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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

1. Introduction

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

The Equilibrium Theory of Island Biogeography (hereafter ETIB) postulates that larger islands have lower extinction rates (*i.e.,* area effect) and more remote islands have lower colonization rates (*i.e.,* distance effect) [10], resulting in the positive species–area and negative species–isolation relationships. In contrast to ETIB, which is generally discussed in the context of biodiversity in natural habitats, countryside biogeography highlights the importance of human-dominated landscapes (*e.g.*, farmland habitats) in supporting biodiversity [11,12]. Linking countryside biogeography and island biogeography thus provides an alternative framework, namely countryside island biogeography, which can be used to frame conservation science in human-dominated landscapes on inhabited islands [13,14]. To date, few 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 km^2 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 TreeAnnonator 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    $$SES = (Obs - Mean_{null})/SD_{null},$$

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　× 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 (|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 (*Ixobrycus*

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

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

582 mUw).

583

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