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# 1 **A simple dynamic model explains island bird diversity worldwide**

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29 Colonisation, speciation and extinction are dynamic processes that influence  
30 global patterns of species richness<sup>1-6</sup>. Island biogeography theory predicts that  
31 the contribution of these processes to the build-up of species diversity depends  
32 on area and isolation<sup>7,8</sup>. Remarkably, there has been no robust global test of this  
33 prediction<sup>9</sup>, because neither the appropriate data nor the analytical tools have  
34 been available. Here, we address both deficiencies to reveal, for island birds, the  
35 empirical shape of the general relationships that determine how colonisation,  
36 extinction and speciation rates covary with island area and isolation. We compile  
37 the first global molecular phylogenetic dataset of birds on islands, based on the  
38 terrestrial avifaunas of 41 oceanic archipelagos worldwide (including 596 avian  
39 taxa), and apply novel methodology to estimate the sensitivity of island-specific  
40 rates of colonisation, speciation and extinction to island features (area, isolation).  
41 Our model predicts, with high explanatory power, several global relationships: a  
42 decline of colonisation with isolation, a decline of extinction with area, and an  
43 increase of speciation with area and isolation. Combining the theoretical  
44 foundations of island biogeography<sup>7,8</sup> with the temporal information contained in  
45 molecular phylogenies<sup>10</sup> proves a powerful approach to unveil the fundamental  
46 relationships that govern variation in biodiversity across the planet.

47

48 A key feature of global diversity is the tendency for some areas to harbour many more  
49 species than others<sup>7,8</sup>. Uncovering the drivers and regulators of spatial differences in  
50 diversity of simple systems such as islands is a crucial step towards understanding the  
51 global distribution of species richness. The two most prominent biodiversity patterns in  
52 fragmented or isolated environments worldwide are the increase of species richness  
53 with area and the decline of richness with isolation<sup>8,11-14</sup>. In their theory of island  
54 biogeography, MacArthur and Wilson proposed how the processes of colonisation and  
55 extinction could explain these patterns<sup>7,8</sup>. They argued that the rates of these processes  
56 are determined by the geographic context: colonisation decreases with isolation and  
57 extinction decreases with area<sup>7,8</sup>. They also suggested that rates of formation of island  
58 endemic species via *in situ* speciation increase with island isolation and area<sup>8</sup>. Despite  
59 an abundance of studies over five decades supporting the general patterns predicted by  
60 MacArthur and Wilson<sup>2,15-18</sup>, tests of predictions regarding the dependence of the  
61 underlying processes – colonisation, speciation and extinction – on island geographic  
62 context (area and isolation) are few in number, and are either restricted in temporal,  
63 geographic, or taxonomic scope<sup>5,19,20</sup> or seek to infer speciation rates in the absence of  
64 data on the relationships among species<sup>2,16</sup>. As a result, there has been no robust and  
65 powerful test of MacArthur and Wilson’s predictions on a global scale, and the effect of  
66 area and isolation on biogeographical processes acting on macro-evolutionary time  
67 scales remains largely unexplored.

68 Here we expand on approaches that leverage the information in time-calibrated  
69 molecular phylogenies of insular species<sup>1,10,21,22</sup> to determine how the processes of  
70 colonisation, speciation and extinction are influenced by area and isolation. The  
71 dynamic stochastic model DAISIE<sup>10</sup> (Dynamic Assembly of Islands through Speciation,  
72 Immigration, and Extinction) can accurately estimate maximum likelihood (ML) rates of  
73 colonisation, extinction and speciation rates (CES rates) from branching times  
74 (colonisation times and any *in situ* diversification events) and endemism status of  
75 species resulting from one or multiple independent colonisations of a given island  
76 system (e.g. all native terrestrial birds on an archipelago)<sup>10</sup>. This method can also detect  
77 the presence or absence of diversity-dependence in rates of colonisation and speciation,  
78 by estimating a carrying capacity (upper bound to the number of species in an island  
79 system). Here we extend DAISIE to estimate, for the first time, the hyperparameters that



80 control the shape of the relationships between CES rates and the area and isolation of  
81 islands worldwide.

82 Accurate estimation of fundamental island biogeographic relationships requires  
83 suitable data from many archipelagos, but divergence-dated phylogenies of complete  
84 communities on islands remain scarce. Hence, we produced new dated molecular  
85 phylogenies for the terrestrial avifaunas of 41 archipelagos worldwide. By ‘archipelago’  
86 we refer to both true archipelagos (composed of multiple islands) and isolated insular  
87 units consisting of single islands (e.g. Saint Helena). For each archipelago we compiled  
88 avian taxon lists (excluding introduced, marine, migratory, and aquatic species, as well  
89 as birds of prey, rails and nocturnal birds, see Methods) and collected physical data (Fig.  
90 1, Supplementary Data 1 and 2). We use archipelagos as our insular unit, because the  
91 high dispersal abilities of birds within archipelagos imply that for birds, archipelagos  
92 can be considered equivalent to single islands for less dispersive taxa<sup>23</sup>, and because  
93 archipelagos constitute the most appropriate spatiotemporal unit for framing analyses  
94 of biodiversity patterns at a large scale<sup>2,24,25</sup>. We extracted colonisation and speciation  
95 times for each archipelago from the phylogenetic trees, producing a ‘global dataset’ for  
96 the 41 archipelagos, which includes each archipelago’s complete extant avifauna, plus  
97 all species known to have become extinct due to anthropogenic causes. The dataset  
98 comprises 596 insular taxa from 491 species. The phylogenies revealed a total of 502  
99 archipelago colonisation events and 26 independent in-situ ‘radiations’ (cases where  
100 diversification has occurred within an archipelago) ranging in size from 2 to 33 species  
101 (the Hawaiian honeycreepers being the largest clade). The distribution of colonisation  
102 times is summarised in Fig. 1 and the full dataset is given in Supplementary Data 1.

103 Our extension of the DAISIE framework allows us to estimate hyperparameters  
104 that control the relationship between archipelago area and isolation and archipelago-  
105 specific local CES rates, i.e., rates of colonisation, cladogenesis (within-archipelago  
106 speciation involving *in situ* lineage splitting), anagenesis (within-archipelago speciation  
107 by divergence from the mainland without lineage splitting), natural extinction rates and  
108 carrying capacity. We tested the hypothesis that area and distance from the nearest  
109 mainland have an effect on the specific CES rates, and, where a significant effect was  
110 identified, estimated its shape and scaling. We developed a set of *a priori* models  
111 (Supplementary Table 1) where CES rates are power law functions of archipelago  
112 features. Area has been proposed to have a positive effect on cladogenesis and carrying

113 capacity<sup>3,5,8</sup>, and a negative effect on extinction rates<sup>8,26</sup>. Archipelago isolation is  
114 hypothesised to reduce colonisation rates<sup>7</sup> and elevate anagenesis rates<sup>27</sup>. Models  
115 including or excluding diversity-dependence in rates of colonisation and cladogenesis<sup>10</sup>  
116 (i.e. estimating a carrying capacity parameter) were compared. We also considered a set  
117 of *post hoc* models with alternative shapes for the relationships (*post hoc* power and  
118 *post hoc* sigmoid models, see Methods, Supplementary Table 1).

119 We fitted a set of 28 candidate models to the global dataset using ML  
120 (Supplementary Table 2). The shape of the relationship of CES rates with area and  
121 distance for the two best models is shown in Fig. 2. Under the preferred *a priori* model  
122 (lowest value of Bayesian Information Criterion (BIC); M14, eight parameters)  
123 colonisation rates decline with archipelago isolation (exponent of the power law = -0.25  
124 (95% confidence interval = -0.17 - -0.34)) and extinction rate decreases with area  
125 (scaling = -0.15 (-0.11 - -0.18)). Rates of cladogenesis increase with area (scaling = 0.26  
126 (0.13 - 0.37)), whilst anagenesis increases with isolation (scaling = 0.42 (0.24 - 0.61)).  
127 The preferred *post hoc* model (M19, eight parameters) was also the preferred model  
128 overall and differs qualitatively from the preferred *a priori* model M14 only in the  
129 cladogenesis function. In M14 cladogenesis is solely a function of area, whereas in M19  
130 cladogenesis depends interactively and positively on both area and distance from the  
131 nearest mainland, such that the cladogenesis-area relationship is steeper for more  
132 isolated archipelagos (Fig. 2 and Extended Data Fig. 1). In addition, we found no  
133 evidence for diversity-dependence, as the carrying capacity ( $K$ ) was estimated to be  
134 much larger than the number of species on the island and models without a  $K$   
135 parameter (no upper bound to diversity), such as M14 and M19, performed better than  
136 models including one (Supplementary Table 2). We also tested whether the inclusion of  
137 a combination of true archipelagos and single islands in our dataset could have affected  
138 our results, for example if opportunities for allopatric speciation are higher when an  
139 area is subdivided into multiple islands<sup>28</sup>. We repeated analyses excluding single island  
140 units and found that the same model (M19) is preferred with similar parameter  
141 estimates. Hence, we discuss only the results for the main dataset (including both single  
142 islands and true archipelagos). Our results are robust to uncertainty in colonisation and  
143 branching times (see section 'Sensitivity to alternative divergence times and tree  
144 topologies').

145 A parametric bootstrap analysis of the two preferred models (M14 and M19)

146 demonstrated that the method is able to recover hyperparameters with high precision  
147 and little bias (Extended Data Fig. 2). In order to test the significance of the  
148 relationships between area, isolation and CES rates, we conducted a randomization test  
149 on the global dataset with reshuffled areas and distances. This test estimated the  
150 exponent hyperparameters as zero in most reshuffled cases (i.e. no effect of area or  
151 isolation detected; Extended Data Fig. 3), confirming that it is the observed  
152 relationships between diversity and archipelago characteristics that generate our  
153 parameter estimates.

154 To assess model fit we simulated archipelago communities under the best model  
155 (M19) and found that for most archipelagos the observed diversity metrics (numbers of  
156 species, cladogenetic species and colonisations) were similar to the expected numbers,  
157 with some exceptions: for example, diversity was underestimated for Comoros and São  
158 Tomé & Príncipe (Fig. 3 and Extended Data Fig. 4). The ability of the model to explain  
159 observed values (pseudo- $R^2$  for total species = 0.72, cladogenetic species = 0.52,  
160 colonisers = 0.60) was very high considering the model includes only eight parameters  
161 (at least 12 parameters would be needed if each rate depended on area and isolation,  
162 and at least 164 parameters if each archipelago was allowed to have its own  
163 parameters) and was able to explain multiple diversity metrics. This represents a very  
164 large proportion of the explanatory power one would expect to obtain for data  
165 generated under the preferred model (Extended Data Fig. 5). Simulations under the best  
166 model reproduced the classic observed relationships between area, distance and  
167 diversity metrics (Fig. 4).

168 Our approach reveals the empirical shape of fundamental biogeographic  
169 relationships that have hitherto largely evaded estimation. In agreement with recent  
170 studies<sup>2,29</sup>, we found strong evidence for a decline of rates of colonisation with isolation  
171 and of rates of extinction with area, confirming two of the key assumptions of island  
172 biogeography theory<sup>7</sup>. The colonisation-isolation effect was detected despite the decline  
173 of avian richness with distance from the nearest mainland in our empirical data not  
174 being as pronounced as in other less mobile taxa<sup>4,11</sup>, revealing isolation to be a clear  
175 determinant of probability of immigration and successful establishment of populations  
176 even in a highly dispersive group such as birds. The extinction-area relationship has  
177 been a fundamental empirical generalization in conservation theory (for example for  
178 the design of protected areas<sup>30</sup>) but this is the first time the shape of this dependence is

179 characterized at the global spatial scale and macro-evolutionary time scale.

180 We provide novel insights into the scaling of speciation with area and isolation.  
181 Contrary to previous work on within-island speciation, which suggested the existence of  
182 an area below which cladogenesis does not take place on single islands<sup>5</sup>, we do not find  
183 evidence for such an area threshold at the archipelago level, and under our model  
184 speciation is predicted to be non-zero even at small areas. In addition, our *post hoc*  
185 finding that rates of cladogenesis increase through an interactive effect of both island  
186 size and distance from the nearest mainland (Fig. 2 and Extended Data Fig. 1) provides a  
187 mechanism that limits radiations to archipelagos that are both large and remote<sup>6,27</sup>.  
188 Why this interaction exists requires further investigation, but one possibility is that  
189 unsaturated niche space provides greater opportunities for diversification<sup>6</sup>. In addition  
190 to the effects of physical features on cladogenesis, we found that rates of anagenesis  
191 increase with island isolation. While impressive insular radiations tend to receive the  
192 most attention from evolutionary biologists (e.g. Darwin's finches or Hawaiian  
193 honeycreepers), our phylogenies revealed that the majority of endemic birds in our  
194 dataset in fact display an anagenetic pattern (at the time of human arrival 231 of 350  
195 endemic species had no extant sister taxa on the archipelago and there were only 26  
196 extant *in situ* radiations). The positive effect of archipelago isolation on rates of  
197 anagenesis that we estimate suggests this fundamental but overlooked process is  
198 impeded by high levels of movement between island and mainland populations.

199 A variety of global patterns of biodiversity have been described – from small  
200 islands and lakes, up to biomes and continents - but the processes underpinning them  
201 remain little explored. Our simulations using parameters estimated from data were able  
202 to reproduce classic global patterns of island biogeography across 41 archipelagos (Fig.  
203 4). This advances our understanding of macro-scale biology, by providing missing links  
204 between local process, environment and global patterns. Over half a century since the  
205 seminal work of MacArthur & Wilson<sup>7</sup>, we now have the data and tools to go beyond  
206 statistical descriptions of diversity patterns, enabling us to quantify community-level  
207 processes that have long been elusive.

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## 279 MAIN TEXT FIGURE LEGENDS

280  
281 **Figure 1 – Archipelago and island bird colonisation time data.** Circles show number  
282 of species belonging to our focal group (both extinct and extant) found in each  
283 archipelago (at the time of human arrival). Numbers on map correspond to numbers to  
284 the left of the archipelago name. Numbers to the right of the archipelago name: number  
285 of species from our focal assemblage on the archipelago | percentage of species sampled  
286 in the phylogenetic trees. Even species not sampled in the trees are accounted for by  
287 including them as missing species that could have colonised any time since emergence  
288 of the archipelago. Colonisation times plot: grey horizontal lines – archipelago ages  
289 (Extended Data Table 1). Violin plots (blue) show the kernel density of the distribution  
290 of times of colonisation of bird species in each archipelago, obtained from the  
291 phylogenetic trees. Thick black line inside violin - interquartile distance; thin black line -  
292 95% CI; black dot - median. Archipelagos with no violin plot or dots are cases for which  
293 no species of our focal assemblage were present at the time of human arrival, or none  
294 were sampled using molecular data. Birds from left to right: Seychelles sunbird,  
295 Seychelles magpie robin, silveryeye, Príncipe thrush, laurel pigeon, dodo (extinct),  
296 Mauritius fody, red-moustached fruit dove (extinct), Galápagos warbler, Norfolk kaka  
297 (extinct). Bird images used with permission from: Cláudia Baeta, Pedro Cascão, Martijn  
298 Hammers, Julian Hume, Dubi Shapiro and Juan Varela. There are no *in-situ* radiations in  
299 the Mascarenes (Mauritius, Reunion and Rodrigues) because we treat the islands as  
300 separate entities (but see sensitivity analyses).

301  
302 **Figure 2 – Estimated relationships between island area and isolation and local**  
303 **island biogeography parameters.** Isolation measured as distance to the nearest  
304 mainland ( $D_m$ ). Based on the maximum likelihood global hyperparameters of the best  
305 models (equations describing the relationships given in Supplementary Table 1).  
306 Darker lines – M14 model, lighter lines – M19 model. Under the M14 model,  
307 cladogenesis rate depends only on area. Under the M19 model, cladogenesis rate  
308 increases with both area and  $D_m$ , and thus lines for more (far, 5,000 km) and less (near,  
309 50 km) isolated islands are shown. See also Extended Data Fig. 1 for the relationship of  
310 cladogenesis with both area and distance under the M19 model.

311  
312 **Figure 3 – Goodness of fit of the preferred model (M19).** The map identifies whether  
313 the diversity metrics were well estimated (empirical value matches 95% confidence  
314 interval of simulations), underestimated (empirical value higher than 95% interval) or  
315 overestimated (empirical value lower than 95% interval). Intervals based on 1000  
316 simulations of each archipelago (see Extended Data Fig. 4). Numbers indicating  
317 archipelagos on the map match those in Fig. 1.

318  
319 **Figure 4 – Observed and predicted island diversity-area and island diversity-**  
320 **distance relationships.** Grey vertical lines show the 95% confidence intervals across  
321 1,000 datasets simulated for each of the 41 archipelagos assuming the M19 model. Blue  
322 points: mean values of the simulations; blue line – fitted line for the simulated data; red  
323 points – observed values in the empirical data; red line – fitted line for the empirical  
324 data; red shaded area is the 95% confidence interval of the predicted relationship for  
325 the empirical data.

## 326 **Methods**

327

### 328 **Archipelago selection**

329

330 We focus on oceanic islands, i.e. volcanic islands that have never been connected to any  
331 other landmass in the past. We also include the Granitic Inner Seychelles, even though  
332 these islands have a continental origin, because they have been separated from other  
333 landmasses for a very long period of time (64 million years (Ma)<sup>31</sup>) and can be  
334 considered quasi-oceanic, as all extant avian species originated in much more recent  
335 times. The 41 archipelagos chosen are located in the Atlantic, Indian and Pacific oceans,  
336 with latitudes between 45° North and South. Islands within these archipelagos are  
337 separated by a maximum of 150 km. The sole exceptions are the Azores and Hawaii, two  
338 very isolated systems where the distances between some islands exceed this value. The  
339 shape files used to plot the maps of Figs. 1 and 3 were obtained from Weigelt, Jetz and  
340 Kreft 2013<sup>32</sup>.

341

### 342 **Physical and geological data**

343

344 Full archipelago data is given in Supplementary Data 2 and Extended Data Table 1. We  
345 obtained data on total contemporary landmass area for each archipelago. For our  
346 isolation metric, we computed the minimum round earth distance to the nearest  
347 mainland ( $D_m$ ) in km using Google Earth. We considered ‘nearest mainland’ to be the  
348 nearest probable source of colonists (but see ‘Sensitivity to archipelago selection and  
349 isolation metrics’ section for different isolation metrics). This is the nearest continent  
350 except for island groups that were closer to Madagascar, New Guinea or New Zealand  
351 than to the continent, in which case we assigned these large continent-like islands as the  
352 mainland. This is supported by our phylogenetic data – for example, many Indian Ocean  
353 island taxa have closest relatives on Madagascar rather than mainland Africa.

354 Island palaeo-areas and past archipelago configurations have been shown to be  
355 better predictors of endemic insular diversity than contemporary area<sup>15,33</sup>. In contrast,  
356 island total native and non-endemic richness is better predicted by present island  
357 characteristics<sup>15,33</sup>. With insufficient data on island ontogeny being available (i.e.  
358 describing empirical area trajectories from island birth to present) we therefore



359 analysed contemporary area and isolation as currently the most appropriate units for  
360 our dataset.

361 We conducted an extensive survey of the literature and consulted geologists to  
362 obtain archipelago geological ages (Extended Data Table 1), treating the age of the  
363 oldest currently emerged island as an upper bound for colonisation. Islands may have  
364 been submerged and emerged multiple times and we consider the age of the last known  
365 emergence. For the Aldabra Group we used an age older than the published estimate.  
366 The current estimated age of re-emergence of Aldabra is 0.125 Ma<sup>34</sup>, but nine out of 12  
367 Aldabra colonisation events in our dataset are older, suggesting the archipelago was not  
368 fully submerged prior to this and may have been available for colonisation for a longer  
369 period. Therefore, for Aldabra we used an older upper bound of 1 Ma for colonisation,  
370 although we acknowledge that the mitochondrial markers used for dating may not  
371 provide sufficient resolution at the shallow temporal scale of the published age. For  
372 Hawaii, the colonisation times we obtained for more than half of the colonisation events  
373 were older than the age of the current high islands that is often used as a maximum age  
374 for colonisation (~5 Ma). Therefore, instead of this age, we used the much older  
375 estimate of 29.8 Ma of the Kure Atoll<sup>35</sup> to account for currently submerged or very low-  
376 lying Hawaiian islands that could have received colonists in the past. For Bermuda and  
377 Marianas, we could not find age estimates in the literature, and we therefore consulted  
378 geologists to obtain these (P. Hearty, R. Stern and M. Reagan, pers. comm., Extended  
379 Data Table 1).

380

### 381 **Island avifaunas**

382

383 Our sampling focused on native resident terrestrial birds and we considered only birds  
384 that colonise by chance events (e.g. hurricanes, rafts). We thus excluded marine and  
385 migratory species, because they are capable of actively colonising an island at a much  
386 higher rate. We focused on songbird-like and pigeon-like birds, which constitute the  
387 majority of terrestrial (land-dwelling) birds on islands. Following a precedent set by  
388 previous work<sup>10,27,36</sup>, we included only species from the same trophic level (in the spirit  
389 of MacArthur and Wilson's model): we excluded aquatic birds, birds of prey, rails (many  
390 are flightless or semi-aquatic) and nightjars (nocturnal). We also excluded introduced  
391 and vagrant species. Including species such as rails and owls (which are components of

392 many island avifaunas) would have led to a higher estimate of the product of  
393 colonisation rate and mainland pool size due to a larger mainland pool, and potentially  
394 to higher estimated rates of anagenesis (many owl or rail species are island endemics  
395 with no close relatives on the islands).

396 For the focal avian groups, we compiled complete taxon lists for each of the 41  
397 archipelagos based on recent checklists from Avibase (<http://avibase.bsc-eoc.org>),  
398 which we cross-checked with the online version of the *Handbook of the Birds of the*  
399 *World* (HBW<sup>37</sup>). We followed HBW's nomenclature and species assignments, except for  
400 12 cases where our phylogenetic data disagree with HBW's scheme (noted in the  
401 column 'Taxonomy' of Supplementary Data 1). For example, in eleven cases  
402 phylogenetic trees support raising endemic island subspecies to species status (we  
403 sampled multiple samples per island taxon and outgroup, and the island individuals  
404 form a reciprocally monophyletic well-supported clade), and for these taxa we decided  
405 it was more appropriate to use a phylogenetic species concept so as not to  
406 underestimate endemism and rates of speciation (Supplementary Data 1). We re-ran  
407 DAISIE analyses using HBW's classification and found that the ML parameters are very  
408 similar and thus we report only the results using the scheme based on the phylogenies  
409 produced for this study.

410 For each bird species found on each archipelago we aimed to sample sequence  
411 data for individuals on the archipelago and the closest relatives outside the archipelago  
412 (outgroup taxa). Our sampling success per archipelago is shown on Fig. 1 and Extended  
413 Data Table 1.

414

415

#### 416 **Extinct species**

417 We do not count extinctions with anthropogenic causes as impacting the natural  
418 background rate of extinction. Therefore, we explicitly include species where there is  
419 strong evidence that they have been extirpated by humans. We treat taxa extirpated on  
420 an archipelago by humans as though they had survived in that archipelago until the  
421 present following the approach of Valente, Etienne and Dávalos 2017<sup>38</sup>.

422 We identified anthropogenic extinctions based on published data<sup>39-46</sup> and  
423 personal comments (Josep Antoni Alcover and Juan Carlos Rando on unpublished  
424 Macaronesian taxa; Ferran Sayol and Søren Faurby). We include the species present on

425 the islands that belong to our archipelago definition as in Supplementary Data 2. We  
426 excluded largely hypothetical accounts or pre-Holocene fossils that greatly pre-date  
427 human arrival. Our dataset accounts for 153 taxa that were present upon first human  
428 contact and have gone extinct since, probably because of human activities including  
429 human introduction of invasive species. To our knowledge 71 of these taxa have  
430 previously been sequenced using ancient DNA or belong to clades present in our trees,  
431 and we were thus able to include them in the phylogenetic analyses as regular data (n =  
432 54), or as missing species by adding them as unsampled species to a designated clade (n  
433 = 17). For the remaining 82 extinct taxa, sequences were not available and we were  
434 unable to obtain samples and to allocate them to clades. We assume that these taxa  
435 represent extinct independent colonisations and we included them in the analyses using  
436 the “Endemic\_MaxAge” and “Non\_endemic\_MaxAge” options in DAISIE, which assume  
437 that they have colonised at any given time since the birth of the archipelago (but before  
438 any *in situ* cladogenesis event). As an example, our dataset includes the 27 species of  
439 Hawaiian birds belonging to our focal group that are known to have gone extinct since  
440 human colonisation. Eight of these species were included using DNA data, 17 were  
441 added as missing species to their clades (14 honeycreepers and 3 *Myadestes*) and two  
442 were added using the Endemic\_MaxAge option in DAISIE (*Corvus impluviatus* and  
443 *Corvus viriosus*).

444

#### 445 **Sequence data: GenBank**

446

447 We conducted an extensive search of GenBank for available DNA sequences from the  
448 596 island bird taxa fitting our sampling criteria and from multiple outgroup taxa, using  
449 software Geneious 11<sup>47</sup>. The molecular markers chosen varied from species to species,  
450 depending on which marker was typically sequenced for the taxon in question, the  
451 commonest being cytochrome b (*cyt-b*). In total, we downloaded 3155 sequences from  
452 GenBank. For some taxa, sequences from both archipelago and close relatives from  
453 outside the archipelago were already available from detailed phylogenetic or  
454 phylogeographic analyses. In some cases, a target species had been sampled, but only  
455 from populations outside the archipelago. In other cases, the species on the archipelago  
456 had been sampled, but the sampling of the relatives outside of the archipelago was  
457 lacking or only from distant regions, which meant a suitable outgroup was not available

458 on GenBank. Finally, for some species there were no previous sequences available on  
459 GenBank. GenBank accession numbers and geographical origin for the downloaded  
460 sequences are provided on the DNA matrices and maximum clade credibility trees  
461 (uploaded to Mendeley Data).

462

### 463 **Sequence data: new samples**

464

465 Sequences available on GenBank covered only 54% (269/502) of the total independent  
466 colonisation events. We improved the sampling by obtaining new sequences for many  
467 island taxa (n = 174 taxa) and from their close relatives from continental regions (n =  
468 78). We obtained new samples from three sources: field trips, research collections and  
469 colleagues who kindly contributed field samples. New samples were obtained during  
470 field trips conducted by M.M. (Gulf of Guinea and African continent); B.H.W. and C.T.  
471 (Comoros, Mauritius Isl., Rodrigues, Seychelles); S.M.C. (New Caledonia); J.C.I.  
472 (Macaronesia, Europe and Africa) and L.V. (New Caledonia), between 1999 and 2017.  
473 Samples of individuals were captured using mist-nets or spring traps baited with larvae.  
474 Blood samples were taken by brachial venipuncture, diluted in ethanol or Queen's lysis  
475 buffer in a microfuge tube. Birds were released at the point of capture. Aldabra Group  
476 samples were obtained from research collections of the Seychelles Islands Foundation.  
477 Museum samples from several Galápagos and Comoros specimens were obtained on  
478 loan from respectively, the California Academy of Sciences and the Natural History  
479 Museum London. Additional samples from various localities (Aldabra Islands, Iberian  
480 Peninsula, Madagascar and Senegal) were kindly provided by collaborators, as indicated  
481 in Supplementary Table 3. Sample information and GenBank accession numbers for all  
482 new specimens are provided in Supplementary Table 3.

483 DNA was extracted from blood, feathers and museum toe-pad samples using  
484 QIAGEN DNeasy Blood and Tissue kits (QIAGEN, USA). For museum samples, we used a  
485 dedicated ancient DNA lab facility at the University of Potsdam to avoid contamination.  
486 The *cyt-b* region (1100 base pairs) was amplified using the primers shown in Extended  
487 Data Table 2. DNA from historical museum samples was degraded and *cyt-b* could not  
488 be amplified as a single fragment. We thus designed internal primers to sequence  
489 different overlapping fragments in a stepwise fashion (Extended Data Table 2).

490 Polymerase chain reactions (PCR) were set up in 25  $\mu$ L total volumes including 5

491  $\mu\text{L}$  of buffer Bioline MyTaq, 1  $\mu\text{L}$  (10 mM) of each primer, and 0.12  $\mu\text{L}$  MyTaq  
492 polymerase. PCRs were performed with the following thermocycler conditions: initial  
493 denaturation at 95° C for 1 min followed by 35 cycles of denaturation at 95° C for 20 s,  
494 with an annealing temperature of 48° C for 20 s, and extension at 72° C for 15 s min and  
495 a final extension at 72° C for 10 min. Amplified products were purified using  
496 Exonuclease I and Antarctic Phosphatase, and sequenced at the University of Potsdam  
497 (Unit of Evolutionary Biology/Systematic Zoology) on an ABI PRISM 3130xl sequencer  
498 (Applied Biosystems) using the BigDye Terminator v3.1 Cycle Sequencing Kit (Applied  
499 Biosystems). We used Geneious 11 to edit chromatograms and align sequences.

500

501

## 502 **Phylogenetic analyses**

503

504 To estimate times of colonisation and speciation for each archipelago we produced new  
505 divergence dated phylogenies or compiled published dated trees, to yield a total of 91  
506 independent phylogenies (maximum clade credibility trees and posterior distribution  
507 deposited in Mendeley for all new trees produced for this study; the 11 previously  
508 published trees are available upon request). Information on all alignments and trees,  
509 including molecular markers, source of data, calibration method and substitution model  
510 are given in Extended Data Tables 3 and 4 and Supplementary Table 4. The majority of  
511 alignments/phylogenies focus on a single genus, but some include multiple closely  
512 related genera or higher order clades (family, order) depending on the diversity and  
513 level of sampling of the relevant group (taxonomic scope indicated in Extended Data  
514 Tables 3 and 4). Most alignments include taxa from a variety of archipelagos.  
515 Alignments were based on a variety of markers, according to which marker had been  
516 mostly sequenced for a given group.

517 For the new dating analyses conducted for this study, we created 80 separate  
518 alignments for different groups using a combination of sequences from GenBank ( $n =$   
519 3155) and new sequences ( $n = 252$ ) produced for this study. In some cases, we obtained  
520 DNA alignments directly from authors of previous studies and these are credited in  
521 Extended Data Table 3. Phylogenetic divergence dating analyses were performed in  
522 BEAST 2<sup>48</sup>. For each alignment we performed substitution model selection in  
523 jModeltest<sup>49</sup> using the Bayesian information criterion. We used rates of molecular

524 evolution for avian mitochondrial sequences, which have been shown to evolve in a  
525 clock-like fashion at an average rate of  $\sim 2\%$  per Ma<sup>50</sup>. Molecular rate calibrations can be  
526 problematic for ancient clades, due to high levels of heterotachy in birds<sup>51</sup>. In addition,  
527 mitochondrial DNA saturates after about 10 to 20 million years, and genetic distances of  
528 more than 20% may provide limited information regarding dating<sup>52</sup>. Therefore, we only  
529 used molecular rate dating to extract node ages for branching events at the tips of the  
530 trees, at the species or population level (oldest colonisation time in our dataset is 15.3  
531 Ma, but most are much younger). Rates of evolution were obtained from the literature  
532 and varied between different markers and taxonomic group (Supplementary Table 4).  
533 We applied the avian mitochondrial rates estimated from *cyt-b* by Weir and Schluter<sup>50</sup>  
534 (but see ‘Sensitivity to alternative divergence times and tree topologies’ section for  
535 different rates).

536 We applied a Bayesian uncorrelated lognormal relaxed clock model. For each  
537 analysis, we ran two independent chains of between 10 and 40 million generations,  
538 with a birth-death tree prior. We assessed convergence of chains and appropriate burn-  
539 ins with Tracer, combined runs using LogCombiner, and produced maximum clade  
540 credibility trees with mean node heights in Tree Annotator. We produced a total of 80  
541 maximum clade credibility trees.

542 For 11 groups (Extended Data Table 4), well-sampled and rigorously-dated  
543 phylogenies were already available from recent publications, all of which conducted  
544 Bayesian divergence dating using a variety of calibration methods, including fossils and  
545 molecular rates. We obtained maximum clade credibility trees from these studies from  
546 online repositories or directly from the authors (Extended Data Table 4).

547

## 548 **Colonisation and branching times**

549 The nodes selected in the dated trees for estimates of colonisation and branching times  
550 are given for each taxon in Supplementary Data 1. Our node selection approach was as  
551 follows. For cases in which samples representing species or populations from  
552 archipelagos formed a monophyletic clade consisting exclusively of archipelago  
553 individuals, we used the stem age of this clade as colonisation time. For cases in which  
554 only one individual of the archipelago was sampled, we used the length of the tip  
555 leading to that individual, which is equivalent to the stem age. For cases in which the  
556 archipelago individuals were embedded in a clade containing mainland individuals of

557 the same species, i.e. paraphyly or polyphyly; we assumed (based on morphological  
558 characteristics) that this is due to incomplete lineage sorting of the insular and  
559 mainland lineages, and we therefore used the MRCA of the archipelago individuals, or  
560 the crown node when the MRCA coincides with the crown. For these later cases using  
561 the stem would most likely have been an overestimation of the colonisation time, as we  
562 assume that colonisation happens from the mainland to the archipelago. For such cases  
563 we applied the ages using the “MaxAge” option in DAISIE, which integrates over the  
564 possible colonisation times between the present and the upper bound. A robustness test  
565 of our results to node choice is given in section “Sensitivity to alternative branching  
566 times and tree topologies”.

567 For a total of 19 endemic taxa we could not obtain sequences, but we could  
568 allocate them to a specific island clade (e.g. Hawaiian honeycreepers and solitaires).  
569 These were added as missing species to that clade. For 96 non-endemic taxa we could  
570 not obtain sequences of individuals from the archipelago, but we could obtain  
571 sequences from the same species from different regions. For these cases we used the  
572 crown or the stem age of the species as an upper bound for the age of the colonisation  
573 event, using the “Non\_endemic\_MaxAge” option in DAISIE. Finally, for 124 taxa (20.8 %)  
574 no sequences of individuals from the archipelago were available on GenBank and we  
575 were not able to obtain samples for sequencing from the species or from close relatives.  
576 We assumed these cases constituted independent colonisations that could have taken  
577 place any time since the origin of the archipelago and the present, and applied the  
578 “Non\_endemic\_MaxAge” and “Endemic\_MaxAge” options in DAISIE with a maximum age  
579 equal to the archipelago age. DAISIE makes use of this information<sup>53</sup>.

580

### 581 **Global dataset characteristics**

582

583 Data points from taxa of the same archipelago were assembled into 41 archipelago-  
584 specific datasets. These 41 datasets were in turn assembled into a single dataset (D1)  
585 which was analysed with DAISIE (D1 DAISIE R object, available in Mendeley Data  
586 <https://doi.org/10.17632/sy58zbv3s2.2>). This dataset (information Supplementary  
587 Data 1) has a total of 596 taxa (independent colonisation events plus species within  
588 radiations), covering 491 species from 203 different genera and eight orders. All taxa  
589 were included in the analyses: those which we sampled in phylogenies, but also those

590 for which sequences or phylogenies could not be obtained and which were included  
591 following the approaches described in the *colonisation and branching time* methods. A  
592 summary of diversity and sampling per archipelago is given in Extended Data Table 1.

593

### 594 **Sampling completeness**

595

596 In total, we produced new sequences from 252 new individuals, comprising 90 different  
597 species from 45 different genera, covering an additional 110 colonisation events that  
598 had never before been sampled (i.e. populations from islands where the species had not  
599 been sampled before). For at least 12 of these 90 species, we found no previous  
600 sequences on GenBank, including island endemics from Comoros, Galápagos, Rodrigues  
601 and São Tomé (Supplementary Table 5). The new sequences from 252 individuals  
602 increase the molecular sampling for extant colonisation events from 60% (223/373) to  
603 89% (332/373). If we include historically extinct colonisations, we increased the  
604 molecular sampling from the existing 54% (269/502) of colonisation events to 75%  
605 (379/502). We also substantially increased molecular sampling of continental relatives,  
606 adding 78 new individuals from the continent or islands surrounding our archipelagos,  
607 covering 43 different species. The percentage of taxa sampled in phylogenies varied  
608 widely between archipelagos (Extended Data Table 1 and Fig. 1). For eight archipelagos  
609 (Bermuda, Fernando de Noronha, Pitcairn, Rapa Nui, Rodrigues, Saint Helena, Society  
610 Islands and Tonga) less than 50% of the species were sampled in phylogenies, and thus  
611 the majority of the species for these island groups were added with maximum ages and  
612 endemism status. For 13 archipelagos, which accounted for more than a third of the  
613 total species, over 90% of the species were sampled in phylogenies.

614

### 615 **DAISIE**

616

617 We used the method DAISIE<sup>10</sup> (Dynamic Assembly of Islands through Speciation,  
618 Immigration, and Extinction) to estimate rates of species accumulation (colonisation,  
619 speciation and extinction) on the archipelagos. The model assumes that after the origin  
620 of an island, species can colonise from a mainland pool. Once a species has colonised, it  
621 may remain similar to its mainland ancestor (non-endemic species), become endemic  
622 through anagenetic speciation (new endemic species is formed without lineage splitting



623 on the island), split into new species via cladogenetic speciation and/or go extinct. A  
624 carrying capacity (i.e. maximum number of species each colonist lineage can attain) is  
625 implemented, such that rates of cladogenesis and colonisation decline with increasing  
626 number of species in the colonising clade.

627 The only effect of anagenesis under DAISIE is that the colonising species becomes  
628 endemic, because further anagenesis events on the endemic species do not leave a  
629 signature in the data. However, the rate of anagenesis is not systematically  
630 underestimated. Suppose the rate was higher; it would then follow that colonising  
631 species would also become endemic faster, and we would see more endemic species.  
632 Thus, the number of endemic species determines the rate of anagenesis, and DAISIE  
633 estimates the true rate of anagenesis without systematic bias. Further anagenesis  
634 events do not have an effect on the state variables, and hence do not enter the equations  
635 anymore.

636 In its parameterization of extinction, DAISIE accounts for the fact that there may  
637 have been several lineages that were present on the insular system in the past but  
638 which went completely extinct due to natural causes, leaving no extant descendants.  
639 Simulations have shown that the rate of natural extinction is usually well estimated in  
640 DAISIE (Methods section *Measuring precision and accuracy* and ref. <sup>53</sup>). Studies on  
641 phylogenies of single clades suggest that phylogenetic data on only extant species  
642 provide less information on extinction than on speciation (or rather diversification  
643 rates<sup>54</sup>). However, there is information-content in such data<sup>55</sup>, especially when  
644 diversification dynamics are diversity-dependent<sup>56</sup>. Moreover, here we use colonisation  
645 times in addition to phylogenetic branching times to estimate extinction rates, and we  
646 are estimating hyperparameters that theory suggests correlate with extinction (i.e.  
647 area). Finally, we use data from many independent colonisations, which increases the  
648 power of our statistical method considerably, and decreases the bias, as ML is known to  
649 asymptotically provide unbiased estimates.

650

### 651 **Estimating global hyperparameters**

652

653 Our aim is to examine the dependencies of the parameters that govern species assembly  
654 (colonisation, extinction, cladogenesis, anagenesis (CES rates), and carrying capacity)  
655 on the features of archipelagos (area, isolation). We developed a new method to

656 estimate global hyperparameters that control the relationship between two key  
657 archipelago features (area and isolation) and archipelago-specific (local) CES rates. One  
658 can estimate directly from the global dataset the shape of the relationship between  
659 isolation and colonisation rate that maximizes the likelihood for the entire dataset.

660 Our method finds the hyperparameters that maximize the likelihood of the entire  
661 dataset, i.e. the sum of the log likelihoods for each archipelago. We tested the hypothesis  
662 that area and distance from the nearest mainland have an effect on CES rates  
663 (cladogenesis, anagenesis, extinction and colonisation). If an effect was identified we  
664 also estimated the scaling of the effect. We developed a set of *a priori* models where CES  
665 rates are affected by archipelago features as is often assumed in the island  
666 biogeography literature (Supplementary Table 1). For the *a priori* models, we  
667 considered that CES rates are determined by a power function of area or distance. In the  
668 power function,  $par = par_0 I^h$ , where  $par$  is the CES rate (e.g. local rate of colonisation),  
669  $par_0$  is the initial value of the biogeographical rate (e.g. global initial rate of  
670 colonisation),  $I$  is the physical variable (area or distance) and  $h$  is the strength of the  
671 relationship. The exponent  $h$  can be negative or positive depending on the nature of the  
672 relationship.  $par_0$  and  $h$  are the hyperparameters. If the exponent  $h$  is estimated as zero,  
673 there is no relationship between  $I$  and the parameter. By including or excluding  $h$  from  
674 the different relationships we can compare different models with the effects switched  
675 on or off (Supplementary Table 1, e.g. in model M1 all relationships are estimated, but in  
676 model M2 the exponent of the relationship between anagenesis and distance is fixed to  
677 zero and thus anagenesis does not vary with distance).

678 In addition to the *a priori* models, we considered a set of *post hoc* models with  
679 alternative shapes of relationships. We fitted two types of *post hoc* models: power  
680 models and sigmoid models (Supplementary Table 1). In the *post hoc* power models we  
681 modelled all parameters as in the *a priori* models, except for cladogenesis: we allowed  
682 cladogenesis to be dependent both on area and distance. The reason for this is that we  
683 found that the predicted number of cladogenetic species under the *a priori* models were  
684 not as high as observed, so we examined whether including a positive effect of distance  
685 would improve the fit. We described the relationship between area, distance and  
686 cladogenesis using different functions – one model where there is an additive effect of  
687 area and distance (M15); and three models (M16, M17, M18) where the effect of area  
688 and distance is interactive. In addition, we fitted a model identical to M16 but with one

689 parameter less (M19). The reason for this was that this parameter ( $\gamma$ ) was being  
690 estimated as zero in M16

691 In the *post hoc* sigmoid models, we allowed the relationship between distance and  
692 a given parameter to follow a sigmoid rather a power function. The rationale for this  
693 was that we wanted to investigate whether for birds the effect of distance on a  
694 parameter only starts to operate after a certain distance from the mainland, as below  
695 certain geographical distances archipelagos are within easy reach for many bird species  
696 by flight so that at these distances the island behaves almost as part of the mainland  
697 from a bird's perspective. We fitted nine different sigmoid models (Supplementary  
698 Table 1), allowing cladogenesis, anagenesis and colonisation to vary with distance  
699 following a sigmoid function. The sigmoid function we used has an additional parameter  
700 in comparison to power functions.

701 In total we fitted 28 candidate models (14 *a priori*, 14 *post hoc*) to the global  
702 dataset using ML. We fitted each model using 20 initial sets of random starting  
703 parameters to reduce the risk of being trapped in local likelihood suboptima. We used  
704 the age of each archipelago (Extended Data Table 1) as the maximum age for  
705 colonisation. We assumed a global mainland species pool  $M$  of 1000 species. The  
706 product of  $M$  and the intrinsic rate of colonisation ( $\sqrt{\gamma_0}$ ) is constant as long as  $M$  is large  
707 enough (larger than the number of island species), and thus the chosen value of  $M$  does  
708 not affect the results.

709 To decide which information criterion to use to select between different models  
710 we compared the performance of the BIC and the Akaike information criterion (AIC).  
711 We simulated 1,000 datasets each with models M9 and M19 and then fitted the M9,  
712 M14, M17 and M19 models to each of these datasets using two initial sets of starting  
713 parameters for each optimisation. We found that for datasets simulated using M9 an  
714 incorrect model was preferred using AIC in 10.4 % of cases, but only in 0.11 % of cases  
715 when using BIC. For datasets simulated using M19 an incorrect model was preferred  
716 12.8 % of cases using AIC and 11.1 % of cases using BIC. We thus compared models  
717 using BIC, as this model has lower error rates.

718 An alternative approach to estimating hyperparameters would be to calculate CES  
719 rates and their uncertainty independently for each archipelago and to then conduct a  
720 meta-analysis of the resulting data, including archipelago area and isolation as  
721 predictors. However, errors in parameter estimates will vary, particularly because some

722 archipelagos have small sample sizes (only a few extant colonisation events, or none at  
723 all, e.g. Chagos) and are thus much less informative about underlying process<sup>53</sup>. Thus,  
724 maximizing the likelihood of all data sets together by estimating the hyperparameters  
725 (which is precisely our aim) is preferable. For completeness, we present CES rates  
726 estimated independently for each archipelago in Supplementary Table 6, excluding  
727 archipelagos with fewer than six species and for which we sampled less than 60% of the  
728 species in the phylogenies. However, as argued above we do not advocate using these  
729 parameter estimates for further analyses because the number of taxa for some of these  
730 archipelagos is still low and by excluding archipelagos with fewer than six taxa we  
731 cannot capture the lower part of the relationship between area/isolation and CES rates.

732 All DAISIE analyses were run using parallel computation on the high-performance  
733 computer clusters of the University of Groningen (Peregrine cluster) and the Museum  
734 für Naturkunde Berlin. The new version of the R package DAISIE is available on Github.

735

### 736 **Randomization analysis**

737

738 We conducted a randomization analysis to evaluate whether there is significant signal  
739 of a relationship between area and distance and local CES rates in our global dataset.  
740 We produced 1,000 datasets with the same phylogenetic data and archipelago ages as  
741 the global dataset, but randomly reshuffled archipelago area and  $D_m$  in each dataset. We  
742 then fitted the best *post hoc* model to each of these 1,000 randomized datasets. If the ML  
743 estimates of exponent hyperparameters (i.e. the strength of the relationship) in the  
744 randomized datasets were non-zero this would indicate that the method is finding  
745 evidence for a relationship even if there is none. If, on the other hand, non-zero  
746 hyperparameters are estimated in the real data but not in the randomized datasets, this  
747 would mean that there is information in the data regarding the putative relationships.

748 The randomization analysis showed that in global datasets with reshuffled areas  
749 and distances the exponent hyperparameters are estimated as zero in most cases,  
750 whereas in the empirical global dataset they are not (Extended Data Fig. 3).

751

### 752 **A posteriori simulations**

753

754 We simulated 1,000 phylogenetic global datasets (41 archipelagos each) with the ML

755 hyperparameters of the best *a priori* (M14) and *post hoc* models (M19). We first  
756 calculated the local CES rates for each archipelago based on their area and isolation and  
757 the hyperparameters for the model, and then used these CES rates as the parameters for  
758 the simulations using the DAISIE R package. The simulated data were used to measure  
759 bias and accuracy of the method, goodness of fit and the ability of our method to recover  
760 observed island biogeographic diversity patterns (see below).

761

### 762 **Measuring precision and accuracy of method**

763

764 DAISIE estimates CES rates with high precision and little bias<sup>10,53</sup>. We conducted  
765 parametric bootstrap analyses to assess whether the ability to estimate  
766 hyperparameters from global datasets is also good (Extended Data Fig. 2), and to obtain  
767 confidence intervals on parameter estimates (Extended Data Table 5). We used DAISIE  
768 to estimate hyperparameters from the M14 and M19 simulated datasets (1,000  
769 replicates each). We measured precision and accuracy by comparing the distribution of  
770 parameters estimated from the 1,000 simulated data set with the real parameters used  
771 to simulate the same datasets. To check whether ML optimisations of the simulated  
772 global datasets converge to the same point in parameter space, we first performed a test  
773 on a subset of the simulated data. We ran optimisations with 10 random sets of initial  
774 starting values for each of 10 simulated datasets. All optimisations converged to the  
775 same likelihood and a very similar hyperparameter set; therefore, we are confident we  
776 found the global optimum for each simulated global dataset, even for models with many  
777 parameters.

778

### 779 **Measuring goodness of fit**

780

781 We measured how well the preferred models fitted the data using different approaches.  
782 First, we examined whether our models successfully reproduce the diversity patterns  
783 found on individual archipelagos. We calculated the total number of species,  
784 cladogenetic species and independent colonisations in each archipelago for each of the  
785 1,000 simulated datasets. We then plotted these metrics versus the observed values in  
786 the empirical data (Extended Data Fig. 4 and Fig. 3). Our preferred models have a slight  
787 tendency to overpredict species richness when there are a few species and

788 underpredict it when there are many. We do not have a clear explanation for this. This  
789 slight deviation does not seem to be due to an additional area- or distance-dependence,  
790 so an explanation should be sought in other factors that we did not model. We note that  
791 the fact that all three plots show this tendency rather than just one is to be expected  
792 because the three metrics of species richness are not entirely independent, with total  
793 species richness being the sum of the other two.

794 Second, we examined whether the models successfully predict the empirical  
795 relationships between area, distance and diversity metrics (total species, cladogenetic  
796 species, and number of independent colonisations). We fitted generalised linear models  
797 (GLM) for each diversity metric, with quasipoisson family errors and log area (or  
798 distance) as predictors. We then repeated this across 1000 independent sets of  
799 simulated data for the 41 archipelagos and compared the mean of slopes and intercepts  
800 for archipelago area and archipelago isolation to the equivalent estimates for the  
801 empirical data (Fig. 4).

802 Third, we estimated the pseudo- $R^2$  of the best model (M19) as a measure of the  
803 model's explanatory power. We simulated two independent sets of 10,000 global  
804 datasets under M19 model (Set 1 and Set 2). We calculated the mean total number of  
805 species, number of cladogenetic species and colonisations for each archipelago across  
806 all datasets from Set 1. For each diversity metric we calculated a pseudo- $R^2$  (pseudo- $R^2$ -  
807 observed) where the total sum of squares was obtained from the empirical data and the  
808 residual sum of squares was obtained as the difference between empirical values and  
809 expected values (i.e. the simulation means). As the model is inherently stochastic, even  
810 if the model is an accurate and complete reflection of the underlying processes then the  
811 pseudo- $R^2$  would tend to be  $< 1$ . To estimate the distribution of pseudo- $R^2$  expected  
812 under the model we treated the set 2 simulations as data and estimated the pseudo- $R^2$   
813 for each (pseudo- $R^2$ -simulated). We then calculated the ratio of the pseudo- $R^2$ -observed  
814 values over the 10,000 pseudo- $R^2$ -simulated values. A ratio approaching 1 would  
815 indicate that the model is explaining the observed data as well as the average dataset  
816 simulated under this process (Extended Data Fig. 5).

817

### 818 **Sensitivity to alternative divergence times and tree topologies**

819

820 Despite having sampled many new individuals from islands worldwide, given the wide

821 geographical scale of our study we still rely on sequence data for thousands of  
822 individuals submitted to GenBank over the years. Whenever multi-loci analyses  
823 including our focal taxa were available we used them, but these are rare (Extended Data  
824 Table 4). Therefore, the majority of our phylogenies are based on a small number of  
825 genes, and most on a single gene, *cyt-b*, which is the most widely sequenced  
826 mitochondrial marker in birds. Although some studies on island birds have shown that  
827 colonisation and diversification times derived from mitochondrial trees often do not  
828 differ much from those obtained using multiple loci (e.g. <sup>57</sup>), it is possible that for some  
829 cases the scaling and topologies of the trees might have been more accurate had we  
830 used multiple loci<sup>58</sup>. This is particularly relevant for recent island colonists, given  
831 incomplete lineage sorting<sup>59</sup>. An additional shortcoming of relying on published  
832 sequence data is that many of our DNA alignments often have substantial sections with  
833 missing data (e.g. because only one small section of the gene could be sequenced and  
834 was uploaded to GenBank), which has been shown to lead to biases in branch lengths  
835 and topology<sup>60</sup>. While future studies using phylogenomic approaches may address these  
836 issues, obtaining tissue samples for all these taxa will remain an obstacle for a long time.

837         Although DAISIE does not directly use topological information (only divergence  
838 times are used), it is possible that the true **topology** for a clade may differ from that of  
839 the gene tree we have estimated and this could have an impact on our results by a)  
840 affecting colonisation and branching times (addressed in the paragraph below); or b) by  
841 altering the number of colonisation events. Alternative topologies may have led to an  
842 increase or decrease in colonisation events – for instance, some species that appear to  
843 have colonised an archipelago only once may have colonised multiple times and if these  
844 re-colonisations are recent they may go undetected when using one or few loci. As with  
845 any phylogenetic study, we cannot rule out this possibility, but we assume that recent  
846 re-colonisation of the archipelagos in our dataset by the same taxon is rare, as these are  
847 all oceanic and isolated. For archipelago lineages with cladogenesis (26 out of 502  
848 lineages), alternative topologies could include non-monophyly of island radiations, with  
849 the corollary being that they would be the result of multiple colonisation events.  
850 However, this seems improbable for these isolated and well-studied radiations, for  
851 which morphological evidence (e.g. HBW<sup>37</sup>) is consistent with their monophyly as  
852 supported by existing molecular data.

853           Regarding **scaling of divergence times**, we assessed how uncertainty in our  
854 estimated node ages could influence our results by running an analysis of 100 datasets.  
855 For each dataset we sampled the node ages (i.e. colonisation and branching times) at  
856 random from a uniform distribution centred on the posterior mean for that node in the  
857 BEAST tree and extending twice the length of the highest posterior density (HPD)  
858 interval. For example, for a node with a 95% HPD interval of 2-3 Ma in our trees, the  
859 uniform distribution was set to between 1.5 and 3.5 Ma. The HPD interval will capture  
860 uncertainty under the selected phylogenetic and substitution models for the loci we  
861 used, but we conduct our sensitivity analysis over a broader interval to accommodate  
862 the potential that the selected models and gene trees are inadequate. For cases where  
863 using this approach meant that the lower bound of the uniform distribution was lower  
864 than 0, we assigned a value of 0.00001 Ma to the lower bound. We fitted the nine best  
865 models to the 100 datasets using five initial starting parameters for each model (total  
866 4,500 optimisations). We found that parameter estimates across the 100 datasets do  
867 not differ strongly from those in the main dataset (Supplementary Table 7).  
868 Importantly, model selection was unaffected, with the M19 model being selected for all  
869 100 datasets. This is because a lot of the information used for model selection is coming  
870 from the other sources of information DAISIE uses (island age, number of species,  
871 endemicity status) rather than colonisation/branching times.

872           The ML parameters of the M19 model and the resulting area and isolation  
873 dependencies for datasets D1 to D6 - discussed below - are shown in Extended Data Fig.  
874 6 and the DAISIE R objects including these alternative datasets are available in  
875 Mendeley Data (<https://doi.org/10.17632/sy58zbv3s2.2>).

876           To account for uncertainty in **rates of molecular evolution**, we repeated all  
877 BEAST dating analyses for markers that were not *cyt-b* using 1) the Weir and Schluter<sup>50</sup>  
878 *cyt-b* rate (dataset D1, equal to main dataset) and 2) marker-specific rates estimated by  
879 Lerner et al.<sup>41</sup>, which are also widely used in the literature (dataset D2). Although the  
880 trees dated using the Lerner et al. rates provide younger ages, we found that the DAISIE  
881 results were very similar using either approach (same model preferred and similar  
882 parameters). Therefore, in the main text we only discuss the results of analyses of D1,  
883 i.e. applying Weir and Schluter's *cyt-b* rate to all markers.

884           For some taxa we did not use the stem age as the estimate of colonisation time,  
885 and instead used alternative nodes (see 'Colonisation and branching times' section). To



886 test whether our **choice of nodes** affects our main conclusions, we recoded all such  
887 taxa by extracting the stem ages and used these ages as an upper bound for colonisation  
888 (DAISIE MaxAge option). We fitted all 28 models to this new dataset (D3) and found  
889 that the M19 model is preferred and that the parameters and area/isolation  
890 relationships vary only slightly from those of the main analysis. We therefore conclude  
891 that our results are robust to the node selection approach.

892 If **extinction has been high on the mainland**, or if we failed to **sample the**  
893 **closest relatives** of the island taxa, this could lead to an overestimation of colonisation  
894 times when using the stem age as the precise time of colonisation. To investigate how  
895 this could have influenced our results, we ran analyses of datasets where we allow  
896 colonisation to have happened at any time since the stem age (i.e. the time of divergence  
897 from the nearest relative of the taxon on the mainland). For this we use the DAISIE  
898 options Endemic\_MaxAge or NonEndemic\_MaxAge, which integrate over all possible  
899 ages between the given maximum age and the present (or the first branching event  
900 within the archipelago for cases where cladogenesis has occurred). We repeated this  
901 analysis coding all stem ages as maximum ages (D4), or coding only the 25% older stem  
902 ages as maximum ages (to account for the fact that on older stems there is potential for  
903 there to be more bias) (D5). We also ran analyses on 100 datasets (D6) for which we  
904 assigned precise younger ages by randomly selecting a value between the stem age and  
905 the present (or crown age for cladogenetic groups). For all these datasets (D4-D6) we  
906 found that the same model (M19) is preferred, but the initial values of the  
907 biogeographical rates (cladogenesis, extinction, colonisation and anagenesis) are  
908 estimated to be higher than in the main dataset. Importantly, the exponent  
909 hyperparameters are similar to those in the main dataset, meaning that the shape of the  
910 relationships between parameters and area/isolation is not much affected (Extended  
911 Data Fig. 6). The only exception is perhaps anagenesis, for which the relationships vary  
912 more markedly – with isolated islands achieving very high rates for this parameter -,  
913 but still agreeing with our main conclusions. Anagenesis is in general the most difficult  
914 parameter to estimate<sup>53</sup>. Thus, our conclusions are robust to the colonisation times  
915 potentially being younger than those in our main dataset.

916

### 917 **Sensitivity to archipelago selection and isolation metrics**

918

919 The results of the following sensitivity analyses are presented in Supplementary Data 3  
920 and the DAISIE R objects including these alternative datasets are available in Mendeley  
921 Data (<https://doi.org/10.17632/sy58zbv3s2.2>).

922 To test whether the **inclusion of both true archipelagos and single islands** in  
923 our dataset could affect the results, we repeated analyses excluding single island units  
924 and found that the same model is preferred. The estimated initial rate of cladogenesis  
925 ( $\lambda_0$ ) is higher if we exclude single islands, but this parameter is not different from a  
926 distribution of parameters estimated from datasets generated using a stratified-random  
927 sampling of both archipelagos and single islands.

928 **Alternative isolation metrics** to  $D_m$  have been shown to explain varying and  
929 often higher amounts of variation in species richness on islands<sup>61</sup>. We tested two  
930 alternative metrics: distance to the nearest larger or equivalent-sized landmass ( $D_b$ ),  
931 and the mean between  $D_m$  and  $D_b$  (metrics given in Supplementary Data 2). We found  
932 that the same DAISIE model with very similar parameters was preferred in both cases,  
933 and thus we used only the  $D_m$  metric, as this is more similar to the original model of  
934 MacArthur & Wilson.

935 The **Mascarenes** (Mauritius Isl., Reunion and Rodrigues) are often treated as a  
936 single biogeographical unit in analyses. We chose to analyse them as independent units  
937 because a) the distance between islands is much greater than our threshold for  
938 archipelago definition (more than 500 km between Mauritius Isl. and Rodrigues; more  
939 than 170 km between Reunion and Mauritius Isl.); b) only two species of our target  
940 group are shared between the islands (*Terpsiphone bourbonnensis* found in Mauritius  
941 Isl. and Reunion; and *Psittacula eques* found in Mauritius Isl. and extirpated from  
942 Reunion), suggesting low connectivity; c) while there are three clades whose branching  
943 events took place within the Mascarenes (*Coracina*, *Pezophaps/Raphus* and *Zosterops*),  
944 the remaining species result from independent colonisations suggesting that the three  
945 islands behave mostly as three different biogeographical units. We nevertheless ran an  
946 analysis treating the islands as a single archipelagic unit and found that the same model  
947 was preferred and with similar parameter estimates, and we therefore discuss only the  
948 results treating them as separate.

949

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- 1155

## 1156 **Data availability**

1157 New sequence data produced for this study have been deposited in GenBank with the  
1158 accession codes: MH307408- MH307656. The following datasets have been deposited in  
1159 Mendeley: DNA alignments (<https://doi.org/10.17632/vf95364vx6.1>), new  
1160 phylogenetic trees produced for this study (<https://doi.org/10.17632/p6hm5w8s3b.2>)  
1161 and DAISIE R objects (<https://doi.org/10.17632/sy58zbv3s2.2>). The 11 previously  
1162 published trees are available upon request.

1163

## 1164 **Code availability**

1165 The custom computer code used for this study is freely available in the DAISIE R  
1166 package (<https://github.com/rsetienne/DAISIE>).

1167

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#### 1216 **Author contributions**

1217 L.V., A.B.P. and R.S.E. designed the study, developed the analytical framework and  
1218 performed statistical analyses. L.V. compiled the data, conducted most of the analyses  
1219 and wrote the first draft. R.S.E. developed the likelihood method. A.B.P. and R.S.E.  
1220 contributed substantially to the writing. M.M., B.H.W., S.M.C., J.C.I. and C.T. provided  
1221 expertise on islands birds and collected bird tissue samples, as well as molecular and/or  
1222 phylogenetic data. K.H. and J.C.I. performed laboratory work. R.T. contributed to  
1223 molecular analyses. T.A. performed analyses. All authors commented on the draft.

1224

1225 **Supplementary information** is available for this paper.

1226

1227 **Competing interests** The authors declare no competing interests.

1228

1229 **Correspondence and requests for materials** should be addressed to L.V.



1230

## Extended Data Figure Legends

1231

### **Extended Data Figure 1 | Variation of cladogenesis with isolation and area.**

1232

Contour plot showing how the local rate of cladogenesis varies with area and distance

1233

from the nearest mainland ( $D_m$ ) assuming the ML global hyperparameters of the M19

1234

model (equations describing the relationships given in Supplementary Table 1).

1235

Numbers correspond to the archipelago numbers from Fig. 1, and show the local

1236

cladogenesis rates for each of the archipelagos in our dataset. Area in log scale.

1237

1238

### **Extended Data Figure 2 | Bootstrap precision estimates of the parameters of the**

1239

**M19 model.** Parametric bootstrap analysis fitting the M19 model to 1,000 global data

1240

sets simulated with ML parameters of the M19 model. Plots are frequency histograms of

1241

estimated parameters. Black lines show the median estimated values across all

1242

simulations and the blue lines the simulated values. Dashed lines show 2.5 – 97.5

1243

percentiles. Parameters explained in Supplementary Table 1. Bootstrap parameter

1244

estimates for the M14 model are shown in Extended Data Table 5.

1245

1246

### **Extended Data Figure 3 | Randomization analysis of the M19 model.**

1247

Distribution of global hyperparameters estimated from each of 1,000 datasets with the same

1248

phylogenetic data as our main global dataset but randomly reshuffling archipelago area

1249

and isolation among the 41 archipelagos in the data. Grey histograms show DAISIE ML

1250

parameter estimates for the M19 model. Red arrow shows the estimated parameter

1251

from the real data. In the majority of cases, the hyperparameters describing the

1252

exponent of the power models ( $x$ ,  $\alpha$ ,  $\beta$  and  $d_0$ ) are estimated as zero in the reshuffled

1253

datasets, which is not the case in the real data (red). Parameters explained in

1254

Supplementary Table 1.

1255

1256

### **Extended Data Figure 4 | Goodness of fit of the preferred model (M19).**

1257

Plots show observed total number of species, cladogenetic species and colonisations versus those

1258

simulated under the model. Median and 95% percentiles shown for 1000 simulations of

1259

each archipelago. Selected archipelagos are highlighted in colour. Dashed line is  $y=x$ . See

1260

also Fig. 3.

1261

1262

### **Extended Data Figure 5 | Ratio of pseudo- $R^2$ -observed over pseudo- $R^2$ -simulated.**

1263

Based on 10,000 datasets simulated under M19 model. A ratio centred on 1 would

1264

indicate that the model explains the observed data as well as it is able to explain the

1265

average dataset simulated under the ML parameters.

1266

1267

### **Extended Data Figure 6 | Sensitivity to colonisation and branching times. a,**

1268

ML parameter estimates of the M19 model (preferred model) for datasets differing in

1269

colonisation and branching times. D6 represents 100 datasets, therefore, the 2.5 and

1270

97.5 percentiles are shown. Parameter symbols as in Supplementary Table 1. **b,**

1271

Estimated relationships between island area and isolation and local island

1272

biogeography parameters for each dataset. Under the M19 model, cladogenesis rate

1273

increases with both area and isolation, and thus plots for more (far, 5,000 km) and less

1274

(near, 50 km) isolated islands are shown.

1275 **Extended Data table titles and footnotes**

1276

1277 **Extended Data Table 1 | Archipelago characteristics and references for the island**  
1278 **geological ages.** More data in Supplementary Data 2. For archipelagos closer to  
1279 Madagascar, New Guinea or New Zealand than to the continent, we use those islands as  
1280 the mainland.

1281 **Footnote:**

1282 \* <sup>34</sup> proposed an age of 0.125 Ma, but we used older age, see Methods.

1283 † At least 2 Ma; Paul Hearty pers. comm.

1284 ‡ Robert Stern & Mark K. Reagan pers. comm.

1285

1286

1287 **Extended Data Table 2 | Primer sequences used in this study.**

1288

1289

1290 **Extended Data Table 3 | The 80 alignments used in the new phylogenetic analyses.**

1291 Main source of sequences is GenBank or the new sequences produced for this study,  
1292 except for the cases noted in the table, where a matrix was directly obtained from a  
1293 specific study. Details on molecular rates and molecular models applied to each  
1294 alignment in Supplementary Table 4.

1295

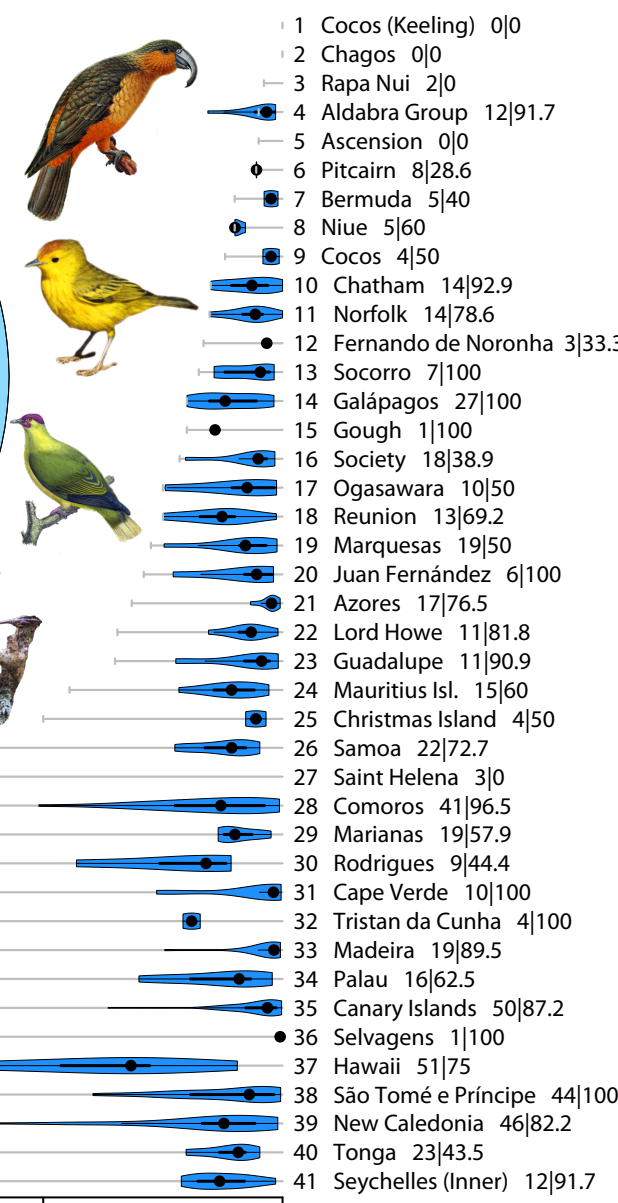
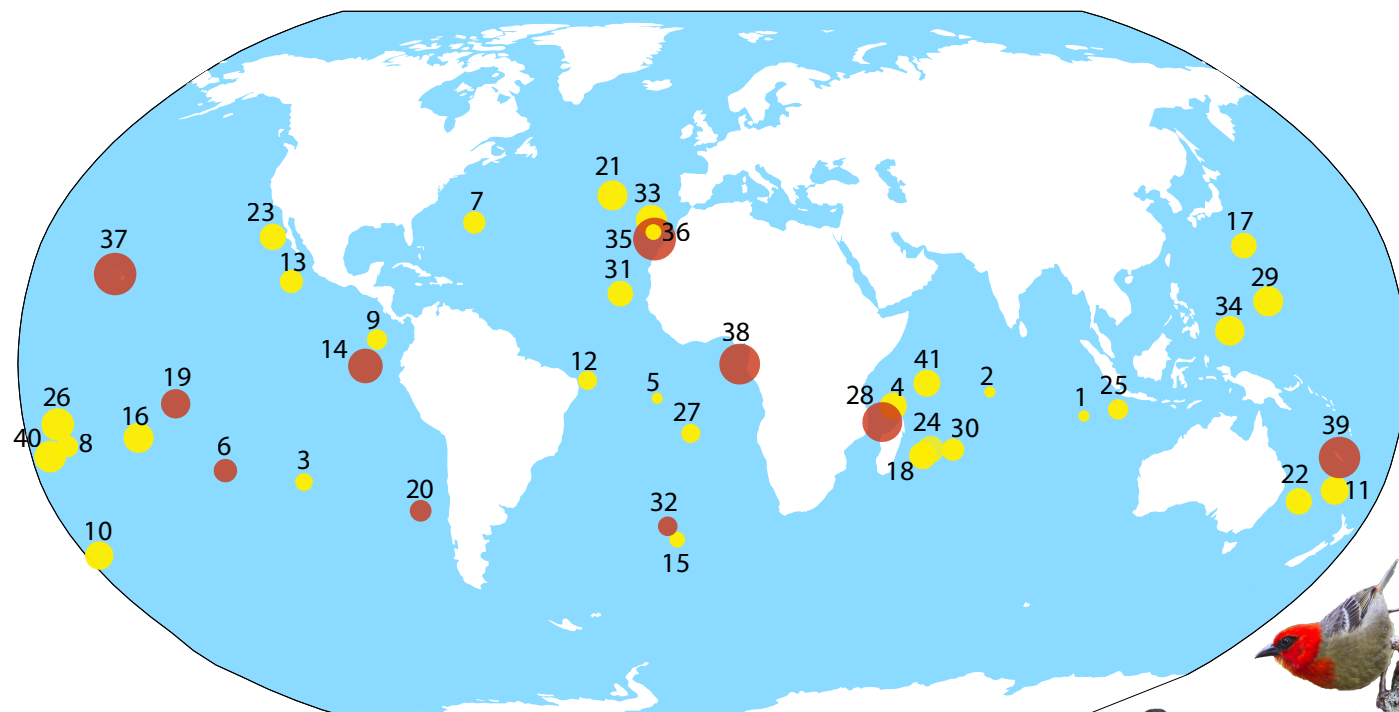
1296

1297 **Extended Data Table 4 | Previously published dated trees used.**

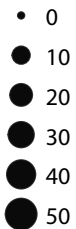
1298

1299

1300 **Extended Data Table 5 | Bootstrap of M14 and M19 models.** ML estimates and 95%  
1301 confidence intervals of the parameters of the two best models. Confidence intervals  
1302 obtained from the bootstrap analyses. Parameter symbols explained in Supplementary  
1303 Table 1.

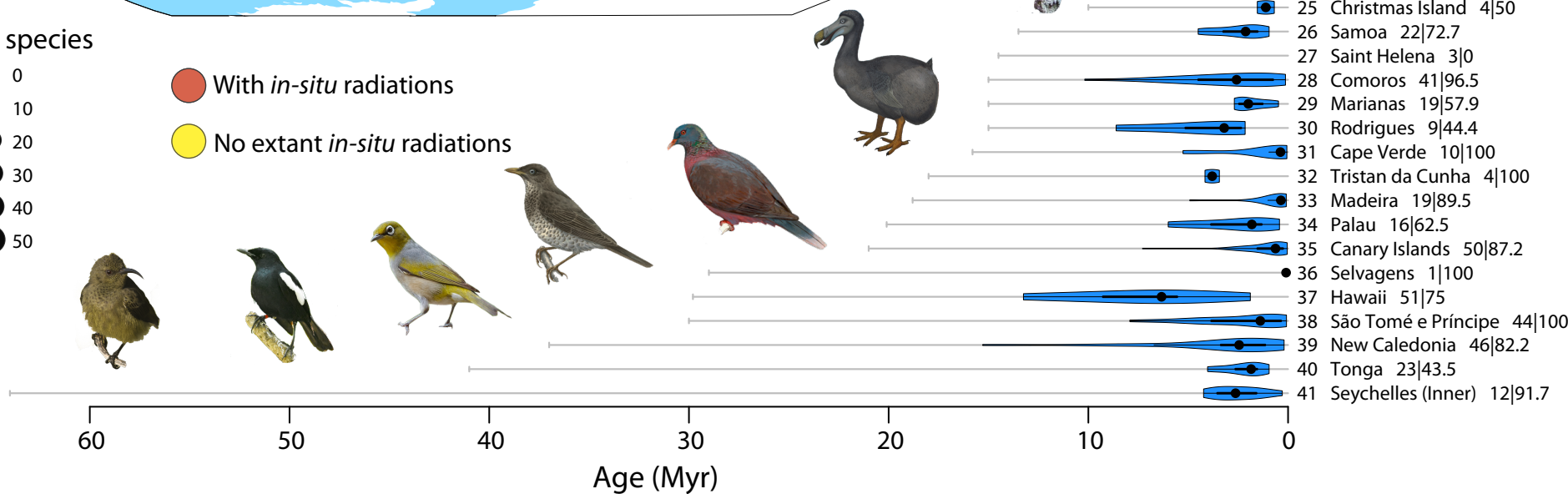


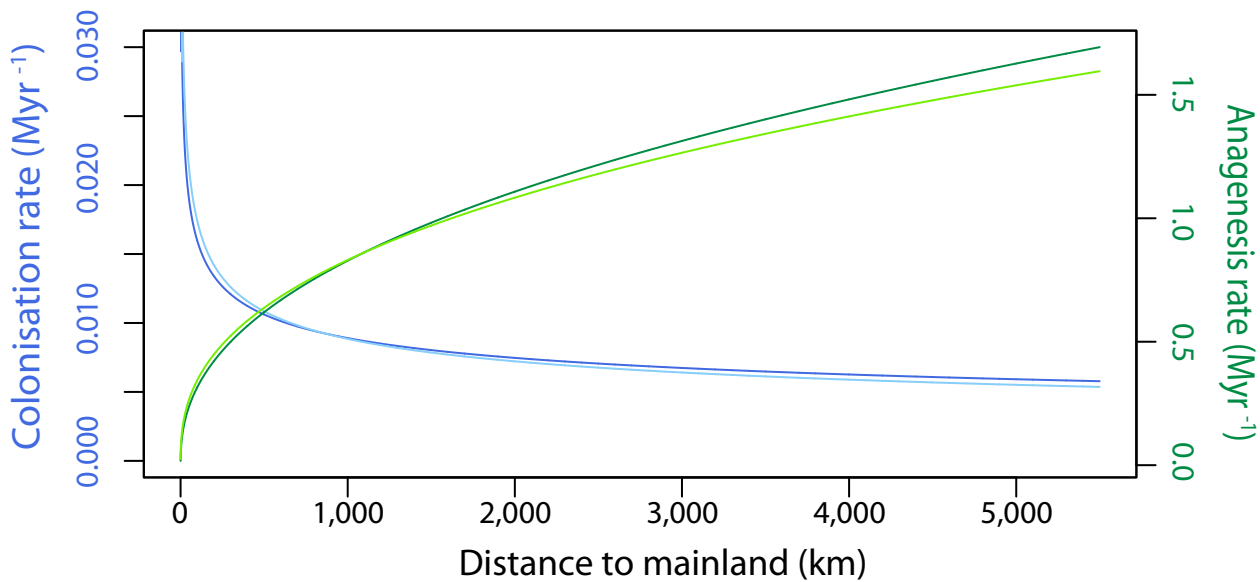
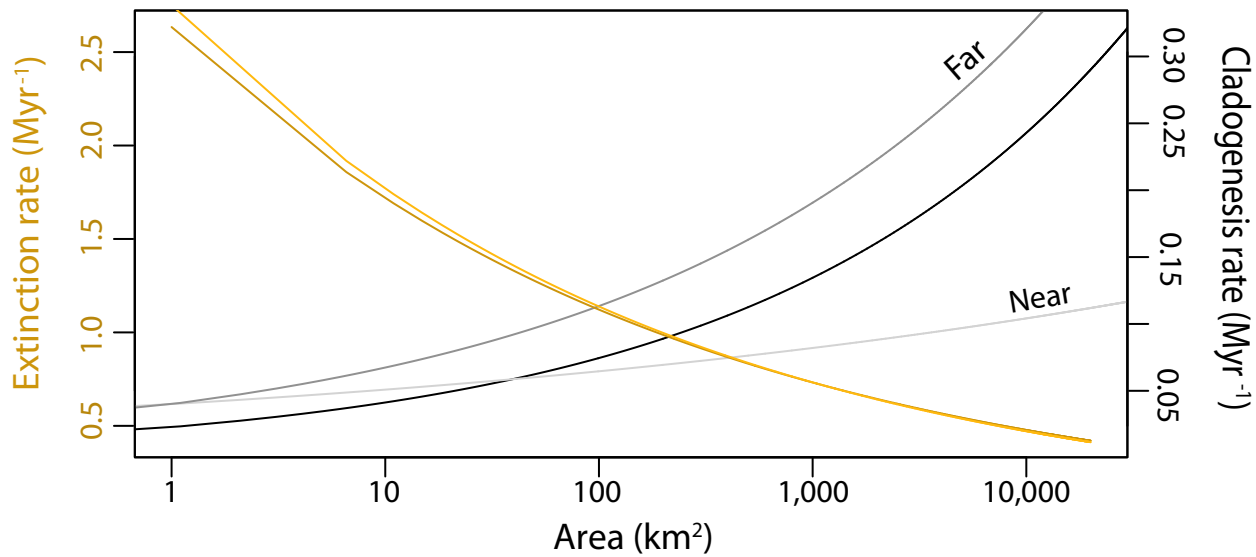
Total species

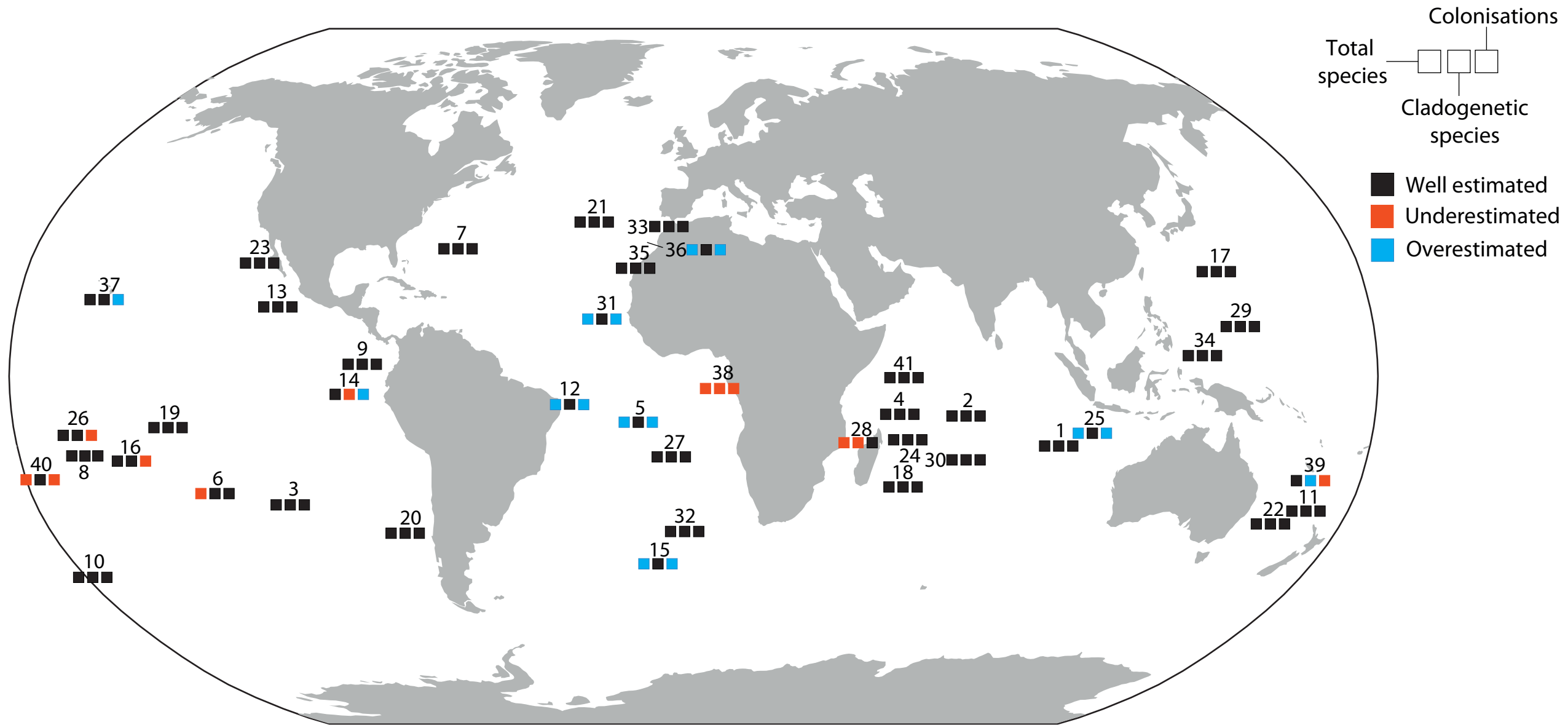


● With *in-situ* radiations

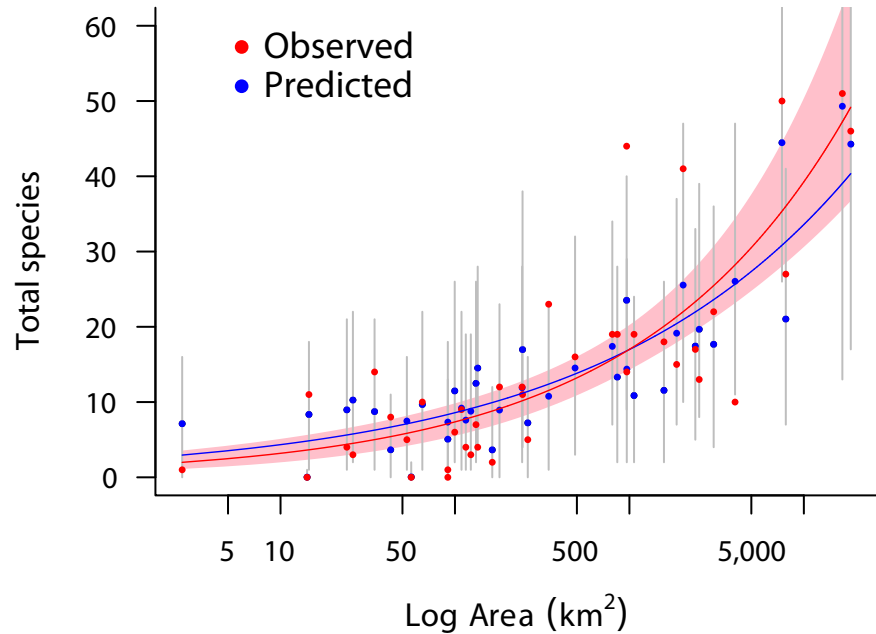
● No extant *in-situ* radiations



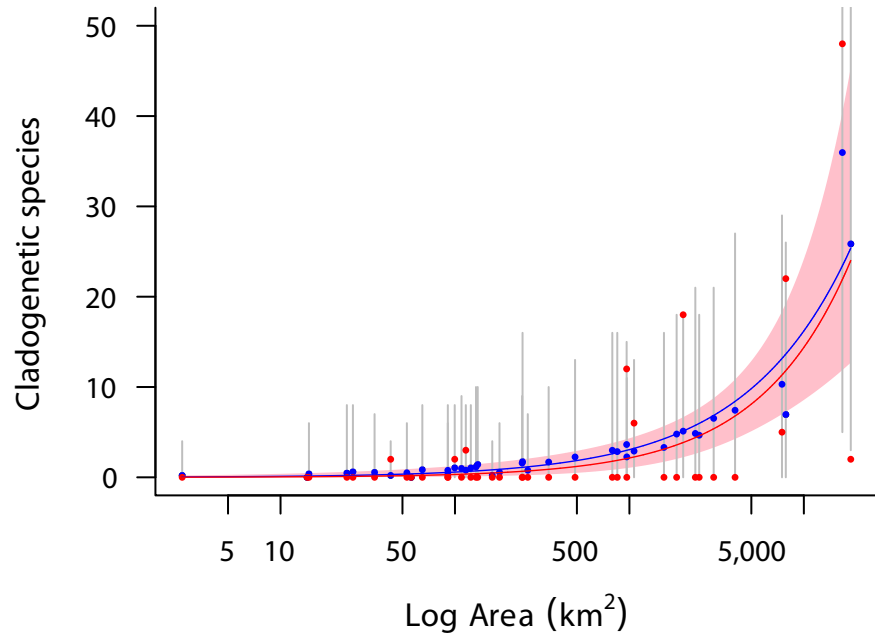




### Total species



### Cladogenetic species



### Colonisations

