Palmerston North, New Zealand, 25 November 2020
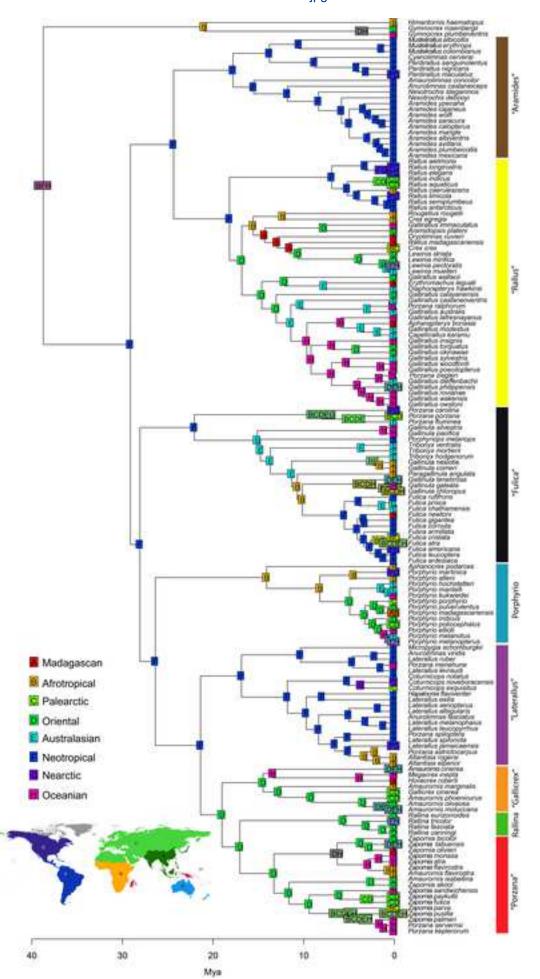
Re: Manuscript submission for consideration at *Molecular Phylogenetics and Evolution*

Dear Dr., Elizabeth A. Zimmer
Editor-in-Chief
Molecular Phylogenetics and Evolution

We are submitting the manuscript entitled "Trait-dependent dispersal in rails (Aves: Rallidae): Historical biogeography of a cosmopolitan bird clade" to be considered for publication in *Molecular Phylogenetics and Evolution*. We have used broad taxonomic sampling and substantial molecular and morphological data to provide the historical biogeography of the cosmopolitan bird family Rallidae. We also examined an evolving biological trait that influence rates of dispersal and diversification in this clade. The study neatly fit into the space left between phylogenetics, biogeographical processes and evolution. This manuscript presents the first total-evidence approach of this group of birds with biogeographic analyses and discussion performed in sufficient detail. This is a valid, interesting and worthy study that will have a high impact and will contribute significantly to the literature of the current evolutionary work. We think that *Molecular Phylogenetics and Evolution* would be the best way to reach scientists interested in evolutionary ecology. We would like to suggest Dr. Shannon Hackett as a potential Academic Editor to handle our submission.

Sincerely,

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1   **Title:** Trait-dependent dispersal in rails (Aves: Rallidae): Historical biogeography of a

2   cosmopolitan bird clade

3

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15

16   **Abstract**

17   The ability of lineages to disperse over evolutionary timescales may be influenced by the gain or

18   loss of traits after adaptation to new ecological conditions. For example, rails (Aves: Rallidae)

19   have many cases of flightless insular endemic species that presumably evolved after flying

20   ancestors dispersed over large ocean barriers and became isolated. Nonetheless, the details of

21   how flying and its loss have influenced the clade's historical biogeography are unknown, as is

22   the importance of other predictors of dispersal such as the geographic distance between regions.

23   Here, we used a dated phylogeny of 158 species of rails to compare trait-dependent and trait-

24   independent biogeography models in BioGeoBEARS. We evaluated a probabilistic historical

25   biogeographical model that allows geographic range and flight to co-evolve and influence

26   dispersal ability on a phylogeny. The best-fitting dispersal model was a trait-dependent dispersal

27   model (DEC+j +x+t_{21}+m_1) that accrued 85.2% of the corrected Akaike Information Criterion

28   (AICc) model weight. The distance-dependence parameter, x was estimated at -0.54, ranging

29   from -0.49 to -0.65 across models, suggesting that a doubling of dispersal distance results in an

30   approximately 31% decrease in dispersal rate ($2^{-0.54}$ = 0.69). The estimated rate of loss of flight

31   (t_{21}) was similar across all models (~0.029 loss events per lineage per million years). The

32   multiplier on dispersal rate when a lineage is non-flying, m_1, is estimated to be 0.38 under this

33   model. Surprisingly, the estimate of m_1 was not 0.0, probably because the loss of flight is so

34   common in the rails that entire clades of flightless species are found in the data, forcing the

35   model to attribute some dispersal to flightless lineages. These results indicate that long-distance

36   dispersal over macroevolutionary timespans can be modelled, rather than simply attributed to

37   chance, allowing support for different hypotheses to be quantified and model limitations to be

38   identified. Overall, by combining new analytical methods with a comprehensive phylogenomic

39   dataset, we use a quantitative framework to show how traits influence dispersal capacity and

40   eventually shape geographical distributions at a macroevolutionary scale.

Introduction

Inferring the evolution of geographic ranges of species and clades in a phylogenetic context is a major focus of historical biogeography (Ronquist and Sanmartín, 2011; Sanmartín, 2012). Biological traits must be important in shaping the dispersal abilities of organisms, and therefore evolutionary changes in traits could strongly influence the distribution and diversification patterns of clades (Sukumaran and Knowles, 2018). An evolving trait that is particularly likely to influence rates of macroevolutionary dispersal is flightlessness. The rails (Aves: Gruiformes: Rallidae), for instance, have colonised very isolated islands and readily evolve distinct forms of endemic flightless species (Garcia-R et al., 2016; Garcia-R et al., 2019; Garcia-R et al., 2017; Garcia-R and Trewick, 2015; Kirchman, 2009; Trewick, 1997a; Wright et al., 2016). Although the general relation of dispersal followed by isolation and loss of flight is obvious in rails, it is important to keep in mind that the detailed history of both flightlessness and biogeography is not known with certainty, but instead inferred on phylogenies using evolutionary models.

In a trait-dependent dispersal model, simultaneously inferring the trait history and dispersal history enables them to influence each other and could compensate for weaknesses in either dataset assessed individually, for example, due to convergent loss of flight in rails. Besides, a quantitative model-based framework allows the inference of parameters that describe the rates of trait change, dispersal, the influence of traits on dispersal, as well as other factors in dispersal probability, such as the geographic distance between regions. None of these parameters has been measured in rails. A study group such as rails, where the link between trait and dispersal ability seems clear, provides an opportunity to further test the inferences made by trait-dependent dispersal models, which have only been deployed in a few recent publications (Blom et al., 2019;

Klaus and Matzke, 2020; Matos-Maraví et al., 2018; Nicolaï and Matzke, 2019). Here, we answer these questions with a dated phylogeny of 158 species of rails and new models implemented in BioGeoBEARS.

Standard probabilistic historical biogeographical models exclude biology, treating all species as interchangeable units, with no differences in the way they interact with any biogeographical process (Sukumaran and Knowles, 2018). The R package BioGeoBEARS (Matzke, 2013) allows an evolving discrete trait to influence dispersal ability for both anagenetic and cladogenetic range change (Klaus and Matzke, 2020). Biogeographical models describe possible ways that geographic range might change during anagenesis and cladogenesis (Matzke, 2013). Different models "turn on" different processes, and statistical model comparison (Burnham and Anderson, 2002, 2008) can be used to assess which model best fit a particular dataset. A similar approach can be used to measure the influence of physical variables, such as distance, on dispersal rate (Van Dam and Matzke, 2016). When the evolutionary history of an evolving trait, such as flightlessness, has to be jointly estimated along with the biogeography history of a clade, these biogeographical models can be expanded further with trait-based dispersal models. These models modify dispersal probability with a free parameter, m, that describes a multiplier on dispersal when a lineage is inhabiting the less-dispersive character state (Klaus and Matzke, 2020). When $m=1$, the model reduces to the "trait-independent" null model, where the log-likelihood of the trait and the geographic data can be calculated independently and summed. Inference under trait-dependent models is computationally slower because they require doubling the size of state space (Sukumaran and Knowles, 2018). This is because the model must track the probability of a lineage occupying each of the possible geographic ranges while in trait state 1, as well as the

87   probability of a lineage occupying each of the possible geographic ranges while in trait state 2.

88   However, for moderate-sized problems (<2000 states total), they are feasible (although slow) on

89   desktop computers.

90

91   To conduct trait-dependent biogeographic inference on rails, we begin with a comprehensive

92   phylogenetic hypothesis that includes the vast majority of the taxa in the clade. Knowledge of the

93   phylogenetic relationships of rails has increased dramatically in the last decade (e.g., Garcia-R

94   and Trewick, 2015; Kirchman, 2009; Kirchman, 2012; Slikas et al., 2002) but the phylogenetic

95   relationships of several species remain poorly known. Although taxonomic coverage using

96   morphology (Livezey, 1998) and DNA-based analyses (Garcia-R et al., 2014a) have been shed

97   light on the evolution and phylogenetics of rails, a total-evidence analysis including both

98   molecular and morphological data has not previously been available for this group. We analyse

99   relationships among rails using all available evidence to allow a comprehensive taxon sampling

100   and a robust phylogenetic hypothesis that provides an exceptional context for studying the

101   evolutionary history of this group of birds.

102

103   **Materials and methods**

104   *Phylogenetic reconstruction and total-evidence dating*

105   Because of the lack of global analyses that include most described extant and extinct taxa,

106   knowledge of the relationships of the total clade of the rails has been limited. We performed the

107   first total-evidence analysis combining morphological data and molecular sequences of 158

108   species of rails (see Supplementary Material). We used morphological characters that were

109   obtained from Livezey (1998) and molecular data collected from previous studies (Garcia-R et

110   al., 2014a; Garcia-R et al., 2020). Morphological data was partitioned in groups of characters

111   with respect to the number of observed states (ranged from two- to six-state characters) evolving

112   under the Lewis M*k*v model (Lewis and Olmstead, 2001). We assumed gamma-distributed rate

113   variation across characters with three or fewer states (Gavryushkina et al., 2017). For molecular

114   data, each locus was assigned to its model of nucleotide substitution, as determined by the

115   Bayesian Information Criterion (BIC) in PartitionFinder 2.1.1 (Lanfear et al., 2016). For nuclear

116   data, both GTR + Γ and HKY + Γ models were estimated, whilst mitochondrial data only used

117   the GTR + Γ model.

118

119   To obtain divergence times from the total-evidence analysis, we used a previously estimated

120   crown age of ralloids (Garcia-R et al., 2014b). The approximate age of the origin of rails has

121   been estimated using different Bayesian and non-Bayesian approaches and fossil calibrations

122   with results varying between 40 and 19 Mya (Garcia-R et al., 2014b; Garcia-R et al., 2020). The

123   differences in age estimations for the origin of this group is due to the scarcity of reliable crown

124   old fossils. A root calibration of 40 Mya with Normal distribution of 33–49 Mya (95% range)

125   was implemented in BEAST 2.4.7 (Bouckaert et al., 2014). We used the wider estimate date for

126   the origin of the clade because comparisons of estimates under a total-evidence approach have

127   obtained younger ages than traditional node dating (Ronquist et al., 2012). The fossils (< 2.5

128   Mya) were treated as terminals, with the ages obtained from published literature (Olson, 1985;

129   Olson, 1977; Ripley, 1977) and online databases (http://fossilworks.org/). The analysis was run

130   for 200 million generations using a Birth-Death process and uncorrelated lognormal relaxed

131   clock. We combined the results of two independent runs with a burn-in of 50% each to obtain

132   effective sample sizes (ESS) above 150 for all parameters. The stationarity of the runs was

133   assessed using Tracer v.1.7 (Rambaut et al., 2018). The tree was viewed using FigTree 1.4.2

134   (http://tree.bio.ed.ac.uk/software/figtree/).

135

136   *Modelling trait-dependent dispersal*

137   The rails have a near-global distribution only being absent in polar regions, waterless deserts,

138   and mountains above the snow line. For biogeographical inference analyses, we defined eight

139   major geographic regions: Nearctic, Neotropical, Palearctic, Afrotropical, Madagascan, Oriental,

140   Oceanian and Australasian. We used a distance matrix measuring the minimum overwater

141   distance between areas. Ancestral range reconstruction was performed using the DEC,

142   DIVALIKE and BAYAREALIKE models (Matzke, 2013). We assessed each model's fitness

143   using sample-size corrected Akaike information criterion (AICc) (Burnham and Anderson,

144   2002). The DEC model takes into account range expansion (dispersal) and extinction (range

145   contraction) with a constant cladogenesis model (Ree and Smith, 2008) where daughter lineages

146   have an equal probability of inheriting various ancestral ranges through allowed speciation

147   events (i.e., subset sympatry and vicariance). The DIVALIKE model (a likelihood version of

148   Ronquist (1997)'s DIVA) disallows subset sympatry but allows more forms of vicariance. The

149   BAYAREALIKE model (a likelihood version of Landis et al. (2013)'s BayArea) allows only

150   "range copying" (both daughters inherit the ancestral range, whatever its size). We created

151   another three modified models by adding jump dispersal at speciation (+j), allowing a daughter

152   species to 'jump' to a new range outside of its ancestor, a process of particular interest in islands

153   and other systems where rare dispersal events followed by isolation and speciation may be

154   common (Matzke, 2014). We are aware of the critique of DEC/DEC+j statistical comparisons

155   put forward by Ree and Sanmartín (2018), but reject its claims based on standard, widely-

156   accepted principles of evaluating models and statistical model comparison (Klaus and Matzke,

157   2020).

158

159   Each of the six base models was further modified to allow an evolving discrete trait to affect

160   dispersal ability, which in turn, allows dispersal history to affect the inference of trait evolution

161   (Klaus and Matzke, 2020). We tested whether or not these trait-dependent model variants

162   outperformed models where dispersal is independent of the trait. Models are compared by their

163   fit to the data, where "the data" consist of both the geographic range and the trait states for each

164   species. Relative fit is measured with AICc weights (Burnham and Anderson, 2002). The trait-

165   dependent dispersal model adds three free parameters to a standard BioGeoBEARS model. First,

166   the parameters t_{12} and t_{21} describe the rate of transition of the morphological character between

167   non-flying (N, state 1) and flying (F, state 2), and the reverse (from F to N). For comparison, 1-

168   and 2-rate models (the Mk model of Lewis (2001)) were run on the trait data, and the log-

169   likelihoods were added to the standard biogeography models. This provides the joint log-

170   likelihood of the trait and geography data in a trait-independent biogeography model. The third

171   parameter, m_1, is a multiplier on the base dispersal probability when a lineage is in state 1.

172   Parameter m_2 is also present in the model, representing a rate multiplier when the lineage is in

173   state 2; this was fixed to $m_2 = 1$ in all analyses, as m_1 and m_2 are not simultaneously identifiable.

174   We also fixed $t_{12} = 0.0$, representing the assumption that flight can never be regained after being

175   lost. We found that fixing this parameter was useful to avoid interactions in the parameter

176   inference and speed convergence. We compared the trait-independent models to trait-based

177   dispersal models (DEC+t_{21}+m_1, DEC+j+t_{21}+m_1, DIVALIKE+t_{21}+m_1, DIVALIKE+j+t_{21}+m_1,

178   BAYAREALIKE+t_{21}+m_1, BAYAREALIKE+j+t_{21}+m_1). In addition, we extended both trait-

9

179 dependent and trait-independent models by the inclusion of geographical distance (+x variants),

180 where the base dispersal rates are multiplied by distance x; when $x = 0$, distance does not affect

181 dispersal probability (Van Dam and Matzke, 2016).

182

183 **Results**

184 *Phylogeny and total-evidence dating*

185 The data matrix consisted of 158 extant and recently extinct (< 2.5 Mya) species of rails (129

186 extant and 29 extinct taxa). This is the most comprehensive taxon set of Rallidae so far

187 generated. The original morphological (osteological and integument) matrix contained 570

188 characters, but only 271 were used for the analysis. We discarded 299 characters because they

189 did not provide any information (i.e., presented only one state in all species). Molecular data

190 from 10 nuclear and three mitochondrial gene fragments were used, which resulted in a total of

191 20,828 nucleotides. Figure 1 shows the dated phylogeny obtained in the total-evidence analysis

192 with BEAST2. The total-evidence analysis yields a topology similar to previous molecular

193 phylogenies (Garcia-R et al., 2014a; Garcia-R et al., 2020) and, regardless of exactly when rails

194 originated, it indicates that all major clades occurred during the Miocene, as previously shown by

195 molecular divergence estimations obtained from different approaches (Garcia-R et al., 2020).

196 This analysis recovered the monophyletic clades "*Aramides*", "*Rallus*", "*Fulica*", "*Laterallus*",

197 "*Porzana*", "*Gallicrex*", *Porphyrio* and *Rallina* and several relationships previously identified

198 (Garcia-R et al., 2014a; Garcia-R et al., 2020). The only major difference, apart from the

199 inclusion of numerous extinct and extant species added for the first time in a robust phylogenetic

200 framework, is that species within *Gymnocrex* are shown as sister taxa of *Himantornis*

201 *haemotopus*. This result hinges on morphological data from *Gymnocrex* species, and this clade

202 forms a basal split, making it the sister of all remaining clades.

203

204 *Biogeography analyses*

205 A trait-dependent dispersal model outperformed all other models (Table 1). The best-fitting

206 model was DEC+j +x+t_{21}+m_1, with an AICc model weight of 85.2%. Specifically, m_1,

207 representing the multiplier on dispersal rate when a lineage is non-flying, is estimated to be 0.38

208 under this model. A similar model, DIVALIKE+j+x +t_{21}+m_1, gathered 2.1% of the model weight

209 and estimated m_1 as 0.22. These results suggest, as expected, a substantial decrease in dispersal

210 capability for flightless rails, although puzzlingly, the dispersal multiplier for flightlessness is not

211 inferred to be 0.0. The trait-dependent dispersal models together had an AICc model weight of

212 87.3%. Interestingly, a non-trait-dependent model, DEC+j+x +t_{21}, (where m_1 is fixed to 1.0) had

213 an AICc weight of 12.7%, indicating that while it is not the best-performing model, it cannot be

214 statistically excluded from the set of plausible models (Burnham et al., 2011). Averaging the

215 parameter estimates across all models (weighting the average by the AICc model weights)

216 returns an all-models estimate for $m_1 = 0.45$ (Burnham and Anderson, 2002).

217

218 Other parameter estimates, however, followed expectations. The x parameter in the best model

219 was estimated at -0.54, ranging from -0.49 to -0.65 across models (Table 1), suggesting that a

220 doubling of dispersal distance results in an approximately 31% decrease in dispersal rate ($2^{-0.54}$ =

221 0.69). The weighted average of x estimates across all models was also -0.54, and the +x model

222 variants together garnered 100% of the model weight. The j parameter was also supported with

223 100% model weight, as is common in systems with isolated areas (e.g. islands) where most

224   species are single-area endemics (Matzke, 2014). The estimated rate of loss of flight (t_{21}) was

225   similar across all models (~0.029 loss events per lineage per million years).

226

227   We estimated ancestral ranges on the phylogeny using the best-fit model. This suggests that the

228   Afrotropical, Neotropical and Oceanian regions are better supported as the centre of origin of

229   rails (Figure 1). Nonetheless, there is high uncertainty in ancestral ranges (Figure S1). The

230   Neotropical region is confidently inferred as the ancestral area for "*Laterallus*" and "*Aramides*"

231   clades with a subsequent expansion to the Nearctic. The most probable ancestral areas for

232   *Porphyrio* and *Rallina* are the Afrotropical and Oriental regions, respectively. Additionally, the

233   Oriental region is showed as the most probable state for "*Porzana*" and "*Gallicrex*", while other

234   clades ("*Fulica*", "*Rallus*", and *Himantornis + Gymnocrex*) presented unresolved ancestral range

235   reconstructions.

236

237   *Evolution of flightlessness in Rallidae*

238   Flightlessness is found in 47 of the 158 species in our study and within all clades except for the

239   most basal split *Himantornis + Gymnocrex* and *Rallina* clades (Figure 2). The "*Rallus*" clade

240   contained the vast majority of flightless species associated with founder events of remote isolate

241   islands in the Oceanian and Australasian regions. Flightless species in other clades are also found

242   in the Madagascan region and islands on the Oriental region, with flying as the most probable

243   inferred ancestral state (Figure S2). We estimate that flight was lost approximately 22 times

244   independently in the evolutionary history of this group.

245

246   **Discussion**

247   In our total-evidence analysis, the phylogenetic position of several fossils, recently extinct and

248   extant taxa without molecular data were determined based on morphological evidence. Adding

249   both types of data inform us of taxa relationships previously unrecognised. Previous

250   controversial propositions and taxonomic conflicts (Livezey, 1998; Olson, 1973) caused by

251   morphological convergence can now be reconciled for different taxa. Although missing

252   molecular data for fossil and extinct taxa can be seen as a concern, we expected that our

253   extensive and informative morphological character states detriment the effects caused by this and

254   have little impact in the topology recovered. Our total-evidence analysis retrieves clade node age

255   estimates that were very similar to those obtained with young node dating calibrations.

256   Unfortunately, older rail-like fossils are poorly preserved and can not be used in node dating

257   analysis or fossilized birth-death (FBD) models due to the large uncertainty in their topological

258   placement.

259

260   Our analyses suggest that a model where dispersal is dependent on the flying condition and

261   geographical distance is better fit to the data than models where dispersal is independent of traits

262   and/or distances. In the best-fitting model (DEC+j +x+t_{21}+m_1), an estimated m_1 of 0.38 suggests

263   that macroevolutionary dispersal rates are 62% lower for lineages with flightless species. Even

264   when m_1 is estimated from a weighted average of all 24 models, the model-averaged estimate of

265    $m_1 = 0.59$ suggests a dispersal rate that is 41% lower for flightless species. An estimated x of -

266   0.54 under the best model suggests a substantial negative correlation between dispersal and

267   increasing distance (an x of -1 indicates a linear relationship between inverse distance and

268   dispersal probability, that is, doubling the distance halves the dispersal probability). An

269   explanation for this result is that there are vagrant lineages in rails reaching new regions and

270 isolated islands via long-distance dispersal (Garcia-R et al., 2016; Garcia-R et al., 2019; Garcia-

271 R et al., 2017; Garcia-R and Trewick, 2015). Long-distance dispersal and colonisations resulting

272 in extended geographic ranges to new areas or isolated islands have been a recognised trait in

273 some rail lineages (Garcia-R et al., 2016; Garcia-R et al., 2017; Garcia-R and Trewick, 2015).

274 Independent evolution of flightlessness is a by-product of adaptation to these colonisations and

275 new environmental conditions where flying was not integral to foraging, social interaction, or

276 predator avoidance.

277

278 Estimation of ancestral ranges under the best-fit model indicates an uncertain origin of the

279 Rallidae. Nonetheless, the most probable ancestral areas are the Afrotropical and Neotropical

280 regions. Two clades have originated in the Neotropical region ("*Laterallus*" and "*Aramides*")

281 and several members of other clades are present in the Afrotropical. The oldest fossils with rail-

282 like traits are found in the Palaearctic and Nearctic regions, including *Belgirallus,* which is

283 considered a stem Ralloidae member (De Pietri and Mayr, 2014; Mayr, 2006; Rasmussen et al.,

284 1987; Wetmore, 1931). Rail fossils from the Miocene, some showing flightless characteristics,

285 are found in the Palearctic and Australasian regions (Mather et al., 2018; Worthy and Boles,

286 2011; Zelenkov et al., 2017). The relationships of these fossils are uncertain (Mayr, 2017), but

287 they show affinities with members of the "*Rallus*" and *Porphyrio* clades. Including these fossils

288 confidently in a phylogeny would benefit the dating and biogeographical analyses. Unequivocal

289 fossils assigned to crown-group lineages have only been found in the Pliocene and Pleistocene

290 on different regions, including Oceanian and Madagascan (Kirchman and Steadman, 2005;

291 Steadman, 2006; Steadman et al., 1999).

292

293   According to our analyses, the earliest transition from flying to non-flying within the Rallideae

294   occurred in the Late Miocene (∼12 Ma), which contrasts with the age of the flightless

295   *Priscaweka* and *Litorallus* from New Zealand (Mather et al., 2018) in the Early Miocene (19─16

296   Ma). This early transition occurred within the clade containing the majority of flightless species.

297   If *Priscaweka* and *Litorallus* are indeed found closely related to members of the "*Rallus*" clade,

298   they would be considered part of the stem group.

299

300   The all-model estimate for m_1 of 0.45 is substantial but greater than might be expected for the

301   flightlessness trait. For example, in trap-jaw ants, closed forest species had an estimated $m = 0.0$,

302   and all dispersal occurred in edge species (Matos-Maraví et al., 2018), and *Cryptoblepharus*

303   skinks with littoral and beach-dwelling species presenting dispersal rates ~14 times higher than

304   non-littoral species (Blom et al., 2019). We suspect that the reason we do not estimate $m_1 = 0.0$ in

305   Rallidae is the high frequency of convergent loss of flight. This process can easily produce an

306   entire clade of flightless species occupying multiple areas. Faced with such data, maximum

307   likelihood inference is forced to attribute some positive dispersal probability to lineages that are

308   flightless. This issue might be overcome via a few approaches. For example, a Bayesian analysis

309   where strong prior pushes m_1 towards 0.0 would force the model to increase the rate of transition

310   to flightlessness to compensate. However, this is arguably "telling the model what the answer

311   is," and also a Bayesian analysis would require 100,000+ calculations of the likelihood,

312   computationally impractical due to the size of the state space of trait-dependent biogeography

313   models. Another approach that could be explored is state-dependent speciation/extinction (SSE)

314   models, as these allow for lineage extinction and missing speciation events that are excluded

315   from DEC-type biogeography models (Klaus and Matzke, 2020). SSE models could allow

316 flighted ancestors to produce flightless descendants and then go extinct. However, SSE models

317 are also dramatically slower than DEC-type models for large state spaces. Technical advances

318 may introduce more feasible strategies in the future, but regardless, researchers should always be

319 aware that models are just an attempt to describe major features of a very complex evolutionary

320 progress, and will always have limitations (Burnham and Anderson, 2002).

321

322 Despite the limitations, our statistical model comparisons do provide support for trait-dependent

323 dispersal in the Rallidae, as well as estimates of key parameters. The loss of flight has

324 independently evolved in different rail lineages with an estimated rate of ~0.029 events per

325 lineage per million years. Rails seem particularly prone to adapt to the ground-dwelling lifestyle

326 leading to rapid morphological changes (Garcia-R et al., 2016; Trewick, 1997a, 1997b) and

327 isolation leading to low gene flow and speciation. This process undoubtedly contributes to

328 diversity in rail clades, although the details of this process – for example, does adaptation to

329 ground-dwelling lead or follow genetic isolation – require further research.

330

342

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473 Figure captions

474 Figure 1. Time-calibrated phylogeny and ancestral range estimation based on total-evidence data

475 of the family Rallidae. Areas were coded as follows: A = Madagascan (red), B = Afrotropical

476 (orange), C = Palearctic (light green), D = Oriental (dark green), E = Australasian (light blue),

477 F= Neotropical (dark blue), G = Nearctic (purple), H = Oceanian (magenta). Coloured bars at the

478 right of the figure indicate the clades.

479

480 Figure 2. Evolution of flightlessness in rails. Ancestral state under the best fitting model

481 (DEC+j+t_{21}+m_1) is shown at each node. Traits are code as follows: Flying (blue) and non-flying

482 (green).

483

484 Figure S1. The most probable state of inferred ancestral ranges using BioGeoBEARS and the

485 DEC+j+t_{21}+m_1 model. Pie charts represent the probabilities of each possible ancestral range.

486 Areas were coded as follows: A = Madagascan (red), B = Afrotropical (orange), C = Palearctic

487 (light green), D = Oriental (dark green), E = Australasian (light blue), F= Neotropical (dark

488 blue), G = Nearctic (purple), H = Oceanian (magenta).

489

490 Figure S2. The most probable ancestral state of flying condition in rails under the best fitting

491 model (DEC+j+t_{21}+m_1). Pie charts represent the probabilities of each possible ancestral

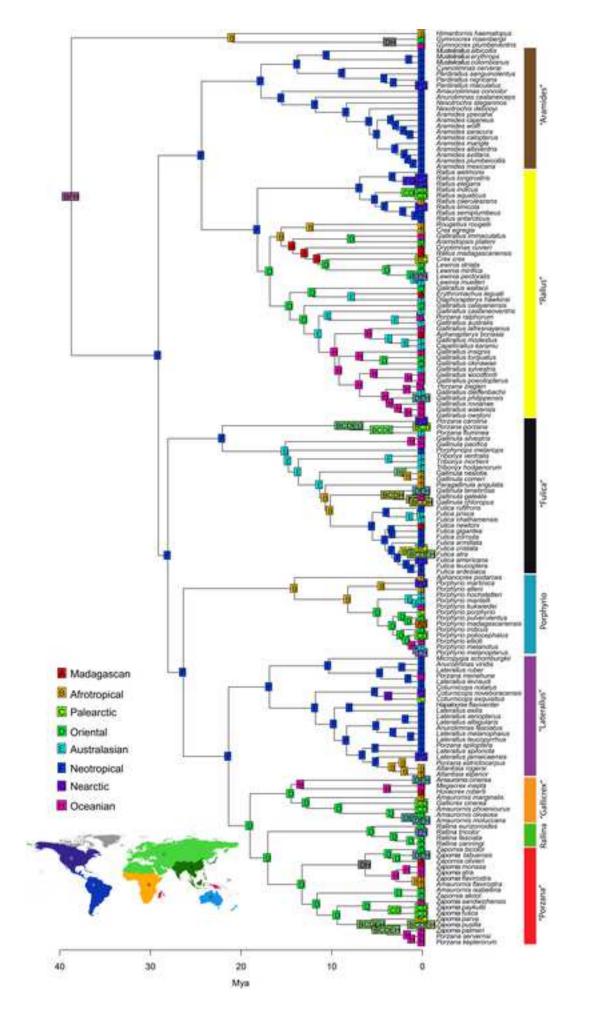492 condition. Ancestral flying conditions are depicted at each node as flying (blue) and non-flying
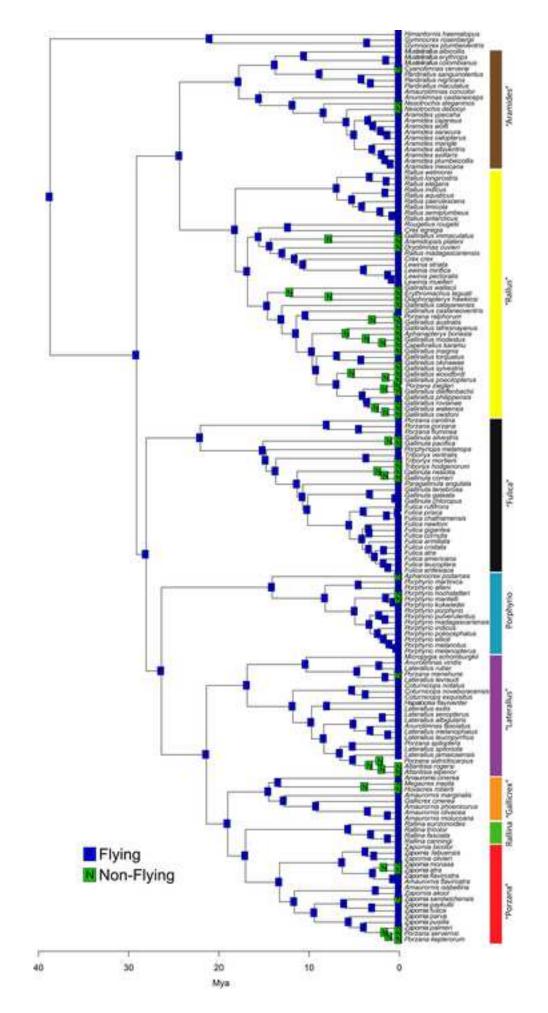
493 (green).

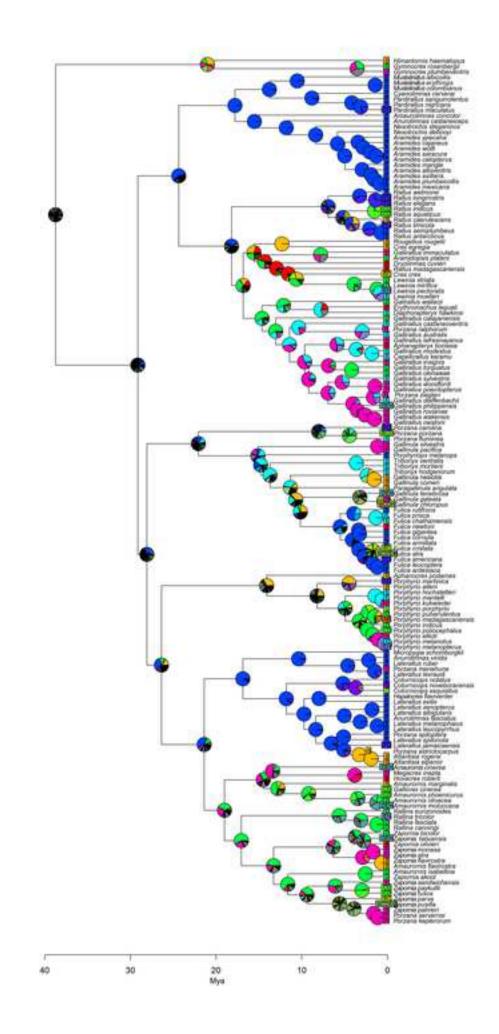494

495

496 Table captions

497 Table 1. BioGeoBEARS analyses of statistical model comparison based on geographical ranges and flying/non-flying discrete traits.
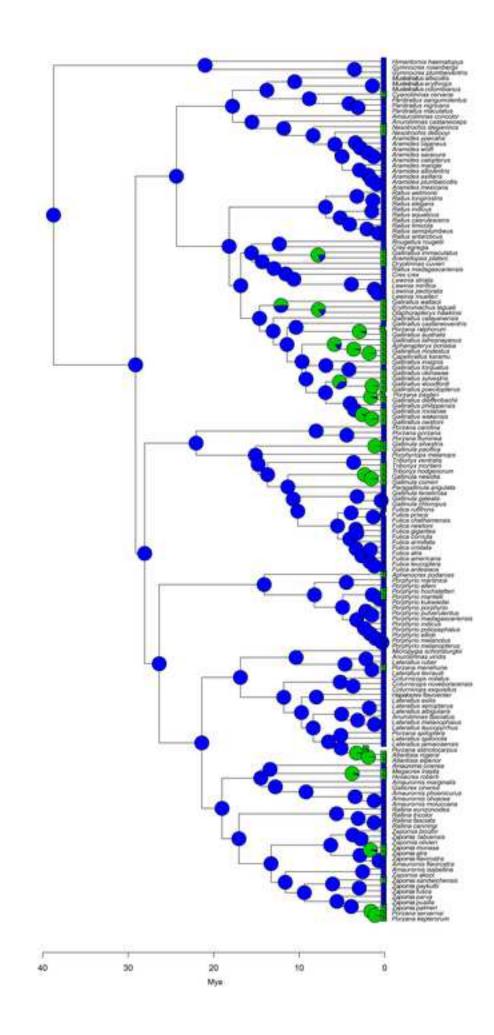
Category	Model	LnL	np	d	e	j	x	t_{21}	m_1	m_2	AICc	AICc wt	LRT
Trait-independent, distance-independent dispersal	DEC+t21	-529.6687	3	0.0099	0.0029	0	0	0.0288	1	1	1065.493	0%	2.266E-30
	DEC+j+t_{21}	-498.4805	4	0.0064	1E-12	0.0347	0	0.0288	1	1	1005.222	0%	2.773E-17
	DIVALIKE+t_{21}	-525.2667	3	0.0116	1E-12	0	0	0.0288	1	1	1056.689	0%	1.85E-28
	DIVALIKE+j+t_{21}	-505.4717	4	0.0078	1E-12	0.0270	0	0.0288	1	1	1019.205	0%	2.551E-20
	BAYAREALIKE+t_{21}	-584.0062	3	0.0100	0.1033	0	0	0.0288	1	1	1174.168	0%	5.713E-54
	BAYAREALIKE+j+t_{21}	-503.9572	4	0.0047	1E-12	0.0479	0	0.0288	1	1	1016.176	0%	1.16E-19
Trait-independent, distance-dependent dispersal (+x models)	DEC+x+t_{21}	-492.7391	4	0.6955	0.0044	0	-0.6065	0.0288	1	1	993.740	0%	8.638E-15
	DEC+j+x+t_{21}	-461.1950	5	0.3030	1E-12	1.1558	-0.5442	0.0288	1	1	932.785	12.7%	0.1488019
	DIVALIKE+x+t_{21}	-486.3943	4	0.6395	1E-12	0	-0.5673	0.0288	1	1	981.050	0%	4.92E-12
	DIVALIKE+j+x+t_{21}	-466.6418	5	0.3844	1E-12	0.8767	-0.5497	0.0288	1	1	943.678	0%	0.0006414
	BAYAREALIKE+x+t_{21}	-557.6819	4	0.7969	0.1084	0	-0.6106	0.0288	1	1	1123.625	0%	5.397E-43
	BAYAREALIKE+j+x+t_{21}	-471.1900	5	0.1570	1E-12	0.6655	-0.4916	0.0288	1	1	952.775	0%	6.79E-06
Trait-dependent, distance-independent dispersal	DEC+t_{21}+m_1	-520.8507	4	0.0115	1E-12	0	0	0.0291	0	1	1049.963	0%	5.342E-27
	DEC+j+t_{21}+m_1	-495.6507	5	0.0073	1E-13	0.0384	0	0.0292	0.380	1	1001.696	0%	1.617E-16
	DIVALIKE+t_{21}+m_1	-515.0783	4	0.0139	1E-12	0	0	0.0293	0	1	1038.418	0%	1.716E-24
	DIVALIKE+j+t_{21}+m_1	-500.9353	5	0.0093	1E-13	0.0277	0	0.0294	0.225	1	1012.265	0%	8.197E-19
	BAYAREALIKE+t_{21}+m_1	-576.9979	4	0.0124	0.1070	0	0	0.0288	0	1	1162.257	0%	2.205E-51
	BAYAREALIKE+j+t_{21}+m_1	-502.1328	5	0.0051	1E-13	0.0525	0	0.0291	0.487	1	1014.660	0%	2.475E-19
Trait-dependent, distance-dependent dispersal (+x models)	DEC+x+t_{21}+m_1	-484.5341	5	0.6346	0.0018	0	-0.5671	0.0291	0	1	979.463	0%	1.088E-11
	DEC+j+x+t_{21}+m_1	-458.2091	6	0.3353	1E-13	1.2509	-0.5424	0.0292	0.376	1	928.975	85.2%	1
	DIVALIKE+x+t_{21}+m_1	-476.3978	5	0.7465	1E-12	0	-0.5641	0.0292	0	1	963.190	0%	3.717E-08
	DIVALIKE+j+x+t_{21}+m_1	-461.9290	6	0.4340	1E-13	0.8785	-0.5417	0.0294	0.218	1	936.414	2.1%	0.0242361
	BAYAREALIKE+x+t_{21}+m_1	-550.4837	5	1.2209	0.1133	0	-0.6455	0.0288	0	1	1111.362	0%	2.483E-40
	BAYAREALIKE+j+x+t_{21}+m_1	-468.9452	6	0.1721	1E-13	0.6942	-0.4918	0.0291	0.440	1	950.447	0%	2.175E-05

498

499   Supplementary Information. Nexus files with morphological and molecular data that were used

500   for the total-evidence phylogenetic analysis.

501

502

503

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Figure 1

Figure 2

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