

Re-assessing species limits in a morphologically cryptic Australasian kingfisher lineage (Coraciiformes: Halcyonidae) using bioacoustic data

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Received 22 December 2021; revised 22 March 2022; accepted for publication 26 March 2022

The common paradise-kingfisher, *Tanysiptera galatea*, species complex comprises 19 taxa distributed across New Guinea and Wallacea. Owing to its highly conserved morphological features, the lineage has been taxonomically confused, with 15 similar-plumaged taxa currently treated as conspecific. To shed light on species limits, we analysed eight bioacoustic parameters across 107 sound recordings using principal component analysis and the Isler criterion, among other methods. Our results show that multiple geographical entities of *Tanysiptera* paradise-kingfishers form discrete bioacoustic clusters across several vocal parameters, suggesting that species diversity of the common paradise-kingfisher complex has been greatly underestimated. Based on our results, we propose splitting *T. galatea* into six species: (1) Obi paradise-kingfisher, *Tanysiptera obiensis*; (2) Rossel paradise-kingfisher, *Tanysiptera rosseliana*; (3) Papuan paradise-kingfisher, *T. galatea*; (4) Halmahera paradise-kingfisher, *Tanysiptera margarethae*; (5) Morotai paradise-kingfisher, *Tanysiptera doris*; and (6) Amboyna paradise-kingfisher, *Tanysiptera nais*. Our work highlights that the non-invasive collection of avian vocal data is a crucial taxonomic tool and adds to increasing evidence that bioacoustic analyses are effective in elucidating cryptic diversity.

ADDITIONAL KEYWORDS: biogeography – evolution – islands – Melanesia – systematics – taxonomy.

INTRODUCTION

With their extravagant plumage and behaviour, kingfishers (families Alcedinidae and Halcyonidae) are among the most well-known bird families in the world. Not only are they well studied by evolutionary biologists and ornithologists, but their unique foraging behaviour has also attracted attention in fields of science such as physics (Crandell *et al.*, 2019) and engineering (Snell-Rood, 2016). This diverse family has >130 species distributed across all continents except for Antarctica (Gill *et al.*, 2021). Their global distribution is highly skewed; only six species are found in the New World, whereas more than half of the species are found in Australasia, owing to their likely Indomalayan origin (Andersen *et al.*, 2018; McCullough *et al.*, 2019). Many taxa are geographically restricted, making

them an interesting subject of biodiversity research; generations of biologists have dedicated decades of effort into resolving their taxonomy, opening up doors to explore topics such as biogeography and cryptic diversification (Sharpe, 1868; Mayr, 1942, 1954, 1963, 1970; Diamond *et al.*, 1976; Moyle, 2006; Fry & Fry, 2010; Andersen *et al.*, 2018; McCullough *et al.*, 2019).

There has been a comparatively large amount of evolutionary research into some species complexes of kingfishers, such as the collared kingfisher, *Todiramphus chloris* (Boddaert, 1783), and variable dwarf kingfisher, *Ceyx lepidus* Temminck, 1836 (Andersen *et al.*, 2013, 2015). Despite the highly conserved plumage features within these complexes, molecular work has revealed their rapid diversification across Australasia, underscoring the presence of genomic divergence among insular taxa, even those separated by short water gaps (Andersen *et al.*, 2013, 2015). Genomic differentiation has even been discovered in the similar looking but elevationally separated

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yellow-bellied kingfisher, *Syma torotoro* Lesson, 1827, and mountain kingfisher, *Syma megarhyncha* Salvadori, 1896, from New Guinea, highlighting that gene flow can be limited even after secondary contact. Given that such convoluted evolutionary histories are prevalent across kingfishers, we can expect diversity to be high in other kingfisher lineages.

Among the taxonomically confusing groups within the Halcyonidae are the paradise-kingfishers of the genus *Tanysiptera* Vigors, 1825, which comprise nine species distributed from north-east Australia through New Guinea to Wallacea (Gill *et al.*, 2021). They are characterized by having elongated central tail feathers, unlike other kingfishers, with variable amounts of blue and black on their upperparts and head (Fry & Fry, 2010). The genus can be divided into two main groups based on coloration (orange vs. white) of the underparts, and molecular work has shown that the white-bellied paradise-kingfishers are monophyletic (Andersen *et al.*, 2018; McCullough *et al.*, 2019). The core white-bellied paradise-kingfishers constitute a taxonomically challenging radiation of 19 taxa, ascribed to five species in almost all modern taxonomies (Fry & Fry, 2010; Dickinson & Christidis, 2014; Billerman *et al.*, 2020; Gill *et al.*, 2021), 15 of which are included as subspecies under the common paradise-kingfisher, *Tanysiptera galatea* Gray, G.R., 1859 (Table 1). The other four species in the complex

are separated from the common paradise-kingfisher based on plumage coloration (Table 1; Billerman *et al.*, 2020). All taxa in the species complex are insular and parapatric, with the exception of the little paradise-kingfisher, *Tanysiptera hydrocharis* Gray, G.R., 1858, which is sympatric but does not interbreed with *Tanysiptera galatea minor* Salvadori & D'Albertis, 1875, in southern New Guinea (Fig. 1).

Musings about the mosaic distribution of this white-bellied paradise-kingfisher complex have featured widely in the literature on evolution and species concepts (Mayr, 1942, 1954, 1963). Their insular distribution makes them particularly relevant, given that genomic and bioacoustic analyses have revealed unexpected diversity on deep-sea islands (Rheindt *et al.*, 2020; Yue *et al.*, 2020). Moreover, various Australasian species groups with a strong dependence on dense forests exhibit deep genomic divergences across insular populations (Irestedt *et al.*, 2013; Marcaigh *et al.*, 2021). The white-bellied paradise-kingfishers are primarily inhabitants of monsoon forests and lowland rainforest, typically with a sedentary lifestyle (Fry & Fry, 2010), making them an excellent study system in which to examine cryptic diversity.

Given that plumage characteristics in this species complex are conserved in comparison to many other kingfishers (Eliason *et al.*, 2019), accounting for the

Table 1. Traditional taxonomic treatment of the white-bellied *Tanysiptera* paradise-kingfisher species complex (following Gill *et al.*, 2021) and the taxonomic revision proposed on the basis of the present work, with sample sizes of sound recordings used for each taxon

Common name	Scientific name	Revised common name	Revised scientific name	Sample size
Common paradise-kingfisher	<i>T. galatea galatea</i>	Papuan paradise-kingfisher	<i>T. galatea galatea</i>	6
Common paradise-kingfisher	<i>T. g. minor</i>	Papuan paradise-kingfisher	<i>T. g. minor</i>	6
Common paradise-kingfisher	<i>T. g. meyeri</i>	Papuan paradise-kingfisher	<i>T. g. meyeri</i>	1
Common paradise-kingfisher	<i>T. g. vulcani</i>	Papuan paradise-kingfisher	<i>T. g. vulcani</i>	0
Common paradise-kingfisher	<i>T. g. margarethae</i>	Halmahera paradise-kingfisher	<i>T. margarethae</i>	1
Common paradise-kingfisher	<i>T. g. sabrina</i>	Halmahera paradise-kingfisher	<i>T. m. sabrina</i>	0
Common paradise-kingfisher	<i>T. g. browningi</i>	Halmahera paradise-kingfisher	<i>T. m. browningi</i>	13
Common paradise-kingfisher	<i>T. g. brunhildae</i>	Halmahera paradise-kingfisher	<i>T. m. brunhildae</i>	0
Common paradise-kingfisher	<i>T. g. nais</i>	Amboyna paradise-kingfisher	<i>T. nais nais</i>	7
Common paradise-kingfisher	<i>T. g. acis</i>	Amboyna paradise-kingfisher	<i>T. n. acis</i>	1
Common paradise-kingfisher	<i>T. g. boanensis</i>	Amboyna paradise-kingfisher	<i>T. n. boanensis</i>	3
Common paradise-kingfisher	<i>T. g. doris</i>	Morotai paradise-kingfisher	<i>T. doris doris</i>	10
Common paradise-kingfisher	<i>T. g. emiliae</i>	Morotai paradise-kingfisher	<i>T. d. emiliae</i>	0
Common paradise-kingfisher	<i>T. g. obiensis</i>	Obi paradise-kingfisher	<i>T. obiensis</i>	4
Common paradise-kingfisher	<i>T. g. rosseliana</i>	Rossel paradise-kingfisher	<i>T. rosseliana</i>	1
Biak paradise-kingfisher	<i>T. riedelii</i>	Biak paradise-kingfisher	<i>T. riedelii</i>	4
Kofiau paradise-kingfisher	<i>T. ellioti</i>	Kofiau paradise-kingfisher	<i>T. ellioti</i>	1
Little paradise-kingfisher	<i>T. hydrocharis</i>	Little paradise-kingfisher	<i>T. hydrocharis</i>	5
Numfor paradise-kingfisher	<i>T. carolinae</i>	Numfor paradise-kingfisher	<i>T. carolinae</i>	3

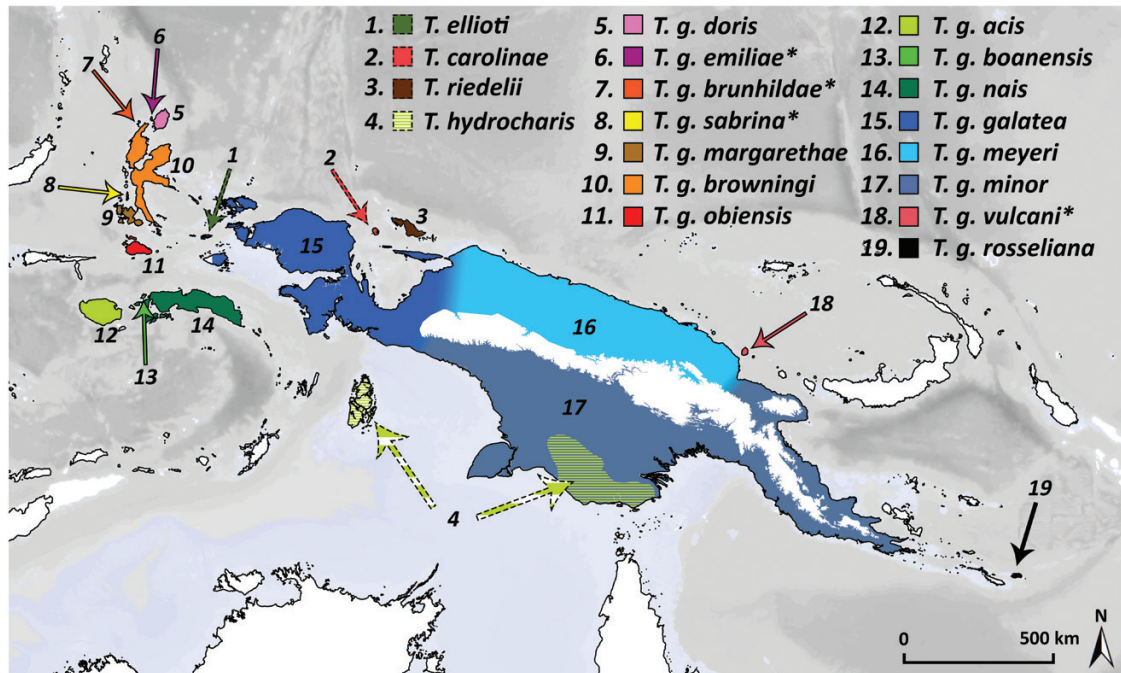


Figure 1. Range map of all 19 taxa within the white-bellied *Tanysiptera* paradise-kingfisher species complex. Asterisks indicate taxa for which sound recordings were not obtained. During the Last Glacial Maximum, the global sea level decreased by ~120 m, leading to a coastline expansion (Voris, 2000), illustrated by the -120 m isobath in lilac-blue. Grey shades represent the ocean depth. Species and subspecies rank are shown according to taxonomic baseline treatment (Gill *et al.*, 2021).

potential of cryptic species diversity through non-visual but reproductively important traits is crucial in taxonomic assessments. In birds, song structure can be governed by various factors, including cultural drift, sexual selection and morphological adaptation (Rheindt *et al.*, 2004; Huber & Podos, 2006; Potvin, 2013; Potvin & Clegg, 2015; Derryberry *et al.*, 2018). Although bioacoustic differences have rarely been found not to be reflected in population divergence (Potvin *et al.*, 2013), avian song serves overwhelmingly as a crucial pre-mating isolation mechanism, creating barriers to gene flow among diverging populations, even those separated by short distances (Diamond, 1998; Uy *et al.*, 2009; Cibois *et al.*, 2019). Work in our study region has corroborated a congruence between bioacoustic differences of insular populations with deep, often species-level genomic divergence (O'Connell *et al.*, 2019; Rheindt *et al.*, 2020). Bioacoustic data have proved to be useful phylogenetic indicators in morphologically cryptic complexes across both passerine (Isler *et al.*, 1998, 2008; Rheindt *et al.*, 2008; Hungnon *et al.*, 2017; Gwee *et al.*, 2019a, 2021; Alström *et al.*, 2020) and non-passerine birds (Sangster & Rozendaal, 2004; Ng *et al.*, 2016; Ng & Rheindt, 2016; Gwee *et al.*, 2017, 2019b). In the present study, we assess species limits within the white-bellied paradise-kingfisher complex by using bioacoustic data.

MATERIAL AND METHODS

We obtained 203 sound recordings from a total of 75 individuals from 15 taxa spanning all five traditional species of the white-bellied paradise-kingfisher complex, primarily sourced from online repositories (Xeno-Canto, AVoCet and Macaulay Library; Supporting Information, Tables S1 and S2). Vocal data for the following taxa could not be obtained (Table 1): *Tanysiptera galatea emiliae* Sharpe, 1871, *Tanysiptera galatea brunhildae* Jany, 1955, *Tanysiptera galatea sabrina* Gray, G.R., 1861 and *Tanysiptera galatea vulcani* Rothschild & Hartert, 1915. Sonograms were analysed using RAVEN PRO v.1.5 (Bioacoustics Research Program, Cornell Laboratory of Ornithology, Ithaca, NY, USA), with consistent contrast and brightness (50) and sharpness (1024) settings across all recordings.

All taxa had songs characterized by a distinct introductory note followed by a trill with similar-shaped notes throughout the rest of the song (Fig. 2). A note is defined here as one unbroken segment of the song, and a motif refers to one repetition of the song. To ensure that vocalizations analysed were homologous across taxa, we only included recordings of single birds singing. Other calls, often in the form of down-slurred whines, were removed because they were variable and limited in sample size. Duets were also excluded despite their similar bioacoustic structure because

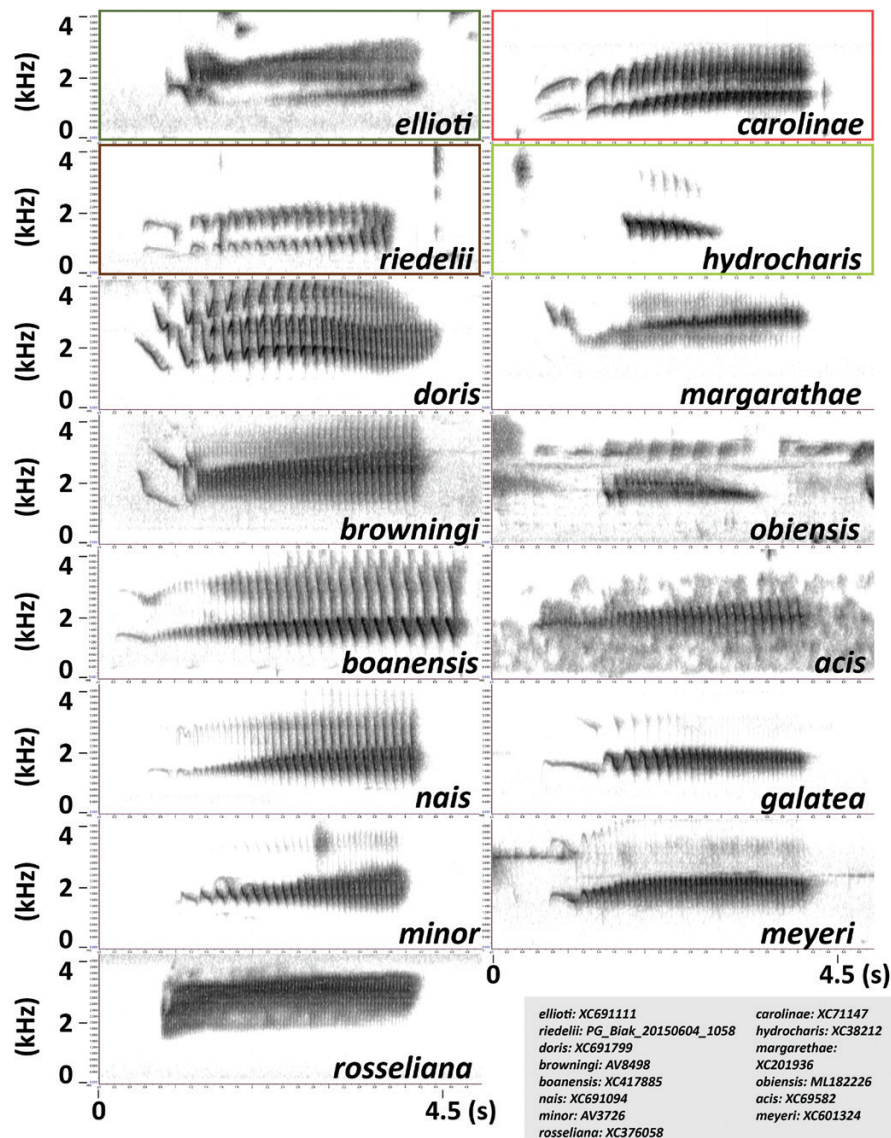


Figure 2. Sonograms of typical song renditions of all 15 taxa examined. Taxa in coloured boxes are treated as full species by most modern taxonomies, and the rest are treated as subspecies of *Tanysepta galatea* (Fry & Fry, 2010; Dickinson & Christidis, 2014; Billerman *et al.*, 2020; Gill *et al.*, 2021). Sound library accession numbers for each recording are given in the grey box in the lower right corner (also see Supporting Information, Table S1).

they were frequently curtailed abruptly, and it was sometimes not possible to ascribe motifs to particular individuals.

We measured a total of eight bioacoustic parameters based on their discernibility within our dataset, which included three frequency parameters (Fig. 3): (1) centre frequency (a horizontal band that divides the energy of the vocalization into two); (2) frequency bandwidth of introductory note (where bandwidth refers to the difference between the highest and lowest frequency); and (3) ratio of frequency bandwidths between second note and last note; and five temporal parameters: (4) ratio of durations between second note and last note;

(5) duration of introductory note; (6) shape of second note; (7) total number of notes; and (8) position of note with lowest centre frequency. Parameter 6 was quantified by taking the duration elapsed for the second note to reach its highest frequency as a fraction of the duration of the entire note (Fig. 3). Parameter 8 was calculated in a similar manner by taking the duration elapsed for the song to reach the note with lowest centre frequency as a fraction of the duration of the trill (Fig. 3). For taxa in which the second note peaked at either the beginning or the end of the note (i.e. not n-shaped), parameter 6 was defined as zero or one, respectively. For every individual, parameters

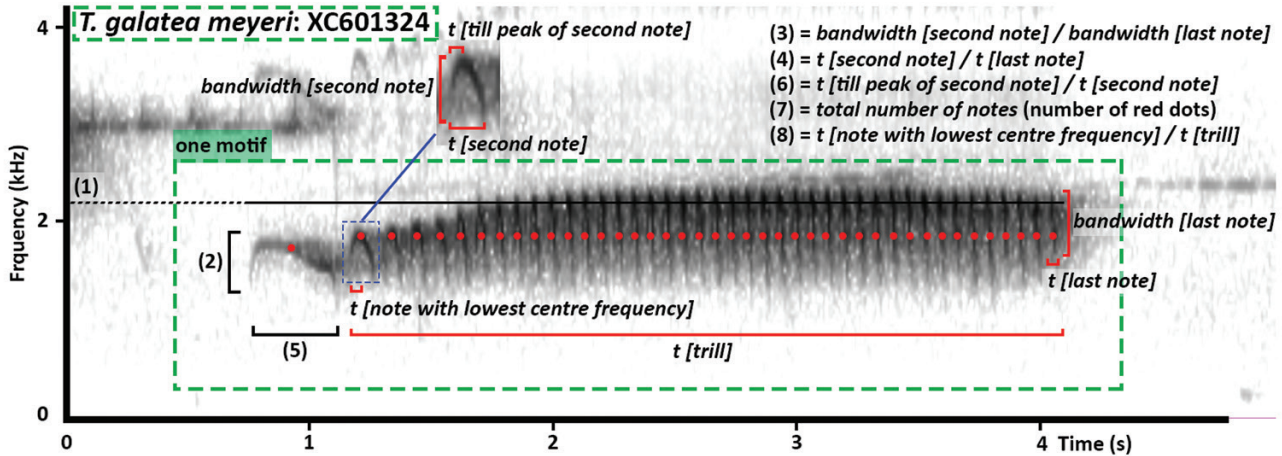


Figure 3. Illustration of vocal parameters analysed for a typical sonogram, where t = time. Parameters: (1) centre frequency (i.e. frequency band that splits the energy of the vocalization into two); (2) frequency bandwidth of introductory note; (3) ratio of frequency bandwidths between second note and last note; (4) ratio of durations between second note and last note; (5) duration of introductory note; (6) shape of second note; (7) total number of notes; and (8) position of note with lowest centre frequency.

were derived from the means of all motifs available in the recording or for a maximum of seven motifs if more were available. A minimum of two motifs were measured for all except eight individuals.

Statistical analyses were conducted using R v.3.6.1 (R Development Core Team, 2019). To account for multicollinearity, we checked that all vocal parameters had a Pearson correlation score < 0.8 before further statistical analysis (Isler *et al.*, 2008; Supporting Information, Table S3).

We conducted principal component analysis (PCA) for all measurements using the ‘prcomp’ function, with variable means centred and rescaled to explore the vocal dataset. We confirmed that all eight parameters could be used appropriately in a PCA by performing Bartlett’s test on the correlation matrix of the vocal parameters using the ‘psych’ package ($P < 0.001$; Bartlett, 1951; Revelle & Revelle, 2015). The ‘ggplot2’ package was used to visualize our PCA results (Wickham, 2011). Diagnosable groups were inferred from the PCA plots, and we performed analysis of variance (ANOVA) and Tukey’s post hoc comparison on the relevant principal components (PCs; eigenvalues > 1) of groups with sample sizes of at least three to test their differences.

Additionally, we examined the vocal diagnosability of each taxon using a formula devised by Isler *et al.* (1998). This diagnosability test was devised originally to examine vocal differentiation among Neotropical suboscines and has since been used successfully to distinguish species complexes of various families of birds across both passerines and non-passerines (Sangster & Rozendaal, 2004; Ng *et al.*, 2016, 2020; Cros & Rheindt, 2017; Gwee *et al.*, 2017, 2019a). This

conservative formula (henceforth, the Isler criterion) requires two conditions to be met: (1) vocal parameters compared between two taxa must not overlap; and (2) means (\bar{x}) and standard deviations (SD) of the two taxa must meet the following requirement: $\bar{x}_a + t_a SD_a < \bar{x}_b - t_b SD_b$, where a is the taxon with smaller measurements, b is the taxon with larger measurements, and t_i is Student’s t -score at the 97.5th percentile at $N - 1$ degrees of freedom of the t distribution. We define Isler diagnosability as two taxa having at least one vocally diagnosable trait. The Isler criterion was only applied to taxa with a sample size of at least three. Given that the Isler criterion cannot be applied to parameters derived from ratios, we conducted a non-parametric bootstrap simulation to test their differences (parameters 3 and 4; Isler *et al.*, 2007). Specifically, the differences between means (DBM; measured by Student’s unpaired t -tests) of the focal pair were compared against the distribution of DBMs of 10 000 simulated populations with the same sample size, sampled with replacement (Isler *et al.*, 2007). We used the ‘boot.t.test’ function from the package ‘MKinfer’ to conduct this bootstrapping approach (Kohl, 2020).

RESULTS

After filtering out poor recordings and duplicate files, 107 recordings from 75 individuals were retained for analysis (Supporting Information, Tables S1 and S2). Visual inspection of the PCA showed that *T. hydrocharis* and *Tansysiptera galatea obiensi* Salvadori, 1877 exhibited a high degree of vocal

divergence from the rest of the *T. galatea* species complex (Fig. 4). These two taxa were also vocally distinct from all other taxa in at least one diagnosable parameter (Table 2). To improve spatial resolution of bioacoustic data, we re-ran the PCA with samples belonging to these two taxa removed. The results indicated that vocal differentiation of *Tanysiptera galatea rosseliana* Tristram, 1889 from other taxa was also pronounced, although it was represented by only a single sample (Fig. 5). To obtain a further improvement of spatial resolution, we ran a final PCA conducted after the removal of *T. g. rosseliana*. The resulting PCA spatially isolated the bioacoustic samples of two taxa currently recognized as full species (*Tanysiptera carolinae* Schlegel, 1871 and *Tanysiptera riedelii* Verreaux, 1866), whereas another widely recognized species (*Tanysiptera ellioti* Sharpe, 1870) remained embedded within the cloud of *T. galatea* samples (Fig. 6). The taxa widely classified as subspecies of *T. galatea* formed four main groups: a New Guinean cluster and three insular clusters (Fig. 6).

A one-way ANOVA demonstrated that clusters identified by PCA showed significant differences for all three relevant PCs ($P < 0.001$). Tukey's post hoc comparison revealed that all the clusters differed from one another by at least one PC, except for *T. riedelii* and *T. carolinae* (Table S5).

Diagnosability tests revealed at least two differences between most taxa assigned as species in our PCA and Tukey's post hoc test (Table 2). The exception to this was *T. doris* Wallace, 1862 and *T. g. minor*, which differed by one diagnosable difference, although this was probably attributable to their limited sample size and slight variability of vocal samples as inferred from the PCA and boxplots (Figs 6, 7). Although the ratio of frequency bandwidths between the second note and the last note (parameter 3) often corroborated diagnosable differences, temporal parameters were generally more effective in distinguishing taxon pairs (Table 2; Table S4). The shape of the second note (parameter 6), for instance, emerged as a crucial character for diagnosing taxa, especially *T. carolinae*, which otherwise did not differ from *Tanysiptera boanensis* Mees, 1964, *T. galatea* and *Tanysiptera nais* Gray, G.R., 1861.

DISCUSSION

The highly conserved plumage features across white-bellied paradise-kingfishers of the genus *Tanysiptera* have led to the treatment of most taxa as members of a single species, *T. galatea*. Nonetheless, field workers have been aware of the great magnitude of geographical differentiation in the territorial songs of these forest-inhabiting kingfishers for approximately a decade now (Eaton *et al.*, 2021). This vocal mosaicism is considered

to go beyond the level of bioacoustic differentiation within single forest kingfisher species (Eaton *et al.*, 2021), hinting at the likelihood of cryptic species-level diversity. Our vocal analyses demonstrate pronounced bioacoustic differences among songs of *Tanysiptera* taxa from different islands. Importantly, our data show that some taxa hitherto treated at the subspecies level exhibit more pronounced vocal differentiation than other taxa which have, for a long time, been treated as distinct species because of their differences in plumage. These results call for a taxonomic revision.

Some *Tanysiptera* kingfishers live on remote islands that have not been visited by ornithologists for years or even decades; hence, vocal material was lacking for four obscure small-island forms. To account for this lack of bioacoustic samples for a number of taxa, we adopt a biogeographical approach in the interpretation of our results. Quaternary sea-level fluctuations have had an all-important impact on the build-up of biotic differentiation in Australasia; the frequent presence of land-bridges between some islands facilitates gene flow and reduces the potential for endemism, and vice versa (Weigelt *et al.*, 2016; Norder *et al.*, 2019; Rheindt *et al.*, 2020). Although most *Tanysiptera* taxa are endemic to their respective islands today, the level of isolation and opportunity for gene flow with neighbouring taxa would have differed among islands. For instance, during the Last Glacial Maximum (LGM) ~20 000 years ago, the global sea level was ~120 m lower than the present-day sea level (Bintanja *et al.*, 2005; Lambeck *et al.*, 2014; Fig. 1). Some islands would have expanded during the LGM in comparison to today, therefore reducing the shortest overwater distance between islands, while land-bridges would have become exposed between other islands to form larger palaeo-islands, facilitating conduits for genetic exchange (see the -120 m isobaths in Fig. 1, showing the coastline during the LGM; Voris, 2000; Becker *et al.*, 2009).

TAXONOMIC IMPLICATIONS

The systematics of *Tanysiptera* kingfishers has been based primarily on morphology to date (Sharpe, 1868; Beehler & Pratt, 2016; Woodall, 2020a, c; Woodall & Sharpe, 2020a, b). Three taxa have been classified unanimously as monotypic species distinct from the common paradise-kingfisher, *T. galatea*: the Numfor paradise-kingfisher, *T. carolinae*, stands out from all other taxa through its remarkably different plumage by having blue instead of white underparts, whereas the Biak paradise-kingfisher, *T. riedelii*, has a bright cobalt head and scapulars, unlike the remaining taxa (Pratt & Beehler, 2016; Woodall, 2020a, c). The little paradise-kingfisher, *T. hydrocharis*, while having similar plumage characteristics to *T. galatea*, is

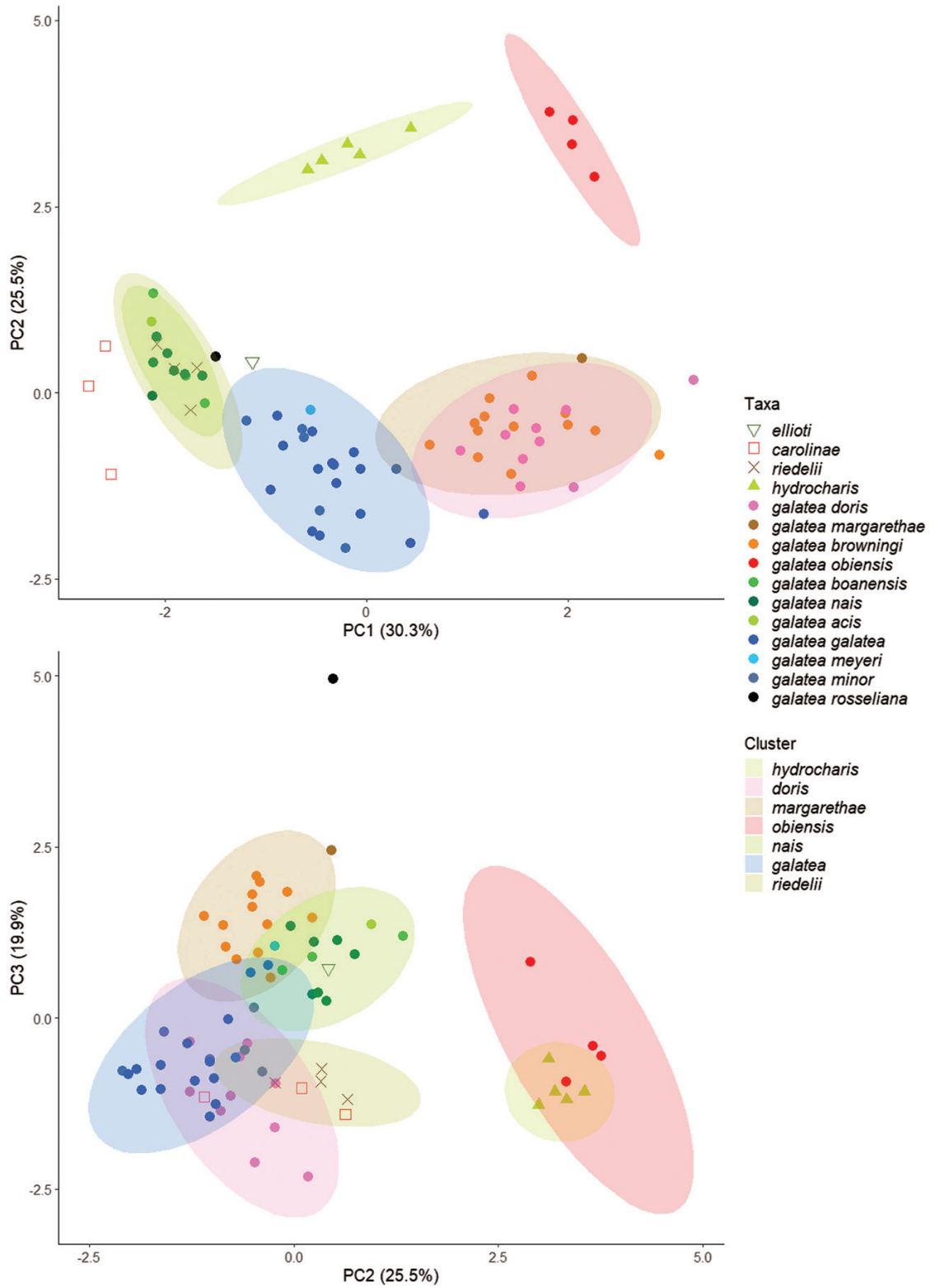


Figure 4. Principal component analysis plot of vocal parameters analysed for all 15 taxa of the white-bellied *Tanysiptera* paradise-kingfisher species complex. Ellipses represent 95% confidence intervals of the displayed principal component (PC) scores, with the points clustered according to our revised taxonomy.

Table 2. Results of pairwise diagnosability test for all eight vocal parameters of *Tanysiptera* kingfishers with sample size of at least three.

Pairwise comparisons	1	2	3	4	5	6	7	8	Total
<i>T. boanensis</i> vs <i>T. nais</i>									0
<i>T. boanensis</i> vs <i>T. carolinae</i>						X			1
<i>T. carolinae</i> vs <i>T. galatea</i>						X			1
<i>T. carolinae</i> vs <i>T. nais</i>						X			1
<i>T. carolinae</i> vs <i>T. riedelii</i>						X			1
<i>T. doris</i> vs <i>T. minor</i>			X						1
<i>T. galatea</i> vs <i>T. minor</i>			X						1
<i>T. minor</i> vs <i>T. riedelii</i>				X					1
<i>T. boanensis</i> vs <i>T. galatea</i>			X	X					2
<i>T. boanensis</i> vs <i>T. minor</i>			X	X					2
<i>T. browningi</i> vs <i>T. carolinae</i>	X					X			2
<i>T. browningi</i> vs <i>T. minor</i>			X	X					2
<i>T. carolinae</i> vs <i>T. hydrocharis</i>						X		X	2
<i>T. carolinae</i> vs <i>T. minor</i>	X					X			2
<i>T. doris</i> vs <i>T. galatea</i>			X			X			2
<i>T. galatea</i> vs <i>T. nais</i>			X	X					2
<i>T. galatea</i> vs <i>T. riedelii</i>			X	X					2
<i>T. hydrocharis</i> vs <i>T. obiensis</i>			X			X			2
<i>T. hydrocharis</i> vs <i>T. riedelii</i>			X					X	2
<i>T. minor</i> vs <i>T. nais</i>			X	X					2
<i>T. nais</i> vs <i>T. riedelii</i>			X	X					2
<i>T. boanensis</i> vs <i>T. browningi</i>			X	X		X			3
<i>T. boanensis</i> vs <i>T. doris</i>			X	X		X			3
<i>T. boanensis</i> vs <i>T. riedelii</i>			X	X			X		3
<i>T. browningi</i> vs <i>T. doris</i>			X	X		X			3
<i>T. browningi</i> vs <i>T. galatea</i>			X	X		X			3
<i>T. carolinae</i> vs <i>T. doris</i>	X		X			X			3
<i>T. doris</i> vs <i>T. nais</i>			X	X		X			3
<i>T. doris</i> vs <i>T. riedelii</i>			X	X		X			3
<i>T. hydrocharis</i> vs <i>T. nais</i>			X				X	X	3
<i>T. minor</i> vs <i>T. obiensis</i>			X	X				X	3
<i>T. boanensis</i> vs <i>T. hydrocharis</i>			X	X			X	X	4
<i>T. boanensis</i> vs <i>T. obiensis</i>			X	X		X		X	4
<i>T. browningi</i> vs <i>T. obiensis</i>			X		X	X		X	4
<i>T. browningi</i> vs <i>T. riedelii</i>	X	X	X			X			4
<i>T. carolinae</i> vs <i>T. obiensis</i>	X		X			X		X	4
<i>T. doris</i> vs <i>T. obiensis</i>				X	X	X		X	4
<i>T. galatea</i> vs <i>T. hydrocharis</i>				X	X		X	X	4
<i>T. galatea</i> vs <i>T.obiensis</i>			X	X	X			X	4
<i>T. hydrocharis</i> vs <i>T.minor</i>			X	X			X	X	4
<i>T. nais</i> vs <i>T. obiensis</i>		X	X			X		X	4
<i>T. obiensis</i> vs <i>T. riedelii</i>		X	X			X		X	4
<i>T. browningi</i> vs <i>T. hydrocharis</i>				X	X	X	X	X	5
<i>T. browningi</i> vs <i>T. nais</i>	X	X	X	X		X			5
<i>T. doris</i> vs <i>T. hydrocharis</i>				X	X	X	X	X	5
Total number of differences	6	4	32	25	6	26	7	16	

Parameters are denoted by numbers 1–8. Diagnosability is denoted by 'X'. The column headed 'Total' refers to the total number of diagnosable parameters. Vocal parameters assessed were as follows: (1) centre frequency; (2) frequency bandwidth of introductory note; (3) ratio of frequency bandwidths between second note and last note; (4) ratio of durations between second note and last note; (5) duration of introductory note; (6) shape of second note; (7) total number of notes; and (8) position of note with lowest centre frequency. The last row, 'Total number of differences', denotes the number of pairs that each vocal parameter distinguished.

significantly smaller and does not interbreed with the latter where they overlap (Fig. 1; Woodall & Sharpe, 2020b). Our results support the species status of these three taxa by confirming their vocal distinctness, both in PCA and through the presence of diagnosable vocal parameters. Intriguingly, the two species with most distinct plumage features, *T. carolinae* and *T. riedelii*, were the only two taxa not significantly different in bioacoustic terms based on our Tukey's post hoc comparison. They were also the taxa with the lowest number of diagnosable characters from others, with vocal differences mainly being their note shape (Table 2).

A fourth taxon that is widely considered a monotypic species is the Kofiau paradise-kingfisher, *T. ellioti*: its plumage differences from *T. galatea* are more modest in comparison to the previous three species (Beehler & Pratt, 2016; Pratt & Beehler, 2016; Woodall & Sharpe, 2020a), and this similarity is reflected in its greater bioacoustic resemblance to *T. galatea* (Fig. 6). Although a firm judgement on the species status of *T. ellioti* cannot be made at present owing to our limited vocal sample size, at a minimum our results call for a re-evaluation of its taxonomic rank in future analyses based on more vocal and genomic data points.

With respect to the polytypic common paradise-kingfisher, *T. galatea*, our analyses reveal one New Guinean bioacoustic clade and multiple insular ones (Fig. 6; Table 2). Based on this evidence, we recommend that the common paradise-kingfisher, *T. galatea*, should be split into six species, namely: (1) Papuan paradise-kingfisher, *T. galatea* (includes subspecies *T. g. galatea*, *T. g. minor*, *Tanysiptera galatea meyeri* Salvadori, 1889 and *T. g. vulcani*); (2) Morotai paradise-kingfisher, *T. doris* Wallace, 1862 (includes subspecies *T. doris doris* and *Tanysiptera doris emiliae*); (3) Halmahera paradise-kingfisher *Tanysiptera margarathae* (includes subspecies *T. m. margarathae* Heine, 1860, *T. m. sabrina*, *T. m. brunhildae* and *T. m. browningi* Ripley, 1983); (4) Obi paradise-kingfisher, *T. obiensis* (monotypic); (5) Amboyna paradise-kingfisher, *T. nais* (includes subspecies *T. n. nais*, *T. n. acis* Wallace, 1863, and *T. n. boanensis* Mees, 1964); and (6) Rossel paradise-kingfisher, *T. rosseliana* (monotypic).

Among traditional subspecies of *T. galatea*, the Obi paradise-kingfisher, *T. obiensis*, is the most vocally divergent. Along with *T. hydrocharis*, it is the first taxon to form a bioacoustic cluster in PCA, even ahead of traditional species-level taxa, such as *T. carolinae* and *T. riedelii* (Fig. 4). The Obi paradise-kingfisher is also the only former subspecies of *T. galatea* to have a descending trill (Figs 2, 7) and consistently to exhibit at least two diagnosable parameters in comparison with all other taxa (Table 2). Morphologically, the plumage of *T. obiensis* is less distinct from *T. galatea* when compared with traditional species, such as *T. carolinae*

and *T. riedelii* (Fry & Fry, 2010), which probably accounts for its overlooked distinctness, underscoring the pitfalls of relying solely on plumage in bird systematics. The deep differentiation of *T. obiensis* is perhaps less surprising when considering that the Obi island group is among the most geographically isolated archipelagos in the Moluccas; this deep-sea island group has been separated permanently by at least ~30 km of open water from Bacan, where the nearest *Tanysiptera* population (*T. margarathae*) resides (Fig. 1). The geographical separation of this island is likely to have produced conditions for the evolution of this endemic species, along with multiple other avian endemics (Mittermeier *et al.*, 2013; Rheindt & Eaton, 2018).

The taxonomic status of the Rossel paradise-kingfisher, *T. rosseliana*, has been contentious; most treat it as a subspecies of *T. galatea* (Fry & Fry, 2010; Woodall, 2020b; Gill *et al.*, 2021), whereas others have adopted a species-level treatment based on multiple plumage traits, including its mostly white (not blue) tail coloration (Beehler & Pratt, 2016), rendering it one of the more distinctly plumaged taxa in the complex. Our bioacoustic results, although restricted to a sample size of one recording, highlight the vocal uniqueness of *T. rosseliana* (Fig. 5). Unlike all other taxa, *T. rosseliana* is characterized uniquely by having a very short introductory note, immediately succeeded by a rapid trill with level pitch (Fig. 2). Molecular works have revealed evidence of avian species complexes with deeply diverged lineages in the Louisiade Archipelago (Kearns *et al.*, 2013; Andersen *et al.*, 2014, 2021; Jönsson *et al.*, 2014; McCullough *et al.*, 2021). Rossel Island, the home of the Rossel paradise-kingfisher, is a deep-sea island almost 400 km east of the nearest *Tanysiptera* population on Papua New Guinea. This isolated range is likely to restrict the opportunity for regular gene flow with its Papuan counterparts, and we support the taxonomic treatment by Beehler & Pratt (2016) in designating this taxon as a full species.

The Halmahera paradise-kingfisher, *T. margarathae*, differs from the rest of the complex in its descending introductory note, uniquely succeeded by a second introductory note, followed by a consistently paced trill that gradually increases in pitch (Fig. 2). We here include taxa from Halmahera (*T. m. browningi*) and three satellite islands (*T. m. sabrina*, *T. m. brunhildae* and *T. m. margarathae*) as subspecies of the Halmahera paradise-kingfisher, although we lacked vocal material from two of them (*T. m. sabrina* and *T. m. brunhildae*) because they are remote and rarely visited, and we had only one sample of the third satellite taxon (*margarathae*). Although *T. m. margarathae* from Bacan seems to differ slightly in PCA space from Halmahera *T. m. browningi* (Fig. 6), a separation of the two is premature based on the sample size of one

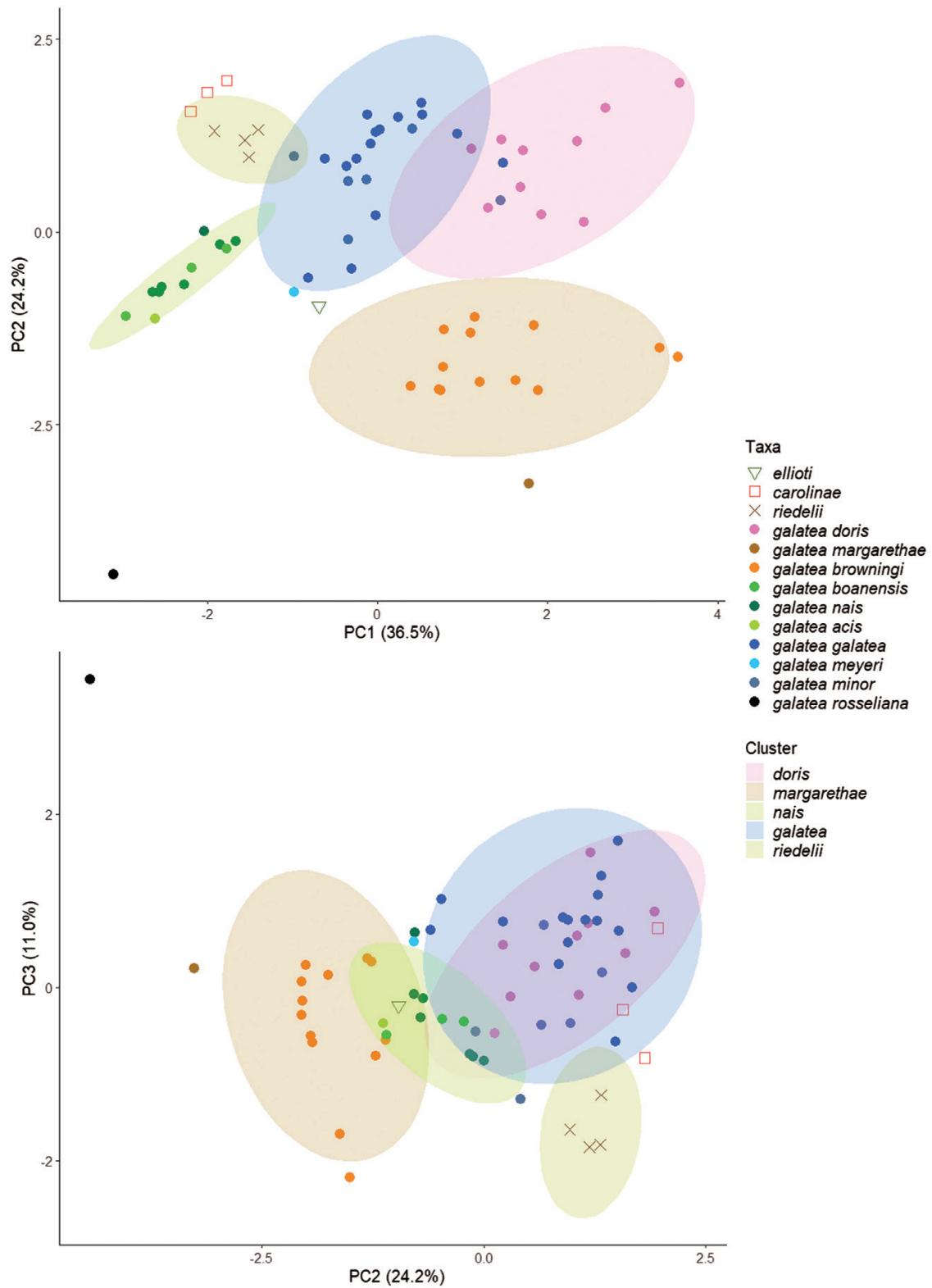


Figure 5. Principal component analysis plot of vocal parameters analysed for the white-bellied *Tanysiptera* paradise-kingfisher species complex after removal of *Tanysiptera hydrocharis* and *Tanysiptera galatea obiensis* from the dataset. Ellipses represent 95% confidence intervals of the displayed principal component (PC) scores, with the points clustered according to our revised taxonomy.

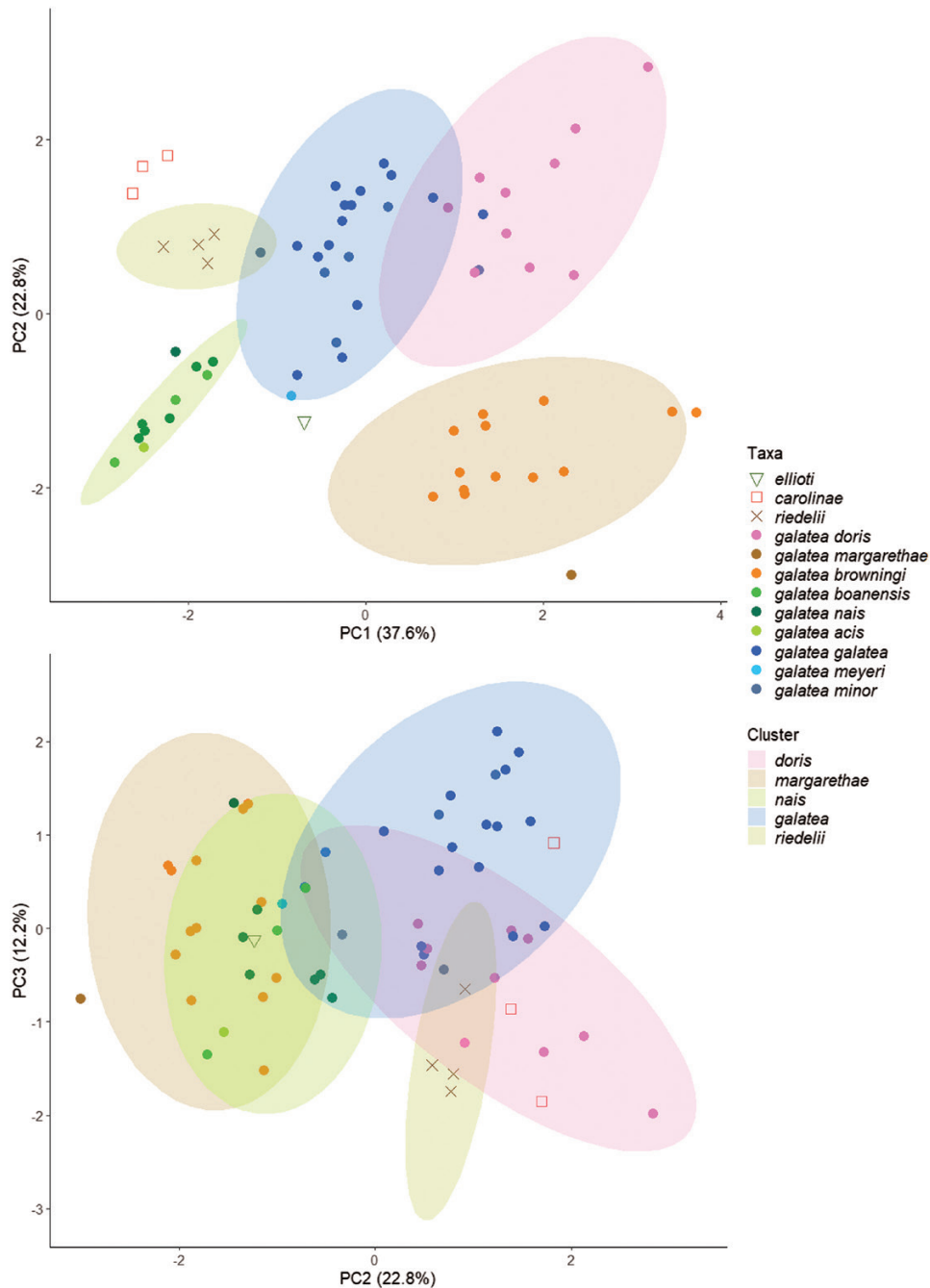


Figure 6. Principal component analysis plot of vocal parameters analysed for the white-bellied *Tanysiptera* paradise-kingfisher species complex after removing taxa that were highly distinct based on earlier inspection (*Tanysiptera hydrocharis*, *Tanysiptera galatea obiensis* and *Tanysiptera galatea rosseliana*) from the dataset. Ellipses represent 95% confidence intervals of the displayed principal component (PC) scores, with the points clustered according to our revised taxonomy. Tukey's post hoc comparisons confirmed that the clusters were significantly different by at least one PC (except *Tanysiptera caroliniae* and *Tanysiptera riedelii*).

T. m. margarethae. Although *T. m. brunhildae* remains vocally unknown at present (Eaton *et al.*, 2021), the islet of Doi, where it resides, has been connected to Halmahera by a land-bridge during the LGM

(Fig. 1; Becker *et al.*, 2009), and we can expect vocal resemblance to *T. m. browningi*. Conversely, Kayoa (where *T. m. sabrina* resides) is a deep-sea island, suggesting a lack of land connection to Halmahera

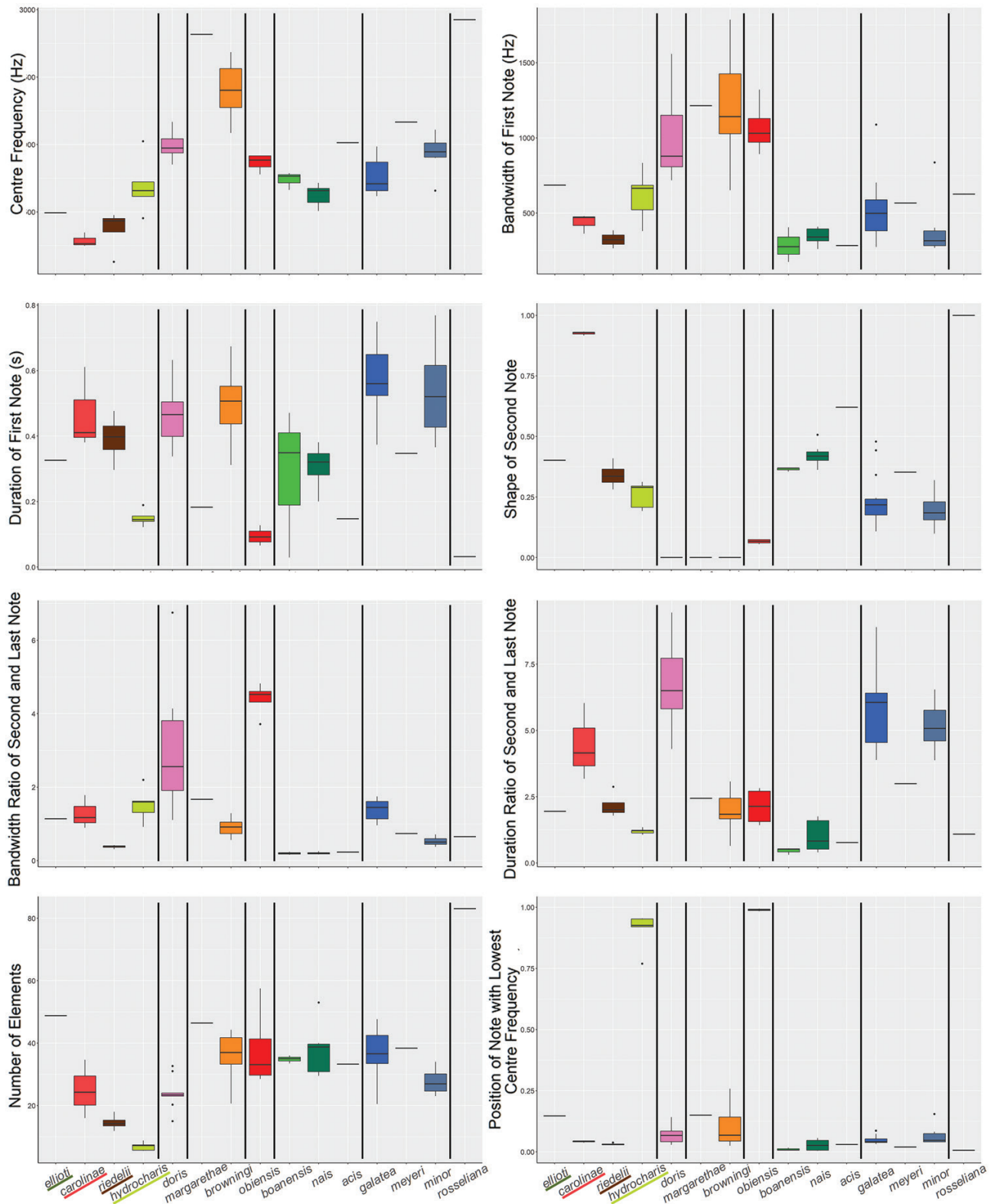


Figure 7. Boxplots of all eight vocal parameters for all taxa. Taxa with labels having coloured underlines are treated as full species by most modern taxonomies, and the rest are treated as subspecies of *Tanyptera galatea* (Fry & Fry, 2010; Dickinson & Christidis, 2014; Billerman *et al.*, 2020; Gill *et al.*, 2021). Black lines indicate boundaries of our revised taxonomy.

or Bacan. Although future genomic or bioacoustic research might reveal *T. m. sabrina* to be distinct, it is justified, on the basis of geographical proximity, to keep it under the Halmahera paradise-kingfisher at present.

Likewise, in our delimitation of the Morotai paradise-kingfisher, *T. doris*, we treat *T. d. emiliae* conservatively as a subspecies owing to the lack of vocal samples. Although *T. d. emiliae* is unknown vocally (Eaton *et al.*, 2021), the island of Rau (where *T. d. emiliae* resides) and Morotai (where *T. doris* resides) formed a palaeo-island during the LGM (Fig. 1; Becker *et al.*, 2009), suggesting a close vocal resemblance between *T. d. emiliae* and *T. doris*. We found only one diagnosable character between *T. doris* and *T. g. minor*, which is attributable to the variability of the latter (Fig. 6; Table 2). Yet in PCA space, *T. doris* is offset from the cloud comprising Papuan samples (Fig. 6). Depending on which vocal parameters and PCA axes are considered, the Morotai paradise-kingfisher, *T. doris*, appears to be more diverged from Halmahera, *T. m. browningi*, than it is from the Papuan samples (Fig. 6). Given the short distance of Morotai from Halmahera (~17 km), this bioacoustic outcome lends support to the separation of *T. doris* as a species separate from *T. margarethae*, although Morotai has always been severed by deep sea and has never had a land connection with Halmahera. This species joins an ever-increasing list of taxa on Morotai being recognized as endemic species (Besson, 2012; Rheindt & Eaton, 2018; Eaton *et al.*, 2021).

Songs of the three subspecies attributed to the Amboyna paradise-kingfisher, *T. nais*, are structurally similar to Papuan populations, but the trill notes in this species are deflected downwards instead of being n-shaped towards the end of the song (Fig. 2). Taxa from the central Moluccan islands form a tight clade in PCA space that is set apart from other traditional subspecies of *T. galatea* and is, unexpectedly, closest to the clusters formed by the two traditional species from the New Guinean satellite islands, *T. carolinae* and *T. riedelii*, along PC1 (Fig. 6). A lack of diagnosable features between *T. boanensis* and *T. nais* supports their vocal similarity (Table 2). In the Moluccan islands, a north vs. south faunal divide has been documented across multiple animal groups (De Boer & Duffels, 1996; Michaux, 1998; Heads, 2001; Rheindt & Hutchinson, 2007; Carstensen & Olesen, 2009) and is also reflected in our analysis (Fig. 6). The north and central/south Moluccan islands have a different geological history; the former originated in the Pacific region before moving westwards along the northern coast of New Guinea and reaching their current position ~5 Mya, whereas the latter originated from the Australian continent before drifting to their present-day position (Hall, 1998).

The Papuan paradise-kingfisher, *T. galatea*, now of reduced composition, is characterized by an extended introductory note, followed by a trill with n-shaped notes at increasing pitch and pace, both of which level out halfway through the song (Fig. 2). We include the Papuan taxa *T. g. galatea*, *T. g. meyeri* and *T. g. minor* in this species, which form a tight PCA cluster (Fig. 6). They are the only taxa in the species complex adjacent to one another via terrestrial contact zones, which presumably permit gene flow, hence the maintenance of a single species (Mayr, 1970). In our delimitation of the Papuan paradise-kingfisher, *T. galatea*, we treat *T. g. vulcani* from the satellite island of Manam conservatively as a subspecies owing to its geographical proximity to *T. g. meyeri*, although we lack vocal recordings of it (Fig. 1). Manam is separated from New Guinea by only a ~15 km water crossing at its shortest distance but is a deep-sea island that would not have been connected to New Guinea by land even during the LGM. The taxon *T. g. vulcani* is characterized by having a primarily white tail, similar to the distinct Rossel paradise-kingfisher, *T. rosseliana* (Woodall, 2020b). Future vocal and genomic data from this remote deep-sea island will be beneficial in elucidating the true status of this endemic taxon, which might well be a monotypic species.

ROLE OF BIOACOUSTIC ANALYSES IN TAXONOMIC INQUIRY

Temporal parameters have been shown to carry a strong phylogenetic signal in non-passerine birds in general (Rheindt *et al.*, 2011; Ng *et al.*, 2016; Ng & Rheindt, 2016). For example, they are known to be more effective in differentiating territorial calls between different individuals of the woodland kingfisher, *Halcyon senegalensis* (Linnaeus, 1766), than are frequency parameters (Taylor & Perrin, 2008). Likewise, in our analyses of *Tanysiptera* kingfishers, temporal characteristics made larger contributions to species delimitation based on the Isler criterion than did frequency parameters (Table 2). Using a large dataset of vocalizations, we uncovered substantial unrecognized species-level diversity in this visually cryptic species complex. At the same time, multiple *Tanysiptera* kingfishers remain vocally unknown owing to the remote nature of their distribution (Eaton *et al.*, 2021), and future additions of new vocal and genomic data will be important to revise our conservative species delimitation approach and add in-depth knowledge on relationships and evolutionary diversification scenarios. Additional details regarding the size and morphometrics of each taxon will also be beneficial to elucidate relationships between their vocalizations and morphology.

Vocalizations provide reliable phylogenetic information in avian systems (McCracken & Sheldon, 1997; Gonzalez-Voyer *et al.*, 2013; Arato & Fitch, 2021) and even in other animal groups, such as anurans (Koehler *et al.*, 2017). In recent years, an increased availability of high-quality sound recordings has facilitated a surge in the integration of bioacoustic data in taxonomic work (Cadena & Cuervo, 2010; Gwee *et al.*, 2019a; Ng *et al.*, 2020; Yue *et al.*, 2020; Marcaigh *et al.*, 2021; Niranjana & Praveen, 2021), and increased screening of online bioacoustic databases could propel further discoveries of cryptic diversity throughout the region. Previous genetic work revealed *T. carolinae* and *T. riedelii* as sister species, with *T. galatea* sister to them and *T. hydrocharis* sister to those three (Andersen *et al.*, 2018; McCullough *et al.*, 2019). However, the widespread and polytypic *T. galatea* was represented only by samples from Papua New Guinea, precluding a fine-scale taxonomic revision within the species complex. Our results underscore the inadequacy of relying solely on morphology and reinforce the importance of considering vocal cues in taxonomy.

ACKNOWLEDGEMENTS

We thank the numerous recordists who have contributed their recordings to public sound archives and Phil Gregory for sharing additional sound collections with us. We are grateful to M. Andersen and one anonymous reviewer for their constructive review, and to J. A. Allen for editorial feedback. We are grateful to E. Ng, W. X. G. Lee, M. Y. Wu, N. Movin and H. Z. Tan for advice and support with this research. This research was funded by a Singapore Ministry of Education Tier 2 grant to F.E.R. (WBS R-154-000-C41-112). We have no conflicts of interest to declare.

DATA AVAILABILITY

The data underlying this article are available in the article and in its online Supporting Information. Additional vocal samples are available upon reasonable request. R script containing relevant codes for analyses is available on Github: <https://github.com/dbssyck/tanysiptera/>.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

- Table S1.** Details and vocal parameters of sound recordings analysed.
- Table S2.** Details of sound recordings excluded from analyses.
- Table S3.** Pearson correlation table of vocal parameters analysed.
- Table S4.** Factor loadings of the eight vocal parameters on the principal components (PCs).
- Table S5.** Summary statistics from Tukey's post hoc comparison after performing a one-way ANOVA on principal components PC1, PC2 and PC3 of the eight vocal parameters.