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1 **Effect of distance, area, and climate on the frequency of introduction and extinction**
2 **events on islands and archipelagos**

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14

15 **Abstract**

16 Change in community similarity (e.g., biotic homogenization) is regulated by different types
17 of introduction and extinction events. However, the spatial patterns and potential drivers of
18 these event types have not yet been addressed to date. Here, we used bird species occurrences
19 on 152 oceanic islands worldwide in both historical (~1500 CE) and current periods with the
20 aim to: 1) elucidate the variations of these events among islands and archipelagos, and 2)
21 disentangle the effects of biogeographical and environmental factors (e.g., spatial distance,
22 island area, climatic conditions, and/or inter-island distance). We found that community
23 similarity increased at both island and archipelago scales after species introductions and
24 extinctions. The introduction and extinction of one species to/from only one island (unique
25 introduction and extinction) comprise most events (> 94%). Island area has a positive effect
26 on nearly all event types at both island and archipelago scales, while climate difference
27 generally has a negative effect on these events. Conversely, responses to spatial distance and
28 inter-island distance on different events is more complex than expected. Overall,
29 biogeographical variables (area and distance) seem to explain most of the events followed by
30 climate variables. Yet extinction events at the archipelago level were also highly associated
31 with inter-island distance as an indicator of dispersal limitation. Our findings provide a solid
32 foundation for understanding the event-mediated processes of homogenization and present
33 essential insights into how biogeographical and environmental factors affect different events
34 on islands.

35

36 **Key Words:** biological invasion; biotic homogenization; community similarity; island

37 biogeography; spatial scale; species extinction.

38

39

40 **Introduction**

41 Human-mediated biological invasion, climate change, and urbanization are currently
42 homogenizing species compositions worldwide (McKinney and Lockwood 1999, McKinney
43 2006, Qian and Ricklefs 2006), and their consequences may lead to irreversible losses in both
44 biodiversity and ecosystem functions (Olden et al. 2004, Sobral et al. 2016). Previous studies
45 have suggested that the strength and direction of changes in community similarity are
46 determined by different types of introduction and extinction events, initial community
47 similarity, and species richness (Olden and Poff 2003, Rosenblad and Sax 2017, Li et al.
48 2019). However, as direct determinants of biotic homogenization, the spatial patterns and
49 potential drivers of different event types have not yet been fully addressed (Olden and Poff
50 2003, Rosenblad and Sax 2017, Longman et al. 2018). This is of utmost importance in order
51 to understand the processes of change in community compositions and better anticipate future
52 consequences under global changes.

53 Two main frameworks are used to categorize the types of introductions and extinctions
54 between paired assemblages (Olden and Poff 2003, Rosenblad and Sax 2017) (Appendix S1:
55 Fig. S1). Unlike Olden and Poff (2003) who use 14 potential scenarios to predict levels of
56 biotic homogenization or differentiation, Rosenblad and Sax (2017) and Longman et al.
57 (2018) provide a more concise framework with just seven types of introduction and
58 extinction events to characterize similarity dynamics. These seven types may be summarized
59 as follows: 1) I01, introduction of a species to one site; 2) I02, introduction of a species to
60 both sites; 3) I12, introduction of a species present on one site to the other site; 4) E10,

61 extinction of a species present on only one site; 5) E20, extinction of a species from both sites;
62 6) E21, extinction of a species present on both sites from one site; and 7) E1/I1, extinction of
63 a species from one site and the introduction of the same species to the other site. These events
64 have different effects on changes in similarity: for example, similarity would increase with
65 more I12, I02, and E10 events but decrease with more I01, E21, and E20 events (Rosenblad
66 and Sax 2017, Li et al. 2019; Appendix S1: Fig. S1). Since the 14 scenarios provided by
67 Olden and Poff (2003) can be decomposed into these new event types (Appendix S1: Fig. S1),
68 Rosenblad and Sax's (2017) framework with only seven event types represents a fundamental
69 classification of introduction and extinction events, which allows us to disentangle the factors
70 associated with each type of event.

71 Understanding the patterns and drivers of community similarity (beta-diversity) is
72 fundamentally important in ecology and biogeography. Previous studies have managed to
73 directly link the change in similarity with the initial similarity, the number of introductions
74 and extinctions, as well as biogeographical factors (Leprieur et al. 2008, Villéger et al. 2014,
75 Longman et al. 2018). Recent studies suggested that the abovementioned event types play a
76 more direct role in governing the changes in similarity (Olden and Poff 2003, Rosenblad and
77 Sax 2017, Li et al. 2019). However, the relative importance of these drivers of extinction and
78 introduction events has yet to be disentangled. This is, nevertheless, of crucial importance,
79 since knowing which factors regulate the frequencies of these event types will lead to: 1) a
80 better understanding of the introduction and extinction processes, and 2) better tools for
81 developing conservation and management strategies in advance.

82 We expect that specific biogeographical and environmental factors may be associated
83 with different event types. Species-area relationships show that sites with large areas support
84 a higher number of native, endemic, and non-native species compared to smaller areas (Harte
85 and Kinzig 1997, Stark et al. 2006, Blackburn et al. 2016). Consequently, we can expect that
86 a higher number of introductions and extinctions will occur in large areas compared to
87 smaller areas. Meanwhile, islands with a greater difference in area should be more dissimilar
88 in terms of species composition, as the numbers of species are quite different, with these
89 differences affecting both the level of homogenization and the frequency of different events
90 (Rosenblad and Sax 2017, Longman et al. 2018). Similarly, heterogeneous environments (e.g.,
91 large elevation range) may support a higher number of native and non-native species
92 (Deutschewitz et al. 2003, Stein et al. 2014) compared to homogeneous environments,
93 because they offer a variety of habitats, which could in turn lead to a high frequency of
94 different events. In addition, species assemblages at a close geodesic distance may have more
95 events involving shared species (i.e., I02, I12, E20, and E21) due to the easy dispersal of
96 non-native species and high initial similarity of native communities (Nekola and White 1999,
97 Soininen et al. 2007, Whittaker and Fernández-Palacios 2007). Furthermore, it was
98 demonstrated that non-native species usually establish successfully in introduced ranges with
99 climatic conditions similar to their native ranges (Duncan et al. 2001, Bomford et al. 2009).
100 Therefore, the same set of species should be able to establish in areas with similar climate
101 conditions. Climatically similar areas also tend to have more shared native species and higher
102 compositional similarity compared to climatically distinct areas (Leprieur et al. 2009), thus

103 leading to higher risks of shared extinctions. To date, the relative importance of these factors
104 to explain different events has remained unaddressed.

105 Among the areas susceptible to massive introductions, we may cite islands, as they are
106 the first victims of species extinctions and introductions (Blackburn et al. 2004, Duncan and
107 Blackburn 2004, Bellard et al. 2017). Regional studies have demonstrated that island flora
108 and fauna are experiencing an ongoing process of homogenization (Castro et al. 2007,
109 Florencio et al. 2013, Rosenblad and Sax 2017, Longman et al. 2018). Thus, an in-depth
110 understanding of the patterns and processes of community dynamics caused by biological
111 invasions on islands is urgently needed. With this aim, we used bird species lists on 152
112 oceanic islands for both historical (before European colonization) and current periods to
113 explore the pattern of change in similarity and the frequency of different event types, and to
114 quantify the effects of the main biogeographical (e.g., area and distance) and environmental
115 factors (e.g., climatic conditions) on these event types.

116

117 **Material and Methods**

118 *Species assemblages on islands*

119 We obtained bird species lists for 152 oceanic islands that vary in terms of geographical and
120 climatic properties from Baiser et al. (2018), which were originally compiled by Blackburn et
121 al. (2004) and Cassey et al. (2007) (Appendix S1: Figs. S2, S3). These islands belong to 4
122 oceans and 20 archipelagos (7 isolated islands were not assigned to any archipelago). The
123 dataset of birds represents both historical and current periods. For the historical period, the

124 species lists reflect species present on the islands at the time of European colonization (not
125 consistent across all the islands) but exclude species that became extinct in the prehistorical
126 period. This represents a total of 927 species. The species list of the current period includes
127 both extant native species (excluding species that became extinct or were extirpated after the
128 arrival of Europeans) and non-native species (with successfully established self-sustaining
129 populations on each island), which includes a total of 919 species. However, the islands
130 included here do not represent all the islands in a given archipelago or ocean, since the data
131 on extinctions or introductions were not available for many of the islands (Cassey et al. 2007).
132 Nevertheless, this dataset is representative and valuable for ecological and biogeographic
133 research, as it includes both historical and current bird species on oceanic islands at a global
134 scale (Blackburn et al. 2004, Cassey et al. 2007, Baiser et al. 2018).

135

136 *Islands characteristics*

137 We extracted the island polygons from the GADM database (<http://www.gadm.org>). For each
138 island, island area (km²) was calculated in cylindrical equal-area projection. The spatial
139 distance (km) between each island pair was measured from the island centroids (König et al.
140 2017). We obtained the maximum elevation (m) of most islands from Blackburn et al. (2004);
141 for the remaining islands, the elevation values were taken from WorldClim raster data
142 (<http://www.worldclim.org/>) at a resolution of 30 arc-second (approximately 1 km at the
143 equator). The elevation data of three remaining islands (Providencia, Penrhyn, and
144 Palmerston) were collected from internet searches (<https://en.wikipedia.org/>;

145 <http://www.cookislands.org.uk>). Although the difference in island area is commonly used to
146 explain community similarity or changes in similarity (Carvalho et al. 2014, Pitta et al. 2017,
147 Longman et al. 2018), the same difference in area can be found between two small islands or
148 two large islands, even though the small islands present very few events. In other words, an
149 island pair with a large area should support more introductions and extinctions compared to a
150 pair with a small area. We thus adopted both the difference in area and the minimum area
151 between paired islands to demonstrate the pairwise difference in area. Similarly, a large
152 difference in topographic heterogeneity would support a high frequency of events, but only
153 when both islands are sufficiently heterogeneous as an island pair; hence, both the difference
154 in maximum elevation and the minimum value of the elevations between islands were
155 calculated.

156 For each island, we also obtained the mean values for annual temperature ($^{\circ}\text{C}$), annual
157 precipitation (mm), temperature seasonality, and precipitation seasonality from WorldClim
158 raster data. We removed 16 small islands without climate information from the analyses of
159 potential drivers of different event types (136 islands and 18 archipelagos) but kept them in
160 the analysis of changes in similarity (152 islands and 20 archipelagos). However, as
161 WorldClim data on islands were interpolated from a limited number of weather stations, we
162 assumed that the differences in interpolated values would reflect the actual differences
163 between islands at the global scale used here (Hijmans et al. 2005).

164 All biogeographical and environmental variables were calculated at the archipelago scale,
165 except for the spatial distance between archipelagos, which was measured as the minimum

166 value of all pairwise distances between islands within different archipelagos. In addition, we
167 also calculated the mean inter-island distance by averaging all pairwise distances between
168 islands within an archipelago. Then, for each archipelago pair, the difference in the mean
169 inter-island distances and the minimum value of the distances were calculated to represent the
170 dispersal limitation at the archipelago level.

171

172 *Change in similarity*

173 We used Jaccard's index to represent the similarity of paired assemblages based on the
174 species lists at the island and archipelago levels (Rosenblad and Sax 2017, Longman et al.
175 2018). Pairwise comparisons were made across all possible pairs separately for the historical
176 and current avian assemblages, resulting in 11,476 and 190 comparisons for islands and
177 archipelagos, respectively. Change in similarity was measured as the difference between the
178 current similarity and historical similarity (initial similarity) for each pair. Positive changes
179 represented homogenization, while negative changes could be associated with differentiation
180 (Cassey et al. 2007). We used a null model approach to test whether the observed biotic
181 homogenization or differentiation differed from random expectations given the species
182 richness. The null model was conducted based on the assumptions that species become
183 randomly extinct and are introduced separately from the local native species pool (at the
184 island or archipelago level) and the non-native species pool (all non-native species introduced
185 to any island or archipelago). In this null model, the numbers of introductions and extinctions
186 on each island or archipelago were kept constant, with only the identity of the species varying.

187 The values of change in similarity were calculated correspondingly. We repeated this
188 procedure 9,999 times to obtain a null distribution of the changes. The observed mean change
189 was considered to be significant if it was less than the 2.5th percentile or greater than the
190 97.5th percentile of those null values.

191

192 *Event types for island avifauna*

193 According to the definition of event types (Rosenblad and Sax 2017, Longman et al. 2018),
194 we calculated the numbers of I01, I02, I12, E10, E20, and E21 events for each island (or
195 archipelago) pair based on the comparison of the species composition between the current
196 and historical periods (E1/I1 would not affect the change in similarity, and given its rarity
197 among assemblages, it was not considered in this study). The correlations among these six
198 event types were examined using the Mantel test (Spearman correlation), and the
199 significances were determined based on 9,999 permutations (Goslee and Urban 2007).

200

201 *Determining the drivers of different event types*

202 Given the overdispersion of the numbers of different event types, we fitted negative binomial
203 regression (NB) models to examine the effects of spatial distance, island area, topographic
204 heterogeneity, climatic conditions, and/or mean inter-island distance on the frequencies of
205 different event types among islands and archipelagos separately. NB has the advantage of
206 incorporating overdispersion and a high frequency of zeros into count datasets (Warton 2005).
207 Thus, it has the potential to efficiently handle lots of zeros that are associated with the

208 ecological or evolutionary restrictions relating to the comparisons of islands or archipelagos
209 such as the numbers of introduction and extinction events among geographically unrelated
210 islands. While zero-inflated models (ZIM) usually handle the overdispersed count variables
211 with excessive zeros in a more effective manner, they model the response in two separate
212 parts with a count model and a logit model (Zeileis et al. 2008), which makes the
213 interpretation of model parameters (or hypothesis testing) difficult (Martin et al. 2005,
214 Warton 2005). In addition, multiple regression on distance matrices (MRM) has the
215 advantage of investigating the relationships between a multivariate response distance matrix
216 and any number of explanatory distance matrices (Lichstein 2007), but it cannot efficiently
217 handle the challenges of overdispersion and excess zeros in our count dataset. For these
218 reasons, ZIM and MRM were not used in this study.

219 As island area and elevation are highly correlated among islands (Spearman correlation r
220 $= 0.81$, $p < 0.001$) and archipelagos ($r = 0.62$, $p = 0.007$), with the differences and minimums
221 in area and elevation also being highly correlated (Appendix S1: Tables S1 and S2), we only
222 kept the comprehensive variables for the area difference and minimum area in our models. To
223 reduce the number of variables and control collinearity between climate variables, we first
224 conducted principal component analysis on the four climate variables and then measured the
225 climate differences using the Euclidean distance on the transformed principal component
226 axes (Qian and Ricklefs 2007). The distance, minimum area, area difference, difference in
227 inter-island distance, and minimum inter-island distance were then log₁₀-transformed before
228 modeling.

229 We are aware that these observations (cells of the distance matrix) are not statistically
230 independent in the regression analysis, which makes the accompanying significance tests of
231 regression coefficients unreliable. Here, we used a permutation method to test the statistical
232 significance of the coefficients. In short, for each event type, all possible values for the
233 number of events were randomly rearranged 9,999 times, and the coefficients were
234 recalculated concurrently; null distributions of the coefficients were generated based on these
235 permutations. We then calculated the proportion of sampled permutations in which the
236 simulated coefficients were greater or less than the observed coefficient. Only if the observed
237 coefficient was outside the 95% confidence interval of the simulated coefficients did we
238 reject the null hypothesis that a given predictor has no effect on a specific event type. All
239 analyses were conducted using R 3.3.0 (R Core Team 2016).

240

241 **Results**

242 *Species extinctions and introductions*

243 The mean number of native species per island was 25.01 ± 1.76 (mean \pm SE) in the historical
244 period, while an average species richness of 27.29 ± 1.95 was observed in the current period
245 (when introduced species were included and extirpated species were removed) (Appendix S1:
246 Fig. S4). Current species richness was significantly higher compared to the calculated
247 richness in the historical period (Wilcoxon signed-rank test p -value < 0.001), with similar
248 results being found at the archipelago level (historical richness: 60.85 ± 11.25 vs current
249 richness: 65.60 ± 12.72 ; p -value = 0.039) (Appendix S1: Fig. S4).

250 We recorded 289 local extirpations involving 206 species on 73 islands (with a mean
251 number of 3.96 ± 0.52 per island), while 137 non-native species were successfully
252 established on 94 islands, resulting in 636 introduction events (with a mean number of $6.77 \pm$
253 0.88 per island). By contrast, 121 species were lost from 14 archipelagos, while 125 were
254 introduced to 15 archipelagos.

255

256 *Change in similarity*

257 Initial similarity (historical period) across all island pairs ranged from 0 to 0.93 with a mean
258 value of $0.050 (\pm 0.001)$. Mean similarity slightly increased to $0.053 (\pm 0.001)$ in the current
259 period. Mean change in similarity was 0.003, which differed significantly from the null
260 distribution based the randomization test (p -value < 0.001). We recorded a higher increase in
261 similarity at the archipelago level (initial similarity: 0.042 ± 0.005 vs current similarity: 0.051
262 ± 0.005 ; p -value < 0.001).

263

264 *Different event types*

265 Event types I01 (unique introduction) and E10 (unique extinction) were the two most
266 frequent events across periods (Fig. 1). I01 events respectively accounted for 64% and 57%
267 of all events among all island and archipelago pairs, while E10 events accounted for 31% and
268 37%. The other event types, which represented less than 6% of all events, were less frequent
269 (Fig. 1). We also found that there were no E20 events among archipelago pairs.

270 We then tested the correlations between these event types. We found a strong positive

271 correlation between I01 and E10 at both the island (Mantel $r = 0.519$) and archipelago levels
272 (Mantel $r = 0.779$) (Appendix S1: Tables S3 and S4). Similar positive correlations between
273 I01 and I02 and between I02 and E10 were also recorded at both scales. However, more
274 significant associations between I02 and other event types, and between E21 and other
275 extinction event types were only detected at the island scale.

276

277 *Drivers of different event types*

278 The NB models show that different event types are governed by slightly different factors
279 (Table 1; Appendix S1: Figs. S5, S6). All events were positively correlated with area
280 difference and minimum area among islands and archipelagos (all p -value < 0.05), although
281 I02 was not correlated with area difference at the archipelago level and E21 was only
282 correlated with minimum area at the island level. Conversely, climatic distance had a
283 significantly negative effect on the frequency of I01, I02, I12, E10, and E21 at the island
284 level, while it negatively affected I01, I02, and E10 at the archipelago level. Spatial distance
285 has different effects on these events: event types involving one species on any single island or
286 archipelago in a pair (i.e., I01 and E10) are more likely to occur on isolated islands or
287 archipelagos, while other events involving two islands (i.e., I02, E20, and E21) are more
288 frequent on proximate islands. At the archipelago level, the difference in inter-island distance
289 was positively correlated with E10 and E21, and the minimum inter-island distance had
290 positive effects on both I02 and E10. The deviance explained by the full models for each
291 event ranged from 14% to 57% at the two spatial scales. We also found that a relatively high

292 proportion of deviance (35% to 50%) was explained by the two most frequent introduction
293 events (i.e., I01 and I02), while more deviance was accounted for at the archipelago level
294 than at the island level (35% vs 18%) for the most frequent extinction event (i.e., E10).

295

296 **Discussion**

297 Based on island avifauna, we found that a large majority of introduction and extinction events
298 occurring among island and archipelago pairs are represented by unique introductions and
299 extinctions, while other events involving the same species on two islands and archipelagos
300 are less frequent. Overall, the homogenization effect (caused by I12, I02, and E10 events)
301 outperformed the differentiation effect (caused by I01, E21, and E20 events), resulting in a
302 slightly more similar bird community composition after European colonization at both the
303 island and archipelago levels. By exploring the potential drivers of these events, we found
304 that island area and climate conditions have consistent effects on event frequencies across
305 nearly all event types and spatial scales, while effects of spatial distance and/or inter-island
306 distance on these events are type- and/or scale-dependent.

307 Mean species richness on islands and archipelagos increased after a series of introduction
308 and extinction events. This result was also documented in previous studies (Sax et al. 2002,
309 Thomas and Palmer 2015, Sobral et al. 2016), especially at local scales. This occurs because
310 the number of non-native species exceeds the number of extirpated native species regionally
311 (Sax and Gaines 2003). However, this situation may also stem from the fact that avian
312 inventories for the current period are more complete than those for the historical period. We

313 also found that the avifauna composition became slightly more similar after species
314 introductions and extinctions, which has been validated with other island taxa such as plants
315 (Castro et al. 2007, Rosenblad and Sax 2017), arthropods (Florencio et al. 2013), and
316 mammals (Longman et al. 2018). By decomposing the changes in community composition
317 into different types of introduction and extinction events, we found that the vast majority of
318 events included the introduction (I01) and extinction (E10) of one species on one of the two
319 sites. Similar findings were also observed with island mammals among islands (Longman et
320 al. 2018) and island birds among archipelagos (Rosenblad and Sax 2017). Besides I01 and
321 E10, other events are less frequent, because their occurrences imply two historically or
322 currently shared native or non-native species, which are not very common. Given that 1) the
323 communities have essentially become more similar, 2) I12, I02, and E10 events
324 mathematically contribute to the increase in similarity (Rosenblad and Sax 2017, Li et al.
325 2019), and 3) the homogenization effect caused by E10 could be offset by I01 events that
326 have a differentiation effect with a smaller number of E10 compared to I01 (Li et al. 2019), it
327 is clear that I02 and I12 events (introductions of the same non-native species) mostly
328 contribute to the observed biotic homogenization. Indeed, several non-native species were
329 introduced to many islands and archipelagos. For example, the common and widespread
330 *Columba livia* has been introduced to 57 islands and 11 archipelagos, and *Acridotheres tristis*
331 to 27 islands and 7 archipelagos (Appendix S1: Fig. S7). However, the shared introductions
332 of these common non-native species mostly contribute to the increase in the frequency of
333 single, but not multiple, I02 or I12 events, because they were generally introduced to

334 different islands but not to specific island pair(s) (Fig. 1). Nevertheless, homogenization and
335 differentiation processes are somehow balanced between assemblage pairs, so the overall rate
336 of similarity only slightly increases. This type of offset has also been confirmed by many
337 other studies (Cassey et al. 2007, Baiser et al. 2012, Rosenblad and Sax 2017). We are aware
338 that there may be other types of cryptic events – for example, species that became extinct
339 after 1500 CE but were later reintroduced, or vice versa – but information on such events is
340 scarce at a global scale.

341 In general, we were able to explain much of the deviance for both introduction and
342 extinction events (average D-squared value of 0.33 across islands and archipelagos) using
343 only a few biogeographical and climate predictors. Overall, our models showed that event
344 types with shared extinct or introduced species (i.e., I02, E20, or E21) are more likely to
345 occur on proximate islands, which may be explained by two reasons. First, proximate islands
346 usually have a similar community composition and share the same native species due to their
347 underlying congruent evolutionary and geological processes (Whittaker and
348 Fernández-Palacios 2007), which contribute to many shared endemic species on the closest
349 islands. Second, the environmental dissimilarities and dispersal limitations are generally
350 weak for proximate islands compared to distant islands (Nekola and White 1999, Soininen et
351 al. 2007), which also contributes to the existence of many shared species on the closest
352 islands. By contrast, we found that both distant islands and archipelagos have more events
353 involving the introduction or extinction of one species on any one site (i.e., I01 and E10),
354 which may be because non-native species introduced to these assemblages are more likely to

355 originate from different sources, while extinctions occurring on distant assemblages have no
356 or few shared species. At the archipelago level, increasing the difference in inter-island
357 distance positively affects the type of extinction events (i.e., E10 and E21), which may be
358 because the dispersal limitation among islands contributes to the generation and maintenance
359 of local endemic species (Losos and Ricklefs 2009) and thus to a high probability of local
360 extinctions after species introductions.

361 The area difference or minimum area positively affects the frequency of all event types at
362 both the island and archipelago levels, except for E21. The minimum area is important for
363 introduction events involving the same species present on both sites (i.e., I02 and I12), which
364 means that the same non-native species are more likely to be introduced on islands with large
365 areas. This may stem from a simple target area effect or from the more extensive exchanges
366 between these large sites. In addition, for these events involving the same species on two sites
367 (i.e., I02, I12, and E20) while keeping the minimum area constant, a site pair with a larger
368 area difference indicates that the large site is more likely to include the species on the small
369 site compared to a site pair with a small area difference. For events involving different
370 species on any single site (i.e., I01 and E10), the positive effect of difference in area could
371 simply be an area effect, because the area difference is highly correlated with the total area
372 (Mantel test based on 9,999 permutations: Spearman $r = 0.95$ at the island level and 0.87 at
373 the archipelago level; all p -value < 0.001).

374 It is well known that more climatically similar areas tend to have more shared native
375 and/or non-native species compared to climatically distinct areas (Duncan et al. 2001,

376 Bomford et al. 2009, Leprieur et al. 2009). Here, we found that paired islands with similar
377 climates could also support more events with the same introduced or extinct species such as
378 I02, I12, and E21. However, among these events, only I02 is more likely to occur with paired
379 archipelagos with similar climates. In addition, climate similarity could also affect the
380 frequency of I01 and E10 events, because the introduced and extinct species are usually
381 clustered into several specific higher taxa (Blackburn and Duncan 2001, Duncan and
382 Blackburn 2004, Dyer et al. 2017, Baiser et al. 2018), while the species within the same taxon
383 may have similar climate requirements (climate niches) due to their closer phylogenetic
384 relationship (Hadly et al. 2009). For example, compared to other taxa, Phasianidae,
385 Estrildidae, and Psittacidae are more frequently introduced to other places among our islands
386 (Appendix S1: Figs. S8a, S9a). Similarly, extinct taxa mostly occurred in specific families
387 such as Psittacidae and Rallidae (Appendix S1: Figs. S8b, S9b). Furthermore, many
388 introduced species have similar geographic origins (Dyer et al. 2017) (Appendix S1: Fig. S10)
389 and are more likely to be successfully established in places with high climate similarity
390 (Duncan et al. 2001, Bomford et al. 2009), with more I01 events being detected among sites
391 with similar climates.

392 We realize that our models only account for part of the deviance for each event type,
393 indicating that other potential factors are yet to be included. For example, the number of
394 extinction or introduction events might be underestimated, because there is usually a time lag
395 before an endemic species becomes extinct or a non-native species becomes established
396 (Kuussaari et al. 2009, Rouget et al. 2016). In addition, other island features such as island

397 age could also play a crucial role in regulating the frequencies of different event types in
398 terms of their effects on the evolutionary dynamics of islands and endemism of island species
399 (Whittaker et al. 2008, Valente et al. 2014, Bellard et al. 2019). Moreover, human activities
400 such as the commodity trade and human movements are a key factor that affects both species
401 introductions and extinctions (Sax and Gaines 2008, Blackburn et al. 2016, Chapman et al.
402 2017), thus influencing community similarity and different events. Although the proxies of
403 these variables are available to us, such drivers are not explicitly available between paired
404 islands, especially in the case of small islands. Similarly, the climate changes since 1500 CE
405 could also influence different event types, with detailed information on these changes being
406 unavailable. Furthermore, information about species introductions and extinctions before
407 European colonization could be of high value to better illustrate the homogenization trends,
408 because some oceanic islands experienced a large number of bird extinctions just after human
409 colonization but before European colonization (Valente et al. 2019). Taxonomic identification
410 on islands could also be very difficult in the case of subspecies previously known as two
411 distinct species, or conversely, two species that are now considered to be a single species
412 based on genetic analyses. Misidentification may alter our results, but we expect that the
413 general trend and main results are robust to this limitation. Lastly, the archipelagos used here
414 do not represent all the islands therein, and thus there may be some sampling biases in
415 estimating species composition at the archipelago level, although the omitted islands may be
416 small in area and low in richness. Nevertheless, our results suggest that further analyses
417 should be conducted to explore some of these effects in the future.

418 By decomposing island introductions and extinctions into different event types, we found
419 that unique introductions and extinctions are the most frequent events among islands and
420 archipelagos. We also observed nearly consistent positive effects of island area and negative
421 effects of climate on all these event types. Our findings provide a better understanding of the
422 patterns and processes of island introductions and extinctions and may also enhance our
423 predictions of biodiversity changes on islands in the future.

424

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427

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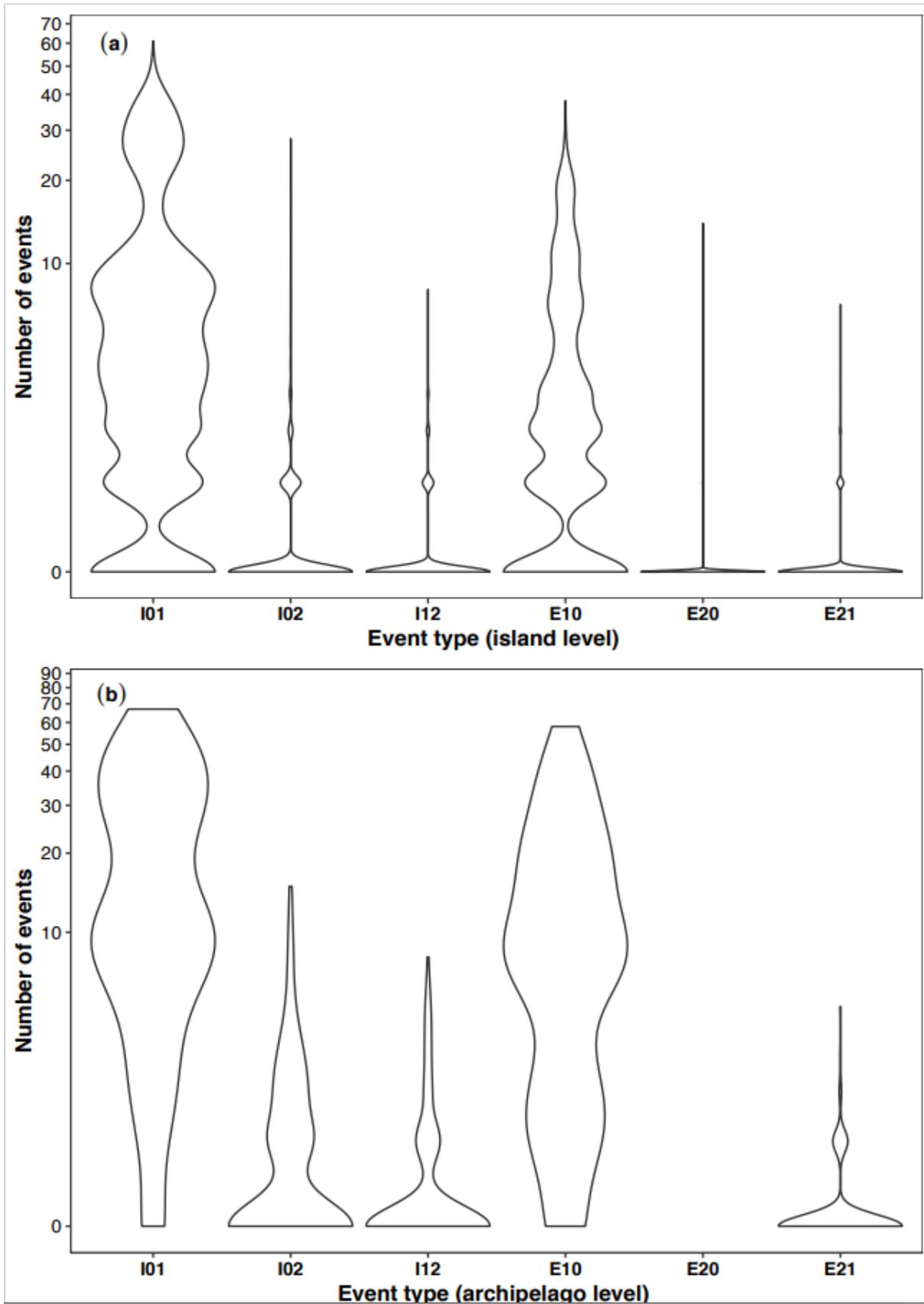
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576 **Table 1. Results of negative binomial regression models testing the effects of spatial distance, island**
577 **area, climatic conditions, and/or inter-island distance on the frequencies of different event types at**
578 **both the island and archipelago scales.**

Event	Scale	Spatial distance	Difference in area	Minimum area	Difference in inter-island distance	Minimum inter-island distance	Climatic distance	D-squared
I01	Island	0.543(***)	0.575(***)	0.295(***)			-0.115(***)	0.348
I01	Archipelago	0.550(*)	0.618(***)	0.470(**)	-0.053(NS)	0.118(NS)	-0.203(**)	0.502
I02	Island	-0.511(***)	0.295(***)	1.187(***)			-0.299(***)	0.399
I02	Archipelago	0.007(NS)	0.290(NS)	0.922(**)	0.018(NS)	1.825(***)	-0.290(*)	0.432
I12	Island	0.134(NS)	0.216(***)	0.803(***)			-0.124(***)	0.148
I12	Archipelago	-0.033(NS)	0.444(*)	0.853(*)	-0.635(NS)	-0.198(NS)	-0.176(NS)	0.138
E10	Island	0.516(***)	0.392(***)	0.271(***)			-0.119(***)	0.182
E10	Archipelago	0.793(**)	0.213(*)	0.360(*)	0.672(***)	0.748(*)	-0.275(***)	0.352
E20	Island	-2.500(***)	0.450(**)	0.831(***)			-0.159(NS)	0.574
E20	Archipelago							
E21	Island	-1.222(***)	0.064(NS)	0.565(***)			-0.209(***)	0.246
E21	Archipelago	-1.091(NS)	-0.396(NS)	0.693(NS)	2.389(***)	0.178(NS)	-0.328(NS)	0.318

579 Note: The significance in parentheses was calculated based on 9,999 permutations for each predictor, and a
580 significance level of 0.05 for a two-sided test was adopted (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, NS, not
581 significant). The amount of deviance accounted for (D-squared) by the model was estimated as (null
582 deviance – deviance) / null deviance. Note the absence of E20 events at the archipelago scale, while
583 inter-island distance was only calculated at the archipelago scale.

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590 **Figure 1. Frequencies of the six event types across island (a) and archipelago (b) pairs.**

591 The mirrored kernel density plot shows the distribution of data. Wider sections represent a

592 higher probability of having the given value, while the thinner sections represent a lower

593 probability.

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