7

8   Original Article

9 **Phylogeography of a "great speciator" (Aves: *Edolisoma tenuirostre*) reveals**

10   **complex dispersal and diversification dynamics across the Indo-Pacific**

11 **Running title:** Phylogeography of a "great speciator"

12

13 Michael Pepke Pedersen[1,2*], Martin Irestedt[3], Leo Joseph[4], Carsten Rahbek[1,5], Knud Andreas
14 Jønsson[1]

15 [1]Center for Macroecology, Evolution and Climate, Natural History Museum of Denmark,
16 University of Copenhagen, DK-2100 Copenhagen Ø, Denmark

17 [2]Centre for Biodiversity Dynamics, Department of Biology, Norwegian University of Science
18 and Technology (NTNU), NO-7491 Trondheim, Norway

19 [3]Department of Bioinformatics and Genetics, Swedish Museum of Natural History, PO Box
20 50007, Stockholm 10405, Sweden

21 [4]Australian National Wildlife Collection, CSIRO National Research Collections, GPO Box 1700,
22 Canberra ACT 2601, Australia

23 [5]Department of Life Sciences, Imperial College London, Silwood Park Campus, Ascot SL5 7PY,
24 UK

25 [*]Correspondence: Michael Pepke Pedersen, Centre for Biodiversity Dynamics, Department of
26 Biology, Norwegian University of Science and Technology, Høgskoleringen 5, NO-7491
27 Trondheim, Norway. Email: michael.p.pedersen@ntnu.no

28   **Word count:** 6348 (abstract, main text and references), figures estimated to 3 pages.

29

30   **ACKNOWLEDGEMENTS**

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 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 out 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, are supported as important factors in generating a "great speciator".

78 **Keywords:** dispersal, great speciators, Indo-Pacific, intraspecific diversification, islands,

79 isolation by distance, phylogeography, Pleistocene diversification, taxon cycles

80

81 **INTRODUCTION**

82 Distribution of biota across island systems have contributed significantly to the development of

83 biogeographical and evolutionary theories (Wallace, 1869; Wilson, 1961; MacArthur & Wilson,

84 1967) and have been important for the understanding of processes underlying the evolution of

85 avian diversity (Losos & Ricklefs, 2010). The Indo-Pacific island region, with its multitude of

86 islands of different size, topography and connectivity (Hall, 2002), provides numerous island

87 colonization events of various complexity (e.g. Moyle *et al.*, 2009; Jønsson *et al.*, 2014, 2017).

88 Furthermore, the Australo-Papuan landmass (known as Sahul when connected at times of lowered

89 sea levels) separates the two geographically extensive archipelagos of Melanesia and

90 Indonesia/Philippines offering two independent replicates of archipelagic radiations. Combined

91 this region provides a unique geographical setting for testing the interaction between continental

92 and island diversifications (Filardi & Moyle, 2005; Schweizer *et al.*, 2015; Jønsson & Holt, 2015)

93 and the build-up of diversity in a dynamic geographical context.

94 The Australo-Papuan region is thought to be the source of several (downstream) colonisations into

95 the Indo-Pacific archipelagos (Kearns *et al.* 2016; Garcia-Ramirez *et al.*, 2017). The

96 Campephagidae (cuckoo-shrikes and allies), which is one of the most species rich families of the

97 Corvides (*sensu* Cracraft, 2014) originated in this region (Jønsson *et al.*, 2011). The focal species

98 herein; *Edolisoma tenuirostre* (Slender-billed or Common Cicadabird) is the most widespread and

99 diversified (in numbers of subspecies) within the Campephagidae and was described by Mayr &

100 Diamond (2001) as one of the "great avian speciators". Mayr & Diamond (2001) developed the

101 "great speciator" concept for Northern Melanesian birds showing a high degree of inter-island

102 geographic variation, defined by their number of subspecies or allospecies per occupied island.

103 The *E. tenuirostre* complex ranges east of Wallace's line into the Near-Pacific, with migratory and

104 sedentary populations of *E. t. tenuirostre* occurring almost along the entire Australian north and

105 east coast (Taylor, 2005; Fig. 1). Few molecular studies have explored intraspecific patterns of

106 diversification with a dense sampling across the range of a great speciator (but see Moyle *et al.*,

107 2009; Irestedt *et al.*, 2013; Jønsson *et al.*, 2014; Garcia-Ramirez & Trewick, 2015; Garcia-Ramirez

et al., 2017). 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 *et al.*, 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 (stage I and II) and old relictual taxa with disjunct distributions inhabiting the higher elevational interior of larger islands (stage III and IV, Ricklefs & Birmingham, 2002). Such evolutionary cycles of shifting range and dispersal ability have been inferred in various island taxa (e.g. Wilson, 1961; Ricklefs & Cox, 1972; Jønsson *et al.*, 2014, 2017). 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.

MATERIALS AND METHODS

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 *et al.*, 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 (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. 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.

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 *et al.*, 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 *et al.*, 2012) was used to estimate phylogenetic relationships. Assuming a birth-death process of speciation (constant speciation rate

167 and a constant, nonzero extinction rate) for the tree prior and all other parameters at default (clock

168 model specified below), the Markov chain Monte Carlo (MCMC) algorithm was run twice for 100

169 million iterations with trees sampled every 1000th generation. Convergence of individual runs was

170 assessed using TRACER 1.6 (Rambaut, *et al.*, 2014) ensuring all ESS > 200 and graphically

171 estimating an appropriate burn-in. TREEANNOTATOR 1.8.2 (Rambaut & Drummond, 2015) was

172 used to summarize a single maximum clade credibility (MCC) tree, which was pruned to remove

173 outgroups and *Lalage* taxa included for calibration (below).

174 **Time-calibration**

175 There are no fossils close to *Edolisoma* to calibrate the phylogeny. Following Jønsson *et al.* (2010),

176 we therefore estimated the age of the split between *Lalage typica* on the isolated island of Mauritius

177 and *L. newtoni* on nearby Réunion by assuming the colonization of the younger Réunion (*c.* 2 Myr

178 old) took place from the older Mauritius. We therefore included previously published ND2

179 sequences of the closely related *Lalage* clade containing these two species (Table S1.2 in Appendix

180 S1) and specified a normally distributed prior for the timing of this split at 1.5 Ma ± 0.25 SD (age

181 within 95% confidence interval: 1.089-1.911 Ma). We assumed an uncorrelated lognormal relaxed

182 molecular clock model (unlinked for mitochondrial and nuclear genes, Drummond *et al.*, 2006).

183 For comparison, we also constructed a phylogeny applying an overall rate of ND2 evolution

184 (Appendix S1).

185 **Ancestral range estimation**

186 Ancestral ranges were estimated using the maximum likelihood framework implemented in the

187 library 'BioGeoBEARS' (Matzke, 2013) in R (R Core Team, 2015). This framework compares

188 several alternative models of geographic ancestral range estimation each of which are included in

189 a version simulating founder-event speciation ("+J", Matzke, 2014), defined as a rare long-distance

190 colonization event, which is likely to be an important process in an oceanic island setting like the

191 Indo-Pacific. All taxa were assigned to four pre-defined geographical regions (Fig. 2): Wallacea

192 (W, defined by Wallace's line to the west and Lydekker's line to east and including Sangihe,

193 Talaud and Palau), Australo-Papua (A, defined as the landmass of Sahul exposed by low

194 Pleistocene sea levels), Melanesia and Micronesia (M) and the Philippines (P). Maximum number

195 of areas was set to 3 to reflect the maximum extent of the *E. tenuirostre* complex. AIC weights

196 and likelihood ratio tests were used to select the model that fits the data best and the probability of

197   each ancestral region was calculated for all nodes. To account for topological uncertainty we also

198   estimated ancestral ranges using RASP 3.2 (Yu *et al.*, 2015) by summarizing over the posterior

199   distribution of 10,000 trees.

Molecular species delimitation and diversification rate analyses

201   We applied the generalized mixed Yule-coalescent (GMYC) model to estimate molecular

202   operational taxonomic units (MOTUs) from sequence divergences (Fujisawa and Barraclough,

203   2013). GMYC uses the time-calibrated (ultrametric) single-locus (ND2) MCC tree to find a

204   threshold in time between inter- and intraspecific branching rates, by maximizing the model

205   likelihood. Splits in tree older than this threshold are assumed to represent speciation events and

206   younger splits reflect intraspecific neutral coalescence events. All branching events older than the

207   threshold are therefore designated as species. For comparison, we also ran the Poisson tree

208   processes (PTP) model (Appendix S1).

209   We constructed a lineage-through-time (LTT) plot using the R package 'ape' (Paradis *et al.*, 2004)

210   after pruning the MCC tree to match the number of species ($n = 18$) according to the species

211   delimitation test. We used the R package 'laser' (Rabosky and Schliep, 2013) and AIC to compare

212   diversification rate models.

Molecular population structure analyses

214   We used POPART (Leigh & Bryant, 2015) to construct a TCS haplotype network of ND2 sequences

215   of the *E. tenuirostre* complex (623 bp excluding gaps). Based on well-supported phylogenetic

216   relationships from the BEAST analyses, the geographic affinities of these relationships and the

217   structure of the haplotype network, we defined nine major putative phylogeographic populations

218   within the complex (Figs. 1). Uncorrected pairwise p-distances based on the ND2 gene were

219   calculated using MEGA 6 (Tamura *et al.*, 2013) and we used a Mantel test to test for a correlation

220   between genetic distance and geographic distance between sample locations (using IBDWS 3.23,

221   Jensen *et al.*, 2005) within the *E. tenuirostre* complex. We removed eight samples found within

222   the species' non-sedentary range (Eastern Australia, Taylor, 2005) to remove confounding effects

223   of seasonally migrating individuals. We also performed three subset analyses of the Australo-

224   Papuan, the Indonesian, and the Melanesian archipelago samples, respectively, to test for differing

225   colonization patterns in different geographical settings (archipelagos and mainland).

226 **Dispersal ability and elevational range**

227 We used the length of the longest primary (wing length, WL) and of the first secondary (secondary

228 length, SL) of the wing measured on 119 adult male and 9 female individuals representing all

229 *Edolisoma* species with at least two specimens and including 35 individuals (representing 7

230 subspecies) of the revised *E. tenuirostre* complex. To assess variation in dispersal ability across

231 *Edolisoma*, we calculated a wing shape aspect ratio (hand-wing index) $\text{HWI} = 100 * \frac{\text{WL}-\text{SL}}{\text{WL}}$,

232 which is believed to be a good proxy for dispersal capacity (Claramunt *et al.*, 2012).

233 We categorized all species into one of three elevational range classes (inhabiting mainly coastal,

234 lowland, and montane habitats, respectively, see Appendix S3) based on information in Taylor

235 (2005). We then investigated correlations of average taxon HWI, its node age (estimated from the

236 time-calibrated MCC tree) and elevational range class.

237

238 **RESULTS**

239 **Phylogenetic analyses and ancestral range estimation**

240 *Edolisoma parvulum* is clearly not a member of *Edolisoma*, but was found to be nested within

241 *Coracina* (M.P. Pedersen, in preparation) and therefore excluded from subsequent analyses. The

242 phylogeny (Figs 2 and 3) reveals extensive para- and polyphyly of nominal taxa at both inter- and

243 intraspecific levels within *Edolisoma* (see Taxonomy), however, several relationships remain

244 poorly resolved. The split between *Edolisoma* and *Lalage* is estimated to be at 9.7 Ma (age within

245 95% highest posterior density (HPD): 4.9-16.1 Ma, not shown). Within the *E. tenuirostre* complex

246 nine distinct phylogeographic groups are recognized (coloured in Figs. 1 and 3). The nominal

247 subspecies *E. t. monacha*, *E. morio salvadorii* and *E. m. talautense* together represent a

248 Micronesian clade, which is sister to the rest of the *E. tenuirostre* complex (Fig. 3). The subspecies

249 *E. t. timoriense* and *E. t. emancipatum* represent an older Lesser Sunda Islands clade together with

250 *E. dispar* and *E. dohertyi* (Fig. 1).

251 The most likely ancestral area reconstruction model estimated by 'BioGeoBEARS' was the

252 dispersal-extinction cladogenesis (DEC) model (Ree *et al.*, 2005) including founder event

253 speciation ("+J", Fig. 2 and Table S2.1 in Appendix S2). The genus originated in the late Miocene

254   and although the area of origin is unresolved, it appears to be based around Australo-Papua. The

255   RASP analysis (Fig. S2.1 in Appendix S2) generally confirmed the most likely areas in

256   'BioGeoBEARS', but with more ambiguity (shared ancestral states).

257   The Wallacean archipelago was colonized earlier than Melanesia by *Edolisoma* species continuing

258   to the Philippines in at least two separate colonization events (*E. ostentum* / *E. coerulescens* and

259   *E. mindanense*). One *Edolisoma* clade diversified 3 Ma (HPD: 1.4-5.0 Ma) in the Lesser Sundas.

260   These islands were not colonized by the more recent (< 1 Ma) *E. tenuirostre* (including *E. sula*

261   and *E. m. morio*) westward expansion across the North Moluccas to Sulawesi. Several waves of

262   colonization of North Melanesia (the Bismarck and Solomon archipelagos) probably occurred via

263   New Guinea and can be recognized as starting at less than 2 Ma with *E. holopolium*, *E. salomonis*,

264   and *E. admiralitatis*. The latter two taxa differentiated on the most peripheral islands to the east

265   (Makira in the Solomons) and to the west (Manus in the Bismarcks), respectively. Two subsequent

266   colonizations of the Solomons (*E. r. saturatius/erythropygium* and *E. r. saturatius/nisorium*)

267   resulted in sympatry with *E. holopolium*, while the Bismarcks were colonized by subspecies of *E.*

268   *remotum*. After dispersal into Wallacea and Melanesia, the Australo-Papuan mainland was back-

269   colonized most likely from the North Melanesian archipelago (Fig. 2). The New Georgian *E. r.*

270   *saturatius* and *E. r. nisorium* on the nearby Russell Island are placed consistently but with low

271   support close to *E. incertum*, which is distributed across New Guinea. Dispersal directly from the

272   Southeast Papuan Islands to New Georgia has been inferred in another widespread great speciator,

273   *Zosterops griseotinctus* (Moyle *et al*., 2009) and cannot be excluded in this case either.

274   **Molecular species delimitation and diversification rate analyses**

275   The GMYC model identified a coalescence time threshold at 0.7 Ma and 18 MOTUs (Table S3.1

276   in Appendix 3) within *Edolisoma*, where PTP and bPTP identified 20 MOTUs. In contrast to

277   GMYC, the PTP and bPTP models designated 1) *E. t. timoriense* as a species separate from *E.*

278   *dispar* and *E. t. emancipatum*, and 2) *E. t. monacha* as separate from *E. m. talautense* and *E. m.*

279   *salvadorii*.

280   In Fig. 4a, the number of lineages were log10-transformed and plotted against branching times.

281   The best fitting diversification rate model for this LTT plot was a pure birth Yule speciation rate

282   model (constant speciation rate with no extinction, see Table S2.2 in Appendix S2).

Molecular population structure analyses

The Mantel test showed a significant positive correlation between genetic and geographic distance within the North Wallacean (r = 0.3197, p < 0.005, Fig. S2.2a in Appendix S2) and North Melanesian archipelagos (r = 0.4755, p < 0.0001, Fig. S2.2b), respectively, but not within the Australo-Papuan clade (r = 0.1623, not significant, Fig. S2.2c). The correlation for the entire *E. tenuirostre* complex remains significant (r = 0.3172, p < 0.0001, Fig. S2.2d). Uncorrected pairwise p-distances ranged from 0-7.5% between subspecies within the currently recognized *E. tenuirostre* complex (0-2.9% after GMYC model revision) and from 0.1-15.5% between *Edolisoma* species (0.9-15.5% after revision).

Dispersal ability, elevational range and evolutionary age

Species in different elevational range classes differ significantly in mean node age (ANOVA, p < 0.001, Fig. 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 = 0.5291, p < 0.01, Fig. 4c).

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 (Voris, 2000; Hall, 2002; Bintanja *et al*., 2005). The constant rate of lineage accumulation (Fig. 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 *et al*., 2012). Furthermore, the ancestral range estimation and the shallow phylogeographic diversity of the *E. tenuirostre* complex (including *E. m. 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

311   Melanesian and the North Wallacean archipelagos followed stepping-stone pathways (Fig. S2.2a-
312   b in Appendix S2). A similar genetic pattern was found for another "great speciator", the
313   *Erythropitta erythrogaster* complex, which colonized the Indo-Pacific in the middle Pleistocene
314   (Irestedt *et al.*, 2013). However, the biogeographic analyses indicate at least one case of "upstream
315   colonization" by *E. tenuirostre* of the Australo-Papuan mainland, probably from the Melanesian
316   Archipelago. Recent studies have emphasized the potential of island systems in generating
317   diversity and back-dispersal to continental landmasses (Filardi & Moyle, 2005; Schweizer *et al*.,
318   2015). This might be more common than previously anticipated (Jønsson & Holt, 2015), especially
319   among highly dispersive "tramp" species such as members of *Edolisoma* (see also Jønsson *et al.*,
320   2008). All areas inhabited by the Australo-Papuan *E. tenuirostre* clade were connected by land
321   during low Pleistocene sea levels (Voris, 2000) forming a single extensive Australo-Papuan
322   mainland (Sahul). Recent mixing of individuals within the entire range may thus have inhibited
323   further differentiation (Weeks & Claramunt, 2014) within the Australo-Papuan clade as indicated
324   by the uncorrelated relationship between genetic and geographical distance (Fig. S2.2c).

325   **Complex Pleistocene diversification**

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

337   Despite examples of recent dispersal across long distances, subspecies differentiated across much
338   smaller water barriers is a more common pattern, e.g. the sister taxa *E. t. rostratum* on Rossel
339   Island and *E. t. tagulanum* on Sudest (35 km) and the populations of *E. remotum* on New Georgia
340   and Choiseul to Guadalcanal (55 km), respectively. The latter was noted by Smith and Filardi

341 (2007) and conforms to a separation described in several species across the Solomon Islands (Uy
342 *et al.*, 2009; Andersen *et al.*, 2014). This probably reflects the effect of land bridges formed during
343 times of low sea levels in the Pleistocene, when global glaciation cycles resulted in sea level
344 changes of up to 120 m (Bintanja *et al.*, 2005). At times of low sea levels, the New Georgia group
345 was connected in "Greater Gatumbangra", and Choiseul and Isabel were connected with Buka,
346 Bougainville and probably Guadalcanal in "Greater Bukida" (Fig. 1; Mayr & Diamond, 2001).
347 However, in contrast to other studies (Uy *et al.*, 2009; Andersen *et al.*, 2014), we do not recover a
348 sister relationship between the Greater Gatumbangra and Bukida populations, suggesting
349 alternative colonization pathways of the Solomon Islands (i.e. directly from New Guinea).
350 Pleistocene island aggregates have been involved in shaping patterns of intraspecific genetic
351 variation across organisms (Lohman *et al.*, 2011). Together with the lack of differentiation of *E.*
352 *tenuirostre* subspecies across the Pleistocene Australo-Papuan mainland, this also suggest a role
353 of recent sea-level changes in shaping the present-day phylogeography of *E. tenuirostre*.

354 **Rapid evolutionary shifts in dispersal ability reflect geography**

355 The present distribution of *E. tenuirostre* on the islands of Palau and Pohnpei (Fig. 1), which
356 remained remote during the evolution of *Edolisoma* (Hall, 2002), almost certainly reflects long-
357 distance dispersal (1000 km) from Wallacea and the Bismarcks, respectively, and illustrates the
358 (historically) high capacity for long-distance dispersal of *E. tenuirostre*. The taxa on these isolated
359 islands have the lowest HWI, while the archipelagic subspecies in Wallacea and Melanesia have
360 "intermediate" HWI values, and *E. t. tenuirostre* of Australo-Papua the highest HWI. This might
361 be the result of reduced selection for dispersal on remote islands, suggesting rapid evolutionary
362 shifts in dispersal ability (Diamond *et al.*, 1976; Moyle *et al.*, 2009). Such shifts in dispersal ability
363 can occur rapidly in insular avian populations; Slikas *et al.* (2002) inferred that some species of
364 Rallidae became flightless within a few hundred thousand years, possibly through adaptation to
365 limited resources on islands and intraspecific competition that reduced the basal rate of metabolism
366 (McNab, 2002).

367 The Australo-Papuan *E. t. tenuirostre* has the highest HWI, consistent with its wide range,
368 migratory behaviour of some populations, and habitat preference (open forest and edge habitat).
369 Thus, this Australo-Papuan clade could be considered a "supertramp" group (*sensu* Diamond,
370 1974), consistent with an interpretation of recent expansion and rapid colonization (from the

371 Melanesian origin). This illustrates the different stages of diversification within the range of the
372 species. That is, isolation by distance generates diversification within archipelagos, but within
373 Australo-Papua (Sahul) periods of landmass connectivity and gene flow together prevent
374 differentiation (Claramunt *et al.*, 2012).

Taxon cycles within *Edolisoma*

376 In a recent study on another Indo-Pacific passerine bird radiation (*Pachycephala*), Jønsson *et al.*
377 (2014) found that old taxa tend to inhabit higher elevations on a few large islands while young
378 taxa inhabit the more disturbed lowlands on many islands. We find a similar pattern within
379 *Edolisoma*, in which the age of a species is positively correlated with elevational range (Fig. 4b):
380 Lowest elevational range class 1 corresponds to early taxon cycle stages (I and II) of relatively
381 recent colonists inhabiting coastal areas. Elevational range class 2 consists of species of stage II or
382 III, which are absent from coastal habitats (due to either competitive exclusion or adaptation to
383 inland habitats), but retain their dispersal ability, and class 3 consists of late stage III or IV species,
384 which are confined to high elevations. This observation supports the prediction of taxa passing
385 through temporal stages of expansions and contractions (Ricklefs & Cox, 1972), but in synchrony
386 with closely related species.

Taxonomy

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

399   In contrast to other *E. tenuirostre* subspecies, the female plumages of *E. sula* and *E. incertum* are

400   highly masculinized. This feature has likely been considered when giving these taxa species status.

401   However, intraspecific variation in the degree of sexual dichromatism is known in other great

402   speciators including *Pachycephala pectoralis* (Andersen *et al.*, 2014) and *Petroica multicolor*

403   (Kearns *et al*., 2016). It might therefore be a characteristic with a common genetic basis (Cornetti

404   *et al*., 2015) that facilitates the early (parapatric) diversification of great speciators.

405   Several molecular studies of avian diversity in the Indo-Pacific have resulted in elevating

406   subspecies to species rank (Irestedt *et al.*, 2013; Kearns *et al*. 2016) or recognizing polytypic taxa

407   as multiple incipient species (Andersen *et al.*, 2015). Contrary to this trend, this study suggests the

408   inclusion of five currently recognized species into one single species complex. In an island setting

409   like the Indo-Pacific, subspecies designation has often been readily assigned based on

410   allopatrically occurring island populations in which each island population is assigned to its own

411   subspecies. This might have contributed to the apparently overestimated intraspecific diversity of

412   the *E. tenuirostre* complex, in combination with the high dispersal ability, the wide distribution,

413   and confounding effects of migratory populations.

414   **A great speciator**

415   Although this study excludes the Lesser Sundas and Micronesia from the range of the most recent

416   *E. tenuirostre* diversification, the morphological and ecological diversity of the species is

417   complemented by the inclusion of *E. incertum*, which has male-like plumage in females and

418   inhabits lower montane areas across New Guinea, *E. morio* across Sulawesi and *E. sula* bridging

419   the gap to Sulawesi (Fig. 1). This study affirms the status of *E. tenuirostre* as a great speciator

420   corresponding to an early expanding taxon cycle stage, where differentiation in isolation is

421   balanced by gene flow due to ongoing dispersal within the range of the species. However, the

422   geographical setting (mainland versus archipelagos) influences the dynamics of this diversification

423   process and shows the importance of water barriers to dispersal. This is further reflected in the

424   decreasing dispersal capacity from mainlands (high) via archipelagos (intermediate) to remote

425   island (low) taxa, respectively. The early dispersive phase of *E. tenuirostre* is illustrated relative

426   to older contraction stage *Edolisoma* species by their elevational ranges. Thus over evolutionary

427   time the oceanic island (or montane) populations of *E. tenuirostre* might differentiate in relative

428   isolation (or become locally extinct), fragmenting the current range of this "great speciator", while

429   the Australo-Papuan *E. tenuirostre* clade maintains the dispersal potential for renewed expansions.

430

431   **REFERENCES**

432   Andersen, M.J., Hosner, P.A., Filardi, C.E. & Moyle, R.G. (2015) Phylogeny of the monarch

433   flycatchers reveals extensive paraphyly and novel relationships within a major Australo-

434   Pacific radiation. *Molecular Phylogenetics and Evolution*, **83**, 118-136.

435   Andersen, M.J., Nyari, A.S., Mason, I., Joseph, L., Dumbacher, J.P., Filardi, C.E. & Moyle, R.G.

436   (2014) Molecular systematics of the world's most polytypic bird: the *Pachycephala*

437   *pectoralis/melanura* (Aves: Pachycephalidae) species complex. *Zoological Journal of the*

438   *Linnean Society*, **170**, 566-588.

439   Bintanja, R., van de Wal, R.S.W., & Oerlemans, J. (2005) Modelled atmospheric temperatures and

440   global sea levels over the past million years. *Nature*, **437**, 125–128.

441   Claramunt, S., Derryberry, E.P., Remsen, J.V. & Brumfield, R.T. (2012) High dispersal ability

442   inhibits speciation in a continental radiation of passerine birds. *Proceedings of the Royal*

443   *Society B-Biological Sciences*, **279**, 1567-1574.

444   Cornetti, L., Valente, L.M., Dunning, L.T., Quan, X.P., Black, R.A., Hebert, O. & Savolainen, V.

445   (2015) The genome of the "great speciator" provides insights into bird diversification.

446   *Genome Biology and Evolution*, **7**, 2680-2691.

447   Cottrell, G.W., Greenway, J.C., Mayr, E., Paynter, R.A., Peters, J.L., Traylor, M.A. & University.,

448   H. (1960) *Check-list of birds of the world*. Harvard University Press, Cambridge.

449   Cracraft, J. (2014) Avian higher-level relationships and classification: Passeriforms. *The Howard*

450   *and Moore Complete Checklist of the Birds of the World* (ed. by E.C. Dickinson and L.

451   Christidis). Aves Press, Eastbourne, U.K.

452   Darriba, D., Taboada, G.L., Doallo, R. & Posada, D. (2012) jModelTest 2: more models, new

453   heuristics and parallel computing. *Nature Methods*, **9**, 772-772.

454   Diamond, J.M. (1974) Colonization of exploded volcanic islands by birds - supertramp strategy.

455   *Science*, **184**, 803-806.

456   Diamond, J.M., Gilpin, M.E. & Mayr, E. (1976) Species-distance relation for birds of Solomon

457   Archipelago, and paradox of great speciators. *Proceedings of the National Academy of*

458   *Sciences of the United States of America*, **73**, 2160-2164.

459 Dickinson, E.C. & Christidis, L. (eds.) (2014) *The Howard and Moore complete checklist of the*
460   *birds of the world*, 4th edn. Aves Press, Eastbourne, U.K.

461 Drummond, A.J., Ho, S.Y.W., Phillips, M.J. & Rambaut, A. (2006) Relaxed phylogenetics and
462   dating with confidence. *Plos Biology*, **4**, 699-710.

463 Drummond, A.J., Suchard, M.A., Xie, D. & Rambaut, A. (2012) Bayesian phylogenetics with
464   BEAUti and the BEAST 1.7. *Molecular Biology and Evolution*, **29**, 1969-1973.

465 Filardi, C.E. & Moyle, R.G. (2005) Single origin of a pan-Pacific bird group and upstream
466   colonization of Australasia. *Nature*, **438**, 216-219.

467 Fritz, S.A., Jønsson, K.A., Fjeldså, J. & Rahbek, C. (2012) Diversification and biogeographic
468   patterns in four island radiations of passerine birds. *Evolution*, **66**, 179-190.

469 Fuchs, J., Cruaud, C., Couloux, A. & Pasquet, E. (2007) Complex biogeographic history of the
470   cuckoo-shrikes and allies (Passeriformes: Campephagidae) revealed by mitochondrial and
471   nuclear sequence data. *Molecular Phylogenetics and Evolution*, **44**, 138.

472 Fujisawa, T. & Barraclough, T.G. (2013) Delimiting species using single-locus data and the
473   Generalized Mixed Yule Coalescent approach: A revised method and evaluation on
474   simulated data sets. *Systematic Biology*, **62**, 707-724.

475 Garcia–Ramirez, J.C., Joseph, L., Lux, F., Adcock, G., Reid, J. and Trewick, S.A. (2017)
476   Interisland gene flow among populations of the buff-banded rail (Aves: Rallidae) and its
477   implications for insular endemism in Oceania. *Journal of Avian Biology*, **48**, 679-690.

478 Garcia-Ramirez, J. C., & Trewick, S. A. (2015) Dispersal and speciation in purple swamphens
479   (Rallidae: *Porphyrio*). *The Auk* **132**: 140–155.

480 Hall, R. (2002) Cenozoic geological and plate tectonic evolution of SE Asia and the SW Pacific:
481   computer-based reconstructions, model and animations. *Journal of Asian Earth Sciences*,
482   **20**, 353-431.

483 Irestedt, M., Fabre, P.-H., Batalha-Filho, H., Jønsson, K.A., Roselaar, C.S., Sangster, G. &
484   Ericson, P.G.P. (2013) The spatio-temporal colonization and diversification across the
485   Indo-Pacific by a "great speciator" (Aves, *Erythropitta erythrogaster*). *Proceedings of the*
486   *Royal Society of London B: Biological Sciences*, **280**, 20130309.

487 Jensen, J.L., Bohonak, A.J. & Kelley, S.T. (2005) Isolation by distance, web service. *BMC*
488   *Genetics*, **6**:13, v.3.23 http://ibdws.sdsu.edu/.

489 Jønsson, K.A., Borregaard, M.K., Carstensen, D.W., Hansen, L.A., Kennedy, J.D., Machac, A.,
490   Marki, P.Z., Fjeldså, J. & Rahbek, C. (2017) Biogeography and biotic assembly of Indo-
491   Pacific corvoid passerine birds. *Annual Review of Ecology, Evolution and Systematics.*
492   **48**:231–53.

493 Jønsson, K.A., Bowie, R.C.K., Nylander, J.A.A., Christidis, L., Norman, J.A. & Fjeldså, J. (2010)
494   Biogeographical history of cuckoo-shrikes (Aves: Passeriformes): transoceanic
495   colonization of Africa from Australo-Papua. *Journal of Biogeography*, **37**, 1767-1781.

496 Jønsson, K.A., Fabre, P.H., Ricklefs, R.E. & Fjeldså, J. (2011) Major global radiation of corvoid
497   birds originated in the proto-Papuan archipelago. *Proceedings of the National Academy of*
498   *Sciences of the United States of America*, **108**, 2328-2333.

499 Jønsson, K.A. & Holt, B.G. (2015) Islands contribute disproportionately high amounts of
500   evolutionary diversity in passerine birds. *Nature Communications*, **6**, 8538.

501 Jønsson, K.A., Irestedt, M., Christidis, L., Clegg, S.M., Holt, B.G. & Fjeldså, J. (2014) Evidence
502   of taxon cycles in an Indo-Pacific passerine bird radiation (Aves: *Pachycephala*).
503   *Proceedings of the Royal Society of London B: Biological Sciences*, **281**, 20131727.

504 Jønsson, K.A., Irestedt, M., Fuchs, J., Ericson, P., Christidis, L., Bowie, R., Norman, J., Pasquet,
505   E. & Fjeldså, J. (2008) Explosive avian radiations and multi-directional dispersal across
506   Wallacea: Evidence from the Campephagidae and other Crown Corvida (Aves). *Molecular*
507   *Phylogenetics and Evolution*, **47**, 221-236.

508 Kearns, A., Joseph, L., White, L.C., Austin, J.J., Baker, C., Driskell, A., Malloy, J., and Omland,
509   K.E. (2016) Norfolk Island Robins are a distinct endangered species: ancient DNA unlocks
510   surprising relationships and phenotypic discordance within the Australo-Pacific Robins.
511   *Conservation Genetics,* **17**, 321-335.

512 Leigh, J.W. & Bryant, D. (2015) POPART: full-feature software for haplotype network
513   construction. *Methods in Ecology and Evolution*, **6**, 1110-1116.

514 Lohman, D.J., de Bruyn, M., Page, T., von Rintelen, K., Hal, R., Ng, P.K.L., Shih, H.T., Carvalho,
515   G.R. & von Rintelen, T. (2011) Biogeography of the Indo-Australian Archipelago. *Annual*
516   *Review of Ecology, Evolution, and Systematics*, **42**, 205-226.

517 Losos, J.B. & Ricklefs, R.E. (2010) *The theory of island biogeography revisited*. Princeton
518   University Press, Princeton.

519 MacArthur, R.H. & Wilson, E.O. (1967) *The theory of island biogeography.* Princeton University

520   Press, Princeton.

521 McNab, B. K. (2002) Minimizing energy expenditure facilitates vertebrate persistence on oceanic
522   islands. *Ecology Letters*, **5**, 693–704.

523 Matzke, N.J. (2013) BioGeoBEARS: BioGeography with Bayesian (and likelihood) Evolutionary
524   Analysis in R Scripts. http://CRAN.R-project.org/package=BioGeoBEARS.

525 Matzke, N.J. (2014) Model selection in historical biogeography reveals that founder-event
526   speciation is a crucial process in island clades. *Systematic Biology*, **63**, 951-970.

527 Mayr, E. & Diamond, J.M. (2001) *The birds of northern Melanesia: speciation, ecology &*
528   *biogeography*. Oxford University Press, New York.

529 Moyle, R.G., Filardi, C.E., Smith, C.E. & Diamond, J. (2009) Explosive Pleistocene diversification
530   and hemispheric expansion of a "great speciator". *Proceedings of the National Academy of*
531   *Sciences of the United States of America*, **106**, 1863-1868.

532 Paradis, E., Claude, J. & Strimmer, K. (2004) APE: Analyses of phylogenetics and evolution in R
533   language. *Bioinformatics*, **20**, 289-290.

534 Rabosky, D. & Schliep, K. (2013) laser: Likelihood analysis of speciation/extinction rates from
535   phylogenies, R package version 2.4-1, http://CRAN.R-project.org/package=laser.

536 Rambaut, A. & Drummond, A.J. (2015) TreeAnnotator v1.8.2: MCMC Output analysis.
537   http://beast.bio.ed.ac.uk.

538 Rambaut, A., Suchard, M.A., Xie, D. & Drummond, A.J. (2014) Tracer v1.6.
539   http://beast.bio.ed.ac.uk/Tracer.

540 Ree, R.H., Moore, B.R., Webb, C.O. & Donoghue, M.J. (2005) A likelihood framework for
541   inferring the evolution of geographic range on phylogenetic trees. *Evolution*, **59**, 2299-
542   2311.

543 Ricklefs, R.E. & Bermingham, E. (2002) The concept of the taxon cycle in biogeography. *Global*
544   *Ecology and Biogeography*, **11**, 353-361.

545 Ricklefs, R.E. & Cox, G.W. (1972) Taxon cycles in West-Indian avifauna. *American Naturalist*,
546   **106**, 195-219.

547 Schweizer, M., Wright, T.F., Penalba, J., Schirtzinger, E.E., & Joseph, L. (2015) Molecular
548   phylogenetics suggests a New Guinean origin and frequent episodes of founder-event
549   speciation in the nectarivorous lories and lorikeets (Aves: Psittaciformes). *Molecular*
550   *Phylogenetics and Evolution*, **90**, 34-48.

551 Slikas, B., Olson, S.L. & Fleischer, R.C. (2002) Rapid, independent evolution of flightlessness in
552   four species of Pacific Island rails (Rallidae): an analysis based on mitochondrial sequence
553   data. *Journal of Avian Biology*, **33**, 5-14.

554 Smith, C.E. & Filardi, C.E. (2007) Patterns of molecular and morphological variation in some
555   Solomon Island land birds. *The Auk*, **124**, 479-493.

556 Tamura, K., Stecher, G., Peterson, D., Filipski, A. & Kumar, S. (2013) MEGA6: Molecular
557   evolutionary genetics analysis version 6.0. *Molecular Biology and Evolution*, **30**, 2725-
558   2729.

559 Taylor, P.B. (2005) Family Campephagidae (cuckoo-shrikes). *Handbook of the Birds of the World.*
560   *Cuckoo-shrikes to Thrushes* (ed. by J. Del Hoyo, A. Elliott and D.A. Christie), pp. 40-123.
561   Lynx Edicions, Barcelona.

562 Uy, J.A.C., Moyle, R.G. & Filardi, C.E. (2009) Plumage and song differences mediate species
563   recognition between incipient flycatcher species of the Solomon Islands. *Evolution*, **63**,
564   153-164.

565 Voris, H.K. (2000) Maps of Pleistocene sea levels in Southeast Asia: shorelines, river systems and
566   time durations. *Journal of Biogeography*, **27**, 1153-1167.

567 Wallace, A.R. (1869) *The Malay Archipelago*. Macmillan, London, U.K.

568 Weeks, B.C. & Claramunt, S. (2014) Dispersal has inhibited avian diversification in Australasian
569   archipelagoes. *Proceedings of the Royal Society B-Biological Sciences*, **281**, 20141257.

570 Wilson, E.O. (1961) The nature of the taxon cycle in the Melanesian ant fauna. *American*
571   *Naturalist*, **95**, 169-193.

572 Yu, Y., Harris, A.J., Blair, C. & He, X.J. (2015) RASP (Reconstruct Ancestral State in
573   Phylogenies): A tool for historical biogeography. *Molecular Phylogenetics and Evolution*,
574   **87**, 46-49.

575 **SUPPORTING INFORMATION**

576 Additional Supporting Information may be found in the online version of this article:

577

578 **Appendix S1** Notes on materials and methods.

579 **Appendix S2** Notes on results.

580 **Appendix S3** Notes on taxonomy.

581

582 **DATA ACCESSIBILITY**

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

584

585 **Biosketch:** Michael Pepke Pedersen is a PhD student at NTNU (Trondheim) and has a broad

586 interest in avian biogeography, phylogenetics and life-history evolution. This paper is part of his

587 master thesis at UCPH (Copenhagen) on the phylogeny and biogeography of the Campephagidae

588 family as a model group for understanding the build-up and distribution of insular avian diversity.

589

590 **Editor:** Sonya Clegg

591

592 **Author contributions:** MPP and KAJ conceived the ideas; MPP, MI and CR collected the data;

593 MPP analysed the data. MPP led the writing with contributions from all authors.
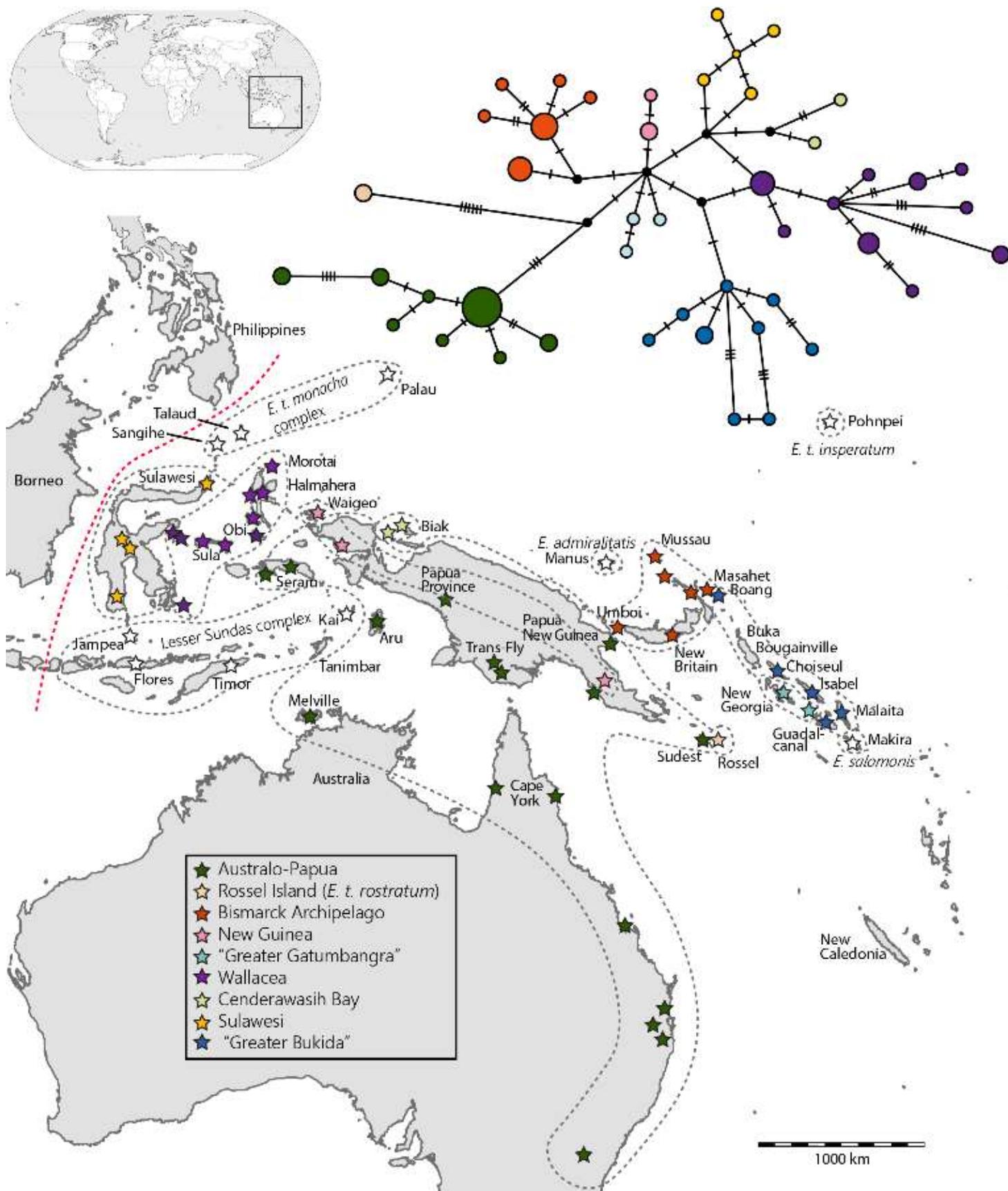
594   **FIGURE LEGENDS**

595   **Fig. 1:** *Edolisoma tenuirostre/remotum* sample locations (coloured stars, there can be multiple

596   samples per star) and closely related allopatrically occuring *Edolisoma* species (white stars).

597   Dotted grey lines delimit the phylogeographic clades indentified within the *E. tenuirostre* complex

598   and allopatrically occuring related species. The dotted red line indicates Wallace's Line. In the

599   haplotype network (based only on ND2 sequences) one bar indicates one mutation, black nodes

600   are hypothetical ancestral states and the size of the circles corresponds to the number of sampled

601   haplotypes.

602   **Fig. 2:** Time-calibrated maximum clade credibility tree of the concatenated dataset of the

603   *Edolisoma* genus with asterisks indicating well-supported nodes with posterior probabilities ≥

604   0.99. Several recent splits have been pruned for clarity. Letters and colours refer to the areas of

605   Australo-Papua (A), Wallacea (W), Melanesia (M), the Philippines (P) and combinations of these.

606   The results of the ancestral range estimation in 'BioGeoBEARS' are shown as pie charts coloured

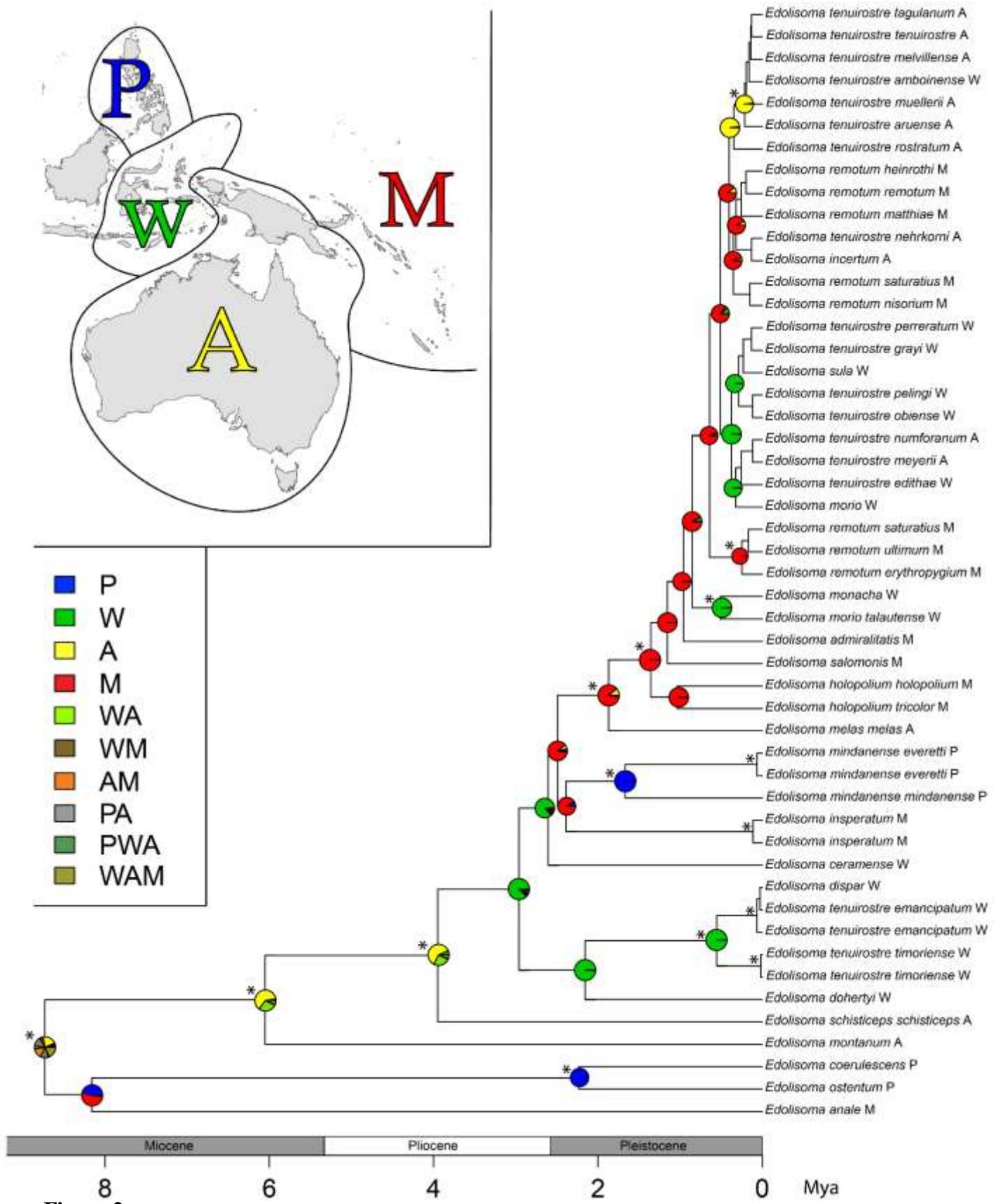607   in relative proportions of the most likely ancestral area.

608   **Fig. 3:** Unpruned section of the maximum clade credibility tree in Fig. 2 showing the *Edolisoma*

609   *tenuirostre* (*E. t.*) / *E. remotum* (*E. r.*) complex with populations coloured according to Fig. 1.

610   Asterisks indicate posterior probabilities ≥ 0.99 and ¤ ≥ 0.97. Figures show males (left) and

611   females (right), illustrating the extreme female plumage variation. Specimen E69 lacks location

612   and is most likely not an *E. t. meyerii* (see Table S1.2 in Appendix S1 for full specimen

613   information). Figures reproduced with permission from del Hoyo, J., Elliott, A., Sargatal, J.,

614   Christie, D.A. & de Juana, E. (eds.) (2017). *Handbook of the Birds of the World Alive*. Lynx

615   Edicions, Barcelona (retrieved from http://www.hbw.com/ on 10 March 2017).

616   **Fig. 4:** a) Lineage-through time plot of log-transformed number of lineages against time in Ma.

617   The solid line represents the maximum clade credibility tree and the grey area shows the

618   phylogenetic uncertainty of 100 randomly sampled trees from the posterior distribution. b) Boxplot

619   showing node ages (in Myr) of species in elevational range class 1 (coastal areas, number of

620   species $n = 13$), class 2 (lowlands, $n = 3$) and class 3 (montane areas, $n = 2$). c) Correlation between

621   HWI and node age (Myr) for subspecies within the revised *Edolisoma tenuirostre* complex and

622   closest relatives (blue, p < 0.01, all < 1.5 Myr old and in Fig. 3) and for species within the genus

623   *Edolisoma* (red, not significant). The Australo-Papuan (mainland) *E. t. tenuirostre* has the largest
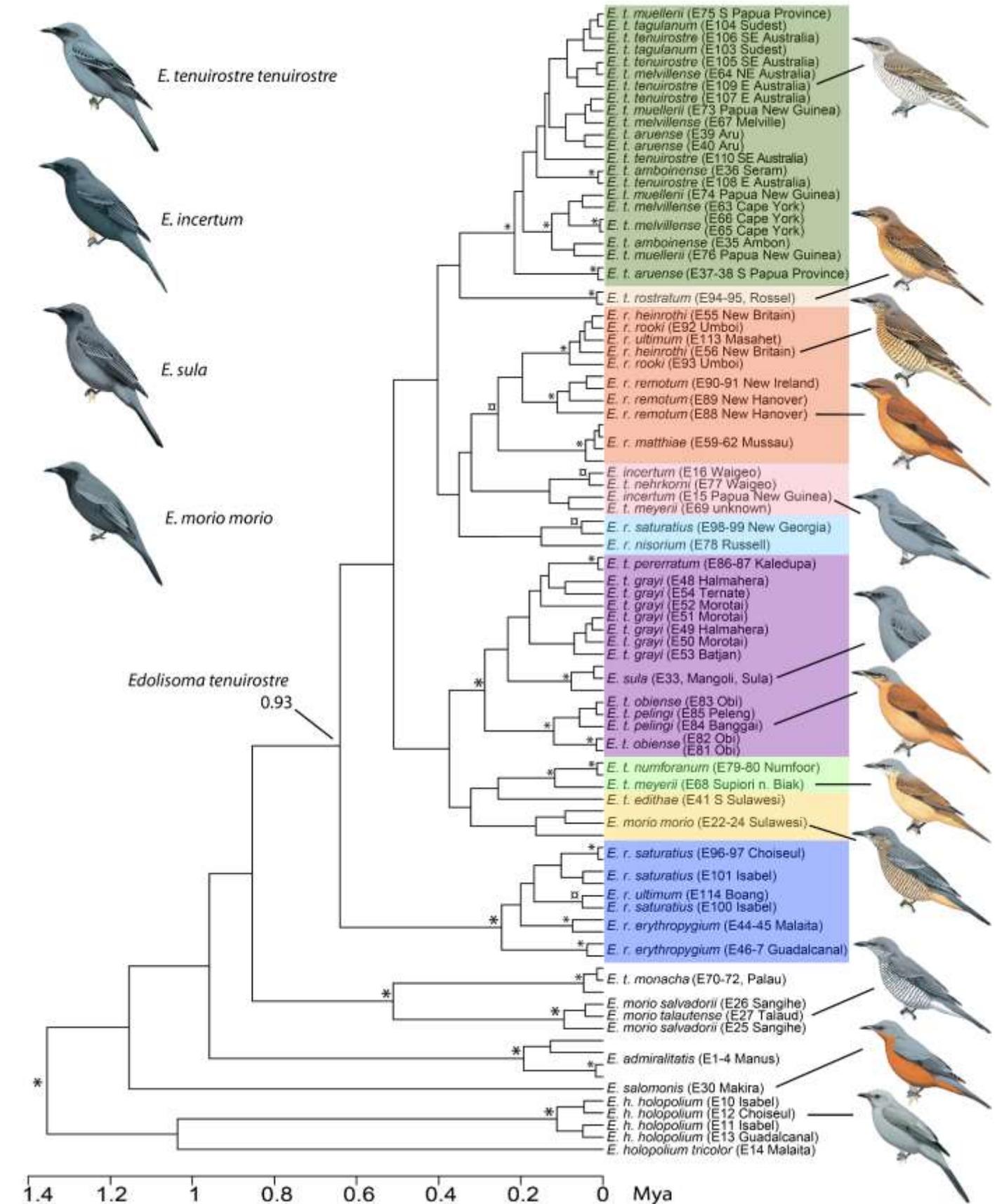
624   HWI, the archipelagic subspecies (black shape, see Appendix S1) have intermediate HWIs and the

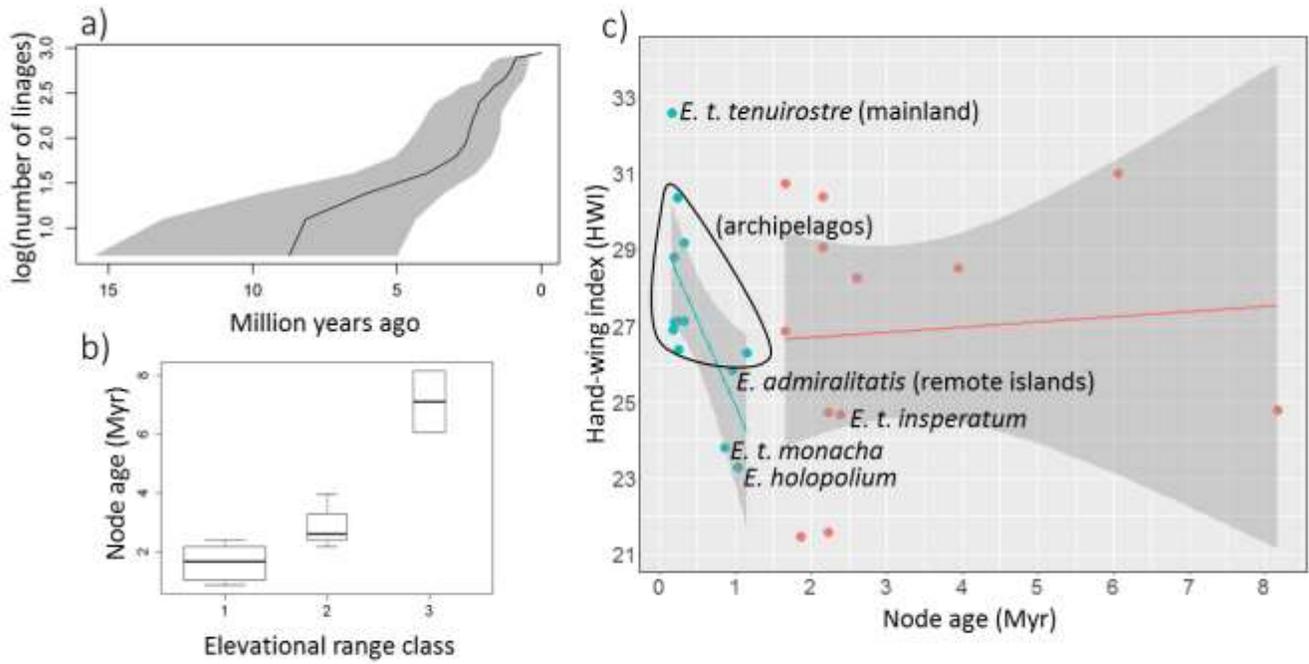625   remote island forms (except *E. holopolium*) have the lowest HWIs.

Legend:
- ★ Australo-Papua
- ☆ Rossel Island (*E. t. rostratum*)
- ★ Bismarck Archipelago
- ★ New Guinea
- ☆ "Greater Gatumbangra"
- ★ Wallacea
- ☆ Cenderawasih Bay
- ★ Sulawesi
- ★ "Greater Bukida"

626   **Figure 1**

Figure 2

E. tenuirostre tenuirostre

E. incertum

E. sula

E. morio morio

Edolisoma tenuirostre
0.93

| 1.4 | 1.2 | 1 | 0.8 | 0.6 | 0.4 | 0.2 | 0 | Mya |

628   **Figure 3**

629   **Figure 4**