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Equilibrium bird species diversity in Atlantic islands

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Abstract:	<p>Half a century ago, MacArthur and Wilson proposed that the number of species on islands tends towards a dynamic equilibrium diversity around which species richness fluctuates. The current prevailing view in island biogeography accepts the fundamentals of MacArthur and Wilson's theory, but questions whether their prediction of equilibrium can be fulfilled over evolutionary time scales, given the unpredictable and ever-changing nature of island geological and biotic features. Here we conduct a complete molecular phylogenetic survey of the terrestrial bird species from four oceanic archipelagos that make up the diverse Macaronesian bioregion - Azores, Canary Islands, Cape Verde and Madeira. We estimate the times at which birds colonized and speciated in the four archipelagos, including many previously unsampled endemic and non-endemic taxa and their closest continental relatives. We develop and fit a new multi-archipelago dynamic stochastic model to these data, explicitly incorporating information from 91 taxa, both extant and extinct. Remarkably, we find that all four archipelagos have independently achieved and maintained a dynamic equilibrium over millions of years. Biogeographical rates are homogenous across archipelagos, except for the Canary Islands, which exhibit higher speciation and colonization. Our finding that the avian communities of the four Macaronesian archipelagos display an equilibrium diversity pattern indicates that a diversity plateau may be rapidly achieved on islands where rates of in situ radiation are low and extinction is high. This study reveals that equilibrium processes may be more prevalent than recently proposed, supporting MacArthur and Wilson's 50 year old theory.</p>

1 **Report**

2
3 **Equilibrium bird species diversity in Atlantic islands**

4
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22 **Keywords:** Dynamic equilibrium, island biogeography, extinction, diversification,
23 phylogeny, colonization, Canary Islands, Azores, Madeira, Cape Verde

24 **SUMMARY**

25

26 **Half a century ago, MacArthur and Wilson proposed that the number of species on**
27 **islands tends towards a dynamic equilibrium diversity around which species richness**
28 **fluctuates [1]. The current prevailing view in island biogeography accepts the**
29 **fundamentals of MacArthur and Wilson's theory [2], but questions whether their**
30 **prediction of equilibrium can be fulfilled over evolutionary time scales, given the**
31 **unpredictable and ever-changing nature of island geological and biotic features [3–7].**
32 **Here we conduct a complete molecular phylogenetic survey of the terrestrial bird species**
33 **from four oceanic archipelagos that make up the diverse Macaronesian bioregion -**
34 **Azores, Canary Islands, Cape Verde and Madeira [8,9]. We estimate the times at which**
35 **birds colonized and speciated in the four archipelagos, including many previously**
36 **unsampled endemic and non-endemic taxa and their closest continental relatives. We**
37 **develop and fit a new multi-archipelago dynamic stochastic model to these data,**
38 **explicitly incorporating information from 91 taxa, both extant and extinct. Remarkably,**
39 **we find that all four archipelagos have independently achieved and maintained a**
40 **dynamic equilibrium over millions of years. Biogeographical rates are homogenous**
41 **across archipelagos, except for the Canary Islands, which exhibit higher speciation and**
42 **colonization. Our finding that the avian communities of the four Macaronesian**
43 **archipelagos display an equilibrium diversity pattern indicates that a diversity plateau**
44 **may be rapidly achieved on islands where rates of *in situ* radiation are low and**
45 **extinction is high. This study reveals that equilibrium processes may be more prevalent**
46 **than recently proposed, supporting MacArthur and Wilson's 50 year old theory.**

RESULTS

The biogeographical region of Macaronesia [8], located in the Northeast Atlantic Ocean, comprises four main volcanic island chains - Azores, Madeira, Canary Islands and Cape Verde (Figure 1, Table 1). In our analyses, we focus on bird species whose ecology is broadly comparable to that of a typical songbird, and therefore we exclude birds of prey and rails. We also exclude marine, aquatic, migratory and introduced species. To estimate times of colonization and speciation of Macaronesian birds, we reconstructed and dated phylogenies covering all known colonization events of native terrestrial birds from our focal group in the islands – including many that had never before been studied (Table S1). We identified a total of 91 independent colonization events (Table S2): 15 on the Azores, 46 on the Canary Islands, 10 on Cape Verde, 19 on Madeira and one on the Selvagens (a small archipelago that we do not include in the main analyses, see STAR Methods). The colonization events comprise 63 species, 29 of which are endemic to a single archipelago, two are endemic to Macaronesia (Berthelot's pipit and the island canary) and 32 are non-endemic (also occur in the continent). We identified only two occasions of cladogenetic events that have extant descendants on the islands, both within the Canary Islands: the blue tits (*Cyanistes*) group of the central islands and one within the blue chaffinches (*Fringilla*, Table S3). The times of colonization of the archipelagos obtained in our Bayesian dating analyses are shown in Figure 1 and Table S2. The average age of colonization of Macaronesia is 0.97 (\pm 0.15) million years (Myr) (Figure S1, Table 1). Endemic species are significantly older (2.71 (\pm 0.54) Myr) than non-endemic species (mean 0.54 (\pm 0.07) Myr) ($P < 0.001$). An analysis of variance revealed no significant differences in colonization times between island chains for both endemic ($P = 0.79$) and non-endemic ($P = 0.69$) species.

71 To estimate rates of colonization, extinction, cladogenesis and anagenesis we used
72 DAISIE (dynamic assembly of islands through speciation, immigration and extinction), an
73 island biogeography process-based model [5]. DAISIE estimates rates of island biota
74 assembly – including extinction – based on phylogenetic information, with high precision
75 [5,10]. Here we develop a new multi-archipelago version of DAISIE that allows us to test
76 whether the different island groups are governed by the same macroevolutionary process. We
77 treat each of the archipelagos as an ‘island’, because the importance of the archipelago as the
78 relevant unit in island biogeography is increasingly recognized [11,12] and birds are vagile
79 taxa that disperse relatively frequently between islands of the same archipelago [13].

80 Using the Bayesian information criterion (BIC), the preferred multi-archipelago
81 DAISIE model is M17, a model with six parameters (Table S4 and S5, Figure 2). Two models
82 that are very similar to M17 - M15 and M24 (Table S5) – also carry a large proportion of BIC
83 weight, and cannot be ruled out (see STAR Methods). According to the M17 model, all
84 Macaronesian islands share the same macroevolutionary rates for extinction – 1.05 events per
85 lineage per Myr; and anagenesis – 0.51 events per lineage per Myr (Table S5). Further, in the
86 Azores, Cape Verde and Madeira cladogenesis is absent and colonization rate is 0.05 events
87 per mainland lineage per Myr (equivalent to 15 events per Myr given a mainland pool size of
88 300 species). The exception is the Canary Islands, which have a different (non-zero) rate of
89 cladogenesis (0.13 events per lineage per Myr) and a higher rate of colonization (0.15
90 colonization events per mainland lineage per Myr, equivalent to 45 colonization events per
91 Myr). The M17 model is diversity-independent (there are no negative feedbacks of diversity
92 on rates of colonization and cladogenesis). A bootstrap analysis using multiple simulated
93 datasets revealed that the model performs well, recovering correct parameter values with little
94 bias (Figure S2).

95 The preferred model for all archipelagos is an equilibrium model, because the rate of
96 extinction exceeds the rate of cladogenesis [10]. Simulations of total species diversity-
97 through-time reveal a general pattern of the number of species in the four Macaronesian
98 archipelagos rapidly reaching an asymptotic phase (Figure 3). The four island chains are thus
99 currently at equilibrium, and this state has been maintained over millions of years.

101 **DISCUSSION**

102
103 Our molecular phylogenetic dating analysis of the terrestrial avian community of Macaronesia
104 covering all known extant and extinct colonization events provides a valuable temporal
105 context for understanding the biogeographical and diversification history of the islands [9,14].
106 Fitting the new multi-archipelago DAISIE models to these phylogenetic data revealed striking
107 homogeneity in rates of bird species accumulation in the Macaronesian bioregion (Figure 2),
108 with diversity resulting from essentially the same biogeographical process. Indeed, three of
109 the archipelagos (Azores, Cape Verde and Madeira) are governed by the same
110 macroevolutionary dynamics model (Table S5). The Canary Islands form the only exception:
111 although they share the same rate of extinction and anagenesis as all other island chains
112 (Figure 2), they exhibit substantially higher rates of cladogenesis and colonization. In
113 addition, while in the other three archipelagos the preferred model was one with no
114 cladogenesis, the phylogenetic data of Canarian birds was best fit by a model where endemic
115 diversity is generated both through cladogenesis and anagenesis. The reason why *in situ*
116 radiation seems to take place in the Canary Islands whilst being absent in the other
117 archipelagos may be linked to the fact that the Canaries have by far the largest area of all
118 Macaronesian archipelagos [9] which may have facilitated allopatry, a key factor in triggering

119 avian radiations [15]. Indeed, the archipelago has been the setting for multiple radiations
120 across other taxonomic groups [16,17].

121 The results regarding the rates of colonization and extinction are striking. While the
122 higher rate of colonization of the Canaries may be expected given their proximity to the
123 African continent (only 96 km), the homogeneity in rates we found for the other three
124 archipelagos is unexpected. A decline of immigration rates with increasing distance from a
125 source pool is a standard feature of most island biogeography models [4,11,18]. However, we
126 find no support for archipelagos with very different levels of isolation (Table 1) having been
127 colonized at different rates by birds. It appears that for a vagile group such as birds the
128 distance-colonization relationship may be more complex than previously thought – birds that
129 are able to cross a certain distance threshold may be able to reach various mid-isolation
130 islands with a similar probability [15,19]. Strictly speaking, we cannot rule out the possibility
131 that differences in the avifaunas of the mainland source areas – e.g. in the proportion of
132 species able to reach and successfully establish islands whose environment is different from
133 the continent – may have cancelled out differences in distance. However, this requires a quite
134 tight negative correlation between the size of the mainland species pool of potential colonizers
135 and dispersal distance for which we see no straightforward explanation.

136 Regarding extinction, the homogeneity in rates across the four archipelagos is also
137 surprising, particularly given the differences in area between them. Models with differential
138 extinction all performed poorly (Table S5) and the precision of our extinction estimates was
139 high (Figure S2), supporting the robustness of this result. The influence of latitude, climate
140 and intra-archipelagic connectivity, which may have enabled greater gene flow and rescue of
141 small populations in the smaller archipelagos, likely overwhelmed the negative effect of area
142 on extinction.

143 As expected, species that have been classified as endemics mostly show deep levels of
144 divergence from continental relatives (Figures 1 and S1, Table 1). The oldest extant endemic
145 species in each of the archipelagos are: the Azores chaffinch (*Fringilla moreletii*), the laurel
146 pigeon of the Canary Islands (*Columba junoniae*), the Razo lark of Cape Verde (*Alauda*
147 *razae*) and the Madeira firecrest (*Regulus madeirensis*) (Table S2). Interestingly, among the
148 taxa with deep divergences, we also find some to which species status has not been assigned
149 and are considered subspecies, despite being older than some archipelagic endemics. For
150 example, the European robin subspecies *Erithacus rubecula* subsp. *marionae* [20] of the
151 Canary Islands colonized the archipelago almost 3 Myr ago and forms a well-supported
152 monophyletic clade. We investigated whether taxonomic scheme affected our results, and
153 found that treating taxa with deep divergences as endemics led to increased estimates of
154 anagenesis in DAISIE but did not affect the preferred model (see STAR Methods).

155 Tests of diversity equilibrium on islands have traditionally been conducted over
156 ecological time scales [21], as MacArthur and Wilson's mathematical work focused on
157 extinction versus immigration. However, in *The Theory of Island Biogeography* [1] they
158 explicitly considered the speciation phase and adaptive radiation – i.e. evolutionary processes.
159 Formal tests of this theory on evolutionary time scales were unfeasible until recently, because
160 they required information on events that took place in the geological past [3]. In the 21st
161 century, the mainstream of the field of island biogeography has fully incorporated the
162 evolutionary aspects of MacArthur and Wilson's theory [2,5,18,22]. In a series of pioneering
163 studies, Ricklefs and Bermingham fitted colonization-extinction models (excluding
164 speciation) to species accumulation curves from several insular communities, finding
165 evidence for evolutionary equilibrium in the number of independent island colonist lineages
166 of Hawaiian birds, West Indian reptiles and New Zealand ferns, but not in Lesser Antillean
167 birds [13,23–25]. More recently, the development of the DAISIE model has allowed explicit

168 consideration of speciation via *in situ* radiation (cladogenesis) and anagenesis, enabling tests
169 of equilibrium not just in the number of lineages, but also in total species diversity. The
170 previous applications of this method have either found no evidence for equilibrium dynamics
171 – in Galápagos birds [5] - or found diversity to be much below equilibrium – in Greater
172 Antillean bats [10].

173 Our results reveal that the avifauna of each of the four Macaronesian archipelagos has
174 independently achieved a diversity steady-state and is at a macroevolutionary equilibrium.
175 The preferred model was diversity-independent, indicating that equilibrium does not arise
176 through negative diversity feedbacks as is the case in other vertebrate insular groups [26,27].
177 Instead, total species richness has reached a plateau in the four island groups (Figure 3)
178 because the rate of extinction is higher than the rate of speciation [10]. By incorporating
179 speciation, our study reveals that a macroevolutionary equilibrium can be achieved in the total
180 number of species.

181 The finding that Macaronesian birds are at equilibrium contrasts with the results of the
182 only other avian study to assess equilibrium including speciation, on the Galápagos avifauna,
183 which found no evidence for steady-state dynamics. However, the Galápagos is an atypical
184 archipelago in that it supports two large endemic radiations of birds [15]. In fact, despite
185 being rich in bird species, oceanic islands are generally home to few or no avian radiations -
186 most of their endemic bird species show an anagenetic pattern, i.e. they have no close
187 relatives on the same island or archipelago [15,28,29]. Whereas in the Galápagos the rate of
188 cladogenesis in birds was high enough to overcome the balancing effects of extinction –
189 leading to non-asymptotic behavior of the species through time plot (Figure 3) - in
190 Macaronesia the rates of *in situ* radiation are too low to allow positive diversification rates.
191 Only two clades, the chaffinches and the blue tits, have undergone cladogenesis within the
192 bioregion, producing two and three species, respectively. These ‘radiations’ are modest when

193 compared to the highly diverse Darwin's finches [30]. Thus, the key to achieving equilibrium
194 appears to be a lack of opportunities for *in situ* diversification in an archipelagic context. The
195 ability of birds to fly and disperse between islands within an archipelago is potentially the
196 main cause for low rates of cladogenesis in most archipelago lineages of birds [15,29]. In
197 addition, extrinsic factors such as island configuration, connectivity and climate (mostly
198 temperate in Macaronesia) may also have contributed to preventing lineage splitting or
199 survival of incipient allopatric species [15].

200 Recent verbal and simulation models have suggested speciation and colonization
201 processes on volcanic islands may operate at rates that are too slow to allow the realized
202 species diversity to match the theoretical equilibrium or carrying-capacity in a context of
203 ongoing geological change and environmental fluctuations [3,4,22,31], i.e. the concept of
204 unattained equilibrium [2]. As a result, the current prevailing view in island biogeography
205 accepts the essentials of MacArthur and Wilson's theory (e.g. colonization and extinction
206 depend on island isolation and size), but doubts their prediction of equilibrium can be fulfilled
207 over long time scales [2]. Indeed, in Macaronesia, detailed paleogeographic reconstructions
208 have provided support for disequilibrium models, by revealing pronounced geological
209 instability as well as variable levels of connectivity between landmasses [8,32]. Surprisingly,
210 our results in birds suggest that equilibrium in this vertebrate group may be attained within a
211 relatively short time frame. When rates of cladogenesis are low (as in the Canary Islands) or
212 absent (Azores, Cape Verde and Madeira), the pace of approach to equilibrium is determined
213 almost solely by the rate of extinction [4,10]. The rate of colonization does affect the
214 approach to equilibrium in the number of non-endemic species, but not in the number of
215 endemic species (see STAR methods). Thus, archipelagos with high rates of natural extinction
216 may rapidly reach equilibrium regardless of how often they are colonized, potentially
217 outpacing major geological change that may otherwise deter steady-state. While volcanic

218 activity and sea level fluctuations have certainly had a dramatic effect on insular diversity on
219 short time scales [3,12,32], the good fit of the model in our analyses suggests that such events
220 may have limited impact on diversity at longer scales.

221 Influenced by the equilibrium theory of island biogeography, research on insular
222 communities in the 20th century was arguably dominated by an equilibrium perspective [31].
223 However, in recent years, the idea that islands tend towards a dynamic equilibrium diversity
224 which is maintained over extended periods has increasingly been replaced by a non-
225 deterministic disequilibrium view, in which diversity is constantly tracking a theoretical
226 equilibrium that is never reached [2,3,6,7,10]. Our results do not support this trend by
227 suggesting the avifaunas of four oceanic archipelagos have achieved and maintained a
228 diversity steady-state for millions of years. The findings on the birds of these North Atlantic
229 islands are particularly relevant because they are representative of the typical oceanic island –
230 they are rich in endemic bird species but poor in *in situ* avian radiations. This suggests that the
231 pattern of long-term evolutionary diversity steady-state being achieved in a short period of
232 time may be the case for many more islands. Future studies on the avifaunas of other island
233 systems worldwide may reveal that MacArthur and Wilson’s prediction of equilibrium is
234 widespread.

235

236 **Author Contributions**

237 L.V. designed the study, performed the analyses and wrote the original draft. R.S.E.
238 developed new statistical tools and contributed to study design. R.T. supervised the molecular
239 analyses and contributed to study design. J.C.I. provided expertise on Macaronesian birds and
240 conducted the fieldwork. K.H., T.P and J.C.I. performed the laboratory work.

241

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REFERENCES

1. MacArthur, R.H., and Wilson, E.O. (1967). *The Theory of Island Biogeography* (Princeton: Princeton University Press).
2. Warren, B., Simberloff, D., Ricklefs, R., Aguilée, R., Condamine, F., Gillespie, R., Gravel, D., H, M., Mouquet, N., Rosindell, J., *et al.* (2015). Islands as model systems in ecology and evolution : progress and prospects fifty years after MacArthur-Wilson. *Ecol. Lett.* *18*, 200–217.
3. Whittaker, R.J., Triantis, K.A., and Ladle, R.J. (2008). A general dynamic theory of oceanic island biogeography. *J. Biogeogr.* *35*, 977–994.
4. Valente, L.M., Etienne, R.S., and Phillimore, A.B. (2014). The effects of island ontogeny on species diversity and phylogeny. *Proc. Biol. Sci.* *281*, 20133227.
5. Valente, L.M., Phillimore, A.B., and Etienne, R.S. (2015). Equilibrium and non-equilibrium dynamics simultaneously operate in the Galápagos islands. *Ecol. Lett.* *18*, 844–852.
6. Marshall, C.R., and Quental, T.B. (2016). The uncertain role of diversity dependence in species diversification and the need to incorporate time-varying carrying capacities. *Philos. Trans. R. Soc. Lond. B. Biol. Sci.* *371*, 20150217-.
7. Borregaard, M.K., Amorim, I.R., Borges, P.A. V, Cabral, J.S., Fernández-Palacios, J.M., Field, R., Heaney, L.R., Kreft, H., Matthews, T.J., Olesen, J.M., *et al.* (2016). Oceanic island biogeography through the lens of the general dynamic model: assessment and prospect. *Biol. Rev. Camb. Philos. Soc.*
8. Fernández-Palacios, J.M., de Nascimento, L., Otto, R., Delgado, J.D., García-del-Rey, E., Arévalo, J.R., and Whittaker, R.J. (2011). A reconstruction of Palaeo-Macaronesia, with particular reference to the long-term biogeography of the Atlantic island laurel forests. *J. Biogeogr.* *38*, 226–246.
9. Illera, J.C., Rando, J.C., Richardson, D.S., and Emerson, B.C. (2012). Age, origins and extinctions of the avifauna of Macaronesia: a synthesis of phylogenetic and fossil information. *Quat. Sci. Rev.* *50*, 14–22.
10. Valente, L., Etienne, R., and Dávalos, L. (2017). Recent extinctions disturb path to equilibrium diversity in Caribbean bats. *Nat. Ecol. Evol.* *1*, 26.
11. Triantis, K.A., Economo, E.P., Guilhaumon, F., and Ricklefs, R.E. (2015). Diversity regulation at macro-scales: species richness on oceanic archipelagos. *Glob. Ecol. Biogeogr.* *24*, 594–605.

- 288 12. Weigelt, P., Steinbauer, M.J., Cabral, J.S., and Kreft, H. (2016). Late Quaternary
289 climate change shapes island biodiversity. *Nature* 532, 99–102.
- 290 13. Ricklefs, R.E., and Bermingham, E. (2001). Nonequilibrium diversity dynamics of the
291 Lesser Antillean avifauna. *Science*. 294, 1522–1524.
- 292 14. Emerson, B.C., and Gillespie, R.G. (2008). Phylogenetic analysis of community
293 assembly and structure over space and time. *Trends Ecol. Evol.* 23, 619–30.
- 294 15. Ricklefs, R.E., and Bermingham, E. (2007). The causes of evolutionary radiations in
295 archipelagoes: passerine birds in the Lesser Antilles. *Am. Nat.* 169, 285–297.
- 296 16. Juan, C., Emerson, B.C., Oromi, P., and Hewitt, G.M. (2000). Colonization and
297 diversification: towards a phylogeographic synthesis for the Canary Islands. *Trends*
298 *Ecol. Evol.* 15, 104–109.
- 299 17. Sanmartín, I., Van Der Mark, P., and Ronquist, F. (2008). Inferring dispersal: A
300 Bayesian approach to phylogeny-based island biogeography, with special reference to
301 the Canary Islands. *J. Biogeogr.* 35, 428–449.
- 302 18. Rosindell, J., and Phillimore, A.B. (2011). A unified model of island biogeography
303 sheds light on the zone of radiation. *Ecol. Lett.* 14, 552–560.
- 304 19. Price, T. (2008). *Speciation in Birds* (Greenwood Village: Roberts & Co.).
- 305 20. Dietzen, C., Michels, J.P., and Wink, M. (2015). Formal description of a new
306 subspecies of the European robin from Gran Canaria island, Spain (Aves:
307 Muscicapidae: *Erithacus rubecula marionae* subsp. nov.). *Open Ornithol. J.* 8, 0.
- 308 21. Diamond, J.M. (1969). Avifaunal equilibria and species turnover rates on the Channel
309 Islands of California. *Proc. Natl. Acad. Sci.* 64, 57–63.
- 310 22. Borregaard, M.K., Matthews, T.J., and Whittaker, R.J. (2015). The general dynamic
311 model: towards a unified theory of island biogeography? *Glob. Ecol. Biogeogr.* 25,
312 805–816.
- 313 23. Ricklefs, R., and Bermingham, E. (2008). The West Indies as a laboratory of
314 biogeography and evolution. *Philos. Trans. R. Soc. B Biol. Sci.* 363, 2393–2413.
- 315 24. Ricklefs, R.E., and Bermingham, E. (2004). Application of Johnson et al’s speciation
316 threshold model to apparent colonization times of island biotas. *Evolution.* 58, 1664–
317 1673.
- 318 25. Ricklefs, R.E. (2009). Dynamics of colonization and extinction on islands. In *The*
319 *theory of island biogeography revisited*, J. B. Losos and R. E. Ricklefs, eds. (Princeton
320 University Press), p. 388.
- 321 26. Rabosky, D.L., and Glor, R.E. (2010). Equilibrium speciation dynamics in a model

- 322 adaptive radiation of island lizards. *Proc. Natl. Acad. Sci.* *107*, 22178–22183.
- 323 27. Scantlebury, D.P. (2013). Diversification rates have declined in the Malagasy
324 herpetofauna. *Proc. Biol. Sci.* *280*, 20131109.
- 325 28. Coyne, J.A., and Price, T.D. (2000). Little evidence for sympatric speciation in island
326 birds. *Evolution (N. Y.)*. *54*, 2166–2171.
- 327 29. Price, T.D. (2011). Adaptive radiations: there’s something about finches. *Curr. Biol.*
328 *21*, R953-5.
- 329 30. Grant, P.R., and Grant, B.R. (2008). How and why species multiply: the radiation of
330 Darwin’s finches (Princeton: Princeton University Press).
- 331 31. Heaney, L.R. (2000). Dynamic disequilibrium: a long-term, large-scale perspective on
332 the equilibrium model of island biogeography. *Glob. Ecol. Biogeogr.* *9*, 59–74.
- 333 32. Fernández-Palacios, J.M., Rijdsdijk, K.F., Norder, S.J., Otto, R., de Nascimento, L.,
334 Fernández-Lugo, S., Tjørve, E., and Whittaker, R.J. (2015). Towards a glacial-sensitive
335 model of island biogeography. *Glob. Ecol. Biogeogr.* *25*, 817–830.
- 336 33. del Hoyo, J., Elliott, A., Sargatal, J., Christie, D.A. & de Juana, E. ed. (2017).
337 Handbook of the Birds of the World Alive (Barcelona: Lynx Edicions).
- 338 34. Arechavaleta, M., Rodriguez, S., Zurita, N., and Garcia, A. (2010). Lista de especies
339 silvestres de Canarias. Hongos, plantas y animales terrestres (Gobierno de Canarias).
- 340 35. Barcelos, L.M.D., Rodrigues, P.R., Bried, J., Mendonça, E.P., Gabriel, R., and Borges,
341 P.A.V. (2015). Birds from the Azores: An updated list with some comments on species
342 distribution. *Biodivers. data J.* *3*, e6604.
- 343 36. Illera, J.C., Spurgin, L.G., Rodriguez-Exposito, E., Nogales, M., and Rando, J.C.
344 (2016). What are we learning about speciation and extinction from the Canary Islands?
345 *Ardeola* *63*, 5–23.
- 346 37. Weir, J.T., and Schluter, D. (2008). Calibrating the avian molecular clock. *Mol. Ecol.*
347 *17*, 2321–2328.
- 348 38. Nguyen, J.M.T., and Ho, S.Y.W. (2016). Mitochondrial rate variation among lineages
349 of passerine birds. *J. Avian Biol.* *47*, 690–696.
- 350 39. Päckert, M., Martens, J., Hering, J., Kvist, L., and Illera, J.C. (2013). Return flight to
351 the Canary Islands – the key role of peripheral populations of Afrocanarian blue tits
352 (*Aves: Cyanistes teneriffae*) in multi-gene reconstructions of colonization pathways.
353 *Mol. Phylogenet. Evol.* *67*, 458–467.
- 354 40. Stervander, M., Illera, J.C., Kvist, L., Barbosa, P., Keehnen, N.P., Pruischer, P.,
355 Bensch, S., and Hansson, B. (2015). Disentangling the complex evolutionary history of

- 356 the Western Palearctic blue tits (*Cyanistes* spp.) - phylogenomic analyses suggest
357 radiation by multiple colonisation events and subsequent isolation. *Mol. Ecol.* *24*,
358 2477–2494.
- 359 41. Kearse, M., Moir, R., Wilson, A., Stones-Havas, S., Cheung, M., Sturrock, S., Buxton,
360 S., Cooper, A., Markowitz, S., Duran, C., *et al.* (2012). Geneious Basic: an integrated
361 and extendable desktop software platform for the organization and analysis of sequence
362 data. *Bioinformatics* *28*, 1647–9.
- 363 42. Dietzen, C., Voigt, C., Wink, M., Gahr, M., and Leitner, S. (2006). Phylogeography of
364 island canary (*Serinus canaria*) populations. *J. Ornithol.* *147*, 485–494.
- 365 43. Illera, J.C., Palmero, A.M., Laiolo, P., Rodríguez, F., Moreno, Á.C., and Navascués,
366 M. (2014). Genetic, morphological, and acoustic evidence reveals lack of
367 diversification in the colonization process in an island bird. *Evolution.* *68*, 2259–2274.
- 368 44. Kocher, T.D., Thomas, W.K., Meyer, A., Edwards, S. V., Paabo, S., Villablanca, F.X.,
369 Wilson, A.C., Pääbo, S., Villablanca, F.X., and Wilson, A.C. (1989). Dynamics of
370 mitochondrial DNA evolution in animals: amplification and sequencing with conserved
371 primers. *Proc. Natl. Acad. Sci. U. S. A.* *86*, 6196–6200.
- 372 45. Dietzen, C., Witt, H.-H., and Wink, M. (2003). The phylogeographic differentiation of
373 the European robin *Erithacus rubecula* on the Canary Islands revealed by
374 mitochondrial DNA sequence data and morphometrics: evidence for a new robin taxon
375 on Gran Canaria? *Avian Sci.* *3*, 115–132.
- 376 46. Edwards, S. V, Arctander, P., and Wilson, A.C. (1991). Mitochondrial resolution of a
377 deep branch in the genealogical tree for perching birds. *Proc. Biol. Sci.* *243*, 99–107.
- 378 47. Helm-Bychowski, K., and Cracraft, J. (1993). Recovering phylogenetic signal from
379 DNA sequences: relationships within the corvine assemblage (class aves) as inferred
380 from complete sequences of the mitochondrial DNA cytochrome-b gene. *Mol. Biol.*
381 *Evol.* *10*, 1196–1214.
- 382 48. Bouckaert, R., Heled, J., Kühnert, D., Vaughan, T., Wu, C.H., Xie, D., Suchard, M.A.,
383 Rambaut, A., and Drummond, A.J. (2014). BEAST 2: a software platform for Bayesian
384 evolutionary analysis. *PLoS Comput. Biol.* *10*, e1003537.
- 385 49. Alström, P., Barnes, K.N., Olsson, U., Barker, F.K., Bloomer, P., Khan, A.A., Qureshi,
386 M.A., Guillaumet, A., Crochet, P.A., and Ryan, P.G. (2013). Multilocus phylogeny of
387 the avian family Alaudidae (larks) reveals complex morphological evolution, non-
388 monophyletic genera and hidden species diversity. *Mol. Phylogenet. Evol.* *69*, 1043–
389 1056.

- 390 50. Posada, D. (2008). jModelTest: Phylogenetic Model Averaging. *Mol Biol Evol* 25,
391 1253–1256.
- 392 51. Alcover, J.A., Pieper, H., Pereira, F., and Rando, J.C. (2015). Five new extinct species
393 of rails (Aves: Gruiformes: Rallidae) from the Macaronesian Islands (North Atlantic
394 Ocean). *Zootaxa* 4057, 151–190.
- 395 52. Ramalho, R., Helffrich, G., Madeira, J., Cosca, M., Quartau, R., Thomas, C., Hipolito,
396 A., and Avila, S.P. (2014). The emergence and evolution of Santa Maria Island
397 (Azores) - the conundrum of uplifting islands revisited. In AGU-Fall-Meeting (San
398 Francisco), p. Abstract V11B–4697.
- 399 53. Carracedo, J.C., and Day, S. (2002). Canary Islands. Classic geology in Europe series
400 (Hertfordshire: Terra Publishing).
- 401 54. Ramalho, R. (2011). Building the Cape Verde Islands (Berlin: Springer).
- 402 55. Mata, J., Fonseca, P.E., Prada, S., Rodrigues, D., Martins, S., and Ramalho, R. (2013).
403 O arquipélago da Madeira - Geografia de Portugal. Esc. Ed. 2, 691–746.
- 404 56. Sangster, G., Rodríguez-Godoy, F., Roselaar, C.S., Robb, M.S., and Luksenburg, J.A.
405 (2016). Integrative taxonomy reveals Europe's rarest songbird species, the Gran
406 Canaria blue chaffinch *Fringilla polatzeki*. *J. Avian Biol.* 47, 159–166.
- 407 57. Clements, J.F., Schulenberg, T.S., Iliff, M.J., Roberson, D., Fredericks, T.A., Sullivan,
408 B.L., and Wood, C.L. (2016). The eBird/Clements checklist of birds of the world:
409 v2016.
- 410
- 411

412 **Figure 1 - Colonization times of Macaronesian bird taxa and map of Macaronesia.** The
413 vertical lines show the maximum geological ages of the archipelagos. Filled circles – non-
414 endemic species; unfilled circles – endemic species, unfilled squares – Macaronesian
415 endemic. Numbers next to the colonization events correspond to codes in Table S2. 95%
416 confidence intervals for the estimates are given in Table S2. Bird drawings used with
417 permission from HBW [33]. See also Table S2.

418
419
420 **Figure 2 - Maximum likelihood estimates of the rates of cladogenesis, extinction,**
421 **colonization and anagenesis for Macaronesia.** Estimated in DAISIE using the M17 model,
422 and for the rates previously found in Galápagos birds [5]. Rates in events per lineage per
423 million years. Error bars show 2.5-97.5 percentiles of bootstrap analyses. See also Tables S5
424 and S6.

425
426
427 **Figure 3 – Number of species through time (Myr) in each of the archipelagos.** Based on
428 5,000 datasets simulated with the ML parameters of the best DAISIE model (M17). Black line
429 shows median value across simulations, and the coloured areas the 2.5 - 97.5 percentiles. The
430 inset shows the same plot for the Galápagos islands [5]. Grey dashed line - pre-human
431 diversity; black dashed line – contemporary diversity (excluding extinct species). See also
432 Table S5.

433

434 **Table 1 – Macaronesia archipelago characteristics and mean colonization times.** Times
 435 obtained in the divergence dating analyses (standard error in brackets).

436

	Archipelago				
	Macaronesia	Azores	Canary Islands	Cape Verde	Madeira
Species (total)	63	15	49	10	19
Endemic species (total)	31	5	16	3	5
Colonizations (total)	91	15	46	10	19
Species (extant)	50	12	42	10	16
Endemic species (extant)	21	2	11	3	3
Colonizations (extant)	78	12	39	10	16
Known extinct species	13	3	7	0	3
Radiations	2	0	2	0	0
Island Age (Myr)	29*	6.3	21	15.8	18.8
Distance to continent (km)	96	1365	96	568	633
Colonization time (Myr)					
All taxa	0.97 (0.15)	0.52 (0.11)	1.09 (0.23)	1.38 (0.6)	0.76 (0.31)
Endemic	2.71 (0.54)	1.21 (0.13)	2.86 (0.84)	3.27 (1.57)	2.73 (1.36)
Non-endemic	0.54 (0.07)	0.39 (0.06)	0.66 (0.12)	0.58 (0.22)	0.34 (0.05)

437 * Age of Selvagens archipelago

438

STAR METHODS

CONTACT FOR REAGENT AND RESOURCE SHARING

Further information and requests for resources and reagents should be directed to and will be fulfilled by the Lead Contact, Luis Valente (luis.valente@mfn-berlin.de).

EXPERIMENTAL MODEL AND SUBJECT DETAILS

Sampling overview

We downloaded cytochrome-*b* (*cyt-b*) sequences from 1,001 individuals from a total of 397 species of Macaronesian taxa and their closest continental relatives from Genbank. In addition, we produced new sequences from 99 fresh samples from 44 species collected in Macaronesia, Europe and North Africa (Table S1). We cover 27 new Macaronesian colonization events that had never before been sampled and greatly expand the sampling of continental relatives.

Taxon sampling

Our sampling focuses on the native resident terrestrial birds from the four main archipelagos that make up Macaronesia – Azores, Canary Islands, Cape Verde, Madeira (Figure 1, Table S2). We based the taxon lists for each of the archipelagos on recent checklists (Refs [34–36], Avibase (<http://avibase.bsc-eoc.org/>) and African Bird Club (<https://www.africanbirdclub.org/>)). For each taxon from each archipelago we aimed to sample individuals from the archipelago as well as from the taxon's closest relatives outside the

464 archipelago. If the taxon was a species endemic to the archipelago, we sampled multiple
465 individuals from that species, as well as from the most closely related species as identified
466 based on available phylogenetic or taxonomic information. If the taxon was not endemic, we
467 sampled individuals from population(s) of the archipelago as well as populations of the
468 species from nearby regions (either from other archipelago or from the continent). The vast
469 majority of Macaronesian birds have a Palearctic origin [9], and we thus focused our sampling
470 from outside Macaronesia on the closest mainland regions in Africa and Europe, with
471 particular focus on the Iberian Peninsula and Morocco.

472 The small archipelago of Selvagens is also part of Macaronesia but only one taxon of
473 our focal group has colonized the islands (*Anthus berthelotti*). We exclude this archipelago
474 from the main analyses because, given its very small area, extinction rates are likely high and
475 colonization rates low, and thus this data point would potentially add more noise than power
476 to the analyses. However, we did sample *Anthus berthelotti* individuals from Selvagens and
477 we provide the estimated age of colonization of this species in the results for reference (Table
478 S2).

479

480 **METHOD DETAILS**

481

482

483 **DNA sequences**

484

485 We conducted analyses using the mitochondrial cytochrome-*b* gene (*cyt-b*) because 1) *cyt-b* is
486 considered a reliable marker for use as molecular clock, as heterogeneity in its substitution
487 rate has been shown to be very low across avian lineages [37,38]; 2) the gene is the most
488 widely used sequenced marker in avian studies and sequences are available from previous
489 studies for the majority of our target taxa; 3) previous studies of Macaronesian birds have

490 found concordance between colonization time estimates obtained using only *cyt-b* and using
491 multiple markers [39,40]; 4) using other less-commonly used markers would have required
492 obtaining hundreds of additional bird DNA samples.

493 Although our age estimates are based on a single mitochondrial marker we believe that
494 the inclusion of multiple markers would not significantly alter our age estimates – indeed, a
495 recent phylogenomic study of blue tits (*Cyanistes*) from the Canary Islands found that a multi-
496 marker dataset did not yield significantly different colonization times from those previously
497 obtained using cytochrome-*b* [39,40]. As our approach uses bird sequences from multiple
498 studies we decided to favor larger taxonomic sampling over greater genetic coverage, and in
499 this respect our dataset is unique among phylogenetic syntheses of island birds in its
500 taxonomic completeness. Focusing on a single well-understood marker with the most well-
501 established molecular clock in birds [37,38] allowed us to obtain relative ages that are
502 comparable across taxa and avoid issues associated with calibration in the absence of fossils.

503

504 **Sequence data: Genbank**

505

506 We used Geneious 8 [41] to conduct an extensive search of Genbank for *cyt-b* sequences of
507 Macaronesian and non-Macaronesian taxa fitting the criteria described in the previous section.
508 We also downloaded sequences from outgroup taxa, selecting the sequences with the top
509 similarity scores in the output of BLAST queries. In total, we downloaded 1,001 *cyt-b*
510 sequences from Genbank, including 397 species across 76 genera and 43 of the independent
511 colonization events. The availability of *cyt-b* sequences in Genbank varied greatly according
512 to taxon. For some taxa, sequences from both archipelago and close relatives from outside the
513 archipelago were already available (e.g. from detailed phylogenetic/phylogeographic
514 analyses, such as *Serinus canarius* [42] and *Sylvia spp.* [43]). In other cases, the target species

515 had been sampled, but only from the continent and not from Macaronesia (e.g. *Alaemon*
516 *alaudipes*, *Emberiza calandra*, *Motacilla cinerea*). In others, the sampling of the continental
517 relatives was very poor or only from very distant regions (e.g. *Eremopterix nigriceps*,
518 *Streptopelia decaocto*, *Turdus merula*). Finally, for two species there were no previous *cyt-b*
519 sequences available on Genbank (*Corvus ruficollis*, *Passer iagoensis*). For one of the species,
520 *Sturnus vulgaris*, *cyt-b* sequences were not available in Genbank from target populations.
521 However, many NADH dehydrogenase 2 (ND2) sequences were available for this species,
522 and we therefore used this marker for this species. Genbank accession numbers and
523 geographical origin for all downloaded sequences are available on the maximum clade
524 credibility trees deposited online.

525

526 **Sequence data: new sequences**

527

528 Overall, sequences available on Genbank covered only 55% of the extant Macaronesia
529 independent colonization events. We thus aimed to substantially improve the sampling by
530 producing new sequences for several Macaronesian taxa and their close relatives from
531 continental regions. We focused on the Macaronesian archipelagos as well as in the Iberian
532 Peninsula and North Africa. New samples were obtained during field trips conducted by JCI
533 between 2008 and 2016 to the Azores, Canary Islands, Cape Verde, Madeira, Selvagens,
534 Iberian Peninsula and Morocco. Individuals were captured using mist-nets or spring traps
535 baited with larvae. Blood samples (c. 40 μ L) were taken by brachial venipuncture, diluted in
536 ethanol in a microfuge tube and stored at room temperature. Birds were released at the point
537 of capture. Further samples were obtained from: Alex Tavares (Cape Verde); Ángel Moreno
538 David P. Padilla, and Mariano Hernández (Canary Islands); J.L. Tella (Iberian Peninsula,

539 Morocco, Mauritania), and Guillermo López (Iberian Peninsula). Sample information and
540 Genbank accession numbers for all new specimens are provided in Table S1.

541 DNA was extracted from blood samples using Qiagen DNeasy Blood and Tissue kits
542 (Qiagen, Inc., USA). The *cyt-b* region was amplified using the following primers: L14841
543 (AAA AAG CTT CCA TCC AAC ATC TCA GCA TGA TGA AA) [44]; L14995 (GCC
544 CCA TCC AAC ATC TCA GCA TGA TGA AAC TTC CG) [45]; L15308 (GGC TAT GTC
545 CTC CCA TGA GGC CAA AT); H15767 (ATG AAG GGA TGT TCT ACT GGT TG) [46];
546 H15917 (TAG TTG GCC AAT GAT GAT GAA TGG GTG TTC TAC TGG TT) [45] and
547 H16065 (GAG TCT TCA GTC TCT GGT TTA CAA GAC) [47]. For species of *Motacilla*,
548 *Passer* and *Petronia* we found that the above primers also amplified nuclear mitochondrial
549 DNA segments (NUMTs). In order to avoid NUMTs, we designed the following new primers
550 that were specific to mitochondrial *cyt-b* copies: L-cytB_Passer (CAC AGG CCT AAT TAA
551 AGC CTA CCT), H-cytB_Passer (TTG ARA ATG CCA GCT TTG GGA G, L-cytB-Mot
552 (CCA AAT YGT TAC AGG MCT CCT G), H-cytB-Mot (GGT GAA TGA GGC TAG TTG
553 CCCA).

554 Polymerase chain reactions (PCR) were set up in 25 µl total volumes including 5 µl of
555 buffer MyTaq, 1 µL (10 µM) of each primer, and 0.12 µl MyTaq polymerase. PCRs were
556 performed with the following thermocycler conditions: initial denaturation at 95° C for 1 min
557 followed by 35 cycles of denaturation at 95° C for 20 s, with an annealing temperature of 48
558 °C for 20 s, and extension at 72 °C for 15 s min and a final extension at 72°C for 10 min.
559 Amplified products were purified using Exonuclease I and Antarctic Phosphatase, and
560 sequenced at the University of Potsdam (Unit of Evolutionary Biology/Systematic Zoology)
561 on an ABI PRISM 3130xl sequencer (Applied Biosystems) using the BigDye Terminator v3.1
562 Cycle Sequencing Kit (Applied Biosystems). We used Geneious 8 to edit chromatograms and
563 align sequences. Alignment was unambiguous in all cases.

564 In total, we added 99 new *cyt-b* sequences from 44 different species, covering an
565 additional 27 Macaronesian colonization events that had never before been sampled. The new
566 sequences increase the sampling of *cyt-b* for extant colonization events from the existing 55%
567 (43/78 colonization events) to 90% (70/78). We also substantially increased sampling of
568 continental relatives, adding 39 new *cyt-b* sequences from the Iberian Peninsula and North
569 Africa, covering 28 species.

570

571 **Phylogenetic analyses**

572

573 In order to estimate the times of colonization and speciation of Macaronesian birds, we
574 produced dated phylogenetic trees in BEAST 2 [48]. We produced an alignment for each
575 genus, with the exception of the following genera, which were combined into a single
576 alignment: *Columba* and *Streptopelia*, because they are the only genera from order
577 Columbiformes in our analyses; *Passer* and *Petronia* because they belong to sister clades; the
578 five genera of the lark family Alaudidae (*Alaemon*, *Alauda*, *Ammomanes*, *Calandrella* and
579 *Eremopterix*) because they were recently analysed in a family-wide phylogenetic analysis
580 [49]. In total we produced and analysed 25 alignments leading to 25 phylogenies (trees
581 deposited Mendeley Data). For each alignment we performed substitution model selection in
582 jModeltest [50] using the Bayesian information criterion (models for each alignment available
583 in Mendeley Data).

584 We used rates of molecular evolution for avian *cyt-b* sequences, which have been
585 shown to evolve in a clock-like fashion at an average rate of ~ 2% per Myr [37]. Recent
586 analyses have confirmed the suitability of *cyt-b* as a molecular clock in birds [38]. We used
587 the average *cyt-b* molecular clock rate for the relevant bird order estimated by [37]:
588 Passeriformes – 2.07% (0.01035 substitutions per site per Myr); Columbiformes 1.96%

589 (0.0098); and Piciformes - 3.30% (0.0165). We applied a Bayesian uncorrelated lognormal
590 relaxed clock model. For each analysis, we ran four independent chains of 10 million
591 generations, with a birth-death tree prior. Convergence of chains and appropriate burn-ins
592 were assessed with Tracer and maximum clade credibility trees with mean node heights were
593 produced in Tree Annotator. We produced 25 maximum clade credibility trees (deposited in
594 Mendeley Data) which were used to extract branching times for island species. Data points
595 from taxa of the same archipelago were then assembled together into archipelago-specific
596 datasets which were analyzed with DAISIE.

597

598 **Colonization times**

599

600 For the majority of colonization events, we sampled two or more individuals from each
601 archipelago (Table S2). In most of these cases, the individuals from the same archipelago
602 formed a monophyletic clade, and we used the stem age of this clade as the time of
603 colonization. For 20 colonization events – all of which corresponded to non-endemic species -
604 the multiple individuals from the same archipelago were embedded in a well-supported clade
605 (PP > 0.99) containing other individuals from that species from other regions. Most of these
606 groupings were young (average age 530,000 years), and within-clade resolution was very
607 poor. We therefore assume that the fact that the individuals do not form a distinctive clade is
608 due to incomplete lineage sorting or insufficient phylogenetic information rather than
609 evidence for multiple colonization events by that species. For all such cases we took the age
610 of the most recent common ancestor of the clade containing the individuals from the same
611 archipelago as a maximum age of colonization, and applied the “Non_endemic_MaxAge”
612 option in DAISIE, which integrates over the possible colonization times between the present
613 and the upper bound.

614 For eight of the extant colonization events, no sequences of individuals from the
615 archipelago were available on Genbank and we were not able to obtain samples for new
616 sequencing. However, for these cases we sampled individuals from the same species from
617 different archipelagos and/or from the mainland, and we thus used the MRCA of these
618 individuals as an upper bound for the age of the colonization event, using again the
619 “Non_endemic_MaxAge” option in DAISIE.

620

621 **Treatment of extinct species**

622

623 Thirteen taxa have gone extinct from Macaronesia (Table 1 and S2), and their extinction has
624 been linked to human activities [9,51]. As anthropogenic extinctions do not count towards the
625 natural background rate of extinction, we explicitly include these species in the analyses,
626 treating them as though they had survived until the present following the approach of Valente
627 *et al.* [10]. Of the 13 extinct species, two taxa have been extirpated from the islands but are
628 still extant elsewhere (the wood pigeon from Madeira, and the alpine chough from the Canary
629 Islands). We included these extirpated species in the phylogenetic analyses mentioned above
630 because we sampled sequences from extant populations from other regions and were able to
631 place an upper bound on the time of colonization. From the taxa that have gone completely
632 extinct we were able to obtain samples from an extinct population of the lesser short-toed lark
633 (*Calandrella rufescens rufescens*) from the Canary Islands.

634 The remaining ten extinct species (Table S2) are only known from fossils or subfossils
635 and we were therefore not able to obtain sequences from them. The ten species were endemic
636 to the archipelago where they occurred and were not closely related to extant species, having
637 most likely resulted from independent colonization events. In order to incorporate these taxa
638 into the analyses we modified the DAISIE framework to allow for a new type of data point

639 corresponding to unsampled endemic species. Given that the age of colonization of these
640 extinct species is unknown, the method assumes they could have colonized anytime between
641 the maximum age of the archipelago and the present. We ran DAISIE analyses including and
642 excluding extinct species and found that the main results were not affected – we thus report
643 only the results including extinct species.

644

645 **QUANTIFICATION AND STATISTICAL ANALYSIS**

646

647 **DAISIE analyses**

648

649 DAISIE is a dynamic stochastic island biogeography model [5]. The general DAISIE
650 framework [4,5] assumes that each species on the mainland (source pool) is equally likely to
651 colonize the island, at a per lineage rate γ (which applies to the number of species on the
652 mainland). Colonization includes both dispersal and successful establishment. Each species
653 present on the island is equally likely to go extinct, at a per lineage rate of μ . Island endemic
654 species can be gained through speciation via anagenesis (where an island population diverges
655 through time and becomes reproductively isolated from the mainland source population,
656 without increase in island species diversity), which occurs at a per lineage rate λ^a ; or via
657 cladogenesis (where one island taxon splits into two island endemic species), which occurs at
658 a per lineage rate λ^c . In models including diversity-dependence (M42-M48 and M50 in Table
659 S5), γ and λ^c decline linearly with the number of species on the island, depending on K' , the
660 maximum number of niches on the island that could be attained in the absence of extinction.

661 We developed a new multi-archipelago version of DAISIE that allows different
662 archipelagos to share all or some macroevolutionary rates. This leads to substantial increase in
663 the number of potential data points used for maximum likelihood optimization, and allows us

664 to test whether rates differ between archipelagos. We used this updated version of the DAISIE
665 R package to estimate archipelago-wide diversification and biogeographical rates. We fitted
666 and compared a large set of candidate models that differed in the number of parameters shared
667 between archipelagos (Tables S4 and S5). We estimated the following parameters: rate of
668 colonization (γ), extinction (μ), speciation via cladogenesis (λ^c), speciation via anagenesis
669 (λ^a) and diversity-limits (K'). Model parameters were estimated via maximum likelihood by
670 fitting models to the times of colonization and branching for each of the archipelagos.

671 We assumed a static mainland pool size of 300 species, approximately the number of
672 species of our target group found in Europe and North Africa. Mainland pool size affects
673 DAISIE estimates of colonization rate, which decline with increasing pool size, but not the
674 other rates (extinction, cladogenesis and anagenesis).

675 We used the following published geological ages for the archipelagos: Azores - 6.3 Myr
676 [52]; Canary Islands – 21 Myr [53]; Cape Verde - 15.8 Myr [54]; Madeira – 18.8 Myr [55].
677 We fitted models to a consensus data set representing the colonization and branching times
678 obtained in the maximum clade credibility trees from BEAST 2 and including extinct species.
679 For each model, we ran maximum likelihood optimisations with 20 different, random, initial
680 starting conditions to ensure searches were not trapped on local suboptima.

681 Model comparison was done using BIC, because in DAISIE this criterion has lower
682 error rates [5] and penalizes more complex models. The preferred model using BIC was M17
683 (discussed in the main text), but two other models – M15 and M24 – also carry a large
684 proportion of BIC weight. M15 has an additional anagenesis parameter for the Canary Islands,
685 which is lower than on the other archipelagos; M24 has a single cladogenesis parameter
686 applying to all archipelagos. Our main conclusions – that the four archipelagos are at
687 equilibrium and that the Canaries exhibit exceptional dynamics – are supported by all three
688 models, and thus we focus on the results of M17 as this model has one parameter less than the

689 second best model (M15), it was marginally preferred using BIC in the main analyses and
690 strongly preferred in the analyses assuming a ‘phylogenetic’ taxonomic scheme (BIC weight
691 for M17 was 0.74, versus 0.02 for M15 and 0.09 for M24) .

692 We assessed bias and precision of the ML inferences using a parametric bootstrap
693 approach (Figure S2). We simulated 1,000 data sets for each archipelago with the parameters
694 of the M17 model and then estimated the ML parameters from each of the simulated data sets
695 and compared them with the simulated values.

696

697 **Equilibrium**

698

699 We simulated islands with the ML parameters of the preferred models for each archipelago.
700 For each model, we simulated 5,000 island biota from the birth of the archipelago to the
701 present (Figure 3). This enabled us to assess visually whether the number of species has
702 achieved an asymptotic value, i.e. equilibrium. We additionally used a deterministic equation
703 available within the DAISIE package [10] to calculate the expected total species diversity at
704 equilibrium for each of the archipelagos. The expected number of species at equilibrium is 46
705 species for the Canary Islands and 14 species each for Azores, Cape Verde and Madeira.
706 Because equilibrium is dynamic, species richness stochastically fluctuates around these values
707 [5]. Therefore, at a particular point in time there can be diversity undershoots (e.g. Cape
708 Verde) or overshoots (e.g. Madeira) with respect to the equilibrium value (Figure 3).

709 Recent extinctions caused by humans have affected how distant the system is to the
710 theoretical equilibrium [10] – for example, as a result of the loss of seven species from the
711 Canary Islands by extinction, contemporary diversity (42 species) is currently below
712 equilibrium (46 species), whereas pre-human diversity was actually above equilibrium (49
713 species) (Figure 3).

714 The rate of colonization can affect the rate of approach to equilibrium of non-endemic
715 species (i.e. equilibrium in the number of non-endemics is reached more rapidly under higher
716 colonization), but does not influence equilibrium in endemic species, which in diversity-
717 independent models is determined by the rate of cladogenesis and extinction (see equations in
718 [10]). Because in the preferred model extinction is estimated to be (much) higher than
719 cladogenesis, the time to reach equilibrium in the total number of species is solely determined
720 by extinction – i.e. higher rates of colonization would not lead to equilibrium being reached
721 more quickly.

722

723 **Taxonomy and species status**

724

725 The taxonomy and status (endemic/non-endemic) of many Macaronesian taxa is ‘work in
726 progress’ by the ornithological community, as more morphological and molecular studies
727 become available [36,56]. To account for taxonomic uncertainty, we analysed datasets
728 assuming three alternative classification schemes: 1) ‘conservative’ classification, based on
729 the Clements checklist [57], which does not confer species status to many Macaronesian
730 endemic taxa; 2) ‘current’, which takes into account recent molecular and morphological
731 results from Macaronesian bird studies [36]; and 3) ‘phylogenetic’, under which we consider
732 as endemic species cases where a taxon from an archipelago forms a well-supported
733 monophyletic group older than 1 Myr on our maximum credibility BEAST trees. The taxa for
734 which alternative taxonomies were used are shown in Table S6. The preferred DAISIE model
735 under the ‘current’ and ‘phylogenetic’ classification schemes was the M17 model (Table S5
736 and Mendeley Data, <http://dx.doi.org/10.17632/r9wt6x7d92.1>), whereas for the ‘conservative’
737 scheme the preferred models were M43 and M44, which show very similar BIC weights
738 (Mendeley Data, <http://dx.doi.org/10.17632/r9wt6x7d92.1>). M43 is a diversity-dependent

739 version of M17. M44 is similar to M43 but the Canary Islands differ only in the rate of
740 colonization; the rate of cladogenesis is equal and non-zero across all archipelagos (Table S4).
741 Because the ‘conservative’ scheme is not up to date with recent findings, and because the
742 ‘phylogenetic’ scheme is too liberal, we favour the ‘current’ scheme. In any case, the results
743 for the three alternative classification schemes are fully in agreement with respect to our main
744 conclusions (equilibrium in all four archipelagos has been achieved, homogeneity in rates
745 across archipelagos and the Canary Islands has decoupled dynamics) and therefore in the
746 main text we discuss only the results of the ‘current’ classification scheme. The results of the
747 optimizations of the 50 candidate models for the ‘conservative’ and ‘phylogenetic’ schemes
748 have been deposited in Mendeley Data whereas those for the ‘current’ scheme are provided in
749 Table S5.

750

751 **DATA AND SOFTWARE AVAILABILITY**

752

753 The new **DNA sequences** produced in this study were deposited in Genbank. Accession
754 numbers are given in Table S1.

755

756 The **25 maximum credibility trees from BEAST** are deposited in Mendeley Data:

757 <http://dx.doi.org/10.17632/62p6fsnyfz.2>. These include Genbank numbers and geographical
758 origin of all individuals as well as information on the models and molecular rates used to
759 build each tree.

760

761 The results of the **optimizations of the 50 candidate models** for the ‘conservative’ and
762 ‘phylogenetic’ schemes are deposited in Mendeley Data:

763 <http://dx.doi.org/10.17632/r9wt6x7d92.1>

764

765 New computer code was implemented in a new version of **DAISIE R package** available in:

766 <https://CRAN.R-project.org/package=DAISIE>

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Antibodies		
Bacterial and Virus Strains		
Biological Samples		
Avian blood samples used for DNA isolation	This paper	Table S1
Chemicals, Peptides, and Recombinant Proteins		
DNeasy®Blood & Tissue Kit	Qiagen	Cat#69506
MyTaq™ DNA Polymerase	Bioline GmbH	Cat#BIO-21107
Exonuclease I	New England Biolabs GmbH	Cat#M0293L
Antarctic Phosphatase	New England Biolabs GmbH	Cat#M0289L
BigDye™ Terminator v3.1 Cycle Sequencing Kit	ThermoFisher Scientific – Applied Biosystems	Cat#4337455
Critical Commercial Assays		
Deposited Data		
New cytochrome- <i>b</i> sequences	This paper	Genbank accession numbers in Table S1
25 Maximum clade credibility trees	This paper	Deposited in Mendeley Data: http://dx.doi.org/10.17632/62p6fsnyfz.2
Optimizations of the 50 candidate models	This paper	Deposited in Mendeley Data, http://dx.doi.org/10.17632/r9wt6x7d92.1

Experimental Models: Cell Lines		
Experimental Models: Organisms/Strains		
Oligonucleotides		
L14841: AAAAAGCTTCCATCCAACATCTCAGCATGATGAAA	[44]	N/A
L14995:GCCCCATCCAACATCTCAGCATGATGAAAC TTCCG	[45]	N/A
H15767: ATGAAGGGATGTTCTACTGGTTG	[46]	N/A
H15917: TAGTTGGCCAATGATGATGAATGGGTGTTCTACTGG TT	[45]	N/A
H16065: GAGTCTTCAGTCTCTGGTTTACAAGAC	[47]	N/A
L-cytB_Passer: CACAGGCCTAATTAAAGCCTACCT	This paper	N/A
H-cytB_Passer: TTGARAATGCCAGCTTTGGGAG	This paper	N/A
L-cytB-Mot: CCAAATYGTACAGGMCTCCTG	This paper	N/A
H-cytB-Mot: GGTGAATGAGGCTAGTTGCCCA	This paper	N/A
Recombinant DNA		
Software and Algorithms		
DAISIE R package v.1.4	This paper; [5]	https://cran.r-project.org/web/packages/DAISIE
BEAST 2	[48]	www.beast2.org
Geneious 8	[41]	www.geneious.com
jModeltest 2.1.5	[50]	https://github.com/ddarriba/jmodeltest2
Other		

Figure 1

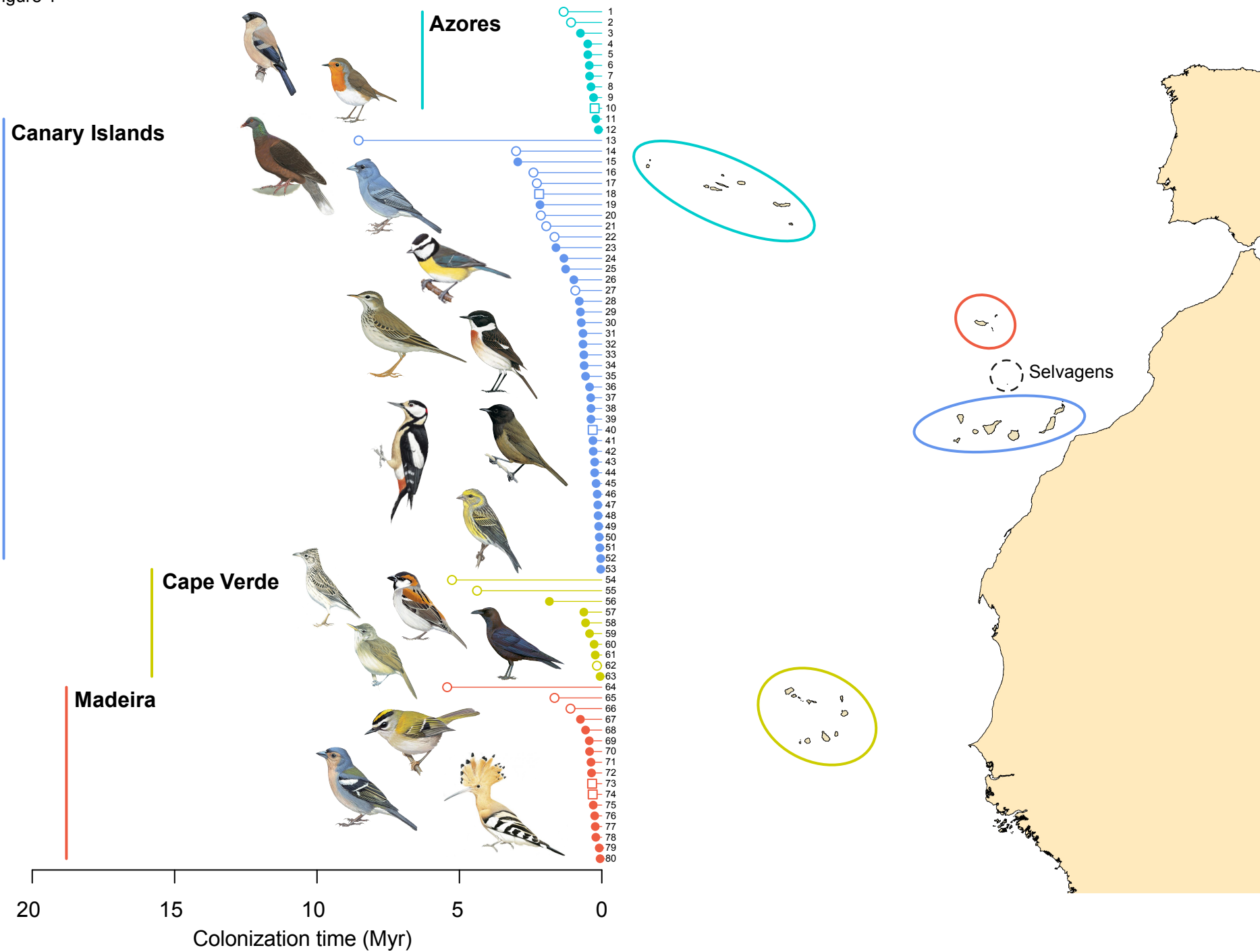


Figure 2

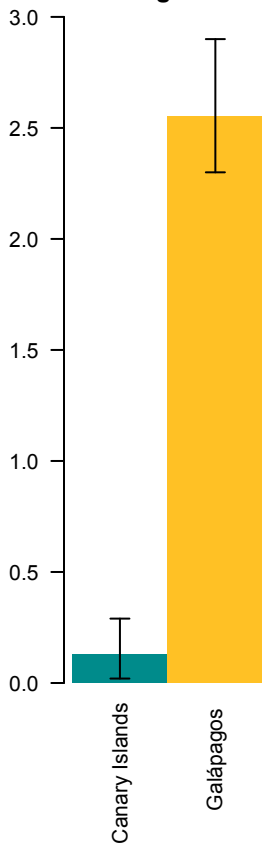
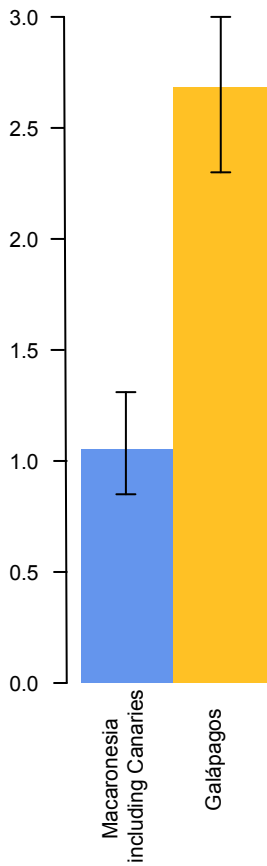
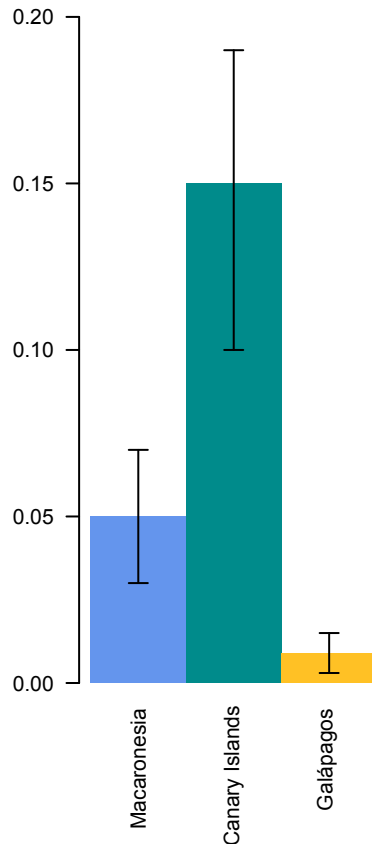
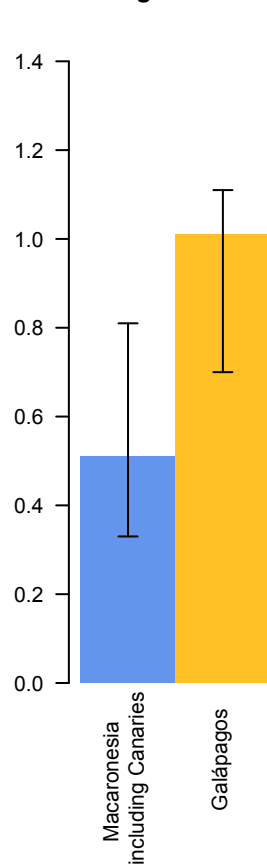
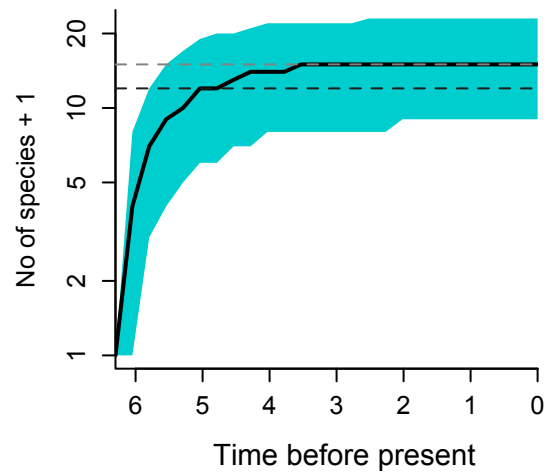
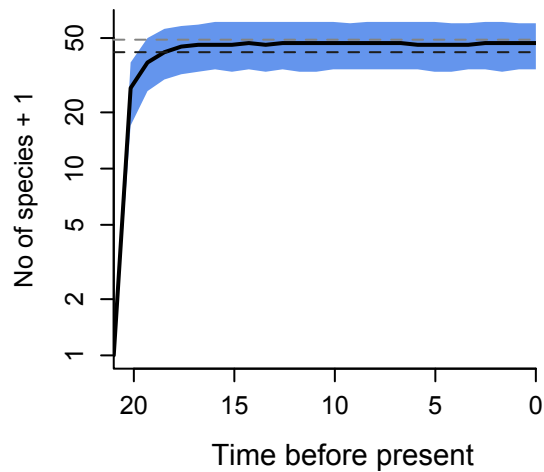
Cladogenesis**Extinction****Colonization****Anagenesis**

Figure 3

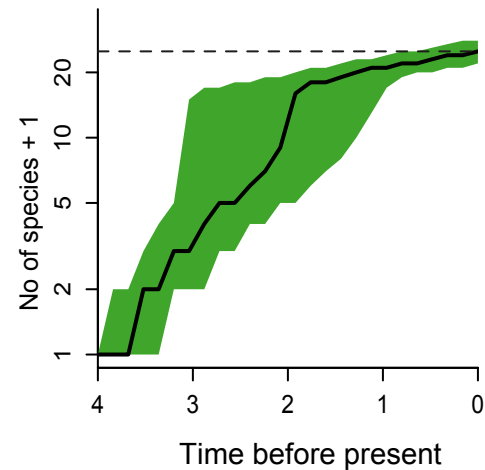
Azores



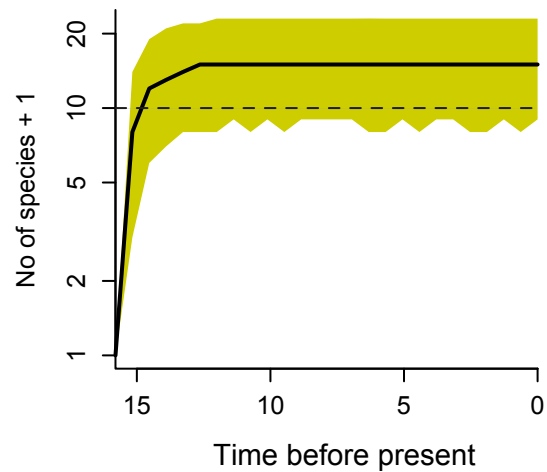
Canary Islands



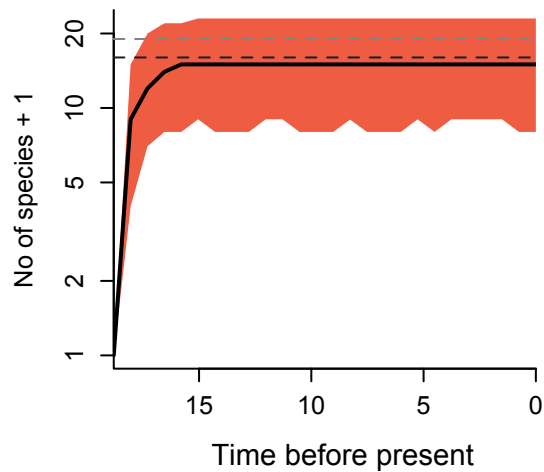
Galápagos



Cape Verde



Madeira



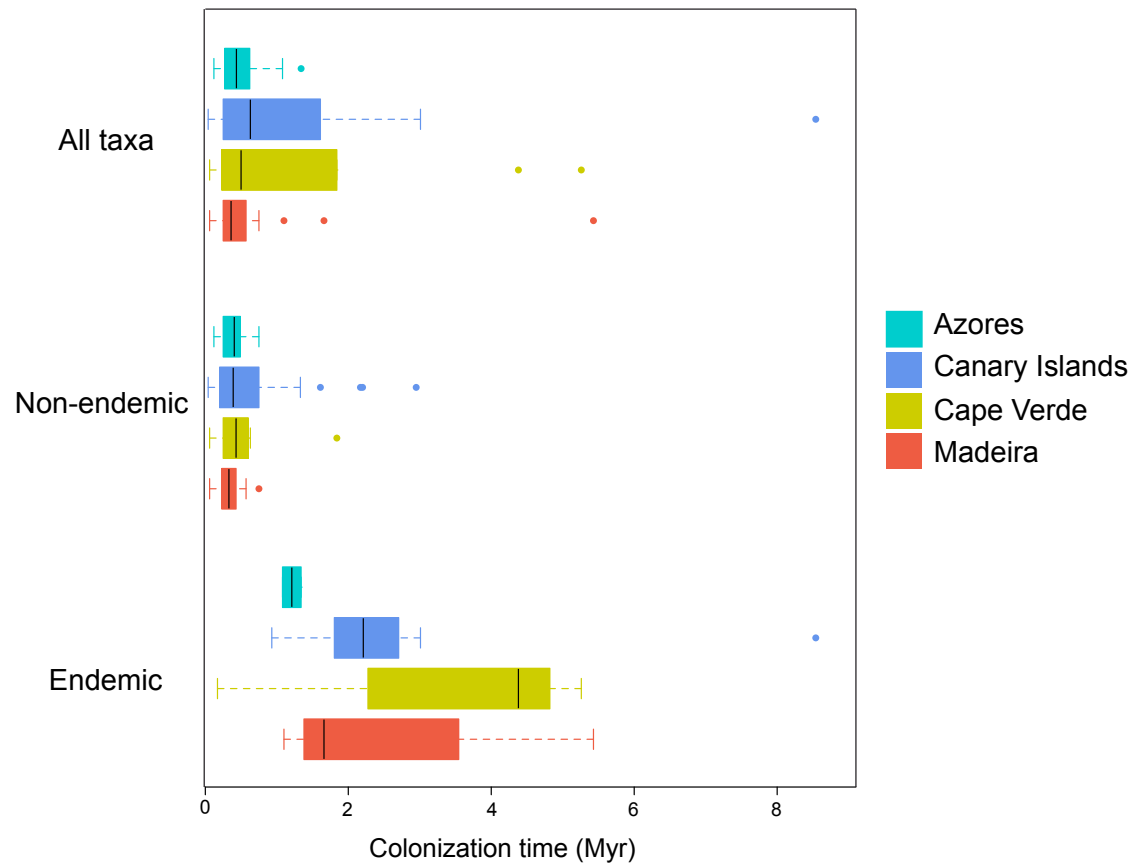


Figure S1 - Distribution of times of colonization of the four archipelagos. Related to Figure 1. Times of colonization obtained from the BEAST analyses.

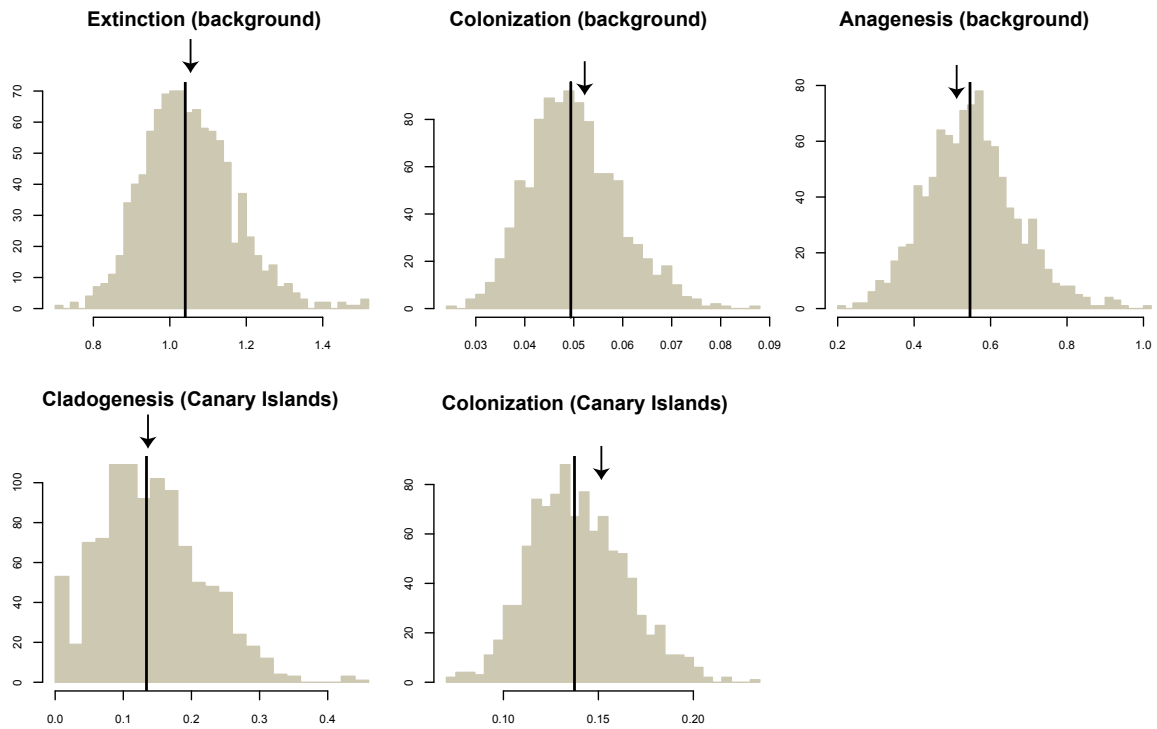


Figure S2 – Bootstrap precision estimates of the parameters of the M17 model. Related to Figure 2. Parametric bootstrap analysis fitting the M17 model to 1,000 datasets simulated with maximum likelihood parameters of M17 model. Plots show frequency histograms of estimated parameters. Black lines show the median estimated values across all simulations and the arrows the simulated values. Background – indicates that the parameter is shared across all archipelagos (extinction and anagenesis) or most archipelagos (colonization).

Table S1 – Sample information for all new samples sequenced for this study. Related to Figure 1 and STAR Methods.

Genus	Species	Subspecies	Region	Locality	Collector	Code	Genbank accession #
<i>Acrocephalus</i>	<i>brevipennis</i>		Cape Verde	Santiago	J.C. Illera	L313_CV1	KY378711
<i>Alaemon</i>	<i>alaudipes</i>		Cape Verde	Maio	Alex Tavares	L578	KY378712
<i>Alaemon</i>	<i>alaudipes</i>		Morocco	Lago Ait-Serji	J.L. Tella	L586_V077710	KY378713
<i>Ammomanes</i>	<i>cinctura</i>		Cape Verde	Santiago	J.C. Illera	L316_CV20	KY378714
<i>Anthus</i>	<i>berthelotii</i>	<i>berthelotii</i>	Canary Islands	Fuerteventura	J.C. Illera	L324_FV6	KY378716
<i>Anthus</i>	<i>campestris</i>		Iberian Peninsula	Sierra Nevada	J.C. Illera	L360_PN442	KY378719
<i>Anthus</i>	<i>berthelotii</i>	<i>maderensis</i>	Madeira	Porto Santo	J.C. Illera	L367_AB814	KY378717
<i>Anthus</i>	<i>berthelotii</i>	<i>maderensis</i>	Madeira	Deserta Grande	J.C. Illera	L368_AB549	KY378718
<i>Anthus</i>	<i>berthelotii</i>		Selvagens	Selvagem Grande	J.C. Illera	L377_AB867	KY378715
<i>Bucanetes</i>	<i>githagineus</i>	<i>amantum</i>	Canary Islands	Fuerteventura	J.C. Illera	L321_FV3	KY378721
<i>Bucanetes</i>	<i>githagineus</i>		Morocco	Lago Ait-Serji	J.L. Tella	L587_L955050	KY378720
<i>Calandrella</i>	<i>rufescens</i>	<i>polatzeki</i>	Canary Islands	Fuerteventura	J.C. Illera	L326_FV8	KY378724
<i>Calandrella</i>	<i>rufescens</i>		Iberian Peninsula	Planerón	J.L. Tella	L341_IP1	KY378722
<i>Calandrella</i>	<i>rufescens</i>		Iberian Peninsula	Planerón	J.L. Tella	L590_N643392	KY378723
<i>Calandrella</i>	<i>rufescens</i>	<i>rufescens</i>	Canary Islands	Captive / Tenerife	Mariano Hernández	L591	KY378725
<i>Carduelis</i>	<i>cannabina</i>	<i>harteri</i>	Canary Islands	Fuerteventura	J.C. Illera	L325_FV7	KY378728
<i>Carduelis</i>	<i>carduelis</i>		Iberian Peninsula	Córdoba	J.C. Illera	L345_IP5	KY378731
<i>Carduelis</i>	<i>cannabina</i>		Iberian Peninsula	Sierra Nevada	J.C. Illera	L350_PN1316	KY378726
<i>Carduelis</i>	<i>chloris</i>		Iberian Peninsula	Sierra Nevada	J.C. Illera	L359_PN357	KY378733
<i>Carduelis</i>	<i>chloris</i>		Morocco	Ain-El-Hallouf	J.C. Illera	L374_MO6	KY378734
<i>Carduelis</i>	<i>cannabina</i>		Morocco	Ain-El-Hallouf	J.C. Illera	L375_MO7	KY378727
<i>Carduelis</i>	<i>cannabina</i>	<i>meadewaldoi</i>	Canary Islands	Tenerife	J.C. Illera	L379_Va2	KY378730
<i>Carduelis</i>	<i>carduelis</i>		Canary Islands	La Gomera	J.C. Illera	L380_Va3	KY378732
<i>Carduelis</i>	<i>chloris</i>		Canary Islands	Tenerife	J.C. Illera	L382_Va5	KY378735
<i>Carduelis</i>	<i>cannabina</i>	<i>harteri</i>	Canary Islands	Lanzarote	J.C. Illera	L390_Va13	KY378729
<i>Columba</i>	<i>livia</i>		Canary Islands	Fuerteventura	J.C. Illera	L323_FV5	KY378736
<i>Columba</i>	<i>livia</i>		Azores	Graciosa	J.C. Illera	L391_Coli1	KY378737
<i>Columba</i>	<i>livia</i>		Azores	Graciosa	J.C. Illera	L392_Coli2	KY378738
<i>Columba</i>	<i>livia</i>		Cape Verde	Cape Verde	Alex Tavares	L579	KY378739
<i>Corvus</i>	<i>ruficollis</i>		Cape Verde	Maio	Alex Tavares	L592_Corvo220	KY378740
<i>Cyanistes</i>	<i>teneriffae</i>	<i>palmensis</i>	Canary Islands	La Palma	J.C. Illera	L332_PN496	KY378743
<i>Cyanistes</i>	<i>teneriffae</i>	<i>degener</i>	Canary Islands	Fuerteventura	J.C. Illera	L338_FV1	KY378742

<i>Cyanistes</i>	<i>caeruleus</i>		Iberian Peninsula	Sierra Nevada	J.C. Illera	L357_PN254	KY378741
<i>Dendrocopos</i>	<i>major</i>		Iberian Peninsula	Sierra Nevada	J.C. Illera	L349_PN1295	KY378744
<i>Emberiza</i>	<i>calandra</i>		Iberian Peninsula	Lumbrales	G. López	L344_IP4	KY378745
<i>Emberiza</i>	<i>calandra</i>		Canary Islands	Tenerife	D.P. Padilla	L581_V021108	KY378746
<i>Eremopterix</i>	<i>nigriceps</i>		Cape Verde	Santiago	J.C. Illera	L315_CV19	KY378747
<i>Eremopterix</i>	<i>nigriceps</i>		Cape Verde	Cape Verde	Alex Tavares	L576	KY378748
<i>Eremopterix</i>	<i>nigriceps</i>		Mauritania	El Metreoka	J.L. Tella	L588_45	KY378749
<i>Erithacus</i>	<i>rubecula</i>	<i>rubecula</i>	Canary Islands	La Palma	J.C. Illera	L330_PN492	KY378751
<i>Erithacus</i>	<i>rubecula</i>		Madeira	Santa Pico Alto	J.C. Illera	L558_MADE05	KY378750
<i>Fringilla</i>	<i>coelebs</i>	<i>palmae</i>	Canary Islands	La Palma	J.C. Illera	L331_PN493	KY378753
<i>Fringilla</i>	<i>coelebs</i>		Iberian Peninsula	Sierra Nevada	J.C. Illera	L352_PN157	KY378752
<i>Fringilla</i>	<i>coelebs</i>		Morocco	Ifrane	J.C. Illera	L369_MO1	KY378754
<i>Lanius</i>	<i>meridionalis</i>	<i>koenigi</i>	Canary Islands	Fuerteventura	J.C. Illera	L322_FV4	KY378755
<i>Motacilla</i>	<i>cinerea</i>		Iberian Peninsula	Sierra Nevada	G. López	L358_PN325	KY378756
<i>Motacilla</i>	<i>cinerea</i>	<i>patriciae</i>	Azores	Terceira	J.C. Illera	L378_Va1	KY378761
<i>Motacilla</i>	<i>cinerea</i>	<i>canariensis</i>	Canary Islands	Tenerife	J.C. Illera	L381_Va4	KY378760
<i>Motacilla</i>	<i>cinerea</i>		Madeira	Lombo do Baixo, Faial	J.C. Illera	L560_MADE74	KY378757
<i>Motacilla</i>	<i>cinerea</i>		Morocco	Morocco	J.C. Illera	L582_0001213	KY378758
<i>Motacilla</i>	<i>cinerea</i>		Iberian Peninsula	Sierra Nevada	J.C. Illera	L583_PN325	KY378759
<i>Passer</i>	<i>iagoensis</i>		Cape Verde	Santiago	J.C. Illera	L314_CV10	KY378765
<i>Passer</i>	<i>hispaniolensis</i>		Cape Verde	Santiago	J.C. Illera	L317_CV6	KY378762
<i>Passer</i>	<i>hispaniolensis</i>		Canary Islands	Fuerteventura	J.C. Illera	L320_FV2	KY378763
<i>Passer</i>	<i>montanus</i>		Iberian Peninsula	Madrid	J.C. Illera	L343_IP3	KY378767
<i>Passer</i>	<i>hispaniolensis</i>		Iberian Peninsula	Córdoba	J.C. Illera	L346_IP6	KY378764
<i>Passer</i>	<i>iagoensis</i>		Cape Verde	Maio	A. Tavares	L577	KY378766
<i>Passer</i>	<i>montanus</i>		Canary Islands	Gran Canaria	A. Moreno	L593_L555950	KY378768
<i>Petronia</i>	<i>petronia</i>	<i>petronia</i>	Canary Islands	Tenerife	J.C. Illera	L383_Va6	KY378769
<i>Phylloscopus</i>	<i>canariensis</i>		Canary Islands	La Palma	J.C. Illera	L333_PN611	KY378770
<i>Phylloscopus</i>	<i>collybita</i>		Iberian Peninsula	Lumbrales	J.C. Illera	L339_GUI1	KY378771
<i>Phylloscopus</i>	<i>ibericus</i>		Iberian Peninsula	Trassierra	J.C. Illera	L340_GUI7	KY378772
<i>Pyrrhonorax</i>	<i>pyrrhonorax</i>		Canary Islands	La Palma	J.C. Illera	L384_Va7	KY378773
<i>Pyrrhula</i>	<i>pyrrhula</i>		Iberian Peninsula	Picos de Europa	J.C. Illera	L361_PN63	KY378774
<i>Regulus</i>	<i>regulus</i>	<i>ellenthalerae</i>	Canary Islands	La Palma	J.C. Illera	L335_PN654	KY378777

<i>Regulus</i>	<i>ignicapillus</i>		Iberian Peninsula	Sierra Nevada	J.C. Illera	L348_PN1226	KY378775
<i>Regulus</i>	<i>regulus</i>		Iberian Peninsula	Picos de Europa	J.C. Illera	L353_PN1918	KY378776
<i>Saxicola</i>	<i>dacotiae</i>	<i>dacotiae</i>	Canary Islands	Fuerteventura	J.C. Illera	L336_Sax 911	KY378778
<i>Saxicola</i>	<i>torquata</i>	<i>rubicola</i>	Iberian Peninsula	Sierra Nevada	J.C. Illera	L354_PN200	KY378779
<i>Serinus</i>	<i>canarius</i>		Canary Islands	La Palma	J.C. Illera	L334_PN645	KY378780
<i>Serinus</i>	<i>serinus</i>		Iberian Peninsula	Sierra Nevada	J.C. Illera	L355_PN207	KY378782
<i>Serinus</i>	<i>canarius</i>		Madeira	Porto Santo	J.C. Illera	L365_SC 444	KY378781
<i>Serinus</i>	<i>serinus</i>		Morocco	Ain-El-Hallouf	J.C. Illera	L373_MO5	KY378783
<i>Serinus</i>	<i>serinus</i>		Canary Islands	Gran Canaria	J.C. Illera	L385_Va8	KY378784
<i>Streptopelia</i>	<i>turtur</i>		Canary Islands	Tenerife	J.C. Illera	L386_Va9	KY378787
<i>Streptopelia</i>	<i>decaocto</i>		Iberian Peninsula	Málaga	G. López	L575	KY378785
<i>Streptopelia</i>	<i>decaocto</i>		Canary Islands	Tenerife	J.C. Illera	L589_Va10	KY378786
<i>Streptopelia</i>	<i>turtur</i>		Iberian Peninsula	Andújar (Jaén)	G. López	L594	KY378788
<i>Sylvia</i>	<i>atricapilla</i>		Cape Verde	Santiago	J.C. Illera	L318_CV7	KY378789
<i>Sylvia</i>	<i>conspicillata</i>		Cape Verde	Maio	J.C. Illera	L319_SC272	KY378792
<i>Sylvia</i>	<i>atricapilla</i>	<i>heineken</i>	Canary Islands	La Palma	J.C. Illera	L328_PN488	KY378791
<i>Sylvia</i>	<i>melanocephalaleucogastra</i>		Canary Islands	La Palma	J.C. Illera	L329_PN491	KY378799
<i>Sylvia</i>	<i>conspicillata</i>	<i>orbitalis</i>	Canary Islands	Tenerife	J.C. Illera	L337_SC61	KY378796
<i>Sylvia</i>	<i>melanocephala</i>		Iberian Peninsula	Sierra Nevada	J.C. Illera	L351_PN155	KY378797
<i>Sylvia</i>	<i>conspicillata</i>	<i>conspicillata</i>	Iberian Peninsula	Granada	J.C. Illera	L363_SC133	KY378794
<i>Sylvia</i>	<i>conspicillata</i>		Madeira	Porto Santo	J.C. Illera	L364_SC 403	KY378793
<i>Sylvia</i>	<i>atricapilla</i>		Madeira	Porto Santo	J.C. Illera	L366_SC 445	KY378790
<i>Sylvia</i>	<i>melanocephala</i>		Morocco	Ain-El-Hallouf	J.C. Illera	L372_MO4	KY378798
<i>Sylvia</i>	<i>conspicillata</i>	<i>conspicillata</i>	Morocco	Ifrane	J.C. Illera	L376_SC8	KY378795
<i>Turdus</i>	<i>merula</i>		Canary Islands	La Palma	J.C. Illera	L327_PN472	KY378800
<i>Turdus</i>	<i>merula</i>		Iberian Peninsula	Sierra Nevada	J.C. Illera	L347_PN1086	KY378801
<i>Turdus</i>	<i>merula</i>		Morocco	Ain-El-Hallouf	J.C. Illera	L370_MO2	KY378802
<i>Turdus</i>	<i>merula</i>		Madeira	Santa Pico Alto	J.C. Illera	L559_MADE08	KY378803
<i>Turdus</i>	<i>merula</i>		Azores	Pico	J.C. Illera	L603_T1	KY378804
<i>Turdus</i>	<i>merula</i>		Azores	Terceira	J.C. Illera	L604_T2	KY378805
<i>Turdus</i>	<i>merula</i>		Azores	Terceira	J.C. Illera	L605_T3	KY378806
<i>Upupa</i>	<i>epops</i>		Iberian Peninsula	Sierra Nevada	J.C. Illera	L342_IP2	KY378807
<i>Upupa</i>	<i>epops</i>		Canary Islands	Tenerife	J.C. Illera	L388_Va11	KY378808
<i>Upupa</i>	<i>epops</i>		Canary Islands	Tenerife	J.C. Illera	L389_Va12	KY378809

Table S2 – Colonization events of Macaronesia for all the taxa in our focal group. Related to Figure 1.
Including extinct species. Times of colonization taken from the maximum clade credibility trees from BEAST.

Archipelago	Taxon	Status	Colonization time (Myr)	95% CI (Myr)	Topology	Node used for age	Fig. 1
Azores	<i>Fringilla moreletii</i>	Endemic	1.34	0.91 - 1.8	A	St	1
Azores	<i>Pyrrhula murina</i>	Endemic	1.08	0.50 - 1.85	A	St	2
Azores	<i>Erithacus rubecula</i>	Non endemic	0.75	0.32 - 1.13	B	Mrca	3
Azores	<i>Turdus merula azorensis</i>	Non endemic	0.493	0.27 - 0.74	B	Mrca	4
Azores	<i>Regulus regulus</i>	Non endemic	0.49	0.26 - 0.75	A	St	5
Azores	<i>Carduelis carduelis</i>	Non endemic	0.44	0.14 - 0.82	D	Cr	6
Azores	<i>Sylvia atricapilla atlantis</i>	Non endemic	0.43	0.18 - 0.73	B	Mrca	7
Azores	<i>Motacilla cinerea</i>	Non endemic	0.38	0.10 - 0.71	C	Mrca	8
Azores	<i>Columba livia atlantis</i>	Non endemic	0.29	0.13 - 0.47	A	St	9
Azores	<i>Serinus canarius</i>	Macaronesian endemic	0.25	0.10 - 0.43	A	St	10
Azores	<i>Columba palumbus azorica</i>	Non endemic	0.21	0.07 - 0.38	B	Mrca	11
Azores	<i>Sturnus vulgaris granti</i>	Non endemic	0.12	0.03 - 0.26	A	St	12
Azores	<i>Pyrrhula</i> spp. †	Extinct	NA	NA	E	Na	-
Azores	Undescribed taxon aff. family Troglodytidae †	Extinct	NA	NA	E	Na	-
Azores	<i>Turdus</i> spp. 1 †	Extinct	NA	NA	E	Na	-
Canary Isl.	<i>Columba junoniae</i>	Endemic	8.54	6.49 - 10.98	A	St	13
Canary Isl.	<i>Fringilla teydea / polatzeki</i>	Endemic	3.01	2.15 - 3.87	A	St	14
Canary Isl.	<i>Erithacus rubecula marionae</i>	Non endemic	2.95	1.46 - 4.59	A	St	15
Canary Isl.	<i>Cyanistes teneriffae palmensis</i>	Endemic	2.4	1.35 - 3.44	A	St	16
Canary Isl.	<i>Phylloscopus canariensis</i>	Endemic	2.28	1.59 - 3.02	A	St	17
Canary Isl.	<i>Anthus berthelotii</i>	Macaronesian endemic	2.2	1.42 - 3.07	A	St	18
Canary Isl.	<i>Erithacus rubecula superbus</i>	Non endemic	2.17	0.99 - 3.25	A	St	19
Canary Isl.	<i>Columba bollii</i>	Endemic	2.14	1.42- 2.91	A	St	20
Canary Isl.	<i>Saxicola dacotiae</i>	Endemic	1.95	1.29 - 2.62	A	St	21
Canary Isl.	<i>Cyanistes teneriffae Central group</i>	Endemic	1.66	1.03 - 2.32	A	St	22
Canary Isl.	<i>Regulus regulus teneriffae</i>	Non endemic	1.61	1.08 - 2.14	A	St	23
Canary Isl.	<i>Regulus regulus ellenthalerae</i>	Non endemic	1.33	0.87 - 1.82	A	St	24
Canary Isl.	<i>Passer hispaniolensis</i>	Non endemic	1.27	0.73 - 1.84	B	Mrca	25
Canary Isl.	<i>Dendrocopos major</i>	Non endemic	0.98	0.21 - 2.25	A	St	26
Canary Isl.	<i>Fringilla canariensis</i>	Endemic	0.93	0.57 - 1.32	A	St	27
Canary Isl.	<i>Calandrella rufescens rufescens</i> †	Extirpated	0.79	0.25 - 1.52	C	Tip	28
Canary Isl.	<i>Erithacus rubecula rubecula</i>	Non endemic	0.75	0.32 - 1.13	B	Mrca	29
Canary Isl.	<i>Bucanetes githagineus</i>	Non endemic	0.72	0.34 - 1.16	B	Mrca	30

Canary Isl.	<i>Pyrrhocorax graculus</i> †	Extirpated	0.66	0.09 - 1.27	D	Cr	31
Canary Isl.	<i>Corvus corax</i>	Non endemic	0.66	0.34 - 1.03	B	Mrca	32
Canary Isl.	<i>Columba livia</i>	Non endemic	0.63	0.30 - 1.07	C	Mrca	33
Canary Isl.	<i>Sylvia melanocephala</i>	Non endemic	0.62	0.32 - 0.97	B	Mrca	34
Canary Isl.	<i>Sylvia conspicillata</i>	Non endemic	0.57	0.27 - 0.95	B	Mrca	35
Canary Isl.	<i>Sylvia atricapilla</i>	Non endemic	0.43	0.18 - 0.73	B	Mrca	36
Canary Isl.	<i>Lanius meridionalis</i>	Non endemic	0.39	0.20 - 0.62	B	Mrca	37
Canary Isl.	<i>Sturnus vulgaris</i>	Non endemic	0.38	0.20 - 0.60	D	Cr	38
Canary Isl.	<i>Motacilla cinerea</i>	Non endemic	0.38	0.10 - 0.71	C	Mrca	39
Canary Isl.	<i>Serinus canarius</i>	Macaronesian endemic	0.32	0.12 - 0.56	B	Mrca	40
Canary Isl.	<i>Pyrrhocorax pyrrhocorax</i>	Non endemic	0.31	0.02 - 0.90	C	Tip	41
Canary Isl.	<i>Carduelis cannabina</i>	Non endemic	0.3	0.08 - 0.56	B	Mrca	42
Canary Isl.	<i>Petronia petronia</i>	Non endemic	0.25	0.03 - 0.51	C	Tip	43
Canary Isl.	<i>Cyanistes teneriffae</i> East	Non endemic	0.25	0.09 - 0.42	B	Mrca	44
Canary Isl.	<i>Carduelis carduelis</i>	Non endemic	0.2	0.03 - 0.41	A	St	45
Canary Isl.	<i>Carduelis chloris</i>	Non endemic	0.16	0.03 - 0.33	A	St	46
Canary Isl.	<i>Passer montanus</i>	Non endemic	0.14	0.004 - 0.3	C	Tip	47
Canary Isl.	<i>Calandrella rufescens polatzeki</i>	Non endemic	0.13	0.01 - 0.28	C	Tip	48
Canary Isl.	<i>Streptopelia decaocto</i>	Non endemic	0.11	0.01 - 0.23	C	Tip	49
Canary Isl.	<i>Upupa epops</i>	Non endemic	0.09	0.003 - 0.22	A	St	50
Canary Isl.	<i>Turdus merula</i>	Non endemic	0.07	0 - 0.16	C	Tip	51
Canary Isl.	<i>Serinus serinus</i>	Non endemic	0.04	0 - 0.13	C	Tip	52
Canary Isl.	<i>Emberiza calandra</i>	Non endemic	0.04	0 - 0.12	C	Tip	53
Canary Isl.	<i>Carduelis aurelioi</i> †	Extinct	NA	NA	E	Na	-
Canary Isl.	<i>Carduelis triasi</i> †	Extinct	NA	NA	E	Na	-
Canary Isl.	<i>Emberiza alcoveri</i> †	Extinct	NA	NA	E	Na	-
Canary Isl.	<i>Erithacus</i> spp. †	Extinct	NA	NA	E	Na	-
Canary Isl.	<i>Turdus</i> spp. 2 †	Extinct	NA	NA	E	Na	-
Cape Verde	<i>Alauda razae</i>	Endemic	5.26	3.90 - 6.73	C	Tip	54
Cape Verde	<i>Passer iagoensis</i>	Endemic	4.38	3.10 - 5.86	A	St	55
Cape Verde	<i>Corvus ruficollis</i>	Non endemic	1.84	0.93 - 2.68	C	Tip	56
Cape Verde	<i>Columba livia</i>	Non endemic	0.63	0.30 - 1.07	C	Mrca	57
Cape Verde	<i>Sylvia conspicillata</i>	Non endemic	0.57	0.27 - 0.95	B	Mrca	58
Cape Verde	<i>Sylvia atricapilla</i>	Non endemic	0.43	0.18 - 0.73	C	Mrca	59
Cape Verde	<i>Eremopterix nigriceps</i>	Non endemic	0.27	0.07 - 0.50	A	St	60
Cape Verde	<i>Ammomanes cinctura</i>	Non endemic	0.23	0.07 - 0.42	C	Tip	61
Cape Verde	<i>Acrocephalus brevipennis</i>	Endemic	0.17	0.03 - 0.34	A	St	62
Cape Verde	<i>Alaemon alaudipes</i>	Non endemic	0.06	0 - 0.17	C	Tip	63
Madeira	<i>Regulus madeirensis</i>	Endemic	5.43	3.39 - 7.45	A	St	64
Madeira	<i>Columba trocaz</i>	Endemic	1.66	1.04 - 2.31	A	St	65
Madeira	<i>Fringilla madeirensis</i>	Endemic	1.1	0.73 - 1.51	A	St	66

Madeira	<i>Erithacus rubecula</i>	Non endemic	0.75	0.32 - 1.13	B	Mrca	67
Madeira	<i>Sylvia conspicillata</i>	Non endemic	0.57	0.27 - 0.95	C	Mrca	68
Madeira	<i>Carduelis carduelis</i>	Non endemic	0.44	0.14 - 0.71	D	Cr	69
Madeira	<i>Sylvia atricapilla</i>	Non endemic	0.43	0.18 - 0.73	B	Mrca	70
Madeira	<i>Motacilla cinerea</i>	Non endemic	0.38	0.10 - 0.71	C	Mrca	71
Madeira	<i>Carduelis chloris</i>	Non endemic	0.36	0.14 - 0.58	D	Cr	72
Madeira	<i>Anthus berthelotti</i>	Macaronesian endemic	0.34	0.13 - 0.58	B	Mrca	73
Madeira	<i>Serinus canarius</i>	Macaronesian endemic	0.32	0.12 - 0.56	B	Mrca	74
Madeira	<i>Carduelis cannabina</i>	Non endemic	0.3	0.08 - 0.56	D	Cr	75
Madeira	<i>Petronia petronia</i>	Non endemic	0.25	0.03 - 0.51	D	Cr	76
Madeira	<i>Streptopelia decaocto</i>	Non endemic	0.23	0.07 - 0.42	D	Cr	77
Madeira	<i>Columba palumbus</i> †	Extirpated	0.21	0.07 - 0.38	D	Cr	78
Madeira	<i>Upupa epops</i>	Non endemic	0.09	0.003 - 0.22	D	Cr	79
Madeira	<i>Turdus merula</i>	Non endemic	0.06	0 - 0.14	C	Tip	80
Madeira	Fringillidae spp. †	Extinct	NA	NA	E	Na	-
Madeira	<i>Turdus</i> spp. 3 †	Extinct	NA	NA	E	Na	-
Selvagens	<i>Anthus berthelotti</i>	Macaronesian endemic	0.34	0.13 - 0.58	C	Cr	-

A - Two or more individuals from archipelago sampled, archipelago individuals form monophyletic clade
B - Two or more individuals from archipelago sampled, archipelago individuals do not form exclusive clade
C - One individual sampled from archipelago
D - Species sampled, but from population outside the archipelago
E - Species not sampled in phylogeny
Cr - Crown age of species used
Mrca - Age of most recent common ancestor of clade containing the individuals from archipelago used
St - Stem age used
Tip - Age of tip of individual sample used
Na - Not available
† - Extinct/extirpated

Table S3 – Cladogenetic events in Macaronesian birds. Related to Figure 1. Branching times taken from the maximum clade credibility trees from BEAST.

Archipelago	Clade name	Species	Branching times (Myr)	95% CI, lower bound (Myr)	95% CI, upper bound(Myr)
Canary Islands	<i>Cyanistes teneriffae</i> (Central)	<i>C. teneriffae</i> , <i>C. hedwigae</i> , <i>C. ombriosus</i>	1.7, 1.1, 0.6	1.0, 0.7, 0.3	2.3, 1.7, 0.9
Canary Islands	<i>Fringilla</i>	<i>F. teydea</i> , <i>F. polatzeki</i>	3.0, 1.2	2.2, 0.7	3.9, 1.8

Table S6 – Taxa for which three alternative classification schemes were used. Related to Figure 1. The ‘conservative’ scheme is based on the Clements Checklist [S1]; the ‘current’ scheme is based on Illera *et al.* [S2] who reviewed latest taxonomic findings; the ‘phylogenetic’ scheme is similar to the ‘current’ scheme, but additionally treats as endemic species cases where a taxon from an archipelago forms a strongly supported monophyletic group older than 1 Myr in our BEAST trees.

Archipelago	‘Conservative’	‘Current’	‘Phylogenetic’
Canary Isl.	<i>Cyanistes teneriffae</i> (non-endemic)	<i>Cyanistes palmensis</i> (endemic)	<i>Cyanistes palmensis</i> (endemic)
Canary Isl.	<i>Cyanistes teneriffae</i> (non-endemic)	<i>Cyanistes teneriffae</i> Central group, (3 endemic species: <i>C. teneriffae</i> , <i>C. hedwigae</i> , <i>C. ombriosus</i>)	<i>Cyanistes teneriffae</i> Central group, (3 endemic species: <i>C. teneriffae</i> , <i>C. hedwigae</i> , <i>C. ombriosus</i>)
Canary Isl.	<i>Erithacus rubecula</i> (non-endemic)	<i>Erithacus rubecula</i> (non-endemic)	<i>Erithacus marionae</i> (endemic)
Canary Isl.	<i>Erithacus rubecula</i> (non-endemic)	<i>Erithacus rubecula</i> (non-endemic)	<i>Erithacus superbus</i> (endemic)
Madeira	<i>Fringilla coelebs</i> (non-endemic)	<i>Fringilla madeirensis</i> (endemic)	<i>Fringilla madeirensis</i> (endemic)
Azores	<i>Fringilla coelebs</i> (non-endemic)	<i>Fringilla moreletii</i> (endemic)	<i>Fringilla moreletii</i> (endemic)
Canary Isl.	<i>Fringilla coelebs</i> (non-endemic)	<i>Fringilla canariensis</i> (endemic)	<i>Fringilla canariensis</i> (endemic)
Canary Isl.	<i>Fringilla teydea</i> (single endemic species)	<i>Fringilla teydea</i> , <i>Fringilla polatzeki</i> (2 endemic species)	<i>Fringilla teydea</i> , <i>Fringilla polatzeki</i> (2 endemic species)
Madeira	<i>Regulus ignicapillus</i> (non-endemic)	<i>Regulus madeirensis</i> (endemic)	<i>Regulus madeirensis</i> (endemic)
Canary Isl.	<i>Regulus regulus</i> (non-endemic)	<i>Regulus regulus</i> (non-endemic)	<i>Regulus teneriffae</i> (endemic)
Canary Isl.	<i>Regulus regulus</i> (non-endemic)	<i>Regulus regulus</i> (non-endemic)	<i>Regulus ellenthalerae</i> (endemic)

SUPPLEMENTAL REFERENCES

- S1. Clements, J.F., Schulenberg, T.S., Iliff, M.J., Roberson, D., Fredericks, T.A., Sullivan, B.L., and Wood, C.L. (2016). The eBird/Clements checklist of birds of the world: v2016.
- S2. Illera, J.C., Spurgin, L.G., Rodriguez-Exposito, E., Nogales, M., and Rando, J.C. (2016). What are we learning about speciation and extinction from the Canary Islands? *Ardeola* 63, 5–23.