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Research

Severity of deforestation mediates biotic homogenisation in an island archipelago

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Anthropogenic-driven species extinctions are radically changing the biosphere. Biological communities may become increasingly similar to or dissimilar from one another via the processes of biotic homogenisation or heterogenisation. A key question is how the conversion of native forests to agriculture may influence these processes by driving changes in the occurrence patterns of restricted-range endemic species versus wide-ranging generalists. We examined biotic homogenisation and heterogenisation in bird communities on the Southeast Asian islands of Borneo, Sulawesi, Seram, Buru, Talaud and Sangihe. Each island is characterised by high levels of avian endemism and unique spatial configuration of forest conversion to agriculture. Forest conversion to agriculture influenced the patterns of biotic homogenisation on five islands. Bird communities became increasingly dissimilar to forest reference communities relative to localised patterns of deforestation. Turnover led to species with larger global range-sizes dominating communities at the expense of island endemics and ecological specialists. Within islands, forest conversion did not result in clear changes to β -diversity, whereas between-island communities became increasingly similar with greater deforestation, implying that patterns of forest conversion profoundly affect biotic homogenisation. Our findings elucidate how continued conversion of forests is causing the replacement of endemic species by a small cohort of shared ubiquitous species with potentially strong negative consequences for ecosystem functioning and resilience. Halting reorganisation of the biosphere via the loss of range-restricted species and spread of wide-ranging generalists will require improved efforts to reduce the impacts of deforestation, particularly in regions with high endemism.

Keywords: avian biogeography, β -diversity, deforestation, endemism, forest loss, land-use change, Southeast Asia, tropical biodiversity, Wallacea



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Introduction

More than 6.7 million km² of the world's tropical land is used for agriculture (Phalan et al. 2011), with an additional ~3 million km² of forest expected to be converted by 2050 (Busch and Engelmann 2017). These vast and ongoing land-use changes have profound implications for the reorganisation of the biosphere via biotic homogenisation and heterogenisation, whereby biological communities become either increasingly similar to or different from one another, respectively (McKinney and Lockwood 2001, Socolar et al. 2016). Biotic homogenisation erodes the resilience of ecosystems, particularly when accompanied by reductions in diversity or function (Isbell et al. 2015). For example, the homogenisation associated with transition from forest to agricultural ecosystems can be associated with both diminished functional (Carvalho et al. 2013) and phylogenetic (Liang et al. 2019) diversity.

Conflicting patterns of homogenisation and heterogenisation suggest our understanding of the factors underlying these processes is still incomplete. Partial deforestation may increase biotic differentiation at landscape scales when both forest and agricultural habitats are present, due to the distinctiveness of the respective faunal communities (Fermon et al. 2005, Shahabuddin et al. 2005). For instance, in the Brazilian Amazon, arable fields supported greater avian β -diversity than forests due to the infrequent appearance of transient species from adjacent habitats (Solar et al. 2015). Similarly, greater primary forest cover at the landscape scale mitigates β -diversity loss in secondary forest bird communities (Kormann et al. 2018). However, at sufficiently large spatial scales the opposite pattern has also been documented, with bird and arthropod communities exhibiting lower β -diversity within agricultural areas than in forests (Hendrickx et al. 2007, Karp et al. 2012). Understanding how patterns of homogenisation differ with varying spatial, taxonomic, biogeographic and land-use contexts will help us predict how future land-use change is likely to affect the biosphere.

Global patterns of biotic homogenisation are often characterised by the loss of native local species, and the proliferation of broad-ranged generalists associated with novel human-modified habitats (Socolar et al. 2016). This rise of the generalists has been detected through decreased β -diversity in Lepidoptera (Ekroos et al. 2010) and plants (Vellend et al. 2007). The spread of generalists into newly available agricultural habitats also expands their global ranges and populations (Dyer et al. 2016), thereby increasing the likelihood of further colonisation events. In contrast, range-restricted, endemic taxa are disproportionately lost from inventories (Böhm et al. 2016), because they tend to have more specialised niches (Socolar et al. 2016, Reside et al. 2019). Such information is potentially useful for conservation science as preserving biodiversity worldwide is a key conservation goal. For example, species' global range data already informs conservation strategies through Key Biodiversity Areas (Kullberg et al. 2019) and Endemic Bird Areas (EBAs; Birdlife 2020).

A recent global analysis highlighted how average species range size is larger for communities in human-modified

habitats than in native habitats, though 'relative community average range' (RCAR; hereafter 'community average range') varies between taxonomic groups (Newbold et al. 2018). Birds and amphibians tend to be more strongly affected by conversion to human-dominated land-use types, while mammals are most strongly affected by degradation from primary to secondary forest. Across all taxa, changes in community average range are most profound in tropical regions characterised by reduced seasonal variation in temperature and precipitation (Newbold et al. 2018). By capturing the level at which widespread species are represented within a single community, community average range represents an index of biotic homogenisation. In principle, community average range can be measured both across and between landscapes and regions as a measure of β -diversity, which is independent of spatial scale. Linking changes in β -diversity to alterations in the proportion of wide-ranged and range-restricted species contextualises variation in β -diversity at the global scale at which conservation effort can be best prioritised.

A mechanistic understanding of how patterns of biotic homogenisation manifest requires a detailed assessment of not only dissimilarity, but also its disaggregated components of turnover (i.e. the replacement of certain species with new ones) and nestedness (i.e. the loss of species). Coupling such approaches with assessment of community average range offers the potential to better understand the context and degree to which patterns of biotic homogenisation are characterised solely by the loss of species from communities or by the replacement of other taxa. However, to our knowledge, no studies have examined these processes in tandem. In this context, understanding how the conversion of tropical forests to agriculture shapes associated changes of community turnover, nestedness and average range provides new insights into the profound ecological consequences of widespread deforestation.

Here we examine patterns of biotic homogenisation on tropical biodiversity, focusing on bird communities of Wallacea and Sundaland in Southeast Asia. Both are highly biodiverse regions with exceptional levels of avian endemism. We investigate: 1) how bird community structure and inter-site β -diversity changes across forest-farmland landscape gradients; 2) how turnover and nestedness from forest communities within islands shape overall changes in community average range; and 3) how patterns of both inter-site and inter-island β -diversity change with forest conversion to agriculture. We undertake our assessment across six discrete areas of endemism of decreasing size: Borneo (743 330 km²), Sulawesi (174 600 km²), Seram (17 100 km²), Buru (9505 km²), Talaud (1281 km²) and Sangihe (737 km²).

Methods

Study system and sampling design

Our study focussed on five islands in Wallacea (Sulawesi, Seram, Buru, Talaud and Sangihe), as well as the Sundaic island of Borneo. Wallacea is among the most biodiverse

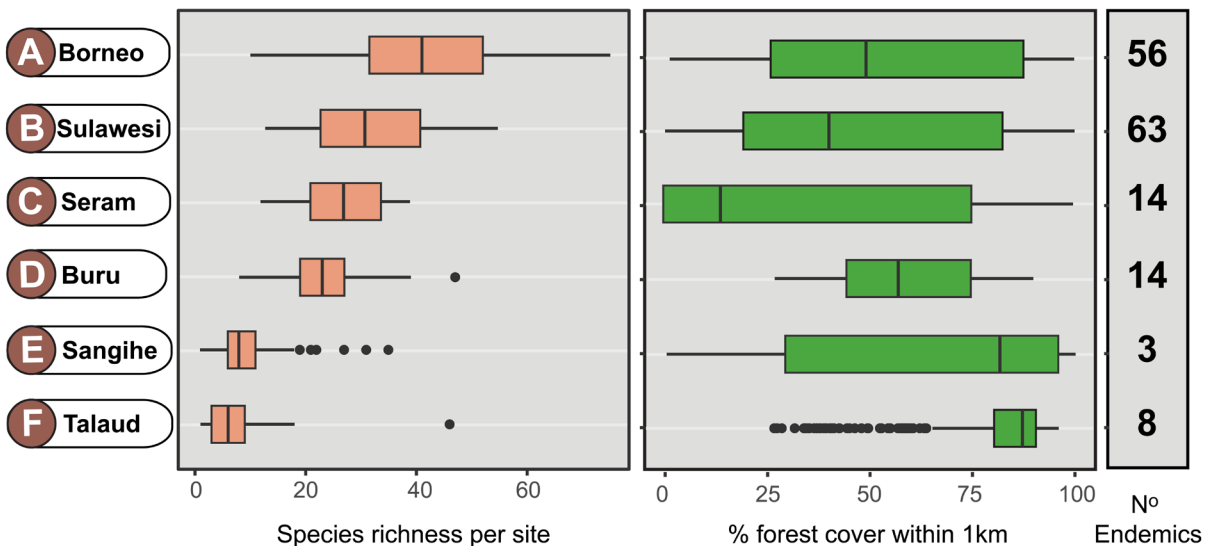
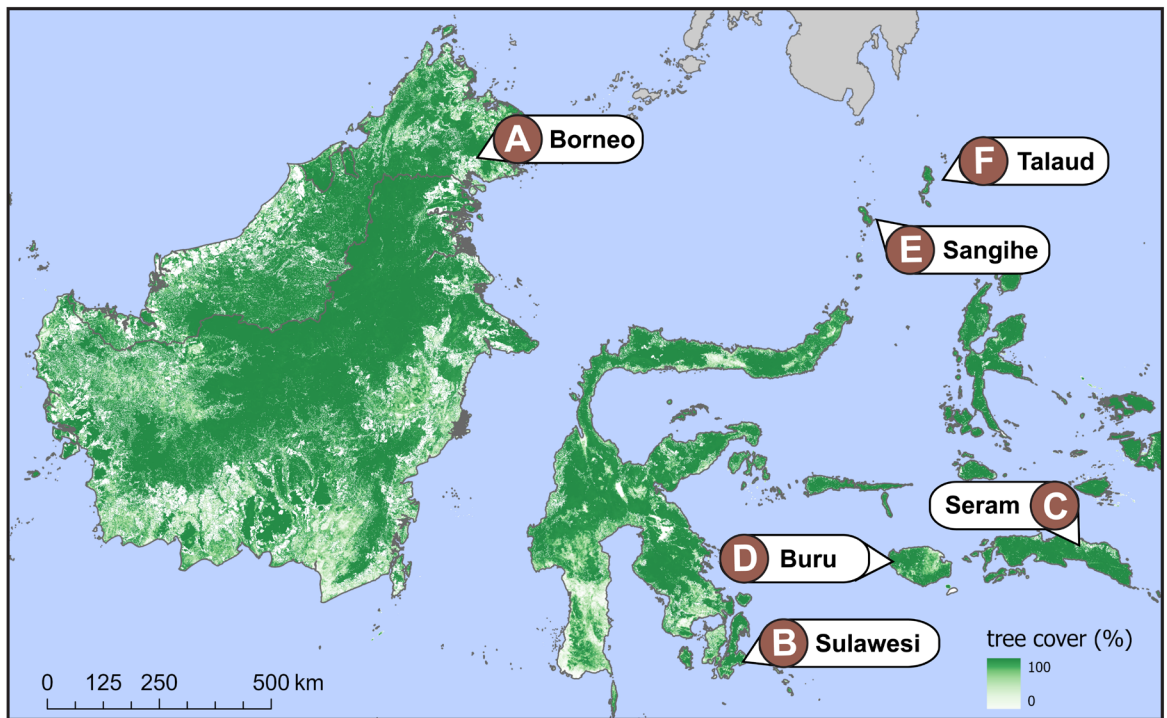


Figure 1. Map of study region representing different areas of endemism: (A) Borneo; (B) Sulawesi; (C) Seram; (D) Buru; (E) Talaud; and (F) Sangihe. Percentage tree cover is shown in shades of green. Inset boxplots of bird species richness are aggregated from point counts at these sites (purple, lower left) and percentage forest cover from the Global Forest Change repository (ver. 1.6, Hansen et al. 2013, Fig. 2) updated to 2017 (see Methods), within 1 km of surveyed sites (green, lower right). The box 'Endemics' (lower right) represents number of endemic species present on each island based on checklists from Lepage and Warnier (2014). Taxonomy for species and endemic classification follows Birdlife (2021).

regions on Earth, harbouring 764 bird species, 250 of which are restricted to single islands (Birdlife 2021), while Borneo has 704 species with 53 being endemic. In both regions, deforestation has been significant with 10 233 km² lost across Wallacea between 2000 and 2018 (Voigt et al. 2021), and 60 300 km² lost across Borneo between 2000 and 2017 (Gaveau et al. 2018).

On each island, we conducted bird point counts across a habitat gradient from forest to agriculture (Supporting information). The proportional coverage and quality of the most intact lowland forest varied on each island (Fig. 1). On Borneo, Sulawesi and Seram, sampling of intact habitat was undertaken in old-growth forest, whereas on other islands the remaining forest largely comprised long-established

secondary regrowth. The agricultural land also varied both within and between islands in terms of crop types: we sampled exclusively in oil palm in Borneo; predominantly cashew and rice in Sulawesi; a mixture of oil palm, coconut, agroforestry of cacao, jackfruit, durian and rice on Seram and Buru; and predominantly coconut and cattle pasture on Talaud and Sangihe (Supporting information).

Bird surveys were undertaken between 2016 and 2020, with work on any given island lasting ~3 months, except for Borneo where surveys were undertaken across 3 years (Mitchell et al. 2018). On each island, we implemented point counts of 100 m sampling distance between 06:00 and 10:00 on mornings without rain. A total of 1349 point count locations were sampled; methodological details are summarised in the Supporting information.

Forest cover

We calculated the proportion of forest cover around point count sites using the tree cover product from the Global Forest Change repository (ver. 1.6, Hansen et al. 2013, Fig. 1). We used the original percentage tree cover estimate for the year 2000 at 30 m resolution and removed cells that had been deforested in subsequent years. To compare forest cover at

multiple spatial scales with avian community attributes, we extracted forest cover as mean values across buffers of 250 m, 1 km and 5 km radii around each point count site using packages ‘raster’, ‘gtools’ and ‘rgdal’ (Bivand et al. 2015, Hijmans 2015, Warnes et al. 2015) in R (<www.r-project.org>).

Analytical framework

Our analysis is based on multiple lines of evidence examining the mechanisms by which deforestation drives biotic homogenisation across bird communities in Southeast Asia. The availability of island land-bridges during the last glacial maximum has not played a discernible role in shaping patterns of β -diversity between the island communities we studied; rather, these are biogeographically distinct communities that have been reshaped by anthropogenic land-use change and potentially human-facilitated dispersal in the modern era. We first explore community structure across all sites on each island in relation to total forest cover. Second, we characterise the changes to community structure associated with forest loss on each island in terms of turnover and nestedness. We highlight the link between community average range and community turnover to demonstrate how deforestation-mediated turnover on islands involves biotic homogenisation. We then assign

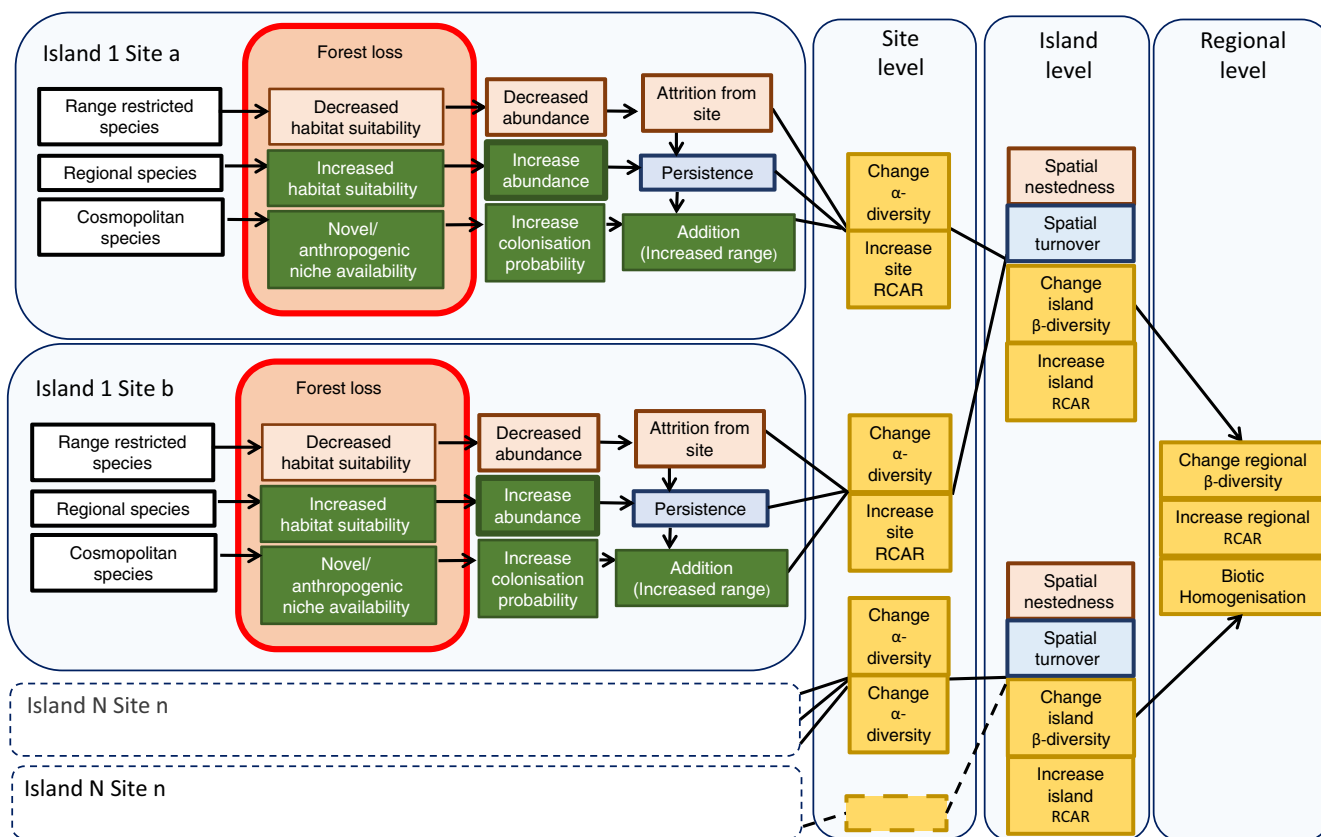


Figure 2. Conceptual diagram showing different factors associated with biotic homogenisation at different levels of spatial abstraction. Bold-outlined boxes are factors examined within our analyses. Pale pink shaded boxes indicate factors associated with species decline, dark green boxes are associated with species increase and blue boxes are neutral. Yellow boxes indicate community level assessments. Community average range is denoted with the acronym ‘RCAR’ (relative community average range).

sites on each island into one of five forest cover categories to compare average levels of pairwise community dissimilarity between sites and demonstrate changes in β -diversity across this gradient. We also examine patterns of dissimilarity between islands for the aggregated communities associated with each of the forest cover categories. We provide a conceptual framework underpinning connections between β -diversity, community average range and both the nestedness and turnover components of community dissimilarity (Fig. 2). To examine the scale-dependence of our results we repeated analyses examining the influence of forest cover at multiple spatial scales, from 250 m to 5 km radii around bird point count sites.

Community structure

We confirmed sampling coverage on each island by producing species accumulation curves using the R package 'iNEXT' (Hsieh et al. 2016). Where point count sites were visited four times (on Borneo, Sulawesi, Seram and Buru), we used non-metric multidimensional scaling (NMDS) ordinations, implemented using the R package 'vegan' (Oksanen et al. 2013), to explore associations between inter-site variation in bird community structure and forest cover on each island at scales of 250 m, 1 km and 5 km. Ordinations based on pairwise Bray–Curtis dissimilarity coefficients were calculated between untransformed species abundances pooled for all visits to each site, and colour and shading gradients based on proportions of forest cover within 1 km to visualise associations between forest cover differences and relative community structure. NMDS ordinations were not implemented for Sangihe and Talaud as point counts were not replicated to the same extent as on other islands. We undertook additional NMDS analysis on Buru, Sulawesi and Seram datasets and confirmed that bird community structure was not measurably influenced by land-cover categorisations based on Indonesian Environment and Forestry (2013) maps (Supporting information).

To explore differences in community composition in detail, we used the R package 'betapart' (Baselga et al. 2018) to partition Bray–Curtis (Soerensen; β_{sor}) dissimilarity from communities at forest reference sites into turnover (β_{sim}) and nestedness (β_{nes}) components (following Baselga and Orme 2012). To confirm these patterns, we also examined dissimilarity due to species replacement (β_{-3}) and dissimilarity due to richness differences (β_{rich}) (Carvalho et al. 2013) using the package BAT (Cardoso et al. 2015). To account for insular variation in forest cover and number of sampling locations, we defined forest reference sites on each island as those with the highest proportions of forest cover across multiple spatial scales. All reference sites had at least 75% forest cover within 1 km, except for Buru where the maximum forest cover available on the island was 60% within 1 km due to high levels of lowland forest loss. Associations between the proportion of forest cover at each spatial scale and Bray–Curtis dissimilarity, turnover (β_{sim}) and nestedness (β_{nes}), compared to forest reference sites, was explored using linear models to test associations on each island. We also assessed how relative levels of nestedness varied within categories of decreasing forest cover

by calculating nestedness based on overlap and decreasing fill (NODF; Almeida-Neto et al. 2008). These calculations were implemented in the R package 'vegan' (Oksanen et al. 2013).

Community average range

To quantify the extent of biotic homogenisation within each island in a global context we used the relative community average range methodology outlined by Newbold et al. (2018). This approach uses log-transformed values of the global species range for every individual recorded in a community to generate an index. For the basis of community average range calculations, we used species range estimates from Birdlife International (Birdlife 2020), which are based on a combination of expert opinion and interpolation from records in the Global Biodiversity Information Facility databases (GBIF 2021). For the community at each site, we calculated the average species range size as the community weighted mean. On each island, associations between community average range and proportion of forest cover within 250 m, 1 km and 5 km were each assessed using linear models. We further examined the breakdown of relative average range contributions by species with differing range species sizes on Talaud and Seram (Supporting information).

Breakdown of feeding guilds

To gain insight into guild-level responses we classified each of the 424 species observed across all sites into dietary guilds following Sheldon et al. (2010), Tobias and Pigot (2019) and Schulenberg (2020). Species were classified as either insectivores, frugivores, granivores, aquatic animal consumers, vertebrate consumers or other. We calculated the proportions of individuals in each guild observed at each site. To examine how feeding guild influenced the relationships between community average range and forest cover we measured the associations between these proportions both graphically and using linear models for each island. Granivores, aquatic animal consumers, vertebrate consumers and other groupings represented an insufficient number of species, so we restricted our feeding guild analysis to insectivores and frugivores.

β -diversity

To assess how β -diversity changed with reduced forest cover we calculated the pairwise Bray–Curtis dissimilarity between all sites in each of five categories of forest cover (100–80; 80–60; 60–40; 40–20; 20–0%) for each island using the R package 'betapart' (Baselga et al. 2018). We evaluated variation in β -diversity at both inter-site and inter-island scales in relation to the forest cover categories. To assess inter-site variation, we calculated pairwise β -diversity between all sites within each forest cover category. We repeated this process independently for each island. To examine inter-island variation in β -diversity, we aggregated community data for all sites in each of our five forest cover categories on each island and divided by the number of sites, to create 'averaged'

communities. We then calculated pairwise Bray–Curtis dissimilarities between the averaged communities for each forest cover category on different islands. Sangihe and Talaud were excluded from this inter-island analysis because comparisons between islands with a single point count per site and those with average communities pooled from four repeated visits necessarily produced far greater community dissimilarity and therefore precluded direct comparisons. We performed ANOVA tests and, where relevant, post-hoc Tukey tests, to examine differences across all categories of forest cover for both inter-site and inter-island β -diversity.

Results

Influence of forest cover on bird community structure

Species accumulation curves confirmed that over 95% of the bird community was sampled within the areas we surveyed

on each island (Supporting information). On the four islands where repeated visits were undertaken (Borneo, Sulawesi, Seram and Buru), NMDS ordinations showed a significant clustering of sites in three of the four islands examined (Borneo, Sulawesi and Seram), based on the proportions of forest cover at scales of 250 m and 1 km (Fig. 3). At the 5 km scale, all four island communities were significantly associated with forest cover (Fig. 3; Supporting information).

Bray–Curtis dissimilarity from the most forested reference sites on Borneo, Sulawesi, Seram and Sangihe increased as the proportion of forest cover within 250 m declined, whereas on Talaud and Buru there were no significant associations (Supporting information). Bray–Curtis dissimilarity from reference sites was also positively related to the proportion of forest cover within 1 km for Borneo, Sulawesi and Sangihe. For forest cover within a 5 km radius, associations were significant for Borneo, Sulawesi and Seram (Supporting information).

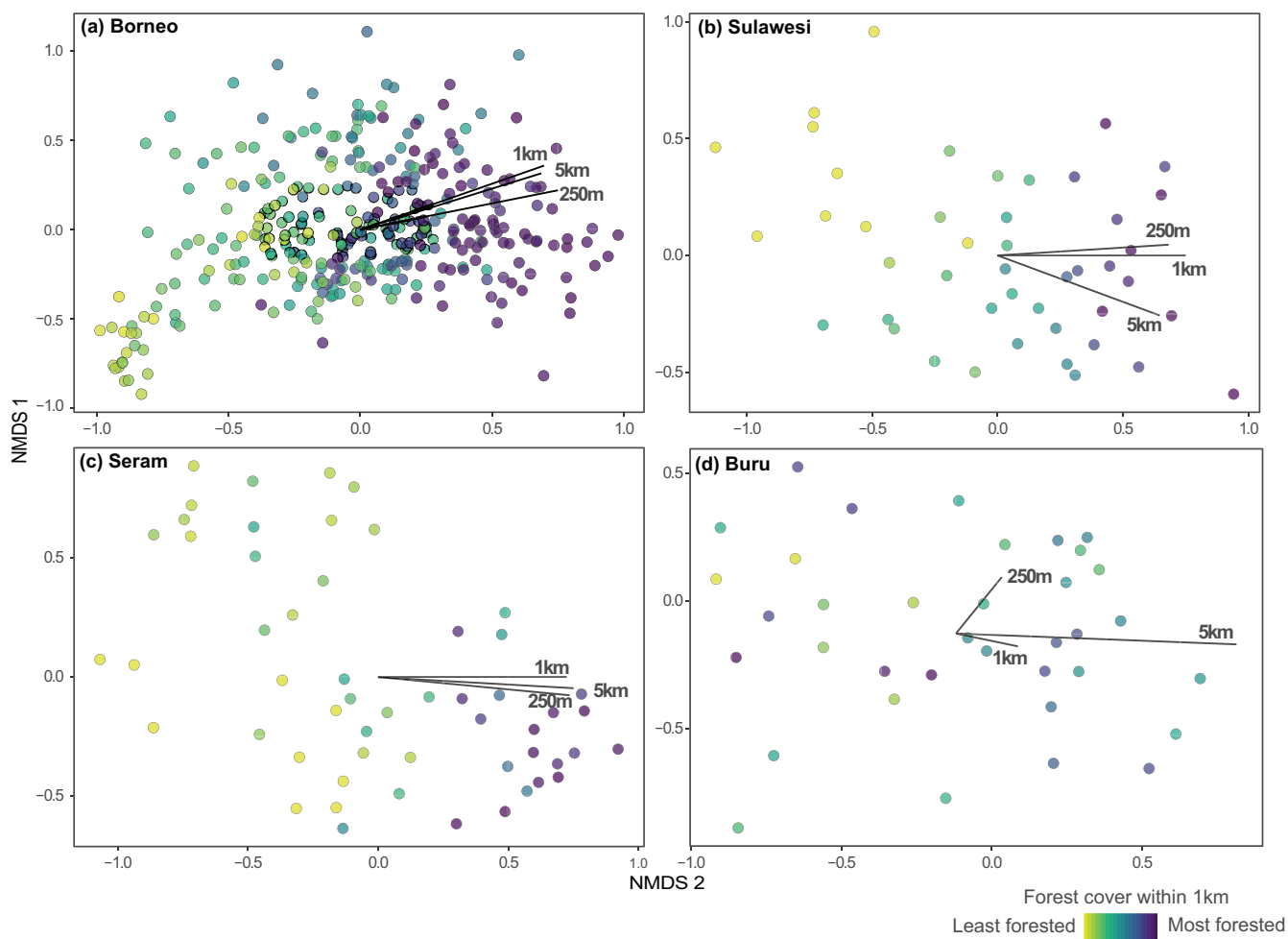


Figure 3. Non-metric multidimensional scaling (NMDS) ordinations for Borneo, Sulawesi, Seram and Buru showing community structure at each survey site. Points represent sites, with the colour gradient indicating percentage forest cover within 1 km. For Borneo, axis NMDS 1 and 2 of a 3-axis solution are presented. For Sulawesi, Seram and Buru a two-axis solution was convergent. Directional lines denote associations between community structure and forest cover at different spatial scales; length representing the relative R^2 value of the relationship (Supporting information).

Turnover, nestedness and community average range

When dissimilarity from forest reference sites was partitioned into turnover and nestedness, there was a significant association between forest cover within 250 m and turnover-driven dissimilarity for Borneo, Sulawesi, Seram and Sangihe (Supporting information). Similarly, forest cover within 1 km was associated with turnover for Borneo, Sulawesi, Seram, Talaud and Sangihe (Supporting information). For forest cover within 5 km, the four largest islands (Borneo, Sulawesi, Seram and Buru) all showed significant associations with turnover, while the two smallest islands (Talaud and Sangihe) did not. Dissimilarity driven by nestedness was significant on Seram and Talaud for forest cover within 250 m, on Buru and Talaud and Sangihe for forest cover within 1 km and on Sulawesi, Seram and Sangihe for forest cover within 5 km (Supporting information).

Partitioning dissimilarity from forest reference sites based on replacement β_{-3} and richness β_{rich} (sensu Carvalho et al. 2013), demonstrated broadly similar patterns in relation to forest cover within 1 km as when dissimilarity was divided into nestedness β_{nes} and turnover β_{sim} components (sensu Basegla et al. 2010). However, R^2 values were consistently lower for richness β_{rich} than for nestedness β_{nes} and Seram presented the inverse pattern (Supporting information).

Relative community average range increased in association with reduced forest cover in Borneo ($r^2=0.23$, $p < 0.001$, Fig. 4d), Seram ($r^2=0.663$, $p < 0.001$, Fig. 4d), Talaud ($r^2=0.24$, $p < 0.001$, Fig. 4d) and Sangihe ($r^2=0.253$, $p=0.003$, Fig. 4d) but not Sulawesi ($r^2=0.039$, $p=0.19$, Fig. 4d) or Buru ($r^2=0.161$, $p=0.057$, Fig. 4d). Patterns of association were reflected at spatial scales of 250 m and 5 km for Borneo and Seram (Supporting information).

Breakdown to feeding guilds

We found that, across all islands, the amount of forest cover within 1 km was positively associated with the proportion of frugivores observed at each site for Borneo, Buru, Seram and Talaud (Supporting information), and negatively associated with the proportion of insectivores on Seram and Talaud (Supporting information). Relative community average range of communities was associated with a reduction in the proportion of frugivores on Borneo, Seram and Talaud (Supporting information), but an increase in the proportion of insectivores present on Talaud and Sangihe (Supporting information).

β -Diversity at different spatial scales

Bray–Curtis dissimilarity between islands differed significantly between forest categories. Post-hoc Tukey test showed that dissimilarity values across all islands (Fig. 5a) were greatest in categories of intermediate forest cover (80–60, 60–40, 40–20%), but lower in those with either high or low amounts of forest cover (100–80, 20–0%; Supporting information). Inter-site Bray–Curtis dissimilarity values within islands

differed significantly between categories of forest cover on Borneo, Seram and Talaud, but not on Sulawesi, Buru or Sangihe (Supporting information), with the direction of differences also reflective of dissimilarity values at levels of intermediate forest cover.

When we expressed forest cover categories numerically based on their median values (i.e. 100–80 defined as 90; 80–60 defined as 70, etc.), dissimilarity between averaged communities for each forest cover category on different islands showed the opposite pattern (Fig. 5b). Greater dissimilarity was significantly associated with the categories of increased forest cover ($n=19$, $R^2=0.26$, $p=0.01$). However, this was not reflected in significant differences between forest cover categories (Fig. 5b, ANOVA $F_{(4,16)}=2.053$, $p=0.13$).

Nestedness based on overlap and decreasing fill within forest categories on each island showed no consistent pattern. Greater nestedness was observed for categories of reduced forest cover on Buton, Seram, Talaud and Sangihe but not for the categories with highest forest cover on Borneo and Buru (Supporting information).

Discussion

Our multi-scale evaluation of bird communities demonstrates that the conversion of tropical forest to agriculture in island archipelagos is a prominent driver of biotic homogenisation. Not only was bird community structure strongly associated with forest cover, but communities in increasingly deforested areas had greater similarity to communities from deforested landscapes on other islands. This contrasted with communities in forested areas that retained greater inter-island dissimilarity. Forest cover is well known to influence bird communities in multiple bioregions, including the Asian tropics (Helms et al. 2018, Mitchell et al. 2018), and similar patterns of biotic homogenisation have been demonstrated within continental Latin America (Karp et al. 2018). However, such findings are novel in the context of patterns of β -diversity between islands with exceptional endemism. Patterns of β -diversity measured from whole-island inventories are expected to be mediated by environmental variations (Otto et al. 2020), including those associated with human development (Kueffer et al. 2010). However, we provide the first empirical evidence for the influence of an environmental gradient on the biotic homogenisation process between evolutionarily isolated island communities.

Community turnover and nestedness associations with forest loss

Across the six islands, reductions in forest cover were mainly associated with turnover from forest communities, rather than nestedness. Forest loss and associated fragmentation drive biotic homogenisation via nested species loss in the Brazilian Atlantic Forest (Vallejos et al. 2016) and in agricultural landscapes in Costa Rica (Karp et al. 2018), but predominantly via turnover in the Brazilian Amazon

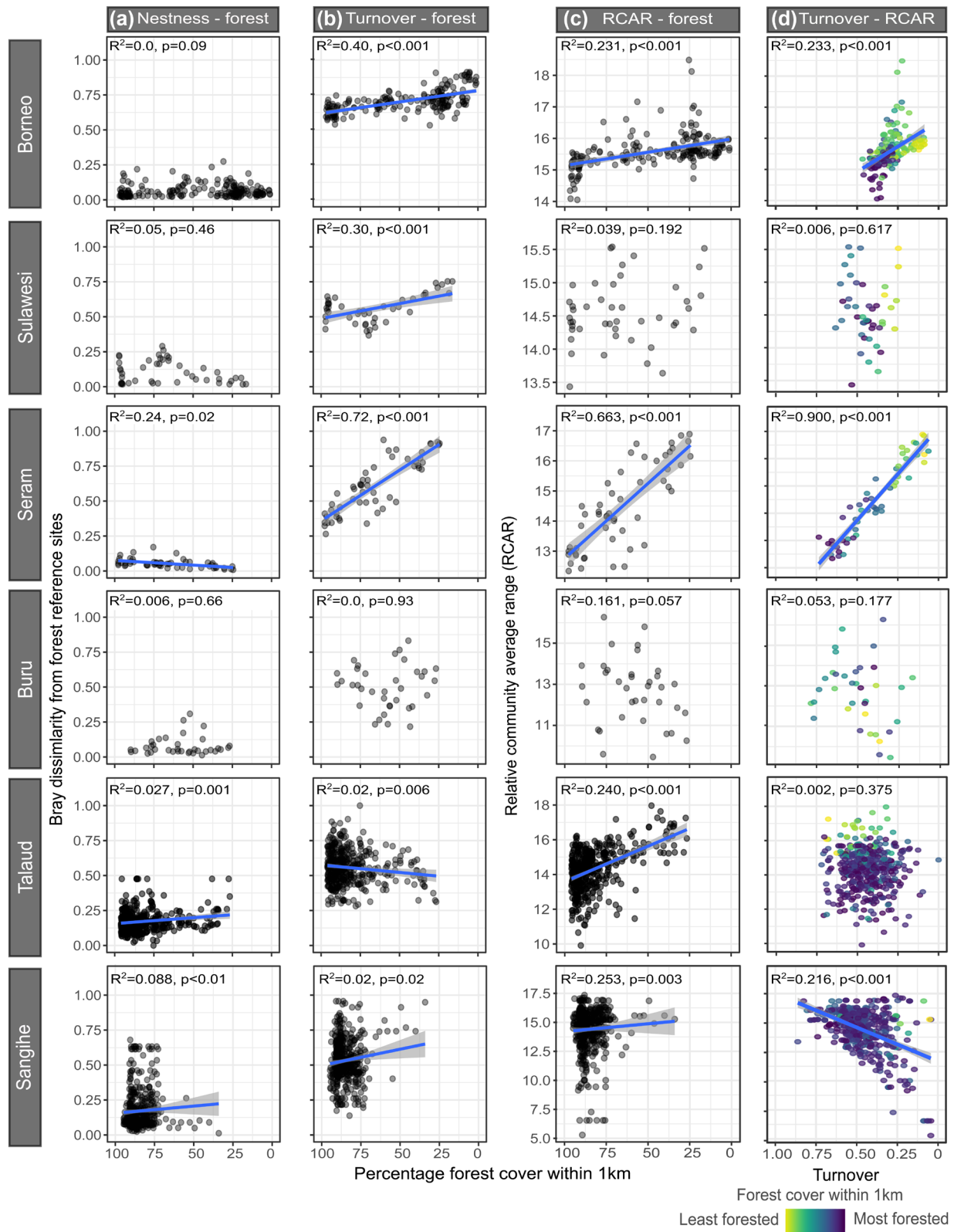


Figure 4. Associations between the proportion of forest cover within 1 km of each site compared to a) nestedness from forest reference sites; b) turnover from forest reference sites; c) community average range; and d) associations between turnover and community average range for each island. Blue lines indicate lines-of-best-fit for each association, with shaded areas denoting 95% confidence intervals. R-values and p-values for each relationship included within panels to highlight the relative strength and statistical significance of associations.

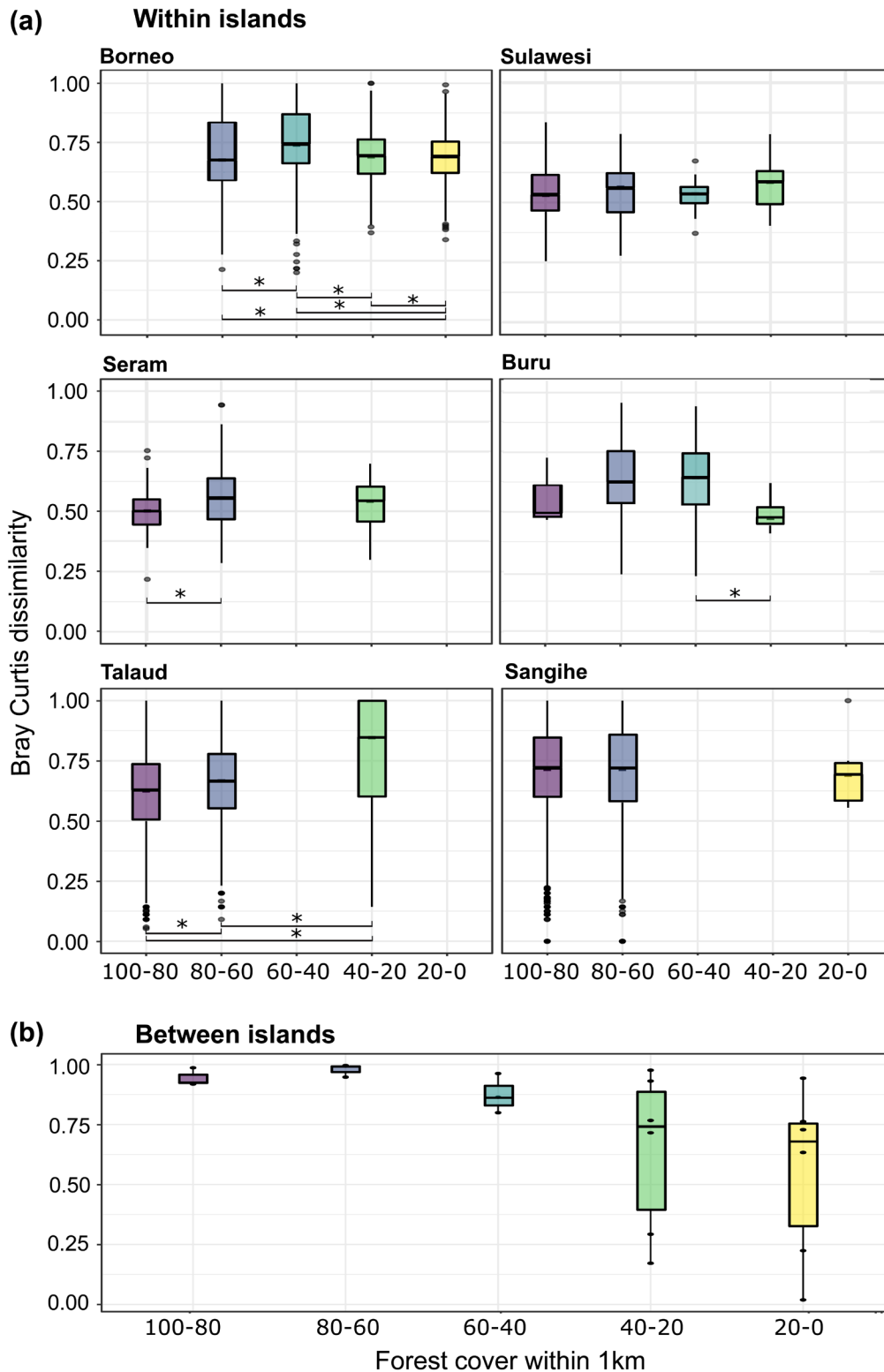


Figure 5. (a) Inter-site Bray–Curtis dissimilarity for categories of decreasing forest cover (100–80 (purple), 80–60 (blue), 60–40 (turquoise), 40–20 (pale green), 20–0% (yellow)) within 1 km for each island. Boxplots show distributions of pairwise dissimilarities within each category on each island. (b) Between-island Bray–Curtis dissimilarity based on pairwise comparisons of aggregated communities of each forest category on Borneo, Sulawesi, Seram and Buru. Boxplot (b) shows the distribution of between- island pairwise dissimilarities. Significant pairwise differences are highlighted with an asterisk. Talaud and Sangihe were excluded from the latter analysis due to differences in sampling completeness.

(Solar et al. 2015). We show that both turnover and nestedness in forest communities are associated with increases in community average range, indicating that the species lost from communities are disproportionately those with smaller ranges, while species gained tend to be those with larger ranges (Fig. 4). These findings, coupled with our demonstration of increasing inter-island community similarity with forest loss (Fig. 5), highlight how continued conversion of forests is causing the replacement of endemic species by a small cohort of ubiquitous species shared across all islands.

There remains some uncertainty concerning the factors that determine whether communities undergo turnover or become nested in response to environmental disturbance. Communities of small, isolated islands are more likely to be nested subsets of larger ones due to selective colonisation and extinction, as well as a reduced number of habitat types available to potential colonists (Cook and Quinn 1995). Indeed, in our study, bird communities on larger islands showed increased turnover (although not nestedness) from forest communities. However, on Talaud nestedness was significantly associated with reduced forest cover, whereas turnover was not. Talaud is significantly smaller (1281 km²) and more isolated than Seram (17 100 km²) and Borneo (743 330 km²), and forests on the island are relatively intact, meaning only a comparatively small area of the island is actively cultivated. Successful colonisation may, therefore, also have been prevented by insufficient total habitat for open-space generalists. The absolute abundance of birds in agricultural habitats on Talaud declined more rapidly than on Seram (Supporting information), where increased numbers of cosmopolitan species offset the reduced abundance of range-restricted and endemic species, resulting in community turnover rather than nestedness.

Our results also highlight how various components of β -diversity respond differently to land-cover change. Specifically, although patterns of turnover (β_{sim} ; Baselga et al. 2013) and replacement (β_{-3} , Carvalho et al. 2013) were similar on all islands (Supporting information), there was consistently higher explanatory power for relationships between turnover (β_{sim}) and forest loss and between replacement (β_{-3}) and forest loss (Supporting information). In Borneo, where species richness in the reference community was comparatively high, weighting nestedness (β_{rich} , Carvalho et al. 2013) based on initial species richness revealed a significant association between richness-based dissimilarity and forest cover, whereas nestedness alone did not (β_{nes} ; Baselga et al. 2013). Conversely, in Seram, where there were relatively fewer species in the forest reference community, nestedness (β_{nes}) was negatively associated with reduced forest cover, while richness-based dissimilarity (β_{rich}) was positively associated (Supporting information). This marked contrast suggests that the richness of reference communities should be accounted for when calculating the degree to which communities are subsets of one another and implies that the two approaches to partitioning β -diversity are complementary.

Community average range associations with forest loss and feeding guild

We show that community turnover and nestedness occur simultaneously with increases in community average range along a continuous gradient of forest conversion. Such examinations along gradients of habitat degradation are rare in the literature, as researchers tend to use discrete classes of land-use or site inventory data (Kueffer et al. 2010, Karp et al. 2018). The severity of deforestation mediating levels of biotic homogenisation along a continuous gradient suggests that even small amounts of forest conversion could result in more homogenised communities where species tend to have larger average range sizes. The implications of this finding are that even small amounts of forest conversion across archipelagos are likely to drive biotic homogenisation within those areas.

Our analysis of species guilds showed that reduced forest cover tends to be associated with community turnover, resulting in a higher proportion of insectivores and a reduced proportion of frugivores. On average, frugivorous birds are larger bodied than insectivorous ones (Russo et al. 2003) and large-bodied species tend to be most susceptible to habitat fragmentation (Ewers and Didham 2006). Avian frugivores may also have a greater degree of dietary specialisation and therefore are comparatively more affected by the loss of specific fruiting trees attendant with reduced forest cover than insectivores. Since diet specialisation is often associated with restricted niches and small species ranges (Socolar et al. 2016, Reside et al. 2019), this would also mean that relative decreases of frugivores and increases of insectivores contributes to turnover to communities with a larger relative community average range, as we observed in our results (Supporting information). An additional possibility which warrants further investigation is that hunting pressure influences relative abundances of some species in more accessible, less forested areas. Hunting may also disproportionately affect larger-bodied species (Stafford et al. 2017). Several Wallacean parrot species (frugivores) are especially popular in the cagebird trade (Setiyani and Ahmadi 2020), for example, and therefore may be disproportionately removed from communities in deforested areas, a phenomenon already documented in songbird species in Sumatra (Harris et al. 2017).

The disproportionate loss of frugivores across our island systems has potentially profound consequences for ecosystem function and forest regeneration due to their importance as seed dispersers (Gardner et al. 2019). The loss of seed-dispersing animals in tropical forest can result in the replacement of fleshy fruiting trees by species with abiotic seed dispersal (Brodie and Aslan 2012). Indeed, it is predicted that the absence of frugivorous birds will result in the loss of up to one third of tree species in some human-modified tropical forests (da Silva and Tabarelli 2000).

Patterns of biotic homogenisation at different spatial scales

In Hawaii, biotic homogenisation across the island archipelago has been characterised by 74 avian extinctions and 51 introductions (Cassey et al. 2007). This has resulted in some

islands with larger inventories than they had at the onset of European colonisation (i.e. biotic heterogenisation), but with reduced dissimilarity between island inventories (i.e. biotic homogenisation) (Blackburn et al. 2004, Cassey et al. 2007). Analyses from Macronesia highlight how spatial scale of inquiry, taxonomic group and environmental variation all mediate β -diversity within island chains (Otto et al. 2020). However, such analyses have often been undertaken at the level of whole-island inventories and do not examine how land-use conversion underpins the dynamics of colonisation and extinction that lead to island community turnover and homogenisation. Studies limited to island-level inventory data will inevitably over-represent small populations of colonist species or even individual vagrants. This, in turn, may result in inferences of biotic homogenisation or heterogenisation that are not indicative of finer scale community change.

We detected no strong change of inter-site β -diversity with decreasing forest cover, although inter-island β -diversity declined significantly across the gradient (Fig. 5). That patterns of β -diversity loss are undetectable at local spatial scales within our study underscores the importance of scale in determining biotic homogenisation and heterogenization. Conflicting β -diversity patterns at different spatial scales have been elucidated in both modelled scenarios (Cassey et al. 2006) and field studies (Arroyo-Rodríguez et al. 2013). Local differentiation might favour species that contribute to biotic homogenisation at larger spatial scales (Olden and Rooney 2006) or result from the loss of native species with more restricted ranges (Rooney et al. 2004), even in island archipelagos (Otto et al. 2020). Our results showed strong patterns of inter-site change in community average range even in the absence of strong signals for inter-site β -diversity. This highlights how community average range can potentially be used to overcome issues relating to scale in assessments of biotic homogenisation.

Forest loss as a driver of biotic homogenisation

The discovery that even small amounts of conversion from forest cover to agriculture are liable to favour wider-ranging species at the cost of restricted-range species across multiple biogeographically isolated islands has potentially important consequences for conservation. For example, on five of six islands we recorded cattle egret *Bubulus ibis*, a human commensal associated with livestock agriculture that has an increasingly cosmopolitan range (Morez-Silva and Del Lama 2014). By contrast, Buru lorikeet *Charmosyna toxopei*, a small frugivorous parrot which occurs only on Buru and has only been recorded on two confirmed occasions in the last century, is thought to have declined largely due to the loss of lowland forests (Birdlife 2021). The implication is that observed turnover to species with wider global ranges is reflective of more than just a general pattern, but rather the first indication of a process in which a small, shared cohort of ubiquitous ‘replacement species’ becomes highly successful at the expense of others. This process, if left unchecked, would ultimately lead to a ‘planet of weeds’ (Quammen et al.

1998). Prior to such worst-case endpoints, the loss of range-restricted species across so many independent biogeographical units should be cause for concern. Wide-ranged species tend to be generalists, whereas range-restricted species tend to be specialists, meaning that increases in community average range are likely to be associated with reductions in ecosystem functioning (Mouillot et al. 2013, Newbold et al. 2018).

Narrow-ranged species are also at greater overall risk of extinction. Indeed, within Indonesia and northern Borneo, 164 bird species are listed as endangered or critically endangered (Birdlife 2021), of which 32 are endemic to islands < 30 000 km². Their replacement by more spatially homogeneous communities implies structural changes that are both more spatially and temporally synchronous (Blüthgen et al. 2016), in turn creating scenarios in which extremes of climate (Mijatović et al. 2013) and disease dynamics (Ezenwa et al. 2006) could have more profound and far-reaching consequences. Such processes could produce self-reinforcing feedbacks, since climate (dos Santos Bertoincin et al. 2019) and disease dynamics (Smith et al. 2009) can themselves drive biotic homogenisation. Similarly, a greater proportion of range-restricted species, compared with large-ranged species, tend to be phylogenetically distinctive in Indonesia (Mooers and Atkins 2003, Jetz et al. 2014). This means that the patterns of homogenisation we observe are likely to result in even greater losses of phylogenetic diversity relative to species diversity.

Less intensive sampling per point on Sangihe and Talaud mean that caution should be exercised when directly comparing patterns between these and other islands. However, previous investigations suggest that both Bray–Curtis dissimilarity and community average range are robust to even severe under-sampling when abundance data are utilised (Beck et al. 2013, Newbold et al. 2018). While under-sampling necessarily reduces precision (Beck et al. 2013) the comparatively high number of total sites sampled on Sangihe and Talaud allowed meaningful patterns to be identified. A further caveat is that community similarities we observed in birds, as a highly motile group, may not be representative of less dispersive taxa, especially given the isolation of islands. More sessile taxonomic groups might be expected to show greater community nestedness and less steep increases in community average range.

Our findings provide robust evidence that the conversion of tropical forests to agriculture in insular Southeast Asia contributes to biotic homogenisation on a regional scale. We highlight how gradients of biotic homogenisation in deforested landscapes reflect the loss of narrow-ranged and endemic species and their replacement by a consistent set of wide-ranged species. Biogeographic processes such as selective colonisation may mediate range expansions and potentially slow biotic homogenisation. However, the general pattern of turnover to wide-ranging species on the study islands is detectable even at low levels of deforestation, suggesting that measurable biotic homogenisation is occurring even in areas where geographic isolation was sufficient to have generated avian speciation.

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Data availability statement

Data is available from the NERC Environmental Information Data Centre (EIDC): <<https://doi.org/10.5285/87f36a61-ca79-40c6-b781-8936ead162cc>> (Mitchell et al. 2022).

Supporting information

The supporting information associated with this article is available from the online version.

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