

1 **Seasonal species richness of birds on the world's islands and its geographical**
2 **correlates**

3

4 Frank A. La Sorte¹, Marius Somveille², Adriaan M. Dokter¹ and Eliot T. Miller¹

5 ¹Cornell Lab of Ornithology, Cornell University, Ithaca, NY 14850 USA

6 ²Centre for Biodiversity and Environment Research, Department of Genetics, Evolution and
7 Environment, University College London, London WC1E 6BT, UK

8 Author for correspondence: Frank A. La Sorte, e-mail: fal42@cornell.edu

9

10 The presence of migratory birds on islands results in seasonal variation in species richness.
11 These patterns and their geographical correlates within the context of island biogeography theory
12 have not been examined. We used 21 years of bird observations on 690 islands from eBird to
13 determine how seasonal species richness estimates vary as a function of island area, isolation,
14 and latitude. Species richness was highest on islands within the northern mid-latitudes during
15 migration and on islands within tropical latitudes during the non-breeding season. Area defined
16 positive, non-linear relationships with species richness across seasons, with the steepest slopes
17 occurring with islands >1,100 km². Distance to mainland defined negative, non-linear
18 relationships with species richness across seasons, with the strongest slopes occurring with
19 islands located >150 km from the mainland. Species-area relationships were weakest for the
20 most remote islands and strongest for islands at intermediate distances to the mainland.
21 Intermediate proximity to other islands was a poor predictor of species richness. Our findings

22 emphasize the presence of seasonally dynamic geographical relationships, the enhanced role of
23 evolutionary processes on larger islands, the unique ecology of the world's most remote islands,
24 and the importance of islands as stopover sites and wintering grounds for migratory bird species.

25

26 **Keywords:** area, island biogeography, isolation, latitude, migratory birds, species richness

27

28 **1. Introduction**

29 Islands are unique places for biodiversity [1]. Although they only make up some 5% of the
30 global land area, islands contain *ca.* 20% of the world's biodiversity [2]. Birds are well
31 represented across the world's islands due in large part to their strong dispersal abilities [3] and
32 the important role islands have played in bird evolution [4, 5]. In addition to resident bird species
33 that occur year-round on islands, islands can also host migratory bird species during the breeding
34 or non-breeding seasons, or as transients during migration [6]. Island stopover events by
35 migrants allow individuals to rest and refuel before continuing their migration journey [7-14].
36 Seasonal variation in the occurrence of migratory birds on islands should therefore result in
37 seasonal variation in species richness. These seasonal patterns and their geographical correlates
38 within the context of island biogeography theory, however, have not been broadly explored.

39 Through the dynamics of colonization, speciation, and extinction, island biogeography
40 theory predicts that species richness should be positively correlated with island area and
41 negatively correlated with island isolation [2, 15, 16]. These predictions have been broadly
42 corroborated for breeding bird assemblages on islands globally [17, 18] and for breeding bird
43 assemblages within island archipelagoes [19-21]. A double sigmodal species-area relationship

44 has been proposed as the expected outcome for island biota based on how stochastic, ecological,
45 and evolutionary processes operate as a function of island size [22, 23]. Stochastic processes are
46 expected to be more pronounced on the smallest islands, resulting in species richness being
47 independent of island area (small island effect). Ecological processes (immigration/extinction
48 dynamics) are expected to dominate with intermediate sized islands, resulting in a deterministic
49 relationship between island area and species richness. With the largest islands, evolutionary
50 processes are expected to increase in prominence through internal geographic isolation,
51 enhancing the strength of species-area relationship through increased opportunities for *in situ*
52 speciation [24]. Current evidence for breeding bird assemblages on islands globally, however,
53 suggests species-area relationships lack a double sigmodal form and are largely linear [17, 18].

54 In addition to the individual relationships with species richness, island biogeography
55 theory predicts an interaction should exist between island area and isolation where the strength of
56 the species-area relationship increases with increasing island isolation [2, 15, 16]. Here,
57 differences in immigration rates between nearshore and remote island is expected to result in
58 different species-area relationships [15]. Higher immigration rates on nearshore islands is
59 expected to maintain higher species numbers on small islands by reducing the chances of
60 extirpations, resulting in weaker species-area relationships [25]. On remote islands, the
61 occurrence of these “rescue effects” are unusual, resulting in fewer species on small islands and
62 stronger species-area relationships [2]. Evidence for an interaction between island area and
63 isolation, however, has not been broadly documented [26], including for breeding bird
64 assemblages on islands worldwide [17].

65 How species-area and species-isolation relationships are defined for birds outside of the
66 breeding season has not been explored. During the non-breeding season, we would expect

67 similar relationships to those documented globally during the breeding season [17, 18]. How
68 these relationships will be affected by the presence of transient species during migration will
69 depend on how island area and isolation affect visitation rates. Larger islands should represent
70 more obvious stopover targets. We would therefore expect the species-area relationship to
71 become steeper during migration as migratory species occur in greater numbers on larger islands.
72 Islands that are located in closer proximity to other islands should also represent more obvious
73 stopover targets, which increase the slope of the species-proximity relationship during migration.
74 Islands that are located closer to the mainland are more likely to be encountered by birds
75 traveling within migration flyways, which are situated over continental landmasses [27]. We
76 would therefore expect the slope of the species-isolation relationship to weaken during migration
77 as the number of migratory species increases on nearshore islands.

78 It has been well documented for birds and other taxa that species richness across the
79 world's continents peaks within the tropics and declines as you move towards the poles [28, 29].
80 This pattern is complicated by the seasonal occurrence of migratory bird species. Most migratory
81 bird species spend the non-breeding season (boreal winter) within tropical latitudes and spend
82 the breeding season (boreal summer) within the temperate latitudes of the Northern Hemisphere
83 [30]. This seasonal redistribution of migratory species from the tropics to northern temperate
84 regions creates a reverse latitudinal gradient in species richness where species richness peaks
85 within the mid-latitudes of the Northern Hemisphere during the breeding season (boreal summer)
86 [31-33]. We would expect these seasonal patterns of species richness to be replicated across the
87 world's islands. Specifically, species richness during the boreal summer should be higher than
88 that of the boreal winter for islands located within the mid-latitudes of the Northern Hemisphere.
89 Species richness during the boreal winter should be higher than that for the boreal summer for

90 islands located within the tropics. During migration, islands located within the mid-latitudes of
91 the Northern Hemisphere should contain the greatest number of species during migration and the
92 fewest species during the boreal winter. Deviation from these predictions would suggest the
93 seasonal movements of migratory birds between the tropics and northern temperate regions does
94 not occur across islands in a similar manner as it does across the mainland.

95 To test these predictions, we use bird occurrence information from eBird over a 21-year
96 period (2002-2022) to estimate avian species richness [34] during four seasons of the annual
97 cycle (boreal winter, spring, summer, and autumn) across a large number of well surveyed
98 islands ($n = 690$). eBird is an online database initiated in 2002 that allows volunteers to submit
99 their observations from any location and time, creating a global full-annual cycle source of
100 occurrence information on the world's birds [35]. To date eBird has sampled over 20% of the
101 world's islands and, based on availability, eBird participants have a propensity to sample islands
102 that are more isolated from the mainland and other islands [36]. By testing these predictions, our
103 objective is to document how the relationships between species richness and island area,
104 isolation, proximity, and latitude are defined across seasons, and where and when migratory
105 birds are visiting the world's islands.

106

107 **2. Methods**

108 **(a) Bird occurrence data**

109 eBird contains bird observations in checklist format where species detected by sight or sound are
110 recorded by one or more observers during a sampling event [37]. eBird represents a semi-
111 structured 'big data' resource where volunteer observers select from a number of predefined

112 sampling protocols where sampling effort is determined by the observer. We compiled bird
113 occurrence information from all available eBird checklists globally from 1 January 2002 to 1
114 May 2022. We queried the database on 2 May 2022, and we included all sampling protocols, all
115 levels of sampling effort, and both designations (yes/no) for the field “all observations reported.”
116 We only considered observations that were identified as valid in the database, we combined
117 observations in grouped checklists into single checklists, and we excluded all pelagic seabird
118 species from the checklists. A total of 70,001,315 checklists were available for analysis
119 containing 10,148 unique species.

120

121 **(b) Island spatial data**

122 We acquired a shoreline vector coverage of the world’s continents and 21,813 of the world’s
123 islands greater than 1 km² in area from [38]. We identified 4,958 islands that contained bird
124 observations from eBird (figure 1a). From these, 4,529 were named islands. Across the 4,958
125 islands, a total of 6,521,894 eBird checklists were available for analysis containing 6,411 unique
126 species. We estimated the distance to the nearest continental shoreline (excluding Antarctica) for
127 all 21,813 islands by rasterizing the shoreline vector coverage of the world’s continents to *ca.* 10
128 km spatial resolution [36]. We first calculated the distance of each non-continental pixel to the
129 nearest continental shoreline pixel. We then found the minimum distance to the continental
130 shoreline for each island. Following the methods of previous island biogeography assessments,
131 we log transformed island area and minimum distance to the continental shoreline to improve
132 their distributional properties for analysis. We estimated the spatial proximity of other islands
133 within a 2,000 km radius from the edge of each island using a proximity metric based on an

134 inverse distance weighting scheme [36]. We applied a power transformation (0.25) to the
135 proximity index to improve its distributional properties for analysis.

136

137 **(c) Seasonal species richness estimates**

138 We used the methodology developed by [34] to estimate seasonal species richness on the 4,958
139 islands, a method used in previous eBird studies investigating global patterns of species richness
140 [35, 36]. Specifically, we estimated survey completeness of bird occurrence information for all
141 years combined during four seasons (boreal winter, spring, summer, and autumn) on the 4,958
142 islands using the “exact” estimator from [39]. We defined the four seasons based on the
143 following dates for the boreal spring (15 March to June 15) and boreal autumn (15 August to 15
144 November). We estimated the relationship between the accumulated number of species and
145 survey effort for each island using the eBird checklists as a unit of survey effort, replicating the
146 approach used in previous studies [35, 36]. We defined survey completeness for each island as
147 the percentage of observed species richness captured by the species richness estimates derived
148 from the species accumulation curves [34]. We removed poorly sampled islands where the ratio
149 between the number of occurrence records and the number of observed species was <3 , the slope
150 of the species accumulation curve was >0.3 , and survey completeness was $<50\%$ [34]. We then
151 removed islands where species richness estimates were not available for all four seasons. We
152 estimated seasonality in species richness for each island based on the maximum seasonal
153 difference in species richness between the migration and non-migration periods. Specifically, the
154 maximum species richness during either the boreal spring or boreal autumn minus the minimum
155 species richness during either the boreal summer or boreal winter.

156

157 **(d) Statistical analysis**

158 We examined how species richness varied among seasons using a one-way repeated measures
159 Poisson mixed-effect ANOVA with a log link function and Tukey corrected post hoc pairwise
160 comparisons with island included as a random effect. We examined the individual relationships
161 between species richness and island area, distance, proximity, and latitude using Poisson
162 generalized additive mixed models (GAMM) with a log link function and exponential spatial
163 correlation structure using the great circle (Haversine) distance [40, 41]. We examined the
164 individual relationships between our estimates of seasonality in species richness (defined above)
165 and island area, distance, proximity, and latitude using the same method. We selected a basis
166 dimension (k) of six as a starting value for the smooth terms in the GAMM fits. We selected this
167 value after it was determined that higher values did not result in statistically important changes in
168 the results [42]. We tested five GAMM spatial correlation structures [43], which we compared
169 using Akaike information criteria [44]. In all cases, the exponential correlation structure
170 performed best. We used the locations of the GAMM fitted lines and 95% confidence bands to
171 assess the level of evidence that the slope of the fitted lines differed significantly from zero and
172 the level of evidence for significant differences among seasons. We report the effective degrees
173 of freedom (edf) and approximate significance of the smooth terms from each GAMM fit to
174 assess the non-linear complexity of the GAMM relationships. We examined the level of evidence
175 for an interaction between island area and distance to mainland for each season using a smooth
176 interaction term in a Poisson GAMM with a log link function and exponential spatial correlation
177 structure using the great circle (Haversine) distance. We interpret the presence of non-linear and
178 non-parallel contour lines in the plot of the smooth interaction term as evidence for an

179 interaction. To assess the non-linear complexity of the smooth interaction term and contour lines,
180 we report edf and approximate significance of the smooth interaction term.

181 All analysis was conducted in the R software environment for statistical computing and
182 graphics, version 4.2.0 [45]. We estimated distance to mainland using the distance function in the
183 raster R package [46]. The survey completeness analysis was implemented using the
184 KnowBPolygon function in the KnowBR R package using the default parameters [34]. We
185 implemented the Poisson mixed-effect ANOVA using the glmer function in the lme4 R package
186 [47] and the Tukey corrected post hoc pairwise comparison using the glht function in the
187 multcomp R package [48]. We implemented GAMM using the gamm function in the mgcv R
188 package [42].

189

190 **3. Results**

191 From a total of 21,813 islands, 4,958 islands (22.7%) contained bird occurrence information in
192 eBird. From these, 3,410 islands (15.6%) contained sufficient occurrence information to estimate
193 survey completeness for at least one season. After removing poorly sampled islands, 690 islands
194 (3.2%) contained enough occurrence information to estimate species richness for all four seasons
195 (figure 1). The 690 islands occurred across the globe with the densest concentrations occurring
196 along the Atlantic and Pacific coasts of North America (figure 1).

197 When the seasonal species richness estimates for the 690 islands were compared across
198 seasons, species richness was highest during the boreal autumn for 293 islands (42.5%) located
199 along the coasts of North America and Europe, within Southeast Asia, and within Australasia
200 (figure 2). Species richness was highest during the boreal spring for 207 islands (30.0%) located

201 primarily within the mid-latitudes of the Northern Hemisphere (figure 2). Species richness was
202 highest during the boreal winter for 179 islands (25.9%) located within the tropical latitudes and
203 within the Southern Hemisphere (figure 2). Lastly, species richness was highest during the boreal
204 summer for 11 islands (1.6%) located across the globe (figure 2).

205 Seasonality in species richness for the 690 islands was generally higher for islands
206 located in the Northern Hemisphere (figure 3a). Island area had a nearly uniform relationship on
207 average with seasonality in species richness (edf = 2.6, $F = 7.2$, $P < 0.001$; figure 3b). Seasonality
208 in species richness displayed on average a negative relationship with distance to the mainland for
209 islands that were located >150 km from the mainland (edf = 3.0, $F = 38.0$, $P < 0.001$; figure 3c).
210 Seasonality in species richness displayed on average a non-linear relationship with proximity to
211 other islands with seasonality peaking at intermediate levels of proximity (edf = 4.0, $F = 8.68$,
212 $P < 0.001$; figure 3d). Seasonality in species richness displayed on average a strong non-linear
213 relationship with latitude with seasonality peaking within the mid-latitudes (centered on *ca.* 30°
214 N latitude) of the Northern Hemisphere (edf = 5.7, $F = 41.0$, $P < 0.001$; figure 3e).

215 Seasonal species richness estimates for the 690 islands varied significantly on average
216 among the four seasons ($\chi^2 = 1083.9$ df = 3, $P < 0.001$; figures 1, 4a). Species richness was higher
217 on average during the boreal spring compared to the boreal autumn ($z = 2.63$, $P = 0.042$), boreal
218 winter ($z = 11.98$, $P < 0.001$), and boreal summer ($z = 26.80$, $P < 0.001$). Species richness was
219 higher on average during the boreal autumn compared to the boreal winter ($z = 14.81$, $P < 0.001$)
220 and boreal summer ($z = 26.80$, $P < 0.001$). Species richness was higher on average during the
221 boreal winter compared to the boreal summer ($z = 14.81$, $P < 0.001$).

222 Species richness estimates increased in a non-linear fashion on average with increasing
223 island area for all four seasons (edf = 5.0, $F = 1151.31$, $P < 0.001$; figure 4b). Species richness

224 was consistently higher on average during the boreal spring and boreal autumn with increasing
225 island area except for the largest islands where values converged across seasons (figure 4b). The
226 strongest species-area relationships during the boreal winter, spring, and autumn occurred on
227 average for islands *ca.* <150 km² and islands *ca.* >1,100 km², and the strongest species-area
228 relationship during the boreal summer occurred on average for islands *ca.* >1,100 km² (figure
229 4b).

230 Species richness decreased in a non-linear fashion on average with increasing island
231 isolation for all four seasons (edf = 5.0, $F = 785.37$, $P < 0.001$; figure 4c). Species richness was
232 consistently higher on average during the boreal spring and boreal autumn with increasing island
233 isolation except for the most isolated islands where the values converged across seasons (figure
234 4c).

235 Species richness increased in a non-linear fashion on average with increasing proximity
236 to other islands for all four seasons (edf = 5.0, $F = 188.76$, $P < 0.001$; figure 4d). Species richness
237 was highest on average across seasons when proximity was greatest, with a peak in species
238 richness occurring at intermediate levels of island proximity, especially during the boreal spring
239 and autumn (figure 4d).

240 Species richness decreased at higher northern and southern latitudes on average for all
241 four seasons (edf = 4.9, $F = 410.20$, $P < 0.001$; figure 4e). Species richness reached its highest
242 levels on average during the boreal spring and boreal autumn within the mid-latitudes of the
243 North Hemisphere (centered between 40° and 50° N latitude; figure 4e). Species richness
244 reached its highest levels on average during the boreal winter within the tropics north of the
245 equator (centered on *ca.* 10° N latitude; figure 4e). Species richness reached its highest levels on
246 average during the boreal summer within the tropics south of the equator (centered on *ca.* 10° S

247 latitude) and within the mid-latitudes in the Northern Hemisphere (centered on *ca.* 50° N
248 latitude; figure 4e).

249 The species richness response surfaces describing the interaction between island area and
250 distance to mainland for each season contained non-linear and non-parallel counter lines whose
251 arrangements differed across seasons ($edf = 28.3$, $F = 393.63$, $P < 0.001$; figure 5). Species
252 richness was lowest across all four seasons on the smallest, most remote islands (figure 5).
253 Species richness was highest across all four seasons on the largest islands located at intermediate
254 distances from the mainland (figure 5). These large, species rich islands were centered on *ca.* 150
255 km from the mainland during the boreal winter and boreal summer and were centered on *ca.* 250
256 km from the mainland during the boreal spring and boreal autumn (figure 5). With increasing
257 distance to the mainland, the positive effect of area on species richness decreased in strength
258 across seasons (figure 5). With increasing island area, the negative effect of distance on species
259 richness decreased in strength across seasons (figure 5).

260

261 **4. Discussion**

262 Across the world's islands, we identified seasonally dynamic relationships between species
263 richness and island area, isolation, and latitude that did not completely follow our expectations.
264 For the majority of islands (72.5%), species richness was highest during migration, emphasizing
265 the role of islands as stopover sites for migrating birds, especially within the mid-latitudes of the
266 Northern Hemisphere. Species richness tended to be higher during the boreal winter compared to
267 the boreal summer, emphasizing the role of islands as wintering grounds for migratory birds
268 within the tropics and the limited role of islands as breeding grounds for migratory birds within

269 the Northern Hemisphere. Seasonal variation in species richness was greatest on islands located
270 near the mainland (<150 km) and on islands located within the mid-latitudes of the Northern
271 Hemisphere. Island area and proximity to other islands had little effect on seasonal variation in
272 species richness. Contrary to previous findings [17, 18], we found non-linear species-area
273 relationships across all four seasons with evidence for a major threshold at 1,100 km² and a
274 minor threshold at 150 km² during the boreal winter, spring, and autumn. These findings
275 highlight the role of evolutionary processes on the largest islands [22, 23] and the importance of
276 small and intermediate sized islands as stopover sites and wintering grounds for migratory birds.
277 We found non-linear relationships with distance to the mainland with a threshold occurring at
278 150 km from the mainland beyond which species numbers declined across seasons. These
279 findings emphasize the ability of birds to dampen the species-isolation effect with nearshore
280 islands and the role of nearshore islands as stopover sites and wintering grounds for migratory
281 birds. We found non-linear relationships with proximity to other islands where intermediate
282 proximity was a poor predictor of species richness across seasons. These results suggest the
283 effects of increasing proximity are strongest for species poor islands that are isolated from other
284 islands and species rich islands that are not isolated from other islands, especially during the
285 boreal winter, spring, and autumn. Contrary to previous findings [17], we found evidence for an
286 interaction between island area and isolation across all four seasons that diverged from the
287 predictions from island biogeography theory [2, 15, 16]. Here, the species-area effect was
288 weakest on small islands and strongest on islands located at intermediate distances from the
289 mainland.

290 The relationships documented in this study between species richness and latitude broadly
291 followed our expectations. The latitudinal species richness gradient during migration peaked

292 within the mid-latitudes of the Northern Hemisphere, where the majority of the world's
293 migratory birds occur during migration [30], emphasizing the importance of islands as stopover
294 sites during migration. The latitudinal species richness gradient during the boreal winter peaked
295 within the tropical latitudes, the region where the majority of the world's migratory birds spend
296 the non-breeding season [30], emphasizing the importance of tropical islands as non-breeding
297 grounds for migratory birds. Latitudinal species richness gradients during the boreal summer
298 contained two peaks, one just south of the equator and one within the mid-latitudes of the
299 Northern Hemisphere. These results reflect the occurrence of large numbers of migratory birds
300 within the mid-latitudes of the Northern Hemisphere during the breeding season [30]. These
301 findings also replicate the reverse latitudinal gradient that has been documented on the North
302 American continent during the boreal summer [31-33].

303 The species-area relationships documented in this study did not display the double
304 sigmoidal form predicted to occur based on how stochastic, ecological, and evolutionary
305 processes are expected to operate as a function of island size [22, 23]. We identified a significant
306 threshold at roughly 1,100 km² beyond which the slope of the species-area relationship increased
307 substantially. These findings suggest the presence of stronger evolutionary processes on larger
308 islands where internal geographic isolation increases the chances of *in situ* speciation [22, 23].
309 We also identified a weaker threshold at roughly 150 km² during the boreal winter, spring, and
310 autumn. These findings suggest transient species occur in large numbers on small to intermediate
311 sized island during these seasons, increasing the strength of the species-area relationship. Our
312 results did not provide strong evidence for a small island effect where the species-area
313 relationship is weakened through stochastic processes. There is a chance the small island effect
314 was not well represented in our data due to the absence of very small islands (<1 km²) and the

315 absence of islands where no birds were observed (empty islands) [49]. In total, our findings
316 suggest we failed to capture the transition from stochastic to ecological processes (ecological
317 threshold T_1) but we did capture the transition from ecological to evolutionary processes
318 (evolutionary threshold T_2) [22, 23]. By capturing the evolutionary threshold, our findings
319 emphasize the ability of speciation to enhance the species-area relationship on larger islands
320 [24].

321 Our analysis of seasonal variation in species richness did not find a significant effect of
322 island area. This outcome could reflect the use of broad migration fronts [27] where all islands,
323 independent of size, have the potential of being encountered during migration. In contrast,
324 seasonal variation in species richness showed a negative relationship with island isolation, which
325 was most pronounced for islands located further than 150 km from the mainland, replicating the
326 threshold identified with the species-isolation relationship. These results suggest that the
327 occurrence of migratory bird species on nearshore islands is an important source of both species
328 numbers and seasonal variation in species richness. For the most remote islands, our estimates of
329 seasonal variation in species richness were very close to zero, suggesting that the occurrence of
330 migratory bird species on these islands is highly unusual. The 150 km threshold may reflect the
331 unwillingness of migrants to deviate from the safety of the coastline or could reflect the use of
332 transoceanic “shortcuts” between continents. For example, migrants crossing the Gulf of Mexico
333 and Caribbean Sea between North and South America [33, 50, 51] and migrants crossing the
334 Mediterranean Sea between Europe and Africa [52, 53]. Current evidence suggests vagrancy is
335 common on nearshore islands, indicating birds are willing to cross relatively short oceanic
336 barriers, especially when the island can be seen from the coast [54, 55]. Traveling further out to

337 sea where islands tend to be smaller and more isolated would substantially increase the chances
338 of mortality.

339 The interactions between island area and isolation documented in this study did not
340 follow expectations based on island biogeography theory [2, 15, 16]. We did not find weaker
341 species-area relationships for nearshore islands and stronger species-area relationships for more
342 remote islands. Rather, we found a stronger species-area relationships for islands at intermediate
343 distances to the mainland and a weaker species-area relationships for the most remote islands.
344 For islands at intermediate distances to the mainland, our findings suggest that the unique
345 combination of stochastic, ecological, evolutionary processes on these islands is responsible for
346 the stronger species-area relationship, with evolutionary processes on the largest islands likely
347 playing a significant role. The weak species-area relationship for the most remote islands is
348 likely a product of several factors including the relatively small size of the islands, the rarity of
349 immigration events on the islands, the dependence on *in situ* speciation to populate the islands,
350 and the recent extinctions of many endemic island bird species [56, 57].

351 The presence of migratory species on islands could have several possible consequences
352 for island biogeography theory. If a migratory species is purely transitory, the presence of these
353 species would likely have little effect on an island's immigration/extinction dynamics. A
354 possible exception could occur if the migratory species interfered with the survival or fitness of
355 resident species, increasing the chances of their extinction. For example, through predation of
356 young or adults, interfering with mating or foraging behavior, the depletion of food resources, or
357 the degradation of habitat. Another exception could occur if the migratory species forms a
358 founder sedentary population. This could occur on islands where, once landfall has been
359 achieved, continuing the migration journey is no longer advantageous due to the island's

360 remoteness and the physical state of the bird. The formation of a sedentary population could also
361 lead to speciation through a variety of processes [58]. Once established, the influx of new
362 individuals during migration could mitigate the risk of extinction through demographic and
363 genetic contributions [25]. Testing the relevance of these different effects would clarify the role
364 of migratory birds as a factor affecting an island's speciation processes and
365 immigration/extinction dynamics.

366 In summary, our study provides the most comprehensive empirical assessment to date on
367 the patterns and geographical correlates of the seasonal species richness of birds across the
368 world's islands. One limitation of our approach is that the dates we used to divide the year into
369 four seasons are not absolute across the world's islands. Using eBird or other data sources to
370 generate island specific migration phenology estimates would likely improve the quality of our
371 seasonal species richness estimates. The thresholds identified in our analysis for island area and
372 distance can be used to inform and guide research, monitoring, and conservation efforts for the
373 world's migratory birds. Evidence for an interaction between area and isolation that is contrary
374 to expectations highlights the ecological isolation of the world's most remote islands and the
375 continuing vulnerability of these systems to effects of anthropogenic activities, and the
376 importance of evolutionary processes on the world's largest islands. Acquiring additional
377 insights into the nature of these seasonal patterns and the role of stochastic, ecological, and
378 evolutionary processes will provide a basis to better understand how resident and migratory bird
379 species function within island systems across their annual life cycles.

380

381 **Data accessibility.** The bird occurrence data are available from <https://ebird.org/science/use->
382 [ebird-data](https://ebird.org/science/use-ebird-data) and the shoreline vector coverage of the world's continents and islands is available
383 from [38]. All data used in the analysis is available at <https://doi.org/10.5061/dryad.m0cfxpp67>

384 **Author's contributions.** F.A. La Sorte and M. Somveille conceived the study. F.A. La Sorte
385 compiled the data and designed and implemented the analysis. F.A. La Sorte wrote the first draft
386 of the paper. All authors contributed suggestions and text to subsequent drafts.

387 **Funding.** This work was supported by The Wolf Creek Charitable Foundation and the National
388 Science Foundation (ABI sustaining: DBI-1939187).

389 **Acknowledgements.** This research would not be possible without the contributions of the eBird
390 participants, expert reviewers, and the many other individuals whose work and engagement make
391 the eBird project successful. We thank A. Phillimore and S. Oppel for helpful comments on an
392 earlier draft.

393

394 **References**

- 395 1. Kier, G, Kreft, H, Lee, TM, Jetz, W, Ibisch, PL, Nowicki, C, Mutke, J, Barthlott, W.
396 2009 A global assessment of endemism and species richness across island and mainland
397 regions. *Proc. Natl. Acad. Sci. U. S. A.* **106**, 9322-9327. (doi:10.1073/pnas.0810306106).
- 398 2. Whittaker, RJ, Fernández-Palacios, JM, Matthews, TJ, Borregaard, MK, Triantis, KA.
399 2017 Island biogeography: Taking the long view of nature's laboratories. *Science* **357**,
400 eaam8326. (doi:10.1126/science.aam8326).
- 401 3. Newton, I. 2003 *The Speciation and Biogeography of Birds*. London, Academic Press;
402 668 p.

- 403 4. Jetz, W, Thomas, GH, Joy, JB, Hartmann, K, Mooers, AO. 2012 The global diversity of
404 birds in space and time. *Nature* **491**, 444-448. (doi:10.1038/nature11631).
- 405 5. Jønsson, KA, Holt, BG. 2015 Islands contribute disproportionately high amounts of
406 evolutionary diversity in passerine birds. *Nat. Commun.* **6**, 8538.
407 (doi:10.1038/ncomms9538).
- 408 6. Stracey, CM, Pimm, SL. 2009 Testing island biogeography theory with visitation rates of
409 birds to British islands. *J. Biogeogr.* **36**, 1532-1539. (doi:10.1111/j.1365-
410 2699.2009.02090.x).
- 411 7. Rebecca, WS, Sara, RM, Kimberly, JB. 2012 Comparison of migrant songbird stopover
412 ecology on two islands in the Gulf of Maine. *Wilson J. Ornithol.* **124**, 217-229.
413 (doi:10.1676/10-067.1).
- 414 8. Saino, N, Rubolini, D, Von Hardenberg, J, Ambrosini, R, Provenzale, A, Romano, M,
415 Spina, F. 2010 Spring migration decisions in relation to weather are predicted by wing
416 morphology among trans-Mediterranean migratory birds. *Funct. Ecol.* **24**, 658-669.
417 (doi:10.1111/j.1365-2435.2009.01659.x).
- 418 9. Morris, SR, Richmond, ME, Holmes, DW. 1994 Patterns of stopover by warblers during
419 spring and fall migration on Appledore Island, Maine. *Wilson Bull.* **106**, 703-718.
- 420 10. Moore, FR, Kerlinger, P, Simons, TR. 1990 Stopover on a gulf coast barrier Island by
421 spring trans-gulf migrants. *Wilson Bull.* **102**, 487-500.
- 422 11. Spina, F, Massi, A, Montemaggiori, A, Baccetti, N. 1993 Spring migration across central
423 Mediterranean: general results from the 'Progetto Piccole Isole'. *Vogelwarte* **37**, 1-94.

- 424 12. Lupi, S, Slezacek, J, Fusani, L. 2019 The physiology of stopover decisions: food, fat and
425 zugunruhe on a Mediterranean island. *J. Ornithol.* **160**, 1205-1212. (doi:10.1007/s10336-
426 019-01693-4).
- 427 13. Goymann, W, Spina, F, Ferri, A, Fusani, L. 2010 Body fat influences departure from
428 stopover sites in migratory birds: evidence from whole-island telemetry. *Biol. Lett.* **6**,
429 478-481. (doi:10.1098/rsbl.2009.1028).
- 430 14. Ferretti, A, Maggini, I, Fusani, L. 2021 How to recover after sea crossing: the importance
431 of small islands for passerines during spring migration. *Ethol. Ecol. Evol.* **33**, 307-320.
432 (doi:10.1080/03949370.2021.1886181).
- 433 15. MacArthur, RH, Wilson, EO. 1967 *The Theory of Island Biogeography*. Princeton, NJ,
434 Princeton University Press.
- 435 16. Losos, JB, Ricklefs, RE. 2010 *The Theory of Island Biogeography Revisited*. Princeton,
436 Princeton University Press; 496 p.
- 437 17. Kalmar, A, Currie, DJ. 2007 A unified model of avian species richness on islands and
438 continents. *Ecology* **88**, 1309-1321. (doi:10.1890/06-1368).
- 439 18. Kalmar, A, Currie, DJ. 2006 A global model of island biogeography. *Glob. Ecol.*
440 *Biogeogr.* **15**, 72-81. (doi:10.1111/j.1466-822X.2006.00205.x).
- 441 19. Ding, T-S, Yuan, H-W, Geng, S, Koh, C-N, Lee, P-F. 2006 Macro-scale bird species
442 richness patterns of the East Asian mainland and islands: energy, area and isolation. *J.*
443 *Biogeogr.* **33**, 683-693. (doi:10.1111/j.1365-2699.2006.01419.x).
- 444 20. Ricklefs, RE, Bermingham, E. 2004 History and the species-area relationship in Lesser
445 Antillean birds. *Am. Nat.* **163**, 227-239. (doi:10.1086/381002).

- 446 21. Ricklefs, RE, Lovette, IJ. 1999 The roles of island area per se and habitat diversity in the
447 species–area relationships of four Lesser Antillean faunal groups. *J. Anim. Ecol.* **68**,
448 1142-1160. (doi:10.1046/j.1365-2656.1999.00358.x).
- 449 22. Lomolino, MV, Weiser, MD. 2001 Towards a more general species–area relationship:
450 diversity on all islands, great and small. *J. Biogeogr.* **28**, 431-445. (doi:10.1046/j.1365-
451 2699.2001.00550.x).
- 452 23. Lomolino, MV. 2000 Ecology’s most general, yet protean pattern: the species-area
453 relationship. *J. Biogeogr.* **27**, 17-26. (doi:10.1046/j.1365-2699.2000.00377.x).
- 454 24. Losos, JB, Schluter, D. 2000 Analysis of an evolutionary species–area relationship.
455 *Nature* **408**, 847-850. (doi:10.1038/35048558).
- 456 25. Brown, JH, Kodric-Brown, A. 1977 Turnover rates in insular biogeography: effect of
457 immigration on extinction. *Ecology* **58**, 445-449. (doi:10.2307/1935620).
- 458 26. Drakare, S, Lennon, JJ, Hillebrand, H. 2006 The imprint of the geographical,
459 evolutionary and ecological context on species–area relationships. *Ecol. Lett.* **9**, 215-227.
460 (doi:10.1111/j.1461-0248.2005.00848.x).
- 461 27. La Sorte, FA, Fink, D, Hochachka, WM, Farnsworth, A, Rodewald, AD, Rosenberg, KV,
462 Sullivan, BL, Winkler, DW, Wood, C, Kelling, S. 2014 The role of atmospheric
463 conditions in the seasonal dynamics of North American migration flyways. *J. Biogeogr.*
464 **41**, 1685-1696. (doi:10.1111/jbi.12328).
- 465 28. Pianka, ER. 1966 Latitudinal gradients in species diversity: a review of concepts. *Am.*
466 *Nat.* **100**, 33-46. (doi:10.1086/282398).

- 467 29. Willig, MR, Kaufman, DM, Stevens, RD. 2003 Latitudinal gradients of biodiversity:
468 pattern, process, scale, and synthesis. *Annu. Rev. Ecol. Evol. Syst.* **34**, 273-309.
469 (doi:10.1146/annurev.ecolsys.34.012103.144032).
- 470 30. Somveille, M, Manica, A, Butchart, SHM, Rodrigues, ASL. 2013 Mapping global
471 diversity patterns for migratory birds. *PLoS ONE* **8**, e70907.
472 (doi:10.1371/journal.pone.0070907).
- 473 31. Rabenold, K. 1993 Latitudinal gradients in avian species diversity and the role of long-
474 distance migration. In *Curr. Ornithol.* (ed. D. Power), pp. 247-274, Springer US.
- 475 32. Mac Arthur, RH. 1959 On the breeding distribution patterns of North American migrant
476 birds. *Auk* **76**, 318-325.
- 477 33. Gauthreaux, SA, Belser, CG. 1999 Bird migration in the region of the Gulf of Mexico. In
478 *Proceedings of the 22nd International Ornithological Congress* (eds. N.J. Adams & R.H.
479 Slotow), pp. 1931-1947. Durban, Birdlife South Africa.
- 480 34. Lobo, JM, Hortal, J, Yela, JL, Millán, A, Sánchez-Fernández, D, García-Roselló, E,
481 González-Dacosta, J, Heine, J, González-Vilas, L, Guisande, C. 2018 KnowBR: An
482 application to map the geographical variation of survey effort and identify well-surveyed
483 areas from biodiversity databases. *Ecol. Indic.* **91**, 241-248.
484 (doi:10.1016/j.ecolind.2018.03.077).
- 485 35. La Sorte, FA, Somveille, M. 2020 Survey completeness of a global citizen-science
486 database of bird occurrence. *Ecography* **43**, 34-43. (doi:10.1111/ecog.04632).
- 487 36. La Sorte, FA, Somveille, M. 2021 The island biogeography of the eBird citizen-science
488 programme. *J. Biogeogr.* **48**, 628-638. (doi:10.1111/jbi.14026).

- 489 37. Sullivan, BL, Aycrigg, JL, Barry, JH, Bonney, RE, Bruns, N, Cooper, CB, Damoulas, T,
490 Dhondt, AA, Dietterich, T, Farnsworth, A, et al. 2014 The eBird enterprise: An integrated
491 approach to development and application of citizen science. *Biol. Conserv.* **169**, 31-40.
492 (doi:10.1016/j.biocon.2013.11.003).
- 493 38. Sayre, R, Noble, S, Hamann, S, Smith, R, Wright, D, Breyer, S, Butler, K, Van
494 Graafeiland, K, Frye, C, Karagulle, D, et al. 2019 A new 30 meter resolution global
495 shoreline vector and associated global islands database for the development of
496 standardized ecological coastal units. *J. Oper. Oceanogr.* **12**, s47-s56.
497 (doi:10.1080/1755876X.2018.1529714).
- 498 39. Ugland, KI, Gray, JS, Ellingsen, KE. 2003 The species-accumulation curve and
499 estimation of species richness. *J. Anim. Ecol.* **72**, 888-897. (doi:10.1046/j.1365-
500 2656.2003.00748.x).
- 501 40. Wood, SN. 2004 Stable and efficient multiple smoothing parameter estimation for
502 generalized additive models. *J. Am. Statist. Assoc.* **99**, 673-686.
503 (doi:10.1198/016214504000000980).
- 504 41. Wood, SN. 2011 Fast stable restricted maximum likelihood and marginal likelihood
505 estimation of semiparametric generalized linear models. *J. R. Stat. Soc. Ser. B-Stat.*
506 *Methodol.* **73**, 3-36.
- 507 42. Wood, SN. 2017 *Generalized Additive Models: An Introduction With R*. 2nd ed. Boca
508 Raton, FL, Chapman & Hall/CRC.
- 509 43. Pinheiro, JC, Bates, DM. 2000 *Mixed-effects models in S and S-PLUS*. New York, New
510 York, USA, Springer.

- 511 44. Akaike, H. 1974 A new look at the statistical model identification. *IEEE Transactions on*
512 *Automatic Control* **19**, 716-723. (doi:10.1109/TAC.1974.1100705).
- 513 45. R Development Core Team. 2022 *R: A language and environment for statistical*
514 *computing*. Vienna, Austria, R Foundation for Statistical Computing [https://www.R-](https://www.R-project.org/)
515 [project.org/](https://www.R-project.org/).
- 516 46. Hijmans, RJ. 2019 raster: Geographic Data Analysis and Modeling. R package version
517 3.0-7. <https://CRAN.R-project.org/package=raster>.
- 518 47. Bates, D, Mächler, M, Bolker, B, Walker, S. 2015 Fitting linear mixed-effects models
519 using lme4. *J. Stat. Softw.* **67**, 1-48. (doi:10.18637/jss.v067.i01).
- 520 48. Hothorn, T, Bretz, F, Westfall, P. 2008 Simultaneous inference in general parametric
521 models. *Biom. J.* **50**, 346-363. (doi:10.1002/bimj.200810425).
- 522 49. Wang, Y, Millien, V, Ding, P. 2016 On empty islands and the small-island effect. *Glob.*
523 *Ecol. Biogeogr.* **25**, 1333-1345. (doi:10.1111/geb.12494).
- 524 50. Lowery, GH. 1946 Evidence of trans-Gulf migration. *Auk* **63**, 175-211.
525 (doi:10.2307/4080010).
- 526 51. Stevenson, HM. 1957 The relative magnitude of the trans-Gulf and circum-Gulf spring
527 migrations. *Wilson Bull.* **69**, 39-77.
- 528 52. Moreau, RE. 1961 Problems of Mediterranean-Saharan migration. *Ibis* **103a**, 373-427.
529 (doi:10.1111/j.1474-919X.1961.tb02454.x).
- 530 53. Biebach, H, Biebach, I, Friedrich, W, Heine, G, Partecke, J, Schmidl, D. 2000 Strategies
531 of passerine migration across the Mediterranean Sea and the Sahara Desert: a radar study.
532 *Ibis* **142**, 623-634. (doi:10.1111/j.1474-919X.2000.tb04462.x).

- 533 54. Rose, MD, Polis, GA. 2000 On the insularity of islands. *Ecography* **23**, 693-701.
534 (doi:10.1111/j.1600-0587.2000.tb00313.x).
- 535 55. Lees, AC, Gilroy, JJ. 2014 Vagrancy fails to predict colonization of oceanic islands.
536 *Glob. Ecol. Biogeogr.* **23**, 405-413. (doi:10.1111/geb.12129).
- 537 56. Biber, E. 2002 Patterns of endemic extinctions among island bird species. *Ecography* **25**,
538 661-676. (doi:10.1034/j.1600-0587.2002.t01-1-250603.x).
- 539 57. Duncan, RP, Blackburn, TM. 2007 Causes of extinction in island birds. *Anim. Conserv.*
540 **10**, 149-150. (doi:10.1111/j.1469-1795.2007.00110.x).
- 541 58. Rolland, J, Jiguet, F, Jønsson, KA, Condamine, FL, Morlon, H. 2014 Settling down of
542 seasonal migrants promotes bird diversification. *Proc. R. Soc. B-Biol. Sci.* **281**.
543 (doi:10.1098/rspb.2014.0473).

544 **Figure 1.** Estimated seasonal species richness of birds on 690 islands during the boreal winter,
545 spring, summer, and autumn. We defined the four seasons based on the following dates for
546 boreal spring (15 March to June 15) and boreal autumn (15 August to 15 November).

547 **Figure 2.** The islands containing the highest estimated seasonal species richness of birds from a
548 total of 690 islands during the boreal winter, spring, summer, and autumn. The percent of the
549 total number of islands for each season is shown in parentheses.

550 **Figure 3.** (a) Seasonality in species richness of birds on 690 islands. Seasonality is defined as the
551 maximum seasonal difference in species richness between the migration (boreal spring and
552 autumn) and non-migration periods (boreal summer and winter). Fitted lines with 95%
553 confidence bands from generalized additive mixed models of seasonality in species richness of
554 birds on 690 islands by (a) island area, (b) distance to mainland (excluding Antarctica), (c)
555 spatial proximity to other islands, and (d) the latitude of the center of the island.

556 **Figure 4.** (a) Boxplot of estimated seasonal species richness of birds on 690 islands during the
557 boreal winter, spring, summer, and autumn. Fitted lines with 95% confidence bands from
558 generalized additive models of estimated seasonal species richness of birds on 690 islands during
559 four seasons by (b) island area, (c) distance to mainland (excluding Antarctica), (d) spatial
560 proximity to other islands, and (e) latitude of the center of the island. Note the different scales on
561 the y-axes.

562 **Figure 5.** Contour plots of estimated seasonal species richness on 690 islands during the boreal
563 winter, spring, summer, and autumn as a function of the smooth interaction between island area
564 and distance to mainland (excluding Antarctica) from generalized additive mixed models. The
565 contour interval scales are identical across the four contour plots.

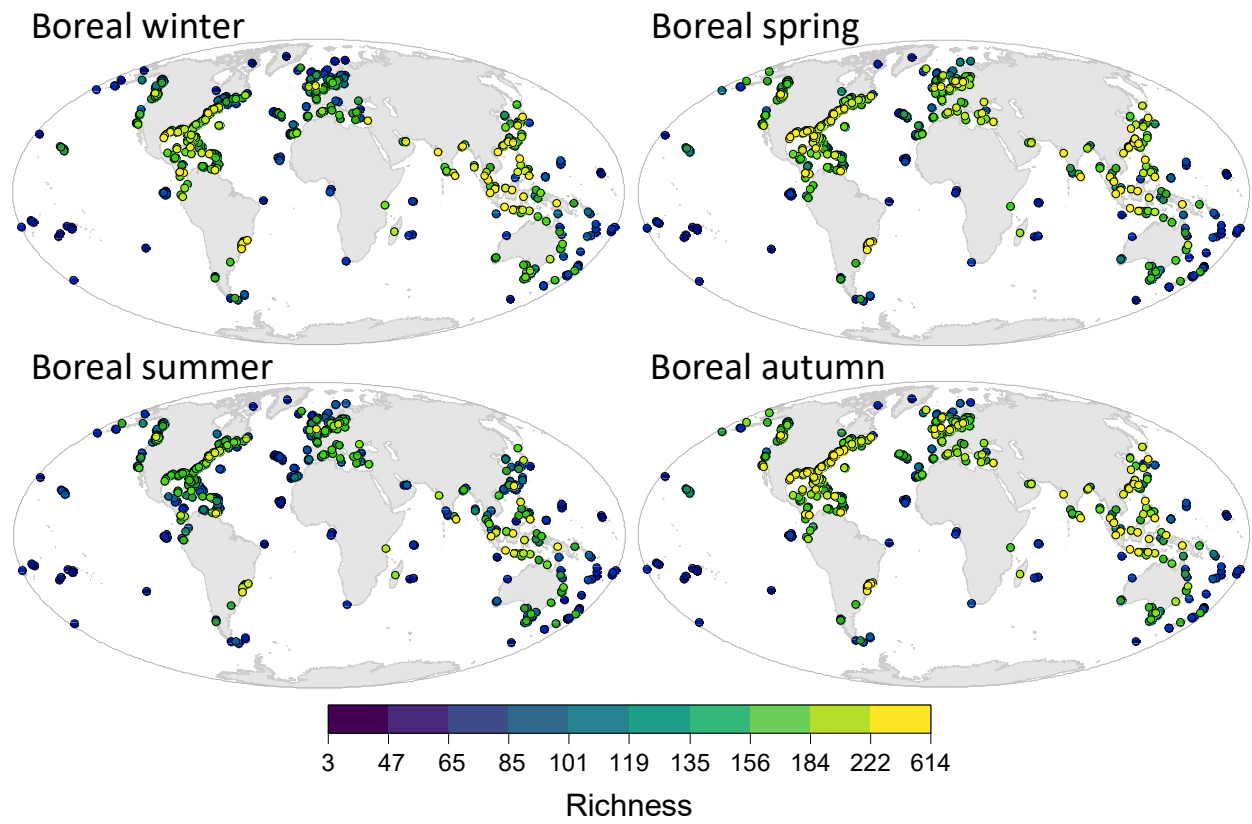
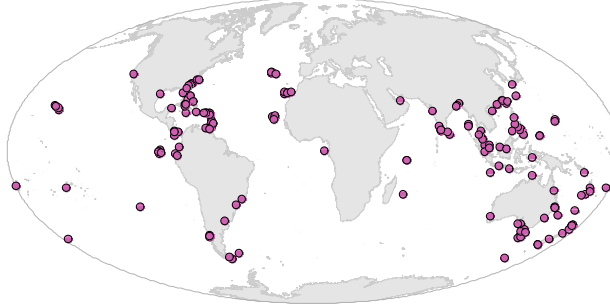
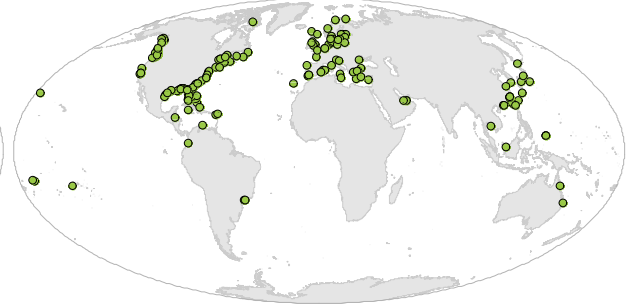


Figure 1

Boreal winter (25.9%)



Boreal spring (30.0%)



Boreal summer (1.6%)



Boreal autumn (42.5%)

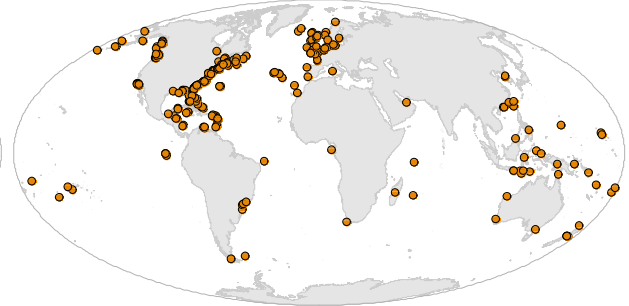


Figure 2

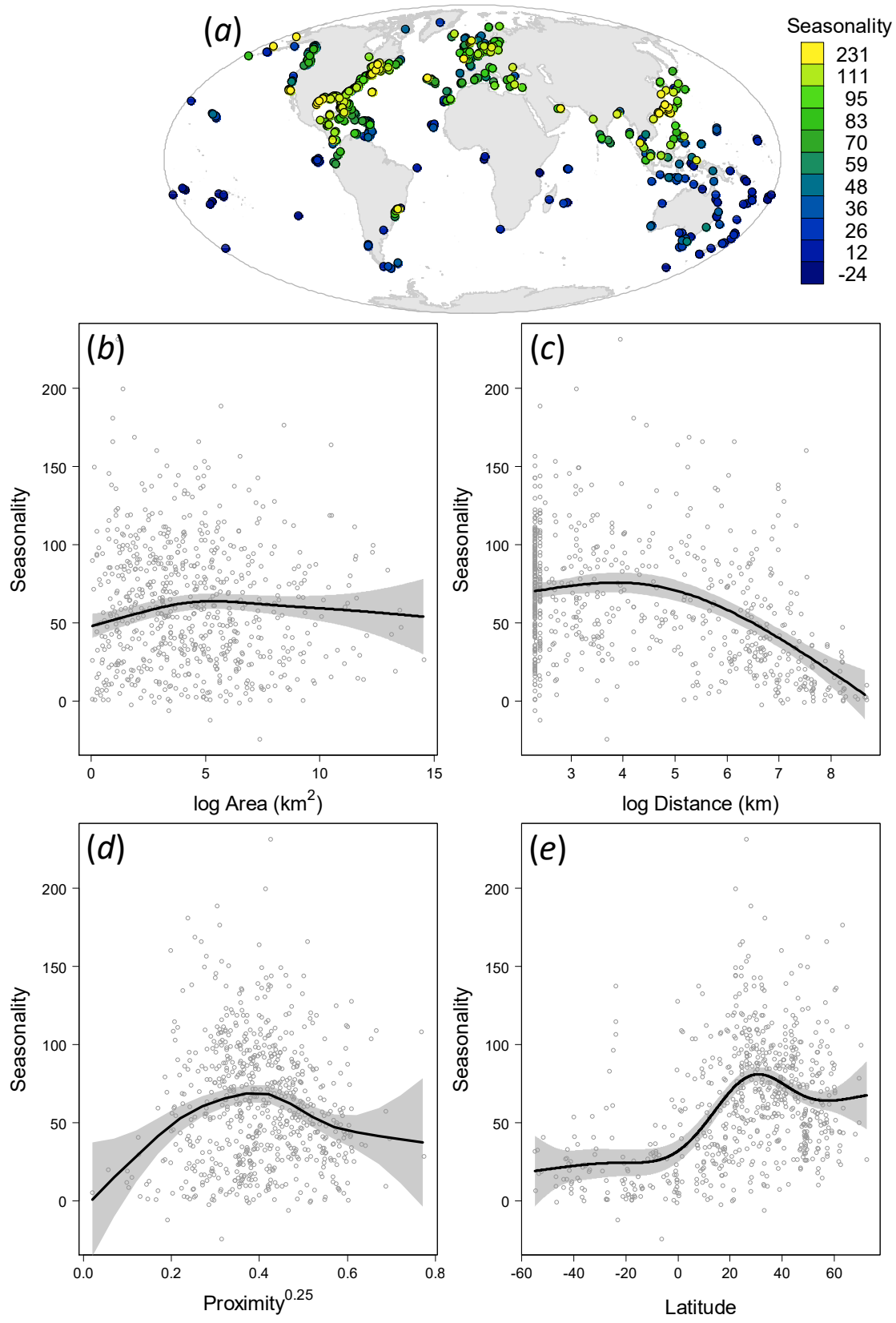


Figure 3

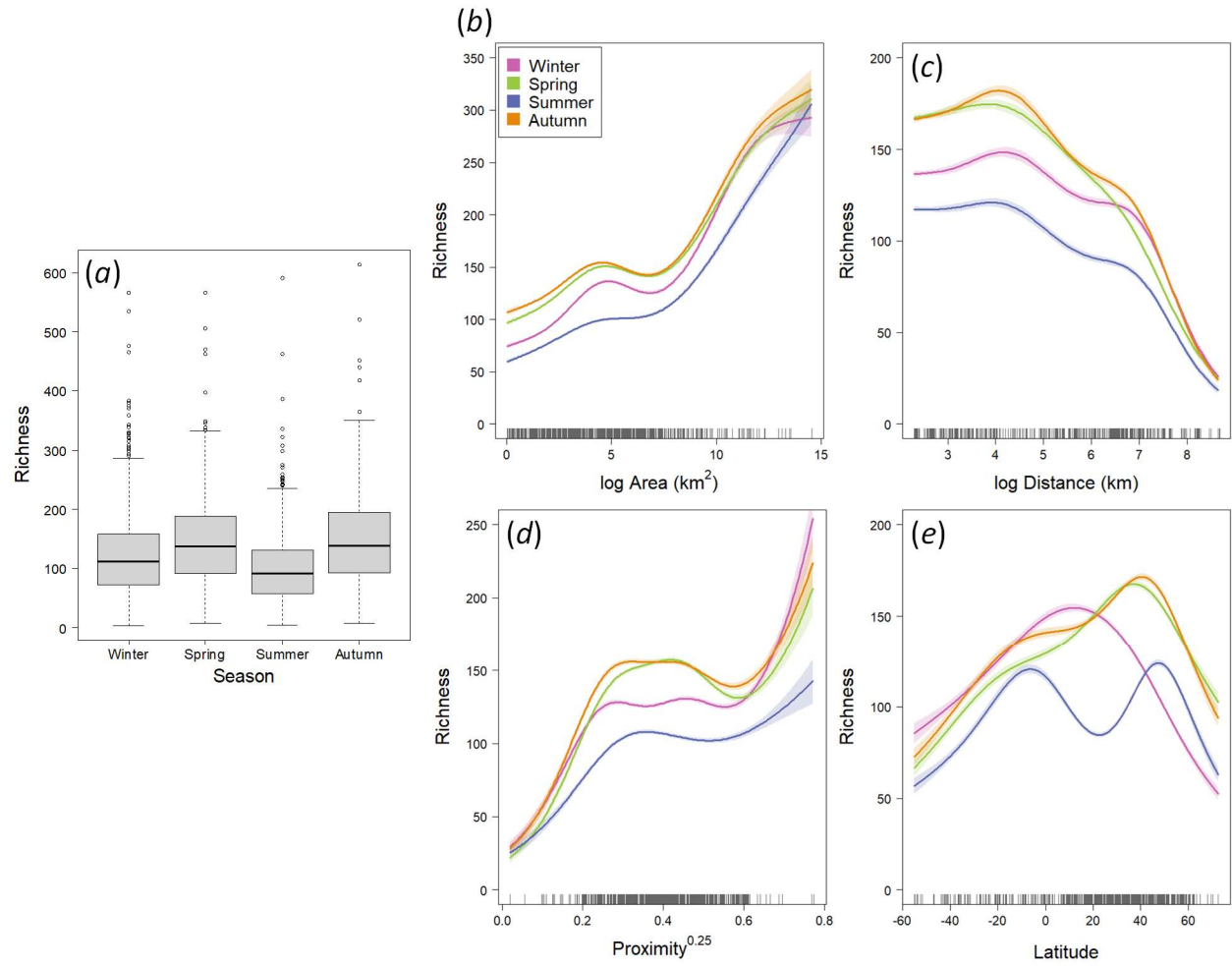


Figure 4

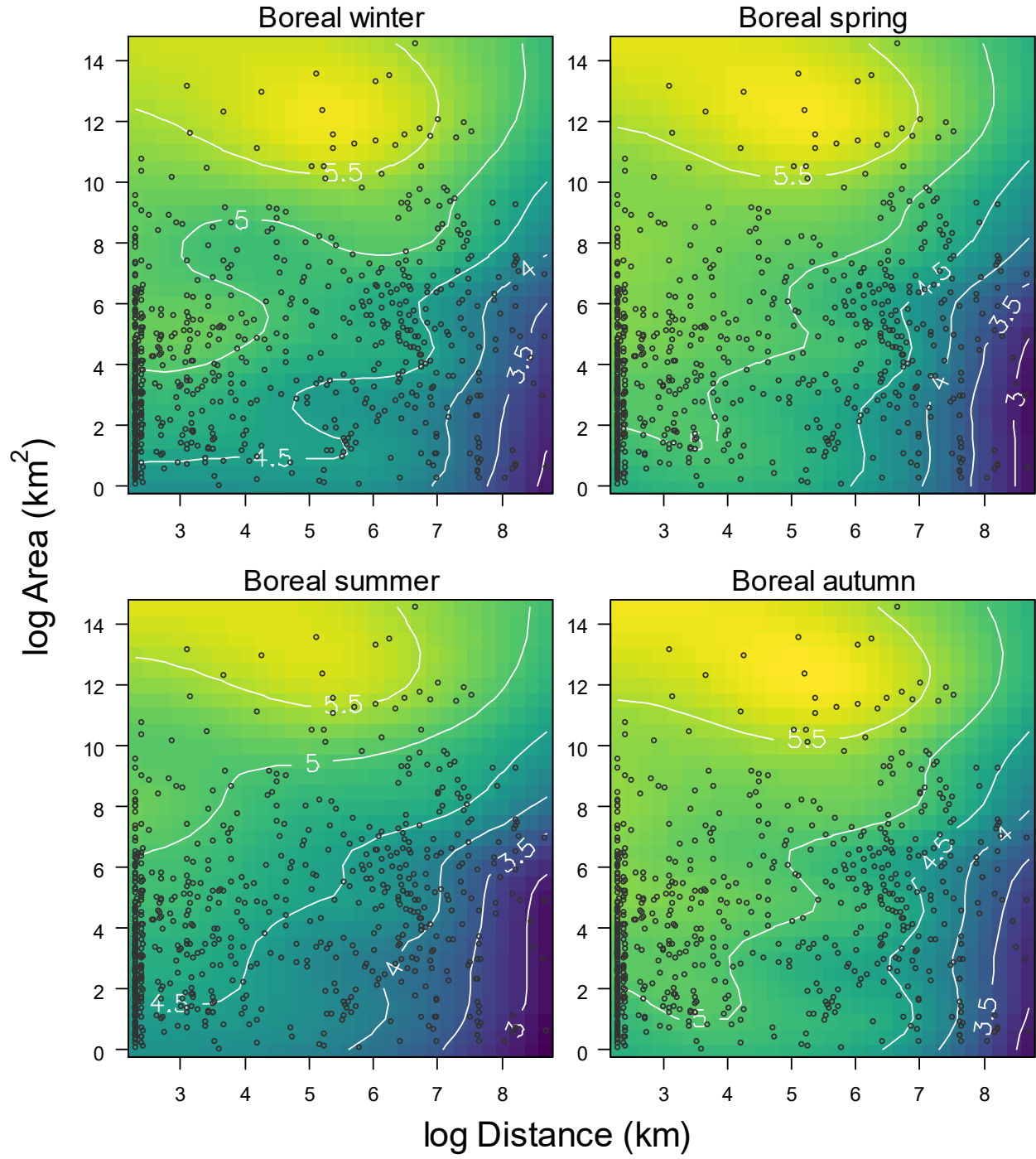


Figure 5