GEOGRAPHIC DRIVERS OF AVIAN DIVERSIFICATION IN THE PHILIPPINE ARCHIPELAGO

By

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Geographic drivers of avian diversification in the Philippine Archipelago

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Abstract

I investigate the relative roles of different classes of geographical barriers in the diversification of the Philippine avifauna, by inferring the evolutionary relationships of avian groups with DNA sequence data. In chapter one, I reconstruct the historical biogeography of the *Aethopyga* sunbirds. In chapter two, I examine the distribution of genetic variation and plumage patterns in *Robsonius* ground-warblers, and identify a new species. In chapter 3, I reconstruct the evolutionary history and ecological niches of eight co-distributed polytypic species of Philippine birds, and infer a paleoclimate barrier that drove diversification. In chapter four, I use molecular markers and plumage characters to reassess species limits in 19 avian species or species groups in the Mindanao Island group of the Philippines. In addition to permanent marine barriers, long understood to isolate insular lineages, I provide evidence that periodic marine barriers, periodic climatic barriers, and complex topography isolate and promote diversification in Philippine birds. Populations inhabiting island groups (bounded by deep-water barriers) are frequently paraphyletic, contrary to the perception that deep-water barriers are the most important geographic isolating feature in insular systems. I document two small avian radiations, the *Robsonius* in Luzon, and *Aethopyga* in Mindanao, that are exceptions to the paradigm that birds do not diversify within single islands. Congruence of molecular markers and plumage characters support that avian taxonomy in the Philippines is extremely conservative, and most Philippines species would be more appropriately treated as sets of allopatric evolutionary lineages, rather than widespread polytypic species.

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Table of contents

List of Figures

List of Tables

List of Appendices

Introduction

The Philippines is a megadiverse county and a biodiversity hotspot. An intense concentration of biodiversity, combined with complex yet well-understood geologic history, makes the archipelago an ideal natural laboratory for phylogeographic inquiry. For the past 30 years, the Pleistocene aggregate island complex (PAIC) model has largely shaped biogeographic inference in the Philippines and other island archipelagos. This model is based on a simple observation: aggregate islands repeatedly formed when sea levels decreased during glacial maxima, increasing connectivity among islands. During periods when dry land connected modern-day islands, populations might have expanded into new areas, and previously isolated island populations could come into contact and potentially interbreed. PAIC boundaries are largely congruent with current day vertebrate species distributions. The PAIC concept has been applied broadly to explain distribution and phylogeographic patterns in other oceanic archipelagos such as the Solomon Islands, and in continental shelf systems such as the Sunda Shelf.

Recently, genetic data from Philippine mammals, reptiles, and amphibians have challenged the notion that isolation among PAICs drove diversification. Rather, they suggest that although PAIC boundaries may explain broad distribution patterns, they do not necessarily explain the complex evolutionary histories of lineages within them. Repeated cycles of isolation and connection caused by sea level and habitat changes, combined with the stochastic process of dispersal, may have created complex biogeographic patterns that are not explained by the PAIC hypothesis. Philippine birds offer a new perspective to previous studies of mammals, reptiles, and amphibians in the PAIC framework because they are often viewed as more capable dispersers. Although the distributional patterns of Philippine birds are well established, the

relative importance of different historical processes in creating these distributions remains poorly understood due to a shortage of molecular phylogenetic studies.

From 2006–present, colleagues and I at the University of Kansas, University of Utah, and the Philippine National Museum conducted fieldwork throughout the Philippine archipelago, establishing a comprehensive modern collection of specimens and tissue samples to better understand the biogeography and evolutionary history of Philippine vertebrates. This new specimen material, supplemented by collections from the Field Museum of Natural History and the Cincinnati Museum Center, provide the dense sampling needed to test complex biogeographical hypotheses.

This dissertation, composed of four chapters, seeks to answer the following questions. 1) To what extent does the PAIC paradigm explain avian diversification in the Philippine archipelago? 2) How does periodic sea level change influence diversification and the distribution of genetic variation in island systems? 3) Do alternative geographic features (intermittent marine barriers, environmental barriers, and topography within islands) isolate avian lineages? 4) To what extent have conservative criteria to infer species limits underestimated diversity and obscured biogeographic and evolutionary patterns? To answer these questions, I used concatenated and coalescent-based phylogenetic inference of multilocus DNA sequence data, including analyses of multiple co-distributed lineages in a comparative phylogeographic framework, to disentangle multiple historical influences and identify common patterns.

In chapter one, I examine the relative roles of deep-water marine barriers, periodic shallow-water marine barriers, and isolation within islands, in the diversification of *Aethopyga*. I present the first molecular phylogenetic hypotheses for these sunbirds, which are most diverse in the Philippines, and used the phylogeny to reconstruct historical biogeography and infer which

barriers were responsible for isolating lineages. Results supported deep-water marine barriers as the most common isolating mechanism, but all three types of barriers contributed to diversification. The phylogeny also demonstrated that a clade of four *Aethopyga* taxa diversified in the montane sky islands of Mindanao, an exception to the idea that birds do not diversify within oceanic islands. Molecular evidence, combined with plumage characters, support that species diversity is greatly underestimated in insular *Aethopyga* sunbirds.

In chapter two, I documented a second example of within-island diversification in the Philippine archipelago, in a lowland bird group endemic to the Luzon Island complex. In the course of fieldwork in 2011, colleagues and I collected new specimen evidence that the *Robsonius* ground-warblers included a third undescribed species. I produced a molecular phylogenetic molecular hypothesis for the group, determined that three allopatric evolutionary lineages inhabit Luzon, and described a new species.

In the third chapter, I expanded beyond physical geographic barriers to examine the role of changing environmental suitability in isolating Philippine bird lineages. I produced molecular phylogenies and ecological niche models for eight co-distributed polytypic bird species, which are distributed in the Luzon and Mindanao Island Groups. A single deep-water barrier separates these island groups. Analyses revealed that each of these species contains between three and seven evolutionary lineages, and populations inhabiting the Mindanao PAIC are paraphyletic in all eight species. Thus, alternative isolating barriers are needed to explain diversification. By comparing paleo-projections of ecological niche models and patterns of genetic differentiation, I identified a novel paleoclimate barrier across the Bohol Sea region. I hypothesize that periodic marine barriers isolated lineages during high-sea level stands (associated with interglacials), and unsuitable environmental conditions isolated lineages during low-sea level stands (associated

with glacial maxima); therefore, the combination of periodic marine and environmental barriers isolated theses lineages throughout the Pleistocene even though land connections occurred.

The first three chapters all suggest that species diversity is grossly underestimated in Philippine birds, and that conservative taxonomy hinders understanding of macroecological and evolutionary processes, as well as conservation strategies. In chapter four, I use an integrative framework utilizing coalescent model-based species delimitation and morphological characters to identify species limits in 19 lowland Philippine bird groups distributed across the Mindanao PAIC. This species delimitation framework recognizes a 74% increase in species diversity over currently accepted taxonomy, and identifies fine-scale endemism within the Mindanao group, with multiple avian endemics restricted to Bohol Island, Samar/Leyte, and the Zamboanga Peninsula of western Mindanao.

In conclusion, my research supports the importance of deep-water in isolating bird lineages and promoting diversification. However, intermittent marine barriers, environmental barriers, and complex topography also played an important role in isolating populations and allowing for diversification— a pattern that has been obscured in part because conservative taxonomy has failed to recognize a large proportion of the evolutionary lineages of birds that inhabit the Philippine archipelago.

Chapter 1*

Water barriers and intra-island isolation contribute to diversification in the insular *Aethopyga* sunbirds (Aves: Nectariniidae)

*Hosner P. A., Nyári, A. S., R. G. Moyle. 2013. Water barriers and intra-island isolation contribute to diversification in the insular *Aethopyga* sunbirds (Aves: Nectariniidae). Journal of Biogeography 64: 1094–1106.

Abstract

Colonization and subsequent isolation across deep-water barriers is thought to be the primary driver of diversification in insular birds. Shallow-water barriers and intra-island isolation are less well-documented drivers of avian diversification. We examined the relative roles of different geographical barriers in the diversification of *Aethopyga* sunbirds, a widespread Southeast Asian genus that has its greatest diversity in the Philippine Archipelago. We reconstructed the phylogenetic relationships among *Aethopyga* sunbirds with mitochondrial and nuclear DNA sequences. Phylogeny was inferred using concatenated and coalescent frameworks, implemented in maximum likelihood and Bayesian analyses. We used maximum-likelihood ancestral state reconstructions to examine the ancestral distribution and colonization history of *Aethopyga*. To determine whether the diversification at each node occurred within a continent, across a shallow-water barrier, across a deep-water barrier or within an island, we used a series of statements based on the phylogeny, current distribution of species and bathymetric reconstructions. Ancestral state reconstructions inferred that the core *Aethopyga* ancestor was continental, and that the diversity of *Aethopyga* on oceanic islands is the result of three or four independent colonization events. Dispersal and subsequent isolation across deep-water barriers was the most common mode of diversification in insular *Aethopyga*, although intra-island isolation contributed to diversity, producing a small montane radiation within Mindanao. Analyses inferred only a single unequivocal event of diversification across a shallow-water barrier. Deep molecular divergences between phenotypically distinct subspecies suggested that *Aethopyga* taxonomy is overly conservative and obscures biogeographical patterns. We recommend elevating five subspecies, all of which are endemic to the Philippines, to full species.

Introduction

Biogeographers have long used the Philippines as a model system to investigate patterns of insular colonization and diversification (Huxley 1868; Dickerson et al. 1928; Diamond and Gilpin 1983; Heaney 1986). Two well-established hypotheses explain patterns of avian biogeography and diversification in the Philippines. The first hypothesis states that lineages colonize the oceanic Philippines from Borneo primarily though two 'umbilici' (long, narrow stretches of land, either an isthmus or a chain of island stepping stones, connecting two larger land masses): Palawan and the Sulu Archipelago (Diamond and Gilpin 1983). The second hypothesis states that dispersal and subsequent isolation across deep-water barriers drives diversification in the Philippines (Heaney 1986; Siler et al. 2010). In the Pleistocene, sea levels periodically fell during glacial maxima (Heaney 1986; Voris 2000; Siddall et al. 2003); during these periods, present-day islands separated by shallow channels repeatedly joined into larger Pleistocene aggregate island complexes (PAICs; Heaney 1986; Brown and Diesmos 2002). Under the PAIC diversification hypothesis, shallow-water barriers are not viewed as effective isolating mechanisms, because periodic land connections allowed dispersal between islands within PAICs, enabling admixture and preventing cladogenesis (Heaney 1986; Brown and Diesmos 2002; Siler et al. 2012). The PAIC hypothesis also implies a Pleistocene diversification of species isolated across PAIC boundaries. Although developed based on mammal distribution patterns (Heaney 1986), the PAIC hypothesis has generally been accepted in birds (Dickinson et al. 1991).

Taken together, the two-umbilici and PAIC hypotheses state that when a new lineage invades the Philippines, dispersal and subsequent isolation across deep-water barriers (between

PAICs) is the major driver of diversification, and that isolation across shallow-water barriers and isolation within larger islands have a limited role in generating diversity. The possibility of intra-island diversification has generally not been supported in birds (Diamond 1977; Coyne and Price 2000). Avian sister taxa are rarely found on the same island, and when they are, studies either cannot reject multiple colonization events (Ryan et al. 2007), suggest that diversification occurred in an earlier geological setting of multiple proto-islands (Sly et al. 2011), or infer that hybridization or ongoing gene flow unite populations (Gill et al. 1973; Vanderwerf et al. 2010).

Several trends are emerging from recent molecular phylogenetic and phylogeographical studies that have implications for Philippine biogeography. 1) Philippine taxa tend to be more genetically distinct and isolated from Sundaic relatives than previously appreciated (Jones and Kennedy 2008; Sheldon et al. 2009; Lohman et al. 2010; Oliveros and Moyle 2010). 2) Many polymorphic Philippine bird species are paraphyletic and/or contain multiple divergent allopatric lineages (Jones and Kennedy 2008; Oliveros and Moyle 2010), and thus are more appropriately viewed as complexes of distinct species (Brown and Diesmos 2002; Peterson 2006; De Queiroz 2007). 3) Support exists for the two-umbilici hypothesis (Oliveros and Moyle 2010), although lineages colonizing Palawan tend not to colonize the oceanic Philippines. 4) Some studies have found diversity partitioned along PAIC boundaries, fulfilling predictions of the PAIC hypothesis (Lim et al. 2010), but other studies have recovered more complex patterns including divergent sister lineages within a single PAIC (Oliveros and Moyle 2010), divergent sister lineages within single islands (Esselstyn et al. 2009), and evidence of pre-Pleistocene diversification (Esselstyn and Brown 2009). Contrary to the predictions of the PAIC hypothesis, Lim *et al*. (Lim et al. 2011) recovered strong genetic differentiation in 11 of 16 species across shallow Sunda Shelf

boundaries, although this differentiation may be better explained by a break in habitat suitability than by the putative shallow-water boundary itself.

With its complex geography and well understood geological history (Hall 1998; 2002; Yumul et al. 2008), the Philippine archipelago is an ideal system to examine the relative roles of water barriers and intra-island factors in the process of diversification. The Philippines comprise several island arc systems that have coalesced over the past 25 million years, although by 5–10 Ma most islands were close to their current position (Hall 1998). Currently, the island of Palawan (which is continental in origin) is narrowly connected by shallow water to the Sunda shelf. The remaining islands are oceanic in origin, and form five major PAICs (Luzon, Mindoro, Visayan, Mindanao and Sulu), each joined by water depths of less than 120 m (Heaney 1986; Voris 2000). This system of islands provides dozens of potential deep- and shallow-water barriers to isolated populations. The large, topographically complex islands of Luzon and Mindanao might provide opportunity for intra-island isolation, especially for montane taxa.

Aethopyga sunbirds (Aves: Passeriformes: Nectariniidae) provide an opportunity to test the relative roles of shallow-water, deep-water and intra-island isolation in the Philippines and Southeast Asia. Several lines of evidence suggest that all three types of barriers have influenced the colonization and diversification history of the genus. First, many *Aethopyga* species and subspecies distributions are bounded by water barriers. Second, islands and island groups harbour different species compositions, suggesting a complex colonization history (e.g. one species on Palawan, three on Luzon and five on Mindanao; (Kennedy et al. 2000). Third, multiple species are endemic to the mountains of Mindanao (Kennedy et al. 1997) and might be the result of an endemic radiation.

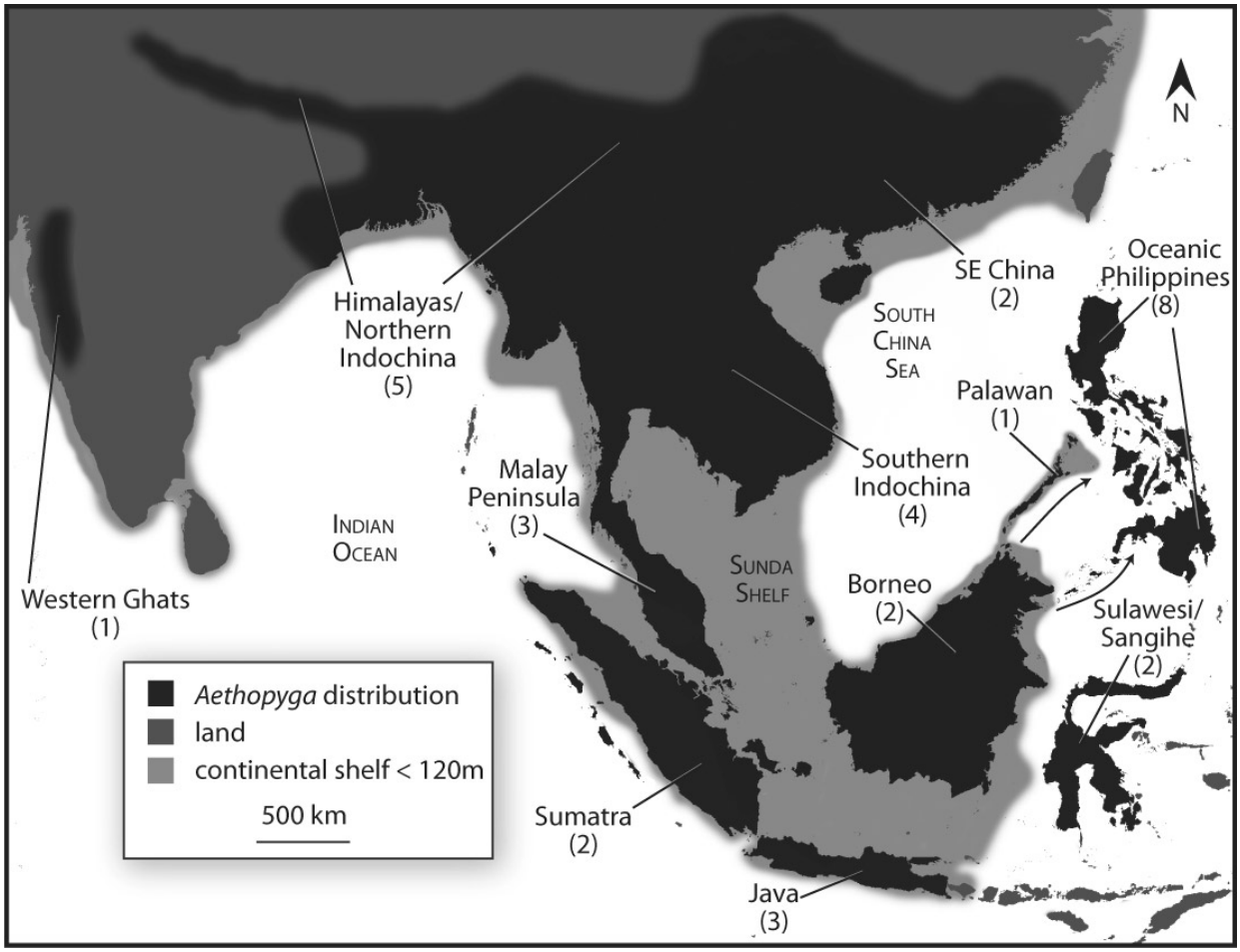


Figure 1-1. Map of Southeast Asia, with the approximate combined distribution of *Aethopyga* sunbirds shown in dark grey, along with species diversity found in selected geographical regions. The approximate boundary of subaerial land on the continental shelf during the Last Glacial Maximum (above the 120 m isobath) is highlighted in light grey. Arrows indicate the two colonization routes from Borneo to the oceanic Philippines (through Palawan and the Sulu archipelago).

Aethopyga comprises 18 recognized species and is the second largest genus of sunbirds. The species are distributed across the Indian subcontinent, Southeast Asia, Sundaland, Sulawesi and the Philippines (Delacour 1944; Cheke and Mann 2001; 2008, Fig. 1-1). The Philippines is a center of diversity for the genus – eight recognized species are found there, seven of which are endemic. Most species are 'polytypic', and many isolated forms have distinctive plumages, suggesting high levels of diversity unrecognized under current taxonomy (McGregor 1909; Peterson 2006; Gill and Donsker 2011). A second region of high *Aethopyga* species diversity is the Himalayan/northern Indochina region, which contains six species. Sundaland and southern

Indochina have relatively low diversity, with two to three species present in most areas. In addition to these regions, the widespread and variable *A. siparaja* is also present on Sulawesi, and single peripheral endemic species occur in the Western Ghats of India and Sangihe Island of northern Sulawesi. Most insular species are restricted to single islands or PAICs, whereas continental and Sundaland species are generally widespread. The more northern, montane species are seasonal altitudinal migrants; all of the other species are resident. Dispersal abilities have not been quantified, but the presence of *Aethopyga* populations in the oceanic Philippines, Sulawesi, Sangihe and the Nicobar Islands suggest that they occasionally cross deep ocean channels.

Aethopyga sunbirds are minute, weighing only 3.1–9.0 g, placing them among the smallest passerine birds. Males of *Aethopyga* are generally ornate – most species have iridescent structural colours such as metallic blues, violets and greens, as well as bright carotenoid pigments such as reds, yellows and oranges. Females of *Aethopyga* are generally dull greyish green above, with yellowish or whitish underparts; identification of some females to species by plumage can be challenging. As is typical of Nectariniidae, they are active and mobile feeders, consuming nectar and small insects, sometimes joining mixed-species foraging flocks. They inhabit a variety of forested and edge habitats, from lowland Dipterocarp forest to high montane heath forest.

No previous phylogenetic hypothesis exists for *Aethopyga*, although Delacour (Delacour 1944) hypothesized a Philippine origin for *Aethopyga* based on species richness, tongue morphology and plumage characters. Allopatric superspecies groups have been suggested based on plumage characteristics: Mindanao endemics *Aethopyga boltoni* and *A. linaraborae* (possibly including Luzon/Visayan *A. flagrans*); Philippine *A. shelleyi* and *A. bella*; Western Ghats

A. vigorsii and widespread *A. siparaja*; and Sundaland *A. temminckii* and *A. mystacalis* (Cheke and Mann 2008). Until recently, the last three species pairs have been considered conspecific (Delacour 1944; Cheke and Mann 2001; Mann 2002; Cheke and Mann 2008).

The purpose of this study is to formulate the first phylogenetic hypothesis for the *Aethopyga* sunbirds, and to use this framework to explore patterns of biogeography, colonization history and diversification, focusing on the roles of different types of isolation barriers (deep-water, shallow-water or intra-island) in the Philippine Archipelago. Additionally, our genetic data will provide a new perspective on species limits in *Aethopyga*, a group in which conservative taxonomy featuring 'polytypic species' may underestimate true species diversity.

Methods

Taxon sampling and molecular markers

We obtained 44 tissue samples for 15 of the 18 recognized *Aethopyga* sunbirds species (Gill and Donsker 2011), including all Philippine species (Appendix 1). In addition to recognized species, we split distinctive described subspecies and subspecies groups into operational taxonomic units, because they have previously been suggested as species (McGregor 1909; Peterson 2006). Species for which no tissue samples were available were not sampled; these were *Aethopyga vigorsii*, *A. eximia* and *A. mystacalis*. We included 10 sunbird (Nectariniidae) and flowerpecker (Dicaeidae) species as outgroups and rooted the tree with *Chloropsis* (Passeriformes: Irenidae), a relative of sunbirds (Barker et al. 2004). Where possible, we included multiple samples for each ingroup species for two reasons. First, we used samples of multiple subspecies or samples from geographically disjunct regions to obtain a preliminary estimate of intra-specific genetic structure. Second, we employed redundancy in the data set to guard against errors of

misidentification (male plumages are distinctive, but females of many *Aethopyga* species are extremely similar), mislabelling, or sample contamination. All samples with the exception of *Aethopyga duyvenbodei* (an unvouchered blood sample) were nitrogen-frozen or ethanol-preserved tissues associated with full voucher specimens deposited in museum collections (Appendix 1).

DNA extraction, amplification, sequencing, and sequence alignment

Genomic DNA was extracted from muscle tissue using a non-commercial guanidine thiocyanate method (Esselstyn et al. 2008). We used polymerase chain reaction (PCR) to amplify two coding mitochondrial genes and three unlinked nuclear introns to provide phylogenetic signal at multiple levels. Mitochondrial genes amplified included the entire coding NADH dehydrogase-2 (ND2) and NADH dehydrogenase-3 (ND3). Nuclear markers included autosomal beta-Fibrinogen intron 5 (Fib-5), autosomal transforming growth factor beta-2 intron 5 (TGFβ2-5), and Z-linked muscle skeletal receptor tyrosine kinase (MUSK). Primers used to amplify gene

Region	Primer name	Primer sequence	Reference
ND2 (1st)	L-5215	5'-TATCGGGCCCATACCCCGAAAAT-3'	Hackett (1996)
	H-5578	5'-CCTTGAAGCACTTCTGGGAATCAGA-3'	Hackett (1996)
ND2 (2nd)	L-347	5'-CCATTCCACTTCTGATTCCC-3'	Drovetski et al. (2004)
	H-6313	5'-CTCTTATTTAAGGCTTTGAAGGC-3'	Sorensen et al. (1999)
ND3	L-10755	5'-ACT TCCAATCTTTAAAATCTGG-3'	Chesser (1999)
	H-11151	5'-GATTTGTTGAGCCGAAATCAAC-3'	Chesser (1999)
Fib-5	Fib5	5'-CGCCATACAGAGTATACTGTGACAT-3'	Kimball et al. (2009)
	Fib6	5'-GCCATCCTGGCGATTCTGAA-3'	Kimball et al. (2009)
MUSK	MUSK-I3F	5'-CTTCCATGCACTACAATGGGAAA-3'	Kimball et al. (2009)
	MUSK-I3R	5'-CTCTGAACATTGTGGATCTCAA-3'	Kimball et al. (2009)
TGFβ2-5	TGFB2.5F	5'-GAAGCGTGCTCTAGATGCTG-3'	Kimball et al. (2009)
	TGFB2.6	5'-AGGCAGCAATTATCCTGCAC-3'	Kimball et al. (2009)

Table 1-1 Primers used for PCR and sequencing reactions.

regions (Hackett 1996; Chesser 1999; Sorenson et al. 1999; Drovetski et al. 2004; Kimball et al. 2009) are summarized below (Table 1-1); PCR reactions followed author-recommended protocols. We purified PCR products with ExoSAP-IT (USB, Cleveland, OH, USA), and performed cycle sequencing of purified PCR products with BigDye Terminator v3.1 Cycle Sequencing kits (Applied Biosystems, Carlsbad, CA, USA). Cycle sequencing reactions used the same primers as PCR, resulting in double stranded sequence reads for all taxa. We purified cycle sequencing products using ethanol precipitation, and analysed sequences on an ABI 3730 automated capillary DNA sequencer (Applied Biosystems). We used SEQUENCHER 4.10 (Genecodes, Ann Arbor, MI, USA) to reconcile chromatograms of complimentary strands. ND2, ND3 and TGFβ2-5 sequences for some taxa were generated for a separate study (Nyári et al. 2009). We reconstructed alignments for each gene using the online version of MUSCLE (Edgar 2004), and then verified alignments by eye. Sequences are archived on GenBank (KC122399–122612

Phylogenetic analysis and divergence time estimation

The mitochondrial ND2 and ND3 genes were concatenated and partitioned by codon in a mitochondrial-only data set. The nuclear introns Fib-5, TGFβ2-5, and MUSK were concatenated and partitioned by gene in a nuclear-only data set. The mitochondrial-only and nuclear-only data were also concatenated into a combined data set. JMODELTEST 0.1 (Posada 2008), using both the Akaike's information criterion (AIC) and Bayesian information criterion (BIC), selected a general time-reversible model with gamma-distributed rates among sites and invariant sites (GTR+I+G) for 1st and 3rd mitochondrial positions, and HKY+I+G model for 2nd positions. The HKY model was selected for the nuclear intron Fib-5, the HKY+G model for TGFβ5, and

the HKY+I+G model for MUSK. These models of sequence evolution were used for each analysis, except when noted.

We implemented Bayesian analysis in MRBAYES 3.1 (Ronquist and Huelsenbeck 2003) using paired Markov chain Monte Carlo (MCMC) runs of 10 million generations sampled every 5000 generations. To explore the potential pitfall of conflicting phylogenetic signal among loci (Maddison 1997; Degnan and Rosenberg 2006; Edwards et al. 2007; Heled and Drummond 2008; Degnan and Rosenberg 2009), we analysed the mitochondrial data set, individual nuclear loci, the nuclear-only data set, and the concatenated (all loci) data set separately. For each MCMC run, we used 2000 trees, minus a burn-in of 500 (after the runs had converged and reached stationarity) to create consensus trees.

To produce an ultrametric tree with divergence time estimates, we used relaxed clock Bayesian analysis invoked in BEAST 1.6.1 (Drummond & Rambaut, 2007) on the concatenated data set. Preliminary BEAST MCMC runs suffered from parameter interaction between the proportion of invariant sites and the gamma-distributed rates (visualized in TRACER 1.5; Rambaut and Drummond 2007), so we selected the simpler SDR06 model (Drummond & Rambaut, 2007) for mitochondrial genes and the HKY+G model for MUSK. We used the random local clock model (Drummond and Suchard 2010), relaxing the assumption of a strict molecular clock, and selected a birth-death process as a tree prior. We executed four independent MCMC runs of 30 million generations, sampled every 3000 generations, and discarded the first 3 million generations (1000 trees) of each run as burn-in, resulting in 9000 trees for each of the four runs. We combined the tree sets from the four runs to produce a maximum-credibility consensus tree. Appropriate fossils or island ages are not available to time-calibrate the *Aethopyga* tree, so we scaled the divergence time to the mitochondrial substitution rate. Using

average mitochondrial substitution rates from other studies of birds may derive a very rough estimate of actual time. We used a range of rates as a calibration to account for uncertainty: 2.4 and 3.3% per lineage per million years for the ND2 gene (Lerner et al. 2011).

In addition to the standard Bayesian analysis on the concatenated data set, we used the coalescent module *BEAST (Heled and Drummond 2010) to estimate a species tree, with settings similar to the standard BEAST 1.6.1 MCMC runs. We reduced the data set by removing outgroups with single samples as well as *Aethopyga duyvenbodei*, and used currently accepted *Aethopyga* species limits (Gill and Donsker 2011) to define branch tips. We implemented eight independent MCMC runs of 50 million generations, sampled every 5000 generations, and discarded the first 5 million generations (1000 trees) as burn-in. We combined tree sets from the eight runs to produce a maximum-credibility consensus tree, and also visualized the posterior distribution of species trees in DENSITREE 2.0 (Bouckaert 2010).

We assessed convergence and stationarity of MCMC runs using three methods. 1) We used the average standard deviation of split frequencies (ASDSF) in MRBAYES to assess topological congruence between independent runs, using 0.01 as the acceptable level of congruence. 2) We used TRACER 1.5 (Rambaut and Drummond 2007) to visualize the stationarity and convergence of parameter estimates and effective sample sizes (ESS, all greater than 200, with most in the thousands) between runs for MRBAYES and BEAST analyses. 3) We used the cumulative, slide, and compare functions in the online version of AWTY (Nylander et al. 2008) to visualize and examine stationarity and convergence of estimates of the posterior probabilities of clades.

For maximum likelihood tree estimation we used RAXML 7.2.6 (Stamatakis 2006; Stamatakis et al. 2008) and assessed support for clades with 1000 bootstrap replicates. ML

analysis was run on the nuclear, mitochondrial, and full matrices with the same partitioning schemes as in Bayesian analysis. All partitions were assigned the GTR+G model (Stamatakis et al. 2008).

Biogeographical reconstructions

To examine the biogeographical history of *Aethopyga*, we reconstructed biogeographical areas as ancestral states, with regions delineated by continental shelf and PAIC boundaries: continental (including Palawan), Mindanao PAIC, Luzon PAIC, Visayan PAIC, and Sulawesi. The Mindoro and Sulu PAICs were not included because they harbour only the widespread *Aethopyga bella*, which is found on all oceanic Philippine PAICs. We implemented ancestral state reconstruction using the maximum likelihood criterion in the multistate module in BAYESTRAITS 1.0 (Pagel et al. 2004) over 1000 trees sampled from the posterior distribution of the BEAST run. Using the Bayesian tree set rather than a single Bayesian consensus tree or maximum likelihood (ML) tree accounts for phylogenetic uncertainly. Likelihood-ratio tests (Pagel 1999) indicated that a single-rate model was a more appropriate fit than a more complex rate-matrix model. We summarized and averaged the 1000 maximum likelihood estimates from each node within the ingroup of the *Aethopyga* phylogeny. We selected biogeographical ML ancestral state reconstructions over other biogeographical reconstruction methods because it involves relatively few assumptions. For example, dispersal–vicariance analysis (DIVA; Ronquist 1997) penalizes dispersal, which is problematic in a dispersal-driven oceanic archipelago.

We also examined the potential role of four types of isolating barriers (intra-island, shallow-water, deep-water and intra-continental) across the *Aethopyga* phylogeny using a set of logical statements based on the following criteria. 1) If two lineages distributed within an island

coalesce, we inferred intra-island diversification for that node. 2) If two lineages currently separated by shallow water < 120 m (different islands within a PAIC) coalesce, we inferred isolation across shallow-water barriers. 3) If two lineages separated by deep water coalesced, we inferred isolation across deep-water barriers (the PAIC diversification hypothesis). 4) If two continental lineages coalesced, we inferred intra-continental diversification. When nodes did not conform to a single criterion due to uncertain biogeographical reconstructions, we did not infer the type of isolation barrier. This method of reconstructing types of isolating barriers assumes correct phylogenetic inference, no extinction, and that the arrangement of islands and PAICs was similar to current arrangements at the time of diversification, which they were for at least the past 5 million years (Hall 1998).

Results

Sequence characteristics

Sequences of the five genes yielded a data matrix of 3164 aligned bases (ND2: 1041, ND3: 351, Fib-5: 599, TGFβ2: 576, MUSK: 597). Of these bases, 1238 were variable (ND2: 561, ND3: 141, Fib-5: 195, TGFβ2: 146, MUSK: 195), and 875 were parsimony-informative (ND2: 489, ND3: 114, Fib-5: 96, TGFβ2: 75, MUSK: 101). All mtDNA sequences appeared to be genuine mitochondrial sequences rather than nuclear copies. Mitochondrial sequences lacked anomalous stop codons, lacked double peaks in chromatograms, and overlapping amplicons contained no conflicts.

We recovered several shared insertions and deletions (indels) in our intron sequences. In TGFβ2-5 sequences, a 14-bp insertion united *Arachnothera, Dicaeum, Chloropsis* and *Prionochilus*, a 3-bp insertion united *Arachnothera magna, Dicaeum, Chloropsis* and

Prionochilus, a 4-bp deletion united *Aethopyga* and *Leptocoma,* 10-bp and 2-bp deletions were shared by *Dicaeum,* a 2-bp deletion unites *Aethopyga shelleyi*/*A. temminckii*, and two separate 1-bp deletions were shared by *Aethopyga bella*/*A. christinae*. At the species level, a 1-bp deletion united *A. christinae*, and a 7-bp deletion united *A. boltoni*. An apparently homoplastic 2-bp deletion was shared by *A. temminckii* and *Cyanomitra olivaceus*. In MUSK sequences, 5-bp and 1-bp insertions united *Dicaeum*. At the species level an 11-bp insertion and a 2-bp deletion united *A. bella*, and a 1-bp insertion united *A. shelleyi*. In Fib-5 sequences, an 18-bp insertion united all samples of *A. siparaja*.

Preliminary results suggested that two female *Aethopyga* sunbird samples had been misidentified, which was confirmed after comparing the voucher specimens to a series of specimens from the species in question. Without voucher specimens and redundancy in the sampling, these misidentifications are likely to have gone unnoticed. The identity of the blood sample of *A. duyvenbodei* could not be confirmed due to the lack of an associated voucher specimen (Peterson et al. 2007).

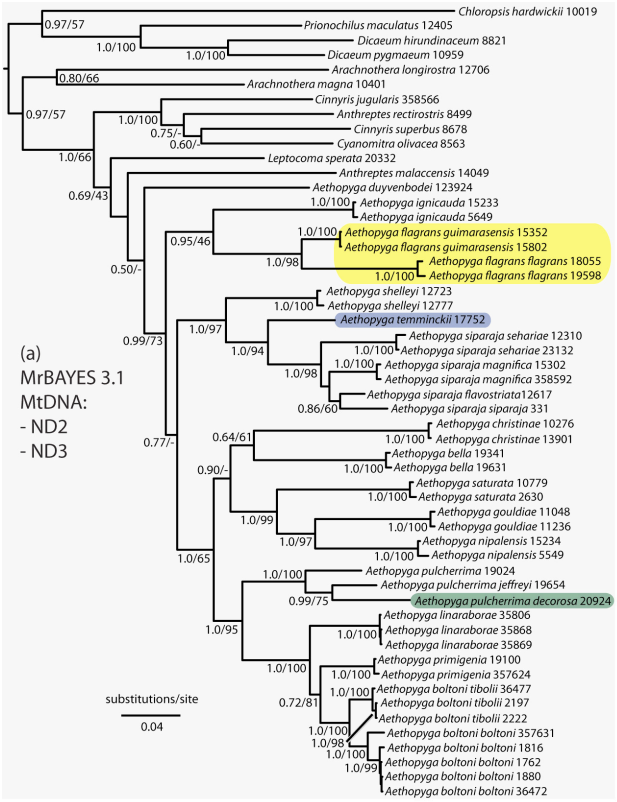
Phylogenetic analyses

Bayesian analysis of individual genes revealed conflicting phylogenetic signals between mitochondrial and nuclear markers (Maddison 1997; Degnan and Rosenberg 2006; Edwards et al. 2007; Degnan and Rosenberg 2009; Heled and Drummond 2010), but no strongly supported conflicts among nuclear loci within the ingroup. The mtDNA gene tree (Fig. 1-2a) supported the *Aethopyga flagrans* complex and *A. ignicauda* being sister taxa (posterior probability 0.95, 46% ML bootstraps), *A. temminckii* and *A. siparaja* being sister taxa (1.0, 94%), and *A. pulcherrima decorosa* and *A. p. jeffreyi* being sister taxa (0.99, 75%). In contrast, the nuclear-only tree (Fig.

1-2b) supported the *A. flagrans* complex and *A. pulcherrima* complex being sister taxa (1.0, 96%), *A. temminckii* and *A. shelleyi* being sister taxa (1.0, 100%), and the sample of *A. pulcherrima decorosa* being sister to *A. p. pulcherrima* and *A. p. jefferyi* (1.0, 100%). The results of the MRBAYES analysis with the full concatenated data set (Fig. 1-2c) were similar to the nuclear-only tree, but with different support for some nodes.

The results of the BEAST analysis with relative divergence times (Fig. 1-3) were similar to the combined MRBAYES analysis, although nodes generally had higher support. One topological difference was evident: *A. duyvenbodei* was sister to *Leptocoma sperata* in the BEAST analysis, rendering *Aethopyga* paraphyletic, although support for the node joining the two taxa was marginally significant (posterior probability 0.95). The *BEAST species tree (Fig. 1-2d) was similar to the BEAST, MRBAYES combined, and MRBAYES nuclear-only trees, but with much lower support for most nodes. Using a conservative range of calibrations of 2.4 and 3.3% per lineage per million years for ND2 (Lerner et al. 2011) as bounds for a molecular clock, most diversification of *Aethopyga* within the Philippines occurred in the Pliocene and Pleistocene when the arrangement of islands was similar to today, although it is possible that some deeper splits occurred in the Miocene when the islands of the Philippine archipelago were more isolated (Hall 1998).

Trees reconstructed with MRBAYES, RAXML, BEAST and *BEAST using the full data alignment were congruent, differing only at poorly supported nodes. These analyses all supported a monophyletic *Aethopyga* with the possible exception of *A. duyvenbodei*, which may be more closely related to the outgroup *Leptocoma sperata*. Within the core *Aethopyga*, *A. ignicauda* was sister to all other *Aethopyga*, which was divided three strongly supported


(a)
MrBAYES 3.1
MtDNA:
- ND2
- ND3
substitutions/site
0.04
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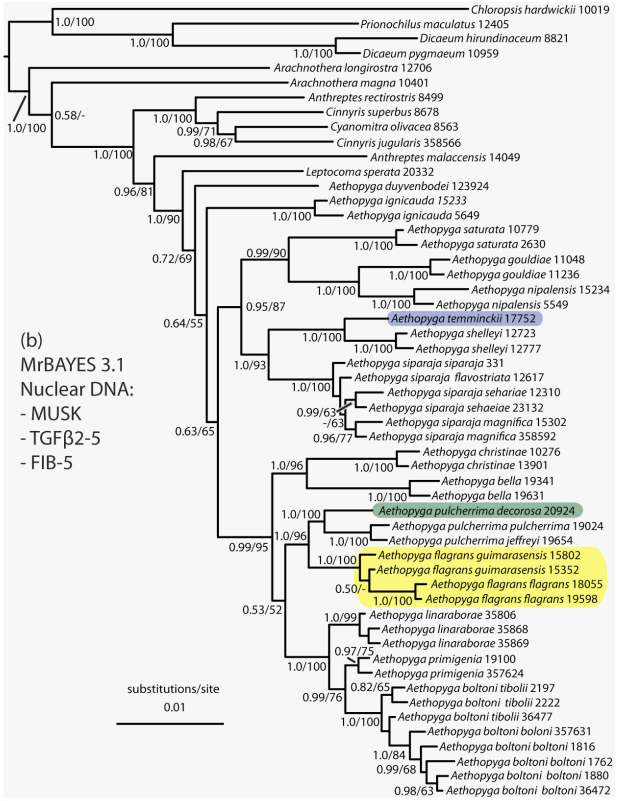
Prionochilus maculatus 12405
Dicaeum hirundinaceum 8821
Dicaeum pygmaeum 10959
Arachnothera longirostra 12706
Arachnothera magna 10401
Cinnyris jugularis 358566
Anthreptes rectirostris 8499
Cinnyris superbus 8678
Cyanomitra olivacea 8563
Leptocoma sperata 20332
Anthreptes malaccensis 14049
Aethopyga duyvenbodei 123924
Aethopyga ignicauda 15233
Aethopyga ignicauda 5649
Aethopyga flagrans guimarasensis 15352
Aethopyga flagrans guimarasensis 15802
Aethopyga flagrans flagrans 18055
Aethopyga flagrans flagrans 19598
Aethopyga shelleyi 12723
Aethopyga shelleyi 12777
Aethopyga temminckii 17752
Aethopyga siparaja sehariae 12310
Aethopyga siparaja sehariae 23132
Aethopyga siparaja magnifica 15302
Aethopyga siparaja magnifica 358592
Aethopyga siparaja flavostriata12617
Aethopyga siparaja siparaja 331
Aethopyga christinae 10276
Aethopyga christinae 13901
Aethopyga bella 19341
Aethopyga bella 19631
Aethopyga saturata 10779
Aethopyga saturata 2630
Aethopyga gouldiae 11048
Aethopyga gouldiae 11236
Aethopyga nipalensis 15234
Aethopyga nipalensis 5549
Aethopyga pulcherrima 19024
Aethopyga pulcherrima jeffreyi 19654
Aethopyga pulcherrima decorosa 20924
Aethopyga linaraborae 35806
Aethopyga linaraborae 35868
Aethopyga linaraborae 35869
Aethopyga primigenia 19100
Aethopyga primigenia 357624
Aethopyga boltoni tibolii 36477
Aethopyga boltoni tibolii 2197
Aethopyga boltoni tibolii 2222
Aethopyga boltoni boltoni 357631
Aethopyga boltoni boltoni 1816
Aethopyga boltoni boltoni 1762
Aethopyga boltoni boltoni 1880
Aethopyga boltoni boltoni 36472


(b)
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Nuclear DNA:
- MUSK
- TGFβ2-5
- FIB-5
substitutions/site
0.01
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Prionochilus maculatus 12405
Dicaeum hirundinaceum 8821
Dicaeum pygmaeum 10959
Arachnothera longirostra 12706
Arachnothera magna 10401
Anthreptes rectirostris 8499
Cinnyris superbus 8678
Cyanomitra olivacea 8563
Cinnyris jugularis 358566
Anthreptes malaccensis 14049
Leptocoma sperata 20332
Aethopyga duyvenbodei 123924
Aethopyga ignicauda 15233
Aethopyga ignicauda 5649
Aethopyga saturata 10779
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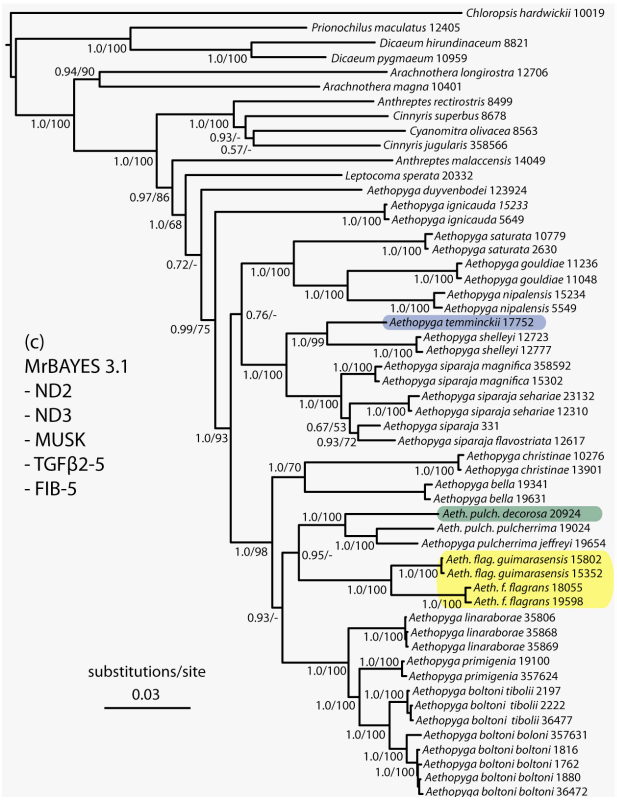
Aethopyga nipalensis 5549
Aethopyga temminckii 17752
Aethopyga shelleyi 12723
Aethopyga shelleyi 12777
Aethopyga siparaja siparaja 331
Aethopyga siparaja flavostriata 12617
Aethopyga siparaja sehariae 12310
Aethopyga siparaja sehaeiae 23132
Aethopyga siparaja magnifica 15302
Aethopyga siparaja magnifica 358592
Aethopyga christinae 10276
Aethopyga christinae 13901
Aethopyga bella 19341
Aethopyga bella 19631
Aethopyga pulcherrima decorosa 20924
Aethopyga pulcherrima pulcherrima 19024
Aethopyga pulcherrima jeffreyi 19654
Aethopyga flagrans guimarasensis 15802
Aethopyga flagrans guimarasensis 15352
Aethopyga flagrans flagrans 18055
Aethopyga flagrans flagrans 19598
Aethopyga linaraborae 35806
Aethopyga linaraborae 35868
Aethopyga linaraborae 35869
Aethopyga primigenia 19100
Aethopyga primigenia 357624
Aethopyga boltoni tibolii 2197
Aethopyga boltoni tibolii 2222
Aethopyga boltoni tibolii 36477
Aethopyga boltoni boloni 357631
Aethopyga boltoni boltoni 1816
Aethopyga boltoni boltoni 1762
Aethopyga boltoni boltoni 1880
Aethopyga boltoni boltoni 36472


(c)
MrBAYES 3.1
- ND2
- ND3
- MUSK
- TGFβ2-5
- FIB-5
substitutions/site
0.03
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Prionochilus maculatus 12405
Dicaeum hirundinaceum 8821
Dicaeum pygmaeum 10959
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Arachnothera magna 10401
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Aethopyga duyvenbodei 123924
Aethopyga ignicauda 15233
Aethopyga ignicauda 5649
Aethopyga saturata 10779
Aethopyga saturata 2630
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Aethopyga gouldiae 11048
Aethopyga nipalensis 15234
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Aethopyga shelleyi 12723
Aethopyga shelleyi 12777
Aethopyga siparaja magnifica 358592
Aethopyga siparaja magnifica 15302
Aethopyga siparaja sehariae 23132
Aethopyga siparaja sehariae 12310
Aethopyga siparaja 331
Aethopyga siparaja flavostriata 12617
Aethopyga christinae 10276
Aethopyga christinae 13901
Aethopyga bella 19341
Aethopyga bella 19631
Aeth. pulch. decorosa 20924
Aeth. pulch. pulcherrima 19024
Aethopyga pulcherrima jeffreyi 19654
Aeth. flag. guimarasensis 15802
Aeth. flag. guimarasensis 15352
Aeth. f. flagrans 18055
Aeth. f. flagrans 19598
Aethopyga linaraborae 35806
Aethopyga linaraborae 35868
Aethopyga linaraborae 35869
Aethopyga primigenia 19100
Aethopyga primigenia 357624
Aethopyga boltoni tibolii 2197
Aethopyga boltoni tibolii 2222
Aethopyga boltoni tibolii 36477
Aethopyga boltoni boloni 357631
Aethopyga boltoni boltoni 1816
Aethopyga boltoni boltoni 1762
Aethopyga boltoni boltoni 1880
Aethopyga boltoni boltoni 36472

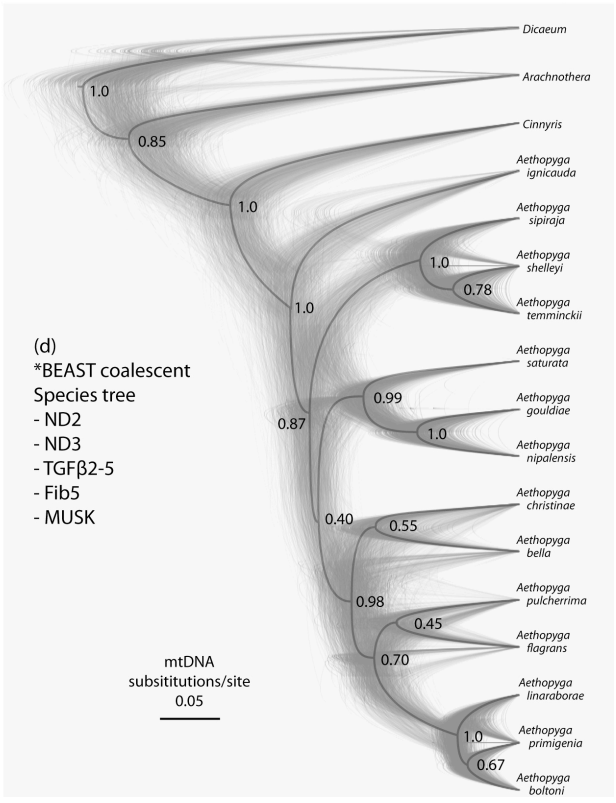
(d)
*BEAST coalescent
Species tree
- ND2
- ND3
- TGFβ2-5
- Fib5
- MUSK
mtDNA
subsititutions/site
0.05
Dicaeum
Arachnothera
Cinnyris
Aethopyga ignicauda
Aethopyga siparaja
Aethopyga shelleyi
Aethopyga temminckii
Aethopyga saturata
Aethopyga gouldiae
Aethopyga nipalensis
Aethopyga christinae
Aethopyga bella
Aethopyga pulcherrima
Aethopyga flagrans
Aethopyga linaraborae
Aethopyga primigenia
Aethopyga boltoni

Figure 1-2 (preceding page) *Aethopyga* phylogenies inferred from (a) mitochondrial DNA sequences only (MRBAYES consensus tree), (b) nuclear DNA sequences only (MRBAYES consensus tree), (c) concatenated nuclear/mitochondrial DNA sequences (MRBAYES consensus tree), and (d) nuclear/mitochondrial coalescent species tree (*BEAST 1.6 maximum clade credibility tree, superimposed on the cloudogram of the posterior tree distribution, visualized with DENSITREE 2.0). Support for each node on trees in panels (a), (b) and (c) is the Bayesian posterior probability followed by the percentage of maximum likelihood (ML) bootstraps performed in RAXML 7.2.6; support for tree in panel (d) is the posterior probability only. Posterior probabilities/ML bootstrap percentages under 50 are not reported. Note the alternative placements of the *Aethopyga flagrans* complex, *A. temminckii* and *A. pulcherrima decorosa* (highlighted) in the mitochondrial only (a) versus all other trees/methodologies. Both concatenated (c) and coalescent (d) trees are similar in topology, but differ strongly in support. For some tip labels, *Aethopyga* and specific epithets have been abbreviated.

clades: a Himalayan/Indochinese clade including *A. saturata*, *A. gouldiae* and *A. nipalensis*; a clade including the widespread *A. siparaja* complex, *A. temminckii* (Sundaland) and *A. shelleyi* (Palawan); and a clade including *A. christinae* (China/Indochina) and taxa endemic to the oceanic Philippine islands. Relationships among these three clades were poorly resolved.

Biogeographical reconstructions

Ancestral state reconstructions using geographical areas defined by sea levels at the Last Glacial Maximum (Fig. 1-3) strongly supported a continental core *Aethopyga* ancestor ($P = 0.98$). This continental distribution was conserved through the Indochina/Himalayan clade of *A. saturata*, *A. gouldiae* and *A. nipalensis*, as well as the Sunda shelf clade of *A. temminckii*, *A. shelleyi* and the *A. siparaja* complex. Within *A. siparaja*, described subspecies separately colonized the Philippines (*A. s. magnifica*) and Sulawesi (*A. s. flavostriata* group). Ancestral state reconstructions within the Philippine + *A. christinae* clade were more complex. The most likely origin for this group was within Mindanao ($P = 0.91$), with upstream colonization of the continental region by an *A. christinae* ancestor, although results do not reject an alternative scenario of multiple colonization events to the Philippines by both *A. bella* and the most recent common ancestor (MRCA) of *A. boltoni and A. pulcherrima*. The MRCA of *A. boltoni* and

A. pulcherrima apparently inhabited the Mindanao PAIC ($P = 0.95$), and both species diversified within the Mindanao PAIC and colonized the Luzon and Visayan PAICs.

Our assessment of the mode of diversification (Fig. 1-4) revealed that intra-island factors, shallow-water barriers (within-PAIC diversification), deep-water barriers (across-PAIC diversification), and intracontinental factors all played a role in the diversification of insular *Aethopyga*. Diversification across deep-water barriers was inferred to be the most common mode in exclusively insular taxa (five events), but intra-island diversification produced a montane radiation of sunbirds in Mindanao (four events). Shallow-water barriers only played a role in isolating *A. shelleyi* on Palawan from Sunda shelf *A. temminckii*.

Discussion

Gene tree incongruence

We observed strong phylogenetic incongruence between the mitochondrial and nuclear loci sequenced in our study. Although phylogenetic incongruence between loci may cause inaccurate estimation of tree topology (Maddison 1997; Degnan and Rosenberg 2006; Edwards et al. 2007; Degnan and Rosenberg 2009; Heled and Drummond 2010), the *BEAST tree (Fig. 1-4), which is free of this assumption, was similar to the nuclear-only MRBAYES (Fig. 1-2B), concatenated MRBAYES (Fig. 1-2c) and BEAST (Fig. 1-3) topologies, differing only in the node joining the three main *Aethopyga* lineages (which was unsupported in all three analyses). We postulate that the mtDNA data are misleading in this case (Degnan and Rosenberg 2009). Our biogeographical interpretations are based on the combined mtDNA/nuclear MRBAYES, BEAST and *BEAST analyses only; all had similar topologies and differed only at nodes without strong statistical support, which we interpreted as polytomies. Because a more complete Nectariniidae phylogeny

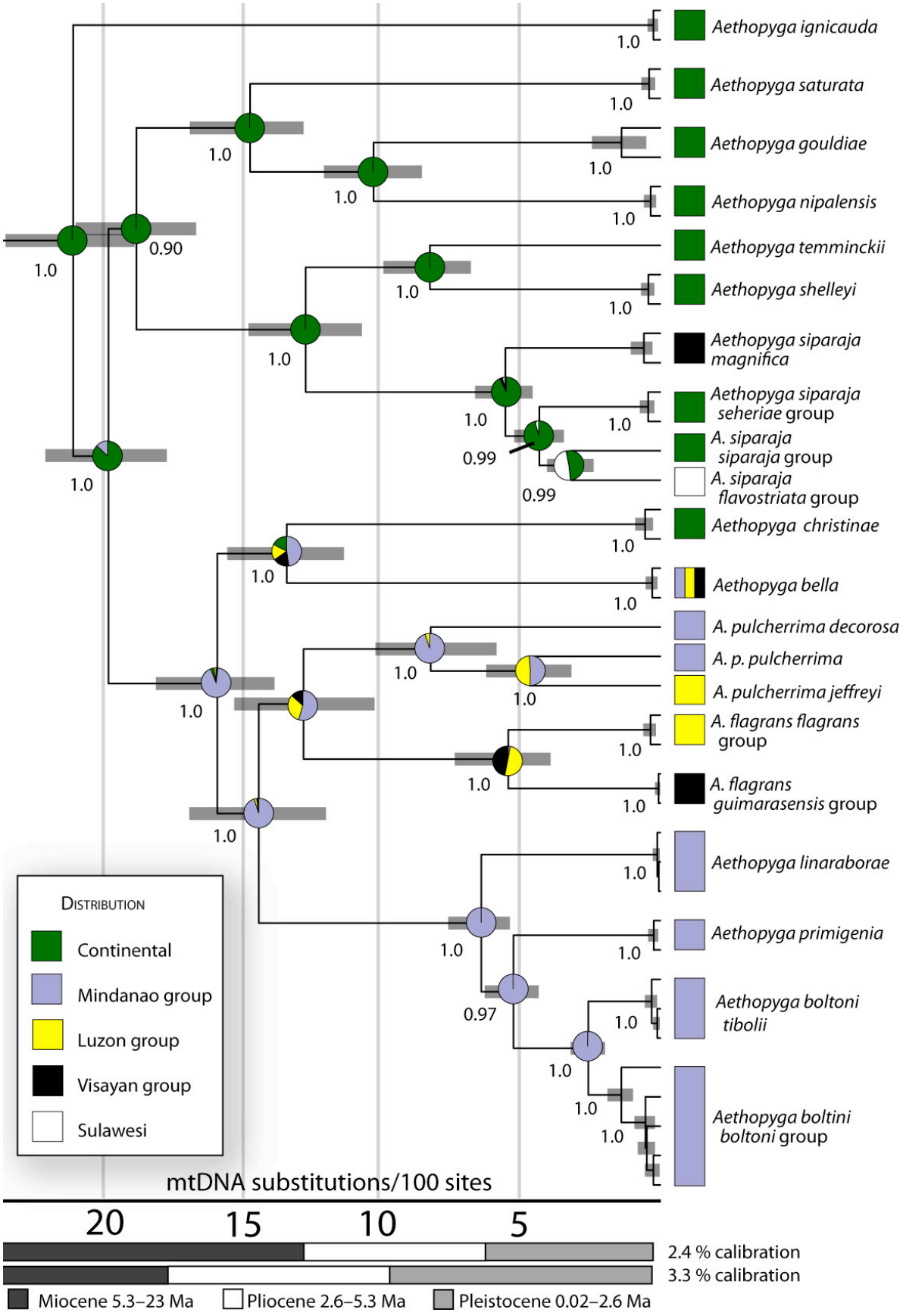
Aethopyga ignicauda
Aethopyga saturata
Aethopyga gouldiae
Aethopyga nipalensis
Aethopyga temminckii
Aethopyga shelleyi
Aethopyga siparaja magnifica
Aethopyga siparaja seheriae group
A. siparaja siparaja group
A. siparaja flavostriata group
Aethopyga christinae
Aethopyga bella
A. pulcherrima decorosa
A. p. pulcherrima
A. pulcherrima jeffreyi
A. flagrans flagrans group
A. flagrans guimarasensis group
Aethopyga linaraborae
Aethopyga primigenia
Aethopyga boltoni tibolii
Aethopyga boltini boltoni group
1.0
0.90
0.99
0.97
Distribution
Continental
Mindanao group
Luzon group
Visayan group
Sulawesi
mtDNA substitutions/100 sites
20
15
10
5
2.4 % calibration
3.3 % calibration
Miocene 5.3–23 Ma
Pliocene 2.6–5.3 Ma
Pleistocene 0.02–2.6 Ma

Figure 1-3 (preceding page) Approximate timescale and ancestral geography of *Aethopyga* diversification in Southeast Asia (maximum clade credibility tree from BEAST analysis, with BAYESTRAITS 1.0 ancestral state reconstruction). Tip labels are species or subspecies groups that we consider as operational taxonomic units; node support values are posterior probabilities; values less than 0.50 are not reported. Divergence times are scaled to the mtDNA substitution rate. Approximate time-scales are based on ND2 substitution rates of 2.4 and 3.3% per lineage per million years. Ancestral state reconstructions infer the ancestral geographical distribution at each node in the phylogeny. All outgroups were included in analysis, but only the core *Aethopyga* taxa are shown.

is needed to determine if *A. duyvenbodei* is sister to the core *Aethopyga*, or if its affinities lie with other sunbird genera, we do not discuss the biogeographical implications for this enigmatic species.

Aethopyga *biogeography and colonization history*

Ancestral state reconstructions strongly supported a continental ancestral of core *Aethopyga*, with four to five colonization events to oceanic islands, refuting Delacour's (1944) hypothesis of a Philippine origin. Most colonization events (*A. shelleyi*, *A. siparaja magnifica* and the *A. siparaja flavostriata* group) resulted in a single taxon colonizing a small area (Palawan, Visayan PAIC and Sulawesi, respectively). The exception to this pattern was the Philippine endemic *A. boltoni*/*A. pulcherrima* clade, which colonized the Mindanao PAIC and subsequently diversified. Ancestral state reconstructions also suggested that *A. christinae* recolonized Asia from a Philippine ancestor, although support was weak and the results do not reject an alternative scenario in which *A. bella* and the *A. boltoni*/*A. pulcherrima* MRCA colonized the Philippines independently from continental ancestors. Molecular results (12.2–14.6% uncorrected pairwise distance for ND2) suggest a long period of isolation between *A. christinae* and *A. bella*. Although they are sister taxa, molecular clock calibrations suggested a MRCA in the Pliocene or late Miocene. The large range gap between *A. christinae* and *A. bella* may be the result of extinction: two surviving geographically isolated species of a formerly more widespread clade.

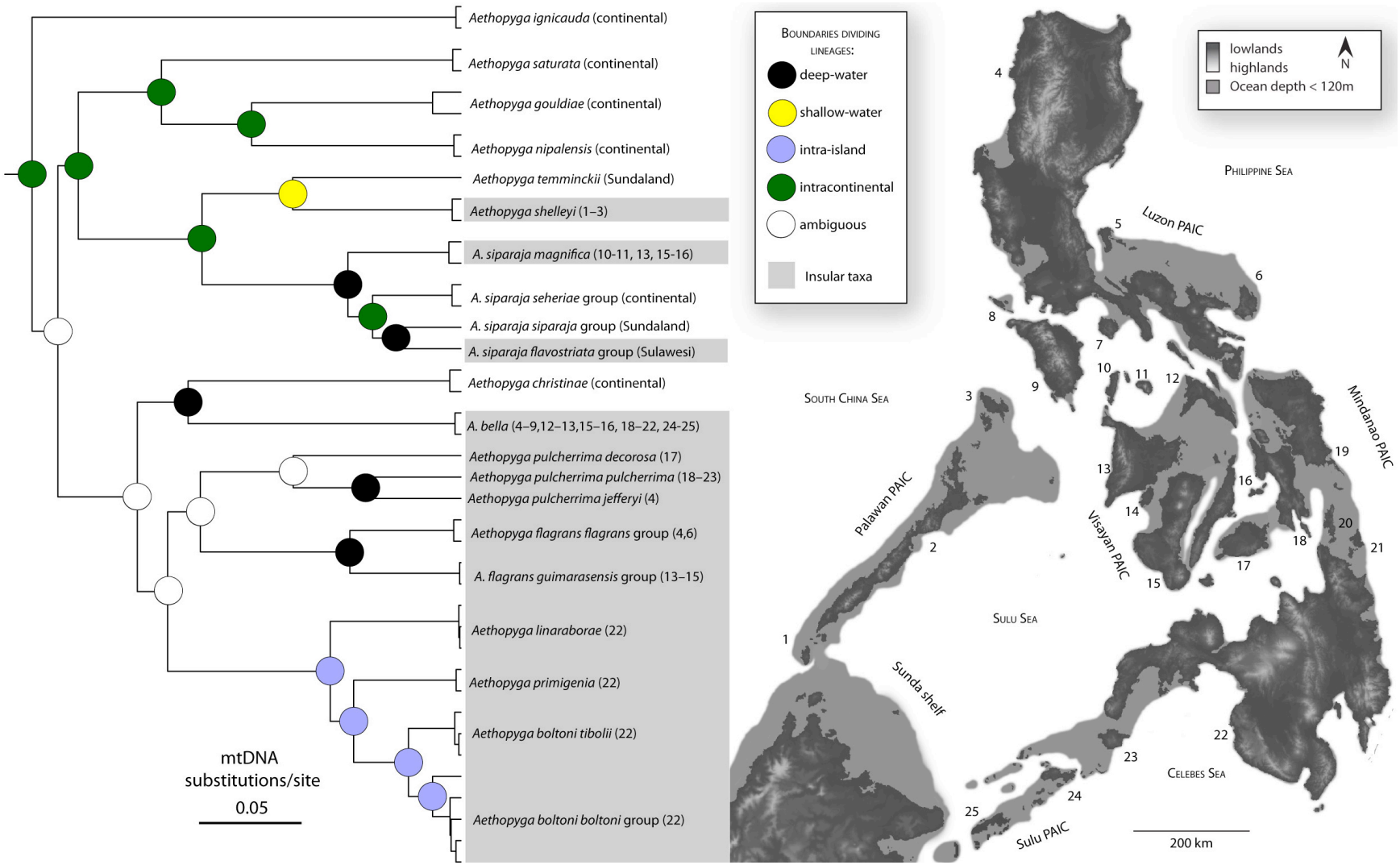
Aethopyga ignicauda (continental)
Aethopyga saturata (continental)
Aethopyga gouldiae (continental)
Aethopyga nipalensis (continental)
Aethopyga temminckii (Sundaland)
Aethopyga shelleyi (1–3)
A. siparaja magnifica (10-11, 13, 15-16)
A. siparaja seheriae group (continental)
A. siparaja siparaja group (Sundaland)
A. siparaja flavostriata group (Sulawesi)
Aethopyga christinae (continental)
A. bella (4–9,12–13,15–16, 18–22, 24-25)
Aethopyga pulcherrima decorosa (17)
Aethopyga pulcherrima pulcherrima (18–23)
Aethopyga pulcherrima jefferyi (4)
Aethopyga flagrans flagrans group (4,6)
A. flagrans guimarasensis group (13–15)
Aethopyga linaraborae (22)
Aethopyga primigenia (22)
Aethopyga boltoni tibolii (22)
Aethopyga boltoni boltoni group (22)
mtDNA substitutions/site
0.05
Boundaries dividing lineages:
deep-water
shallow-water
intra-island
intracontinental
ambiguous
Insular taxa
lowlands
highlands
Ocean depth < 120m
N
Philippine Sea
South China Sea
Sulu Sea
Celebes Sea
Luzon PAIC
Mindanao PAIC
Palawan PAIC
Visayan PAIC
Sulu PAIC
Sunda shelf
200 km

Figure 1-4 (preceding page) Inferred geographical barriers (deep-water, shallow-water, intracontinental, intra-island) reconstructed on the *Aethopyga* phylogeny (maximum clade credibility tree from BEAST). Insular taxa are outlined in grey boxes; tip labels are species or subspecies groups that we consider as operational taxonomic units. Numbers following each Philippine taxon refer to their geographical distribution in the Philippines, also shown on the map: 1, Balabac; 2, Palawan; 3, Calamian group; 4, Luzon; 5, Polillo; 6, Catanduanes; 7, Marinduque; 8, Lubang; 9, Mindoro; 10, Tablas; 11, Sibuyan; 12, Masbate/Ticao; 13, Panay; 14, Guimaras; 15, Negros; 16, Cebu; 17, Bohol; 18, Leyte; 19, Samar; 20, Dinagat; 21, Siargao; 22, Mindanao; 23, Basilan; 24, Jolo; 25, Tawi-Tawi. Philippine map highlights Pleistocene aggregate island complexes (PAICs) and Sunda Shelf boundaries, defined by the 120 m isobath (highlighted in grey). All outgroups were included in analysis, but only core *Aethopyga* taxa are shown; in some tips *Aethopyga* has been abbreviated.

The Javan endemic *A. eximia* has been considered closely related to *A. christinae* (Cheke and Mann 2008). If this assertion is correct, then *A. eximia* may fill part of the large range gap between Asian *A. christinae* and Philippine *A. bella* populations.

Consistent with the two-umbilici colonization hypothesis (Diamond and Gilpin 1983), our analyses supported *Aethopyga* colonization of the Philippines through both the northern umbilicus from the Sunda shelf to Palawan (one event), as well as the southern umbilicus from the Sunda shelf to Mindanao via the Sulu Archipelago (one to two events). However, we observed different patterns of diversification associated with each colonization route. Through the northern umbilicus, the ancestor of *A. shelleyi* colonized Palawan from Borneo, but there is no evidence that either *A. shelleyi* or its ancestors further colonized or diversified in the Philippines. Through the southern umbilicus, the *A. boltoni*/*A. pulcherrima* MRCA diversified within Mindanao, and further colonized the Luzon and Visayan PAICs, giving rise to nine operational taxonomic units (see taxonomic recommendations). These results support a pattern observed in other recent phylogenetic studies of Philippine birds: lineages that colonized via Palawan usually failed to invade the oceanic Philippines; lineages that colonize via the Sulu Archipelago to Mindanao continue to colonize further islands in the oceanic Philippines and to diversify (Jones and Kennedy 2008; Oliveros and Moyle 2010; Moyle et al. 2011).

Curiously, *A. siparaja magnifica* occurs only in the central Philippines (the Visayan PAIC, as well as the small islands of Tablas and Sibuyan), with no close relatives found in either the northern or the southern umbilici. This unique avian distribution is presumably the result of colonization of the Philippines via an umbilicus from Borneo, and subsequent extirpation of connecting populations. However, the *Aethopyga siparaja* complex has colonized across wider spans of ocean than any other *Aethopyga* taxon, with isolated taxa on Sulawesi and the Nicobar Islands. Our samples of *A. siparaja magnifica* from the islands of Sibuyan and Panay are from islands isolated across a deep-water barrier and show low sequence divergence (0.38% uncorrected *p*-distance for ND2); all other Philippine *Aethopyga* populations isolated across deep-water boundaries are strongly structured, except *A. bella* (Fig. 1-4). Given the apparent vagility of *A. siparaja*, direct colonization of the Visayas from Borneo is feasible.

Pleistocene sea-level change appears to have played a role in the biogeography and distributions of *Aethopyga* taxa in the Philippines and Sundaland, consistent with the PAIC hypothesis (Heaney 1986; Siler et al. 2010). Deep-water barriers between Philippine PAICs are congruent with phylogenetic structure in several lineages, notably between the *A. flagrans flagrans* and *A. f. guimarasensis* groups (Luzon PAIC/Visayan PAIC) and *A. pulcherrima pulcherrima* and *A. p. jefferyi* (Mindanao PAIC/Luzon PAIC). The timing of diversification in these lineages is consistent with Pleistocene climate fluctuations under the calibrations of 2.4% and 3.3% per lineage per million years.

The sister relationship between *A. shelleyi* and *A. temminckii* lends some support to the classic biogeographical hypothesis that the fauna of Palawan is more similar to that of Borneo than to the rest of the Philippines (Huxley 1868). However, high genetic divergence between *A. shelleyi* and *A. temminckii* suggests a long period of isolation between the two taxa, which

pre-dates the Pleistocene under the 2.4% and 3.3% rate calibrations. This long period of isolation between taxa supports an emerging view of a distinctive Palawan vertebrate fauna (Esselstyn et al. 2010).

Our reconstruction of the mode of diversification in the Philippines suggests that isolation within islands, and across shallow- and deep-water barriers all contribute to Philippine bird diversification. Consistent with the PAIC hypothesis, deep-water barriers are congruent with the majority (five) of insular cladogenic events. Of these five events, three coincide with the initial colonization of the Philippines (*A. siparaja magnifica*, *A. bella*, and the *A. boltoni*/*A. pulcherrima* MRCA), and two conform to boundaries between PAICs (*A. flagrans flagrans* group/*A. f. guimarasensis* group; *A. pulcherrima pulcherrima*/*A. p. jefferyi*). Only a single species pair (*A. temminckii*/*A. shelleyi*) is isolated across a shallow-water barrier. It is possible that isolation across shallow-water barriers is more prevalent in *Aethopyga*, but we lack samples of the two Javan endemic species, *A. eximia* (hypothesized to be related to *A. christinae*) and *A. mystacalis* (hypothesized to be closely related to and sometimes treated as conspecific with *A. temminckii*). If these hypothetical relationships (Cheke and Mann 2008) were supported, then isolation across shallow-water barriers would be consistent with three cladogenic events.

Diversification within Mindanao

In situ diversification best explains the radiation of four montane *Aethopyga* taxa in Mindanao because: 1) biogeographical reconstruction was unambiguous; 2) some taxa are sympatric, with no evidence of interbreeding, supporting reproductive isolation; and 3) the timescale is consistent with diversification after the proto-islands that comprise current-day Mindanao coalesced. We recovered four well-supported clades in this radiation: *A. linaraborae*, *A. primigenia*, the

A. boltoni boltoni group and *A. b. tibolii*. Populations of *A. linaraborae* (south-eastern Mindanao), the *A. b. boltoni* group (central and western Mindanao) and *A. b. tibolii* (south-western Mindanao) are allopatric, but *A. primigenia* (Mindanao except the south-east) overlaps broadly with the *A. b. boltoni* group without any evidence of interbreeding. The time-scale of the Mindanao *Aethopyga* radiation, given our multiple calibrations (montane Mindanao *Aethopyga* MRCA estimated at 1.6–3.0 Ma) is more consistent with Pleistocene/late Pliocene diversification within a consolidated Mindanao (Hall 1998; Sanguila et al. 2011) than Miocene diversification on a landscape of multiple proto-islands, a scenario invoked for island-arc systems of Sulawesi (Evans et al. 2003) and Hispaniola (Sly et al. 2011).

Mindanao is the world's 19th largest island, at 97,000 km^2, but it is a small island to hold an endemic bird radiation (Coyne and Price 2000; Kisel and Barraclough 2010). The only other single islands to contain such radiations are the much larger Madagascar (587,000 km^2) and New Guinea (785,000 km^2: a continental island that was joined with Australia in the Pleistocene; (Diamond 1977). We hypothesize that the isolated mountain ranges in Mindanao (approximately 18,000 km^2 of montane forest is above 1000 m) are themselves an archipelago of sky-islands, which have allowed isolation and allopatric speciation, as has occurred in many island archipelagos of similar area, such as the Galapagos (45,000 km^2), the Solomon Islands (28,000 km^2), Hawaii (28,000 km^2) and Fiji (18,000 km^2). Montane Mindanao hosts many birds with distinctive subspecies distributed across isolated mountain ranges (Dickinson et al. 1991; Kennedy et al. 2000), and a detailed phylogeographical inquiry may further expand the pattern of intra-Mindanao allopatric diversification to a variety of avian groups.

Taxonomic recommendations

Our analysis strongly supports a monophyletic core *Aethopyga*, containing all species except *A. duyvenbodei*. Placement of this enigmatic taxon, endemic to Sangihe Island in Indonesia, is uncertain. Molecular results suggest that *A. duyvenbodei* is an isolated relict with no close relatives, which is mirrored by several unique plumage and morphological characters not found in other *Aethopyga* species: yellow eye-arcs and lore stripes; a straighter, thicker, longer bill; and an evenly rounded tail with a white web on the outer rectrices. Additionally, it is unclear if *A. duyvenbodei* has the distinctive tongue morphology of the core *Aethopyga*, and thus uncertain if Delacour (1944) used tongue morphology or plumage similarity to place *A. duyvenbodei* within *Aethopyga*. A wide sampling of Nectariniidae will be necessary to resolve the relationship of *A. duyvenbodei* within the sunbirds, and until then it may be tentatively maintained in *Aethopyga*, or resurrected as the monotypic *Duyvena* (Mathews 1925).

Our molecular results suggest that the taxonomy of *Aethopyga* is overly conservative, especially in the Philippine archipelago. All the operational taxonomic groups that are focused on the Philippines differ substantially from their geographically isolated sister groups, both in the genetic markers in our study and also by distinctive plumage characters. We recommend treating *Aethopyga magnifica*, *A. decorosa*, *A. jefferyi*, *A. guimarasensis* and *A. tibolii* as distinct species (McGregor 1909; Delacour 1944; Kennedy et al. 1997; Peterson 2006).

We recovered two clades within *A. flagrans* pertaining to subspecies groups (Peterson 2006) which differed by 7.8–10.4% ND2 *p*-distance and four fixed plumage differences in males (*A. f. flagrans* group: green nape and back, red–orange belly spot, dull greenish flanks, iridescent crown patch extends only to eyes; *A. f. guimarasensis* group: maroon nape and back, yellow–orange belly spot, bright yellow flanks, iridescent crown patch extends beyond eyes). These

clades were originally described as separate species – *Aethopyga flagrans*, endemic to Luzon and Catanduanes, and *Aethopyga guimarasensis*, endemic to Panay, Negros and Guimaras. The two species were subsequently lumped by Delacour (1944) even though he noted that the two forms were 'well-marked'. Parkes (1963) described two more subspecies, but these are likely to represent subtle seasonal, clinal or individual variation (Parkes 1963; Peterson 2006). We thus recommend resurrecting *Aethopyga flagrans* (flaming sunbird) and *Aethopyga guimarasensis* (maroon-naped sunbird) as distinct species.

Phylogenetic results and genetic divergences among subspecies of *Aethopyga pulcherrima* suggest a unique biogeographical scenario in the Philippines. Three recognized subspecies (*A. p. jefferyi*, Luzon; *A. p. decorosa*, Bohol; and *A. p. pulcherrima*, Mindanao PAIC except Bohol) were originally described as species but later lumped (Delacour 1944). Our genetic data suggest that each of the three subspecies is highly distinct; mtDNA *p*-distances range from 7.3% between *A. p. jefferyi* and *A. p. pulcherrima* to 10.9% between *A. decorosa* and *A. pulcherrima*, and nuclear introns unequivocally differentiate each taxon (Fig. 1-2b). Furthermore, fixed plumage characters can separate males from each taxon: *A. decorosa* has iridescent steel-blue wing coverts rather than green, and the red–orange breast spot is greatly reduced or lacking (McGregor 1909; Peterson 2006; Cheke and Mann 2008). *Aethopyga pulcherrima pulcherrima* and *A. p. jefferyi* differ more subtly. *Aethopyga p. jefferyi* has a larger bill, iridescent green edging on the tertials and secondaries, and has a blue-green iridescent tail; *A. p. pulcherrima* has a smaller bill, lacks iridescent tertials and secondary edging, and has a green iridescent tail. Although some plant species are endemic to Bohol (Barcelona et al. 2006), no vertebrate species is currently considered a Bohol endemic (Heaney 1986; Kennedy et al. 2000); R. M. Brown, Univ. Kansas, pers. comm.). Future evaluation of distinctive bird

subspecies described from Bohol, such as *Rhinomyias ruficauda* and *Sterrhoptilus nigrocapitata*, may show that avian endemism in Bohol is more prevalent than previously appreciated. We recommend resurrecting all three forms as species: *Aethopyga pulcherrima* (metallic-winged sunbird), *Aethopyga jefferyi* (Luzon sunbird; McGregor 1909), and *Aethopyga decorosa* (Bohol sunbird; McGregor 1909).

Within *Aethopyga siparaja*, the mitochondrial data revealed deep divergences between morphologically distinct subspecies groups, which suggest that *A. siparaja* might be treated as a complex of allospecies. Molecular results and plumage/morphology characters support at least four groups (each with 4.8–7.5% mtDNA *p*-distance, but undifferentiated in nuclear loci used in this study): *A. magnifica* (Philippines), *A. flavostriata* group (Sulawesi; including *A. beccarii*), *A. siparaja* group (Sundaland; including *A. nicobarica*, *A. heliogona*, *A. natunae* and *A. trangensis*) and the *A. seheriae* group (Indochina/Indian subcontinent, including *A. owstoni*, *A. tonkinensis*, *A. mangini*, *A. insularis* and *A. cara*). The strongly supported placement of the distinctive Philippine species *A. magnifica* as sister to all other *A. siparaja* samples supports other research documenting isolation of Philippine bird populations (Lohman et al. 2010). Molecular results, supported by current geographical isolation and distinctive fixed plumage and morphological characters including large size, black underparts in the male, and the combination of red wings/tail and a plain back in the female (Peterson 2006; Cheke and Mann 2008), support species status of *Aethopyga magnifica* (magnificent sunbird; McGregor 1909). Further splits in the *A. siparaja* complex may be warranted but require denser geographic sampling of genetic markers and/or a rigorous examination of specimen material.

The phylogeny rejects previous taxonomic treatments which have lumped the phenotypically similar *A. shelleyi* of Palawan and *A. bella* of the oceanic Philippines into a single

species (Delacour 1944), or as a pair of closely related sister species (Cheke and Mann 2008). Overall similarity in these species appears to be a remarkable example of plumage phenotype convergence.

When describing *Aethopyga linaraborae*, Kennedy et al. (1997) considered the new species to be most similar to *A. boltoni* based on plumage characters. However, they refrained from suggesting a sister relationship because the affinities of other *Aethopyga* species in the Mindanao region were unclear. Despite overall plumage similarity between *A. boltoni* and *A. linaraborae*, we found *A. boltoni* to be sister to *A. primigenia*, justifying the caution of Kennedy et al. (1997). Within *A. boltoni*, we found mtDNA divergence between subspecies *A. b. boltoni*/ *A. b. malindangensis* and *A. b. tibolii* (3.8–4.1% *p*-distance), and nuclear introns support two groups (Fig. 1-2b). These relationships, combined with subtle phenotypic differences (smaller body size and overall paler plumage in *A. b. tibolii*; (Kennedy et al. 1997; Peterson 2006) support treating *A. tibolii* (T'boli sunbird) as a species. Although we interpret this evidence as supporting treatment as two species, *A. boltoni* and *A. tibolii* are the least well-differentiated *Aethopyga* taxa that we consider splitting. We advocate further evidence from future sampling efforts, increased sampling of genetic markers, and a deeper examination of specimen material to increase support for a taxonomic change.

Chapter 2*

Phylogeography of the *Robsonius* ground-warblers (Passeriformes: Locustellidae) reveals an undescribed species from northeastern Luzon, Philippines

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Abstract

The *Robsonius* ground-warblers are forest birds endemic to the Luzon Island complex in the Philippine archipelago. Their systematic relationships have long remained ambiguous; until recently they were included in the Timaliid genus *Napothera*. Two *Robsonius* species are currently recognized based on plumage differences: *R. rabori* from northern Luzon in the Cordillera Central and the northern Sierra Madre, and *R. sorsogonensis* from southern Luzon and Catanduanes Island. Recent specimen collections, including the first adult specimen from the Cordillera Central, establish plumage differences between Cordillera and Sierra Madre *Robsonius rabori* populations, indicating a third diagnosable population within Luzon. These differences have gone unnoticed because *R. rabori* was described from a single juvenile specimen. Molecular phylogenetic data further support the hypothesis that three highly-divergent taxa occur across the Luzon Island complex: *Robsonius rabori* is known only from the northern Cordillera Central in Ilocos Norte; an undescribed taxon (formerly included in *R. rabori*) occurs in the northern Sierra Madre Mountains in Cagayan, Isabela, Aurora, and Nueva Vizcaya provinces; and *R. sorsogonensis* occurs in southern Luzon (Bulacan and Laguna provinces), the Bicol Peninsula, and on Catanduanes Island. The existence of three putatively allopatric species within the Luzon island complex highlights the role of *in situ* diversification in island systems, and brings attention to the need for forest conservation efforts to protect geographically restricted populations throughout the Luzon Island complex.

Introduction

In 1959, D. S. Rabor led an expedition to Ilocos Norte Province in northwestern Luzon Island, Philippines. Inland from the small, coastal village Pagudpud, the team collected a single juvenile of a long-legged, long-tailed, medium-sized passerine that differed strikingly from any known species. Rand (1960) described the species as *Napothera rabori*, believing it was related to Southeast Asian *Napothera* babblers (Timaliidae). Rabor secured two more juveniles at Mt. Cagua in Cagayan Province, northeastern Luzon, the following year; and four more specimens (adults and juveniles) from Sorsogon Province in the southern end of Luzon in 1961. The southern birds differed from the northern ones in lacking the rusty tinge on the head present in the juvenile northern specimens. Rand and Rabor (1967) named the southern birds *N. sorsogonensis*, after the type locality. Thus, within two years, two species of a unique and enigmatic passerine group were discovered from the distant ends of Luzon Island.

Approximately a decade after the initial discoveries, DuPont (1971a,b) received a specimen from Laguna, in central Luzon, and declared that it was intermediate between *N. rabori* and *N. sorsogonensis*, notwithstanding that he was comparing adults and juveniles. He lumped *N. rabori* and *N. sorsogonensis* into a single species, and named the Laguna birds as a new subspecies, *N. r. mesoluzonica*.

Ornithological exploration in the 1980s and 1990s began to clarify the natural history and distribution of these birds, until then virtually unknown in life, which led to questions about their systematic relationships. Goodman and Gonzales (1990) observed an individual flipping leaf litter and wood debris while walking on the ground, presumably foraging for insects. De Roever (1990) observed an individual walking and running with its tail cocked, and likened it to a small rail or a Neotropical antthrush. Lambert (1993) observed a pair walking and foraging on the

forest floor, noted that this behavior would be unusual for *Napothera* (other *Napothera* species hop), and suggested that the species may belong in another genus. Harrap and Mitchell (1994) described the song—high-pitched phrases given from a horizontal branch or log—as similar to those of *Bradypterus* or *Urosphena* warblers, and advocated placing the complex in its own genus based on song and behavior.

Collar (2006) synthesized the natural history observations and morphological evidence, and moved the *rabori* complex to a new genus within the Timaliidae, which he named *Robsonius*. He also returned to Rand and Rabor's (1967) treatment of two species, *R. rabori* and *R. sorsogonensis* (including *R. s. mesoluzonica*), based on four distinctive plumage differences between the two taxa. In a comprehensive molecular phylogeny of the babblers, Moyle et al. (2012) determined that *Robsonius* fell far outside of the main babbler lineages; thus, removal from *Napothera* was justified. Most recently, Oliveros et al. (2012) determined that *Robsonius* represents a lineage sister to the grassbirds and allies (Locustellidae), and coined a new English name for the genus, the ground-warblers.

In June 2011, a field team from the University of Kansas Biodiversity Institute, Philippine National Museum, and University of Utah visited the forests of Ilocos Norte to survey terrestrial vertebrates and their parasites. The team surveyed two localities south of the small village of Adams, only 5–10 km from where Rabor and his team collected the unique, juvenile type specimen of *R. rabori*. We collected an adult *Robsonius* specimen, salvaged from a mammal trap, which differed in several plumage characters from all other adult *Robsonius* specimens. Because of these plumage differences, we investigated the molecular phylogeographic structure within the *Robsonius* ground-warblers to assess whether the

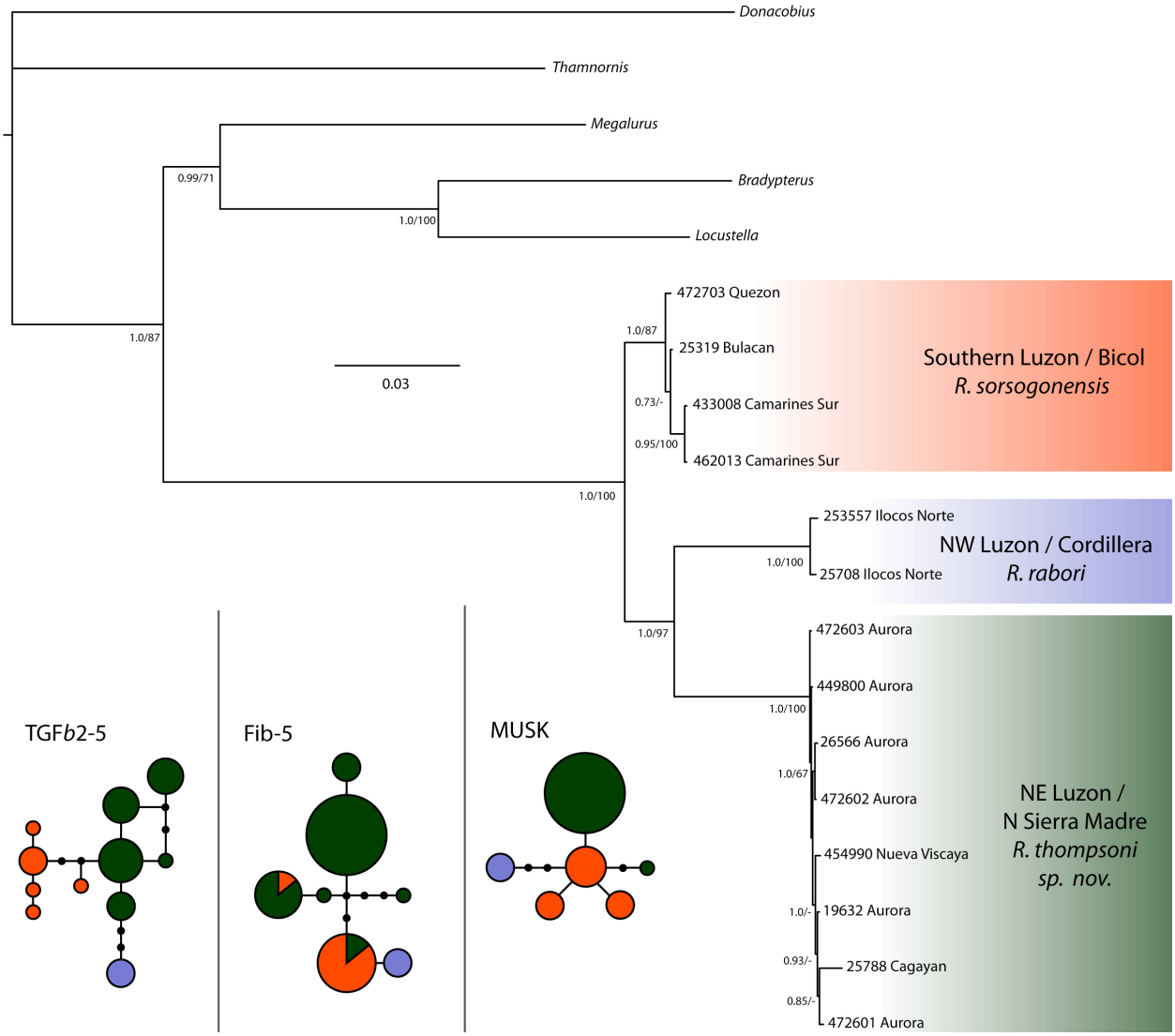

Figure 2-1. Bayesian consensus tree of the concatenated six-gene dataset (cytochrome *b*, ND2, ND3, TGF*b*2-5, Fib-5, MUSK) and phased haplotype networks of the three nuclear introns. Each color in the haplotype networks corresponds to one of the three *Robsonius* clades; black circles represent unsampled haplotypes. Node support values indicate Bayesian posterior probability/maximum likelihood bootstrap percentages; scale bar indicates 0.03 substitutions per site.

differences reflected individual variation in a poorly known group, or a suite of distinct, diagnosable taxa. Analysis of the data revealed (Fig. 2-1) that *Robsonius* populations from the southern, northeastern, and northwestern sectors of Luzon are genetically (based on mitochondrial DNA and nuclear introns) and morphologically distinct, and that an un-named lineage of ground-warbler is present in the northern Sierra Madre Mountains of northeastern

Luzon Island (Fig. 2-2). Because the name *R. rabori* applies to the species occurring in the Cordillera in Ilocos Norte (northwestern Luzon), the northern Sierra Madre birds, long attributed to *R. rabori*, remain undescribed, long hidden from taxonomic recognition because the adult plumage of *R. rabori sensu stricto* was unknown. We proudly name this species:

Robsonius thompsoni

Sierra Madre Ground-Warbler

Holotype. Philippine National Museum (PNM) 20006; originally catalogued as University of Kansas Biodiversity Institute (KU) 114678, adult female (skull 100% ossified, no bursa), KU tissue number 19632, collected on 18 June 2009 in the Philippines, Luzon Island, Aurora Province, San Luis Municipality, 12 km SW Baler (N 15.680°, E 121.529°, 525 m). This individual was net-captured in secondary lowland forest, and prepared as a study skin by Jameson B. Reynon.

Description of Holotype. Adult female; ovary 6 x 3 mm; light fat; mass 63 g; molt on wing, breast, and nape; stomach contents insect parts; maxilla dark brown, mandible pale gray; iris dark brown; legs and feet light brown. Plumage color descriptions follow Smithe (1975). Crown and nape amber, with dusky brown tips to individual feathers, auriculars amber. Lores white with black tips to individual feathers, thin eyering whitish; small area of bare gray skin behind eye. Throat white, with black tips to individual feathers; malar stripe black, formed of feathers with white bases; submoustachial stripe white with black feather edging. Black feather tips on the lower throat and upper breast form a necklace of spots, which separates the primarily white throat from the gray breast. Breast medium neutral gray, with feather shafts slightly paler;

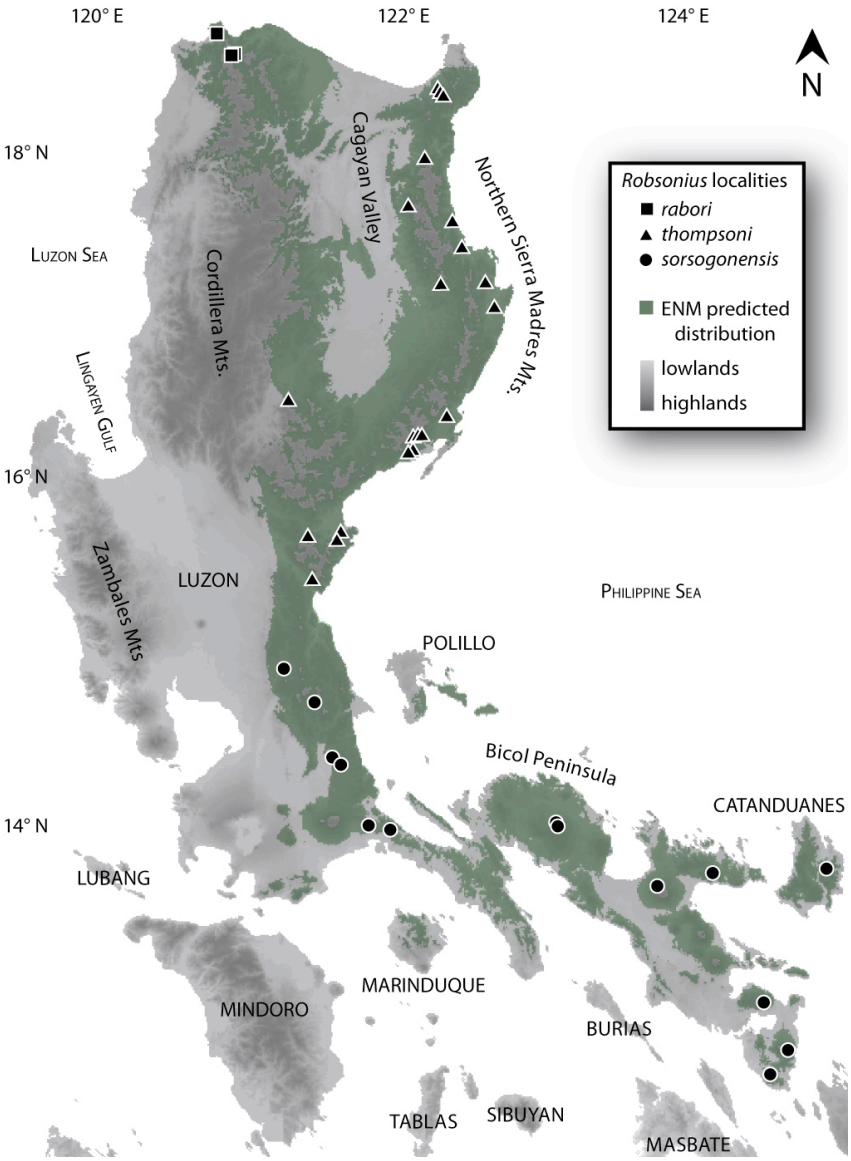

Figure 2-2. *Robsonius* distribution in the Luzon Island Complex in the Philippine Archipelago, which includes Luzon, Catanduanes, Polillo, and Marinduque. Areas presenting suitable environmental conditions for *Robsonius* (inferred from ecological niche models) are shown in green. All known *Robsonius* localities (specimens and observations), used to train models, are displayed on top of the modeled distribution.

belly whitish; flanks dusky brown, with cinnamon-brown to chestnut tinge. Back cinnamon-brown with dusky brown tips to individual feathers, long fluffy rump feathers form a thick mat and are dusky brown with a chestnut tinge; white feather tips form a concealed white rump-band; uppertail and undertail coverts, and tail dusky brown with chestnut tinge. Wings chestnut to dusky brown, with individual feathers dusky brown with broad chestnut edging, so that the wing

appears mostly chestnut when folded. Alula and wing coverts broadly tipped with white, so that the folded wing has several bars of white spots. Outer three primaries also tipped with white, although not visible in the folded wing.

Diagnosis. Adult plumage: *Robsonius thompsoni* (Fig. 2-3C) is most similar to *R. rabori* (Fig. 2-3A), but differs in three plumage characters: presence of a necklace of black spots (lacking in *R. rabori*), black feather tips on the throat / submoustachial (pale gray in *R. rabori*), and a uniform gray breast with pale feather shafts and faint darker edging (in *R. rabori,* breast feathers have broad white bases and centers and gray edges, lending to a scaled appearance). *Robsonius thompsoni* differs from *R. sorsogonensis* (Fig. 2-3E) in four plumage characters: amber crown, nape, and auriculars (uniform dark gray with white feather shafts on the auriculars in *R. sorsogonensis*), dark gray to blackish tips on throat feathers (unmarked white in *R. sorsogonensis*), and pale feather shafts in the gray breast band (uniform gray without pale feather shafts or feather bases in *R. sorsogonensis*). Juvenile plumage: from a limited number of specimens, *R. thompsoni* ($N = 4$) and *R. rabori* ($N = 1$) are not distinguishable from one another (Fig. 2-3B and 2-3D). Overall juvenile plumage is similar to adults, but throat, back, and underparts variable cinnamon-brown to olive brown with paler feather bases; crown, nape, and auriculars similar to those of adults, but with uniform amber lores and eyering. Juvenile *R. sorsogonensis* (Fig. 2-3F; $N = 4$) are similar to *R. rabori* and *R. thompsoni*, except that underparts (especially flanks) are richer chestnut brown, and the crown, nape, auriculars, lores, and eyering are cinnamon brown.

Vocalizations. All three *Robsonius* species give similar, extremely high-pitch (7.5–10.0 kHz) songs, from the ground or an elevated perch. Each song bout is approximately 1.6–2.2 sec in duration, and generally consists of 3–4 variable phrases with ascending and descending notes.

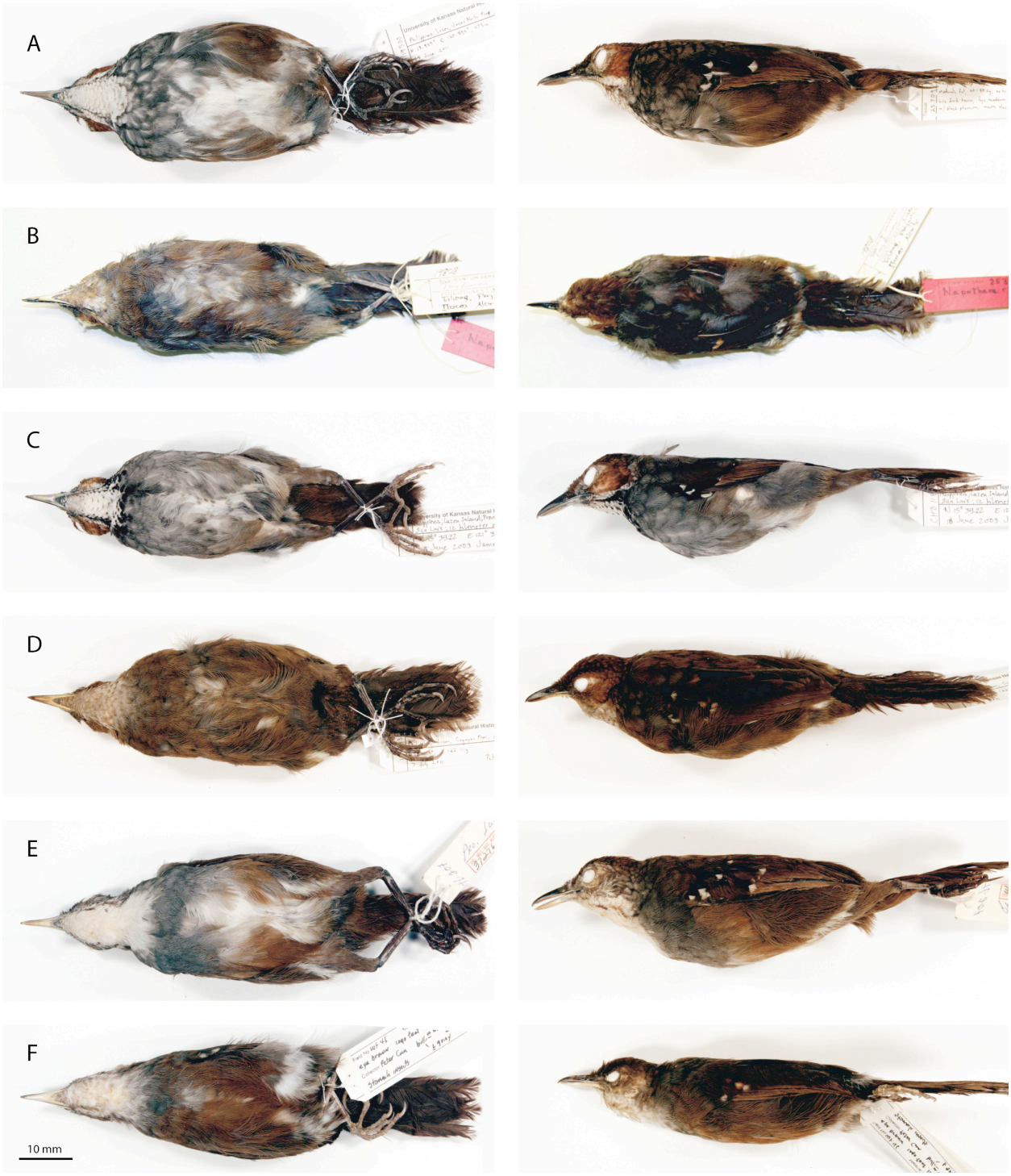

Figure 2-3. Representative specimens of adult and juvenile plumages of all three *Robsonius* species, viewed ventrally (first column) and laterally (second column). A: adult *R. rabori* KU 119500), B: juvenile *R. rabori* (FMNH 253557, holotype), C: adult *R. thompsoni* (PNM 20144, holotype), D: juvenile *R. thompsoni* (KU 119893), E: adult *R. sorsogonensis* (DMNH 37276), F: juvenile *R. sorsogonensis* (CM 153961).

Each phrase is separated by a brief (0.1–0.2 sec) pause. Individuals give song bouts approximately every 5–10 sec when singing regularly. Because of small sample sizes (*rabori*, $N = 1$; *thompsoni*, $N = 10$; *sorsogonensis*, $N = 2$), it is currently unclear whether slight differences in songs represent geographic or individual variation. More recordings are needed from additional localities to assess whether or not each species may be identified solely by vocalizations. In addition to the song, a rapid trill, thought to be an alarm call, has been recorded from an individual bird in a group of *R. thompsoni* (P. Noakes, Xeno-canto [XC] 40990).

Designation of Paratypes. Field Museum of Natural History (FMNH) 472602; adult male (skull ossified, no bursa) captured 10 April 2010, Philippines, Luzon Island, Aurora Province, Dunalungan Municipality, 1.9 km S, 4.0 km E Mt. Anacuao (16.237° N, 121.927° E; 1300 m), in primary lower montane forest. This specimen was originally prepared as a fluid specimen in formalin (DSB 7110) but re-prepared as a skin by PAH: mass 57 g; fat moderate; stomach with scleritized insect fragments; molt on wing and body; testes 5 x 4 mm. KU 119893; juvenile male (skull unossified, bursa 10 x 8 mm), tissue number KU 25788. This individual was net-captured on 7 July 2011 in the Philippines, Luzon Island, Cagayan Province, Gonzaga Municipality, Mt. Cagua crater (13. 219° N, 122.111° E; 780 m) and prepared as a study skin by PAH: fat light; mass 52.5 g; stomach empty; iris dark brown; legs dusky; maxilla dusky with yellow tomium; mandible yellow with dusky tomium; molt on body; mouth lining yellow.

Etymology. We name this species in honor of Max C. Thompson, for his decades of contributions to natural history collections and ornithology in particular. Long employed as a professor of biology at Southwestern College, in Winfield, Kansas, USA, his involvement in diverse initiatives has produced scientific insights and extensive specimen collections not only from the Philippines, but also from Africa, Asia, Australia, the Southwestern Pacific, and

	bill length	bill depth	bill width	wing chord	tail	tarsus
Robsonius rabori	13.5 (2)	5.3 (1)	4.5 (2)	78.6 (2)	75.8 (2)	29.9 (2)
	12.7–14.3	5.3	4.1–4.8	76.6–80.5	70.7–80.8	29.8–30.0
R. sorsogonensis	13.7 (21)	5.5 (17)	5.0 (19)	85.3 (21)	74.6 (17)	30.2 (21)
	10.0–15.6	4.7–6.2	4.1–6.2	71.5–96.0	67.0–87.7	28.0–31.8
R. thompsoni	12.9 (9)	5.1 (8)	5.0 (10)	79.8 (10)	73.3 (9)	29.7 (10)
	12.1–14.5	4.3–5.8	4.6–5.7	71.0–87.0	64.3–81.7	27.4–32.3

Table 2-1. Measurements from specimens of each of the three *Robsonius* species. Mean values are given followed by the sample size in parentheses, the ranges of measurements are indicated below the mean values. We found no significant differences between species or sexes, although juveniles had significantly shorter bills than adults. Sample sizes varied because some measurements were not possible on some specimens.

numerous sites in the New World. His collections are deposited at the University of Kansas, Smithsonian Institution, Bishop Museum, and American Museum of Natural History, and have provided an invaluable resource for the world ornithological community.

English names currently and recently used for *Robsonius* are misleading because they refer to previous taxonomic treatments when *Robsonius* was considered a babbler (Rabor's wren-babbler / Luzon wren-babbler), or because they refer to plumage characters that do not diagnose *Robsonius* to species (rusty-headed babbler / gray-banded babbler; two species have a rusty head, all three have a gray breast band, albeit with slight differences between species). We suggest new English names that highlight the restricted distributions and areas of endemism occupied by each species within Luzon: *Robsonius rabori,* Cordillera ground-warbler; *R. thompsoni*, Sierra Madre ground-warbler; and *R. sorsogonensis*, Bicol ground-warbler.

Specimen material examined. ***Robsonius rabori***: FMNH 253557 (holotype); KU 119500. ***Robsonius sorsogonensis***: American Museum of Natural History (AMNH) 807095 (photos

only); British Museum of Natural History (BMNH) 1977.16.65–6 (photos only); Carnegie Museum (CM) 151227, 153961; Delaware Museum of Natural History (DMNH) 17443, 21812, 37275–6, 37928–33, 43771, 55857; FMNH 275745 (holotype), 399710, 462013, 472703; PNM 16656, 16795, 17532, 20144; Rijksmuseum van Natuurlijke Histoire (RMNH) 99810 (photos only, from Collar 2006), University of the Philippines Los Baños (UPLB) 3554; United States National Museum (USNM) 608086 (photos only). ***Robsonius thompsoni***: Cincinnati Museum of Natural History (CMNH) 37710–1; FMNH 259385, 449800, 454990, 472601–3; KU 114634, 119893; PNM 16801, 19167, 20006 (holotype), University of Michigan Museum of Zoology (UMMZ) 226770 (photos only), USNM 607458, Yale Peabody Museum (YPM) 39989.

Audio records examined. ***Robsonius rabori***: Macaulay Library (ML) 166395. ***Robsonius thompsoni***: Xeno-Canto (XC) 23080, 35259–61, 40988–92, 57572–3. ***Robsonius sorsogonensis***: 2 recordings (Scharringa 2005).

Remarks

Systematics. We used an initial molecular phylogenetic framework from recent higher-level systematic studies that included *Robsonius* (Moyle et al. 2012; Oliveros et al. 2012) to clarify the systematic relationships among *Robsonius* populations. Character sampling (4092 bp) included three mitochondrial genes (1143 bp cytochrome *b*, 1041 bp ND2, 351 bp ND3), and three nuclear introns (544 bp TGF*b*2-5, 570 bp Fib-5, 443 bp MUSK). Sequences for 13 individuals (GenBank KC603622–603686) were derived from fresh tissue samples, whereas sequence for the juvenile type specimen of *Robsonius rabori* was derived from DNA extracted from a toepad clip. Outgroups included *Donacobius, Thamnornis, Megalurus, Locustella,* and *Bradypterus*. (Oliveros et al. 2012). We implemented Bayesian (MRBAYES 3.1, Ronquist and Huelsenbeck

2003; 20 million generations) and Maximum Likelihood (RAxML, Stamatakis 2006; 1000 bootstrap replicates) tree inference on the concatenated dataset. Preliminary analyses of independent loci indicated no strongly supported conflicts in phylogenetic signal between loci, justifying concatenation. See Moyle et al. (2012) and Oliveros et al. (2012) for descriptions of gene regions sequenced, laboratory protocols, and details of analysis. In addition to analyses described in Moyle et al. (2012), phased haplotype networks were reconstructed for each nuclear locus using TCS (Clement et al. 2000).

Bayesian and ML analyses recovered three strongly supported geographic clades within the *Robsonius* complex (Fig. 2-1). One clade comprised samples from southern Luzon, including the Bicol Peninsula and Bulacan Province (1.0 Bayesian posterior probability [BP], 87% ML bootstraps [BS]); a second clade comprised samples from the northern Sierra Madre Mountains in northeastern Luzon, including Aurora, Nueva Vizcaya, and Cagayan provinces (1.0 BP, 100% BS); and a third clade comprised samples from the Cordillera Mountains in Ilocos Norte Province, northwestern Luzon (1.0 BP, 100% BS). The northwestern clade (Cordillera, including the type specimen of *R. rabori*) and the northeastern clade (Northern Sierra Madres, *R. thompsoni*) were strongly supported as sister taxa (1.0 BP, 97% BS), which together were sister to the southern Luzon clade (*R. sorsogonensis*).

Mitochondrial haplotypes of the three clades were widely divergent; uncorrected ND2 pairwise distances between the three populations ranged 7.4–8.7 % (*rabori–thompsoni*, 8.3–8.7 %; *rabori–sorsogonensis*, 7.9–8.2 %; *thompsoni–sorsogonensis*, 7.4–8.1 %), cytochrome *b* uncorrected pairwise distances between populations ranged 5.2–7.4 %. For comparison, mtDNA divergences of most recently described species have been less than 5% (Voelker et al. 2010; Pyle et al. 2011; Lara et al. 2012) and many are less than 2% (O'Neill et al. 2011; Carneiro et al.

2012; Seeholzer et al. 2012). Nuclear gene haplotype networks (Fig. 2-1) showed no haplotype sharing among species, except in Fib-5 where *R. sorsogonensis* and *R. thompsoni* shared two haplotypes. The ND3 sequence amplified from a toepad of the *R. rabori* type specimen was the same haplotype as sample KU 25708, and included no stop codons or heterozygous sites, lending additional confidence that the DNA amplified is of true mitochondrial origin.

Phylogenetic data and plumage independently indicate that three diagnosable lineages of *Robsonius* exist within Luzon, consistent with treatment of three species under the phylogenetic, evolutionary, and general lineage species concepts (De Queiroz 2007). Distributions of the three lineages are currently not known to overlap, precluding direct evaluation of reproductive isolation and determination of species status under the biological species concept. However, indirect evidence strongly suggests reproductive isolation between the three species. First, deep genetic divergences between lineages support a long independent history with no evidence of hybridization even though there are no obvious physical barriers between them. For example, specimens of *R. thompsoni* and *R. sorsogonensis* collected from northern Bulacan and southern Aurora Provinces show no evidence of phenotypic or genetic intergradation, despite a separation of only 60 km and no intervening break in continuous lowland forest. Second, all plumage differences between the lineages are 100% diagnosable, discrete and fixed; no specimens present intermediate character states.

Distribution. We used ecological niche modeling to produce a model of environmental requirements of *Robsonius* as a clade, with which we could assess distributional patterns, and whether phylogenetic breaks coincide with zones of low environmental suitability. Occurrence data consisted of specimen records (data accessed via the Global Biodiversity Information Facility, or museum collection managers), supplemented with observations from the literature

(De Roever 1990; Lambert 1993; Harrap and Mitchell 1994; Poulsen 1995; Collar 2006), web-reported sightings (eBird; Wood et al. 2011), and data associated with vocal archives (XC, ML). The occurrence data thus included 26 unique localities with voucher specimens and 12 additional unique localities based on observations and audio recordings, for a total of 38 occurrence points, adequate for producing robust models (Pearson et al. 2006). We chose to model *Robsonius* at the genus level in light of the small sample size, and because ecological niches of allopatric replacement species tend to be similar (Peterson 1999; 2011). Climate data (30" spatial resolution, or about 1 km) were drawn from the WorldClim climate archive (Hijmans et al. 2005); we used the following data layers: annual mean temperature, mean diurnal temperature range, maximum temperature of warmest month, minimum temperature of coldest month, annual precipitation, and precipitation of the wettest and driest months. Niche models were developed using GARP (Stockwell and Peters 1999) and Maxent (Phillips et al. 2006).

Suitable areas identified by the niche models (Fig. 2-2) suggest that the distribution of *Robsonius* is limited by environmental factors within Luzon. Analysis of variable contributions in Maxent indicate that precipitation in the driest month (62.5 %), minimum temperature in the coldest month (18.8 %), and annual mean temperature (11.9 %) explain the most variance, all other variable contributed less than 5 % of the variance. Thus, niche models suggest that *Robsonius* are confined to wetter rainforest and sub-montane forests, and absent from seasonally dry monsoon areas in western Luzon and the Cagayan Valley, and from montane forest areas above ~1500 m. The environmentally unsuitable Cagayan Valley potentially isolates populations of *R. rabori* and *R. thompsoni*, whereas *R. thompsoni* and *R. sorsogonensis* do not appear to be isolated currently by gaps in suitable environmental conditions.

Discussion

Systematic relationships, biogeography, and distribution. The three species of *Robsonius* on Luzon appear to constitute a case of intra-island diversification in a lowland forest bird. Generally, birds are not thought to speciate readily within the confines of islands (Diamond 1977; Coyne and Price 2000), although recent molecular genetic studies suggest that this phenomenon may be more widespread than previously appreciated (Ryan et al. 2007; Hosner et al. 2013a).

Robsonius is limited to the Luzon Pleistocene aggregate island complex (Heaney 1986; Brown and Diesmos 2002, Fig 2-2), with records from Catanduanes Island, as well as Luzon Island *per se*. Ecological niche models suggest that climatically suitable areas also exist on the smaller satellite islands Polillo and Marinduque (Fig. 2-2), to which the complex evidently had access during Pleistocene low sea-level stands. Recent survey efforts on Polillo have not encountered *Robsonius*; however, Marinduque has received little ornithological attention since the voice of *Robsonius* was described (Harrap and Mitchell 1994), such that its presence there could have been overlooked.

Robsonius thompsoni replaces *R. rabori* east of the Cagayan Valley in forests associated with the northern Sierra Madre Mountains, and has been recorded in Cagayan, Isabela, Aurora, and Nueva Vizcaya provinces; niche models indicate potential for occurrence also in Quirino Province (Fig. 2-2). *Robsonius sorsogonensis* replaces *R. thompsoni* south of the Mid-Sierra Madre Filter Zone, a region that has been hypothesized as an important isolating barrier in birds (e.g., *Sterrhoptilus nigrocapitata* and *S. dennistouni*; (Kennedy et al. 2000) and other vertebrate species (Welton et al. 2010). *Robsonius sorsogonensis* has been recorded in Bulacan, Laguna,

Quezon, Camarines Norte, Camarines Sur, and Sorsogon provinces; ecological niche models suggest it may also occur in Rizal, Marinduque, and Albay provinces.

Robsonius rabori has only been recorded at three localities (the type locality and two localities explored near Adams in 2011) in northernmost Ilocos Norte Province; hence, the first species of this genus to be described is by far the least well known. Ecological niche models identify broader environmental suitability in northwestern Luzon (Fig. 2-2), including parts of Apayao, Kalinga, Mountain, and Ifugao provinces. This northern Cordillera lowland forest block is presumably occupied by *R. rabori*, but is poorly known by biologists and requires further surveys. Alternatively, the distribution of *R. thompsoni* could potentially extend into the southern Cordillera. It is known from Mt. Palali, an outlying peak of the Sierra Madres just east of the Magat River (the largest tributary of the Cagayan River, which separates the Sierra Madres from the Cordillera Mountains). We encourage researchers working in Apayao, Kalinga, Mountain, and Ifugao provinces to search for *Robsonius* to clarify the range limits of each species and determine whether contact zones exist.

Variation within Robsonius *species*. Size variation (Baldwin et al. 1931; Winker 1998) in the three *Robsonius* species (Table 2-1) indicates no apparent significant differences between species (ANOVA, $P > 0.01$) or between sexes *t*-test, $P > 0.01$). Juvenile-plumaged birds tend to have shorter bills (12.3 mm) than adults (13.8 mm; *t*-test $P = 0.0007$); all other differences in measurements were not significant (*t*-test, $P > 0.01$). Most adult plumage variation within *Robsonius* species results from varying amounts of dark feather edging on the back, throat, and breast, which are strongly affected by feather wear. Overall, *R. sorsogonensis* has the least dusky feather edging; some specimens show faint, dusky scalloping on the back, but none has scalloping on the throat and upper breast as in *R. rabori* and *R. thompsoni*. The malar stripe,

formed from grayish or blackish feather tips, is reduced in *R. sorsogonensis* and *R. thompsoni* compared to *R. rabori*. The distinctive necklace of black spots in *R. thompsoni* is variable and influenced by feather wear; in some specimens, the throat is clean white and only a few black spots on the upper breast form the necklace, whereas other specimens have spotted or scalloped throats and prominent black necklaces. The size of the white throat patch, thickness of the breast band, and amount of white on the belly are also variable within species, apparently mostly as a function of feather wear and specimen preparation style, so the biological significance of this variation remains unclear.

In our examination of *Robsonius* specimens, we found no diagnosable differences between *R. s. sorsogonensis* and *R. s. mesoluzonica*. Each of DuPont's (DuPont 1971a) characters is variable individually, and influenced strongly by preparation style and feather wear. Our DNA sequence data also suggest no population structure within *R. sorsogonensis*. As a consequence, we suggest that *R. s. mesoluzonica* is not a diagnosable geographic form, and recommend treating *R. sorsogonensis* as monotypic, with the name *mesoluzonica* DuPont as a junior synonym.

Habitat. Limited data indicate that the three *Robsonius* species have similar habitat requirements. *Robsonius* have been collected and observed in broad-leaved lowland and lower montane forest, including primary, secondary, forest edge, logged second growth, and forest on karst, from sea level to at least 1300 m. In these habitats, *Robsonius* seem to prefer areas of dark, thick undergrowth, including level areas with limestone rocks, outcrops, and fallen logs; steep slopes with bamboo and moss-covered boulders (De Roever 1990; Lambert 1993; Harrap and Mitchell 1994; Poulsen 1995; Kennedy et al. 2000; Collar and Robson 2007); tree-fall gaps; and steep, shrub-filled ravines (PAH, pers. observ.). Occasionally, *Robsonius* have been found in tall,

thick grass near the edge of secondary forests (Poulsen 1995, PAH pers. observ. at Mt. Cagua, Cagayan Prov.). In areas presenting mixed primary and secondary habitats, our limited observations suggest that *Robsonius* may be more frequent in younger second growth. For example, at Adams, Ilocos Norte, only two *R. rabori* were heard in 10 days of survey effort at the tall forest site on Mt. Pao; however, up to five birds were heard in a single day in secondary forest on nearby Mt. Cabacan. Higher abundance in secondary forest may be a function of suitable dense undergrowth, rather than preference for secondary habitats *per se*; we are unaware of records of *Robsonius* populations in isolated patches of secondary forest away from large tracts of tall forest.

Ecology and behavior. Because of their secretive habits and occurrence in dense undergrowth, *Robsonius* ecology and behavior remain poorly understood. Most sightings are of individuals or family groups (adults with juveniles) walking slowly on the ground, flipping over leaves and woody debris in search of invertebrates (Goodman and Gonzales 1990; De Roever 1990; Lambert 1993; Harrap and Mitchell 1994; Poulsen 1995; Collar and Robson 2007). Stomach contents ($N = 4$) included primarily scleritized insect parts. *Robsonius* walk or run across the forest floor, with the tail held straight out or cocked at a 30–60° angle, occasionally to 90° when startled or agitated (De Roever 1990). In addition to its typical ground-walking habits, in response to playback, an agitated *R. sorsogonensis* made short wing-assisted jumps between several small vertical stems, and perched vertically in a posture similar to many wrens (Troglodytidae) and Neotropical antbirds (i.e. *Pithys* or *Gymnopithys;* PAH, pers. observ. at Mt. Labo, Camarines Norte Prov.).

Collar and Robson (2007) and Sánchez-González et al. (2010) described *Robsonius sorsogonensis* and *thompsoni* nest architecture as a large ball structure with a side entrance

placed in understory vegetation, reminiscent of nests of *Pitta* and some *Bradypterus* and *Megalurus*. Sánchez-González et al. (Sánchez-González et al. 2010) referred to the northern Sierra Madre populations as *R. rabori*, consistent with past taxonomic treatments, but the nest actually belonged to *R. thompsoni*, such that the nest was described before the species had a name. The nest of *R. rabori* remains undescribed. Clutch size in each described nest was two, and eggs were white with reddish-brown speckles.

Conservation. In the most recent conservation assessments, *R. "rabori"* (including both *R. rabori* and *R. thompsoni*) and *R. sorsogonensis* have each been treated as Vulnerable based on extent of occurrence (< 6000 km^2), small numbers of known occurrence localities, and suspected population declines from forest fragmentation (BirdLife International 2012). *Robsonius* species are now known from more localities and a larger area than in previous conservation assessments (Fig 2-2): *R. rabori* (3 localities), *R. thompsoni* (21 localities) and *R. sorsogonensis* (14 localities). Recognizing *R. thompsoni* as a separate species results in smaller distributional areas; based on this information and revised species taxonomy, we recommend elevating *R. rabori* to Endangered, but treating *R. thompsoni* and *R. sorsogonensis* as Vulnerable, in each case following IUCN criteria (IUCN 2010).

In recent years, the forests of the northern Sierra Madre have received a great deal of attention from the conservation community. They harbor the largest areas of forest within Luzon, and protect large numbers of endemic, endangered, and threatened species (Mallari and Jensen 1993; Poulsen 1995). However, the discovery reported herein illustrates that conserving small portions of species' ranges may leave differentiated populations unprotected, particularly in a highly beta-diverse landscape such as the Philippines (Peterson 2006; Welton et al. 2010). We hope that *R. rabori*, now the only known bird species endemic to the lowland forests around the

Cordillera Mountains, can become a flagship species for forest conservation in the region. Tracts of lowland forest persist in Ilocos Norte, Apayao, Kalinga, and Mountain provinces. Compared with the northern Sierra Madre region, the lowland avifauna of the Cordillera Mountains is poorly known, and renewed interest in the area will likely result in discovery of other bird populations important for conservation.

Chapter 3*

Phylogeographic structure and paleo-environmental niche modeling support climate-driven diversification in Philippine birds

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Abstract

Avian diversification in oceanic archipelagos is largely attributed to isolation across marine barriers. During glacial maxima, lowered sea levels resulted in repeated land connections between islands joined by shallow seas. Consequently, such islands are not expected to show endemism. However, if climate fluctuations simultaneously caused shifts in suitable environmental conditions, limiting populations to refugia, then occurrence on and dispersal across periodic land bridges is not tenable. To assess the degree to which paleoclimate barriers, rather than marine barriers, drove avian diversification in the Philippine archipelago, we produced ecological niche models for current-day, glacial maxima, and interglacial climate scenarios to infer Pleistocene paleoclimate barriers. We then tested marine and paleoclimate barriers for correspondence to geographic patterns of population divergence, inferred from DNA sequences from eight co-distributed bird species. In all species, deep-water channels corresponded to zones of genetic differentiation, but six species exhibited deeper divergence across a periodic land bridge. Ecological niche models for these species identified a common paleoclimate barrier in the southern Philippines that coincided with deep genetic structure among populations. Although dry land connections joined southern Philippine islands during low sea level stands, unfavorable environmental conditions limited populations within landmasses, resulting in long-term isolation and genetic differentiation. These results highlight the complex nature of diversification in archipelagos: marine barriers, changes in connectivity due to sea level change, and climate-induced refugia acted in concert to produce extraordinary levels of species diversity and endemism in the Philippines.

Introduction

A central goal in phylogeography and distributional ecology is to identify factors that limit species' distributions, partition biodiversity, and promote diversification and differentiation. Processes that limit distributions fall into three broad categories: physical barriers, abiotic factors, and biological interactions (Peterson et al. 2011). Physical geographic barriers, such as marine barriers, large rivers, and mountain ranges, isolate populations by preventing dispersal of individuals. Abiotic factors, such as areas of unsuitable environmental conditions or unsuitable habitats (e.g., a desert may limit the distribution of a humid forest species), similarly isolate populations. Biological interactions, such as the presence of a competitors or predators (e.g., competition with a close relative may prevent range expansion into an otherwise suitable area), may also limit distribution. Each of these factors may limit distributions individually, or multiple factors may reinforce one another.

In birds, sympatric speciation is rare, and perhaps limited to a few examples on extremely remote islands with exceptional environmental conditions (Coyne and Price 2000; Ryan et al. 2007). Hence, isolation of populations across barriers is thought to be the main driver of avian diversification (Wallace 1876; Mayr 1942; 1963). This idea is the basis of classic geographic diversification models, such as the Riverine Barrier Hypothesis (Wallace 1852; Gascon et al. 2000; Ribas et al. 2012), which invokes physical barriers, and the Pleistocene Refugium Hypothesis (Haffer 1969), which invokes abiotic factors (intermittent barriers in environmental suitability). Deciphering the relative importance of physical barriers, abiotic factors, and biotic factors in diversification is a major challenge, in part because across some landscapes different

factors may result similar empirical expectations, or because multiple factors may function in tandem (Endler 1982; Haffer 2008).

The Pleistocene diversification model in the Philippine archipelago

The Philippine archipelago has long served as a model system for biogeographic inquiry (Huxley 1868; Dickerson et al. 1928; Mayr 1944; Diamond and Gilpin 1983; Heaney 1985; 1986). Its complex, yet well-understood, geologic history (Hall 1998; Yumul et al. 2004; 2009), intense concentration of biodiversity (Brown and Diesmos 2009), and relatively well-known faunal distribution patterns (Steere 1894; Dickerson et al. 1928; Heaney 1985; Dickinson et al. 1991), make the archipelago ideal for studies of phylogeography and diversification. The archipelago holds staggering levels of terrestrial vertebrate endemism given its land area, and deeper understanding of drivers of diversification will assist in designation of conservation units and development of effective long-term conservation strategies in megadiverse country and global biodiversity hotspot (Myers et al. 2000; Brooks 2006).

As in other oceanic archipelagos, deep-water barriers between island groups are regarded as key geographic features isolating lineages and limiting distributions of organisms in the Philippines. For several decades, the Pleistocene aggregate island complex (PAIC) model has framed biogeographic inference in the Philippines (Heaney 1985; 1986; Brown and Diesmos 2002; Steppan et al. 2003; Esselstyn et al. 2009; Siler et al. 2010; Oaks et al. 2013). This elegant model is based on the observation that larger, aggregate islands formed repeatedly when sea levels decreased during globally cool periods (during glacial maxima; e.g., approximately 20,000, 150,000 and 250,000 years before present; Siddall et al. 2003), increasing dry-land connectivity among islands (Voris 2000). During these periods of increased connectivity, which

occurred throughout the Pleistocene and into the late Pliocene (Miller 2005), populations might have expanded and dispersed into new areas. Previously isolated island populations could come into contact and potentially interbreed, homogenizing formerly differentiated populations. Alternatively, formation and fragmentation of aggregate islands may have operated as a "species pump," with repeated opportunities for isolation and population differentiation (Oaks et al. 2013). Originally inferred based on mammal distributions and the 120 m isobath (Heaney 1986), PAIC boundaries are largely congruent with current-day Philippine bird (Dickinson et al. 1991), amphibian, and reptile (Brown and Diesmos 2002) distributions. The PAIC concept has been applied broadly to explain distribution and phylogeographic patterns in other archipelagos and continental shelf systems, such as the Solomon Islands (Mayr and Diamond 2001) and the Sunda Shelf (Lim et al. 2011).

The PAIC model offers clear predictions and expectations that are readily testable with distributional and genetic data (Brown et al. 2013): (1) Species or lineage distributions should be congruent with PAIC boundaries, (2) species or lineages distributed across multiple PAICs should exhibit greater genetic structure among PAICs than within PAICs, (3) within-PAIC populations should be monophyletic, (4) timing of diversification should be consistent with Pleistocene to late Pliocene population divergence (i.e., 20,000–3.3 Mybp), and (5) current-day island population divergences should be consistent with recent isolation (<20,000 ybp). Deviations from PAIC model expectations suggest other processes at work; for example, within-PAIC genetic structure indicates isolation mechanisms in addition to deep-water barriers.

Recently, molecular systematic studies of terrestrial vertebrates have identified examples of sister lineages occurring within islands and island groups, challenging the notion that isolation among PAICs drives diversification (Jansa et al. 2006; Jones and Kennedy 2008; Esselstyn et al.

2009; Siler et al. 2010; Sanguila et al. 2011; Brown et al. 2013; Hosner et al. 2013a). Rather, although PAIC boundaries are generally congruent with broad distributional patterns, they do not necessarily explain complex evolutionary histories of lineages contained within them. Alternative scenarios include population divergence due to stochastic processes such as sweepstakes dispersal (Esselstyn et al. 2009), geologic explanations such as isolation between proto-islands (Sanguila et al. 2011), and isolation of montane "sky-islands" within single islands (Jones and Kennedy 2008; Hosner et al. 2013a). These studies question whether Pleistocene sea level fluctuations actually drove diversification, or simply served to redistribute populations, which diversified by other means. Such deviations from PAIC expectations suggest that additional mechanisms are needed to explain geographic patterns of avian diversification in insular systems.

In addition to sea-level changes that underpin the PAIC diversification model, Pleistocene climate cycles likely influenced distributions of organisms by shifting environmental conditions (Peterson and Ammann 2013). In continental systems such as South America (Haffer 1969; Peterson and Nyári 2007), North America (Weir and Schluter 2004), and Asia (Heaney 1991; Cannon et al. 2009; Lim et al. 2011), glacial maxima refugia are thought to have promoted diversification via climate-driven population fragmentation. Implications of historical climate changes on environmental suitability and forest cover in the Philippines and other oceanic islands nonetheless remain little studied. Heaney (1991) suggested that western portions of the Philippine archipelago were drier during glacial maxima and likely were not forested; meanwhile humid montane forests likely expanded. Peterson and Ammann (2013) demonstrated that forest connectivity increased overall in the Philippines during glacial maxima, in tandem with increased land connectivity (associated with PAIC formation). More generally, these studies

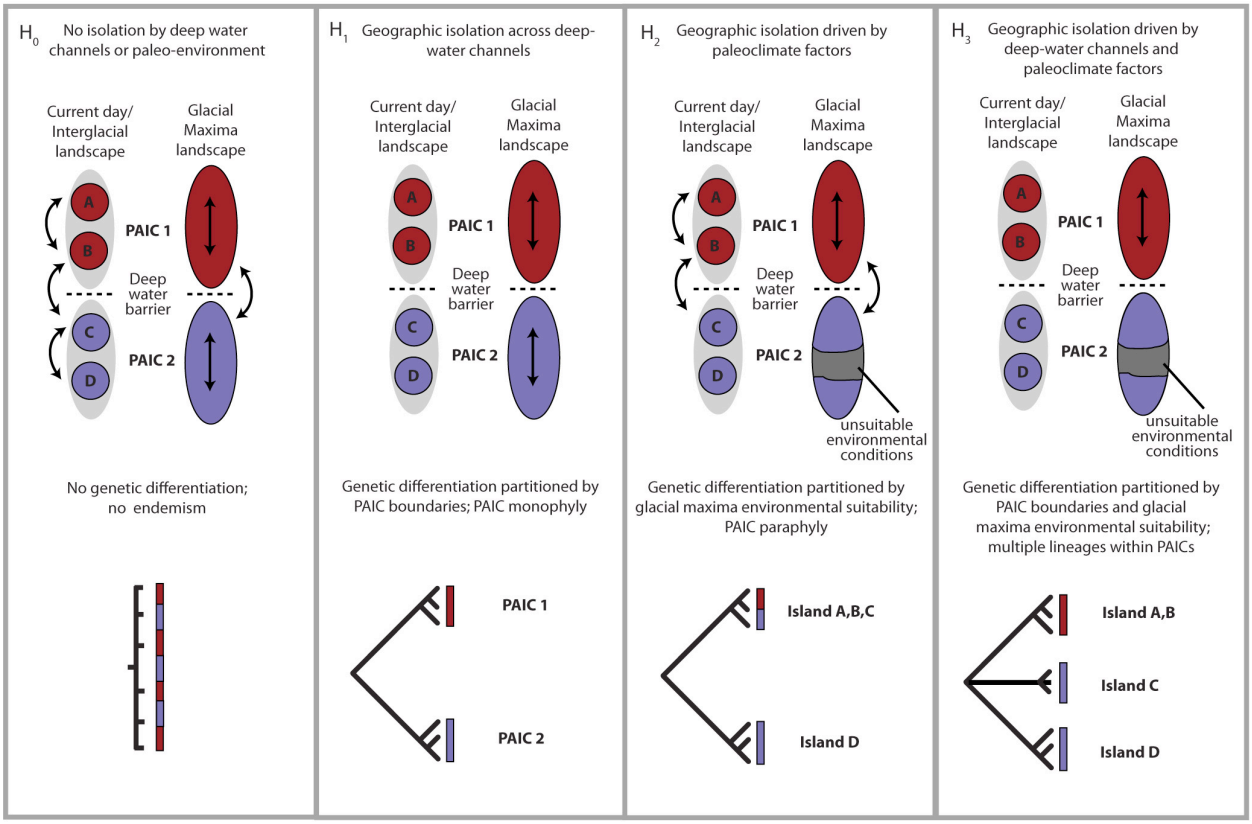


Figure 3-1. Graphical representation of hypotheses and phylogenetic expectations for hypothetical organism populations inhabiting an archipelago consisting to two PAICs, each consisting of two current-day islands joined by an area of shallow seas (light gray). PAIC 1 (red) comprises current-day islands A and B; PAIC 2 (blue) comprise current day islands C and D). Large conglomerate islands form during low sea level stands, which allows admixture between periodically isolated islands within PAICs (A and B; C and D) without a water crossing (arrows represent ability to disperse implicit in each). H_2 and H_3 include and area of environmental unsuitability (dark gray) within PAIC 2.

suggest that Pleistocene environments in the Philippines differed substantially from today, and may have played crucial roles in structuring species' distributions. Barriers in environmental suitability could function to reinforce deep-water barriers if they coincide, or could present additional isolating mechanisms.

In this paper, we integrate insights from phylogeography and distributional ecology to examine the relative roles of geographic barriers and environmental suitability in limiting species' distributions (Peterson and Nyári 2007; Waltari et al. 2007) in the Philippine archipelago. To identify processes that isolated lineages and promoted diversification, we

produced ecological niche models and DNA sequence data for eight co-distributed bird species. Our objective was to test a hierarchical set of biogeographic hypotheses, each with different empirical expectations (Fig. 3-1). Specifically, we tested an overall null hypothesis (H_0) that lineages function as single panmictic populations with no genetic structure: here, neither water barriers nor paleoclimate barriers are effective isolation mechanisms, and no genetic differentiation is observed. For species departing from the null, we tested the strict PAIC diversification hypothesis (H_1) that genetic structure is a function solely of isolation across deep-water channels. Under the strict PAIC diversification hypothesis, populations within PAICs disperse freely during glacial maxima, preventing genetic differentiation within island groups. Deep-water barriers are the only effective isolation mechanisms; as a result each PAIC contains an endemic, differentiated lineage. A second alternate hypothesis (H_2) predicts that paleoclimate suitability, not deep-water barriers, isolates lineages. Under this hypothesis, genetic structure is expected, but lineages will not be divided by PAIC boundaries. Rather, genetic structure will correspond to lineage-specific paleoclimate barriers (inferred from ecological niche models), and may potentially result in panmixia across deep marine barriers, multiple lineages within PAICs, and PAIC paraphyly. The PAIC (H_1) and paleoclimate suitability (H_2) hypotheses are not mutually exclusive; we consider a synergistic third hypothesis (H_3) that the union of marine and paleoclimatic barriers drives diversification.

Methods

Taxa and sampling

To reduce the spatial complexity of the Philippine archipelago and simplify hypothesis testing, we selected bird species restricted to the union of the two largest PAICs: Greater Mindanao and

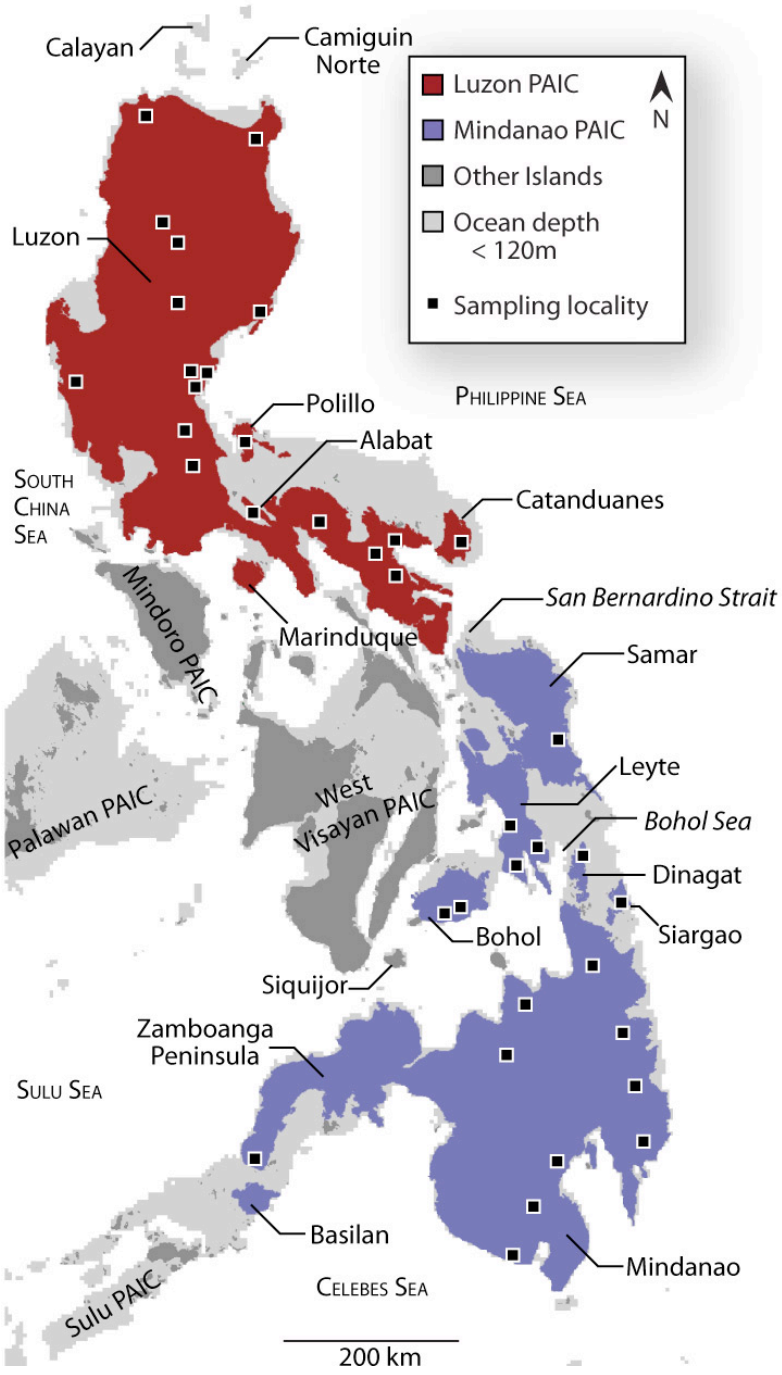


Figure 3-2 Map of the Philippine archipelago, illustrating the two Pleistocene Aggregate Island Complexes (PAICs) of the eastern arc that are the focus of this study: Luzon (in red, composed of Luzon, Polillo, Alabat, Catanduanes, and Marinduque) and Mindanao (in blue, composed of Samar, Leyte, Bohol, Dinagat, Siargao, Mindanao, and Basilan); other Philippine islands are illustrated in dark gray. Light gray indicates the 120m isobath, which was periodically exposed as dry land during Pleistocene low sea level stands, which increased connectivity among current-day islands. Sampling localities are indicated with black squares.

Greater Luzon, which together compose the eastern arc of the Philippines. These islands of this arc form a roughly linear geographic arrangement (Fig. 3-2), simplifying colonization patterns. We selected species inhabiting primarily lowland forests, including primary and secondary forests. Montane species were not selected, because forest connectively and colonization patterns among montane regions differ from those of lowland forests (Jones and Kennedy 2008). More than 15 polytypic avian species fit these requirements (Dickinson et al. 1991; Kennedy et al. 2000); of these, we selected the eight with the densest available genetic sampling for robust phylogeographic and ecological niche modeling analysis.

Each focal taxon (*Harpactes ardens, Ceyx melanurus, Pachycephala philippinensis, Pycnonotus urostictus, Irena cyanogastra, Dicaeum hypoleucum, Prionochilus olivaceus, Aethopyga pulcherrima*) has traditionally been considered a single species (Dickinson et al. 1991; Kennedy et al. 2000; Gill and Donsker 2013); although under lineage-focused species recognition criteria, each could be considered a suite of allopatric replacement species (Peterson 2006; Moltesen et al. 2012; Andersen et al. 2013; Hosner et al. 2013a). These eight species span three avian orders and seven avian families, and feature a diversity of life history characteristics (canopy and understory species; insectivores, frugivores, and nectarivores). Each species includes three to seven described subspecies, but subspecies distinctiveness is variable among species. For example, *C. melanurus* and *A. pulcherrima* each include three subspecies, each of which (adult males only in *A. pulcherrima*) is easily diagnosed by discrete differences in plumage or morphological characters. At the other extreme, subspecific differences in *H. ardens* and *P. urostictus* are subtle; described plumage differences between subspecies may be better explained by plumage aspect (molt and feather wear) than true geographic variation. *D. hypoleucum, I. cyanogastra, P. philippinensis,* and *P. olivaceus* include some subspecies easily

diagnosed by discrete characters, whereas others are not. Although subspecies' distributions are generally bounded by PAIC limits, PAICs can include multiple subspecies (e.g., *C. melanurus* has a single subspecies across the Luzon PAIC, but two allopatric subspecies within the Mindanao PAIC).

In addition to Luzon-Mindanao PAIC populations, *D. hypoleucum* also occurs in the Sulu PAIC southwest of Mindanao, and *P. philippinensis* also occurs on three small oceanic islands peripheral to the Luzon and Mindanao PAICs (Siquijor, Camiguin Norte, Calayan). However, occurrence on these additional islands does not disrupt the near-linear island distributional pattern common to other focal species. Kennedy et al. (2000) included observational records of *P. urostictus* from Negros (Hornskov 1995) as evidence of occurrence there; we regard these records as provisional in absence of physical evidence of occurrence on Negros, a well-surveyed island. The Luzon population of *A. pulcherrima* appears to be restricted to montane and lower montane forest; otherwise, species inhabit a variety of lowland and lower montane forested habitats (Kennedy et al. 2000).

Ecological niche modeling

Occurrence data were obtained for each species from museum specimens accessed via the Global Biodiversity Information Facility, (http://www.gbif.org/) and from observational records submitted to eBird, (http://www.ebird.org/, Wood et al. 2011). Museum specimens without geographic coordinates were georeferenced based on Dickinson et al. (1991) and Collar et al. (1999). Georeferenced points were quality controlled by checking congruence of specimen elevation data with the ETOPO topographic model (Amante and Eakins 2009).

Climate data for present-day were drawn from WorldClim climate archive bioclimatic layers: Bio1, Bio 2, Bio5, Bio6, Bio12, Bio13, Bio14 (Hijmans et al. 2005); all analyses were developed at a spatial resolution of 30''. We limited the area of model calibration (Barve et al. 2011), to the Luzon and Mindanao PAICs, reflecting the probable long-term restriction of the focal species to this area.

To summarize Pleistocene climates (Last Glacial Maximum [LGM] 20,000 yr bp; Last Interglacial [LIG], 135,000 yr bp) at 2.5' resolution, we used layer sets developed to be parallel to each bioclimatic variable used in model calibration (Peterson and Ammann 2013). These layers were developed from outputs of general circulation model (GCM) simulations from the Community Climate System Model (CCSM; Kiehl and Gent 2004). Overall, environmental conditions during the repeated glacial maxima and interglacials throughout the Pleistocene are thought to have been more or less similar (Siddall et al. 2003; Miller 2005), therefore the LGM and LIG layer sets serve as a proxy for environmental conditions during all glacial maxima and interglacial periods, respectively.

We used the Genetic Algorithm for Rule-Set Prediction, (GARP; Stockwell and Peters 1999), implemented in the 'Desktop' module in OPENMODELLER 1.2 (Souza Muñoz et al. 2011) and MAXENT (Phillips et al. 2006) to generate initial ecological niche models for each species. MAXENT models, however, showed odd behavior, with increasing suitability at high elevations, despite the fact that each focal taxon is primarily lowland and known to be absent from high elevations. As a consequence, we used GARP in the remaining analyses, following best-practice recommendations (Anderson et al. 2003). Specifically, we allotted occurrence points randomly into calibration (70%) and extrinsic evaluation (30%) partitions. Of the calibration data partition, 50% of occurrence points were used for developing models, and 50% were used for intrinsic

tests of model quality. We employed up to 10,000 replicate runs enforcing low omission (E = 5%); we used a convergence criterion of 0.01, and ran each model for up to 1000 generations. We evaluated ENMs using a partial ROC approach on the extrinsic data partition (Peterson et al. 2008). Each ENM was thresholded to the highest level of suitability that includes 95% of the calibration data; thresholds were established based on present-day models, and then applied to LGM and LIG coverages. To visualize environmental factors associated with putative paleoclimate barriers, we generated bivariate plots integrating the thresholded ENM predictions for each species with values from LGM climate data extracted from 5000 random points from across the study region.

Phylogenetic analyses

We sequenced mitochondrial and nuclear DNA markers from 443 individuals from the eight focal species, sampled from across their geographic distributions (Fig. 1-1, Appendix 1). Genomic DNA was extracted from muscle tissue using a non-commercial guanidine thiocyanate method (Esselstyn et al. 2008). We used polymerase chain reaction (PCR) to amplify the entire coding NADH dehydrogase-2 (ND2) gene for each sample (Hackett 1996; Sorenson et al. 1999; Drovetski et al. 2004). We screened 10 single-copy autosomal nuclear introns widely used in avian systematics (Sorenson 2003; Backström et al. 2008; Kimball et al. 2009) for amplification and variability by sequencing eight individuals for each species, and then selected the most informative locus that amplified well for each species. All individuals were then sequenced for that nuclear gene region (for primers used to amplify gene regions, see Table 3-1). We purified PCR products with ExoSAP-IT (USB, Cleveland, OH, USA), and performed cycle sequencing of purified PCR products with BigDye Terminator v3.1 Cycle Sequencing kits (Applied

Region	Location (*Gallus*)	Primer	Primer sequence	Reference
ND2 (1st fragment)	MtDNA	L-5215	5'-TATCGGGCCCATACCCCGAAAAT-3'	(Hackett 1996)
		H-5578	5'-CCTTGAAGCACTTCTGGGAATCAGA-3'	(Hackett 1996)
ND2 (2nd fragment)		L-347	5'-CCATTCCACTTCTGATTCCC-3'	(Drovetski et al. 2004)
		H-6313	5'-CTCTTATTTAAGGCTTTGAAGGC-3'	(Sorenson et al. 1999)
CDC132	Chr 2	CDC132F	5'-TCTGGGAACAGATCTGTC-3'	(Backström et al. 2008)
		CDC132R	5'-AAACTTCAGACTTACTGCC-3'	(Backström et al. 2008)
HMG2	Chr 23	HMG2F	5'-GAAATGTGGTCTGAACAGTC-3'	(Kimball et al. 2009)
		HMG2R	5'-TTGCTCTTGGCACGATATGC-3'	(Kimball et al. 2009)
PEPCK (initial)	Chr 20	GTP1601F	5'-ACGAGGCCTTTAACTGGCAGCA-3'	(Sorenson 2003)
		GTP1793R	5'-CTTGGCTGTCTTTCCGGAACC-3'	(Sorenson 2003)
PEPCK (second)		PEPCK9F	5'-GGAGCAGCCATGAGATCTGAAGC-3'	(Sorenson 2003)
		PEPCK9R	5'-GTGCCATGCTAAGCCAGTGGG-3'	(Sorenson 2003)

Table 3-1. Primers used in PCR reactions to amplify DNA sequences. ND2 was amplified and sequenced in two fragments, PEPCK amplification utilized nested PCR with an initial amplification using GTP1601F and GTP1793R and a second amplification using PEPCK9F and PEPCK9R.

Biosystems, Carlsbad, CA, USA). We purified cycle sequencing products using ethanol precipitation, and analysed sequences on an ABI 3730 automated capillary DNA sequencer (Applied Biosystems). We used SEQUENCHER 4.10 (Genecodes, Ann Arbor, MI, USA) to reconcile chromatograms of complimentary strands. All DNA sequences generated are available on GenBank (#s pending). We reconstructed alignments for each intron using the online version of MUSCLE (Edgar 2004) using default parameters, and then verified alignments by eye.

We analyzed sequence data in both concatenated and coalescent frameworks. For concatenated analyses, mitochondrial and nuclear sequences were concatenated and partitioned by locus and codon position. JMODELTEST 0.1 (Posada 2008), using both the Akaike's Information Criterion corrected for small sample size (Arc) and Bayesian Information Criterion (BIC), was used to select models of DNA sequence evolution for each partition (generally the HKY model; with the exceptions of CDC132 for *D. hypoleucum* [HKY+I], PEPCK for *H.*

ardens [HKY+G], ND2 for *I. cyanogastra* [HKY+I], ND2 for *P. philippinensis* [HKY+G], CDC132 for *P. olivaceus* [HKY+I], and CDC132 for P. urostictus [HKY+I]). Phylogenies were rooted to sequences from closely related species indicated by previous higher level studies; sister taxa to focal species occur on either the Sunda Shelf or montane regions of Mindanao (Jønsson et al. 2008; Nyári et al. 2009; Oliveros and Moyle 2010; Hosner et al. 2010; Moltesen et al. 2012; Andersen et al. 2013; Hosner et al. 2013a). We implemented Bayesian phylogenetic inference in BEAST 1.7 (Drummond et al. 2012). For lineages that rejected clock-like evolution of DNA sequences, we selected the uncorrelated lognormal relaxed clock; we selected a birth-death tree prior for each focal species. We executed four independent MCMC runs of 50 million generations, sampled every 50,000 generations, and discarded the first 10 million generations as burnin.

We analyzed DNA sequences in a coalescent framework using *BEAST (invoked in BEAST 1.7, Heled and Drummond 2010). Settings were similar to concatenated BEAST 1.7 runs, but utilized a Yule process species tree prior and a piecewise linear and constant root population size model. We used well-supported, geographically circumscribed clades identified in concatenated analyses to designate species tree tips *a priori*. We executed two independent MCMC runs of 50 million generations, sampled every 50,000 generations, and discarded the first 10 million generations as burnin. We examined parameter convergence, stationarity, and effective samples size (ESS, all > 200, with most in the thousands for each parameter) for each run in TRACER 1.5 (Rambaut and Drummond 2007). For maximum likelihood tree inference, we used GARLI 2.0 (Zwickl 2006) and assessed support for clades with 500 bootstrap replicates.

No fossil or island age evidence is available for calibrating divergence time estimates in the focal species. However, coarse estimates of divergence times can be inferred by scaling DNA

substitution rates to those documented in other bird species (Lovette 2004; Weir and Schluter 2008). To asses if cladogenesis is consistent with Pleistocene divergence (assumed in the PAIC diversification model), we calibrated the range of the 95% confidence interval for relevant nodes in each BEAST and *BEAST phylogeny with a conservative range of rates (2.4–3.3% pairwise divergence per million years for the ND2 gene; Lerner et al. 2011).

When we recovered topologies inconsistent with PAIC monophyly, we evaluated significance by calculating the posterior probability of PAIC monophyly in the credible tree sets from BEAST and *BEAST analyses, percentage of ML bootstrap replicates supporting PAIC monophyly, and the *P*-value of PAIC monophyly utilizing the Approximately Unbiased (AU) test invoked in CONSEL 0.1 (Shimodaira and Hasegawa 2001). We also tested for genetic differentiation across putative paleoclimate breaks in each locus (identified via ENMs outputs) by calculating F_{ST} and the Exact Test of Population Differentiation (Raymond and Rousset 1995), in ARLEQUIN 3.0 (Excoffier et al. 2005) utilizing phased haplotypes for nuclear markers (Stephens et al. 2001).

Results

Ecological niche modeling

Tests of the predictive power of models established that each GARP model developed had excellent ability to predict present-day distributions for each focal taxon. In all eight models, partial ROC tests had ROC curves elevated above null expectations ($P < 0.001$). Evaluation of model transferability supported that the range of LGM environmental conditions within the Philippines in general were largely similar to the range of present-day conditions, justifying projections onto paleoclimate scenarios.

Present-day projections of models were similar in all eight species (Figs. 3-3, 3-4, Appendix 2) and showed broad distributions across the Luzon and Mindanao PAICs, mirroring raw occurrence data. Unsuitable conditions for all species were predicted in the floor of the Cagayan Valley, a dry rain-shadow valley in northern Luzon, as well as in seasonally dry areas north and west of Manila. Interglacial projections corresponded closely to present-day projections.

Contrasting with current-day and interglacial model projections, LGM projections indicated two distinct patterns: five species (*C. melanurus, H. ardens, I. cyanogastra, P. olivaceus, P. urostictus*; Figs. 3-3, Appendix 2) exhibited a broad swath of unsuitable conditions on the windward (eastern) side of the Philippines, from present-day Catanduanes Island south to present-day eastern Mindanao. In these five species, model results indicated a break in environmental suitability separating two widely disjunct refugia of suitable conditions: a small refugium in the northern Mindanao PAIC comprised of present-day western Samar, Leyte, and Bohol; and a larger refugium comprising present-day central/western Mindanao and Basilan.

Thresholded ENMs for the three remaining species (*A. pulcherrima, D. hypoleucum, P. philippinensis*; Figs. 3-4, Appendix 2) exhibited continuous suitable areas at LGM along the entire north-south extent of the study region, and thus no paleoclimate breaks or distinct refugia. More generally, for all eight species, with the exception of the east coast zone described above, all models showed increased connectivity of suitable areas at LGM compared to present-day and interglacial projections (Peterson and Ammann 2013).

Bivariate plots of mean annual temperature and annual precipitation suggested that the five species with the glacial maxima paleoclimate break across the Bohol Sea Land Bridge (Figs. 3-3, 3-5; Appendix 2) have narrower climate tolerances than the other three species (Figs. 3-4, 3-

5; Appendix 2). Models for the former set of species suggested that they are confined to areas of relatively high annual mean temperature and relatively low precipitation, and that the high LGM precipitation across the Bohol Sea Land Bridge renders the area unsuitable in the models. The other three species had wider environmental tolerances, such that most LGM environmental conditions across the region were suitable.

Phylogeography

All eight focal species were highly structured genetically; each comprising three to seven strongly supported geographic clades, rejecting our initial null hypothesis of unstructured populations. In each species, Bayesian inference and ML bootstrapping strongly supported Luzon PAIC monophyly, upholding the San Bernardino Strait (separating Luzon and Samar) as an important deep-water biogeographic break. Contrary to the strict interpretation of the PAIC hypothesis, phylogenetic analyses generally supported Mindanao PAIC paraphyly (Figs. 3-3, 3-4, Table 3-2), with populations from the Luzon PAIC nested within the Mindanao PAIC in all eight species.

The most frequent topology reconstructed (*C. melanurus, H. ardens, I. cyanogastra, P. olivaceus*) indicated a break across the Bohol Sea (within the Mindanao PAIC), with populations on the islands of Samar, Leyte, and Bohol (in *I. cyanogastra*, also Dinagat) sister to Luzon PAIC populations rather than to those of Mindanao Island (Fig. 3-3). A fifth species, *Pycnonotus*

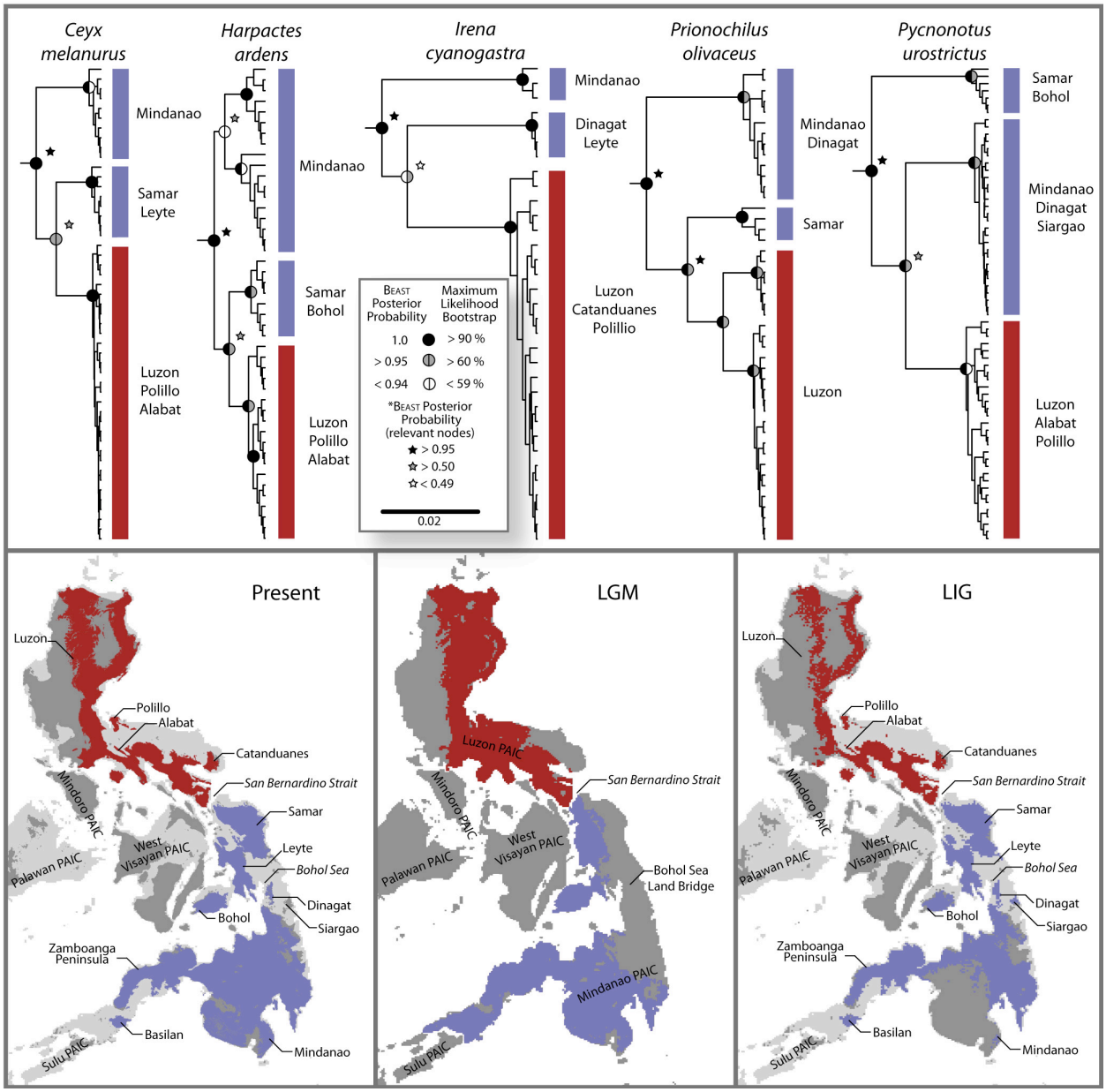


Figure 3-3 Phylogenetic hypotheses (BEAST maximum clade credibility tree, with clade posterior probabilities, GARLI ML bootstraps, and *BEAST posterior probabilities) and ecological niche model (ENM) projections for five bird species predicted to be absent from the Bohol Sea Land Bridge region during Pleistocene low sea level stands. Branch lengths are scaled to the ND2 substitution rate. Detailed phylogenetic trees are included in supporting information (Appendix 2). ENMs shown were developed for *Harpactes ardens*, but ENMs for all five species (including *Ceyx melanurus*, *Irena cyanogastra*, *Prionochilus olivaceus*, and *Pycnonotus urostictus*) were similar (Appendix 2). For ENMs, red denotes suitable environmental conditions within the Luzon PAIC, and blue denotes suitable environmental conditions within the Mindanao PAIC.

Species	BEAST Posterior probability	*BEAST Posterior probability	ML bootstrap (%)	ML tree (ln)	ML PAIC constrained tree (ln)	delta	AU test (*P*)
A. pulcherrima	**0.00**	**0.00**	**0.06**	-4554.88	-4570.76	15.87	**0.05**
C. melanurus	**0.02**	0.22	**0.19**	-3039.23	-3044.17	4.93	0.19
D. hypoleucum	**0.02**	**0.01**	**0.10**	-3332.03	-	-	-
H. ardens	**0.00**	0.19	**0.01**	-2381.47	-2386.25	4.77	0.17
I. cyanogastra	0.29	0.65	**0.06**	-3651.13	-3659.88	8.744	0.08
P. philippinensis	**0.00**	**0.00**	**0.00**	-5080.76	-5136.65	55.88	**0.001**
P. olivaceus	**0.00**	**0.05**	**0.20**	-4324.31	-4332.13	7.81	**0.03**
P. urostictus	**0.00**	0.39	**0.05**	-4508.71	-4512.11	3.39	0.12

Table 3-2. Support for PAIC monophyly in each of eight avian polytypic species: posterior probability of PAIC monophyly in the creditable tree set (BEAST 1.7); proportion of ML bootstrap replicates supporting PAIC monophyly (GARLI 2.0); ML scores of the best and PAIC constrained trees; and the *P*-value of the Approximately Unbiased (AU) test. Values considered strong support for PAIC paraphyly are in bold typeface.

urostictus, was also partitioned into these same three geographic groups (Luzon PAIC, Samar/Bohol, Mindanao/Dinagat/Siargao) but the topology differed, with the Luzon PAIC sister to Mindanao/Dinagat/Siargao.

Two of three remaining species (*A. pulcherrima* and *D. hypoleucum*) lacked genetic structure across the Bohol Sea in both mitochondrial and nuclear loci (Table 3-3). However, each of these species includes a highly divergent lineage restricted to a small subset of the Mindanao PAIC: *A. pulcherrima decorosa* restricted to Bohol, *D. hypoleucum mindanense* restricted to the Zamboanga Peninsula in western Mindanao. Otherwise, patterns in these two species show only a single deep-water break isolating lineages across the San Bernardino Strait.

Genetic structure within *P. philippinensis* is complex, and largely incongruent with all *a priori* hypotheses. Luzon PAIC monophyly was supported, as in the other seven focal species. However, four strongly supported geographic clades were recovered within the Mindanao PAIC, including structure across the Bohol Sea even though ENM did not identify barriers in

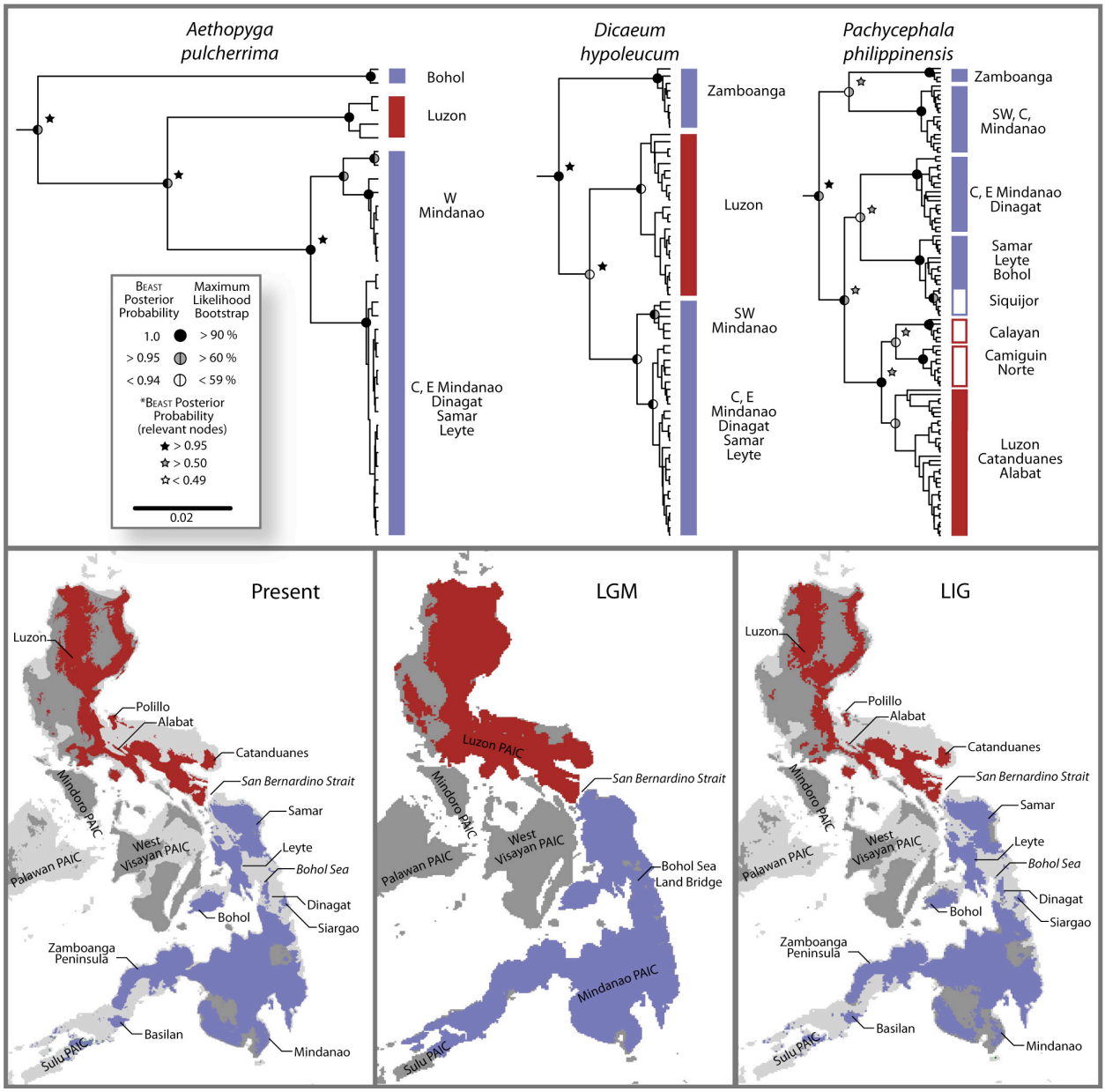


Figure 3-4 Phylogenetic hypotheses (BEAST maximum clade credibility tree, clade posterior probabilities, GARLI ML bootstraps, and *BEAST posterior probabilities), and ENMs for three bird species for which the Bohol Sea Land Bridge region was identified as suitable during Pleistocene low sea level stands. Branch lengths are scaled to ND2 substitution rate. Detailed phylogenetic trees are reported in supporting information (Appendix 2). ENMs shown were developed for *Dicaeum hypoleucum*, but ENMs for all three species (including *Aethopyga pulcherrima* and *Pachycephala philippinensis*) were similar (Appendix 2). For ENMs, red denotes suitable environmental conditions within the Luzon PAIC, and blue denotes suitable environmental conditions within the Mindanao PAIC.

environmental suitability for this species. Unlike the other seven species, *P. philippinensis* occurs on three small peripheral islands isolated by deep-water barriers (Calayan and Camiguin Norte north of Luzon, and Siquijor in the Bohol Sea), each of which was recovered as a monophyletic group with strong support.

All divergence time estimates of major clades (Appendix 2) were consistent with Pleistocene or late Pliocene divergence in each of the eight focal species. Estimates suggest only a single cladogenic event (*A. pulcherrima decorosa* versus *A. p. pulcherrima and A. p. jefferyi*) possibly predated the period of rapid sea level fluctuations [approximately 20,000–3.3 Mybp to present (Miller 2005)], with this event estimated at 1.7–3.5 Mybp (BEAST) or 1.6–3.6 Mybp (*BEAST).

Discussion

Drivers of diversification in the Philippine archipelago

Molecular phylogenetic hypotheses for eight species of Philippine birds clearly indicate that neither deep-water barriers nor paleoclimate refugia adequately explain patterns of genetic differentiation and diversification in the Philippines when take separately. However, when considered together, deep-water and paleoclimate barriers are congruent with the majority of genetic structure within each focal species. That is, shallow seas powered isolation during interglacial periods, and unsuitable environmental conditions powered isolation during glacial maxima, in spite of the existence of land bridges. Thus, paleoclimate factors are a key addition to

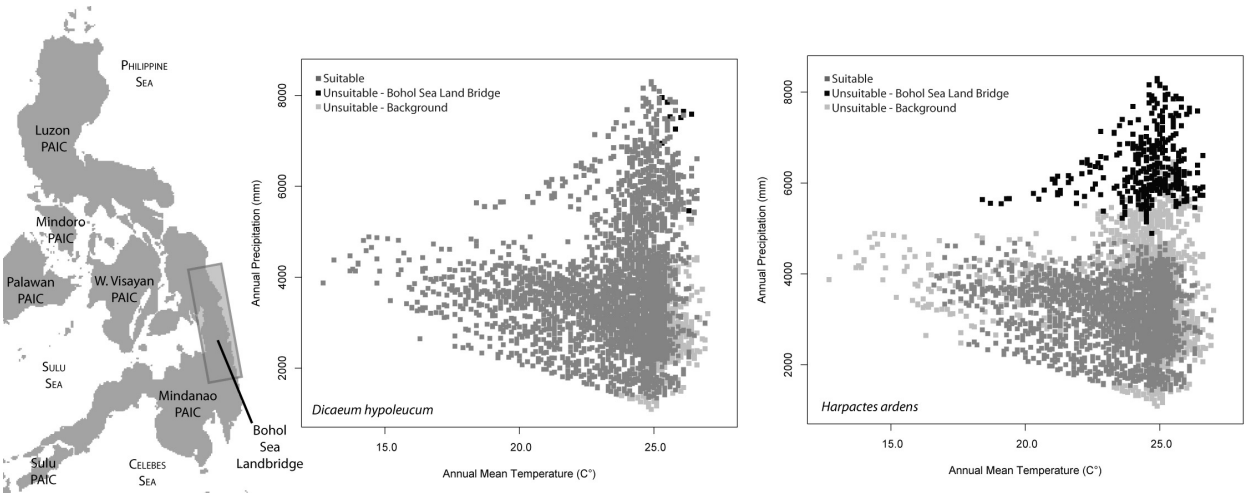


Figure 3-5 Bivariate plots comparing suitable and unsuitable combinations of annual mean temperature and annual precipitation in species predicted to be present (*Dicaeum hypoleucum* shown) or absent (*Harpactes ardens* shown) across the Bohol Sea Land Bridge. Note wide suitability across most combinations in *Dicaeum hypoleucum,* versus a more restricted set of suitable conditions in *Harpactes ardens*. Other species show similar patterns (Appendix 2).

Deviations from strict PAIC model expectations have been documented in several recent phylogenetic studies, but few causal mechanisms have been proposed to explain them. Unlike *ad hoc* mechanisms, such as stochastic dispersal, paleoclimate suitability and refugia provide a testable hypothesis virtually any organism, assuming that adequate occurrence data are available to build robust models (Pearson et al. 2006), and that model transfer from present-day to paleoclimate conditions is justified (Owens et al. 2013). Integration of independent data streams (e.g. ENMs and DNA sequences) and testing for coincidence among different sets of results is a powerful comparative approach to complex biogeographic questions (Peterson 2009).

An examination of glacial maxima models of environmental conditions (temperature and precipitation) suggests that the environmental factor that limits occurrence across the Bohol Sea Land Bridge (Fig. 3-5) is increased precipitation. Periods of increased precipitation result in strong physiological costs to tropical forest birds, including limited foraging time, decrease in fat

Species	LGM Suit-ability break	Average p-dist (%)		Pairwise F_{ST}		F_{ST} *P*-value		Exact test *P*-value	
		ND2	Nuclear loci	ND2	Nuclear loci	ND2	Nuclear loci	ND2	Nuclear loci
A. pulcherrima	No	0.62	0.000	0.12	0.02	0.15	0.19	0.621	0.416
C. melanurus	Yes	2.37	0.122	0.89	0.10	**<0.001**	**<0.001**	**<0.001**	0.085
D. hypoleucum	No	0.03	0.008	0.02	0.00	0.29	0.351	0.855	0.302
H. ardens	Yes	1.10	0.000	0.65	0.01	**<0.001**	0.26	**<0.001**	0.138
I. cyanogastra	Yes	5.04	0.062	0.95	0.12	**0.018**	**0.036**	**0.014**	**0.002**
P. philippinensis	No	1.95	0.003	0.49	0.05	**<0.001**	**<0.001**	**0.012**	**0.003**
P. olivaceus	Yes	3.53	0.002	0.92	0.22	**<0.001**	**<0.001**	**0.006**	0.148
P. urostictus	Yes	4.24	0.164	0.90	0.17	**<0.001**	**<0.001**	**0.005**	0.204

Table 3-3. Support for genetic differentiation across the Bohol Sea (within the Mindanao PAIC) in eight species of Philippine birds. Environmental suitability breaks based on ecological niche models correspond to genetic differentiation in seven of eight species. In *Pachycephala philippinensis,* the lone exception, populations are differentiated across the Sea of Bohol, although no break in environmental suitability was inferred from models. Significant genetic differentiation (*P* < 0.05) is indicated in bold typeface

stores, increased stress, and limited reproductive effort (Boyle et al. 2010; 2011). In light of these observations, we hypothesize that the almost twofold increase in precipitation during globally cool periods rendered the Bohol Sea Land Bridge area unsuitable to *C. melanurus*, *H. ardens*, *I. cyanogastra*, *P. olivaceus*, and *P. urostictus* (Figs. 3-5, Appendix 2). These five species had narrower overall climatic tolerances than *A. pulcherrima*, *D. hypoleucum*, and *P. philippinensis*, for which the Bohol Sea Land Bridge area was reconstructed as suitable. In general, these empirical and modeling results suggest that, over a given landscape, species with narrower environmental tolerances are more likely to become isolated as a result of changing environmental conditions.

Apart from deep phylogenetic divergences across the Bohol Sea Land Bridge, expectations of the PAIC diversification model were largely met by the eight focal species; all eight exhibited genetic divergences across the San Bernardino Strait, which separated a Luzon PAIC clade from all other populations. Luzon PAIC populations generally displayed no genetic

structure within the PAIC, with the exception of *H. ardens*, for which we recovered very slight mitochondrial differentiation between northern and southern populations (Appendix 2). Genetic differentiation within the Luzon PAIC has been reported in other bird (Sánchez-González and Moyle 2011; Sheldon et al. 2012; Hosner et al. 2013b) and vertebrate groups (Welton et al. 2010), but the potential role of paleoclimate in causing this differentiation has not been assessed. Model projections in these eight taxa suggest that suitable environmental conditions for forest species were widespread and continuous within the Luzon PAIC throughout Pleistocene/late Pliocene climate oscillations. Therefore, non-climate-related mechanisms may be needed to explain the genetic differentiation observed within Luzon in some vertebrates.

Two phylogenetic results were incongruent with both the PAIC hypothesis and paleoclimate models. Divergent, diagnosable lineages within *A. pulcherrima* (*decorosa*, Bohol; (Hosner et al. 2013a) and *Dicaeum hypoleucum* (*mindanense,* Zamboanga Peninsula) present additional examples of diversification within the Mindanao PAIC not associated with modeled breaks in climate suitability. Clearly, Philippine biogeography is complex, and additional mechanisms are needed to explain these deviations from current diversification models. *Aethopyga pulcherrima decorosa* is strongly divergent (genetically and phenotypically) from other *A. pulcherrima* populations, and is the only taxon in our study that possibly originated prior to Pleistocene/late Pliocene climate fluctuations. *Dicaeum hypoleucum mindananse* is genetically and phenotypically divergent from all other subspecies sampled (Appendix 2), but is phenotypically similar to *D. h. hypoleucum* of the Sulu Archipelago. If phenotype indeed reflects close relationships between Sulu *D. h. hypoleucum* and *D. h. mindanense*, then presence of two deeply divergent lineages on Mindanao could be the result of differentiation across a deep-water barrier (between Basilan and Jolo islands in the Sulu archipelago), followed by subsequent

colonization of Basilan and the Zamboanga Peninsula. Genetic sampling from the Sulu Archipelago is needed to test this hypothesis.

Mindanao Island comprises several distinct geologic blocks that have merged over the past 5–10 Mybp (Hall 1998; Yumul et al. 2004). Sanguila et al. (2011) demonstrated strong correlations between these geologic blocks and genetic structure in *Ansonia* slender toads, and hypothesized that these geologic blocks played a role in isolating lineages of organisms. In four bird species (*A. pulcherrima, D. hypoleucum, H. ardens,* and *P. philippinensis*), we detected genetic structure more or less corresponding to these geologic blocks within Mindanao (Appendix 2), but this structure was slight compared to that associated with deep-water and paleoclimate factors, suggesting an age much younger than the hypothesized geological events. However, these results do support a potential role of landscape complexity in refining the PAIC model at very fine scales.

The coarse estimates of divergence times obtained from calibrated phylogenies are consistent with the hypothesis that diversification in the focal taxa occurred throughout the Pleistocene, perhaps into the late Pliocene in one species (*A. pulcherrima*; Appendix 2) Estimates for diversification across the San Bernardino Strait (inferred from *BEAST) vary from 0.58–2.2 Mybp (in *A. pulcherrima*) to 0.06–0.3 Mybp (in *H. ardens*). These results suggest that changing environmental conditions and seas levels associated with Pleistocene climate fluctuations function as a "species pump" providing multiple opportunities for population fragmentation and ensuing diversification throughout the past 3.3 Mybp (Miller 2005; Oaks et al. 2013). However, we consider these results regarding the timing of diversification preliminary; more robust estimates of timing require deeper sampling of loci and additional data (fossils and island ages) for improved calibration.

Patterns of endemism and conservation implications

This study adds to other recent avian molecular studies (Sánchez-González and Moyle 2011; Sheldon et al. 2012; Moltesen et al. 2012; Andersen et al. 2013) and general distributional patterns of subspecies (Dickinson et al. 1991) suggesting that isolation and subsequent differentiation within the Mindanao PAIC is widespread in birds. Treating these differentiated populations as multiple, range-restricted species (under lineage-based species concepts), rather than subspecies of single widespread lineages, have profound conservation implications (Peterson 2006). Conservation assessments and priorities based on widespread, polytypic species may overlook threatened populations that would be treated as species under lineage-based criteria (Peterson and Navarro-Sigüenza 1999). For example, *Aethopyga pulcherrima decorosa* is genetically divergent (~10 % uncorrected ND2 pairwise distance from other *pulcherrima* subspecies), and differs in breast, tail, crown and wing coloration. It is endemic to Bohol Island, which is largely deforested, and may now be restricted to two protected areas (Rajah Sikatuna Protected Landscape and the Loboc Watershed) within that island.

Using congruence between operational criteria from both genetic markers (strongly-supported monophyly, strong genetic differentiation between geographically-circumscribed groups) and phenotypic characters (fixed, diagnosable differences in plumage/morphology; assessed from museum specimens), the eight focal species would instead be partitioned into 16: *C. melanurus* partitioned into *Ceyx melanurus, C. samarensis, C. mindanensis* (Collar 2011; Andersen et al. 2013)*; I. cyanogastra* partitioned into *I. cyanogastra I. ellae, I. melanochlamys* (including *hoogstraali*; Moltesen et al. 2012); *D. hypoleucum* partitioned into *D. hypoleucum* (including *mindanense*), *D. pontifex, D. obscurum* (including *cagayanense*); *Aethopyga*

pulcherrima, partitioned into *A. pulcherrima A. jefferyi*, *A. decorosa* (Hosner et al. 2013a). Two species require further evaluation because evidence from molecular markers and phenotype conflict. *Pachycephala philippinensis* is genetically highly structured, yet the only populations differing in fixed plumage characters are the two distinctive populations inhabiting Calayan and Camiguin Norte islands to the north of Luzon, which form a nested clade within all other populations. Similarly, Luzon and Mindanao PAIC populations of *P. olivaceus* are each distinctive and diagnosable in plumage, but we recovered birds from Samar sister to the Luzon PAIC rather than Mindanao. *Harpactes ardens* and *P. urostictus* each contain strongly differentiated populations, but these populations differ subtly in appearance and are not diagnosable by fixed plumage or morphological differences.

In addition to underestimation of species diversity, conservative taxonomy also underestimates species turnover and overlooks fine-scale areas of endemism. We suggest that the Eastern Visayas (Samar, Leyte, Bohol) be recognized as a distinct area of endemism in the Philippine archipelago, and that conservation efforts consider remaining forests on these islands as unique from those of Mindanao. At a finer scale still, Bohol Island and the Zamboanga Peninsula of western Mindanao likely hold additional examples of unrecognized avian diversity, and require further study.

During Pleistocene/late Pliocene climate oscillations, periodic increases in landscape connectivity were offset by periodic decreases in landscape environmental suitability, resulting in long-term isolation across a periodic land bridge in the Philippine archipelago. Deep-water barriers correspond to zones of genetic differentiation in Philippine forest birds, supporting the long-held view that these barriers are key drivers of allopatric differentiation. However, results support that barriers in environmental suitability also correspond to zones of genetic

differentiation, and are also key drivers of differentiation. Thus, insights from ecological niche modeling are an important addition to insular diversification models. Deep divergences in DNA sequence data recovered from co-distributed, polytypic "species" provide new evidence that recognized Philippine avian diversity is drastically underestimated. Insular species limits, and thus the evolutionary/ecological studies and conservation assessments that rely on them, are in need of refinement.

Chapter 4*

Widespread unrecognized and cryptic avian diversity and endemism in the Philippine Archipelago

*Hosner, P. A., Campillo, L. C., Oliveros, C. H., Urriza, R. Siler, C. D., and R. G. Moyle. Widespread unrecognized and cryptic avian diversity and endemism in the Philippine Archipelago.

Abstract

The Philippine archipelago is recognized as a biodiversity hotspot because of its high levels of vertebrate endemism and threatened species. Like many island systems, avian species in the archipelago feature distinctive allopatric subspecies that may alternatively be treated as species, such that recognized diversity and endemism may be a gross underestimate. To understand how alternative species limits would alter metrics and patterns of diversity and endemism, we selected 19 allopatric species/subspecies groups of forest birds inhabiting the Mindanao Island Group, the largest and most biodiverse island group in the Philippines. We delimited species in an integrated framework, using three operation criteria: 1) well-supported, geographically circumscribed clades, 2) coalescent model-based molecular species delimitation, and 3) fixed differences in phenotypic characters. The union of these criteria identified 40 species in the focal groups, a 74% increase over recent comprehensive taxonomic treatments. These criteria also identified fine scale endemism within the Mindanao group, with multiple unrecognized avian endemics restricted to Samar/Leyte, Bohol Island, and the Zamboanga Peninsula of western Mindanao. Molecular analyses also recovered groups not identified by morphological characters, which may be cryptic species in need of further study. We conclude that polytypic bird species in the Philippines tend to be sets of evolutionarily distinct, range-restricted, allopatric replacement lineages rather than single, variable, widespread lineages.

Introduction

Species are the fundamental units in evolutionary biology, macroecology and conservation biology. Studies in these fields often hinge on reliable and accurate metrics of species diversity; therefore, choice and application of criteria to assess species limits have a strong effect on inference of ecological patterns and evolutionary processes. In birds, assessments of species limits often yield widespread polytypic species composed of similar, yet distinct allopatric subspecies (Mayr 1942; Mayr and Amadon 1951). Alternative assessment criteria might treat these same subspecies as multiple species, which are unrecognized in accepted taxonomies and frequently ignored by biologists. Underestimation of species diversity can impact measures of diversity, estimates of species turnover across landscapes, geographic patterns of endemism (Peterson and Navarro-Sigüenza 1999), and estimates of diversification rates (Smith et al. 2013).

A growing consensus among biologists holds that species are evolutionarily distinct lineages (Simpson 1951; Wiley 1978; Cracraft 1983), or metapopulation segments of ancestor-descendant series through time (De Queiroz 2007). Diagnosing evolutionarily distinct lineages in sympatry is straightforward through use of the reproductive isolation criterion (Mayr 1942), but diagnosis in allopatry remains a major challenge to empirical biologists (Sangster 2000; Fujita et al. 2012; Carstens et al. 2013). Because reproductive isolation cannot be directly assessed in allopatry, biologists often invoke a 'yardstick approach,' a measure of similarity or distance to infer if allopatric lineages would hypothetically interbreed (Will et al. 2005; Tobias et al. 2010). However, determining species limits in this fashion usually involves arbitrary decisions, such as appropriate thresholds in sequence divergence (Moritz and Cicero 2004) or judgment of the relative importance of morphological characters (Tobias et al. 2010). These thresholds and judgments are subject to individual interpretation, and often result in conflicting limits drawn

from differing data sources, for example, between morphological characters and genetic markers. Ideally, more objective species limits may be drawn from the same data sources using diagnostic morphological characters (Wiens and Servedio 2000) and model-based analyses of molecular data (Pons et al. 2006; Fujita et al. 2012; Reid and Carstens 2012; Carstens et al. 2013).

To reconcile differing results from different data sources, there is growing interest in the practice of 'integrative taxonomy' in systematics (Dayrat 2005; Will et al. 2005; Padial et al. 2010; Fujita et al. 2012). Integrative taxonomy accepts that different data sources will inherently result in different interpretations of species limits, and that evaluating the insights and limitations of diverse data sources result in a more robust overall assessment. In allopatry, interpretation of any single species delimitation criterion alone may mislead species diagnosis. For example, differences in morphology could be the result of local adaptation within a widespread lineage, or the result of independent evolutionary history. Likewise, differences in genetic markers may be the result of divergent gene sequences evolving within a single lineage (through either ancestral polymorphism or past population structure), or the result of true population divergence (McKay and Zink 2010). However, congruence between morphological and genetic character sets should only identify evolutionarily distinct lineages.

Biodiversity hotspots (Myers et al. 2000) are areas that feature the combination of exceptional concentrations of biodiversity and exceptional habitat loss. These areas are not distributed evenly across the earth's surface; they are concentrated in low-latitude zones that often include island archipelagos and complex topography. These landscapes often feature a large number of distinctive, allopatric avian subspecies. Therefore, the application of different species diagnosis criteria are likely to have a proportionally stronger effect on measures of species diversity than in more basic landscapes (Sangster 2009). However, the impact of

alternative species diagnosis criteria on assessing biodiversity hotspots is unknown because taxonomic revisions and empirical studies of species delimitation (especially those including DNA sequence data) usually focus on clades of interest rather than geographic areas of interest. Thus, there is little information about the degree to which underestimation of species diversity confounds comparative studies of biodiversity in these threatened landscapes.

The Philippine archipelago is a biodiversity hotspot and a megadiverse country, widely recognized for its endemism and intense concentration of vertebrate diversity (Brown et al. 2013). Biogeographers have traditionally recognized six island groups (Palawan, Luzon, Mindoro, West Visayan, Mindanao, Sulu) within the Philippines, each united by the 120 m isobath and faunal similarities (Dickerson et al. 1928; Heaney 1985; 1986). During periodic Pleistocene climate fluctuations, sea levels were as much as 120 m lower than current day (Voris 2000; Siddall et al. 2003; Miller 2005), and islands within each group formed large conglomerate islands. These island groups are referred to as faunal areas (Heaney 1986), or Pleistocene aggregate island complexes (PAICs, Brown and Diesmos 2002). Each is considered an Endemic Bird Area (EBA), as is the single island of Cebu in the West Visayan PAIC (Stattersfield et al. 1998).

Recent systematic studies based on new genetic information (Oliveros and Moyle 2010; Hosner et al. 2013a,b) and reassessments based on plumage and morphology of specimens (Peterson 2006; Collar 2007; 2011) broadly suggest that avian diversity and endemism within the Philippine archipelago are drastically underestimated (Brown et al. 2013). To reassess avian species limits, and understand how these reassessments alter inference of macroecological patterns, inference of evolutionary processes, and conservation implications in a biodiversity hotspot, we studied a diverse set of avian lineages found throughout the largest Philippine island

group, Greater Mindanao (also known as the Mindanao PAIC). Our inference of species limits follows an integrative framework, using congruence of three criteria to recognize species limits: 1) well-supported monophyly of geographic clades, 2) significant genetic differentiation, as identified by automated coalescent species delimitation, and 3) fixed differences in plumage/morphology.

Methods

Genetic sampling and data collection

We selected 19 lowland bird species/allopatric species groups distributed throughout the Mindanao PAIC with dense available sampling for DNA sequencing (Table 4-1). Some species are endemic to the Mindanao PAIC, some are Philippine endemics found on additional Philippine islands, and one species, *Cyornis* (*Rhinomyias*) *ruficauda*, is also found on Borneo. Species limits follow Kennedy et al. (2000), the most recent comprehensive work on Philippine birds. We note that numerous taxonomic recommendations have been suggested since its publication, including several taxa included this study (Peterson 2006; Collar 2007; 2011; Miranda et al. 2011; Sánchez-González and Moyle 2011; Moltesen et al. 2012; Andersen et al. 2013; Hosner et al. 2013a). We selected up to five individuals per species per locality, resulting in 764 sampled individuals, each with a specimen voucher (Appendix 1).

We sequenced a single mitochondrial gene for DNA sequencing. For most species (18), we sequenced the NADH dehydrogenase subunit 2 (ND2) gene. For one species (*Cyornis ruficauda*) we sequenced the Cytochrome *b* (Cyt*b*) gene so that our sequence dataset was more congruent with existing sequences of closely related taxa on GenBank. We selected outgroups based on results of previously published phylogenetic results (Jønsson et al. 2008; Jones and

Kennedy 2008; Nyári et al. 2009; Hosner et al. 2010; Oliveros and Moyle 2010; Sánchez-González and Moyle 2011; Miranda et al. 2011; Sheldon et al. 2012; Moyle et al. 2012; Moltesen et al. 2012; Andersen et al. 2013; Hosner et al. 2013a).

Species/group	English name	Family	#species/ subspecies	# genetic samples
Otus megalotis	Philippine scops owl	Strigidae	1 / 3	12
Harpactes ardens	Philippine trogon	Trogonidae	1 / 5	44
Ceyx melanurus	Philippine dwarf kingfisher	Alcedinidae	1 / 3	49
Ceyx (*Alcedo*) *argentatus*	silvery kingfisher	Alcedinidae	1 / 2	17
Sarcophanops (*Eurylaimus*) *steerii*	wattled broadbill	Eurylaimidae	1 / 3	14
Pachycephala philippinensis	yellow-bellied whistler	Pachycephalidae	1 / 7	108
Pycnonotus urostictus	yellow-wattled bulbul	Pycnonotidae	1 / 5	66
Phylloscopus olivaceus	Philippine leaf warbler	Phylloscopidae	1 / 1	18
Orthotomus cinereiceps group	tailorbirds	Cisticolidae	3 / 4	16
Rhipidura superciliaris	blue fantail	Rhipiduridae	1 / 3	24
Macronus striaticeps	brown tit-babbler	Timaliidae	1 / 4	32
Ptilocichla mindanensis	striated wren-babbler	Pellorneidae	1 / 4	23
Sterrhoptilus (*Stachyris*) *capitalis* group	'crowned' babblers	Zosteropidae	3 / 8	33
Irena cyanogastra	Philippine fairy bluebird	Irenidae	1 / 3	33
Ficedula basilanica	little slaty flycatcher	Muscicapidae	1 / 2	17
Cyornis (*Rhinomyias*) *ruficauda*	rufous-tailed jungle flycatcher	Muscicapidae	1 / 7	25
Aethopyga pulcherrima	metallic-winged sunbird	Nectariniidae	1 / 3	35
Prionochilus olivaceus	olive-backed flowerpecker	Dicaeidae	1 / 3	45
Dicaeum hypoleucum	buzzing flowerpecker	Dicaeidae	1 / 5	63
Totals			23 / 73	764

Table 1. Scientific names, English names, avian families, recognized species and subspecies, and number of genetic samples sequenced for focal allopatric species complexes.

Genomic DNA was extracted from ethanol-preserved muscle tissue using a non-commercial guanidine thiocyanate protocol (Esselstyn et al. 2008). Gene regions were amplified using published primer sets (ND2, Hackett 1996; Sorenson et al. 1999; Drovetski et al. 2004; Cyt*b*, Moyle et al. 2012). We purified PCR products using 0.25μL Shrimp Alkaline Phosphatase and 0.025μL Exonuclease I (New England Biolabs, Ipswich, MA, USA), and cycle-sequenced both strands of PCR products with BigDye Terminator v3.1 Cycle Sequencing kits (Applied Biosystems, Foster City, CA, USA). Cycle-sequencing products were purified using 70% ethanol precipitation and analyzed on an ABI 3730 capillary DNA sequencer. We used Geneious 6.1 (Kearse et al. 2012) to reconcile chromatograms and align sequences, and then verified alignments by eye. All DNA sequences are available on GenBank (#'s pending).

Phylogenetic analyses

We partitioned DNA sequences for each dataset into first+second codon vs. third codon positions, and selected appropriate models of DNA sequence evolution in jModeltest 0.1 using the Bayesian Information Criterion (BIC; Posada 2008). For most datasets, the BIC selected the HKY model of sequence evolution, exceptions being *Irena* (HKY+I), *Pachycephala* (HKY+G) and *Cyornis* (HKY+I). Each mitochondrial genealogy was inferred using Beast 1.7 (Drummond et al. 2012) using a birth-death tree prior and a strict clock (preliminary runs utilizing a uncorrelated lognormal clock all resulted in the estimate of the standard deviation of rates including zero, justifying use of a strict clock with each dataset). We executed two independent 50 million generation runs, sampled every 50,000 generations, resulting in 1,000 samples from the posterior for each run. We discarded the first 20% of the MCMC samples as burnin. To

assess convergence between runs, we examined convergence of all parameter estimates between runs with Tracer 1.5 (Rambaut and Drummond 2007).

To identify geographically circumscribed clades, we classified each locality according to sub-regions within the Mindanao PAIC identified in recent molecular phylogenetic studies (Sanguila et al. 2011; Brown et al. 2013; Hosner et al. 2013a; Fig. 4-1): Samar/Leyte, Bohol, Dinagat/Siargao, Eastern Mindanao, and the Zamboanga Peninsula (Western Mindanao). We considered well-supported clades to be geographically circumscribed if all members of a mitochondrial clade were sampled from single or adjoining sub-regions within the Mindanao group. We considered the following combinations of sub-regions to be adjoining: Samar/Leyte and Bohol, Samar/Leyte and Dinagat/Siargao, Samar/Leyte and Eastern Mindanao, Dinagat/Siargao and Eastern Mindanao, and Eastern Mindanao and Zamboanga.

To identify statistically significant genetic differentiation in mitochondrial genealogies, we used a Bayesian implementation of the General Mixed Yule-Coalescent model (bGMYC, Pons et al. 2006; Reid and Carstens 2012; Fujita et al. 2012; Carstens et al. 2013). The bGMYC model offers several advantages over the original likelihood-based GMYC, namely that results are inferred over a posterior distribution of trees, which accounts for uncertainty in estimation of tree topology and branch lengths. We analyzed each genealogy separately in R using the bGMYC package (Reid and Carstens 2012). For each dataset, we randomly subsampled 100 trees from the posterior distribution of trees inferred in Beast. We ran each bGMYC MCMC 50,000 generations, discarding the first 40,000 generations as burnin and sampling every 100 generations, which resulted 100 samples per tree and 10,000 total samples for each treeset, following recommended guidelines (Reid and Carstens 2012). We set the t1 parameter to 1 and the t2 parameter to the total number of tips in each genealogy. For each dataset, we summarized

bGMYC results as probability matrix plots, and interpreted clades with $P > 0.5$ as significant genetic differentiation. This probability value threshold represents the best estimate of species limits given the bGMYC model and our sequence data (a compromise between failing to recognize true species and recognizing false species).

Assessment of plumage/morphology

To further validate candidate lineages identified by bGMYC analyses and geographically circumscribed monophyly we assessed phenotypic characters discussed in the literature (McGregor 1909; Kennedy et al. 2000; Peterson 2006) and searched for novel characters in series of specimens from the University of Kansas Biodiversity Institute, the Field Museum of Natural History, and the Philippine National Museum. We considered diagnosable phenotypic characters, including fixed differences in plumage characters and non-overlapping differences in mensural characters, as independent evidence for delimiting species. Ideally, we would assess vocal characters as well, especially for groups in which plumage characters are often uninformative in species identification (i.e. *Otus*, *Phylloscopus*), but available material in sound archives is not adequate for formal analysis.

Results

Identification of evolutionary lineages

We identified a total of 63 geographically circumscribed clades across all 19 focal allopatric species complexes, (Figs. 4-2, 4-3, 4-4, Table 4-2). A similar number of clades (62) were identified by bGMYC analysis (hereafter, bGMYC clades). In 18 of 19 complexes, bGMYC

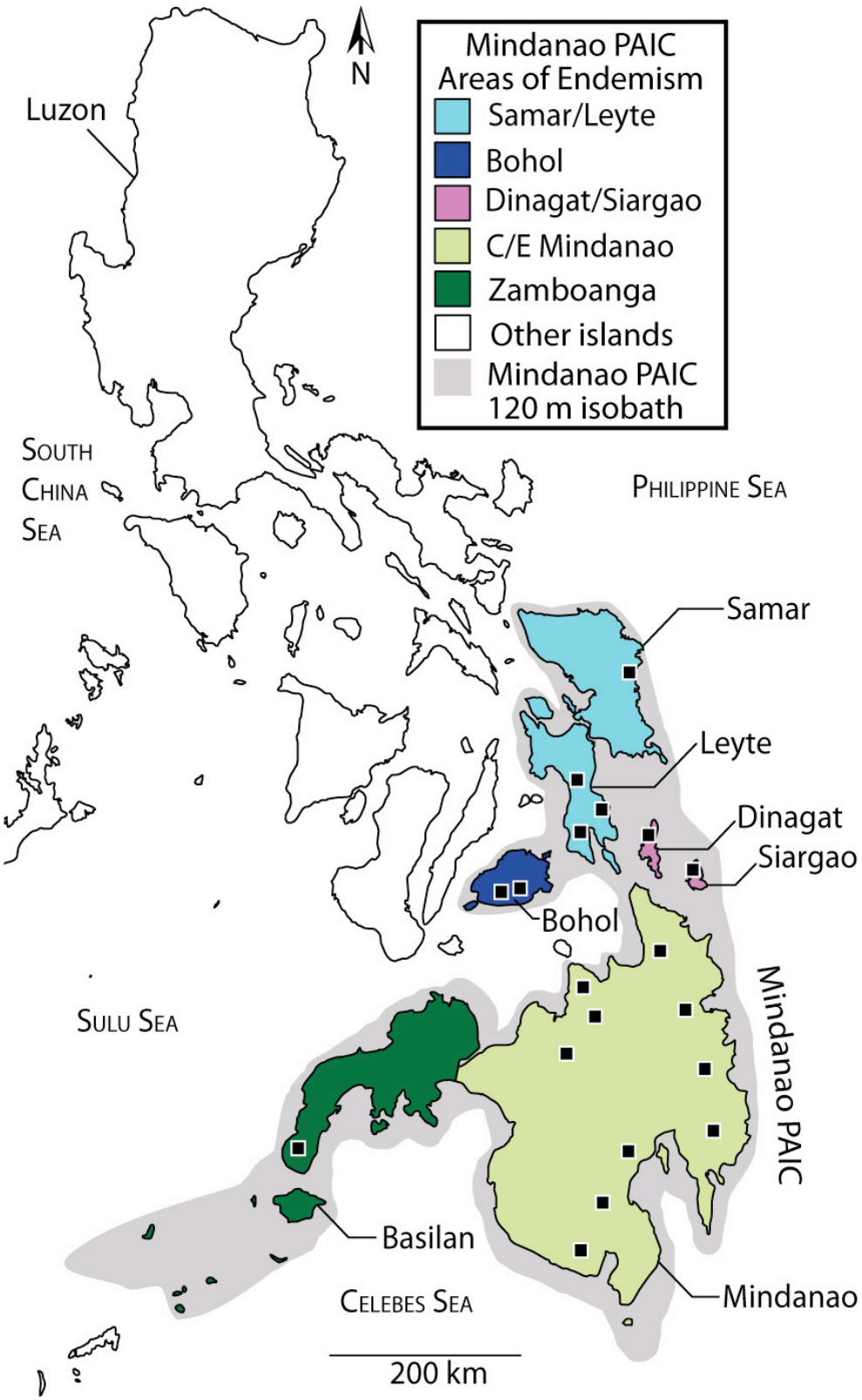


Figure 4-1. Map of the Philippine archipelago, highlighting sub-regions of the Mindanao Island Group. Sampling localities are marked by black squares.

identified multiple clades as candidate species (hereafter, bGMYC clades), with *Phylloscopus olivaceus* being the lone exception (Figs 4-2, 4-3, 4-4, Table 4-2). Comparison of phylogeographic patterns among species revealed multiple shared patterns, most notably a break between Mindanao and the more northern islands of the Mindanao group (Samar/Leyte/Bohol). In addition, geographically circumscribed clades and bGMYC clades all suggested endemism within each sub-region of the Mindanao group: Samar/Leyte (5 lineages), Bohol (4 lineages), Eastern Mindanao (3 lineages), Zamboanga (4 lineages) and Dinagat/Siargao (1 lineage). In *Cyornis ruficauda* (the only focal species found outside the Philippine archipeligo), Philippine populations were monophyletic but were not sister to the Borneo population (only Philippine samples shown in Fig 4-3).

The phylogeographic break (as identified by bGMYC) across the Bohol Sea region (between Bohol/Leyte and Mindanao/Dinagat) was recovered in 15 of 19 complexes. In most species complexes (*Otus*, *Harpactes*, both *Ceyx*, *Sarcophanops*, *Pycnonotus*, *Orthotomus*, *Ptilocichla*, *Sterroptilus*, *Ficedula*, and *Prionochilus*) populations from Samar/Leyte/Bohol and populations from Mindanao/Dinagat/Siargao were reciprocally monophyletic. We also recovered phylogeographic structure across this area in *Irena* and *Macronus*, but populations inhabiting Dinagat and Siargao were sister to those of Samar/Leyte/Bohol rather than those of Mindanao. We also documented differentiation between populations inhabiting Samar/Leyte and Bohol Island. Six bGMYC clades (*Ceyx melanurus*, *Ptilocichla*, *Sterrhoptilus*, *Ficedula*, *Cyornis*, and *Prionochilus*) were recovered as endemic to Samar/Leyte, whereas four mitochondrial lineages were endemic to Bohol (*Ptilocichla*, *Sterrhoptilus*, *Cyornis*, and *Aethopyga*). Of these,

Species/group	Phenotypic group 1	Phenotypic group 2	Phenotypic group 3
Otus megalotis	*O. m. everetti* Mindanao, Basilan, Dinagat, Biliran, Samar, Leyte, Bohol Brownish, small size	*O. m. megalotis* Luzon, Catanduanes, Marinduque Brownish, large size	*O. m. nigrorum* Negros, Panay Face reddish, underparts grayish, small size
Ceyx melanurus	*C. m. mindanensis*: Mindanao, Basilan Auricular white; wing coverts black with tawny edging; outer rectrices tawny; large size	*C. m. samarensis*: Samar, Leyte Auricular blue/white; wing coverts black with blue spots; outer rectrices black; large size	*C. m. melanurus*: Luzon PAIC Auricular blue/white; wing coverts black with blue spots; outer rectrices black; large size
Ceyx (*Alcedo*) *argentatus*	*C. a. argentatus*: Mindanao, Basilan, Dinagat, Siargao Throat, underwing coverts white; underparts metallic teal	*C. a. flumenicolis*: Samar, Leyte, Bohol Throat, underwing coverts buff; underparts metallic indigo	
Sarcophanops (*Eurylaimus*) *steerii*	*S. steerii steerii*/*S. s. mayri*: Mindanao, Basilan, Dinagat, Siargao Back gray; wingstripe yellow/white; nape band plain white	*S. s. samarensis*: Samar, Leyte, Bohol Back maroon; wingstrip maroon/white; nape band scaly	
Pachycephala philippinensis	*P. p. philippinensis*/*P. p. siquijorensis*/*P. p. apoensis*/*P. p. basilanica*/*P. p. boholensis*: Mindanao PAIC/Luzon PAIC/Siquijor Underparts bright yellow; upperparts green	*P. p. fallax*: Calayan Belly whitish/undertail coverts dull yellow; upperparts olive	*P. p. illex*: Camiguin Underparts dull yellow; upperparts olive
Orthotomus cinereiceps group	*O. cinereiceps cinereiceps*/*O. c. obscurior*: Zamboanga/W Mindanao, Basilan Male: Gray crown; white auricular; belly whitish. Female: Similar, but with white throat and streaking on chest	*O. nigriceps*: E Mindanao Male: Black crown; white eyeline; belly dark gray. Female: Similar, but with white throat and streaking on chest	*O. samarensis*: Samar, Leyte, Bohol Male: Black crown; white chin; belly yellow. Female: Similar, but with white throat and streaking on chest
Rhipidura superciliaris	*R. s. superciliaris* Mindanao, Basilan Male: belly bright blue	*R. s. samarensis* Samar, Leyte, Bohol Male: belly bluish-gray	
Macronus striaticeps	*M. s. striaticeps*/*M. s. mindanensis*: Mindanao, Basilan, Samar, Leyte, Bohol Upperparts dark; underparts dark; chest heavily streaked	*M. s. alcasidi*: Dinagat, Siargao Upperparts pale; underparts pale; chest little to no streaking	

Species/group	Phenotypic group 1	Phenotypic group 2	Phenotypic group 3
Ptilocichla mindanensis	*P. m. mindanensis*/*P. m. basilanica*: Mindanao Upperparts plain; large size	*P. m. minuta*/*P. m. fortichi*: Samar, Leyte, Bohol Upperparts streaked with white; small size	
Sterrhoptilus (Stachyris) capitalis	*S. capitalis*: Mindanao, Basilan, Dinagat Crown rufus, throat rufous; belly whitish		
Sterrhoptilus (*Stachyris*) *nigrocapitatus*	*S. n. nigrocapitatus*: Samar, Leyte Crown black; throat yellow with faint rufous edging to feathers; belly whitish	*S. n. boholensis*: Bohol Crown black; throat yellow w/ rufous malar, belly whitish	*S. n. affinis*: S Luzon PAIC Crown black; throat rufous, belly yellowish
Sterrhoptilus (*Stachyris*) *dennistouni*	*S. dennistouni*: N Luzon Crown yellow; throat yellow, belly yellowish		
Irena cyanogastra	*I. c. melanochlamys*/*I. c. hoogstraali*: Mindanao, Basilan Upperparts black; underparts dark blue	*I. c. ellae*: Samar, Leyte, Bohol, Dinagat Upperparts black; underparts black	*I. c. cyanogastra*: Luzon PAIC Upperparts dark blue; underparts dark blue
Ficedula basilanica	*F. b. basilanica*: Mindanao, Basilan Male: tail gray with base of outer tailed feathers white	*F. b. samarensis*: Samar, Leyte Male: tail gray	
Aethopyga pulcherrima	*A. pulcherrima*: Mindanao, Dinagat, Samar, Leyte Wing coverts iridescent green; no iridescence on tertials; tail iridescent blue-green; frontlet small; orange breast spot; bill small	*A. decorosa*: Bohol Wing coverts iridescent steel blue to blue-green; no iridescence on tertials; tail iridescent blue-green; frontlet large; breast spot reduced or lacking; bill small	*A. jefferyi*: Luzon Wing coverts iridescent green; green iridescence on tertials; tail iridescent green; frontlet small; orange breast spot; bill large
Prionochilus olivaceus	*P. o. olivaceus*/*P. o. samarensis*: Mindanao, Dinagat, Samar, Leyte, Bohol Male: Malar dark gray	*P. o. parsoni*: Luzon PAIC Male: Malar black	
Dicaeum hypoleucum	*D. h. hypoleucum*/*D. h. mindanense*: Zamboanga, Basilan Male: Upperparts black, underparts white. Female: Upperparts dusky, underparts whitish	*D. h. pontifex*: E. Mindanao, Samar, Leyte, Bohol Upperparts dusky-brown, underparts whitish	*D. h. obscurum*/ *cagayanense*: Luzon PAIC Uniform greenish, slightly paler below

Table 4-2. (Including preceding page) Phenotypic characters that diagnose geographic groups within each Philippine avian species or species group.

Ptilocichla and *Sterrhoptilus* populations on Samar/Leyte and Bohol were strongly supported as sisters. In *Cyornis*, Bohol was sister to Samar/Leyte + Eastern Mindanao, and in *Aethopyga* Bohol was sister to all other Philippine populations. An assessment of differentiation between Samar/Leyte and Bohol could not be made for *Ceyx melanurus*, *Ficedula,* and *Prionochilus,* because the first two taxa are not known from Bohol, and no *Prionochilus* tissues were available from Bohol.

In addition to genetic structure observed between adjacent islands within Greater Mindanao, we detected evidence for isolation and endemism within Mindanao Island itself. In four species complexes (*Macronus*, *Ficedula*, *Cyornis*, and *Dicaeum*), we identified bGMYC clades from the Zamboanga Peninsula in western Mindanao as distinct from those of Eastern Mindanao. In two groups, *Cyornis* and *Dicaeum*, Zamboanga populations were sister to all other Philippine populations, whereas Zamboanga populations of *Macronus* and *Ficedula* were sister to populations from Eastern Mindanao.

Identification of fixed phenotypic differences

We identified groups of individuals diagnosed by plumage and non-overlapping mensural characters in 15 of 19 focal complexes (Table 4-2). All groups identified by these characters correspond to described subspecies, or groups of subspecies. We found no diagnosable differences within *Harpactes*, *Pycnonotus*, *Phylloscopus*, or *Cyornis*, even though all but *Phylloscopus* are polytypic. In these taxa, plumage variation appears to be individual, based on molt or feather wear, or clinal. In other species groups, we identified two (*Ceyx argentatus*,

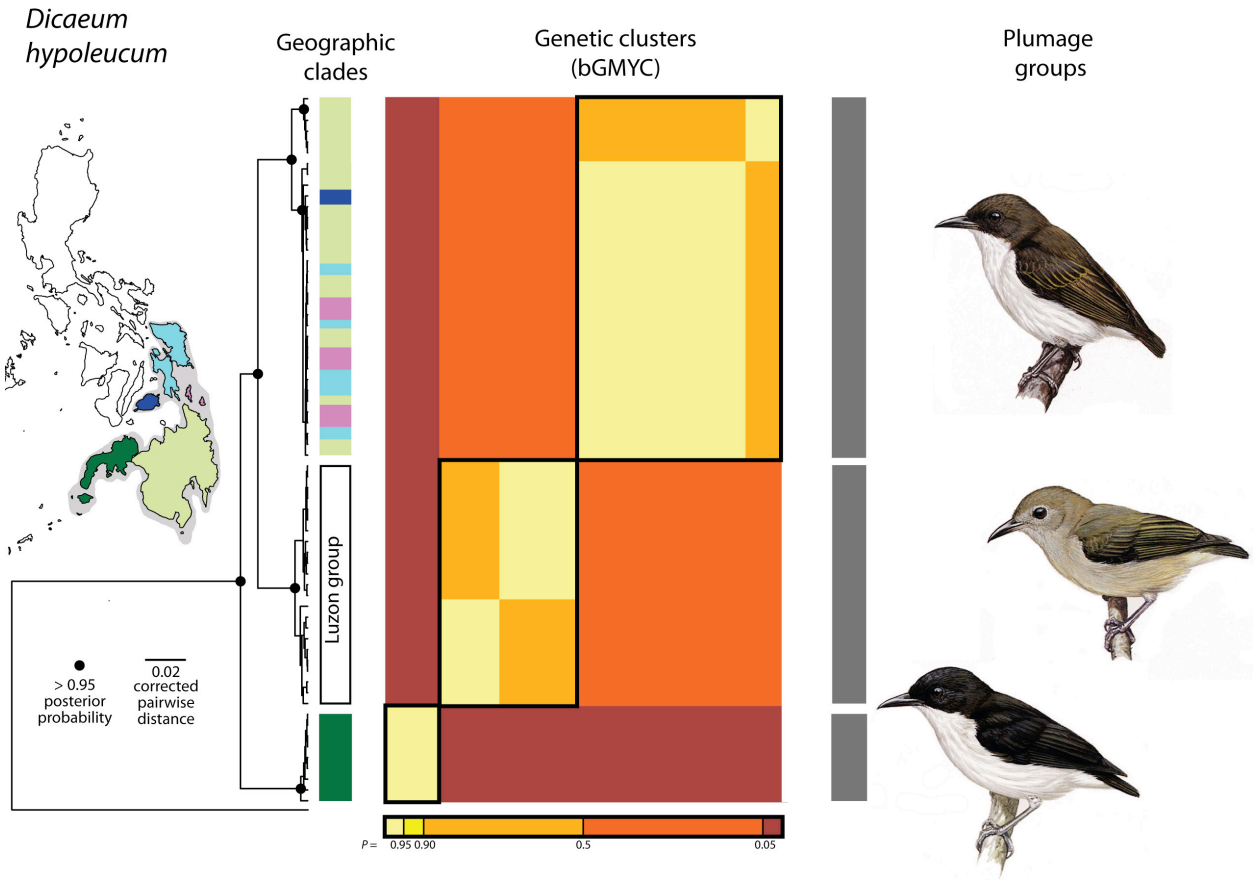


Figure 4-2. Species delimitation of *Dicaeum hypoleucum*, which includes three geographic clades (Zamboanga, Samar/Leyte/Bohol/Dinagat/E. Mindanao, and the Luzon group), each corresponding to a distinct genetic cluster identified by the bGMYC model (black boxes identify each clade on the probability matrix) and distinctive plumage differences. Illustrations copyright Lynx Ediciones, used with permission.

Sarcophanops, *Rhipidura*, *Macronus*, *Ptilocichla*, *Ficedula*, and *Prionochilus*), three (*Otus*, *Ceyx melanurus*, *Orthotomus*, *Irena*, *Aethopyga*) or five (*Sterrhoptilus*) separate phenotypic groups.

Congruence between genetic structure and phenotype

We observed strong congruence between geographically circumscribed clades, bGMYC clades, and groups delimited by phenotypic characters. Using congruence between these character sets as evidence, we recommend recognition of three species within *Ceyx melanurus* (*C. melanurus*, *C. samarensis*, *C. kaupi*), two species within *Ceyx argentatus* (*C. argentatus*, *C. flumenicola*), two species within *Sarcophanops* (*S. steerii*, *S. samarensis*), three species within *Orthotomus* (*O.*

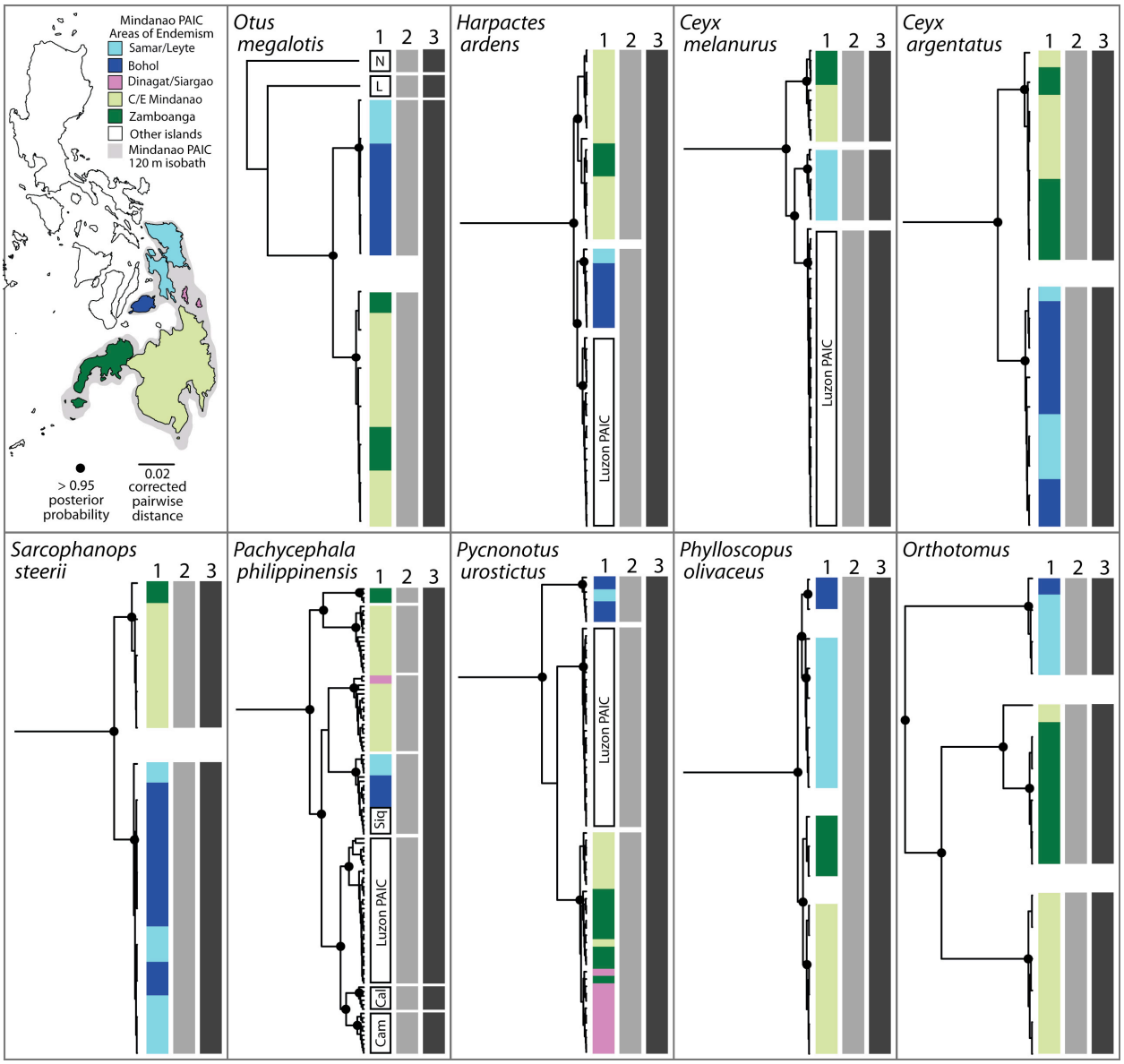


Figure 4-3. Species delimitation of nine Philippine bird species/species groups. The three criteria used to evaluate species limits are 1) Geographic clades, 2) genetic clusters identified with the bGMYC model, and 3) groups identified by fixed differences in plumage/morphology. Congruence between these three criteria is strong evidence for species recognition in *Otus, Ceyx melanurus, Ceyx argentatus, Sarcophanops, and Orthotomus*.

cinereiceps, *O. nigriceps*, *O. samarensis*), two species within *Ptilochichla* (*P. mindanensis* and *P. minuta*) five species of *Sterrhoptilus* (*S. capitalis*, *S. boholensis*, *S. nigrocapitatus*, *S. affinis*, *S. dennistouni*), three species within *Irena cyanogastra* (*I. cyanogastra*, *I. ellae*, *I. melanochlamys*), two species within *Ficedula basilanica* (*F. basilanica*, *F. samarensis*), three

species within *Aethopyga pulcherrima*, (*A. pulcherrima*, *A. jefferyi*, *A. decorosa*), and three species within *Dicaeum hypoleucum* (*D. hypoleucum*, *D. pontifex*, *D. obscurum*).

In *Pachycephala philippinensis*, *Macronus striaticeps*, and *Prionochilus olivaceus*, all three criteria identified subgroups, but group membership conflicted between data sources (i.e., plumage groups were not reciprocally monophyletic in mtDNA sequences). These results could be an artifact of incongruence between gene trees and species trees, or the result of underestimation of species due to symplesiomorphy in morphological characters.

In addition to lineages identified by all three criteria, some lineages were identified as geographically circumscribed clades and bGMYC clades, but not by phenotypic characters. These groups may either represent cryptic species, or results could be an artifact of strong population structure despite ongoing gene flow. Possible cryptic species to be evaluated with additional criteria include mtDNA lineages within *Otus everetti* (two groups), *Harpactes ardens* (two groups), *Pycnonotus urostictus* (three groups) and *Cyornis rufigastra* (four groups, not including the fifth non-sister group on Borneo), as well as additional mtDNA lineages within *Pachycephala philippinensis*, *Macronus striaticeps*, *Ptilocichla mindanensis*, *Ptilocichla minuta*, *Ficedula basilanica*, and *Prionochilus olivaceus*.

Discussion

Species diversity

Our integrative taxonomic assessments of species limits using genetic and phenotypic data support the growing body of evidence that Philippine avian species limits are overly inclusive, resulting in gross underestimates of alpha diversity, beta diversity, and endemism. Our results corroborate and reinforce recent molecular and plumage-based taxonomic updates, several of

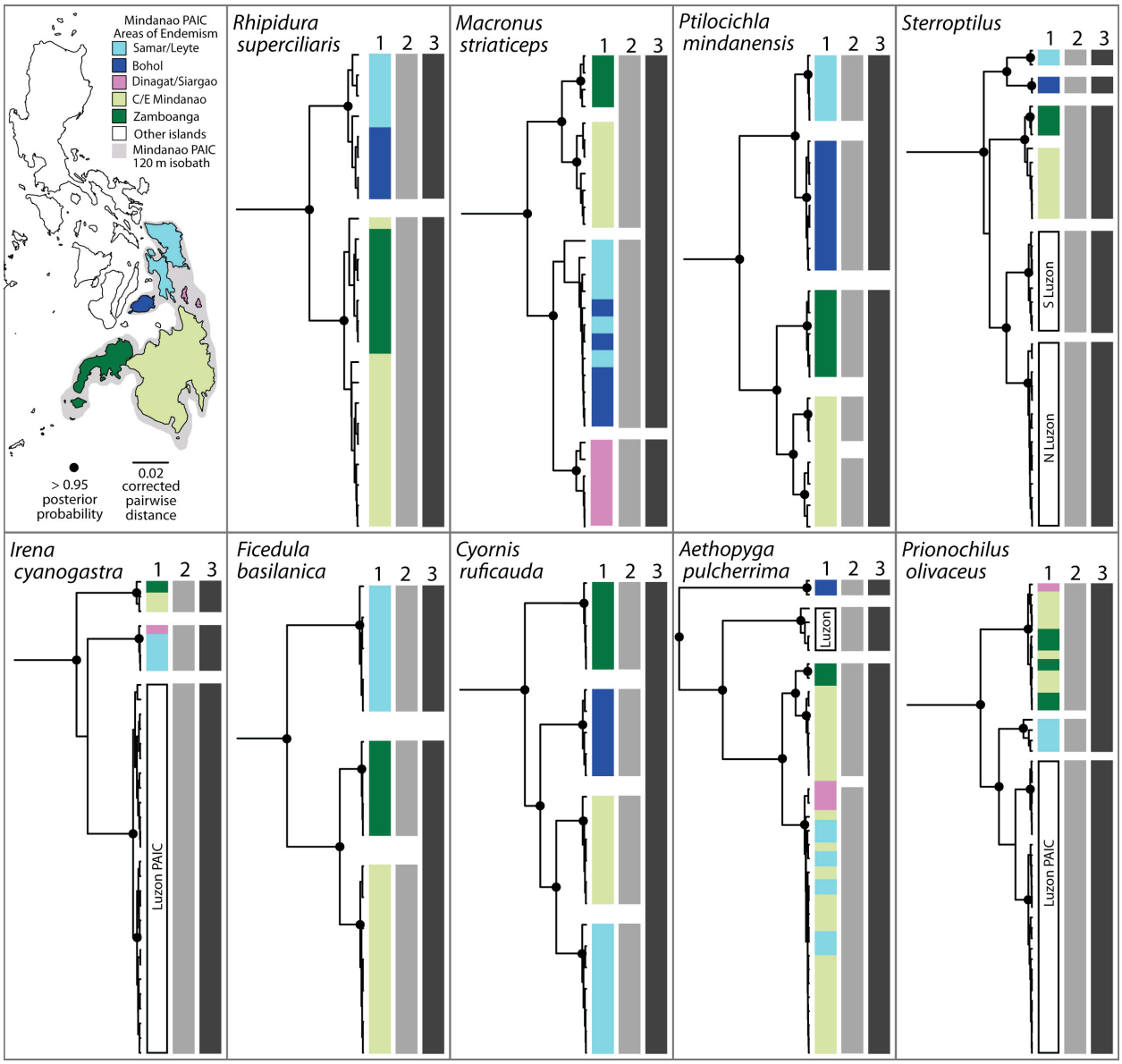


Figure 4-4. Species delimitation of nine more Philippine bird species/species groups. The three criteria used to evaluate species limits are 1) Geographic clades, 2) genetic clusters identified with the bGMYC model, and 3) groups identified by fixed differences in plumage/morphology. Congruence between these three criteria is considered strong evidence for additional species recognition within *Rhipidura*, *Ptilocichla*, *Sterroptilus*, *Irena*, *Ficedula*, and *Aethopyga*.

which motivated this expanded study (Peterson 2006; Oliveros and Moyle 2010; Miranda et al. 2011; Collar 2011; Sánchez-González and Moyle 2011; Sheldon et al. 2012; Moltesen et al. 2012; Andersen et al. 2013; Hosner et al. 2013a). Under the most recent comprehensive taxonomic assessment of Philippine birds (Kennedy et al. 2000), these 19 allopatric species

groups comprise a total of 23 species, yet our integrative assessment supports recognition of 40 species, an increase of 74%. Gill and Donsker (2013), a worldwide taxonomy that already incorporates some of these recent taxonomic recommendations, recognize 31 of these species. The majority of taxa we recommend elevating to species level were originally described as species (McGregor 1909). However, they were later lumped with little comment (Delacour and Mayr 1945) during an active period of taxonomic lumping (Sangster 2009). Our results highlight an important distinction between unrecognized species (species that have been described, are diagnosable and distinctive, yet are not recognized as species due to historical interpretations of species limits), and true cryptic species (species that are not diagnosable by morphological characters, and must be diagnosed by the combination of ecological, behavioral, and genetic characters).

Our results support the possibility of cryptic species in several groups of Philippine birds. Because our validation focused on plumage characters, it is possible (or even likely) that our results were biased towards recognizing more species in taxonomic groups that possess colorful or distinctive plumage patterns. Several of our focal taxonomic groups (e.g., *Otus*, *Phylloscopus*) are widely recognized by ornithologists to have uniform plumage, but also feature distinctive vocalizations that aid in species identification (Irwin et al. 2001; Sangster et al. 2013). Indeed, the divergent clade of *Otus* inhabiting Samar/Leyte/Bohol isn't currently recognized at the subspecific level, although the name *boholensis* appears to be available for it (McGregor 1909). We recommend reassessing 'cryptic' bGMYC clades when adequate material is available for robust analysis of vocal variation in these groups.

Endemism and conservation

Recognition of additional endemic bird species within the Mindanao PAIC suggests that the island group is more a conglomerate of multiple areas of endemism, rather than one large area of endemism. This realization has important implications for avian conservation and highlights the need for conservation strategies and protected areas throughout the Mindanao group, especially in small islands/areas like Bohol Island and the Zamboanga Peninsula. The Philippines hosts a growing grassroots conservation movement (Posa et al. 2008), and we encourage groups working in the archipelago to focus on protected areas and watersheds that hold not only localized endemic bird species, but localized and distinctive endemic bird subspecies as well.

Our results also provide further challenge the paradigm that periodic land connections within PAICs are not substantial biogeographic barriers (Dickinson et al. 1991; Peterson et al. 2000). These data support that current island boundaries and within-island features are important in isolation, maintenance of avian species, and generation of avian endemism. This pattern has been obscured, in part, by conservative taxonomy (Peterson 2006; Brown et al. 2013).

Limitations and improvements

Although these results provide strong support for revising our perspectives on diversity and endemism in Philippine birds, several important limitations exist which could be alleviated by future data collection. First, our molecular data were limited to mtDNA sequences. Although mtDNA can effectively elucidate the evolutionary history of populations, deep coalescence and horizontal gene transfer can lead to conflict between gene trees and the species tree in any single locus (Maddison 1997; Degnan and Rosenberg 2009; Fujita et al. 2012). Nuclear sequence data that support mitochondrial patterns are available for many of these groups (Oliveros and Moyle

2010; Sánchez-González and Moyle 2011; Sheldon et al. 2012; Moltesen et al. 2012; Andersen et al. 2013; Hosner et al. 2013a). However, because bGMYC is a single-locus method, these data were not incorporated herein. Future assessments would benefit from genome-wide sampling (McCormack et al. 2013) to infer population structure, evolutionary history, and the plausibility of additional mtDNA lineages as cryptic species.

The Mindanao PAIC is the largest and most diverse Philippine island group, yet it contains a fraction of the total biological diversity in the Philippine archipelago. Based on numbers of distinctive subspecies once recognized as species (McGregor 1909), several other areas likely contain substantial unrecognized diversity and demand further investigation. Luzon island contains many distinctive north/south replacement subspecies, some of which have recently been re-evaluated and elevated to full species (Sheldon et al. 2012; Hosner et al. 2013b). Similarly, Palawan has many diagnosable subspecies distinct from those of Borneo, some of which have recently been elevated to species (Oliveros and Moyle 2010; Moltesen et al. 2012). Cebu, already classified as its own EBA, has many distinctive subspecies compared to those of other Philippine islands (several of which may already be extinct; Paguntalan and Jakosalem 2008). The Sulu Archipelago, also already considered its own EBA, has distinctive subspecies and is extremely poorly known due to difficult access and political instability. In addition to these large islands found within PAICs, several small, oceanic islands in the Philippines have never had land connections to larger islands (Camiguin Norte, Calayan, Tablas, Siquijor, and Camiguin Sur); each houses distinctive subspecies. If this species delimitation framework were expanded to the entire Philippine archipelago, we would anticipate a tremendous increase in recognized avian diversity in an imperiled landscape already considered a biodiversity hotspot.

Literature Cited

Amante, C., and B. W. Eakins. 2009. ETOPO1: 1 arc-minute global relief model: procedures, data sources and analysis. NOAA Technical Memorandum NESDIS NGDC-24, Washington, D.C.

Andersen, M. J., C. H. Oliveros, C. E. Filardi, and R. G. Moyle. 2013. Phylogeography of the Variable Dwarf-Kingfisher *Ceyx lepidus* (Aves: Alcedinidae) inferred from mitochondrial and nuclear DNA sequences. Auk 130:118–131.

Anderson, R. P., D. Lew, and A. T. Peterson. 2003. Evaluating predictive models of species' distributions: criteria for selecting optimal models. Ecol. Model. 162:211–232.

Backström, N., S. Fagerberg, and H. Ellegren. 2008. Genomics of natural bird populations: a gene-based set of reference markers evenly spread across the avian genome. Mol. Ecol. 17:964–980.

Baldwin, S. P., H. C. Oberholser, and L. G. Worley. 1931. Measurements of birds. Sci. Pub. Cleveland Mus. Nat. Hist. 2:165.

Barcelona, J. R., N. E. Dolotina, G. S. Madronera, W. G. Granert, and D. D. Sopot. 2006. The ferns and fern allies of the karst forests of Bohol Island, Philippines. Am. Fern. J. 96:1–20.

Barker, F., A. Cibois, P. Schikler, J. Feinstein, and J. Cracraft. 2004. Phylogeny and diversification of the largest avian radiation. Proc. Nat. Acad. Sci. USA 101:11040.

Barve, N., V. Barve, A. Jiménez-Valverde, A. Lira-Noriega, S. P. Maher, A. T. Peterson, J. Soberón, and F. Villalobos. 2011. The crucial role of the accessible area in ecological niche modeling and species distribution modeling. Ecol. Model. 222:1810–1819.

BirdLife International. 2012. IUCN Red List for birds. http://www.birdlife.org/

Bouckaert, R. R. 2010. DensiTree: making sense of sets of phylogenetic trees. Bioinformatics 26:1372–1373.

Boyle, W. A., C. G. Guglielmo, K. A. Hobson, and D. R. Norris. 2011. Lekking birds in a tropical forest forego sex for migration. Biol. Lett. 7:661–663.

Boyle, W. A., D. R. Norris, and C. G. Guglielmo. 2010. Storms drive altitudinal migration in a tropical bird. Proc. Roy. Soc. B 277:2511–2519.

Brooks, T. M. 2006. Global biodiversity conservation priorities. Science 313:58–61.

Brown, R. M., and A. C. Diesmos. 2002. Application of lineage-based species concepts to oceanic island frog populations: the effects of differing taxonomic philosophies on the estimation of Philippine biodiversity. Silliman J. 42:133–162.

Brown, R. M., and A. C. Diesmos. 2009. Philippines, biology. Pp. 723–732 *in* R. Gillespie and

D. Clague, eds. Encyclopedia of Islands. University of California Press, Berkeley, California, USA.

Brown, R. M., C. D. Siler, C. H. Oliveros, J. A. Esselstyn, A. C. Diesmos, P. A. Hosner, C. W. Linkem, A. J. Barley, J. R. Oaks, M. B. Sanguila, L. J. Welton, D. C. Blackburn, R. G. Moyle, A. T. Peterson, and A. C. Alcala. 2013. Evolutionary processes of diversification in a model island archipelago. Ann. Rev. Ecol. Syst. 44:24.1–24.25.

Cannon, C. H., R. J. Morley, and A. B. G. Bush. 2009. The current refugial rainforests of Sundaland are unrepresentative of their biogeographic past and highly vulnerable to disturbance. Proc. Nat. Acad. Sci. USA 106:11188–11193.

Carneiro, L. S., L. P. Gonzaga, P. S. Rêgo, I. Sampaio, H. Schneider, and A. Aleixo. 2012. Systematic revision of the Spotted Antpitta (Grallariidae: *Hylopezus macularius*), with description of a cryptic new species from Brazilian Amazonia. Auk 129:338–351.

Carstens, B. C., T. A. Pelletier, N. M. Reid, and J. D. Satler. 2013. How to fail at species delimitation. Mol. Ecol. 22:4369–4383.

Cheke, R. A., and C. F. Mann. 2001. Sunbirds: a guide to sunbirds, flowerpeckers, spiderhunters and sugarbirds of the world. Christopher Helm, London, UK.

Cheke, R. A., and C. Mann. 2008. Family Nectariniidae (sunbirds). Pp. 196–243 *in* J. Del Hoyo, A. Elliott, and D. A. Christie, eds. Handbook of birds of the world: penduline-tits to shrikes. Lynx Ediciones, Barcelona, Spain.

Chesser, R. 1999. Molecular systematics of the Rhinocryptid genus *Pteroptochos*. Condor 101:439–446.

Clement, M., D. Posada, and K. A. Crandall. 2000. TCS: a computer program to estimate gene genealogies. Mol. Ecol. 9:1657–1659.

Collar, N. 2007. Philippine bird taxonomy and conservation: a commentary on Peterson (2006). Bird Conserv. Int. 17:103–113.

Collar, N. J. 2006. A partial revision of the Asian babblers (Timaliidae). Forktail 22:85–112.

Collar, N. J. 2011. Species limits in some Philippine birds including the Greater Flameback *Chrysocolaptes lucidus*. Forktail 27:29–38.

Collar, N. J., and C. Robson. 2007. Family Timaliidae (Babblers). Pp. 70–291 *in* J. Del Hoyo, A. Elliott, and D. A. Christie, eds. Handbook of the birds of the world. Vol. 12: *Picathartes* to tits and chicadees. Lynx Ediciones, Barcelona, Spain.

Coyne, J. A., and T. D. Price. 2000. Little evidence for sympatric speciation in island birds. Evolution 54:2166–2171.

Cracraft, J. 1983. Species concepts and speciation analysis. Pp. 159–187 *in* Current ornithology.

Springer US, Boston, MA.

Dayrat, B. 2005. Towards integrative taxonomy. Biol. J. Linnean Soc. 85:407–415.

De Queiroz, K. 2007. Species concepts and species delimitation. Syst. Biol. 56:879.

De Roever, J. 1990. Notes on the Luzon Wren-babbler. Bull. Oriental Bird Club 12:33–34.

Degnan, J. H., and N. A. Rosenberg. 2009. Gene tree discordance, phylogenetic inference and the multispecies coalescent. Trends Ecol. Evol. 24:332–340.

Degnan, J., and N. Rosenberg. 2006. Discordance of species trees with their most likely gene trees. PLoS Genet. 2:e68.

Delacour, J. 1944. A revision of the family Nectariniidae (sunbirds). Zoologica 29:17–38.

Delacour, J., and E. Mayr. 1945. Notes on the taxonomy of the birds of the Philippines. Zoologica 30:105–117.

Diamond, J. M. 1977. Continental and insular speciation in Pacific land birds. Syst. Biol. 26:263–268.

Diamond, J., and M. Gilpin. 1983. Biogeographic umbilici and the origin of the Philippine avifauna. Oikos 41:307–321.

Dickerson, R. E., E. D. Merrill, R. C. McGregor, W. Schultze, E. H. Taylor, and A. W. Herre. 1928. Distribution of life in the Philippines. Bureau of Printing, Manila, Philippines.

Dickinson, E. C., R. S. Kennedy, and K. C. Parkes. 1991. The birds of the Philippines. BOU checklist No. 12. British Ornithologists' Union, Cambridge, UK.

Drovetski, S., R. M Zink, I. V Fadeev, E. V Nesterov, E. A Koblik, Y. A Red'kin, and S. Rohwer. 2004. Mitochondrial phylogeny of *Locustella* and related genera. J. Avian Biol. 35:105–110.

Drummond, A. J., and M. A. Suchard. 2010. Bayesian random local clocks, or one rate to rule them all. BMC Biol. 8:114

Drummond, A. J., M. A. Suchard, D. Xie, and A. Rambaut. 2012. Bayesian phylogenetics with BEAUti and the BEAST 1.7. Mol. Biol. Evol. 29:1969–1973.

DuPont, J. E. 1971a. Notes on Philippine birds (no. 1). Nemouria 3:1–6.

DuPont, J. E. 1971b. Philippine Birds. Delaware Museum of Natural History, Greenville, USA.

Edgar, R. C. 2004. MUSCLE: a multiple sequence alignment method with reduced time and space complexity. BMC Bioinf. 5:113

Edwards, S. V., L. Liu, and D. Pearl. 2007. High-resolution species trees without concatenation.

Proc. Nat. Acad. Sci. 104:5936–5941

Endler, J. A. 1982. Problems in distinguishing historical from ecological factors in biogeography. Am. Zool. 22:441–452.

Esselstyn, J. A., and R. M. Brown. 2009. The role of repeated sea-level fluctuations in the generation of shrew (Soricidae: *Crocidura*) diversity in the Philippine Archipelago. Mol. Phylogen. Evol. 53:171–181.

Esselstyn, J. A., C. H. Oliveros, R. G. Moyle, A. T. Peterson, J. A. Mcguire, and R. M. Brown. 2010. Integrating phylogenetic and taxonomic evidence illuminates complex biogeographic patterns along Huxley's modification of Wallace's Line. J. Biogeogr. 37:2054–2066.

Esselstyn, J. A., H. J. D. Garcia, M. G. Saulog, and L. R. Heaney. 2008. A new species of *Desmalopex* (Pteropodidae) from the Philippines, with a phylogenetic analysis of the Pteropodini. J Mammal. 89:815–825.

Esselstyn, J. A., R. M. Timm, and R. M. Brown. 2009. Do geological or climatic processes drive speciation in dynamic archipelagos? The tempo and mode of diversification in Southeast Asian shrews. Evolution 63:2595–2610.

Evans, B. J., J. Supriatna, N. Andayani, M. I. Setiadi, D. C. Cannatella, and D. J. Melnick. 2003. Monkeys and toads define areas of endemism on Sulawesi. Evolution 57:1436–1443.

Excoffier, L., G. Laval, and S. Schneider. 2005. Arlequin (version 3.0): An integrated software package for population genetics data analysis. Evol. Bioinform. Online 1:47.

Fujita, M. K., A. D. Leaché, F. T. Burbrink, J. A. Mcguire, and C. Moritz. 2012. Coalescent-based species delimitation in an integrative taxonomy. Trends Ecol. Evol. 27:480–488.

Gascon, C., J. R. Malcolm, J. L. Patton, M. N. da Silva, J. P. Bogart, S. C. Lougheed, C. A. Peres, S. Neckel, and P. T. Boag. 2000. Riverine barriers and the geographic distribution of Amazonian species. Proc. Nat. Acad. Sci. USA 97:13672–13677.

Gill, F. B., F. J. Stokes, and C. Stokes. 1973. Contact zones and hybridization in the Jamaican hummingbird, *Trochilus polytmus* (L.). Condor 75:170–176.

Gill, F., and D. Donsker. 2011. IOC world bird names (version 2.9). http://www.worldbirdnames.org.

Gill, F., and D. Donsker. 2013. IOC world bird names (version 3.0). http://www.worldbirdnames.org.

Goodman, S. M., and P. C. Gonzales. 1990. The birds of Mt. Isarog National Park, southern Luzon, Philippines, with particular reference to altitudinal distribution. Fieldiana Zool. 60:1–39.

Hackett, S. 1996. Molecular phylogenetics and biogeography of tanagers in the genus *Ramphocelus* (Aves). Mol. Phylogen. Evol. 5:368–382.

Haffer, J. 2008. Hypotheses to explain the origin of species in Amazonia. Braz. J. Biol. 68:917–947.

Haffer, J. 1969. Speciation in Amazonian forest birds. Science 165:131–137.

Hall, R. 2002. Cenozoic geological and plate tectonic evolution of SE Asia and the SW Pacific: computer-based reconstructions, model and animations. J. Asian Earth Sci. 20:353–431.

Hall, R. 1998. The plate tectonics of Cenozoic SE Asia and the distribution of land and sea. Pp. 99–131 *in* R. Hall and J. D. Holloway, eds. Biogeography and geological evolution of Southeast Asia. Backhuys Publishers, Leiden, Netherlands.

Harrap, S., and K. Mitchell. 1994. More notes on Rabor's wren-babbler *Napothera rabori*. Bull. Oriental Bird Club 20:50–51.

Heaney, L. 1986. Biogeography of mammals in SE Asia: estimates of rates of colonization, extinction and speciation. Biol. J. Linnean Soc. 28:127–165.

Heaney, L. R. 1991. A synopsis of climatic and vegetational change in Southeast Asia. Climatic Change 19:53–61.

Heaney, L. R. 1985. Zoogeographic evidence for middle and late Pleistocene land bridges to the Philippine Islands. Mod. Quat. Res. Southe. Asia 9:127–144.

Heled, J., and A. Drummond. 2008. Bayesian inference of population size history from multiple loci. BMC Evol. Biol. 8:289.

Heled, J., and A. J. Drummond. 2010. Bayesian inference of species trees from multilocus data. Mol. Biol. Evol. 27:570–580.

Hijmans, R. J., S. E. Cameron, and J. L. Parra. 2005. Very high resolution interpolated climate surfaces for global land areas. Int. J. Climatol. 25:1965–1978.

Hornskov, J. 1995. Recent observations of birds in the Philippine Archipelago. Forktail 11:1–10.

Hosner, P. A., Á. S. Nyári, and R. G. Moyle. 2013a. Water barriers and intra-island isolation contribute to diversification in the insular *Aethopyga* sunbirds (Aves: Nectariniidae). J. Biogeogr. 64:1094–1106.

Hosner, P. A., F. H. Sheldon, H. C. Lim, and R. G. Moyle. 2010. Phylogeny and biogeography of the Asian trogons (Aves: Trogoniformes) inferred from nuclear and mitochondrial DNA sequences. Mol. Phylogen. Evol. 57:1219–1225.

Hosner, P. A., N. C. Boggess, and P. Alviola. 2013b. Phylogeography of the *Robsonius* ground-warblers (Passeriformes: Locustellidae) reveals an undescribed species from northeastern Luzon, Philippines. Condor 115:630–639.

Huxley, T. H. 1868. On the classification and distribution of the Alectoromorphae and

Heteromorphae. Proc. Zool. Soc. Lond. 6:249–319.

Irwin, D. E., P. Alström, U. Olsson, and Z. M. Benowitz-Fredericks. 2001. Cryptic species in the genus *Phylloscopus* (Old World leaf warblers). Ibis 143:233–247.

IUCN. 2010. Guidelines for using the IUCN Red List categories and criteria. Version 8.1. http://www.iucn.org/

Jansa, S., F. Barker, and L. Heaney. 2006. The pattern and timing of diversification of Philippine endemic rodents: evidence from mitochondrial and nuclear gene sequences. Syst. Biol. 55:73–88.

Jones, A., and R. Kennedy. 2008. Evolution in a tropical archipelago: comparative phylogeography of Philippine fauna and flora reveals complex patterns of colonization and diversification. Biol. J. Linnean Soc. 95:620–639.

Jønsson, K. A., R. Bowie, R. Moyle, L. Christidis, C. Filardi, J. Norman, and J. Fjeldså. 2008. Molecular phylogenetics and diversification within one of the most geographically variable bird species complexes *Pachycephala pectoralis/melanura*. J. Avian Biol. 39:473–478.

Kearse, M., R. Moir, A. Wilson, S. Stones-Havas, M. Cheung, S. Sturrock, S. Buxton, A. Cooper, S. Markowitz, C. Duran, T. Thierer, B. Ashton, P. Meintjes, and A. Drummond. 2012. Geneious Basic: an integrated and extendable desktop software platform for the organization and analysis of sequence data. Bioinformatics 28:1647–1649.

Kennedy, R. S., P. C. Gonzales, and E. C. Dickinson. 2000. A guide to the birds of the Philippines. Oxford University Press, New York, USA.

Kennedy, R. S., P. C. Gonzales, and H. C. Miranda. 1997. New *Aethopyga* sunbirds (Aves: Nectariniidae) from the island of Mindanao, Philippines. Auk 114:1–10. Ornithological Societies North America.

Kiehl, J. T., and P. R. Gent. 2004. The community climate system model, Version 2. J. Climate 3666–3682.

Kimball, R. T., E. L. Braun, F. K. Barker, R. C. K. Bowie, M. J. Braun, J. L. Chojnowski, S. J. Hackett, K.-L. Han, J. Harshman, V. Heimer-Torres, W. Holznagel, C. J. Huddleston, B. D. Marks, K. J. Miglia, W. S. Moore, S. Reddy, F. H. Sheldon, J. V. Smith, C. C. Witt, and T. Yuri. 2009. A well-tested set of primers to amplify regions spread across the avian genome. Mol. Phylogen. Evol. 50:654–660.

Kisel, Y., and T. G. Barraclough. 2010. Speciation has a spatial scale that depends on levels of gene flow. Am. Nat. 175:316–334.

Lambert, F. R. 1993. Some key sites and significant records of birds in the Philippines and Sabah. Bird Conserv. Int. 3:281–297.

Lara, C. E., A. M. Cuervo, S. V. Valderrama, D. Calderon-F, and C. Daniel Cadena. 2012. A

new species of wren (Troglodytidae: *Thryophilus*) from the dry Cauca River Canyon, northwestern Colombia. Auk 129:537–550.

Lerner, H. R. L., M. Meyer, H. F. James, M. Hofreiter, and R. C. Fleischer. 2011. Multilocus resolution of phylogeny and timescale in the extant adaptive radiation of Hawaiian honeycreepers. Curr. Biol. 21:1838–1844.

Lim, H. C., F. Zou, S. S. Taylor, B. D. Marks, R. G. Moyle, G. Voelker, and F. H. Sheldon. 2010. Phylogeny of magpie-robins and shamas (Aves: Turdidae: *Copsychus* and *Trichixos*): implications for island biogeography in Southeast Asia. J. Biogeogr. 37:1894–1906.

Lim, H. C., M. A. Rahman, S. L. Lim, R. G. Moyle, and F. H. Sheldon. 2011. Revisiting Wallace's haunt: coalescent simulations and comparative niche modeling reveal historical mechanisms that promoted avian population divergence in the Malay Archipelago. Evolution 65:321–334.

Lohman, D. J., K. K. Ingram, D. M. Prawiradilaga, K. Winker, F. H. Sheldon, R. G. Moyle, P. K. L. Ng, P. S. Ong, L. K. Wang, T. M. Braile, D. Astuti, and R. Meier. 2010. Cryptic genetic diversity in "widespread" Southeast Asian bird species suggests that Philippine avian endemism is gravely underestimated. Biol. Conserv. 143:1885–1890.

Lovette, I. 2004. Mitochondrial dating and mixed support for the "2% rule" in birds. Auk 121:1–6.

Maddison, W. 1997. Gene trees in species trees. Syst. Biol. 46:523.

Mallari, N., and A. Jensen. 1993. Biological diversity in Northern Sierra Madre, Philippines: its implication for conservation and management. Asia Life Sci. 2:1–12.

Mann, C. F. 2002. Systematic notes on Asian birds. 28. Taxonomic comments on some south and south-east Asian members of the family Nectariniidae. Zoologische Verhandelingen 340:179–189.

Mathews, G. M. 1925. Descriptions of new genera of birds. Bull. BOC 45:86–87.

Mayr, E. 1963. Animal species and evolution. Harvard University Press, Cambridge, MA.

Mayr, E. 1942. Systematics and the origin of species, from the viewpoint of a zoologist. Columbia University Press, New York, NY.

Mayr, E. 1944. Wallace's line in the light of recent zoogeographic studies. Q. Rev. Biol. 19:1–14.

Mayr, E., and D. Amadon. 1951. A classification of recent birds. Am. Mus. Nov. 1496:1–42.

Mayr, E., and J. Diamond. 2001. The birds of Northern Melanesia: speciation, ecology, and biogeography. Oxford University Press, New York, USA.

McCormack, J. E., S. M. Hird, A. J. Zellmer, B. C. Carstens, and R. T. Brumfield. 2013.

Applications of next-generation sequencing to phylogeography and phylogenetics. Mol. Phylogen. Evol. 66:526–538.

McGregor, R. C. 1909. A manual of Philippine birds. Bureau of Printing, Manila, Philippines.

Mckay, B. D., and R. M. Zink. 2010. The causes of mitochondrial DNA gene tree paraphyly in birds. Mol. Phylogen. Evol. 54:647–650.

Miller, K. G. 2005. The Phanerozoic record of global sea-level change. Science 310:1293–1298.

Miranda, H. C., Jr, D. M. Brooks, and R. S. Kennedy. 2011. Phylogeny and taxonomic review of Philippine lowland scops owls (Strigiformes): parallel diversification of highland and lowland clades. Wilson J. Ornithology 123:441–453.

Moltesen, M., M. Irestedt, J. Fjeldså, P. G. P. Ericson, and K. A. Jønsson. 2012. Molecular phylogeny of Chloropseidae and Irenidae: cryptic species and biogeography. Mol. Phylogen. Evol. 65:903–914.

Moritz, C., and C. Cicero. 2004. DNA barcoding: promise and pitfalls. PLoS Biol. 2:e279–e354.

Moyle, R. G., M. J. Andersen, C. H. Oliveros, F. D. Steinheimer, and S. Reddy. 2012. Phylogeny and biogeography of the core babblers (Aves: Timaliidae). Syst. Biol. 61:631–651.

Moyle, R. G., S. S. Taylor, C. H. Oliveros, H. C. Lim, C. L. Haines, M. A. Rahman, and F. H. Sheldon. 2011. Diversification of an endemic southeast Asian genus: phylogenetic relationships of the spiderhunters (Nectariniidae: *Arachnothera*). Auk 128:777–788.

Myers, N., R. A. Mittermeier, C. G. Mittermeier, G. da Fonseca, and J. Kent. 2000. Biodiversity hotspots for conservation priorities. Nature 403:853–858.

Nyári, Á. S., A. T. Peterson, N. H. Rice, and R. G. Moyle. 2009. Phylogenetic relationships of flowerpeckers (Aves: Dicaeidae): novel insights into the evolution of a tropical passerine clade. Mol. Phylogen. Evol. 53:613–619.

Nylander, J. A. A., J. C. Wilgenbusch, D. L. Warren, and D. L. Swofford. 2008. AWTY (are we there yet?): a system for graphical exploration of MCMC convergence in Bayesian phylogenetics. Bioinformatics 24:581–583.

Oaks, J. R., J. Sukumaran, J. A. Esselstyn, C. W. Linkem, C. D. Siler, M. T. Holder, and R. M. Brown. 2013. Evidence for climate-driven diversification? a caution for interpreting ABC inferences of simultaneous historical events. Evolution 67:991–1010.

Oliveros, C. H., and R. G. Moyle. 2010. Origin and diversification of Philippine bulbuls. Mol. Phylogen. Evol. 54:822–832.

Oliveros, C. H., S. Reddy, and R. G. Moyle. 2012. The phylogenetic position of some Philippine "babblers" spans the muscicapoid and sylvioid bird radiations. Mol. Phylogen. Evol. 65:799–804.

Owens, H. L., L. P. Campbell, L. Dornak, E. Saupe, N. Barve, J. Soberón, K. Ingenloff, A. Lira-Noriega, C. M. Hensz, C. E. Myers, and A. T. Peterson. 2013. Constraints on interpretation of ecological niche models by limited environmental ranges on calibration areas. Ecol. Model. 263:10–18.

O'Neill, J. P., D. F. Lane, and L. N. Naka. 2011. A cryptic new species of thrush (Turdidae: *Turdus*) from Amazonia. Condor 113:869–880.

Padial, J., A. Miralles, I. De la Riva, and M. Vences. 2010. The integrative future of taxonomy. Front. Zool. 7:16.

Pagel, M. 1999. The maximum likelihood approach to reconstructing ancestral character states of discrete characters on phylogenies. Syst. Biol. 48:612–622.

Pagel, M., A. Meade, and D. Barker. 2004. Bayesian estimation of ancestral character states on phylogenies. Syst. Biol. 53:673–684.

Paguntalan, L., and P. G. Jakosalem. 2008. Significant records of birds in forests on Cebu island, central Philippines. Forktail 24:48–56

Parkes, K. C. 1963. The races of the Flaming Sunbird (*Aethopyga flagrans*). Bull. BOC 83:7–8.

Pearson, R. G., C. J. Raxworthy, M. Nakamura, and A. T. Peterson. 2006. Predicting species distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. J. Biogeogr. 34:102–117.

Peterson, A. T. 1999. Conservatism of ecological niches in evolutionary time. Science 285:1265–1267.

Peterson, A. T. 2011. Ecological niche conservatism: a time-structured review of evidence. J. Biogeogr. 38:817–827.

Peterson, A. T. 2009. Phylogeography is not enough: the need for multiple lines of evidence. Front. Biogeogr. 1.1:19–25.

Peterson, A. T. 2006. Taxonomy is important in conservation: a preliminary reassessment of Philippine species-level bird taxonomy. Bird Conserv. Int. 16:155–173.

Peterson, A. T., and A. G. Navarro-Sigüenza. 1999. Alternate species concepts as bases for determining priority conservation areas. Conserv. Biol. 13:427–431.

Peterson, A. T., and Á. S. Nyári. 2007. Ecological niche conservatism and Pleistocene refugia in the thrush-like mourner, *Schiffornis* sp., in the Neotropics. Evolution 62:173–183.

Peterson, A. T., and C. M. Ammann. 2013. Global patterns of connectivity and isolation of populations of forest bird species in the late Pleistocene. Global. Ecol. Biogeogr. 22:596–606.

Peterson, A. T., J. Soberón, R. G. Pearson, R. P. Anderson, E. Martínez-Meyer, M. Nakamura,

and M. B. Araújo. 2011. Ecological niches and geographic distributions. Princeton University Press, Princeton, NJ.

Peterson, A. T., L. G. Ball, and K. W. Brady. 2000. Distribution of the birds of the Philippines: biogeography and conservation priorities. Bird Conserv. Int. 10:149–167.

Peterson, A. T., M. Papeş, and J. Soberón. 2008. Rethinking receiver operating characteristic analysis applications in ecological niche modeling. Ecol. Model. 213:63–72.

Peterson, A. T., R. G. Moyle, Á. S. Nyári, M. B. Robbins, R. T. Brumfield, and J. V. J. Remsen. 2007. The need for proper vouchering in phylogenetic studies of birds. Mol. Phylogen. Evol. 45:1042–1044.

Phillips, S. J., R. P. Anderson, and R. E. Schapire. 2006. Maximum entropy modeling of species geographic distributions. Ecol. Model. 190:231–259.

Pons, J., T. Barraclough, J. Gomez-Zurita, A. Cardoso, D. Duran, S. Hazell, S. Kamoun, W. Sumlin, and A. Vogler. 2006. Sequence-based species delimitation for the DNA taxonomy of undescribed insects. Syst. Biol. 55:595–609.

Posa, M. R. C., A. C. Diesmos, N. S. Sodhi, and T. M. Brooks. 2008. Hope for threatened tropical biodiversity: lessons from the Philippines. BioScience 58:231–240.

Posada, D. 2008. jModelTest: phylogenetic model averaging. Mol. Biol. Evol. 25:1253–1256.

Poulsen, M. K. 1995. The threatened and near-threatened birds of Luzon, Philippines, and the role of the Sierra Madre mountains in their conservation. Bird Conserv. Int. 5:79–115.

Pyle, P., A. Welch, and R. Fleischer. 2011. A new species of shearwater (*Puffinus*) recorded from Midway Atoll, northwestern Hawaiian Islands. Condor 113:518–527.

Rambaut, A., and A. J. Drummond. 2007. Tracer version 1.5. available from http://beast.bio.ed.ac.uk.

Rand, A. L. 1960. A new species of babbling thrush from the Philippines. Fieldiana Zool. 39:377–379.

Rand, A. L., and D. S. Rabor. 1967. New birds from Luzon, Philippine Islands. Fieldiana Zool. 51:85–99.

Raymond, M., and F. Rousset. 1995. An exact test for population differentiation. Evolution 49:1280–1283.

Reid, N. M., and B. C. Carstens. 2012. Phylogenetic estimation error can decrease the accuracy of species delimitation: a Bayesian implementation of the general mixed Yule-coalescent model. BMC Evol. Biol. 12:1–1.

Ribas, C. C., A. Aleixo, A. C. R. Nogueira, C. Y. Miyaki, and J. Cracraft. 2012. A

palaeobiogeographic model for biotic diversification within Amazonia over the past three million years. Proc. Roy. Soc. B 279:681–689.

Ronquist, F. 1997. Dispersal-vicariance analysis: A new approach to the quantification of historical biogeography. Syst. Biol. 46:195–203.

Ronquist, F., and J. P. Huelsenbeck. 2003. MrBayes 3: Bayesian phylogenetic inference under mixed models. Bioinformatics 19:1572–1574.

Ryan, P. G., P. Bloomer, C. L. Moloney, T. J. Grant, and W. Delport. 2007. Ecological speciation in South Atlantic island finches. Science 315:1420–1423.

Sangster, G. 2009. Increasing numbers of bird species result from taxonomic progress, not taxonomic inflation. Proc. Roy. Soc. B 276:3185–3191.

Sangster, G. 2000. Taxonomic stability and avian extinctions. Conserv. Biol. 14:579–581.

Sangster, G., Ben F King, P. Verbelen, and C. R. Trainor. 2013. A new owl species of the genus *Otus* (Aves: Strigidae) from Lombok, Indonesia. PLoS One 8:e53712.

Sanguila, M. B., C. D. Siler, A. C. Diesmos, O. Nuñeza, and R. M. Brown. 2011. Phylogeography, geographic structure, genetic variation, and potential species boundaries in Philippine slender toads. Mol. Phylogen. Evol. 61:333–350.

Sánchez-González, L. A., and R. G. Moyle. 2011. Molecular systematics and species limits in the Philippine fantails (Aves: *Rhipidura*). Mol. Phylogen. Evol. 61:290–299.

Sánchez-González, L. A., C. Oliveros, N. Puna, and R. G. Moyle. 2010. Nests, nest placement, and eggs of three Philippine endemic birds. Wilson J. Ornithol. 122:587–591.

Scharringa, J. 2005. Birds of tropical Asia 3.0. Bird Songs International, Enschede, Netherlands.

Seeholzer, G. F., B. M. Winger, M. G. Harvey, D. Caceres A, and J. D. Weckstein. 2012. A new species of barbet (Capitonidae: *Capito*) from the Cerros Del Sira, Ucayali, Peru. Auk 129:551–559.

Sheldon, F. H., C. H. Oliveros, S. S. Taylor, B. Mckay, H. C. Lim, M. A. Rahman, H. Mays, and R. G. Moyle. 2012. Molecular phylogeny and insular biogeography of the lowland tailorbirds of Southeast Asia (Cisticolidae: *Orthotomus*). Mol. Phylogen. Evol. 65:54–63.

Sheldon, F. H., D. J. Lohman, H. C. Lim, F. Zou, S. M. Goodman, D. M. Prawiradilaga, K. Winker, T. M. Braile, and R. G. Moyle. 2009. Phylogeography of the magpie-robin species complex (Aves: Turdidae: *Copsychus*) reveals a Philippine species, an interesting isolating barrier and unusual dispersal patterns in the Indian Ocean and Southeast Asia. J. Biogeogr. 36:1070–1083.

Shimodaira, H., and M. Hasegawa. 2001. CONSEL: for assessing the confidence of phylogenetic tree selection. 17:1246–1247.

Siddall, M., E. Rohling, A. Almogi-Labin, C. Hemleben, D. Meischner, I. Schmelzer, and D. Smeed. 2003. Sea-level fluctuations during the last glacial cycle. Nature 423:853–858.

Siler, C. D., J. R. Oaks, J. A. Esselstyn, A. C. Diesmos, and R. M. Brown. 2010. Phylogeny and biogeography of Philippine bent-toed geckos (Gekkonidae: *Cyrtodactylus*) contradict a prevailing model of Pleistocene diversification. Mol. Phylogen. Evol. 55:699–710.

Siler, C. D., J. R. Oaks, L. J. Welton, C. W. Linkem, J. C. Swab, A. C. Diesmos, and R. M. Brown. 2012. Did geckos ride the Palawan raft to the Philippines? J. Biogeogr. 39:1217–1234.

Simpson, G. G. 1951. The species concept. Evolution 5:285.

Sly, N. D., A. K. Townsend, C. C. Rimmer, J. M. Townsend, S. C. Latta, and I. J. Lovette. 2011. Ancient islands and modern invasions: disparate phylogeographic histories among Hispaniola's endemic birds. Mol. Ecol. 20:5012–5024.

Smith, B. T., C. C. Ribas, B. M. Whitney, B. E. Hernández-Baños, and J. Klicka. 2013. Identifying biases at different spatial and temporal scales of diversification: a case study in the Neotropical parrotlet genus *Forpus*. Mol. Ecol. 22:483–494.

Smithe, F. B. 1975. Naturalist's color guide. American Museum of Natural History, New York, USA.

Sorenson, M. D. 2003. More taxa, more characters: the hoatzin problem is still unresolved. Mol. Biol. Evol. 20:1484–1498.

Sorenson, M., J. Ast, D. Dimcheff, T. Yuri, and D. Mindell. 1999. Primers for a PCR-based approach to mitochondrial genome sequencing in birds and other vertebrates. Mol. Phylogen. Evol. 12:105–114.

Souza Muñoz, M. E., R. Giovanni, M. F. Siqueira, T. Sutton, P. Brewer, R. S. Pereira, D. A. L. Canhos, and V. P. Canhos. 2011. openModeller: a generic approach to species' potential distribution modelling. Geoinformatica 15:111–135.

Stamatakis, A. 2006. RAxML-VI-HPC: Maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. Bioinformatics 22:2688–2690.

Stamatakis, A., P. Hoover, and J. Rougemont. 2008. A rapid bootstrap algorithm for the RAxML web servers. Syst. Biol. 57:758–771.

Stattersfield, A. J., M. J. Crosby, and A. J. Long. 1998. Endemic bird areas of the world. BirdLife International, Cambridge U.K.

Steere, J. B. 1894. On the distribution of genera and species of non-migratory land-birds in the Philippines. Ibis 36:411–420.

Stephens, M., N. J. Smith, and P. Donnelly. 2001. A new statistical method for haplotype reconstruction from population data. Am. J. Hum. Gen. 68:978–989.

Steppan, S., C. Zawadski, and L. R. Heaney. 2003. Molecular phylogeny of the endemic Philippine rodent *Apomys* (Muridae) and the dynamics of diversification in an oceanic archipelago. Biol. J. Linnean Soc. 80:699–715.

Stockwell, D., and D. Peters. 1999. The GARP modelling system: problems and solutions to automated spatial prediction. Int. J. Geogr. Inf. Sci. 13:143–158.

Tobias, J. A., N. Seddon, C. N. Spottiswoode, J. D. Pilgrim, L. D. C. Fishpool, and N. J. Collar. 2010. Quantitative criteria for species delimitation. Ibis 152:724–746.

Vanderwerf, E. A., L. C. Young, N. W. Yeung, and D. B. Carlon. 2010. Stepping stone speciation in Hawaii's flycatchers: molecular divergence supports new island endemics within the elepaio. Conserv. Genet. 11:1283–1298.

Voelker, G., R. Outlaw, S. Reddy, M. Tobler, J. Bates, S. Hackett, C. Kahindo, B. Marks, J. Kerbis Peterhans, and T. Gnoske. 2010. A new species of boubou (Malaconotidae: *Laniarius*) from the Albertine Rift. Auk 127:678–689.

Voris, H. 2000. Maps of Pleistocene sea levels in Southeast Asia: shorelines, river systems and time durations. J. Biogeogr. 27:1153–1167.

Wallace, A. R. 1852. On the monkeys of the Amazon. Proc. Zool. Soc. Lond. 20:107–110.

Wallace, A. R. 1876. The geographical distibution of animals, with a study of the relations of living and extinct faunas as elucidating the past changes of the earth's surface. Macmillan, London, GB.

Waltari, E., R. J. Hijmans, A. T. Peterson, Á. S. Nyári, S. L. Perkins, and R. P. Guralnick. 2007. Locating Pleistocene refugia: comparing phylogeographic and ecological niche model predictions. PLoS One 2:e563.

Weir, J. T., and D. Schluter. 2008. Calibrating the avian molecular clock. Mol. Ecol. 17:2321–2328.

Weir, J. T., and D. Schluter. 2004. Ice sheets promote speciation in boreal birds. Proc. Roy. Soc. B 271:1881–1887.

Welton, L. J., C. D. Siler, D. Bennett, A. Diesmos, M. R. Duya, R. Dugay, E. L. B. Rico, M. Van Weerd, and R. M. Brown. 2010. A spectacular new Philippine monitor lizard reveals a hidden biogeographic boundary and a novel flagship species for conservation. Biol. Lett. 6:1–6.

Wiens, J. J., and M. R. Servedio. 2000. Species delimitation in systematics: inferring diagnostic differences between species.

Wiley, E. O. 1978. The evolutionary species concept reconsidered. Syst. Biol. 27:17–26.

Will, K., B. Mishler, and Q. Wheeler. 2005. The perils of DNA barcoding and the need for integrative taxonomy. Syst. Biol. 54:844–851.

Winker, K. 1998. Suggestions for measuring external characters of birds. Ornitol. Neotrop 23–30.

Wood, C., B. Sullivan, M. Iliff, D. Fink, and S. Kelling. 2011. eBird: engaging birders in science and conservation. PLoS Biology 9:e1001220.

Yumul, G. P., C. B. Dimalanta, R. A. Tamayo, R. C. Maury, H. Bellon, M. Polvé, V. B. Maglambayan, C. L. Querubin, and J. Cotten. 2004. Geology of the Zamboanga Peninsula, Mindanao, Philippines: an enigmatic South China continental fragment? Pp. 289–312 *in* J. Malpas, C. J. N. Fletcher, J. R. Ali, and J. C. Aitchison, eds. Aspects of the tectonic evolution of China. Geological Society, London, UK.

Yumul, G. P., Jr., C. B. Dimalanta, V. B. Maglambayan, and E. J. Marquez. 2008. Tectonic setting of a composite terrane: A review of the Philippine island arc system. Geosci J. 12:7–17.

Yumul, G., C. Dimalanta, K. Queaño, E. Marquez, and R. Gillespie. 2009. Philippines, geology. Pp. 732–738 *in* R. Gillespie and D. Clague, eds. Encyclopedia of islands. University of California Press, Berkeley, California, USA.

Zwickl, D. J. 2006. GARLI: genetic algorithm for rapid likelihood inference. http://www. bio. utexas. edu/faculty/antisense/garli/Garli. html.

Appendix 1. All avian tissue samples used in DNA sequencing

Institution	Tissue	*Species*	Country	Island	Province	Locality
KU	19341	*Aethopyga bella*	Philippines	Lubang	Occidental Mindoro	
KU	19631	*Aethopyga bella*	Philippines	Luzon	Aurora	
CMC	1762	*Aethopyga boltoni*	Philippines	Mindanao	Davao del Sur	
CMC	1816	*Aethopyga boltoni*	Philippines	Mindanao	North Cotabato	
CMC	1880	*Aethopyga boltoni*	Philippines	Mindanao	North Cotabato	
CMC	2197	*Aethopyga boltoni*	Philippines	Mindanao	Sarangani	
CMC	2222	*Aethopyga boltoni*	Philippines	Mindanao	Sarangani	
CMC	B36472	*Aethopyga boltoni*	Philippines	Mindanao	North Cotabato	
CMC	B36477	*Aethopyga boltoni*	Philippines	Mindanao	Sarangani	
FMNH	357631	*Aethopyga boltoni*	Philippines	Mindanao	Bukidnon	
KU	10276	*Aethopyga christinae*	China		Guangxi	
KU	13901	*Aethopyga christinae*	China		Guizhou	
ZMUC	123924	*Aethopyga duyvenbodei*	Indonesia	Sangihe	North Sulawesi	
KU	15352	*Aethopyga flagrans*	Philippines	Panay	Antique	
KU	15802	*Aethopyga flagrans*	Philippines	Panay	Antique	
KU	18055	*Aethopyga flagrans*	Philippines	Luzon	Caminares Sur	
KU	19598	*Aethopyga flagrans*	Philippines	Luzon	Aurora	
KU	11048	*Aethopyga gouldiae*	China		Guizhou	
KU	11236	*Aethopyga gouldiae*	China		Guizhou	
AMNH	DOT5649	*Aethopyga ignicauda*	Vietnam		Quag Nam	
KU	15233	*Aethopyga ignicauda*	Myanmar		Jed Lwe	
CMC	B35806	*Aethopyga linaraborae*	Philippines	Mindanao	Davao del Norte	
CMC	B35868	*Aethopyga linaraborae*	Philippines	Mindanao	Davao del Norte	
CMC	B35869	*Aethopyga linaraborae*	Philippines	Mindanao	Davao del Norte	
AMNH	DOT5549	*Aethopyga nipalensis*	Vietnam		Quag Nam	
KU	15234	*Aethopyga nipalensis*	Myanmar		Jed Lwe	
FMNH	357624	*Aethopyga primigenia*	Philippines	Mindanao	Bukidnon	
KU	19100	*Aethopyga primigenia*	Philippines	Mindanao	Agusan del Norte	
CMC	1982	*Aethopyga pulcherrima*	Philippines	Mindanao	Sarangani	Mt. Busa
CMC	2100	*Aethopyga pulcherrima*	Philippines	Mindanao	Sarangani	Mt. Busa
CMC	2125	*Aethopyga pulcherrima*	Philippines	Mindanao	Sarangani	Mt. Busa
CMC	2126	*Aethopyga pulcherrima*	Philippines	Mindanao	Sarangani	Mt. Busa
CMC	2131	*Aethopyga pulcherrima*	Philippines	Mindanao	Sarangani	Mt. Busa
CMC	2146	*Aethopyga pulcherrima*	Philippines	Mindanao	Sarangani	Mt. Busa
CMC	2148	*Aethopyga pulcherrima*	Philippines	Mindanao	Sarangani	Mt. Busa
CMC	3194	*Aethopyga pulcherrima*	Philippines	Mindanao	Davao del Norte	Mt. Pasian
CMC	3204	*Aethopyga pulcherrima*	Philippines	Mindanao	Davao del Norte	Mt. Pasian
CMC	3207	*Aethopyga pulcherrima*	Philippines	Mindanao	Davao del Norte	Mt. Pasian
CMC	3213	*Aethopyga pulcherrima*	Philippines	Mindanao	Davao del Norte	Mt. Pasian
CMC	3242	*Aethopyga pulcherrima*	Philippines	Mindanao	Davao del Norte	Mt. Pasian
CMC	3267	*Aethopyga pulcherrima*	Philippines	Mindanao	Davao del Norte	Mt. Pasian
CMC	3300	*Aethopyga pulcherrima*	Philippines	Mindanao	Davao del Norte	Mt. Pasian
FMNH	454951	*Aethopyga pulcherrima*	Philippines	Luzon	Mountain	Barlig
FMNH	455038	*Aethopyga pulcherrima*	Philippines	Luzon	Albay	Malinao
KU	14043	*Aethopyga pulcherrima*	Philippines	Dinagat	Surigao del Norte	Loreto
KU	14058	*Aethopyga pulcherrima*	Philippines	Dinagat	Surigao del Norte	Loreto
KU	14239	*Aethopyga pulcherrima*	Philippines	Samar	Eastern Samar	Taft
KU	14247	*Aethopyga pulcherrima*	Philippines	Samar	Eastern Samar	Taft
KU	14305	*Aethopyga pulcherrima*	Philippines	Leyte	Leyte	Baybay
KU	19024	*Aethopyga pulcherrima*	Philippines	Mindanao	Aguasan del Sur	Mt. Magdiwata
KU	19052	*Aethopyga pulcherrima*	Philippines	Mindanao	Aguasan del Sur	Mt. Magdiwata
KU	19232	*Aethopyga pulcherrima*	Philippines	Mindanao	Zamboanga del Sur	Pasononca
KU	19237	*Aethopyga pulcherrima*	Philippines	Mindanao	Zamboanga del Sur	Pasononca
KU	19654	*Aethopyga pulcherrima*	Philippines	Luzon	Aurora	Baler
KU	20924	*Aethopyga pulcherrima*	Philippines	Bohol	Bohol	Bilar
KU	21746	*Aethopyga pulcherrima*	Philippines	Luzon	Aurora	Baler
KU	27367	*Aethopyga pulcherrima*	Philippines	Leyte	Southern Leyte	Silago
KU	27447	*Aethopyga pulcherrima*	Philippines	Leyte	Southern Leyte	Silago
KU	27461	*Aethopyga pulcherrima*	Philippines	Leyte	Southern Leyte	Sogod
KU	27466	*Aethopyga pulcherrima*	Philippines	Leyte	Southern Leyte	Sogod
KU	28217	*Aethopyga pulcherrima*	Philippines	Bohol	Bohol	Valencia

KU	28306	*Aethopyga pulcherrima*	Philippines	Mindanao	Aguasan del Norte	Mt. Hilong-Hilong
KU	28316	*Aethopyga pulcherrima*	Philippines	Mindanao	Aguasan del Norte	Mt. Hilong-Hilong
AMNH	DOT10779	*Aethopyga saturata*	Vietnam		Quag Nam	
AMNH	DOT2630	*Aethopyga saturata*	Vietnam		Ha Giang	
KU	12723	*Aethopyga shelleyi*	Philippines	Palawan	Palawan	
KU	12776	*Aethopyga shelleyi*	Philippines	Palawan	Palawan	
AMNH	DOT12310	*Aethopyga siparaja*	Vietnam		Quag Nam	
AMNH	DOT12617	*Aethopyga siparaja*	Indonesia	Sulawesi	Central Sulawesi	
AMNH	DOT331	*Aethopyga siparaja*	Malaysia	Borneo	Sabah	
KU	15302	*Aethopyga siparaja*	Philippines	Panay	Antique	
KU	23182	*Aethopyga siparaja*	Vietnam		Ha Giang	
KU	358592	*Aethopyga siparaja*	Philippines	Sibuyan	Romblon	
KU	17752	*Aethopyga temminckii*	Malaysia	Borneo	Sabah	
KU	14241	*Alcedo argentata*	Philippines	Samar	Eastern Samar	Taft
KU	14284	*Alcedo argentata*	Philippines	Leyte	Leyte	Baybay
KU	14289	*Alcedo argentata*	Philippines	Leyte	Leyte	Baybay
KU	14298	*Alcedo argentata*	Philippines	Leyte	Leyte	Baybay
KU	18103	*Alcedo argentata*	Philippines	Mindanao	Zamboanga del Sur	Pasonanca
KU	18240	*Alcedo argentata*	Philippines	Mindanao	Zamboanga del Sur	Pasonanca
KU	18243	*Alcedo argentata*	Philippines	Mindanao	Zamboanga del Sur	Pasonanca
KU	19071	*Alcedo argentata*	Philippines	Mindanao	Agusan del Sur	Mt. Magdiwata
KU	19252	*Alcedo argentata*	Philippines	Mindanao	Agusan del Sur	Pasonanca
KU	19268	*Alcedo argentata*	Philippines	Mindanao	Zamboanga del Sur	Pasonanca
KU	19269	*Alcedo argentata*	Philippines	Mindanao	Zamboanga del Sur	Pasonanca
KU	20934	*Alcedo argentata*	Philippines	Bohol	Bohol	Sierra Bullones
KU	20940	*Alcedo argentata*	Philippines	Bohol	Bohol	Sierra Bullones
KU	20943	*Alcedo argentata*	Philippines	Bohol	Bohol	Sierra Bullones
KU	20964	*Alcedo argentata*	Philippines	Bohol	Bohol	Sierra Bullones
KU	20972	*Alcedo argentata*	Philippines	Bohol	Bohol	Sierra Bullones
KU	28469	*Alcedo argentata*	Philippines	Mindanao	Agusan del Norte	Mt. Hilong-Hilong
KU	12359	*Ceyx erithacus*	Malaysia	Borneo		
KU	14485	*Ceyx lepidus*	Philippines	Camiguin S.		
AMNH	14995	*Ceyx melanurus*	Philippines	Luzon	Quezon	Alabat
FMNH	461991	*Ceyx melanurus*	Philippines	Luzon	Camarines Sur	Lagonoy
FMNH	472748	*Ceyx melanurus*	Philippines	Luzon	Rizal	Mt. Irid
KU	14226	*Ceyx melanurus*	Philippines	Samar	Eastern Samar	Taft
KU	14255	*Ceyx melanurus*	Philippines	Samar	Eastern Samar	Taft
KU	14275	*Ceyx melanurus*	Philippines	Samar	Eastern Samar	Taft
KU	14282	*Ceyx melanurus*	Philippines	Leyte	Leyte	Baybay
KU	14304	*Ceyx melanurus*	Philippines	Leyte	Leyte	Baybay
KU	18002	*Ceyx melanurus*	Philippines	Luzon	Caminares Norte	Mt. Labo
KU	18032	*Ceyx melanurus*	Philippines	Luzon	Caminares Norte	Mt. Labo
KU	18046	*Ceyx melanurus*	Philippines	Luzon	Caminares Norte	Mt. Labo
KU	18053	*Ceyx melanurus*	Philippines	Luzon	Caminares Norte	Mt. Labo
KU	18100	*Ceyx melanurus*	Philippines	Mindanao	Zamboanga del Sur	Pasonanca: Intake
KU	18102	*Ceyx melanurus*	Philippines	Mindanao	Zamboanga del Sur	Pasonanca: Intake
KU	18127	*Ceyx melanurus*	Philippines	Mindanao	Zamboanga del Sur	Pasonanca: Intake
KU	18149	*Ceyx melanurus*	Philippines	Mindanao	Zamboanga del Sur	Pasonanca: Intake
KU	18184	*Ceyx melanurus*	Philippines	Mindanao	Zamboanga del Sur	Pasonanca: Baluno
KU	18218	*Ceyx melanurus*	Philippines	Mindanao	Zamboanga del Sur	Pasonanca: Baluno
KU	19006	*Ceyx melanurus*	Philippines	Mindanao	Aguasan del Sur	Mt. Magdiwata
KU	19368	*Ceyx melanurus*	Philippines	Luzon	Aurora	Aurora N.P
KU	20200	*Ceyx melanurus*	Philippines	Luzon	Aurora	Aurora N.P
KU	20203	*Ceyx melanurus*	Philippines	Luzon	Aurora	Aurora N.P
KU	20211	*Ceyx melanurus*	Philippines	Luzon	Aurora	Aurora N.P
KU	21766	*Ceyx melanurus*	Philippines	Luzon	Aurora	Baler
KU	25327	*Ceyx melanurus*	Philippines	Luzon	Bulacan	Angat Watershed
KU	25552	*Ceyx melanurus*	Philippines	Luzon	Bulacan	Angat Watershed
KU	25572	*Ceyx melanurus*	Philippines	Luzon	Bulacan	Angat Watershed
KU	25577	*Ceyx melanurus*	Philippines	Luzon	Bulacan	Angat Watershed
KU	25580	*Ceyx melanurus*	Philippines	Luzon	Bulacan	Angat Watershed
KU	25581	*Ceyx melanurus*	Philippines	Luzon	Bulacan	Angat Watershed
KU	25793	*Ceyx melanurus*	Philippines	Luzon	Cagayan	Mt. Cagua
KU	25800	*Ceyx melanurus*	Philippines	Luzon	Cagayan	Mt. Cagua

KU	25822	*Ceyx melanurus*	Philippines	Luzon	Cagayan	Mt. Cagua
KU	25884	*Ceyx melanurus*	Philippines	Luzon	Cagayan	Mt. Cagua
KU	25886	*Ceyx melanurus*	Philippines	Luzon	Cagayan	Mt. Cagua
KU	25946	*Ceyx melanurus*	Philippines	Luzon	Cagayan	Mt. Cagua
KU	25952	*Ceyx melanurus*	Philippines	Luzon	Cagayan	Mt. Cagua
KU	25963	*Ceyx melanurus*	Philippines	Polillo	Quezon	Burdeos
KU	26941	*Ceyx melanurus*	Philippines	Polillo	Quezon	Burdeos
KU	26953	*Ceyx melanurus*	Philippines	Polillo	Quezon	Burdeos
KU	26999	*Ceyx melanurus*	Philippines	Polillo	Quezon	Burdeos
KU	27005	*Ceyx melanurus*	Philippines	Polillo	Quezon	Burdeos
KU	27033	*Ceyx melanurus*	Philippines	Polillo	Quezon	Burdeos
KU	27364	*Ceyx melanurus*	Philippines	Leyte	Southern Leyte	Silago
KU	27371	*Ceyx melanurus*	Philippines	Leyte	Southern Leyte	Silago
KU	27455	*Ceyx melanurus*	Philippines	Leyte	Southern Leyte	Sogod
KU	28287	*Ceyx melanurus*	Philippines	Mindanao	Agusan del Norte	Mt. Hilong-Hilong
KU	28320	*Ceyx melanurus*	Philippines	Mindanao	Agusan del Norte	Mt. Hilong-Hilong
KU	28321	*Ceyx melanurus*	Philippines	Mindanao	Agusan del Norte	Mt. Hilong-Hilong
KU	14042	*Cinnyris jugularis*	Philippines	Camiguin S.		
CMC	142	*Dicaeum hypoleucum*	Philippines	Luzon	Camarines Sur	Mt. Isarog
CMC	1271	*Dicaeum hypoleucum*	Philippines	Mindanao	Davao City	Mt. Talmo
CMC	1273	*Dicaeum hypoleucum*	Philippines	Mindanao	Davao City	Mt. Talmo
CMC	1275	*Dicaeum hypoleucum*	Philippines	Mindanao	Davao City	Mt. Talmo
CMC	1956	*Dicaeum hypoleucum*	Philippines	Mindanao	Sarangani	Mt. Busa
CMC	2208	*Dicaeum hypoleucum*	Philippines	Mindanao	Sarangani	Mt. Busa
CMC	2253	*Dicaeum hypoleucum*	Philippines	Mindanao	Sarangani	Mt. Busa
CMC	3095	*Dicaeum hypoleucum*	Philippines	Mindanao	Davao del Norte	Mt. Pasian
CMC	3158	*Dicaeum hypoleucum*	Philippines	Mindanao	Davao del Norte	Mt. Pasian
CMC	3208	*Dicaeum hypoleucum*	Philippines	Mindanao	Davao del Norte	Mt. Pasian
CMC	3230	*Dicaeum hypoleucum*	Philippines	Mindanao	Davao del Norte	Mt. Pasian
CMC	3274	*Dicaeum hypoleucum*	Philippines	Mindanao	Davao del Norte	Mt. Pasian
CMC	3275	*Dicaeum hypoleucum*	Philippines	Mindanao	Davao del Norte	Mt. Pasian
CMC	3314	*Dicaeum hypoleucum*	Philippines	Mindanao	Davao del Norte	Mt. Pasian
FMNH	357608	*Dicaeum hypoleucum*	Philippines	Mindanao	Bukidnon	Mt. Kitanglad Range
FMNH	357611	*Dicaeum hypoleucum*	Philippines	Mindanao	Bukidnon	Mt. Kitanglad Range
FMNH	357614	*Dicaeum hypoleucum*	Philippines	Mindanao	Bukidnon	Mt. Kitanglad Range
FMNH	449787	*Dicaeum hypoleucum*	Philippines	Luzon	Aurora	Dingalan
FMNH	454950	*Dicaeum hypoleucum*	Philippines	Luzon	Mountain	Mt. Amnyao Peak
FMNH	472816	*Dicaeum hypoleucum*	Philippines	Luzon	Rizal	Mt. Irid
KU	14037	*Dicaeum hypoleucum*	Philippines	Dinagat	Surigao del Norte	Loreto
KU	14048	*Dicaeum hypoleucum*	Philippines	Dinagat	Surigao del Norte	Loreto
KU	14061	*Dicaeum hypoleucum*	Philippines	Dinagat	Surigao del Norte	Loreto
KU	14065	*Dicaeum hypoleucum*	Philippines	Dinagat	Surigao del Norte	Loreto
KU	14181	*Dicaeum hypoleucum*	Philippines	Samar	Eastern Samar	Taft
KU	17969	*Dicaeum hypoleucum*	Philippines	Luzon	Caminares Norte	Mt. Labo
KU	17976	*Dicaeum hypoleucum*	Philippines	Luzon	Caminares Norte	Mt. Labo
KU	18070	*Dicaeum hypoleucum*	Philippines	Luzon	Caminares Norte	Mt. Labo
KU	18159	*Dicaeum hypoleucum*	Philippines	Mindanao	Zamboanga del Sur	Pasonanca: Baluno
KU	18188	*Dicaeum hypoleucum*	Philippines	Mindanao	Zamboanga del Sur	Pasonanca: Baluno
KU	18191	*Dicaeum hypoleucum*	Philippines	Mindanao	Zamboanga del Sur	Pasonanca: Baluno
KU	18193	*Dicaeum hypoleucum*	Philippines	Mindanao	Zamboanga del Sur	Pasonanca: Baluno
KU	18233	*Dicaeum hypoleucum*	Philippines	Mindanao	Zamboanga del Sur	Pasonanca: Baluno
KU	19066	*Dicaeum hypoleucum*	Philippines	Mindanao	Aguasan del Sur	Mt. Magdiwata
KU	19177	*Dicaeum hypoleucum*	Philippines	Mindanao	Zamboanga del Sur	Pasonanca: San. Clara
KU	19178	*Dicaeum hypoleucum*	Philippines	Mindanao	Zamboanga del Sur	Pasonanca: San. Clara
KU	19254	*Dicaeum hypoleucum*	Philippines	Mindanao	Zamboanga del Sur	Pasonanca: San. Clara
KU	19256	*Dicaeum hypoleucum*	Philippines	Mindanao	Zamboanga del Sur	Pasonanca: San. Clara
KU	20193	*Dicaeum hypoleucum*	Philippines	Luzon	Aurora	Aurora N.P
KU	20213	*Dicaeum hypoleucum*	Philippines	Luzon	Aurora	Aurora N.P
KU	20214	*Dicaeum hypoleucum*	Philippines	Luzon	Aurora	Aurora N.P
KU	20218	*Dicaeum hypoleucum*	Philippines	Luzon	Aurora	Aurora N.P
KU	20246	*Dicaeum hypoleucum*	Philippines	Luzon	Aurora	Aurora N.P
KU	20276	*Dicaeum hypoleucum*	Philippines	Luzon	Aurora	Aurora N.P
KU	20360	*Dicaeum hypoleucum*	Philippines	Luzon	Aurora	Aurora N.P
KU	20921	*Dicaeum hypoleucum*	Philippines	Bohol	Bohol	Bilar

KU	25622	*Dicaeum hypoleucum*	Philippines	Luzon	Ilocos Norte	Mt. Pao
KU	25637	*Dicaeum hypoleucum*	Philippines	Luzon	Ilocos Norte	Mt. Pao
KU	25653	*Dicaeum hypoleucum*	Philippines	Luzon	Ilocos Norte	Mt. Pao
KU	25672	*Dicaeum hypoleucum*	Philippines	Luzon	Ilocos Norte	Mt. Pao
KU	25868	*Dicaeum hypoleucum*	Philippines	Luzon	Cagayan	Mt. Cagua
KU	25880	*Dicaeum hypoleucum*	Philippines	Luzon	Cagayan	Mt. Cagua
KU	25921	*Dicaeum hypoleucum*	Philippines	Luzon	Cagayan	Mt. Cagua
KU	26975	*Dicaeum hypoleucum*	Philippines	Luzon	Cagayan	Mt. Cagua
KU	26984	*Dicaeum hypoleucum*	Philippines	Luzon	Cagayan	Mt. Cagua
KU	27182	*Dicaeum hypoleucum*	Philippines	Mindanao	South Cotabato	Tampakan
KU	27450	*Dicaeum hypoleucum*	Philippines	Leyte	Southern Leyte	Hinunangan
KU	27454	*Dicaeum hypoleucum*	Philippines	Leyte	Southern Leyte	Hinunangan
KU	27468	*Dicaeum hypoleucum*	Philippines	Leyte	Southern Leyte	Sogod
KU	27471	*Dicaeum hypoleucum*	Philippines	Leyte	Southern Leyte	Sogod
KU	28294	*Dicaeum hypoleucum*	Philippines	Mindanao	Agusan del Norte	Mt. Hilong-Hilong
KU	28376	*Dicaeum hypoleucum*	Philippines	Mindanao	Agusan del Norte	Mt. Hilong-Hilong
KU	28584	*Dicaeum hypoleucum*	Philippines	Mindanao	Misamis Oriental	Mt. Lumot
KU	14270	*Eurylaimus steerii*	Philippines	Samar	Eastern Samar	Taft
KU	19047	*Eurylaimus steerii*	Philippines	Mindanao	Agusan del Sur	Mt. Magdiwata
KU	19050	*Eurylaimus steerii*	Philippines	Mindanao	Agusan del Sur	Mt. Magdiwata
KU	19061	*Eurylaimus steerii*	Philippines	Mindanao	Agusan del Sur	Mt. Magdiwata
KU	19186	*Eurylaimus steerii*	Philippines	Mindanao	Zamboanga del Sur	Pasonanca
KU	20929	*Eurylaimus steerii*	Philippines	Bohol	Bohol	Bilar
KU	27374	*Eurylaimus steerii*	Philippines	Leyte	Southern Leyte	Silago
KU	27376	*Eurylaimus steerii*	Philippines	Leyte	Southern Leyte	Silago
KU	27448	*Eurylaimus steerii*	Philippines	Leyte	Southern Leyte	Sogod
KU	28182	*Eurylaimus steerii*	Philippines	Bohol	Bohol	Bilar
KU	28213	*Eurylaimus steerii*	Philippines	Bohol	Bohol	Bilar
KU	28231	*Eurylaimus steerii*	Philippines	Bohol	Bohol	Valencia
KU	28247	*Eurylaimus steerii*	Philippines	Bohol	Bohol	Valencia
KU	28295	*Eurylaimus steerii*	Philippines	Mindanao	Agussan del Norte	Mt. Hilong-Hilong
KU	14143	*Ficedula basilanica*	Philippines	Samar	Eastern Samar	Taft
KU	14152	*Ficedula basilanica*	Philippines	Samar	Eastern Samar	Taft
KU	14153	*Ficedula basilanica*	Philippines	Samar	Eastern Samar	Taft
KU	14224	*Ficedula basilanica*	Philippines	Samar	Eastern Samar	Taft
KU	14265	*Ficedula basilanica*	Philippines	Samar	Eastern Samar	Taft
KU	18114	*Ficedula basilanica*	Philippines	Mindanao	Zamboanga del Sur	Pasonanca
KU	18120	*Ficedula basilanica*	Philippines	Mindanao	Zamboanga del Sur	Pasonanca
KU	18166	*Ficedula basilanica*	Philippines	Mindanao	Zamboanga del Sur	Pasonanca
KU	18201	*Ficedula basilanica*	Philippines	Mindanao	Zamboanga del Sur	Pasonanca
KU	18235	*Ficedula basilanica*	Philippines	Mindanao	Zamboanga del Sur	Pasonanca
KU	19005	*Ficedula basilanica*	Philippines	Mindanao	Agusan del Sur	Mt. Magdiwata
KU	19009	*Ficedula basilanica*	Philippines	Mindanao	Agusan del Sur	Mt. Magdiwata
KU	19036	*Ficedula basilanica*	Philippines	Mindanao	Agusan del Sur	Mt. Magdiwata
KU	28280	*Ficedula basilanica*	Philippines	Mindanao	Agusan del Norte	Mt. Hilong-Hilong
KU	28317	*Ficedula basilanica*	Philippines	Mindanao	Agusan del Norte	Mt. Hilong-Hilong
KU	28472	*Ficedula basilanica*	Philippines	Mindanao	Agusan del Norte	Mt. Hilong-Hilong
KU	28481	*Ficedula basilanica*	Philippines	Mindanao	Agusan del Norte	Mt. Hilong-Hilong
LSUMZ	52627	*Hapractes whiteheadi*	Malaysia	Borneo		
AMNH	15002	*Harpactes ardens*	Philippines	Alabat	Quezon	Alabat
CMC	1417	*Harpactes ardens*	Philippines	Mindanao	Davao City	Mt. Talmo
CMC	1955	*Harpactes ardens*	Philippines	Mindanao	Sarangani	Mt. Busa
CMC	2037	*Harpactes ardens*	Philippines	Mindanao	Sarangani	Mt. Busa
CMC	2234	*Harpactes ardens*	Philippines	Mindanao	Sarangani	Mt. Busa
CMC	2235	*Harpactes ardens*	Philippines	Mindanao	Sarangani	Mt. Busa
CMC	2239	*Harpactes ardens*	Philippines	Mindanao	Sarangani	Mt. Busa
FMNH	429208	*Harpactes ardens*	Philippines	Luzon	Kalinga	Mapga River
KU	14176	*Harpactes ardens*	Philippines	Samar	Eastern Samar	Taft
KU	14220	*Harpactes ardens*	Philippines	Samar	Eastern Samar	Taft
KU	18219	*Harpactes ardens*	Philippines	Mindanao	Zamboanga del Sur	Pasonanca: Baluno
KU	18227	*Harpactes ardens*	Philippines	Mindanao	Zamboanga del Sur	Pasonanca: Baluno
KU	18246	*Harpactes ardens*	Philippines	Mindanao	Zamboanga del Sur	Pasonanca: Baluno
KU	19031	*Harpactes ardens*	Philippines	Mindanao	Aguasan del Sur	Mt. Magdiwata
KU	19035	*Harpactes ardens*	Philippines	Mindanao	Aguasan del Sur	Mt. Magdiwata

KU	19040	*Harpactes ardens*	Philippines	Mindanao	Aguasan del Sur	Mt. Magdiwata
KU	19065	*Harpactes ardens*	Philippines	Mindanao	Aguasan del Sur	Mt. Magdiwata
KU	19646	*Harpactes ardens*	Philippines	Luzon	Aurora	Baler
KU	20178	*Harpactes ardens*	Philippines	Luzon	Aurora	Aurora N.P.
KU	20256	*Harpactes ardens*	Philippines	Luzon	Aurora	Aurora N.P.
KU	20257	*Harpactes ardens*	Philippines	Luzon	Aurora	Aurora N.P.
KU	20318	*Harpactes ardens*	Philippines	Luzon	Aurora	Aurora N.P.
KU	20922	*Harpactes ardens*	Philippines	Bohol	Bohol	Bilar
KU	20927	*Harpactes ardens*	Philippines	Bohol	Bohol	Bilar
KU	25560	*Harpactes ardens*	Philippines	Luzon	Bulacan	Angat Watershed
KU	25599	*Harpactes ardens*	Philippines	Luzon	Ilocos Norte	Mt. Pao
KU	25667	*Harpactes ardens*	Philippines	Luzon	Ilocos Norte	Mt. Pao
KU	25864	*Harpactes ardens*	Philippines	Luzon	Cagayan	Mt. Cagua
KU	25927	*Harpactes ardens*	Philippines	Luzon	Cagayan	Mt. Cagua
KU	25938	*Harpactes ardens*	Philippines	Luzon	Cagayan	Mt. Cagua
KU	25973	*Harpactes ardens*	Philippines	Luzon	Cagayan	Mt. Cagua
KU	25989	*Harpactes ardens*	Philippines	Luzon	Cagayan	Mt. Cagua
KU	26929	*Harpactes ardens*	Philippines	Polillo	Quezon	Burdeos
KU	26958	*Harpactes ardens*	Philippines	Polillo	Quezon	Burdeos
KU	26995	*Harpactes ardens*	Philippines	Polillo	Quezon	Burdeos
KU	28216	*Harpactes ardens*	Philippines	Bohol	Bohol	Valencia
KU	28228	*Harpactes ardens*	Philippines	Bohol	Bohol	Valencia
KU	28237	*Harpactes ardens*	Philippines	Bohol	Bohol	Valencia
KU	28260	*Harpactes ardens*	Philippines	Bohol	Bohol	Valencia
KU	28279	*Harpactes ardens*	Philippines	Mindanao	Agusan del Norte	Mt. Hilong-Hilong
KU	28337	*Harpactes ardens*	Philippines	Mindanao	Agusan del Norte	Mt. Hilong-Hilong
KU	28352	*Harpactes ardens*	Philippines	Mindanao	Agusan del Norte	Mt. Hilong-Hilong
KU	28435	*Harpactes ardens*	Philippines	Mindanao	Agusan del Norte	Mt. Hilong-Hilong
KU	28507	*Harpactes ardens*	Philippines	Mindanao	Misamis Oriental	Mt. Lumot
KU	12388	*Harpactes kasumba*	Malaysia	Borneo		
CMC	1963	*Irena cyanogastra*	Philippines	Mindanao	Sarangani	Mt. Busa
CMC	2133	*Irena cyanogastra*	Philippines	Mindanao	Sarangani	Mt. Busa
FMNH	350955	*Irena cyanogastra*	Philippines	Luzon	Camarines Sur	Lagonoy
FMNH	462007	*Irena cyanogastra*	Philippines	Catanduanes	Gigmoto	Gigmoto
KU	14081	*Irena cyanogastra*	Philippines	Dinagat	Surigao del Norte	Loreto
KU	14293	*Irena cyanogastra*	Philippines	Leyte	Leyte	Baybay
KU	14294	*Irena cyanogastra*	Philippines	Leyte	Leyte	Baybay
KU	14309	*Irena cyanogastra*	Philippines	Leyte	Leyte	Baybay
KU	17963	*Irena cyanogastra*	Philippines	Luzon	Caminares Norte	Mt. Labo
KU	17964	*Irena cyanogastra*	Philippines	Luzon	Caminares Norte	Mt. Labo
KU	17982	*Irena cyanogastra*	Philippines	Luzon	Caminares Norte	Mt. Labo
KU	17989	*Irena cyanogastra*	Philippines	Luzon	Caminares Norte	Mt. Labo
KU	17998	*Irena cyanogastra*	Philippines	Luzon	Caminares Norte	Mt. Labo
KU	18003	*Irena cyanogastra*	Philippines	Luzon	Caminares Norte	Mt. Labo
KU	18094	*Irena cyanogastra*	Philippines	Luzon	Caminares Norte	Mt. Labo
KU	18212	*Irena cyanogastra*	Philippines	Mindanao	Zamboanga del Sur	Pasonanca: Baluno
KU	19621	*Irena cyanogastra*	Philippines	Luzon	Aurora	Baler
KU	19626	*Irena cyanogastra*	Philippines	Luzon	Aurora	Baler
KU	19629	*Irena cyanogastra*	Philippines	Luzon	Aurora	Baler
KU	20258	*Irena cyanogastra*	Philippines	Luzon	Aurora	Aurora N.P.
KU	20271	*Irena cyanogastra*	Philippines	Luzon	Aurora	Aurora N.P.
KU	21765	*Irena cyanogastra*	Philippines	Luzon	Aurora	Baler
KU	25554	*Irena cyanogastra*	Philippines	Luzon	Cagayan	Mt. Cagua
KU	25561	*Irena cyanogastra*	Philippines	Luzon	Cagayan	Mt. Cagua
KU	25780	*Irena cyanogastra*	Philippines	Luzon	Cagayan	Mt. Cagua
KU	25789	*Irena cyanogastra*	Philippines	Luzon	Cagayan	Mt. Cagua
KU	25830	*Irena cyanogastra*	Philippines	Luzon	Cagayan	Mt. Cagua
KU	25834	*Irena cyanogastra*	Philippines	Luzon	Cagayan	Mt. Cagua
KU	25840	*Irena cyanogastra*	Philippines	Luzon	Cagayan	Mt. Cagua
KU	25841	*Irena cyanogastra*	Philippines	Luzon	Cagayan	Mt. Cagua
KU	25891	*Irena cyanogastra*	Philippines	Luzon	Cagayan	Mt. Cagua
KU	27015	*Irena cyanogastra*	Philippines	Polillo	Quezon	Burdeos
KU	27017	*Irena cyanogastra*	Philippines	Polillo	Quezon	Burdeos
KU	12369	*Irena puella*	Malaysia	Borneo		

KU	14040	*Macronous striaticeps*	Philippines	Dinagat	Dinagat	Loreto
KU	14050	*Macronous striaticeps*	Philippines	Dinagat	Dinagat	Loreto
KU	14054	*Macronous striaticeps*	Philippines	Dinagat	Dinagat	Loreto
KU	14080	*Macronous striaticeps*	Philippines	Dinagat	Dinagat	Loreto
KU	14130	*Macronous striaticeps*	Philippines	Samar	Eastern Samar	Taft
KU	14140	*Macronous striaticeps*	Philippines	Samar	Eastern Samar	Taft
KU	14177	*Macronous striaticeps*	Philippines	Samar	Eastern Samar	Taft
KU	14263	*Macronous striaticeps*	Philippines	Samar	Eastern Samar	Taft
KU	14280	*Macronous striaticeps*	Philippines	Leyte	Leyte	Baybay
KU	14291	*Macronous striaticeps*	Philippines	Leyte	Leyte	Baybay
KU	18133	*Macronous striaticeps*	Philippines	Mindanao	Zamboanga del Sur	Pasonanca
KU	18139	*Macronous striaticeps*	Philippines	Mindanao	Zamboanga del Sur	Pasonanca
KU	19013	*Macronous striaticeps*	Philippines	Mindanao	Agusan del Sur	Mt. Magdiwata
KU	19017	*Macronous striaticeps*	Philippines	Mindanao	Agusan del Sur	Mt. Magdiwata
KU	19068	*Macronous striaticeps*	Philippines	Mindanao	Agusan del Sur	Mt. Magdiwata
KU	19134	*Macronous striaticeps*	Philippines	Mindanao	Misamis Oriental	Mt. Balatukan
KU	19144	*Macronous striaticeps*	Philippines	Mindanao	Misamis Oriental	Mt. Balatukan
KU	19149	*Macronous striaticeps*	Philippines	Mindanao	Misamis Oriental	Mt. Balatukan
KU	19181	*Macronous striaticeps*	Philippines	Mindanao	Zamboanga del Sur	Pasonanca
KU	19205	*Macronous striaticeps*	Philippines	Mindanao	Zamboanga del Sur	Pasonanca
KU	20954	*Macronous striaticeps*	Philippines	Bohol	Bohol	Bilar
KU	20962	*Macronous striaticeps*	Philippines	Bohol	Bohol	Bilar
KU	27386	*Macronous striaticeps*	Philippines	Siargao	Surigao del Norte	Pilar
KU	27397	*Macronous striaticeps*	Philippines	Siargao	Surigao del Norte	Pilar
KU	27428	*Macronous striaticeps*	Philippines	Siargao	Surigao del Norte	Pilar
KU	27444	*Macronous striaticeps*	Philippines	Leyte	Southern Leyte	Sogod
KU	27460	*Macronous striaticeps*	Philippines	Leyte	Southern Leyte	Sogod
KU	28199	*Macronous striaticeps*	Philippines	Bohol	Bohol	Bilar
KU	28210	*Macronous striaticeps*	Philippines	Bohol	Bohol	Bilar
KU	28271	*Macronous striaticeps*	Philippines	Mindanao	Agusan del Norte	Mt. Hilong-Hilong
KU	28322	*Macronous striaticeps*	Philippines	Mindanao	Agusan del Norte	Mt. Hilong-Hilong
KU	28583	*Macronous striaticeps*	Philippines	Mindanao	Misamis Oriental	Mt. Lumot
CMC	2068	*Orthotomus cinereiceps*	Philippines	Mindanao	South Cotabato	Mt. Busa
KU	18104	*Orthotomus cinereiceps*	Philippines	Mindanao	Zamboanga del Sur	Pasonanca
KU	18112	*Orthotomus cinereiceps*	Philippines	Mindanao	Zamboanga del Sur	Pasonanca
KU	18167	*Orthotomus cinereiceps*	Philippines	Mindanao	Zamboanga del Sur	Pasonanca
KU	18215	*Orthotomus cinereiceps*	Philippines	Mindanao	Zamboanga del Sur	Pasonanca
KU	18228	*Orthotomus cinereiceps*	Philippines	Mindanao	Zamboanga del Sur	Pasonanca
KU	14063	*Orthotomus nigriceps*	Philippines	Dinagat	Dinagat	Loreto
KU	19057	*Orthotomus nigriceps*	Philippines	Mindanao	Agusan del Sur	Mt. Magdiwata
KU	19058	*Orthotomus nigriceps*	Philippines	Mindanao	Agusan del Sur	Mt. Magdiwata
KU	19069	*Orthotomus nigriceps*	Philippines	Mindanao	Agusan del Sur	Mt. Magdiwata
KU	28324	*Orthotomus nigriceps*	Philippines	Mindanao	Agusan del Norte	Mt. Hilong-Hilong
KU	28437	*Orthotomus nigriceps*	Philippines	Mindanao	Agusan del Norte	Mt. Hilong-Hilong
KU	14147	*Orthotomus samarensis*	Philippines	Samar	Eastern Samar	Taft
KU	14197	*Orthotomus samarensis*	Philippines	Samar	Eastern Samar	Taft
KU	14204	*Orthotomus samarensis*	Philippines	Samar	Eastern Samar	Taft
KU	14242	*Orthotomus samarensis*	Philippines	Samar	Eastern Samar	Taft
KU	28209	*Orthotomus samarensis*	Philippines	Bohol	Bohol	Bilar
CMC	1391	*Otus megalotis*	Philippines	Mindanao	Davao del Norte	Mt. Talomo
CMC	1392	*Otus megalotis*	Philippines	Mindanao	Davao del Norte	Mt. Talomo
CMC	1746	*Otus megalotis*	Philippines	Mindanao	Davao del Norte	Mt. Talomo
CMC	2211	*Otus megalotis*	Philippines	Mindanao	Sarangani	Mt. Busa
KU	14230	*Otus megalotis*	Philippines	Samar	Eastern Samar	Taft
KU	18205	*Otus megalotis*	Philippines	Mindanao	Zamboanga del Sur	Pasonanca
KU	18206	*Otus megalotis*	Philippines	Mindanao	Zamboanga del Sur	Pasonanca
KU	28198	*Otus megalotis*	Philippines	Bohol	Bohol	Bilar
KU	28200	*Otus megalotis*	Philippines	Bohol	Bohol	Bilar
KU	28225	*Otus megalotis*	Philippines	Bohol	Bohol	Valencia
KU	28229	*Otus megalotis*	Philippines	Bohol	Bohol	Valencia
KU	28302	*Otus megalotis*	Philippines	Mindanao	Agusan del Norte	Mt. Hilong-Hilong
KU	25745	*Pachycephala albiventris*	Philippines	Luzon		
KU	6175	*Pachycephala pectoralis*	Australia			
AMNH	15004	*Pachycephala philippinensis*	Philippines	Alabat	Quezon	Alabat

CMC	153	*Pachycephala philippinensis*	Philippines	Luzon	Zambales	Masinioc
CMC	167	*Pachycephala philippinensis*	Philippines	Luzon	Zambales	Masinioc
CMC	1251	*Pachycephala philippinensis*	Philippines	Mindanao	Davao City	Mt. Talmo
CMC	1252	*Pachycephala philippinensis*	Philippines	Mindanao	Davao City	Mt. Talmo
CMC	1256	*Pachycephala philippinensis*	Philippines	Mindanao	Davao City	Mt. Talmo
CMC	1289	*Pachycephala philippinensis*	Philippines	Mindanao	Davao City	Mt. Talmo
CMC	1679	*Pachycephala philippinensis*	Philippines	Mindanao	Davao City	Mt. Talmo
CMC	1741	*Pachycephala philippinensis*	Philippines	Mindanao	Davao City	Mt. Talmo
CMC	1767	*Pachycephala philippinensis*	Philippines	Mindanao	Davao City	Mt. Talmo
CMC	1797	*Pachycephala philippinensis*	Philippines	Mindanao	South Cotabato	Mt. Apo
CMC	3265	*Pachycephala philippinensis*	Philippines	Mindanao	Davao del Norte	Mt. Pasian
CMC	3299	*Pachycephala philippinensis*	Philippines	Mindanao	Davao del Norte	Mt. Pasian
CMC	3312	*Pachycephala philippinensis*	Philippines	Mindanao	Davao del Norte	Mt. Pasian
FMNH	350976	*Pachycephala philippinensis*	Philippines	Catanduanes	Gigmoto	Gigmoto
FMNH	357555	*Pachycephala philippinensis*	Philippines	Mindanao	Bukidnon	Mt. Kitanglad Range
FMNH	357557	*Pachycephala philippinensis*	Philippines	Mindanao	Bukidnon	Mt. Kitanglad Range
FMNH	357558	*Pachycephala philippinensis*	Philippines	Mindanao	Bukidnon	Mt. Kitanglad Range
FMNH	357559	*Pachycephala philippinensis*	Philippines	Mindanao	Bukidnon	Mt. Kitanglad Range
FMNH	392305	*Pachycephala philippinensis*	Philippines	Mindanao	Bukidnon	Mt. Kitanglad Range
FMNH	392306	*Pachycephala philippinensis*	Philippines	Mindanao	Bukidnon	Mt. Kitanglad Range
FMNH	455032	*Pachycephala philippinensis*	Philippines	Luzon	Nueva Vizcaya	Mt. Palali
FMNH	472720	*Pachycephala philippinensis*	Philippines	Mindanao	Davao Oriental	Mt. Kampalili
KU	10842	*Pachycephala philippinensis*	Philippines	Camiguin N.	Cagayan	Limandok
KU	10843	*Pachycephala philippinensis*	Philippines	Camiguin N.	Cagayan	Limandok
KU	10860	*Pachycephala philippinensis*	Philippines	Camiguin N.	Cagayan	Limandok
KU	10869	*Pachycephala philippinensis*	Philippines	Camiguin N.	Cagayan	Limandok
KU	10873	*Pachycephala philippinensis*	Philippines	Camiguin N.	Cagayan	Limandok
KU	10880	*Pachycephala philippinensis*	Philippines	Camiguin N.	Cagayan	Limandok
KU	10921	*Pachycephala philippinensis*	Philippines	Calayan	Cagayan	Macarra
KU	10936	*Pachycephala philippinensis*	Philippines	Calayan	Cagayan	Macarra
KU	10942	*Pachycephala philippinensis*	Philippines	Calayan	Cagayan	Macarra
KU	10965	*Pachycephala philippinensis*	Philippines	Calayan	Cagayan	Longog
KU	10968	*Pachycephala philippinensis*	Philippines	Calayan	Cagayan	Longog
KU	10976	*Pachycephala philippinensis*	Philippines	Calayan	Cagayan	Longog
KU	12440	*Pachycephala philippinensis*	Philippines	Camiguin N.	Cagayan	Kauringan
KU	12451	*Pachycephala philippinensis*	Philippines	Camiguin N.	Cagayan	Kauringan
KU	12458	*Pachycephala philippinensis*	Philippines	Camiguin N.	Cagayan	Kauringan
KU	12475	*Pachycephala philippinensis*	Philippines	Camiguin N.	Cagayan	Kauringan
KU	14066	*Pachycephala philippinensis*	Philippines	Dinagat	Dinagat	Loreto
KU	14117	*Pachycephala philippinensis*	Philippines	Samar	Eastern Samar	Taft
KU	14159	*Pachycephala philippinensis*	Philippines	Samar	Eastern Samar	Taft
KU	14236	*Pachycephala philippinensis*	Philippines	Samar	Eastern Samar	Taft
KU	16003	*Pachycephala philippinensis*	Philippines	Mindanao	Zamboanga del Sur	Pasonanca: Baluno
KU	17983	*Pachycephala philippinensis*	Philippines	Luzon	Caminares Norte	Mt. Labo
KU	18005	*Pachycephala philippinensis*	Philippines	Luzon	Caminares Norte	Mt. Labo
KU	18065	*Pachycephala philippinensis*	Philippines	Luzon	Caminares Norte	Mt. Labo
KU	18084	*Pachycephala philippinensis*	Philippines	Luzon	Caminares Norte	Mt. Labo
KU	18251	*Pachycephala philippinensis*	Philippines	Mindanao	Zamboanga del Sur	Pasonanca: Baluno
KU	19091	*Pachycephala philippinensis*	Philippines	Mindanao	Misamis Oriental	Mt. Balatukan
KU	19101	*Pachycephala philippinensis*	Philippines	Mindanao	Misamis Oriental	Mt. Balatukan
KU	19112	*Pachycephala philippinensis*	Philippines	Mindanao	Misamis Oriental	Mt. Balatukan
KU	19126	*Pachycephala philippinensis*	Philippines	Mindanao	Misamis Oriental	Mt. Balatukan
KU	19128	*Pachycephala philippinensis*	Philippines	Mindanao	Misamis Oriental	Mt. Balatukan
KU	19145	*Pachycephala philippinensis*	Philippines	Mindanao	Misamis Oriental	Mt. Balatukan
KU	19154	*Pachycephala philippinensis*	Philippines	Mindanao	Misamis Oriental	Mt. Balatukan
KU	19192	*Pachycephala philippinensis*	Philippines	Mindanao	Zamboanga del Sur	Pasonanca: San. Clara
KU	19214	*Pachycephala philippinensis*	Philippines	Mindanao	Zamboanga del Sur	Pasononca: Nancy
KU	19608	*Pachycephala philippinensis*	Philippines	Luzon	Aurora	Baler
KU	20180	*Pachycephala philippinensis*	Philippines	Luzon	Aurora	Baler
KU	20205	*Pachycephala philippinensis*	Philippines	Luzon	Aurora	Aurora N.P
KU	20242	*Pachycephala philippinensis*	Philippines	Luzon	Aurora	Aurora N.P
KU	20946	*Pachycephala philippinensis*	Philippines	Bohol	Bohol	Sierra Bullones
KU	20948	*Pachycephala philippinensis*	Philippines	Bohol	Bohol	Sierra Bullones
KU	20949	*Pachycephala philippinensis*	Philippines	Bohol	Bohol	Sierra Bullones

KU	20951	*Pachycephala philippinensis*	Philippines	Bohol	Bohol	Sierra Bullones
KU	20952	*Pachycephala philippinensis*	Philippines	Bohol	Bohol	Sierra Bullones
KU	25321	*Pachycephala philippinensis*	Philippines	Luzon	Bulacan	Angat Watershed
KU	25578	*Pachycephala philippinensis*	Philippines	Luzon	Bulacan	Angat Watershed
KU	25677	*Pachycephala philippinensis*	Philippines	Luzon	Ilocos Norte	Mt. Cabacan
KU	25686	*Pachycephala philippinensis*	Philippines	Luzon	Ilocos Norte	Mt. Cabacan
KU	25693	*Pachycephala philippinensis*	Philippines	Luzon	Ilocos Norte	Mt. Cabacan
KU	25695	*Pachycephala philippinensis*	Philippines	Luzon	Ilocos Norte	Mt. Cabacan
KU	25766	*Pachycephala philippinensis*	Philippines	Luzon	Ilocos Norte	Mt. Cabacan
KU	25768	*Pachycephala philippinensis*	Philippines	Luzon	Ilocos Norte	Mt. Cabacan
KU	25772	*Pachycephala philippinensis*	Philippines	Luzon	Ilocos Norte	Mt. Cabacan
KU	25779	*Pachycephala philippinensis*	Philippines	Luzon	Cagayan	Mt. Cagua
KU	25782	*Pachycephala philippinensis*	Philippines	Luzon	Cagayan	Mt. Cagua
KU	25792	*Pachycephala philippinensis*	Philippines	Luzon	Cagayan	Mt. Cagua
KU	25804	*Pachycephala philippinensis*	Philippines	Luzon	Cagayan	Mt. Cagua
KU	25809	*Pachycephala philippinensis*	Philippines	Luzon	Cagayan	Mt. Cagua
KU	25826	*Pachycephala philippinensis*	Philippines	Luzon	Cagayan	Mt. Cagua
KU	25833	*Pachycephala philippinensis*	Philippines	Luzon	Cagayan	Mt. Cagua
KU	25904	*Pachycephala philippinensis*	Philippines	Luzon	Cagayan	Mt. Cagua
KU	25956	*Pachycephala philippinensis*	Philippines	Luzon	Cagayan	Mt. Cagua
KU	27019	*Pachycephala philippinensis*	Philippines	Alabat	Quezon	Alabat
KU	27083	*Pachycephala philippinensis*	Philippines	Alabat	Quezon	Alabat
KU	27086	*Pachycephala philippinensis*	Philippines	Alabat	Quezon	Alabat
KU	27107	*Pachycephala philippinensis*	Philippines	Alabat	Quezon	Alabat
KU	27146	*Pachycephala philippinensis*	Philippines	Mindanao	South Cotabato	Tampakan
KU	27192	*Pachycephala philippinensis*	Philippines	Mindanao	South Cotabato	Tampakan
KU	27237	*Pachycephala philippinensis*	Philippines	Siquijor	Siquijor	Mt. Bandilaan
KU	27238	*Pachycephala philippinensis*	Philippines	Siquijor	Siquijor	Mt. Bandilaan
KU	27242	*Pachycephala philippinensis*	Philippines	Siquijor	Siquijor	Mt. Bandilaan
KU	27243	*Pachycephala philippinensis*	Philippines	Siquijor	Siquijor	Mt. Bandilaan
KU	27249	*Pachycephala philippinensis*	Philippines	Siquijor	Siquijor	Mt. Bandilaan
KU	27255	*Pachycephala philippinensis*	Philippines	Siquijor	Siquijor	Mt. Bandilaan
KU	27268	*Pachycephala philippinensis*	Philippines	Siquijor	Siquijor	Mt. Bandilaan
KU	27369	*Pachycephala philippinensis*	Philippines	Leyte	Southern Leyte	Silago
KU	27477	*Pachycephala philippinensis*	Philippines	Leyte	Southern Leyte	Sogod
KU	28187	*Pachycephala philippinensis*	Philippines	Bohol	Bohol	Bilar
KU	28222	*Pachycephala philippinensis*	Philippines	Bohol	Bohol	Valencia
KU	28312	*Pachycephala philippinensis*	Philippines	Mindanao	Agusan del Norte	Mt. Hilong-Hilong
KU	28368	*Pachycephala philippinensis*	Philippines	Mindanao	Agusan del Norte	Mt. Hilong-Hilong
KU	28369	*Pachycephala philippinensis*	Philippines	Mindanao	Agusan del Norte	Mt. Hilong-Hilong
KU	28523	*Pachycephala philippinensis*	Philippines	Mindanao	Misamis Oriental	Mt. Lumot
KU	28546	*Pachycephala philippinensis*	Philippines	Mindanao	Misamis Oriental	Mt. Lumot
KU	28638	*Pachycephala philippinensis*	Philippines	Mindanao	Misamis Oriental	Mt. Lumot
KU	14118	*Phylloscopus olivaceus*	Philippines	Samar	Eastern Samar	Taft
KU	14169	*Phylloscopus olivaceus*	Philippines	Samar	Eastern Samar	Taft
KU	14170	*Phylloscopus olivaceus*	Philippines	Samar	Eastern Samar	Taft
KU	14229	*Phylloscopus olivaceus*	Philippines	Samar	Eastern Samar	Taft
KU	14269	*Phylloscopus olivaceus*	Philippines	Samar	Eastern Samar	Taft
KU	14290	*Phylloscopus olivaceus*	Philippines	Leyte	Leyte	Baybay
KU	14303	*Phylloscopus olivaceus*	Philippines	Leyte	Leyte	Baybay
KU	18234	*Phylloscopus olivaceus*	Philippines	Mindanao	Zamboanga del Sur	Pasonanca
KU	19012	*Phylloscopus olivaceus*	Philippines	Samar	Agusan del Sur	Mt. Magdiwata
KU	27372	*Phylloscopus olivaceus*	Philippines	Leyte	Leyte	Silago
KU	28226	*Phylloscopus olivaceus*	Philippines	Bohol	Bohol	Valencia
KU	28227	*Phylloscopus olivaceus*	Philippines	Bohol	Bohol	Valencia
KU	28290	*Phylloscopus olivaceus*	Philippines	Mindanao	Agusan del Norte	Mt. Hilong-Hilong
KU	28311	*Phylloscopus olivaceus*	Philippines	Mindanao	Agusan del Norte	Mt. Hilong-Hilong
KU	28365	*Phylloscopus olivaceus*	Philippines	Mindanao	Agusan del Norte	Mt. Hilong-Hilong
KU	29931	*Phylloscopus olivaceus*	Philippines	Mindanao	Zamboanga del Sur	Pasonanca
KU	29972	*Phylloscopus olivaceus*	Philippines	Mindanao	Zamboanga del Sur	Pasonanca
FMNH	357587	*Prionochilus olivaceus*	Philippines	Mindanao	Bukidnon	Mt. Kitanglad Range
FMNH	357588	*Prionochilus olivaceus*	Philippines	Mindanao	Bukidnon	Mt. Kitanglad Range
FMNH	357589	*Prionochilus olivaceus*	Philippines	Mindanao	Bukidnon	Mt. Kitanglad Range
FMNH	455039	*Prionochilus olivaceus*	Philippines	Luzon	Nueva Vizcaya	Mt. Palali

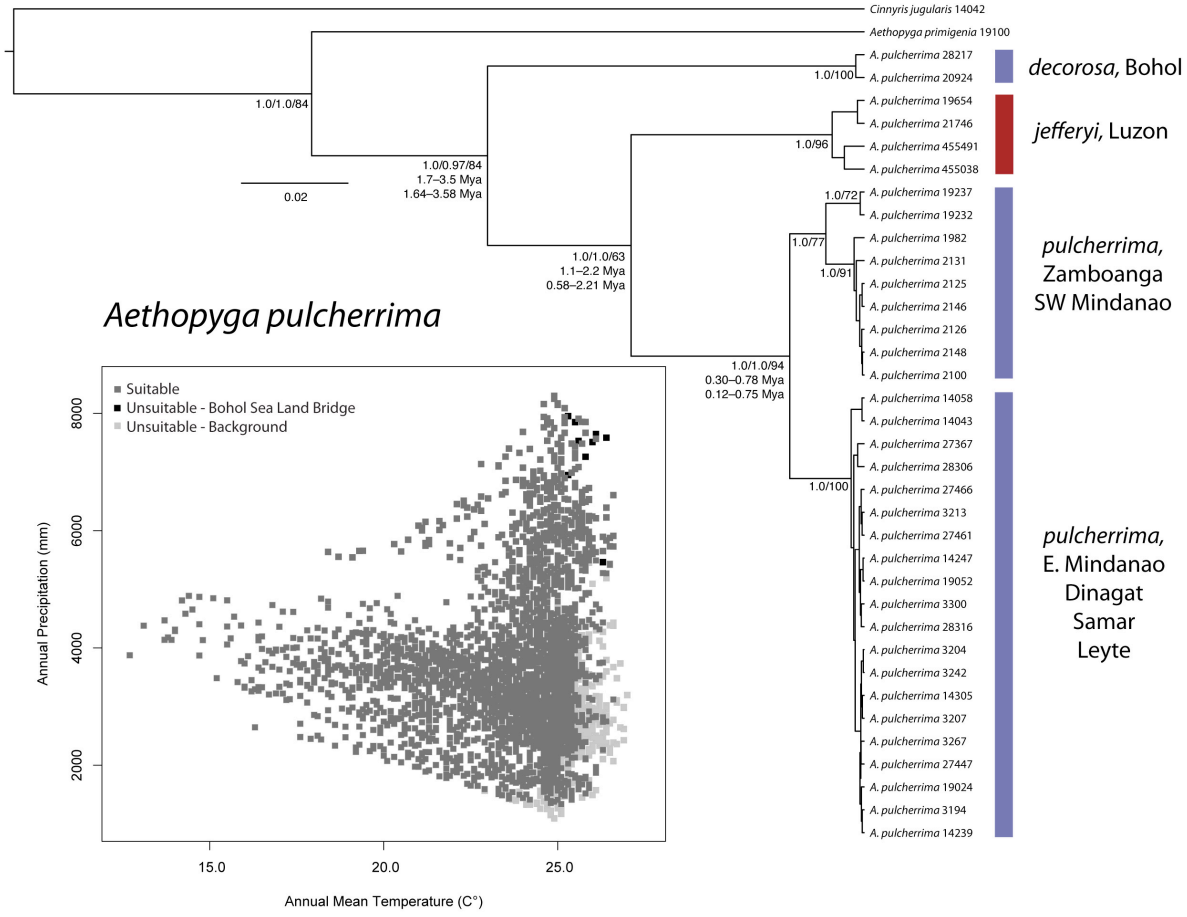
FMNH	462068	*Prionochilus olivaceus*	Philippines	Luzon	Camarines Sur	Lagonoy
FMNH	462069	*Prionochilus olivaceus*	Philippines	Luzon	Camarines Sur	Lagonoy
KU	14047	*Prionochilus olivaceus*	Philippines	Dinagat	Surigao del Norte	Loreto
KU	14131	*Prionochilus olivaceus*	Philippines	Samar	Eastern Samar	Taft
KU	14194	*Prionochilus olivaceus*	Philippines	Samar	Eastern Samar	Taft
KU	14195	*Prionochilus olivaceus*	Philippines	Samar	Eastern Samar	Taft
KU	14196	*Prionochilus olivaceus*	Philippines	Samar	Eastern Samar	Taft
KU	16004	*Prionochilus olivaceus*	Philippines	Mindanao	Zamboanga del Sur	Pasonanca: Baluno
KU	17956	*Prionochilus olivaceus*	Philippines	Luzon	Caminares Norte	Mt. Labo
KU	17987	*Prionochilus olivaceus*	Philippines	Luzon	Caminares Norte	Mt. Labo
KU	18062	*Prionochilus olivaceus*	Philippines	Luzon	Caminares Norte	Mt. Labo
KU	18063	*Prionochilus olivaceus*	Philippines	Luzon	Caminares Norte	Mt. Labo
KU	18182	*Prionochilus olivaceus*	Philippines	Mindanao	Zamboanga del Sur	Pasonanca: Baluno
KU	18220	*Prionochilus olivaceus*	Philippines	Mindanao	Zamboanga del Sur	Pasonanca: Baluno
KU	18244	*Prionochilus olivaceus*	Philippines	Mindanao	Zamboanga del Sur	Pasonanca: Baluno
KU	19051	*Prionochilus olivaceus*	Philippines	Mindanao	Aguasan del Sur	Mt. Magdiwata
KU	19184	*Prionochilus olivaceus*	Philippines	Mindanao	Zamboanga del Sur	Pasonanca: San. Clara
KU	19614	*Prionochilus olivaceus*	Philippines	Luzon	Aurora	Baler
KU	19615	*Prionochilus olivaceus*	Philippines	Luzon	Aurora	Baler
KU	20244	*Prionochilus olivaceus*	Philippines	Luzon	Aurora	Aurora N.P
KU	20253	*Prionochilus olivaceus*	Philippines	Luzon	Aurora	Aurora N.P
KU	20254	*Prionochilus olivaceus*	Philippines	Luzon	Aurora	Aurora N.P
KU	20259	*Prionochilus olivaceus*	Philippines	Luzon	Aurora	Aurora N.P
KU	20358	*Prionochilus olivaceus*	Philippines	Luzon	Aurora	Baler
KU	20359	*Prionochilus olivaceus*	Philippines	Luzon	Aurora	Baler
KU	21048	*Prionochilus olivaceus*	Philippines	Luzon	Nueva Vizcaya	Mt. Palali
KU	21063	*Prionochilus olivaceus*	Philippines	Luzon	Nueva Vizcaya	Mt. Palali
KU	25727	*Prionochilus olivaceus*	Philippines	Luzon	Ilocos Norte	Mt. Cabacan
KU	25769	*Prionochilus olivaceus*	Philippines	Luzon	Ilocos Norte	Mt. Cabacan
KU	25770	*Prionochilus olivaceus*	Philippines	Luzon	Ilocos Norte	Mt. Cabacan
KU	25771	*Prionochilus olivaceus*	Philippines	Luzon	Ilocos Norte	Mt. Cabacan
KU	25794	*Prionochilus olivaceus*	Philippines	Luzon	Cagayan	Mt. Cagua
KU	25797	*Prionochilus olivaceus*	Philippines	Luzon	Cagayan	Mt. Cagua
KU	25879	*Prionochilus olivaceus*	Philippines	Luzon	Cagayan	Mt. Cagua
KU	25895	*Prionochilus olivaceus*	Philippines	Luzon	Cagayan	Mt. Cagua
KU	25909	*Prionochilus olivaceus*	Philippines	Luzon	Cagayan	Mt. Cagua
KU	25916	*Prionochilus olivaceus*	Philippines	Luzon	Cagayan	Mt. Cagua
KU	25947	*Prionochilus olivaceus*	Philippines	Luzon	Cagayan	Mt. Cagua
KU	27156	*Prionochilus olivaceus*	Philippines	Mindanao	South Cotabato	Tampakan
KU	28286	*Prionochilus olivaceus*	Philippines	Mindanao	Agusan del Norte	Mt. Hilong-Hilong
KU	28358	*Prionochilus olivaceus*	Philippines	Mindanao	Agusan del Norte	Mt. Hilong-Hilong
KU	12333	*Prionochilus xanthopygius*	Malaysia	Borneo		
CMNH	B35763	*Ptilocichla mindanensis*	Philippines	Mindanao	Davao del Norte	Mt. Pasian
CMNH	B39115	*Ptilocichla mindanensis*	Philippines	Mindanao	South Cotabato	Mt. Busa
FMNH	472764	*Ptilocichla mindanensis*	Philippines	Mindanao	Sultan Kudara	Ninoy Aquino
KU	14193	*Ptilocichla mindanensis*	Philippines	Samar	Eastern Samar	Taft
KU	14272	*Ptilocichla mindanensis*	Philippines	Samar	Eastern Samar	Taft
KU	14273	*Ptilocichla mindanensis*	Philippines	Samar	Eastern Samar	Taft
KU	14274	*Ptilocichla mindanensis*	Philippines	Samar	Eastern Samar	Taft
KU	18187	*Ptilocichla mindanensis*	Philippines	Mindanao	Zamboanga del Sur	Pasonanca
KU	19070	*Ptilocichla mindanensis*	Philippines	Mindanao	Agusan del Sur	Mt. Magdiwata
KU	19191	*Ptilocichla mindanensis*	Philippines	Mindanao	Zamboanga del Sur	Pasonanca
KU	19245	*Ptilocichla mindanensis*	Philippines	Mindanao	Zamboanga del Sur	Pasonanca
KU	27196	*Ptilocichla mindanensis*	Philippines	Mindanao	South Cotabato	Tampakan
KU	27197	*Ptilocichla mindanensis*	Philippines	Mindanao	South Cotabato	Tampakan
KU	28201	*Ptilocichla mindanensis*	Philippines	Bohol	Bohol	Bilar
KU	28202	*Ptilocichla mindanensis*	Philippines	Bohol	Bohol	Bilar
KU	28208	*Ptilocichla mindanensis*	Philippines	Bohol	Bohol	Bilar
KU	28221	*Ptilocichla mindanensis*	Philippines	Bohol	Bohol	Valencia
KU	28238	*Ptilocichla mindanensis*	Philippines	Bohol	Bohol	Valencia
KU	28241	*Ptilocichla mindanensis*	Philippines	Bohol	Bohol	Valencia
KU	28242	*Ptilocichla mindanensis*	Philippines	Bohol	Bohol	Valencia
KU	28336	*Ptilocichla mindanensis*	Philippines	Mindanao	Agusan del Norte	Mt. Hilong-Hilong
KU	29950	*Ptilocichla mindanensis*	Philippines	Mindanao	Zamboanga del Sur	Pasonanca

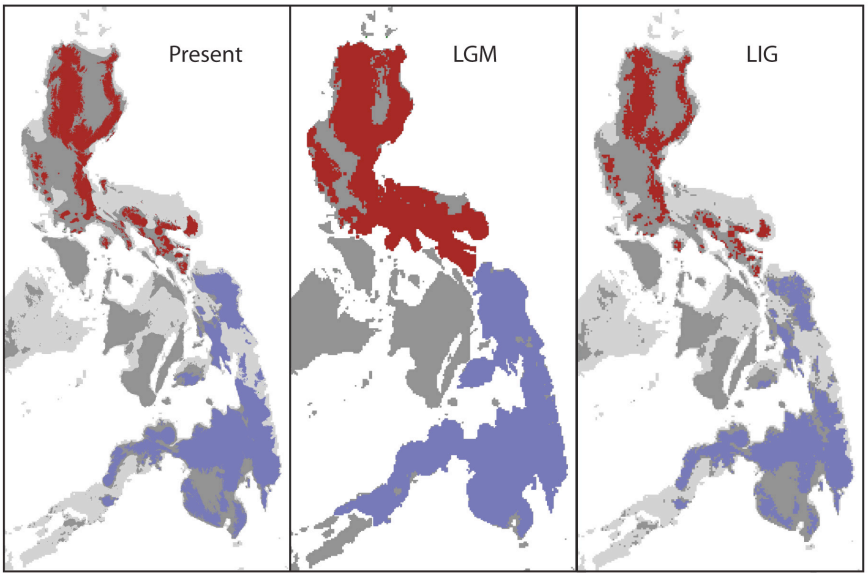
KU	29952	*Ptilocichla mindanensis*	Philippines	Mindanao	Zamboanga del Sur	Pasonanca
KU	12641	*Pycnonotus atriceps*	Philippines	Palawan		
LSUMZ	36351	*Pycnonotus goavier*	Malaysia	Borneo		
AMNH	14987	*Pycnonotus urostictus*	Philippines	Alabat	Quezon	Alabat
FMNH	449746	*Pycnonotus urostictus*	Philippines	Luzon	Aurora	Dingalan
FMNH	449747	*Pycnonotus urostictus*	Philippines	Luzon	Aurora	Dingalan
FMNH	461999	*Pycnonotus urostictus*	Philippines	Luzon	Camarines Sur	Caramoan Park
KU	14038	*Pycnonotus urostictus*	Philippines	Dinagat	Surigao del Norte	Loreto
KU	14052	*Pycnonotus urostictus*	Philippines	Dinagat	Surigao del Norte	Loreto
KU	14070	*Pycnonotus urostictus*	Philippines	Dinagat	Surigao del Norte	Loreto
KU	14072	*Pycnonotus urostictus*	Philippines	Dinagat	Surigao del Norte	Loreto
KU	14074	*Pycnonotus urostictus*	Philippines	Dinagat	Surigao del Norte	Loreto
KU	14233	*Pycnonotus urostictus*	Philippines	Samar	Eastern Samar	Taft
KU	14238	*Pycnonotus urostictus*	Philippines	Samar	Eastern Samar	Taft
KU	18105	*Pycnonotus urostictus*	Philippines	Mindanao	Zamboanga del Sur	Pasonanca: Intake
KU	18128	*Pycnonotus urostictus*	Philippines	Mindanao	Zamboanga del Sur	Pasonanca: Intake
KU	18131	*Pycnonotus urostictus*	Philippines	Mindanao	Zamboanga del Sur	Pasonanca: Intake
KU	18132	*Pycnonotus urostictus*	Philippines	Mindanao	Zamboanga del Sur	Pasonanca: Intake
KU	18136	*Pycnonotus urostictus*	Philippines	Mindanao	Zamboanga del Sur	Pasonanca: Intake
KU	18153	*Pycnonotus urostictus*	Philippines	Mindanao	Zamboanga del Sur	Pasonanca: Intake
KU	18165	*Pycnonotus urostictus*	Philippines	Mindanao	Zamboanga del Sur	Pasonanca: Baluno
KU	18172	*Pycnonotus urostictus*	Philippines	Mindanao	Zamboanga del Sur	Pasonanca: Baluno
KU	18173	*Pycnonotus urostictus*	Philippines	Mindanao	Zamboanga del Sur	Pasonanca: Baluno
KU	19002	*Pycnonotus urostictus*	Philippines	Mindanao	Aguasan del Sur	Mt. Magdiwata
KU	19004	*Pycnonotus urostictus*	Philippines	Mindanao	Aguasan del Sur	Mt. Magdiwata
KU	19026	*Pycnonotus urostictus*	Philippines	Mindanao	Aguasan del Sur	Mt. Magdiwata
KU	19037	*Pycnonotus urostictus*	Philippines	Mindanao	Aguasan del Sur	Mt. Magdiwata
KU	19188	*Pycnonotus urostictus*	Philippines	Mindanao	Zamboanga del Sur	Pasonanca: San. Clara
KU	19267	*Pycnonotus urostictus*	Philippines	Mindanao	Zamboanga del Sur	Pasonanca: Intake
KU	19375	*Pycnonotus urostictus*	Philippines	Luzon	Aurora	Casiguran
KU	20338	*Pycnonotus urostictus*	Philippines	Luzon	Aurora	ASCOT
KU	20346	*Pycnonotus urostictus*	Philippines	Luzon	Aurora	ASCOT
KU	20347	*Pycnonotus urostictus*	Philippines	Luzon	Aurora	ASCOT
KU	20352	*Pycnonotus urostictus*	Philippines	Luzon	Aurora	ASCOT
KU	20353	*Pycnonotus urostictus*	Philippines	Luzon	Aurora	ASCOT
KU	20937	*Pycnonotus urostictus*	Philippines	Bohol	Bohol	Sierra Bullones
KU	21770	*Pycnonotus urostictus*	Philippines	Luzon	Aurora	Casiguran
KU	21771	*Pycnonotus urostictus*	Philippines	Luzon	Aurora	Casiguran
KU	25542	*Pycnonotus urostictus*	Philippines	Luzon	Bulacan	Angat Watershed
KU	25812	*Pycnonotus urostictus*	Philippines	Luzon	Cagayan	Mt. Cagua
KU	25816	*Pycnonotus urostictus*	Philippines	Luzon	Cagayan	Mt. Cagua
KU	25853	*Pycnonotus urostictus*	Philippines	Luzon	Cagayan	Mt. Cagua
KU	25883	*Pycnonotus urostictus*	Philippines	Luzon	Cagayan	Mt. Cagua
KU	25922	*Pycnonotus urostictus*	Philippines	Luzon	Cagayan	Mt. Cagua
KU	25926	*Pycnonotus urostictus*	Philippines	Luzon	Cagayan	Mt. Cagua
KU	25967	*Pycnonotus urostictus*	Philippines	Luzon	Cagayan	Mt. Cagua
KU	25968	*Pycnonotus urostictus*	Philippines	Luzon	Cagayan	Mt. Cagua
KU	25972	*Pycnonotus urostictus*	Philippines	Luzon	Cagayan	Mt. Cagua
KU	26936	*Pycnonotus urostictus*	Philippines	Polillo	Cagayan	Mt. Cagua
KU	26997	*Pycnonotus urostictus*	Philippines	Polillo	Quezon	Burdeos
KU	26998	*Pycnonotus urostictus*	Philippines	Polillo	Quezon	Burdeos
KU	27001	*Pycnonotus urostictus*	Philippines	Polillo	Quezon	Burdeos
KU	27012	*Pycnonotus urostictus*	Philippines	Polillo	Quezon	Burdeos
KU	27023	*Pycnonotus urostictus*	Philippines	Polillo	Quezon	Burdeos
KU	27381	*Pycnonotus urostictus*	Philippines	Siargao	Surigao del Norte	Pilar
KU	27382	*Pycnonotus urostictus*	Philippines	Siargao	Surigao del Norte	Pilar
KU	27420	*Pycnonotus urostictus*	Philippines	Siargao	Surigao del Norte	Pilar
KU	27427	*Pycnonotus urostictus*	Philippines	Siargao	Surigao del Norte	Pilar
KU	27430	*Pycnonotus urostictus*	Philippines	Siargao	Surigao del Norte	Pilar
KU	28179	*Pycnonotus urostictus*	Philippines	Bohol	Bohol	Bilar
KU	28184	*Pycnonotus urostictus*	Philippines	Bohol	Bohol	Bilar
KU	28204	*Pycnonotus urostictus*	Philippines	Bohol	Bohol	Bilar
KU	28212	*Pycnonotus urostictus*	Philippines	Bohol	Bohol	Bilar
KU	28276	*Pycnonotus urostictus*	Philippines	Mindanao	Agusan del Norte	Mt. Hilong-Hilong

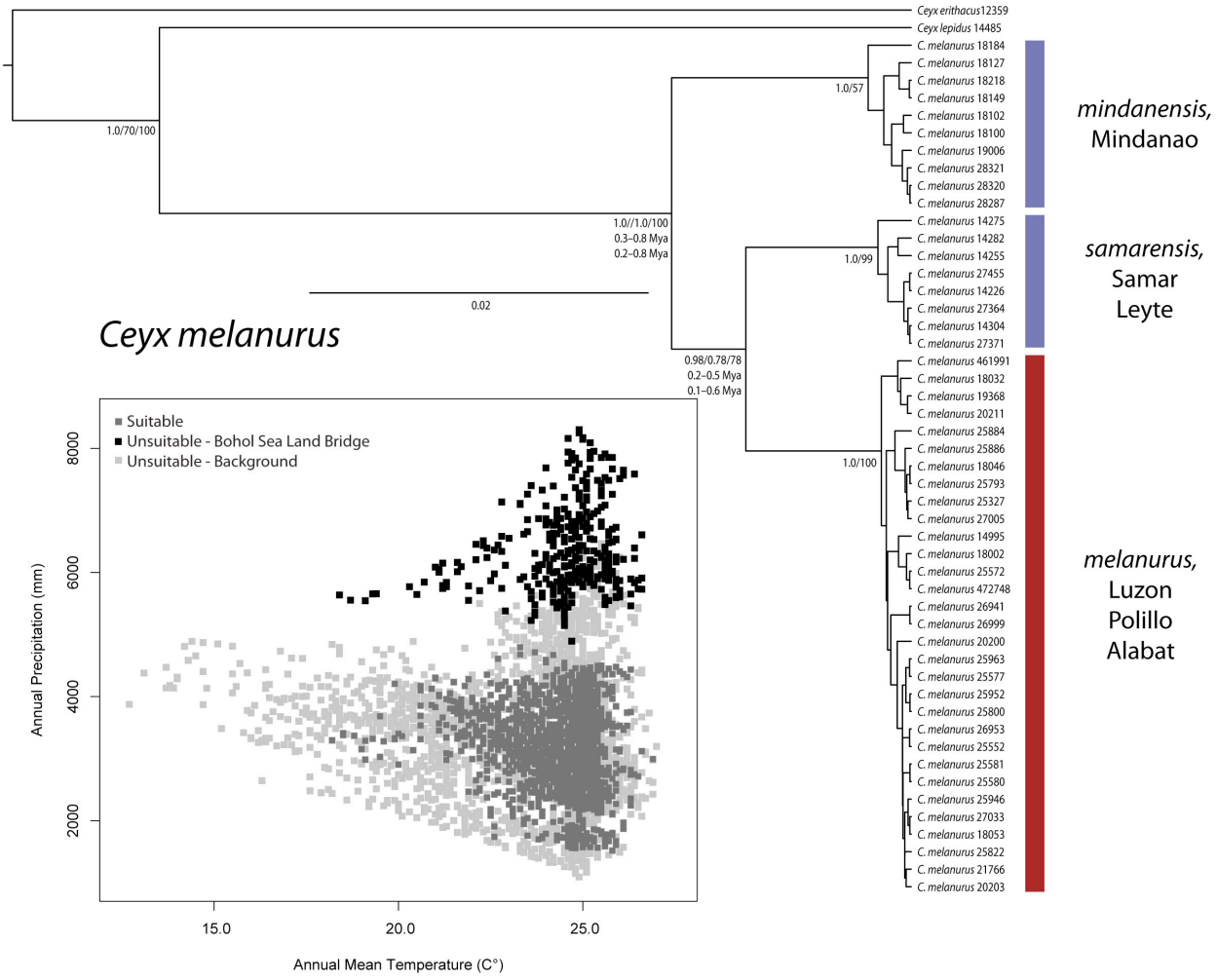
KU	28277	*Pycnonotus urostictus*	Philippines	Mindanao	Agusan del Norte	Mt. Hilong-Hilong
KU	28465	*Pycnonotus urostictus*	Philippines	Mindanao	Agusan del Norte	Mt. Hilong-Hilong
KU	28629	*Pycnonotus urostictus*	Philippines	Mindanao	Misamis Oriental	Mt. Lumot
KU	28632	*Pycnonotus urostictus*	Philippines	Mindanao	Misamis Oriental	Mt. Lumot
KU	28644	*Pycnonotus urostictus*	Philippines	Mindanao	Misamis Oriental	Mt. Lumot
KU	14144	*Rhipidura superciliaris*	Philippines	Samar	Eastern Samar	Taft
KU	14182	*Rhipidura superciliaris*	Philippines	Samar	Eastern Samar	Taft
KU	14202	*Rhipidura superciliaris*	Philippines	Samar	Eastern Samar	Taft
KU	14208	*Rhipidura superciliaris*	Philippines	Samar	Eastern Samar	Taft
KU	14228	*Rhipidura superciliaris*	Philippines	Samar	Eastern Samar	Taft
KU	18176	*Rhipidura superciliaris*	Philippines	Mindanao	Zamboanga del Sur	Pasonanca
KU	18192	*Rhipidura superciliaris*	Philippines	Mindanao	Zamboanga del Sur	Pasonanca
KU	18198	*Rhipidura superciliaris*	Philippines	Mindanao	Zamboanga del Sur	Pasonanca
KU	18242	*Rhipidura superciliaris*	Philippines	Mindanao	Zamboanga del Sur	Pasonanca
KU	18249	*Rhipidura superciliaris*	Philippines	Mindanao	Zamboanga del Sur	Pasonanca
KU	19007	*Rhipidura superciliaris*	Philippines	Mindanao	Agusan del Sur	Mt. Magdiwata
KU	19015	*Rhipidura superciliaris*	Philippines	Mindanao	Agusan del Sur	Mt. Magdiwata
KU	19021	*Rhipidura superciliaris*	Philippines	Mindanao	Agusan del Sur	Mt. Magdiwata
KU	19023	*Rhipidura superciliaris*	Philippines	Mindanao	Agusan del Sur	Mt. Magdiwata
KU	20920	*Rhipidura superciliaris*	Philippines	Bohol	Bohol	Bilar
KU	20931	*Rhipidura superciliaris*	Philippines	Bohol	Bohol	Bilar
KU	27149	*Rhipidura superciliaris*	Philippines	Mindanao	South Cotabato	Tampakan
KU	27150	*Rhipidura superciliaris*	Philippines	Mindanao	South Cotabato	Tampakan
KU	27169	*Rhipidura superciliaris*	Philippines	Mindanao	South Cotabato	Tampakan
KU	28220	*Rhipidura superciliaris*	Philippines	Bohol	Bohol	Valencia
KU	28252	*Rhipidura superciliaris*	Philippines	Bohol	Bohol	Valencia
KU	28278	*Rhipidura superciliaris*	Philippines	Mindanao	Agusan del Norte	Mt. Hilong-Hilong
KU	28319	*Rhipidura superciliaris*	Philippines	Mindanao	Agusan del Norte	Mt. Hilong-Hilong
KU	28332	*Rhipidura superciliaris*	Philippines	Mindanao	Agusan del Norte	Mt. Hilong-Hilong
FMNH	253557	*Robsonius rabori*	Philippines	Luzon	Ilocos Norte	Tabbug
KU	25708	*Robsonius rabori*	Philippines	Luzon	Ilocos Norte	Mt Cabacan
FMNH	462013	*Robsonius sorsogonensis*	Philippines	Luzon	Camarines Sur	Saddle Peak
FMNH	472703	*Robsonius sorsogonensis*	Philippines	Luzon	Quezon	Tayabas City
PNM	25319	*Robsonius sorsogonensis*	Philippines	Luzon	Bulacan	Angat Watershead
USNM	433008	*Robsonius sorsogonensis*	Philippines	Luzon	Camarines Sur	Mount Isarog
FMNH	449800	*Robsonius thompsoni*	Philippines	Luzon	Aurora	Mingan Peak
FMNH	454990	*Robsonius thompsoni*	Philippines	Luzon	Nueva Vizcaya	Mt Palali
FMNH	472601	*Robsonius thompsoni*	Philippines	Luzon	Aurora	Mt Anacuao
FMNH	472602	*Robsonius thompsoni*	Philippines	Luzon	Aurora	Mt Anacuao
FMNH	472603	*Robsonius thompsoni*	Philippines	Luzon	Aurora	Mt Anacuao
KU	19632	*Robsonius thompsoni*	Philippines	Luzon	Aurora	SW of Baler
KU	25788	*Robsonius thompsoni*	Philippines	Luzon	Cagayan	Mt. Cagua
KU	26566	*Robsonius thompsoni*	Philippines	Luzon	Aurora	Sitio Minoli
CMNH	B37769	*Sterrhoptilus capitalis*	Philippines	Mindanao	South Cotabato	Mt. Busa
KU	28326	*Sterrhoptilus capitalis*	Philippines	Mindanao	Agusan del Norte	Mt. Hilong-Hilong
KU	28338	*Sterrhoptilus capitalis*	Philippines	Mindanao	Agusan del Norte	Mt. Hilong-Hilong
KU	28339	*Sterrhoptilus capitalis*	Philippines	Mindanao	Agusan del Norte	Mt. Hilong-Hilong
KU	28342	*Sterrhoptilus capitalis*	Philippines	Mindanao	Agusan del Norte	Mt. Hilong-Hilong
KU	28343	*Sterrhoptilus capitalis*	Philippines	Mindanao	Agusan del Norte	Mt. Hilong-Hilong
KU	29959	*Sterrhoptilus capitalis*	Philippines	Mindanao	Zamboanga del Sur	Pasonanca
KU	29965	*Sterrhoptilus capitalis*	Philippines	Mindanao	Zamboanga del Sur	Pasonanca
KU	29968	*Sterrhoptilus capitalis*	Philippines	Mindanao	Zamboanga del Sur	Pasonanca
KU	19648	*Sterrhoptilus dennistouni*	Philippines	Luzon	Aurora	San Luis
KU	20186	*Sterrhoptilus dennistouni*	Philippines	Luzon	Aurora	Aurora N.P.
KU	20225	*Sterrhoptilus dennistouni*	Philippines	Luzon	Aurora	Aurora N.P.
KU	20335	*Sterrhoptilus dennistouni*	Philippines	Luzon	Aurora	Baler
KU	21084	*Sterrhoptilus dennistouni*	Philippines	Luzon	Nueva Vizcaya	Mt. Palali
KU	21086	*Sterrhoptilus dennistouni*	Philippines	Luzon	Nueva Vizcaya	Mt. Palali
KU	25702	*Sterrhoptilus dennistouni*	Philippines	Luzon	Ilocos Norte	Mt. Cabacan
KU	25713	*Sterrhoptilus dennistouni*	Philippines	Luzon	Ilocos Norte	Mt. Cabacan
KU	25817	*Sterrhoptilus dennistouni*	Philippines	Luzon	Gonzaga	Mt. Cabacan
KU	25829	*Sterrhoptilus dennistouni*	Philippines	Luzon	Gonzaga	Mt. Cabacan
KU	25950	*Sterrhoptilus dennistouni*	Philippines	Luzon	Gonzaga	Mt. Cabacan
FMNH	449754	*Sterrhoptilus nigrocapitata*	Philippines	Luzon	Aurora	Dingalan

FMNH	449755	*Sterrhoptilus nigrocapitata*	Philippines	Luzon	Aurora	Dingalan
FMNH	449756	*Sterrhoptilus nigrocapitata*	Philippines	Luzon	Aurora	Dingalan
FMNH	472765	*Sterrhoptilus nigrocapitata*	Philippines	Luzon	Rizal	Dingalan
KU	14192	*Sterrhoptilus nigrocapitata*	Philippines	Samar	Eastern Samar	Taft
KU	14199	*Sterrhoptilus nigrocapitata*	Philippines	Samar	Eastern Samar	Taft
KU	18034	*Sterrhoptilus nigrocapitata*	Philippines	Luzon	Caminares Sur	Mt. Labo
KU	18040	*Sterrhoptilus nigrocapitata*	Philippines	Luzon	Caminares Sur	Mt. Labo
KU	18083	*Sterrhoptilus nigrocapitata*	Philippines	Luzon	Caminares Sur	Mt. Labo
KU	25550	*Sterrhoptilus nigrocapitata*	Philippines	Luzon	Bulacan	Angat Watershed
KU	25551	*Sterrhoptilus nigrocapitata*	Philippines	Luzon	Bulacan	Angat Watershed
KU	28214	*Sterrhoptilus nigrocapitata*	Philippines	Bohol	Bohol	Valencia
KU	28215	*Sterrhoptilus nigrocapitata*	Philippines	Bohol	Bohol	Valencia

Appendix 2: Detailed phylogenies, ENMs, and bivariate plots for 8 co-distributed Philippine bird species



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Ceyx lepidus 14485
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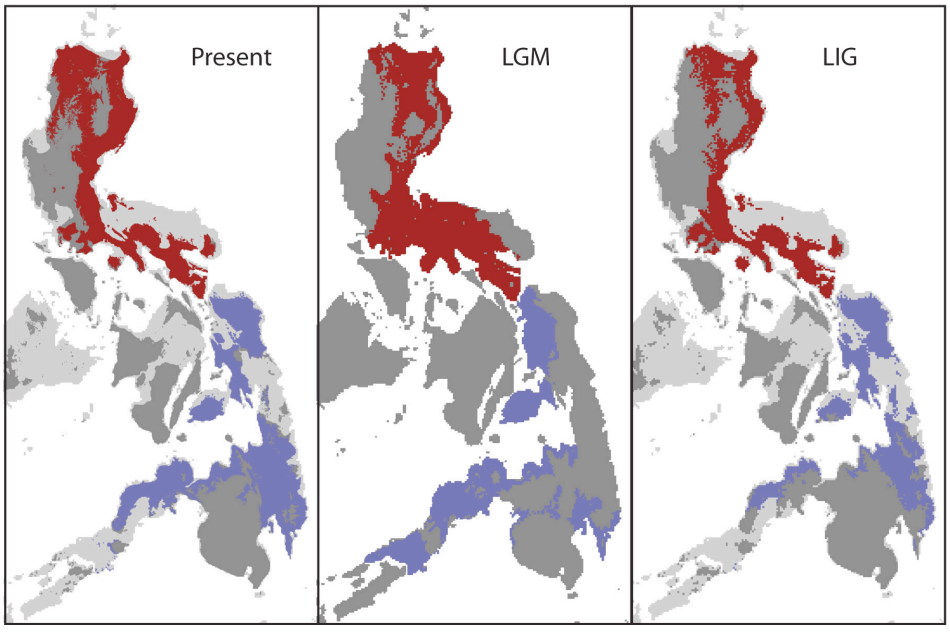
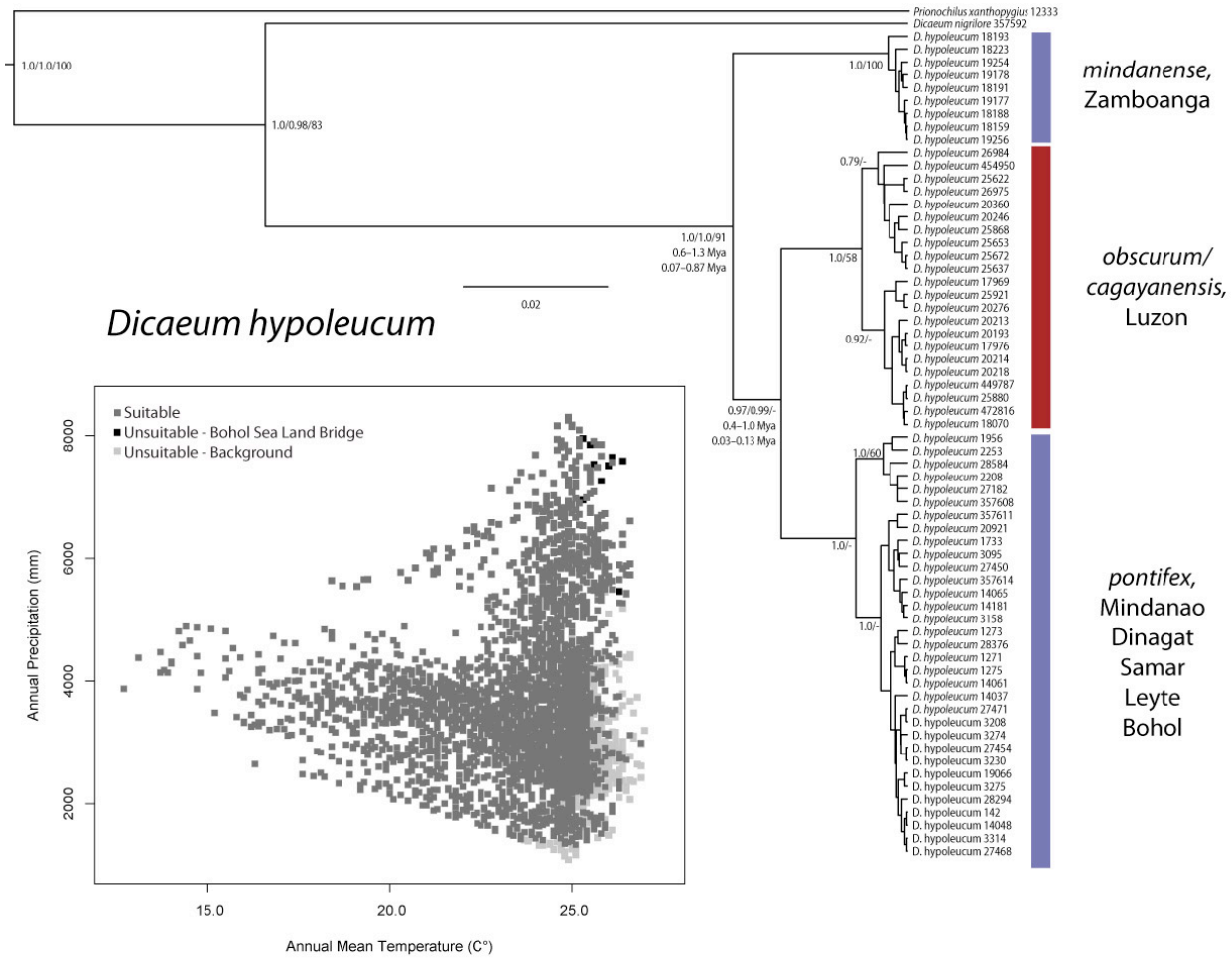
C. melanurus 18218
C. melanurus 18149
C. melanurus 18102
C. melanurus 18100
C. melanurus 19006
C. melanurus 28321
C. melanurus 28320
C. melanurus 28287
C. melanurus 14275
C. melanurus 14282
C. melanurus 14255
C. melanurus 27455
C. melanurus 14226
C. melanurus 27364
C. melanurus 14304
C. melanurus 27371
C. melanurus 461991
C. melanurus 18032
C. melanurus 19368
C. melanurus 20211
C. melanurus 25884
C. melanurus 25886
C. melanurus 18046
C. melanurus 25793
C. melanurus 25327
C. melanurus 27005
C. melanurus 14995
C. melanurus 18002
C. melanurus 25572
C. melanurus 472748
C. melanurus 26941
C. melanurus 26999
C. melanurus 20200
C. melanurus 25963
C. melanurus 25577
C. melanurus 25952
C. melanurus 25800
C. melanurus 26953
C. melanurus 25552
C. melanurus 25581
C. melanurus 25580
C. melanurus 25946
C. melanurus 27033
C. melanurus 18053
C. melanurus 25822
C. melanurus 21766
C. melanurus 20203
1.0/70/100
1.0/57
1.0//1.0/100
0.3–0.8 Mya
0.2–0.8 Mya
0.02
1.0/99
0.98/0.78/78
0.2–0.5 Mya
0.1–0.6 Mya
1.0/100
mindanensis,
Mindanao
samarensis,
Samar
Leyte
melanurus,
Luzon
Polillo
Alabat
Ceyx melanurus
Suitable
Unsuitable - Bohol Sea Land Bridge
Unsuitable - Background
Annual Precipitation (mm)
2000
4000
6000
8000
15.0
20.0
25.0
Annual Mean Temperature (C°)


Present
LGM
LIG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Dicaeum nigrilore 357592
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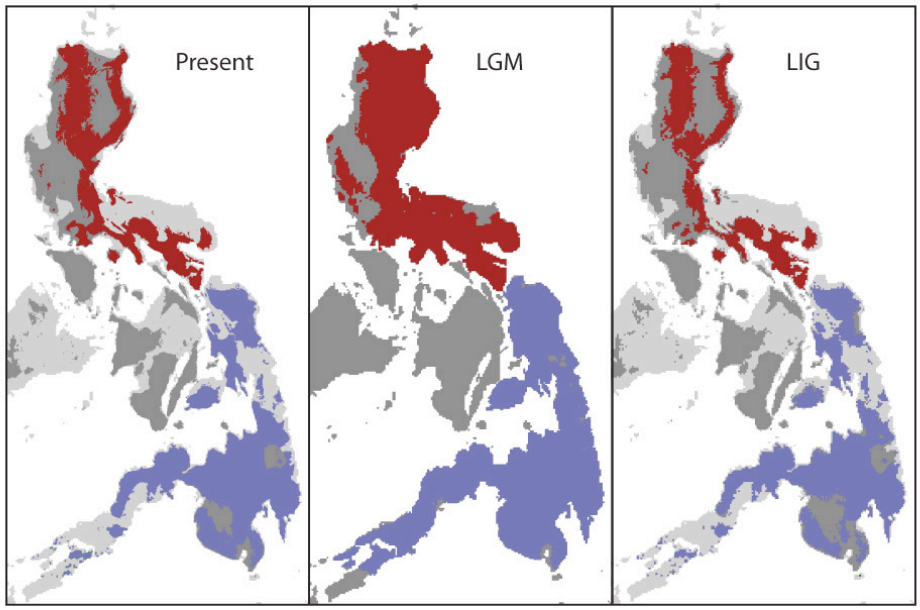
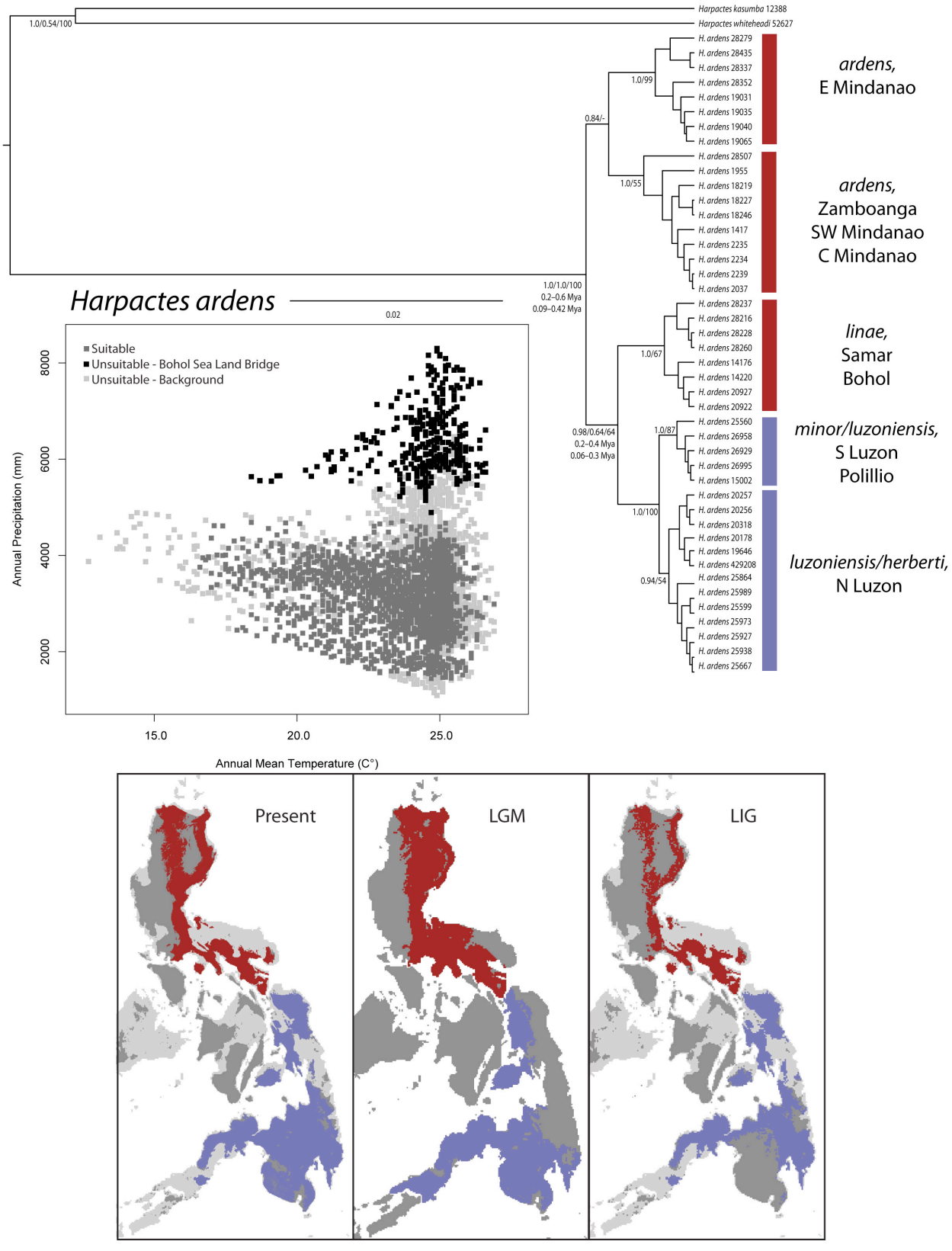
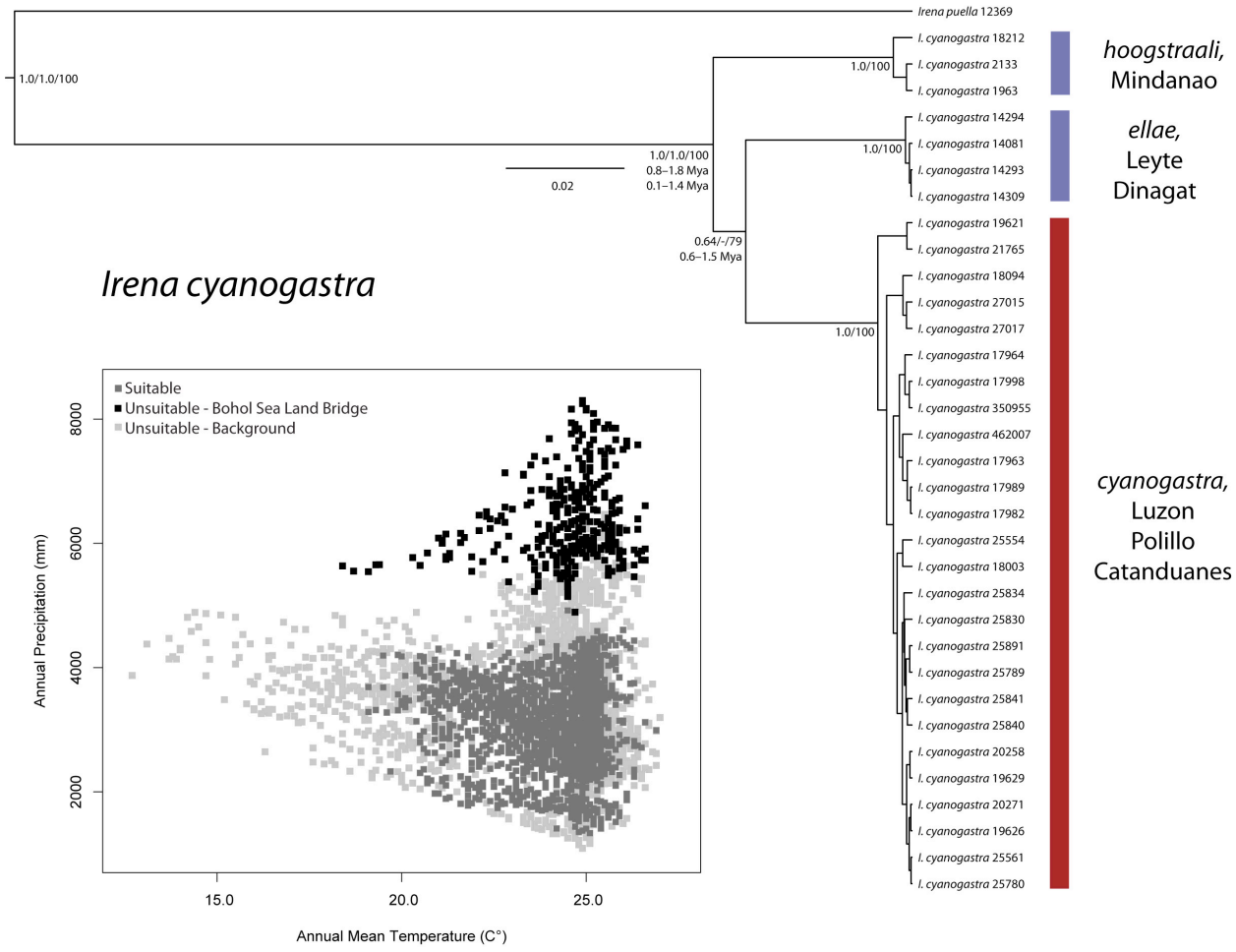
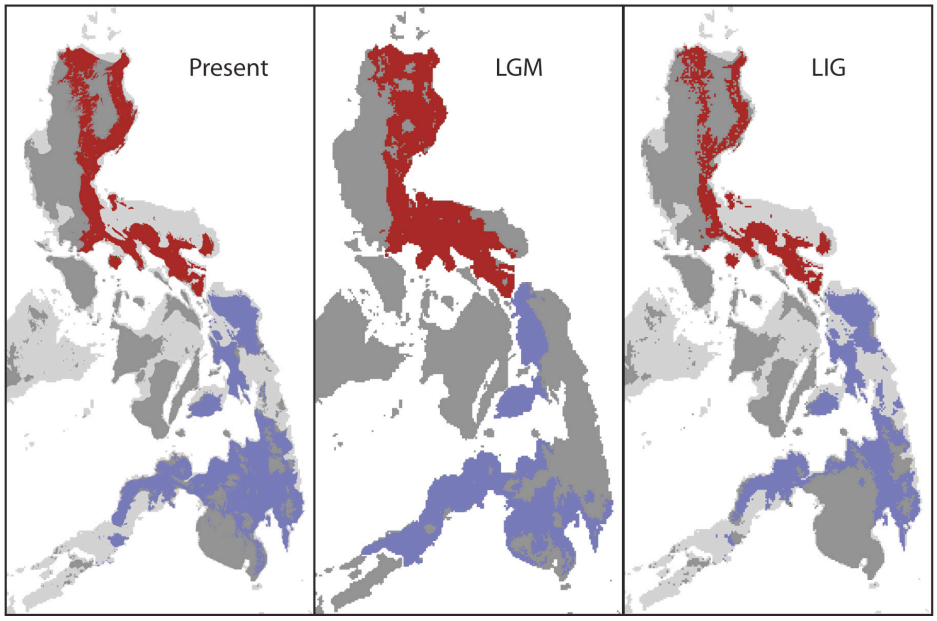
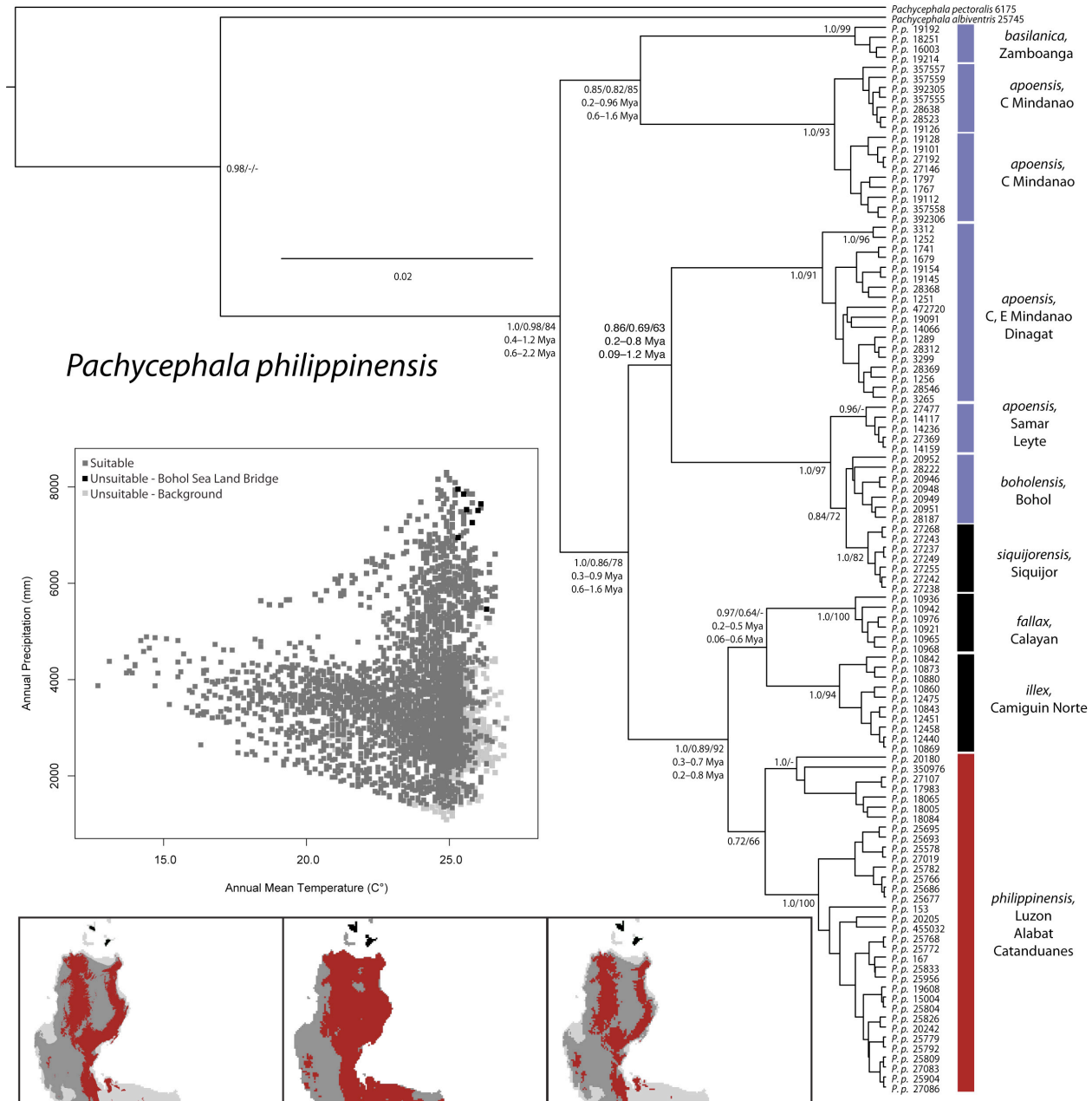
D. hypoleucum 18223
D. hypoleucum 19254
D. hypoleucum 19178
D. hypoleucum 18191
D. hypoleucum 19177
D. hypoleucum 18188
D. hypoleucum 18159
D. hypoleucum 19256
D. hypoleucum 26984
D. hypoleucum 454950
D. hypoleucum 25622
D. hypoleucum 26975
D. hypoleucum 20360
D. hypoleucum 20246
D. hypoleucum 25868
D. hypoleucum 25653
D. hypoleucum 25672
D. hypoleucum 25637
D. hypoleucum 17969
D. hypoleucum 25921
D. hypoleucum 20276
D. hypoleucum 20213
D. hypoleucum 20193
D. hypoleucum 17976
D. hypoleucum 20214
D. hypoleucum 20218
D. hypoleucum 449787
D. hypoleucum 25880
D. hypoleucum 472816
D. hypoleucum 18070
D. hypoleucum 1956
D. hypoleucum 2253
D. hypoleucum 28584
D. hypoleucum 2208
D. hypoleucum 27182
D. hypoleucum 357608
D. hypoleucum 357611
D. hypoleucum 20921
D. hypoleucum 1733
D. hypoleucum 3095
D. hypoleucum 27450
D. hypoleucum 357614
D. hypoleucum 14065
D. hypoleucum 14181
D. hypoleucum 3158
D. hypoleucum 1273
D. hypoleucum 28376
D. hypoleucum 1271
D. hypoleucum 1275
D. hypoleucum 14061
D. hypoleucum 14037
D. hypoleucum 27471
D. hypoleucum 3208
D. hypoleucum 3274
D. hypoleucum 27454
D. hypoleucum 3230
D. hypoleucum 19066
D. hypoleucum 3275
D. hypoleucum 28294
D. hypoleucum 142
D. hypoleucum 14048
D. hypoleucum 3314
D. hypoleucum 27468
1.0/1.0/100
1.0/0.98/83
1.0/100
0.79/-
1.0/58
0.92/-
1.0/1.0/91
0.6–1.3 Mya
0.07–0.87 Mya
0.97/0.99/-
0.4–1.0 Mya
0.03–0.13 Mya
1.0/60
1.0/-
1.0/-
0.02
mindanense,
Zamboanga
obscurum/
cagayanensis,
Luzon
pontifex,
Mindanao
Dinagat
Samar
Leyte
Bohol
Dicaeum hypoleucum
Suitable
Unsuitable - Bohol Sea Land Bridge
Unsuitable - Background
Annual Precipitation (mm)
2000
4000
6000
8000
15.0
20.0
25.0
Annual Mean Temperature (C°)

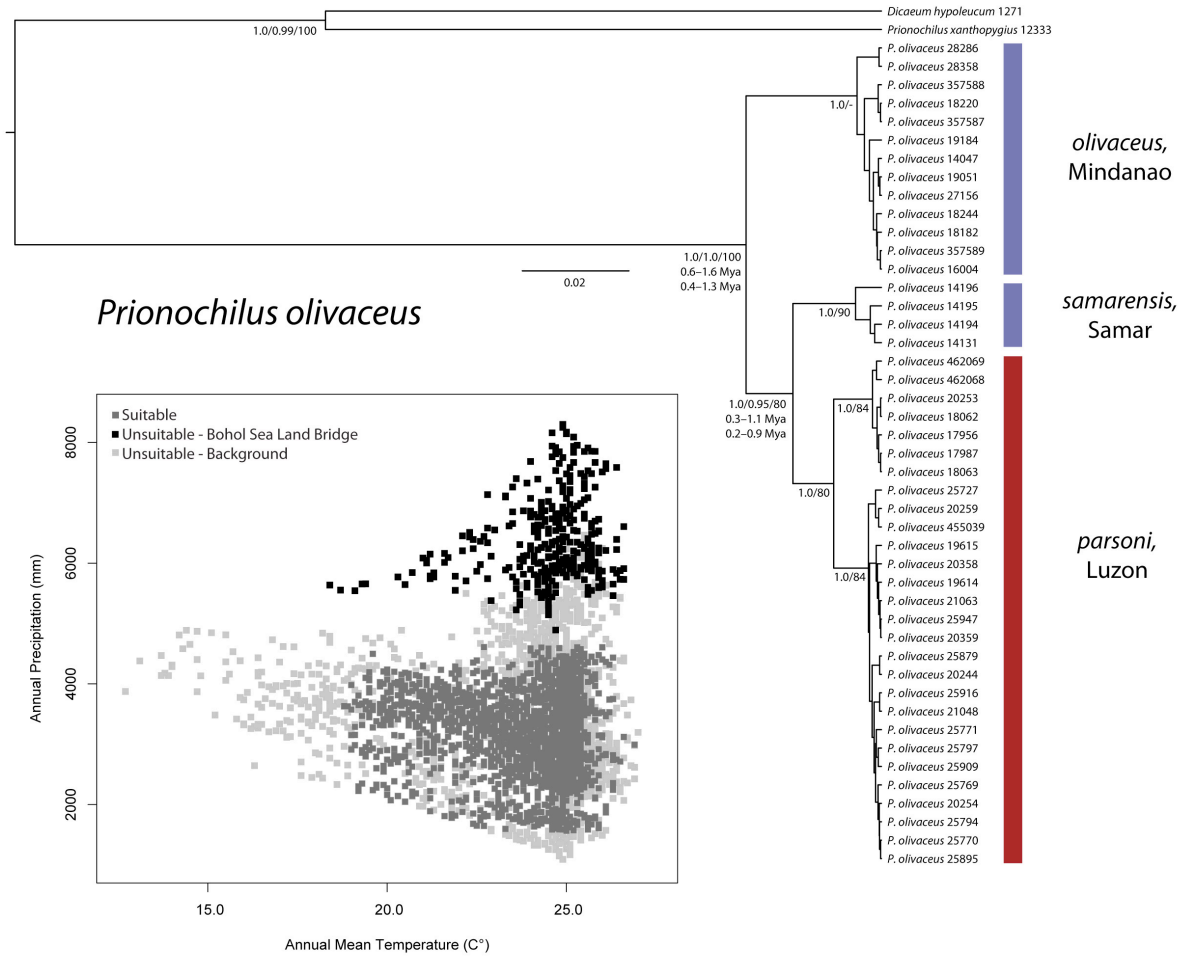

Present
LGM
LIG


Harpactes kasumba 12388
Harpactes whiteheadi 52627
1.0/0.54/100
H. ardens 28279
H. ardens 28435
H. ardens 28337
1.0/99
H. ardens 28352
H. ardens 19031
H. ardens 19035
H. ardens 19040
H. ardens 19065
0.84/-
H. ardens 28507
H. ardens 1955
1.0/55
H. ardens 18219
H. ardens 18227
H. ardens 18246
H. ardens 1417
H. ardens 2235
H. ardens 2234
H. ardens 2239
H. ardens 2037
1.0/1.0/100
0.2–0.6 Mya
0.09–0.42 Mya
H. ardens 28237
H. ardens 28216
H. ardens 28228
1.0/67
H. ardens 28260
H. ardens 14176
H. ardens 14220
H. ardens 20927
H. ardens 20922
0.98/0.64/64
0.2–0.4 Mya
0.06–0.3 Mya
H. ardens 25560
1.0/87
H. ardens 26958
H. ardens 26929
H. ardens 26995
H. ardens 15002
H. ardens 20257
H. ardens 20256
1.0/100
H. ardens 20318
H. ardens 20178
H. ardens 19646
H. ardens 429208
0.94/54
H. ardens 25864
H. ardens 25989
H. ardens 25599
H. ardens 25973
H. ardens 25927
H. ardens 25938
H. ardens 25667
ardens, E Mindanao
ardens, Zamboanga SW Mindanao C Mindanao
linae, Samar Bohol
minor/luzoniensis, S Luzon Polillio
luzoniensis/herberti, N Luzon
Harpactes ardens
0.02
Suitable
Unsuitable - Bohol Sea Land Bridge
Unsuitable - Background
Annual Precipitation (mm)
8000
6000
4000
2000
15.0
20.0
25.0
Annual Mean Temperature (C°)
Present
LGM
LIG


Irena puella 12369
I. cyanogastra 18212
I. cyanogastra 2133
I. cyanogastra 1963
I. cyanogastra 14294
I. cyanogastra 14081
I. cyanogastra 14293
I. cyanogastra 14309
I. cyanogastra 19621
I. cyanogastra 21765
I. cyanogastra 18094
I. cyanogastra 27015
I. cyanogastra 27017
I. cyanogastra 17964
I. cyanogastra 17998
I. cyanogastra 350955
I. cyanogastra 462007
I. cyanogastra 17963
I. cyanogastra 17989
I. cyanogastra 17982
I. cyanogastra 25554
I. cyanogastra 18003
I. cyanogastra 25834
I. cyanogastra 25830
I. cyanogastra 25891
I. cyanogastra 25789
I. cyanogastra 25841
I. cyanogastra 25840
I. cyanogastra 20258
I. cyanogastra 19629
I. cyanogastra 20271
I. cyanogastra 19626
I. cyanogastra 25561
I. cyanogastra 25780
1.0/1.0/100
1.0/100
1.0/100
1.0/1.0/100
0.8–1.8 Mya
0.1–1.4 Mya
0.02
0.64/-/79
0.6–1.5 Mya
1.0/100
hoogstraali,
Mindanao
ellae,
Leyte
Dinagat
cyanogastra,
Luzon
Polillo
Catanduanes
Irena cyanogastra
Suitable
Unsuitable - Bohol Sea Land Bridge
Unsuitable - Background
Annual Precipitation (mm)
8000
6000
4000
2000
15.0
20.0
25.0
Annual Mean Temperature (C°)


Present
LGM
LIG


Pachycephala philippinensis
Pachycephala pectoralis 6175
Pachycephala albiventris 25745
basilanica, Zamboanga
apoensis, C Mindanao
apoensis, C Mindanao
apoensis, C, E Mindanao Dinagat
apoensis, Samar Leyte
boholensis, Bohol
siquijorensis, Siquijor
fallax, Calayan
illex, Camiguin Norte
philippinensis, Luzon Alabat Catanduanes
0.98/-/-
0.02
1.0/0.98/84
0.4–1.2 Mya
0.6–2.2 Mya
0.86/0.69/63
0.2–0.8 Mya
0.09–1.2 Mya
0.85/0.82/85
0.2–0.96 Mya
0.6–1.6 Mya
1.0/0.86/78
0.3–0.9 Mya
0.6–1.6 Mya
1.0/0.89/92
0.3–0.7 Mya
0.2–0.8 Mya
0.97/0.64/-
0.2–0.5 Mya
0.06–0.6 Mya
0.72/66
Suitable
Unsuitable - Bohol Sea Land Bridge
Unsuitable - Background
Annual Precipitation (mm)
Annual Mean Temperature (C°)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Prionochilus xanthopygius 12333
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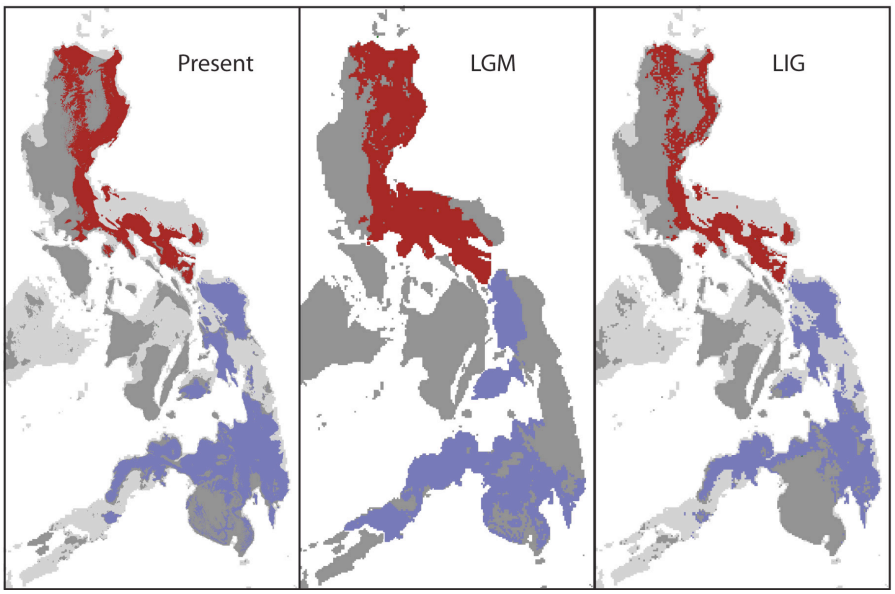
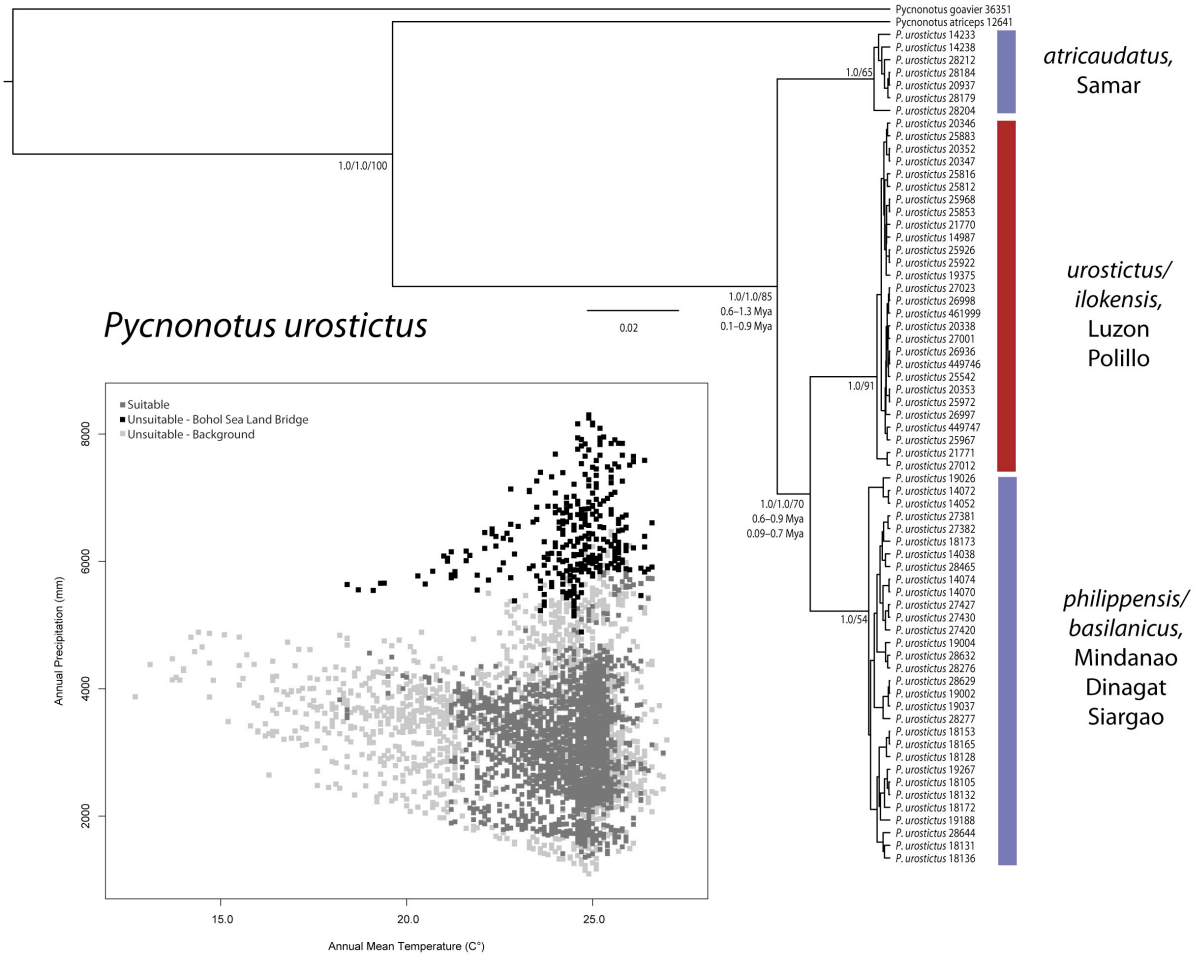
P. olivaceus 28286
P. olivaceus 28358
P. olivaceus 357588
1.0/-
P. olivaceus 18220
P. olivaceus 357587
P. olivaceus 19184
P. olivaceus 14047
P. olivaceus 19051
P. olivaceus 27156
P. olivaceus 18244
P. olivaceus 18182
P. olivaceus 357589
P. olivaceus 16004
olivaceus, Mindanao
1.0/1.0/100
0.6–1.6 Mya
0.4–1.3 Mya
0.02
Prionochilus olivaceus
P. olivaceus 14196
1.0/90
P. olivaceus 14195
P. olivaceus 14194
P. olivaceus 14131
samarensis, Samar
P. olivaceus 462069
P. olivaceus 462068
1.0/0.95/80
0.3–1.1 Mya
0.2–0.9 Mya
1.0/84
P. olivaceus 20253
P. olivaceus 18062
P. olivaceus 17956
P. olivaceus 17987
P. olivaceus 18063
1.0/80
P. olivaceus 25727
P. olivaceus 20259
P. olivaceus 455039
P. olivaceus 19615
1.0/84
P. olivaceus 20358
P. olivaceus 19614
P. olivaceus 21063
P. olivaceus 25947
P. olivaceus 20359
P. olivaceus 25879
P. olivaceus 20244
P. olivaceus 25916
P. olivaceus 21048
P. olivaceus 25771
P. olivaceus 25797
P. olivaceus 25909
P. olivaceus 25769
P. olivaceus 20254
P. olivaceus 25794
P. olivaceus 25770
P. olivaceus 25895
parsoni, Luzon
Suitable
Unsuitable - Bohol Sea Land Bridge
Unsuitable - Background
Annual Precipitation (mm)
8000
6000
4000
2000
15.0
20.0
25.0
Annual Mean Temperature (C°)


Present
LGM
LIG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Pycnonotus atriceps 12641
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P. urostictus 14238
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P. urostictus 28184
P. urostictus 20937
P. urostictus 28179
P. urostictus 28204
P. urostictus 20346
P. urostictus 25883
P. urostictus 20352
P. urostictus 20347
P. urostictus 25816
P. urostictus 25812
P. urostictus 25968
P. urostictus 25853
P. urostictus 21770
P. urostictus 14987
P. urostictus 25926
P. urostictus 25922
P. urostictus 19375
P. urostictus 27023
P. urostictus 26998
P. urostictus 461999
P. urostictus 20338
P. urostictus 27001
P. urostictus 26936
P. urostictus 449746
P. urostictus 25542
P. urostictus 20353
P. urostictus 25972
P. urostictus 26997
P. urostictus 449747
P. urostictus 25967
P. urostictus 21771
P. urostictus 27012
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P. urostictus 14072
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P. urostictus 27381
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P. urostictus 18173
P. urostictus 14038
P. urostictus 28465
P. urostictus 14074
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P. urostictus 27427
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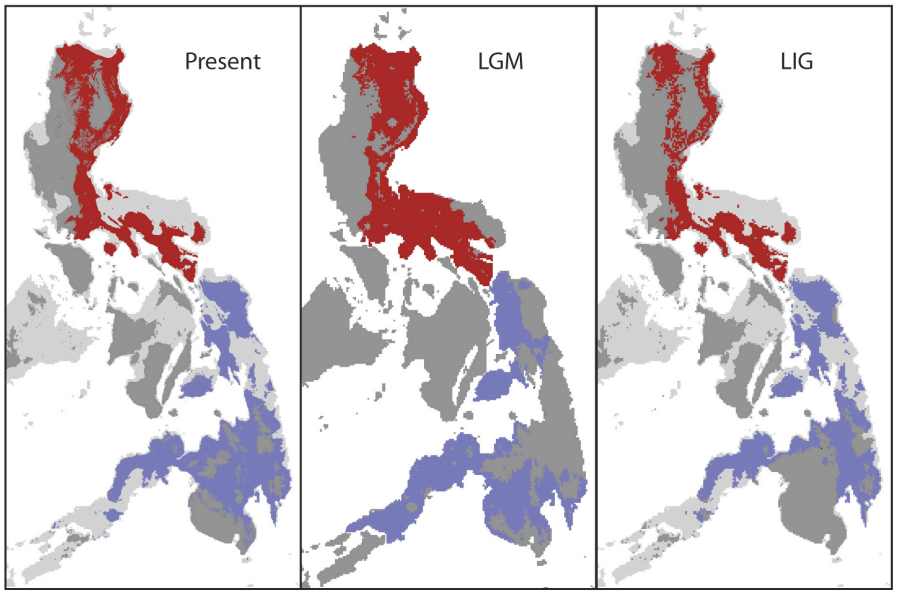
P. urostictus 19037
P. urostictus 28277
P. urostictus 18153
P. urostictus 18165
P. urostictus 18128
P. urostictus 19267
P. urostictus 18105
P. urostictus 18132
P. urostictus 18172
P. urostictus 19188
P. urostictus 28644
P. urostictus 18131
P. urostictus 18136
1.0/1.0/100
1.0/65
1.0/1.0/85
0.6–1.3 Mya
0.1–0.9 Mya
1.0/91
1.0/1.0/70
0.6–0.9 Mya
0.09–0.7 Mya
1.0/54
0.02
Pycnonotus urostictus
atricaudatus,
Samar
urostictus/
ilokensis,
Luzon
Polillo
philippensis/
basilanicus,
Mindanao
Dinagat
Siargao
Suitable
Unsuitable - Bohol Sea Land Bridge
Unsuitable - Background
Annual Precipitation (mm)
8000
6000
4000
2000
15.0
20.0
25.0
Annual Mean Temperature (C°)


Present
LGM
LIG