

Genetic differentiation in two widespread, open-forest bird species of Southeast Asia (*Copsychus saularis* and *Megalaima haemacephala*): Insights from ecological niche modeling

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Abstract Ecological niche modeling has emerged as an useful tool in the investigation of the phylogeographic histories of species or communities in a region. The high biodiversity (oftentimes cryptic), and complex geography and geological history of Southeast Asia particularly call for multipronged approaches in phylogeographic investigations. Past studies have focused on taxa that are associated with lowland rainforests, which is the dominant natural vegetation type. Here, we combine published phylogenetic data, ecological niche modeling and paleo-climate models to reveal potential drivers of divergence in two open-forest bird species, the oriental magpie-robin *Copsychus saularis* and Coppersmith barbet *Megalaima haemacephala*. In spite of broad overlap in current distributions, there are subtle differences in their climatic niches, which result in different responses to past climatic changes. For *C. saularis*, both Last Glacial Maximum climate models indicated that the entire Sundaland was climatically suitable, while phylogenetic analyses found divergent eastern and western Sundaland lineages. We thus postulate that this genetic divergence was a result of past separations of coastal habitats into eastern and western portions due to the emergence of Sunda shelf as sea-level fell. The current separation of morphological subspecies in Borneo is maintained by low climatic suitability (high annual rainfall) in certain regions. The extirpation of *M. haemacephala* from Borneo and southern Malay Peninsula might have been driven by unsuitable conditions (high temperature seasonality) in central Sundaland and/or the lack of open woodlands. Our study shows that ecological niche modeling adds a powerful dimension to our attempt to understand lineage evolution in space [*Current Zoology* 61 (5): 922–934, 2015].

Keywords Barbet, Indo-Burma, Malay Archipelago, Magpie-robin, Phylogeography, Species distribution modeling

Understanding modern distributions of taxa requires not only a consideration of current habitat occurrence but also how habitats have shifted through time (Wiens and Donoghue, 2004). In Asia, like elsewhere in the world, changes in habitat types and their distributions occurred numerous times, having been driven by global climatic changes induced by Earth's orbital cycles, solar-energy fluctuations and other large scale factors (Dynerius and Jansson, 2000). During the Pleistocene (2.5 million years ago [mya] to 11.7 thousand years ago [kya]), the oscillating glacial cycles had a particularly strong influence on paleo-habitat distributions and organismal movements, such as causing montane forests to descend, wet forests to dry out, and islands to be connected to one another and the mainland (Flenley, 1998; Voris, 2000). Because of the strong influences past climatic changes likely have on the present distribution of biological and genetic diversity, numerous studies focu-

sing on Asian taxa have begun to include paleo-projections of ecological niche models as a part of the investigative toolbox (Cannon et al., 2009; Liu et al., 2012; Sheldon et al., 2015). Among the difficulties in assessing the effects of climate change on distributions are that past climate itself is a very complex phenomenon to model (Kohfeld and Harrison, 2000), the inherently idiosyncratic responses different species have to climatic changes, and unaccounted changes to biological interactions (Bullock et al., 2000). These problems are exacerbated in the case of Pleistocene glacial-interglacial climate fluctuations, because there have been at least 7–8 glacial events in the last million years (Lambeck et al., 2002). Even so, organisms can be expected to have required the same conditions in the modern era as in the relatively recent past (Peterson et al., 1999), and thus might have responded to past climatic changes in a concerted manner (Carstens and Richards, 2007). Here, we

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focus our phylogeographic and ecological niche modeling study on two largely co-distributed bird species that are found across Asia mainland and Southeast Asia. We seek to understand, in view of their broadly similar current distributions, whether they possessed similar paleodistributions, and how this influenced their patterns of population divergence.

The two species under comparison—oriental magpie-robin (*Copsychus saularis*, Muscicapidae) and Coppersmith barbet (*Megalaima haemacephala*, Megalaimidae)—have distributions that overlap substantially in south and Southeast Asia, from India to China and south into Sundaland. One of the key differences in their distributions is in Borneo, where *C. saularis* is present but *M. haemacephala* is not. On the other hand, in the Philippines, the reverse is true. In the Philippines, taxa that were considered subspecies of *C. saularis* (ssp. *deuteronymus* and *mindanensis*) have recently been elevated to *C. mindanensis* because of their large divergences from *C. saularis* sensu stricto (Sheldon et al., 2009). *Copsychus saularis* consists of 13 subspecies, several of which are restricted to small islands or groups of small islands (Gill and Donsker, 2014). The species is part of the clade that includes Madagascan magpie-robin *C. albospecularis*, Seychelles magpie-robin *C. sechellarum*, and the above-mentioned Philippine magpie-robin *C. mindanensis*. All species show affinity to coastal environments and the clade as a whole appears to diversify via long-distance over-water dispersals (Lim et al., 2010b). *Megalaima haemacephala* belongs to a clade of Asian Barbets (~30 spp.) that are dependent on terrestrial forests or woodlands (Hone and Short, 2002; den Tex and Leonard, 2013). Nine subspecies are recognized in *M. haemacephala*, and, unlike *C. saularis*, no populations occur on small isolated islands (den Tex and Leonard, 2014).

Paleo-distributions of these two taxa were computed via ecological niche modeling methods using climate data for the Last Glacial Maximum (LGM, ~ 21 kya) and the Last Interglacial (LIG, ~ 125 kya). Their distributional similarities and differences were then used to shed light on their phylogenies, which have recently been reconstructed using DNA sequence data (Sheldon et al., 2009; den Tex and Leonard, 2014). These comparisons allowed us to assess common and disparate evolutionary influences on the biogeography of the two taxa. Because past ecological niche modeling studies have focused on rainforest species, our study, by focusing on open-habitat species, aims to shed new light on how climatic conditions (past and present) influence and

maintain population divergence of SE Asian taxa.

1 Materials and Methods

1.1 Phylogenetic analysis

To assemble genetic data, we downloaded sequence data from GenBank. For *Copsychus saularis*, we obtained 33 *ND2* and 32 *CO1* sequences, plus two each of *C. albospecularis* as the outgroup (Table 1). For *Megalaima haemacephala* comparisons, we obtained 21 *Cyt b* sequences, 20 *ND2* sequences, and 17 *βFib7* sequences, plus two each of *M. rubricapillus* and three each of *M. malabaricus* as outgroups (Table 2). These outgroup taxa were selected based on strong evidence from comprehensive phylogenetic studies that they are sister to the ingroup taxa (Lim et al., 2010b; den Tex and Leonard, 2013). To determine optimal partitioning schemes for phylogenetic analysis of the *Copsychus* and *Megalaima* sequences, we first defined codon positions in the coding genes as data blocks (e.g., in *Copsychus*, there are six data blocks corresponding to three codon positions in each gene). The entire *βFib7* intron was considered as a single data block. Separately for each dataset, we then used PartitionFinder v1.1.1 to determine the best partitioning scheme among all possible partitions (option: search = all; selection criterion = Bayesian information criterion) (Lanfear et al., 2014). These analyses resulted in three data partitions for *Copsychus* and two for *Megalaima* (see results). PartitionFinder also provided the optimal nucleotide substitution model for each data partition.

To construct phylogenetic trees, we used MrBayes v.3.2.1 (Ronquist et al., 2012) and RAxML v.7.0.4 (Stamatakis, 2006). In MrBayes, we performed two simultaneous runs, each with the following specifications: four MCMC chains (default heating scheme), total chain length equal to 10 million generations, and sampling every 1,000 generations. The first 25% of saved generations was discarded as burn-in. We used average standard deviation of split frequencies (< 0.004 for both species) and visualization of log-likelihood traces in Tracer v.1.6 (Rambaut et al., 2014) to determine that convergence was achieved. For RAxML, we conducted rapid bootstrap ($n = 100$) analysis and searched for the best-scoring ML tree in a single run (option: -f a).

1.2 Ecological niche modeling

1.2.1 Distributional Data and Environmental Data

We downloaded occurrence data for our study taxa from the Global Biodiversity Information Facility database (www.gbif.org), on 4–5 August 2014, and then applied the following quality control steps to the data.

First, we removed records with imprecise locality information (i.e., latitude-longitude coordinates with fewer than two decimal places and records with only vague descriptions of locality) and those requiring additional verification (based on observers' explicit statements). In addition, duplicates from exactly the same location were removed. Because our study species are land birds, localities of birds in the ocean more than 5 km from the coast were also removed (to account for imprecision in

GPS devices and GIS layers). The resulting data were then visualized in ArcMap v.10 (Environmental Systems Research Institute) to identify records that fell well outside of the known distributions of the species (e.g., misidentifications and captive birds). The final locational datasets of *C. saularis* and *M. haemacephala* comprised 1,636 and 696 records, respectively (Table S1).

The climatic data we used for niche modeling comprise four datasets: the WorldClim data that are a spatial

Table 1 Samples of *Copsychus* used in this study (Lim et al., 2010, Sheldon et al., 2009). *C.s.* = *Copsychus saularis*.

Species	Museum ¹	Tissue No.	Location	GenBank No.	
				ND2	CO1
<i>C. s. prosthopellus</i>	KUMNH	11116	Guizhou, China	FJ473262	FJ473012
<i>C. s. prosthopellus</i>	LSUMNS	B51252	Guangdong, China	FJ473279	FJ473028
<i>C. s. prosthopellus</i>	LSUMNS	B51265	Guangdong, China	FJ473280	FJ473029
<i>C. s. prosthopellus</i>	LSUMNS	B51266	Guangdong, China	FJ473281	FJ473030
<i>C. s. prosthopellus</i>	LSUMNS	B51267	Guangdong, China	FJ473282	FJ473031
<i>C. s. prosthopellus</i>	LSUMNS	B51268	Guangdong, China	FJ473283	FJ473032
<i>C. s. prosthopellus</i>	LSUMNS	B51270	Guangdong, China	FJ473284	FJ473033
<i>C. s. erimelas</i>	MNHN	04.8H	Tak Prov., Thailand	DQ125977	
<i>C. s. erimelas</i>	NRM	20026683	Hanoi, Vietnam (captive)	FJ473286	FJ473035
<i>C. s. erimelas</i>	AMNH	DOT2661	Ha Giang, Vietnam	FJ473246	FJ472996
<i>C. s. erimelas</i>	AMNH	DOT6510	Ha Giang, Vietnam	FH473269	FJ473019
<i>C. s. saularis</i>	AMNH	DOT5740	Betrabati, Nepal	FJ473260	FJ473010
<i>C. s. erimelas</i>	USNM	B02486	Sagaing, Myanmar	FJ473298	FJ473047
<i>C. s. erimelas</i>	USNM	B05612	Sagaing, Myanmar	FJ473299	FJ473048
<i>C. s. erimelas</i>	USNM	B05629	Sagaing, Myanmar	FJ473300	FJ473049
<i>C. s. erimelas</i>	USNM	B05735	Sagaing, Myanmar	FJ473301	FJ473050
<i>C. s. erimelas</i>	USNM	B06155	Sagaing, Myanmar	FJ473302	FJ473051
<i>C. s. erimelas</i>	USNM	B06160	Sagaing, Myanmar	FJ473303	FJ473052
<i>C. s. adamsi</i>	LSUMNS	B36327	Sabah Malaysia	FJ473270	EU541454
<i>C. s. adamsi</i>	LSUMNS	B46962	Sabah, Malaysia	FJ473271	FJ473020
<i>C. s. adamsi</i>	LSUMNS	B46966	Sabah, Malaysia	FJ473272	FJ473021
<i>C. s. adamsi</i>	LSUMNS	B46967	Sabah, Malaysia	FJ473273	FJ473022
<i>C. s. adamsi</i>	LSUMNS	B47166	Sabah, Malaysia	FJ473275	FJ473024
<i>C. s. adamsi</i>	LSUMNS	B47215	Sabah, Malaysia	FJ473276	FJ473025
<i>C. s. adamsi</i>	LSUMNS	B51004	Sabah, Malaysia	FJ473277	FJ473026
<i>C. s. adamsi</i>	LSUMNS	B51045	Sabah, Malaysia	FJ473278	FJ473027
<i>C. s. musicus</i>	LSUMNS	B57071	Sarawak, Malaysia	FJ473285	FJ473034
<i>C. s. pluto</i>	MZB	BS06	Kalimantan, Indonesia	FJ473245	FJ472995
<i>C. s. musicus</i>	MZB	SPS32	W. Sumatra, Indonesia	FJ473288	FJ473037
<i>C. s. musicus</i>	MZB	SPS33	W. Sumatra, Indonesia	FJ473289	FJ473038
<i>C. s. musicus</i>	MZB	SPS34	W. Sumatra, Indonesia	FJ473290	FJ473039
<i>C. s. musicus</i>	RMBR	102907	Singapore (salvage)	FJ473287	FJ473036
<i>C. s. musicus</i>	UAM	KSW4072	Singapore (salvage)	FJ473261	FJ473011
<i>C. albospecularis</i>	FMNH	393324	Madagascar	FJ473258	FJ473008
<i>C. albospecularis</i>	FMNH	393325	Madagascar	FJ473259	FJ473009

¹ AMNH = American Museum of Natural History (New York), FMNH = Field Museum of Natural History (Chicago), KUNHM = University of Kansas Natural History Museum, LSUMNS = Louisiana State University Museum of Natural Science, MNHN = Muséum National d'Histoire Naturelle (Paris), MZB = Museum Zoologicum Bogoriense (Bogor), NRM = Naturhistoriska riksmuseet (Stockholm), PNM = National Museum of the Philippines, RMBR = Raffles Museum of Biodiversity Research (Singapore), SNHM = Swedish Natural History Museum, UAM = University of Alaska Museum, USNM = National Museum of Natural History (Washington, DC), UWBM = University of Washington Burke Museum.

interpolation of weather data collected from 1950–2000 (Hijmans et al., 2005), data from two different LGM climate models, CCSM4 and MIROC-ESM (Brady et al., 2012; Sueyoshi et al., 2013), and a LIG climate model (Otto-Bliesner et al., 2006). These climatic data are available from the website www.worldclim.org. To avoid over-specification of niche models, we selected seven, relatively independent variables to represent different aspects of the climate. These variables are: annual mean temperature, mean diurnal temperature range, maximum temperature of warmest month, minimum temperature of coldest month, annual precipitation, precipitation of wettest month and precipitation of driest month (Table 3).

1.2.2 Model calibration and evaluation

To construct climatic niche models for each species and to evaluate these models, we split occurrence re-

ords of each species into two halves (training and evaluation). Using Maxent v.3.3.3 (Phillips and Dudik, 2008), we applied the training data of each species to the seven WorldClim climate variable layers. The area used for model calibration (the accessible area, or M) was different for each species and was delineated based on the following considerations (see Barve et al., 2011 for a discussion). Each M area has to be reasonably accessible in its entirety to the study species across evolutionary times so that absence at a particular location is likely due to a lack of appropriate conditions, not the result of dispersal limitations. The initial step for defining M area consisted of delimiting areas falling within a 500 km buffer zone around each occurrence point. Because *C. saularis* and other Magpie-Robins are good overwater dispersers (Sheldon et al., 2009; Lim et al., 2010b), landmasses or islands less than 500 km from an

Table 2 Samples of *Megalaima* used in this study (from den Tex and Leonard, 2014). *M. h.* = *M. haemacephala*.

Species	Museum ¹	Tissue No.	Location	GenBank No.		
				<i>Cyt b</i>	<i>ND2</i>	<i>βFib7</i>
<i>M. h. indica</i>	RMNH	162750	Sri Lanka	HQ877152	HQ874471	HQ874513
<i>M. h. indica</i>	RMNH	162749	Sri Lanka	HQ877153	HQ874472	HQ874499
<i>M. h. indica</i>	RMNH	27059	India	HQ877154	HQ874473	HQ874500
<i>M. h. indica</i>	NHM	570386	Thailand	HQ877155	HQ874474	
<i>M. h. indica</i>	NHM	570387	Cambodia	HQ877156	HQ874475	
<i>M. h. delica</i>	RMNH	162745	Sumatra	HQ877157	HQ874476	HQ874511
<i>M. h. delica</i>	RMNH	162746	Sumatra	HQ877158	HQ874477	HQ874501
<i>M. h. rosea</i>	RMNH	81987	W. Java	HQ877160	HQ874479	HQ874503
<i>M. h. rosea</i>	RMNH	66822	W. Java	HQ877159	HQ874478	HQ874502
<i>M. h. rosea</i>	RMNH	23429	E. Java	HQ877161	HQ874480	HQ874504
<i>M. h. rosea</i>	RMNH	10151	Bali	HQ877162	HQ874481	HQ874505
<i>M. h. rosea</i>	RMNH	10152	Bali	HQ877163	HQ874482	HQ874512
<i>M. h. haemacephala</i>	RMNH	162747	Mindoro	HQ877164	HQ874483	HQ874506
<i>M. h. haemacephala</i>	RMNH	99703	Mindoro	HQ877165	HQ874484	HQ874514
<i>M. h. mindanensis</i>	RMNH	162748	Mindanao	HQ877170	HQ874489	HQ874510
<i>M. h. mindanensis</i>	RMNH	97137	Mindanao	HQ877171	HQ874490	
<i>M. h. intermedia</i>	RMNH	99704	Negros	HQ877167	HQ874486	HQ874508
<i>M. h. intermedia</i>	RMNH	99702	Negros	HQ877168	HQ874487	HQ874509
<i>M. h. celestinoi</i>	RMNH	99706	Leyte	HQ877166	HQ874485	HQ874507
<i>M. h. cebuensis</i>	NHM	570385	Cebu	HQ877169	HQ874488	
<i>M. h. indica</i>	AMNH	PRS703	Singapore	DQ182306		AY279230
<i>M. rubricapillus</i>	RMNH	162752	Sri Lanka	HQ877172	HQ874491	HQ874515
<i>M. rubricapillus</i>	RMNH	162751	Sri Lanka	HQ877173	HQ874492	HQ874516
<i>M. malabarica</i>	AMNH	462210	India	HQ877174	HQ874493	HQ874517
<i>M. malabarica</i>	AMNH	777391	India	HQ877175	HQ874494	HQ874518
<i>M. malabarica</i>	AMNH	462209	India	HQ877176	HQ874495	HQ874519

¹ AMNH = American Museum of Natural History (New York), NHM = Naturhistoriska riksmuseet (Stockholm), RMNH = Netherlands Center for Biodiversity (NCB) Naturalis, and ZMUC = Zoological Museum University of Copenhagen.

Table 3 Estimates of relative contributions of the environmental variables to the Maxent model of each study species

Climatic variable	Description	<i>C. saularis</i>		<i>M. haemacephala</i>	
		Percent contribution	Permutation importance	Percent contribution	Permutation importance
bio1	Annual Mean Temperature	8.3	5	12.6	14.6
bio2	Mean Diurnal Temperature Range (mean of monthly maximum temperature - minimum temperature)	8.5	10.8	8.3	8.9
bio5	Maximum Temperature of Warmest Month	14.7	21.7	15.7	17.6
bio6	Minimum Temperature of Coldest Month	29.5	26.9	34.5	26.9
bio12	Annual Precipitation	4.8	10.2	10.5	13.4
bio13	Precipitation of Wettest Month	28.5	21	13.1	15.2
bio14	Precipitation of Driest Month	5.7	4.5	5.3	3.5

Percent contribution is calculated based on how much the variable contributes to increases in regularized gains during model construction. Permutation importance is determined from drop in AUC when values of a climatic variable are permuted among the training points.

occurrence point were considered accessible. The M area for *C. saularis* does not include Palawan, where Magpie-Robins are absent (presumably because of competition from *C. niger*, the White-vented Shama), or the Sulu islands, which are occupied by *C. mindanensis*. It also does not include islands east of Wallace's Line, because no *Copsychus* species have crossed this line. In continental Asia, the northwestern limit of *C. saularis* M area is constrained by an elevational limit of 4,000 m. We considered mountain ranges of this height to be a significant dispersal barrier to *C. saularis* since the species is generally found no higher than 2,000 m (Mann, 2008). The same principles were applied to delineating the M area of *M. haemacephala*, except that this species is not considered to be a good over-water disperser. Thus, landmasses or islands not connected by land bridges during eustatic sea-level lowstands (i.e., when seas fell ~120 m below their current level) were not considered accessible.

For each species, we ran 100 bootstrap Maxent replicate analyses using the training dataset and the seven current environmental layers (other run configurations were set to default). For each species, we determined if the statistical median of the 100 bootstrap logistic outputs (indicating median probability of presence) was a good predictor of the distribution of species-specific evaluation points using the following approach. First, we overlaid the evaluation points (comprising 50% of occurrence points of each species) over the map of median suitability values and extracted the latter. We then compared Area under the Receiver Operating Characteristic curve (AUC) of the evaluation points against those expected by chance using the program partial ROC (Barve, 2008). When running partial ROC (1,000 bootstrap replicate analyses were conducted), we assumed omission error rate (E) to be 5%.

1.2.3 Final model development and projections

After model evaluation, we combined all occurrence records (training plus evaluation) of each species and repeated the construction of species-specific niche models. These models were then projected onto current climatic conditions, and across time onto climatic conditions of the LGM and LIG. As in model evaluation, we ran 100 bootstrap replicate analyses and took the median logistic output grids as results. To convert the original output grids containing continuous suitability values into output grids with binary data (presence or absence), we identified threshold suitability values for each species that include 95% of the occurrence points. "Thresholded" outputs (showing predicted presence and absence) and median logistic outputs are presented in the results and supplementary materials, respectively.

1.2.4 Comparison of climatic niche space and requirements

We used ENMTools v1.3 to measure niche dissimilarity between the two species and also to compare their niche breadths (Warren et al., 2008). To test niche dissimilarity, we used ENMTools's "background test" to determine if climatic niches of the two species are more or less similar (two-tailed test) based on differences in the environmental conditions available to them. In this test, actual occurrence points of a focal species (*C. saularis* or *M. haemacephala*) were compared to an equal number of random points generated from the M area of the other species. Maxent was then used to generate environmental niche models from these two sets of points, which were then used by ENMTools to calculate niche similarity scores (Schoener's *D* and Similarity Statistic *I*) (Warren et al., 2008). For both metrics, a score of zero is equivalent to no niche overlap, whereas a score of one implies niche identity. This procedure was carried out 100 times (each time using a new set of random points

from the M area of the non-focal species) and in both directions. The simulated distributions of Schoener's D and Similarity Statistic I were then compared against the observed values. We also used ENMTools to calculate niche breadths of both species (Nakazato et al., 2010). The two metrics used—Inverse Concentration score and Uncertainty score—were first introduced to the ecology literature by Levins (1968). Similar to the niche similarity scores, zero represents the minimum possible breadth (only one grid cell in the geographic space is suitable) and one represents maximum breadth (every grid cell is equally suitable) (Mandle et al., 2010).

2 Results

2.1 Phylogeography

The tree of *Copsychus saularis* populations (Fig. 1A) is consistent with previous studies of oriental magpie-robin phylogeography (Sheldon et al., 2009; Lim et al., 2010b). The populations of eastern Borneo (Sabah and eastern Indonesian Kalimantan) are sister to a large clade comprising all other populations. Within the large clade are populations from western Borneo, western Sundaland (Sumatra and Singapore), the Indian subcontinent, Indo-Burma, and China. Populations in the last three areas—the Sino-Indian region—form a monophyletic group that is divided into two clades. The first subclade comprises individuals from Indo-Burma, while the second subclade comprises individuals from the whole

Sino-Indian region.

The tree of *Megalaima haemacephala* (Fig. 1B) is consistent with the phylogeographic study from which its sequences were derived (den Tex and Leonard, 2014). It consists of two main clades, each containing 1–2 clades. The first group comprises Philippine populations as sister to Indian and Sri Lankan populations, and the second comprises Sumatran and Javan populations nested within individuals from Singapore and Indo-Burma.

2.2 Niche modeling

Both *C. saularis* and *M. haemacephala* have reliable occurrence records from throughout their ranges. This is because both are conspicuous—Magpie-Robin by sight and the Barbet by sound—and are easily identified by bird watchers. Both are also well represented in museum collections, and thus specimens contributed a moderate number of records to the analysis. Maxent produced models that fit evaluation occurrence points of each species well. For each species, out of 1,000 bootstrap iterations in partial ROC, all of the $AUC_{model}:AUC_{null}$ ratios fell above one, suggesting significantly good fit of the models to the data (a ratio of > 1 indicates that the model predicted occurrence of evaluation points better than chance). For both species, minimum temperature in the coldest month (bio6) was the most important climatic variable, followed by maximum temperature in the warmest month (bio5) and precipitation in the wettest month (bio13) (Table 3).

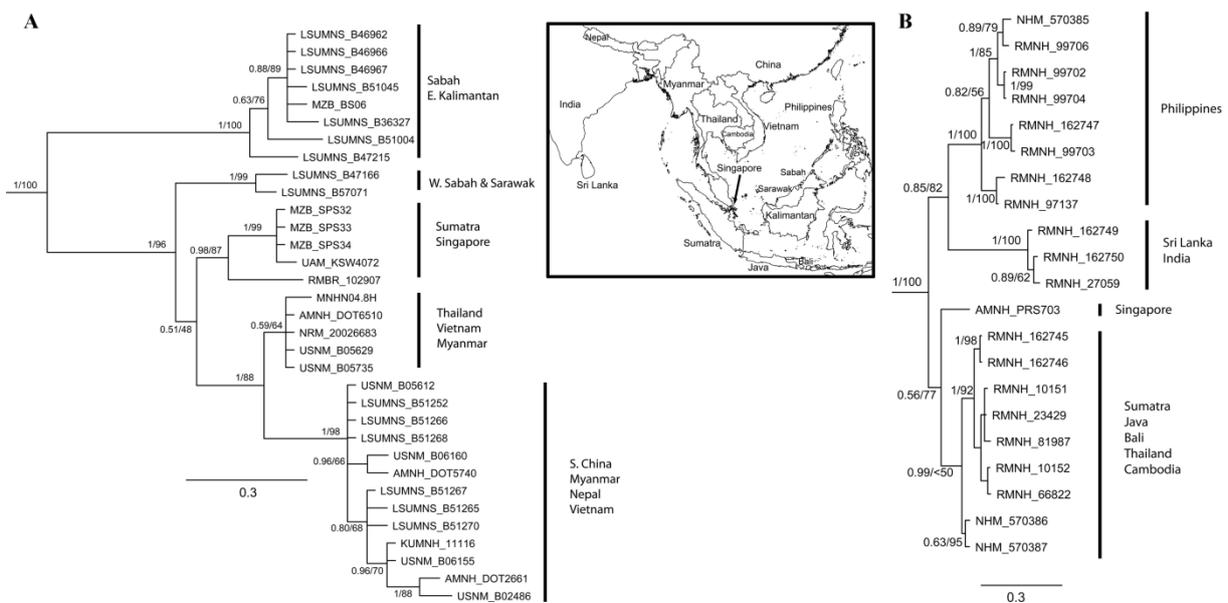


Fig. 1 Phylogenetic trees of (A) *Copsychus saularis* and (B) *Megalaima haemacephala* populations built using MrBayes with methods described in the text

Number adjacent to branches indicate Bayesian posterior probability/RAxML bootstrap support values (out of 100). Outgroup taxa in both phylogenetic trees (located at the left of each tree) have been trimmed. Insert map shows names of areas where samples were collected from.

Projection of *C. saularis*' niche model to the current environment in our study area shows a predicted distribution that conforms well with what we know of *C. saularis*' distribution (Figs. 2 and S1). In the north, its

distribution largely follows the classic contour of the Indomalayan zoogeographic realm (Wallace, 1876; Cox, 2001). In eastern China, this means that *C. saularis*' range ends where subtropical climate gives way to tem-

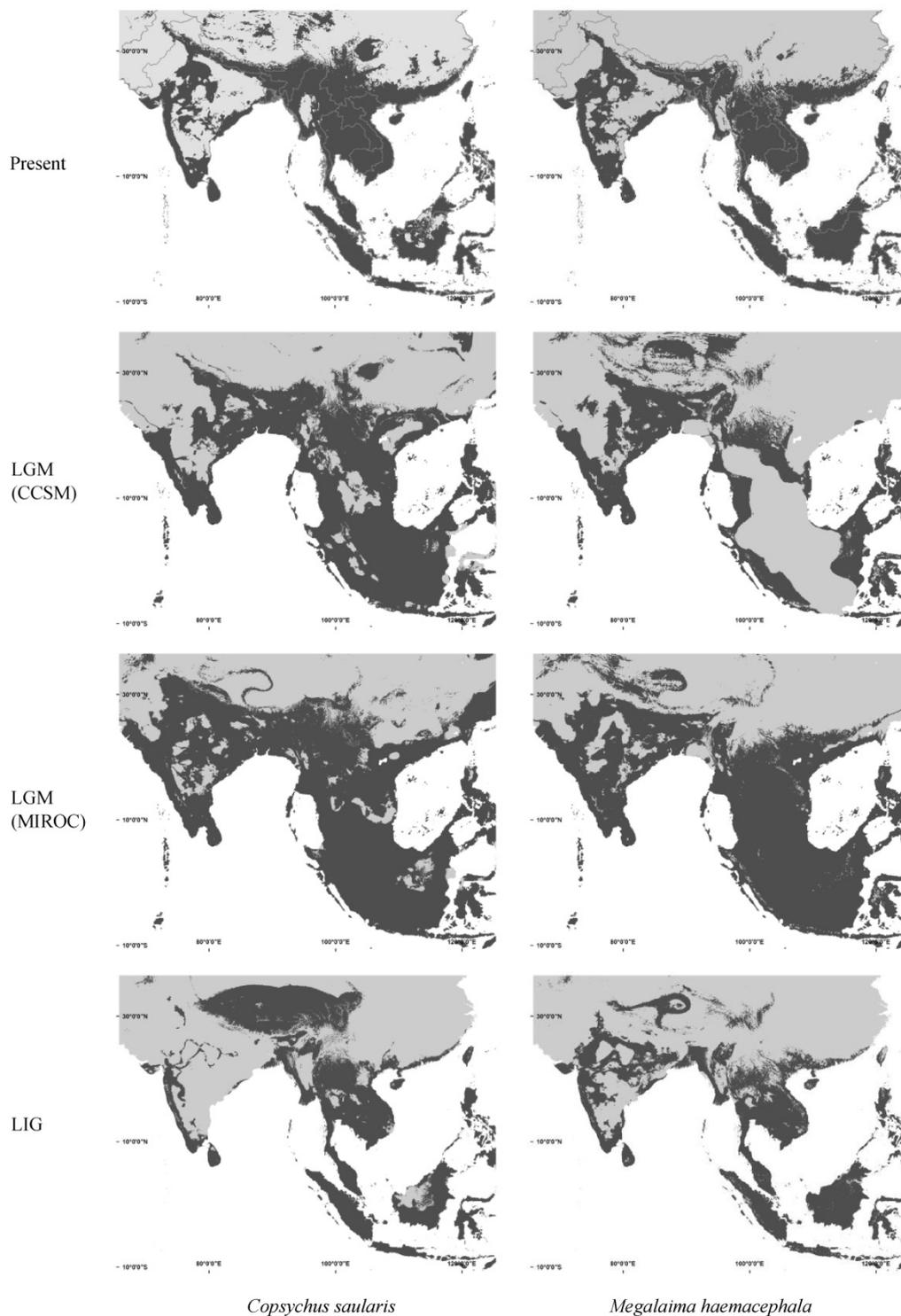


Fig. 2 Predicted climatic suitability for *Copsychus saularis* (left column) and *Megalaima haemacephala* (right column) at present (top), during the last glacial maximum (CCSM second row, MIROC third row), and during the last interglacial (bottom row)

Black indicates predicted presence of species, gray indicates absence.

perate conditions, as approximated by the 0°C isotherm of average January temperate and an isohyet of 800 mm annual precipitation (Chen et al., 2008). Areas predicted to be climatically suitable for *C. saularis* but where the species is absent are either occupied by close congeners, e.g., *C. mindanensis* in most of the Philippines and *C. niger* on Palawan, or are beyond the range of colonization (e.g., areas east of Wallace's Line). Within *C. saularis*' known distributional limits, some areas seem to be climatically less suitable for the species, for example, central India, the central dry valley of Myanmar, southeastern China, and central Borneo. An examination of climatic variables and their contributions to Maxent's output logit scores indicates that different variables are limiting *C. saularis*' presence in these areas. In central India and Myanmar, limitation is mainly due to low rainfall (bio13) and/or high temperatures (bio5). In central Borneo, it is mainly due to high precipitation (bio 12 and 14), and in eastern China, it is mainly due to low temperatures (bio6).

Projection of *C. saularis*' niche models onto LGM-CCSM and LGM-MIROC models indicated that virtually the entirety of the Indomalayan region, including the emergent Sunda shelf, was climatically suitable for this species (Figs. 2 and S1). In the LGM-CCSM model, a swath of land in central Sundaland had mean diurnal temperature range values (bio2) outside of those of the training data (i.e., current climate experienced by *C. saularis*) (Fig. S2). As a result "clamping" (intentional flattening of the response surface to the calibration area-edge value when extrapolating) was imposed during model projection (Elith et al., 2011). Without clamping, the high bio2 values in central Sundaland under CCSM would have made central Sundaland even more suitable for *C. saularis* during the LGM (see Fig. S2 for bio2 maps and *C. saularis* response curves with and without clamping). Clamping was not an issue when projecting the *C. saularis* niche model onto the LGM-MIROC model. When applied to LIG climatic conditions, the *C. saularis* niche model produced a distribution map that is similar to today's, but with a slight contraction of range in the northeast. We consider the predicted presence of *C. saularis* in the Tibetan plateau during LIG to be improbable, an artifact caused by a failure in model training to take into account non-analogous Tibetan climatic conditions presented by the LIG model. In particular, the LIG climatic model specified the Tibetan plateau as having a much lower minimum temperature during its coldest month than today (bio6; generally 10°C lower during the LIG), but the negative effects of such low temperatures were not fully accounted for by our niche

model because such extreme values were not encountered during model training.

The predicted modern range for *M. haemacephala* is largely coincident with its known distribution, except in southeastern China and in Borneo (Fig. 2). Maxent predicts that this species should occupy coastal southeastern China (comprised mainly of monsoon tropical forests), but the species has only been recorded up to northern Laos and central Vietnam, at least a few hundred kilometers southwest of its the predicted northeastern limits. Present-day Borneo is modeled as highly suitable for *M. haemacephala*, but the barbet is absent from there as well. Examination of climatic layers suggest that areas unsuitable for *M. haemacephala* are characterized by a combination of low rainfall in the wettest month (bio13) and high temperatures in the warmest month (bio5). The predicted LGM-CCSM range of *M. haemacephala* differed from that of *C. saularis* in that the central swath of Sundaland was unsuitable for the barbet. The areas's lack of suitability under this model was a result of high variability in diurnal temperature (high bio2) and high temperature in the warmest month (high bio5) (Figs. S2 and S3). However, the LGM-MIROC model indicated that central Sundaland was suitable because under this model, central Sundaland did not possess high bio2 or high bio5, highlighting important differences between the two LGM models (Figs. S2 and S3). The projected LIG distribution of *M. haemacephala* is quite similar to that of *C. saularis*. The unexpected occurrence of the Barbet in the Tibetan plateau is again due to projection of the model into non-analogous conditions.

2.3 Comparison of niche similarity and breadth

The empirical Schoener's *D* and Similarity Statistic *I* values between *C. saularis* and *M. haemacephala* are 0.856 and 0.964, respectively, suggesting that they occupy similar environmental niches. Background tests using *C. saularis* or *M. haemacephala* as the focal species show that their niches are more similar than expected by chance. For each statistic, the empirical value was greater than the 95th percentile value of the simulated distributions (*M. haemacephala* as focal: *D* = 0.635, *I* = 0.855; *C. saularis* as focal: *D* = 0.704, *I* = 0.891) (Fig. 3). Based on the two niche breadth metrics, *C. saularis* has a greater niche breadth than *M. haemacephala* (Inverse Concentration score: *C. saularis* = 0.745, *M. haemacephala* = 0.710; Uncertainty score: *C. saularis* = 0.983; *M. haemacephala* = 0.979).

3 Discussion

In *C. saularis*, the eastern Borneo black-bellied sub-

species (*pluto* and *adamsi*) form a sister clade to the rest of the species (from western Borneo, western Sundaland and the Sino-Indian region), which has white belly (see Mees 1986 for further discussion of other plumage differences). This east-west genetic and morphological divergence, dated to about 1 mya, is interesting because it mirrors those of species inhabiting lowland rainforest and even montane species (Lim et al., 2010a; Lim and Sheldon, 2011; Gawin et al., 2014). However, the mechanism underlying lineage divergence of *C. saularis* may be different from those of rainforest species since *C. saularis* is an open area species, preferring habitats such as mangrove, forest edge, coastal scrub vegetation, and, in more recent times, man-made open areas such as gardens (Sheldon et al., 2001; Wells, 2007; Mann, 2008).

For LGM, our niche modeling did not indicate any major distributional break in Southeast Asia for *C. sau-*

laris, as have been suggested for birds and mammals that occupy lowland rainforests due to postulated emergence of seasonal forests (Brandon-Jones, 1996; Gorog et al., 2004; Bird et al., 2005; Lim et al., 2010a). One possible mechanism for past distributional disjunction undetected by our method is that the coastal habitats preferred by *C. saularis* have been separated between western and eastern Sundaland by fallen sea-levels. During glacial maxima, because sea-levels fell below the shelf margin, mangroves (which require sheltered, gentle slopes and constant sediment supply) would have likely been restricted to narrow coastal belts (Bird et al., 2004; Cannon et al., 2009). The only places likely to have extensive mangroves were at the deltas of large Sundaic paleo-rivers, which, during the LGM, were the Siam River, the North Sunda River (both exiting into South China Sea northeast of Natuna Islands), East

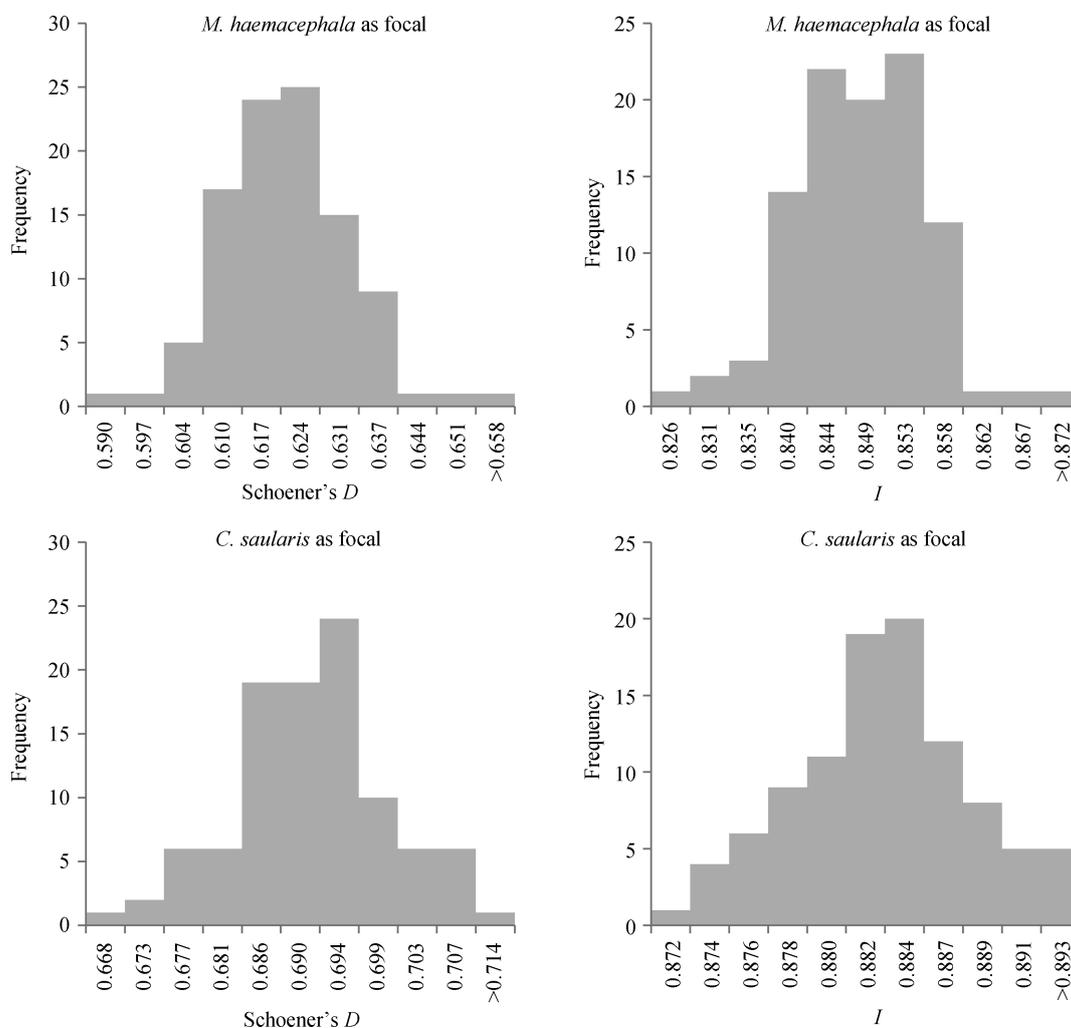


Fig. 3 Distribution of simulated Schoener's D and Similarity Statistic I values generated by background tests using *C. saularis* and *M. haemacephala* as focal species

Empirical values of D and I are 0.856 and 0.964, respectively, indicating that climatic niches of these two species are more similar than expected by chance. These empirical values lie outside of the graphs, to the right.

Sunda River (exiting around Bali) and Malacca Strait River (exiting near northern Sumatra) (Solihuddin, 2014). These deltas could have maintained distinct habitat patches that contributed to divergence of mangrove-associated birds. To confirm that this mechanism influenced population divergence of mangrove and mangrove-associated birds, further phylogeographic studies on these species need to be carried out in Southeast Asia.

Under current climatic conditions, Maxent analyses indicate areas where lowered suitability could have contributed to the separation of the three Borneo *C. saularis* subspecies (*musicus*, *adamsi* and *pluto*). The subspecies *adamsi* is found in northeastern Borneo while *pluto* is found in the rest of eastern Borneo. Mees (1986) put their zone of integration around the boundary between Malaysian Sabah and Indonesian Kalimantan, matching an area of lower climatic suitability for *C. saularis* (Figs. 2 and 4). A similar zone of low suitability separates the range of *adamsi* and from that of the western Borneo *musicus*. Low climatic suitability of these areas is mainly driven by high annual precipitation (bio12), which in turn is directly impacted by the northeast monsoon rainfall pattern (Camerlengo et al., 1998). In spite of the less than favorable climatic conditions in parts of Borneo, extensive deforestation and urbanization could have improved habitat suitability for these open-habitat birds to the extent that it increases contact and admix-

ture among the subspecies above the natural level (D.F. Gawin, unpublished data)

In the Asian mainland, niche modeling shows that there was continuous paleo-distribution for *C. saularis* through glacial cycles. However, this appears to be at odds with the available phylogenetic information: mainland and Sumatran *musicus*, and Sino-Indian individuals (comprising subspecies *erimelas*, *saularis* and *prosthopellus*) form reciprocally monophyletic clades, suggesting long-term divergence. This apparent north-south genetic distinction, however, could diminish if more individuals along the Thai-Malay Peninsula are sampled since the only mainland *musicus* available for sequencing were from the extreme southern tip of Malaya (Sheldon et al., 2009). Based on the distribution of conditions during glacial and interglacial periods, the one possible region where a population could accumulate genetic differentiation is the west coast of India. This is because this area appears to be continuously isolated from other portions of *C. saularis*' range by areas of low suitability. Sampling of birds from here and/or Sri Lanka is needed to confirm this suspicion.

The Coppersmith barbet, *M. haemacephala*, like *C. saularis*, is not a bird of the closed forest. It prefers more open terrestrial woodlands and invades green urban areas and orchards quite readily (Hone and Short, 2002; Lok and Lee, 2009). As a result of forest clearing, it expanded from northern Malay Peninsula (Robinson, 1927) and arrived at the southern terminus (Singapore) in the 1940's–50's (Gibson, 1949). Based on niche modeling, *M. haemacephala* finds Borneo highly suitable climatically, but is obviously not found there currently. The parsimonious interpretation (based on biogeographic and phylogenetic data) is that Borneo was once occupied by a widespread ancestral *M. haemacephala* population, which gave rise to the populations in India/Sri Lanka and the Philippines. However, *M. haemacephala* subsequently retreated from Borneo. One possible explanation for this retreat is that Borneo's climate (especially in terms of seasonality in temperature) during LGM (based on the CCSM4 model) or other glacial periods was largely unsuitable for *M. haemacephala*. The absence of *M. haemacephala* from most of the Malay Peninsula until recently also supports the argument that a corridor of unsuitable area running down the middle of Sundaland existed during LGM or other glacial periods. However, this phenomenon is not supported by paleo-distribution reconstruction based on the LGM-MIROC model. The alternative explanation for *M. haemacephala*'s absence in the Malay Peninsula and

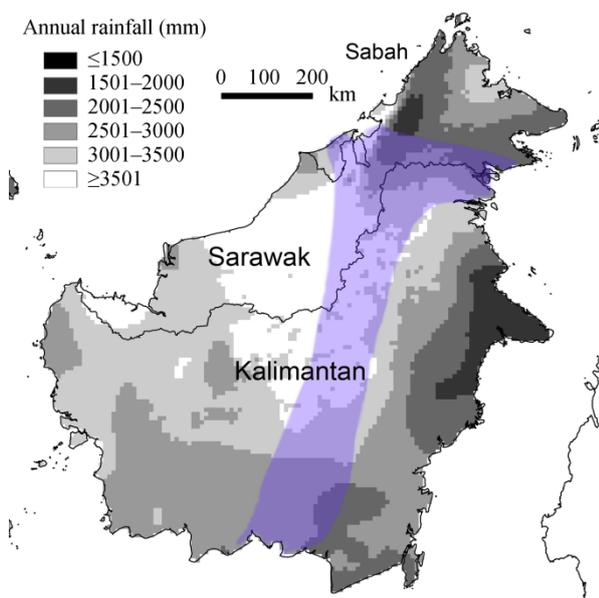


Fig. 4 Annual rainfall pattern in Borneo and zones of intergradation (in blue) between the three morphological subspecies of *C. saularis* (*musicus*, *adamsi* and *pluto*) as depicted in Mees (1986)

Borneo is that Sundaland had remained heavily forested during the LGM (Raes et al., 2014), and there was little open woodland available to *M. haemacephala*—a habitat type that would have been available further in the north (current transition from evergreen rainforest to mixed moist deciduous occurred around the Isthmus of Kra) or peripheral areas such as Java (van den Bergh et al., 2001; Woodruff, 2010). Regardless of the actual cause of its extirpation from Borneo, it does not recolonize Borneo, despite the presence of suitable climate and/or more open woodlands due to deforestation, because of its apparent poor over-water dispersal ability.

Despite the fact that *C. saularis* and *M. haemacephala* are broadly co-distributed, and that they occupy very similar climatic niches (with the former's being slightly broader), niche model projections showed that even subtle differences in climatic niche can result in disparate paleo-distributions, at least under the LGM-CCSM model. This suggests that broad coincidence in geographic range should not be taken as a sign that the species had responded to climatic changes in the same way (Carstens and Richards, 2007). Further, other dimensions of the species' ecology (e.g., dispersal ability and habitat preferences) are needed to better explain their responses to past climatic changes and patterns of population divergence. Our study, like numerous others, shows that ecological niche modeling adds a powerful dimension to our attempt to understand lineage evolution in space. Ecological niche modeling will become an increasingly important tool in the biogeographer's toolbox, even as the scientific community resolves outstanding technical and philosophical challenges and questions, such as whether occurrence data are allowing us to measure fundamental niche (Saupe et al., 2012), difficulties of modeling species that are not in equilibrium with the environment (Elith et al., 2010), and whether to treat co-occurring species as integrated communities or to model their responses individually (Ricklefs, 2008).

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