RESEARCH ARTICLE

Bird diversity on shelf islands does not benefit from recent land-bridge connections

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Abstract

Aim: Research in island biogeography has long focused mainly on present-day island configurations. Recently, there has been an increasing focus on islands' past histories of land connection, shape and size. Moreover, continental islands (=shelf islands) have received less attention than oceanic islands, and species inventories from extremely small islands are lacking in many datasets. We examine the effects of sea-level rise since the Last Glacial Maximum (LGM) on bird species diversity and composition of tropical shelf islands in Southeast Asia.

Location: Sundaland.

Taxon: Birds.

Methods: We compiled avifaunal island inventories for 94 islands using an exhaustive literature review of historic surveys of larger islands combined with our own comprehensive island surveys from both small and large islands. Using generalised least-squares models with spatial autocorrelation, we assessed the importance of traditional biogeographical parameters including area, maximum elevation, distance from mainland and geographical isolation, along with post-LGM effects of change in island area and duration since isolation. We also compared the species composition on similar-sized shelf islands from two categories—recently submerged and unsubmerged—using non-metric multidimensional scaling.

Results: Post-LGM effects on species diversity are minimal and insular diversity is instead well explained by present-day island characteristics, such as area, distance to mainland and proportion of land surrounding an island within a 10 km radius (Cox and Snell Pseudo-$R^2 = 0.803$). Avifaunal diversity is similar across recently submerged and unsubmerged small shelf islands.

Main conclusion: Avifaunal diversity on tropical shelf islands equilibrates rapidly after isolation, indicating that both extinction and immigration rates are high. In particular, a high immigration rate of dispersive species maintains diversity, especially on small islands. Over-water dispersal is generally restricted to short distances among Sundaic birds. Consequently, the diversity of an island can be maintained by the presence of large or stepping-stone islands near it.

KEYWORDS
birds, dispersal, extinction, island biogeography, quaternary climate oscillations, shelf islands, Sundaland

1 | INTRODUCTION

Geographical patterns of species diversity have long intrigued scientists. Islands have served as natural laboratories in biodiversity research and the theory of island biogeography (MacArthur & Wilson, 1967) revolutionised the study of diversity patterns by providing a rigorous quantitative footing. The theory's main tenet is that species diversity on islands is primarily determined by island size and distance from the mainland. Generations of biologists have since dedicated their careers to refining and corroborating the predictions of island biogeography (Patiño et al., 2017). Many studies have focused on oceanic archipelagos (Valente et al., 2020; Weigelt et al., 2016; Whittaker et al., 2008), but a recent global analysis estimated that over 70% of the world's islands bigger than 1 km^2 were continental, that is, those with a mainland connection during times of global sea-level recession (Weigelt et al., 2013). Research on continental islands, also known as shelf islands, has been limited, especially in the tropics (Diamond, 1972; Heaney, 1984, 2000).

Processes underpinning diversity patterns on shelf islands differ from those of oceanic islands (=deep-sea islands; Ali, 2017; Hammoud et al., 2021; K. A. Triantis et al., 2012; Whittaker et al., 2017). Sundaland is the Earth's largest shelf archipelago and has become a natural laboratory to investigate the influence of cyclical land-bridges on island assemblages (Figure 1; Cros, Chattopadhyay, et al., 2020; Sadanandan & Rheindt, 2015). Comprising the entire Sunda shelf and bordered roughly by the present Isthmus of Kra around 9°N to the north and by Wallace's line to the east (Bird et al., 2005),

the archipelago presently encompasses approximately 17,000 islands (Whitten et al., 2004). While some of them are continental fore-arc islands formed by tectonic processes at oceanic-continental subduction zones, the overwhelming majority of them are continental shelf islands (Ali, 2017, 2018). Sitting atop the Sunda shelf, islands belonging to the latter category were all connected to the mainland during the Last Glacial Maximum (LGM) approximately 20,000 years ago when the sea level was about 120 m below present (Bintanja et al., 2005; Lambeck et al., 2014; Sathiamurthy & Voris, 2006; Voris, 2000).

Historically, the whole of Sundaland was permanently exposed as land; only ~400,000 years ago consistent subsidence of its landmass led to its partial drowning (Sarr et al., 2019). Since then, its biogeography has been governed by a highly dynamic process with sea-level change constantly altering the islands' characteristics and configurations (Husson et al., 2020; Sarr et al., 2019; Sathiamurthy & Voris, 2006; Voris, 2000). As a consequence of the uneven topology of Sundaland, there is variation in the ages of islands—here referring to the duration an island has been isolated from the mainland as a result of post-LGM sea-level rises (Sathiamurthy & Voris, 2006; Voris, 2000). In the context of small Sundaic islands, the large landmasses of Sumatra, Java and Borneo, where source populations for the islands are present, operate as mainland together with continental Asia. Furthermore, each island's historic area has considerably fluctuated and differed from those of neighbouring islands over time, largely depending on surrounding relief (Sathiamurthy & Voris, 2006; Voris, 2000). Consequently, two islands of equal size today may have differed extensively in size and level of geographical isolation during
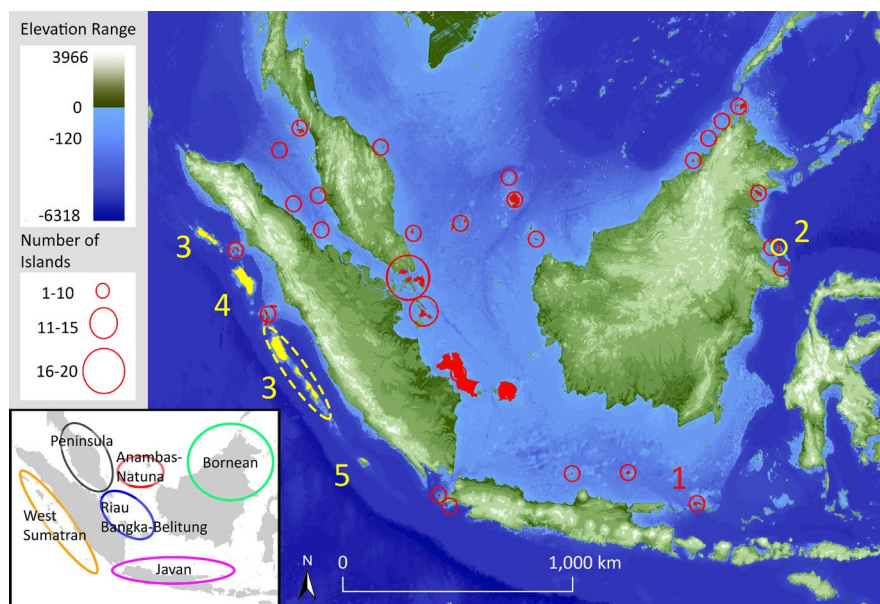

FIGURE 1 Map of Sundaland delineated by the Sunda shelf in light blue. The islands included in this study (*n* = 94) are highlighted, with deep-sea islands in yellow and shelf islands in red. Many small islands are not visible at this scale and circle sizes indicate the number of study islands within a 50 km radius. The number of endemic species-level bird taxa, if any, is indicated adjacent to islands following the same colour scheme (only one shelf island—Kangean, in the extreme southeast of the shelf—has an endemic species-level taxon) (for more details, see Table S1). In the case of the Mentawai islands (dotted yellow ellipse), three taxa are endemic to the whole island group, which forms one connected paleo-island. Inset (bottom left) refers to the island grouping scheme for the non-metric multidimensional scaling analysis (for more details, see Table S2).

various times in the past. An island that was recently connected to the mainland could be supersaturated, having a species richness higher than expected from its present-day area (Diamond, 1972; Simaiakis et al., 2017; Wilcox, 1978); by the same token, a presently small island with a vast former extent can be more diverse than expected (Simpson, 1974). In addition, during the Holocene sea-level peak merely 7000 years ago, the relative sea level in the region was about 3–5 m above the current one (Bird et al., 2007), which caused low-lying and typically small-area islands in the region to be completely submerged. Conversely, deep-sea islands (islands surrounded by sea deeper than 120 m) have vastly different life cycles as they have never experienced land connections to the mainland before (Sathiamurthy & Voris, 2006; Voris, 2000). These discrepancies in environmental history are not encapsulated by current island configurations and therefore remain unaccounted for by classical island biogeography (Norder et al., 2018). Heterogeneity in island history cannot be disregarded when studying shelf regions such as Sundaland.

To investigate the effects of past and present island characteristics on insular communities, we evaluated the species diversity and distribution of native terrestrial breeding birds on Sundaic islands. In particular, we tested the hypotheses that (1) shelf islands with a larger historical area and more recent land connection to the mainland have higher diversity; (2) shelf islands have higher diversity than deep-sea islands of a similar present-day geographical configuration; (3) the species composition of recently submerged islands differs from compositions of unsubmerged islands of similar island size class; and (4) species endemism is distributed unevenly across Sundaic islands.

Ornithological knowledge of the region is relatively comprehensive (Eaton et al., 2021; Wells, 1999, 2007). However, despite the extensive avian work that has been conducted thus far, most expeditions in the region have concentrated on bigger islands, including recent ones (Rheindt, Gwee, et al., 2020; Rheindt et al., 2019). Many surveys have been comparatively insubstantial due to the relatively standard Sundaic avifaunal assemblage—the lack of a pronounced endemic element on shelf islands has limited researchers' focus on them (Chasen, 1924, 1925). To overcome this major survey bias from the published literature, we produced novel island inventories through comprehensive field surveys. We focused on a subset of islands whose source populations have exclusively originated from large Sundaic landmasses. Palawan and its associated islands, despite their affiliations to the Sunda shelf, were not included to avoid the potential confounding effects of their zoogeographical influences from the Philippine archipelago (Bird et al., 2005; Esselstyn et al., 2010).

2 | MATERIALS AND METHODS

2.1 | Study area and island parameters

Island coastlines were obtained from the GADM database of Global Administrative Areas (version 3.6, gadm.org) with the exception of five islands absent in that database, which were traced out using Google Earth satellite imagery (Google, 2020; Table S2.1). Island area was derived from these coastline data. Distance to the mainland for each island was calculated as the shortest straight-line distance to the nearest mainland, defined as either continental Asia or the large landmasses of Sumatra, Java and Borneo. Isolation indices for each island were obtained by calculating the proportion of area covered by land at buffer distances of 10, 50, 100 and 200 km from each island's shoreline (Figure 2; metric $A17_I$ in Weigelt and Kreft (2013)).

Historical coastlines were estimated at 5-m intervals from LGM sea level to present-day sea level using bathymetric data from the General Bathymetric Chart of the Oceans GEBCO_2020 Grid (gebco.net). We calculated the historical area of each island at every 5-m interval (Figure 2). The difference between the average historical area and the present-day area was taken as the average change in area since the LGM. The existence of a shelf island was interpreted to commence after the land connection to the mainland was severed (Figure 2). Maximum island elevation was obtained from the GEBCO database. For 20 islands, the maximum elevation was estimated from Google Earth (Google, 2020) as there were mismatches between the polygons of the tiny islands and the GEBCO database. To examine the effects of the Holocene sea-level peak ~7000 years ago, we classified islands with a present-day maximum elevation ≤4 m as 'recently submerged' (Bird et al., 2007).

A proxy for isolation time since the LGM was calculated by estimating the duration for which an island was connected to the mainland as a fraction of 20,000 years (Figure 2; Lambeck et al., 2014). Deep-sea islands, which have never been connected to the mainland over the last 20,000 years, were assigned a value of 0%. The island of Siberut, whose possible connection to the mainland via a narrow land bridge during the LGM remains ambiguous (Abegg, 2002; Batchelor, 1979; Sathiamurthy & Voris, 2006; Voris, 2000), was assigned a value of 1%. Since shelf islands classified as 'recently submerged' have not experienced any mainland connection since their re-emergence, their duration of mainland connection was set to 0%.

2.2 | Island bird inventories

Bird species inventories were compiled for each island from a comprehensive assessment of published species lists. Although methods have been proposed to account for uneven survey effort (Pardo et al., 2013; Santos et al., 2010), we instead excluded islands with poor sampling to preclude bias (Weigelt & Kreft, 2013; Tables S1.7 and S2.2). We removed islands on which there were no records of multiple widespread species that are highly unlikely to be absent based on the islands' size classes. Islands for which poor collecting conditions were noted in the primary literature were also excluded. To reduce the confounding effects of anthropogenic extinctions that prevail throughout islands in the region (Sodhi, Wilcove, Lee, et al., 2010; Symes et al., 2018; Verma et al., 2020), islands described to have been heavily ecologically altered at the time of survey were also filtered out.
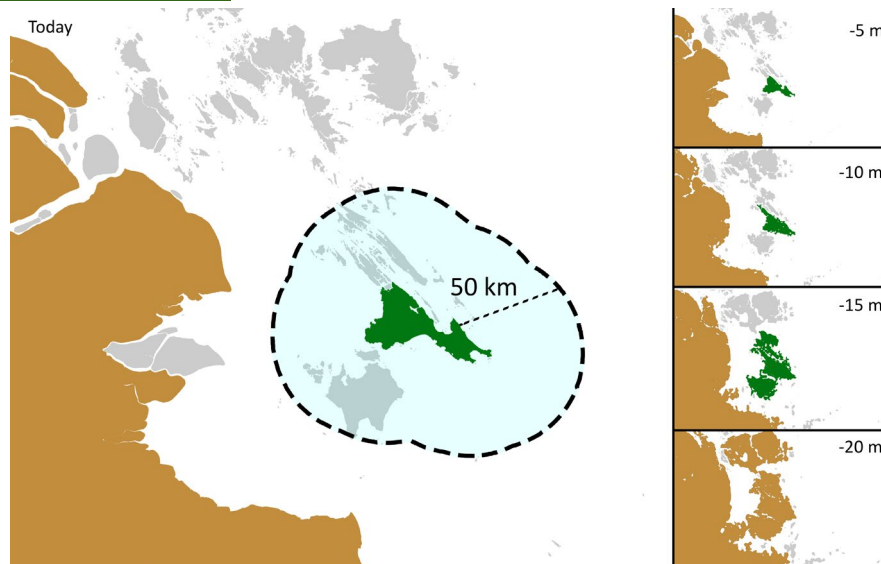
FIGURE 2 Illustration of geographical parameters calculated for an example focal island, Lingga, in green, with the mainland, Sumatra, in brown. The buffer area shown in the main panel encompasses land and water within a distance of 50 km. The isolation index was obtained by calculating the proportion of the buffer area (light blue) covered by land (grey). Panels on the right show the coastlines at sea levels of 5–20 m below present, with the historical coastlines of Lingga in green. Lingga was connected to the mainland when the sea level was 20 m below present; the isolation time was estimated by taking the time corresponding to the sea level being 15 m below present following Lambeck et al. (2014)

Comprehensive avifaunal surveys focusing on small islands <10 km^2 were led by YCKS from June 2019 to January 2020 (30 islands in the Riau region; Tables S2.1 and S2.2). Of the ~2000 islands in the Riau region, islands were selected based on accessibility by boat and proximity to inhabited islands. Islands dominated by mangroves were avoided due to poor accessibility. Those with clear signs of anthropogenic damage, with scarcely any remnant natural vegetation, were also avoided. Due to the lack of suitable trails for systematic counts, we walked through the islands as conditions permitted and recorded all birds detected (Sodhi, Wilcove, Lee, et al., 2010). Playback trials of potential resident birds were conducted during all surveys and ceased once a particular species was detected. Inventory completeness was assessed by constructing species accumulation curves using the R package 'vegan' 2.5-6 (Oksanen et al., 2019). The inventories were supplemented with surveys led by FER from 2015 to 2020 (five islands in the West Sumatran region; refer to Rheindt, Gwee, et al., 2020; Rheindt et al., 2019).

We followed Eaton et al. (2021) for taxonomy on Indonesian birds and Gill et al. (2020) for the remaining species (n = 11). Introduced, nocturnal, aquatic, pelagic and coastal species, as well as those not breeding on these islands (migratory species and flyby birds of prey), were excluded. While the avifauna of Southeast Asia is relatively well understood, deep genomic divergences and cryptic species continue to be discovered with advances in research (Chua et al., 2015; Cros, Chattopadhyay, et al., 2020; Gwee et al., 2019, 2020; Lim et al., 2019; Manawatthana et al., 2017; Ng et al., 2021). As an underestimation of endemism could bias the analysis (Gray & Cavers, 2014), we adjusted species

delimitation based on these most recent insights (Tables S1.5 and S1.6).

2.3 | Statistical analysis

2.3.1 | Factors affecting species diversity

We used island characteristics (area, distance to mainland, isolation index, maximum elevation, average change in area, isolation time, submerged status, deep sea vs. shelf island) as predictors for native species richness. All numerical variables were $\log_{10}$ transformed prior to analysis. Isolation index, average change in area and isolation time were $\log_{10}$ transformed after adding 0.1 to avoid taking the logarithms of zero. As spatial autocorrelation among closely distributed islands had to be accounted for, we used the *gls* function in R package 'nlme' (Pinheiro et al., 2013) to apply generalised least-square models (Beale et al., 2010). Models were fitted with and without the spherical autocorrelation structures for all possible combinations of the explanatory variables using the *dredge* function in R package 'MuMIn' (Barton, 2020). We used the Akaike Information Criterion (AIC) to select the best models, and the set of models with ΔAIC <2 from the model with the lowest AIC score were selected (Burnham & Anderson, 2002) and the pseudo-R^2 of the best set of models was calculated using the R package 'rcompanion' (Mangiafico, 2017).

Climatic variables were not included in our analysis as they are largely similar across the Sundaic islands (Weigelt et al., 2013). The impacts of historical climate on species diversity have been shown to

be weak in other archipelagos (Dalsgaard et al., 2014; Weigelt et al., 2016) and their effects would likely either be minimal or uniform across the islands in our study area as well.

2.3.2 | Factors affecting species distribution

Our dataset presented a unique opportunity to distinguish between two basic island biogeographical mechanisms—immigration and extinction (MacArthur & Wilson, 1967). The diversity of recently submerged islands should generally reflect immigration as all bird populations on an island would have been extirpated when the island sank, whereas the diversity of similar-sized islands that have not been submerged should reflect a balance between immigration and extinction since the LGM. We thus compared species composition among small islands that have been recently submerged and those that have not. We focused on small islands to control for area effects: we extracted a subset of all shelf islands smaller than the largest recently submerged island (hereafter we refer to this as the small-island dataset). To investigate the drivers of species assemblages, we carried out non-metric multidimensional scaling (NMDS) ordination on the species presence–absence matrix of the small-island dataset using a Bray–Curtis dissimilarity coefficient with the *metaMDS* function in the R package 'Vegan' (Oksanen et al., 2019). To account for the effects of different landmasses having provided the source populations for each island, we classified islands into groups based on their geographical location (Figure 1; Table S2). We then used vector fitting to quantitatively characterise the correlation among various island characteristics ($\log_{10}$ transformed) with the observed pattern (Dargie, 1984).

All analyses were conducted using ArcMap 10.4 (ESRI, 2016) and R version 3.6.1 (R Development Core Team, 2019).

3 | RESULTS

The initial dataset included 182 islands. Seven islands surveyed by us were excluded from the analysis as their species accumulation curves did not plateau. After filtering for poor inventories, the final dataset totalled 94 islands and 322 bird species, 18 of which were island or island-group endemics (excluding nocturnal species; Figure 1; Table S1.1; Figure S1). Island sizes ranged from 0.00260 to 11,654 km^2 (Panggal Kecil and Bangka respectively, both from the Riau-Bangka Belitung island group; Table S2.1). A small proportion of islands were deep sea, with all but one of these belonging to the West Sumatran islands (Figure 1; Table S2).

Deep-sea islands, with the exception of two islands of small size (Lasia = 14.9 km^2; Babi = 45.8 km^2), all harboured endemic species-level taxa. Conversely, only one shelf island carried an endemic according to the taxonomic treatment we followed (Figure 1).

A single best model had a ΔAIC value <2.0 relative to the other models (Table 1; Tables S3.1 and S3.2). The best model suggested that island area, distance to mainland and isolation index at a 10 km

TABLE 1 Model statistics for the best generalised least-squares (GLS) model of avian diversity for all study islands (n = 94). Cox and Snell Pseudo-R^2 = 0.803. GLS$_{best}$: AIC = −3.79, GLS$_{null}$: ΔAIC = 127.6

Predictors	Estimate
(Intercept)	0.180
$\log_{10}$(area)	0.246
$\log_{10}$(distance)	−0.135
$\log_{10}$(isolation_10km)	0.107

buffer distance (isolation_10km) most appropriately explained island species richness, in decreasing order of importance (Figure 3; Table 1). The three parameters were weakly correlated (Table S3.3).

The small-island dataset comprised 42 shelf islands and 88 bird species, with the biggest recently submerged island being 4.09 km^2 in area (number of recently submerged islands = 19, unsubmerged islands = 23). The majority of islands in the small-island dataset were from the Riau-Bangka Belitung, Bornean and Peninsular island groups and the NMDS plot showed that species composition among recently submerged and unsubmerged islands was similar (Figure 4). The ordination had two dimensions (stress = 0.162) and composition among these islands was best explained by isolation_10km (r^2 = 0.476, p = 0.001) and island group (r^2 = 0.419, p = 0.001). The submerged status of an island was not a statistically significant predictor (r^2 = 0.018, p = 0.512). Species distribution among the small-island dataset was highly skewed, with 80.7% of species absent from over 80% of the islands (Figure 4; Table S1.2).

4 | DISCUSSION

Our key finding is that the historical characteristics of islands in Sundaland have little effect on present-day bird diversity. For equal-sized islands, diversity was similar irrespective of their duration of isolation, which implies rapid extinction on islands following a decrease in area. These results contradicted our hypothesis that shelf islands with a larger historical area and more recent land connection to the mainland would have retained a higher diversity as a legacy of their historic properties, and that shelf islands have a higher diversity than deep-sea islands of similar present-day geographical configuration. Whether a small shelf island was recently submerged or not did not affect species diversity either, contradicting our third hypothesis. Moreover, species composition was similar comparing between these two classes of islands, indicating that the subset of species common on the two groups of islands can rapidly colonise new islands. The observation that the proportion of land within a 10 km buffer was a significant predictor of diversity demonstrates that even for a relatively mobile taxonomic group like birds, overwater dispersal is typically restricted to short distances. While our data indicate that historical characteristics of an island have little effect on bird diversity, the same does not hold for endemism: most island
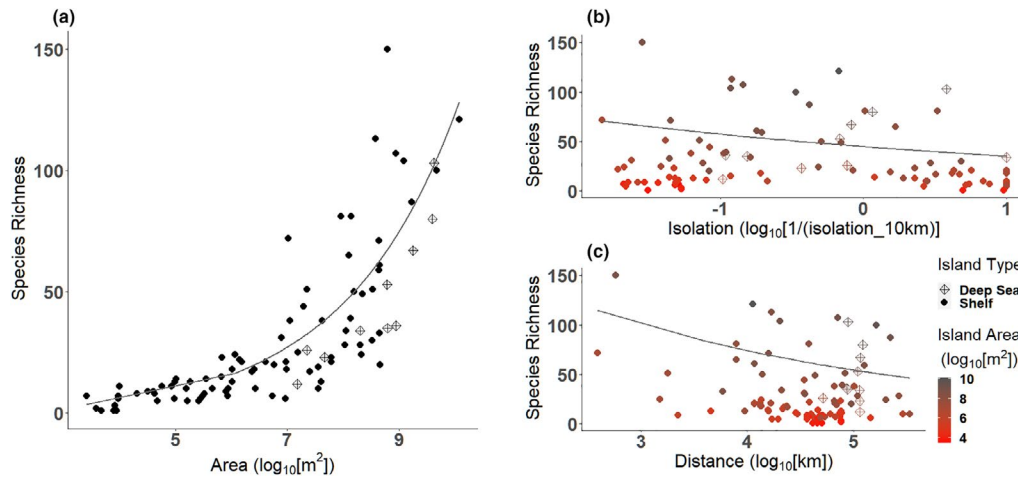
FIGURE 3 Relationship of avian species richness on Sundaic islands ($n = 94$) with (a) island area, (b) island isolation index at 10 km buffer distance (isolation_10km) and (c) distance from mainland, using the best generalised least-squares model—$\log_{10}$(species richness) ~ $\log_{10}$(area) + $\log_{10}$(distance) + $\log_{10}$(isolation_10km). Each graph is drawn by controlling for all other covariates in the best generalised least-square model by taking their averages.

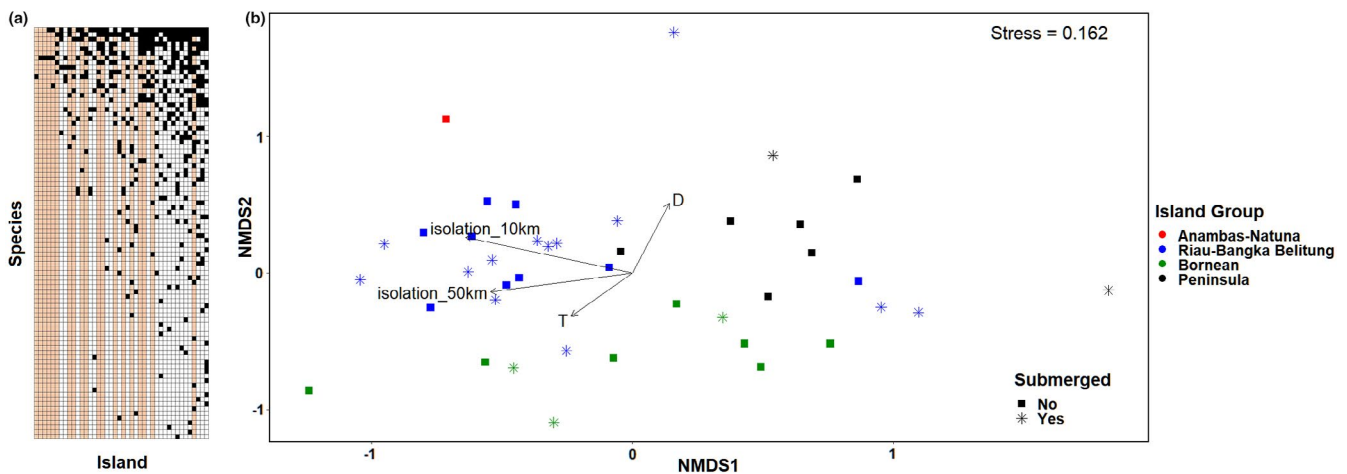**FIGURE 4** (a) Illustration of the species presence–absence matrix in the small-island dataset (n species $= 88$, n island $= 42$). Each cell represents the status of a species on an island where black indicates presence and an empty cell indicates absence. Recently submerged islands are highlighted in orange. The species are ordered by commonness and islands are ordered by species richness. (b) Non-metric multidimensional scaling (NMDS) of the small-island dataset based on the species presence–absence matrix with the significant environmental vectors at $p < 0.05$ shown. (*D*: distance from mainland, *T*: isolation time, *isolation_10km* and *isolation_50km*: isolation indices at 10 and 50 km buffer distance, respectively)

endemics were found on deep-sea islands with no historic land connection to the mainland, aligning with our fourth hypothesis.

4.1 | Rapid extinction leads to diversity loss soon after isolation

Theory predicts that islands with a historically larger area or past connection to the mainland may retain greater species diversity than similar islands with a more stable history (Diamond, 1972; Simaiakis et al., 2017; Simpson, 1974; Wilcox, 1978). This expectation is based on a process akin to extinction debt (Halley et al., 2014): loss of area and increased geographical isolation shifts the balance between extinction and colonisation processes (MacArthur & Wilson, 1967);

however, it takes time for diversity to reach its new, lower equilibrium. During the last 3–4 glacial maxima, the most recent one of which occurred ~20,000 years ago, the shelf islands of Sundaland were part of a large subcontinental expanse of land. Sundaland was broken up into its present archipelagic layout following the rapid rise in sea level since the LGM. Therefore, present-day diversity patterns may be expected to retain the signal of past island configuration and duration of land connections.

However, contrary to expectations, we did not find evidence for an effect of the historical geographical configurations of islands in Sundaland on present-day bird species diversity. Neither isolation time nor average change in area were included in the best model (Table 1; Table S3.2), indicating their poor explanatory power. This result implies that islands of similar size and present geographical

isolation exhibit similar diversities even if one of them had enjoyed ample continental connectivity during the last 20,000 years compared to the other. Moreover, despite recurring connection to the mainland, shelf islands were not more species-rich than deep-sea islands of similar geographical characteristics. Instead, our data show that species richness on shelf islands and deep-sea islands exhibit similar relationships to area and present geographical isolation (Figure 3; Table 1). All else being equal, a decrease in island area by a factor of 10 leads to a diversity drop of ~57% (Table 1).

Our result implies that local extinction of bird species occurred soon after islands were disconnected due to rising sea levels and shrank, with equilibration likely occurring within a few thousand years. A combination of factors may contribute to the high natural extinction rates that drive patterns of species diversity on these dynamic islands. One of them may be the small overall composite area of islands across Sundaland; the vast majority of the ~17,000 Sundaic islands are much smaller than 100 km^2 (Weigelt et al., 2013; Whitten et al., 2004). The population density of birds compared to other animal groups such as reptiles and insects is generally low. Their correspondingly low population sizes for any given initial island area possibly accelerate extinctions after a decrease in area to cause species diversity to equilibrate rapidly (Ricklefs & Lovette, 1999). As a result, the diversity that may have built up on these now-small islands over the course of their extensive existence as part of the mainland could have easily diminished within a short time frame after mainland connections disappeared (Diamond, 1972; Heaney, 1986).

Our observations are similar to patterns in Sundaic mammalian fauna, where diversity is unaffected by isolation time (Heaney, 1984). However, they contrast with the supersaturated diversity of lizards on land-bridge islands in Baja California (Wilcox, 1978) and with certain avifauna on the satellite islands of New Guinea (Diamond, 1972). Working on a purely oceanic island dataset, Weigelt et al. (2016) demonstrated that past geographical island attributes are similarly inconsequential to the native angiosperm diversities of islands with differing historic extents. Our study—perhaps surprisingly—extends this notion even to the class of shelf islands despite their extremely different geologic history from oceanic islands. We here show that, at least in birds, shelf islands and deep-sea islands behave similarly in terms of species richness as long as their diversity stems from a similar source population (Figure 3; Table 1).

4.2 | Stepping-stone islands counteract effects of distance to mainland

Our data indicate that distance to the mainland alone does not sufficiently capture the effects of isolation on species diversity. An increasing distance from the mainland, unsurprisingly, results in an island having a lower species diversity (Figure 3c; MacArthur & Wilson, 1967). In addition, at similar distances from the mainland, isolated islands tend to be more species poor than those in close proximity to other islands (Figure 3b). Low isolation, specifically the

presence of other nearby islands, can boost a focal island's diversity by providing additional potential source populations or serving as stepping stones (Dalsgaard et al., 2014; Gilpin, 1980; MacArthur & Wilson, 1967). A variety of metrics have been presented to quantify the level of an island's isolation (Itescu et al., 2020; Weigelt & Kreft, 2013). Incorporating the effects of proximity to other landmasses, regardless of whether they are considered part of the mainland, emerged as a powerful predictor of diversity in our work (Figure 3; Table 1) and should continue to be included in future diversity studies.

The proportion of land within a 10 km buffer distance emerged as the best isolation index compared to larger buffer distances (Table 1; Figure 3b). This short buffer distance puts the scale of overwater dispersal in Sundaic birds into perspective: although birds are thought to be one of the most vagile animal groups, this result suggests that overwater dispersal mostly occurs across relatively short distances among the resident regional birds. Many tropical species are reluctant to fly across ecological barriers such as waterbodies and in some, even just habitat fragmented by road (Cros, Ng, et al., 2020; Develey & Stouffer, 2001; Laurance et al., 2004; Moore et al., 2008; Sadanandan & Rheindt, 2015). The maintenance of diversity on islands is highly reliant on the presence of larger or stepping-stone islands within close proximity.

4.3 | Highly dispersive species rapidly colonise new, small islands

The present warm inter-glacial period is thought to have undergone its peak at about 7000 years ago, leading to an all-time high at 3–5 m above the current sea level (Bird et al., 2007). Low-lying islands would have been completely inundated at the time; their present-day species assemblages can safely be assumed to have originated entirely from colonisers, as opposed to assemblages on other islands, whose communities may be a combination of colonisers and surviving populations from the time of continental land connection. Yet, both species diversity and composition were similar across similar-sized submerged and unsubmerged islands in our small-island dataset (Table 1; Figure 4b). Using the avifauna on recently submerged islands as a baseline for dispersive species, our results indicate that only a subset of species are capable of long-term survival on small islands, chiefly those with a high colonising capability (Figure 4).

We infer that a high immigration rate of strongly dispersive species has shaped the diversity of small Sundaic islands. In post-LGM Sundaland, rising sea levels have increasingly isolated islands from one another. As islands shrink, they become more unstable and populations become more prone to extinction (Burkey, 1995; Pimm et al., 1988). Inevitably, the smallest islands will converge on a set of species with the highest dispersal capability as they are the ones able to successfully re-colonise islands that are undergoing constant extinction events.

The highly skewed species distribution across both island classes is a further testament that persistence on small islands is dominated

by a subset of strongly dispersive species (Figure 4a). While only a fifth of the species were present in >80% of the islands, only one species (pied imperial pigeon *Ducula bicolor*) was an island specialist: a classic supertramp of Diamond (1974). A majority of the species instead perform well on the mainland too, with most of them inhabiting coastal or mangrove forests, or highly disturbed habitats such as secondary forests and parks (Tables S1.2 and S1.3; Wells, 1999, 2007). It follows that diversity on small islands is maintained by repeated colonisation from the mainland and constant exchange among the small islands.

There has been no direct study of the difference in colonisation capabilities of birds in Sundaland, perhaps with the exception of Krakatau, where arrivals of land birds and other organisms have been carefully documented since the island volcano's catastrophic eruption in 1883 (MacArthur & Wilson, 1967; Thornton et al., 1988, 1993). Ringing records have provided information regarding certain species' dispersal abilities (Wells, 1999, 2007) and recent molecular work has added insights (Cros, Ng, et al., 2020; Sadanandan & Rheindt, 2015; Tang et al., 2016). Our results further improve our understanding of the ecological traits of the Sundaic avifauna by highlighting those species that are capable of accomplishing the feat of surviving on small islands.

4.4 | Land-bridge connections counteract the build-up of endemism

Quaternary processes such as cyclical sea-level fluctuations and glaciations are known to be of immense importance in the accumulation of genetic differentiation and endemism (Cros, Chattopadhyay, et al., 2020; Ericson et al., 2019; Garg et al., 2018; Hammoud et al., 2021; Norder et al., 2019; Rheindt, Prawiradilaga, et al., 2020; Weigelt et al., 2016). The results of our study support these findings in that only deep-sea islands exhibited any appreciable endemism (Figure 1). Such a pattern is observed despite the presence of many shelf islands that are currently more geographically isolated than the deep-sea islands in our dataset. Maratua island is a case in point— despite its geographical proximity to Borneo compared to other shelf islands, such as those from the Anambas-Natuna group, it still harbours endemics unlike the numerous shelf islands (Figure 1); all shelf islands in our dataset were part of the mainland on the order of only a few thousand years ago, precluding any deep genetic isolation of their avifauna. Furthermore, some of the deep-sea islands such as Maratua and Enggano host endemic species despite being smaller than many shelf islands (two and five species, respectively; Figure 1). Unlike shelf islands where extinction kicks in soon after their disconnection from the mainland, the sizes of many deep-sea islands are relatively stable (Sathiamurthy & Voris, 2006; Voris, 2000). The presence of deeply diverged lineages on deep-sea islands is a testament of the persistence of resident populations of successful colonisers.

The patterns of diversity and endemism observed in our results parallel those in other animal groups in Sundaland (Harrison et al.,

2006; Wilting et al., 2012). However, there are differences in dispersal mechanisms and life history among animals groups (Ali & Vences, 2019; Ricklefs & Lovette, 1999), and Sundaic island biogeography will benefit from future studies focusing on additional taxa. Because of their ability to fly, birds are generally thought of as being more dispersive than most other animal groups. Yet with the exception of the subset of highly dispersive species, our results support the view that long-distance overwater colonisation is in general unsuccessful in resident Sundaic birds.

4.5 | Crucial inventories for future island biogeography research

The study of island biogeography is heavily reliant on rigorous checklists and species inventories. Many studies have benefited from published datasets, and citizen science data are increasingly becoming a powerful engine to drive such research (La Sorte & Somveille, 2020; Sullivan et al., 2009). Yet although birds are the most well-studied animal group in the world (F. B. Gill, 2006; Troudet et al., 2017), many bird island inventories thus far have been restricted to model archipelagos; thorough inventories from small Sundaic islands have so far been lacking. Our study supplies over two-dozen novel inventories from among the most geologically exciting archipelagos in the world, providing reliable census results for one of the world's major playgrounds for island biogeography research. We also compiled reliable historic surveys that can serve as crucial data in future work.

Many species in the region have been experiencing rapid range expansions within recent historical times (Hutchinson & Mears, 2006; Lok & Subaraj, 2009; Low et al., 2016; Wang & Hails, 2007; Wells, 1999, 2007). Simultaneously, extinction is plagueing biodiversity in the region, with immense effects on isolated islands (Sodhi, Wilcove, Lee, et al., 2010; Sodhi, Wilcove, Subaraj, et al., 2010). The results from our surveys provide a wealth of updated baseline data for future works.

5 | OUTLOOK

With ~17,000 islands of varying history and sizes, Sundaland has great potential to serve as a hotspot for island biogeography research. As the natural history of many avian species in the region is relatively well known, vegetation surveys will be beneficial in supplementing information to assimilate methods such as the Choros model that factors in habitat diversity (K. Triantis et al., 2003; K. Triantis et al., 2005). Vastly varying island sizes across the archipelago bring to attention the possibilities of investigating the small-island effect, where diversity below a certain island area plateaus instead of following a typical species–area relationship (Chisholm et al., 2016; Panitsa et al., 2006; K. Triantis et al., 2006). However, the number of island-specific inventories for other taxonomic groups in the region is either scarce or contains large knowledge gaps (Das & van Dijk, 2013; Grismer & Aun, 2008; Okie & Brown, 2009).

Increasing research is being put into consolidating various sources of information (Joyce et al., 2020; Orr et al., 2021) and it is hoped that an increase in reliable fine-scale data will allow similar works to be conducted across different taxonomic groups. Pronounced differences in dispersal capabilities and life history will no doubt add insights in to our understanding of biogeographical mechanisms (Brown, 1971; Hammoud et al., 2021; Hausdorf & Hennig, 2005). For example, the species composition between recently submerged and unsubmerged small islands might differ in less dispersive taxonomic groups.

Using multiple approaches, our study identifies key factors defining island biogeographical patterns of avian species richness, composition and endemism in Sundaland. Rapid extinction on islands is a strong driver of regional diversity patterns; many species are rapidly pushed to extinction once an island is severed from the mainland and shrinks due to rising sea levels. However, a high immigration rate of a subset of strongly dispersive species helps maintain diversity, especially on smaller islands. For most species, overwater colonisation across Sundaland is limited to short geographical distances, resulting in endemism on isolated deep-sea islands.

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CONFLICT OF INTEREST

The authors declare that there is no conflict of interest.

DATA AVAILABILITY STATEMENT

Island parameters and inventories used in this study and model statistics are all available in Supporting Information.

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BIOSKETCH

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SUPPORTING INFORMATION

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