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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Introduction

The Philippines is a megadiverse country 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)

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.
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 unvouchedered 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 dehydrogenase-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

<table>
<thead>
<tr>
<th>Region</th>
<th>Primer name</th>
<th>Primer sequence</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>ND2</td>
<td>L-5215</td>
<td>5’-TATCGGGGCCCATAACCCCGAAAAT-3’</td>
<td>Hackett (1996)</td>
</tr>
<tr>
<td>(1st)</td>
<td>H-5578</td>
<td>5’-CCTTGAGCAGCTCTGGGAATCAGA-3’</td>
<td>Hackett (1996)</td>
</tr>
<tr>
<td>ND2</td>
<td>L-347</td>
<td>5’-CCATTCCACTTCTGTCC-3’</td>
<td>Drovetski et al. (2004)</td>
</tr>
<tr>
<td>(2nd)</td>
<td>H-6313</td>
<td>5’-CTCTTATTTAAGGCTTTGAGGC-3’</td>
<td>Sorensen et al. (1999)</td>
</tr>
<tr>
<td>ND3</td>
<td>L-10755</td>
<td>5’-ACTTCAATCTTTAAAATCTGG-3’</td>
<td>Chesser (1999)</td>
</tr>
<tr>
<td></td>
<td>H-11151</td>
<td>5’-GATTGTGGAGCCGAAATCAAC-3’</td>
<td>Chesser (1999)</td>
</tr>
<tr>
<td>Fib-5</td>
<td>Fib5</td>
<td>5’-CAGCCAATAAGTATACTGTGACAT-3’</td>
<td>Kimball et al. (2009)</td>
</tr>
<tr>
<td></td>
<td>Fib6</td>
<td>5’-GCCATCCTGGCGATGCTTGA-3’</td>
<td>Kimball et al. (2009)</td>
</tr>
<tr>
<td>MUSK</td>
<td>MUSK-I3F</td>
<td>5’-CTTCCATGCATACTAATGGGAAA-3’</td>
<td>Kimball et al. (2009)</td>
</tr>
<tr>
<td></td>
<td>MUSK-I3R</td>
<td>5’-CTCTGAAACTTTGATATCTCAA-3’</td>
<td>Kimball et al. (2009)</td>
</tr>
<tr>
<td>TGFβ2-5</td>
<td>TGFβ2.5F</td>
<td>5’-GAAAGCGGTCTCTAGATGCTG-3’</td>
<td>Kimball et al. (2009)</td>
</tr>
<tr>
<td></td>
<td>TGFβ2.6</td>
<td>5’-AGGCCAGCATTATCTCGCAC-3’</td>
<td>Kimball et al. (2009)</td>
</tr>
</tbody>
</table>

Table 1-1 Primers used for PCR and sequencing reactions.
regions (Hackett 1996; Chesser 1999; Sorenson et al. 1999; Drovettski 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 SEQUENCER 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 uncertainty. 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
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
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.
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. boltini/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 colonizion of the Philippines (A. siparaja magnifica, A. bella, and the A. boltonii/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 km², 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 km²) and New Guinea (785,000 km²: 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 km² 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 km²), the Solomon Islands (28,000 km²), Hawaii (28,000 km²) and Fiji (18,000 km²). 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.
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

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, TGFb2-5, 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.
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, auriculares 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;
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, Dinalungan 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
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.

<table>
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<tr>
<th></th>
<th>bill length</th>
<th>bill depth</th>
<th>bill width</th>
<th>wing chord</th>
<th>tail</th>
<th>tarsus</th>
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<tr>
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<td>13.5 (2)</td>
<td>5.3 (1)</td>
<td>4.5 (2)</td>
<td>78.6 (2)</td>
<td>75.8 (2)</td>
<td>29.9 (2)</td>
</tr>
<tr>
<td>R. sorsogonensis</td>
<td>12.7–14.3</td>
<td>5.3</td>
<td>4.1–4.8</td>
<td>76.6–80.5</td>
<td>70.7–80.8</td>
<td>29.8–30.0</td>
</tr>
<tr>
<td>R. thompsoni</td>
<td>13.7 (21)</td>
<td>5.5 (17)</td>
<td>5.0 (19)</td>
<td>85.3 (21)</td>
<td>74.6 (17)</td>
<td>30.2 (21)</td>
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<td></td>
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<td>4.1–6.2</td>
<td>71.5–96.0</td>
<td>67.0–87.7</td>
<td>28.0–31.8</td>
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<tr>
<td></td>
<td>12.9 (9)</td>
<td>5.1 (8)</td>
<td>5.0 (10)</td>
<td>79.8 (10)</td>
<td>73.3 (9)</td>
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<td>64.3–81.7</td>
<td>27.4–32.3</td>
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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.


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 TGFb2-5, 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. 2011).
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 (Trogodytidae) 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 km²), 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


Phylogeographic structure and paleo-environmental niche modeling support climate-driven diversification in Philippine birds. *Evolution*. 
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. 2011).
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
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,
ocurrence 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
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 dehydrogenase-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
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.

<table>
<thead>
<tr>
<th>Region</th>
<th>Location (Gallus)</th>
<th>Primer</th>
<th>Primer sequence</th>
<th>Reference</th>
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<tbody>
<tr>
<td>ND2 (1st fragment)</td>
<td>MtDNA</td>
<td>L-5215</td>
<td>5'-TATCGGGGCCCTACCCGAAAT-3'</td>
<td>(Hackett 1996)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>H-5578</td>
<td>5'-CTTTGAAAGCAGTTCTGGAAATCAGA-3'</td>
<td>(Hackett 1996)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>L-347</td>
<td>5'-CCATTCCACCTGTTCCTGC-3'</td>
<td>(Drovetski et al. 2004)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>H-6313</td>
<td>5'-CTCTTATTTAAGGCTTTGAAGGC-3'</td>
<td>(Sorenson et al. 1999)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>CDC132F</td>
<td>5'-TCTGGGAAACAGATCTGTC-3'</td>
<td>(Backström et al. 2008)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>CDC132R</td>
<td>5'-AAACTCAGACTTTACTGCC-3'</td>
<td>(Backström et al. 2008)</td>
</tr>
<tr>
<td>CDC132</td>
<td>Chr 2</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>HMG2</td>
<td>Chr 23</td>
<td>HMG2F</td>
<td>5'-GAAATGTGGTCTGAACAGTC-3'</td>
<td>(Kimball et al. 2009)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>HMG2R</td>
<td>5'-TTGCTCTTTGGCAAGATGC-3'</td>
<td>(Kimball et al. 2009)</td>
</tr>
<tr>
<td>PEPCK (initial)</td>
<td>Chr 20</td>
<td>GTP1601F</td>
<td>5'-ACGAGGCTTATACTGGACGCA-3'</td>
<td>(Sorenson 2003)</td>
</tr>
<tr>
<td>PEPCK (second)</td>
<td></td>
<td>GTP1793R</td>
<td>5'-CTTGGCTGTCTTTCCGGACCC-3'</td>
<td>(Sorenson 2003)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>PEPCK9F</td>
<td>5'-GGAGCAGCCATGATCTGGAAGC-3'</td>
<td>(Sorenson 2003)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>PEPCK9R</td>
<td>5'-GTGCCATGCTAAGCCGATGG-3'</td>
<td>(Sorenson 2003)</td>
</tr>
</tbody>
</table>

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 SEQUENCER 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 assess 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-
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.
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.

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

_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
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 pulcherima 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, \textit{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 (\textit{A. pulcherrima decorosa} versus \textit{A. p. pulcherrima} and \textit{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).

\textbf{Discussion}

\textit{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 taken 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
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...
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.

<table>
<thead>
<tr>
<th>Species</th>
<th>LGM Suitability break</th>
<th>Average p-dist (%)</th>
<th>Pairwise $F_{st}$</th>
<th>$F_{st}$ P-value</th>
<th>Exact test P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>ND2</td>
<td>Nuclear loci</td>
<td>ND2</td>
<td>Nuclear loci</td>
</tr>
<tr>
<td><em>A. pulcherrima</em></td>
<td>No</td>
<td>0.62</td>
<td>0.000</td>
<td>0.12</td>
<td>0.02</td>
</tr>
<tr>
<td><em>C. melanurus</em></td>
<td>Yes</td>
<td>2.37</td>
<td>0.122</td>
<td>0.89</td>
<td>0.10</td>
</tr>
<tr>
<td><em>D. hypoleucum</em></td>
<td>No</td>
<td>0.03</td>
<td>0.008</td>
<td>0.02</td>
<td>0.00</td>
</tr>
<tr>
<td><em>H. ardens</em></td>
<td>Yes</td>
<td>1.10</td>
<td>0.000</td>
<td>0.65</td>
<td>0.01</td>
</tr>
<tr>
<td><em>I. cyanogastra</em></td>
<td>Yes</td>
<td>5.04</td>
<td>0.062</td>
<td>0.95</td>
<td>0.12</td>
</tr>
<tr>
<td><em>P. philippinensis</em></td>
<td>No</td>
<td>1.95</td>
<td>0.003</td>
<td>0.49</td>
<td>0.05</td>
</tr>
<tr>
<td><em>P. olivaceus</em></td>
<td>Yes</td>
<td>3.53</td>
<td>0.002</td>
<td>0.92</td>
<td>0.22</td>
</tr>
<tr>
<td><em>P. urostictus</em></td>
<td>Yes</td>
<td>4.24</td>
<td>0.164</td>
<td>0.90</td>
<td>0.17</td>
</tr>
</tbody>
</table>

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.

*Aetopyga 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 mindanense* 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


Widespread unrecognized and cryptic avian diversity and endemism in the Philippine Archipelago.
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 (Cytb) 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 (Jönnson et al. 2008; Jones and

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; Cytb, 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, Sterrhopilus, 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, Sterrhopilus, Ficedula, Cyornis*, and *Prionochilus*) were recovered as endemic to Samar/Leyte, whereas four mitochondrial lineages were endemic to Bohol (*Ptilocichla, Sterrhopilus, Cyornis*, and *Aethopyga*). Of these,
<table>
<thead>
<tr>
<th>Species/group</th>
<th>Phenotypic group 1</th>
<th>Phenotypic group 2</th>
<th>Phenotypic group 3</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Otus megalotis</em></td>
<td><em>O. m. everetti</em> Mindanao, Basilan, Dinagat, Biliran, Samar, Leyte, Bohol</td>
<td><em>O. m. megalotis</em> Luzon, Catanduanes, Marinduque</td>
<td><em>O. m. nigrorum</em> Negros, Panay</td>
</tr>
<tr>
<td></td>
<td>Brownish, small size</td>
<td>Brownish, large size</td>
<td>Face reddish, underparts grayish, small size</td>
</tr>
<tr>
<td><em>Ceyx melanurus</em></td>
<td><em>C. m. mindanensis</em>: Mindanao, Basilan, Dinagat, Siargao</td>
<td><em>C. m. samarensis</em>: Samar, Leyte</td>
<td><em>C. m. melanurus</em>: Luzon PAIC</td>
</tr>
<tr>
<td></td>
<td>Auricular white; wing coverts black with tawny edging; outer rectrices tawny; large size</td>
<td>Auricular blue/white; wing coverts black with blue spots; outer rectrices black; large size</td>
<td>Auricular blue/white; wing coverts black with blue spots; outer rectrices black; large size</td>
</tr>
<tr>
<td><em>Ceyx (Alcedo) argenatum</em></td>
<td><em>C. a. argentatus</em>: Mindanao, Basilan, Dinagat, Siargao</td>
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<tr>
<td></td>
<td>Throat, underwing coverts white; underparts metallic teal</td>
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<tr>
<td><em>Sarcophanops (Eurylaimus) steerii</em></td>
<td><em>S. steerii steerii/S. s. mayri</em>: Mindanao, Basilan, Dinagat, Siargao</td>
<td><em>S. s. samarensis</em>: Samar, Leyte, Bohol</td>
<td></td>
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<tr>
<td></td>
<td>Back gray; wingstripe yellow/white; nape band plain white</td>
<td>Back maroon; wingstripe maroon/white; nape band scaly</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Underparts bright yellow; upperparts green</td>
<td>Belly whitish/undertail coverts dull yellow; upperparts olive</td>
<td>Underparts dull yellow; upperparts olive</td>
</tr>
<tr>
<td><em>Orthotomus cinereiceps</em></td>
<td><em>O. cinereiceps cinereiceps/O. c. obscurior</em>: Zamboanga/W Mindanao, Basilan</td>
<td><em>O. nigriceps</em>: E Mindanao</td>
<td><em>O. samarensis</em>: Samar, Leyte, Bohol</td>
</tr>
<tr>
<td>group</td>
<td>Male: Gray crown; white auricular; belly whitish. Female: Similar, but with white throat and streaking on chest</td>
<td>Male: Black crown; white eyeine; belly dark gray. Female: Similar, but with white throat and streaking on chest</td>
<td>Male: Black crown; white chin; belly yellow. Female: Similar, but with white throat and streaking on chest</td>
</tr>
<tr>
<td><em>Rhipidura superciliaris</em></td>
<td><em>R. s. superciliaris</em>: Mindanao, Basilan</td>
<td><em>R. s. samarensis</em>: Samar, Leyte, Bohol</td>
<td></td>
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<tr>
<td></td>
<td>Male: belly bright blue</td>
<td>Male: belly bluish-gray</td>
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<tr>
<td><em>Macronus striaticeps</em></td>
<td><em>M. s. striaticeps/M. s. mindanensis</em>: Mindanao, Basilan, Samar, Leyte, Bohol</td>
<td><em>M. s. alcasidi</em>: Dinagat, Siargao</td>
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<tr>
<td></td>
<td>Upperparts dark; underparts dark; chest heavily streaked</td>
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<tr>
<td>Species/group</td>
<td>Phenotypic group 1</td>
<td>Phenotypic group 2</td>
<td>Phenotypic group 3</td>
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<tr>
<td><em>Ptilocichla</em></td>
<td><em>P. m. mindanensis</em>/P. m. *</td>
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<tr>
<td><em>mindanensis</em></td>
<td>basilanica: Mindanao</td>
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<tr>
<td></td>
<td>Upperparts plain; large size</td>
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<td><em>Sternhootilus</em></td>
<td><em>S. capitalis:</em> Mindanao, Basilan, Dinagat</td>
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<tr>
<td><em>(Stachyris)</em></td>
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<tr>
<td><em>capitalis</em></td>
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<td></td>
<td>Crown rufus, throat rufous;</td>
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<tr>
<td></td>
<td>belly whitish</td>
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<tr>
<td><em>Sternhootilus</em></td>
<td><em>S. n. nigrocapitatus:</em> Samar, Leyte</td>
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<tr>
<td><em>(Stachyris)</em></td>
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<td><em>nigrocapitatus</em></td>
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<td></td>
<td>Crown black; throat yellow with faint rufous edging to</td>
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<tr>
<td></td>
<td>feathers; belly whitish</td>
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<tr>
<td><em>Sternhootilus</em></td>
<td><em>S. dennistouni:</em> N Luzon</td>
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<tr>
<td><em>(Stachyris)</em></td>
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<tr>
<td><em>dennistouni</em></td>
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<tr>
<td></td>
<td>Crown yellow; throat yellow, belly yellowish</td>
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<tr>
<td><em>Irena</em></td>
<td><em>I. c. melanochlamys</em>/I. c. *</td>
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<tr>
<td><em>cyanogastra</em></td>
<td><em>hoogstraali:</em> Mindanao, Basilan</td>
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<td></td>
<td>Upperparts black; underparts dark blue</td>
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<tr>
<td><em>Ficedula</em></td>
<td><em>F. b. basilanica:</em> Mindanao, Basilan</td>
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<td><em>basilanica</em></td>
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<td></td>
<td>Male: tail gray with base of outer tailed feathers white</td>
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<td><em>Aethopyga</em></td>
<td><em>A. pulcherrima:</em> Mindanao, Dinagat, Samar, Leyte</td>
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<td><em>pulcherrima</em></td>
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<td></td>
<td>Wing coverts iridescent green; no iridescence on</td>
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<td></td>
<td>tertials; tail iridescent blue-green; frontlet small;</td>
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<td></td>
<td>orange breast spot; bill small</td>
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<td><em>Prionochilus</em></td>
<td><em>P. o. olivaceus</em>/P. o. *</td>
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<td><em>olivaceus</em></td>
<td><em>samarensis:</em> Mindanao, Dinagat, Samar, Leyte, Bohol</td>
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<tr>
<td></td>
<td>Male: Malar dark gray</td>
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<tr>
<td><em>Dicaeum</em></td>
<td><em>D. h. hypoleucum</em>/D. h. *</td>
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<tr>
<td><em>hypoleucum</em></td>
<td><em>mindanense:</em> Zamboanga, Basilan</td>
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</table>
*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*, *Ceyx melanurus*,...
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. dennisstouni*), 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.
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.
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## Appendix 1. All avian tissue samples used in DNA sequencing

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<td>Zamboanga del Sur</td>
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<td>Mindanao</td>
<td>Zamboanga del Sur</td>
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<td>Mindanao</td>
<td>Agusan del Sur</td>
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<td>Harpactes ardens</td>
<td>Philippines</td>
<td>Mindanao</td>
<td>Agusan del Sur</td>
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KU 19040  Harpactes ardens  Philippines  Mindanao  Agusan del Sur  Mt. Magdiwata
KU 19065  Harpactes ardens  Philippines  Mindanao  Agusan 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
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KU 28282  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 359955  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  Camarines Norte  Mt. Labo
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KU 18003  Irena cyanogastra  Philippines  Luzon  Camarines Norte  Mt. Labo
KU 18094  Irena cyanogastra  Philippines  Luzon  Camarines 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
Macronous striaticeps Philippines Dinagat Dinagat Loreto
Macronous striaticeps Philippines Dinagat Dinagat Loreto
Macronous striaticeps Philippines Dinagat Dinagat Loreto
Macronous striaticeps Philippines Samar Eastern Samar Taft
Macronous striaticeps Philippines Samar Eastern Samar Taft
Macronous striaticeps Philippines Samar Eastern Samar Taft
Macronous striaticeps Philippines Samar Eastern Samar Taft
Macronous striaticeps Philippines Leyte Leyte Baybay
Macronous striaticeps Philippines Leyte Leyte Baybay
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Macronous striaticeps Philippines Mindanao Zamboanga del Sur Pasonanca
Macronous striaticeps Philippines Mindanao Agusan del Sur Mt. Magdiwata
Macronous striaticeps Philippines Mindanao Agusan del Sur Mt. Magdiwata
Macronous striaticeps Philippines Mindanao Agusan del Sur Mt. Magdiwata
Macronous striaticeps Philippines Mindanao Misamis Oriental Mt. Balatukan
Macronous striaticeps Philippines Mindanao Misamis Oriental Mt. Balatukan
Macronous striaticeps Philippines Mindanao Misamis Oriental Mt. Balatukan
Macronous striaticeps Philippines Mindanao Zamboanga del Sur Pasonanca
Macronous striaticeps Philippines Mindanao Zamboanga del Sur Pasonanca
Macronous striaticeps Bohol Bohol Bilar
Macronous striaticeps Siargao Surigao del Norte Pilar
Macronous striaticeps Siargao Surigao del Norte Pilar
Macronous striaticeps Siargao Surigao del Norte Pilar
Macronous striaticeps Leyte Southern Leyte Sogod
Macronous striaticeps Leyte Southern Leyte Sogod
Macronous striaticeps Bohol Bohol Bilar
Macronous striaticeps Bohol Bohol Bilar
Macronous striaticeps Mindanao Agusan del Norte Mt. Hilong-Hilong
Macronous striaticeps Mindanao Agusan del Norte Mt. Hilong-Hilong
Macronous striaticeps Mindanao Misamis Oriental Mt. Lumot
Macronous striaticeps Mindanao Zamboanga del Sur Pasonanca
Macronous striaticeps Mindanao Zamboanga del Sur Pasonanca
Macronous striaticeps Mindanao Zamboanga del Sur Pasonanca
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Macronous striaticeps Mindanao Zamboanga del Sur Pasonanca
Macronous striaticeps Dinagat Dinagat Loreto
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Macronous striaticeps Samar Eastern Samar Taft
Macronous striaticeps Samar Eastern Samar Taft
Macronous striaticeps Samar Eastern Samar Taft
Macronous striaticeps Samar Eastern Samar Taft
Macronous striaticeps Bohol Bohol Bilar
Macronous striaticeps Bohol Bohol Bilar
Macronous striaticeps Bohol Bohol Bilar
Macronous striaticeps Bohol Bohol Bilar
Macronous striaticeps Bohol Bohol Valencia
Macronous striaticeps Bohol Bohol Valencia
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Macronous striaticeps Luzon
Pachycephala albiventris Philippines Alabat Quezon Alabat
Pachycephala pectoralis Australia
CMC 153 Pachycephala philippinensis Philippines Luzon Zambales Masinloc
CMC 167 Pachycephala philippinensis Philippines Luzon Zambales Masinloc
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
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KU 10843 Pachycephala philippinensis Philippines Camiguin N. Cagayan Limandok
KU 10860 Pachycephala philippinensis Philippines Camiguin N. Cagayan Limandok
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KU 10880 Pachycephala philippinensis Philippines Camiguin N. Cagayan Limandok
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KU 10942 Pachycephala philippinensis Philippines Calayan Cagayan Macarra
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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
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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 Pasonanca: 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 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 | 25789 | 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 |
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| KU | 25833 | Pachycephala philippinensis | Philippines | Luzon | Cagayan | Mt. Cagua |
| KU | 25904 | Pachycephala philippinensis | Philippines | Luzon | Cagayan | Mt. Cagua |
| KU | 25936 | 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 | Sibuyan |
| KU | 27477 | Pachycephala philippinensis | Philippines | Leyte | Southern Leyte | Sibuyan |
| KU | 28187 | Pachycephala philippinensis | Philippines | Bohol | Bohol | Bilar |
| KU | 28222 | Pachycephala philippinensis | Philippines | Bohol | Bohol | Bilar |
| KU | 28312 | Pachycephala philippinensis | Philippines | Mindanao | Agusan del Norte | Mt. Hilo-Hilo |
| KU | 28368 | Pachycephala philippinensis | Philippines | Mindanao | Agusan del Norte | Mt. Hilo-Hilo |
| KU | 28369 | Pachycephala philippinensis | Philippines | Mindanao | Agusan del Norte | Mt. Hilo-Hilo |
| 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 olivaceous | Philippines | Samar | Eastern Samar | Taft |
| KU | 14169 | Phylloscopus olivaceous | Philippines | Samar | Eastern Samar | Taft |
| KU | 14170 | Phylloscopus olivaceous | Philippines | Samar | Eastern Samar | Taft |
| KU | 14229 | Phylloscopus olivaceous | Philippines | Samar | Eastern Samar | Taft |
| KU | 14269 | Phylloscopus olivaceous | Philippines | Samar | Eastern Samar | Taft |
| KU | 14290 | Phylloscopus olivaceous | Philippines | Leyte | Leyte | Baybay |
| KU | 14303 | Phylloscopus olivaceous | Philippines | Leyte | Leyte | Baybay |
| KU | 18234 | Phylloscopus olivaceous | Philippines | Mindanao | Zamboanga del Sur | Pasonanca |
| KU | 19012 | Phylloscopus olivaceous | Philippines | Samar | Agusan del Sur | Mt. Magdiwata |
| KU | 23732 | Phylloscopus olivaceous | Philippines | Leyte | Leyte | Silago |
| KU | 28226 | Phylloscopus olivaceous | Philippines | Bohol | Bohol | Valencia |
| KU | 28227 | Phylloscopus olivaceous | Philippines | Bohol | Bohol | Valencia |
| KU | 28290 | Phylloscopus olivaceous | Philippines | Mindanao | Agusan del Norte | Mt. Hilo-Hilo |
| KU | 28311 | Phylloscopus olivaceous | Philippines | Mindanao | Agusan del Norte | Mt. Hilo-Hilo |
| KU | 28365 | Phylloscopus olivaceous | Philippines | Mindanao | Agusan del Norte | Mt. Hilo-Hilo |
| KU | 29931 | Phylloscopus olivaceous | Philippines | Mindanao | Zamboanga del Sur | Pasonanca |
| KU | 29972 | Phylloscopus olivaceous | Philippines | Mindanao | Zamboanga del Sur | Pasonanca |
| FMNH | 357587 | Priornichus olivaceous | Philippines | Mindanao | Bukidnon | Mt. Kitanglad Range |
| FMNH | 357588 | Priornichus olivaceous | Philippines | Mindanao | Bukidnon | Mt. Kitanglad Range |
| FMNH | 357589 | Priornichus olivaceous | Philippines | Mindanao | Bukidnon | Mt. Kitanglad Range |
| FMNH | 455039 | Priornichus olivaceous | Philippines | Luzon | Nueva Vizcaya | Mt. Palali |
Ptilocichla mindanensis

Philippines

Mindanao

Zamboanga del Sur

Pasonanca: Baluno

Prionochilus olivaceus

Philippines

Luzon

Camiguin Norte

Mt. Labo

Philippines

Zamboanga del Sur

Pasonanca: Baluno

Philippines

Mindanao

Aguasan del Norte

Mt. Magdiwata

Philippines

Mindanao

Aguasan del Norte

Mt. Hilong-Hilong

Philippines

Mindanao

Davao del Norte

Mt. Pasian

Philippines

Mindanao

South Cotabato

Tampakan

Philippines

Mindanao

Agusan del Norte

Mt. Hilong-Hilong
KU 29952  *Prilochichla mindanaensis*  Philippines Mindanao Zamboanga del Sur Pasonanca
KU 12641  *Pycnonotus atriceps*  Philippines Palawan
LSUMZ 36531  *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
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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: Intake
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 Agusan del Sur Mt. Magdiwata
KU 19004  *Pycnonotus urostictus*  Philippines Mindanao Agusan del Sur Mt. Magdiwata
KU 19026  *Pycnonotus urostictus*  Philippines Mindanao Agusan del Sur Mt. Magdiwata
KU 19037  *Pycnonotus urostictus*  Philippines Mindanao Agusan 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
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KU 26997  *Pycnonotus urostictus*  Philippines Polillo Quezon Burdeos
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KU 27012  *Pycnonotus urostictus*  Philippines Polillo Quezon Burdeos
KU 27023  *Pycnonotus urostictus*  Philippines Polillo Quezon Burdeos
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KU 28212  *Pycnonotus urostictus*  Philippines Bohol Bohol Bilar
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KU 14202  *Rhipidura superciliaris*  Philippines  Samar  Eastern Samar  Taft
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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 Watershed
USNM 433008  *Robsonius sorsogonensis*  Philippines  Luzon  Camarines Sur  Mount Isarog
FMNH 449800  *Robsonius thompsoni*  Philippines  Luzon  Aurora  Mignan 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
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KU 29968  *Sterrhophtis capitalis*  Philippines  Mindanao  Zamboanga del Sur  Pasonanca
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KU 20186  *Sterrhophtis dennistouni*  Philippines  Luzon  Aurora  Aurora N.P.
KU 20225  *Sterrhophtis dennistouni*  Philippines  Luzon  Aurora  Aurora N.P.
KU 20335  *Sterrhophtis dennistouni*  Philippines  Luzon  Aurora  Baler
KU 21084  *Sterrhophtis dennistouni*  Philippines  Luzon  Nueva Vizcaya  Mt. Palali
KU 21086  *Sterrhophtis dennistouni*  Philippines  Luzon  Nueva Vizcaya  Mt. Palali
KU 25702  *Sterrhophtis dennistouni*  Philippines  Luzon  Ilocos Norte  Mt. Cabacan
KU 25713  *Sterrhophtis dennistouni*  Philippines  Luzon  Ilocos Norte  Mt. Cabacan
KU 25817  *Sterrhophtis dennistouni*  Philippines  Luzon  Gonzaga  Mt. Cabacan
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Appendix 2: Detailed phylogenies, ENMs, and bivariate plots for 8 co-distributed Philippine bird species

Aethopyga pulcherrima

Present | LGM | LIG
Ceyx melanurus

- Suitable
- Unsuitable - Bohol Sea Land Bridge
- Unsuitable - Background

Annual Precipitation (mm)

Annual Mean Temperature (°C)

Present  |  LGM  |  LIG