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CONSERVATION OF HERPETOFAUNAL COMMUNITIES IN FRAGMENTED LOWLAND RAINFORESTS IN THE PHILIPPINES

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SUMMARY

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. Through strip transects, I characterized patterns of species richness and endemism, abundance, distribution, and ecological guilds between the herpetofauna in a contiguous forest and 10 forest fragments in response to forest loss and other anthropogenic disturbance. An information theoretic approach helped us identify correlates of extinction proneness by examining a combination of ecological and life history variables. Microclimate and habitat structure significantly influenced the observed patterns of herpetofaunal distribution. The fauna in forest fragments consisted of subsets of the species pool in contiguous forest. Frogs, lizards, and snakes responded variedly to fragmentation, which is attributed to differences in their ecological guilds and life history traits. Fragments tend to support higher densities of lizards. In contrast to other studies, the results of this study indicate that large body size is not an important correlate of extinction risk in the herpetofauna. Forest fragmentation resulted in a cascading loss of species and had profound effects on the community structure of the herpetofauna. Species extinctions in the fragments ranged from 15% to as high as 94% of the species found in contiguous forest. Snakes manifested the sharpest decline in richness and abundance and are the most sensitive to habitat transformation compared with frogs and lizards. I classified 48 species that are vulnerable to extinction and identified reproductive mode as an important trait to predict extinction proneness. Although the preservation of large forest areas is the best strategy to maintain herpetofaunal diversity, habitat 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.

INTRODUCTION

Habitat fragmentation is among the greatest threat 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 imperilled (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; Alcala et al. 2004).

Of the countries in the region, the Philippines has likely suffered the most devastating consequences of large-scale deforestation. 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 centres 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. 2002b). The Global Amphibian Assessment (IUCN, Conservation International, and NatureServe 2006) 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. 2002b; 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.

METHODS

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. 1). 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 1000 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). Climate varies markedly on either side of the range. The east slope is predominantly wet throughout the year with annual rainfall of 2500–5000 mm. The west slope has a pronounced dry season (December to May) and an average annual rainfall of 2000 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, harbouring 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$_2$ of forest annually. By 1981 over 80% of its lowland forest has been logged (Tan 2000; van den Top 2003). The Philippine government instated 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).

Forest sites

The study encompassed 11 sites in lowland dipterocarp forest (Whitmore 1998) on the west slope of the Sierra Madres (Fig. 1, Table 1). 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 centres surrounds the ten study fragments. Forest re-growth 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 isolates 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).

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 1). 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 behaviour 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 = 400–1000, 3 = > 1000), classified according to sex and age, and released at sites of capture. Frog advertisement calls were recorded to aid in species identification. Nomenclature follows Alcala (1986), the Global Amphibian Assessment (http://www.globalamphibians.org/), and the Reptile Database (http://reptiledatabase. org/).

Transect sampling detected 95% (81of 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), I collected voucher specimens (as per stipulated protocols detailed in research and collecting permits granted by the Philippine wildlife authority) that represented un-described 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.

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), understory 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_2 plots that were randomly placed within the same points. Understory density was estimated by recording the number of contacts between a 5-m vertical pole and understory 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 1).

Ecological correlates of extinction-prone species

I determined the correlates of extinction proneness of species by examining their 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 1); (3) were rare based on an index of rarity (Watling & Donnelly 2007); (3) fragmentation-sensitive (Fig. 2); and (4) were extirpated in ≥ 50% of the fragments (Appendix 1). 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 2004). 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 2). 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 = non-extinction- 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 modelled 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, I restricted the *a priori* model set to include seven models that best represented thematic hypothesis to test (Table 3). 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*c*) 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).

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 (± SE) generated from various non-parametric estimators was used as a measure of the overall herpetofaunal richness of each forest site (Table 4). 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 1000 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).

RESULTS

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 & Alcala 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 2004; CITES 2005), some of which occurs in the forest fragments (Appendix 1). 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 chinensis*; both are invasive alien species in the Philippines (Diesmos et al. 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 4). 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. 3a, 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. 4a). 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 4). The proportion of endemic species and abundance similarly showed a linear relationship with area (Fig. 4b, 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.

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.3c, Fig. 5a). 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. 5b) 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. 5c). Vertical stratum distributions shifted between forest sites for some groups (Fig. 5d). 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 ($T = 16.8°$, $p = 7.17 \times 10^{-6}$ for frogs; $T = 23.2°$, $p = 6.13 \times 10^{-8}$ for lizards; $T = 13.5°$, $p = 2.30 \times 10^{-4}$ 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. 6a; MRPP pair wise comparison tests, $p < 0.001$). The herpetofauna (Fig. 6b) 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 (Table 2). 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 2). 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.

Extinction-proneness

I identified reproductive development mode as the most significant predictor of extinction proneness of the herpetofauna (Table 5). The most parsimonious model exhibited a remarkable *w*AIC*c* of 57.4%, which explained 7.3% of the variation in the probability of extinction. The next highest-ranked model (*w*AIC*c* = 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 (*w*AIC*c* < 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 2). 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 2004; Stuart et al. 2004). I excluded these traits from the analysis to avoid potential circularity in explaining for extinction proneness.

DISCUSSION

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 (≤ 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. 6). 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. 5d) 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 harboured 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 2005), 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. 5a, 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 (≥ 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 we 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. 5c), 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. 4) 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.

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; Alcala 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.

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. 2002a; 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.

Conservation implications

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.

I have shown that localized extinctions of herpetofaunal species are an inevitable consequence of forest fragmentation. Patches below 1000 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 (FAO 2005; Laurance & Peres 2006; Sodhi & Brook 2006).

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Table 1. Description of the study sites 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	17º01’43” N, 122º11’37” E; 17º00’55” N, 122º12’13” E	5000 plots	150–350	–	–	25 (2.5)	1.17	0.07
1	Nassiping	17º58’12” N, 122º39’12” E	700	10–60	1970	37	11 (1.1)	1.47	0.15
2	Dunoy	16º59’34” N, 122º09’24” E	650	150–300	1990	4	11 (1.1)	1.13	0.05
3	Binatug	16º57’15” N, 122º04’01” E	10	100–160	1980	14.9	6 (0.6)	1.33	0.07
4	Del Pilar	16º51’33” N, 122º06’19” E	9	150–260	1980	3.2	6 (0.6)	1.11	0.67
5	Maldam	16º56’18” N, 122º03’20” E	5	100–150	1990	13	5 (0.5)	1.08	0.11
6	Puerta	17º25’34” N, 121º55’04” E	4	150–200	1990	2	4 (0.4)	0.33	0.15
7	San Jose 2	16º56’12” N, 122º07’45” E	2.5	150–190	1990	4.1	3 (0.3)	1.15	0.30
8	Garita	17º24’25” N, 121º49’11” E	2	40–70	1970	15	3 (0.3)	0.75	0.44
9	San Jose 1	16º56’03” N, 122º07’39” E	1.5	150–190	1990	4.1	2 (0.2)	1.07	0.22
10	Alibadabad	16º57’48” N, 122º02’46” E	0.5	85–100	1980	14.2	1 (0.1)	1.02	0.10

Table 2. 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	*Kaloula kalingensis*	2	1.52	1	0.06	3	2	3	1
F2	*Kaloula picta*	1	1.63	1	0.10	1	1	1	0
F3	*Kaloula rigida*	2	1.64	1	0.05	1	1	1	1
F4	*Fejervarya vittigera*	1	1.88	1	0.04	1	1	2	0
F5	*Limnonectes macrocephalus*	2	1.98	1	0.04	1	1	2	1
F6	*Limnonectes woodworthi*	2	1.81	1	0.19	1	1	2	0
F7	*Limnonectes* sp.	2	1.88	1	0.16	1	1	2	0
F8	*Occidozyga* cf. *laevis*	0	1.61	1	0.19	1	1	2	0
F9	*Platymantis cornutus*	2	1.48	3	0.05	3	2	3	1
F10	*Platymantis corrugatus*	1	1.57	3	0.08	2	1	1	1
F11	*Platymantis luzonensis*	2	1.54	3	0.06	3	2	3	1
F12	*Platymantis pygmaeus*	2	1.11	3	0.26	2	1	1	1
F13	*Platymantis taylori*	2	1.46	3	0.27	2	1	1	1
F14	*Platymantis* sp. A	2	1.45	3	0.19	2	1	1	1
F15	*Platymantis* sp. B	2	1.28	3	0.18	2	1	1	1
F16	*Platymantis* sp. C	2	1.43	3	0.65	2	1	1	0
F17	*Platymantis* sp. D	2	1.57	3	0.22	2	1	1	1
F18	*Platymantis* sp. E	2	1.45	3	0.22	2	1	1	1
F19	*Rana luzonensis*	2	1.64	1	0.04	1	3	2	1
F20	*Rana similis*	2	1.69	1	0.13	1	1	2	1
F21	*Polypedates leucomystax*	0	1.79	1	0.36	1	3	3	0
F22	*Rhacophorus pardalis*	0	1.64	1	0.06	1	3	3	1
L1	*Bronchocela cristatella*	0	2.01	1	0.01	2	3	3	0
L2	*Draco spilopterus*	1	1.82	1	0.19	2	2	3	0
L3	*Cyrtodactylus philippinicus*	1	1.93	1	0.09	2	3	3	1
L4	*Gehyra mutilata*	0	1.74	1	0.03	2	3	3	0
L5	*Gekko gecko*	0	2.13	1	0.03	3	3	3	0
L6	*Gekko monarchus*	0	1.89	1	0.05	3	3	3	0
L7	*Hemidactylus frenatus*	0	1.70	1	0.06	3	3	3	0

L8	*Hemidactylus stejnegeri*	0	1.74	1	0.01	3	3	3	0
L9	*Lepidodactylus* cf. *planicaudus*	1	1.57	1	0.05	3	3	3	1
L10	*Luperosaurus kubli*	2	2.02	1	0.03	3	2	3	1
L11	*Brachymeles bicolor*	2	2.13	2	0.08	2	1	1	1
L12	*Brachymeles bonitae*	1	1.86	2	0.08	2	1	1	1
L13	*Brachymeles b. boulengeri*	2	2.00	2	0.18	2	1	1	0
L14	*Brachymeles talinis*	1	1.75	2	0.06	2	1	1	1
L15	*Brachymeles* sp.	2	1.58	2	0.04	2	1	1	1
L16	*Eutropis cumingi*	0	1.72	1	0.18	2	1	1	1
L17	*Eutropis m. borealis*	1	1.83	1	0.68	2	1	1	0
L18	*Eutropis multifasciata*	0	2.03	1	0.23	2	1	1	0
L19	*Lamprolepis s. philippinica*	1	2.00	1	0.10	3	3	3	0
L20	*Lipinia* cf. *vulcania*	1	1.58	1	0.01	3	2	3	1
L21	*Sphenomorphus cumingi*	1	2.08	1	0.04	2	1	1	1
L22	*Sphenomorphus decipiens*	1	1.58	1	0.21	2	1	1	0
L23	*Sphenomorphus jagori*	1	1.91	1	0.30	2	1	1	0
L24	*Sphenomorphus leucospilos*	2	1.66	1	0.08	2	1	2	1
L25	*Sphenomorphus steerei*	1	1.58	1	0.42	2	1	1	0
L26	*Sphenomorphus* sp.	2	1.43	1	0.13	2	1	1	1
L27	*Tropidophorus grayi*	1	2.01	2	0.01	2	1	2	1
L28	*Varanus olivaceus*	2	2.71	1	0.01	3	3	3	1
L29	*Varanus s. marmoratus*	1	2.70	1	0.14	2	3	1	0
S1	*Ramphotyphlops braminus*	0	2.13	1	0.04	2	1	1	0
S2	*Typhlops* cf. *luzonensis*	1	2.33	1	0.05	2	1	1	1
S3	*Python reticulatus*	0	3.60	1	0.03	2	3	1	0
S4	*Ahaetulla p. preocularis*	1	2.85	1	0.05	3	2	3	0
S5	*Boiga angulata*	1	3.10	1	0.01	3	3	3	1
S6	*Boiga d. divergens*	2	3.00	1	0.01	2	3	1	1
S7	*Boiga philippina*	1	3.04	1	0.03	3	3	3	1
S8	*Calamaria bitorques*	1	2.33	1	0.04	2	1	1	1
S9	*Calamaria gervaisii*	1	2.15	1	0.03	2	1	1	1
S10	*Coelognathus e. manillensis*	1	3.07	1	0.03	2	1	1	0
S11	*Cyclocorus lineatus*	1	2.55	1	0.08	2	1	1	1

S12	*Dendrelaphis c. luzonensis*	1	2.81	1	0.05	3	3	1	0
S13	*Dendrelaphis p. pictus*	1	2.74	1	0.03	3	1	1	1
S14	*Dryophiops philippina*	1	2.74	1	0.01	2	1	1	1
S15	*Gonyosoma oxycephalum*	0	2.90	1	0.01	3	3	3	0
S16	*Lycodon aulicus*	0	2.71	1	0.01	2	1	1	0
S17	*Lycodon muelleri*	2	2.61	1	0.04	2	3	2	1
S18	*Oligodon modestum*	1	2.43	1	0.01	2	1	1	1
S19	*Psammodynastes pulverulentus*	0	2.60	1	0.03	3	3	3	1
S20	*Pseudorabion oxycephalum*	1	2.36	1	0.13	2	1	1	1
S21	*Ptyas luzonensis*	1	3.03	1	0.04	3	3	1	1
S22	*Rhabdophis spilogaster*	2	2.67	1	0.12	2	1	2	1
S23	*Tropidonophis dendrophiops*	1	2.75	1	0.03	2	1	2	1
S24	*Hemibungarus calligaster*	2	2.70	1	0.01	2	1	1	1
S25	*Naja philippinensis*	2	3.00	1	0.01	2	1	1	0
S26	*Ophiophagus hannah*	0	3.40	1	0.01	2	1	1	1
S27	*Trimeresurus flavomaculatus*	1	2.82	1	0.08	3	3	3	1

Table 3. Generalized linear mixed-effects models 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 4. Species richness estimates (± 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 ± 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 ± 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 ± 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 ± 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 ± 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 ± 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 ± 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 ± 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 ± 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 ± 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 ± 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 ± 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 ± 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 ± 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 ± 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 ± 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 ± 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 ± 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 ± 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 ± 0.13	0.91
	Snakes	4	5	10.	11.5	5.5	5.1	6.3	7.4	5.0	14.6	15.2	8.5 ± 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 ± 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 ± 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 ± 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 ± 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 ± 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 ± 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	0.0	0.0	0.0	4.2 ± 0.92	n/a
	Lizards	7	17	7.3	7.0	7.3	7.0	7.0	0.0	0.0	0.0	0.0	5.0 ± 1.08	n/a
	Snakes	3	3	*	*	*	*	*	*	*	*	*	*	*

Table 5. 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 (∆AIC*c*), AIC*c* weight (*w*AIC*c*), and the percent deviance (%DE) explained in the response variable by the model under consideration.

Models	*k*	*-LL*	∆AIC*c*	*w*AIC*c*	%DE	∆%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

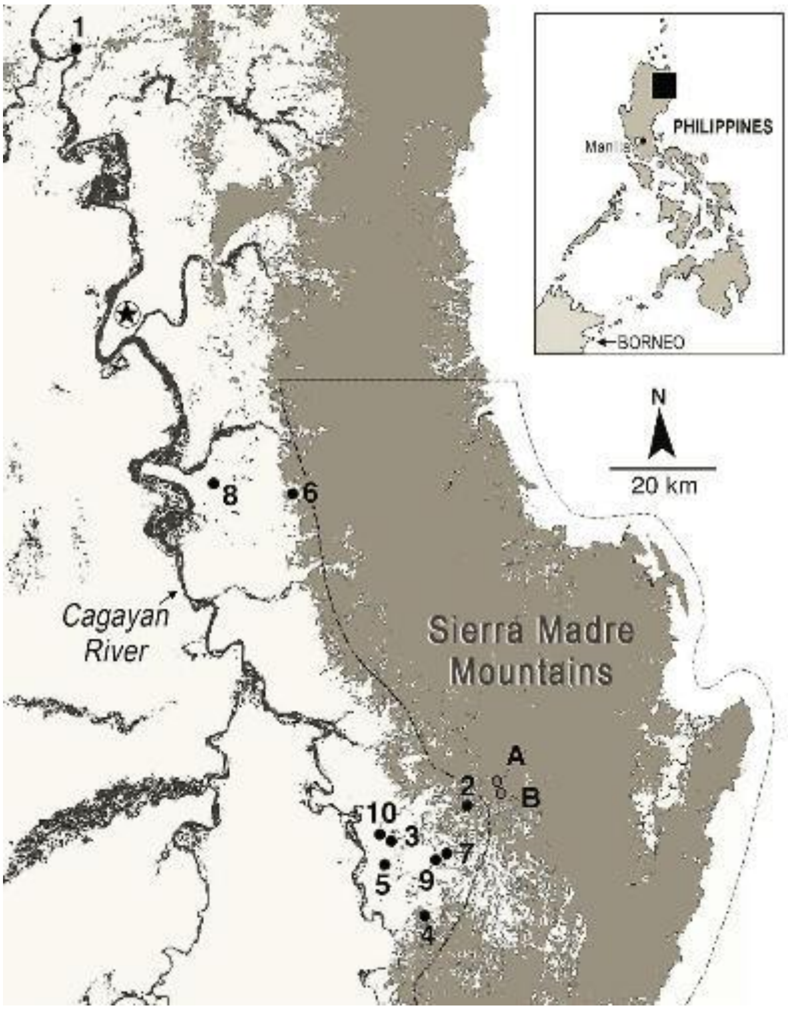

Figure 1. Location of the study fragments (solid circles 1–10) and the control site in continuous forest (open circles, plots A and B) on the west slopes of the Sierra Madre Mountains of Luzon Island, Republic of the Philippines. Study sites are described in Table 1. Gray-shaded areas represent the extent of forest, solid lines are river systems, and enclosed star depicts a major urban centre (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.

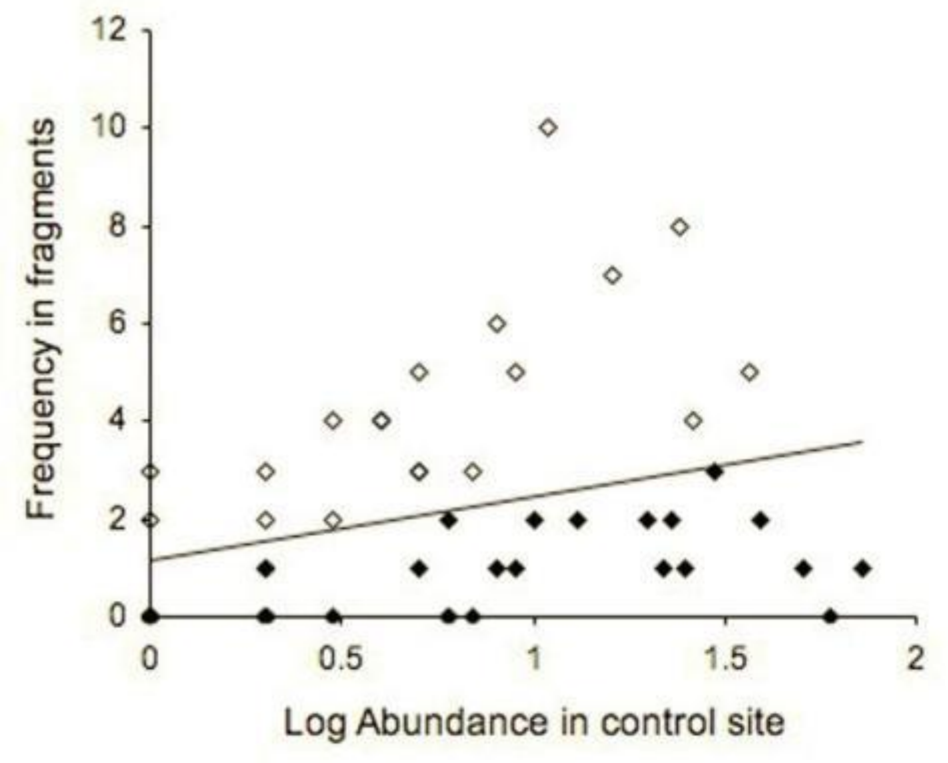

Figure 2. The plot shows a positive relationship between abundance ($\log_{10}$) of species in continuous forest and the number of fragments in which they occur ($R^2 = 0.09$, df = 48, $P = 0.035$), such that those species that are rare in the control site occurred in fewer fragments. Solid diamonds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

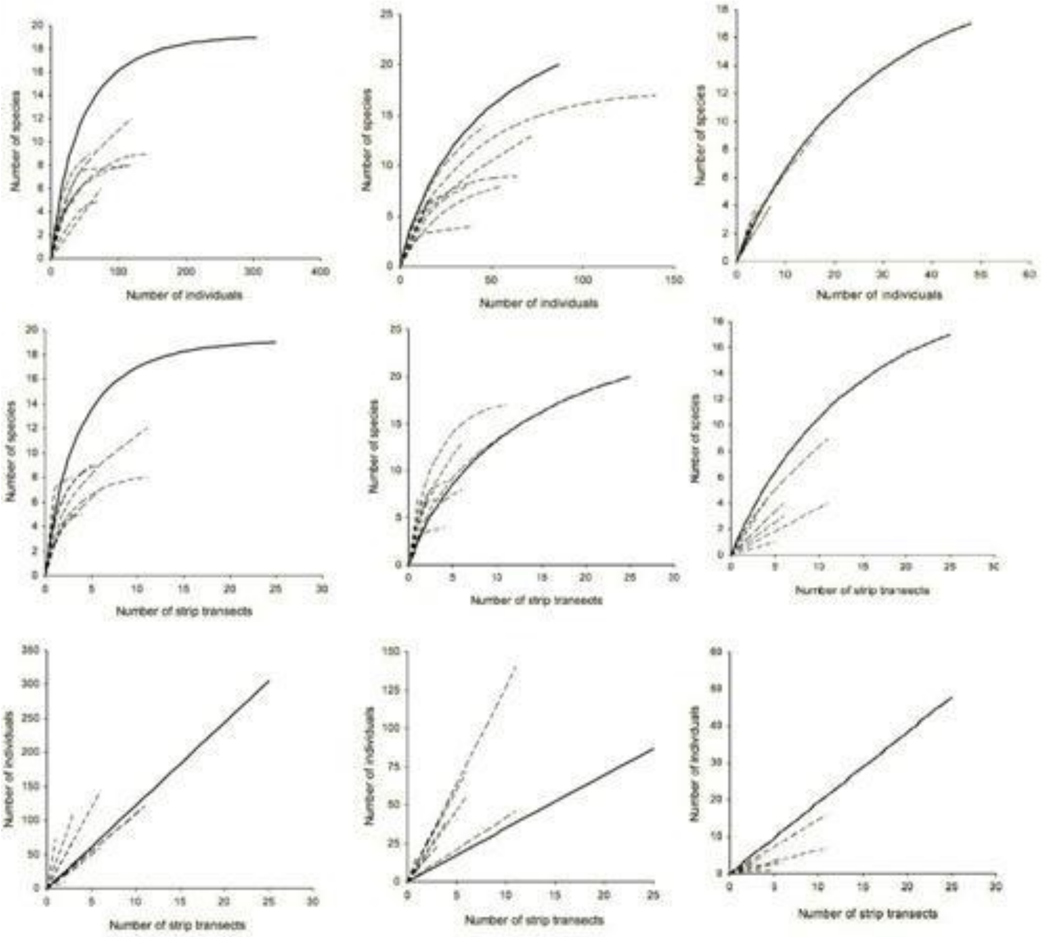

Figure 3. Individual-based species accumulation curves (A), species density (B), and population density (C) of frogs, snakes, and lizards in continuous forest (solid line) and forest fragments (dashed lines).

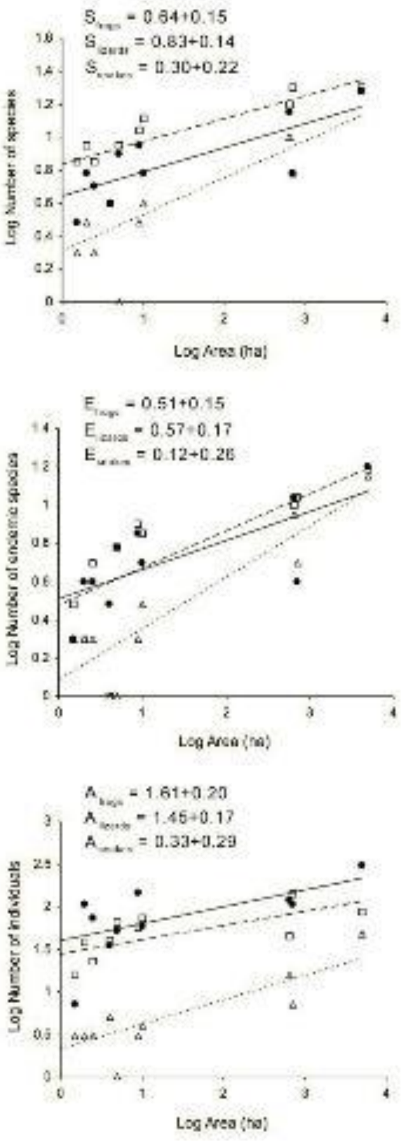

Figure 4. Univariate relationships between (A) complementary $\log_{10}$-$\log_{10}$ transformation of species richness and forest area, (B) number of endemic species and area, and (C) faunal abundance and area. Frogs = circles and solid lines, lizards = squares and dashed lines, snakes = triangles and dotted lines.

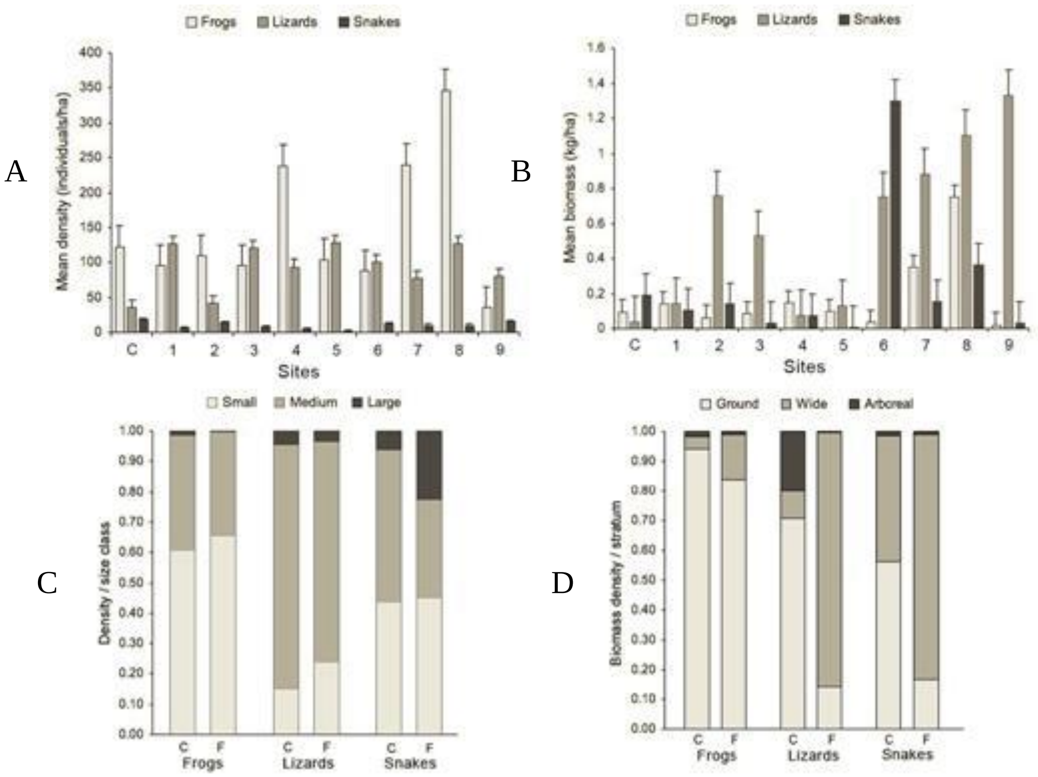

Figure 5. Population densities (A) and fresh biomass (B) of frogs, lizards, and snakes and their proportions (%) in body size classes (C) and vertical stratum distributions (D). One of the forest fragments (Site 10) was excluded because of the small sample size (*n* = 1). Bars represent the standard error.

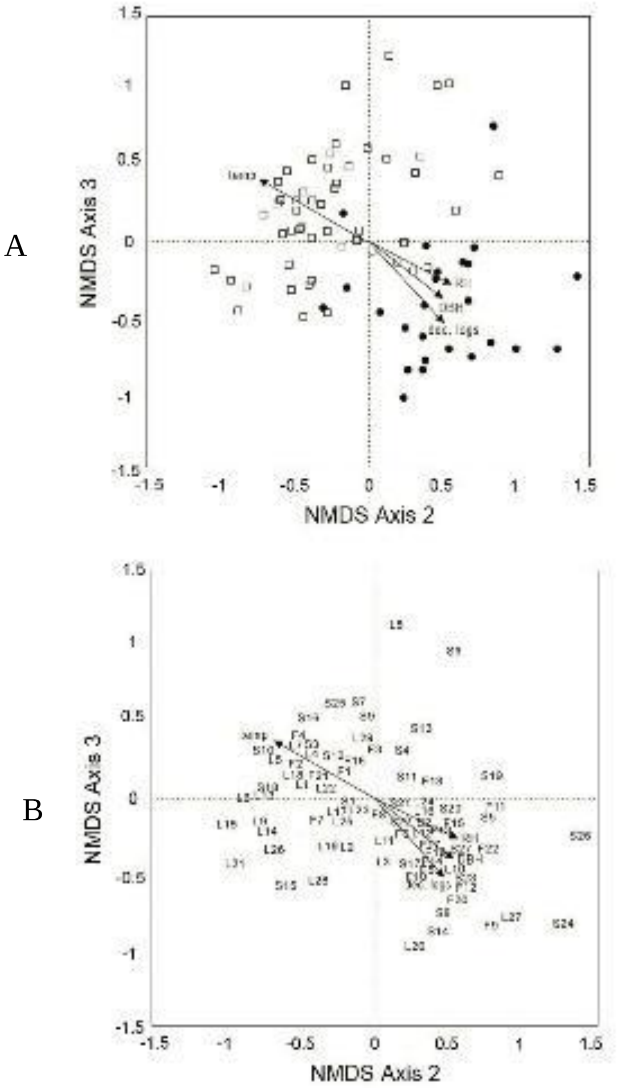

Figure 6. Non-metric multidimensional scaling plot of 77 locality scores (A; circles = continuous forest, squares = forest fragments) and 78 species scores (B; frogs = F1– F22, lizards = L1–L29, snakes = S1–S27) grouped by similarity in community composition. Overlaid were four ecological variables that strongly correlate with the ordination (temperature, relative humidity, mean DBH of trees, and mean number of decayed logs). Refer to Table 2 for the species codes.

Appendix 1. 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 2004). *Appendix* status is from CITES (2005).

Taxon	Mean Abundance / Site											Matrix tolerant?	No. of local extinctions	Range	Status
	C	1	2	3	4	5	6	7	8	9	10°				
AMPHIBIA															
Order Anura															
Bufonidae															
Bufo marinus (Linnaeus)	0	0.82	0	0.33	0	1.2	0.75	0	1	1.5	2	Yes	-	Widespread	Introduced species
Microhylidae															
Kaloula kalingensis Taylor	0	0	0	0.17	2.33	0	0	0	0.33	0	0	No	7	LE	VU; needs taxonomic study
K. picta (Duméril & Bibron)	0	0.10	0	0	0	0.4	0.25	0	0	0.05	1	Yes	-	PE	
K. rigida Taylor	0.04	0.18	0.18	0	0	0	0	0	0	0	0	No	8	LE	VU; needs taxonomic study
Ranidae															
Fejervarya cancrivora (Gravenhorst)	0	0	0	0	0	0	0	0	0	0	0	Yes	-	Asia	
F. vittigera (Wiegmann)	0	0	0	0	0	0	0	0	0	133	0	Yes	-	PE	
Hoplobatrachus chinensis (Osbeck)	0	0.64	0	0	0	0	0	0	2	0	9	Yes	-	Asia	Introduced species
Limnonectes macrocephalus (Inger)	0.20	0	0.27	0	0	0	0	0	0	0	0	No	9	LE	NT
L. woodworthi (Taylor)	1.12	0	0.18	0	2	1	0	9.33	0	0	8	Yes	5	LE	
Limnonectes sp.	0.16	2.45	0	0	0	0.6	0	0.67	12	0	0	Yes	6	LE	Probable new species
Occidozyga cf. *laevis* (Günther)	0.80	0.18	0	0	3	0.4	0	0	2	0	0	No	6	SE Asia	Needs taxonomic study
Platymantis cf. *cornutus* (Taylor)	0.24	0	0	0	0	0	0	0	0	0	0	No	10	LE	VU; needs taxonomic study
P. corrugatus (Duméril)	0.2	0	0	0.17	0	0	0	0	0	0	0	No	9	PE	
P. luzonensis Brown, Alcala, Diesmos & Alcala	0.24	0	0	0	0	0	0	0	0	0	0	No	10	LE	NT
P. pygmaeus Alcala, Brown & Diesmos	2.56	0	0.36	0	0	0	0	0	0	0	0	No	9	LE	VU
P. taylori Brown, Alcala & Diesmos	0.88	0	2.64	0.67	2.17	0.8	0	0	0	0	0	No	6	LE	EN
Platymantis sp. A	1.28	0	0.45	0	0	2.75	0	0	0	0	0	No	8	LE	New species
Platymantis sp. B	0.36	0	0.82	0	0.67	0	0	0	0	0	0	No	8	LE	New species
Platymantis sp. C	0.44	5.55	3.91	4.67	7.5	4.8	5.25	12.33	7.67	2.5	4.9	No	0	LE	New species
Platymantis sp. D	1	0	0.64	0	0.5	0	0	0.33	0	0	0	No	7	LE	New species
Platymantis sp. E	0.2	0	1.27	0	4.83	1.4	0	0	0	0	0	No	7	LE	New species

Rana luzonensis Boulenger	0.64	0	0	0	0	0	0	0	0	0	0	No	10	LE	NT
R. similis (Günther)	1.36	0	0	0	0	0	0	0	0	0	0	No	10	LE	NT
Rhacophoridae															
Polypedates leucomystax (Gravenhorst)	0.16	1	0.09	0	0.83	0.83	0.5	1.33	11.33	0.5	0	Yes	-	Asia	
Rhacophorus pardalis Günther	0.32	0	0.09	0	0	0	0	0	0	0	0	No	9	SE Asia	
REPTILIA															
Order Testudines															
Bataguridae															
Cuora amboinensis amboinensis (Daudin)	0.04	0.09	0.09	0.17	0	0.2	0	0	0.33	0	0	*b*	-	Asia	VU; Appendix II
Trionychidae															
Pelochelys cantorii 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															
Bronchocela cristatella (Kuhl)	0	0.27	0	0	0	0	0	0	0	0	0	No	9	SE Asia	
Draco spilopterus (Wiegmann)	0.2	0.45	0.27	0.33	0.33	0.4	0	0	0	0	0	No	5	PE	
Gekkonidae															
Cosymbotus platyurus (Schneider)	0	0	0	0	0	0	0	0	0.67	0	0	Yes	-	Asia	
Cyrtodactylus philippinicus (Steindachner)	0.12	0.18	0	0	0	0	0	0	0	0	0	No	8	PE	
Gehyra mutilata (Wiegmann)	0	0	0	0	0	0	0	0	0.33	0.5	0	Yes	-	Widespread	
Gekko gecko Linnaeus	0	0	0	0	0	0	0	0	0.67	0	0	Yes	-	Asia	
Gekko monarchus (Schlegel)	0.08	0.36	0	0.17	0	0	0	0	0	1	0	Yes	-	SE Asia	
Hemidactylus frenatus Schlegel	0	0	0	0.17	0	0.4	0	0	4	0	0	Yes	-	Widespread	
H. stejnegeri Ota & Hikida	0	0	0.90	0	0	0	0	0	0	0	0	Yes	-	Asia	
Lepidodactylus cf. *planicaudus* Stejneger	0.08	0.27	0	0	0	0	0	0	0	0	0	No	9	PE	Needs taxonomic study
Luperosaurus kubli Brown, Diesmos & Duya	0.08	0	0	0	0	00	0	0	0	0	0	No	10	LE	
Scincidae															
Brachymeles bicolor (Gray)	0.08	0	0.09	0	0	0	0	0.67	0	1	0	No	7	PE	
B. bonitae Duméril & Bibron	0.12	0	0.09	0	0	0	0	0.33	0	0.5	0	No	7	LE	
B. boulengeri boulengeri Taylor	0	1.55	0	0.33	0.17	0.4	0	0	1	0	0	No	4	PE	
B. talinis (Brown)	0.04	0.36	0	0.17	0	0	0	0	0	0	0	No	8	LE	Probable new species
Brachymeles sp.	0	0.18	0	0	0	0	0	0	0	0	1	No	8	Philippines, Taiwan	

Eutropis cumingi Brown & Alcala	0.56	0	0.36	0	0	0	2.5	0	0	0	0	No	8	PE	
E. multicarinata borealis Brown & Alcala	1.16	2.45	0.91	7	7	5.8	5.75	2.33	3.67	3.5	4	Yes	-	Asia	
E. multifasciata (Kuhl)	0.04	1.36	0.09	0.17	0.17	0.8	1.5	0	1	0	2	Yes	-	PE	
Lamprolepis smaragdina philippinica (Mertens)	0.08	0.45	0.09	0.17	0.17	0	0	0	0	0	0	Yes	6	PE	
Lipinia cf. *vulcania* Girard	0.04	0	0	0	0	0	0	0	0	0	0	No	10	PE	Last recorded in 1909
Sphenomorphus cumingi (Gray)	0.04	0.18	0	0	0	0	0	0	0	0	0	No	9	PE	
S. decipiens (Boulenger)	0.12	2.18	0.27	0.83	0	1.4	0	1.33	0	0	4	No	4	PE	
S. jagori jagori (Peters)	0.2	0.18	0.36	1.33	0.5	1.4	0	0	1	0	3	No	3	PE	
S. leucospilos (Peters)	0.12	0	0.09	0	2.5	0	0	0	0	0	0	No	8	LE	Last recorded in 1870
S. steerei Stejneger	0.2	0.55	1.18	1	1	1.8	0	1.67	0	0	0	No	2	PE	
Sphenomorphus sp.	0.08	1.64	0	0.17	0	0	0	1	0	0	0	No	7	LE	Probable new species
Tropidophorus grayi Günther	0.04	0	0	0	0	0	0	0	0	0	0	No	10	PE	
Varanidae															
Varanus olivaceus Hallowell	0	0	0.09	0	0	0	0	0	0	0	0	No	9	LE	VU; Appendix II
V. salvator marmoratus (Wiegmann)	0.08	0.09	0.18	0.17	0	0	0.25	0.33	0.33	0.5	2	Yes	-	PE	Appendix II
Suboder Serpentes															
Typhlopidae															
Ramphotyphlops braminus (Daudin)	0	0	0.09	0	0.17	0	0	0	0	0	1	Yes	-	Widespread	
Typhlops cf. *luzonensis* Taylor	0.08	0	0.09	0	0	0	0	0	0	0.5	0	No	8	PE	Needs taxonomic study
Boidae															
Python reticulatus (Schneider)	0	0	0	0	0	0	0.25	0	0	0	1	Yes	-	Asia	Appendix II
Colubridae															
Ahaetulla prasina preocularis (Taylor)	0.08	0.27	0	0	0	0	0.25	0	0	0	0	No	8	PE	
Boiga angulata (Peters)	0.04	0	0	0	0	0	0	0	0	0	0	No	10	PE	
B. dendrophila divergens (Taylor)	0	0	0.09	0	0	0	0	0	0	0	0	No	9	LE	
B. philippina (Peters)	0	0.09	0.09	0	0	0	0	0	0	0	0	No	8	PE	
Calamaria bitorques Peters	0.16	0	0	0	0	0	0	0	0	0	0	No	10	PE	
C. gervaisii Duméril, Bibron & Duméril	0	0	0.09	0.17	0	0	0	0	0	0	0	No	8	PE	
Coelognathus erythrurus manillensis Jan	0	0.18	0	0	0	0	0	0	0.33	0	0	Yes	-	PE	
Cyclocorus lineatus(Reinhardt)	0.08	0	0.45	0	0	0	0	0.67	0	1	0	No	7	PE	

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

[a] Site 10 has only one strip transect (*n* = 1), thus, the high abundance values.

[b] These species are affiliated with riparian habitats that transcend both forest sites and matrix.