

Research



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

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

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.

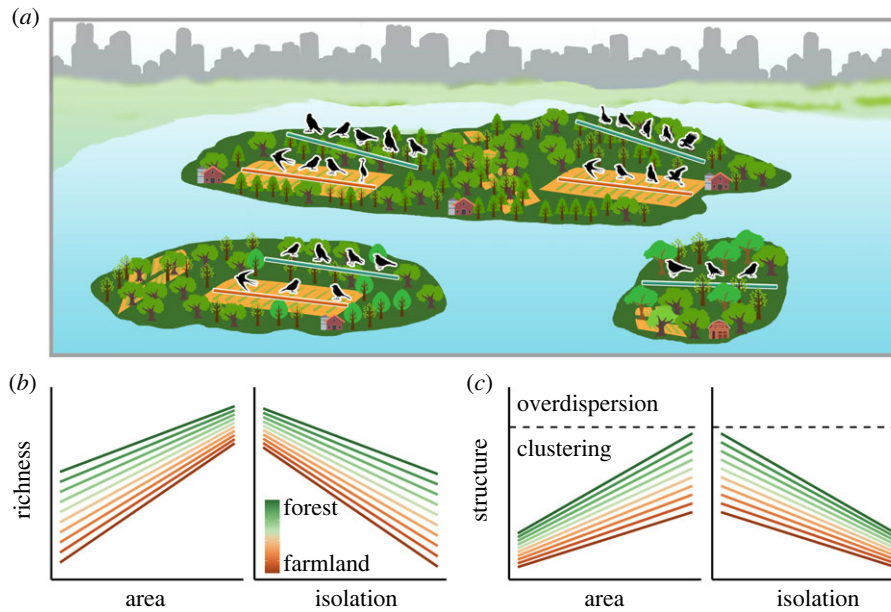


Figure 1. The framework of countryside island biogeography illustrating the predicted relationships between bird richness and community structure in habitats (i.e. transects in our study) dominated by forest or farmland on islands of various sizes and degrees of isolation. (a) Inhabited islands of different areas, where green and brown lines indicate survey transects running through forest-dominated and farmland-dominated habitats. Birds and land-use types are illustrated. (b) We predict an interactive effect between land-use types and island attributes (i.e. area and isolation) and expect smaller intercepts and steeper slopes of species–area and –isolation relationships for assemblages in farmland-dominated habitats compared to assemblages in forest-dominated habitats. (c) Farmland assemblages will tend to be more functionally and phylogenetically clustered compared to forest assemblages, and we expect flat structure–area and –isolation relationships for farmland assemblages due to functional and phylogenetic redundancy. Colours in (b) and (c) represent the relative proportion of forest habitats (towards green meaning that the sites are increasingly covered by forest) and farmland (towards brown meaning that the sites are increasingly covered by farmland) along transects. See §1 for detailed hypotheses and methods relating to the calculation of functional and phylogenetic community structure.

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

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

Clarifying the processes and mechanisms underpinning community assembly is key to understanding the maintenance of biodiversity [22]. Researchers have recently incorporated species traits and evolutionary histories into the ETIB to try to better understand community assembly processes on islands [23,24]. Suppose that species with strong dispersal abilities are more likely to successfully colonize islands and/or that their subsequent probability of survival is related to specific habitat availability on different islands (e.g. the availability of mature trees on islands is essential for tree-roosting species). Under these circumstances, relative to a larger species pool, insular assemblages will comprise a subset of species that share similar functional traits (i.e. functional clustering) [25,26] that confer a survival advantage in specific insular environments [27]. If these traits are phylogenetically conserved, which is generally common [28], insular assemblages will also comprise groups of species that are more similar in terms of their evolutionary history than expected (i.e. phylogenetic clustering). A contrasting theoretical prediction is that closely related species that share similar traits or resource requirements are more likely to compete due to the limited resources on (particularly small) islands [29]. In this case, island biotas are expected to comprise species with distinct traits and/or evolutionary histories (i.e. functional and/or phylogenetic overdispersion) [25,26] through competitive exclusion of closely related species. However, empirical studies of various taxa have found that the structure of island assemblages is, in general, phylogenetically and functionally clustered [26,30,31]. Given the presence of severe environmental filters and limited habitat diversity on small

and remote islands—in addition to the increased role of dispersal filtering—one may expect community structure on these types of islands to be even more phylogenetically and functionally clustered [32] (figure 1c). As such, we may expect that community structure patterns will change across island area and isolation gradients (i.e. structure–area and structure–isolation relationships).

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

In this study, we examined whether there are interactive effects of land-use type and island attributes (area and isolation) on bird assemblages in the Zhoushan Archipelago, the largest archipelago in China with more than 1000 continental (oceanic land-bridge) islands. To address this question, we surveyed birds during the breeding season along transects with varying proportions of land-use types (primarily forest and farmland) on 34 islands that span a gradient of island area and isolation in the archipelago. We used these data to test three predictions. 1) The species richness of bird assemblages will increase with island area and decrease with isolation, in accordance with the predictions of the ETIB (figure 1b). 2) The phylogenetic and functional community structure of bird assemblages will be clustered on the study islands, and the degree of clustering will decrease with island area and increase with isolation (figure 1c). 3) There will be an interactive effect of land-use change (i.e. the presence of human-modified habitats) and island biogeographic variables on insular bird richness and community assembly. Specifically, the species–area relationship and species–isolation relationship are expected to be steeper along transects with an increasing proportion of farmland and a decreasing proportion of forest (figure 1b). In addition, birds inhabiting farmland-dominated transects are predicted to be more compositionally similar across islands (i.e. phylogenetic and functional redundancy) compared to those in forest-dominated transects, resulting in flatter structure–area and structure–isolation relationships with increasing farmland cover along a transect (figure 1c).

2. Methods

(a) Study site

Our study is situated in the Zhoushan Archipelago (29°31′–31°04′N, 121°30′–123°25′E), in eastern China (figure 2). The region belongs to the subtropical oceanic monsoon zone, with a strong seasonal climate (i.e. hot summers and cold winters). The average temperature between April to June in 2020 and 2021 (i.e. surveying period) was 20.73°C (data from China Meteorological Administration; <http://lishi.tianqi.com>). The subtropical evergreen broadleaf forest is the dominant vegetation on the islands of the Zhoushan Archipelago, along with coniferous forests, grasslands and shrubs [37,38]. The Zhoushan Archipelago provides an excellent opportunity to test the interactive effects of human land-use and island biophysical characteristics on island community diversity and assembly for a number of reasons. First, archaeological evidence indicates that humans have continuously occupied the archipelago since at least the Neolithic (i.e. 5000 years ago) [39], resulting in complex landscapes (including some agricultural lands) on most islands. The primary agricultural crops cultivated on the islands include rice, maize, sweet potato, oilseed rape, as well as various vegetables and fruits, all of which are patchily distributed within and across islands (<http://zstj.zhoushan.gov.cn/col/col1229615782/index.html>). Second, background information on the region's biota is well-known, given that research on the archipelago has been undertaken since the 1850s [40,41]. Lastly, as the focus is on birds, the effect of evolutionary processes (e.g. *in situ* speciation) can be largely ignored, given the relatively short geological history of the islands being separated from the mainland (about 7000–9000 years).

We selected 34 islands across a gradient of island area and isolation (i.e. island size and the nearest coast-to-coast distance from each island to the mainland), and considering the habitat types present on the islands. In other words, we particularly looked for small and remote islands that have farmland habitats (e.g. island S31, with area = 0.24 km² and isolation = 65.82 km). We calculated island area and isolation using ArcGIS based on a metre-resolution dataset of global coastlines [42] (electronic supplementary material, table S1).

(b) Field survey and bird data

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

We conducted breeding bird surveys along each transect from April to June in 2020 and 2021. During each breeding season, the survey was conducted twice within a one-month interval, which is the maximum effort we could afford in the field [44], so we undertook four replicated surveys for each transect during two sampling years. In each survey, at least two trained observers walked the transect at a constant speed (1–2 km h⁻¹ depending on the terrain) while maintaining the overall surveying time of around 1.5 h to make the sampling efforts comparable. The observers recorded the numbers of individuals of all bird species seen or heard within a 50 m distance on both sides of the transect. Surveys ran from half an hour after dawn to 11:00 h, and from 15:00 h to half an hour before sunset. We did not conduct bird surveys when it was rainy or windy.

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

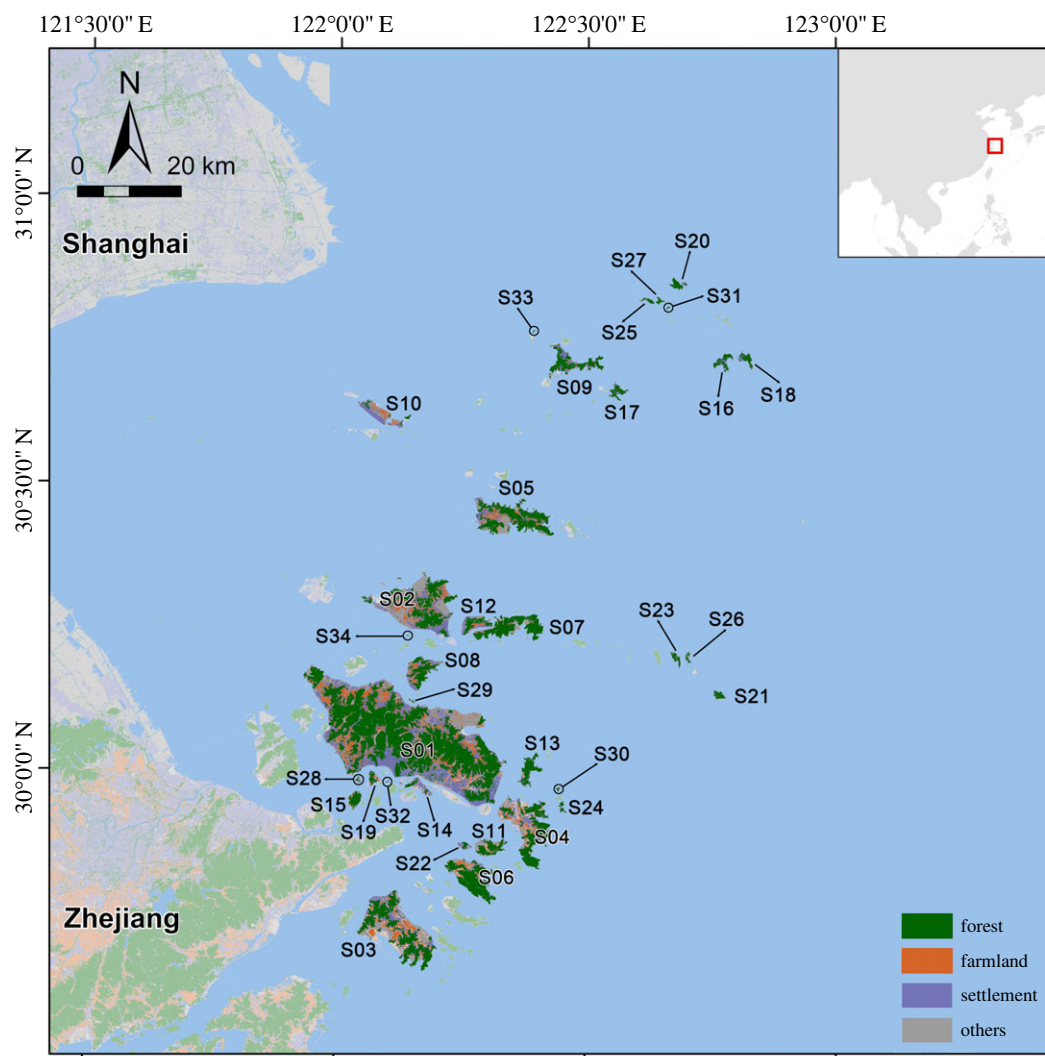


Figure 2. The 34 study islands in the Zhoushan Archipelago, eastern China. The map was derived from the WorldCover 2021 v.200 product (<https://esa-worldcover.org/en>).

(c) Land-use types along each transect

To assess the land-use types along each transect, we used the WorldCover 2021 v.200 product (<https://esa-worldcover.org/en>), which provides land-use information at a resolution of 10 m worldwide. This product includes 11 primary land-use classes and has an overall accuracy of 76.7% based on the validation report [45]. While our primary focus was on forest and farmland habitats, we also recognized the significance of human settlements as habitats for certain species, such as the barn swallow (*Hirundo rustica*) and red-rumped swallow (*Hirundo daurica*) on the study islands. Therefore, we selected three land-use types to represent the transect habitat composition: farmland, forest and settlements. These three land-use types accounted for nearly 87% of the total land-use cover across the 70 transects. We manually checked and corrected the land-use type along each transect based on Google Earth and field observations, where necessary (electronic supplementary material, figure S1).

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

(d) Species traits and phylogeny

For each species, we sourced data on body length, body mass, bill length, wing length, tail length and tarsus length from a bird trait dataset specific to China [46]. The traits we chose are highly associated with birds' ecological niches (i.e. diets and behaviours) [47] (see electronic supplementary material, text S1 for more details on the choice of traits and sources). Before conducting the analyses, we \log_{10} -transformed body mass to stabilize the variance and to normalize the distribution [48]. Bill length, wing length, tail length and tarsus length were divided by body length to ensure that these trait values are independent of body size [49] (electronic supplementary material, table S6). Because body mass and body length were highly correlated (Pearson's $r = 0.92$, $p < 0.001$), we excluded body length from the analyses.

We then built a functional dendrogram using a modified version of neighbour-joining clustering [50] based on a Gower dissimilarity distance matrix of the five morphological traits (scaled and centred). This clustering method minimizes functional space distortion [51] and we observed that the functional dendrogram provided a high-quality representation of the distances between species in the

Gower dissimilarity distance matrix (0.98, measured by the standardized inverse of mean squared deviation [52], with 1 representing the maximum quality). The functional dendrogram was built using the *tree.build* function in the 'BAT' package [53].

To obtain an avian phylogeny, we downloaded 5000 posterior phylogenetic trees under the option of 'Hackett All Species: a set of 10 000 trees with 9993 OTUs each' from BirdTree (<http://birdtree.org>) [54], including only the species recorded in our study. We then constructed a maximum clade credibility tree across 5000 pseudo-posterior samples using the software TreeAnnotator v.1.8.2 [55]. The resulting consensus tree was used for subsequent phylogenetic analyses.

(e) Sampling completeness and phylogenetic signal

Before undertaking statistical analyses, we tested the sampling completeness of each transect based on the species presence/absence matrix derived from four replicated surveys. The sampling completeness was calculated using the *iNEXT* function in the 'iNEXT' package [56]. Most transects had relatively high sampling completeness, with the exception of a single small island (S33, 64%; electronic supplementary material, table S1).

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

(f) Metrics of bird richness and community structure

We first calculated the number of species (species richness, SR) along each transect. To estimate phylogenetic community structure, we used the standardized effect size (SES) of mean pairwise phylogenetic distance (MPD), denoted as SES.MPD, which represents the phylogenetic relatedness of species within an assemblage [28]. Similarly, for functional community structure, we calculated the SES of mean pairwise functional distance (MFD), denoted as SES.MFD [60].

MPD and MFD were calculated using our maximum clade credibility phylogenetic tree and functional dendrogram, respectively. The values of SES.MPD and SES.MFD were calculated using the 'shuffling tip' null model approach. This null model randomly shuffled the taxa labels of each phylogenetic tree or functional dendrogram (i.e. the species pool of the null model was the archipelago species list; see also below) while retaining the structure of the community data [61]. We ran the null model 999 times and recalculated the MPD and MFD of each randomized community. The equation of SES is:

$$SES = \frac{(\text{Obs} - \text{Mean}_{\text{null}})}{SD_{\text{null}}}$$

where Obs is the observed MPD or MFD on each transect and $\text{Mean}_{\text{null}}$ and SD_{null} are the mean and standard deviation values of 999 randomisations for the MPD and MFD of each transect, respectively.

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

During our sampling, we found several species that occurred on all islands (e.g. light-vented bulbul (*Pycnonotus sinensis*)). Thus, based on the concept of dispersion-field species pools [63], we considered the species pool to comprise all species that were observed on the study islands. However, we recognize that the selection of a specific species pool could potentially affect the community structure results [64]. To confirm the robustness of our results, we ran additional analyses where we expanded the species pool by incorporating bird species occurring on (i) the study islands but that were not sampled by us, and (ii) the surrounding mainland, based on a citizen bird surveying database (i.e. China Bird Report; <http://www.birdreport.cn/>), and in both cases we recalculated the community structure metrics. We found that the results based on the different species pools are qualitatively the same. We thus only report in the main manuscript the findings from the analyses including all observed species from the study islands as the species pool. Please see electronic supplementary material, text S2 for more information about the results from the analyses of alternative species pools.

(g) Statistical analyses

Our study was conducted at the transect level (i.e. the unit of analysis is a transect), so we applied linear mixed-effect regression models (LMM), with island identity as a random effect (i.e. random intercept), to regress bird richness and community structure per transect against the fixed effects using the *lmer* function in the 'lme4' package [65]. To test whether bird richness and community structure follow the predictions of the ETIB, we used either island area or isolation as the fixed effect in the LMM. In a separate model, we used the percentage cover of each land-use type (forest, farmland and settlement) as a fixed effect to test the bivariate relationships between bird richness and community structure and land-use type. Finally, to test whether there are any interactive effects of land-use change and island attributes on bird richness and community structure, we fitted a model with island area/isolation and the percentage cover of each land-use type, including an interaction term between island area/isolation and each land-use type (e.g. island area \times farmland cover). Note that we also conducted analyses using multivariate models (i.e. models containing island area, isolation, the percentage cover of forest, farmland, and settlement, as well as the interaction term between island area/isolation and each land-use type as fixed effects) and the results were qualitatively the same as the univariate models described above (see electronic supplementary material, text S3, and tables S8–S11). We thus put the results based on multivariate models into the supplementary material and only report the results based on univariate models in the main text. Island area was \log_{10} -transformed to normalize model residuals. There were only weak correlations between the percentage cover of each land-use type and island area or isolation ($|\text{Pearson's } r| < 0.4$; electronic supplementary material, table S12). Model residual assumptions were visually checked, and the residuals met the assumptions of linear models. All analyses were conducted in R v. 4.1.2 [66].

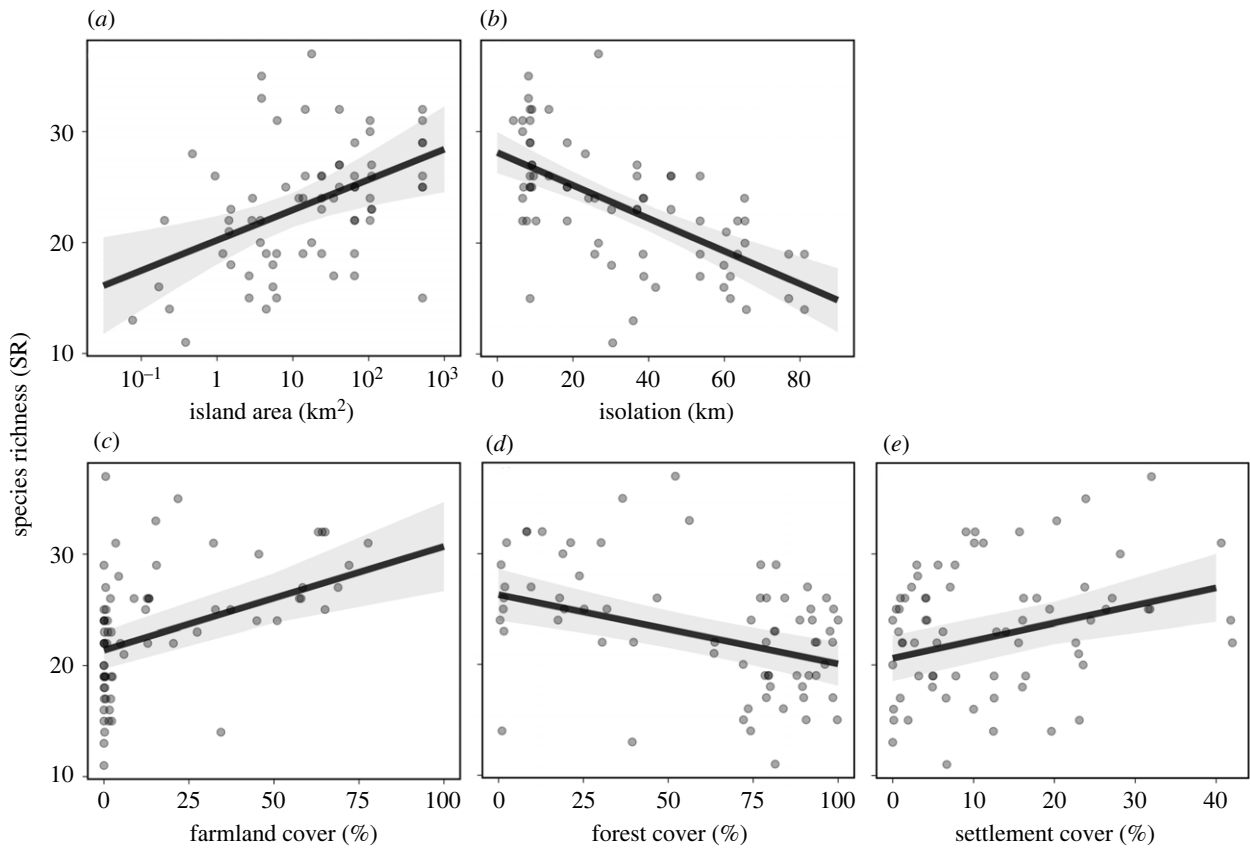


Figure 3. The effects of island area (a), isolation (distance to the mainland) (b), farmland cover (c), forest cover (d) and settlement cover (e) on the species richness (SR) of bird assemblages in 70 transects on 34 islands in the Zhoushan Archipelago, China. The solid lines indicate significant relationships derived from univariate regression models at the significance level of $\alpha = 0.05$. The polygons represent the standard errors.

3. Results

(a) Effect of island area, isolation and land-use types on species richness

Consistent with the predictions of the ETIB, transect-level SR significantly increased with island area ($t = 3.22$, d.f. = 24.6, $p < 0.01$; figure 3a) and decreased with isolation ($t = -6.33$, d.f. = 68, $p < 0.001$; figure 3b), according to our LMMs. We note, however, that the effect of island area on SR could be partially explained by the transect length (i.e. sampling effect) as we also found that transect length had a positive effect on SR (please see electronic supplementary material, text S4 for more details).

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

(b) Effects of island area, isolation and land-use types on bird phylogenetic and functional community structure

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

Furthermore, SES.MFD was affected by the interactive effect of island area and farmland cover ($t = 2.17$, d.f. = 65, $p = 0.03$; electronic supplementary material, table S14). Transects with a larger proportion of farmland on larger islands and transects with less farmland cover on smaller islands tended to support bird assemblages with less clustered functional structure (figure 4e). Additionally, the patterns of bird phylogenetic and functional community structure (i.e. SES.MPD and SES.MFD) showed similar trends along the interactive gradient of area and isolation with forest cover (island area \times forest cover for SES.MPD: $t = -2.8$, d.f. = 65.6, $p < 0.01$, for SES.MFD: $t = -2.8$, d.f. = 64.6, $p < 0.01$; isolation \times forest cover for SES.MPD: $t = 2.92$, d.f. = 58.5, $p < 0.01$, for SES.MFD: $t = 2.25$, d.f. = 63.7, $p = 0.03$; electronic supplementary material, table S14). This indicated clustered community structure

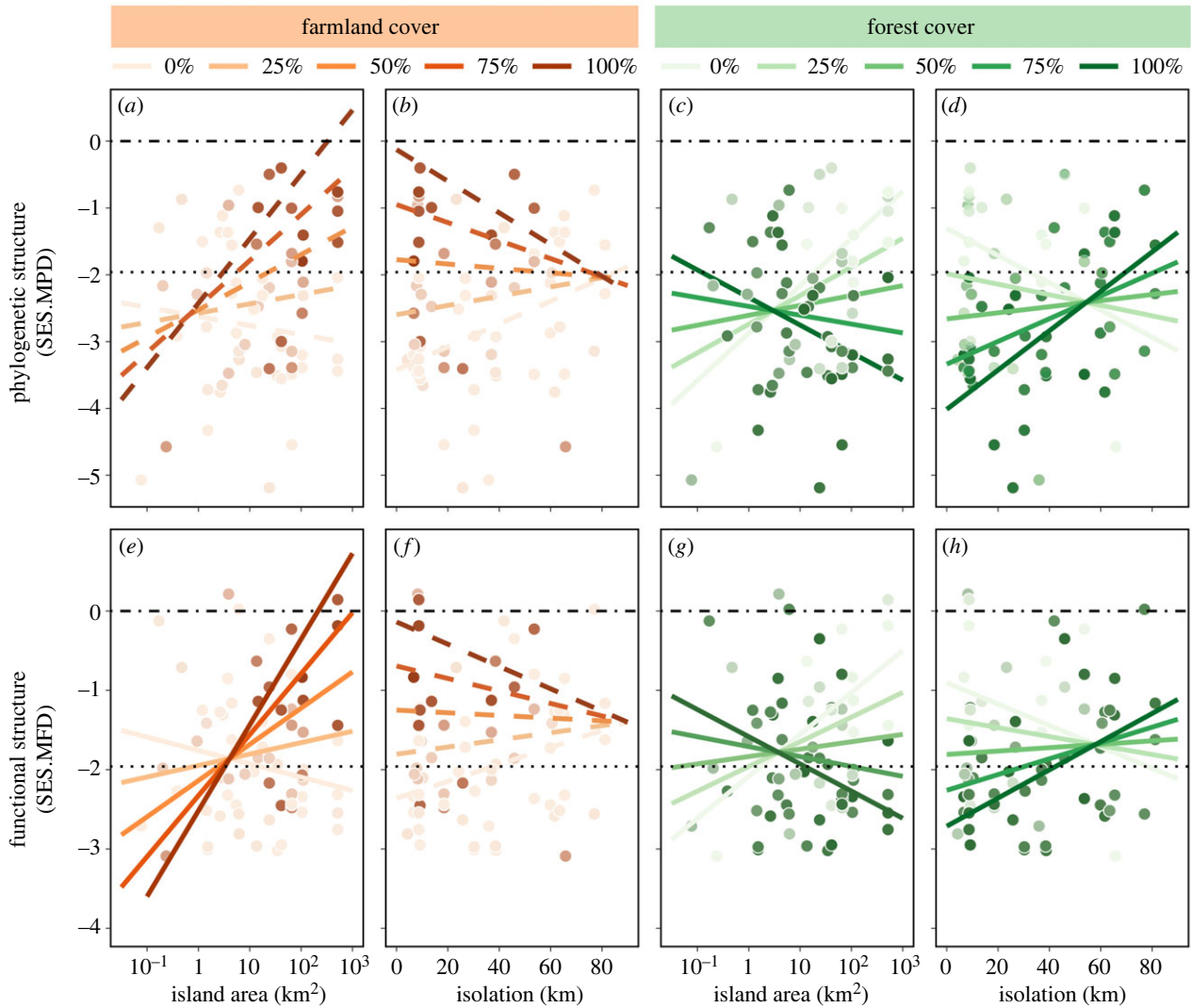


Figure 4. The interactive effects of island attributes (island area (*a, c, e, g*) and isolation (*b, d, f, h*)) and land-use (percentage cover of farmland (*a, b, e, f*) and forest (*c, d, g, h*)) on the phylogenetic and functional structure (i.e. SES.MPD and SES.MFD; the standardized effect size of the mean phylogenetic or functional pairwise distances) of bird assemblages in 70 transects on 34 islands in the Zhoushan Archipelago, China. The solid lines indicate that the effect of the interactive term is significant at the significance level of $\alpha = 0.05$, whereas the dashed lines indicate non-significant relationships. Black dot-dashed and dotted horizontal lines indicate the SES value thresholds of 0 and -1.96 (i.e. significantly clustered structure at $\alpha = 0.05$), respectively. Note that each individual-coloured line in each panel represents the predicted relationships between island area (or isolation) and SES.MPD (or SES.MFD) when the farmland cover (or forest cover) was held at a constant value.

in transects on large and close islands with a high proportion of forest cover, as well as clustered community structure on small and remote islands with a low proportion of forest cover (figure 4*c,d,g* and *h*; electronic supplementary material, figures S6*b, S6e, S7b* and *S7e*). Settlement cover did not exhibit an interactive effect with island attributes on bird community structure (electronic supplementary material, figures S6*c, S6f, S7c* and *S7f*, table S14).

4. Discussion

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

We found that both the phylogenetic and functional structure (SES.MPD and SES.MFD) of island bird assemblages were clustered relative to random assemblages. Specifically, bird assemblages in farmland-dominated habitats tended to be more phylogenetically and functionally clustered on small islands. By contrast, forest bird assemblages were more clustered on large islands and islands close to the mainland. These results suggest that there is indeed an interaction between land-use change and classic island biogeographic variables in shaping bird community assembly.

(a) Variations in species richness across island attributes and land-use types

We found positive species–area relationships and negative species–isolation relationships in this study (figure 3*a*; electronic supplementary material, text S5 and figure S8*a, S8b*). The positive species–area relationship is well-studied: larger islands harbour more species as

they support larger populations and contain more diverse habitat types, a greater number of habitats and more diverse resources [67,68]. This near-universal pattern has been observed in butterflies [69], frogs [70] and bryophyte [71] species in the same island system.

Dispersal limitation may be a driver of the negative species–isolation relationships observed (see also [44] for the use of more comprehensive measures of isolation in examining dispersal limitation in the same archipelago). Although most bird species (especially the summer migrants; table S2) can fly over open water, some species are seemingly unwilling to do this due to a natural fear of water [72]. For example, two summer migrants with good dispersal ability, the black bulbul (*Hypsipetes leucocephalus*) and Swinhoe's minivet (*Pericrocotus cantonensis*), are distributed widely across most of the study islands but do not occur on several remote islands with a distance of over 65 km from the mainland. Additionally, extended analysis showed that remote islands possess bird species with higher average dispersal abilities (measured by the hand–wing index; see electronic supplementary material, text S6 and figure S9b for more details). Taken together, these results indicate that a 'landscape of fear' and/or limited dispersal ability may restrict the distribution of some species during the breeding season in our study system [30].

Surprisingly, bird species richness was relatively high in transects dominated by farmland, despite the fact that there are more bird species preferring forest habitats (41 of 96 species) than farmland habitats (27 of 96 species; see electronic supplementary material, table S2). We also found that bird species richness increased with the proportion of human-modified habitats (i.e. farmland and settlement), while decreasing with increasing forest cover. These findings contrast with studies conducted on mainland areas, where forests should typically have more species than surrounding agricultural lands [21,73]. Several reasons may explain these patterns. (a) On inhabited islands, the resources in farmland and settlements (e.g. food and nesting substrates) may be abundant and relatively easy to access for certain species. Thus, many species may be able to utilize the human-modified habitats, leading to higher species richness in sites with a greater coverage of farmland and settlements. In this study, many species disproportionately occur in farmland-dominated habitats, including common moorhen (*Gallinula chloropus*), scaly-breasted munia (*Lonchura punctulata*) and intermediate egret (*Mesophoyx intermedia*)—all species that are known to associate strongly with agricultural habitats [73] (electronic supplementary material, table S2, figures S10 and S11). (b) Although we found more forest bird species in our study islands (electronic supplementary material, table S2), bird species in forest-dominated habitats have lower average dispersal ability (electronic supplementary material, figure S9d), indicating that forest species tend to be more dispersal-limited. By contrast, bird species in farmland habitats had higher average dispersal ability (electronic supplementary material, figure S9c), indicating that bird species in farmland have better abilities to disperse between habitat patches, which in turn leads to higher observed richness. (c) Alternatively, it is also possible that forests are important for birds to roost at night, but our surveys were only conducted in the daytime, ignoring this function that forests provide.

(b) Bird phylogenetic and functional community structure across island attributes and land-use types

Phylogenetic and functional community structure (i.e. SES.MPD and SES.MFD) were clustered on almost all islands, indicating the possibility that environmental filtering is an important assembly process in the archipelago [27]. However, unlike species richness, bird community structure did not show clear patterns along the gradients of island area and isolation, indicating increasing phylogenetic and functional redundancy with increasing species richness. In other words, the higher species richness of bird assemblages on large and close islands does not involve the addition of extra functional roles.

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

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

The relationship between bird community structure in forest-dominated habitats and isolation is broadly consistent (i.e. decreasing clustering with increasing isolation). In this study, forest-dominated habitats on remote islands contain several species that are functionally and phylogenetically distinct from other species (electronic supplementary material, figures S10 and S11), such as Eurasian hoopoe (*Upupa epops*), Chinese pond heron (*A. bacchus*), cattle egret (*B. ibis*) and yellow bittern (*Ixobrychus sinensis*). Most of these species are summer migrants and are known to be able to persist in farmland habitats with shallow water [73]. We argue that they may preferentially inhabit more remote islands to avoid the intense human disturbance and exploit food resources in more pristine forests. It is worth noting that these species have relatively long bills that may facilitate capturing mobile prey (e.g. insects and reptiles) in forest habitats [77]. In addition, some individuals may travel to islands close to the mainland where they prefer to look for external

food resources supplemented by farmland. Consequently, only forest habitats on less isolated islands lack these distinct species, resulting in a relatively high clustering pattern.

(c) Conservation implications

We found that farmland-dominated habitats support more species than forest-dominated habitats on the study islands (electronic supplementary material, figure S4). The importance of agricultural land in supporting substantial biodiversity in fragmented landscapes on the mainland [12,78,79] is a key component of the framework of countryside biogeography. Here, we moved a step further to identify that farmland habitats also support high bird diversity on islands in our study system, providing evidence that species can tolerate or thrive in insular human-modified habitats [80]. Countryside island biogeography can thus provide valuable perspectives for the conservation of island biodiversity, particularly on islands with large amounts of human-modified habitats [81]. Importantly, we found that the effect of farmland depends on the relative proportion of various land-use types, as well as the size of a particular island. Birds in farmland-dominated habitats have relatively less clustered structure on large islands than in forest-dominated habitats and *vice versa* (figure 4a,c,e,g). Meanwhile, forest-dominated habitats on remote islands also have relatively less clustered bird assemblages (figure 4d,h). Thus, concerning further anthropogenic development on the islands studied here, we argue that it is better to leave small and remote islands where the remaining natural forest habitat can support—relatively higher biodiversity undeveloped.

(d) Caveats

Our study is limited by the uneven sampling design across islands, necessitated by logistical restrictions related to small island size. Although we conducted additional analyses to account for this sampling effect (see electronic supplementary material, text S4), our results should still be interpreted with caution as we cannot fully exclude the sampling effect in the analyses. Additionally, our use of continuous proportional land-use variables inherently produces collinearity issues (e.g. forest and farmland covers were negatively correlated: Pearson's $r = -0.86$). The existence of collinearity issues results in a difficulty in interpreting the effect of cover type because an observed effect of increasing farmland could actually be an effect of decreasing forest cover, and *vice versa*. An alternative way to solve the collinearity issue is to use categorical land-use variables (i.e. designating transects as forest or farmland). However, categorical land-use variables will lose detailed information, such as the pattern of community structure shifting along a gradient of forest/farmland cover (as shown in figure 4). We suggest that further studies should pinpoint the location of each bird record and measure point-based land-use changes to tease apart the precise effects of land-use types in this system.

The lower richness and clustered structure of bird communities in forest-dominated habitats could also relate to the legacy effect associated with historical landscape configurations [82,83]. Unfortunately, suitable historical land-use data were unavailable to investigate this phenomenon. However, legacy effects in our study archipelago should be relatively weak for several reasons. First, land-use change on the study islands has a long history (approx. 5000 years), indicating that contemporary communities have had considerable time to respond to past modifications. Second, the larger number of forest species in the species pool, including the pools that incorporated nearby mainland species (electronic supplementary material, tables S2 and S15), indicates that historic human activities have not substantially restricted these taxa from occupying the study islands.

5. Conclusion

Our results emphasize the need to better understand how anthropogenic effects and standard island biogeographic variables interact to determine community assembly mechanisms in human-dominated island landscapes. Although the relationships between species richness and island area and isolation remained consistent across land-use types, functional and phylogenetic community structure (measured by SES.MPD and SES.MFD) were higher in farmland-dominated habitats on large islands, illustrating the importance of farmland in sustaining island bird diversity. Examining the interactive effect of land use and island attributes, a novel frontier in countryside island biogeography, provides a promising research avenue to better understand the distribution of island biodiversity across human-dominated ecosystems, ultimately enabling more accurate predictions of the future trajectory of biodiversity changes in the Anthropocene.

Ethics. This work did not require ethical approval from a human subject or animal welfare committee.

Data accessibility. The data used in this study can be found on Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.kh18932c5> [84] and the land-use information of each transect is available in the electronic supplementary material [85].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. Y.Z.: conceptualization, data curation, formal analysis, methodology, software, visualization, writing—original draft, writing—review and editing; C.D.M.: methodology, validation, writing—review and editing; T.J.M.: methodology, validation, writing—review and editing; D.W.: data curation, visualization, writing—review and editing; W.L.: data curation, writing—review and editing; X.L.: data curation, methodology, visualization; S.T.: data curation, resources; P.H.: data curation, resources; G.W.: data curation, resources; Y.K.: data curation, resources; C.W.: data curation, methodology, writing—review and editing; R.W.: data curation, methodology, writing—review and editing; D.Z.: data curation, methodology, writing—review and editing; L.O.F.: writing—review and editing; X.S.: conceptualization, data curation, funding acquisition, investigation, methodology, project administration, resources, supervision, validation, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

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