

Phylogeography of a 'great speciator' (Aves: *Edolisoma tenuirostre*) reveals complex dispersal and diversification dynamics across the Indo-Pacific

Michael Pepke Pedersen^{1,2}  | Martin Irestedt³ | Leo Joseph⁴ | Carsten Rahbek^{1,5} | Knud Andreas Jønsson¹

¹Center for Macroecology, Evolution and Climate, Natural History Museum of Denmark, University of Copenhagen, Copenhagen Ø, Denmark

²Department of Biology, Centre for Biodiversity Dynamics, Norwegian University of Science and Technology (NTNU), Trondheim, Norway

³Department of Bioinformatics and Genetics, Swedish Museum of Natural History, Stockholm, Sweden

⁴Australian National Wildlife Collection, CSIRO National Research Collections, Canberra, ACT, Australia

⁵Department of Life Sciences, Imperial College London, Ascot, UK

Correspondence

Michael Pepke Pedersen, Centre for Biodiversity Dynamics, Department of Biology, Norwegian University of Science and Technology, Trondheim, Norway.
Email: michael.p.pedersen@ntnu.no

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Abstract

Aim: We derive a new phylogenetic framework of the Indo-Pacific avian genus *Edolisoma* based on a dense taxon sampling and use it in an explicit spatiotemporal framework to understand the history of intraspecific diversification dynamics in a 'great speciator', the Cicadabird *Edolisoma tenuirostre/remotum* complex.

Location: The Indo-Pacific island region, Australia and New Guinea.

Taxon: Corvoid passerine birds (Passeriformes).

Methods: We used Bayesian phylogenetic methods (BEAST) to construct a time-calibrated molecular phylogeny of all 19 species in the genus *Edolisoma* and 27 of 29 subspecies of the *E. tenuirostre/remotum* complex (previously *Coracina tenuirostris*) primarily based on one mitochondrial DNA marker. Ancestral area reconstruction methods ('BioGeoBEARS') were used to infer the historical biogeography of the genus. We used population-level analyses to assess intraspecific phylogeography and a molecular species delimitation test to evaluate the current taxonomy. A morphometric dataset was used to discuss differential dispersal ability among taxa.

Results: *Edolisoma* originated in the late Miocene and diversification within the *E. tenuirostre/remotum* complex began in the Pleistocene. Within the North Melanesian and North Wallacean archipelagos, which have experienced several waves of diversification, we find significant patterns of genetic isolation by distance, but not within the Australo-Papuan 'mainland', which was recently back-colonized from these archipelagos. Based on the phylogeny, we suggest several taxonomic changes. We also discuss evidence of taxon cycles within *Edolisoma* based on correlations of species age, elevational ranges and dispersal ability.

Main conclusions: The biogeographical history and patterns of differentiation between phylogroups within *E. tenuirostre* support the importance of barriers to gene flow in island systems. Examples of both recent genetic exchange across significant sea barriers and differentiation across much smaller water gaps suggest complex dispersal and diversification dynamics. The capacity for dispersal away from islands, and gradual shifts in dispersal ability in relation to the geographical setting, is supported as important factors in generating a 'great speciator'.

KEYWORDS

dispersal, great speciators, Indo-Pacific, intraspecific diversification, islands, isolation by distance, phylogeography, Pleistocene diversification, taxon cycles

1 | INTRODUCTION

Distribution of biota across island systems has contributed significantly to the development of biogeographical and evolutionary theories (MacArthur & Wilson, 1967; Wallace, 1869; Wilson, 1961) and has been important for the understanding of processes underlying the evolution of avian diversity (Losos & Ricklefs, 2010). The Indo-Pacific island region, with its multitude of islands of different size, topography and connectivity (Hall, 2002), provides numerous island colonization events of various complexity (e.g. Jønsson et al., 2014, 2017; Moyle, Filardi, Smith, & Diamond, 2009). Furthermore, the Australo-Papuan land mass (known as Sahul when connected at times of lowered sea levels) separates the two geographically extensive archipelagos of Melanesia and Indonesia/Philippines offering two independent replicates of archipelagic radiations. Combined this region provides a unique geographical setting for testing the interaction between continental and island diversifications (Filardi & Moyle, 2005; Jønsson & Holt, 2015; Schweizer, Wright, Penalba, Schirtzinger, & Joseph, 2015) and the build-up of diversity in a dynamic geographical context.

The Australo-Papuan region is thought to be the source of several (downstream) colonizations into the Indo-Pacific archipelagos (García-Ramírez et al., 2017; Kearns et al., 2016). The Campephagidae (cuckoo-shrikes and allies), which is one of the most species-rich families of the Corvidae (sensu Cracraft, 2014), originated in this region (Jønsson, Fabre, Ricklefs, & Fjeldså, 2011). The focal species herein, *Edolisoma tenuirostre* (Slender-billed or Common Cicadabird), is the most widespread and diversified (in numbers of subspecies) within the Campephagidae and was described by Mayr and Diamond (2001) as one of the 'great avian speciators'. Mayr and Diamond (2001) developed the 'great speciator' concept for Northern Melanesian birds showing a high degree of interisland geographic variation, defined by their number of subspecies or allospecies per occupied island. The *E. tenuirostre* complex ranges east of Wallace's line into the Near-Pacific, with migratory and sedentary populations of *E. t. tenuirostre* occurring almost along the entire Australian north and east coast (Taylor, 2005; Figure 1). Few molecular studies have explored intraspecific patterns of diversification with a dense sampling across the range of a great speciator (but see García-Ramírez & Trewick, 2015; García-Ramírez et al., 2017; Irestedt et al., 2013; Jønsson et al., 2014; Moyle et al., 2009). In this study, we initially reconstruct phylogenetic relationships and colonization history of the genus *Edolisoma* and in particular the hyperdiverse *E. tenuirostre* subspecies complex.

Great speciators have been characterized as abundant, lowland species of intermediate dispersal ability and as good short-distance colonizers (Diamond, Gilpin, & Mayr, 1976). However, other widely distributed species show little or no geographic variation, creating an

apparent paradox: How do great speciators readily colonize and diversify across island systems, when at the same time, homogenizing gene flow should work counter to this? Rapid evolutionary shifts in dispersal ability have been invoked to explain this paradox, but no single explanation for the diversification patterns of great speciators has emerged (Diamond et al., 1976). Here, we use wing morphology as a proxy of dispersal ability to test if the *E. tenuirostre* complex has undergone shifts in dispersal ability, potentially in relation to landscape connectivity (water barriers), that could have generated the high geographic variation. In particular, we predict that selection against dispersal on small, remote islands would result in birds with shorter and stubbier wings compared to populations, which remain in a dispersive phase.

Evolutionary shifts in dispersal ability have been suggested to correlate with several geographical and ecological traits throughout the speciation process in island settings. The concept of taxon cycles (Wilson, 1961) thus predicts that species pass through stages of range expansions and range contractions, with young expanding taxa widely and continuously distributed in lowland habitats (stages I and II) and old relictual taxa with disjunct distributions inhabiting the higher elevational interior of larger islands (stages III and IV, Ricklefs & Bermingham, 2002). Such evolutionary cycles of shifting range and dispersal ability have been inferred in various island taxa (e.g. Jønsson et al., 2014, 2017; Ricklefs & Cox, 1972; Wilson, 1961). Here, we draw on patterns of elevational distribution, dispersal ability and species age of *Edolisoma* taxa to discuss the diversification dynamics of this radiation in the context of taxon cycles. Finally, we re-evaluate the complex taxonomy and 'great speciator' status of *E. tenuirostre* in light of the new molecular data presented here.

2 | MATERIALS AND METHODS

2.1 | Taxon sampling and laboratory procedures

The genus *Edolisoma* was recently reinstated as a genus separate from Cuckoo-shrikes (*Coracina*; see Dickinson & Christidis, 2014) based on molecular studies indicating paraphyly of this group with respect to Trillers (*Lalage*, see Fuchs, Cruaud, Couloux, & Pasquet, 2007; Jønsson et al., 2008, 2010). These studies also resulted in a preliminary circumscription of the Slender-billed Cicadabird (*Coracina tenuirostris*) into a Melanesian species *E. remotum* (8 subspecies) and its remaining 21 subspecies into *E. tenuirostre*, while elevating the Manus Island endemic *E. admiralitatis* to species rank (Dickinson & Christidis, 2014). Here, we include all 19 species of *Edolisoma* and 27 of the 29 currently recognized subspecies in the *E. tenuirostre/remotum* complex, except *E. t. kalaotuae* and the endangered *E. t. nesiotis* from the small islands of Kalaotoa (Lesser Sundas) and Yap

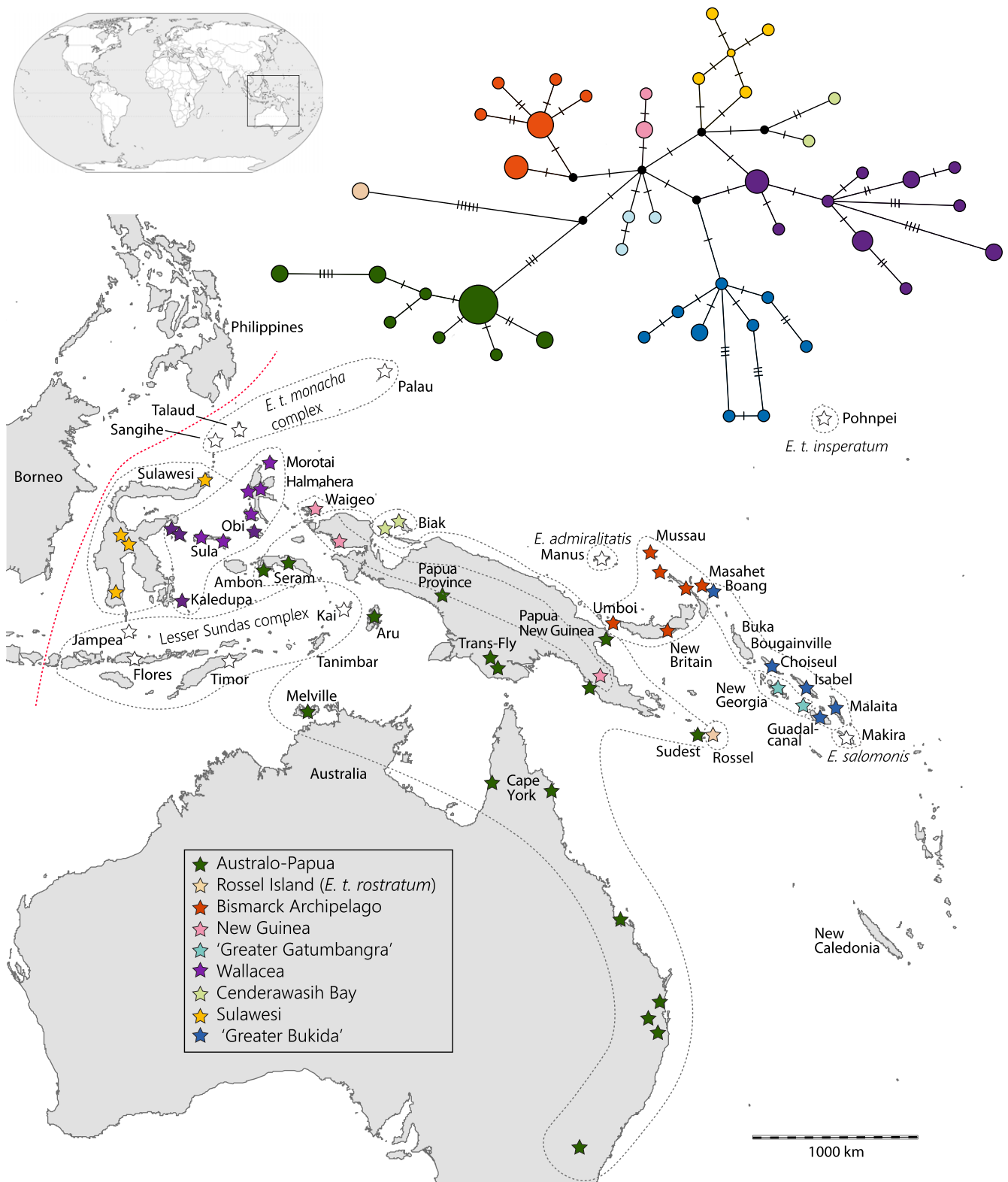


FIGURE 1 *Edolisoma tenuirostre/remotum* sample locations (coloured stars, a star may represent multiple samples) and closely related allopatrically occurring *Edolisoma* species (white stars). Dotted grey lines delimit the phylogeographic clades identified within the *E. tenuirostre* complex and allopatrically occurring related species. The dotted red line indicates Wallace's Line. In the haplotype network (based only on ND2 sequences), one bar indicates one mutation, black nodes are hypothetical ancestral states and the size of the circles corresponds to the number of sampled haplotypes [Colour figure can be viewed at wileyonlinelibrary.com]

(Micronesia), respectively. For simplicity, we refer hereafter to the *E. tenuirostre/remotum* complex as 'the *E. tenuirostre* complex' due to the polyphyly of *E. tenuirostre* and *E. remotum* shown in this study.

We included 119 samples from 19 *Edolisoma* species: 71 samples were derived from museum specimens (toepads) and for these one fast-evolving mitochondrial marker, NADH dehydrogenase subunit 2 (ND2, 1041 bp) was sequenced in seven fragments of 154–190 bp. A total of 12 samples were freshly collected tissue samples, and from these ND2 and three nuclear gene regions, ornithine decarboxylase introns 6 to 7 (ODC, 601 bp), glyceraldehyde-3-phosphodehydrogenase intron 11 (GAPDH, 291 bp) and myoglobin gene intron 2 (Myo, 708 bp) were sequenced. Full laboratory procedures, primer pairs, list of locations, accession numbers and specimens including 31 samples downloaded from GenBank are detailed in Table S1.1 and S1.2 in Appendix S1. Two closely related monotypic genera *Celebesica* and *Campochaera* were included as outgroups.

2.2 | Alignment and phylogenetic analyses

Contigs were assembled and primers trimmed with SEQMAN PRO 12.3.1.4 (DNASTAR Inc., Madison, WI, USA). Previously published sequences from GenBank (28 individuals from 16 *Edolisoma* species and 11 *Lalage* species) were added to the alignment. Alignment procedures are specified in Appendix S1. We used jMODELTEST2 (Darriba, Taboada, Doallo, & Posada, 2012) to identify appropriate nucleotide substitution models for each gene using the Akaike information criterion (AIC). Bayesian inference as implemented in BEAST 1.8.2 (Drummond, Suchard, Xie, & Rambaut, 2012) was used to estimate phylogenetic relationships. Assuming a birth-death process of speciation (constant speciation rate and a constant, nonzero extinction rate) for the tree prior and all other parameters at default (clock model specified below), the Markov chain Monte Carlo (MCMC) algorithm was run twice for 100 million iterations with trees sampled every 1000th generation. Convergence of individual runs was assessed using TRACER 1.6 (Rambaut, Suchard, Xie, & Drummond, 2014) ensuring all ESS > 200 and graphically estimating an appropriate burn-in. TREEANNOTATOR 1.8.2 (Rambaut & Drummond, 2015) was used to summarize a single maximum clade credibility (MCC) tree, which was pruned to remove outgroups and *Lalage* taxa included for calibration (below).

2.3 | Time-calibration

There are no fossils close to *Edolisoma* to calibrate the phylogeny. Following Jönsson et al. (2010), we therefore estimated the age of the split between *Lalage typica* on the isolated island of Mauritius and *L. newtoni* on nearby Réunion by assuming the colonization of the younger Réunion (c. 2 Myr old) took place from the older Mauritius. We therefore included previously published ND2 sequences of the closely related *Lalage* clade containing these two species (Table S1.2 in Appendix S1) and specified a normally distributed prior for the timing of this split at 1.5 Ma \pm 0.25 SD (age within

95% confidence interval: 1.089–1.911 Ma). We assumed an uncorrelated lognormal relaxed molecular clock model (unlinked for mitochondrial and nuclear genes, Drummond, Ho, Phillips, & Rambaut, 2006). For comparison, we also constructed a phylogeny applying an overall rate of ND2 evolution (Appendix S1).

2.4 | Ancestral range estimation

Ancestral ranges were estimated using the maximum likelihood framework implemented in the library 'BioGeoBEARS' (Matzke, 2013) in R (R Core Team, 2015). This framework compares several alternative models of geographic ancestral range estimation each of which are included in a version simulating founder-event speciation ('+J', Matzke, 2014), defined as a rare long-distance colonization event, which is likely to be an important process in an oceanic island setting like the Indo-Pacific. All taxa were assigned to four pre-defined geographical regions (Figure 2): Wallacea (W, defined by Wallace's line to the west and Lydekker's line to east and including Sangihe, Talaud and Palau), Australo-Papua (A, defined as the land mass of Sahul exposed by low Pleistocene sea levels), Melanesia and Micronesia (M) and the Philippines (P). Maximum number of areas was set to 3 to reflect the maximum extent of the *E. tenuirostre* complex. AIC weights and likelihood ratio tests were used to select the model that fits the data best, and the probability of each ancestral region was calculated for all nodes. To account for topological uncertainty, we also estimated ancestral ranges using RASP 3.2 (Yu, Harris, Blair, & He, 2015) by summarizing over the posterior distribution of 10,000 trees.

2.5 | Molecular species delimitation and diversification rate analyses

We applied the generalized mixed Yule-coalescent (GMYC) model to estimate molecular operational taxonomic units (MOTUs) from sequence divergences (Fujisawa & Barraclough, 2013). GMYC uses the time-calibrated (ultrametric) single-locus (ND2) MCC tree to find a threshold in time between inter- and intraspecific branching rates, by maximizing the model likelihood. Splits in tree older than this threshold are assumed to represent speciation events, and younger splits reflect intraspecific neutral coalescence events. All branching events older than the threshold are therefore designated as species. For comparison, we also ran the Poisson tree processes (PTP) model (Appendix S1).

We constructed a lineage-through-time (LTT) plot using the R package 'ape' (Paradis, Claude, & Strimmer, 2004) after pruning the MCC tree to match the number of species ($n = 18$) according to the species delimitation test. We used the R package 'laser' (Rabosky & Schliep, 2013) and AIC to compare diversification rate models.

2.6 | Molecular population structure analyses

We used POPART (Leigh & Bryant, 2015) to construct a TCS haplotype network of ND2 sequences of the *E. tenuirostre* complex

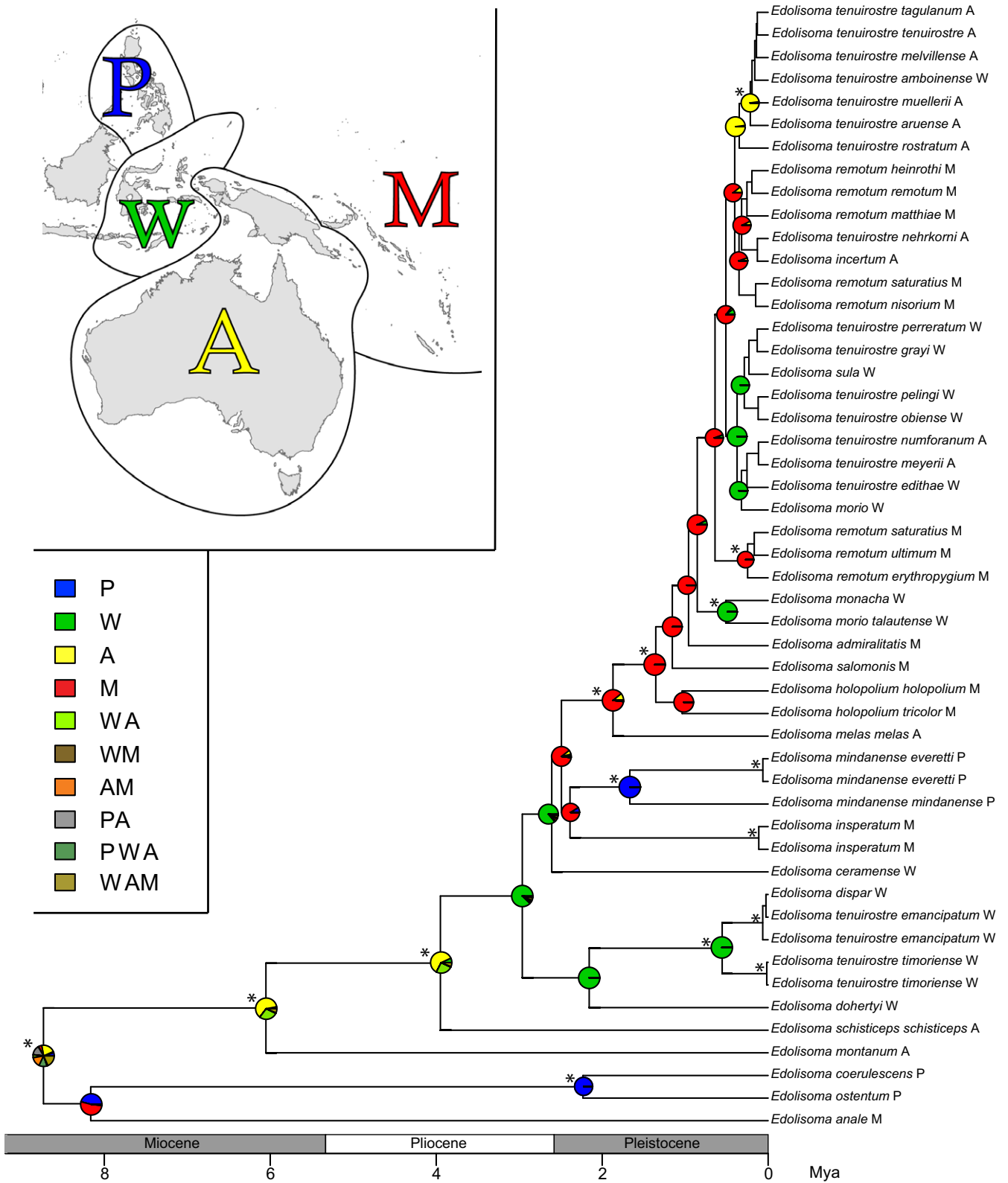


FIGURE 2 Time-calibrated maximum clade credibility tree of the concatenated dataset of the *Edolisoma* genus with asterisks indicating well-supported nodes with posterior $p \geq .99$. Several recent splits have been pruned for clarity. Letters and colours refer to the areas of Australo-Papua (A), Wallacea (W), Melanesia (M), the Philippines (P) and combinations of these. The results of the ancestral range estimation in 'BioGeoBEARS' are shown as pie charts coloured in relative proportions of the most likely ancestral area [Colour figure can be viewed at wileyonlinelibrary.com]

(623 bp excluding gaps). Based on well-supported phylogenetic relationships from the BEAST analyses, the geographic affinities of these relationships and the structure of the haplotype network, we defined nine major putative phylogeographic populations within the complex (Figure 1). Uncorrected pairwise p-distances based on the ND2 gene were calculated using MEGA 6 (Tamura, Stecher, Peterson, Filipski, & Kumar, 2013), and we used a Mantel test to test for a correlation between genetic distance and geographic distance between sample locations (using *IBDWS* 3.23, Jensen, Bohonak, & Kelley, 2005) within the *E. tenuirostre* complex. We removed eight samples found within the species' non-sedentary range (Eastern Australia, Taylor, 2005) to remove confounding effects of seasonally migrating individuals. We also performed three subset analyses of the Australo-Papuan, the Indonesian and the Melanesian archipelago samples, respectively, to test for differing colonization patterns in different geographical settings (archipelagos and mainland).

2.7 | Dispersal ability and elevational range

We used the length of the longest primary (wing length, WL) and of the first secondary (secondary length, SL) of the wing measured on 119 adult male and nine female individuals representing all *Edolisoma* species with at least two specimens and including 35 individuals (representing seven subspecies) of the revised *E. tenuirostre* complex. To assess variation in dispersal ability across *Edolisoma*, we calculated a wing shape aspect ratio (hand-wing index) $HWI = 100 \times \frac{WL - SL}{WL}$, which is believed to be a good proxy for dispersal capacity (Claramunt, Derryberry, Remsen, & Brumfield, 2012).

We categorized all species into one of three elevational range classes (inhabiting mainly coastal, lowland and montane habitats, respectively, see Appendix S3) based on information in Taylor (2005). We then investigated correlations of average taxon HWI, its node age (estimated from the time-calibrated MCC tree) and elevational range class.

3 | RESULTS

3.1 | Phylogenetic analyses and ancestral range estimation

Edolisoma parvulum is clearly not a member of *Edolisoma*, but was found to be nested within *Coracina* (M.P. Pedersen, in preparation) and therefore excluded from subsequent analyses. The phylogeny (Figures 2 and 3) reveals extensive para- and polyphyly of nominal taxa at both inter- and intraspecific levels within *Edolisoma* (see Taxonomy), however, several relationships remain poorly resolved. The split between *Edolisoma* and *Lalage* is estimated to be at 9.7 Ma (age within 95% highest posterior density (HPD): 4.9–16.1 Ma, not shown). Within the *E. tenuirostre* complex, nine distinct phylogeographic groups are recognized (coloured in Figures 1 and 3). The nominal subspecies *E. t. monacha*, *E. morio salvadorii* and *E. m. talautense* together represent a Micronesian clade, which

is sister to the rest of the *E. tenuirostre* complex (Figure 3). The subspecies *E. t. timoriense* and *E. t. emancipatum* represent an older Lesser Sunda Islands clade together with *E. dispar* and *E. doherityi* (Figure 1).

The most likely ancestral area reconstruction model estimated by 'BioGeoBEARS' was the dispersal-extinction cladogenesis (DEC) model (Ree, Moore, Webb, & Donoghue, 2005) including founder-event speciation ('+J', Figure 2 and Table S2.1 in Appendix S2). The genus originated in the late Miocene and although the area of origin is unresolved, it appears to be based around Australo-Papua. The RASP analysis (Figure S2.1 in Appendix S2) generally confirmed the most likely areas in 'BioGeoBEARS', but with more ambiguity (shared ancestral states).

The Wallacean archipelago was colonized earlier than Melanesia by *Edolisoma* species continuing to the Philippines in at least two separate colonization events (*E. ostentum* / *E. coeruleescens* and *E. mindanense*). One *Edolisoma* clade diversified 3 Ma (HPD: 1.4–5.0 Ma) in the Lesser Sundas. These islands were not colonized by the more recent (<1 Ma) *E. tenuirostre* (including *E. sula* and *E. m. morio*) westward expansion across the North Moluccas to Sulawesi. Several waves of colonization of North Melanesia (the Bismarck and Solomon archipelagos) probably occurred via New Guinea and can be recognized as starting at less than 2 Ma with *E. holopolium*, *E. salomonis* and *E. admiralitatis*. The latter two taxa differentiated on the most peripheral islands to the east (Makira in the Solomons) and to the west (Manus in the Bismarcks), respectively. Two subsequent colonizations of the Solomons (*E. r. saturatius/erythropygium* and *E. r. saturatius/nisorium*) resulted in sympatry with *E. holopolium*, while the Bismarcks were colonized by subspecies of *E. remotum*. After dispersal into Wallacea and Melanesia, the Australo-Papuan mainland was back-colonized most likely from the North Melanesian archipelago (Figure 2). The New Georgian *E. r. saturatius* and *E. r. nisorium* on the nearby Russell Island are placed consistently but with low support close to *E. incertum*, which is distributed across New Guinea. Dispersal directly from the Southeast Papuan Islands to New Georgia has been inferred in another widespread great speciator, *Zosterops griseotinctus* (Moyle et al., 2009) and cannot be excluded in this case either.

3.2 | Molecular species delimitation and diversification rate analyses

The GMYC model identified a coalescence time threshold at 0.7 Ma and 18 MOTUs (Table S3.1 in Appendix S3) within *Edolisoma*, where PTP and bPTP identified 20 MOTUs. In contrast to GMYC, the PTP and bPTP models designated (1) *E. t. timoriense* as a species separate from *E. dispar* and *E. t. emancipatum*, and (2) *E. t. monacha* as separate from *E. m. talautense* and *E. m. salvadorii*.

In Figure 4a, the number of lineages was log₁₀-transformed and plotted against branching times. The best fitting diversification rate model for this LTT plot was a pure birth Yule speciation rate model (constant speciation rate with no extinction, see Table S2.2 in Appendix S2).

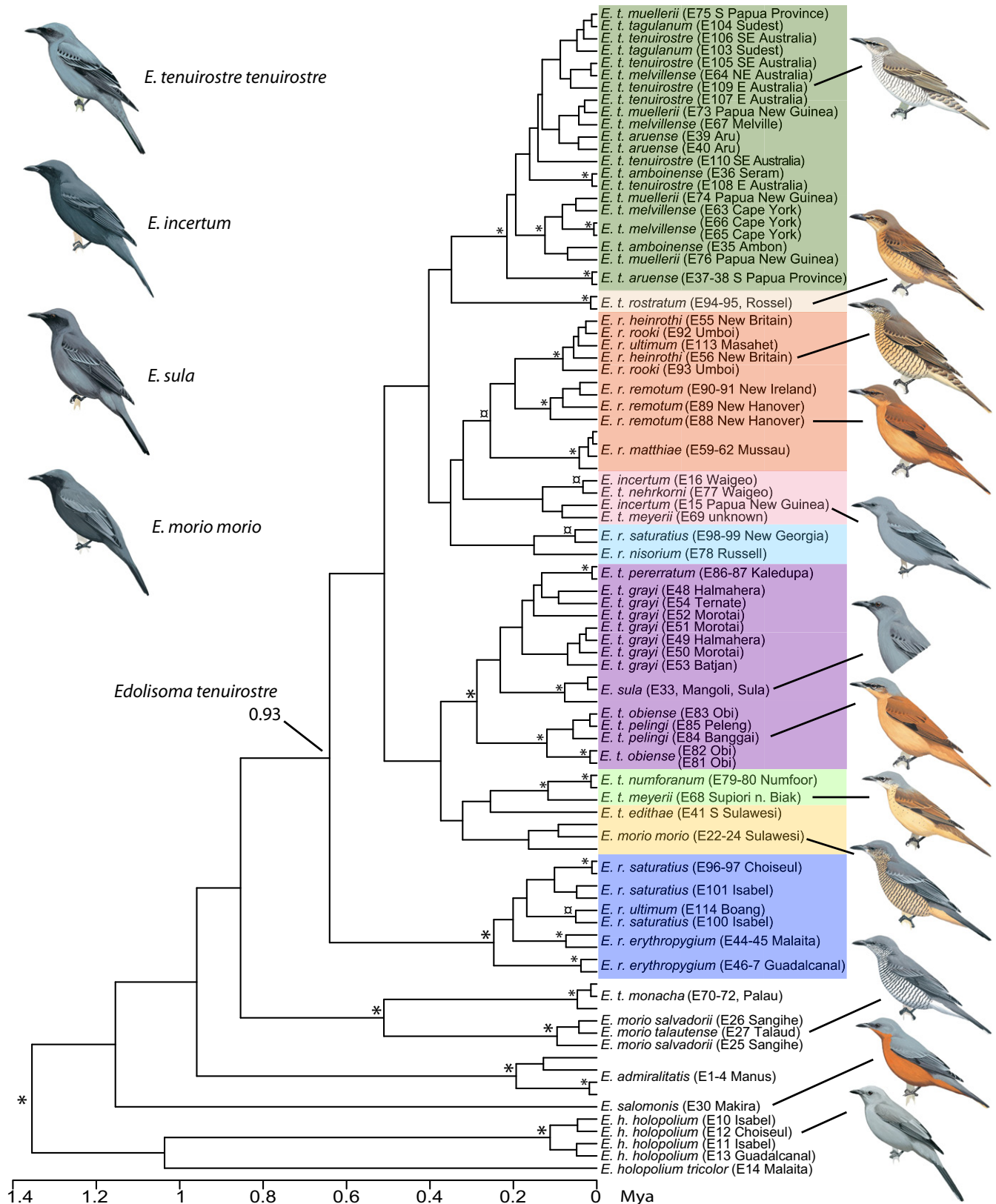


FIGURE 3 Unpruned section of the maximum clade credibility tree in Figure 2 showing the *Edolisoma tenuirostre* (*E. t.*)/*E. remotum* (*E. r.*) complex with populations coloured according to Figure 1. Asterisks indicate posterior $p \geq .99$ and $\square \geq .97$. Figures show males (left) and females (right), illustrating the extreme female plumage variation. Specimen E69 lacks location and is most likely not an *E. t. meyerii* (see Table S1.2 in Appendix S1 for full specimen information). Figures reproduced with permission from del Hoyo, J., Elliott, A., Sargatal, J., Christie, D.A. & de Juana, E. (eds.) (2017). *Handbook of the Birds of the World Alive*. Lynx Edicions, Barcelona (retrieved from <http://www.hbw.com/> on 10 March 2017) [Colour figure can be viewed at wileyonlinelibrary.com]

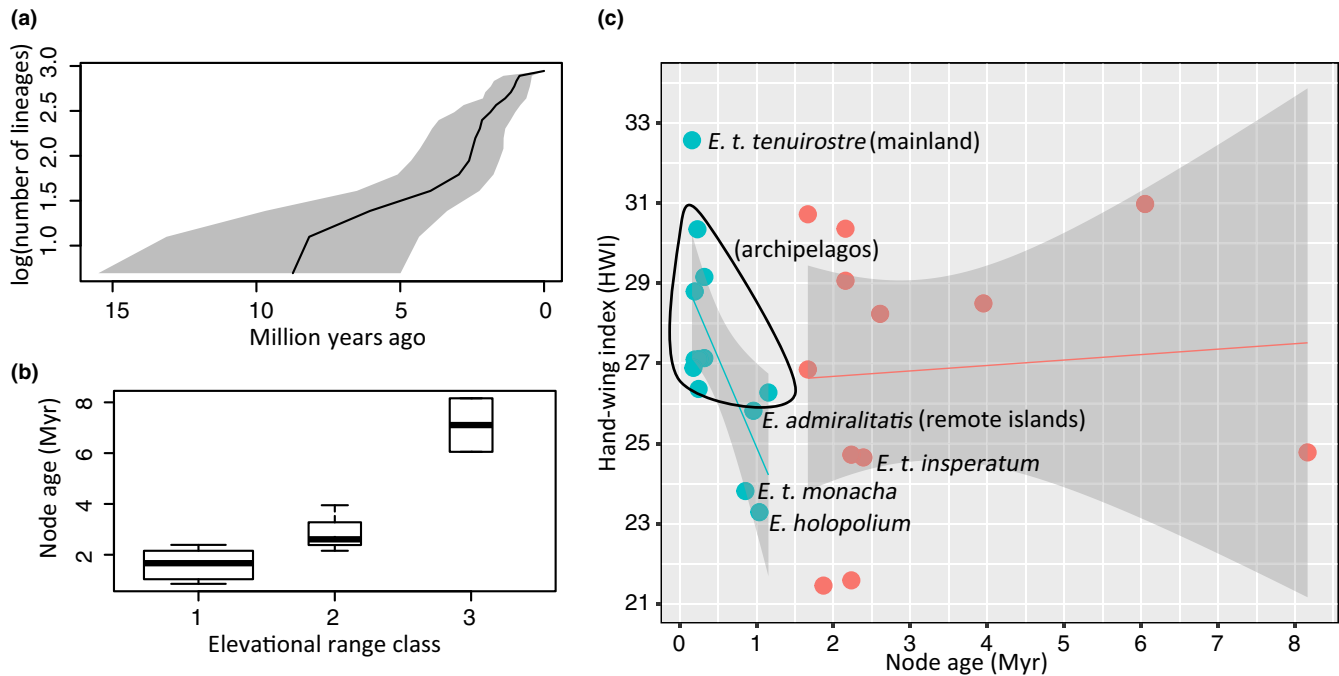


FIGURE 4 (a) Lineage-through time plot of log-transformed number of lineages against time in million years. The solid line represents the maximum clade credibility tree and the grey area shows the phylogenetic uncertainty of 100 randomly sampled trees from the posterior distribution. (b) Boxplot showing node ages (in Myr) of species in elevational range class 1 (coastal areas, number of species $n = 13$), class 2 (lowlands, $n = 3$) and class 3 (montane areas, $n = 2$). (c) Correlation between HWI and node age (Myr) for subspecies within the revised *Edolisoma tenuirostre* complex and closest relatives (blue, $p < .01$, all <1.5 Myr old and in Figure 3) and for species within the genus *Edolisoma* (red, not significant). The Australo-Papuan (mainland) *E. t. tenuirostre* has the largest HWI, the archipelagic subspecies (black shape, see Appendix S1) have intermediate HWIs and the remote island forms (except *E. holopolium*) have the lowest HWIs [Colour figure can be viewed at wileyonlinelibrary.com]

3.3 | Molecular population structure analyses

The Mantel test showed a significant positive correlation between genetic and geographic distance within the North Wallacean ($r = .3197$, $p < .005$, Figure S2.2a in Appendix S2) and North Melanesian archipelagos ($r = .4755$, $p < .0001$, Figure S2.2b in Appendix S2), respectively, but not within the Australo-Papuan clade ($r = .1623$, not significant, Figure S2.2c in Appendix S2). The correlation for the entire *E. tenuirostre* complex remains significant ($r = .3172$, $p < .0001$, Figure S2.2d in Appendix S2). Uncorrected pairwise p -distances ranged from 0 to 7.5% between subspecies within the currently recognized *E. tenuirostre* complex (0–2.9% after GMYC model revision) and from 0.1 to 15.5% between *Edolisoma* species (0.9–15.5% after revision).

3.4 | Dispersal ability, elevational range and evolutionary age

Species in different elevational range classes differ significantly in mean node age (ANOVA, $p < .001$, Figure 4b, see Appendix S3 for examples) with species inhabiting the highest elevations (class 3) being oldest ($n = 2$, mean age = 7.2 Myr), species at sea level (class 1) being youngest ($n = 13$, mean age = 1.6 Myr) and species in elevational class 2 being of intermediate ages ($n = 3$, mean age = 2.9 Myr). Within the *E. tenuirostre* subspecies complex,

average subspecies HWI is negatively correlated with the age of subspecies ($n = 12$, $R^2 = .5291$, $p < .01$, Figure 4c).

4 | DISCUSSION

While *Edolisoma* originated in the late Miocene, diversification within the *E. tenuirostre* complex mostly occurred more recently during the late Pleistocene. Thus, their current distribution appears to mainly be the result of dispersal or range expansion facilitated by Pleistocene sea level changes (Bintanja, van de Wal, & Oerlemans, 2005; Hall, 2002; Voris, 2000). The constant rate of lineage accumulation (Figure 4a) suggests that the genus has maintained high net diversification rates perhaps as a result of continued expansion and high colonization success (e.g. Fritz, Jönsson, Fjeldså, & Rahbek, 2012). Furthermore, the ancestral range estimation and the shallow phylogeographic diversity of the *E. tenuirostre* complex (including *E. morio*, *E. sula* and *E. incertum*) suggest that these birds are good dispersers that recently colonized the entire Indo-Pacific island region east of Wallace's Line except the Lesser Sundas, which were colonized by an older, closely related clade. The colonization of the North Melanesian and the North Wallacean archipelagos followed stepping-stone pathways (Figure S2.2a–b in Appendix S2). A similar genetic pattern was found for another 'great speciator', the *Erythropitta erythrogaster* complex, which colonized the Indo-Pacific in the

middle Pleistocene (Irestedt et al., 2013). However, the biogeographic analyses indicate at least one case of 'upstream colonization' by *E. tenuirostre* of the Australo-Papuan mainland, probably from the Melanesian Archipelago. Recent studies have emphasized the potential of island systems in generating diversity and back-dispersal to continental land masses (Filardi & Moyle, 2005; Schweizer et al., 2015). This might be more common than previously anticipated (Jönsson & Holt, 2015), especially among highly dispersive 'tramp' species such as members of *Edolisoma* (see also Jönsson et al., 2008). All areas inhabited by the Australo-Papuan *E. tenuirostre* clade were connected by land during low Pleistocene sea levels (Voris, 2000) forming a single extensive Australo-Papuan mainland (Sahul). Recent mixing of individuals within the entire range may thus have inhibited further differentiation (Weeks & Claramunt, 2014) within the Australo-Papuan clade as indicated by the uncorrelated relationship between genetic and geographical distance (Figure S2.2c in Appendix S2).

4.1 | Complex Pleistocene diversification

In the North Melanesian archipelago, a well-supported relationship between the Solomon populations and an individual from Boang (*E. r. ultimum* E114, Figures 1 and 3) north-east of New Ireland confirms recent exchange between the Bismarcks and the Solomons. Also in the North Moluccas, the phenotypically and genetically similar *E. t. pelingi* (Banggai) and *E. t. obiense* (Obi) form a group separated by 500 km of deep ocean on either side of the Sula Islands, which are occupied by the closely related but distinctive *E. sula*. However, in light of the high dispersal ability of *E. tenuirostre*, populations might sustain exchange of individuals across large distances. Ecological (competitive) interactions between inhabitants on intervening islands might then explain why sister populations are separated by islands with apparently suitable habitat. Alternatively, recent local (and possibly anthropogenic) extinctions could have produced a similar pattern.

Despite examples of recent dispersal across long distances, subspecies differentiation across much smaller water barriers is a more common pattern, for example the sister taxa *E. t. rostratum* on Rossel Island and *E. t. tagulanum* on Sudest (35 km) and the populations of *E. remotum* on New Georgia and Choiseul to Guadalcanal (55 km), respectively. The latter was noted by Smith and Filardi (2007) and conforms to a separation described in several species across the Solomon Islands (Andersen et al., 2014; Uy, Moyle, & Filardi, 2009). This probably reflects the effect of land bridges formed during times of low sea levels in the Pleistocene, when global glaciation cycles resulted in sea level changes of up to 120 m (Bintanja et al., 2005). At times of low sea levels, the New Georgia group was connected in 'Greater Gatumbangra', and Choiseul and Isabel were connected with Buka, Bougainville and probably Guadalcanal in 'Greater Bukida' (Figure 1; Mayr & Diamond, 2001). However, in contrast to other studies (Andersen et al., 2014; Uy et al., 2009), we do not recover a sister relationship between the Greater Gatumbangra and Bukida populations, suggesting alternative colonization pathways of the Solomon Islands (i.e. directly from New Guinea). Pleistocene island

aggregates have been involved in shaping patterns of intraspecific genetic variation across organisms (Lohman et al., 2011). Together with the lack of differentiation of *E. tenuirostre* subspecies across the Pleistocene Australo-Papuan mainland, this also suggests a role of recent sea level changes in shaping the present-day phylogeography of *E. tenuirostre*.

4.2 | Rapid evolutionary shifts in dispersal ability reflect geography

The present distribution of *E. tenuirostre* on the islands of Palau and Pohnpei (Figure 1), which remained remote during the evolution of *Edolisoma* (Hall, 2002), almost certainly reflects long-distance dispersal (1,000 km) from Wallacea and the Bismarcks, respectively, and illustrates the (historically) high capacity for long-distance dispersal of *E. tenuirostre*. The taxa on these isolated islands have the lowest HWI, while the archipelagic subspecies in Wallacea and Melanesia have 'intermediate' HWI values, and *E. t. tenuirostre* of Australo-Papua the highest HWI. This might be the result of reduced selection for dispersal on remote islands, suggesting rapid evolutionary shifts in dispersal ability (Diamond et al., 1976; Moyle et al., 2009). Such shifts in dispersal ability can occur rapidly in insular avian populations; Slikas, Olson, and Fleischer (2002) inferred that some species of Rallidae became flightless within a few hundred thousand years, possibly through adaptation to limited resources on islands and intraspecific competition that reduced the basal rate of metabolism (McNab, 2002).

The Australo-Papuan *E. t. tenuirostre* has the highest HWI, consistent with its wide range, migratory behaviour of some populations, and habitat preference (open forest and edge habitat). Thus, this Australo-Papuan clade could be considered a 'supertramp' group (sensu Diamond, 1974), consistent with an interpretation of recent expansion and rapid colonization (from the Melanesian origin). This illustrates the different stages of diversification within the range of the species. That is, isolation by distance generates diversification within archipelagos, but within Australo-Papua (Sahul) periods of land mass connectivity and gene flow together prevent differentiation (Claramunt et al., 2012).

4.3 | Taxon cycles within *Edolisoma*

In a recent study on another Indo-Pacific passerine bird radiation (*Pachycephala*), Jönsson et al. (2014) found that old taxa tend to inhabit higher elevations on a few large islands while young taxa inhabit the more disturbed lowlands on many islands. We find a similar pattern within *Edolisoma*, in which the age of a species is positively correlated with elevational range (Figure 4b): Lowest elevational range class 1 corresponds to early taxon cycle stages (I and II) of relatively recent colonists inhabiting coastal areas. Elevational range class 2 consists of species of stage II or III, which are absent from coastal habitats (due to either competitive exclusion or adaptation to inland habitats), but retain their dispersal ability, and class 3 consists of late stage III or IV species, which are confined to

high elevations. This observation supports the prediction of taxa passing through temporal stages of expansions and contractions (Ricklefs & Cox, 1972), but in synchrony with closely related species.

4.4 | Taxonomy

Apart from *E. parvulum*, which should be placed in *Coracina*, our data affirm the monophyly of *Edolisoma* and corroborate the phylogeny of Jønsson et al. (2010) in that the *E. tenuirostre* complex is polyphyletic. Based on the GMYC model, we suggest the following tentative taxonomic changes at species-level (checklist in Table S3.1 in Appendix S3 modified from Dickinson & Christidis, 2014): (1) *E. t. insperatum*, *E. t. monacha* (including *E. m. salvadorii/talautense*), *E. holopolium tricolor* and *E. mindanense everetti* should each be elevated to species rank. (2) *E. incertum*, *E. morio morio* and *E. sula*, which were originally lumped by Peters (Cottrell et al., 1960), are each nested deeply within the *E. tenuirostre/remotum* complex and should therefore all be lumped. (3) *E. t. emancipatum*, *E. t. timoriense* and *E. dispar* are conspecific and should be lumped. The identity of *E. t. edithae* remains unclear (Table S3.1 in Appendix S3).

In contrast to other *E. tenuirostre* subspecies, the female plumages of *E. sula* and *E. incertum* are highly masculinized. This feature has likely been considered when giving these taxa species status. However, intraspecific variation in the degree of sexual dichromatism is known in other great speciators including *Pachycephala pectoralis* (Andersen et al., 2014) and *Petroica multicolor* (Kearns et al., 2016). It might therefore be a characteristic with a common genetic basis (Cornetti et al., 2015) that facilitates the early (parapatric) diversification of great speciators.

Several molecular studies of avian diversity in the Indo-Pacific have resulted in elevating subspecies to species rank (Irestedt et al., 2013; Kearns et al., 2016) or recognizing polytypic taxa as multiple incipient species (Andersen, Hosner, Filardi, & Moyle, 2015). Contrary to this trend, this study suggests the inclusion of five currently recognized species into one single species complex. In an island setting like the Indo-Pacific, subspecies designation has often been readily assigned based on allopatrically occurring island populations in which each island population is assigned to its own subspecies. This might have contributed to the apparently overestimated intraspecific diversity of the *E. tenuirostre* complex, in combination with the high dispersal ability, the wide distribution and confounding effects of migratory populations.

4.5 | A great speciator

Although this study excludes the Lesser Sundas and Micronesia from the range of the most recent *E. tenuirostre* diversification, the morphological and ecological diversity of the species is complemented by the inclusion of *E. incertum*, which has male-like plumage in females and inhabits lower montane areas across New Guinea, *E. morio* across Sulawesi and *E. sula* bridging the gap to Sulawesi (Figure 1). This study affirms the status of *E. tenuirostre* as a great speciator corresponding to an early expanding taxon cycle stage, in which

differentiation in isolation is balanced by gene flow due to ongoing dispersal within the range of the species. However, the geographical setting (mainland versus archipelagos) influences the dynamics of this diversification process and shows the importance of water barriers to dispersal. This is further reflected in the decreasing dispersal capacity from mainlands (high) via archipelagos (intermediate) to remote island (low) taxa, respectively. The early dispersive phase of *E. tenuirostre* is illustrated relative to older contraction stage *Edolisoma* species by their elevational ranges. Thus, over evolutionary time, the oceanic island (or montane) populations of *E. tenuirostre* might differentiate in relative isolation (or become locally extinct), fragmenting the current range of this 'great speciator', while the Australo-Papuan *E. tenuirostre* clade maintains the dispersal potential for renewed expansions.

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DATA ACCESSIBILITY

All sequence data have been deposited on GenBank (Table S1.2 in Appendix S1).

ORCID

Michael Pepke Pedersen  <http://orcid.org/0000-0002-6280-1829>

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BIOSKETCH

Michael Pepke Pedersen is a PhD student at NTNU (Trondheim) and has a broad interest in avian biogeography, phylogenetics and life-history evolution. This study is part of his master thesis at UCPH (Copenhagen) on the phylogeny and biogeography of the Campephagidae family as a model group for understanding the build-up and distribution of insular avian diversity.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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