Short Communication

Cryptic diversity and population genetic structure in the rare, endemic, forest-obligate, slender geckos of the Philippines

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ARTICLE INFO

Article history:
Received 8 April 2013
Revised 5 August 2013
Accepted 16 September 2013
Available online 25 September 2013

Keywords:
Conservation
Deforestation
Endemicity
Enigmatic taxa
Lepidodactylus
Pseudogekko

ABSTRACT

Recent studies of forest lizards in Southeast Asia have highlighted spectacular morphological and cryptic genetic diversity in several poorly known clades. Unfortunately, many of the included species have microhabitat preferences for forested environments, and therefore they are threatened by extensive forest destruction throughout the region. This is particularly true in the Philippines, an archipelago with a strikingly high proportion (84%) of endemic geckos. Abundances inferred from historical museum collections suggests that we are in a critical period where apparent declines in population viability and species’ abundance have taken place faster than the growth in our understanding of alpha diversity. This phenomenon is exemplified in the exceedingly rare Philippine slender forest geckos of the genus Pseudogekko. Most of the known species are rarely encountered by field biologists, and species boundaries are unclear; this poor state of knowledge impedes effective conservation measures. Using the first multilocus phylogeny for these taxa, and phylogenetic and population genetic approaches, we elucidate evolutionary lineages and delimit species-level conservation targets in this unique radiation of endemic Philippine geckos. The results support the presence of widespread cryptic diversity in the genus, providing a framework for the re-evaluation of conservation priorities aimed at protecting these rare, forest-obligate species.

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1. Introduction

Over the last decade, the diversity of gekkonid lizards in the Philippines has blossomed as a result of renewed survey efforts throughout the country, focused investigations of widespread taxa, and use of phylogenetic approaches with molecular data in combination with traditional morphological characters (Brown and Diesmos, 2009; Siler et al., 2010, 2012a). Presently, 50 gekkonid species (representing nine genera) are recognized: Cyrtodactylus (9 species), Gekko (14), Gehyra (1), Hemidactylus (5), Hemiphyllodactylus (2), Lepidodactylus (6), Luperosaurus (8), Pseudogekko (4), and Ptychozoon (1) (for recent reviews, see Brown et al., 2011; Linkem et al., 2010; Welton et al., 2010). Notably, with the exception of common house geckos (genera Gehyra and Hemidactylus), and two species in the genus Gekko (G. gecko and G. monarchus), all species are endemic to the Philippines, resulting in a remarkable endemic community of gekkonid lizards (84% endemicity).

Unfortunately, because many of these species are dependent on primary forest microhabitats, they are threatened by extensive habitat destruction throughout the archipelago (Brown and Diesmos, 2009; Heaney and Regaldo, 1998; Lasco et al., 2001; Liu et al., 1993). With only 4–8% of the country’s primary forest remaining (Brown and Diesmos, 2009; Lasco and Pulhin, 1998; Lasco et al., 2001; Liu et al., 1993), the conservation of species with obligate forest requirements represents a critical challenge for government agencies, wildlife managers, and conservation biologists (Brown and Diesmos, 2009; Catbog-Sinha and Heaney, 2006). Complicating the conservation issues in the Philippines is the rapidly growing realization that our current understanding of terrestrial vertebrate diversity in the archipelago is significantly underestimated for reptiles and amphibians (Brown and Diesmos, 2002, 2009).

For geckos (last reviewed by Brown and Alcala (1978)), a nascent body of research over the last few years has allowed for more stable estimates of alpha diversity throughout the archipelago (for recent reviews, see: Brown et al., 2011, 2012a, 2012b; Linkem et al., 2010; Welton et al., 2010); however, we remain in a critical period where observed decreases in population health and abundance (IUCN, 2012) have taken place faster than the growth in...
our understanding of gekkonid diversity (CDS and RMB, personal observations; PhilIBREO, 2013). Few Philippine endemic genera provide more poignant examples of this than the genus *Pseudogekko*.

Members of this genus are so rare, that over the last two decades of comprehensive biodiversity surveys throughout the country, only 28 vouchered genetic samples have been collected. With the exception of a single specimen (CAS 139713) from the small isolated island of Tablas in the Romblon Island Group in the central Philippines, these rare, forest-obligate species are known to occur in only three major faunal regions in the Philippines, or Pleistocene aggregate island complexes (PAICs: Brown and Diesmos, 2002, 2009); the Luzon, Mindanao, and Visayan PAICs (PhilIBREO, 2013; Fig. S1). Although only four species currently are recognized, the genus has had a complex taxonomic history, with multiple members of *Pseudogekko* previously being assigned to or derived from the genera *Luperosaurus* (Taylor, 1915) and *Lepidodactylus* (Brown and Alcala, 1978; Kluge, 1968).

We undertook the present study with two main objectives: (1) To screen for divergent lineages (likely conservation targets, putative unrecognized species) and determine whether these correspond to currently recognized species, and (2) To question whether *P. brevipes* and *P. compressicorpus*, whose distributions span multiple distinct biogeographic regions (separate PAICs; Fig. S1), are single entities (evolutionary lineages). Contrary to many other Philippine amphibians and reptiles that exhibit more limited geographical ranges, the widespread distributions (across recognized faunal boundaries) of *P. brevipes* and *P. compressicorpus* suggests a need for closer investigation. Here we use a newly collected, multi-locus molecular dataset and phylogenetic and population genetic approaches to elucidate evolutionary lineages and delimit species–level conservation targets in this unique radiation of endemic Philippine geckos. Members of the genus *Pseudogekko* represent a critical extreme of the conservation urgency spectrum because: (i) the entire genus is endemic to the Philippines, (ii) all species are primary forest obligates or possess microhabitat preferences for *Pandanus* plants, (iii) over the last 25 years, members of the genus have been rarely encountered in the wild, (iv) judging from the few known historical collections, populations apparently have decreased over the last 100 years, and (v) near complete removal of their required habitat (primary forest) has occurred. These five factors underscore the urgent need to resolve species boundaries within the genus in order to facilitate conservation status assessments and identify conservation targets in this unique radiation.

## 2. Materials and methods

### 2.1. Taxon sampling and data collection

Ingroup sampling included 28 individuals collected from 12 localities, with three of the four currently recognized species of *Pseudogekko* represented (Figs. 1, 2 and S2; Appendix 1). Tissue samples of true *P. labialis* have never been collected, and therefore were unavailable for this study (but see Discussion for questions on the taxonomic affinity of *P. labialis*). To assess the monophyly of the genus, test taxonomic hypotheses, and investigate appropriate taxa, a broad sampling (28 taxa) of species from the families Gekkonidae and Phyllodactylidae were included based on the data presented in recent phylogenetic studies of geckos in the Philippines (Brown et al., 2012a, 2012b; Siler et al., 2012a), using sequence data available on GenBank (Appendix 1).

In addition to these data, genomic DNA was extracted from liver tissues stored in 95% ethanol for 28 vouchered specimens of *Pseudogekko*. We sequenced a 1321 nucleotide fragment consisting of the mitochondrial gene NADH Dehydrogenase Subunit 2 (ND2) and components of three flanking transfer RNA genes (trNA^{p}, trNA^{aa}, trNA^{asn}) using the primers and protocols of Siler et al. (2012a). Additionally, we sequenced completely the nuclear loci Phosducin (PDC), proeglandin E receptor 4 (PTGER4), and oocyte maturation factor (C-mos), using the primers of Jackson et al. (2008) and Siler et al. (2012b). Protocols for PCR and sequencing followed Siler et al. (2012a, 2012b). All novel sequences were deposited in GenBank (Appendix 1).

### 2.2. Phylogenetic analyses and support for topological hypotheses

Initial alignments were produced in MUSCLE (Edgar, 2004) with minimal manual adjustments. Following the observation of no strongly supported incongruence between datasets, we felt justified in using the combined, concatenated data for subsequent analyses. Partitioned Bayesian analyses were conducted in MrBayes v3.2.1 (Ronquist and Huelsenbeck, 2003). All gene datasets were partitioned by codon position for protein-coding regions, and the three flanking tRNAs for ND2 were analyzed as a single subset. The Akaike Information Criterion (AIC), as implemented in jModelTest v0.1.1 (Posada, 2008), was used to select the best model of nucleotide substitution for each partition (Table S1). A rate multiplier model was used to allow substitution rates to vary among subsets, and default priors were used for all model parameters. We ran four independent MCMC analyses, each with four Metropolis-coupled chains, an incremental heating temperature of 0.02, and an exponential distribution with a rate parameter of 25 as the prior on branch lengths (Marshall, 2010). All analyses were run for 10 million generations, with parameters and topologies sampled every 3000 generations. We assessed stationarity with Tracer v1.4 (Rambaut and Drummond, 2007) and confirmed convergence with AWTY (Wilgenbusch et al., 2004). Stationarity was achieved after 3 million generations (i.e., the first 15%), and we conservatively discarded the first 20% of samples as burn-in.

Partitioned maximum likelihood (ML) analyses were conducted in RAxML-VI-HPC v7.0 (Stamatakis, 2006) on the concatenated dataset using the same partitioning strategy as for Bayesian analysis. The more complex model (GTR + Γ) was used for all subsets (Table S1), and 100 replicate ML inferences were performed for each analysis. Each inference was initiated with a random starting tree and nodal support was assessed with 100 bootstrap pseudoreplicates (Stamatakis et al., 2008). All alignments and resulting topologies are deposited in Dryad (http://dx.doi.org/10.5061/dryad.1g9g7).

### 2.3. Analyses of population genetic structure

To visualize population genetic structure, we generated phylogenetic networks for the mitochondrial and concatenated nuclear datasets, respectively, by employing the Neighbor-Net algorithm (Bryant and Moulton, 2004) in the program SplitsTree v4.10 (Huelsen and Bryant, 2006; Fig. 2). To assess the support for inferred splits in the network, a bootstrap analysis was conducted with 1000 pseudoreplicates.

To estimate the number of cohesive genetic populations represented by the genetically divergent *P. compressicorpus* species complex, we used the Bayesian clustering method of the program STRUCTURE v2.3.3 (Pritchard et al., 2000), with allelic data from our three nuclear loci to infer the number of populations and the probabilities of individuals belonging to each of the estimated genetic clusters. We phased each nuclear locus using the program PHASE v2.1.1 (Stephens and Donnelly, 2003), and retained haplotypes with the highest probabilities for subsequent analyses. We considered the number of possible populations, represented by K, for each species complex to range from one (all samples represent
a single panmictic population) to the number of unique sampling localities (each sampled population represents a unique genetic cluster; Appendix 1). We conducted 20 replicate runs in STRUCTURE for each of the values of $K$ (for each species) to verify stationarity of parameter estimates. We ran each analysis for 1 million iterations, with a burn-in of 500,000. The preferred value of $K$ was determined using the program STRUCTURE HARVESTER (Earl and vonHoldt, 2012) following the method of Evanno et al. (2005), with results visualized using the program DISTRUCT v1.1 (Rosenberg, 2004).

3. Results

3.1. Taxon sampling, data collection, and sequence alignment

The complete, aligned matrix contains 28 samples of Pseudogekko (all genetic samples amassed in the last 22 years of field work), representing three of the four currently recognized species ($P. \text{brevipes}$, $P. \text{compressorcorpus}$, and $P. \text{smaragdinus}$). Twenty-eight additional samples are included from the families Gekkonidae and Phyllodactylidae (Fig. S2, Appendix 1). Following initial unrooted analyses, and other recent gekkonid phylogenetic analyses (Brown et al., 2012a, 2012b; Gamble et al., 2011), we rooted the tree using a representative sample of $Tarentola \text{mauritanica}$ (Phyllodactylidae). Variable characters are: 960 of 1321 (ND2); 73 of 430 (PDC); 14 of 348 (C-mos); 15 of 488 (PTGER4).

3.2. Phylogenetic analyses

All analyses result in topologies with high ML bootstrap support and posterior probabilities among species and divergent populations of Pseudogekko. General topological patterns among the major clades of outgroup species included in this study are congruent with recently published gekkonid studies (Brown et al., 2012a, 2012b; Siler et al., 2012a), and some members of the genus Lepidodactylus continue to be supported as sister to the genus Pseudogekko (Figs. 1 and S2).

With the exception of the shallow divergence observed between sampled allopatric populations of $P. \text{smaragdinus}$, populations of $P. \text{brevipes}$ and $P. \text{compressorcorpus}$ are recovered as monophyletic clades of deeply divergent, allopatric populations (Fig. 1). We confirm the first published record of $P. \text{smaragdinus}$ on mainland Luzon, with a population from the northern Bicol Peninsula (Mt. Labo) recovered as sister to the population on Polillo Is-
land (Fig. 1). Analyses support three major clades within the *P. compressicorpus* Complex (Fig. 1, Clades A–C), all of which possess high degrees of inter-population genetic divergence (Table 1). Interestingly, the results of phylogenetic analyses confirm the presence of multiple distinct species or lineages occurring sympatrically on multiple islands in the Philippines: *P. compressicorpus* and *P. smaragdinus* on Polillo and Luzon islands; *P. compressicorpus*, *P. cf. compressicorpus*, and *P. brevipes* on Leyte Island; and *P. compressicorpus* and *P. cf. compressicorpus* on Mindanao Island (Fig. 1).

### 3.3. Population structure and hypothesized species boundaries

The results of network analyses corroborate the major results observed from phylogenetic analyses (Fig. 2). Both our mtDNA (ND2) and concatenated nuDNA networks (PDC + C-mos + PTGER4) revealed highly divergent, well-supported splits corresponding to all divergent lineages recovered in phylogenetic analyses (Fig. 2). STRUCTURE analyses focused on the *P. compressicorpus* Complex support the presence of five genetically distinct populations (*K* = 5) within *P. compressicorpus* (Fig. 2). Two of these genetic clusters correspond to groups distributed together in the Luzon PAIC, and the remaining three genetic clusters correspond to groups of allopatric populations distributed in the Mindanao PAIC (Figs. 2 and S1).

### 4. Discussion

#### 4.1. Phylogeny and species diversity

Phylogenetic analyses of our multilocus dataset reveal extensive cryptic inter-population genetic diversity across the archipelago. Even with a conservative approach of identifying unique genetic diversity, analyses recover six major lineages with high support: two divergent lineages within the *Pseudogekko brevipes* Complex, three divergent lineages within the *P. compressicorpus* Complex, and *P. smaragdinus* (Figs. 1 and 2). Uncorrected *p*-distances (Table 1) among these lineages far exceed those observed in all previous studies focused on widespread complexes of endemic Philippine geckos (*Cyrtodactylus*, *Gekko*, and *Luperosaurus*; Brown et al., 2011, 2012b; Siler et al., 2012a; Welton et al., 2010) or gekkonid lizards in general (Gamble et al., 2012). Furthermore, intraspecific genetic diversity within the three major clades of the *P. compressicorpus* Complex indicate that many allopatric populations warrant closer investigation, as they may represent additional cryptic species (Table 1; Figs. 1 and 2).

For half a century, confusion over the systematic affinities of species of *Lepidodactylus* and *Pseudogekko* (Brown, 1964; Brown and Alcala, 1978; Kluge, 1968) has prevailed, in a large part due to poor sampling available for many rare taxa within these genera.

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**Table 1**

Uncorrected pairwise sequence divergence (%) for mitochondrial data (below diagonal) and nuclear data (above diagonal) for the six major lineages recovered in phylogenetic analyses (Figs. 1 and 2). Percentages on the diagonal represent intraspecific genetic diversity for mitochondrial data, when sampling permits (bolded for emphasis).

<table>
<thead>
<tr>
<th></th>
<th>brevipes</th>
<th>cf. brevipes</th>
<th><em>compressicorpus</em> (Clade C)</th>
<th>cf. <em>compressicorpus</em> (Clade B)</th>
<th>cf. <em>compressicorpus</em> (Clade A)</th>
<th><em>smaragdinus</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>brevipes</td>
<td>-</td>
<td>1.0</td>
<td>0.9–1.0</td>
<td>0.9–1.4</td>
<td>0.8–1.0</td>
<td>1.1–1.2</td>
</tr>
<tr>
<td>cf. brevipes</td>
<td>20.4–20.6</td>
<td><strong>0.0–0.1</strong></td>
<td>1.6–1.7</td>
<td>1.5–1.8</td>
<td>1.6–1.7</td>
<td>1.4–1.5</td>
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<tr>
<td><em>compressicorpus</em> (Clade C)</td>
<td>24.0–27.0</td>
<td>25.0–25.8</td>
<td><strong>0.9–14.8</strong></td>
<td>0.1–1.1</td>
<td>0.8–0.9</td>
<td>1.0–1.2</td>
</tr>
<tr>
<td>cf. <em>compressicorpus</em> (Clade B)</td>
<td>23.0–24.1</td>
<td>25.4–28.3</td>
<td>20.5–26.1</td>
<td><strong>0.0–12.0</strong></td>
<td>0.7–0.9</td>
<td>0.8–1.3</td>
</tr>
<tr>
<td>cf. <em>compressicorpus</em> (Clade A)</td>
<td>24.0–30.5</td>
<td>23.5–28.8</td>
<td>21.0–26.4</td>
<td>17.3–22.3</td>
<td><strong>0.0–19.0</strong></td>
<td>0.8–1.1</td>
</tr>
<tr>
<td><em>smaragdinus</em></td>
<td>23.4–23.6</td>
<td>22.8–23.8</td>
<td>20.7–21.4</td>
<td>21.2–24.0</td>
<td>20.6–23.6</td>
<td><strong>0.0–4.7</strong></td>
</tr>
</tbody>
</table>
This is most acute in the case of *P. labialis*, a species that for many years was considered a member of the genus *Lepidodactylus* (for review, see Brown and Alcala, 1978). Of the morphological characters used to diagnose members of the two genera, the only external morphological character used to differentiate *Pseudogecko* from *Lepidodactylus*, is the preanofemoral pore series. In *Pseudogecko*, the series is described as being significantly arched anteromedially (versus non-arched in *Lepidodactylus*; Kluge, 1968). Superficially, *P. labialis* looks morphologically more similar to species in the genus *Pseudogecko* (CDS and RMB, personal observations), and even early reviews cited *P. labialis* as having larger, relatively more robust body proportions than all the remaining, elongate, slender species of *Pseudogecko* (Brown and Alcala, 1978). *Pseudogecko labialis* also possesses non-arched preanofemoral pore series, a diagnostic characteristic of the genus *Lepidodactylus* (Kluge, 1968). Unfortunately, no tissue samples are available for true *P. labialis* from Mt. Hilong-hilong, Northeastern Mindanao (Fig. 2) and a recent (2012) 5-week biodiversity survey to the type locality produced no specimens (RMB and M.B. Sanguila, unpublished data) despite a concerted effort to Rediscover this species. Based on examination of external morphology of the available specimens, we anticipate that *P. labialis* eventually will be placed back in the genus *Lepidodactylus*. Genetic material from *P. labialis* would be instrumental in resolving this taxonomic problem.

4.2. Morphological variation and diversification

A comprehensive study exploring morphological diversity among genetically divergent populations of *Pseudogecko* will be necessary to resolve what appears to be widespread underesti- mated species diversity (Figs. 1 and 2). Although species in this genus are considered rare (Brown et al., 2013; PhilBREO, 2013), and many divergent lineages are represented by few voucher samples in museum collections, preliminary data indicate there may be substantial morphological differences among allopatric populations. Among the three major clades within the *P. compressicorpus* Complex, large, inter-clade differences in body size measurements and preanofemoral pore counts are apparent (CDS, personal observations); both characters used as traditional diagnostic traits in the recognition of species in the family Gekkonidae (e.g., Brown et al., 2011, 2012a, 2012b; Linkem et al., 2010; Welton et al., 2010). Thus, we anticipate that the recognition of these genetically divergent lineages as new species will be non-controversial.

As no species of *Pseudogecko* have ever been documented from the western islands of the Philippines (Palawan and Mindoro PAICs), it is plausible that the genus evolved from an eastern arc origin via Mindanao Island in the southeast (Figs. 2 and S1). This might explain why the majority of divergent lineages occur in the Luzon and Mindanao PAICs, with only a single lineage currently known from the Visayan PAIC in the central Philippines (*P. cf. brevipes*; Figs. 1, 2 and S1). Although the nature of this study (and size of the dataset) precluded us from conducting biogeographic analy- ses, the results of our phylogenetic analyses support the possibility that species diversity in the Visayan and Luzon PAICs were the result of multiple, independent dispersal events out of the Mindanao PAIC (Fig. 1). With these species dependent on primary forest habitat, it is plausible that chance dispersal events out of the southern Philippine islands were followed by subsequent isolation in forested habitat. This mechanism might explain the observation of both deeply divergent lineages throughout the central and northern Philippines, and the disproportionate number of non-monophyletic, divergent lineages on Leyte Island (an intervening island in this putative pathway; Figs. 1, 2 and S1).

4.3. Conservation significance and strategic planning

The results of this study suggest multiple changes to our understanding of species boundaries, taxonomic diversity, conservation status assessments (IUCN, 2012; Table 2), and applied conservation targets in the genus *Pseudogecko*. First, the brilliantly colored and attractive forest species *P. smaragdinus* appears more widespread than previously known, and in addition to our new record from Mt. Labo, we anticipate that this species is present throughout much of the Quezon region and northern extent of the Bicol Peninsula, including Caramoan and Catanduanes (Fig. 2). However, this species has appeared in the illegal international pet trade (personal observations) and possesses a microhabitat preference for *Panda-nus* plants (Taylor, 1922). As similar anthropogenic activities have been linked to the rapid decline of other rare, critically endangered geckos (Flecks et al., 2012), populations on Polillo and the Bicol Peninsula of Luzon should be monitored and protected, and therefore may qualify for “Near Threatened” status (Table 2). *Pseudogecko brevipes* has been classified by IUCN as “Vulnerable” (IUCN, 2012) based on small area of occurrence and fewer than ten observations of the species in the wild. Our data increase the conservation urgency concerning this species further by suggesting that the eastern Visayan populations (Leyte, possibly Samar and Bohol) may be a separate evolutionary lineage (putative species) from western Visayan populations (Negros and Panay), an arrangement that would not be surprising given biogeographical considerations (Brown and Diesmos, 2009). Each of these genetically distinct lineages should be assessed separately; our data suggest that two species with even smaller known areas of occurrence would provide justification for elevated levels of threat and IUCN (2012) status designation (Table 2). Finally *P. compressicorpus*, previously considered widespread, common and formerly “Least Concern” (IUCN, 2012; Table 2), appears to harbor three or four independent evolutionary lineages (putative species). It is notable that at least two of these lineages (*true* *P. compressicorpus* from Luzon [Fig. 1, Clade C] and *P. cf. compressicorpus* from Leyte, Bohol, and Mindanao [Fig. 1, Clade B] are widespread and most likely appropriately considered of lower relative conservation importance. Future studies will have to determine whether Clade A (Fig. 1) is composed of one species or two. In summary, if future taxonomic investigations support the divergent lineages identified

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<th>Current IUCN classification</th>
<th>Suggested IUCN classification</th>
<th>Criteria</th>
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<td><em>Pseudogecko brevipes</em></td>
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<td>Endangered</td>
<td>EN A2ac; B1ab(iii)</td>
</tr>
<tr>
<td><em>Pseudogecko cf. brevipes</em></td>
<td>Vulnerable</td>
<td>Endangered</td>
<td>EN A2ac; B1ab(iii)</td>
</tr>
<tr>
<td><em>Pseudogecko cf. compressicorpus</em> (Clade A)</td>
<td>Least Concern</td>
<td>Vulnerable</td>
<td>VU A2ac; B2ab(ii); D2</td>
</tr>
<tr>
<td><em>Pseudogecko cf. compressicorpus</em> (Clade B)</td>
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<td>Least Concern</td>
<td>Does not qualify at this time</td>
</tr>
<tr>
<td><em>Pseudogecko compressicorpus</em> (Clade C)</td>
<td>Least Concern</td>
<td>Least Concern</td>
<td>Does not qualify at this time</td>
</tr>
<tr>
<td><em>Pseudogecko smaragdinus</em></td>
<td>Least Concern</td>
<td>Near Threatened</td>
<td>VU A3cd; B2ab(ii); D2</td>
</tr>
</tbody>
</table>
in this study as diagnosable evolutionary lineages worthy of taxonomic recognition, then some IUCN conservation status designations will need to be elevated (IUCN, 2012; Table 2). Whatever the result of future research, our data suggest that the Philippine endemic forest gecko genus *Pseudogecko* is most likely composed of more species with smaller ranges than previously believed. Given that the recognized and putative new taxa are all obligatory forest species in a country characterized by rapid and near-complete forest removal over the last century, our sense of urgency has increased for a resolved taxonomy, updated assessments of conservation status, and appropriate conservation measures.

**Acknowledgments**

We thank the Protected Areas and Wildlife Bureau (PAWB) of the Philippine Department of Environment and Natural Resources (in particular T.M. Lim, C. Custodio, J. de Leon, A. Manila, and A. Tagtag) for facilitating this study. Thanks are due to A. Diesmos for logistical support. Sampling efforts followed protocols approved by the University of Kansas (KU) IACUC and Memorandum of Agreement between KU and PAWB, as outlined in a GP administered by PAWB. Fieldwork was supported by a National Science Foundation Doctoral Dissertation Improvement Grant (DEB 0804115 to CDS), Fulbright and Fulbright-Hayes Fellowships (to CDS); and an NSF Biotic Surveys and Inventories Grant (DEB 0743491 to RMB). This study resulted from a Biodiversity Research workshop led by CDS at the University of South Dakota, with team-driven contributions from postdoctoral researchers, undergraduates, and graduate students. We thank K. Kozak, D. Scantlebury, and graduate students. We thank K. Kozak, D. Scantlebury, and graduate students. We thank K. Kozak, D. Scantlebury, and graduate students. We thank K. Kozak, D. Scantlebury, and graduate students.

**Appendix A. Supplementary material**

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ympev.2013.09.014.

**References**


