

Evolution in the understory: The Sulawesi babbler *Pellorneum celebense* (Passeriformes: Pellorneidae) has diverged rapidly on land-bridge islands in the Wallacean biodiversity hotspot

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ABSTRACT

Tropical islands hold great treasures of Earth's biodiversity, but these fragile ecosystems may be lost before their diversity is fully catalogued or the evolutionary processes that birthed it are understood. We ran comparative analyses on the ND2 and ND3 mitochondrial genes of the Sulawesi babbler *Pellorneum celebense*, an understory bird endemic to Sulawesi and its continental islands, along with its morphology and song. Genetic, acoustic, and morphological data agree on multiple isolated populations, likely representing independently evolving lineages. The Sulawesi babbler shows signs of rapid speciation, with populations diverging between Central and Southeast Sulawesi, and even on land-bridge islands which were connected within the last few tens of thousands of years. The genetic divergence between Sulawesi babbler populations in this time has been around 33% of their divergence from sister species which have been isolated from Sulawesi for millions of years. This is likely facilitated by the Sulawesi babbler's understory lifestyle, which inhibits gene flow and promotes speciation. Similar patterns of endemism are seen in Sulawesi's mammals and amphibians. This work highlights the undocumented biodiversity of a threatened hotspot, wrought by complex processes of speciation which interact with ecology and geology. Subspecific taxonomy has at times been controversial, but we argue that discrete populations such as these play a key role in evolution. Lying as they do at the heart of the biodiversity hotspot of Wallacea, these islands can reveal much about the evolution of biodiversity at all of its levels, from the gene to the ecosystem.

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1. Introduction

The 20th century Biological Species Concept cemented the importance of isolation in evolutionary biology, with pivotal works like those of Mayr (1942, 1959) and Dobzhansky (1937, 1940) showing that populations become species when they are isolated, first geographically and then reproductively. The role of geographic isolation in speciation continues to inspire debate, particularly in the evolutionary marvels that are the world's islands (e.g. Flantua et al., 2020; Itescu et al., 2020). Early biogeographers such as

Wallace (1880) noted that islands vary in their geographical isolation, with important consequences for evolution. Some, which they termed oceanic islands, were created by volcanic eruptions or uplift of coral far out at sea. Oceanic islands are separated from continents and other large landmasses by deep seas, and thus have never been connected to them by land. Continental land-bridge islands, on the other hand, are formed from parts of the continental shelf, and so at times of reduced sea level they were a continuous part of the mainland. Though later work has elaborated on this original classification (Ali, 2017, 2018), much research on island speciation still focuses on highly isolated oceanic islands such as Hawaii and the Galápagos (Whittaker et al., 2017). A smaller, but growing, body of literature has drawn important evolutionary conclusions from the faunas of land-bridge islands (e.g. Lister, 1989; Vartanyan et al.,

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1993; Keogh et al., 2005; Itescu et al., 2020), which are numerically more numerous, ecologically more complex, and zoologically richer than are oceanic islands (Meiri, 2017). As land-bridge islands have been isolated only briefly, these studies provide evidence of evolution which has taken place at a rapid rate.

Isolation of an island population results from features of the species as well as the island, as some organisms are more likely to maintain gene flow across water barriers than others. Thus, studies of evolution on land-bridge islands tend to focus on particularly weak dispersers, such as terrestrial mammals and reptiles (e.g. Lister, 1989; Vartanyan et al., 1993; Keogh et al., 2005). However, even among birds and other strongly dispersing animals, certain ecological and behavioural traits will inhibit gene flow across barriers which the organism should be physically capable of crossing (Harris & Reed, 2002). Some birds that fly long distances over land will not cross even narrow bodies of water (Diamond, 1981), and even the dispersive species that do colonise remote islands can develop “behavioural flightlessness” in these isolated populations (Moyle et al., 2009). The habit of foraging in forest understorey seems to be particularly significant in limiting gene flow and driving speciation (Burney & Brumfield, 2009; Smith et al., 2014). This study aims to investigate evolution on the land-bridge islands surrounding Sulawesi using a bird which is limited to the forest understorey, the endemic Sulawesi babbler *Pellorneum celebensis*. This species was first described, as *Trichastoma celebensis*, by Strickland (1849). The genus *Trichastoma* (Blyth, 1842) was subsumed into *Pellorneum* (Swainson, 1831) by Moyle et al. (2012) and Cai et al. (2019). Our taxonomy follows Gill et al. (2021).

Sulawesi is the largest island of the Wallacea region, one of Earth's threatened biodiversity hotspots (Myers et al., 2000). Sulawesi's complex geology has shaped an “anomalous” biogeography (Wallace, 1880) and a high level of endemism (Stattersfield et al., 1998), with the island divided into four distinct peninsulæ or “arms”, here referred to as North, Central, South, and Southeast Sulawesi (Fig. 1) (the centre of the island, between the arms, also forms part of Central Sulawesi). Southeast Sulawesi and the islands of Kabaena, Muna, and Wawonii (or Wowoni) all sit on a small fragment of continental lithosphere (Hall, 2013), which collided

with an adjoining microcontinent to form Buton (or Butung) Island (Satyana & Purwaningsih, 2011). The seas between these five islands are both shallow and narrow, and they were connected by land within the last 20,000 years (Nugraha & Hall, 2018).

The diversity of islands and species found in Sulawesi make it an ideal place to study evolutionary divergence across islands. As well as the land-bridge islands described here, there are more isolated islands, including the Sula group and the Wakatobi (or Tukangbesi) archipelago, which have never been connected to Sulawesi by land (Nugraha & Hall, 2018). Descriptions of endemic species from these more isolated islands indicate that birds readily speciate when separated by such permanent barriers (Kelly et al., 2014; O'Connell et al., 2019b; Rheindt et al., 2020). The Sulawesi babbler is found on all the land-bridge islands of Southeast Sulawesi, making it an ideal candidate for studies of evolutionary divergence on this shorter time scale. As the populations on Sulawesi, Buton, Kabaena, Muna, and Wawonii have been separated for an evolutionarily brief period of time, any divergence between them is evidence of evolution occurring at a rapid pace. These islands remain poorly known ornithologically, with species inventories emerging only recently (Martin et al., 2012; Martin et al., 2015; Martin et al., 2017; O'Connell et al., 2017; O'Connell et al., 2019a). As pressures on Indonesia's birds continue to mount (Rentschlar et al., 2018), it becomes increasingly urgent that we study recently documented populations such as these, in order to estimate their evolutionary distinctiveness and consider their conservation.

The Sulawesi babbler belongs to the family Pellorneidae (ground babblers), which was formed after species were split from the Timaliidae, Sylviidae, and Cisticolidae on molecular evidence (Cai et al., 2019). Babbler systematics are complex, and scientists' interpretations of them have changed repeatedly over the years (Cibois et al., 2002; Cibois, 2003; Gelang et al., 2009; Moyle et al., 2012; Cai et al., 2019). Pellorneid species richness reflects their biogeographic history (Cai et al., 2020), being highest in the Sino-Himalayan Mountains (where the group originated) and in the Sundaland region. Though Wallacea lies immediately to Sundaland's east, babblers colonised it more recently and thus their species richness is lower in this region. Aspects of the natural

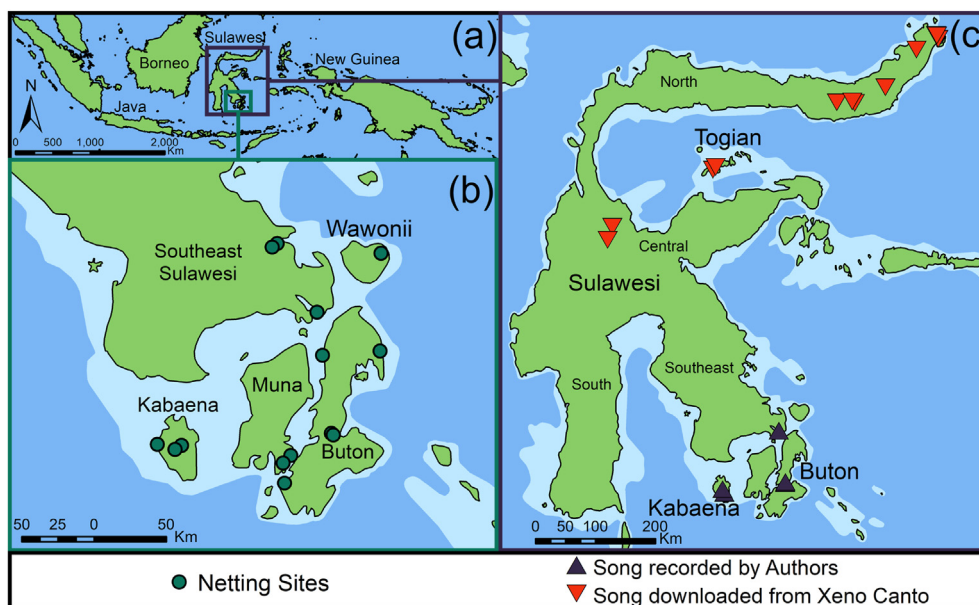


Fig. 1. a) Map of Indonesia with study region outlined. b) Map of Southeast Sulawesi with sampling sites marked with circles. c) Map of Sulawesi with song recording locations marked with triangles.

history and ecology of babblers remain enigmatic (Ó Marcaigh et al., 2020). As the Sulawesi babbler is “smallish [and] relatively featureless” (Billerman et al., 2020) and tends to skulk in the understorey, it is of the kind of bird most likely to be overlooked (Diamond, 1985; Gaston & Blackburn, 1994). Its “mouse-like” behaviour (Billerman et al., 2020) suggests that, biogeographically, such understorey birds may have more in common with terrestrial mammals than more dispersive species.

If we are to understand how populations become species, it is natural that we must study populations as well as species. Variation below the species level provides the raw material for natural selection, as populations will begin to diverge before they evolve physiological barriers to reproduction (Dobzhansky, 1940). Therefore, targeting the species level and below allows us to study both current and past speciation (e.g. Brelsford & Irwin, 2009; Everson et al., 2018). Units of diversity below the species level have been defined differently through scientific history, as varieties (Linnaeus, 1766), subspecies (Esper, 1781; Mayr, 1963), incipient species (Dobzhansky & Pavlovsky, 1967), conservation units (Coates et al., 2018) or Evolutionarily Significant Units (ESUs) (Moritz, 1994). Though division of subspecific diversity into units has often generated controversy, it is evident that this diversity is pivotal to evolution (O'Brien & Mayr, 1991; Phillimore & Owens, 2006). Indeed, while the species features in the title of evolutionary biology's founding text (Darwin, 1859), the subtitle refers to subspecific “races”. The Convention on Biological Diversity (1992) recognises biodiversity at the levels of genes, species, and ecosystems, but conservation at the gene level is hampered by lack of data, particularly in the biodiverse tropics (Bickford et al., 2007). Around 2% of vertebrate species are endemic to Wallacea (Myers et al., 2000), making it an urgent conservation priority that we understand Sulawesi's endemism, both above and below the species level.

The Sulawesi babbler provides one example of a bird species divided into subspecies based on plumage and other typological characteristics, where genetic data have been lacking. Current taxonomy (Gill et al., 2021) assigns all populations from Central and Southeast Sulawesi, as well as the land-bridge islands, to a single subspecies *P. c. rufofuscum* (Stresemann, 1931). The wide range thus attributed to this subspecies crosses several present-day mountain ranges and seas. Central and Southeast Sulawesi were separate islands in the past, leading to differences between their monkeys, toads (Evans et al., 2003), hoofed mammals (Frantz et al., 2018), and trees (Trethowan et al., 2020). If flight allowed all birds to transcend this pattern, we would expect the widely distributed babblers designated as *rufofuscum* to present one genetically uniform population, following the current taxonomy. Alternatively, if the understorey lifestyle of babblers limited their gene flow in a manner similar to land mammals, we would expect to see diversification between Central and Southeast Sulawesi populations and potentially across land-bridge islands as well.

2. Materials and methods

2.1. Sampling and data collection

We mist netted birds in Southeast Sulawesi (Fig. 1, Table S1) and the land-bridge islands of Kabaena, Muna, Buton, and Wawonii, between 1999 and 2017. We used the methods outlined in Redfern & Clark (2001) to photograph our birds (Fig. S1) and measure a range of morphological traits including wing length (maximum chord), bill length (tip of bill to the base), and skull length (from back of skull to base of bill). Only adult birds measured by a single recorder (NMM) were used for morphological analyses. This gave a morphological sample size of 22 for Southeast Sulawesi, 18 for

Kabaena, 6 for Muna, and 22 for Buton. Birds were also sampled for genetic analysis by taking a small number of contour feathers from the flank. Compared to other feather tracts, sampling of contour feathers minimises the risk of injury to the bird and avoids disrupting its flight ability and any plumage-based visual signals (McDonald & Griffith, 2011). Genetic sample size was 5 for Southeast Sulawesi, 1 for Central Sulawesi, 8 for Kabaena, 6 for Muna, 5 for Buton, and 1 for Wawonii. We recorded the babbler songs using a Zoom H2 Handy Recorder, with a Sennheiser Me62 external microphone and a Telinga V2 parabolic reflector, and downloaded additional recordings from the website xeno-canto (<https://www.xeno-canto.org/>). The combined acoustic sample size from both sources was 15 for Southeast Sulawesi, 2 for Central Sulawesi, 12 for North Sulawesi, 2 for Togian, 17 for Kabaena, and 16 for Buton. Our acoustic sampling thus included three of the four Sulawesi babbler subspecies recognised by Gill et al. (2021). These are the North Sulawesi subspecies *P. c. celebensis* (Strickland, 1849), the Togian subspecies *P. c. togianense* (Voous, 1952), and *P. c. rufofuscum* which supposedly covers all of Central and Southeast Sulawesi and the land-bridge islands. Previous taxonomic treatments had a subspecies endemic to Southeast Sulawesi, named *sordidum* by Stresemann (1938) and renamed *improbatum* by Deignan (1964) as there was already a *sordidum* subspecies in the same genus. However, White & Bruce (1986) merged *improbatum* into *rufofuscum* based on their similar flank colour, and this move has been retained by Gill et al. (2021). The fourth subspecies, not covered by our sampling, is *P. c. finschi* (Walden, 1876), endemic to South Sulawesi.

2.2. Genetic analyses

It has been demonstrated that divergence in mitochondrial genes correlates with speciation rate in tropical birds (Harvey et al., 2017). We used the mitochondrial DNA (mtDNA) genes NADH dehydrogenase subunits 2 and 3 (hereafter ND2 and ND3), to investigate population genetics of babblers. Barcoding approaches with mtDNA have proved successful in species delimitation (Hebert et al., 2004; Kerr et al., 2007; Hebert et al., 2016). While some evolutionary histories inferred from mtDNA differ from those inferred from nuclear DNA (Rubinoff & Holland, 2005; Phillimore et al., 2008), and biogeographic patterns inferred from mtDNA can be obscured by introgression and male-mediated gene flow (Toews & Brelsford, 2012), ND2 has shown a particularly high level of concordance with nuclear markers (Campillo et al., 2019), and studies on young radiations have found ND2 and ND3 to provide the best phylogenetic resolution (Andersen et al., 2015). This makes them appropriate to study divergence at the level of populations and subspecies, as we aimed to do.

DNA was extracted from feathers using a Qiagen DNeasy Blood and Tissue Kit (Qiagen, California, USA), following the manufacturer's instructions, but with the addition of 5 µL of 1M dithiothreitol (DTT). The DTT was added before the samples were vortexed prior to incubation, to break down the keratin from the base of the feather, which encased the genetic material. Polymerase Chain Reactions (PCRs) were carried out in 20 µL reactions to target the ND2 and ND3 genes, using a touchdown cycling protocol to increase yield (Korbie & Mattick, 2008). We amplified the ND3 gene using the L10755-F and DOC-ND3-R1 primer pair (Chesser, 1999; O'Connell et al., 2019b), while ND2 was sequenced in two halves using established and novel internal and external primers (Table S2). The reactions were screened using 2% electrophoresis gels stained with GelRed (Biotium), then sequenced by GATC EuroFins using a Sanger sequencing protocol. These sequences were aligned using the ClustalW function in BioEdit (Hall, 1999) and the ND2 and ND3 sequences were concatenated using Mesquite (Maddison & Maddison, 2018), for a total of 1392bp. We

used GenBank to obtain the sequences of the sole individual of *P. celebense* that had been sequenced previously (ND2 ccession JN826691, ND3 accession JN826966), and those of its two sister species: *Pellorneum rostratum*, described by Blyth (1842) (ND2 JN826692, ND3 JN826967), and *Pellorneum bicolor*, described by Lesson (1839) (ND2 JN826690, ND3 JN826965). These sequences of the three *Pellorneum* species were published in Moyle et al. (2012), with the *P. celebense* material supplied by a bird from Banggai Province in Central Sulawesi. Our outgroup included other babbler genera (Cai et al., 2019) and outgroup taxa used by Moyle et al. (2012) (a full list with accession numbers is in Table S3). Our new ND2 and ND3 sequences have been deposited in GenBank under accession numbers MW387438–MW387487.

We used POPART (Leigh et al., 2015) to draw a TCS Network of the haplotypes we sequenced (Fig. 2), to help visualise any potential population structure. The TCS algorithm uses an agglomerative approach, progressively combining clusters with one or more connecting edge (Templeton et al., 1992). A complete list of samples and their corresponding haplotypes is available in the Supplementary Information (Table S3). Only one representative of each ND2/ND3 haplotype was included in the Maximum Likelihood and Bayesian analyses. We used MEGA X (Kumar et al., 2018) to generate pairwise proportion differences (p-distances) between our concatenated ND2/ND3 haplotypes (Table S4) and to choose a nucleotide substitution model based on the Bayesian Information Criterion (BIC). It selected a Hasegawa–Kishino–Yano (HKY) model, which we used to perform Maximum Likelihood analysis with 1000 bootstraps and a level 5 Subtree-Pruning-Regrafting heuristic. We carried out Bayesian phylogenetic inference in MrBayes version 3.2.7 (Huelsenbeck & Ronquist, 2001), using a HKY model with burn in set to 25%. This consisted of two independent Markov chain Monte Carlo (MCMC) runs, with four chains per run, sampling every 1000 generations. We used TRACER version 1.7.1 (Rambaut et al., 2018) to assess convergence, accepting once average standard deviation in split frequencies (ASDSF) reached 0.01 and Effective Sample Size (ESS) of model parameters reached 200. These thresholds had been passed by 2 million generations. We exported a 50% majority rule consensus tree from MrBayes and merged it with the Maximum Likelihood tree using the merge_tree function in the ggtree R package (Yu et al., 2016). This merged tree is shown in Fig. 3, with the outgroup collapsed and with Bayesian probabilities and ML bootstrap values displayed. A version with all outgroup taxa displayed is available in Fig. S2.

To check for potential cryptic species within our babblers, we carried out distance-based molecular species delimitation using Automatic Barcode Gap Discovery (ABGD) (Puillandre et al., 2012). This analysis uses pairwise genetic distances to group sequences into “species” so that genetic distances within these “species” are smaller than those than between them. It takes a range of prior

maximum intraspecific divergences, and for each of them it calculates a “barcode gap” which is equal to the minimum threshold interspecific distance. It then splits the sequences into groups separated by the barcode gap. The range of prior maximum intraspecific divergences allows the analysis to be calibrated for different genes and species. We ran ABGD analysis on the web-server <https://bioinfo.mnhn.fr/abi/public/abgd/> using default settings (Pmin = 0.001, Pmax = 0.1, Steps = 10, relative gap width = 1.5, Number of bins = 20) and a Kimura-2-Parameter (K2P) model.

2.3. Phylogeographic analysis

Phylogeographic analyses were carried out in R version 4.0.2 (R Core Team, 2020) using the package Geneland (Guillot et al., 2005a). This is one of several clustering algorithms useful in assigning genetic data to groups without prior knowledge (Carstens et al., 2013). These algorithms search for the number of genetic populations that maximises Hardy–Weinberg Equilibrium (HWE) and Linkage Equilibrium. Because of this basis in HWE, the package creators advise caution in the interpretation of clustering in non-recombining DNA, such as mtDNA (The Geneland Development Group, 2020). Nevertheless, previous studies using the Geneland package have found clustering of the ND2 gene to agree with that of nuclear DNA (Trier et al., 2014; Klein et al., 2016). We ran a spatial MCMC algorithm on the 51 polymorphic sites of our concatenated babbler sequences for 45,000 iterations with thinning set to 100. We used Geneland’s “haploid” setting as our sequences were of mtDNA. This model’s output was then used to estimate the number of populations at HWE and assign each individual to a population (Fig. 4). The Geneland model accomplishes this by dividing the study area using a Voronoi tessellation and using genetic and geographic distance to calculate the probability of individuals originating from the same population (Guillot et al., 2005b). As all sequenced birds came from Central and Southeast Sulawesi and are currently grouped as the *P. c. rufofuscum* subspecies, the current taxonomy of the species would be supported if this analysis found only one cluster. By the same token, multiple clusters would indicate more genetic populations than captured by current taxonomy.

2.4. Acoustic analysis

Comparative analysis of bird song has come to play a central role in species delimitation and integrative taxonomy, as differences in song have been shown to lead to reproductive isolation and speciation (Isler et al., 1998; O'Reilly et al., 2018). The Sulawesi babbler often sings in duet, with the “main song” produced by one individual (presumed to be the male of a pair) answered with a distinct vocalisation from the presumed female (Billerman et al.,

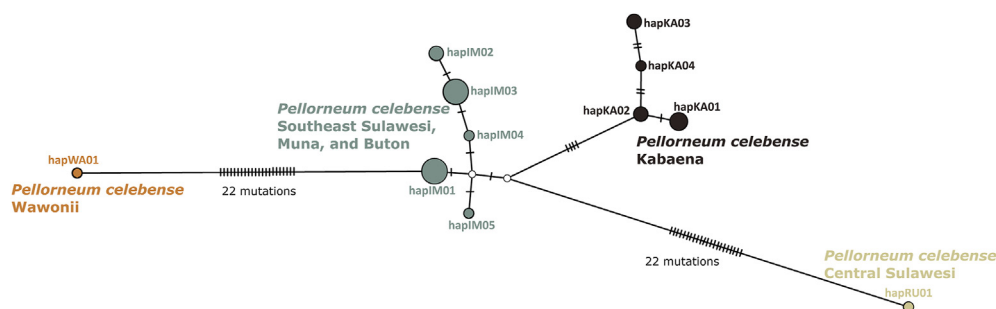


Fig. 2. Haplotype Network of concatenated babbler ND2/ND3 sequences. Each coloured circle represents a haplotype, sized to represent the number of corresponding samples and coloured to represent our proposed delineation of populations. Each bar across the interconnecting lines represents one mutation. The small, unfilled white nodes represent hypothetical ancestral states.

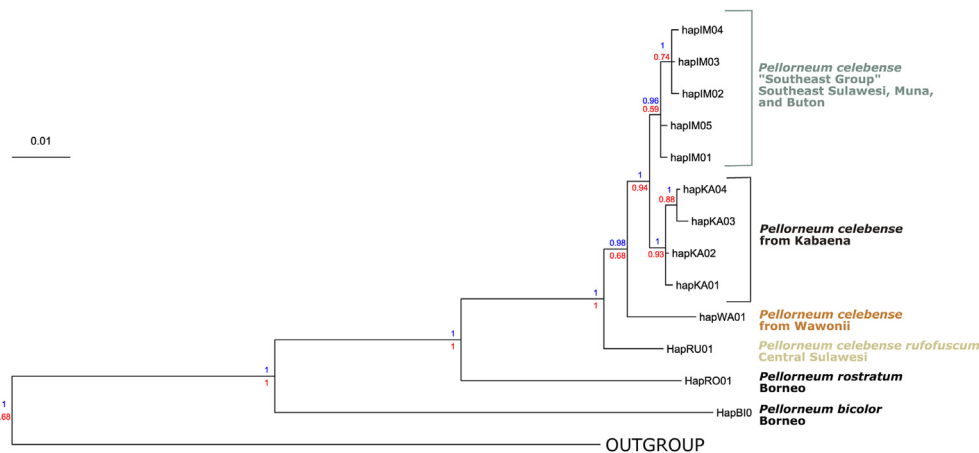


Fig. 3. Consensus phylogenetic tree of babler haplotypes, incorporating both Bayesian and Maximum Likelihood (ML) analyses. Nodes are labelled with Bayesian probabilities (above, in blue) and ML bootstrap supports (below, in red). The tree shows the outgroup taxa collapsed into one tip, a full list of the outgroup taxa used in the analyses can be found in Table S3 while Fig. S2 shows them included in the tree.

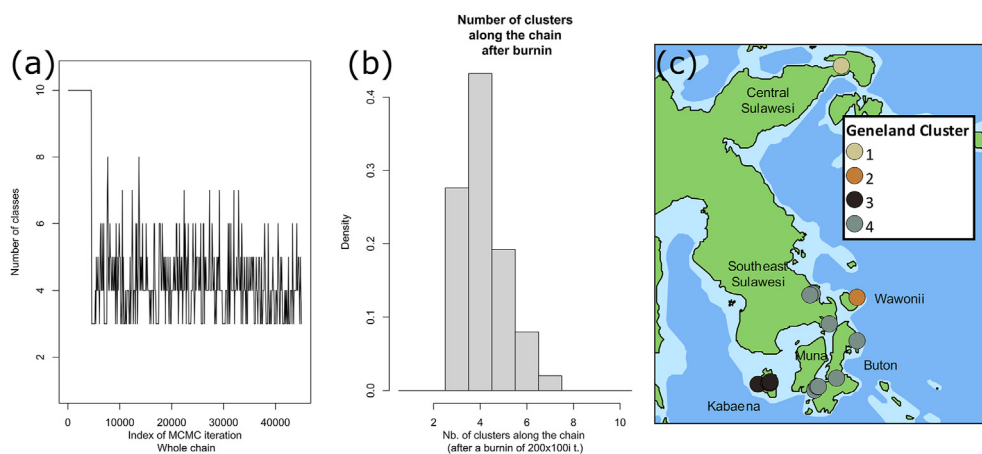


Fig. 4. a) Plot of the Geneland MCMC estimating the number of clusters, i.e. populations at HWE in the babblers of Central and Southeast Sulawesi. b) Histogram summarising the MCMC results and finding four clusters to be the most likely result. c) Map of babler concatenated sequences with the clusters they were assigned to by the Geneland analysis.

2020). We analysed the main, “male” song, and not the answering song of the presumed female, as there were more uninterrupted song bursts available and male song is more likely to be relevant to speciation, as mate choice by females based on male song may reinforce reproductive isolation if song diverges between populations (Catchpole, 1987). We used Raven Pro version 1.6 (Center for Conservation Bioacoustics, 2019) to create spectrograms from the babler recordings and measured these using on-screen cursors to collect data. Our acoustic dataset consisted of standard spectral and temporal song traits: peak frequency, duration, minimum frequency, maximum frequency, bandwidth, number of notes, and pace (Tobias et al., 2010; O'Connell et al., 2019b). To aid in visualisation, contrast and brightness were set to an equal value and the “Jet” colormap was selected; all other settings were left at their defaults (Ng et al., 2016). To account for intra-individual variation, intra-individual means were calculated from a minimum of two independent bursts of song (average of 8.1 songs, range 2–26) (Ng et al., 2016). These means served as our sample points (Supplementary File 2).

To give an impression of whether babler populations could be distinguished by song, we used the “random forest” algorithm in WEKA version 3.8.4 (Frank et al., 2016). This allowed us to look for clusters independently in our different datasets. As Geneland and

our haplotype network and phylogenetic tree had suggested certain patterns of genetic clustering in the purported *rufofuscum* subspecies, we were able to test whether this was reflected by song differences while also extending the comparison to two other recognised babler subspecies (*celebense* from North Sulawesi and *togianense* from Togian).

A random forest is a supervised classification algorithm which uses a series of decision trees to partition the dataset. A random subset of input variables are used to create bootstrapped subsets of training data to combine into a final model, splitting the data in a way that is unbiased and robust (Breiman, 2001). Random forests have been used to diagnose samples by their origin in other fields, such as geology (Dornan et al., 2020) and botany (Finch et al., 2017), and are increasingly used in similar fashion in species delimitation and population genetics (Derkarabetian et al., 2019; Smith & Carstens, 2020). Diagnosability is key to defining taxa, and is emphasised in particular by the Phylogenetic Species Concept (Cracraft, 1983; Archer et al., 2017). We used the “training set” setting for WEKA's random forest. A subset of the babler data was used to train the algorithm, by dividing these training examples by subspecies and additional divisions suggested by the genetic and phylogeographic analyses. In keeping with the current taxonomy, we labelled birds from North Sulawesi as *celebense*, those from

Togian *togianense*, and those from Central Sulawesi *rufofuscum*. Based on genetic divisions we grouped together the birds from Southeast Sulawesi and Buton as the “southeast group” and gave separate labels to those from Kabaena. We did not have songs from Wawonii or Muna (Table 1). The algorithm then attempted to classify the rest of the data based on differences in the training set. For comparison, we also ran Random Forest analyses which tried to group the birds by island, i.e. with Buton, Southeast Sulawesi, and Muna treated separately.

To confirm the pattern suggested by the Random Forest analysis, we used R to carry out a multivariate ANOVA (or MANOVA) on the acoustic data to see if differences between songs of populations were statistically significant. This MANOVA tested the difference between the North Sulawesi, Togian, Central Sulawesi, “southeast group” (Southeast Sulawesi and Buton) and Kabaena populations in peak frequency, duration, minimum frequency, high frequency, bandwidth, number of notes, and pace. We visualised the acoustic data using box plots (Fig. 5).

2.5. Morphological analyses

Only adult birds measured by NMM were included in morphometric analyses, and male and female babblers were analysed separately as males are considerably larger (Ó Marcaigh et al., 2020). The morphometric analyses thus included only birds from the Kabaena (n = 18) and “southeast group” (n = 50) populations, where the southeast group comprised Southeast Sulawesi, Muna, and Buton. We selected wing length, bill length, and skull length for the morphological analyses as they are independent variables that correspond to different aspects of the birds’ ecology (Ó Marcaigh et al., 2020). As with the acoustic data, we first carried out a random forest classification to see if these populations could be distinguished based on these three traits, then a MANOVA to test whether the differences were statistically significant. We constructed box plots to visualise the morphological data (Fig. 6).

2.6. Tobias scoring

We subjected our putative babbler populations to the quantitative scoring criteria outlined by Tobias et al. (2010), where populations with a “score” of 7 or more are seen as deserving of species status. This score is a combination of differences in morphology, vocalisations, plumage, ecology or behaviour, and geography. The geography category awards points for situations of sympatry and hybrid zones, and so does not apply to island populations. We had no data on ecology or behaviour, and our photographs of live birds in the field (Fig. S1) could not demonstrate plumage differences due to varying light conditions, so we were unable to score those areas. Therefore we calculated a partial Tobias score for the Kabaena population on acoustics and morphology, using the “effsize” package in R (Torchiano, 2020) to calculate Cohen’s *d*. Effect sizes are more suitable than *p*-values for informing taxonomic judgments as they are less correlated with sample size (Tobias et al., 2010). We used male morphology for our Tobias score because the acoustic score was based on the male song. We also made

similar comparisons with female morphology and the effect sizes were such that the score would have been the same.

3. Results

3.1. Genetics and phylogeography

Genetic analysis provided evidence of population structure within the ostensible *P. c. rufofuscum* subspecies of Central and Southeast Sulawesi. Southeast Sulawesi shared concatenated ND2-ND3 haplotypes with Muna and Buton, but not with Wawonii, Kabaena, or Central Sulawesi (Fig. 2). For that reason, in further analyses we grouped Southeast Sulawesi, Buton, and Muna as the “southeast group”, separate to Central Sulawesi. The Central Sulawesi haplotype (HapRU01) was between 1.7% and 1.9% different from the southeast group haplotypes, while it was 2.4% different from the Wawonii haplotype (hapWA01) and 1.9–2.2% different from the Kabaena haplotypes (Table S4). Babblers from Kabaena and the southeast group are distinct, monophyletic clusters on the phylogenetic tree (Fig. 3), each diverging from a common ancestor.

The Geneland MCMC analysis found best support for a 4-cluster model (Fig. 4), followed by a 3-cluster model. This indicates that there is more population structure in these babbler populations than is recognised by the current taxonomy, where all of these birds are considered to belong to one subspecies (*P. c. rufofuscum*). Furthermore, its proposed populations line up with the divisions suggested by the phylogenetic tree, with the Kabaena, Wawonii, southeast group, and Central Sulawesi clusters all apparent (Fig. 4c).

The ABGD analysis found the most support for three species in *Pellorneum* (*P. rostratum*, *P. bicolor*, and *P. celebense*), with five different barcode gaps between 0.8% and 6% difference in concatenated ND2-ND3 producing this grouping. At the lowest prior intraspecific divergences, however, the analysis calculated the barcode gap distance to be 0.1% and with this it created six groups: *P. rostratum*, *P. bicolor*, *P. celebense* from Central Sulawesi, *P. celebense* from Wawonii, *P. celebense* from Kabaena, and *P. celebense* from the southeast group.

3.2. Acoustic results

The Random Forest analysis on the seven acoustic traits had a 100% success rate in classifying birds according to our population divisions of Togian, North Sulawesi, Central Sulawesi, the “southeast group” (Southeast Sulawesi and Buton), and Kabaena. The Kappa statistic, F-Measure and ROC Area for each division was equal to 1, indicating an optimal classifying model. MANOVA on the seven traits agreed, finding a statistically significant difference between the same population divisions (*p* < 0.001). The full output from this MANOVA is in the Supplementary Information (Table S5). The Random Forest acoustic analysis which treated each island individually was much less successful, as it classified 31 birds incorrectly (48%). The Kappa statistic was 0.37, indicating a sub-optimal model.

Table 1
Number of individual babblers from each area available for each analysis. Mainland Sulawesi areas are bolded, offshore islands are italicised.

n	Southeast Sulawesi	Central Sulawesi	North Sulawesi	<i>Togian</i>	<i>Kabaena</i>	<i>Muna</i>	<i>Buton</i>	<i>Wawonii</i>
DNA	5	1	0	0	8	6	5	1
Morphology	22	0	0	0	18	6	22	0
Song	15	2	12	2	17	0	16	0

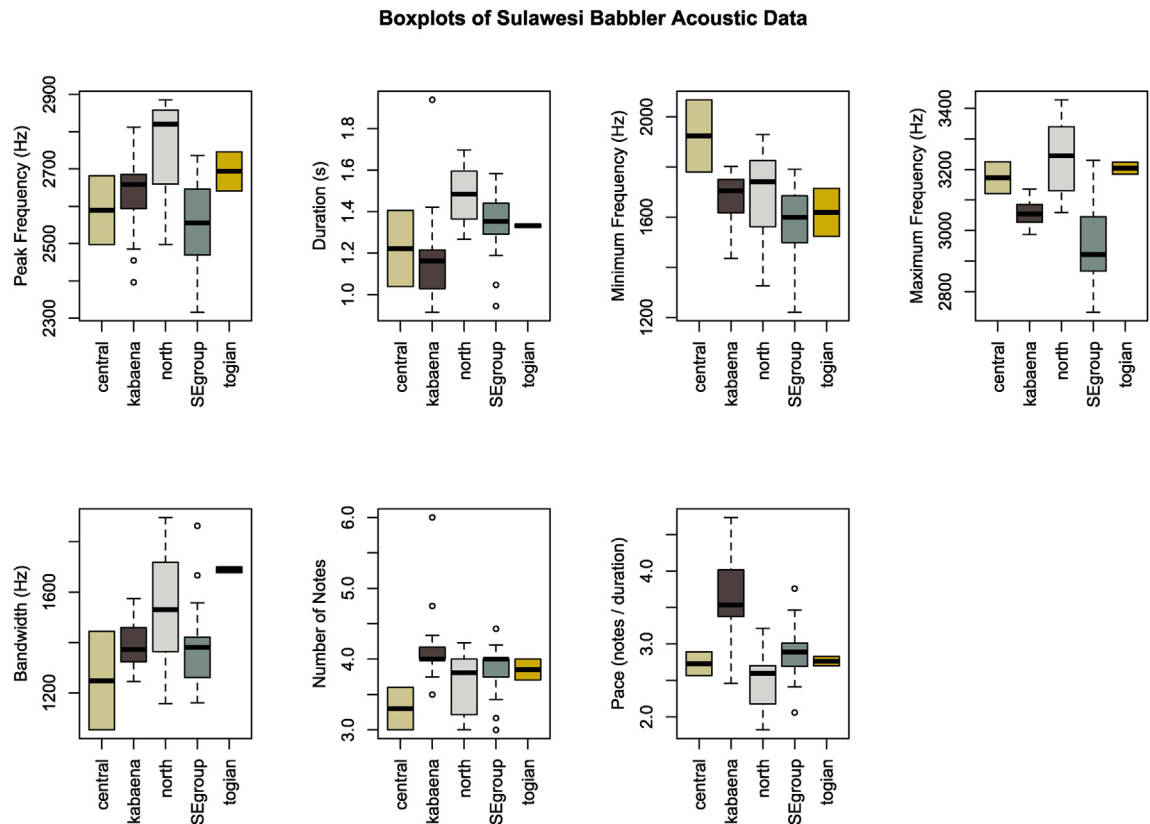


Fig. 5. Box plots of acoustic traits of Sulawesi babblers from Central Sulawesi, Kabaena, North Sulawesi, the Southeast Group (including mainland Southeast Sulawesi and Buton), and Togian.

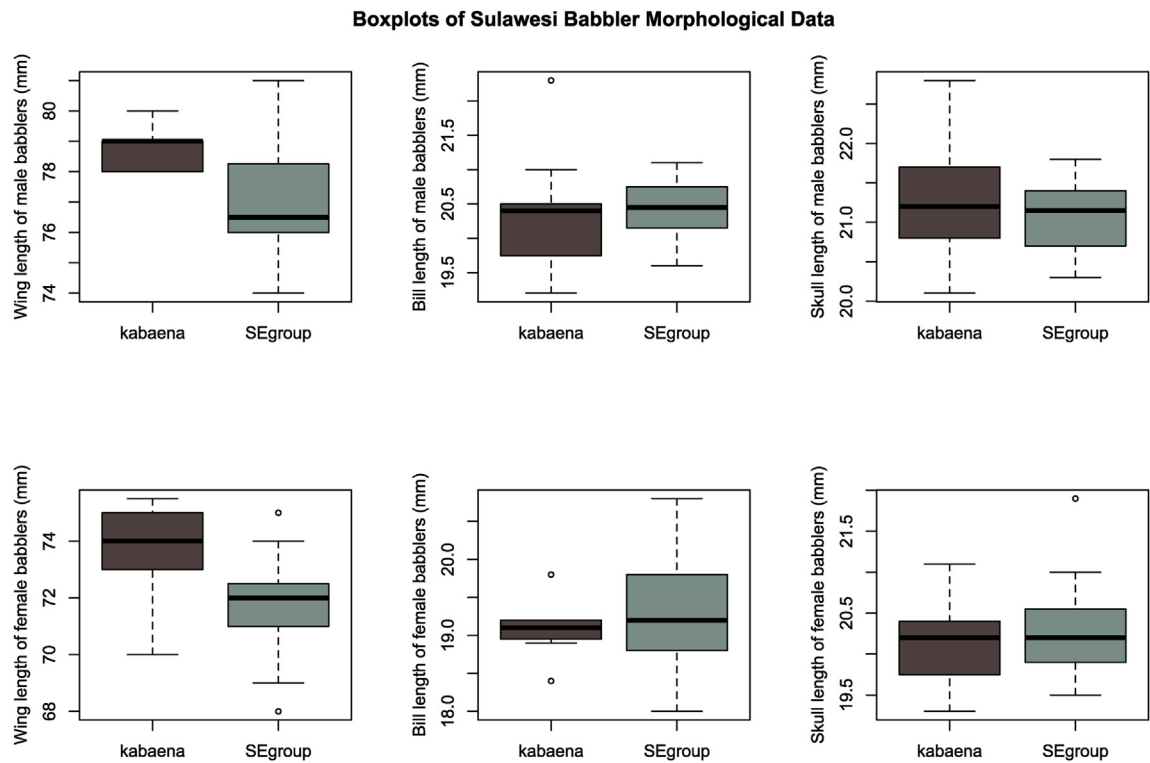


Fig. 6. Box plots of morphological traits of Sulawesi babblers from Kabaena and the Southeast Group (including mainland Southeast Sulawesi, Buton, and Muna). The top row of box plots represent the male babblers, the bottom row the females.

3.3. Morphological results

Once juvenile birds were excluded from the morphological dataset, this left only the southeast group and the Kabaena population. Even so, the Random Forest analysis categorised each dataset with 100% accuracy and with Kappa statistics, F-Measures and ROC Areas equal to 1. The MANOVA on male babblers from the southeast group and from Kabaena found that they were statistically significantly different in wing length, bill length and skull length ($p < 0.05$), as did the MANOVA on female babblers from the same two populations, using the same traits ($p < 0.05$). The full output from these MANOVAs are in the Supplementary Information (male babblers in Table S6, females in Table S7). When treating each island separately, the accuracy of morphological Random Forest analysis on males declined to 35%, while accuracy on females was reduced to 40%.

3.4. Tobias scoring

We applied the Tobias species delimitation system (Tobias et al., 2010) to our division between the Kabaena population and the southeast group (consisting of Southeast Sulawesi, Muna, and Buton), because this division had been supported by all of our previous analyses. This system allows use of one spectral acoustic character and one temporal in distinguishing between bird populations. Peak frequency was the most divergent spectral character between Kabaena and the southeast group, with a Cohen's d of 0.36. Pace was the most divergent temporal character, with a Cohen's d of 1.77. These constitute “minor” differences under the Tobias system, scoring 1 point each.

Two morphological traits may be included in calculating a Tobias score: that showing the largest increase, and that showing the largest decrease. When comparing birds from Kabaena to those from the southeast group, these were wing length (Cohen's d of 1.28) and bill length (Cohen's d of -0.25). The system ranks these effect sizes as “minor” and awards 1 point for each of them. Added together, these give a Tobias score of 4 for the Kabaena population when compared to babblers from Southeast Sulawesi, Buton, and Muna.

4. Discussion

Wallace (1887) set the priorities of biogeographers for centuries when he wrote that “The continental islands, still attached as they are to the base of the mainland, are to all intents and purposes a portion of the continent, as well in structure as in the forms of animal and vegetable life which they afford. It is in the oceanic islands that we should meet with limited and peculiar types.” Oceanic islands continue to receive the most attention in speciation studies today (Tobias et al., 2020). While continental land-bridge islands indeed harbour fewer endemic species, their populations may yet represent unique components of the species, important for both current biodiversity and future evolution. The fact that land-bridge islands are numerous and tend to be richer in species makes their populations more interesting still (Meiri, 2017; Tobias et al., 2020). It is apparent that babblers on the land-bridge islands of Kabaena and Wawonii have diverged from mainland populations in the brief time since these landmasses became physically disconnected. Previous work has shown that babblers on the land-bridge islands of Sulawesi exhibit stronger sexual dimorphism than those on the mainland (Ó Marcaigh et al., 2020). This study adds that babblers on Kabaena are distinct in acoustics, morphology, and mtDNA, and that the Wawonii population is strongly divergent in mtDNA. Combined with the division we found between Southeast Sulawesi and Central Sulawesi, this indicates that the subspecies

Pellorneum celebense rufosum is actually comprised of four independently evolving lineages.

The babblers of Southeast Sulawesi were formerly recognised as a distinct subspecies, *P. c. improbatum*, originally described by Stresemann (1938) from a type specimen from Lalolai in Southeast Sulawesi (latitude -4.05 , longitude 121.88). Though this taxon was abolished by White & Bruce (1986) and Gill et al. (2021), our analyses have reaffirmed that the babblers of the southeast group (Southeast Sulawesi, Buton, and Muna), do in fact represent an evolutionarily distinct population. The Southeast population has diverged from Central Sulawesi both acoustically and morphologically, mirroring the patterns of endemism seen in trees, monkeys, toads, and hoofed mammals (Evans et al., 2003; Frantz et al., 2018; Trethowan et al., 2020). This supports the hypothesis that these understorey birds are as disinclined to disperse as are non-volant organisms, with corresponding impacts on evolutionary trajectories. This is in keeping with findings from other understorey babbler species, which have also diverged genetically in areas that were recently connected by land bridges (Cros et al., 2020).

The distances involved would appear to be too short to fully explain the divergence seen. Kabaena is the most distant of the land-bridge islands at around 18 km from the Sulawesi mainland (Robinson-Dean et al., 2002), still a relatively short distance in terms of speciation. Wawonii is only 7 km from Sulawesi, comparable to Buton which is 6 km from the mainland at its closest point. Muna is separated from Buton by only 0.6 km. Habitats on Kabaena and Wawonii may be isolated by geology more than distance, as both islands are dominated by a distinct ultramafic geology that produces soils poor in nutrients and rich in phytotoxic minerals (Galey et al., 2017). Such soils present distinct selection pressures for organisms and are noted for very high levels of plant endemism (Anacker, 2014), which would in turn present a distinct evolutionary environment for animals including babblers. Populations of other taxa on Kabaena and Wawonii have been noted for their distinctness from neighbouring islands, showing the potential for evolutionary and ecological divergence despite the short time scale. Tweedley et al. (2013) observed a pronounced difference between the composition of the freshwater fish faunas of Kabaena and Buton. Trethowan et al. (2020) found the tree communities of Wawonii to comprise different species than those of Central Sulawesi.

Within birds, the patterns of evolutionary divergence in the region can be linked to life history. *Zosterops* white-eyes (Vigors & Horsfield, 1826) are famous for their dispersal abilities, though more isolated populations are known to develop behavioural flightlessness (Moyle et al., 2009). *Zosterops* populations on Kabaena and Wawonii show no sign of divergence (O'Connell et al., 2019b). The olive-backed sunbird *Cinnyris jugularis* (Linnaeus, 1766) and grey-sided flowerpecker *Dicaeum celebicum* (Müller, 1843) both inhabit marginal habitats such as forest edges, scrubland and mangroves (Billerman et al., 2020), a trait that makes a bird more likely to cross habitat gaps and open spaces (Burney & Brumfield, 2009). They too share populations across Kabaena and Sulawesi (Kelly, 2014; Kelly et al., 2014; O'Connell et al., 2019c). The red-backed thrush *Geokichla erythronota* (Sclater, 1859) presents a notable contrast to these species, having diverged strongly enough on Kabaena to produce an endemic subspecies *G. e. kabaena* (Robinson-Dean et al., 2002). Like the Sulawesi babbler, the rusty-backed thrush is a bird of the forest understorey, and the two species have even been observed foraging together (Billerman et al., 2020).

Evolutionary divergence within the babblers of Sulawesi and its land-bridge islands can be compared to that between more geographically isolated lineages. This study found Moyle et al.'s (2012) *P. rostratum* sequence from Borneo to be 7% different from

all *Pellorneum celebense* haplotypes. Borneo and Sulawesi have been separated for the duration of their existence by the Makassar Strait, part of the permanent barrier of deep water known to biogeographers as Wallace's Line (Wallace, 1880; Tweedley et al., 2013). This 7% difference in concatenated ND2-ND3 is thus the result of millions of years of evolution, while the populations of Sulawesi and its land-bridge islands have developed a p-distance around 1/3 of this in only 12,000 years or so (Table S4). This illustrates the remarkable speed with which speciation can act on dispersal-limited species, as well as the impact of genetic drift on these relatively small island populations.

Our work highlights the importance of units below the species level to the evolutionary potential of the Sulawesi babbler. This joins a long-standing debate in evolutionary biology, where approaches to species and subspecies often generate controversy. Earlier naturalists named many subspecies based on typological traits and came in for some contemporary criticism (Wilson & Brown, 1953). While modern methods overturned many of their designations, they reaffirmed others: Hartert (1903), for example, named two endemic species from the Wakatobi islands which were later demoted to subspecies (White & Bruce, 1986), before being confirmed as reproductively isolated species a century later (Kelly et al., 2014; O'Connell et al., 2019b). The higher levels of the Linnaean hierarchy were prioritised early in the molecular age, but a broad consensus persisted that the subspecies concept is useful in naming distinct populations with geographical boundaries between them, using multiple lines of evidence (Wiens et al., 1982). Phillimore & Owens (2006) found that island subspecies are the most likely to reflect evolution accurately and suggested that subspecies can aid conservation in the tropics. We have sought to follow these recommendations by analysing geographically delimited populations on tropical islands using multiple lines of evidence.

Modern ornithologists delimit species with an integrative approach based on comparison to recognised species and ultimately derived from the Biological Species Concept (Tobias et al., 2010). This integrative approach is particularly important when genetic data are absent or, as here, based on relatively low genetic sample sizes. Based on two of the five scoring criteria, the Kabaena population attains a Tobias score of 4, three points short of species status. Despite the lack of data on plumage, ecology, and behaviour, this partial score was more than half of that required to identify a distinct species, strongly suggesting that the Kabaena birds and the southeast group represent separate populations. The Wawonii population cannot be scored as it lacks acoustic and morphological data. Note that this system does not incorporate genetic data. We thus propose the distinct babbler populations as subspecies and not as independent species. Our ABGD analysis supports this conclusion, as it separated these four *P. celebense* populations from one another using a small barcode gap of 0.1% difference in concatenated ND2-ND3, appropriate for splits between subspecies. When the barcode gap was between 0.8% and 6%, similar to that between ND2 sequences of other bird species (e.g. Pellegrino et al., 2017; O'Connell et al., 2019b), ABGD grouped *P. celebense* together as a single species. Fuller Tobias assessments, incorporating plumage, ecology, and behaviour, might lead to other conclusions.

We thus recommend that the subspecies *Pellorneum celebense improbatum* be reinstated for babblers from Southeast Sulawesi, Buton, and Muna, as these are genetically and acoustically divergent from the *P. c. rufofuscum* population of Central Sulawesi. We propose that babblers from Kabaena be named as a new subspecies for their genetic, acoustic, and morphological divergence from Southeast Sulawesi, Buton, and Muna. This would require collection of a voucher specimen from Kabaena, as historical collectors did not visit the island (White & Bruce, 1986) and as a result very few

species have ever been collected there, in fact the island was almost unknown ornithologically until recently (O'Connell et al., 2017). Lack of museum material should not delay conservation (O'Connell et al., 2020). We therefore suggest the provisional name of *P. c. kabaena* for the Kabaena babblers and recommend that they be subjected to formal description. The Wawonii population shows strong divergence in mtDNA, but as this is based on one sample and lacks acoustic or morphological data, we recommend that it be studied in more detail before a taxonomic judgement is made.

Separate to any taxonomic revision, characterising the divergence of populations on Wallacean islands is key to our understanding of how speciation creates the biodiversity of this global hotspot. The concept of the Evolutionarily Significant Unit, or ESU, aims to sidestep taxonomic debate by targeting conservation at lineages that are evolving independently, regardless of how these are assigned to taxa (Ryder, 1986; Moritz, 1994; Coates et al., 2018; Neal et al., 2018). We believe that four independent ESUs are present in the populations currently assigned to this one babbler subspecies, one each from Central Sulawesi, Southeast Sulawesi, Kabaena, and Wawonii.

These populations of the supposed *rufofuscum* subspecies have undergone divergent evolution, despite being physically capable of maintaining gene flow between the land-bridge islands and the mainland. As Mayr (1969) noted, "Most tropical birds are highly sedentary and respect water barriers to a high degree". This also applies to the division between Central Sulawesi and Southeast Sulawesi, which were separated by water barriers for much of their geological history. Taxonomists should be wary of lumping the taxa of these two "areas of endemism" (Evans et al., 2003) together. Just as our understanding of a species and its evolution is improved by analysing its constituent populations, there is an urgent need to consider which areas within the threatened biodiversity hotspots are most important in generating this biodiversity through speciation. Sometimes these areas are imperilled by the very traits that make them evolutionarily significant: the ultramafic nickel deposits of Kabaena and Wawonii also make them attractive to large-scale mining (Morse, 2019b, a). Time is therefore running out to build a full picture of the biodiversity of these islands and their evolutionary dynamics.

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Availability of data and material

All new ND2 and ND3 DNA sequences from this study have been submitted to GenBank under accession numbers MW387438 – MW387487. Recordings of vocalisations will be uploaded to xeno-canto. The acoustic and morphological data have been made available in Supplementary Files 2 and 3, respectively.

Code availability

The R code used in our analyses is available in Supplementary File 1.

Authors' contributions

FÓM, DJK, and NMM conceived this study and led the writing of the manuscript. DJK, NMM, DOC, FÓM, AK, and KA carried out the fieldwork. FÓM, NL, DOC, DD, and AC carried out the labwork. FÓM and DD processed the song recordings and DNA sequences. FÓM

analysed the data, with input from DOC on phylogenetics. All authors contributed to revising and improving the manuscript.

Ethics approval

Kementerian Riset Teknologi Dan Pendidikan Tinggi (RISTEKDIKTI) provided the necessary permits and approvals, under permit numbers 0143/SIP/FRP/SM/VII/2010, 278/SIP/FRP/SM/VII/2012, 279/SIP/FRP/SM/VIII/2012, 174/SIP/FRP/E5/Dit. KI/V/2016, 159/SIP/FRP/E5/Fit.KIVII/2017, and 160/SIP/FRP/E5/Fit.KIVII/2017.

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.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jcz.2021.07.006>.

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