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1 **Main Manuscript for**

2 The importance of migratory drop-off for island colonization in birds

3

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28

29 **Author contributions:** PD and SF conceived the study. PD, FS, RC and MG collected the data.  
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31 authors read, made substantial comments, and approved the final manuscript.

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33

34

39 **Abstract**

40 Seasonal migration is an underappreciated driver of animal speciation and diversification.  
41 Changes in migratory behavior may favor the establishment of sedentary founder populations  
42 and promote speciation if there is sufficient reproductive isolation between sedentary and  
43 migratory populations. From a systematic literature review, we here quantify the role of  
44 migratory drop-off – the loss of migratory behavior – in promoting speciation in birds on  
45 islands. We identify at least 157 independent colonization events likely initiated by migratory  
46 species and that led to speciation, including 44 cases among recently extinct species. We  
47 compared the proportion of island endemic species that evolved by migratory drop-off with the  
48 proportion of migratory species in the source area for 40 islands and show that seasonal  
49 migration (movements between breeding and non-breeding locations) has a larger effect on  
50 island endemic richness than direct dispersal. We also found that the role of migration in island  
51 colonization increases with the geographic isolation of archipelagos. Furthermore, the success  
52 of speciation events depends in part on species biogeographic and ecological factors, here  
53 positively associated with greater range size and larger flock sizes. These results highlight the  
54 importance of shifts in migratory behavior in speciation process and calls for greater  
55 consideration of migratory drop-off in the biogeographic distribution of birds.

56

57 **Keywords:** Seasonal migration – long-distance dispersal – birds – island biogeography –  
58 extinct species

## 59 **Introduction**

60 Billions of birds travel twice a year between their breeding and wintering grounds, on journeys  
61 covering hundreds to thousands of kilometers [1]. In fact, birds undertake some of the most  
62 spectacular seasonal migrations in the animal kingdom and while seasonal migration is a  
63 globally well-studied phenomenon, little research has assessed its role in population divergence  
64 and diversification processes (see [2–4]).

65 Seasonal migration is here defined as regularly timed movements of organisms between  
66 breeding and non-breeding locations [5]. Most bird species, sedentary or migratory, exhibit  
67 some level of breeding site fidelity and/or philopatry and indeed, many migratory species return  
68 to their breeding grounds with exceptional precision [6]. There is thus no direct relationship  
69 between migration distance and dispersal distance (i.e., movement between birth and first  
70 breeding, or between breeding events [7]; see [8,9]). However, migratory movements may also  
71 increase the opportunities to encounter, settle and breed in, locations far from the place of birth  
72 or previous breeding [10]. In those rare cases where migratory birds attempt to breed far from  
73 their birthplace or previous breeding locations, migratory movements can effectively result in  
74 long-distance dispersal [11]. When the settlement is associated with a loss of migratory  
75 behavior (i.e., a shift towards sedentariness, called migratory drop-off), it may result in  
76 speciation if accompanied by an interruption of gene flow between migratory and sedentary  
77 populations [12].

78 Phylogenetic studies in several bird clades have identified migratory drop-off as an  
79 important mechanism of speciation (e.g., [13–16]) and previous studies have underscored the  
80 significance of this phenomenon on large scales [4,12,17]. Despite these insights, a thorough  
81 evaluation in the specific context of island environments is lacking. Yet, island environments  
82 offer an optimal study system for delving into this mechanism, as island endemism must result  
83 from over-water dispersal that then leads to speciation in oceanic islands (i.e. those surrounded  
84 by water since their emergence) [18].

85 Bird immigration from continents to islands via over-water dispersal can result either  
86 from exploratory movements, which we refer to here as direct dispersal, or from migratory  
87 movements (Fig. 1). Migratory movements can be either seasonal or irruptive, and performed  
88 in response to environmental variation [19]. By contrast, exploratory movements are generally  
89 performed to explore the environment, regardless of any variation of the latter, and can occur  
90 before or after the breeding season, with the primary objective of finding new breeding  
91 territories [20]. Both migratory and sedentary species can perform exploratory movements, but  
92 the distances are relatively short compared to those covered during migratory movements [21].

93 In addition, visitation of island environments also depends on the species' degree of vagrancy,  
94 i.e., the appearance of an individual outside the normal distribution range of its species, often  
95 due to navigational errors or severe weather events, a phenomenon that is more frequent in  
96 migratory species [11,22]. Interestingly, the relative contributions of different bird movements  
97 (migration by-products vs. exploration) to island colonization remain unknown.

98 Despite its importance in island biogeography, the process of immigration remains  
99 poorly understood [23]. Alternating phases of selection for high and low dispersal ability have  
100 long been considered a key feature in the colonization and speciation process [24–26]. In the  
101 context of trans-oceanic speciation in migratory species, variations in the use of migration  
102 routes, and the large climatic fluctuations that occurred during the Pleistocene, may also have  
103 acted as alternating phases that either favored or prevented the arrival and settlement of  
104 migratory species on archipelagos [27]. For example, during ice-age conditions, migratory  
105 movements were considerably reduced [28,29]. Thus, an established island population may  
106 have diverged rapidly from its original migratory population, and reproductive barriers may  
107 have continued to promote divergence once migratory movements were restored.

108 In this study, we assess the influence of migratory movements in promoting speciation  
109 in insular environments. We take advantage of the availability of recent comprehensive  
110 phylogenies for most bird clades (e.g., [30]) and the increase of data availability on recently  
111 extinct species (e.g., [31–33]). We first completed an exhaustive literature review, looking for  
112 evidence of trans-oceanic speciation associated with migratory drop-off on islands [18]. By  
113 comparing, for all islands and archipelagos, the proportion of island endemic species that  
114 derived from speciation associated with migratory drop-off with the proportion of migratory  
115 species among potential colonizers, we tested whether seasonal migration is an important driver  
116 of speciation on islands. We then separately analyzed the geographic and taxonomic variation  
117 in the importance of migratory drop-off. We tested whether the contribution of migratory drop-  
118 off changes with geographical features of islands (e.g., latitude, distance from the nearest  
119 landmass). We also tested whether traits thought to influence over-water long-distance dispersal  
120 and speciation in birds (Table 1), including flight efficiency (hand-wing index), relative brain  
121 size, flock size or diet breadth, may drive the success of speciation by migratory drop-off.

122

## 123 **Materials and Methods**

124 All analyses were performed in R version 4.2.2 using the packages ape 5.7-1 [34], foreign 0.8-  
125 84 [35], ggplot2 3.4.4 [36], mapplots 1.5.1 [37], phylolm 2.6.2 [38], Rphylopars 0.3.9 [39], and  
126 scales 1.2.1 [40].

127

128 *Speciation process*

129 To identify island endemic species that evolved from trans-oceanic speciation associated with  
130 migratory drop-off, we collected information on phylogenetic relationships, migratory  
131 movements and distributions for mainland and close relative species of all island endemic  
132 species. To examine the biogeographic history of lineages with minimum uncertainty, we chose  
133 to rely on comprehensive phylogenies for each clade (see below) rather than on the available  
134 global bird phylogeny [41].

135 First, we compiled a list of island endemic bird species, including 316 recently extinct  
136 species (i.e., from the Late Pleistocene onward; [33,42]). We were interested in most recent  
137 cases of speciation (less than 5 million years ago) and our list therefore excluded families that  
138 are entirely endemic to islands (e.g. Acanthisittidae, Brachypteraciidae). We also excluded  
139 seabirds (here defined as Suliformes, Procellariiformes, Sphenisciformes, Stercorariidae and  
140 Alcidae) due to their complex movements outside of the breeding period. We excluded the few  
141 island endemic species that undertake seasonal migration (e.g., *Progne cryptoleuca*, *Progne*  
142 *dominicensis*). We also excluded Rallidae which, despite the presence of many endemic species  
143 on numerous archipelagos, likely contain a disproportionately large number of unrecorded  
144 anthropogenic extinct species [43], which could bias our analyses.

145 Second, we identified the closest mainland relative (i.e., the continental species that  
146 shared the same most common ancestor) of each island endemic species. Mainland was here  
147 defined as continents as well as islands larger than 100,000 km<sup>2</sup> (e.g., Madagascar, Cuba or  
148 New Zealand). These larger islands were considered both as “islands” and “mainland”, acting  
149 as sources for species that have speciated on surrounding islands (i.e., mainland) but also  
150 allowing speciation of migrants from continents (i.e., island). We distinguished species derived  
151 from trans-oceanic speciation from species derived from within-island speciation (i.e., clades  
152 of multiple species derived from a unique colonization event which occupy the same island or  
153 the same archipelago). We omitted species derived from within-island speciation in the  
154 subsequent analyses since we were interested in island colonization events.

155 Third, we assessed whether island endemic species evolved from trans-oceanic species  
156 induced by migratory drop-off or direct dispersal movements, based on information on  
157 migratory behavior, seasonal movements and distributions of mainland and close relatives  
158 found in reference handbooks [44,45]. Evaluating whether island endemic species have  
159 emerged via migratory drop-off or direct dispersal is not straightforward for all species and can  
160 be subject to debate. To account for the uncertainty associated with this inference, we have

161 created 4 categories reflecting whether island endemic species have evolved from migratory  
162 drop-off: (1) very likely (conservative set, with clear and convincing evidence), (2) likely  
163 (liberal set, with reasonable suspicion), (3) unlikely, and (4) data deficient (not sufficient  
164 evidence). A species has *very likely* evolved by migratory drop-off if the closest-relative is a  
165 strict migrant, related species (i.e., other species that share the same evolutionary history and  
166 that are grouped together on the phylogenetic tree) are strict or partial migrants, and the island  
167 is an extension of, or near, current migration routes. A species has *likely* evolved by migratory  
168 drop-off if the island is an extension of, or near, current migration routes, but the closest-relative  
169 (and related species) includes sedentary populations (i.e., is a partial migrant) and colonization  
170 by a direct dispersal event from current or past sedentary populations cannot be ruled out. A  
171 species has *unlikely* evolved via migratory drop-off, but rather from direct dispersal  
172 movements, if the closest-relative and related species are mostly sedentary (see Supplementary  
173 Information for more details).

174

#### 175 *Seasonal migration as a driver of speciation on islands*

176 Because island endemic species that evolved from migratory drop-off must have derived from  
177 migratory ancestors, we investigated if seasonal migration is a driver of speciation on islands.  
178 We tested this hypothesis by comparing the proportion of island endemic species derived by  
179 migratory drop-off to the proportion of migratory species in the source area. If, in the majority  
180 of archipelagos, the proportion of island endemic species resulting from migratory drop-off  
181 surpasses the percentage of migratory species in the source area, it suggests that migratory  
182 species are more likely to drive the evolution of island endemic species, emphasizing the  
183 importance of drop-off speciation as an important phenomenon.

184 The proportion of colonization events derived by migratory drop-off was estimated from  
185 the number of island/archipelago endemic species identified to have evolved from migratory  
186 drop-off (likely + very likely) against the number of species derived from direct dispersal  
187 events. The proportion of migratory species in the source area was estimated as follow. For  
188 each island, the source area was defined as the polygon encompassing the distribution of all  
189 mainland sister groups of all island endemic species. We used the breeding range maps of  
190 Birdlife International [42] gridded at a 50x50km resolution to delineate the polygon and then  
191 extracted the number of migratory (partial and strict) and the number of sedentary species (i.e.,  
192 the overall species richness), considering species with at least 25% of their range overlapping  
193 the polygon (migration strategies can be found in Supplementary Data 1). We considered that

194 25% of the breeding distribution of a species represents a sufficiently significant part of its  
195 population but also tested whether different values of overlap threshold could affect the results.

196 Subsequently, we calculated the number of archipelagos where the ratio of endemic  
197 species derived by migratory drop-off surpassed the proportion of migratory species in the  
198 source area. A binomial test was then employed to determine whether this count significantly  
199 deviates from the null hypothesis ( $H_0 = 50\%$ ). To account for uncertainties in our categorization  
200 of migratory drop-off events, we conducted a parallel analysis only including events identified  
201 as *very likely* (with events identified as *likely* reclassified as direct dispersal events).

202 To ensure that we only consider trans-oceanic speciation events (i.e., exclude vicariance  
203 events), we excluded islands and archipelagos that have been connected to continental  
204 landmasses in the last five million years and which have been too close (less than 100  
205 kilometers) to landmasses to consider that long-distance dispersal events occurred (details can  
206 be found in Figure S1).

207

#### 208 *Geographical structure of migratory drop-off*

209 We tested for potential geographic structure of migratory drop-off, using three different  
210 variables for this purpose: 1) absolute latitude, 2) distance from the nearest equivalent or larger  
211 landmass and 3) ocean identity (categorical). We expected to find a positive correlation between  
212 the proportion of island endemic species derived by migratory drop-off and the absolute latitude  
213 of islands, as the occurrence of migratory species may increase in high latitude islands because  
214 both the proportion and the number of migratory species increase with latitude. The distance  
215 from the nearest equivalent or larger landmass was defined as the distance between the island  
216 and the nearest continent or island of similar area. This variable assessed whether migratory  
217 drop-offs are more frequent on isolated islands, as we suspected that sedentary species may  
218 colonize islands located far from continents only if they manage successively to colonize  
219 islands located near each other using them as steppingstones. We used the distance values  
220 published in Valente et al. [46], available for most of the archipelagos, and followed their  
221 methods to estimate the distance to the nearest mainland or to the nearest equivalent or larger  
222 landmass for missing values (see details in Supplementary Data 1). Finally, we used the third  
223 variable, ocean, indicating the ocean (Atlantic, Pacific, Indian; considering the Mediterranean  
224 and the Caribbean as part of the Atlantic Ocean) in which the island is located to test for  
225 potential regional effects.

226 We tested the relative influence of these three variables on the proportion of island  
227 endemic species derived by migratory drop-off (likely + very likely; against the number of



228 species derived by direct dispersal events). Again, we omitted species derived from within-  
229 island speciation. We examined correlations between variables prior to the analysis and fitted a  
230 binomial model using the *glm* function with the proportion of island endemic species derived  
231 by migratory drop-off as the explanatory variable. Because differences in the number of island  
232 endemic species mostly depend on the age and surface area of the island [46], we weighted the  
233 model by the total number of endemic species in each island. We considered the same set of  
234 islands and archipelagos as in the previous analysis.

235

### 236 *Biogeographic and ecological traits*

237 We wanted to investigate whether, and if so why, some families exhibit a greater number of  
238 migratory drop-off events than others. To do so, and for migratory species only, we selected  
239 five different variables considered as relevant for influencing over-water long-distance  
240 dispersal and island speciation: 1) range size, 2) flock size, 3) diet breadth, 4) relative brain size  
241 and 5) hand-wing index (for definitions and predictions see Table 1 and Supplementary  
242 Information). We tested for the relative influence of these biogeographic and ecological traits  
243 on the number of migratory drop-off events per migratory family using phylogenetic regression.

244 We modelled rate of migratory drop-off per family, calculated by multiplying the total  
245 number of drop-offs (likely + very likely) by the proportion of migratory species and divided  
246 by total evolutionary time (sum of all branch lengths). Our null expectation was that all families  
247 have the same rate of drop-off per million years per lineage and we assumed that the fraction  
248 of migratory species within each family remained constant over time (even though we do not  
249 have evidence supporting this assumption). Exploratory analyses found that the number of  
250 migratory drop-off events per family scaled linearly with the proportion of migratory species  
251 (correlation coefficient = 0.77) and with total evolutionary time (correlation coefficient = 0.58),  
252 suggesting that the approach is justified (more details can be found in Supplementary  
253 Information).

254 Using the package *phylolm* [38], we then fitted phylogenetic generalized least square  
255 (PGLS) models to test how our five explanatory variables were associated with the rate of  
256 migratory drop-off events per family, while controlling for phylogenetic relatedness with  
257 Pagel's lambda [47]. We computed a family-level phylogeny, following the BirdLife  
258 International taxonomy, by pruning the maximum clade credibility (MCC) tree of Jetz et al.  
259 [41], modified with the backbone of Prum et al. ([48]; see method in [49]). All variables were  
260 centered and scaled prior to analyses to facilitate interpretation (effect sizes were obtained from  
261 regression coefficients of the model) and correlations between variables were examined prior

262 to the analysis (all had variance inflation factors below five). Variable importance was  
 263 calculated with a function where each variable was randomly permuted (1,000 times) to  
 264 simulate its absence in the model while keeping the number of degrees of freedom constant  
 265 [50]. We considered a total of 91 families for this analysis, including 43 families with at least  
 266 one migratory drop-off event identified and 48 families with no drop-off identified but  
 267 including at least one migratory species.

268 To evaluate the importance of anthropogenic extinction and the need to consider extinct  
 269 species in understanding evolutionary patterns, we repeated the phylogenetic regression by  
 270 either excluding species extinct before 1500 CE or excluding all extinct species. Finally, to test  
 271 whether these variables are specific to over-water long-distance dispersal and island speciation  
 272 in migratory species, we also repeated the analysis for species having derived by direct dispersal  
 273 events. Following the same method, we modelled the corrected number of direct dispersal  
 274 events per family, excluding species derived from within-island speciation, considering a total  
 275 of 180 families including 47 families with at least one island endemic species derived by direct  
 276 dispersal.

277 It is analytically challenging to know when to rely only on available data only and when  
 278 to rely on complete but potentially imprecise data coming from imputation. For the main  
 279 analyses, we used only the available data for flock size (87% of species) and relative brain size  
 280 (26% of species) but we ran supplementary analyses where we imputed all missing values  
 281 before taking means (details in Supplementary Information). The results were very similar  
 282 between these approaches (Table S1 vs S2) and the imputed results will not be discussed further.  
 283

284 **Table 1.** Definitions and predictions for the association between ecological and  
 285 biogeographical traits and island colonization and speciation by migratory drop-off. We  
 286 calculated mean values per family. Additional details can be found in the Supplementary  
 287 Information.

288

289

<b>Traits</b>	<b>Definition</b>	<b>Prediction</b>	<b>Data source</b>
Range size	The number of grid cells occupied by each species	Families that occupy a larger geographic area are more likely to colonize more archipelagos	[42]
Flock size	The average of mean flock size of each month of each species	Probability of establishment of a sustainable population increases with the number of arriving individuals [51]	[52]

Diet breadth	The number of diet categories used by each species	Families with a broader diet (generalists) would be more likely to colonize islands, because of their greater ability to find resources and survive compared to dietary specialist species [53]	[54]
Relative brain size	The residuals from a log-log phylogenetic generalized least square regression of absolute brain size against body size	Larger relative brain sizes have been shown to reflect a disproportionate enlargement of the pallial areas and enhanced flexibility [55,56], and are suggested to be associated with island living [57]	[58,59]
Hand-wing index	The Kipp's distance (the distance between the tip of the first secondary feather and the tip of the longest primary feather) corrected for wing size	Hand-wing index is a surrogate for flight capacity [60]; families with a high flight capacity (i.e., strong fliers) could reach isolated archipelagos more easily than weak flyers	[61]

290

291

292 **Results**

293 We identified 157 events of migratory drop-off that led to speciation (67 identified as very  
 294 likely, 90 as likely; Fig. 2). From these 157 unique colonization events, a total of 318 island  
 295 endemic species (221 extant, 46 extinct after 1500 CE and 51 extinct before 1500 CE) likely  
 296 evolved as a result of within-island speciation (Fig. S2).

297 Migratory drop-off represents a significant proportion of the colonization events for  
 298 some islands and archipelagos. We found that very likely and likely migratory drop-offs  
 299 together represent at least 7 out of 14 colonization events in the Canaries (representing 11 out  
 300 of 18 species), 10 out of 17 in Hawaii (representing 78 out of 95 species), 3 out of 4 in Saint  
 301 Helena (representing 3 out of 4 species), and 8 out of 24 in Mauritius and Reunion islands  
 302 (representing 14 out of 39 species; Fig. 3a; Supplementary Data 2). The proportion of island  
 303 endemic species that evolved by migratory drop-off was higher than the proportion of migratory  
 304 species in the source area in 31 out of 38 islands or archipelagos ( $H_0 = 50\%$ ; confidence-interval  
 305 = 0.66-0.92;  $p$ -value < 0.001; Fig. 3b) suggesting that seasonal migration was important for  
 306 speciation. We obtained very similar results when considering only the migratory drop-off  
 307 events identified as very likely, and when considering different values of overlap threshold (Fig.  
 308 S3).

309 We found that the proportion of island endemic species derived from trans-oceanic  
 310 speciation induced by migratory drop-off (against the number of trans-oceanic speciation

311 induced by direct dispersal events) significantly increased with the distance of the nearest larger  
 312 or equivalent land mass (Table 2), suggesting that migratory drop-off is more frequent on  
 313 isolated islands. These patterns were not influenced by latitude. We also found strong regional  
 314 effects in the proportion of island endemic species that evolved by migratory drop-off according  
 315 to the location of the islands or archipelagos, with drop-off events occurring more often in the  
 316 Atlantic Ocean (Table 2).

317 Biogeographic and ecological characteristics can facilitate speciation by migratory  
 318 drop-off and may explain why some migratory families were more successful in speciating in  
 319 island environments than others. Our models identified a positive effect of range size and flock  
 320 size on the corrected number of migratory drop-off events identified per family (Fig. 4a; Table  
 321 S1): migratory families travelling in large flocks and/or species that occupy large geographic  
 322 area are more likely to colonize an island to speciate (respective p-values = 0.004 and 0.044).  
 323 By contrast, we did not find any effect of diet breadth, relative brain size or hand-wing index.  
 324 Notably, analyses that excluded either species extinct before 1500 CE or all extinct species  
 325 failed to recover any significant effects (Fig. 4a) and the strong phylogenetic signal that we  
 326 found when all species were included ( $\lambda = 1$ ) disappeared when all extinct species were  
 327 excluded ( $\lambda < 0.001$ ; Table S1).

328

329 **Table 2.** Results of the binomial regression modelling the effect of geographical variables on  
 330 the proportion of island endemic species derived per migratory drop-off. The distance to  
 331 equivalent island represents the distance of the nearest larger or equivalent land mass and  
 332 assesses whether migratory drop-offs are more frequent on isolated islands. S.E. is the standard-  
 333 error and significant p-values are denoted with asterisks;  $p < 0.05$  (\*),  $p < 0.01$  (\*\*) and  $p < 0.001$   
 334 (\*\*\*).

335

Variable	Estimate	SE	z-value	p-value
Atlantic Ocean	-0.8	0.3	-2.8	0.005 **
Indian Ocean	-1.5	0.4	-3.9	<0.001 ***
Pacific Ocean	-1.6	0.4	-4.2	<0.001 ***
Latitude	1.0	0.7	1.4	0.156
Distance to equivalent island	2.4	0.7	3.5	<0.001 ***

336

## 337 Discussion

### 338 *Seasonal migration and island speciation*

339 Here, we identify endemic species on most of the world's islands that evolved from trans-  
340 oceanic speciation induced by migratory drop-off of a likely migratory ancestor. In most  
341 archipelagos, we found a higher proportion of island endemic species that evolved from  
342 migratory ancestors than the proportion of migratory species among potential colonizers, hence  
343 suggesting that seasonal migration plays an important role in the immigration process in island  
344 biogeography. Our results indicate a positive influence of migratory behavior on speciation rate  
345 by promoting long-distance dispersals on remote archipelagos where divergence can rapidly  
346 occur, and hence corroborate the main results of Rolland *et al.* [4].

347 While we have identified island endemic species that likely evolved from migratory  
348 drop-off on most islands, the relative importance of this phenomenon compared to direct  
349 dispersal events appears to be variable across islands or archipelagos. As examples, we  
350 identified few migratory drop-off events in proportion to direct dispersal events (or species  
351 evolved via within-island speciation) in the southern Pacific Ocean, while migratory drop-off  
352 events constitute most of the colonization events for the mid-Atlantic islands (e.g., Azores, St  
353 Helena). We found that the proportion of migratory drop-off events increases on isolated  
354 islands, suggesting that migratory species are disproportionately more likely to occur, settle and  
355 diverge on islands isolated from the continents, and from other islands of at least similar size,  
356 than non-migratory species. This result also suggests that isolated islands are less accessible for  
357 sedentary species, which can only reach islands close to the mainland or close to each other.  
358 This pattern is consistent with the idea of the stepping-stone model of island colonization,  
359 mostly proposed for sedentary lineages, where the first settlers come from the nearest mainland  
360 and then follow a chronological sequence of colonization of the nearest island [62].

361 Our results also suggest that the proportion of drop-offs increases for islands or  
362 archipelagos located within or close to major migratory flyways. We found many drop-offs for  
363 the Caribbean islands or the Canary Islands, but few drop-offs in the many archipelagos of the  
364 Pacific Ocean. Even though the Caribbean and the Canary Islands are close to the continental  
365 masses (or to other islands of similar size) where gene flow may be favored and thus inhibit the  
366 speciation process, their proximity to major migratory flyways probably compensates for this.  
367 Indeed, their geographical location makes these islands more likely to be visited by migratory  
368 species, which may be trapped and/or encounter environmental conditions that influence their  
369 decision to migrate and promote migratory drop-off [13].

370 The location of insular endemic species with respect to the geographical origin of  
371 migratory lineages corroborates the hypothesis that migratory species have a high propensity  
372 for vagrancy, and therefore to occur on isolated archipelagos where they may act as a propagule

373 in the colonization phase [63]. Several cases of migratory drop-off indicate that migratory birds  
374 do not necessarily originate from the nearest land. In Hawaii for example, although the  
375 archipelago is almost twice as close to America as it is to Asia, several island endemic lineages  
376 derive from Asian migratory species (e.g., honeycreepers: [60]; crows: [61]). The same is true  
377 for several island endemic species of the Mascarene archipelago which derived from migratory  
378 lineages that ancestrally migrated within Asia or between Asia and East Africa [66,67].  
379 Migratory individuals departing alone on their first migrations can occasionally misinterpret  
380 their migratory program and take erroneous orientations (e.g., mirror-image, reverse-migration  
381 [64]). In addition, external meteorological factors (e.g., storms) can displace migratory birds  
382 off their usual migration routes [69]. Nevertheless, Lees & Gilroy [70], who focused on the  
383 contemporary distribution and occurrence patterns of species (thus excluding island endemic  
384 species and past colonization events), failed to find an association between colonization of  
385 oceanic islands and vagrancy in their analysis. Their study nevertheless attests that island  
386 colonization by vagrant individuals is a well-established phenomenon, more frequent in  
387 migratory species.

388

### 389 *Ecological drivers of migratory drop-off*

390 Our results showed that some families are more likely to perform trans-oceanic speciation  
391 through migratory drop-off than others, depending notably on the average range size and flock  
392 size of species within the families.

393 The positive relationship between range size and speciation would suggest that part of  
394 the variation in migratory drop-off may be driven by variation in population size. All else being  
395 equal, species with larger ranges should have more individuals and likely also more individuals  
396 outside the regular ranges (i.e., vagrants). Moreover, as hypothesized by Lees & Gilroy [70],  
397 the positive relationship could suggest that families occupying large global ranges are likely to  
398 have increased opportunities for visiting islands, as their regular range more likely encompasses  
399 or lies relatively close to multiple islands or archipelagos – greater encounter potential.

400 Migratory drop-off occurred particularly in families migrating in large flocks,  
401 suggesting, that the number of arriving individuals influences the probability of establishment  
402 of a sustainable population [51]. It is expected that a large group of individuals, rather than  
403 several colonization events of small groups of individuals, will allow for more successful  
404 colonization and divergence. In addition, species migrating in large flocks are partly species  
405 migrating by following conspecifics (e.g., Anatidae and Gruidae [66]). Such species can more  
406 easily be trapped and become sedentary if they reach an unknown destination or if non-

407 experienced individuals become separated from experienced individuals (e.g., [36]).  
408 Nevertheless, it must be noted that most vagrancy events involve single individuals which may  
409 not be inconsequential for dispersal and colonization if frequent and pervasive.

410         Despite strong biological expectation, we found little evidence for a relationship at the  
411 family-level between speciation induced by migratory drop-off and other plausible traits  
412 directly linked to migration capacity and establishment success. Our analysis did not support  
413 an association between migratory drop-off and diet breadth, relative brain size and hand-wing  
414 index. We hypothesized that dietary generalists should have higher chances of finding suitable  
415 resources and may cope better with seasonally available resources than dietary specialists upon  
416 establishment on islands [72], which could also influence the decision to settle [73,74]. It is  
417 possible that the categorization of the diet data used was too coarse to detect an effect.  
418 Regarding relative brain size, previous work found that larger brain sizes were not associated  
419 with the propensity of island colonization, but instead seem to be favored after the colonization  
420 event [57]. This, together with the fact that migratory species tend to have relatively small  
421 brains [75] may partially explain the non-significant result. A further aspect to consider is the  
422 unimodal relationship between diversification rate and dispersal ability found in several studies,  
423 where efficacy of barriers to gene flow decreases as the dispersal capacity of families increases  
424 [60,76]. A species that has colonized an archipelago but still reaches it frequently, because of  
425 high dispersal capacity and/or frequent departure from its migratory route, could potentially  
426 maintain a sufficient gene flow to prevent divergence of populations and evolution of new  
427 species, as the case for example in Eurasian Woodcock *Scolopax rusticola* and Common Wood  
428 Pigeon *Columba palumbus* in the Canaries and Azores [77,78]. In fact, migratory species that  
429 frequently disperse to insular environments would likely have frequent short-term populations  
430 on islands during suitable periods, and their local adaptation could only depend on the change  
431 of migration routes, linked to fitness consequences [79] or climatic variations [28].

432         Finally, our results highlight the importance of integrating extinct species into analyses  
433 when studying global evolutionary and ecological patterns. When excluding extinct species in  
434 the comparative analyses, we missed the significant role of ecological traits (range size and  
435 flock size) as drivers of migratory drop-off colonization success and lost the phylogenetic  
436 signal. Biases in trait effects have frequently been reported previously [33,80], but the loss of  
437 phylogenetic signal when extinct species are excluded is a somewhat unexpected result. These  
438 results stress the importance of analyzing the full natural diversity rather than the diminished  
439 current diversity whenever possible in macro-scale analyses. If this study stresses the  
440 importance of shifts in migratory behavior in speciation process in island environments, the

441 number of events identified is also likely minimized given the large number of species that have  
442 gone extinct recently without leaving any trace in the fossil record [81].

443

#### 444 *Perspectives and conclusion*

445 Several studies have shown that migratory drop-off is an important mechanism of speciation  
446 and migratory behaviour is known to be a labile trait on evolutionary time scales (e.g.  
447 [4,17,45]). Interestingly, previous work reported that losses of migratory behaviour were more  
448 frequent than gains [4]. However, the alternative scenario of a gain in migration following a  
449 dispersal event is also theoretically plausible and might be difficult to detect from phylogeny.  
450 In the island context, such a scenario seems unlikely as the number of island migrants is limited  
451 to a few species (e.g., Cuban Martin *Progne cryptoleuca*, Caribbean Martin *Progne*  
452 *dominicensis* in the Caribbean) but invites further research to understand the context in which  
453 these species evolved.

454 Many movements, whether migratory or exploratory (here qualified as direct dispersal,  
455 and which can be performed by sedentary or migratory species), can lead to island colonization  
456 and result, by definition, in a dispersal movement once breeding has occurred [7]. Interestingly,  
457 it has long been suspected that migratory behavior has a strong effect on dispersal distance [82]  
458 but recent studies suggest instead that migration and dispersal may be decoupled [9,83]. In fact,  
459 most migratory species show a trend of increasing dispersal distances with increasing flight  
460 efficiency that is very similar to the one shown by non-migratory species [8]. What makes  
461 migratory species truly unique is the long-distance movements they make twice a year, which  
462 allow them to cross a multitude of localities and habitats, and which can also take them more  
463 frequently to isolated localities, like islands. In most cases identified here, the colonization of  
464 islands located thousands of kilometers away from the regular breeding grounds of the species  
465 is more likely to result as by-products of migratory movements than from exploratory  
466 movements [21]. However, the highly dispersive character of some clades that do not undertake  
467 seasonal migration movements but can perform long over-water flights (e.g., *Caloenas* sp.;  
468 [84]) still invites further research of the links between dispersal and migration, especially in  
469 these so-called highly dispersive species (see [85]).

470

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474



475 **Data accessibility statement:**

476 Bird range maps are available from [www.birdlife.org](http://www.birdlife.org). A table containing all species' migration  
 477 characteristics, range size, inferred flock size, and relative brain size data is available in the  
 478 Supporting Information (Supplementary Data 1), as well as a table with details regarding the  
 479 evolutionary history and migratory behavior of island endemic and related species  
 480 (Supplementary Data 2). We confirm that once the manuscript is accepted, the data supporting  
 481 the results will be archived in an appropriate public repository and the DOI of the data will be  
 482 included at the end of the article.

483

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- 709

## 710 Figure legends

711 **Figure 1.** Schematic examples of the role of bird movements in the evolution of island endemic  
712 species. Trans-oceanic speciation represents a dispersal event associated with speciation, which  
713 can be induced by (a) migratory drop-off or (b) direct dispersal movements (as a result of  
714 exploratory behavior, not related to migration). In the case of migratory drop-off, speciation

715 results from the settlement of a migratory species on an island, accompanied by an interruption  
716 of gene flow between migratory and sedentary populations. Such events can, for example, be  
717 identified when an island endemic lineage is embedded in a migratory group of species that  
718 undertake migratory movements between breeding (pink) and non-breeding (blue) zones that  
719 pass nearby the island. The double arrow in panel (a) indicates the migratory routes of the  
720 closest relative, while the dotted arrow represents the one-way migratory movement that led to  
721 the colonization of the island. Conversely, speciation by direct dispersal generally concerns  
722 island endemic species embedded in a group of species restricted to a nearby continental region,  
723 mostly sedentary or which do not express (partial or strict) migratory behavior (i.e., year-round  
724 distribution). Within-island speciation represents species derived from a unique colonization  
725 event that occupy the same island or archipelago. Silhouettes were downloaded from  
726 phylopic.org. The different grey colors indicate island endemic species whereas the black  
727 silhouette represents the closest mainland relative.

728

729 **Figure 2.** (a) The number of island endemic species that evolved from trans-oceanic dispersal  
730 induced by migratory drop-off identified by family, with extant and extinct (within the last  
731 130,000 years) species depicted by different colors. (b) Geographic distribution of these cases  
732 of speciation induced by migratory drop-off. Silhouettes represent some examples of island  
733 endemic species (extant or extinct: †) that likely evolved from migratory drop-off. Details about  
734 species and names of the archipelagos can be found in Supplementary Information. Silhouettes  
735 were downloaded from phylopic.org.

736

737 **Figure 3.** (a) Relative contribution of migratory drop-off in bird island endemism. We  
738 differentiated species that evolved from trans-oceanic speciation associated with migratory  
739 drop-off (red) or with direct dispersal movements (orange). We also represented endemic  
740 species that evolved from within-island speciation (yellow) and species for which current  
741 knowledge does not allow any conclusion (data deficient; grey). The size of the pie is  
742 proportional to the number of described endemic species on the archipelago. Double arrows  
743 indicate main migratory flyways. (b) Comparison of the proportion of island endemic species  
744 that derived from migratory drop-off (likely + very likely; calculated against the number of  
745 island endemic species that derived from direct dispersal movements) with the proportion of  
746 migratory species in the source area (against the number of sedentary species). For each island  
747 or archipelago, the source area was defined as a polygon delimited by the distribution of all  
748 mainland species (see Materials and methods). 82% of islands and archipelagos studied, located

749 above this line, have a higher-than-expected number of migratory drop-off events ( $H_0 = 50\%$ ;  
750  $z$ -statistic = 3.98,  $p$ -value < 0.001). Names of the island or archipelago can be found in  
751 Supplementary Information.

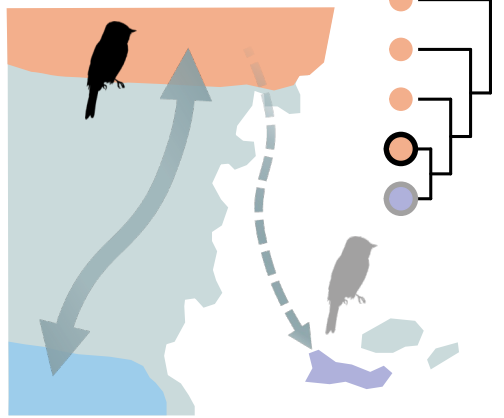
752

753 **Figure 4.** Effects of biogeographic and ecological traits on trans-oceanic speciation by  
754 migratory drop-off (a) or direct dispersal (b), based on differences found between families. We  
755 tested different models considering all extant and extinct species, only species alive to at least  
756 1500 CE and only extant species. Effect size and relative importance were estimated from  
757 phylogenetic generalized least squares (PGLS) regression models. Lambda values are indicated  
758 in the bottom right of each box. Asterisks denote a significant effect size at  $p$ -value = 0.05  
759 (details can be found in Table S1).

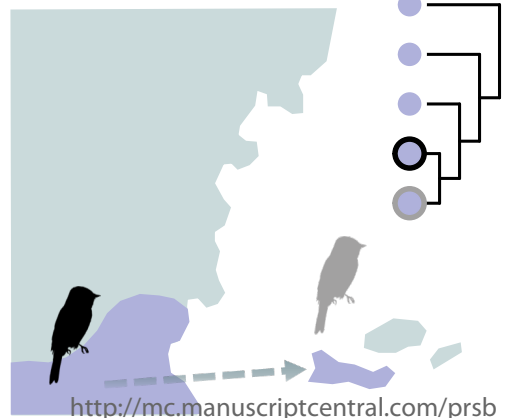
760

Trans-oceanic speciation:

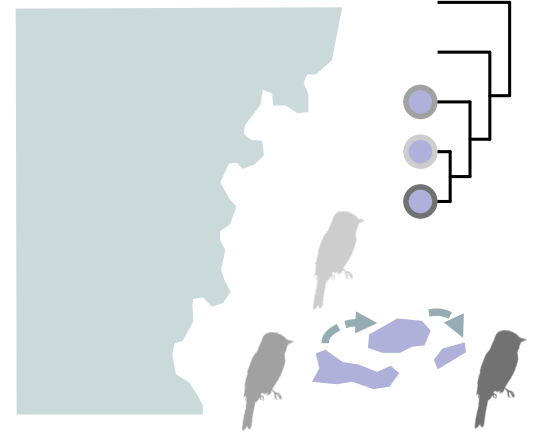
a) By migratory drop-off



b) By direct dispersal



Within-island speciation:



Distribution:

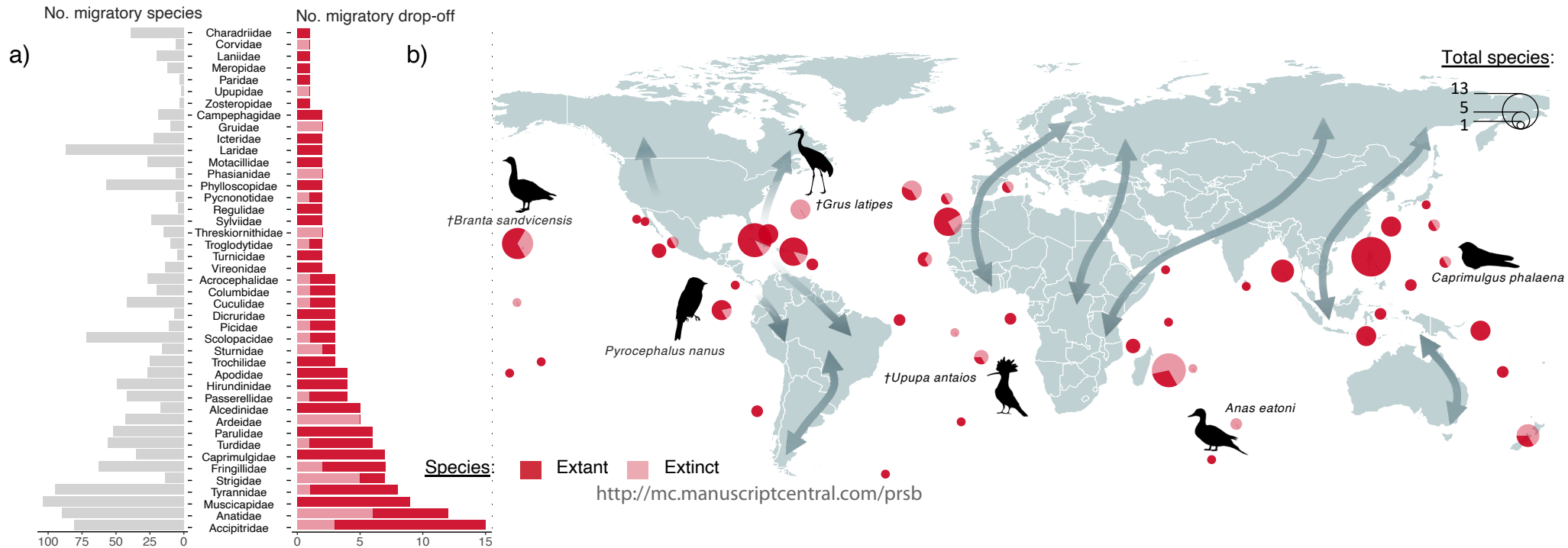
- breeding
- non-breeding
- year-round

Migration strategy:

- migratory
- sedentary

<http://mc.manuscriptcentral.com/prsb>





Number of endemic species:

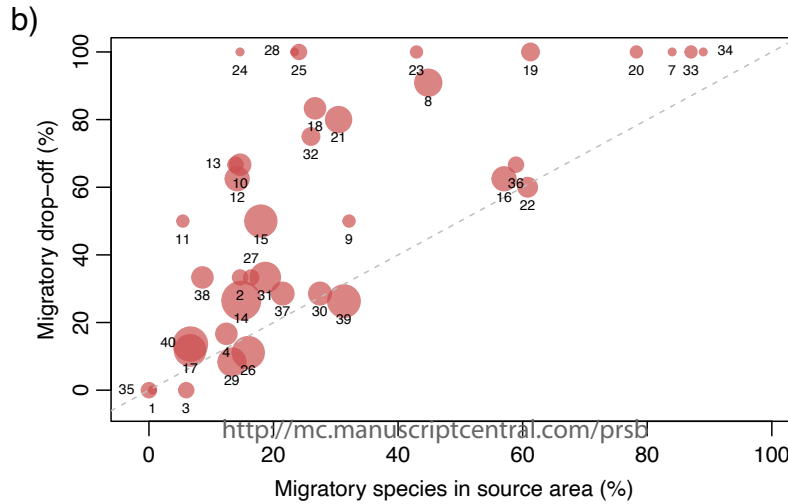
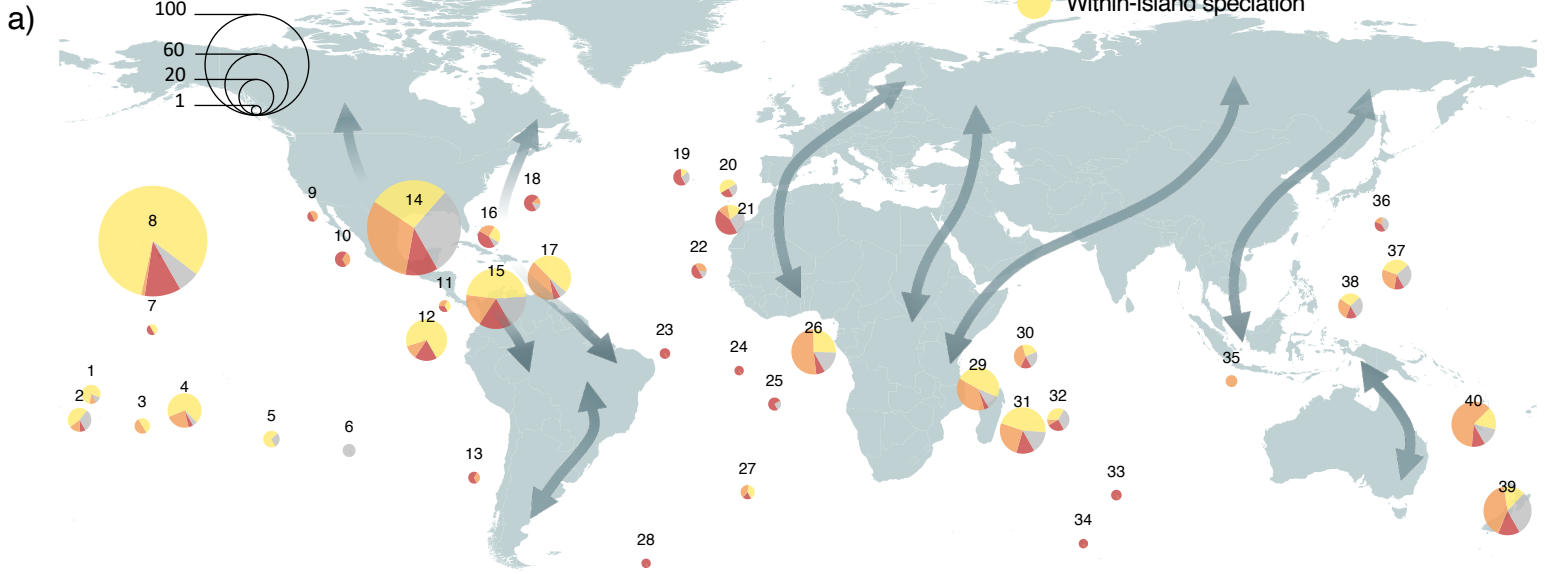
Colonization likely induced by:

● Migratory drop-off

● Direct dispersal

● Data deficient

● Within-island speciation



## a) Migratory drop-off

## b) Direct dispersal

