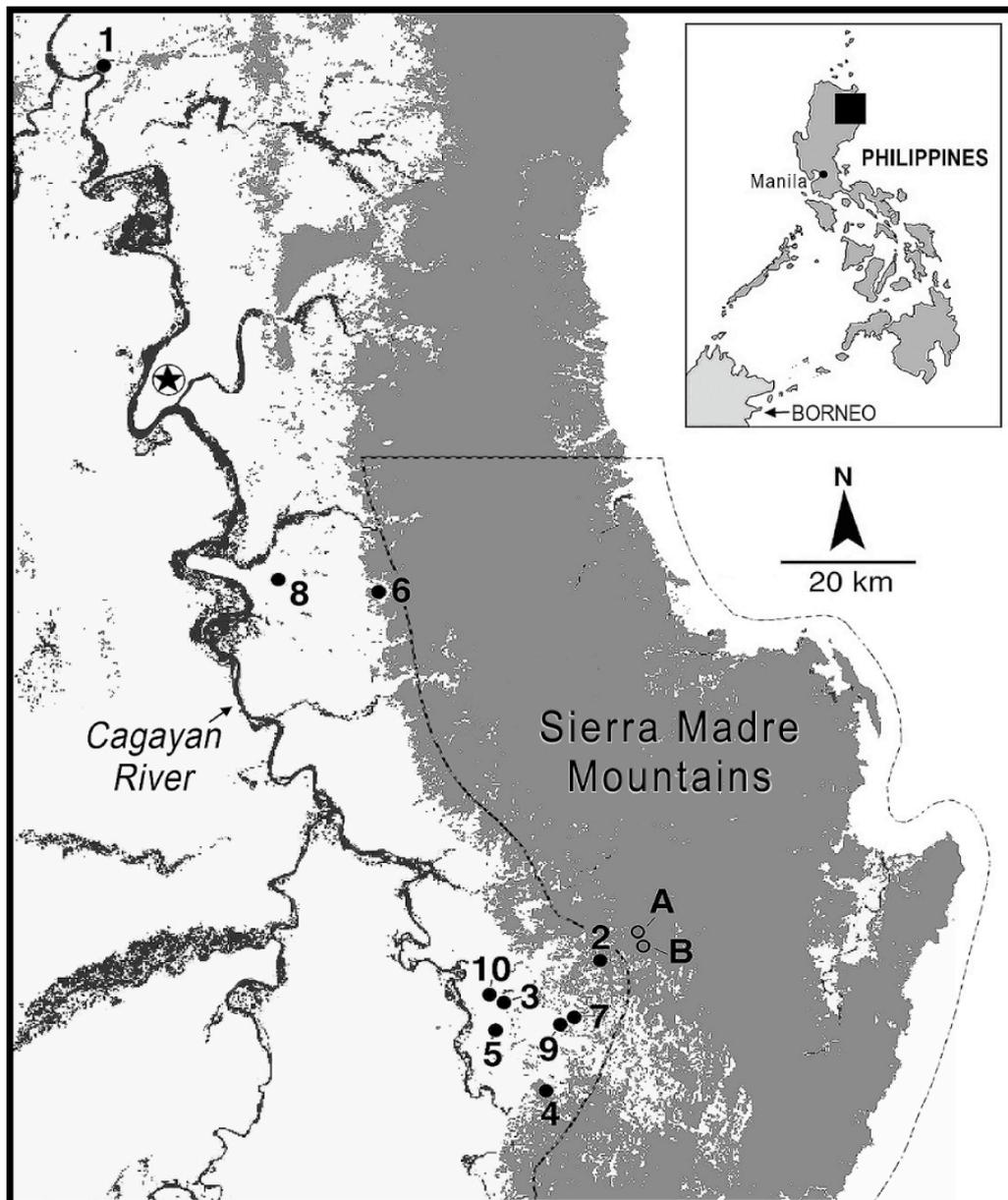


Figure 4. Location of the study fragments (solid circles 1–10) and the control site in continuous forest (open circles, plots A and B) on the west slopes of the Sierra Madre Mountains of Luzon Island, Republic of the Philippines. Study sites are described in Table 4. Gray-shaded areas represent the extent of forest, solid lines are river systems, and enclosed star depicts a major urban center (Tuguegarao City). Dashed lines depict the boundaries of the Northern Sierra Madre Natural Park. Modified from maps of the Sierra Madre Biodiversity Corridor Program of Conservation International Philippines.

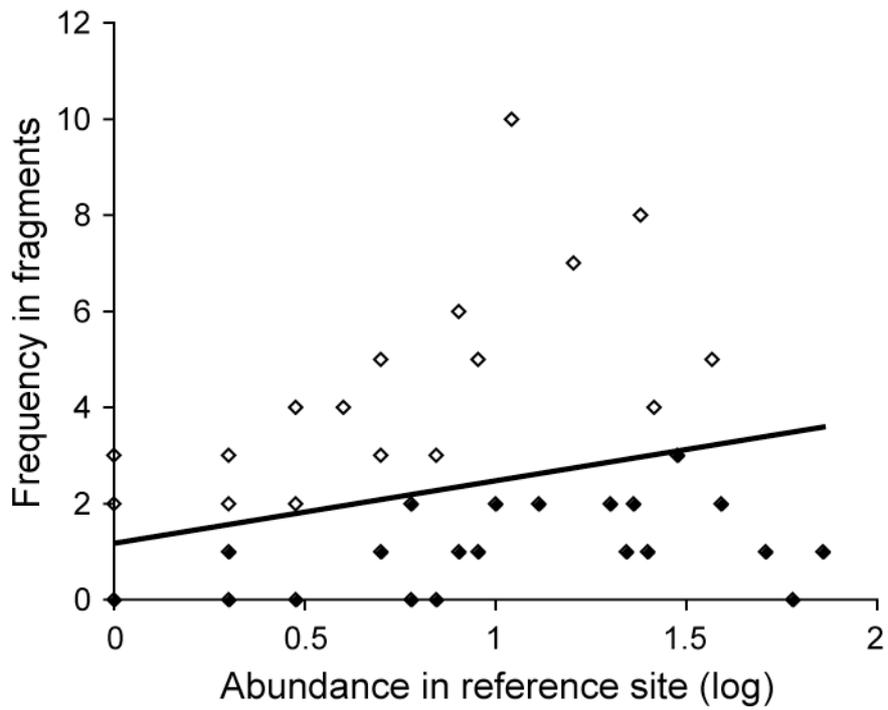


Figure 5. The plot shows a positive relationship between abundance ( $\log_{10}$ ) of species in continuous forest and the number of fragments in which they occur ( $R^2 = 0.09$ ,  $df = 48$ ,  $p = 0.035$ ), such that those species that are rare in the control site occurred in fewer fragments. Solid diamonds depict species that are fragmentation-sensitive.

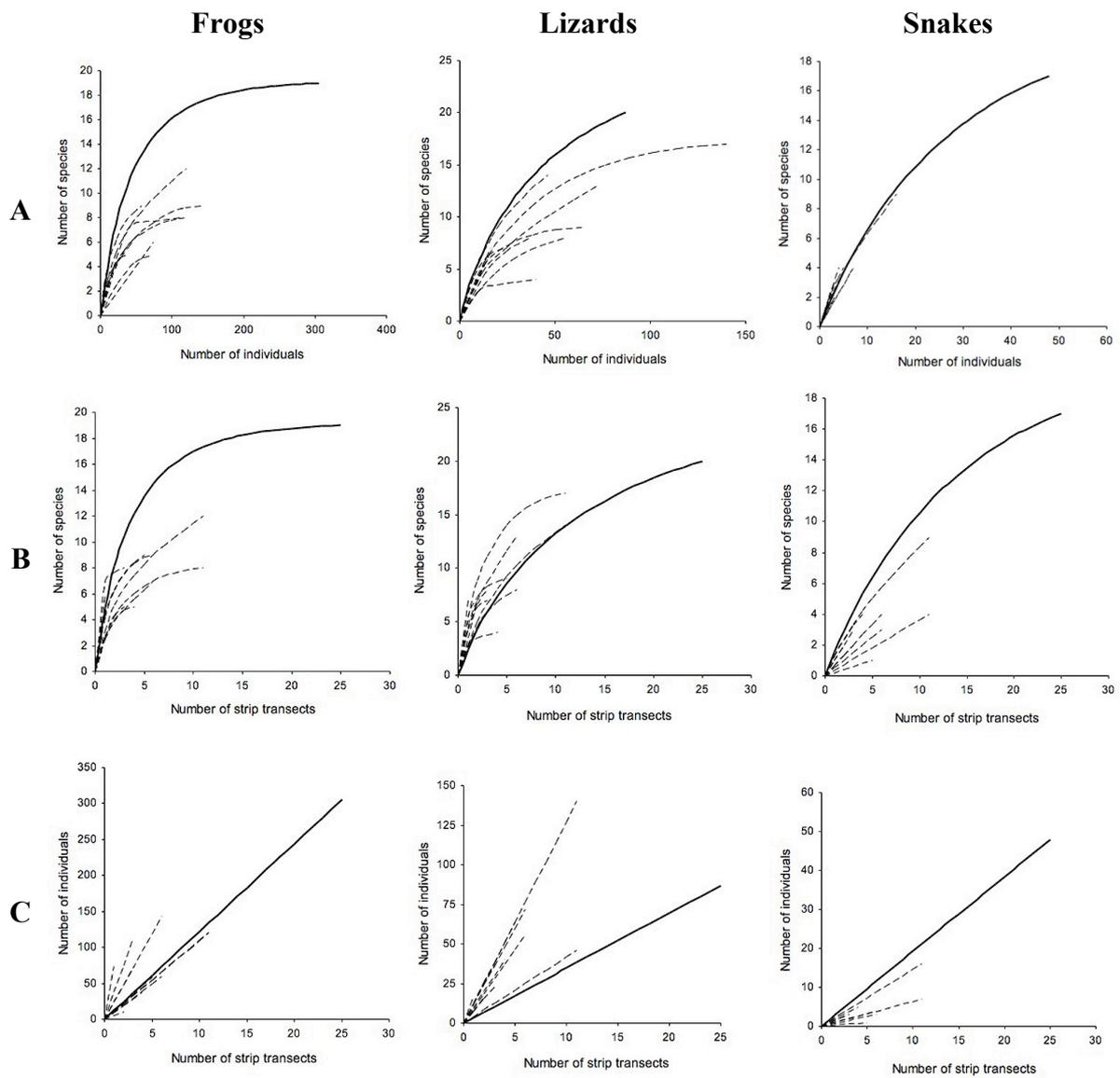


Figure 6. Individual-based species accumulation curves (A), species density (B), and population density (C) of frogs, snakes, and lizards in continuous forest (solid lines) and forest fragments (dashed lines).



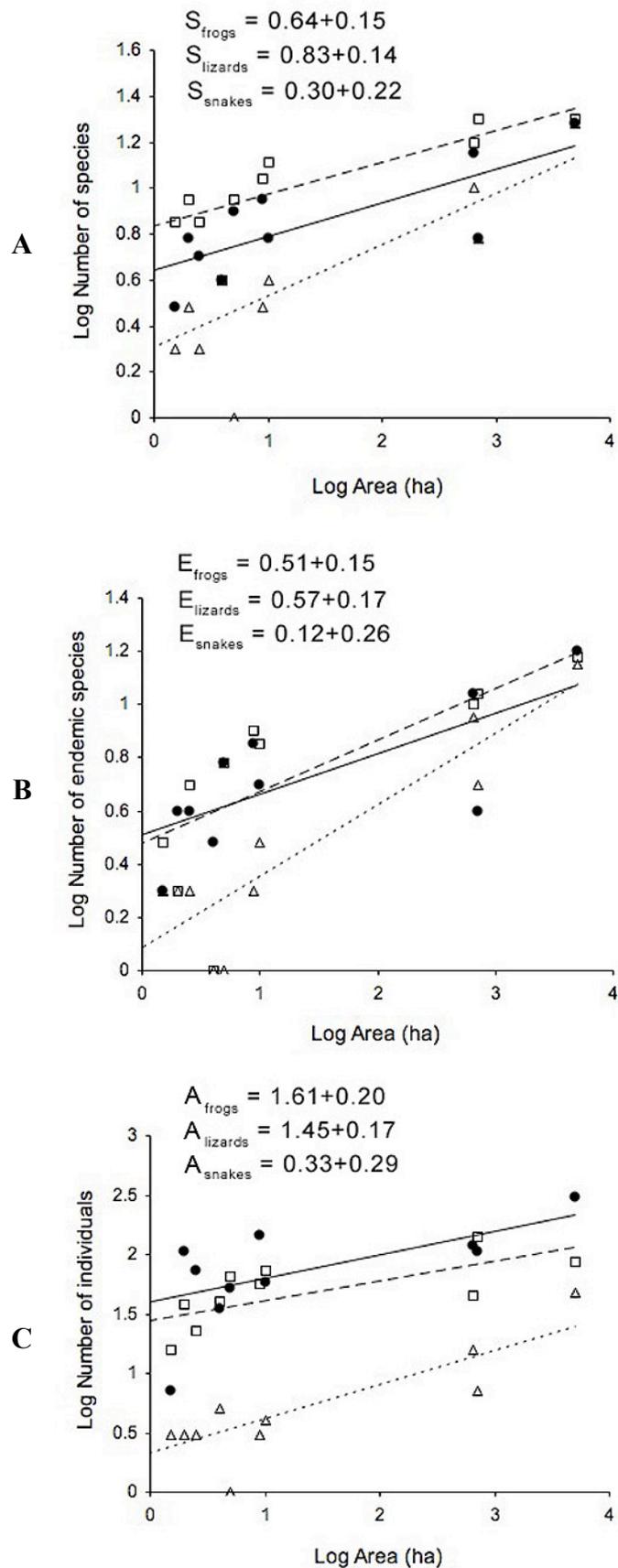


Figure 7. Univariate relationships between (A) complementary  $\log_{10}$ - $\log_{10}$  transformation of species richness and forest area, (B) number of endemic species and area, and (C) faunal abundance and area. Frogs = circles and solid lines, lizards = squares and dashed lines, snakes = triangles and dotted lines.

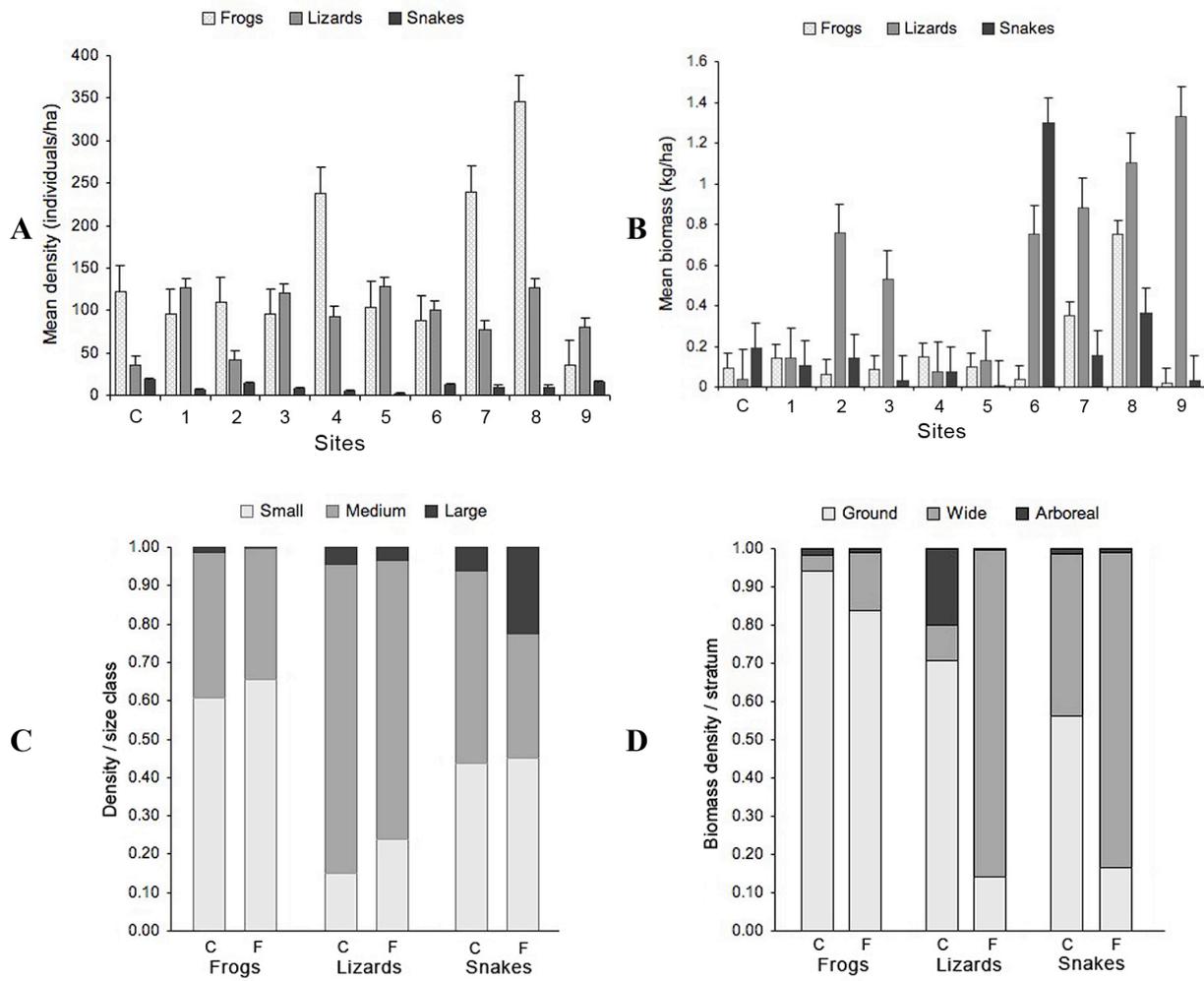


Figure 8. Population densities (A) and fresh biomass (B) of frogs, lizards, and snakes and their proportions (%) in body size classes (C) and vertical stratum distributions (D). One of the forest fragments (Site 10) was excluded because of the small sample size ( $n = 1$ ). Bars represent the standard error.

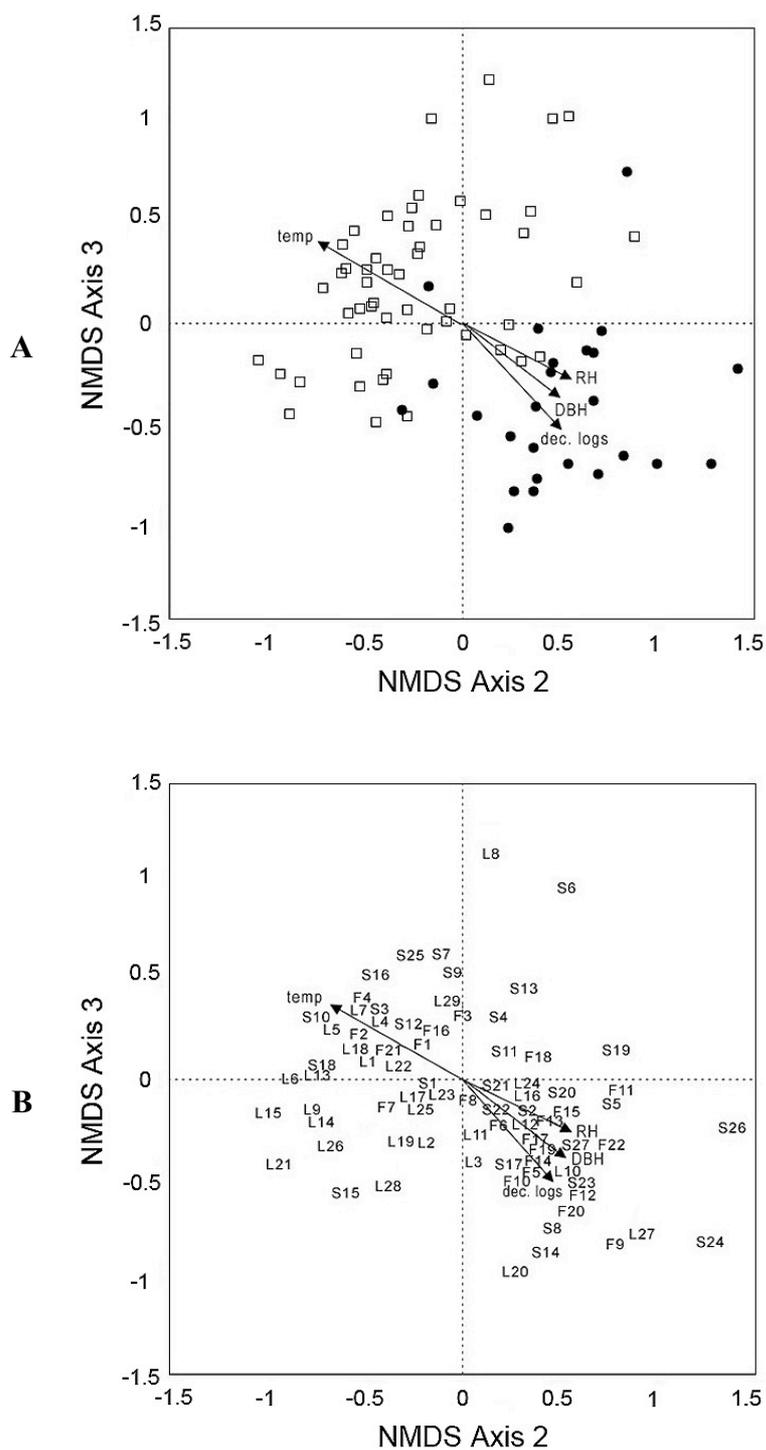


Figure 9. Non-metric multidimensional scaling plot of 77 locality scores (A; circles = continuous forest, squares = forest fragments) and 78 species scores (B; frogs = F1–F22, lizards = L1–L29, snakes = S1–S27) grouped by similarity in community composition. Overlaid were four ecological variables that strongly correlate with the ordination (temperature, relative humidity, mean DBH of trees, and mean number of decayed logs). Refer to Table 5 for the species codes.

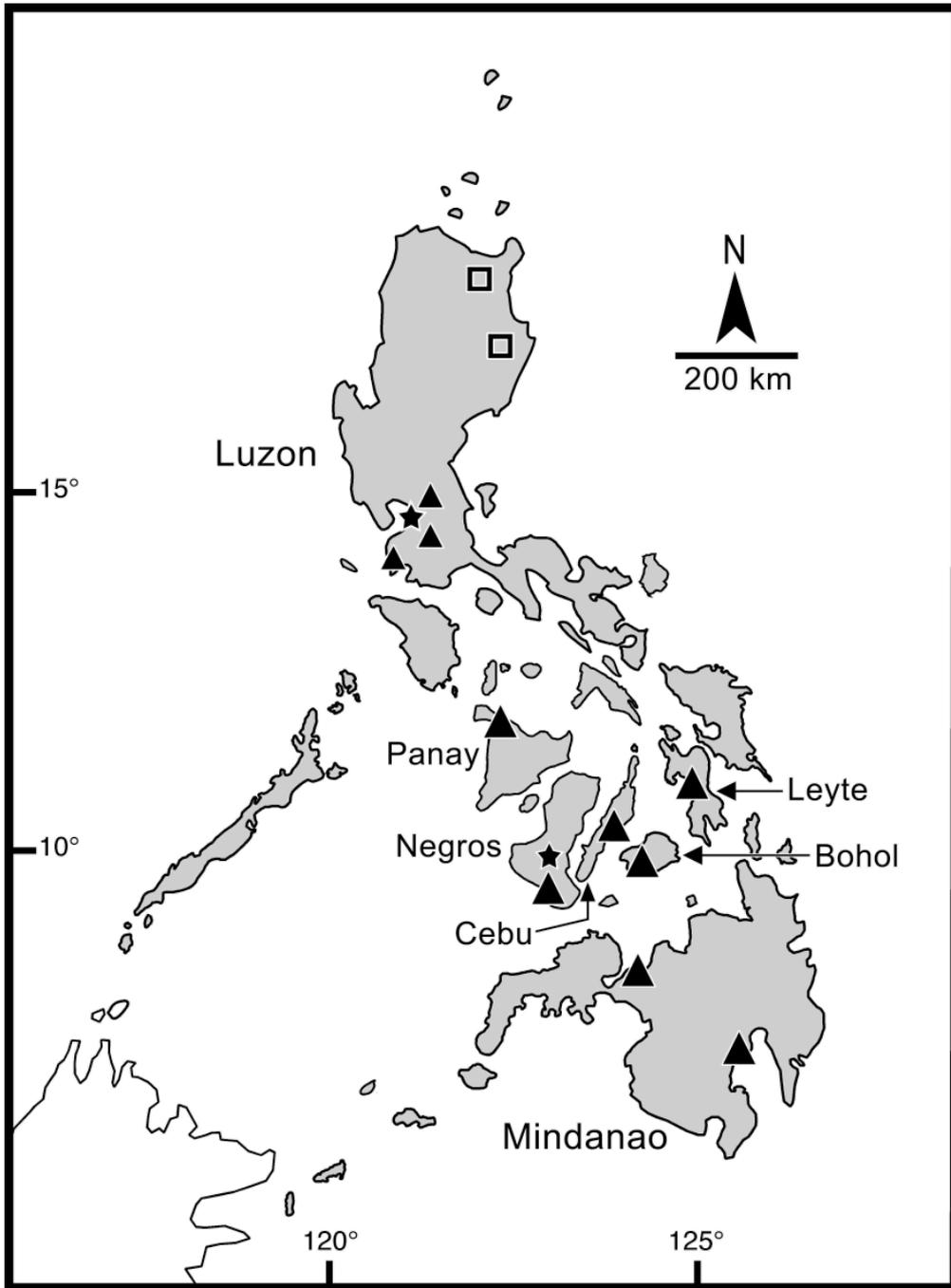


Figure 10. Study plots (open squares) on Luzon Island, Philippines and sampling localities of *Bufo marinus* (triangles) from seven island populations. Localities where the species was initially introduced are marked with a star.

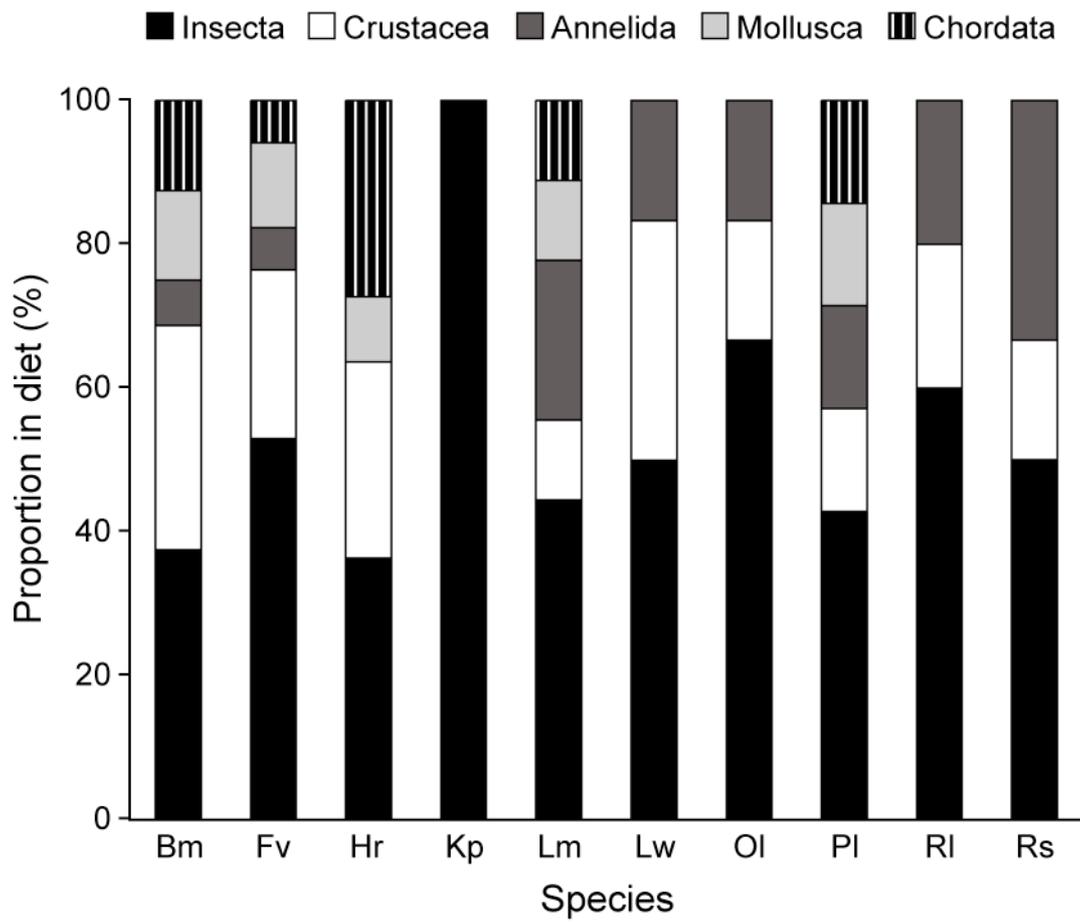


Figure 11. Proportion of food types consumed by introduced and native anurans from the study sites. See Table 9 for species abbreviations.

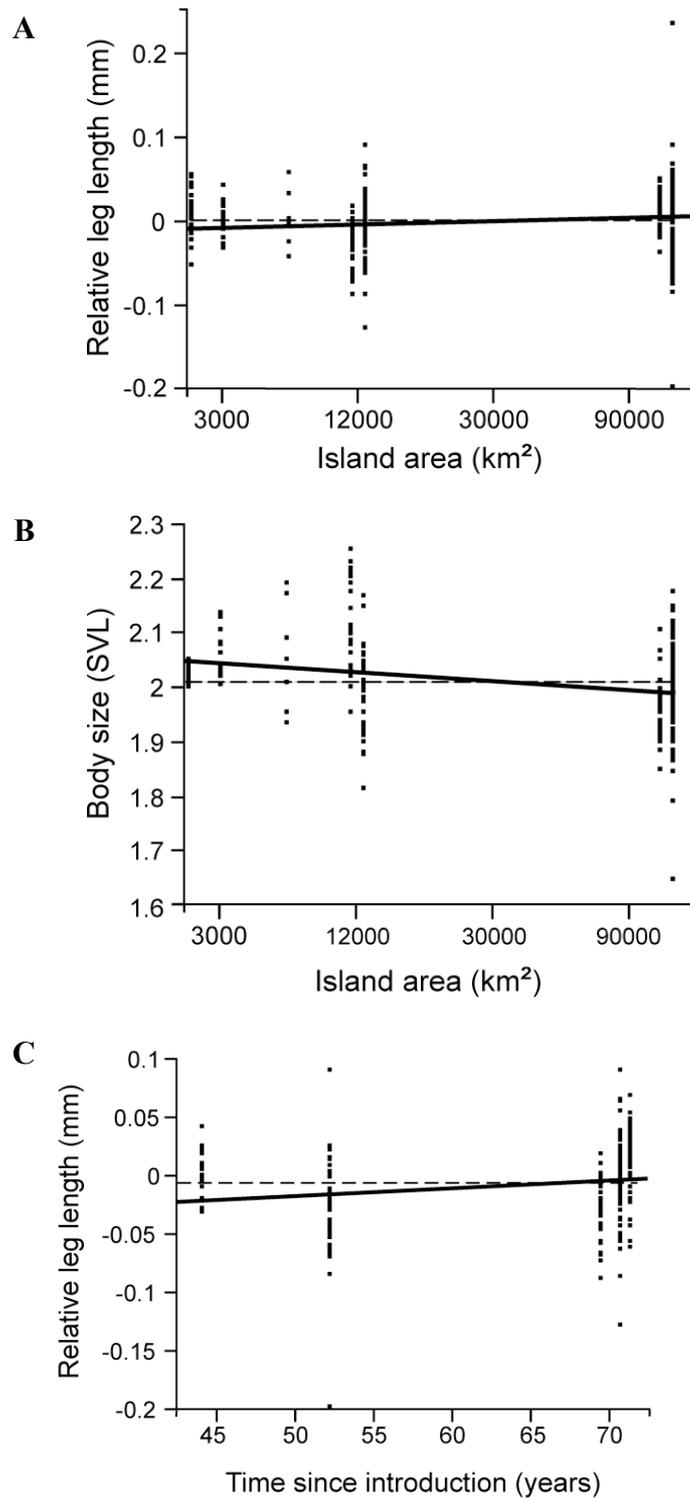


Figure 12. Univariate relationships between log-transformed island size and relative leg length of *Bufo marinus* ( $R^2 = 0.017$ ,  $p = 0.024$ ) revealed a detectable increase in leg length of toad populations in larger islands (A). Toads in smaller islands had a larger body size (B). Legs were slightly longer in older populations of *B. marinus* ( $R^2 = 0.033$ ,  $p = 0.009$ ) compared with younger populations (C).

## Appendices

Appendix 1. Total number of species of amphibians and reptiles, number of threatened species, and the proportion (%) of lowland forest on each island. Islands are grouped to corresponding herpetofaunal provinces or PAIC (Pleistocene Aggregate Island Complex).

PAIC and islands	Land area (km <sup>2</sup> )	Lowland forest (km <sup>2</sup> )	Forest cover (%)	Total species*	Threatened species
<b>BATANES</b>					
Itbayat	84.1	10.2	12.2	13	0
Batan	68.7	17.2	25.5	22	0
Sabtang	33.5	8.2	24.6	12	0
<b>BABUYAN</b>					
Calayan	174.4	52.5	30.1	12	2
Dalupiri	64.4	2.2	3.5	11	1
Fuga	95.5	13.5	14.1	3	0
Camiguin Norte	166.7	55.2	33.1	20	1
<b>LUZON</b>					
Luzon	104674.9	17187.5	19.2	136	13
Palaui	25.1	4.0	16.0	13	2
Polillo	634.1	166.7	26.3	72	4
Alabat	183.8	49.0	26.7	8	0
Catanduanes	1445.0	539.0	37.3	49	2
Marinduque	890.7	170.5	19.2	44	2
<b>MINDORO</b>					
Mindoro	9785.8	961.7	11.9	66	6
Verde	16.2	2.2	13.9	14	1
LUBANG	186.9	49.7	26.6	23	1
BURIAS	407.1	13.2	3.3	7	0
<b>ROMBLON-SIBUYAN</b>					
Romblon	665.4	43.5	6.5	20	1
Tablas	451.5	183.5	46.1	36	2
Sibuyan	78.5	13.2	16.9	36	4
<b>PALAWAN</b>					
Palawan	11398.0	4689.7	43.3	89	6
Calauit	31.9	265.5	29.8	32	1
Busuanga	891.3	6.5	20.4	34	2
Calamianes	379.2	93.5	24.7	34	1
Dumaran	321.7	25.5	7.9	23	2
Balabac	311.2	95.7	30.8	40	5

WEST VISAYAS					
Panay	11477.1	642.7	5.9	74	8
Negros	12726.0	334.7	2.8	85	9
Cebu	4390.4	160.7	3.7	62	4
Masbate	3174.4	109.2	3.4	39	4
Guimaras	572.7	11.0	1.9	27	2
GIGANTE					
North Gigante	7.0	1.0	14.3	6	2
South Gigante	8.0	1.5	18.8	14	2
SIQUIJOR	317.4	16.2	5.1	27	1
CAMIGUIN	243.5	57.0	26.3	54	2
MINDANAO					
Samar	12397.3	5308.4	42.8	83	6
Leyte	6964.6	1704.2	25.0	88	9
Biliran	497.4	106.5	23.5	27	4
Bohol	3731.5	545.2	14.9	84	8
Mindanao	93807.0	15628.2	20.0	141	16
Dinagat	809.9	295.2	36.6	48	5
Siargao	418.2	126.2	30.2	22	0
Basilan	1231.1	585.0	48.7	65	5
JOLO-TAWITAWI					
Jolo	835.1	257.7	30.9	50	6
Tawitawi	608.2	365.0	60.0	39	5

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\* These are all presently known native Philippine species. See text for the criteria used in including species for the analysis.



Appendix 2. Amphibians and reptiles from low elevation tropical moist forests in the Philippines and their distribution in 11 PAIC (Pleistocene Aggregate Island Complex) herpetofaunal provinces. Abbreviations: A = Batanes, B = Babuyan, C = Luzon, D = Mindoro, E = Romblon–Sibuyan, F = Palawan, G = West Visayas, H = Gigante, I = Camiguin, J = Mindanao, K = Jolo–Tawitawi, CR = Critically Endangered, EN = Endangered, VU = Vulnerable, NT = Near Threatened, DD = Data Deficient. Conservation status of species is based on IUCN (2007) and the Global Reptile Assessment (unpublished data; assessed in 2007). Species in boldface are endemic taxa (species/subspecies).

Species	A	B	C	D	E	F	G	H	I	J	K	Remarks
Anurans												
<i>Barbourula busuangensis</i>						X						VU
<i>Ansonia mcgregori</i>										X		VU
<i>Pelophryne brevipes</i>										X		
<i>Ingerana mariae</i>						X						DD
<i>Platymantis cagayanensis</i>			X									EN
<i>Platymantis corrugatus</i>			X				X		X			
<i>Platymantis dorsalis</i>			X									
<i>Platymantis guentheri</i>										X		VU
<i>Platymantis hazelae</i>							X					EN
<i>Platymantis indeprensus</i>			X									VU
<i>Platymantis insulatus</i>									X			CR
<i>Platymantis levigatus</i>					X							EN
<i>Platymantis luzonensis</i>			X									NT
<i>Platymantis mimulus</i>			X									NT
<i>Platymantis negrosensis</i>							X					EN
<i>Platymantis paengi</i>							X					Not assessed
<i>Platymantis polillensis</i>			X									EN
<i>Platymantis pygmaeus</i>			X									VU
<i>Platymantis rabori</i>										X		VU
<i>Platymantis sierramadrensis</i>			X									VU
<i>Platymantis spelaeus</i>							X					EN
<i>Platymantis taylori</i>			X									EN
<i>Platymantis</i> new species A <sup>a</sup>	X											Not assessed
<i>Platymantis</i> new species B <sup>a</sup>		X										Not assessed
<i>Platymantis</i> new species C <sup>a</sup>			X									Not assessed
<i>Platymantis</i> new species D <sup>a</sup>			X									Not assessed
<i>Platymantis</i> new species E <sup>a</sup>			X									Not assessed
<i>Platymantis</i> new species F <sup>a</sup>			X									Not assessed
<i>Platymantis</i> new species G <sup>a</sup>			X									Not assessed
<i>Platymantis</i> new species H <sup>a</sup>			X									Not assessed
<i>Platymantis</i> new species I <sup>a</sup>			X									Not assessed
<i>Platymantis</i> new species J <sup>a</sup>			X									Not assessed
<i>Platymantis</i> new species K <sup>a</sup>			X									Not assessed
<i>Platymantis</i> new species L <sup>a</sup>							X					Not assessed
<i>Platymantis</i> new species M <sup>a</sup>			X									Not assessed
<i>Platymantis</i> new species N <sup>a</sup>			X									Not assessed
<i>Platymantis</i> new species O <sup>a</sup>							X					Not assessed
<i>Platymantis</i> new species P <sup>a</sup>										X		Not assessed
<i>Platymantis</i> new species Q <sup>a</sup>					X							Not assessed
<i>Platymantis</i> new species R <sup>a</sup>				X								Not assessed
<i>Platymantis</i> new species S <sup>a</sup>										X		Not assessed

<i>Platymantis</i> new species T <sup>a</sup>	X								Not assessed	
<i>Platymantis</i> new species U <sup>a</sup>	X								Not assessed	
<i>Platymantis</i> new species V <sup>a</sup>	X								Not assessed	
<i>Platymantis</i> new species W <sup>a</sup>			X						Not assessed	
<i>Platymantis</i> new species X <sup>a</sup>	X								Not assessed	
<i>Fejervarya nicobariensis</i>				X				X		
<i>Limnonectes acanthi</i>				X					VU	
<i>Limnonectes diuatus</i>								X	VU	
<i>Limnonectes macrocephalus</i>	X	X							NT	
<i>Limnonectes magnus</i>							X	X	NT	
<i>Limnonectes micrixalus</i>								X	DD	
<i>Limnonectes palavanensis</i>				X						
<i>Limnonectes parvus</i>								X	VU	
<i>Limnonectes visayanus</i>					X				VU	
<i>Limnonectes</i> cf. <i>acanthi</i> <sup>a</sup>		X							Not assessed	
<i>Limnonectes</i> cf. <i>magnus</i> <sup>a</sup>								X	Not assessed	
<i>Occidozyga diminutivus</i>								X	X	VU
<i>Occidozyga</i> cf. <i>laevis</i>	X	X	X	X	X	X	X	X	X	
<i>Leptobrachium</i> new species A <sup>a</sup>								X		Not assessed
<i>Leptobrachium</i> new species B <sup>a</sup>				X						Not assessed
<i>Leptobrachium</i> new species C <sup>a</sup>		X								Not assessed
<i>Megophrys ligayae</i>				X						EN
<i>Megophrys stejneri</i>								X		VU
<i>Chaperina fusca</i>				X				X	X	
<i>Kaloula kalingensis</i>	X									VU
<i>Kaloula</i> new species <sup>a</sup>					X			X		Not assessed
<i>Kaloula kokacii</i>	X									NT
<i>Kaloula rigida</i>	X									VU
<i>Kaloula walteri</i>	X									DD
<i>Microhyla petrigena</i>									X	NT
<i>Rana albotuberculata</i>								X		DD
<i>Rana everetti</i>					X					DD
<i>Rana grandocula</i>								X	X	
<i>Rana luzonensis</i>	X									NT
<i>Rana mangyanum</i>		X								EN
<i>Rana melanomenta</i>									X	DD
<i>Rana moellendorffi</i>					X					NT
<i>Rana sanguinea</i>					X					
<i>Rana similis</i>	X									NT
<i>Rana tipanan</i>	X									VU
<i>Staurois natator</i>					X			X		
<i>Nyctixalus pictus</i>					X					NT
<i>Nyctixalus spinosus</i>								X		VU
<i>Philautus leitensis</i>								X		VU
<i>Philautus schmackeri</i>		X								EN
<i>Polypedates hecticus</i>								X		DD
<i>Rhacophorus appendiculatus</i>	X				X			X		
<i>Rhacophorus bimaculatus</i>	X							X		VU
<i>Rhacophorus everetti everetti</i>					X					NT
<i>Rhacophorus pardalis</i>	X				X	X	X	X	X	
Caecilians										
<i>Caudacaecilia weberi</i>					X					DD
<i>Ichthyophis glandulosus</i>								X		DD
<i>Ichthyophis mindanaoensis</i>								X		DD

Turtles										
<i>Cyclemys dentata</i>							X		X	
<i>Heosemys spinosa</i>									X	Threatened
<i>Siebenrockiella leytensis</i>							X			Threatened
Lizards										
<i>Bronchocela cristatella</i>		X	X	X	X	X	X	X	X	
<i>Bronchocela marmorata marmorata</i>			X	X	X		X			DD
<i>Draco bimaculatus</i>									X	X
<i>Draco guentheri</i>									X	X
<i>Draco jareckii</i>	X	X								
<i>Draco mindanensis</i>									X	Threatened
<i>Draco ornatus</i>									X	
<i>Gonocephalus interruptus</i>			X	X					X	DD
<i>Gonocephalus semperi</i>			X	X				X	X	DD
<i>Gonocephalus sophiae</i>					X	X			X	DD
<i>Hydrosaurus amboinensis</i>									X	DD
<i>Hydrosaurus pustulatus</i>			X	X	X		X	X		Threatened
<i>Cyrtodactylus agusanensis</i>									X	
<i>Cyrtodactylus annulatus</i>						X		X	X	X
<i>Cyrtodactylus philippinus</i>	X	X	X	X		X				
<i>Cyrtodactylus redimiculus</i>					X					
<i>Cyrtodactylus</i> new species <sup>b</sup>					X					Not assessed
<i>Gekko athymus</i>					X					
<i>Gekko</i> new species <sup>c</sup>	X									Not assessed
<i>Gekko ernstkelleri</i>						X				Threatened
<i>Gekko gigante</i>							X			Threatened
<i>Gekko palawanensis</i>					X					
<i>Gekko porosus</i>	X									
<i>Gekko romblon</i>				X						
<i>Hemiphyllodactylus insularis</i>						X				DD
<i>Lepidodactylus aureolineatus</i>								X	X	
<i>Lepidodactylus balioburius</i>	X									
<i>Lepidodactylus christiani</i>				X	X					
<i>Luperosaurus corfieldi</i>						X				
<i>Luperosaurus cumingii</i>	X	X				X	X			DD
<i>Luperosaurus joloensis</i>								X	X	Threatened
<i>Luperosaurus kubli</i>		X								DD
<i>Luperosaurus macgregori</i>	X									Threatened
<i>Luperosaurus palawanensis</i>					X					DD
<i>Pseudogekko brevipes</i>					X	X	X	X		Threatened
<i>Pseudogekko compressicarpus</i>		X				X	X	X		
<i>Pseudogekko labialis</i>								X		
<i>Pseudogekko smaragdinus</i>	X									
<i>Ptychozoon intermedium</i>									X	
<i>Dibamus leucurus</i>								X	X	
<i>Dibamus novaeguineae</i>			X		X	X		X	X	
<i>Brachymeles bicolor</i>		X								
<i>Brachymeles bonitae</i>		X	X	X		X				
<i>Brachymeles boulengeri boulengeri</i>		X								
<i>Brachymeles boulengeri boholensis</i>									X	
<i>Brachymeles boulengeri taylora</i>			X							
<i>Brachymeles boulengeri mindorensis</i>						X				
<i>Brachymeles cebuensis</i>						X				Threatened
<i>Brachymeles elerae</i>										DD
<i>Brachymeles gracilis gracilis</i>									X	
<i>Brachymeles gracilis hilong</i>								X	X	
<i>Brachymeles minimus</i>		X				X		X		
<i>Brachymeles pathfinderi</i>								X	X	DD

<i>Brachymeles samarensis</i>			X						X	
<i>Brachymeles schadenbergi schadenbergi</i>									X	
<i>Brachymeles schadenbergi orientalis</i>								X	X	
<i>Brachymeles talinis</i>		X	X	X						
<i>Brachymeles tridactylus</i>					X					
<i>Brachymeles vermis</i>									X	Threatened
<i>Dasia griffini</i>					X					Threatened
<i>Dasia grisea</i>	X	X	X							
<i>Dasia semicineta</i>						X		X		DD
<i>Eutropis bontocensis</i>			X							
<i>Eutropis cumingi</i>	X	X	X							
<i>Eutropis englei</i>									X	
<i>Eutropis indeprensa</i>		X	X	X	X	X	X	X	X	
<i>Eutropis multicarinata borealis</i>		X	X	X	X	X				
<i>Eutropis multicarinata multicarinata</i>								X	X	
<i>Lipinia auriculata auriculata</i>						X				
<i>Lipinia auriculata herrei</i>		X							X	
<i>Lipinia auriculata kempfi</i>		X	X	X						
<i>Lipinia pulchella pulchella</i>		X							X	
<i>Lipinia pulchella levitoni</i>		X								
<i>Lipinia pulchella taylori</i>						X				
<i>Lipinia quadrivittata quadrivittata</i>					X	X		X	X	
<i>Lipinia rabori</i>						X				DD
<i>Lipinia semperi</i>							X	X		DD
<i>Lygosoma bowringii</i>					X			X	X	
<i>Lygosoma quadrupes</i>					X					
<i>Parvoscincus palawanensis</i>					X					DD
<i>Sphenomorphus abdictus abdictus</i>								X	X	
<i>Sphenomorphus abdictus aquilonius</i>	X	X	X							
<i>Sphenomorphus acutus</i>									X	
<i>Sphenomorphus arborens</i>						X				
<i>Sphenomorphus atrigularis</i>									X	
<i>Sphenomorphus biparietalis</i>								X	X	Threatened
<i>Sphenomorphus coxi coxi</i>								X	X	
<i>Sphenomorphus coxi divergens</i>		X	X							
<i>Sphenomorphus cumingii</i>		X	X						X	
<i>Sphenomorphus decipiens</i>		X	X						X	
<i>Sphenomorphus diwata</i>									X	DD
<i>Sphenomorphus fasciatus</i>								X	X	
<i>Sphenomorphus jagori jagori</i>	X	X	X	X				X	X	
<i>Sphenomorphus jagori grandis</i>						X	X			
<i>Sphenomorphus laterimaculatus</i>		X								DD
<i>Sphenomorphus leucospilos</i>		X								
<i>Sphenomorphus llanosi</i>									X	
<i>Sphenomorphus mindanensis</i>									X	
<i>Sphenomorphus tagapayo</i>		X								
<i>Sphenomorphus variegatus</i>								X	X	X
<i>Sphenomorphus victoria</i>					X					
<i>Tropidophorus davaoensis</i>									X	
<i>Tropidophorus grayi</i>	X					X	X	X	X	
<i>Tropidophorus misaminius</i>									X	
<i>Tropidophorus partelloi</i>									X	
<i>Varanus mabitang</i>					X					Threatened
<i>Varanus olivaceus</i>	X									Threatened
Snakes										
<i>Ramphotyphlops cumingii</i>	X	X	X	X	X	X	X	X		DD
<i>Ramphotyphlops olivaceus</i>								X		DD
<i>Ramphotyphlops suluensis</i>									X	Threatened



<i>Oxyrhabdium leporinum leporinum</i>	X	X		X	X			
<i>Oxyrhabdium leporinum visayanum</i>					X			
<i>Oxyrhabdium modestum</i>	X	X		X		X		
<i>Psammodynastes pulverulentus</i>	X	X		X	X	X	X	X
<i>Pseudorabdion ater</i>								X
<i>Pseudorabdion oxycephalum</i>		X		X	X		X	
<i>Pseudorabdion taylori</i>							X	DD
<i>Ptyas carinatus</i>				X				
<i>Ptyas luzonensis</i>		X		X		X		
<i>Rhabdophis auriculata myersi</i>							X	
<i>Rhabdophis chrysarga</i>				X				
<i>Rhabdophis lineata</i>							X	
<i>Rhabdophis spilogaster</i>	X	X	X	X	X		X	
<i>Sibynophis bivittatus</i>				X				
<i>Sibynophis geminatus</i>							X	Threatened
<i>Stegonotus muelleri</i>							X	
<i>Tropidonophis dendrophiops</i>		X				X	X	
<i>Tropidonophis negrosensis</i>			X		X			Threatened
<i>Calliophis intestinalis bilineata</i>				X				
<i>Calliophis intestinalis philippina</i>	X						X	
<i>Calliophis intestinalis suluensis</i>								X
<i>Hemibungarus calligaster calligaster</i>	X	X					X	
<i>Hemibungarus calligaster gemianulis</i>					X	X	X	
<i>Hemibungarus calligaster mcclungi</i>	X							
<i>Ophiophagus hannah</i>	X	X	X	X		X	X	
<i>Trimeresurus flavomaculatus flavomaculatus</i>	X	X		X		X	X	X
<i>Trimeresurus flavomaculatus halieus</i>		X						
<i>Trimeresurus mcgregori</i>	X	X						
<i>Trimeresurus schultzei</i>				X				
<i>Tropidolaemus philippensis</i>							X	Not Assessed
<i>Tropidolaemus subannulatus</i>	X	X	X	X		X	X	

<sup>a</sup> R. Brown, A. Diesmos, et al., in preparation.

<sup>b</sup> L. Welton, C. Siler, A. Diesmos, R. Brown, in preparation.

<sup>c</sup> R. Brown, C. Oliveros, C. Siler, A. Diesmos, in press.

<sup>d</sup> W. Addison, R. Brown, A. Diesmos, et al., in preparation.

Appendix 3. Amphibians and reptiles recorded from the study area in the lowland rainforest of the Sierra Madre Mountains, Philippines. Abbreviations: PE = endemic to the Philippines, LE = confined to Luzon biogeographic region, CR = Critically Endangered, EN = Endangered, VU = Vulnerable, NT = Near Threatened (IUCN 2007). "Appendix" status is from CITES (2005).

Species	Mean Abundance / Site											Matrix tolerant?	Local extinctions	Range	Status	
	C	1	2	3	4	5	6	7	8	9	10 <sup>a</sup>					
AMPHIBIA																
Order Anura																
Bufonidae																
<i>Bufo marinus</i> (Linnaeus)	0	0.82	0	0.33	0	1.2	0.75	0	1	1.5	2	Yes	–	Widespread	Introduced species	
Microhylidae																
<i>Kaloula kalingensis</i> Taylor	0	0	0	0.17	2.33	0	0	0	0.33	0	0	No	7	LE	VU; needs taxonomic study	
<i>K. picta</i> (Duméril & Bibron)	0	0.18	0	0	0	0.4	0.25	0	0	0.05	1	Yes	–	PE		
<i>K. rigida</i> Taylor	0.04	0.18	0.18	0	0	0	0	0	0	0	0	No	8	LE	VU; needs taxonomic study	
Ranidae																
<i>Fejervarya cancrivora</i> (Gravenhorst)	0	0	0	0	0	0	0	0	0	0	0	Yes	–	Asia		
<i>F. vittigera</i> (Wiegmann)	0	0	0	0	0	0	0	0	0	1.33	0	Yes	–	PE		
<i>Hoplobatrachus rugulosus</i> (Wiegmann)	0	0.64	0	0	0	0	0	0	2	0	9	Yes	–	Asia	Introduced species	
<i>Limnonectes macrocephalus</i> (Inger)	0.20	0	0.27	0	0	0	0	0	0	0	0	No	9	LE	NT	
<i>L. woodworthi</i> (Taylor)	1.12	0	0.18	0	2	1	0	9.33	0	0	8	Yes	5	LE		
<i>Limnonectes</i> sp.	0.16	2.45	0	0	0	0.6	0	0.67	12	0	0	Yes	6	LE	Probable new species	
<i>Occidozyga</i> cf. <i>laevis</i> (Günther)	0.80	0.18	0	0	3	0.4	0	0	2	0	0	No	6	SE Asia	Needs taxonomic study	
<i>Platymantis</i> cf. <i>cornutus</i> (Taylor)	0.24	0	0	0	0	0	0	0	0	0	0	No	10	LE	VU; needs taxonomic study	
<i>P. corrugatus</i> (Duméril)	0.2	0	0	0.17	0	0	0	0	0	0	0	No	9	PE		
<i>P. luzonensis</i> Brown, Alcalá, Diesmos & Alcalá	0.24	0	0	0	0	0	0	0	0	0	0	No	10	LE	NT	
<i>P. pygmaeus</i> Alcalá, Brown & Diesmos	2.56	0	0.36	0	0	0	0	0	0	0	0	No	9	LE	VU	
<i>P. taylori</i> Brown, Alcalá & Diesmos	0.88	0	2.64	0.67	2.17	0.8	0	0	0	0	0	No	6	LE	EN	
<i>Platymantis</i> sp. A	1.28	0	0.45	0	0	0	2.75	0	0	0	0	No	8	LE	New species	
<i>Platymantis</i> sp. B	0.36	0	0.82	0	0.67	0	0	0	0	0	0	No	8	LE	New species	
<i>Platymantis</i> sp. C	0.44	5.55	3.91	4.67	7.5	4.8	5.25	12.33	7.67	2.5	49	No	0	LE	New species	

<i>Platymantis</i> sp. D	1	0	0.64	0	0.5	0	0	0.33	0	0	0	No	7	LE	New species
<i>Platymantis</i> sp. E	0.2	0	1.27	0	4.83	1.4	0	0	0	0	0	No	7	LE	New species
<i>Rana luzonensis</i> Boulenger	0.64	0	0	0	0	0	0	0	0	0	0	No	10	LE	NT
<i>R. similis</i> (Günther)	1.36	0	0	0	0	0	0	0	0	0	0	No	10	LE	NT
Rhacophoridae															
<i>Polypedates leucomystax</i> (Gravenhorst)	0.16	1	0.09	3.17	0.83	0.83	0.5	1.33	11.33	0.5	0	Yes	–	Asia	
<i>Rhacophorus pardalis</i> Günther	0.32	0	0.09	0	0	0	0	0	0	0	0	No	9	SE Asia	
REPTILIA															
Order Testudines															
Bataguridae															
<i>Cuora amboinensis amboinensis</i> (Daudin)	0.04	0.09	0.09	0.17	0	0.2	0	0	0.33	0	0	b	–	Asia	VU; Appendix II
Trionychidae															
<i>Pelochelys cantorii</i> Gray	0	0.09	0	0	0	0	0	0	0	0	0	b	–	Asia	EN; Appendix II; last recorded on Luzon in 1918
Suborder Lacertilia															
Agamidae															
<i>Bronchocela cristatella</i> (Kuhl)	0	0.27	0	0	0	0	0	0	0	0	0	No	9	SE Asia	
<i>Draco spilopterus</i> (Wiegmann)	0.2	0.45	0.27	0.33	0.33	0.4	0	0	0	0	0	No	5	PE	
Gekkonidae															
<i>Cosymbotus platyurus</i> (Schneider)	0	0	0	0	0	0	0	0	0.67	0	0	Yes	–	Asia	
<i>Cyrtodactylus philippinicus</i> (Steindachner)	0.12	0.18	0	0	0	0	0	0	0	0	0	No	8	PE	
<i>Gehyra mutilata</i> (Wiegmann)	0	0	0	0	0	0	0	0	0.33	0.5	0	Yes	–	Widespread	
<i>Gekko gecko</i> Linnaeus	0	0	0	0	0	0	0	0	0.67	0	0	Yes	–	Asia	
<i>Gekko monarchus</i> (Schlegel)	0.08	0.36	0	0.17	0	0	0	0	0	1	0	Yes	–	SE Asia	
<i>Hemidactylus frenatus</i> Schlegel	0	0	0	0.17	0	0.4	0	0	4	0	0	Yes	–	Widespread	
<i>H. stejnegeri</i> Ota & Hikida	0	0	0.90	0	0	0	0	0	0	0	0	Yes	–	Asia	
<i>Lepidodactylus</i> cf. <i>planicaudus</i> Stejneger	0.08	0.27	0	0	0	0	0	0	0	0	0	No	9	PE	Needs taxonomic study
<i>Luperosaurus kubli</i> Brown, Diesmos & Duya	0.08	0	0	0	0	0	0	0	0	0	0	No	10	LE	
Scincidae															
<i>Brachymeles bicolor</i> (Gray)	0.08	0	0.09	0	0	0	0	0.67	0	1	0	No	7	LE	



<i>B. bonita</i> Duméril & Bibron	0.12	0	0.09	0	0	0	0	0.33	0	0.5	0	No	7	PE	
<i>B. boulengeri boulengeri</i> Taylor	0	1.55	0	0.33	0.17	0.4	0	0	1	0	0	No	4	LE	
<i>B. talinis</i> (Brown)	0.04	0.36	0	0.17	0	0	0	0	0	0	0	No	8	PE	
<i>Brachymeles</i> sp.	0	0.18	0	0	0	0	0	0	0	0	1	No	8	LE	Probable new species
<i>Eutropis cumingi</i> Brown & Alcala	0.56	0	0.36	0	0	0	2.5	0	0	0	0	No	8	Philippines, Taiwan	
<i>E. multicarinata borealis</i> Brown & Alcala	1.16	2.45	0.91	7	7	5.8	5.75	2.33	3.67	3.5	4	Yes	–	PE	
<i>E. multifasciata</i> (Kuhl)	0.04	1.36	0.09	0.17	0.17	0.8	1.5	0	1	0	2	Yes	–	Asia	
<i>Lamprolepis smaragdina philippinica</i> (Mertens)	0.08	0.45	0.09	0.17	0.17	0	0	0	0	0	0	Yes	6	PE	
<i>Lipinia</i> cf. <i>vulcania</i> Girard	0.04	0	0	0	0	0	0	0	0	0	0	No	10	PE	Last recorded in 1909
<i>Sphenomorphus cumingi</i> (Gray)	0.04	0.18	0	0	0	0	0	0	0	0	0	No	9	PE	
<i>S. decipiens</i> (Boulenger)	0.12	2.18	0.27	0.83	0	1.4	0	1.33	0	0	4	No	4	PE	
<i>S. jagori jagori</i> (Peters)	0.2	0.18	0.36	1.33	0.5	1.4	0	0	1	0	3	No	3	PE	
<i>S. leucospilos</i> (Peters)	0.12	0	0.09	0	2.5	0	0	0	0	0	0	No	8	LE	Last recorded in 1870
<i>S. steerei</i> Stejneger	0.2	0.55	1.18	1	1	1.8	0	1.67	0	1	1	No	2	PE	
<i>Sphenomorphus</i> sp.	0.08	1.64	0	0.17	0	0	0	1	0	0	0	No	7	LE	Probable new species
<i>Tropidophorus grayi</i> Günther	0.04	0	0	0	0	0	0	0	0	0	0	No	10	PE	
Varanidae															
<i>Varanus olivaceus</i> Hallowell	0	0	0.09	0	0	0	0	0	0	0	0	No	9	LE	VU; Appendix II
<i>V. salvator marmoratus</i> (Wiegmann)	0.08	0.09	0.18	0.17	0	0	0.25	0.33	0.33	0.5	2	Yes	–	PE	Appendix II
Suborder Serpentes															
Typhlopidae															
<i>Ramphotyphlops braminus</i> (Daudin)	0	0	0.09	0	0.17	0	0	0	0	0	1	Yes	–	Widespread	
<i>Typhlops</i> cf. <i>luzonensis</i> Taylor	0.08	0	0.09	0	0	0	0	0	0	0.5	0	No	8	PE	Needs taxonomic study
Boidae															
<i>Python reticulatus</i> (Schneider)	0	0	0	0	0	0	0.25	0	0	0	1	Yes	–	Asia	Appendix II
Colubridae															
<i>Ahaetulla prasina preocularis</i> (Taylor)	0.08	0.27	0	0	0	0	0.25	0	0	0	0	No	8	PE	
<i>Boiga angulata</i> (Peters)	0.04	0	0	0	0	0	0	0	0	0	0	No	10	PE	
<i>B. dendrophila divergens</i> (Taylor)	0	0	0.09	0	0	0	0	0	0	0	0	No	9	LE	
<i>B. philippina</i> (Peters)	0	0.09	0.09	0	0	0	0	0	0	0	0	No	8	PE	
<i>Calamaria bitorques</i> Peters	0.16	0	0	0	0	0	0	0	0	0	0	No	10	PE	
<i>C. gervaisii</i> Duméril, Bibron & Duméril	0	0	0.09	0.17	0	0	0	0	0	0	0	No	8	PE	

<i>Coelognathus erythrurus manillensis</i> Jan	0	0.18	0	0	0	0	0	0	0.33	0	0	Yes	–	PE	
<i>Cyclocorus lineatus</i> (Reinhardt)	0.08	0	0.45	0	0	0	0	0.67	0	1	0	No	7	PE	
<i>Dendrelaphis caudolineatus luzonensis</i> (Leviton)	0.04	0	0	0	0	0	0.5	0	0.33	0	0	Yes	–	PE	
<i>D. pictus pictus</i> (Gmelin)	0.08	0	0	0	0	0	0	0	0	0	0	No	10	PE	
<i>Dryophiops philippina</i> Boulenger	0.04	0	0	0	0	0	0	0	0	0	0	No	10	PE	
<i>Gonyosoma oxycephalum</i> (Reinwardt)	0	0	0	0.17	0	0	0	0	0	0	0	Yes	–	Asia	
<i>Lycodon aulicus</i> (Boie)	0	0	0	0	0	0	0.25	0	0	0	0	Yes	–	Asia	
<i>L. muelleri</i> Duméril, Bibron & Duméril	0.08	0	0.09	0	0	0	0	0	0	0	0	No	9	LE	
<i>Oligodon modestum</i> (Günther)	0	0	0	0.17	0	0	0	0	0	0	0	No	9	PE	
<i>Psammodynastes pulverulentus</i> (Boie)	0.08	0	0	0	0	0	0	0	0	0	0	No	10	Asia	
<i>Pseudorabion oxycephalum</i> (Günther)	0.52	0	0.36	0	0	0	0	0	0	0	0	No	9	PE	
<i>Ptyas luzonensis</i> (Günther)	0.04	0	0	0	0.17	0	0	0.33	0	0	0	No	8	PE	
<i>Rhabdophis spilogaster</i> (Boie)	0.20	0.09	0	0.17	0.17	0.2	0	0	0	0	1	No	5	LE	
<i>Tropidonophis dendrophiops</i> (Günther)	0.08	0	0	0	0	0	0	0	0	0	0	No	10	PE	
Elapidae															
<i>Hemibungarus calligaster calligaster</i> Wiegmann	0.04	0	0	0	0	0	0	0	0	0	0	No	10	LE	
<i>Naja philippinensis</i> Taylor	0	0	0	0	0	0	0	0	0.33	0	0	Yes	–	LE	Appendix II
<i>Ophiophagus hannah</i> (Cantor)	0.04	0	0	0	0	0	0	0	0	0	0	No	10	Asia	Appendix II
Viperidae															
<i>Trimeresurus flavomaculatus</i> (Gray)	0.24	0	0.09	0	0	0	0	0	0	0	0	No	9	PE	
Order Crocodylia															
Crocodylidae															
<i>Crocodylus mindorensis</i> Schmidt	0.04	0	0.73	0	0	0	0	0	0	0	0	<sup>b</sup>	–	PE	CR; Appendix I

<sup>a</sup> Site 10 includes one strip transect ( $n = 1$ ), hence the high abundance values.

<sup>b</sup> These species are affiliated with riparian habitats that transcend both forest sites and matrix.

Appendix 4. Summary data of log-transformed snout-vent length (SVL) and tibia length of 309 individuals of *Bufo marinus* from seven island populations in the Philippines. Residuals were based on regression of SVL versus tibia length.

Island/locality	SVL	Tibia length	Residuals	Year introduced	Reference
LUZON					
Marikina	1.991	1.587	0.007	1934	Rabor 1952
Marikina	1.975	1.592	0.025	1934	Rabor 1952
Marikina	2.077	1.661	0.010	1934	Rabor 1952
Marikina	2.027	1.588	-0.022	1934	Rabor 1952
Marikina	1.986	1.623	0.047	1934	Rabor 1952
Marikina	1.990	1.581	0.002	1934	Rabor 1952
Marikina	2.015	1.633	0.033	1934	Rabor 1952
Marikina	2.037	1.619	0.001	1934	Rabor 1952
Marikina	2.020	1.619	0.015	1934	Rabor 1952
Marikina	2.009	1.663	0.068	1934	Rabor 1952
Marikina	1.981	1.594	0.022	1934	Rabor 1952
Marikina	1.982	1.562	-0.011	1934	Rabor 1952
Marikina	1.969	1.584	0.022	1934	Rabor 1952
Marikina	1.952	1.589	0.041	1934	Rabor 1952
Marikina	1.975	1.598	0.031	1934	Rabor 1952
Marikina	1.974	1.615	0.049	1934	Rabor 1952
Marikina	1.912	1.553	0.038	1934	Rabor 1952
Marikina	1.993	1.635	0.053	1934	Rabor 1952
Marikina	1.918	1.517	-0.003	1934	Rabor 1952
Marikina	1.958	1.563	0.010	1934	Rabor 1952
Los Baños	2.120	1.630	-0.057	1934	Rabor 1952
Los Baños	2.032	1.660	0.046	1934	Rabor 1952
Los Baños	1.956	1.589	0.038	1934	Rabor 1952
Los Baños	1.957	1.558	0.006	1934	Rabor 1952
Los Baños	1.998	1.622	0.036	1934	Rabor 1952
Los Baños	1.943	1.573	0.033	1934	Rabor 1952
Los Baños	1.997	1.562	-0.023	1934	Rabor 1952
Los Baños	1.970	1.597	0.034	1934	Rabor 1952
Los Baños	2.061	1.623	-0.015	1934	Rabor 1952
Los Baños	2.000	1.602	0.014	1934	Rabor 1952
Los Baños	2.041	1.602	-0.020	1934	Rabor 1952
Los Baños	2.021	1.544	-0.061	1934	Rabor 1952
Los Baños	2.063	1.602	-0.038	1934	Rabor 1952
Los Baños	2.058	1.659	0.023	1934	Rabor 1952
Los Baños	1.975	1.588	0.021	1934	Rabor 1952
Los Baños	2.074	1.605	-0.044	1934	Rabor 1952
Los Baños	2.020	1.638	0.034	1934	Rabor 1952
Los Baños	1.991	1.607	0.027	1934	Rabor 1952
Los Baños	1.979	1.606	0.036	1934	Rabor 1952
Los Baños	1.975	1.604	0.037	1934	Rabor 1952
Los Baños	2.017	1.640	0.038	1934	Rabor 1952
Los Baños	1.993	1.607	0.025	1934	Rabor 1952
Los Baños	2.040	1.617	-0.004	1934	Rabor 1952
Los Baños	2.008	1.617	0.023	1934	Rabor 1952
Los Baños	2.042	1.654	0.032	1934	Rabor 1952
Los Baños	2.014	1.632	0.033	1934	Rabor 1952
Los Baños	2.059	1.643	0.007	1934	Rabor 1952
Los Baños	1.988	1.617	0.039	1934	Rabor 1952
Los Baños	2.009	1.609	0.014	1934	Rabor 1952
Los Baños	2.012	1.615	0.017	1934	Rabor 1952
Los Baños	2.000	1.627	0.039	1934	Rabor 1952

Los Baños	2.013	1.643	0.045	1934	Rabor 1952
Los Baños	1.978	1.600	0.031	1934	Rabor 1952
Los Baños	1.972	1.606	0.042	1934	Rabor 1952
Los Baños	1.996	1.602	0.018	1934	Rabor 1952
Los Baños	1.977	1.604	0.035	1934	Rabor 1952
Los Baños	2.038	1.639	0.020	1934	Rabor 1952
Los Baños	1.991	1.606	0.026	1934	Rabor 1952
Los Baños	1.933	1.531	-0.001	1934	Rabor 1952
Los Baños	1.995	1.614	0.031	1934	Rabor 1952
Cavite	2.033	1.587	-0.028	1940	Rabor 1952
Cavite	2.105	1.615	-0.060	1940	Rabor 1952
Cavite	2.064	1.625	-0.016	1940	Rabor 1952
Cavite	2.139	1.744	0.041	1940	Rabor 1952
Cavite	1.970	1.798	0.235	1940	Rabor 1952
Cavite	1.989	1.625	0.046	1940	Rabor 1952
Cavite	1.998	1.511	-0.075	1940	Rabor 1952
Cavite	2.116	1.683	-0.001	1940	Rabor 1952
Cavite	2.029	1.627	0.015	1940	Rabor 1952
Cavite	2.091	1.631	-0.032	1940	Rabor 1952
Cavite	1.992	1.584	0.003	1940	Rabor 1952
Cavite	2.078	1.713	0.061	1940	Rabor 1952
Cavite	2.036	1.639	0.022	1940	Rabor 1952
Cavite	2.066	1.667	0.025	1940	Rabor 1952
Cavite	1.965	1.567	0.008	1940	Rabor 1952
Cavite	1.993	1.594	0.012	1940	Rabor 1952
Cavite	2.079	1.681	0.028	1940	Rabor 1952
Cavite	1.988	1.613	0.035	1940	Rabor 1952
Cavite	2.008	1.623	0.029	1940	Rabor 1952
Cavite	2.080	1.667	0.013	1940	Rabor 1952
Cavite	2.041	1.648	0.026	1940	Rabor 1952
Cavite	2.027	1.621	0.011	1940	Rabor 1952
Cavite	2.053	1.638	0.007	1940	Rabor 1952
Cavite	1.993	1.638	0.056	1940	Rabor 1952
Cavite	1.905	1.494	-0.015	1940	Rabor 1952
Cavite	2.045	1.648	0.023	1940	Rabor 1952
Cavite	1.944	1.548	0.007	1940	Rabor 1952
Cavite	1.972	1.575	0.011	1940	Rabor 1952
Cavite	2.059	1.662	0.026	1940	Rabor 1952
Cavite	2.039	1.641	0.021	1940	Rabor 1952
Isabela	2.176	1.747	0.014	1960	Espiritu 1985
Isabela	1.876	1.431	-0.054	1960	Espiritu 1985
Isabela	2.099	1.692	0.022	1960	Espiritu 1985
Isabela	2.096	1.692	0.025	1960	Espiritu 1985
Isabela	1.792	1.346	-0.069	1960	Espiritu 1985
Isabela	1.881	1.450	-0.039	1960	Espiritu 1985
Isabela	1.648	1.212	-0.084	1960	Espiritu 1985
Isabela	1.865	1.474	-0.002	1960	Espiritu 1985
Isabela	2.117	1.655	-0.029	1960	Espiritu 1985
Isabela	2.090	1.638	-0.024	1960	Espiritu 1985
Isabela	1.974	1.481	-0.085	1960	Espiritu 1985
Isabela	1.899	1.464	-0.040	1960	Espiritu 1985
Isabela	1.987	1.551	-0.026	1960	Espiritu 1985
Isabela	2.061	1.618	-0.020	1960	Espiritu 1985
Isabela	1.950	1.497	-0.049	1960	Espiritu 1985
Isabela	2.057	1.604	-0.031	1960	Espiritu 1985
Isabela	2.150	1.715	0.003	1960	Espiritu 1985
Isabela	2.073	1.649	0.001	1960	Espiritu 1985
Isabela	1.988	1.531	-0.047	1960	Espiritu 1985
Isabela	2.059	1.639	0.003	1960	Espiritu 1985
Isabela	2.111	1.677	-0.002	1960	Espiritu 1985

Isabela	2.149	1.726	0.015	1960	Espiritu 1985
Isabela	2.077	1.677	0.026	1960	Espiritu 1985
Isabela	1.903	1.481	-0.026	1960	Espiritu 1985
Isabela	1.939	1.477	-0.060	1960	Espiritu 1985
Isabela	1.944	1.473	-0.068	1960	Espiritu 1985
Isabela	1.960	1.526	-0.029	1960	Espiritu 1985
Isabela	1.903	1.442	-0.065	1960	Espiritu 1985
Cagayan	1.902	1.441	-0.066	1960	Espiritu 1985
Cagayan	2.023	1.591	-0.016	1960	Espiritu 1985
Cagayan	2.101	1.645	-0.026	1960	Espiritu 1985
Cagayan	1.918	1.481	-0.039	1960	Espiritu 1985
Cagayan	1.870	1.418	-0.062	1960	Espiritu 1985
Cagayan	1.863	1.444	-0.030	1960	Espiritu 1985
Cagayan	1.884	1.446	-0.046	1960	Espiritu 1985
Cagayan	1.877	1.439	-0.047	1960	Espiritu 1985
Cagayan	1.844	1.415	-0.044	1960	Espiritu 1985
Cagayan	1.922	1.531	0.008	1960	Espiritu 1985
Cagayan	1.975	1.544	-0.023	1960	Espiritu 1985
Cagayan	2.045	1.606	-0.019	1960	Espiritu 1985
Cagayan	2.022	1.604	-0.002	1960	Espiritu 1985
Cagayan	1.905	1.599	0.090	1960	Espiritu 1985
Cagayan	2.053	1.433	-0.198	1960	Espiritu 1985
Cagayan	2.031	1.602	-0.011	1960	Espiritu 1985
Cagayan	1.989	1.581	0.002	1960	Espiritu 1985

NEGROS

Bacong	2.047	1.644	0.017	1935	Rabor 1952
Bacong	2.150	1.700	-0.012	1935	Rabor 1952
Bacong	2.060	1.668	0.031	1935	Rabor 1952
Bacong	2.061	1.581	-0.057	1935	Rabor 1952
Bacong	2.005	1.548	-0.044	1935	Rabor 1952
Bacong	1.993	1.573	-0.009	1935	Rabor 1952
Bacong	2.075	1.643	-0.007	1935	Rabor 1952
Bacong	2.014	1.607	0.008	1935	Rabor 1952
Bacong	2.043	1.629	0.006	1935	Rabor 1952
Bacong	2.035	1.610	-0.007	1935	Rabor 1952
Bacong	2.034	1.572	-0.044	1935	Rabor 1952
Bacong	2.048	1.577	-0.050	1935	Rabor 1952
Bacong	2.031	1.588	-0.025	1935	Rabor 1952
Bacong	2.033	1.627	0.012	1935	Rabor 1952
Bacong	1.992	1.544	-0.037	1935	Rabor 1952
Bacong	1.955	1.497	-0.053	1935	Rabor 1952
Bacong	2.002	1.624	0.035	1935	Rabor 1952
Bacong	1.974	1.544	-0.022	1935	Rabor 1952
Bacong	2.006	1.574	-0.019	1935	Rabor 1952
Bacong	2.057	1.610	-0.025	1935	Rabor 1952
Bacong	1.980	1.577	0.006	1935	Rabor 1952
Bacong	2.001	1.559	-0.029	1935	Rabor 1952
Bacong	2.029	1.556	-0.056	1935	Rabor 1952
Bacong	2.004	1.528	-0.063	1935	Rabor 1952
Bacong	2.006	1.593	0.000	1935	Rabor 1952
Bacong	1.915	1.389	-0.128	1935	Rabor 1952
Bacong	2.039	1.533	-0.087	1935	Rabor 1952
Bacong	1.929	1.491	-0.038	1935	Rabor 1952
Bacong	2.030	1.618	0.006	1935	Rabor 1952
Bacong	1.980	1.636	0.065	1935	Rabor 1952
Dumaguete	1.931	1.539	0.008	1935	Rabor 1952
Dumaguete	1.932	1.535	0.004	1935	Rabor 1952
Dumaguete	1.922	1.561	0.038	1935	Rabor 1952
Dumaguete	1.912	1.504	-0.011	1935	Rabor 1952

Dumaguete	1.878	1.471	-0.016	1935	Rabor 1952
Dumaguete	1.880	1.480	-0.008	1935	Rabor 1952
Dumaguete	1.922	1.532	0.009	1935	Rabor 1952
Dumaguete	1.917	1.516	-0.003	1935	Rabor 1952
Dumaguete	1.936	1.564	0.029	1935	Rabor 1952
Dumaguete	1.901	1.531	0.025	1935	Rabor 1952
Dumaguete	1.813	1.380	-0.053	1935	Rabor 1952
Bacolod	2.002	1.602	0.013	1935	Rabor 1952
Bacolod	1.973	1.604	0.039	1935	Rabor 1952
Bacolod	2.006	1.682	0.089	1935	Rabor 1952
Bacolod	2.166	1.744	0.019	1935	Rabor 1952
Bacolod	2.058	1.632	-0.004	1935	Rabor 1952
Bacolod	2.009	1.593	-0.002	1935	Rabor 1952
Bacolod	2.079	1.716	0.063	1935	Rabor 1952
Bacolod	2.076	1.671	0.020	1935	Rabor 1952
Bacolod	1.995	1.597	0.014	1935	Rabor 1952
Bacolod	2.034	1.606	-0.010	1935	Rabor 1952
Bacolod	2.049	1.649	0.021	1935	Rabor 1952
Bacolod	2.064	1.672	0.031	1935	Rabor 1952
Bacolod	2.049	1.683	0.055	1935	Rabor 1952
Bacolod	2.037	1.650	0.032	1935	Rabor 1952
Bacolod	2.002	1.601	0.012	1935	Rabor 1952
PANAY					
Pandan	2.204	1.699	-0.057	1936–1939	Rabor 1952
Pandan	2.255	1.778	-0.021	1936–1939	Rabor 1952
Pandan	2.230	1.778	0.000	1936–1939	Rabor 1952
Pandan	2.146	1.699	-0.009	1936–1939	Rabor 1952
Pandan	2.097	1.602	-0.066	1936–1939	Rabor 1952
Pandan	2.217	1.699	-0.068	1936–1939	Rabor 1952
Pandan	1.954	1.477	-0.073	1936–1939	Rabor 1952
Pandan	2.021	1.602	-0.003	1936–1939	Rabor 1952
Pandan	2.176	1.699	-0.034	1936–1939	Rabor 1952
Pandan	2.190	1.699	-0.046	1936–1939	Rabor 1952
Pandan	2.079	1.663	0.010	1936–1939	Rabor 1952
Pandan	2.021	1.580	-0.025	1936–1939	Rabor 1952
Pandan	2.041	1.623	0.001	1936–1939	Rabor 1952
Pandan	2.041	1.580	-0.042	1936–1939	Rabor 1952
Pandan	2.041	1.580	-0.042	1936–1939	Rabor 1952
Pandan	2.000	1.556	-0.032	1936–1939	Rabor 1952
Pandan	2.000	1.556	-0.032	1936–1939	Rabor 1952
Pandan	1.954	1.519	-0.031	1936–1939	Rabor 1952
Pandan	1.954	1.544	-0.006	1936–1939	Rabor 1952
Pandan	2.000	1.580	-0.008	1936–1939	Rabor 1952
Pandan	2.086	1.602	-0.057	1936–1939	Rabor 1952
Pandan	2.061	1.580	-0.058	1936–1939	Rabor 1952
Pandan	2.107	1.633	-0.043	1936–1939	Rabor 1952
Pandan	2.021	1.623	0.018	1936–1939	Rabor 1952
Pandan	2.097	1.653	-0.015	1936–1939	Rabor 1952
Pandan	2.114	1.653	-0.029	1936–1939	Rabor 1952
Pandan	2.097	1.580	-0.088	1936–1939	Rabor 1952
Pandan	2.079	1.580	-0.073	1936–1939	Rabor 1952
Pandan	2.033	1.556	-0.059	1936–1939	Rabor 1952
Pandan	2.079	1.580	-0.073	1936–1939	Rabor 1952
Pandan	2.210	1.740	-0.021	1936–1939	Rabor 1952
CEBU					
Argao	2.079	1.653	0.000	1968	CAS <sup>a</sup>
Argao	2.061	1.663	0.025	1968	CAS
Argao	2.079	1.663	0.010	1968	CAS

Argao	2.137	1.681	-0.020	1968	CAS
Argao	2.130	1.663	-0.032	1968	CAS
Argao	2.041	1.643	0.021	1968	CAS
Argao	2.033	1.613	-0.002	1968	CAS
Argao	2.004	1.613	0.022	1968	CAS
Argao	2.083	1.653	-0.003	1968	CAS
Argao	2.064	1.613	-0.028	1968	CAS
Argao	2.104	1.681	0.007	1968	CAS
Argao	2.033	1.633	0.018	1968	CAS
Argao	2.137	1.699	-0.002	1968	CAS
Argao	2.079	1.643	-0.010	1968	CAS
Argao	2.029	1.653	0.041	1968	CAS
Argao	2.021	1.623	0.018	1968	CAS
Argao	2.037	1.623	0.005	1968	CAS
Argao	2.061	1.633	-0.005	1968	CAS
Argao	2.033	1.623	0.008	1968	CAS
BOHOL					
Tagbilaran	2.018	1.606	0.003	No data	
Tagbilaran	2.028	1.626	0.015	No data	
Tagbilaran	2.015	1.609	0.009	No data	
Tagbilaran	2.009	1.634	0.039	No data	
Tagbilaran	2.043	1.653	0.030	No data	
Tagbilaran	2.027	1.666	0.056	No data	
Tagbilaran	2.015	1.604	0.004	No data	
Tagbilaran	2.002	1.643	0.054	No data	
Tagbilaran	2.014	1.588	-0.011	No data	
Tagbilaran	2.003	1.568	-0.022	No data	
Tagbilaran	2.030	1.635	0.023	No data	
Tagbilaran	1.999	1.573	-0.014	No data	
Tagbilaran	2.000	1.582	-0.006	No data	
Tagbilaran	2.018	1.623	0.020	No data	
Tagbilaran	2.052	1.649	0.018	No data	
Tagbilaran	2.033	1.621	0.006	No data	
Tagbilaran	2.009	1.563	-0.032	No data	
Tagbilaran	2.022	1.652	0.046	No data	
Tagbilaran	2.000	1.534	-0.054	No data	
Tagbilaran	2.035	1.610	-0.007	No data	
LEYTE					
Baybay	1.954	1.508	-0.042	No data	
Baybay	1.934	1.508	-0.025	No data	
Baybay	2.190	1.777	0.032	No data	
Baybay	2.170	1.727	-0.001	No data	
Baybay	2.090	1.663	0.001	No data	
Baybay	2.009	1.597	0.002	No data	
Baybay	1.934	1.508	-0.025	No data	
Baybay	2.053	1.688	0.057	No data	
MINDANAO					
Iligan	1.972	1.612	0.048	No data <sup>b</sup>	
Iligan	1.917	1.550	0.031	No data	
Iligan	1.974	1.613	0.047	No data	
Iligan	1.967	1.584	0.024	No data	
Iligan	1.977	1.598	0.029	No data	
Iligan	1.972	1.575	0.011	No data	
Iligan	1.997	1.603	0.018	No data	
Iligan	1.955	1.597	0.047	No data	
Iligan	1.963	1.561	0.004	No data	
Iligan	1.939	1.532	-0.005	No data	

Iligan	1.962	1.563	0.007	No data
Iligan	1.938	1.558	0.022	No data
Iligan	1.968	1.592	0.031	No data
Iligan	1.907	1.535	0.024	No data
Iligan	1.919	1.535	0.014	No data
Iligan	1.884	1.479	-0.013	No data
Iligan	1.882	1.483	-0.007	No data
Iligan	1.963	1.570	0.013	No data
Iligan	1.911	1.552	0.038	No data
Iligan	1.849	1.476	0.013	No data
Iligan	1.915	1.499	-0.018	No data
Iligan	1.988	1.614	0.036	No data
Iligan	1.952	1.557	0.009	No data
Iligan	1.901	1.543	0.037	No data
Iligan	1.936	1.567	0.032	No data
Iligan	1.927	1.566	0.039	No data
Iligan	1.900	1.512	0.007	No data
Iligan	1.931	1.533	0.002	No data
Iligan	1.900	1.512	0.007	No data
Iligan	1.906	1.544	0.034	No data
Iligan	1.912	1.494	-0.021	No data
Malagos	2.068	1.646	0.002	No data
Davao	2.051	1.679	0.049	No data
Davao	2.013	1.630	0.032	No data
Davao	1.883	1.476	-0.015	No data
Davao	2.107	1.710	0.034	No data
Davao	1.902	1.530	0.023	No data
Davao	1.967	1.597	0.037	No data
Davao	1.981	1.584	0.012	No data
Davao	1.901	1.467	-0.039	No data

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<sup>a</sup> Data from the California Academy of Sciences herpetological registry.

<sup>b</sup> Rabor (1952) mentioned that *Bufo marinus* was introduced to Cotabato Province in southern Mindanao in 1949.