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# Using bioacoustic data to test species limits in an Indo-Pacific island radiation of *Macropygia* cuckoo doves

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The characterization of species limits and diversification patterns across the geographically complex Indo-Pacific region has presented biogeographers and evolutionary biologists with great challenges. In the present study, we investigated the brown cuckoo dove (*Macropygia amboinensis s.l.*) species complex, whose distribution spans this entire region. We analyzed whether bioacoustic data are congruent with previous plumage-based classifications and whether glacial land bridges have impacted bioacoustic diversification in these doves. Using an unusually large vocal dataset of > 300 recordings from over 30 islands and 24 taxa, we analyzed 29 bioacoustic frequency and temporal parameters and tested for a correlation between geographical and bioacoustic distances. We found a weak correlation between geographical and bioacoustic distances. We identified numerous lineages that are bioacoustically distinct and proposed their elevation to the species level, leading to a doubling of the number of species in this complex and indicating a high proportion of cryptic species-level diversity that has previously gone unrecognized. © 2016 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2016, **00**, 000–000.

KEYWORDS: allopatry – Columbidae – isolation-by-distance – Wallacea.

## INTRODUCTION

The Indo-Pacific region is a biogeographically important crossroads between the Asian and Australian realms (Wallace, 1859). It is an area of high endemicity (Mittermeier *et al.*, 1998; Myers *et al.*, 2000) and rich biodiversity (Corlett, 2009). The region comprises more than 20 000 islands (Lohman *et al.*, 2011), some of which are periodically connected during the glacial periods, whereas others are not (Bintanja, van de Wal & Oerlemans, 2005). Additionally, the region is characterized by some of the most dramatic tectonic shifts of landmasses in Pleistocene times (Hall, 1996).

Despite previous research into the evolutionary histories of Indo-Pacific fauna and flora (Ziegler *et al.*, 2007; Jønsson *et al.*, 2008; Muellner *et al.*, 2008; Müller & Beheregaray, 2010), much remains to be learned about diversification mechanisms across this vast archipelago. Although populations on islands connected by glacial land bridges are expected to have higher levels of gene flow than those of unconnected islands, few studies have investigated faunal groups of a sufficiently wide distribution to test the impact of land bridges on patterns of diversification (Hosner, Nyari & Moyle, 2013; Weeks & Claramunt, 2014).

Birds are an important model group for examining faunal diversification patterns because they are taxonomically and biologically well known. However, even within birds, areas such as the Indo-Pacific region are thought to harbour cryptic diversity that is unrecognized by current taxonomic treatments (Collar, 2003). Recent efforts have applied various techniques, including molecular and bioacoustic ones, to diagnose cryptic Indo-Pacific species (Jønsson *et al.*, 2009, 2011, 2014; Moyle *et al.*, 2009; Irestedt *et al.*, 2013; Andersen *et al.*, 2015). In the present study, we examine Indo-Pacific faunal diversification using a collection of field

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sound recordings of unprecedented scale in a dove (Columbidae) species complex that has diversified extensively across the archipelago.

Vocalizations are an important form of communication in birds (Catchpole & Slater, 2008), especially with regard to the recognition and attraction of conspecifics during courtship. Avian vocalization is thus a target of sexual selection (Searcy & Brenowitz, 1988) that is crucial in mediating reproductive isolation (Kroodsma & Byers, 1991) and acts as a sensitive indicator of speciation (Payne, 1986; Päckert *et al.*, 2003; Rheindt, Norman & Christidis, 2008; Seneviratne, Jones & Carr, 2012). This is especially so for groups with innate vocalizations, such as pigeons and doves (Miller & Baker, 2009). Bioacoustics is a powerful tool for determining species limits and has allowed the recognition of allopatric taxa with distinct vocalizations as species rather than subspecies, especially in elusive and morphologically similar groups (Jones, 1997; Isler, Isler & Whitney, 1999; Isler *et al.*, 2001; Alström & Ranft, 2003).

The brown cuckoo dove (*Macropygia amboinensis s.l.*) complex is a group of forest-dwelling doves that has had a checkered taxonomic history, with treatments describing from one to six species (Fig. 1; Table 1). The multitude of islands inhabited within each species-level group has rendered the exact circumscription of specific boundaries difficult. With respect to the six species widely acknowledged in recent accounts, Baptista, Trail & Horblit (1997) recognized 29 subspecies, whereas Gibbs, Barnes & Cox (2001) recognized 37 subspecies. Some island subspecies differ greatly in coloration (Baptista *et al.*, 1997), which further complicates the use of plumage characters in species delimitation. Other characters, such as bioacoustic ones, are needed to understand species limits and biogeographical patterns of diversification.

The present study investigates whether bioacoustic data across the brown cuckoo dove species complex are congruent with the plumage-based baseline taxonomy reported by Gibbs *et al.* (2001) or whether additional cryptic taxa are revealed by vocal differentiation. We then examined whether there is bioacoustic evidence for isolation-by-distance over landmasses and, at the same time, taking into account overwater distances that would have to be crossed at the glacial maxima. The aim is to test whether bioacoustic data provide support for the inclusion of various island taxa into broad species. In the absence of isolation-by-distance, some island taxa with distinct vocalizations would have remained isolated from one another, despite glacial land connections. This would suggest that other evolutionary mechanisms played a role in the diversification of the brown cuckoo dove species complex.

## MATERIAL AND METHODS

### Vocal samples

A total of 315 recordings of the brown cuckoo dove complex across 24 taxa (see Supporting information, Table S1) were obtained, with 126 (40%) from the Xeno-Canto bird sound collection (http://www.xeno-canto.org) and a further 189 recordings obtained in the field by ourselves. Recordings were made by 42 different recordists from across the range of the brown cuckoo dove complex (see Supporting information, Table S1). Recordings were converted to WAV format, if not obtained in that format. Recording equipment differed among recordists, although sonogram inspection revealed a negligible equipment bias. Among recordings from the same recordist, variability in background noise and slight differences in note shape are most often equivalent to the variability among recordings from different recordists, implying that differences in recording quality have greater importance than equipment differences (Rheindt, Eaton & Verbelen, 2011; van Balen, Eaton & Rheindt, 2013).

### Vocal analysis

Sonograms of vocalizations were prepared and analyzed using RAVEN PRO, version 1.5 (Bioacoustics Research Program, Cornell Laboratory of Ornithology, Ithaca, NY, USA). Contrast and brightness were set to an equal level and the sharpness was set at 2000 (Fig. 2); all other settings were left at default. Only recordings with homologous vocalizations for each taxon were included in the analysis (MacKinnon & Phillipps, 1993; Coates & Bishop, 1997; del Hoyo *et al.*, 2014; Pratt & Beehler, 2014).

All taxa had vocalizations containing between one and three elements per call motif (Fig. 3). A motif is defined here as one repeat of a call, and an element comprises an unbroken segment of a call motif (Fig. 2), as similarly defined in previous bioacoustic studies (Nemeth & Brumm, 2009; Rheindt *et al.*, 2011; Nemeth *et al.*, 2013; Harris *et al.*, 2014). A total of 29 vocal parameters, where applicable, were measured: (1) number of elements per motif; (2–4) lowest frequency of elements 1–3; (5–7) highest frequency of elements 1–3; (8–10) peak frequency of elements 1–3; (11–13) bandwidth frequency of elements 1–3; (14) total lowest frequency; (15) total highest frequency; (16) total peak frequency; (17) total bandwidth frequency; (18) break length between elements 1 and 2; (19) break length between elements 2 and 3; (20) total intra-motif break length; (21) break length between motifs; (22–24) duration of elements 1–3; (25) total motif length; (26) ratio between total break length and total motif length;

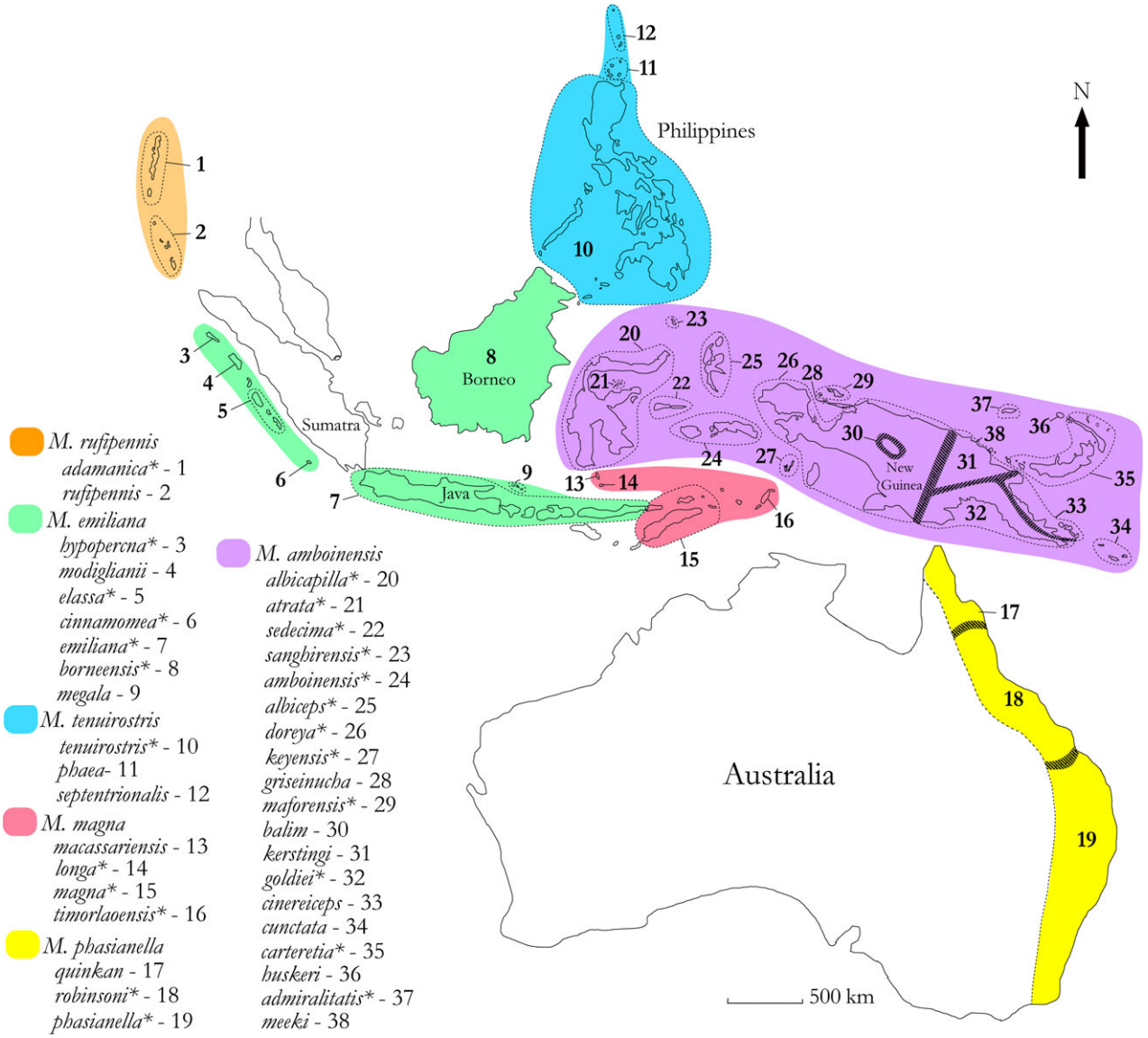



**Figure 1.** Distribution of the brown cuckoo dove species complex *sensu* Gibbs *et al.* (2001) across the Indo-Pacific Archipelago, from the Andaman Islands to Australia. Asterisks (*) indicate taxa that were included in the present study. Taxon *goldiei* was not recognized by Gibbs *et al.* (2001) but was by Baptista *et al.* (1997) and was included in the present study. Distribution of taxon *kerstingi* was revised based on new vocal recording; for rationale, see Discussion. The exact distributions and demarcation of adjacent taxa are uncertain; this uncertainty is indicated by the black barred areas.

and (27–29) differential frequency of elements 1–3. The vocal parameters are further illustrated in Figure 2. We attempted to be comprehensive in our selection of vocal parameters, including those that are likely to be taxonomically informative and those that are potentially uninformative.

To ensure that equal weight was given to each recorded individual, intra-individual means were computed from an average of 10 calls per individual for applicable vocal characters. The means became sample points from which ranges, means and SDs were computed for each taxon.

### Statistical analysis

For each recording, vocal parameters that apply to an entire vocalization as opposed to those that only apply to single elements [(1), (14), (15), (16), (17), (20), (21), (25), and (26)] were subjected to principal component analysis (PCA). PCA was conducted with

**Table 1.** Past and recent taxonomic classification of Macropygia amboinensis species complex

| Taxa | Peters (1937), Goodwin (1983) | Condon (1975) | Frith (1982), Christidis and Boles (2008) | White and Bruce (1986), Sibley and Monroe (1990), Andrew (1992), Baptista *et al*. (1997), Gibbs *et al*. (2001), del Hoyo *et al*. (2014) | Inskipp, Lindsey & Duckworth (1996) | Dickinson & Christidis (2014) |
|---|---|---|---|---|---|---|
| *rufipennis* | *M. rufipennis* | | | *M. rufipennis* | *M. rufipennis* | *M. rufipennis* |
| ***andamanica*** | | | | | | |
| ***hypopercna*** | *M. phasianella* | *M. amboinensis* | *M. emiliana* | *M. emiliana* | *M. amboinensis* | *M. emiliana* |
| *modiglianii* | | | | | | |
| ***elassa*** | | | | | | |
| ***cinnamomea*** | | | | | | |
| ***borneensis*** | | | | | | |
| *megala* | | | | | | |
| ***emiliana*** | | | | | | |
| ***tenuirostris*** | | | *M. tenuirostris* | *M. tenuirostris* | | *M. tenuirostris* |
| *phaea* | | | | | | |
| *septentrionalis* | | | | | | |
| ***magna*** | *M. magna* | | *M. amboinensis* | *M. magna* | | *M. magna* |
| ***longa*** | | | | | | |
| *macassariensis* | | | | | | |
| ***timorlaoensis*** | | | | | | |
| ***sanghirensis*** | *M. amboinensis* | | | *M. amboinensis* | | *M. amboinensis* |
| ***albicapilla*** | | | | | | |
| ***albiceps*** | | | | | | |
| ***amboinensis*** | | | | | | |
| ***keyensis*** | | | | | | |
| ***doreya*** | | | | | | |
| ***maforensis*** | | | | | | |
| *griseinucha* | | | | | | |
| *kerstingi* | | | | | | |
| *cunctata* | | | | | | |
| *meeki* | | | | | | |
| ***carteretia*** | | | | | | |
| *hueskeri* | | | | | | |
| *cinereiceps* | | | | | | |
| ***goldiei**** | | | | | | |
| ***arata*** | | | | | | |
| ***sedecima*** | | | | | | |
| *balim* | | | | | | |
| ***admiralitatis*** | | | | | | |
| ***phasianella*** | *M. phasianella* | | | *M. phasianella* | | |
| ***robinsoni*** | | | | | | |
| *quinkan* | | | | | | |

All taxa listed are recognized by Gibbs et al. (2001) with the exception of asterisk (*) marked goldiei, which is recognized by Baptista et al. (1997). Back cells indicate species that were omitted in the classification. Taxa in shown bold are considered in the present study with baseline taxonomy by Gibbs et al. (2001).

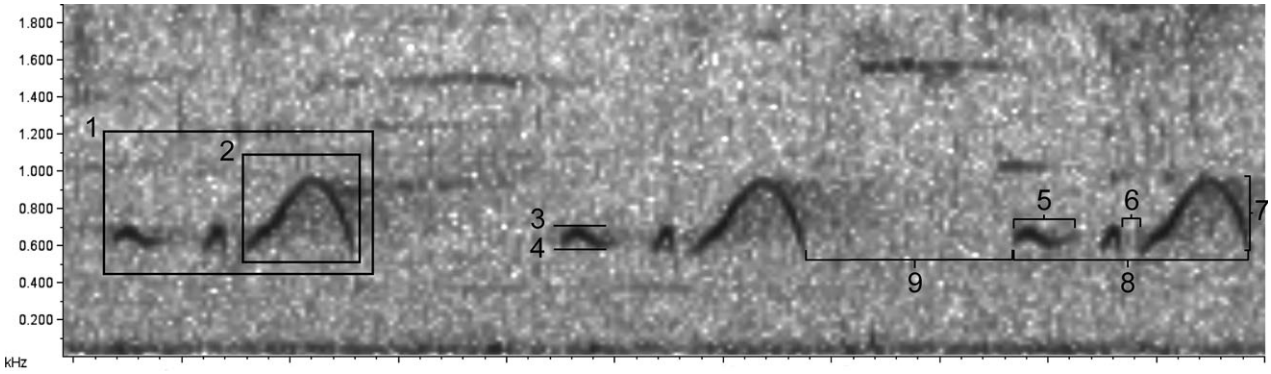



**Figure 2.** An example of a typical sonogram used for analysis. Vocal characters: (1) a motif and (2) an element. Parameters measured: (3) highest frequency; (4) lowest frequency; (5) duration of an element; (6) break length between elements; (7) bandwidth frequency; (8) total motif length; and (9) break length between motifs.

the 'prcomp' function in R, version 3.1.1 (R Development Core Team, 2014). Recordings with any of these nine characters absent were omitted because PCA cannot be conducted with missing values. Distinct vocal clusters are encompassed within the 95% confidence ellipses, with an allowance of < 5% overlap.

Isler, Isler & Whitney (1998) formulated and tested their vocal diagnosability criterion (i.e. the Isler criterion) using well established limits within antbird (Passeriformes: Thamnophilidae) species pairs. Although designed for suboscine passerines, the Isler criterion has been successfully applied to doves and was shown to discriminate between vocally divergent lineages (Rheindt *et al.*, 2011). As such, the Isler criterion was strategically applied to geographically proximate taxon pairs. The Isler criterion is based on two conditions: (1) the vocal parameters measured for taxa compared must not overlap and (2) mean ± SD values of the taxon with the smaller measurement set (a) and the taxon with the larger measurement set (b) had to meet the requirement

$$\bar{x_a} + t_a \mathrm{SD}_a < \bar{x_b} - t_b \mathrm{SD}_b$$

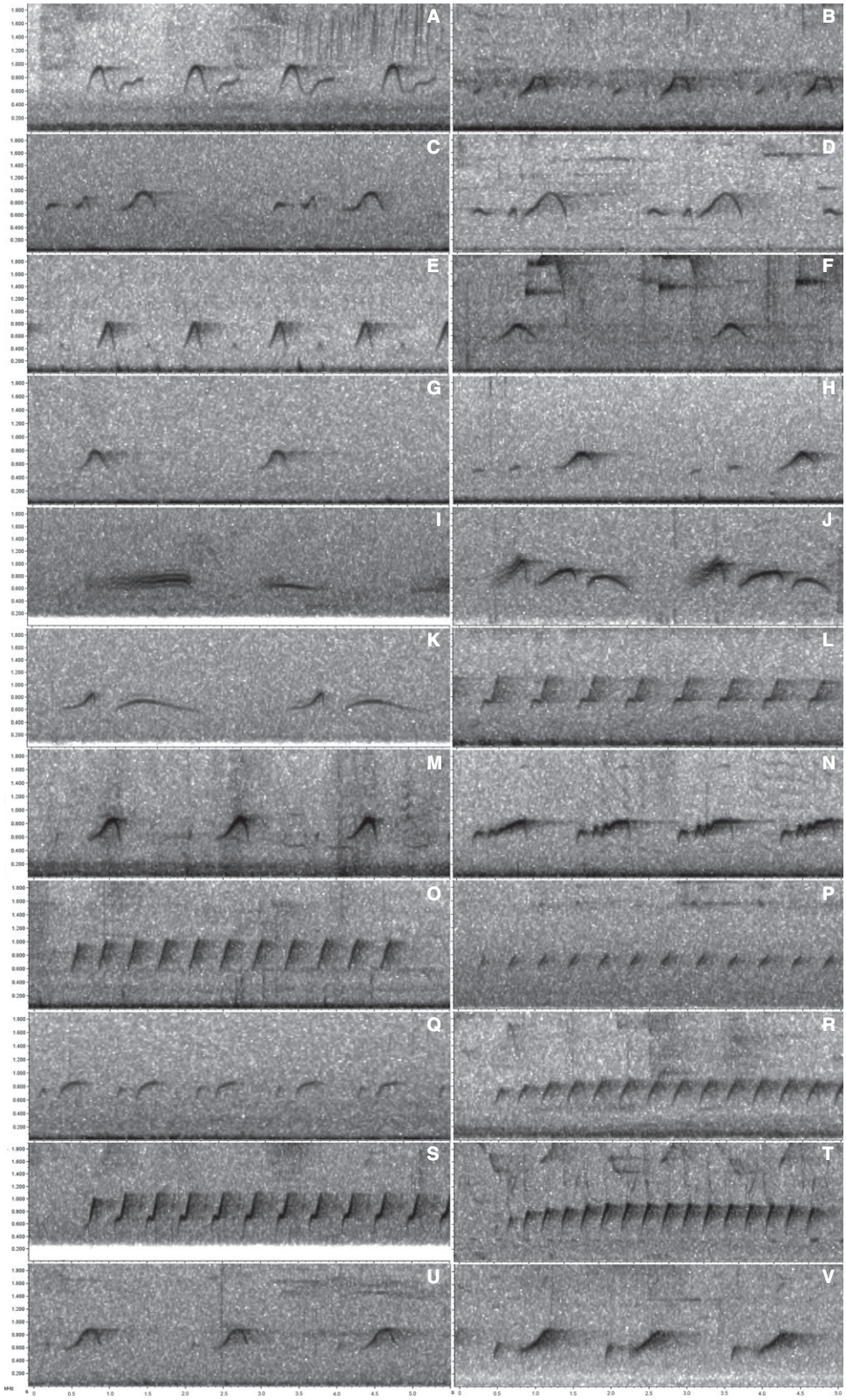
where $t_i$ is Student's $t$-score at the 97.5 percentile at $N - 1$ degrees of freedom of the $t$ distribution. The second condition of the criterion (Isler *et al.*, 1998) was modified with respect to the original formulation to account for characters with little variation that resulted in null values. The criterion has been altered to diagnose vocal differentiation only when the set of measurements of one population is greater than (and not equal to) the set of measurements of the other population. Isler diagnosability is defined here as the presence of at least one or more vocally diagnosable characters between taxa. Species delimitation in the present study is based on Isler's criterion and also in accordance with the biological species concept (Mayr, 1942).

### Distance analysis

Little is known about the modes of gene flow within Australasian biota but, depending on the oceanic vs. continental nature of the landmass inhabited, certain patterns of connectivity are more likely than others. In particular, there would be fewer obstacles to gene flow between taxa ranging on islands regularly connected by Pleistocene land bridges and taxa from other connected islands. Conversely, taxa from unconnected deep-sea islands would only be connected with neighbouring populations by overwater dispersal, with the level of gene flow in an approximately negative correlation with the overwater distance to be bridged. We have taken these geographical factors into account by computing distances between populations and taxa in two different ways.

First, we investigated the presence of isolation-by-distance with the correlation between inter-individual geographical distances and Euclidean bioacoustic distances of principal component (PC) coordinates from when each recording was first examined. PC1 and 2 coordinates extracted from PCA (data not shown) were used to determine interspecific pairwise Euclidean distances between recorded individuals. The geographical longitudes and latitudes of each recorded individual were obtained either from the recordist or, when no coordinates were included, the location was inferred from Google Maps (https://maps.google.co.uk). Geographical distances between all recorded individuals were calculated with function 'earth.dist' from R package 'fossil' (Vavrek, 2011).

Next, we investigated the possibility that gene flow between dove populations may be governed less by


A
B
C
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R
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T
U
V

**Figure 3.** Sample sonograms of taxa included in the present study. A, *Macropygia rufipennis andamanica;* B, *Macropygia emiliana borneensis;* C, *Macropygia emiliana cinnamomea;* D, *Macropygia emiliana elassa;* E, *Macropygia emiliana emiliana;* F, *Macropygia emiliana hypopercna;* G, *Macropygia tenuirostris tenuirostris* (Palawan)*;* H, *Macropygia tenuirostris tenuirostris;* I, *Macropygia magna longa;* J, *Macropygia magna magna;* K, *Macropygia magna timorlaoensis;* L, *Macropygia amboinensis admiralitatis*; M, *Macropygia amboinensis albicapilla*, *Macropygia amboinensis atrata*, *Macropygia amboinensis sedecima;* N, *Macropygia amboinensis albiceps;* O, *Macropygia amboinensis amboinensis;* P, *Macropygia amboinensis carteretia;* Q, *Macropygia amboinensis doreya;* R, *Macropygia amboinensis goldiei;* S, *Macropygia amboinensis maforensis;* T, *Macropygia amboinensis keyensis;* U, *Macropygia amboinensis sanghirensis;* and V, *Macropygia phasianella.*

absolute geographical proximity and more by the overwater distance that must be crossed to establish connectivity. Global sea levels are known to have dropped by up to 120 m during the 20–30 Pleistocene glaciations, creating land bridges between many islands in the Indo-Pacific realm (Bintanja *et al.*, 2005) (Fig. 4). We tested for a correlation between Euclidean distances of PC coordinates from each taxon and the shortest –120 m sea level isobath distances between two populations. The shortest distance between palaeo-landmasses at –120 m isobaths was calculated by summing the distances between islands and landmasses along the shortest summed route. For each taxon, the mean of each of the nine non-element specific vocal characters that were applicable [(1), (14), (15), (16), (17), (20), (21), (25), and (26)] was calculated. This mean was then subjected to PCA in which PC1 and 2 were used to determine pairwise Euclidean distances. Isobaths at –120 m sea level were obtained with the function 'getNOAA.bathy' from the R package 'marmap', which imports bathymetric data from NOAA's server (Pante & Simon-Bouhet, 2013). Spearman's correlation coefficient was applied to determine the correlations because the data were not normally distributed (see Supporting information Fig. S1).

## RESULTS

There was a weak correlation ($r = -0.0455$, $P < 0.001$) between the pairwise comparison of Euclidean distance of PC coordinates and pairwise geographical distance between each pair of individuals

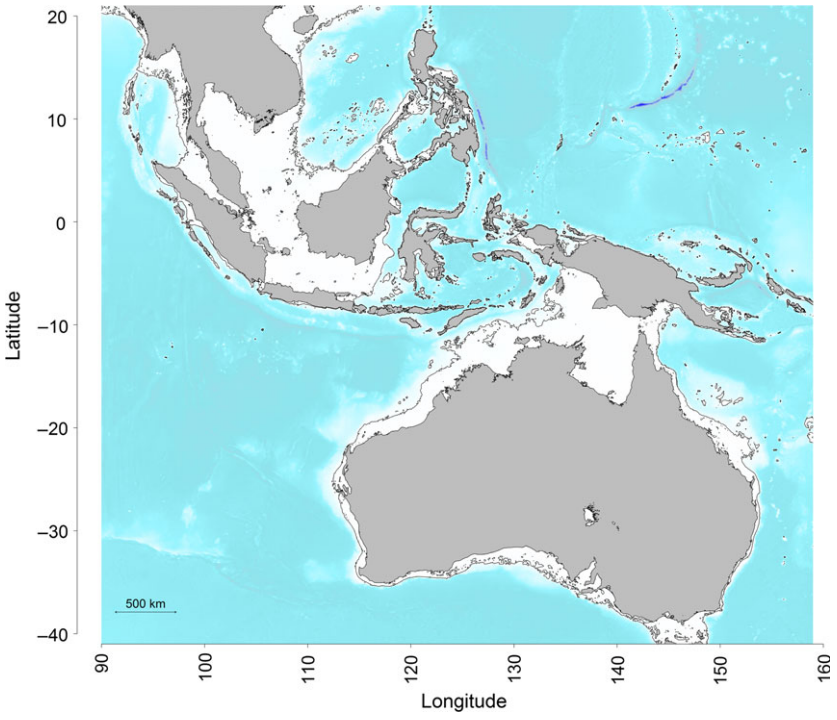


**Figure 4.** Distribution range of the brown cuckoo dove species complex at –120 m isobaths indicated in white and landmasses indicated in grey.

(Fig. 5A). A similar weak correlation ($r = 0.2019$, $P = 0.07253$) was also observed when a pairwise comparison was conducted between the Euclidean distance of PC coordinates and the shortest pairwise –120 m isobath distance for each taxon (Fig. 5B).

*Macropygia amboinensis* (*sensu* Gibbs *et al.*, 2001) divided into two distinct PCA clusters (Fig. 6). Clusters comprised up to six taxa with either one (*admiralitatis*, *maforensis*, *amboinensis*, *carteretia*, *goldiei*, and *keyensis*) or two (*albiceps*, *albicapilla*, *doreya*, *sedecima*, and *sanghirensis*) elements per call motif. Because taxon *Macropygia amboinensis sedecima* was embedded within *albicapilla* (Fig. 6), they were treated as a single unit and differentiation between them was not investigated further. Taxa *Macropygia amboinensis albicapilla* (including *M. a. sedecima*) and *Macropygia amboinensis sanghirensis* potentially constituted separate spatial PCA clusters from *Macropygia amboinensis albiceps* and *Macropygia amboinensis doreya* (Fig. 6); however, *M. a. albicapilla* was not diagnosable against *M. a. albiceps* based on the more conservative Isler criterion (Table 2). When comparing geographically proximate taxa with each other, *M. a. albicapilla*, *M. a. albiceps* and *M. a. doreya* were Isler-diagnosable against *Macropygia amboinensis amboinensis* (Table 2), as were *Macropygia amboinensis keyensis* from *M. a. doreya* and *Macropygia amboinensis maforensis* from

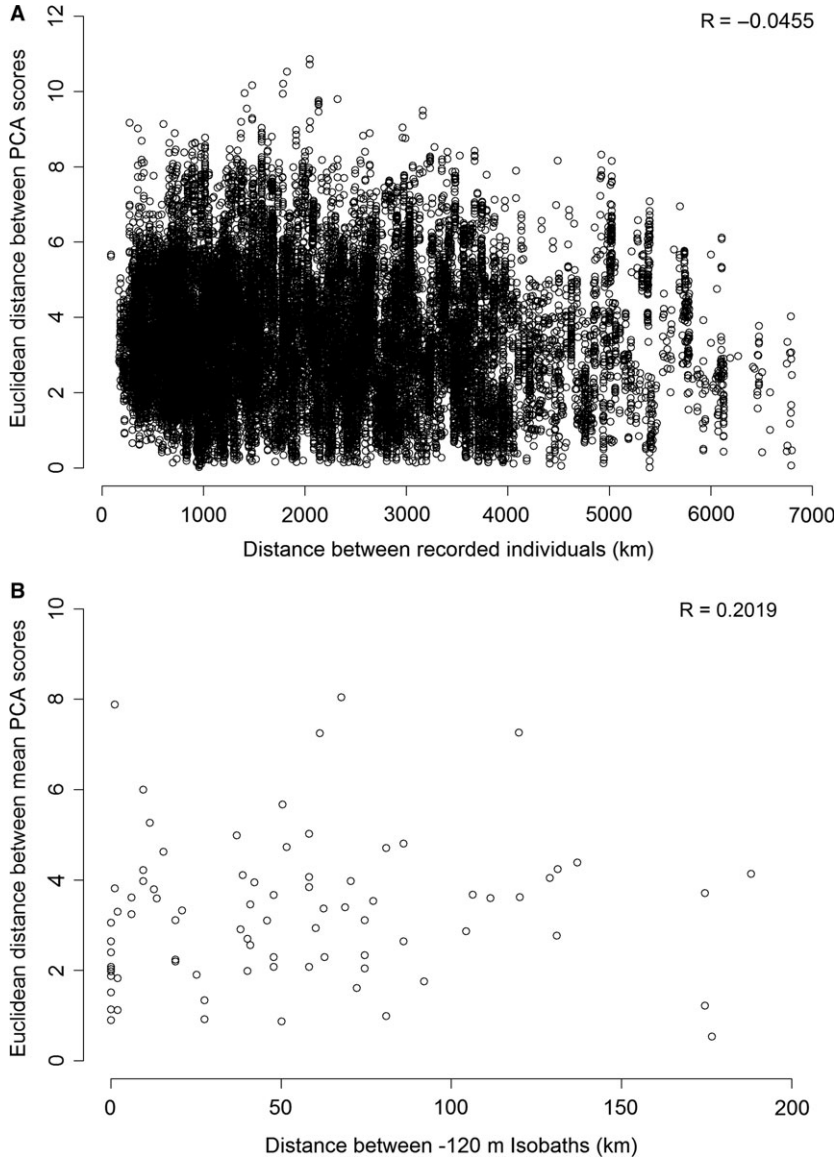


**Figure 5.** Plot of Euclidean distance of principal component (PC) scores with geographical distance between each pair of recorded individuals (A) and shortest –120 m isobaths distance between each taxon pair (B).

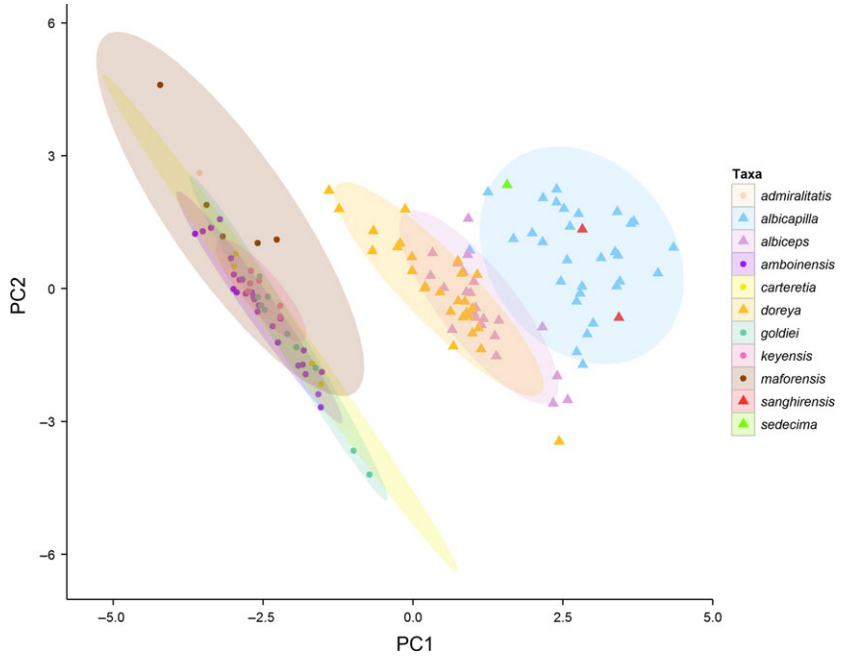


**Figure 6.** Principal component (PC) plot of PC1 against PC2 for *Macropygia amboinensis sensu* Gibbs *et al.* (2001). PC1, explaining 57% of total variance, was positively correlated with the number of elements total intra-motif break and motif lengths, break length between motifs, and the ratio of total break length and total motif length. PC2, explaining 20% of total variance, was positively correlated with total highest, peak, and bandwidth frequencies. Taxon *atrata* was omitted from PCA because of the absence of more than one non-element specific vocal character. Two distinct symbols (circles and triangles) represent the two distinct vocalizations in *M. amboinensis*. Ellipses represent 95% confidence intervals of the PC scores for each taxon.

*M. a. doreya*. These comparisons confirmed the presence of at least two distinct song types in *M. amboinensis* that are diagnosable according to the conservative Isler criterion (Table 2). *Macropygia phasianella* was Isler-diagnosable against the geographically proximate taxa *Macropygia amboinensis goldiei* and *M. a. doreya*, although not against the disjunct taxa *M. a. albicapilla* and *M. a. albiceps* (Table 2).

Preliminary inspection indicated that the Flores population may be vocally differentiated within the taxon *Macropygia emiliana emiliana*. Therefore, recordings from Flores were analyzed separately from Javan recordings. PCA and Isler criterion showed that the Flores population of the nominate taxon *M. e. emiliana* was distinct and diagnosable from the remaining populations (Fig. 7, Table 2). For ease of discussion, the Flores population is referred to as *M. e. emiliana* (F), with *M. e. emiliana* referring to the remaining populations. According to PCA, *M. emiliana* segregated into four distinct song types (Fig. 7). Taxa *Macropygia emiliana elassa* and *Macropygia emiliana borneensis* segregated from each other and were distinct from both *M. e. emiliana* populations (Fig. 7). Taxon *Macropygia emiliana hypopercna* was embedded within *M. e. elassa*, whereas the clusters of *Macropygia emiliana cinnamomea* and *M. e. elassa* abutted each other (Fig. 7). The Isler criterion confirmed that all subspecies were diagnosable from each other, except *M. e. hypopercna*, which was only diagnosable against both *emiliana* populations (Table 2).

Interspecific comparisons among geographically proximate taxa indicated that both *M. e. emiliana* populations were diagnosable from taxa *Macropygia magna magna*, *Macropygia magna longa*, and *Macropygia phasianella phasianella* (Table 2). Taxa *M. e. borneensis* and *M. a. albicapilla* were also found to be diagnosable. Pairwise comparisons of *M. a. albicapilla* with disjunct *M. e. emiliana*, and *M. e. borneensis* with geographically proximate *Macropygia tenuirostris tenuirostris*, came out nondistinct and undiagnosable based on Isler criterion (Table 2).

Taxa in *M. magna* segregated into three distinct PCA clusters (Fig. 8). Taxon *M. m. longa* was the most vocally distinct based on PCA (Fig. 8). All three taxa were Isler-diagnosable against one another (Table 2). Hence, there are three distinct song types

**Table 2.** Summary of diagnosable vocal characters from the Isler criterion for geographically proximate taxa in the brown cuckoo dove species complex

| | Non-element specific parameters | | | | | | | | | Element specific parameters | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Taxa | 1 | 14 | 15 | 16 | 17 | 20 | 21 | 25 | 26 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 18 | 19 | 22 | 23 | 24 | 27 | 28 | 29 | Total |
| *Macropygia amboinensis admiralitatis/Macropygia amboinensis carteretia* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 0 |
| *Macropygia amboinensis admiralitatis/Macropygia amboinensis goldiei* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 0 |
| *Macropygia amboinensis admiralitatis/Macropygia amboinensis doreya* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 0 |
| *Macropygia amboinensis admiralitatis/Macropygia phasianella* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 0 |
| *Macropygia amboinensis albicapilla/Macropygia amboinensis albiceps* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 0 |
| *Macropygia amboinensis albicapilla/Macropygia amboinensis amboinensis* | X | | | | | X | X | X | X | | | | | | | | | | | | | | | | | | | | | 5 |
| *Macropygia amboinensis albicapilla/Macropygia amboinensis andamanica* | | | | | | | | | | | | | | | | | | | | | | | | X | | | | | | 1 |
| *Macropygia amboinensis albicapilla/Macropygia amboinensis arata* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 0 |
| *Macropygia amboinensis albicapilla/Macropygia emiliana borneensis* | X | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 |
| *Macropygia amboinensis albicapilla/Macropygia amboinensis doreya* | | | | | | X | X | X | | | | | | | | | | | | | | X | | | | | | | | 4 |
| *Macropygia amboinensis albicapilla/Macropygia emiliana emiliana* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 0 |
| *Macropygia amboinensis albicapilla/Macropygia emiliana emiliana* (F) | | | | | | | | | | | | | | X | | | X | | | | | | | | | | | | | 2 |

**Table 2.** *Continued*

| | Non-element specific parameters | | | | | | | | | Element specific parameters | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Taxa | 1 | 14 | 15 | 16 | 17 | 20 | 21 | 25 | 26 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 18 | 19 | 22 | 23 | 24 | 27 | 28 | 29 | Total |
| *Macropygia amboinensis albicapilla/Macropygia magna longa* | | | | | | X | | | | | | | | | | | | | | | | | | | | | | | | 1 |
| *Macropygia amboinensis albicapilla/Macropygia amboinensis sanghirensis* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 0 |
| *Macropygia amboinensis albicapilla/Macropygia amboinensis sedecima* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 0 |
| *Macropygia amboinensis albicapilla/Macropygia tenuirostris tenuirostris* (P) | X | | | | | X | | X | X | | | | | | | | | | | | | | | | | | | | | 4 |
| *Macropygia amboinensis albicapilla/Macropygia tenuirostris tenuirostris* | X | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 |
| *Macropygia amboinensis albiceps/Macropygia amboinensis amboinensis* | X | | | | | X | X | X | X | | | | | | | | | | | | | | | | | | | | | 5 |
| *Macropygia amboinensis albiceps/Macropygia amboinensis doreya* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 0 |
| *Macropygia amboinensis albiceps/Macropygia emiliana emiliana* | | | | | | X | | | X | | | | X | | | | | | | | | X | | | | | | | | 4 |
| *Macropygia amboinensis albiceps/Macropygia emiliana emiliana* (F) | | | | | | | | | | | X | | | X | | | X | | | | | | | | | | | | | 3 |
| *Macropygia amboinensis albiceps/Macropygia phasianella* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 0 |
| *Macropygia amboinensis albiceps/Macropygia amboinensis sedecima* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 0 |
| *Macropygia amboinensis amboinensis/Macropygia amboinensis doreya* | X | | | | | X | X | X | X | | | | | | | | | | | | | | | | | | | | | 5 |

**Table 2.** *Continued*

| Taxa | Non-element specific parameters | | | | | | | | | Element specific parameters | | | | | | | | | | | | | | | | | | | | | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1 | 14 | 15 | 16 | 17 | 20 | 21 | 25 | 26 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 18 | 19 | 22 | 23 | 24 | 27 | 28 | 29 | |
| *Macropygia amboinensis amboinensis/Macropygia amboinensis keyensis* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 0 |
| *Macropygia amboinensis amboinensis / Macropygia magna magna* | X | | | | | X | X | X | X | | | | | | | | | | | | | | | | | | | | | 5 |
| *Macropygia amboinensis amboinensis/Macropygia amboinensis sedecima* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 0 |
| *Macropygia amboinensis amboinensis / Macropygia magna timorlaoensis* | X | | | | | X | X | X | X | | | | | | | | | | | | | | | | | | | | | 5 |
| *Macropygia amboinensis andamanica/Macropygia amboinensis albiceps* | | | | | | | | | | | | | | | | | | | | | | | | X | | | | | | 1 |
| *Macropygia amboinensis andamanica/Macropygia emiliana borneensis* | X | | | | | | | X | | | | | | | | | | | | | | | | | | | | | | 2 |
| *Macropygia amboinensis andamanica/Macropygia amboinensis doreya* | | | | | | | | X | | | | | | | | | | | | | | | | X | | | | | | 2 |
| *Macropygia amboinensis andamanica/Macropygia emiliana hypopercna* | X | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 |
| *Macropygia amboinensis andamanica / Macropygia phasianella* | | | | | | | | | | | | | | | | | | | | | | | | X | | | | | | 1 |
| *Macropygia emiliana borneensis/ Macropygia emiliana cinanamomea* | | | | | | | | | | | X | | X | X | | X | X | | | | | | | | | | | | | 5 |
| *Macropygia emiliana borneensis/Macropygia emiliana elassa* | | | | | | | | | | | | | | | | | | | | | | | | | | X | | | | 1 |
| *Macropygia emiliana borneensis/Macropygia emiliana emiliana* | X | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 |

**Table 2.** *Continued*

| | Non-element specific parameters | | | | | | | | | Element specific parameters | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Taxa | 1 | 14 | 15 | 16 | 17 | 20 | 21 | 25 | 26 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 18 | 19 | 22 | 23 | 24 | 27 | 28 | 29 | Total |
| *Macropygia emiliana borneensis/Macropygia emiliana emiliana* (F) | X | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 |
| *Macropygia emiliana borneensis/Macropygia emiliana hypopercna* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 0 |
| *Macropygia emiliana borneensis/Macropygia tenuirostris tenuirostris* (P) | X | | | | | X | X | X | X | | | | | | | | | | | | | | | | | | | | | 5 |
| *Macropygia emiliana borneensis/Macropygia tenuirostris tenuirostris* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 0 |
| *Macropygia amboinensis carteretia/Macropygia amboinensis goldiei* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 0 |
| *Macropygia emiliana cinanamomea/Macropygia emiliana emiliana* | X | | | | | | X | X | | | | | | | | | | | | | | | | | | | | | | 3 |
| *Macropygia emiliana cinnamomea/Macropygia emiliana elassa* | | | | | | | | | | | X | | X | | | | X | | | | | | | | | | | | | 3 |
| *Macropygia emiliana cinnamomea/Macropygia emiliana emiliana* (F) | X | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 |
| *Macropygia amboinensis doreya/Macropygia amboinensis keyensis* | X | | | | | X | X | X | X | | | | | | | | | | | | | | | | | | | | | 5 |
| *Macropygia amboinensis doreya/Macropygia amboinensis maforensis* | X | | | | | X | | | X | | | | | | | | | | | | | | | | | | | | | 3 |
| *Macropygia amboinensis doreya/Macropygia phasianella* | | | | | | | X | X | | | | | | | | | | | | | | | | | X | | | | | 3 |
| *Macropygia amboinensis doreya/Macropygia amboinensis sedecima* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 0 |

**Table 2.** *Continued*

| Taxa | Non-element specific parameters | | | | | | | | | Element specific parameters | | | | | | | | | | | | | | | | | | | | | | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1 | 14 | 15 | 16 | 17 | 20 | 21 | 25 | 26 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 18 | 19 | 22 | 23 | 24 | 27 | 28 | 29 | |
| *Macropygia amboinensis doreya*/*Macropygia magna timorlaoensis* | | | | | | | X | X | | | | | | | | | | | | | | | | | | | | | | 2 |
| *Macropygia emiliana elassa*/*Macropygia emiliana emiliana* | X | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 |
| *Macropygia emiliana elassa*/*Macropygia emiliana emiliana* (F) | X | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 |
| *Macropygia emiliana elassa*/*Macropygia emiliana hypopercna* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 0 |
| *Macropygia emiliana emiliana* (F)/*Macropygia magna longa* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 0 |
| *Macropygia emiliana emiliana* (F)/*Macropygia phasianella* | | | | | | | | | | | X | | | X | | | X | | | | | | | | | | | | | 3 |
| *Macropygia emiliana emiliana* (F)/*Macropygia emiliana hypopercna* | X | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 |
| *Macropygia emiliana emiliana*/*Macropygia emiliana emiliana* (F) | | | | | | | | | | | | | | X | | | X | | | | | | | | | | | | | 2 |
| *Macropygia emiliana emiliana*/*Macropygia emiliana hypopercna* | X | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 |
| *Macropygia emiliana emiliana*/*Macropygia magna longa* | | | | | | | | | | | | | X | | | | | | | | | | | | | | | | | 1 |
| *Macropygia emiliana emiliana*/*Macropygia magna magna* | X | | | | | | | X | | | | | | | | | | | | | | | | | | | | | | 2 |
| *Macropygia emiliana emiliana*/*Macropygia phasianella* | | | | | | | | | X | | | | | | | | | | | | | | | | | | | | | 1 |

**Table 2.** *Continued*

| | Non-element specific parameters | | | | | | | | | Element specific parameters | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Taxa | 1 | 14 | 15 | 16 | 17 | 20 | 21 | 25 | 26 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 18 | 19 | 22 | 23 | 24 | 27 | 28 | 29 | Total |
| *Macropygia amboinensis goldiei/Macropygia amboinensis doreya* | X | | | | | X | | X | X | | | | | | | | | | | | | | | | | | | | | 4 |
| *Macropygia amboinensis goldiei/M. phasianella* | X | | | | | X | X | X | X | | | | | | | | | | | | | | | | | | | | | 5 |
| *Macropygia amboinensis keyensis/Macropygia magna timorlaoensis* | X | | | | | X | X | X | X | | | | | | | | | | | | | | | | | | | | | 5 |
| *Macropygia magna longa/ Macropygia magna magna* | X | | X | | | X | | | | | | | | | | | | | | | | | | | | | | | | 3 |
| *Macropygia magna longa/ Macropygia magna timorlaoensis* | | | X | | | X | | | | | | | X | | | | X | | | | | X | | | | | | | | 5 |
| *Macropygia magna magna/ Macropygia magna timorlaoensis* | X | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 |
| *Macropygia phasianella phasianella/Macropygia phasianella robinsoni* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 0 |
| *Macropygia amboinensis sanghirensis/Macropygia tenuirostris tenuirostris* | X | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 |
| *Macropygia tenuirostris tenuirostris/Macropygia tenuirostris tenuirostris* (P) | X | | | | | X | | X | X | | | | | | | | | | | | | | | | | | | | | 4 |
| Total | 30 | 0 | 2 | 0 | 0 | 19 | 14 | 21 | 16 | 0 | 4 | 0 | 5 | 5 | 0 | 1 | 7 | 0 | 0 | 0 | 0 | 3 | 0 | 5 | 1 | 1 | 0 | 0 | 0 | 73 |

*Macropygia phasianella includes both M. p. phasianella and M. p. robinsoni*, and subspecies are indicated respectively. *Macropygia e. emiliana* (F) refers to the Flores population of *M. e. emiliana*, and *M. t. tenuirostris* (P) refers to the Palawan population of *M. t. tenuirostris* (for rationale, refer to the Results section). 1 = number of elements per motif; 2 = lowest frequency (element 1); 3 = lowest frequency (element 2); 4 = lowest frequency (element 3); 5 = highest frequency (element 1); 6 = highest frequency (element 2); 7 = highest frequency (element 3); 8 = peak frequency (element 1); 9 = peak frequency (element 2); 10 = peak frequency (element 3); 11 = bandwidth frequency (element 1); 12 = bandwidth frequency (element 2); 13 = bandwidth frequency (element 3); 14 = total lowest frequency; 15 = total highest frequency; 16 = total peak frequency; 17 = total bandwidth frequency; 18 = break length between elements 1 and 2; 19 = break length between elements 2 and 3; 20 = total intra-motif break length; 21 = break length between motifs; 22 = duration (element 1); 23 = duration (element 2); 24 = duration (element 3); 25 = total motif length; 26 = ratio between total break length and total motif length; 27 = differential frequency (element 1); 28 = differential frequency (element 2); 29 = differential frequency (element 3).

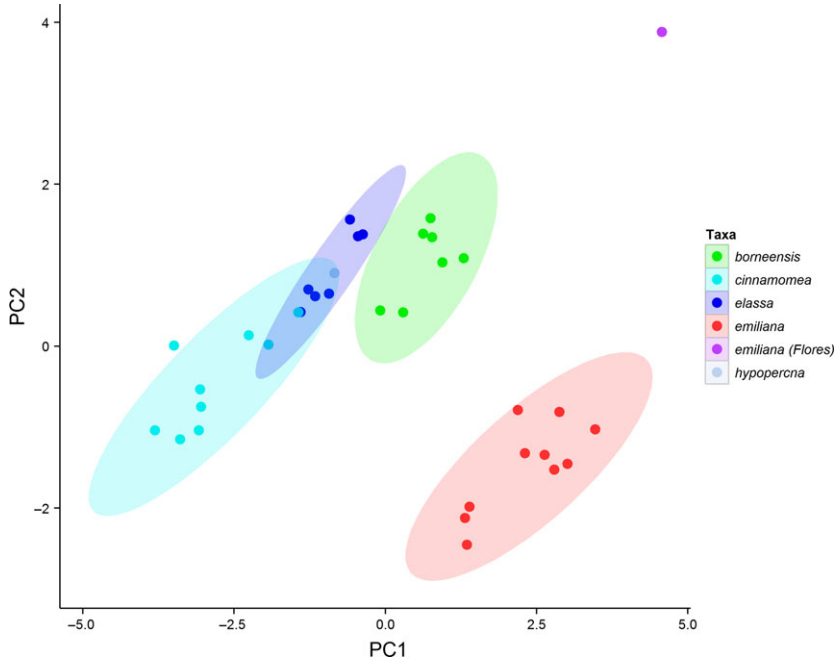


**Figure 7.** Principal component (PC) plot of PC1 against PC2 for *Macropygia emiliana sensu* Gibbs *et al.* (2001). PC1, explaining 55% of total variance, was negatively correlated with the number of elements, total lowest and highest frequencies, break length between motifs, and total motif length. PC2, explaining 20% of total variance, was positively correlated with the number of elements, whereas it was negatively correlated with total intra-motif break length and the ratio of total break length and total motif length. The Flores population of *M. emiliana* is referred to as *emiliana* (Flores), with *emiliana* referring to the remaining populations. Ellipses represent 95% confidence intervals of the PC scores for each taxon.

within *M. magna*. Neighbouring taxon pairs (*M. m. magna* and both *M. e. emiliana* populations; *M. a. albicapilla* and *M. m. longa*; *Macropygia magna timorlaoensis* and *M. a. keyensis*) were Isler-diagnosable (Table 2).

*Macropygia phasianella* did not cluster into discrete subspecific song types in the vocal PCA plot (Fig. 9). Recordings from Queensland, which could not be unequivocally attributed to either subspecies based on geography, also fell within the range of vocal variation of all other recordings (Fig. 9). There was no diagnosable difference between taxa *Macropygia phasianella robinsoni* and *M. p. phasianella* (Table 2). This indicated that there is only one song type within *M. phasianella*.

Preliminary inspection of *M. tenuirostris* recordings indicated that the Palawan population may be vocally differentiated and hence this was analyzed separately. Analysis showed that the Palawan population was distinct and diagnosable from the rest of *tenuirostris* (Fig. 10; Table 2). For ease of discussion, the Palawan population is referred to as *M. t. tenuirostris* (P), with *M. t. tenuirostris* referring to the remaining populations on the main Philippine islands. Interspecific comparisons with neighbouring taxa indicated that only *M. t. tenuirostris* (P), and not *M. t. tenuirostris* from the main Philippines, was Isler-diagnosable against *M. e. borneensis* (Table 2). In addition, both *M. t. tenuirostris* populations were also Isler-diagnosable against *M. a. albiceps* and *M. a. albicapilla*.

Based on PCA, *Macropygia rufipennis andamanica* was clearly distinct from all taxa within *M. magna*, *M. tenuirostris*, and *M. emiliana* but not necessarily from widely disjunct *M. phasianella* and some of the taxa within *M. amboinensis* (data not shown). However, based on the Isler criterion, *M. r. andamanica* was diagnosable from both *M. phasianella* and most taxa of *M. amboinensis* (Table 2).

Vocal analyses among bioacoustically well-differentiated groups revealed that the number of elements (see Supporting information, Table S2) and temporal parameters (see Supporting information, Fig. S2) were more critical in distinguishing between discrete geographical song types compared to frequency parameters (see Supporting information, Fig. S3). This result is in agreement with conclusions made by Rheindt *et al.* (2011).

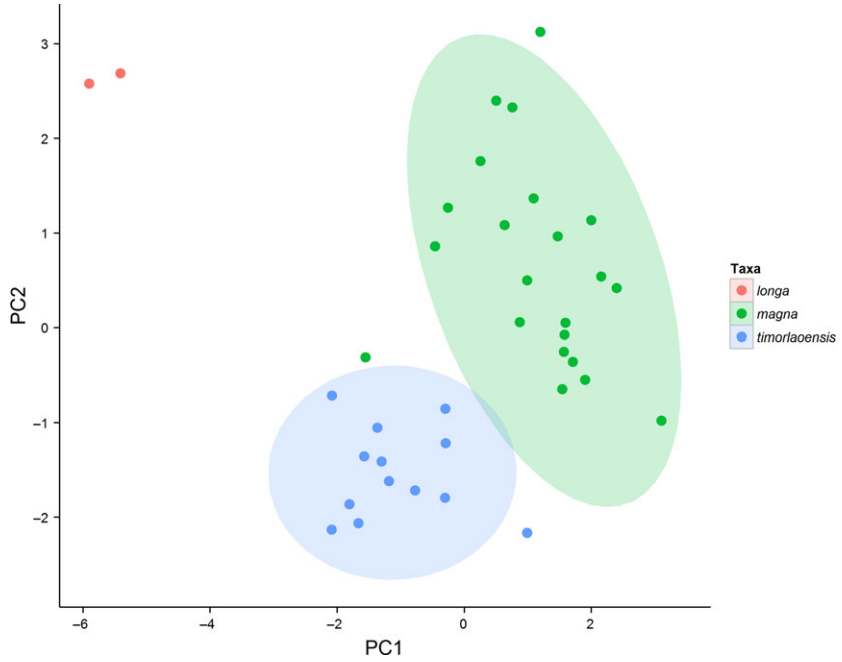


**Figure 8.** Principal component (PC) plot of PC1 against PC2 for *Macropygia magna sensu* Gibbs *et al.* (2001). PC1, explaining 43% of total variance, was positively correlated with number of elements and total highest, peak, and bandwidth frequencies, whereas it was negatively correlated with total motif length. PC2, explaining 25% of total variance, was positively correlated with number of elements, total intra-motif break length, and ratio of total break length and total motif length. Ellipses represent 95% confidence intervals of the PC scores for each taxon.

## DISCUSSION

Little is known about the evolutionary history of the brown cuckoo dove species complex, an Australasian lineage with a wide distribution across the geographically complex Indo-Pacific Archipelago (Gibbs *et al.*, 2001). Uncertainty about relationships within the brown cuckoo dove species complex is reflected in its taxonomy, which has been revised multiple times (Table 1). The taxonomic revisions classified the species complex into anything between one and six species, depending on the rationale of the reviser. The fact that so many plumage-based classifications of cuckoo doves by competent ornithologists are at odds with one another (Table 1) reflects the great level of lability of plumage traits in these doves, calling into question their value as a marker for taxonomy and for the detection of patterns of gene flow. Vocal traits can be more reliable than plumage traits as taxonomic indicators of birds (Rheindt *et al.*, 2008), including doves (Beckers & Ten Cate, 2001; Rheindt *et al.*, 2011).

The biological species concept was applied when delimiting species within the brown cuckoo dove species complex distributed in the Indo-Pacific Archipelago. Despite constituent species being allopatric populations at present, some of these populations inhabit islands that have been periodically connected during Pleistocene glaciations (Voris, 2000). Even historically unconnected island populations can occasionally be linked by gene flow given that these pigeons, as frugivores, undertake regular movements to exploit the shifting availability of fruit resources (Moran *et al.*, 2004; Price, 2004). Overwater dispersal has been suggested and reported in the brown cuckoo dove species complex (Thornton, Compton & Wilson, 1996; Mayr & Diamond, 2001), indicating that geographically disconnected island populations may not always speciate allopatrically.

Our vocal analysis demonstrated discrete geographical song types and suggested the presence of vocally distinct clusters within the brown cuckoo dove species complex. Populations on individual landmasses such as Australia (*M. phasianella*), Enggano (*M. e. cinnamomea*), Tanimbar (*M. m. timorlaoensis*), the Philippines (*M. t. tenuirostris*), and many others formed their own distinct vocal clusters with respect to multiple characters (see Supporting information, Table S1). The distinct vocal clusters formed by populations in close geographical proximity indicated that the nine vocal parameters used in the analysis were sufficient to resolve the brown cuckoo dove species complex into its constituent taxa.

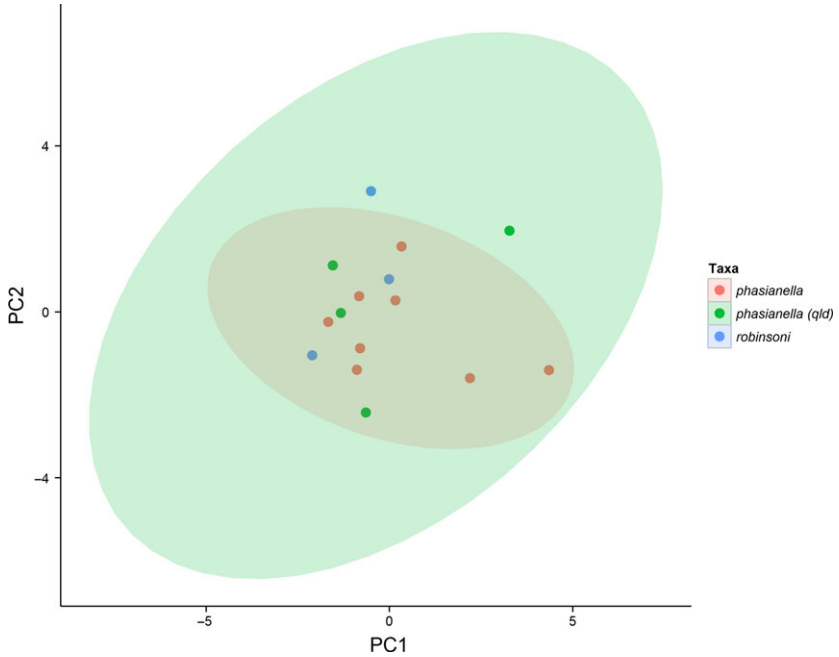


**Figure 9.** Principal component (PC) plot of PC1 against PC2 for *Macropygia phasianella sensu* Gibbs *et al.* (2001). PC1, explaining 43% of total variance, was positively correlated with total intra-motif break and motif lengths, break length between motifs, and the ratio of total break length and total motif length. PC2, explaining 28% of total variance, was negatively correlated with total highest, peak, and bandwidth frequencies. Recordings from Queensland, marked '*phasianella* (Qld)', were analyzed separately because localities could not be unequivocally attributed to the ranges of either subspecies. Ellipses represent 95% confidence intervals of the PC scores for each taxon.

From the interspecific distance plots, the weak correlation between Euclidean distances and both isobaths and geographical distances (Fig. 5) indicates that the brown cuckoo dove species complex is unlikely to form a contiguous vocal cline across the Indo-Pacific region. Instead, the presence of geographically proximate but vocally distinct forms, as well as of geographically distant but vocally conservative forms (Fig. 5), precludes such a pattern of vocal differentiation-by-distance, and suggests that the evolution of this complex is not easily explained by a clear stepping-stone model. This result contradicts the treatment of all forms as members of a single biological species by Condon (1975), although it is in agreement with previous classifications of the brown cuckoo dove complex as multiple species through divergent song types (Table 1). Under this scenario, ancestral versions of the cuckoo dove song would still be present in widely disjunct areas of the range, whereas an unexpected number of geographically proximate taxon pairs with highly different songs would have been created by rapid vocal differentiation, perhaps through sexual selection and reinforcement along Pleistocene zones of potential contact (Pérez Mena & Mora, 2011; Bell *et al.*, 2012). Alternatively, some of the distinct vocal clusters of the brown cuckoo dove complex may only be distantly related to the main complex, although this remains inconclusive in the absence of molecular data.

## Taxonomic implications

### *Vocal differentiation in M. amboinensis*

*Macropygia amboinensis* (*sensu* Gibbs *et al.*, 2001) is the largest polytypic species in the complex consisting of 18 subspecies. Analysis revealed two distinct song types that are separated by the presence of one vs. two elements per motif (Fig. 6; see also Supporting information, Table S2). Taxa with two elements range over larger islands, whereas those with one element inhabit the former's peripheral regions (Fig. 11). The two vocal groups were recognized as being dissimilar in previous bioacoustic descriptions (Gibbs *et al.*, 2001; del Hoyo *et al.*, 2014), which have, however, not been as thorough and quantitative as the present one. Within the two-element group, *M. a. albicapilla*, *Macropygia amboinensis atrata*, *M. a. doreya*, *M. a. sanghirensis*, and *M. a. sedecima* were described to be very similar in plumage but distinct from the nominate

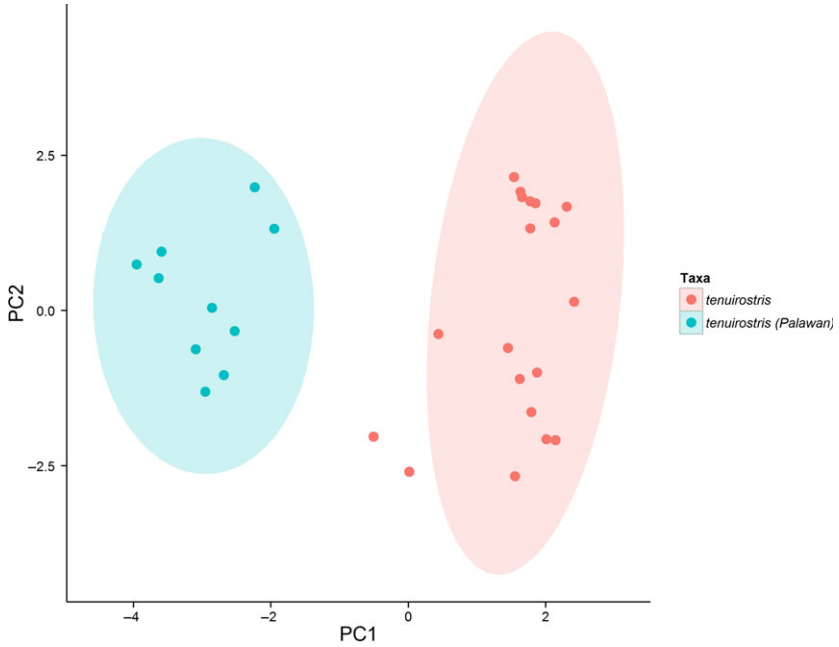


**Figure 10.** Principal component (PC) plot of PC1 against PC2 for *Macropygia tenuirostris sensu* Gibbs *et al.* (2001). PC1, explaining 58% of total variance, was positively correlated with number of elements, total intra-motif break, and motif lengths and the ratio of total break length and total motif length, whereas it was negatively correlated with break length between motifs. PC2, explaining 27% of total variance, was negatively correlated with total highest, peak, and bandwidth frequency. The Palawan population of *M. tenuirostris* is referred to as *tenuirostris* (Palawan), with *tenuirostris* referring to the remaining population. Ellipses represent 95% confidence intervals of the PC scores for each taxon.

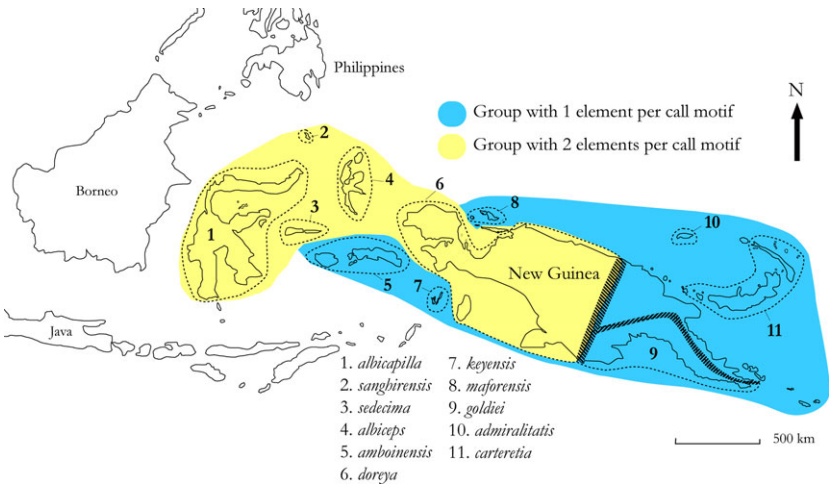


**Figure 11.** Map showing the distribution of *Macropygia amboinensis* (*sensu* Gibbs *et al.*, 2001) based on the number of elements per call motif. Only taxa that were considered in the present study were included. The distributions of *doreya* and *goldiei* are adjacent to each other and the exact demarcation of their distribution is uncertain as indicated by the black barred area.

subspecies (Gibbs *et al.*, 2001). Taxon *M. a. albiceps* differs from both the nominate and the above group of taxa including *M. a. doreya* in multiple plumage details (Gibbs *et al.*, 2001). However, vocally, *M. a. albiceps* is firmly embedded within the *M. a. doreya* group. Given the distinct bioacoustic differences,

which are corroborated for most taxa by morphological differences, the two groups should be afforded species status as *M. amboinensis s.s.* and *M. doreya.* The latter name was simultaneously published with *albicapilla* by Bonaparte in 1854 but is chosen here for priority based on the Principle of First Reviser (ICZN, 1999: Article 24.2). The contact zone of *M. amboinensis* and *M. doreya* (as defined here) on the island of New Guinea is poorly understood: *M. a. goldiei* is only known from the south-eastern parts of New Guinea, although it is not known whether there is a hybrid zone or any other type of contact zone between it and *M. doreya* on the rest of the island.

According to PCA, *M. doreya* (as defined here) could be further divided into (1) *M. albicapilla* (including the taxa *albicapilla*, *sedecima*, and *sanghirensis*) centered in the Sulawesi subregion and (2) *M. doreya s.s.* (including taxa *albiceps* and *doreya*) from the northern Moluccas and parts of New Guinea. These latter two forms make a quite distinct impression on the human ear, and they divide out into different vocal PCA clusters (Fig. 6), although they fail to be diagnosable by the Isler criterion. Accordingly, we retain them here as *M. doreya*, at the same time acknowledging that future insights may change this treatment.

Earlier classifications placed *M. phasianella* and *M. amboinensis* together (Table 1). However, taxa *M. a. doreya* and *M. a. goldiei* (*sensu* Gibbs *et al.*, 2001) are vocally well-differentiated from adjacent *M. phasianella*. Vocal characters could have diverged as a result of sexual selection, character displacement or other modes of evolution because these populations would have interacted repeatedly with recurrent land connections between New Guinea and Australia during the Pleistocene (Voris, 2000). Alternatively, adjacent taxa with differentiated vocalization may have evolved independently of each other. By contrast, the more distant taxa *M. a. albiceps* and *M. a. albicapilla* (*sensu* Gibbs *et al.*, 2001) are poorly differentiated vocally from *M. phasianella* (Table 2). The similarity could reflect bioacoustic symplesiomorphy when there are pronounced plumage differences (Baptista *et al.*, 1997; Gibbs *et al.*, 2001): *albicapilla* and *albiceps* have an overall orangey–buff plumage and breast barring that are both absent in chocolate-brown *phasianella*.

*Vocal differentiation in M. emiliana*

*Macropygia emiliana* (*sensu* Gibbs *et al.*, 2001) has a wide yet disjunct geographical distribution comprising seven subspecies (Fig. 1). Among the five studied subspecies, five distinct vocal types were uncovered (Fig. 7; Table 2). The presence of multiple vocal types is in agreement with del Hoyo *et al.* (2014), who further suggested the prospect of multiple species within *M. emiliana* (*sensu* Gibbs *et al.*, 2001).

The lack of land bridge formation during the Pleistocene (Whitten *et al.*, 1987; Voris, 2000; Meijaard, 2003; Sathiamurthy & Voris, 2006) and the large distances between *cinnamomea* on Enggano and *elassa* on Mentawai islands prevent regular gene flow between them. Furthermore, *cinnamomea* has a distinct call that complements its strongly differentiated plumage (Baptista *et al.*, 1997; Gibbs *et al.*, 2001). Hence, *M. e. cinnamomea* should be recognized as a separate species and this would be in agreement with the proposal by Gibbs *et al.* (2001) to recognize it as an allospecies. By contrast, *M. e. hypopercna* and *M. e. elassa* are vocally undifferentiated and connected through stepping stone islands in between that shorten the distance between them. Taxon *M. e. hypopercna* is characterized to be larger and paler brighter rufous in plumage than the nominate (Gibbs *et al.*, 2001). Gibbs *et al.* (2001) further characterized *M. e. elassa* as distinct from *M. e. hypopercna* based only on its paler plumage. Therefore, *M. e. hypopercna* and *M. e. elassa* should be recognized as one species.

Taxon *M. e. borneensis* is geographically and vocally distant from other taxa (Fig. 7 and Table 2). Although land bridges have been connecting Borneo to Java (Voris, 2000), *M. e. borneensis* is Isler-diagnosable from Javan *M. e. emiliana* (Fig. 7 and Table 2). Morphologically, *M. e. borneensis* is larger than the nominate taxon; has a darker chestnut face and ear coverts; the hindneck is more green–gold iridescent than purple; and the outer tail feathers have more defined subterminal black bands (Gibbs *et al.*, 2001).

In *M. e. emiliana*, Javan and Flores population differed in two diagnosable characters, despite the high penalties imposed by the Isler criterion on the low sample size from Flores ($N = 4$). However, a sampling gap in intervening areas from Bali to Sumbawa leaves open the possibility of a vocal cline. Flores populations may refer to an undescribed species, although further sampling is required for substantiation or to confirm that our vocal sample does not refer to a misidentified recording. Given the low sample size for Flores, we prefer to keep this population subsumed under Java for now.

Earlier treatments included the *M. e. emiliana* assemblage within *M. phasianella* or *M. amboinensis* (Table 1), although vocal analysis showed it to be differentiated from both, except for comparisons between Javan *M. e. emiliana* and *M. a. albicapilla* (Table 2). Taxa *emiliana* and *albicapilla* are separated by pronounced morphological differences: *M. e. emiliana* has chestnut plumage with no breast barring, whereas *M. a. albicapilla* has a lighter orangey–buff head, grey crown, and strongly barred

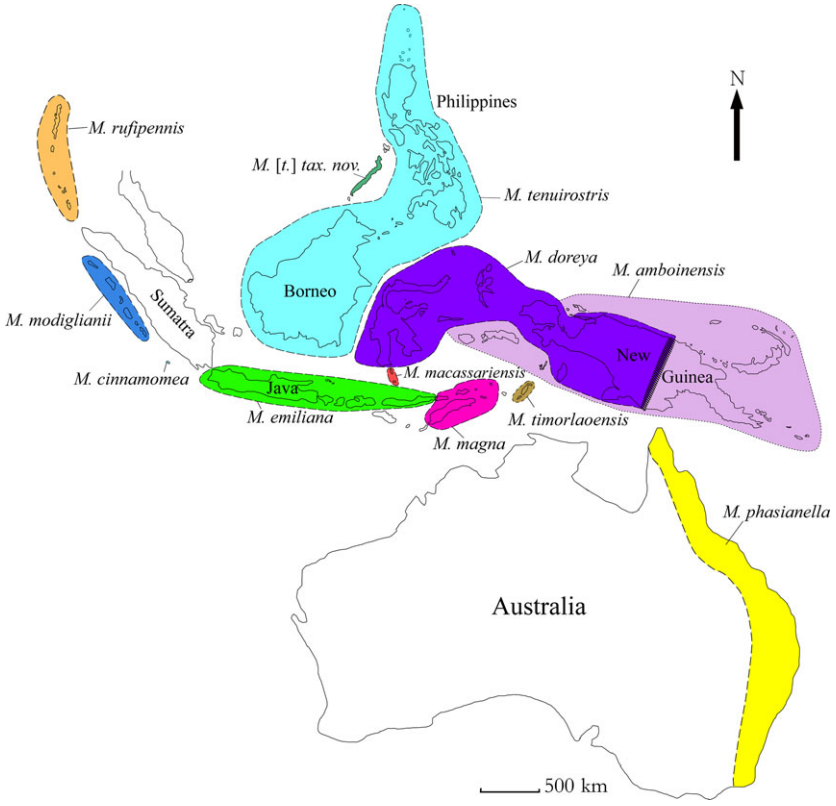


**Figure 12.** Distribution of the brown cuckoo dove species complex based on the newly proposed classification. The distributions of *Macropygia doreya* and *Macropygia amboinensis* are adjacent to each other and the exact demarcation of their distribution is uncertain as indicated by the black barred area.

yellow–buff underparts (Gibbs *et al.*, 2001). The low level of differentiation between *M. e. emiliana* and *M. a. albicapilla* could be a case of symplesiomorphy or convergence, although our current data are unable to distinguish between these scenarios. Furthermore, no land bridge has ever connected Sulawesi and Java that would allow for regular terrestrial gene flow between them (Voris, 2000).

*Vocal differentiation in M. magna*

*Macropygia magna* (*sensu* Gibbs *et al.*, 2001) is polytypic with four subspecies: *macassariensis*, *longa*, *magna*, and *timorlaoensis*. In the present study, the latter three subspecies were examined and found to be vocally differentiated from one another (Fig. 8; Table 2). The island ranges of these subspecies are geographically disjunct (Fig. 1) and were never connected during the Pleistocene (Voris, 2000). Despite penalties imposed by the Isler criterion for its low sample size ($N = 2$), *M. m. longa* emerged with extremely distinct vocalizations from *M. m. magna* and *M. m. timorlaoensis* and should be recognized as an independent species. Morphologically, *longa* has a much paler grey–brown plumage than the nominate, its throat is pale buff, and its underparts are pale creamy–buff with blackish–grey barring (Gibbs *et al.*, 2001; del Hoyo *et al.*, 2014).

Taxa *M. m. magna* and *M. m. timorlaoensis* fundamentally differed in the number of elements per motif (Table 2). Taxon *M. m. timorlaoensis* has a darker plumage that lacks the warm rufous tone present in *M. m. magna* (Gibbs *et al.*, 2001). Underparts of *M. m. timorlaoensis* have more distinct black barring (Gibbs *et al.*, 2001). The distinct differences present in the vocalizations and plumage suggest separate species status for *M. m. timorlaoensis* and *M. m. magna*.

Earlier classifications incorporated *M. magna* within *M. amboinensis* (Table 1), even though Peters (1937) recognized it as a species. Taxon *M. m. longa* showed Isler diagnosability against neighbouring taxon *M. a. albicapilla* on Sulawesi but not against *M. e. emiliana* on Java (Table 2), despite being distinct with PCA (not shown). However, nondiagnosability can probably be attributed to the small sample size ($N = 2$) for *M. m. longa* because the vocal characters were mostly distinct (see Supporting information, Figs S2, S3) and emerged in separate

**Table 3.** Revised classification of the species and subspecies of the brown cuckoo dove species complex

| Proposed species | Distribution |
|---|---|
| *Macropygia amboinensis* (Amboyna cuckoo dove) | |
| *Macropygia amboinensis amboinensis* (Linnaeus,1766) | Central Moluccas: Buru, Seram, Ambon and Seram Laut |
| *Macropygia amboinensis admiralitatis* Mayr, 1937 | Admiralty Islands |
| *Macropygia amboinensis carteretia* Bonaparte, 1854 | Bismarck Archipelago (except Admiralty Islands and New Hanover) |
| *Macropygia amboinensis goldiei* Salvadori, 1893 | South Coast of South-East New Guinea from Merauke region to Milne Bay |
| *Macropygia amboinensis keyensis* Salvadori, 1876 | Kai Islands (South-East Moluccas) |
| *Macropygia amboinensis maforensis* Salvadori, 1878 | Numfor Island (Geelvink Bay) |
| *Macropygia amboinensis griseinucha* Salvadori, 1876 | Mios Num Island (Geelvink Bay) |
| *Macropygia amboinensis meeki*, Rothschild & Hartert, 1915 | Manam Island |
| *Macropygia amboinensis cinereiceps* Tristram, 1889 | D'Entrecasteaux Islands |
| *Macropygia amboinensis cunctata* Hartert, 1899 | Louisiade Archipelago (Misima, Tagula and Rossel) |
| *Macropygia amboinensis huskeri* Neumann, 1922 | New Hanover |
| *Macropygia amboinensis kerstingi* Reichenow, 1897 | North-eastern New Guinea (probably from East Sepik east to Astrolabe Bay) |
| *Macropygia doreya* (Sultan's cuckoo dove) | |
| *Macropygia doreya doreya* Bonaparte 1854 | Western New Guinea; almost the entire Indonesian part (former Irian Jaya), Waigeo, Batanta, Salawati, Misool, Yapen and Aru Islands |
| *Macropygia doreya albicapilla* Bonaparte 1854 | Sulawesi and satellite Islands: Manadotua, Manterawu, Bangka, Lembeh, Muna, Butung, Banggai, Butung, Wangiwangi, Kaledupa and Binongka |
| *Macropygia doreya albiceps* Bonaparte, 1856 | North Moluccas: Morotai, Kayoa, Ternate, Halmahera, Bacan and Obi |
| *Macropygia doreya atrata* Ripley 1941 | Togian Islands |
| *Macropygia doreya sanghirensis* Salvadori, 1878 | Sangihe and Talaud Islands |
| *Macropygia doreya sedecima* Neumann, 1939 | Sula Islands |
| *Macropygia doreya balim* Rand, 1941 | Balim Valley |
| *Macropygia emiliana emiliana* (Parzudaki's Cuckoo Dove) | |
| *Macropygia emiliana emiliana* Bonaparte, 1854 | Krakatau, Java, Bali, Lombok, Sumbawa, Flores |
| *Macropygia emiliana megala*, Siebers, 1929 | Kangean Islands |
| *Macropygia cinnamomea* (Enggano Cuckoo Dove) Salvador, 1892 | Enggano |
| *Macropygia modiglianii* (Barusan Cuckoo Dove) | |
| *Macropygia modiglianii modiglianii* Salvadori, 1887 | Nias |
| *Macropygia modiglianii elassa* Oberholser, 1912 | Mentawai Islands |
| *Macropygia modiglianii hypopercna* Oberholser, 1912 | Simeulue |
| *Macropygia magna* (Timor Cuckoo Dove) Wallace, 1864 | Alor, Timor, Wetar, Romang, Moa, Kisar, Leti, Sermata, Damar |
| *Macropygia timorlaoensis* (Tanimbar Cuckoo Dove) Meyer, 1884 | Tanimbar |
| *Macropygia macassariensis* (Flores Sea cuckoo dove) | |
| *Macropygia macassariensis macassariensis* Wallace, 1865 | Tana Keke and Salayar |
| *Macropygia macassariensis longa* Meise, 1930 | Tanahjampea and Kalaotoa |
| *Macropygia tenuirostris* (Slender-billed cuckoo dove) | |
| *Macropygia tenuirostris tenuirostris* Bonaparte, 1854 | Philippines (excluding Palawan) |
| *Macropygia tenuirostris borneensis* Robinson & Kloss, 1921 | Borneo |
| *Macropygia tenuirostris phaea* McGregor, 1904 | Calayan Island |

**Table 3.** *Continued*

| Proposed species | Distribution |
|---|---|
| *Macropygia tenuirostris septentrionalis* Hachisuka, 1930 | Batan, Itbayat and Sabtan Island, north Philippines; and Lanyu Island |
| *Macropygia tenuirostris* tax. nov. | Palawan, Philippines |
| *Macropygia phasianella* (Australian cuckoo dove) (Temminck, 1821) | East Australia from tip of Cape York Peninsula (North Queensland) to East Victoria |
| *Macropygia rufipennis* (Andaman Cuckoo Dove) | |
| *Macropygia rufipennis rufipennis* Blyth, 1846 | Nicobar Islands |
| *Macropygia rufipennis andamanica* Abdulaii, 1967 | Andaman Islands |

PCA space. With these pronounced differences, *M. m. magna*, *M. m. longa*, and *M. m. timorlaoensis* should be recognized as distinct species.

*Vocal differentiation in M. phasianella*

*Macropygia phasianella* (*sensu* Gibbs *et al.*, 2001) is restricted to eastern Australia (Fig. 1). The vocalizations of subspecies *M. p. robinsoni* and *M. p. phasianella* were undifferentiated (Fig. 9). Because the subspecies abut each other, extensive gene flow between the populations is likely. Two subspecies, *M. p. robinsoni* and *Macropygia phasianella quinkan*, were recognized to be almost identical to the nominate (*phasianella*) and were proposed on the basis of very subtle plumage differences, such as paler plumage (*quinkan*) or bolder bars on belly (*robinsoni*) (Gibbs *et al.*, 2001). These subspecies were not recognized by Baptista *et al.* (1997) and our vocal analysis also failed to distinguish between them. Thus, synonymization of these subspecies by Baptista *et al.* (1997) was probably valid and *M. phasianella* should best be considered monotypic.

*Vocal differentiation in M. tenuirostris*

*Macropygia tenuirostris* (*sensu* Gibbs *et al.*, 2001) is distributed across the Philippine archipelago (Fig. 1). Analysis revealed two distinct vocalizations, with the presence of a distinct population on Palawan (Philippines) (Fig. 10; Table 2). Based on the substantial vocal differences between both *M. tenuirostris* taxa, we have provisionally treated the Palawan population of *M. tenuirostris* as a new taxon within *M. tenuirostris*. Little is known about the biology and plumage of this unnamed Palawan population. This further emphasizes the importance of this bioacoustic dataset with respect to taxon delimitation.

Both Philippine taxa have vocal characters that are substantially differentiated in bioacoustic terms from *M. phasianella* and from geographically adjacent taxa within *M. amboinensis* (Table 2). This rules out earlier classifications that placed *M. tenuirostris* within *M. phasianella* or *M. amboinensis* (Table 1). On the other hand, *M. t. tenuirostris* from the main Philippine islands is not deeply differentiated vocally from *M. e. borneensis*. Interaction between these taxa could have occurred via the Sulu islands between Borneo and the Philippines, a colonization route that has been proposed for a number of avian taxa (Jones & Kennedy, 2008; Oliveros & Moyle, 2010). Furthermore, land bridges formed during the Pleistocene (Voris, 2000). Although the land bridges had gaps, these were likely to be sufficiently narrow for movement between Borneo and the Philippines. Plumage characters are also largely similar, except that *M. e. borneensis* has a darker crown and blue orbital skin that is absent in *M. t. tenuirostris* (Gibbs *et al.*, 2001). Hence, we provisionally treat taxa *M. t. tenuirostris* and *M. e. borneensis* as one species until DNA becomes available to test whether phenotypic similarities between them are symplesiomorphic, maintained through regular gene flow or otherwise.

*Vocal differentiation in M. rufipennis*

*Macropygia rufipennis* (*sensu* Gibbs *et al.*, 2001) is restricted to the Andaman and Nicobar Islands and hence isolated from the remaining taxa within the *M. amboinensis* species complex (Fig. 1). Taxon *M. r. andamanica* is vocally differentiated from all other taxa analyzed (Table 2) (PCA data not shown). Previous classifications recognized *M. rufipennis* as a species based on plumage differences with the remaining species within the complex, except when omitted entirely (Table 1). Land bridges have never connected the Andaman and Nicobar Islands to nearby landmasses (Voris, 2000); thus, it is unlikely for *rufipennis* to have maintained gene flow with other species-level taxa. *Macropygia rufipennis* should therefore remain as a separate species.

*Revised taxonomic arrangements and future work*

The present study has considerably advanced past classifications of the brown cuckoo dove species

complex, which can be further refined into 11 species based on corroboration of distinct morphological and bioacoustic differences (Fig 12; Table 3). *Macropygia amboinensis* (*sensu* Gibbs *et al.*, 2001) is recognized here as *M. amboinensis s.s.* and *M. doreya*. The vocally unsampled subspecies *griseinucha*, *meeki*, *cinereiceps*, *cunctata*, *kerstingi*, and *huskeri* are attributed to *M. amboinensis s.s.* based on geographical proximity to other subspecies that were vocally assigned here. Confusion has surrounded the exact range of *Macropygia amboinensis kerstingi* (for which we included no vocal samples), with the type specimen originating from the Madang area in Papua New Guinea, although the distribution purported to extend all the way to Geelvink Bay in Indonesia (Baptista *et al.*, 1997; Gibbs *et al.*, 2001; del Hoyo *et al.*, 2014). The subspecies was also described to be morphologically similar to *M. a. albicapilla*, *M. a. atrata*, *M. a. doreya*, *M. a. sanghirensis*, and *M. a. sedecima*. However, new vocal data from Xeno-Canto (XC267889), which were unavailable at the time of our analyses, reveal that *M. a. kerstingi* has a one-note song placing it within *M. amboinensis s.s.* (for interpretations, see the Results). The new vocal data demonstrate that birds in the western half of this range (eastwards at least to Jayapura) should be re-assigned to *M. a. doreya*. The morphological characterization by Gibbs *et al.* (2001) may therefore have been based on specimens being incorrectly assigned to *M. a. kerstingi*, leading to its erroneous diagnosis as a *M. a. doreya*-like plumage. *Macropygia doreya balim* was included as a subspecies of *M. doreya* based on its previous synonymization with *doreya* (Baptista *et al.*, 1997). *Macropygia emiliana megala* is classified within *M. emiliana* because it has been decribed to be morphologically very similar to the Javan population (Gibbs *et al.*, 2001). *Macropygia modiglianii modiglianii* was classified together with *M. m. elassa* and *M. m. hypopercna* because it is geographically intermediate between both populations and also morphologically more similar to *hypopercna* than to *emiliana* (Gibbs *et al.*, 2001). *Macropygia macassariensis macassariensis* was classified as conspecific with *M. m. longa* as a result of great similarities in plumage and geographical proximity (Gibbs *et al.*, 2001).

Future work on brown cuckoo dove species complex should focus on the acquisition of additional sound recordings for island forms not yet represented in the present dataset (e.g. the collection of subspecies from the Melanesian islands). Of equal importance is the potential integration of phylogenetics into the current bioacoustics framework reported in the present study, which would require the procurement of DNA material for a large number of taxa in the complex to clarify patterns of gene flow and differentiation.

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## SUPPORTING INFORMATION

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

**Figure S1.** Normal Q-Q plots for inter-individual geographical distances (A); inter-individual Euclidean bioacoustic distances of principal component (PC) coordinates (A); shortest –120m sea level isobath distances between each taxa (C); and Euclidean distances of PC coordinates from each taxon mean (D).
**Figure S2.** Box plots of the four non-element specific temporal vocal parameters on the well-differentiated groups derived from bioacoustic analysis.
**Figure S3.** Box plots of the four non-element specific vocal frequency parameters on the vocally differentiated groups derived from bioacoustic analysis.
**Table S1.** Recordings and their details; sample means for each parameter analyzed.
**Table S2.** Number of elements per call motif across the vocally differentiated groups derived from bioacoustic analysis.