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1 **Land-use change interacts with island biogeography to alter**
2 **bird community assembly**

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23 **Abstract:** Anthropogenic activities have reshaped biodiversity on islands worldwide.
24 However, it remains unclear how island attributes and land-use change interactively
25 shape multiple facets of island biodiversity through community assembly processes.
26 To answer this, we conducted bird surveys in various land-use types (mainly forest
27 and farmland) using transects on 34 oceanic land-bridge islands in the largest
28 archipelago of China. We found that bird species richness increases with island area
29 and decreases with isolation, regardless of the intensity of land-use change. However,
30 forest-dominated habitats exhibited lower richness than farmland-dominated habitats.
31 Island bird assemblages generally comprised species that share more similar traits or
32 evolutionary histories (*i.e.*, functional and/or phylogenetic clustering) than expected if
33 assemblages were randomly assembled. Contrary to our expectations, we observed
34 that bird assemblages in forest-dominated habitats were more clustered on large and
35 close islands, whereas assemblages in farmland-dominated habitats were more
36 clustered on small islands. These contrasting results indicate that land-use change
37 interacts with island biogeography to alter the community assembly of birds on
38 inhabited islands. Our findings emphasize the importance of incorporating human-
39 modified habitats when examining the community assembly of island biota, and
40 further suggest that agricultural landscapes on large islands may play essential roles in
41 protecting countryside island biodiversity.

42 **Keywords:** Anthropocene, biodiversity conservation, countryside island
43 biogeography, farmland, functional trait, oceanic island

44 **1. Introduction**

45 Islands are hotspots of biodiversity that make up 5.3% of the global land area but
46 support around 20% of the world's species [1,2]. However, the decline and turnover
47 of biodiversity on islands due to anthropogenic activities are more rapid than
48 anywhere else [3]. A primary driver of island biodiversity decline is land-use change
49 [4,5], especially the conversion of natural forests into agricultural lands and
50 settlements [6-8]. Therefore, it is critical to disentangle the effects of human activities
51 on island biodiversity from those of natural biophysical island characteristics [9] to
52 better understand the drivers of biodiversity loss and to inform conservation strategies
53 aimed at mitigating further biodiversity declines.

54 The Equilibrium Theory of Island Biogeography (hereafter ETIB) postulates that
55 larger islands have lower extinction rates (*i.e.*, area effect) and more remote islands
56 have lower colonization rates (*i.e.*, distance effect) [10], resulting in the positive
57 species–area and negative species–isolation relationships. In contrast to ETIB, which
58 is generally discussed in the context of biodiversity in natural habitats, countryside
59 biogeography highlights the importance of human-dominated landscapes (*e.g.*,
60 farmland habitats) in supporting biodiversity [11,12]. Linking countryside
61 biogeography and island biogeography thus provides an alternative framework,
62 namely countryside island biogeography, which can be used to frame conservation
63 science in human-dominated landscapes on inhabited islands [13,14]. To date, few
64 studies have explored how human-modified habitats affect species diversity patterns

65 in true island systems (*i.e.*, islands surrounded by water). Moreover, these studies
66 often do so by surveying only one or a small number of island(s) [15-17], probably
67 due to the efforts required to sample multiple habitats across different islands. To the
68 best of our knowledge, no study has explored the *interactive* effect of island
69 biogeography (*e.g.*, island area and isolation) and land-use change on biodiversity
70 across multiple inhabited true islands — a key component of countryside island
71 biogeography.

72 In naturally forested regions, ecological theory predicts that all else being equal
73 farmland habitats harbour lower richness than forest habitats because they provide
74 fewer complex niches and resources, and have generally been present for a much
75 shorter period of time than adjacent forests (*i.e.*, there has been little time for new taxa
76 to originate via speciation), especially on small and remote islands (figure 1a) [18-
77 21]. In other words, species richness on small and remote islands should be more
78 affected by land-use change than on large and close islands (*i.e.*, there is expected to
79 be an interactive effect between island characteristics and land-use change) (figure
80 1b).

81 Clarifying the processes and mechanisms underpinning community assembly is
82 key to understanding the maintenance of biodiversity [22]. Researchers have recently
83 incorporated species traits and evolutionary histories into ETIB to try to better
84 understand community assembly processes on islands [23,24]. Suppose species with
85 strong dispersal abilities are more likely to successfully colonise islands and/or that

86 the subsequent probability of survival is related to specific habitat availability on
87 different islands (*e.g.*, the availability of mature trees on islands is essential for tree-
88 roosting species). Under these circumstances, relative to a larger species pool, insular
89 assemblages will comprise a subset of species that share similar functional traits (*i.e.*,
90 functional clustering) [25,26] which confer a survival advantage in specific insular
91 environments [27]. If these traits are phylogenetically conserved, which is generally
92 common [28], insular assemblages will also comprise groups of species that are more
93 similar in terms of their evolutionary history than expected (*i.e.*, phylogenetic
94 clustering). A contrasting theoretical prediction is that closely related species that
95 share similar traits or resource requirements are more likely to compete due to the
96 limited resource on (particularly small) islands [29]. In this case, island biotas are
97 expected to comprise species with distinct traits and/or evolutionary histories (*i.e.*,
98 functional and/or phylogenetic overdispersion) [25,26] through competitive exclusion
99 of closely related species. However, empirical studies of various taxa have found the
100 structure of island assemblages is, in general, phylogenetically and functionally
101 clustered [26,30,31]. Given the presence of severe environmental filters and limited
102 habitat diversity, in addition to the increased role of dispersal filtering, on small and
103 remote islands, one may expect community structure on these types of islands to be
104 even more phylogenetically and functionally clustered [32] (figure 1c). As such, we
105 may expect that community structure patterns will change across island area and
106 isolation gradients (*i.e.*, structure–area and structure–isolation relationships).

107 The aforementioned expectations relate to assemblages on islands that still
108 maintain full forest cover [33]. However, land-use change, a feature of almost all
109 inhabited islands globally, may impact community assembly in insular biotas, leading
110 to altered community structure. The transformation of forests to farmland typically
111 reduces habitat diversity and complexity at certain scales (*e.g.*, per transect), resulting
112 in more homogenised assemblages in farmland, especially on large and close islands
113 where human activities are more frequent [34,35]. Thus, we predict that community
114 structure in farmland-dominated habitats on islands will be even more clustered (*i.e.*,
115 species are more closely related and functionally similar than expected) than in forest-
116 dominated habitats, as only a few insular species can likely tolerate significant human
117 disturbance (*i.e.*, the conversion of forest to farmland acts as a strong environmental
118 filter) [18,36].

119 In this study, we examined whether there are interactive effects of land-use type
120 and island attributes (area and isolation) on bird assemblages in the Zhoushan
121 Archipelago, the largest archipelago in China with > 1,000 continental (oceanic land-
122 bridge) islands. To address this question, we surveyed birds during the breeding
123 season along transects with varying proportions of land-use types (primarily forest
124 and farmland) on 34 islands that span a gradient of island area and isolation in the
125 archipelago. We used these data to test three predictions. 1) The species richness of
126 bird assemblages will increase with island area and decrease with isolation, in
127 accordance with the predictions of ETIB (figure 1b). 2) The phylogenetic and

128 functional community structure of bird assemblages will be clustered on the study
129 islands, and the degree of clustering will decrease with island area and increase with
130 isolation (figure 1c). 3) There will be an interactive effect of land-use change (*i.e.*, the
131 presence of human-modified habitats) and island biogeographic variables on insular
132 bird richness and community assembly. Specifically, the species–area relationship and
133 species–isolation relationship are expected to be steeper along transects with an
134 increasing proportion of farmland and a decreasing proportion of forest (figure 1b). In
135 addition, birds inhabiting farmland-dominated transects are predicted to be more
136 compositionally similar across islands (*i.e.*, phylogenetic and functional redundancy)
137 compared to those in forest-dominated transects, resulting in flatter structure–area and
138 structure–isolation relationships with increasing farmland cover along a transect
139 (figure 1c).

140

141 **2. Methods**

142 **2.1 Study site**

143 Our study is situated in the Zhoushan Archipelago (29°31'–31°04'N, 121°30'–
144 123°25'E), in eastern China (figure 2). The region belongs to the subtropical oceanic
145 monsoon zone, with a strong seasonal climate (*i.e.*, hot summers and cold winters).
146 The average temperature between April to June in 2020 and 2021 (*i.e.*, surveying
147 period) was 20.73°C (data from China Meteorological Administration;
148 <http://lishi.tianqi.com>). The subtropical evergreen broadleaf forest is the dominant

149 vegetation on the islands of the Zhoushan Archipelago, along with coniferous forests,
150 grasslands, and shrubs [37,38]. The Zhoushan Archipelago provides an excellent
151 opportunity to test the interactive effects of human land use and island biophysical
152 characteristics on island community diversity and assembly for a number of reasons.
153 First, archaeological evidence indicates that humans have continuously occupied the
154 archipelago since at least the Neolithic (*i.e.*, 5,000 years ago) [39], resulting in
155 complex landscapes (including some agricultural lands) on most islands. The primary
156 agricultural crops cultivated on the islands include rice, maize, sweet potato, oilseed
157 rape, as well as various vegetables and fruits, all of which are patchily distributed
158 within and across islands (<http://zstj.zhoushan.gov.cn/col/col1229615782/index.html>).
159 Second, background information on the region's biota is well-known, given that
160 research on the archipelago has been undertaken since the 1850s [40,41]. Lastly, as
161 the focus is on birds, the effect of evolutionary processes (*e.g.*, *in situ* speciation) can
162 be largely ignored, given the relatively short geological history of the islands being
163 separated from the mainland (about 7,000–9,000 years).

164 We selected 34 islands across a gradient of island area and isolation (*i.e.*, island
165 size and the nearest coast-to-coast distance from each island to the mainland), and
166 considering the habitat types present on the islands. In other words, we particularly
167 looked for small and remote islands that have farmland habitats (*e.g.*, Island S31, with
168 area = 0.24 km² and isolation = 65.82 km). We calculated island area and isolation

169 using ArcGIS based on a meter-resolution dataset of global coastlines [42] (electronic
170 supplementary material, table S1).

171

172 **2.2 Field survey and bird data**

173 We located transects for bird surveys on each island based on the available forest (*i.e.*,
174 the dominant vegetation along the transect is evergreen broadleaf forest) and farmland
175 (*i.e.*, the transect runs through multiple crops in farmers' fields). The number of
176 transects on each island was roughly proportional to island area [43]. The length of
177 most transects was around 2 km, with a few being 1 km because of logistical
178 restrictions (*i.e.*, cliffs or inaccessible terrain on, the mostly smaller, islands) (see
179 more details in electronic supplementary material, table S1). As a result, we set a total
180 of 70 transects on 34 study islands.

181 We conducted breeding bird surveys along each transect from April to June in
182 2020 and 2021, respectively. During each breeding season, the survey was conducted
183 twice within a one-month interval, which is the maximum effort we could afford in
184 the field [44], so we undertook four replicated surveys for each transect during two
185 sampling years. In each survey, at least two trained observers walked the transect at a
186 constant speed (1–2 km/h depending on the terrain) while maintaining the overall
187 surveying time of around 1.5 hours to make the sampling efforts comparable. The
188 observers recorded the number of individuals of all bird species seen or heard within a
189 50 m distance on both sides of the transect. Surveys ran from half an hour after dawn

190 to 11:00 h, and from 15:00 h to half an hour before sunset. We did not conduct
191 surveys when it was rainy or windy.

192 All bird species recorded were native species (*i.e.*, there are no introduced
193 species in the study region). This study only considered breeding birds (resident and
194 summer species) that mainly use terrestrial habitats on islands, excluding species that
195 rely on aquatic habitats (*e.g.*, diving birds, ducks, and gulls) or are only active at night
196 (*i.e.*, *Caprimulgus indicus*) (electronic supplementary material, table S2).

197

198 **2.3 Land-use types along each transect**

199 To assess the land-use types along each transect, we utilized the WorldCover 2021
200 v200 product (<https://esa-worldcover.org/en>), which provides land-use information at
201 a resolution of 10 m worldwide. The product includes 11 primary land-use classes and
202 has an overall accuracy of 76.7% based on the validation report [45]. While our
203 primary focus was on forest and farmland habitats, we also recognized the
204 significance of human settlements as habitats for certain species, such as the barn
205 swallow (*Hirundo rustica*) and red-rumped swallow (*Hirundo daurica*) on the study
206 islands. Therefore, we selected three land-use types to represent the transect habitat
207 composition: farmland, forest, and settlements. These three land-use types accounted
208 for nearly 87% of the total land-use cover across the 70 transects. We manually
209 checked and corrected the land-use type along each transect based on Google Earth

210 and field observations, where necessary (electronic supplementary material, figure
211 S1).

212 To calculate the percentage cover of the three land-use types, we chose a 50-m
213 buffer area. This buffer area was selected because we recorded bird observations
214 within a 50 m distance on both sides of the transect. Note that we have also calculated
215 the land-use cover using 100-m and 200-m buffer areas, and the results were
216 qualitatively similar (electronic supplementary material, tables S3–S5). Therefore, for
217 the subsequent analyses, we used the results obtained from 50-m buffer areas. We did
218 not consider larger buffer areas as the study was conducted on islands – including
219 many small islands – and using larger buffers would often result in the inclusion of
220 large areas of water.

221

222 **2.4 Species traits and phylogeny**

223 For each species, we sourced data on body length, body mass, bill length, wing
224 length, tail length, and tarsus length from a bird trait dataset specific to China [46].
225 The traits we chose are highly associated with birds' ecological niches (*i.e.*, diets and
226 behaviours) [47] (See electronic supplementary material, text S1 for more details on
227 the choice of traits and sources). Before conducting the analyses, we \log_{10} -
228 transformed body mass to stabilize the variance and to normalize the distribution [48].
229 Bill length, wing length, tail length, and tarsus length were divided by body length to
230 ensure these trait values are independent of body size [49] (electronic supplementary

231 material, table S6). Because body mass and body length were highly correlated
232 (Pearson's $r = 0.92$, $p < 0.001$), we excluded body length from the analyses.

233 We then built a functional dendrogram using a modified version of neighbor-
234 joining clustering [50] based on a Gower dissimilarity distance matrix of the five
235 morphological traits (scaled and centered). This clustering method minimizes
236 functional space distortion [51], and we observed that the functional dendrogram
237 provided a high quality representation of the distances between species in the Gower
238 dissimilarity distance matrix (0.98, measured by the standardised inverse of mean
239 squared deviation [52], with 1 representing the maximum quality). The functional
240 dendrogram was built using the *tree.build* function in the 'BAT' package [53].

241 To obtain an avian phylogeny, we downloaded 5,000 posterior phylogenetic
242 trees under the option of 'Hackett All Species: a set of 10,000 trees with 9,993 OTUs
243 each' from BirdTree (<http://birdtree.org>) [54], including only the species recorded in
244 our study. We then constructed a maximum clade credibility tree across 5,000
245 pseudo-posterior samples using the software TreeAnnotator v1.8.2 [55]. The
246 resulting consensus tree was used for subsequent phylogenetic analyses.

247

248 **2.5 Sampling completeness and phylogenetic signal**

249 Before undertaking statistical analyses, we tested the sampling completeness of each
250 transect based on the species presence/absence matrix derived from four replicated
251 surveys. The sampling completeness was calculated using the *iNEXT* function in the

252 'iNEXT' package [56]. Most transects had relatively high sampling completeness,
253 with the exception of a single small island (S33, 64%; electronic supplementary
254 material, table S1).

255 We estimated the phylogenetic signal of species traits (*i.e.*, body mass, relative
256 bill length, relative wing length, relative tail length, and relative tarsus length) with
257 Blomberg's K [57] and Pagel's λ [58] using the *phylosig* function in the 'phytools'
258 package [59]. All morphological traits had significant phylogenetic signals ($p <$
259 0.001 ; electronic supplementary material, table S7), indicating that the selected traits
260 are phylogenetically conserved.

261

262 **2.6 Metrics of bird richness and community structure**

263 We first calculated the number of species (species richness, SR) along each transect.
264 To estimate phylogenetic community structure, we used the standardized effect size
265 (SES) of mean pairwise phylogenetic distance (MPD), denoted as SES.MPD, which
266 represents the phylogenetic relatedness of species within an assemblage [28].

267 Similarly, for functional community structure, we calculated the standardized effect
268 size (SES) of mean pairwise functional distance (MFD), denoted as SES.MFD [60].

269 MPD and MFD were calculated using our maximum clade credibility
270 phylogenetic tree and functional dendrogram, respectively. The values of SES.MPD
271 and SES.MFD were calculated using the 'shuffling tip' null model approach. This
272 null model randomly shuffled the taxa labels of each phylogenetic tree or functional

273 dendrogram (*i.e.*, the species pool of the null model was the archipelago species list,
274 see also below) while retaining the structure of the community data [61]. We ran the
275 null model 999 times and recalculated the MPD and MFD of each randomised
276 community. The equation of SES is:

$$277 \quad \text{SES} = (\text{Obs} - \text{Mean}_{\text{null}}) / \text{SD}_{\text{null}},$$

278 where Obs is the observed MPD or MFD on each transect, and Mean_{null} and SD_{null} are
279 the mean and standard deviation values of 999 randomisations for the MPD and MFD
280 of each transect.

281 SES.MPD and SES.MFD measure species relatedness in the observed
282 community compared to species randomly sampled from the species pool.
283 Specifically, SES values of MPD and MFD < 0 suggest phylogenetic or functional
284 clustering (species share similar traits or evolutionary histories), SES values > 0
285 suggest phylogenetic or functional overdispersion (species share distinct traits or
286 evolutionary histories), and SES values ≈ 0 indicate a random phylogenetic or
287 functional community structure [28]. SES values less than -1.96 or greater than 1.96
288 indicate significant clustering or overdispersion, respectively ($\alpha = 0.05$). The
289 SES.MPD and SES.MFD metrics were calculated using the *ses.mpd* function in
290 'picante' package [62].

291 During our sampling, we found several species that occurred on all islands (*e.g.*,
292 light-vented bulbul [*Pycnonotus sinensis*]). Thus, based on the concept of dispersion-
293 field species pools [63], we considered the species pool to comprise all species that

294 were observed on the study islands. However, we recognise that the selection of a
295 specific species pool could potentially affect the community structure results [64]. To
296 confirm the robustness of our results, we ran additional analyses where we expanded
297 the species pool by incorporating bird species occurring on (i) the study islands but
298 that were not sampled by us, and (ii) the surrounding mainland, based on a citizen
299 bird surveying database (*i.e.*, China Bird Report; <http://www.birdreport.cn/>), and in
300 both cases recalculated the community structure metrics. We found that the results
301 based on the different species pools are qualitatively the same. We thus only report in
302 the main manuscript the findings from the analyses including all observed species
303 from the study islands as the species pool. Please see electronic supplementary
304 material, text S2 for more information about the results from analyses of alternative
305 species pools.

306

307 **2.7 Statistical analyses**

308 Our study was conducted at the transect level (*i.e.*, the unit of analysis is a transect),
309 so we applied linear mixed-effect regression models (LMM), with island identity as a
310 random effect (*i.e.*, random intercept), to regress bird richness and community
311 structure per transect against the fixed effects using the *lmer* function in the ‘lme4’
312 package [65]. To test if bird richness and community structure follow the predictions
313 of the Equilibrium Theory of Island Biogeography, we used either island area or
314 isolation as the fixed effect in the LMM. In a separate model, we used the percentage

315 cover of each land-use type (forest, farmland, and settlement) as a fixed effect to test
316 the bivariate relationships between bird richness and community structure and land-
317 use type. Finally, to test if there are any interactive effects of land-use change and
318 island attributes on bird richness and community structure, we fitted a model with
319 island area/isolation and the percentage cover of each land-use type, including an
320 interaction term between island area/isolation and each land-use type (*e.g.*, island area
321 \times farmland cover). Note we also conducted analyses using multivariate models (*i.e.*,
322 models contain island area, isolation, the percentage cover of forest, farmland, and
323 settlement, as well as the interaction term between island area/isolation and each land-
324 use type as fixed effect) and the results are qualitatively the same as univariate models
325 described above (see electronic supplementary material, text 3 and tables S8–S11).
326 We thus put the results based on multivariate models into the supplementary material
327 and only reported the results based on univariate models in the main text. Island area
328 was \log_{10} -transformed to normalize model residuals. There were only weak
329 correlations between the percentage cover of each land-use type and island area or
330 isolation ($|\text{Pearson's } r| < 0.4$; electronic supplementary material, table S12). Model
331 residual assumptions were visually checked, and the residuals met the assumptions of
332 linear models. All analyses were conducted in R version 4.1.2 [66].

333

334 **3. Results**

335 **3.1 Effect of island area, isolation, and land-use types on species richness**

336 Consistent with the predictions of the Equilibrium Theory of Island Biogeography,
337 transect-level species richness (SR) significantly increased with island area ($t = 3.22$,
338 $df = 24.6$, $p < 0.01$; figure 3a) and decreased with isolation ($t = -6.33$, $df = 68$, $p <$
339 0.001 ; figure 3b), according to our LMMs. We note, however, the effect of island area
340 on SR could be partially explained by the transect length (*i.e.*, sampling effect) as we
341 also found transect length had a positive effect on SR (please see electronic
342 supplementary material, text S3 for more details).

343 In addition, transect-level SR had significant relationships with the three land-
344 use types (electronic supplementary material, table S13). Specifically, SR increased
345 with increasing farmland cover ($t = 4.4$, $df = 41.5$, $p < 0.001$; figure 3c) and settlement
346 cover ($t = 3.51$, $df = 46$, $p < 0.01$; figure 3d), but decreased with increasing forest
347 cover ($t = -4.63$, $df = 41.9$, $p < 0.001$; figure 3e). However, the land-use type did not
348 affect SR–area and –isolation relationships as we did not find any interactive effects
349 of island area (or isolation) and the percentage cover of each land-use type (electronic
350 supplementary material, figures S2 and S3, table S14). In general, SR was higher in
351 farmland-dominated habitats than in forest-dominated habitats (electronic
352 supplementary material, figure S4a).

353

354 **3.2 Effects of island area, isolation, and land-use types on bird phylogenetic and**
355 **functional community structure**

356 The overall phylogenetic and functional community structure (SES.MPD and
357 SES.MFD) was more clustered than expected by chance in most transects (figure 4),
358 indicating that phylogenetic and functional clustering of bird assemblages on all study
359 islands was pervasive. Community structure in farmland-dominated transects was less
360 clustered than forest-dominated transects (electronic supplementary material, figure
361 S4b). SES.MPD and SES.MFD did not vary systematically with island area and
362 isolation (electronic supplementary material, table S13), but they both increased with
363 increasing farmland cover (SES.MPD: $t = 4.39$, $df = 47.3$, $p < 0.001$; SES.MFD: $t =$
364 3.47 , $df = 66.6$, $p < 0.001$; electronic supplementary material, figure S5c) and
365 settlement cover (SES.MPD: $t = 2$, $df = 57.4$, $p = 0.05$; SES.MFD: $t = 1.78$, $df = 68$, p
366 $= 0.08$; electronic supplementary material, figure S5e), and decreased with increasing
367 forest cover (SES.MPD: $t = -3.78$, $df = 42.8$, $p < 0.001$; SES.MFD: $t = -2.96$, $df = 61$,
368 $p < 0.01$; electronic supplementary material, figure S5d).

369 Furthermore, SES.MFD was affected by the interactive effect of island area and
370 farmland cover ($t = 2.17$, $df = 65$, $p = 0.03$; electronic supplementary material, table
371 S14). Transects with a larger proportion of farmland on larger islands and transects
372 with less farmland cover on smaller islands tended to support bird assemblages with
373 less clustered functional structure (figure 4e). Additionally, the patterns of bird
374 phylogenetic and functional community structure (*i.e.*, SES.MPD and SES.MFD)
375 showed similar trends along the interactive gradient of area and isolation with forest
376 cover (island area x forest cover for SES.MPD: $t = -2.8$, $df = 65.6$, $p < 0.01$, for

377 SES.MFD: $t = -2.8$, $df = 64.6$, $p < 0.01$; isolation x forest cover for SES.MPD: $t =$
378 2.92 , $df = 58.5$, $p < 0.01$, for SES.MFD: $t = 2.25$, $df = 63.7$, $p = 0.03$; electronic
379 supplementary material, table S14). This indicates clustered community structure in
380 transects on large and close islands with a high proportion of forest cover, as well as
381 clustered community structure on small and remote islands with a low proportion of
382 forest cover (figure 4c, 4d, 4g, and 4h; electronic supplementary material, figures S6b,
383 S6e, S7b, and S7e). Settlement cover did not exhibit an interactive effect with island
384 attributes on bird community structure (electronic supplementary material, figures
385 S6c, S6f, S7c, and S7f, table S14).

386

387 **4 Discussion**

388 Human activities have extensively modified habitats on 75% of the global land
389 surface, including many islands worldwide. However, assessing the impact of land-
390 use change on islands presents challenges as it is generally unclear whether there are
391 interactive effects between land-use change and natural island attributes (*e.g.*, area
392 and isolation) on the diversity and community assembly of island faunas. To answer
393 this question, we undertook sampling across multiple habitats on islands within the
394 largest Chinese archipelago.

395 We found that both the phylogenetic and functional structure (SES.MPD and
396 SES.MFD) of island bird assemblages were clustered relative to random assemblages.
397 Specifically, bird assemblages in farmland-dominated habitats tended to be more

398 phylogenetically and functionally clustered on small islands. In contrast, forest bird
399 assemblages were more clustered on large islands and islands close to the mainland.
400 These results suggest that there is indeed an interaction between land-use change and
401 classic island biogeographic variables in shaping bird community assembly.

402

403 **4.1 Variations in species richness across island attributes and land-use types**

404 We found positive species–area relationships and negative species–isolation
405 relationships in this study (figure 3a; electronic supplementary material, text S4 and
406 figure S8a, S8b). The positive species–area relationship is well-studied: larger islands
407 harbour more species as they support larger populations and contain more diverse
408 habitat types, a greater number of habitats, and more diverse resources [67,68]. This
409 near-universal pattern has been observed in butterflies [69], frogs [70], and bryophyte
410 [71] species in the same island system.

411 Dispersal limitation may be a driver of the negative species–isolation
412 relationships observed (see also [44] for a more comprehensive measures of isolation
413 in examining dispersal limitation in the same archipelago). Although most bird
414 species (especially the summer migrants; electronic supplementary material, table S2)
415 can fly over open water, some species are seemingly unwilling to due to a natural fear
416 of water [72]. For example, two summer migrants with good dispersal ability, the
417 black bulbul (*Hypsipetes leucocephalus*) and Swinhoe's minivet (*Pericrocotus*
418 *cantonensis*), are distributed widely across most of the study islands but do not occur

419 on several remote islands with a distance > 65 km from the mainland. Additionally,
420 extended analysis showed that remote islands possess bird species with higher
421 average dispersal abilities (measured by the hand-wing index, see electronic
422 supplementary material, text S5 and figure S9b for more details). Taken together,
423 these results indicate that a ‘landscape of fear’ and/or limited dispersal ability may
424 restrict the distribution of some species during the breeding season in our study
425 system [30].

426 Surprisingly, bird species richness was relatively high in transects dominated by
427 farmland, despite the fact that there are more bird species preferring forest habitats
428 [41 of 96 species] than farmland habitats [27 of 96 species] (electronic supplementary
429 material, table S2). We also found bird species richness increased with the proportion
430 of human-modified habitats (*i.e.*, farmland and settlement), while decreasing with
431 increasing forest cover. These findings contrast with studies conducted on mainland
432 areas, where forests should typically have more species than surrounding agricultural
433 lands [21,73]. Several reasons may explain these patterns. (a) On inhabited islands,
434 the resources in farmland and settlements (*e.g.*, food and nesting substrate) may be
435 abundant and relatively easy to access for certain species. Thus, many species may be
436 able to utilize the human-modified habitats, leading to higher species richness in sites
437 with a greater coverage of farmland and settlements. In this study, many species
438 disproportionately occur in farmland-dominated habitats, including common moorhen
439 [*Gallinula chloropus*], scaly-breasted munia [*Lonchura punctulata*], and intermediate

440 egret [*Mesophoyx intermedia*] — all species that are known to associate strongly
441 with agricultural habitats [73] (electronic supplementary material, table S2, figures
442 S10 and S11). (b) Although we found more forest bird species in our study islands
443 (electronic supplementary material, table S2), bird species in forest-dominated
444 habitats have lower average dispersal ability (electronic supplementary material,
445 figure S9d), indicating that forest species tend to be more dispersal limited. In
446 contrast, bird species in farmland habitats had higher average dispersal ability
447 (electronic supplementary material, figure S9c), indicating that bird species in
448 farmland have better abilities to disperse between habitat patches, and in turn lead to
449 higher observed richness. (c) Alternatively, it is also possible that forests are
450 important for birds to roost at night, but our surveys were only conducted in the
451 daytime, ignoring this function forests provide.

452

453 **4.2 Bird phylogenetic and functional community structure across island**

454 **attributes and land-use types**

455 Phylogenetic and functional community structure (*i.e.*, SES.MPD and SES.MFD) was
456 clustered on almost all islands, indicating the possibility that environmental filtering
457 is an important assembly process in the archipelago [27]. However, unlike species
458 richness, bird community structure did not show clear patterns along the gradients of
459 island area and isolation, indicating increasing phylogenetic and functional
460 redundancy with increasing species richness. In other words, the higher species

461 richness of bird assemblages on large and close islands does not involve the addition
462 of extra functional roles.

463 As shown above, we found that there was an interaction between the structure–
464 area and –isolation relationships and land-use types. Specifically, bird assemblages in
465 farmland-dominated habitats on small islands were more phylogenetically and
466 functionally clustered than larger ones, consistent with our prediction (figures 1c, 4a,
467 and 4e; electronic supplementary material, figures S6a and S7a). Farmland on small
468 islands often contains limited types of crops. For example, on island S31, the crops
469 are mainly vegetables that are sparsely cultivated by local farmers (electronic
470 supplementary material, figure S12). As a result, only disturbance-tolerant bird
471 species can persist in such habitats. Indeed, we found species on this transect are all
472 passerines, and several common (*i.e.*, present on other farmland habitats) but
473 functionally and phylogenetically distinct species in this region were lacking, such as
474 cattle egret (*Bubulcus ibis*) and Chinese pond heron (*Ardeola bacchus*) (electronic
475 supplementary material, figures S10 and S11), resulting in a highly redundant
476 community [36]. Conversely, farmland on large islands may have higher net primary
477 productivity due to more diverse agricultures and more intensive management
478 [74,75]. The greater niche opportunities provided by farmland on large islands not
479 only support more species, but also support species with a broader range of life-
480 history traits [76], leading to less clustered structure.

481 Contrary to our expectation, assemblages in forest-dominated habitats were more
482 clustered on large and close islands, and we observed a positive functional and
483 phylogenetic clustering–area relationship on islands covered by forest (figures 4c and
484 4g). A possible explanation is that, on large islands, while the amount of total forested
485 area is often relatively large, vegetation composition is similar (electronic
486 supplementary material, figure S13) and often fragmented, separated by roads,
487 villages, and farmland [37,38]. This fragmented forest mosaic is likely only able to
488 support a set of phylogenetically and functionally similar species that are able to
489 persist in these conditions (*i.e.*, high species turnover but low phylogenetic and
490 functional turnover) [26], leading to high clustering on forest transects on large
491 islands.

492 The relationship between bird community structure in forest-dominated habitats
493 and isolation is broadly consistent (*i.e.*, decreasing clustering with increasing isolation).
494 In this study, forest-dominated habitats on remote islands contain several species that
495 are functionally and phylogenetically distinct from other species (electronic
496 supplementary material, figures S8 and S9), such as Eurasian hoopoe (*Upupa epops*),
497 Chinese pond heron (*A. bacchus*), cattle egret (*B. ibis*), and yellow bittern (*Ixobrychus*
498 *sinensis*). Most of these species are summer migrants and are known to be able to persist
499 in farmland habitats with shallow water [73]. We argue that they may preferentially
500 inhabit more remote islands to avoid the intense human disturbance and exploit food
501 resources in more pristine forests. It is worth noting that these species have relatively

502 long bills which may facilitate capturing mobile prey (*e.g.*, insects and reptiles) in forest
503 habitats [77]. In addition, some individuals may travel to islands close to the mainland
504 where they prefer to look for external food resources supplemented by farmland.
505 Consequently, only forest habitats on less isolated islands lack these distinct species,
506 resulting in a relatively high clustering pattern.

507

508 **4.3 Conservation implications**

509 We found that farmland-dominated habitats support more species than forest-
510 dominated habitats on the study islands (electronic supplementary material, figure
511 S4). The importance of agricultural land in supporting substantial biodiversity in
512 fragmented landscapes on the mainland [12,78,79] is a key component of the
513 framework of countryside biogeography. Here, we moved a step further to identify
514 that farmland habitats also support high bird diversity on islands in our study system,
515 providing evidence that species can tolerate or thrive in insular human-modified
516 habitats [80]. Countryside island biogeography can thus provide valuable perspectives
517 for the conservation of island biodiversity, particularly on islands with large amounts
518 of human-modified habitats [81]. Importantly, we found that the effect of farmland
519 depends on the relative proportion of various land-use types, as well as the size of a
520 particular island. Birds in farmland-dominated habitats have relatively less clustered
521 structure on large islands than in forest-dominated habitats and vice versa (figures 4a,
522 4c, 4e, and 4g). Meanwhile, forest-dominated habitats on remote islands also have

523 relatively less clustered bird assemblages (figures 4d and 4h). Thus, concerning
524 further anthropogenic development on the islands studied here, we argue that it is
525 better to leave small and remote islands – where the remaining natural forest habitat
526 can support relatively higher biodiversity – undeveloped.

527

528 **4.4 Caveats**

529 Our study is limited by the uneven sampling design across islands, necessitated by
530 logistical restrictions related to small island size. Although we conducted additional
531 analyses to account for this sampling effect (see electronic supplementary material,
532 text S3), our results should still be interpreted with caution as we cannot fully exclude
533 the sampling effect in the analyses. Additionally, our use of continuous proportional
534 land-use variables inherently produces collinearity issues (*e.g.*, forest and farmland
535 covers were negatively correlated: Pearson's $r = -0.86$). The existence of collinearity
536 issues results in the difficulty of interpreting the effect of cover type because an
537 observed effect of increasing farmland could actually be an effect of decreasing forest
538 cover, and vice versa. An alternative way to solve the collinearity issue is to use
539 categorical land-use variables (*i.e.*, designating transects as forest or farmland).
540 However, categorical land-use variables will loss detailed information, such as the
541 pattern of community structure shifting along a gradient of forest/farmland cover (as
542 shown in Figure 4). We suggest that further studies should pinpoint the location of

543 each bird record and measure point-based land uses to fully tease apart the precise
544 effects of land-use types in this system.

545 The lower richness and clustered structure of bird communities in forest-
546 dominated habitats could also relate to the legacy effect associated with historical
547 landscape configurations [82,83]. Unfortunately, suitable historical land-use data were
548 unavailable to investigate this phenomenon. However, legacy effects in our study
549 archipelago should be relatively weak for several reasons. First, land-use change on
550 the study islands has a long history (~5,000 years), indicating contemporary
551 communities have had considerable time to respond to past modifications. Second, the
552 larger number of forest species in the species pool, including the pools that
553 incorporated nearby mainland species (electronic supplementary material, tables S2
554 and S15), indicates that historic human activities have not substantially restricted
555 these taxa from occupying study islands.

556

557 **5 Conclusion**

558 Our results emphasize the need to better understand how anthropogenic effects and
559 standard island biogeographic variables interact to determine community assembly
560 mechanisms in human-dominated island landscapes. Although the relationship between
561 species richness and island area and isolation remained consistent across land use types,
562 functional and phylogenetic community structure (measured by SES.MPD and
563 SES.MFD) were higher in farmland-dominated habitats on large islands, illustrating the

564 importance of farmland in sustaining island bird diversity. Examining the interactive
565 effect of land-use and island attributes, a novel frontier in countryside island
566 biogeography, provides a promising research avenue to better understand the
567 distribution of island biodiversity across human-dominated ecosystems, ultimately
568 enabling more accurate predictions of the future trajectory of biodiversity in the
569 Anthropocene.

570

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577

578 **Competing Interest Statement:** The authors declare no conflict of interest.

579

580 **Data availability:** The data used in this study have been uploaded on Dryad (link:
581 [https://datadryad.org/stash/share/38izdimqLPECiQW5Kd42Ct7aF6AzslwHx27JLF6b](https://datadryad.org/stash/share/38izdimqLPECiQW5Kd42Ct7aF6AzslwHx27JLF6bmUw)
582 [mUw](https://datadryad.org/stash/share/38izdimqLPECiQW5Kd42Ct7aF6AzslwHx27JLF6bmUw)).

583

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