Timaliidae: recognize *Mixornis woodi* as a species and move Striped Tit-babbler subspecies of Anambas and Natuna Islands from *Mixornis bornensis* to *Mixornis gularis*

Following data presented in Berman et al. 2024, supplemented by data from Cros & Rheindt 2017

Introduction

Old world Babblers from the family Timaliidae are a group of forest-dwelling songbirds which are mostly understory and social species (although some members are monogamous).

Two social species of this group are the Pin-striped Tit-Babbler (*Mixornis gularis*) and Bold-striped Tit-Babbler (*M. bornensis*). These taxa are distributed in South East Asia, with the former having a wider range of distribution – they were previously regarded as conspecific but were subsequently split on the basis of plumage (Collar 2006, Collar & Robson 2007) and genetics which revealed that they constitute two deeply diverged species (Lim et al. 2011, 2017).

Here, we propose (a) recognizing *Mixornis gularis woodi* as a full species and (b) shifting three taxa (*everetti*, *zaperissus* and *zophera*) currently classified under Bold-striped Tit-Babbler *Mixornis bornensis* to Pin-Striped Tit-babbler *Mixornis gularis* on the basis of morphological, genomic and biogeographic evidence presented in Berman *et al.* 2024, and vocal data from Cros & Rheindt (2017).

Table 1 Current classification of Pin-striped Tit-Babbler *Mixornis gularis* and Bold-striped Tit-Babbler *Mixornis bornensis* taxa as per AviList v2025

Common name	**Scientific name**	**Range**
Pin-striped Tit-babbler	***Mixornis gularis***	
	Mixornis gularis rubicapilla	lowlands of eastern Nepal to northeastern India and far northern Myanmar
	Mixornis gularis ticehursti	western Myanmar (Upper Chindwin District to Arakan)

	Mixornis gularis sulphureus	southern China (southwestern Yunnan) to eastern Myanmar and northern plateau of Thailand
	Mixornis gularis lutescens	southern China (southeastern Yunnan) to northern and eastern Thailand, Laos, and Tonkin
	Mixornis gularis kinneari	central Vietnam
	Mixornis gularis saraburiensis	eastern Thailand and western Cambodia
	Mixornis gularis versuricola	eastern Cambodia and southern Vietnam
	Mixornis gularis condorensis	Pulau Kundur (South China Sea)
	Mixornis gularis connectens	Tenasserim (southeastern Myanmar), coastal Gulf of Thailand to central Malay Peninsula
	Mixornis gularis archipelagicus	Mergui Archipelago (off southwestern Myanmar)
	Mixornis gularis inveteratus	coastal islets off southeastern Thailand and Cambodia
	Mixornis gularis gularis	southern Malay Peninsula, Sumatra, and Banyak, Batu, Lingga, and Riau islands
	Mixornis gularis woodi	southwestern Philippines (Balabac and Palawan)
Bold-striped Tit-Babbler	***Mixornis bornensis***	
	Mixornis bornensis zopherus	Anambas Islands
	Mixornis bornensis everetti	Pulau Bunguran (North Natuna Islands)
	Mixornis bornensis zaperissus	North Natuna Islands

	Mixornis bornensis argenteus	Banggai Islands (off northern Borneo)
	Mixornis bornensis cagayanensis	Mapun (southern Philippines)
	Mixornis bornensis bornensis	Borneo, and Bangka and Belitung islands (off eastern Sumatra)
	Mixornis bornensis montanus	northeastern Borneo
	Mixornis bornensis javanicus	western and central Java

Whereas the other *Mixornis* species (e.g. Grey-faced Tit-babbler *M. kelleyi*, Grey-cheeked Tit-babbler *M. flavicollis* and Kangean Tit-babbler *M. prillwitzi*) in Southeast Asia are monotypic, *M. gularis* and *M. bornensis* each comprise numerous subspecies (Table 1).

One of the subspecies, *M. gularis woodi* from Balabac and Palawan, has long been attributed to Pin-striped Tit-babblers on the basis of its sparsely streaked underparts. However, some publications have suggested that it may warrant species status distinct from *M. gularis* on account of its overall distinctive plumage (including indistinct streaking on underparts, greyish face, mantle, back and scapulars, and its paler underparts [Collar & Robson, 2007]). Further, three of the subspecies – *everetti*, *zaperissus* and *zophera*, residing on Anambas and Natuna Islands at the centre of the Sunda Shelf – are of uncertain taxonomic affinity. Currently, they are assigned to the Bold-striped Tit-babbler (AviList v2025, Collar 2006, Collar & Robson 2020, Eaton et al. 2021) following plumage traits characterized in the original taxon description (Oberholser 1917).

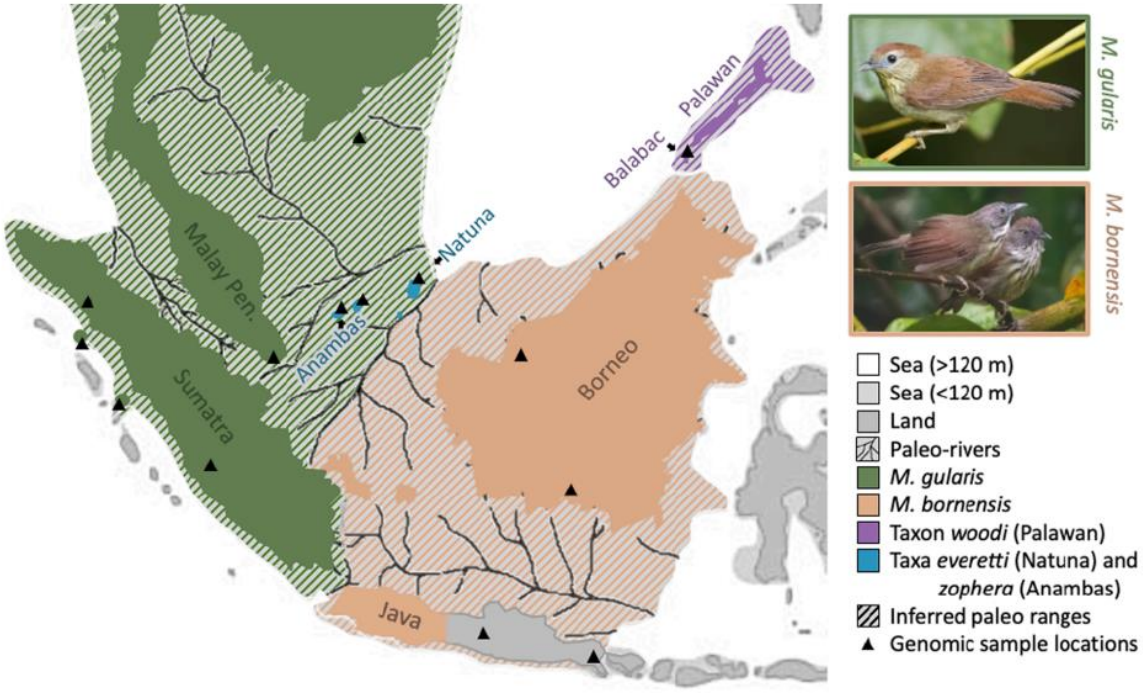

Figure 1 Range of Pin-striped and Bold-striped Tit-babblers (*Mixornis gularis* and *M. bornensis* respectively). Hashed areas show the Sunda shelf, an area currently characterized by shallow seas which would have been connected during Pleistocene glaciations, with major Paleo-rivers illustrated. Note that the complete range of *M. gularis* extends beyond the extent of this map to northeast India [figure from Berman et al. 2024]

Morphology

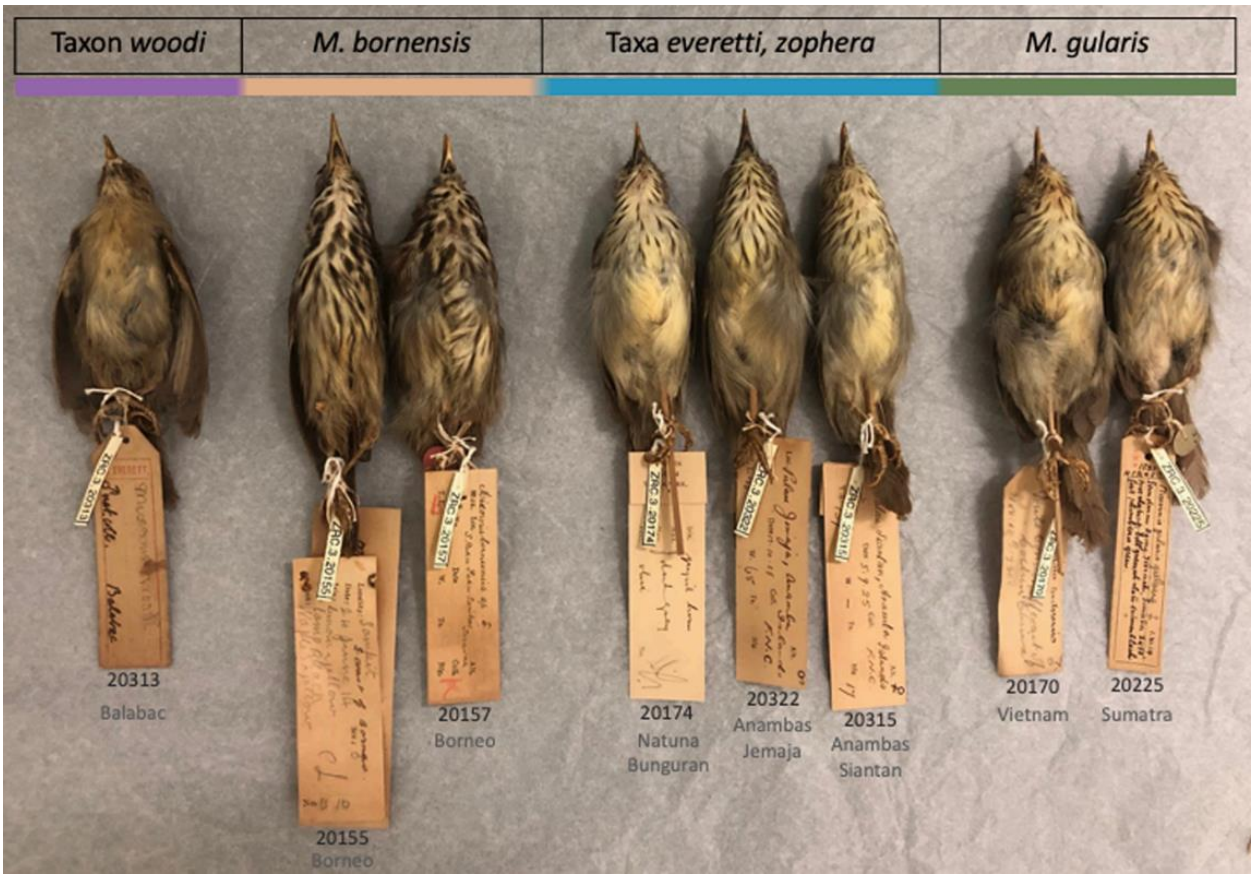

Figure 2 Plumage phenotypes of museum specimens representing typical individuals of *M. bornensis* and *M. gularis*, as well as populations from Anambas (*zophera*) and Natuna (*everetti*) as well as a virtually unstreaked individual from Balabac near Palawan (*woodi*). Note the streaking on the breast of the individuals from the Natuna and Anambas Archipelagos is most similar to *M. gularis*. The individual from Balabac appears virtually unstriped [figure and caption from Berman et al. 2024]

The width of breast stripes of the two taxa sampled from Natuna and Anambas fall completely within the range seen in Pin-striped Tit-Babbler *M. gularis* (Fig. 2, Fig. 3: t-test, p-value = 1.5 x 10^{-09}). All *M. bornensis* individuals sampled had stripes exceeding 1mm in diameter. Note that the initial split of Bold-striped Tit-Babbler from Pin-striped Tit-babbler was also on the basis of throat and breast streaking. Further, the study states this of the *woodi* specimen: *The sole individual from Balabac (off Palawan, Philippines) was morphologically distinct; its breast was nearly unstriped, with a dark rachis only on a few feathers* (Berman et al. 2024). This unstreaked plumage is especially remarkable given the geographic proximity of *woodi* to *bornensis*, the most prominently streaked *Mixornis* taxon.

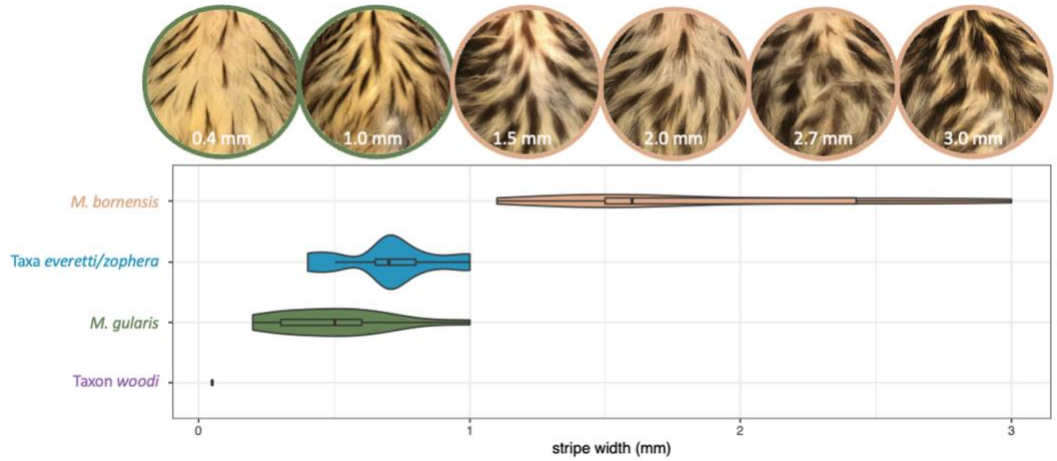

Figure 3 Analysis on breast stripes showed that the width of breast stripes of taxa *everetti/zophera* falls within the range of *M. gularis* [figure from Berman et al. 2024]

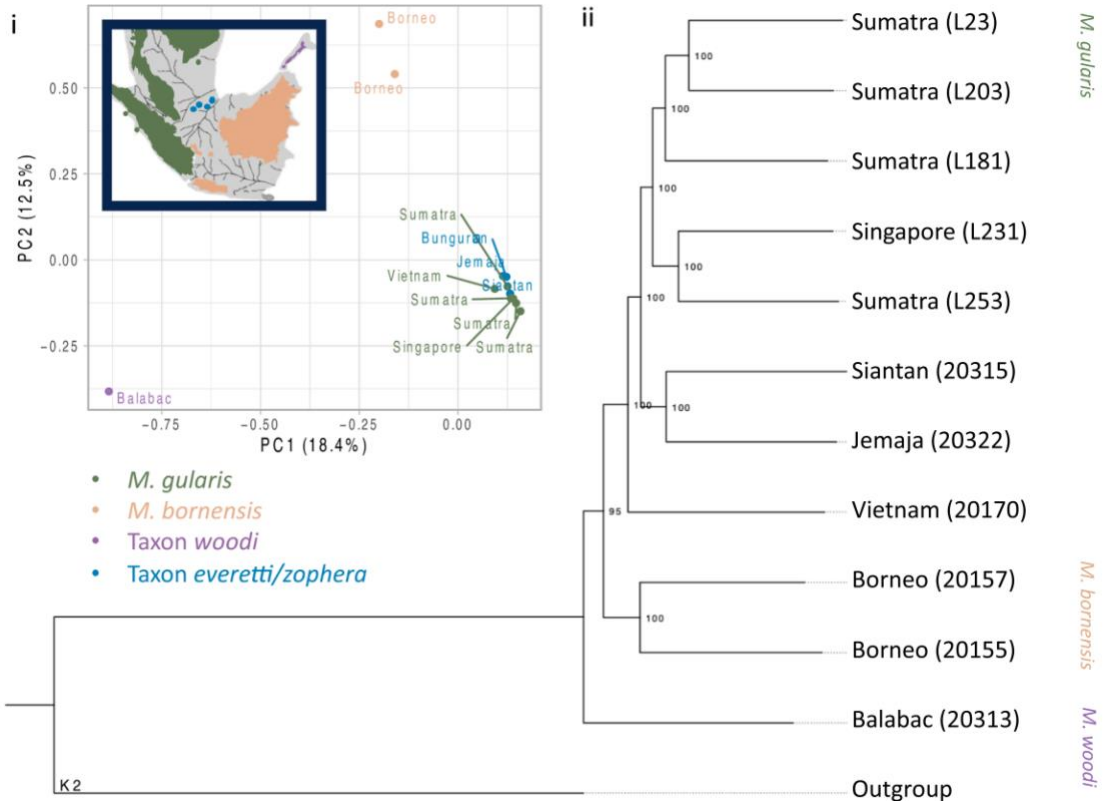

Figure 4 Genomic analyses. i) Principal component analysis based on 448,761 genome-wide SNPs, excluding the outgroup. Percentages along each principal component (PC) show the amount of total variation accounted for. Bunguran (home of *everetti*) is an island in the Natuna Archipelago. Jemaja and Siantan (home of *zophera*) are islands in the Anambas Archipelago. Balabac lies off the coast of Palawan (home of *woodi*). ii) Maximum-likelihood tree, based on 10,459 concatenated loci, each 10,000 bp long, run with 1,000 bootstrap iterations. Individuals from the Anambas Archipelago (Siantan and Jemaja, home of *zophera*) are highlighted in turquoise. Outgroup: *M. flavicollis* from Java [figure and caption from Berman et al. 2024]

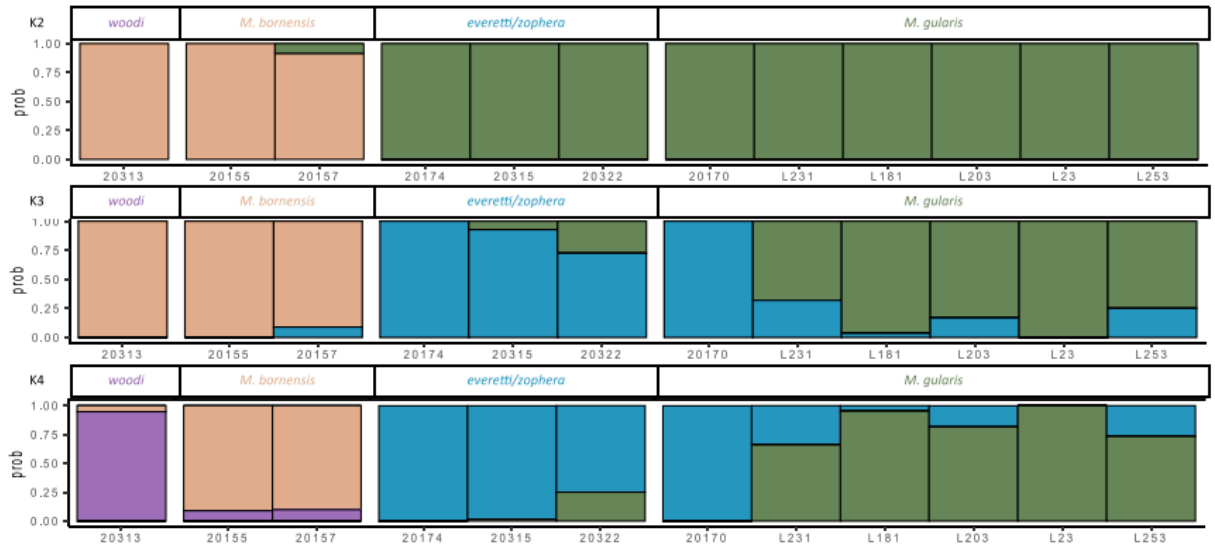

Figure 5 STRUCTURE analysis [from Berman et al. 2024] *M. gularis* and *M. bornensis* individuals at K = 2 to K = 4, aggregated across ten replicates, with 200,000 MCMC bootstraps, a burn-in of 100,000, using 448,761 genome wide SNPs

Genomics

A population genomic dataset of 448,761 SNPs showed that (a) the *woodi* individual appeared to be the most highly diverged of all 12 *Mixornis* samples in the dataset and that (b) Natuna and Anambas individuals show greater affinity with *gularis* than *bornensis* (Fig 4, 5). Specifically, Natuna and Anambas individuals were embedded within the monophyletic *M. gularis* clade in the maximum likelihood tree (Fig. 4). Note that *woodi* appears distinct in STRUCTURE at k=4 (optimum k) (Fig. 5), and emerged as basal to both *gularis* and *bornensis* in the Maximum Likelihood tree (Fig. 4).

Bioacoustics

This complex of Tit-babblers is known to produce a stereotyped "chonk chonk chonk..." song which is easily recognizable in the field. Additionally, a more irregularly spaced song has been reported in the *M. bornensis* taxa (Cros & Rheindt 2017).

Bioacoustic analysis indicated that *everetti* from Natuna is intermediate between *M. gularis* and *M. bornensis*. It does not exhibit the song type characteristic of the Bornean taxa, yet it performs duets, a characteristic shared with some *M. bornensis* taxa and *M. prillwitzi* (Cros & Rheindt, 2017). Both the PCA and dot plot of vocal characters further support this intermediacy, with *everetti* positioned between mainland and Bornean populations (Fig. 6 and 7). Although *M. bornensis* and *M. gularis* are Isler-diagnosable for nine parameters, *everetti* is not Isler-diagnosable from either taxon (Table 2).

Bioacoustics analysis of *woodi* did not show it to be vocally distinct from *gularis* from the Malay Peninsula (Fig. 6).

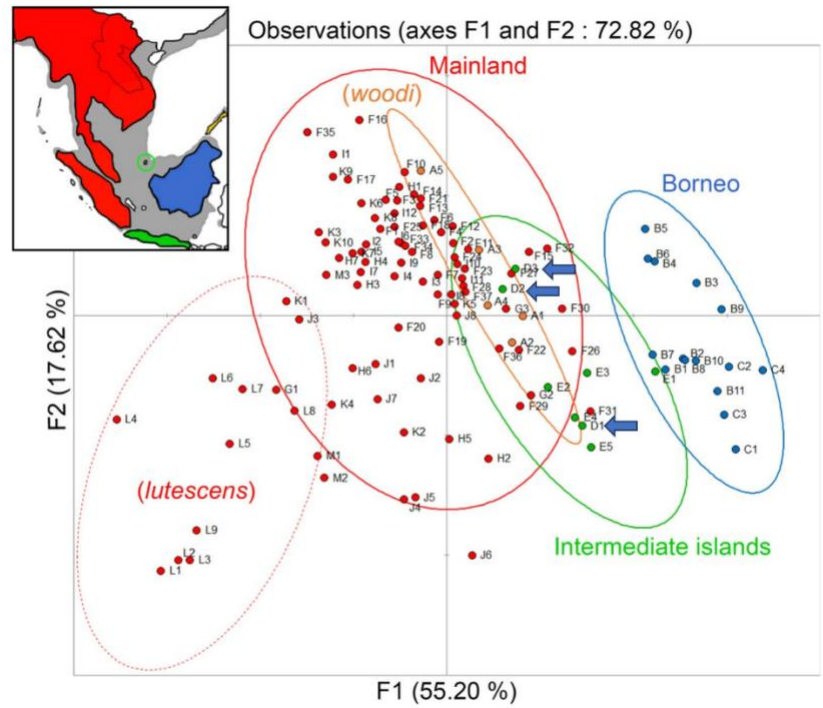

Figure 6 PCA analysis of song type 1 acoustics parameters of the tit babbler complex with 95% confidence ellipses. Arrows indicate the position of Natuna taxon *everetti* [Figure from Cros & Rheindt, 2017]

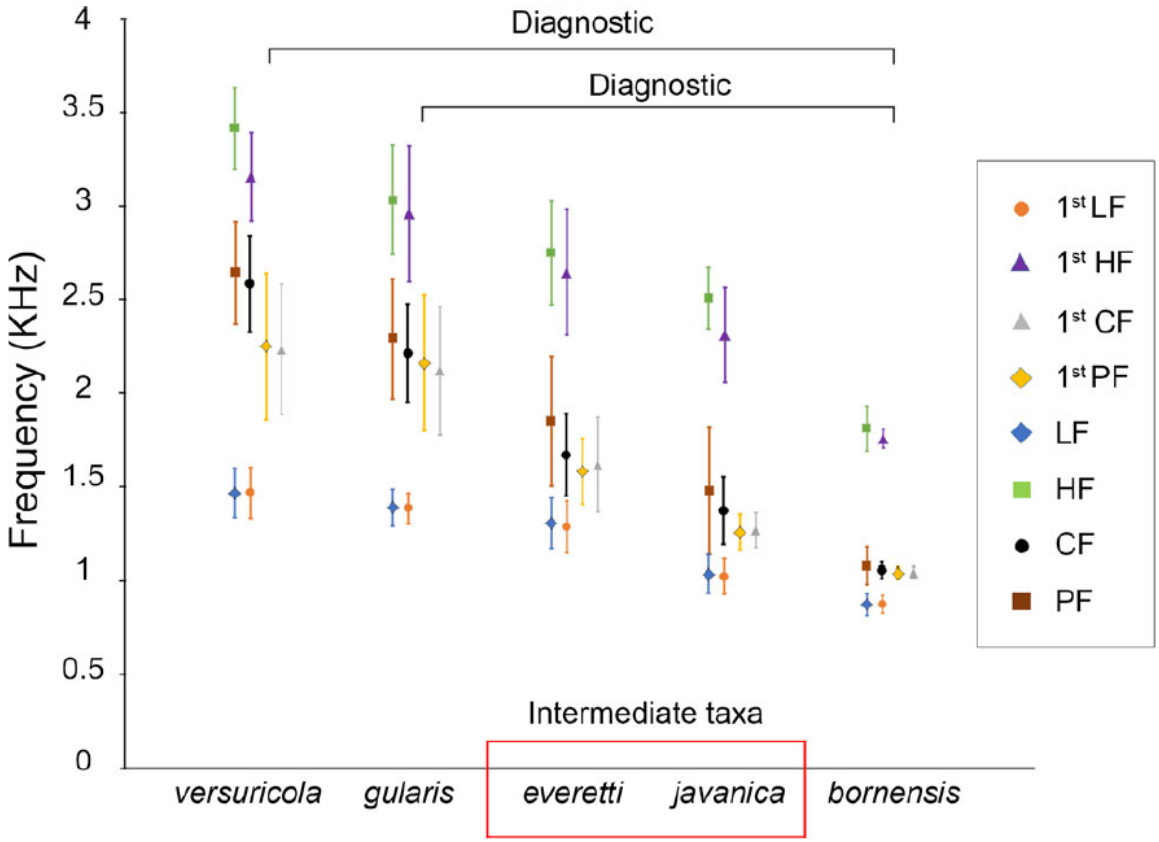

Figure 7 Mean and standard deviation of the bio-acoustic measurements of the song type 1 of subspecies *versuricola*, *gularis*, *everetti*, *javanica*, and *bornensis*. Only parameters found diagnosable for all comparisons between *gularis* and *bornensis*; and *bornensis* and *versuricola* are shown. LF low frequency, HF high frequency, CF center frequency, PF peak frequency [caption and figure from Cros & Rhinedt 2017]

Table 2 Diagnosability for acoustic parameters across pairwise comparisons within the Striped Tit-Babbler complex (non-diagnosable comparisons between neighbouring taxa not shown) according to the Isler criterion (see "Methods")

Type of comparison	Species	1st element							Main element							Bout	Total
		LF	HF	FB	CF	PF	ED	EI	LF	HF	FB	CF	PF	ED	EI	ER	
Between neighbouring taxa	*lutescens/versuricola*		X														1
	lutescens/saraburiensis	X			X												2
	lutescens/kinneari	X															1
Between adjacent taxa	*gularis/javanica*																0
	bornensis/javanica																0
	bornensis/everetti																0
	versuricola/everetti																0
	gularis/everetti																0
Between distant taxa	*gularis/bornensis*	X	X		X	X			X	X		X	X				8
	versuricola/bornensis	X	X		X	X			X	X	X	X	X				9
	gularis/rubicapilla																0
	gularis/versuricola																0

LF low frequency, *HF* high frequency, *DF* frequency bandwidth, *CF* center frequency, *PF* peak frequency, *ED* element duration, *ER* element rate, *EI* element interval

Biogeography

The genomic distinctiveness of *woodi* is perhaps unsurprising, as there are several other instances in which Palawan populations have been recognized as distinct species from the larger taxa they are associated with (for example, Melodious Babbler *Malacopteron palawanense* has been recognized as distinct from Rufous-crowned Babbler *M. magnum*; Ashy-headed Babbler *Pellorneum cinereiceps* is distinct from Short-tailed Babbler *P. malaccense*; and Palawan Fairy Bluebird *Irena tweeddalii* is distinct from Asian Fairy Bluebird *I. puella*). Palawan and its neighboring islands (including Balabac) would not have been connected to the Philippines during Pleistocene glaciations – these islands are actually geographically closer to Borneo (although it is unclear whether they were actually stably connected during glacial cycles) (Berman et al. 2024). Given these complex dynamics, it is not unprecedented that the *Mixornis* taxon on Palawan and Balabac is genomically highly differentiated from others in the region.

Similarly, the results for the Natuna and Anambas *Mixornis* taxa are also unsurprising. Although the Natuna islands are geographically closer to Borneo than the Malay Peninsula, the course of paleo-rivers and the associated interfluvia formed mean that Natuna and Anambas islands may have stronger connectivity with the Malay Peninsula. A large paleo-river originating in Sumatra is known to have run across the Sunda Shelf (Voris 2000), just east of the Natuna and Anambas islands. This river would have potentially minimized gene flow between these islands and Borneo - from Berman et al. (2024): "*the position of paleo-river catchments would suggest that these islands had a closer connectivity with the Malay Peninsula and Sumatra than with Borneo, so that tit-babblers inhabiting them would more likely pertain to pin-striped M. gularis, akin to populations of other songbirds on Natuna and Anambas (Garg et al. 2022).*" We note that these other songbirds referenced here are also babblers.

Conclusion

Tropical Asia RAG proposes recognizing *Mixornis gularis woodi* from Balabac and Palawan as a full species (Palawan Tit-babbler *Mixornis woodi*), on the basis of morphological and genomic analyses presented in Berman et al. (2024) (we also include supplementary comparative photos of this taxon and its original description in the Appendix). Genome-wide analysis shows this taxon to be basal to *M. gularis* and *M. bornensis* – therefore, its current taxonomic treatment is untenable and we recommend recognizing it as a distinct species.

Berman et al. (2024) also provides strong morphological and genomic evidence that the taxa *everetti* and *zophera* have more affinity with *Mixornis gularis* than *M. bornensis*. Therefore, Tropical Asia RAG proposes recognizing these two taxa as well as *zaperissus* as subspecies of *M. gularis* rather than the current treatment whereby they are recognized as subspecies of *M. bornensis*. We note that *zaperissus* from N Natunas (except Bunguran) was not sampled in this study nor the Cros & Rheindt (2017) bioacoustic study – however, *everetti*, *zophera* and *zaperissus* are all found in close proximity to each other in the Anambas and Natuna islands, and are described as being morphologically similar. Therefore, we also include this taxon in our recommendation.

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Appendix

Appendix 1 Top row: Photos of *woodi* taxon from Palawan (Philippines), showing its lightly streaked breast and greyish head (Macaulay Library ML 49131761 and ML 72544681) Bottom row: Comparison photos of *Mixornis gularis* from Yunnan (China) and Kaeng Krachan (Thailand) (Macaulay Library ML 187183921 and ML656030129)

MIXORNIS, Hodgson.

69. MIXORNIS WOODI, sp. n.

Ad. similis *M. pileatæ*, sed facie laterali cinerea, mento albo et dorso olivascenti-cineraceo distinguendus. Long. tot. 5·2, culm. 0·6, alæ 2·35, caudæ 2·25, tarsi 0·8.

a, *b*. ♂. Puerto Princesa, Palawan.
c. ♂. Puerto Princesa. Eyes flesh-colour.
d. ♂. Puerto Princesa. Eyes hazel.

[Only found in the deep brush.—J. B. S.]

Appendix 2 original description of *Mixornis woodi* as a species by Sharpe 1877.

“Adult similar to *M. pileata*, but distinguished by the lateral face being grey, the chin white, and the back olive-grey.
Total length 5.2, culmen 0.6, wing 2.35, tail 2.25, tarsus 0.8.”