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The Effects of Land-Use Dynamics on Avian Phylogenetic Diversity Across Island Ecosystems

Halvina G. Saiya[1] | David P. Edwards[2,3] | Matthew J. Struebig[4] | David J. I. Seaman[4] | Robby Butarbutar[4] | Nurul L. Winarni[5] | Simon L. Mitchell[4] | Jatna Supriatna[5] | Rob W. Martin[6] | Adi Karya[7,8] | Robert P. Freckleton[1]

[1]Ecology and Evolutionary Biology, School of Biosciences, University of Sheffield, Sheffield, UK | [2]Department of Plant Sciences and Centre for Global Wood Security, University of Cambridge, Cambridge, UK | [3]Conservation Research Institute, University of Cambridge, Cambridge, UK | [4]Durrell Institute of Conservation and Ecology (DICE), University of Kent, Canterbury, UK | [5]Research Centre for Climate Change, Universitas Indonesia, Depok, Indonesia | [6]Birdlife International, Cambridge, UK | [7]Department of Biology, Faculty of Mathematics and Natural Sciences, Halu Oleo University, Kendari, Indonesia | [8]Operation Wallacea, Spilsby, UK

Correspondence: Halvina G. Saiya (hgsaiya1@sheffield.ac.uk)

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ABSTRACT

Aim: To test whether forest extent and recent forest-cover change are associated with avian phylogenetic diversity and community-level evolutionary value across islands.

Location: Seven islands spanning Borneo and Wallacea in the Malay Archipelago.

Taxon: Terrestrial birds.

Methods: We sampled 1410 sites (2010–2022). We calculated phylogenetic diversity (PD), mean phylogenetic distance (MPD), mean nearest taxon distance (MNTD) and their standardised effect sizes (SES), as well as community-level EDGE (Evolutionarily Distinct and Globally Endangered). Responses to (i) average forest proportion (250-m radius) and (ii) recent forest-cover change were analysed with spatial linear mixed-effects.

Results: Observed PD showed a negative visual trend with increasing forest proportion, whereas SES PD declined. MPD showed only a weak positive visual trend with forest proportion, whereas SES MPD showed no clear response. Although observed MNTD appeared to increase in the binned visual summaries, both observed MNTD and SES MNTD showed significant negative associations with forest cover in the spatial models, indicating stronger nearest-neighbour phylogenetic clustering in more forested sites. Effects of recent forest loss (2010–2022) on SES metrics were generally weak and inconsistent. Although PD also declined with decreasing rates of forest change, community-level EDGE was higher where forest cover was greater, indicating higher average evolutionary distinctiveness and extinction risk.

Main Conclusions: In this archipelagic system, forest amount is a key correlate of phylogenetic structure and the retention of evolutionarily distinctive, high-risk lineages. By contrast, recent forest-cover change showed weaker and more context-dependent associations. Conserving intact forests remains crucial for safeguarding the evolutionary legacy of island bird communities.

1 | Introduction

The geographic isolation of island ecosystems can promote independent evolutionary trajectories and, in some cases, high levels of endemism (MacArthur and Wilson 1967; Whittaker et al. 2008, 2017). However, patterns of diversity and endemism on islands are shaped not by isolation alone, but also by factors such as island size, geological history, environmental heterogeneity and colonisation dynamics (MacArthur and Wilson 1967; Whittaker et al. 2008, 2014, 2017). As a result, island biotas often

contain distinctive assemblages that may be especially vulnerable to external disturbances such as habitat destruction, biological invasions and population decline, thereby increasing the risk of species extinction (Russell and Kueffer 2019; Whittaker et al. 2017).

Habitat loss due to deforestation and fragmentation is a significant threat to island ecosystems, reducing habitat availability and reshaping community composition (Margono et al. 2012; Mitchell et al. 2022; Voigt et al. 2021). For example, on several islands in Wallacea, conversion of forest to agriculture has led to declines in habitat-specialist bird species and increasing dominance of widespread generalists, with implications for both biodiversity and ecosystem functioning (Mitchell et al. 2022). In addition, many island species face an elevated risk of extinction due to small populations and declining habitat quality (Russell and Kueffer 2019; Triantis et al. 2010). For example, in the Azores, more than half of the forest-dependent endemic arthropods are predicted to go extinct due to past habitat loss, despite many still occurring in small, isolated populations (Triantis et al. 2010). Also, many island-dwelling bird and reptile species, already constrained by small ranges and population sizes, have rapidly declined following habitat degradation and novel pressures (Russell and Kueffer 2019).

Given these threats, it is important to understand not only how many species occur in island communities, but also how evolutionary history is distributed among them. Phylogenetic Diversity (PD) and Evolutionarily Distinctiveness provide insight into the evolutionary history and uniqueness of species, capturing dimensions beyond taxonomic counts (Barker 2008; Chapman et al. 2018; Cosset and Edwards 2017). Metrics such as PD, Mean Pairwise Distance (MPD), Mean Nearest Taxon Distance (MNTD) and Evolutionary Distinctiveness and Globally Endangered (EDGE) scores help identify lineages that are both evolutionarily unique and potentially vulnerable (Barker 2008; Chapman et al. 2018; Cosset and Edwards 2017). These metrics are particularly relevant for guiding conservation priorities, as they provide essential information about species whose loss would represent a disproportionate erosion of evolutionary history and irreplaceability of evolutionary lineages (Barker 2008; Chapman et al. 2018).

Changes in forest structure and composition significantly affect the phylogenetic diversity of multiple taxa, including birds, mammals and insects (Cardoso et al. 2021; Chapman et al. 2018; Cosset and Edwards 2017; Mestre et al. 2020; Mitchell et al. 2022; Triantis et al. 2022). For instance, in Borneo, selective logging and the conversion of forests to oil palm plantations reduce phylogenetic and functional diversity by disproportionately removing evolutionarily distinct species (Chapman et al. 2018). Similarly, in the Amazon, selective logging reduces the phylogenetic and functional diversity of bird communities by eroding evolutionary history and ecological traits (Mestre et al. 2020). More extensive deforestation can lead to community homogenization dominated by generalist species, indicating substantial phylogenetic erosion (Mitchell et al. 2022). This loss of evolutionary distinctiveness is not limited to primary forest degradation. Similar patterns are also evident in restored forests, where environmental filtering often favours closely related, disturbance-tolerant species, resulting in lower phylogenetic and functional diversity. These trends have been documented in birds and dung beetles in lowland Amazonian and Andean systems (Cerullo et al. 2023, 2019; López-Bedoya et al. 2024). Finally, deforestation and anthropogenic pressures on islands such as the Mascarenes drive community convergence across islands, eliminating unique taxa and narrowing the phylogenetic spectrum (Triantis et al. 2022).

Here, we examine how forest extent and forest dynamics (2010–2022) shape avian phylogenetic diversity and evolutionary uniqueness across seven islands in the Malay Archipelago. We ask how variation in forest amount and recent forest loss influences the phylogenetic structure of island bird assemblages. Specifically, we address three questions: (1) Does greater forest extent correlate with higher phylogenetic diversity and the retention of evolutionarily distinctive lineages? (Chapman et al. 2018; Mestre et al. 2020; Triantis et al. 2010; Whittaker et al. 2014); (2) Does recent forest loss reduce phylogenetic diversity and increase relatedness, indicating disturbance-driven homogenization through the expansion of generalist or closely related species? (Margono et al. 2012; Mestre et al. 2020; Russell and Kueffer 2019; Triantis et al. 2022); and (3) Are bird communities in more stable forests characterised by higher community-level EDGE scores, indicating the persistence of distinctive and threatened evolutionary lineages? (Cardoso et al. 2021; Whittaker et al. 2017).

2 | Methods

2.1 | Study Area and Bird Community Data

We focus on birds as effective bioindicators whose abundance reflects habitat quality, ecosystem stability and human pressures such as urbanisation and fragmentation (Beauchamp 2021; Isaksson 2018; Rajpar and Zakaria 2011), while also supporting ecosystems through pest control, pollination, seed dispersal and nutrient cycling (Sekercioglu 2012). Therefore, understanding the drivers of avian diversity is essential to maintaining ecosystem functioning and long-term sustainability (Beauchamp 2021; Isaksson 2018; Rajpar and Zakaria 2011; Sekercioglu 2012).

Our study encompasses seven islands in the Malay Archipelago surveyed between 2010 and 2022: Borneo (312 sampling points), Buru (36 sampling points), Buton (45 sampling points), Sangihe (457 sampling points), Seram (54 sampling points), Sulawesi (69 sampling points) and Talaud (437 sampling points). Details of the sampling areas on each island can be seen in Supporting Information Appendix A1. The sampling data were taken from the presence-absence dataset from Mitchell et al. (2018, 2022), Maas et al. (2015) and Winarni et al. (2024). Point counts were carried out with 100 m sampling radius between 06.00 and 10.00 in the morning under dry conditions, and all bird species were detected visually and acoustically. Sampling effort varied among studies and islands, although several site-level inventories were based on multiple point-count stations and repeated visits rather than single brief counts (Maas et al. 2015; Mitchell et al. 2018, 2022; Winarni et al. 2024). Sites were surveyed on up to seven occasions, points were revisited four times, or detections were pooled across 10 stations surveyed on three occasions (Maas et al. 2015; Mitchell et al. 2018, 2022; Winarni et al. 2024). These designs likely improved inventory completeness and should

have minimised differences in detection among studies and islands. Across all islands, point counts were located mainly in lowland forest below 500 m above sea level (m.a.s.l) elevation, with only a subset of sites on Sangihe and mainland Sulawesi extending slightly above this threshold into lower montane forest (Supporting Information Appendix A2).

2.2 | Phylogenetic Data and Taxonomic Harmonisation

We used the global avian phylogeny of Jetz et al. (2012), based on the Hackett backbone, as the source tree for all phylogenetic analyses. This resource provides a pseudo-posterior distribution of dated bird trees, in which species with and without molecular data are incorporated using a Bayesian framework and taxonomic constraints to account for phylogenetic uncertainty (Jetz et al. 2012). From this distribution, we sampled one tree and used it as the starting phylogeny for the present study.

The community dataset contained 430 bird taxa across the seven islands. Species names in the field dataset were reconciled to the phylogeny using a two-step taxonomic harmonisation procedure. First, we carried out an automated reconciliation using harmonised taxonomic fields based on eBird, Eaton et al. (2016), GBIF and Jetz et al. (2012). This step identified 82 mismatches, most of which reflected nomenclatural differences only. Second, we manually reviewed each unmatched taxon to verify its taxonomic status and determine the appropriate correspondence in the phylogeny (Jetz et al. 2012). After this harmonisation step, we pruned the sampled Jetz tree to retain only taxa represented in our dataset, yielding a study-specific phylogeny for downstream analyses. The final pruned tree used for PD, MPD and MNTD contained 422 tips because eight taxa in the community dataset were not represented as separate terminal units in the source phylogeny, most of them being subspecies or recently split taxa that have not yet been incorporated into molecular studies.

We confirmed that the final phylogeny was rooted, binary and ultrametric before calculating community-level phylogenetic metrics. PD, MPD and MNTD were then calculated from the presence–absence matrix using the 422 taxa represented in the phylogeny. For EDGE analyses, we further restricted the dataset to taxa for which both phylogenetic placement and complete conservation data were available. Of the 422 taxa in the final phylogeny, 419 had complete information on evolutionary distinctiveness, IUCN status and population trend and these taxa were used in the community-level EDGE calculations.

2.3 | Forest Proportion and Forest Change

We extracted data on the proportion of forest habitat from Tropical Forest Monitoring (TMF) (Vancutsem et al. 2021) within a 250-m radius around each coordinate point from 2010 to 2022. We used this radius as a standardised measure (Bibby 2000; Ralph 1985) of the local forest context surrounding each sampling point. We acknowledge that the relevant spatial scale may vary among bird species with different body sizes, mobility and foraging strategies, but a single radius provides a consistent basis for comparison across sites and islands. Although a few sampling points were located within 500 m of one another, most were separated by substantially greater distances, as indicated by the mean and median inter-point distances across islands (Supporting Information Appendix A3). Accordingly, overlap among 250-m buffers was limited.

We used annual forest cover data at a 30-m resolution from TMF, containing six land cover classes (Vancutsem et al. 2021). For each year from 2010 to 2022, we created a binary forest/non-forest map by classifying undisturbed and degraded tropical moist forest as 'forest' and other classes as 'non-forest'. This allowed us to track forest temporal changes in forest cover relevant to bird occurrence data.

The average proportion of forest cover in the vicinity of each point count location was calculated from 2010 to 2022 at each observation location for a radius of 250 m, representing the average condition of forest cover during the period. Forest-cover change was estimated for each sampling location by fitting a simple linear regression of forest cover against year. The resulting slope was used as a standardised summary of the average annual direction and rate of forest-cover change between 2010 and 2022 across 1410 sampling sites. We acknowledge that forest loss may be non-linear and may include abrupt changes associated with discrete land-use events; however, the linear slope provides a simple and comparable approximation of the net temporal change over the whole study period and is comparable across sites.

2.4 | Phylogenetic Diversity Analysis

Analysis of three main metrics, Phylogenetic Diversity (PD), Mean Pairwise Distance (MPD) and Mean Nearest Taxon Distance (MNTD), was based on the presence-absence matrix of bird species at each observation location that had been aligned with the pruned phylogenetic tree so that it only included taxa that were detected (Pavoine et al. 2005; Redding and Mooers 2006). The PD metric measures the total length of branches in the phylogenetic tree connecting all species in a community (Barker 2008; Chapman et al. 2018; Cosset and Edwards 2017), thus representing the accumulation of evolutionary lineages owned by the community. MPD calculates the average evolutionary distance between all pairs of species in a community (Barker 2008; Chapman et al. 2018; Cosset and Edwards 2017), while MNTD estimates the average distance between each species and its closest relative (Barker 2008; Chapman et al. 2018; Cosset and Edwards 2017). By utilising these three metrics together, this analysis allows the identification of patterns of phylogenetic shrinkage or homogenization that may occur due to changes in forest cover, both spatially and temporally (Pavoine et al. 2005; Redding and Mooers 2006).

To understand whether the bird community has a greater or lesser phylogenetic uniqueness than random expectations, we calculated the Standardised Effect Size (SES) for PD, MPD and MNTD. This used the independent swap algorithm, which maintains the richness and occurrence frequencies of species at each site, as is standard practice in ecophylogenetic studies (Cosset and Edwards 2017; Kembel et al. 2020). Given the high number of observation points in this study, running the analysis 9999

times with 1000 iterations was sufficient to generate a stable random distribution and estimate SES values robustly (Kembel et al. 2020; Tsirogiannis and Sandel 2016). Finally, spatial linear mixed-effects models were fitted separately for PD, MPD, MNTD, SES PD, SES MPD and SES MNTD to examine the effects of forest cover and forest temporal change on phylogenetic community structure. Mean forest proportion (250 m) and forest-change slope (250 m) were fitted as single fixed effects in separate models, with island included as a random intercept to account for among-island variation. An exponential spatial correlation structure based on site coordinates (x and y) within islands was included to account for residual spatial autocorrelation. This framework enabled the analysis of broad phylogenetic patterns across sites while accommodating both inter-island heterogeneity (Chapman et al. 2018; Cosset and Edwards 2017) and spatial non-independence.

Assumptions for all spatial mixed-effects models used in the study were evaluated by inspecting normal Q–Q plots and residuals-versus-fitted plots, together with Moran's I tests of residual spatial autocorrelation (Supporting Information Appendices A4.1–A4.4). The graphical diagnostics were used to assess departures from normality, heteroscedasticity, non-linearity and unusual residual structure. Moran's I was calculated both for the full dataset and within individual islands because sampling sites were distributed across separate island systems. The diagnostics indicated that some non-spatial models departed from ideal residual expectations, and Moran's I showed evidence of residual spatial autocorrelation across the full dataset and, in several cases, within individual islands (Supporting Information Appendices A4.2 and A4.3). We therefore used spatial mixed-effects models, as described above. Representative residual plots are provided for the principal spatial mixed-effects models most central to the study hypotheses, including SES PD, MNTD, SES MNTD and mean EDGE scores under forest cover, together with SES PD under forest-cover change (Supporting Information Appendix A4.4). These models are therefore interpreted primarily as describing overall cross-island associations rather than precise site-specific relationships.

2.5 | EDGE Scores Analysis

We conducted an EDGE analysis to assess the conservation value of bird species based on evolutionary distinctiveness and extinction risk. ED values were derived from a pruned ultrametric phylogenetic tree (Jetz et al. 2012), containing only species observed in the field. This pruning enables ecologically meaningful comparisons among sites while applying standard community-level phylogenetic approaches (Chapman et al. 2018). ED was calculated by summing branch lengths from tip to root, weighted by the inverse number of descendant species and log-transformed as $\ln(1 + \text{ED})$ (Isaac et al. 2007; Supporting Information Appendix A5).

To capture extinction risk, we applied a modified Global Endangerment (GE) score that integrates IUCN Red List categories with population trends. Extinction probabilities were assigned to Red List statuses (LC = 0.0001 to CR = 0.5), representing an approximate tenfold increase in extinction risk per category (Butchart et al. 2004; Isaac et al. 2007; Supporting Information Appendix A5). Population trend categories were weighted as Increasing = 0.5, Stable = 1, Unknown = 2 and Decreasing = 3, consistent with CITES and IUCN prioritisation frameworks (Lacher et al. 2022; McClure et al. 2023; UNEP-WCMC 2022, CoP19 Inf. 101; Supporting Information Appendix A5).

Final EDGE scores were calculated by combining the normalised ED values with the modified GE scores (Supporting Information Appendix A5). Presence-absence data were then used to compute mean site-level EDGE scores, which were analysed in their relation to environmental variables: forest cover and forest change. Then, we fitted spatial linear mixed-effects models using mean EDGE score, mean IUCN status, mean population trend and log-transformed species richness as response variables. Forest proportion or forest-cover change was included as a single fixed effect in separate models, while island was treated as a random intercept to account for among-island variation. An exponential spatial correlation structure based on site coordinates (x and y) within islands was included to account for residual spatial clustering. These models were used to test whether community-level conservation metrics varied along gradients of forest cover and recent forest change.

Model assumptions for the EDGE-related spatial mixed-effects models were evaluated using the same diagnostic procedures described above (Supporting Information Appendices A4.1–A4.4). A representative set of residual plots for the mean EDGE model under forest proportion is shown in Supporting Information Appendix A4.4. As with the phylogenetic-diversity models, these results are interpreted as overall cross-island associations rather than precise site-specific relationships.

2.6 | Software

All analyses were conducted in R within RStudio version 2024.12.0.467 (Posit Team 2024). Phylogenetic tree import, pruning, matching and diagnostics were conducted using ape, geiger and phytools (Harmon et al. 2007; Paradis et al. 2004; Revell 2018). Community phylogenetic metrics (PD, MPD, MNTD and SES) were calculated using picante (Kembel et al. 2020). EDGE calculations used ape, picante and tidyverse (Kembel et al. 2020; Paradis et al. 2004; Wickham et al. 2019). Spatial linear mixed-effects models were fitted using nlme (Pinheiro et al. 2026), with island included as a random intercept and an exponential spatial correlation structure based on site coordinates within islands. Separate models were fitted for each response variable against each predictor, and model summaries were extracted directly from the fitted objects. Supporting Information Appendices F–I model tables were generated using sjPlot (Lüdecke et al. 2025), whereas diagnostic checks were based on graphical inspection of normal Q–Q plots and residuals-versus-fitted plots, supported by model-performance summaries from performance and Moran's I tests of residual spatial autocorrelation implemented in spdep (Bivand et al. 2026; Lüdecke et al. 2026). Spatial processing of forest-cover data was conducted using raster and sf, whereas data manipulation and reshaping were performed using tidyverse (Hijmans 2010; Pebesma 2018; Wickham et al. 2019). Figures were assembled using patchwork (Pedersen 2019).

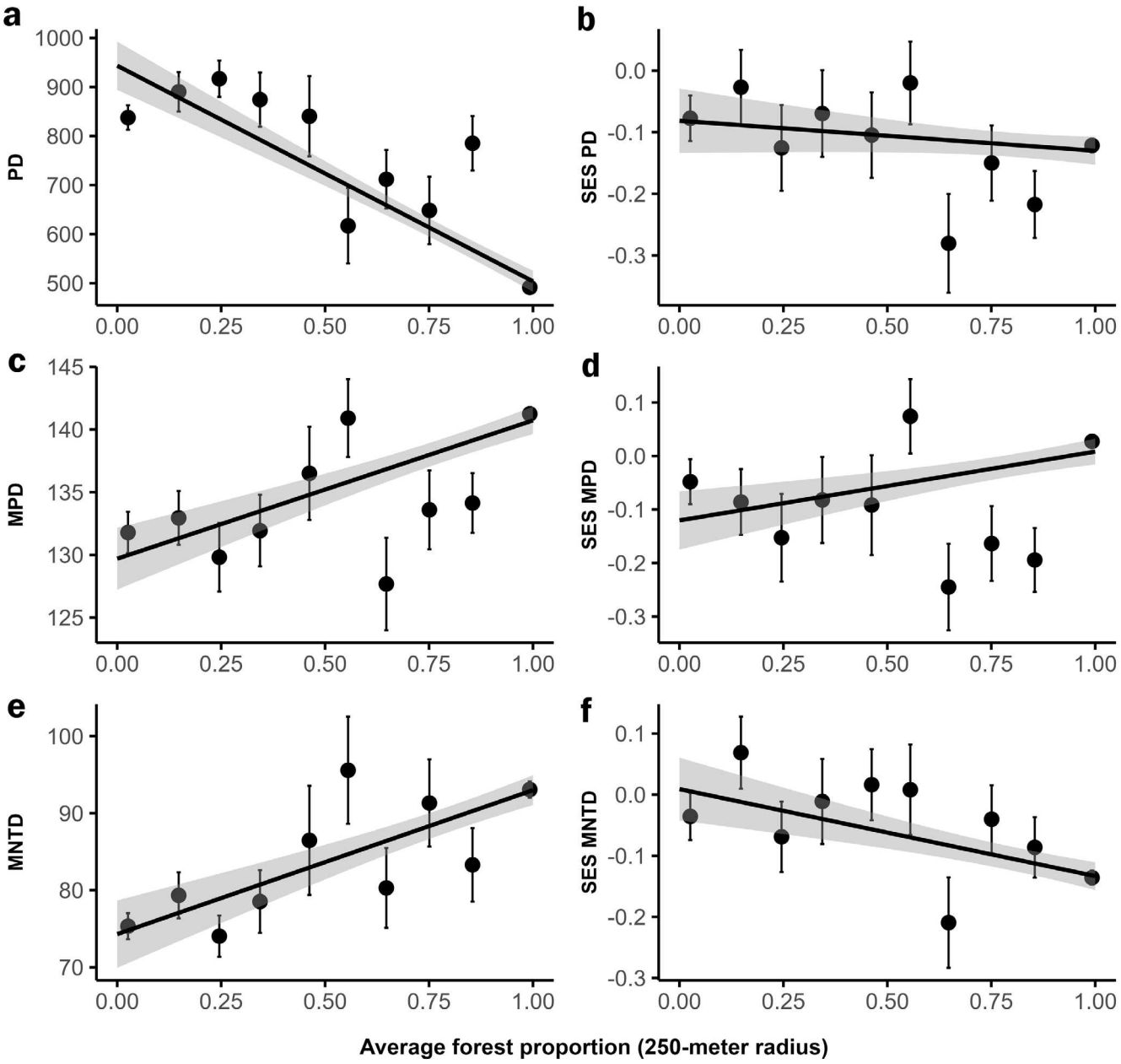

FIGURE 1 | Relationships between forest-cover proportion (250-m radius) and avian phylogenetic metrics across seven islands (Borneo, Buru, Buton, Sangihe, Seram, Sulawesi and Talaud), 2010–2022. Points show bin means (10 equal bins) ± SE for visualisation only. Solid lines and 95% confidence intervals are fitted to the full unbinned dataset. Statistical significance refers to the corresponding spatial linear mixed-effects models with island included as a random intercept (Supporting Information Appendix F). Panels show both observed metrics and their standardised effect sizes (SES): (a) PD; (b) SES PD; (c) MPD; (d) SES MPD; (e) MNTD; and (f) SES MNTD.

3 | Results

3.1 | Forest Proportion Influences Island Bird Community Phylogenetic Diversity

Phylogenetic diversity (PD) appeared to decline with increasing forest proportion in the binned visual summary (Figure 1a), but the corresponding spatial mixed-effects model did not detect a significant association with forest cover (estimate = 52.17, $p = 0.175$; Supporting Information Appendix F). By contrast, SES PD showed a significant negative association with forest cover (estimate = −0.22, $p < 0.001$; Supporting Information Appendix F). MPD showed an increase across the forest-cover gradient in the visual summary (Figure 1c), but this relationship was not supported by the spatial model (estimate = 1.41, $p = 0.560$; Supporting Information Appendix F) and SES MPD likewise showed no significant response (estimate = −0.04, $p = 0.395$; Supporting Information Appendix F). For the nearest-neighbour structure, the MNTD appeared to increase in the binned visual summary (Figure 1e), whereas the spatial model identified a significant negative association with forest cover (estimate = −13.07, $p = 0.002$; Supporting Information Appendix F). SES MNTD declined significantly with increasing forest cover (estimate = −0.19, $p < 0.001$; Supporting Information Appendix F). Thus, the strongest and most consistent signal in the spatial models was a decline in SES PD and SES MNTD with increasing forest cover,

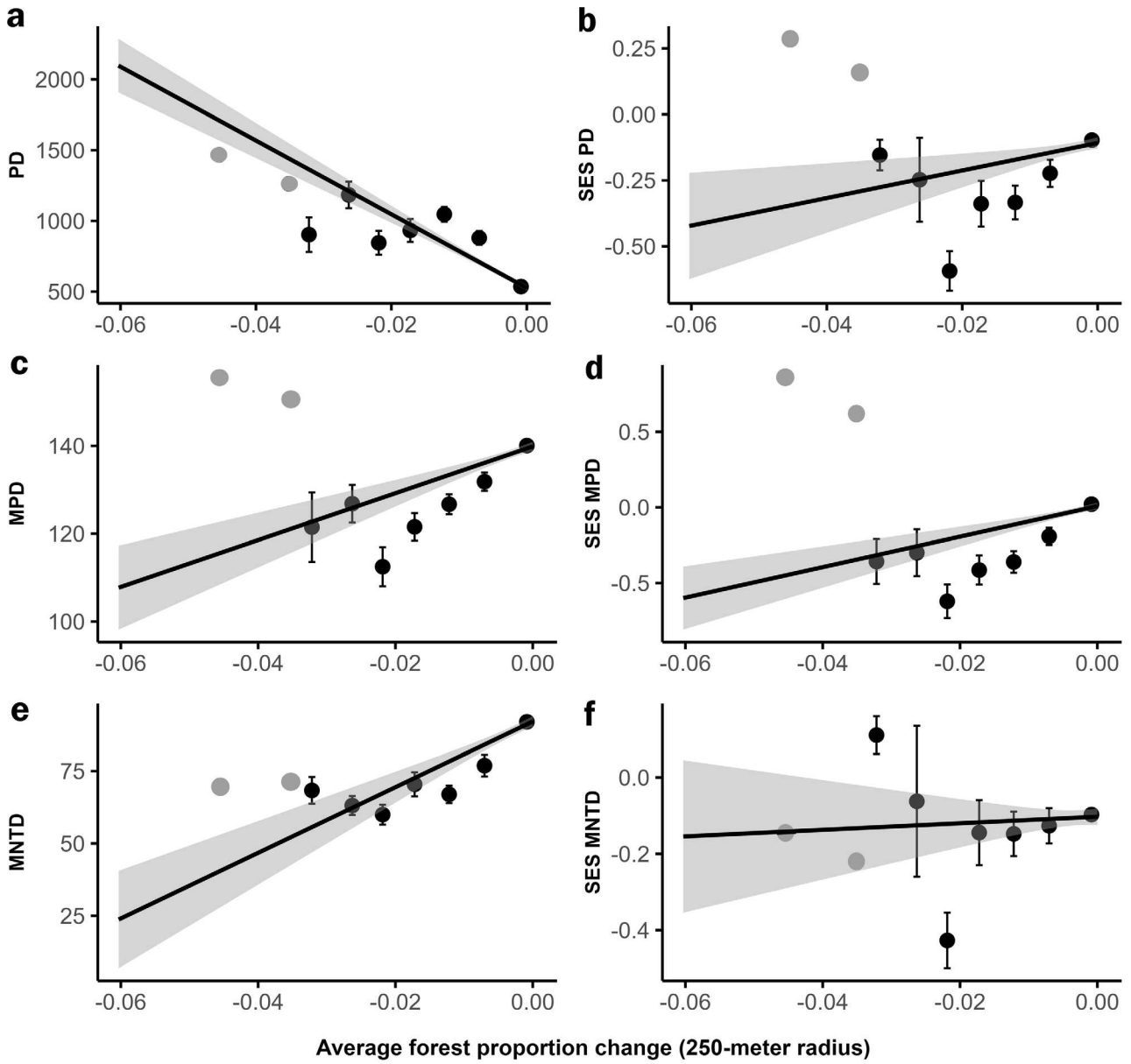

FIGURE 2 | Relationships between forest-cover change (slope, 2010–2022; 250-m radius) and avian phylogenetic metrics across seven islands (Borneo, Buru, Buton, Sangihe, Seram, Sulawesi and Talaud). Points show forest-change bin means (bin width = 0.005) ± SE for visualisation only. Solid lines and 95% confidence intervals are fitted to the full unbinned dataset. Statistical significance refers to the corresponding spatial linear mixed-effects models with island included as a random intercept (Supporting Information Appendix G). Grey points indicate the two Sulawesi sites with extreme forest-loss slopes. These bins contained single observations only and therefore do not show SE bars. The mixed-model results were qualitatively unchanged when these sites were excluded (Supporting Information Appendix G). Panels show both observed metrics and their standardised effect sizes (SES): (a) PD; (b) SES PD; (c) MPD; (d) SES MPD; (e) MNTD; and (f) SES MNTD.

indicating greater phylogenetic clustering than expected in more forested sites. As Figure 1 presents binned means for visualisation, the differences between the plotted patterns and the model estimates should be interpreted cautiously.

3.2 | Forest Change Influences Bird Phylogenetic Diversity

Phylogenetic diversity (PD) declined along the forest-change gradient, with lower PD in sites showing less forest loss (Figure 2a). The corresponding spatial mixed-effects model detected a significant negative association between PD and forest change (estimate = −4283.84, $p = 0.026$; Supporting Information Appendix G). However, SES PD did not respond significantly to forest change (estimate = −1.92, $p = 0.251$; Figure 2b, Supporting Information Appendix G), indicating no clear richness-standardised shift in phylogenetic structure. MPD and MNTD tended to increase towards sites with less forest loss in the binned visual summaries (Figure 2c,e), but neither relationship was supported by the spatial models (MPD: estimate = −3.48, $p = 0.975$; MNTD: estimate = −6.97, $p = 0.973$; Supporting Information Appendix G). Likewise, the corresponding SES metrics remained non-significant (SES MPD:

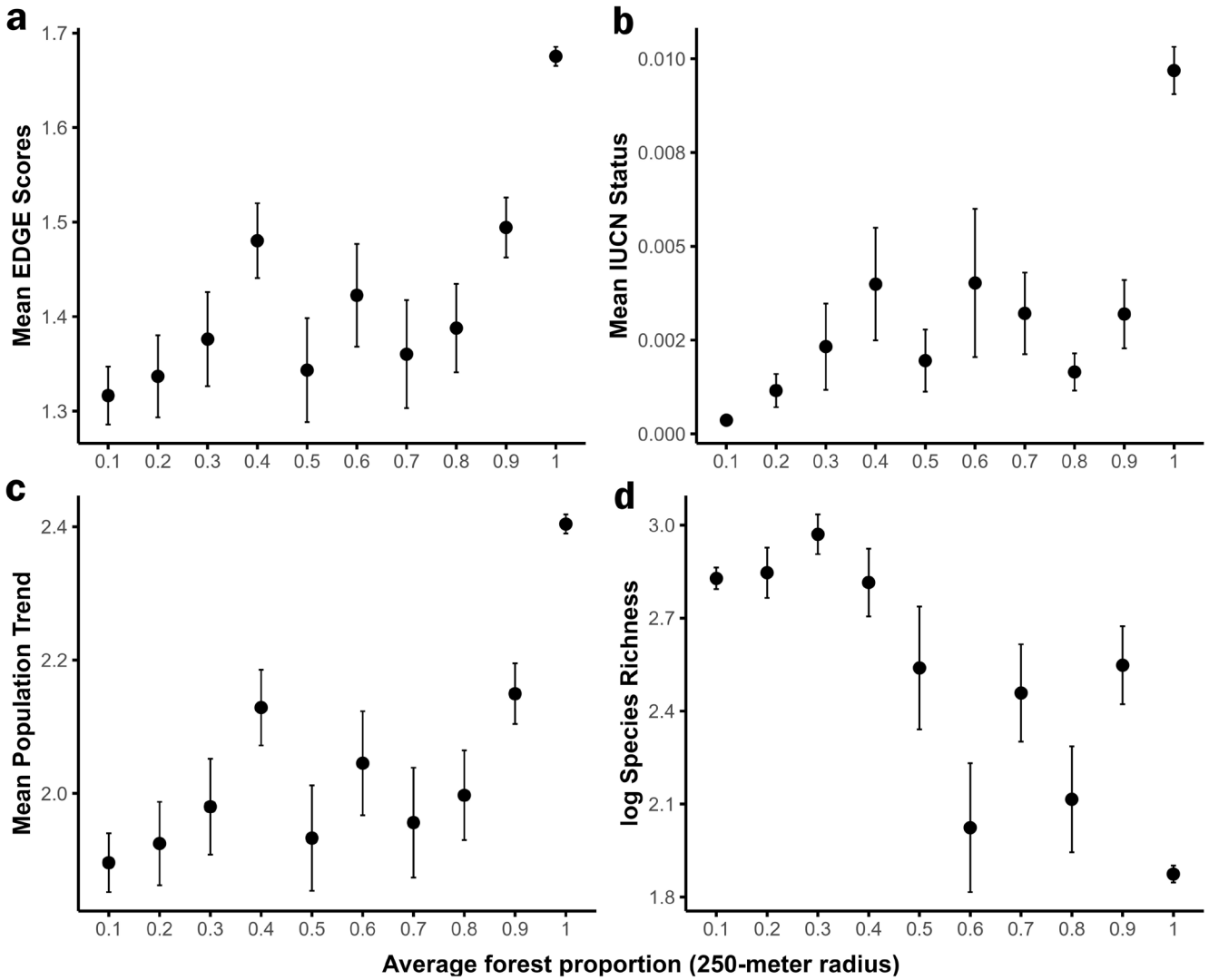

FIGURE 3 | Relationships between forest-cover proportion (250 m radius) and four community metrics across seven islands (Borneo, Buru, Buton, Sangihe, Seram, Sulawesi and Talaud), 2010–2022: (a) mean EDGE score (higher = more evolutionarily distinct and threatened), (b) mean IUCN status (higher = greater extinction risk), (c) mean population-trend score (higher = stronger declines) and (d) log species richness. Points show means ± SE from 10 equal forest-cover classes for visualisation only. Statistical significance refers to the corresponding spatial linear mixed-effects models fitted to the full unbinned dataset, with island included as a random intercept (Supporting Information Appendix H).

estimate = −1.33, $p = 0.469$; SES MNTD: estimate = −0.53, $p = 0.779$; Figure 2d,f; Supporting Information Appendix G). Taken together, the forest-change models provide little evidence that recent forest loss consistently altered phylogenetic structure beyond variation in PD. Thus, unlike forest-cover proportion, recent forest-cover change did not produce a consistent signal in the richness-standardised phylogenetic metrics.

3.3 | Forest Dynamics Shape the Phylogenetic Uniqueness of Island Bird Communities

3.3.1 | Forest Proportion

EDGE scores generally increased with forest cover, with particularly high values in the most forested sites (Figure 3a). This pattern was broadly consistent across islands (Supporting Information Appendix D), suggesting that more forested habitats tended to support communities with higher average evolutionary distinctiveness and extinction risk. The spatial mixed-effects model supported this pattern, showing a statistically significant positive association between forest cover and community-level EDGE scores (estimate = 0.40, $p < 0.001$; Supporting Information Appendix H).

Across the forest-cover gradient, average IUCN status remained low, suggesting that most species were not highly threatened overall (Figure 3b). However, mean IUCN status tended to increase in the most densely forested areas, particularly on smaller and more remote islands such as Sangihe and Talaud (Supporting Information Appendix D), where forest-dependent bird species may be more prevalent. The spatial linear mixed-effects model also detected a statistically significant but weak positive relationship between forest cover and average IUCN status (estimate = 0.01, $p < 0.001$; Supporting Information Appendix H).

Across the seven islands, bird communities were generally composed of species experiencing population declines and these declines tended to be steeper in areas with the highest forest cover (Figure 3c, Supporting Information Appendix D). This suggests that forest-dependent species may remain vulnerable even in apparently suitable habitats because of sensitivity, endemism or historical pressures. The spatial mixed-effects model showed a significant positive association between forest cover and average population-trend scores (estimate = 0.58, $p < 0.001$; Supporting Information Appendix H), indicating that declining populations were more concentrated in more forested areas.

Species richness tended to be lower in areas with the highest forest cover, with log-transformed richness peaking at low to intermediate forest cover (~20%–40%) and declining at higher values in the binned visual summaries (Figure 3d), although patterns varied among islands (Supporting Information Appendix D). In contrast, the corresponding spatial mixed-effects model detected a weak but statistically significant positive association between forest cover and log-transformed species richness (estimate = 0.24, $p = 0.006$; Supporting Information Appendix H). Most of the variation was explained by inter-island differences (ICC = 0.72), and the low marginal R^2 (0.007) indicates that forest cover alone explained only a very small proportion of the variation in richness. Accordingly, the biological importance of this effect should be interpreted with caution.

3.3.2 | Forest Proportion Change

Mean EDGE scores within bird communities tended to be higher in places with slower forest loss (i.e., forest-change values closer to zero; Figure 4a). Island-level patterns (Supporting Information Appendix E) show that Buru, Buton, Sangihe, Seram and Talaud exhibited a marked increase in mean EDGE scores under slower forest loss, whereas Borneo and Sulawesi showed relatively stable trends. However, the corresponding spatial mixed-effects model did not detect a statistically significant relationship between forest change and EDGE scores (estimate = 4.08, $p = 0.164$; Supporting Information Appendix I), indicating that this pattern should be interpreted cautiously.

Mean IUCN status appeared to increase as the rate of forest loss decreased in the binned visual summary (Figure 4b). However, the pattern was variable across bins, with broad confidence intervals in parts of the forest-change gradient and the spatial mixed-effects model did not support a statistically significant relationship between forest-cover change and mean IUCN status (estimate = 0.07, $p = 0.484$; Supporting Information Appendix I). This visual pattern should therefore be interpreted cautiously, although it may be consistent with species-level patterns on islands such as Sangihe and Talaud, where the most threatened species tended to occur in less disturbed habitats (Supporting Information Appendix E).

Higher population-trend values indicate steeper declines. In the binned visual summary, population-trend values appeared higher in areas with less forest loss, where forest-change values were closer to zero (Figure 4c). However, the spatial mixed-effects model did not detect a statistically significant relationship between forest change and population trend (estimate = 5.85, $p = 0.164$; Supporting Information Appendix I). This apparent pattern should therefore be interpreted cautiously, although similar species-level patterns were more apparent on Buru, Buton, Sangihe, Seram and Talaud than on larger islands such as Borneo and Sulawesi (Supporting Information Appendix E).

Species richness showed a slight decline as deforestation decreased in the binned visual summary (Figure 4d). However, the spatial mixed-effects model did not detect a statistically significant relationship between forest change and log-transformed species richness (estimate = −4.31, $p = 0.326$; Supporting Information Appendix I), so this apparent visual pattern should be interpreted cautiously. At the island level, patterns varied: Sangihe and Talaud showed higher richness in less disturbed forests, whereas richness on Borneo, Buru and Seram remained relatively stable across the forest-change gradient, and Buton and Sulawesi showed lower richness with lower forest loss (Supporting Information Appendix E).

4 | Discussion

At the archipelago scale, forest extent serves as a key environmental filter shaping the composition of island bird communities. Intact and long-standing forests tend to support assemblages dominated by forest specialists, which in turn harbour a higher concentration of evolutionarily distinctive and threatened species. Taken together, these patterns appear to indicate that habitat amount and continuity are major correlates of phylogenetic structure and conservation importance across islands, although island-specific histories and biogeographic context still contribute to local variation.

In line with this interpretation, phylogenetic diversity (PD) was lower in areas with greater forest cover. Standardised metrics also suggested increased relatedness among species, evidenced by negative SES PD and SES MNTD values, whereas SES MPD showed only a weak and non-significant negative trend, indicating stronger environmental filtering in more forested habitats. Community-level EDGE scores were also higher in more forested sites, reinforcing the importance of forest continuity for retaining irreplaceable evolutionary history. By contrast, associations with recent forest change were generally weaker and more context dependent, suggesting that habitat amount provides the clearest ecological signal at this scale.

4.1 | Effects of Forestation on Island Bird Phylogenetic Diversity

PD declined with increasing forest cover, and SES PD also showed a significant negative association with forest proportion (Figure 1a,b), indicating that more forested sites tended to contain assemblages that were more phylogenetically clustered than expected under null expectations. This suggests that dense forest habitats may favour species with similar ecological traits, reducing local evolutionary breadth rather than increasing the number of lineages (Dehling et al. 2014; Hanz et al. 2019). Thus, greater forest extent does not always equate to broader lineage representation. Similar patterns have been noted elsewhere, for example where parrots (Psittacidae) are largely associated with

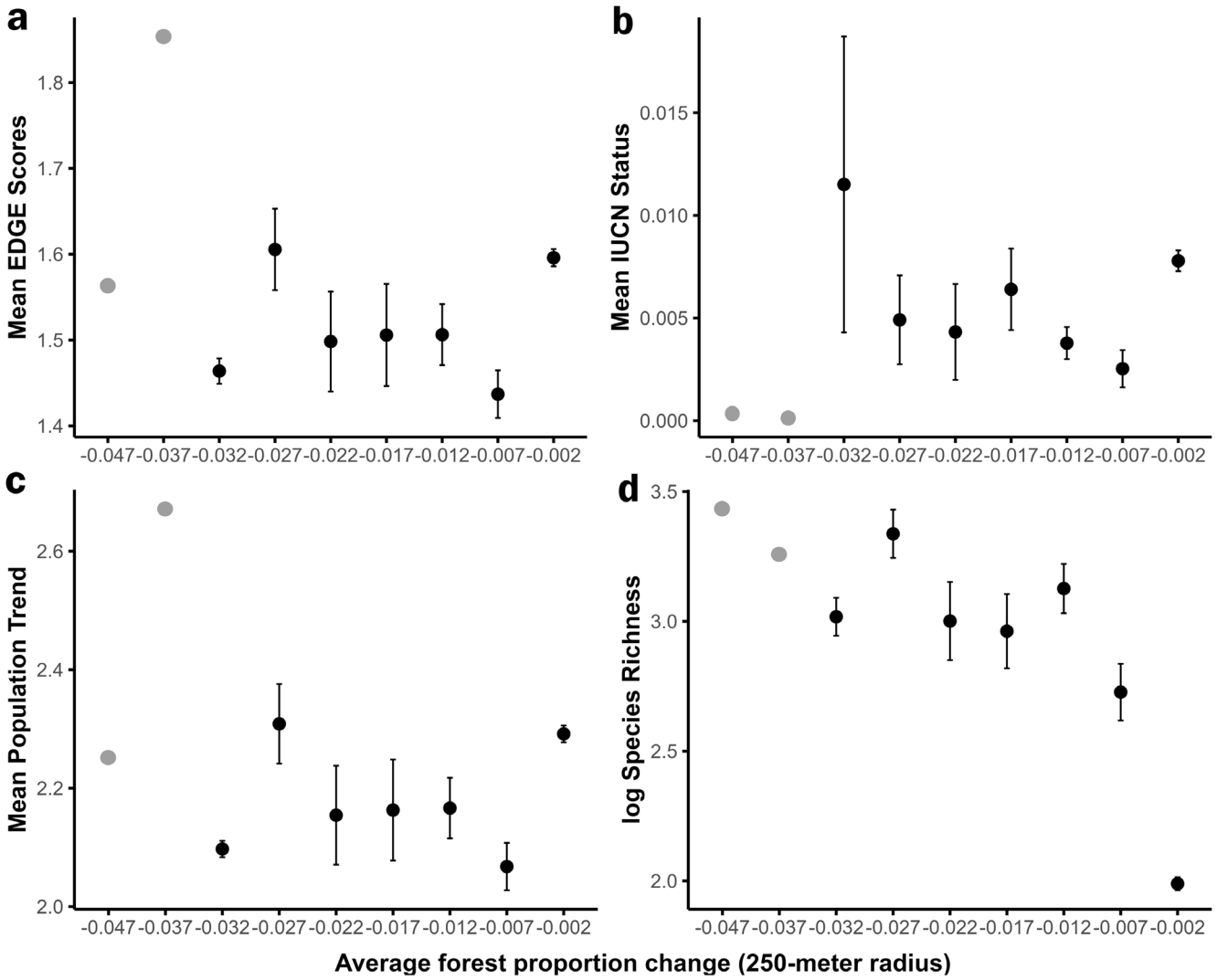

FIGURE 4 | Relationships between forest-cover change (slope 2010–2022; 250 m radius) and four community metrics across seven islands (Borneo, Buru, Buton, Sangihe, Seram, Sulawesi and Talaud). Panels show: (a) mean EDGE score (significant), (b) mean IUCN status (non-significant), (c) mean population-trend score (significant) and (d) log species richness (non-significant). Points represent forest-loss slope bin means (bin width = 0.005) ± SE for visualisation only. Statistical significance refers to the corresponding spatial linear mixed-effects models fitted to the full unbinned dataset with island included as a random intercept (Supporting Information Appendix I). Models include two Sulawesi sites with extreme forest-loss slopes, shown in grey. These bins contained single observations only and therefore do not show SE bars. The model results were qualitatively unchanged when these sites were excluded (Supporting Information Appendix I).

lowlands, whereas uplands may include more generalist groups such as tyrant flycatchers (Tyrannidae) (Hanz et al. 2019). In Buru, SES PD remained low despite relatively stable forests (Supporting Information Appendix B), which may reflect the dominance of endemic birds but relatively closely related or ecologically tolerant species such as *Philemon moluccensis* and *Dicaeum erythrothorax* (Jones et al. 2003; Marsden et al. 1997; Reeve et al. 2014).

Although MPD showed a slight positive trend with increasing forest cover in the visual summary (Figure 1c), neither observed MPD nor SES MPD showed a significant association with forest proportion in the spatial models (Figure 1d; Supporting Information Appendix F). This suggests that the positive raw MPD trend should not be interpreted straightforwardly as evidence of broader deep evolutionary structure in more forested sites. Instead, variation in SES MPD may reflect turnover within similar clades or other shifts in community composition. In Sulawesi and Buru, relatively stable community composition across forest types may be linked to the persistent dominance of groups such as Zosteropidae and Dicaeidae (Mitchell et al. 2022), which may help obscure deeper phylogenetic differentiation in the observed metric.

Trends in MNTD (Figure 1e,f) suggest that environmental filtering may favour closely related species in more forested habitats (Mitchell et al. 2022; Sobral and Cianciaruso 2016). In the spatial models, both observed MNTD and SES MNTD showed significant negative associations with forest proportion (Figure 1e,f; Supporting Information Appendix F), indicating stronger nearest-neighbour clustering in more forested sites. This pattern is consistent with the idea that less disturbed forest habitats favour assemblages drawn from more similar lineages. In Talaud and Seram, higher forest cover coincided with

increased presence of insectivorous taxa from similar clades, indicating filtering effects (Mitchell et al. 2022). In contrast, SES MNTD remained relatively stable in Borneo, Buru and Buton (Supporting Information Appendix B), likely due to within-clade replacement. In Buton, geological heterogeneity (karst and ultrabasic substrates) shapes relatively low vegetation diversity, favouring insectivores and nectarivores such as *Dicrurus montanus*, *Leptocoma sericea*, *Dicaeum aureolimbatum* and *Ducula forsteni* (Martin et al. 2012, 2017), which may contribute little to broader nearest-neighbour phylogenetic dispersion.

The contrasting patterns in PD, MPD and MNTD reflect how habitat structure, ecological filtering and historical biogeography jointly shape bird communities (Mitchell et al. 2022; Voigt et al. 2021). PD captures historical lineage diversity, while MPD and MNTD reflect phylogenetic structure at broader and shallower scales of turnover, respectively (Sobral and Cianciaruso 2016; Socolar et al. 2016). More importantly, the negative responses of SES PD and SES MNTD indicate that greater forest cover was associated with stronger phylogenetic clustering after accounting for richness effects. In Buru, dominance by flexible species such as *Dicaeum erythrothorax*, *Prioniturus mada* and *Eos bornea* suggests that increased forest cover does not necessarily ensure broader phylogenetic representation if adaptable clades prevail (Marsden et al. 1997; Mitchell et al. 2022; Reeve et al. 2014; Socolar et al. 2016).

4.2 | Impact of Forest Cover Changes on Phylogenetic Diversity

PD declined with decreasing rates of forest change (Figure 2a), and the model also detected a significant negative association with forest change, suggesting that recent forest loss may still be associated with shifts in present-day bird community composition. However, SES PD showed no significant response to forest change (Figure 2b; Supporting Information Appendix G), indicating that this pattern was not clearly distinguishable from richness-controlled expectations. This suggests that while forest change may influence the raw accumulation of lineages, it did not produce a consistent richness shift in phylogenetic structure across islands. One possible explanation is that forest degradation may remove some evolutionarily distinct species in certain settings (Russell and Kueffer 2019; Triantis et al. 2022), whereas in other cases apparently stable forests may already reflect historical filtering dominated by relatively closely related survivors (de Lima et al. 2013; Jones et al. 2003; Mitchell et al. 2022).

Although MPD increased slightly with decreasing forest loss in the visual summaries (Figure 2c,d), this relationship was not statistically significant in either the observed or standardised spatial models (Supporting Information Appendix G). This suggests that recent forest change did not consistently affect deeper phylogenetic structure across the study system. Intact or less disturbed forests may nevertheless allow the persistence of more distantly related species through niche differentiation and habitat partitioning (Lung et al. 2012; Ralph 1985; Sobral and Cianciaruso 2016), but such effects appear to be context dependent rather than general across islands. On fragmented islands such as Sangihe, for example, the continued dominance of generalist clades may help maintain relatively limited deep phylogenetic spread despite variation in forest change (Mitchell et al. 2022; Voigt et al. 2021).

Although MNTD increased with decreasing forest loss (Figure 2e), neither observed MNTD nor SES MNTD showed a significant response in the models (Figure 2f; Supporting Information Appendix G), indicating little evidence that recent forest change consistently altered nearest-neighbour phylogenetic structure beyond raw turnover. However, island-level patterns still suggest context dependence. In Sangihe and Talaud, SES MNTD tended to decline in more stable forests, which is consistent with phylogenetic clustering under persistent filtering (Mitchell et al. 2022; Socolar et al. 2016; Supporting Information Appendix C). By contrast, relatively stable MNTD in Seram and Buru may reflect greater habitat complexity or the continued dominance of tolerant species such as *Prioniturus mada* and *Philemon moluccensis* (Jones et al. 2003; Marsden et al. 1997; Supporting Information Appendix C). Taken together, these contrasting island-level tendencies reinforce that forest-change effects were weaker and more heterogeneous than those associated with forest extent.

4.3 | Forest Dynamics Drive the Phylogenetic Distinctiveness of Island Birds

4.3.1 | Forest Proportion

Community-level EDGE scores increased with forest cover (Figure 3a), indicating that more forested sites tended to support communities with higher average evolutionary distinctiveness and extinction risk. Because habitat loss disproportionately affects range-restricted species with few close relatives, it can promote phylogenetic homogenization through the erosion of distinctive lineages (Redding and Mooers 2006). On islands such as Sangihe and Talaud, where forest-dependent and range-restricted species are especially prominent, preserving forest cover is likely to be important for protecting irreplaceable evolutionary history (Triantis et al. 2022; Supporting Information Appendix D). This pattern is consistent with broader assessments highlighting the conservation importance of areas harbouring species with high evolutionary distinctiveness and extinction risk (Butchart et al. 2004; Cardoso et al. 2021).

These patterns largely reflect lowland forests, with exceptions in Sangihe and parts of Sulawesi (Supporting Information Appendix A2). Borneo is another partial exception, as its extensive and topographically complex landscape supports rich endemic biotas (Moss and Wilson 1998), but our transects sampled only part of this gradient. Consequently, strictly montane endemics on some islands may be under-represented, making our community-level EDGE estimates conservative. Nevertheless, within this predominantly lowland forest context, our findings still indicate that sites with greater forest cover tend to support communities with higher EDGE scores.

Although average IUCN status scores were low overall, more densely forested sites tended to support species with slightly higher mean extinction risk (Figure 3b), especially on small and remote islands (Supporting Information Appendix D). This suggests that intact or less disturbed forests may function as refuges for

extinction-prone species with narrow tolerances or legacies of past declines (Gray and Cavers 2014; Sodhi 2002; Symes et al. 2018).

Higher population-trend values (indicating steeper declines) occurred in areas with greater forest cover (Figure 3c), suggesting that forest-dependent species may remain vulnerable to threats such as hunting, invasive species or climate change even where forest habitat persists (Sekercioglu 2012; Symes et al. 2018). Many of these species are island endemics with small populations, implying that effective conservation may require measures beyond habitat protection alone (Russell and Kueffer 2019; Triantis et al. 2010).

In the binned visual summaries, species richness peaked at intermediate forest cover (~20%–40%) and declined in the most heavily forested areas (Figure 3d), although the corresponding mixed-model effect of forest cover was weak. This pattern may reflect a trade-off between generalist dominance in more degraded habitats and environmental filtering favouring forest specialists in less disturbed forest (Sodhi 2002). Beyond local habitat conditions, richness may also reflect broader historical and biogeographic context (MacArthur and Wilson 1963; Whittaker et al. 2017). For example, Buton's avifauna closely resembles that of Sulawesi because of the shallow straits separating them (Moss and Wilson 1998).

4.3.2 | Forest Proportion Change

Mean EDGE scores tended to be higher in areas with slower deforestation in the binned visual summary (Figure 4a), suggesting that greater recent forest stability may help retain communities with higher average evolutionary distinctiveness and extinction risk (Cardoso et al. 2021; Redding and Mooers 2006; Triantis et al. 2022; Whittaker et al. 2017). However, this relationship was not statistically significant in the model (Supporting Information Appendix I) and should therefore be interpreted cautiously. Although mean IUCN status also tended to indicate greater extinction risk in forests with slower loss (Figure 4b), this relationship was likewise not statistically significant (Supporting Information Appendix I), even if it remains broadly consistent with ecological filtering on small, isolated islands (Sekercioglu 2012; Sodhi 2002; Supporting Information Appendix E).

Steeper population declines were more apparent in forests experiencing slower recent loss in the binned visual summaries, particularly on smaller islands (Figure 4c; Supporting Information Appendix E), suggesting that species persisting in less disturbed habitats may remain vulnerable to hunting, invasive species or climate-related stressors (Sekercioglu 2012; Symes et al. 2018). In the binned visual summaries, richness was also lower in these forests (Figure 4d), which may be consistent with ecological filtering, although the overall mixed-model relationships were not statistically significant. Variation among islands (Supporting Information Appendix E) further suggests that these patterns are shaped not only by recent forest change but also by broader biogeographic and ecological influences (MacArthur and Wilson 1963; Sodhi et al. 2004; Triantis et al. 2010).

A limitation of our dataset is that sampling effort was not identical across all source studies. However, several site-level inventories were assembled from repeated point counts and multiple stations within sites, rather than from single brief visits. This likely improved inventory completeness and, in some cases, may have brought site-level inventories closer to sampling saturation. It may also have reduced, though not eliminated, differences in detectability among studies. We nevertheless acknowledge that unequal effort may still influence observed richness and other raw community metrics. SES-based phylogenetic metrics are likely to be more robust, although they are not entirely immune if detectability varies systematically among taxa, habitats or islands. Our results should therefore be interpreted as broad cross-island patterns in phylogenetic structure and conservation value, while recognising that unequal sampling effort may add noise to site-level comparisons.

Across this archipelago, forest amount and continuity emerge as dominant environmental filters shaping avian assemblages and concentrating evolutionarily distinctive, threatened lineages. Protecting large, stable forest blocks, especially on small and isolated islands, offers the greatest opportunity for maintaining community-level EDGE. Incorporating phylogenetic diversity (PD) and EDGE scores alongside species richness in spatial planning can identify high-EDGE refugia for strict protection or Other Effective area-based Conservation Measures (OECMs) (Hughes et al. 2023; Struebig et al. 2025). These priorities can align with jurisdictional REDD+ schemes and other nature-based climate finance or deforestation-free trade mechanisms (Cannon et al. 2019; Marsh et al. 2025; Struebig et al. 2025). Although our sampling focuses on lowland forests, the general pattern, greater forest continuity, higher community-level EDGE should apply broadly, with exceptions where montane endemism dominates.

Our cross-island analysis suggests that habitat amount, rather than recent change, plays a stronger role in shaping avian phylogenetic assemblages across the Malay Archipelago. Intact and long-standing forests support communities that are both evolutionarily distinctive and at higher risk of extinction. In contrast, recent forest loss exerts a weaker and more context-dependent influence on phylogenetic structure. These findings highlight the importance of forest extent and continuity in conservation strategies. Incorporating phylogenetic diversity (PD) and EDGE scores into island-level planning will be essential for safeguarding the evolutionary heritage of tropical archipelagos in the face of ongoing environmental pressures.

Author Contributions

Halvina G. Saiya conceived the study with Robert P. Freckleton and David P. Edwards; led all analyses; performed final editing/formatting; and wrote the original draft. Matthew J. Struebig, David J.I. Seaman, Nurul L. Winarni, Simon L. Mitchell, Jatna Supriatna, Rob W. Martin and Adi Karya conducted and curated field data; Matthew J. Struebig and Jatna Supriatna acquired funding. Robby Butarbutar coded taxonomy reconciliation. All authors contributed to review and editing, with substantial input from Robert P. Freckleton, David P. Edwards, Matthew J. Struebig and Simon L. Mitchell.

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Disclosure

Statement on inclusion: Our study took place on six Indonesian islands and Malaysian Borneo and involved locally based scientists (N. L. Winarni, J. Supriatna, A. Karya, R. Butarbutar and lead author H. G. Saiya); work was conducted under the relevant permits with landowner cooperation, and we will share results and archived data with local universities.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data and R code supporting this study are archived in Dryad: https://doi.org/10.5061/dryad.b5mkkwhsv.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Appendix A4.1.** Summary of model fit statistics for all spatial linear mixed-effects models. This table presents model fit statistics for all mixed-effects models fitted in the study, including models for observed phylogenetic diversity, standardised effect size (SES) metrics and conservation-related response variables. For all models, the table reports Akaike Information Criterion (AIC), Bayesian Information Criterion (BIC), log-likelihood (logLik), marginal R^2 and conditional R^2. All models were fitted with a single fixed effect (forest proportion or forest-cover change), a random intercept for island and an exponential spatial correlation structure based on site coordinates (x and y) within islands. Lower AIC and BIC values indicate better relative fit among comparable models. **Appendix A4.2**. Summary of Moran's I tests for residual spatial autocorrelation in all spatial linear mixed-effects models. This table summarises global and within-island Moran's I statistics calculated from the residuals of all spatial mixed-effects models fitted with an island random intercept and an exponential spatial correlation structure based on site coordinates (x and y) within islands. **Appendix A4.3**. Interpretation of Moran's I results for residual spatial autocorrelation in all spatial linear mixed-effects models. This table provides simplified verbal summaries of the global and within-island Moran's I results for each spatial mixed-effects model, indicating whether residual spatial autocorrelation remained after model fitting. **Appendix A4.4**. Representative residual diagnostics for the main spatial linear mixed-effects models. The plots shown here were selected not as an exhaustive set of all fitted models, but as representative examples of the models most central to the study's main hypotheses and interpretation. This appendix presents representative normal Q–Q plots and residuals-versus-fitted plots for selected spatial mixed-effects models for SES PD, MNTD and mean EDGE scores under forest cover. All models included island as a random intercept and an exponential spatial correlation structure based on site coordinates (x and y) within islands. The Q–Q plots were used to assess departures from normality, whereas the residuals-versus-fitted plots were used to inspect linearity, heteroscedasticity and unusual residual structure. These plots are presented as visual complements to the tabulated diagnostic summaries and Moran's I residual tests reported in Appendices 1d.1–1d.3, with the Q–Q plot shown on the left and the residuals-versus-fitted plot on the right.