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When colors mislead: Genomics and bioacoustics prompt re-classification of Asian flycatcher radiation (Aves: Niltavinae)

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ABSTRACT

Traditional classification of many animals, including birds, has been highly dependent on external morphological characters like plumage coloration. However, both bioacoustics and genetic or genomic data have revolutionized our understanding of the relationships of certain lineages and led to sweeping taxonomic re-organizations. In this study, we present a case of erroneous delimitation of genus boundaries in the species-rich flycatcher subfamily Niltavinae. Genera within this subfamily have historically been delineated based on blue versus brown male body plumage until recent studies based on a few mitochondrial and nuclear loci unearthed several cases of generic misclassification. Here we use extensive bioacoustic data from 43 species and genomic data from 28 species for a fundamental reclassification of species in the Niltavinae. Our study reveals that song is an important trait to classify these birds even at the genus level, whereas plumage traits exhibit ample convergence and have led to numerous historic misattributions. Our taxonomic re-organization leads to new biogeographic limits of major genera, such that the genus *Cyornis* now only extends as far east as the islands of Sulawesi, Sula, and Banggai, whereas *Eumyias* is redefined to extend far beyond Wallace's Line to the islands of Seram and Timor. Our conclusions advise against an over-reliance on morphological traits and underscore the importance of integrative datasets.

1. Introduction

Ever since the adoption of Carl von Linné's hierarchical classification of organisms (Linnaeus, 1758), generations of museum taxonomists have refined our understanding of the evolutionary relationships of the world's animals. In their quest, they have had to rely on the external and

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internal character traits that museum specimens exhibit, with only rare recourse to life-history data on behavior, lifestyle, habitat and vocalizations (Dyke and Van Tuinen, 2004, Gadow, 1892, Huxley, 1867, Livezey and Zusi, 2007, Töpfer, 2018, Webster, 2017). Meanwhile, over the past half-century, the genetic revolution has helped uncover numerous instances in which traditional museum taxonomists may have been misled. Some of the more consequential DNA-driven taxonomic rearrangements include the demonstration of reptile paraphyly along with major rearrangements in other vertebrates (Chiari et al., 2012, Jarvis et al., 2014, Jebb et al., 2020, Sibley and Ahlquist, 1990, Wang et al., 2013, Wilson et al., 1977). Even so, a majority of taxonomic arrangements in lower-level animal groups, such as genera and families, continue to be based on traditional insights gained from museum specimens (Kaliontzopoulou, 2011, Kasinathan et al., 2021, Lee and Palci, 2015, Wiens, 2004).

Skeletal features and shape have been a primary guide for higher-level classification into families, orders and classes among many organismic groups (Horovitz and Sánchez-Villagra, 2003, Kasinathan et al., 2021, Lee and Palci, 2015, Livezey and Zusi, 2007). However, taxonomists have often utilized coloration as a primary indicator for classification among the more closely related members of genera and subfamilies, especially in animal groups that rely on visual cues for sexual selection such as many birds (Aves).

Here we uncover a case of manifestly erroneous genus delimitation in an Asian songbird radiation, the flycatcher subfamily Niltavinae. Even before the subfamily was defined in its present circumscription (Sangster, et al., 2010, 2016, Zhao et al., 2023), its members had long been classified into five to six primary genera chiefly based on the presence or absence of a blue versus brown body coloration in males. Setting aside the smaller genera *Cyanoptila* and *Niltava*, whose generic

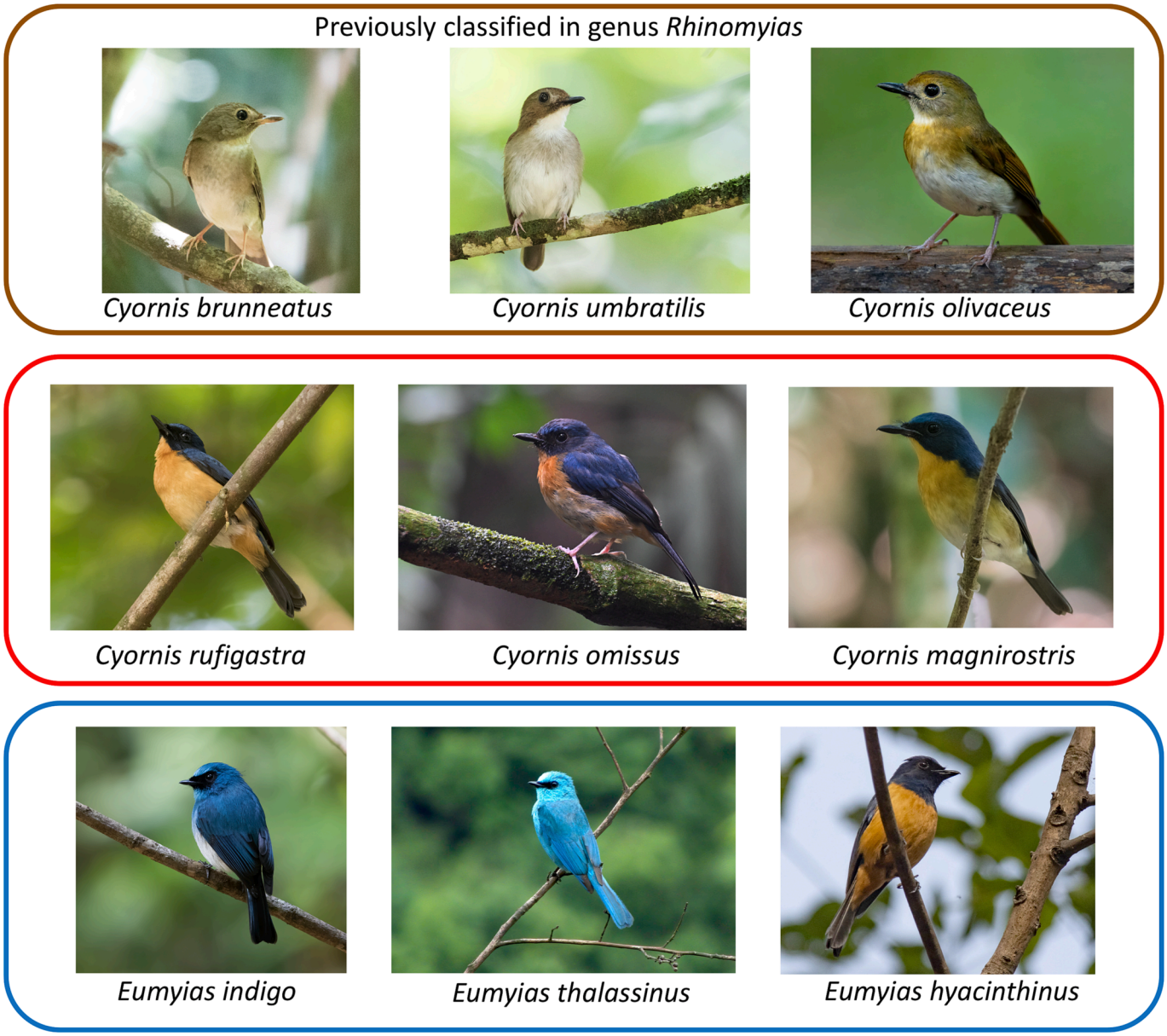

Fig. 1. Male representative members of the Niltavinae subfamily. Birds with a sexually monomorphic brown plumage were previously mostly classified in the genus *Rhinomyias* (brown box), sexually dimorphic birds with a male blue plumage with red underparts are mostly but not universally classified in the genus *Cyornis* (red box), and most monomorphic species with a blue plumage are ascribed to the genus *Eumyias*, although this study adds a number of red-bellied ones to the genus (blue box). Photo credits: Yong Chee Keita Sin (*Cyornis brunneatus*, *C. umbratilis*, *C. rufigastra*, and *Eumyias indigo*); John J. Harrison (*C. olivaceus*); Ting-Wei Hung (*C. omissus*); John le Rond (*C. magnirostris*); P.A. (*E. thalassinus*); Robert Tizard (*E. hyacinthinus*). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

circumscription has been stable for a long time, species have traditionally been divided into three main groups (Clement, 2006): (1) *Rhinomyias* "jungle-flycatchers", comprising ~ 7–12 sexually monomorphic species with a drab all-brown plumage; (2) *Cyornis* "blue-flycatchers", encompassing ~ 19–26 mostly sexually dimorphic species, overwhelmingly with bright blue males (often exhibiting rufous underparts); and (3) *Eumyias* "verditer flycatchers", with five species that usually have a mostly blue plumage in both sexes (Fig. 1).

Phylogenetic work based on mitochondrial DNA (mtDNA) and a few nuclear markers has clarified the relationships among these five genera and added further genera to the subfamily (Zhao et al., 2023), such as *Anthipes* (Sangster et al., 2010), *Leucoptilon* (Sangster et al., 2021) and *Sholicola* (Robin et al., 2017), most of which contain species previously misattributed to other subfamilies. In addition, traditional sequence data based on a combination of two to three dozen markers have unveiled that the brown *Rhinomyias* jungle-flycatchers and male-blue *Cyornis* blue-flycatchers are phylogenetically interdigitated (Sangster et al., 2010, Zhao et al., 2023), leading to a merger of both genera in most modern classifications (e.g., Clement et al., 2022, del Hoyo and Collar, 2016, Eaton et al., 2016, 2021, Gill et al., 2022). However, a large part of the classical Niltavinae arrangement continues to stand, especially with regards to *Eumyias* "verditer flycatchers".

In this study, we use thousands of genome-wide loci as well as a suite of bioacoustic characters to demonstrate that the color-based delimitation of the subfamily Niltavinae is erroneous. Instead the songs of these flycatchers provide an easy guide to their actual relationships in agreement with genome-wide data, but *contra* the traditional plumage-based classification.

2. Methods

2.1. Vocal sampling and analysis

We collected a total of 574 sound recordings from various sources, including our private collections, Xeno-canto (https://www.xeno-canto.org), Macaulay Library (https://macaulaylibrary.org), and the Avian Vocalization Center (https://avocet.zoology.msu.edu). A number of taxa were represented by variable song types across recordings. Therefore, we screened through all recordings to ensure only the homologous territorial song was used for analysis. The screening was conducted by selecting the typical song type of each taxon and filtering out calls, such as juvenile begging calls and short alarm calls. After removal of non-homologous, poor-quality, duplicate, and misidentified recordings, we retained a total of 471 recordings for analysis (Table S1). Altogether, our sound collection represents 68.75 % of *Cyornis* species (n = 22 out 32 recognized species), all *Eumyias* species (n = 11), 85.71 % of *Niltava* species (n = 6 out of 7 recognized species), as well as all recognized *Cyanoptila* (n = 2) and *Anthipes* species (n = 2) (species count following newly revised classification according to the present data; see Table S1 and Fig. S2 for details). Parameter variance was minimal across different motif measurements within one recording (i.e., within one individual), allowing us to use parameter means for downstream analyses.

For bioacoustic analysis, we classified and measured songs following the methodology of Gwee et al. (2019). In brief, default settings in Raven Pro 1.4 were used with the window size adjusted to 1024 to obtain best resolution across all recordings. Pre-analysis inspection revealed no systematic differences in the distribution of temporal and frequency parameters across recordings of different formats of the same species (data not shown). Hence, recordings of different sound file formats were merged into one dataset.

A song motif was defined as being composed of a constant and consistently repeated set and arrangement of song elements (i.e., continuous trace elements on a sonogram) within a song bout. We measured a total of six parameters for each homologous song motif (see Gwee et al., 2019): (i) average number of elements on the sonogram per motif, (ii) average duration of a motif, (iii) average minimum frequency of a motif, (iv) average maximum frequency of a motif, (v) average peak frequency (i.e., the frequency with the highest amplitude) of a motif, and (vi) average bandwidth (i.e., maximum minus minimum frequency) of a motif. We measured at least five motifs for each recording, or we measured all motifs when the recording contained less than five motifs. The mean for each vocal parameter was then calculated for each species from the means of each individual recording. Subsequently, R version 3.5.0 (R Core Team, 2018) on RStudio (https://www.rstudio.com) was used to conduct principal component analysis (PCA) on the vocal dataset to distinguish among the five flycatcher genera.

2.2. Molecular sampling and DNA extraction

We sampled representatives of all the currently recognized constituent genera (*Anthipes*, *Leucoptilon*, *Cyornis*, *Niltava*, *Cyanoptila* and *Eumyias*) within the newly described subfamily Niltavinae except the divergent *Sholicola* (Robin et al., 2017). We obtained tissue samples (blood or muscle) for 117 individuals belonging to 28 species (~51 % of the recognized species) from various museum collections as well as our own field efforts; details of sample localities and sources are provided in Table S2. We extracted DNA using the DNeasy Blood and Tissue Kit (QIAGEN, Germany) following the manufacturer's instructions and quantified double-stranded DNA using a Qubit high sensitivity DNA Assay kit (Invitrogen, USA). This study complied with all ethical regulations, and protocols were approved by the National University of Singapore Institutional Animal Care and Use Committee (IACUC, Protocol Number: L2017-00459).

2.3. ddRAD-Seq library preparation, data filtering and data matrix generation

We employed a double digest restriction-enzyme associated DNA sequencing (ddRAD-Seq) methodology to obtain genome-wide markers. We prepared ddRAD-Seq libraries following an established protocol (Peterson et al., 2012) with modifications (Chattopadhyay et al., 2016). We used EcoRI and MspI restriction enzymes for digesting the DNA and either used Sera-Mag magnetic beads (Thermo Scientific, USA) or Pippin prep (Sage Science, USA) for size selection (250–500 bp fragments). For final library amplification, we performed 12 PCR cycles. Then libraries were pooled at equimolar concentrations and run on two 150 bp paired end lanes on a HiSeq 4000 platform at Novogene, Beijing, and the Genome Institute of Singapore.

We performed quality checks on the raw reads in FastQC (Andrews, 2010) and used default settings in ipyrad v.0.7.23 (Eaton and Overcast, 2020) to demultiplex and clean the sequence data. We trimmed the 3′ ends of all reads by removing the last 10 bases. Further, any read containing more than five bases with PHRED scores lower than 20 was removed. We used strict settings for adapter removal and allowed for no mismatch in barcodes during demultiplexing steps. Finally, any read less than 35 bp after adapter removal was discarded during this step. We generated multiple datasets (read 1 only, read 2 only and both reads together) with two different levels of missing data allowance (30 % and 50 %) for each dataset (Table 1). In addition, we generated datasets with two levels of clustering thresholds (default 85 %, and a lower threshold of 80 %) to identify the optimal value for *de novo* locus generation. The clustering threshold is the most important parameter for identifying and assembling ddRAD-Seq loci. We used the default setting equivalent to the minimum read depth for statistical base calling (six reads). The parameter files used for ipyrad are provided as supplementary information.

In total, we generated 12 datasets varying in the level of missing data and clustering thresholds as summarized in Table 1. As there was no considerable difference in the number of loci generated between 80 % and 85 % clustering thresholds (Table 1), we continued with the default clustering threshold of 85 % for all downstream analyses. We retained only few loci when including both reads for data generation in ipyrad,

Table 1
Summary of different genomic data matrices generated in this study. Datasets in bold were used for phylogenetic analysis. Abbreviation: NA = not applicable.

Dataset ID	Read type	Clustering level	Level of missing data	Number of loci isolated	Number of loci retained after adding outgroup	Total data matrix length (in bp)
Dataset 1	Read 1 only	0.80	30 %	944	NA	NA
Dataset 2	Read 2 only	0.80	30 %	979	NA	NA
Dataset 3	Both reads	0.80	30 %	228	NA	NA
Dataset 4	Read 1 only	0.80	50 %	2,686	NA	NA
Dataset 5	Read 2 only	0.80	50 %	3,066	NA	NA
Dataset 6	Both reads	0.80	50 %	737	NA	NA
Dataset 7	**Read 1 only**	**0.85**	**30 %**	**951**	**909**	**124,538**
Dataset 8	**Read 2 only**	**0.85**	**30 %**	**1007**	**955**	**130,681**
Dataset 9	Both reads	0.85	30 %	249	NA	NA
Dataset 10	**Read 1 only**	**0.85**	**50 %**	**2,733**	**2,490**	**340,501**
Dataset 11	**Read 2 only**	**0.85**	**50 %**	**3,162**	**2,882**	**394,032**
Dataset 12	Both reads	0.85	50 %	806	NA	NA

potentially due to differences in the size selection protocols used across samples (bead-based and automated size selection using Pippin prep) (Table 1). Therefore, we discarded the datasets containing both reads. This filtering regime resulted in four primary datasets for phylogenomic analysis (datasets 7, 8, 10 and 11; Table 1), all of them based on a clustering threshold of 85 %. Datasets 7 and 10 were generated using on only read 1 and allowing for 30 % and 50 % missing data, respectively, whereas datasets 8 and 11 were generated using only read 2 and allowing for 30 % and 50 % missing data, respectively (Table 1). The number of ddRAD-Seq loci varied between 961 and 3,162 across these datasets (Table 1).

We included the collared flycatcher *Ficedula albicollis* as an outgroup. The sequence for the outgroup was isolated from its available genome sequence (GCA_000247815.2; Ellegren et al., 2012) following the method outlined by Chattopadhyay et al. (2020) (for general workflow and code see https://github.com/gargkritika/append_sequences_to_existing_alignments). In brief, we used BLASTn (Altschul et al., 1990) to identify similar region for each locus identified using ipyrad in the *Ficedula albicollis* genome. Only single BLAST hits with an e-value < 10E-15 were filtered and isolated from the *Ficedula albicollis* genome. We employed MAFFT (Katoh and Standley, 2013) to realign the outgroup sequence with the sequences isolated using ipyrad. Finally, we only retained loci for which an outgroup sequence was available for further phylogenomic analysis (see Table 1 for the number of loci retained).

2.4. Phylogenomic analysis

We employed both concatenation and species tree approaches to reconstruct the phylogenetic relationships among members of the Niltavinae subfamily. We generated phylogenetic trees for all four main datasets selected for downstream analyses. For the concatenated tree approach, we used the maximum likelihood framework as implemented in RAxML 8.2.4 (Stamatakis, 2014), applying a GTR + Gamma model of sequence evolution and performing a single full maximum likelihood tree search using the rapid bootstrap algorithm with 1,000 replicates. The *Ficedula albicollis* sample served as an outgroup, and the tree was visualized in FigTree 1.4.2 (Rambaut, 2015).

We utilized MP-EST 1.6 (Liu et al., 2010) and ASTRAL 5.6.3 (Rabiee et al., 2019, Zhang et al., 2018) to generate species trees. MP-EST generates species trees by maximizing the pseudo-likelihood function from a set of rooted gene trees (Liu et al., 2010), whereas ASTRAL estimates unrooted species trees from a set of unrooted gene trees using a multi-species coalescent model (Zhang et al., 2018). We constructed gene trees using RAxML within the phyluce pipeline 1.6.6 (Faircloth, 2016), with 100 bootstrap trees generated for each gene tree. The gene trees were rooted using the STRAW server (http://bioinformatics.publichealth.uga.edu/SpeciesTreeAnalysis/) for MP-EST analysis following Chattopadhyay et al. (2020). In brief, we reconstructed the species tree for each bootstrap file in MP-EST. The 100 MP-EST trees were used as input to build a majority-rule consensus tree using Phylip v3.69 (Felsenstein, 2005). For ASTRAL analysis, RAxML gene trees were used to compute ASTRAL support values as an equivalent of local posterior probabilities. All final trees were viewed in FigTree 1.4.2 (Rambaut, A. 2015).

3. Results

3.1. Vocal analysis

For members of the genera *Eumyias* and *Cyornis*, two distinct bioacoustic clusters emerged that were consistent with a redefinition of each genus according to genomic data (green and blue clusters in Fig. 2). These two clusters were largely distinct in bioacoustic space from *Anthipes*, but overlapped fully with *Cyanoptila* and partly with *Niltava* (Fig. 2). Two distinct vocal clusters were found within the genus *Niltava*, one of which was vocally offset from all the other flycatcher genera in the study (Fig. 2).

The genus *Eumyias*, as redefined in this study, is characterized by species with long "reeling" song motifs that contain more elements on average that those of the other genera (Fig. 2, S1, S2). In contrast, members of the reconstituted genus *Cyornis* typically utter songs composed of no more than a handful to a dozen elements, melodiously assembled into a "tinkling" song strophe (Fig. 2, S1, S2). Both these genera have song profiles that are largely distinct from the smaller genera which have traditionally been placed apart, such as *Niltava, Anthipes* or *Cyanoptila*.

We repeated PCA to account for the low sample size of a few taxa, and removed species for which there were fewer than 3 sound recordings available for analysis. This rarefied dataset produced equal results (Fig. S3). Further, linear discriminant analysis was also performed on the vocal data (see supporting information), which could accurately predict and assign 81.8 % of the observations to the correct genera (Fig. S4). Both the rarified PCA and the linear discriminant analysis underscore the importance of song in the generic classification within the subfamily Niltavinae.

3.2. Genomic data matrix

We obtained a total of ~ 455 million clean reads. The number of reads per sample varied between 33,261 and 8,537,711, with an average of 3.9 million reads (±1.4 million, standard deviation). We discarded four samples due to low number of reads (Table S2), resulting in 113

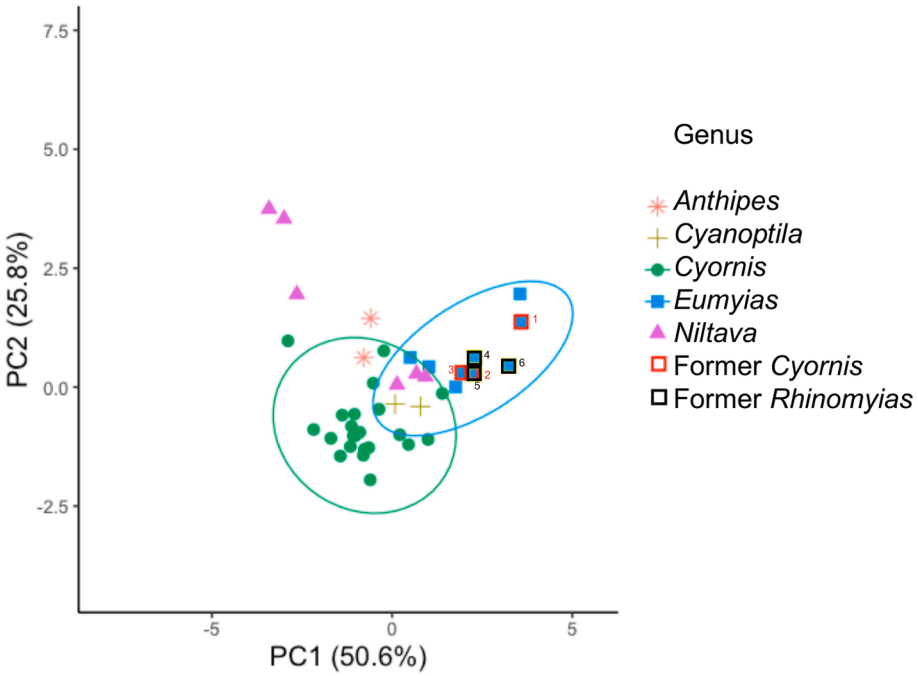

Fig. 2. Principal component analysis based on six vocal parameters, each symbol representing one species, with the green and blue ellipses representing 95% confidence intervals of the principal component scores for the genera *Cyornis* (green circles) and *Eumyias* (blue squares), respectively. Genera are assigned based on the results of this study. Six *Eumyias* species labelled in Arabic numbers 1 to 6 (*E. sanfordi, E. hoevelli, E. hyacinthinus, E. additus, E. oscillans, E. stresemanni*) are marked with red and black frames, indicating their former classification as *Cyornis* and *Rhinomyias*, respectively, which is here shown to be erroneous based on bioacoustic (and in some cases genetic) data. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

samples with between 228 and 3,162 loci in ipyrad (Table 1). For phylogenomic analysis we constrained ourselves to four datasets (datasets 7, 8, 10 and 11; Table 1), retaining 909 to 2,882 loci after the inclusion of the outgroup (Table 1). Total sequence length of the phylogenomic alignments varied between 124,538 bp and 394,032 bp (Table 1).

3.3. Phylogenomic reconstruction

All four datasets returned the same overall relationships among the genera within Niltavinae for both the concatenated and species tree-based approaches (Fig. 3, S5–S15). Branch support values varied minimally across datasets, and resolution improved with an increase in size of the data matrix (Fig. 3, S5–S15). Overall, we observed better phylogenetic resolution with the concatenated tree in comparison with the species tree-based approach (Fig. 3, S5–S15). The relatively poorer support values for the two species tree approaches may be due to the generally low level of resolution obtained from the individual gene trees that are based on short ddRAD-Seq loci (~135 bp in length).

In all trees, *Leucoptilon concretum* was basal to all other Niltavinae (corroborating Sangster et al., 2021). The re-circumscribed *Eumyias* always emerged as sister to *Cyanoptila*, while the re-circumscribed *Cyornis* always came out as the sister lineage to *Anthipes* (Fig. 3, S5–S15); the two large and re-circumscribed genera were never reflected as closely related to each other within the Niltavinae, corroborating bioacoustic results (Fig. 2). The position of *Niltava* varied among trees, but it never emerged as a closely related sister group to any traditional niltavine genus (Fig. 3, S5–S15).

4. Discussion

4.1. Color is not an adequate indicator of generic relationships in Niltavinae

Bioacoustic analysis of 43 Niltavinae species indicates that five species from the genus *Cyornis* (including formerly *Rhinomyias*) should be reassigned to *Eumyias*. Two Wallacean species, *E. hoevelli* and *E. hyacinthinus*, are currently widely attributed to *Cyornis* because of their obvious sexual dimorphism, with bright males sporting blue upperparts and reddish underparts in contrast to drab all-brown females (Fig. 1). Furthermore, despite their overall drab plumages in both males and females, *E. sanfordi, E. oscillans* and *E. stresemanni* are also widely attributed to *Cyornis* (the latter two previously to *Rhinomyias* before that genus had been sunk into *Cyornis*) (e.g., Coates and Bishop, 1997). However, the long reeling songs of these five species are similar in character to those of other members of *Eumyias*, as corroborated by bioacoustic PCA (Fig. 2), and underscore that plumage coloration is often convergent and does not reliably reflect phylogenetic relationships.

Although based on fewer taxa, our phylogenomic analyses corroborate the results of bioacoustic inquiry. Out of the five species reassigned to *Eumyias* based on acoustic data, our genomic sampling covers "*Cyornis hyacinthinus*" from Timor (eastern Indonesia), which indeed emerges as embedded within *Eumyias* (Fig. 3). *Eumyias hyacinthinus* is perhaps the best example of a species with a bright blue-and-red male plumage (Fig. 1) that had never been associated with the all-blue members of the genus *Eumyias* before our bioacoustic and genomic datasets suggested its placement there, as also reflected in a recently-published bird identification guide (Eaton et al., 2021) co-authored by one of us.

4.2. The importance of song traits in Niltavinae

Museum taxonomists predominantly know their objects from inspection on a specimen tray, with limited insights from the field. Our new acoustics-based classification of Niltavinae will be less surprising to field ornithologists intimately familiar with these flycatchers' vocalizations from the forest. Describing the rationale for the new generic treatment of *Eumyias* and *Cyornis* in a recent bird identification field guide, Rheindt (2021) stated that some "…'blue-flycatchers' (former

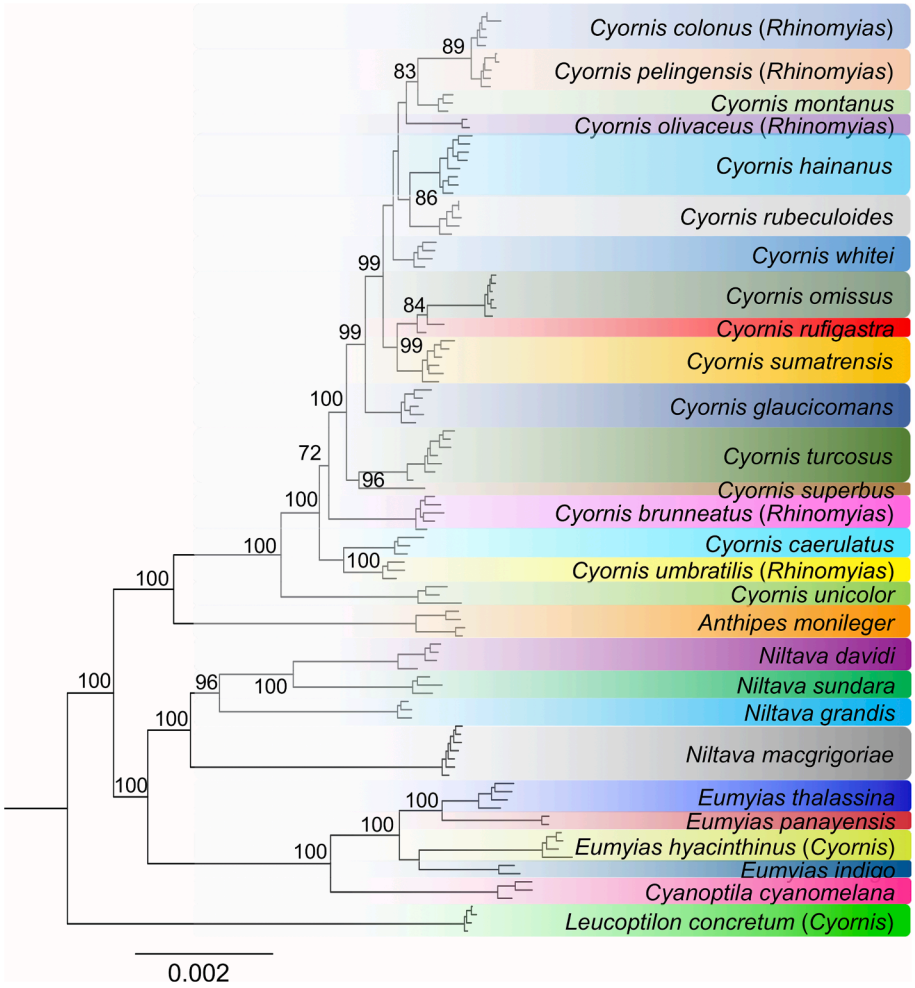

Fig. 3. Phylogenetic relationships among various members of the Niltavinae subfamily based on 909 concatenated ddRAD-Seq loci amounting to a 124,538 bp alignment (dataset 7, see Table 1). RAxML was used to construct the maximum likelihood tree. Outgroup (*Ficedula albicollis*) not shown. For species traditionally classified under a different genus, former genus names are provided in brackets following the species name. Nodal values indicate bootstrap support. Support values shown only for major nodes. Scale bar represents substitutions per nucleotide site. Colors are used to identify samples belonging to individual taxa on the tree.

Cyornis) and 'jungle-flycatchers' (former *Rhinomyias*) from eastern Indonesia share with members of *Eumyias* a continuous, endless, reeling warble that sets them apart from the tinkling, metallic sounds of true jungle-flycatchers. All these species require to be assigned to *Eumyias*, which now – with its larger composition – is best referred to as 'warbling-flycatchers'…". The two general song types described in that account are congruent with the two clouds of song types reflected in our bioacoustic PCA (Fig. 2). We recommend that the four global avian taxonomic checklists as of 2023 (Clements et al., 2022, del Hoyo and Collar, 2016, Dickinson and Christidis, 2014, Gill et al., 2022), which often await peer-reviewed results before implementing taxonomic change to avoid mistakes, consider the adoption of the present treatment of all *Eumyias* under the name "warbling-flycatchers", while classifying members of the reconstituted *Cyornis* exclusively under the more appropriate name "jungle-flycatchers", eliminating the name "blue-fly-catchers", which – although still widely used – does not refer to a monophyletic lineage and would be inappropriate to refer to all-brown species.

4.3. Biogeographic implications

With the considerable rearrangement of genera within Niltavinae (see taxonomic synopsis below), numerous important biogeographic ramifications arise. The genus *Eumyias* in its new circumscription is a tropical to subtropical Asian assemblage of species now reaching far beyond the borders of Asia and Wallace's Line to islands as far east as Buru and Timor (Fig. 4). In contrast, the jungle-flycatchers of the genus *Cyornis* are no longer known to occur in southern and eastern parts of Wallacea, only reaching Sulawesi, Sula and a number of satellite islands (Fig. 4).

4.4. Taxonomic recommendations

Based on the current study and previous work (Eaton et al., 2016, 2021, Garg et al., 2018, Gwee et al., 2019, Robin et al., 2017, Sangster, et al., 2010, 2016, 2021, Zhao et al., 2023), we suggest the following taxonomic recommendations for the genera *Cyornis* and *Eumyias*. The order of species generally follows del Hoyo and Collar (2016). We exclusively use the English name "jungle-flycatcher" for members of *Cyornis* following Rheindt (2021) as opposed to the widespread mixed usage of "blue-flycatcher" and "jungle-flycatcher". Following the same source, we also use "warbling-flycatcher" for members of *Eumyias*. Otherwise, our English names largely follow Eaton et al. (2021) or – for species not covered therein – del Hoyo and Collar (2016). Taxa in bold font were included in this study (see Table S1 and S2 for details).

GENUS *Cyornis* Blyth, 1843 – jungle-flycatchers.

- *Cyornis ruckii* (Oustalet, 1881) – monotypic – Rück's jungle-flycatcher – taxon unknown in life, provisionally retained in *Cyornis* in the absence of molecular data, although its plumage

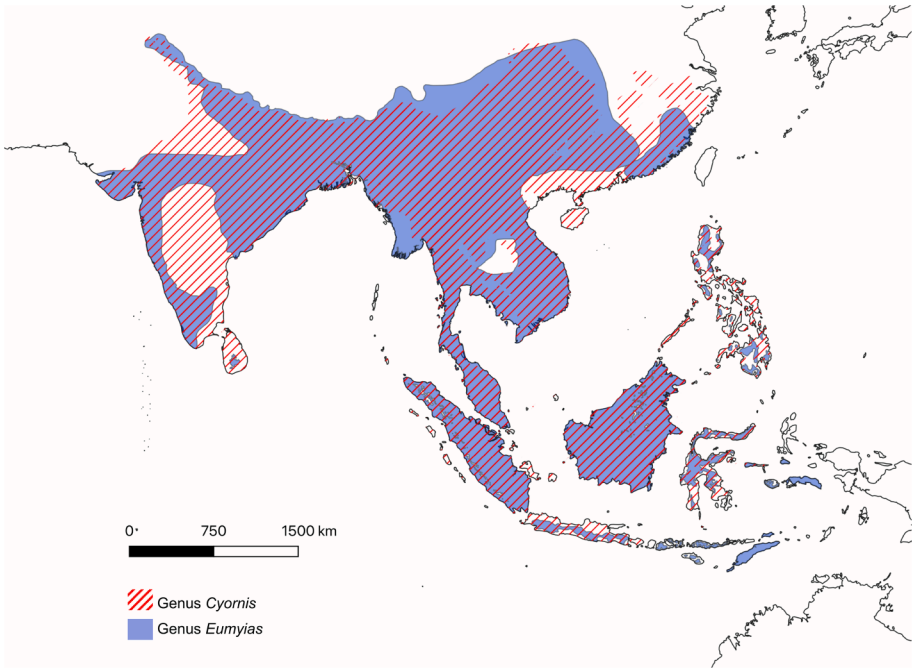

Fig. 4. Revised distribution of the genus *Cyornis* depicted in red oblique lines, and of the genus *Eumyias* depicted in solid blue color. The distribution of the genus *Eumyias* now extends beyond Wallace's Line to islands as far east as Seram and Timor, whereas that of the genus *Cyornis* only extends as far east as the Banggai and Sula archipelagos. The shape files for the species were obtained from the International Union for the Conservation of Nature. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

resemblance to *Leucoptilon concretum* may require future transfer to the latter's genus

- *Cyornis herioti* Wardlaw-Ramsay, 1886 – monotypic – Blue-breasted jungle-flycatcher – placement in *Cyornis* confirmed molecularly by Zhao et al. (2023)
- *Cyornis camarinensis* (Rand and Rabor, 1967) – monotypic – Rufous-breasted jungle-flycatcher – for a long time included under *C. herioti*, but separated on account of its distinct plumage by del Hoyo and Collar (2016)
- ***Cyornis hainanus*** (Ogilvie-Grant, 1900) – Hainan jungle-flycatcher – placement in *Cyornis* first confirmed molecularly by Zhang et al. (2016)
  - o *C. h. hainanus*
  - o *C. h. klossi* Robinson, 1921 – see Zhang et al. (2016) and Ng et al. (2023) for reassignment of this taxon from *C. rubeculoides* to *C. hainanus*
  - o *felsenstein C. h. dialilaemus* Salvadori, 1889 – traditionally placed under *C. rubeculoides*, but Singh et al. (2019) presented molecular evidence for probable inclusion as subspecies of *C. hainanus*, where we place it provisionally
- *Cyornis pallidipes* (Jerdon, 1840) – monotypic – White-bellied jungle-flycatcher – placement in *Cyornis* confirmed molecularly by Zhao et al. (2023)
- *Cyornis poliogenys* Brooks, 1880 – Pale-chinned jungle-flycatcher – placement in *Cyornis* first confirmed molecularly by Sangster et al. (2010):
  - o *C. p. poliogenys*
  - o *C. p. cachariensis* (von Madarász, 1884)
  - o *C. p. laurentei* (La Touche, 1921)
  - o *C. p. vernayi* Whistler, 1931
- ***Cyornis unicolor*** Blyth, 1843 – Pale-blue jungle-flycatcher – placement in *Cyornis* first confirmed molecularly by Sangster et al. (2010); a continued treatment of the following three taxa as subspecies (not species) was supported by bioacoustic analysis (Gwee et al., 2019):
  - o *C. u. unicolor*
  - o *C. u. diaoluoensis* (Zheng, Yang, and Lu, 1981)
  - o *C. u. cyanopolia* Blyth, 1870
- ***Cyornis rubeculoides*** (Vigors, 1831) – Blue-throated jungle-flycatcher – type species of *Cyornis* by subsequent designation (Gray, 1846); see *C. hainanus* for status of taxon *dialilaemus*, often attributed to this species
  - o *C. r. rubeculoides*
  - o *C. r. rogersi* Robinson and Kinnear, 1928 – see Singh et al. (2019) for status of *rogersi* as a deeply diverged subspecies of *C. rubeculoides*
- ***Cyornis glaucicomans*** Thayer and Bangs, 1909 – Chinese jungle-flycatcher – monotypic – see Zhang et al. (2016) and Ng et al. (2023) for molecular and vocal support for placement in *Cyornis* and for separation from *C. rubeculoides*
- ***Cyornis magnirostris*** Blyth, 1849 – Large jungle-flycatcher – monotypic – previously included in *C. banyumas* but now separated based on bioacoustic (Gwee et al., 2019) and molecular evidence (Zhao et al., 2023), the latter confirming placement in *Cyornis*
- ***Cyornis whitei*** Harington, 1908 – Hill jungle-flycatcher – previously included in *C. banyumas* but now separated based on bioacoustic (Gwee et al., 2019) and molecular evidence (Zhang et al., 2016, Zhao et al., 2023), the latter confirming placement in *Cyornis*
  - o *C. w. whitei*
  - o *C. w. lekhakuni* (Deignan, 1956)
  - o *C. w. deignani* Meyer de Schauensee, 1939
  - o *C. w. coerulifrons* Baker, 1918
- ***Cyornis banyumas*** Horsfield, 1821 – Javan jungle-flycatcher – see Gwee et al. (2019), Zhang et al. (2016), Eaton et al. (2021) and Zhao et al. (2023) for evidence to separate various taxa which had previously been subsumed under *C. banyumas*, and for corroboration of placement in *Cyornis*
  - o *C. b. banyumas*
  - o *C. b. ligus* (Deignan, 1947)
- ***Cyornis montanus*** Robinson and Kinnear, 1928 – Dayak jungle-flycatcher – monotypic – previously included in *C. banyumas* but now separated based on bioacoustic (Gwee et al., 2019) and

molecular evidence (Zhang et al., 2016, Zhao et al., 2023), the latter confirming placement in *Cyornis*

- *Cyornis kadayangensis* Irham, Haryoko, Shakya et al., 2022 – Meratus jungle-flycatcher – monotypic – newly described by Irham et al. (2022) who molecularly confirmed placement within *Cyornis*
- ***Cyornis caerulatus*** (Bonaparte, 1857) – Sunda jungle-flycatcher – placement in *Cyornis* first molecularly confirmed by Zhang et al. (2016); a continued treatment of the following three taxa as subspecies (not separate species) was supported by bioacoustic analysis (Gwee et al., 2019):
  - o *C. c. caerulatus*
  - o *C. c. albiventer* Junge, 1933
  - o *C. c. rufifrons* Wallace, 1865
- ***Cyornis turcosus*** Brüggemann, 1877 – Malaysian jungle-flycatcher – monotypic – placement in *Cyornis* first molecularly confirmed by Zhang et al. (2016)
- ***Cyornis lemprieri*** (Sharpe, 1884) – Palawan jungle-flycatcher – monotypic – placement in *Cyornis* molecularly confirmed by Zhao et al. (2023)
- ***Cyornis superbus*** Stresemann, 1925 – Bornean jungle-flycatcher – monotypic – placement in *Cyornis* molecularly confirmed by Zhao et al. (2023)
- ***Cyornis tickelliae*** Blyth, 1843 – Tickell's jungle-flycatcher – placement in *Cyornis* first molecularly confirmed by Zhang et al. (2016); see *C. sumatrensis* for the latter's previous inclusion under *C. tickelliae*
  - o *C. t. tickelliae*
  - o *C. t. jerdoni* Holdsworth, 1872
- ***Cyornis sumatrensis*** (Sharpe, 1879) – Indochinese jungle-flycatcher – for a long time included under *C. tickelliae*, but now separated based on bioacoustic evidence (Gwee et al., 2019) and plumage traits (del Hoyo and Collar, 2016):
  - o *C. s. sumatrensis*
  - o *C. s. indochina* Chasen and Kloss, 1928
  - o *C. s. lamprus* Oberholser, 1917
- ***Cyornis rufigastra*** (Raffles, 1822) – Mangrove jungle-flycatcher – placement in *Cyornis* first molecularly confirmed by Zhang et al. (2016); a continued treatment of some of the following taxa as subspecies (not separate species) was supported by bioacoustic analysis (Gwee et al., 2019):
  - o *C. r. rufigastra*
  - o *C. r. longipennis* Chasen and Kloss, 1930
  - o *C. r. rhizophorae* Stresemann, 1925
  - o *C. r. karimatensis* Oberholser, 1924
  - o *C. r. blythi* Giebel, 1875
  - o *C. r. marinduquensis* duPont, 1972
  - o *C. r. philippinensis* Sharpe, 1877
- ***Cyornis omissus*** (Hartert, 1896) – Sulawesi jungle-flycatcher – for a long time included with *C. rufigastra* but see Gwee et al. (2019) and Rheindt et al. (2020) for molecular and bioacoustic evidence for separation:
  - o *C. o. omissus*
  - o *C. o. omississimus* Rheindt, Prawiradilaga, Ashari, Suparno and Gwee, 2020
  - o *C. o. peromissus* Hartert, 1920
  - o *C. o. djampeanus* (Hartert, 1896) – see Gwee et al. (2019) for bioacoustic evidence supporting placement under *C. omissus*
- ***Cyornis kalaoensis*** (Hartert, 1896) – Kalao jungle-flycatcher – monotypic – for a long time subsumed under *C. omissus* and earlier under *C. rufigastra*, but see Gwee et al. (2019) for bioacoustic evidence for separation
- ***Cyornis brunneatus*** (Slater, 1897) – Brown-chested jungle-flycatcher – monotypic – traditionally placed in *Rhinomyias* and transferred to *Cyornis* following the dissolution of the former, but hitherto not analyzed molecularly or bioacoustically; see *C. nicobaricus* regarding the latter's separation from *C. brunneatus*
- *Cyornis nicobaricus* (Richmond, 1902) – Nicobar jungle-flycatcher – monotypic – until recently placed with *C. brunneatus* but now separated based on a combination of morphological and bioacoustic traits (del Hoyo and Collar, 2016)
- ***Cyornis umbratilis*** (Strickland, 1849) – Gray-chested jungle-flycatcher – monotypic – placement in *Cyornis* first confirmed molecularly by Sangster et al. (2010)
- ***Cyornis olivaceus*** Hume, 1877 – Fulvous-chested jungle-flycatcher – placement in *Cyornis* first confirmed molecularly by Sangster et al. (2010)
  - o *C. o. olivaceus*
  - o *C. o. perolivaceus* Chasen and Kloss, 1929
- ***Cyornis ruficauda*** (Sharpe, 1877) – Philippine jungle-flycatcher – placement in *Cyornis* confirmed molecularly by Zhao et al. (2023); see Gwee et al. (2019) for bioacoustic evidence for separation of *C. ocularis* and *C. ruficrissa*
  - o *C. r. ruficauda*
  - o *C. r. samarensis* (Steere, 1890)
  - o *C. r. boholensis* (Rand and Rabor, 1957)
  - o *C. r. zamboanga* (Rand and Rabor, 1957)
- ***Cyornis ocularis*** (Bourns and Worcester, 1894) – Sulu jungle-flycatcher – monotypic – for a long time included with *C. ruficauda*, but see Gwee et al. (2019) for bioacoustic evidence for separation
- ***Cyornis ruficrissa*** (Sharpe, 1887) – Crocker jungle-flycatcher – for a long time included with *C. ruficauda*, but see Gwee et al. (2019) for bioacoustic evidence for separation:
  - o *C. r. ruficrissa*
  - o *C. r. isola* (Hachisuka, 1932)
- ***Cyornis colonus*** (Hartert, 1898) – Sula jungle-flycatcher – monotypic – placement within *Cyornis* confirmed molecularly by Zhao et al. (2023); see *C. pelingensis* for the separation of that species
- ***Cyornis pelingensis*** (Vaurie, 1952) – Banggai jungle-flycatcher – monotypic – for a long time subsumed under *C. colonus*, but see Garg et al. (2018) for molecular and Gwee et al. (2019) for bioacoustic evidence for the separation of *C. pelingensis*

GENUS *Eumyias* Cabanis, 1851.

- ***Eumyias sanfordi*** (Stresemann, 1931) – Matinan warbling-flycatcher – monotypic – previously placed in *Cyornis* but here re-assigned based on our bioacoustic data (Fig. 2), which is also the basis for Eaton et al.'s (2021) re-assignment to *Eumyias*
- ***Eumyias hoevelli*** (Meyer, 1903) – Hoevell's warbling-flycatcher – monotypic – previously placed in *Cyornis* or *Niltava* but here re-assigned based on our bioacoustic data (Fig. 2), which is also the basis for Eaton et al.'s (2021) re-assignment to *Eumyias*
- ***Eumyias hyacinthinus*** (Temminck, 1820) – Timor warbling-flycatcher – previously placed in *Cyornis* or *Niltava* but here re-assigned based on our bioacoustic (Fig. 2) and genomic data (Fig. 3), which is also the basis for Eaton et al.'s (2021) re-assignment to *Eumyias*
  - o *E. h. hyacinthinus*
  - o *E. h. kuehni* (Hartert, 1904)
- ***Eumyias oscillans*** (Hartert, 1897) – Flores warbling-flycatcher – monotypic – previously placed in *Rhinomyias* and – later – *Cyornis*, but here re-assigned based on our bioacoustic (Fig. 2) evidence, which is also the basis for Eaton et al.'s (2021) re-assignment to *Eumyias*
- ***Eumyias stresemanni*** (Siebers, 1928) – Sumba warbling-flycatcher – monotypic – for a long time subsumed under *E. oscillans* and placed in *Rhinomyias* and – later – *Cyornis*, but here elevated to species level and re-assigned to *Eumyias* based on our bioacoustic (Fig. 2) evidence, which is also the basis for Eaton et al.'s (2021) treatment as separate species within *Eumyias*

- ***Eumyias sordidus*** (Walden, 1870) – Dull-blue warbling-flycatcher – monotypic – traditional placement within *Eumyias* here confirmed for the first time on the basis of bioacoustic analysis (Fig. 2)
- ***Eumyias albicaudatus*** (Jerdon, 1840) – Nilgiri warbling-flycatcher – monotypic – placement in *Eumyias* confirmed molecularly by Zhao et al. (2023)
- ***Eumyias indigo*** (Horsfield, 1821) – Indigo warbling-flycatcher – type species of *Eumyias* by monotypy
  - o *E. i. indigo*
  - o *E. i. ruficrissa* (Salvadori, 1879)
  - o *E. i. cerviniventris* (Sharpe, 1887)
- ***Eumyias thalassinus*** (Swainson, 1838) – Verditer warbling-flycatcher – placement in *Eumyias* first confirmed molecularly by Sangster et al. (2010)
  - o *E. t. thalassinus*
  - o *E. t. thalassoides* (Cabanis, 1851)
- ***Eumyias additus*** (Hartert, 1900) – Buru warbling-flycatcher – monotypic – traditionally placed in *Rhinomyias* but placement in *Eumyias* first confirmed molecularly by Sangster et al. (2010)
- ***Eumyias panayensis*** Sharpe, 1877 – Turquoise warbling-flycatcher – placement in *Eumyias* first confirmed molecularly by Sangster et al. (2010)
  - o *E. p. panayensis*
  - o *E. p. septentrionalis* (Büttikofer, 1893)
  - o *E. p. meridionalis* (Büttikofer, 1893)
  - o *E. p. obiensis* (Hartert, 1912)
  - o *E. p. harterti* (van Oort, 1911)
  - o *E. p. nigrimentalis* (Ogilvie-Grant, 1894)
  - o *E. p. nigriloris* (Hartert, 1904)

CRediT authorship contribution statement

Kritika M. Garg: Conceptualization, Formal analysis, Writing – original draft, Writing – review & editing, Visualization. **Chyi Yin Gwee:** Formal analysis, Writing – original draft, Writing – review & editing, Visualization. **Balaji Chattopadhyay:** Formal analysis. **Nathaniel S. Ng:** Resources. **Dewi M. Prawiradilaga:** Resources. **Gabriel David:** Resources. **Jérôme Fuchs:** Resources, Writing – original draft. **Hung Le Manh:** Resources. **Jonathan Martinez:** Resources. **Urban Olsson:** Resources, Writing – original draft. **Vuong Tan Tu:** Resources. **Sophea Chhin:** Resources. **Per Alström:** Resources, Writing – original draft. **Fumin Lei:** Resources. **Frank E. Rheindt:** Conceptualization, Writing – original draft, Writing – review & editing, Supervision, Project administration, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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DATA Accessibility.

Sequence data generated in this study have been submitted to NCBI Sequence Read Archive (PRJNA1015018). See table S2 for individual BioSample accession ID.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ympev.2023.107999.

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