



# Avian functional diversity retained in a tropical rainforest fragment after more than 120 years of turnover

Bing Wen LOW<sup>1</sup> · Shelby Qi Wei WEE<sup>1</sup> · Malcolm Chu Keong SOH<sup>1</sup> · Kenneth Boon Hwee ER<sup>1</sup>

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## Abstract

Deforestation is linked to the increasing prevalence of small forest fragments worldwide and an associated loss in functional diversity. However, our long-term understanding on how biodiversity and functional roles respond in such isolated fragments is limited, especially in Southeast Asia. We compared the bird community in a small primary rainforest fragment in the Singapore Botanic Gardens, a UNESCO World Heritage Site, using historical records in 1898 and contemporary surveys conducted in 1998 and 2018–2021. Species composition was expectedly dissimilar between the 1898 and contemporary bird communities (50%), driven mostly by turnover (45.5%) rather than nestedness (4.5%). Despite the changes in community composition and species extirpations, both species richness and functional diversity were retained. Our results suggest that small forest fragments can form novel bird communities that are functionally similar to previous communities that inhabited the fragment, leading to the retention of functional diversity. Such functional redundancy may be encouraged through habitat restoration initiatives adjacent to fragmented forests.

**Keywords** Bird communities · Rainforest · Functional diversity · Feeding guilds

## Introduction

Tropical forests are one of the most diverse ecosystems in the world and harbour more than half of the world's known species (Wilson 1988; Wright 2005). These forests contain 62% of all terrestrial vertebrate species, of which up to 29% are endemic to tropical forests (Pillay et al. 2021). Despite providing critical refugia for biodiversity, large areas of tropical forests have been lost, largely due to agriculture, forestry, and urbanization (Achard et al. 2014; Lewis et al. 2015; Song et al. 2018). This has led to widespread forest fragmentation with significant impacts to biodiversity (Gibson et al.

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✉ Bing Wen LOW  
low\_bing\_wen@nparks.gov.sg

<sup>1</sup> National Parks Board, 1 Cluny Road, Singapore 259569, Singapore

2011; Haddad et al. 2015; Fischer et al. 2021). Between 9–11% of formerly forested tropical landscapes typically contained small forest fragments between 13–17 ha in size (Taubert et al. 2018). In the next 50 years, under current deforestation rates, the number of fragments is projected to increase 33-fold with a reduction in mean fragment size to 0.25 ha (Taubert et al. 2018). This trend of decreasing fragment size with sustained deforestation also applies to protected areas (Hansen et al. 2020). Greater conservation attention should be paid to small forest fragments, particularly in landscapes where these represent the remaining forest habitat. Preservation of tropical forests including small fragments is pertinent to attain the 2020-Global Biodiversity Framework's 30 by 30 commitment to protect and manage 30% of habitats globally by 2030 (Riva et al. 2022).

In the absence of large forest tracts, small forest fragments can provide important habitats for biodiversity in highly degraded landscapes (Turner and Corlett 1996; Tull-och et al. 2016; Wintle et al. 2019; Volenec and Dobson 2020). The conservation value of these fragments is influenced by the surrounding landscape matrix, presence of habitat corridors, and the extent of connectedness to other habitat fragments (Arroyo-Rodríguez et al. 2020). Lowering the contrast in the landscape matrix (de Souza et al. 2022; Ramírez-Delgado et al. 2022) and increasing connectivity between forest fragments can facilitate dispersal and prevent extirpation of isolated populations (Taylor et al. 1993; Rosenburg et al. 1997).

Increasingly, functional diversity is considered a more informative metric than species richness in evaluating the conservation value of forests, since it reflects the utilisation of habitats by wildlife (Zambrano et al. 2019) and quantifies the range of ecological functions provided by communities as predicted by morphological traits. Changes in functional diversity of a community in response to habitat disturbance are therefore dependent on constituent species' morphological traits and their ecological functions (De Coster et al. 2015; Dehling et al. 2016). Birds are well-suited to studies in functional diversity studies as they are easily studied, possess a wide range of well-characterised morphological traits and perform a multitude of ecological functions in various ecosystems globally (Sekercioglu 2006; Alexander et al. 2019). For example, in the rainforests of southern Chile, the functional diversity of birds in secondary forests was lower than old growth forests, probably due to the lack of natural tree cavities in the former (Fontúrbel et al. 2022). A recurring theme in this field of research is the concept of functional redundancy, where the maintenance of ecological roles within an ecosystem is maintained despite changes in species richness (Walker 1992; Diaz and Cabido 2001). Greater functional redundancy is associated with improved ecosystem stability and has been documented in both protected forests and reforestation sites in various landscapes (Ikin et al. 2019; Oliveira and dos Anjos 2022).

Aside from the Neotropics where studies of avian functional diversity have been conducted in the Brazilian Atlantic Forest and Brazilian Amazon (Mariano-Neto and Santos 2023; Coddington et al. 2023), information regarding the long-term (i.e., > 50 years) persistence of bird communities and associated changes to functional diversity in isolated forest fragments in Southeast Asia is lacking. This is due to the dearth of comparable historical data associated with isolated forest fragments in this biodiversity and deforestation hotspot (Myers et al. 2000; Sodhi et al. 2004a, b; Estoque et al. 2019). Only two Southeast Asian studies to our knowledge have assessed the long-term implications of avian communities in isolated forest fragments. Both studies involved the 86 ha Bogor Botanical Gardens (BBG) in Java, Indonesia and found that larger, forest-dependent birds were more prone to extirpation (Diamond et al. 1987; Sodhi et al. 2006).

Besides BBG, a 6 ha primary rainforest fragment at the Singapore Botanic Gardens or SBG (hereafter, SBGR with reference to the forest fragment) has historical data of its avian community dating back to 1898. This fragment was re-surveyed between 1997 and 1999 (referred to as the 1998 survey) (Sodhi et al. 2005). Between 1898 and 1998, the avian community in SBGR had lost 18 species (49%) and gained 20 species and the species composition resembled that of a young secondary forest fragment in Singapore (Sodhi et al. 2005). Data from recent field surveys provide a unique opportunity to examine the bird species turnover at the SBGR over 123 years, potentially making this the longest interval study of any tropical forest fragment in Southeast Asia.

Here, we examined changes in the bird community across three time periods over 123 years—1898 (Ridley 1898), 1998 (Sodhi et al. 2005), and 2018–2021 (present study). We also compared SBGR's bird community to that of two other forest fragments in Singapore—(a) Bukit Timah Nature Reserve (BTNR), a larger forest fragment which comprises of both primary and mature secondary rainforest, and (b) Tyersall Learning Forest, a nearby patch of secondary forest within the grounds of the SBG. This comparison was undertaken to determine if the SBGR bird community at different time points was more similar to a larger primary and mature secondary rainforest fragment in Singapore (BTNR), or a younger secondary forest (Tyersall Learning Forest). We predicted that the contemporary bird species richness in the SBGR would be similar to the 1898 community but differ in species composition and would not resemble the bird community found in BTNR. We also predicted that among the birds in SBGR, species that are larger, from specialist foraging guilds and with smaller wing length to tarsus ratios would be more prone to extirpation. We expected high community turnover in SBGR and predicted that the functional diversity would remain similar as new species with comparable traits colonise the fragment (Ikin et al. 2019; Oliveira and dos Anjos 2022).

## Methods

### Study sites

The SBG is one of the oldest botanic gardens in Southeast Asia. The SBGR (1.3112° N, 103.8162°), measuring 6.2 ha, has been isolated for more than 170 years with the nearest tract of primary forest, the Central Catchment Nature Reserve, located about 3 km away (Fig. 1) (Turner et al. 1996; Sodhi et al. 2005).

Our other study site is the 10 ha Learning Forest (henceforth, LF), located about 500 m away from the centre of SBGR. The site on which LF is currently situated was largely cleared by the 1860s and subsequently replanted in the 1920s as a rubber plantation. The forest has been regenerating over the past century and today it is a secondary forest dominated by trees such as *Syzgium grande*, *Rhodamnia cinerea* and *Prunus polystachya*. The site was restored as an extension of the SBG in 2017 (Fig. 1).

Data collected from our current and historical surveys were compared against a recent bird survey conducted at BTNR. In Singapore, primary rainforest occupies less than 0.5% of the country's land area due to large-scale forest clearance since 1819 (Corlett 1992; Yee et al. 2011). This 163 ha reserve encompasses almost 120 ha of primary rainforest (Yee et al. 2011, 2019), making it one of the most important habitats for forest birds in Singapore. As part of this survey, surveyors had concurrently surveyed four 1 km long transects along the reserve's trail network once a month for a year (Lim 2019).



**Fig. 1** Overview of Singapore and where the Singapore Botanic Gardens (SBG) is situated in relation to Bukit Timah Nature Reserve (BTNR). The insert shows the location of the Singapore Botanic Gardens Rainforest (SBGR) and Learning Forest (LF) as well as the associated survey transects within the wider SBG

## Survey methods

Prior to our study, the bird community in SBGR had been surveyed in 1898 and 1998. The former are the detailed personal observations of H.N. Ridley, the first director of the SBG, while the latter involved bimonthly surveys over 11 months (Ridley 1898; Sodhi et al. 2005).

In our study, transect surveys were conducted over two years in the SBGR and LF. The first survey period was from October 2018 to September 2019 and surveys were carried out monthly. The second survey period was from January 2021 to December 2021 and surveys were carried out twice a month. The increase in survey intensity was due to preliminary data analysis which revealed that the monthly surveys conducted from 2018 to 2019 were insufficient to attain sampling saturation. For species accumulation curves covering the recent surveys used in this study, see Online Resource 1. In total, 36 surveys were completed for each site.

All surveys were conducted along a transect measuring 700 m in length at both the SBGR and LF from 0730 to 0930 h at a walking speed of 1 km/h (Fig. 1). Both transects followed existing footpaths located within the confines of the two sites. All bird species were identified and recorded if they were observed or heard within 50 m of either side of the transects. Additionally, birds that flew overhead were excluded if they did not interact with the surrounding environment. Only one observer conducted the surveys. The birds recorded during these surveys will hereafter be collectively referred to as the Contemporary SBGR and LF bird community respectively.

## Data analysis

The origin of all the bird species from both historical and current surveys were first verified using the Checklist of the Birds of Singapore (Nature Society (Singapore) (2022)) (Online Resource 2). All species were classified according to their habitat specialisation and functional groups based on feeding guild and foraging strata using Wells (1999, 2009) supplemented by personal observations from the authors (Online Resource 3). Aerial species were excluded from data analysis because they were not observed in the contemporary surveys due to substantial canopy growth obscuring a view of the sky. In line with the 1998 surveys,

migratory species (i.e. both passage migrants and overwintering species) were also excluded from subsequent analysis as their use of forest fragments like the SBGR is opportunistic, and there is no certainty that they will return to the SBGR every migration season.

To examine the differences between the bird community at SBGR in 1898, 1998, and Contemporary SBGR, as well as at the LF and BTNR, Sorensen's dissimilarity index and the corresponding turnover and nestedness components were calculated (Baselga 2009). Turnover is the degree to which species have been replaced between communities, whereas nestedness refers to the extent to which a community is a subset of another. Both are important metrics of beta diversity. We used betapart (version 1.5.6) (Baselga 2009) in R version 4.1.1 (R Core Team 2021) to obtain the Sorensen's Dissimilarity indices, and to calculate the nestedness and turnover components of beta diversity. Hierarchical cluster analysis using an average linkage method was performed in R to visualise the clustering of communities based on the generated Sorensen's dissimilarity values. To compare the differences in communities based on species traits, vegan (version 2.5–7) (Oksanen et al. 2020) was used to perform Non-metric Multidimensional Scaling (NMDS) to ordinate the communities in relation to origin and habitat specialization, feeding guild and activity strata.

Three species traits were investigated for extinction probability: feeding guild, body mass and wing-to-tarsus ratio. Feeding guild was chosen as multiple studies have found a link between diet and extinction probability for tropical birds (Sodhi et al. 2004a, b; Curtis et al. 2021). There were four levels defining different feeding guilds. As they all have plant-based diets, frugivores, nectarivores, and granivores were combined into one level, and omnivores, insectivores, and carnivores made up the other three. Omnivores were used as the reference variable. Body mass was included because studies have shown a positive relationship between it and a higher probability of extinction (Ripple et al. 2017; Ali et al. 2022). Wing-to-tarsus ratio was chosen because it is generally indicative of the main foraging strata (e.g., birds like babblers and pittas that typically forage closer to ground and in the understorey have lower wing to tarsus ratio than birds that forage in the canopy), and had also been shown to influence extinction probability for tropical birds (Sekercioglu 2007). Body mass, wing and tarsus lengths were obtained from AVONET (Tobias et al. 2022).

We used Firth's logistic regression model to determine the species traits that affected the extinction probability of species from the 1898 SBGR community. This method was chosen due to our small sample size that frequently led to complete separation during model fitting (Heinze & Schemper 2002). Model selection was carried out by fitting a model for every possible combination of species traits followed by model-averaging candidate models with  $\Delta AIC < 2$  (Burnham & Anderson 2004). Model averaging was conducted as an extension to model selection as it is a multimodel approach that reduces potential biases or risks associated with conventional model selection (Peng & Yang 2022; Burnham & Anderson 2004). The package *logistf* (version 1.24) was used to fit Firth's regression models, while *MuMIn* (version 1.43.17) was used for model selection and averaging (Bartoni 2020; Heinze et al. 2020). Next, to ascertain if the functional diversity of the SBGR had changed substantially from 1898 to the Contemporary surveys, we used package *fundiversity* (version 1.1.1) to produce three functional diversity indices which were standardized for comparison – functional richness, functional evenness, and functional divergence – based on the species traits: body mass and wing-to-tarsus ratio (Grenié & Gruson 2024). We excluded feeding guild because the inclusion of categorical variables has been shown to reduce the quality of the functional space on which these indices are calculated, and their inclusion has been advised against. (Maire et al. 2015; Schleuter et al. 2010). Instead, we conducted Fisher's exact tests for feeding guild and foraging strata to compare the proportion of species in each category across the three survey periods.

**Table 1** Sorensen's dissimilarity indices between avian communities with the top value showing overall dissimilarity, middle value showing the turnover component, and bottom value showing the nestedness component

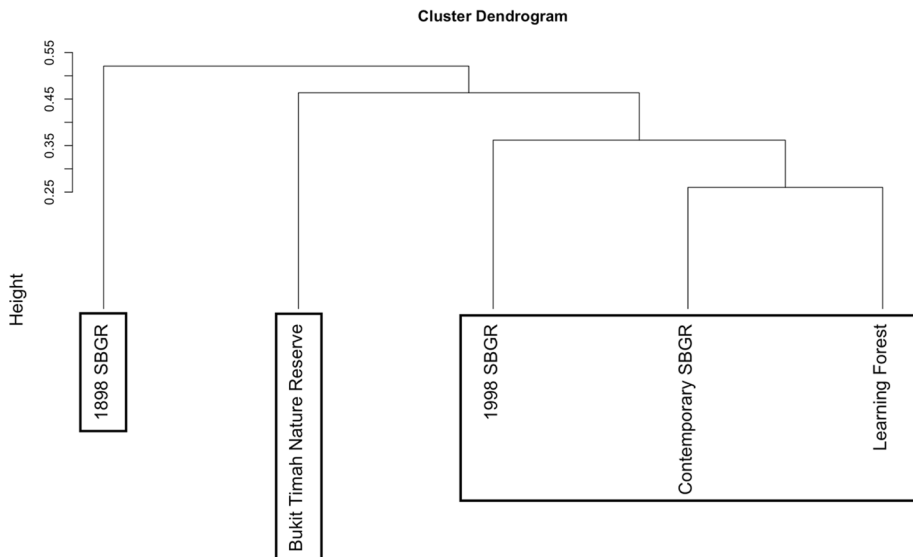
	1898 SBGR <sup>a</sup>	1998 SBGR	Contemporary SBGR	Learning Forest
1998 SBGR	0.507 0.485 0.022	-	-	-
Contemporary SBGR	0.500 0.455 0.045	0.280 0.250 0.030	-	-
Learning Forest	0.554 0.364 0.190	0.443 0.250 0.193	0.260 0.051 0.209	-
Bukit Timah Nature Reserve	0.523 0.364 0.159	0.516 0.389 0.128	0.426 0.308 0.118	0.448 0.418 0.030

<sup>a</sup>SBGR refers to Singapore Botanic Gardens Rainforest

## Results

We documented a total of 39 species in the SBGR during transect surveys, compared to 36 species in 1998, and 33 species in 1898 (Online Resource 4). Between 1898 and 1998, 16 species had gone extinct, 17 species had persisted, and 19 new species were recorded, of which four were introduced species to Singapore. In both SBGR and LF, as at BTNR, the number of species detected approached asymptote (Online Resource 1). Between 1898 and the contemporary surveys, 15 species had gone extinct, 18 species persisted, and 21 new species were recorded, of which five were introduced species to Singapore. The common flameback (*Dinopium javanese*) is the only species which was recorded as extinct in 1998 that was observed in the contemporary surveys. Although the number of introduced species recorded in 1998 and contemporary surveys were similar, the species composition differed. In 1998, four introduced species were reported—the house crow (*Corvus splendens*), Javan myna (*Acridotheres javanicus*), rock pigeon (*Columba livia*), and tanimbar corella (*Cacatua goffiniana*). In contrast, only the Javan myna and tanimbar corella were recorded in the contemporary surveys. Another three introduced species, namely the lineated barbet (*Megalaima lineata*), red-whiskered bulbul (*Pycnonotus jocosus*), and white-crested laughingthrush (*Garrulax leucolophus*) were newly recorded.

Sorensen's dissimilarity index revealed that the 1898 and Contemporary SBGR bird communities were 50% dissimilar, with much of this difference attributed to turnover (45.5%) rather than nestedness (4.5%) (Table 1). When comparing the Contemporary SBGR bird community to the LF and BTNR bird communities, the SBGR's community was more like the LF (26% dissimilar) than the BTNR (43% dissimilar). The dissimilarity between the Contemporary SBGR and LF bird communities was mainly due to nestedness (21%), rather than turnover (5%). Out of the 39 recorded species, the Contemporary SBGR shared 37 of them with LF and only contained two unique species – changeable hawk-eagle (*Nisaetus cirrhatus*) and tanimbar corella. On the other hand, LF contained 24 unique species (Online Resource 4).

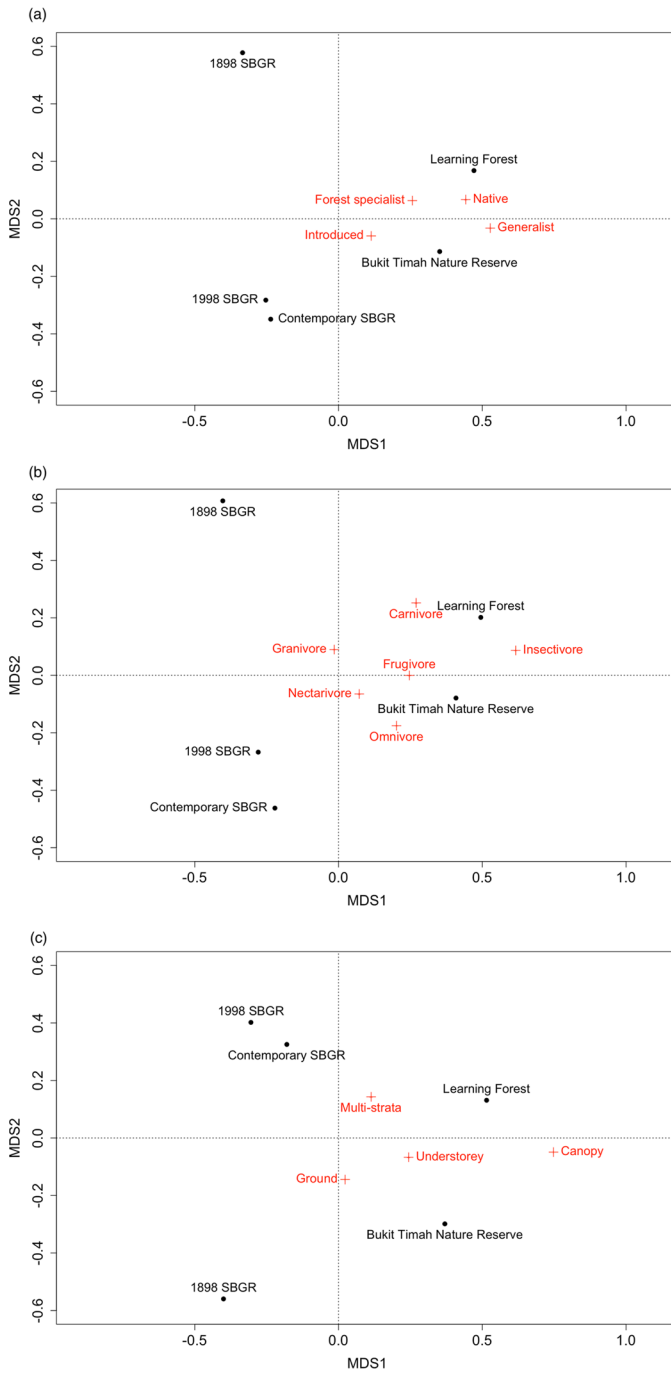


**Fig. 2** Cluster dendrogram obtained from hierarchical clustering using the average clustering method. The five communities are divided into three clusters delineated by rectangles surrounding each distinct cluster. SBGR refers to the Singapore Botanic Gardens Rainforest

The cluster dendrogram based on Sorensen's dissimilarity indices similarly showed that the Contemporary and 1898 SBGR communities were dissimilar. It also showed the large similarity between the former and the LF bird community. When divided into three clusters, the 1898 SBGR community was grouped distinctly from the 1998 and Contemporary SBGR communities, which were grouped with LF instead (Fig. 2). The 1898 and Contemporary SBGR communities were not only different in terms of species composition, but were also different in terms of species traits (Fig. 3). The Contemporary SBGR community was more associated with omnivores and species that utilised multiple strata, in comparison to the 1898 SBGR community (Fig. 3b & c). Neither appeared strongly associated to a particular origin or habitat specialization (Fig. 3a). Like the cluster dendrogram, the 1898 SBGR and BTNR communities were distinct across all NMDs plots. The 1998 and Contemporary SBGR communities were consistently ordinated close to each other indicating their relative similarity. The LF and the Contemporary SBGR community, however, were dissimilar in relation to species traits, despite their compositional similarity. Nevertheless, this was expected, in view that the Contemporary SBGR was highly nested within LF. Their compositions are thus similar, while the observed differences in species traits could be attributed to the many additional species in LF. Overall, the results of the NMDs largely aligned with that from the Sorensen's dissimilarity index. In addition, stress plots showed that the stress values for all three NMDs plots were less than 0.05, indicating that the results were representative. Hence, our analysis showed that the SBGR community had undergone changes in both species composition and traits.

Eight Firth's regression models for extinction probability were fitted (Online Resource 5), of which two were averaged to yield a final model that included two explanatory variables. Body mass and wing-tarsus ratio showed no significant effect (Table 2). Functional diversity indices showed that functional richness had declined in SBGR, while





**Fig. 3** Non-metric multi-dimensional scaling with communities ordinated with respect to (a) origin and habitat specialization, (b) feeding guild, and (c) foraging strata



**Table 2** Final averaged model for extinction probability in the SBGR, with top row of numbers corresponding to the full averaged model, and bottom row corresponding to the conditional averaged model

	Estimate	Standard Error	p-value
Intercept	-0.122	0.852	0.886
	-0.122	0.852	0.886
Wing-to-tarsus ratio	-0.038	0.141	0.341
	-0.061	0.176	0.341
Weight	0.0005	0.001	0.790
	0.0005	0.001	0.729

**Table 3** Functional diversity indices of the five avian communities

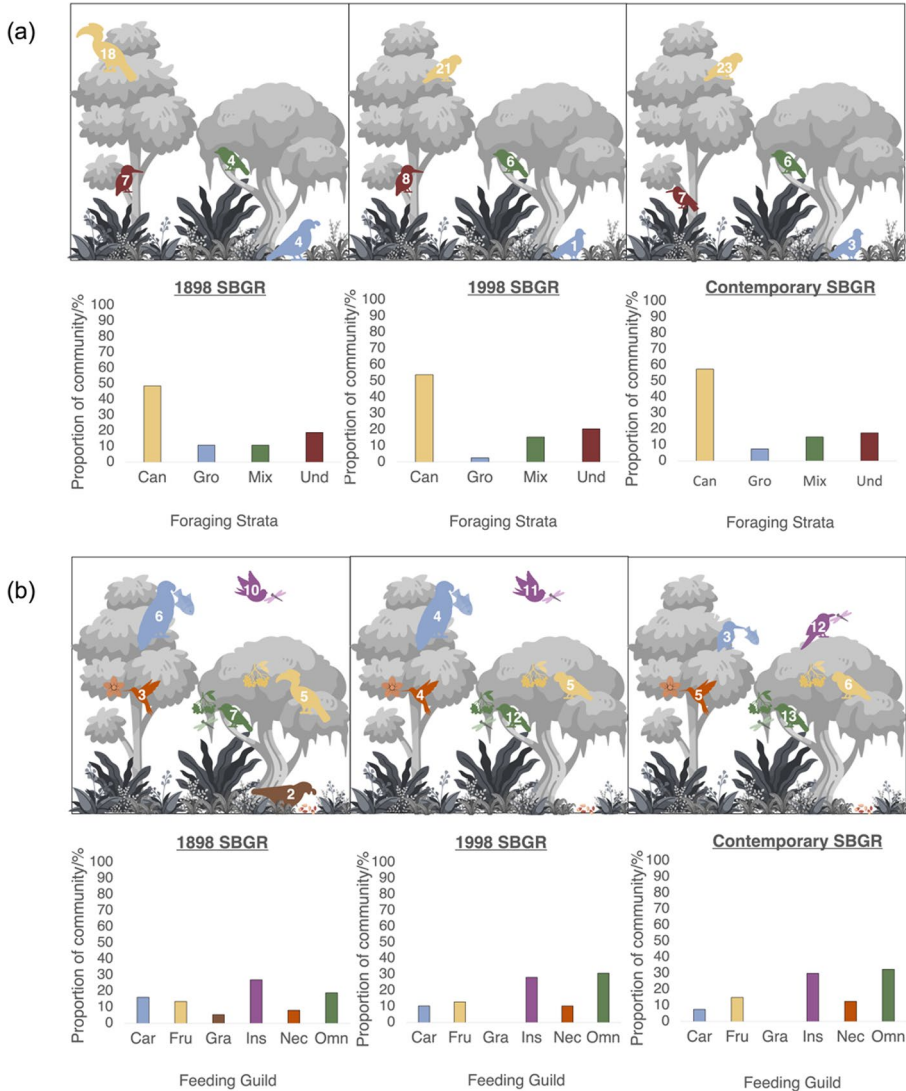
	Functional Richness	Functional Evenness	Functional Divergence
1898 SBGR	0.705	0.175	0.837
1998 SBGR	0.443	0.254	0.757
Contemporary SBGR	0.434	0.283	0.788
Learning Forest	0.961	0.203	0.798
Bukit Timah Nature Reserve	0.723	0.136	0.865

functional evenness slightly increased and functional divergence remained largely unchanged (Table 3). This indicates that despite the loss in functional richness, there is now a slightly more even abundance across all niche groups. Additionally, most of the loss took place between 1898 and 1998, with all three indices remaining largely unchanged between 1998 and the current study. Fisher's exact tests revealed no significant differences in the proportion of species in each feeding guild ( $p=0.827$ ) and foraging strata ( $p=0.882$ ) between the 1898, 1998 and Contemporary SBGR bird communities (Fig. 4).

In summary, our study showed that: (a) the contemporary SBGR bird community had a different species composition to the 1898 SBGR bird community, but the overall species richness remained similar. Some aspects of functional diversity (functional evenness and divergence) were also retained since 1898 despite changes in species composition, and (b) the contemporary SBGR bird community did not resemble the contemporary bird community found in a primary and mature secondary rainforest fragment.

## Discussion

Forest fragmentation is typically associated with the loss of native and forest-dependent species, and colonisation by non-native and generalist species (Filgueiras et al. 2021). This is often brought about by the establishment of human-modified landscapes, which results in the species spillover across habitats, such as generalists or matrix-specialists from open habitats to edge-affected habitats (i.e. small forest fragments and forest edges) (Filgueiras et al. 2021; Liu et al. 2023). This has been reported in the small forest fragments nestled within the urban landscape matrix of Singapore (Castelletta et al. 2005; Sodhi et al. 2005). The observed dissimilarity between the 1898 and contemporary bird communities, coupled with the increased proportion of non-native species, is consistent with this observation. Notwithstanding this influx of non-native species, much of the dissimilarity was brought about by turnover in the bird species, rather than the loss in species (i.e. nestedness).



**Fig. 4** (a) Change in proportion and number of species in each feeding guild and (b) each foraging strata over the three study periods. Feeding guilds Car, Fru, Gra, Ins, Omn, and Nec refer to Carnivore, Frugivore, Insectivore, Omnivore, and Nectarivore respectively. Foraging stratas Can, Gro, Mix, and Und refer to Canopy, Ground, Mixed, and Understory respectively. SBGR refers to the Singapore Botanic Gardens Rainforest

Hence, the functional diversity in terms of feeding guild and foraging strata remained largely unchanged across the 1898, 1998 and contemporary surveys. This suggests that even a small forest fragment like SBGR can maintain a degree of functional redundancy and ecosystem resilience through the colonisation of species from the surrounding landscape (Walker 1992). In 1898, the functional role of large-gaped frugivores was filled by the Green Broadbill (*Calyptomena viridis*) and Rhinoceros Hornbill (*Buceros rhinoceros*).

Both species were considered extinct in Singapore by 1998 and no functional replacements were recorded during previous surveys of the SBGR (Sodhi et al. 2005). By the 21st Century, this niche was occupied by no fewer than three species that had colonized the site during the intervening two decades – the native Pied Imperial Pigeon (*Ducula bicolor*) and Oriental Pied Hornbill (*Anthracoceros albirostris*), as well as the introduced Lineated Barbet (*Psilopogon lineatus*). These three species have been expanding their range across Singapore since the start of the 21st Century (Yong et al. 2017), and have become a regular sight around SBG within the last decade.

The SBGR bird community was also different from the contemporary bird community at BTNR. In terms of species composition, the current community was most like the bird community recorded during the 1998 SBGR surveys. This is corroborated by the fact that the bird community recorded within the SBGR in 1998 already had some combination of the following ecological traits– (i) omnivores, (ii) species that utilised multiple strata for foraging and (iii) species introduced to Singapore. Furthermore, the 1998 and contemporary SBGR bird community collectively differed substantially from the 1898 community, implying that a new baseline had been reached by 1998 and subsequently maintained over the past 23 years. This corroborates the findings of Stouffer et al. (2020) in Amazonian forest fragments, which showed that the bird communities in secondary growth and fragments will approach a new baseline that is completely different from their historical state in the long-term, and that omnivores tended to be more successful in such a human-modified landscape.

We also acknowledge that the SBGR was most likely no longer a pristine rainforest when Ridley started documenting his observations in 1898. Further support for this can be found in the observations of birds during the 1898 surveys, such as the Blue-breasted Quail (*Coturnix chinensis*) and Barred Buttonquail (*Turnix suscitator*). These two species are associated with open country habitats (Yong et al. 2017), thereby suggesting that by 1898, the SBGR was possibly already an isolated fragment. Consequently, the functional diversity of the 1898 SBGR bird community would not have been representative of an undisturbed lowland rainforest. Nevertheless, in view that bird communities even in undisturbed rainforest are dynamic (Stouffer et al. 2020), we deem our findings still noteworthy that both avian species richness and functional diversity in the SBGR had remained relatively stable since 1898.

Globally, larger birds with functionally unique dimensions, such as shorter wing-tarsus ratios have been shown to have the highest risk of extinction (Ali et al. 2022). Among the birds recorded in SBGR, body mass and wing-tarsus ratio had no effect on their extinction proneness. Despite the extirpations in SBGR during the study period, the proportion of species in each feeding guild also remained largely unchanged over the study period as new species fulfilled the vacant functional roles. The structural integrity of the SBGR, and ongoing habitat restoration initiatives in the surrounding landscape matrix may explain the stability in avian species richness and functional diversity in the SBGR during the study period. It has been shown that the structural complexity of forests is positively associated with species richness across many taxon groups (Tews et al. 2004; Carrasco et al. 2019), and retention of the structural integrity can lower the risk of extinction in tropical vertebrates including birds (Pillay et al. 2022). A 1994 survey conducted in the SBGR concluded that areas of forest with good structural complexity were still present, albeit with limited ongoing regeneration (Turner et al. 1996). Since then, there have been intensive efforts to naturalise the parks and gardens in Singapore, including the SBG, as part of the nation's vision to be a City in Nature. These efforts are guided by various planting schemes using native plant species to emulate Singapore's

natural forests (Er 2021). Such efforts could have buffered the SBGR against edge effects. Furthermore, added tree cover within the Gardens would also have facilitated the movement of native birds into the SBGR from the surrounding habitat, and helped to maintain the functional diversity (Uezu et al. 2005; de Souza et al. 2022). This is aligned with a study, which found that habitat fragments in landscapes with high tree cover were colonised by species belonging to functional groups that were previously present within the fragments. The resultant gain in novel, but functionally similar species, improved the stability of ecological functions within the fragments, leading to the retention of functional diversity (Ikin et al. 2019). In contrast, fragments isolated amidst a harsh urban environment, such as BBG, recorded substantial declines in species richness over a 70-year period (Sodhi et al. 2006). This was probably reflective of the erosion of bird populations in the agricultural landscape surrounding the forest fragments (Diamond et al. 1987).

The habitat restoration initiatives in SBG have also resulted in the observation of previously unrecorded bird species within its restored forest fragments. During LF's restoration, a freshwater wetland was created adjacent to the forest fragment. As a result, birds associated with forested waterbodies such as the Grey-headed Fish Eagle (*Haliaeetus ichthyaeus*) and Straw-headed Bulbul (*Pycnonotus zeylanicus*) were observed at LF, but not in the SBGR. The added occurrences of such species aligned with a recent study in Singapore, which showed that freshwater wetlands within urban green spaces can increase bird diversity (Wong et al. 2022).

A limitation in this study relates to the usage of historical data, particularly the accuracy of the data and its suitability for addressing scientific hypotheses (Primack et al. 2022). Our historical data were collected over approximately 14 years by Henry Nicholas Ridley, the first director of the Singapore Botanic Gardens between 1888 to 1912 (Tinsley 2009). While Ridley's primary interest was in botany, his observations of SBG's birds demonstrated a familiarity with both resident and migratory birds within the gardens, as well as a high degree of scientific rigour. With reference to the three-step framework outlined in Primack et al. (2022), Ridley had taken detailed notes of the birds observed in the gardens, including accurate observations of their foraging and breeding behaviour. For example, in an era without comprehensive field guides and capable optics, he was able to identify a Black-capped Kingfisher (*Halcyon pileata*), an uncommonly observed migratory species that would only be present in SBG at certain times of the year. Ridley's observations of the birdlife were also anecdotal and may have potentially included detections in other parts of the Gardens beyond the SBGR. In this regard, other studies have noted that utilising historical data to determine shifts in community composition tend to require less detailed information (Tingley and Beissinger 2009; Kopecky and Macek 2015). Hence, we are of the view that Ridley's observations are sufficiently robust to serve as a baseline for comparison.

To conclude, our study provides long-term evidence that a small forest fragment in the tropics can form novel bird communities that are functionally similar to previous communities that inhabited the fragment, leading to the retention of functional diversity. Conservation managers working in fragmented landscapes, particularly in highly urbanised areas, should consider habitat restoration initiatives surrounding small fragments. Such initiatives like tree planting in the landscape matrix, will improve the resilience of the avian communities residing in these fragments, as well as facilitate the movement of native birds into the fragment (Uezu et al. 2005; Ikin et al. 2019). In turn, this will contribute to the overall ecological stability of the fragment and its associated biodiversity. These activities also

provide opportunities for public involvement (Wong et al. 2022), and can raise awareness of the value of small fragments for biodiversity conservation.

**Supplementary Information** The online version contains supplementary material available at <https://doi.org/10.1007/s10531-024-02855-4>.

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**Data availability** No datasets were generated or analysed during the current study.

## Declarations

**Competing interests** The authors have no relevant financial or non-financial interests to disclose.

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## References

- Achard F, Beuchle R, Mayaux P, Stibig HJ, Bodart C, Brink A, Carboni S, Desclée B, Donnay F, Eva HD, Lupi A (2014) Determination of tropical deforestation rates and related carbon losses from 1990 to 2010. *Glob Chang Biol* 20(8):2540–2554. <https://doi.org/10.1111/gcb.12605>
- Alexander J, Ehlers Smith DA, Ehlers Smith YC, Downs CT (2019) Drivers of fine-scale avian functional diversity with changing land use: an assessment of the effects of eco-estate housing development and management. *Landsc Ecol* 34:537–549
- Ali JR, Blonder BW, Pigot AL, Tobias JA (2022) Bird extinctions threaten to cause disproportionate reductions of functional diversity and uniqueness. *Func Ecol* 37:162–175
- Arroyo-Rodríguez V, Fahrig L, Tabarelli M, Watling JI, Tischendorf L, Benchimol M, Cazetta E, Faria D, Leal IR, Melo FPL, Morante-Filho JC, Santos BA, Arasa-Gisbert R, Arce-Peña N, Cervantes-López MJ, Cudney-Valenzuela S, Galán-Acedo C, San-José M, Vieira ICG, Slik JWF, Nowakowski AJ, Tschardtke T (2020) Designing optimal human-modified landscapes for forest biodiversity conservation. *Ecol Lett* 23:1404–1420
- Bartoń K (2020) MuMIn: Multi-Model Inference. R package version 1.43.17. <https://CRAN.R-project.org/package=MuMIn>. Accessed 9 November 2023
- Baselga A (2009) Partitioning the turnover and nestedness components of beta diversity. *Glob Ecol Biogeogr* 19(1):134–143. <https://doi.org/10.1111/j.1466-8238.2009.00490.x>
- Burnham KP, Anderson DR (2004) Multimodel inference: understanding AIC and BIC in model selection. *Socio Met Res* 33(2):261–304
- Carrasco L, Giam X, Papeş M, Sheldon K (2019) Metrics of lidar-derived 3D vegetation structure reveal contrasting effects of horizontal and vertical forest heterogeneity on bird species richness. *Remote Sens* 11(7):743

- Castelletta M, Thiollay J-M, Sodhi NS (2005) The effects of extreme forest fragmentation on the bird community of Singapore Island. *Biol Conserv* 121:135–155
- Coddington CPI, Cooper WJ, Mokross K, Luther DA (2023) Forest structure predicts species richness and functional diversity in Amazonian mixed-species bird flocks. *Biotropica* 55:467–479
- Corlett RT (1992) The ecological transformation of Singapore, 1819–1990. *J Biogeogr* 19:411–420
- Curtis JR, Robinson WD, Rompre G, Randall PM, McCune B (2021) Erosion of tropical bird diversity over a century is influenced by abundance, diet and subtle climatic tolerances. *Sci Rep* 11:10045
- de Coster G, Banks-Leite C, Metzger JP (2015) Atlantic forest bird communities provide different but not fewer functions after habitat loss. *Proc R Soc b: Biol Sci* 282:20142844
- de Souza LM, Boesing AL, Metzger JP, Prado PI (2022) Matrix quality determines the strength of habitat loss filtering on bird communities at the landscape scale. *J Appl Ecol* 59:2790–2802
- Dehling DM, Jordano P, Schaefer HM, Bohning-Gaese K, Schleuning M (2016) Morphology predicts species' functional roles and their degree of specialization in plant-frugivore interactions. *Proc R Soc B* 283:20152444
- Diamond JM, Bishop KD, van Balen S (1987) Bird survival in an isolated javan woodland: island or mirror? *Conserv Biol* 1:132–142
- Diaz S, Cabido M (2001) Vive la difference: plant functional diversity matters to ecosystem processes. *Trends Ecol Evol* 16(11):646–655
- Er K (2021) Transforming Singapore into a city in nature. *Urb Solut* 19:68–77
- Estoque RC, Ooba M, Avitabile V, Hijioka Y, Dasgupta R, Togawa T, Murayama Y (2019) The future of Southeast Asia's forests. *Nat Commun* 10:1829
- Filgueiras BKC, Peres CA, Melo FPL, Leal IR, Tabarelli M (2021) Winner-loser species replacements in human-modified landscapes. *Trends Ecol Evol* 36(6):545–555
- Fischer R, Taubert F, Muller MS, Groeneveld J, Lehmann S, Wiegand T, Huth A (2021) Accelerated forest fragmentation leads to critical increase in tropical forest edge area. *Sci Adv* 7:eabg7012
- Fontúrbel FE, Betancurt-Grisales JF, Vargas-Daza AM, Castaño-Villa GJ (2022) Effects of habitat degradation on bird functional diversity: A field test in the Valdivian rainforest. *For Ecol Manag* 522:120466
- Gibson L, Lee TM, Koh LP, Brook BW, Gardner TA, Barlow J, Peres CA, Bradshaw CJA, Laurance WF, Lovejoy TE, Sodhi NS (2011) Primary forests are irreplaceable for sustaining tropical biodiversity. *Nature* 478:378–381
- Grenié M, Gruson H (2024) *\_fundiversity*: Easy computation of Functional Diversity Indices. <https://doi.org/10.5281/zenodo.4761754>, R package version 1.1.1, <https://CRAN.R-project.org/package=fundiversity>. Accessed 23 Apr 2024
- Haddad NM, Brudvig LA, Clobert J, Davies KF, Gonzalez A, Holt RD, Lovejoy TE et al (2015) Habitat fragmentation and its lasting impact on Earth's ecosystems. *Sci Adv* 1:e1500052
- Hansen AJ, Burns P, Ervin J, Goetz SJ, Hansen M, Venter O, Watson JE, Jantz PA, Virnig AL, Barnett K, Pillay R (2020) A policy-driven framework for conserving the best of Earth's remaining moist tropical forests. *Nat Ecol Evol* 4(10):1377–1384. 10.1038/s41559-020-1274-7. <https://doi.org/10.1038/s41559-020-1274-7>
- Heinze G, Ploner M, Jiricka L (2020) *logistf*: Firth's Bias-Reduced Logistic Regression. R package version 1.24. <https://CRAN.R-project.org/package=logistf>. Accessed 9 November 2023
- Heinze G, Schemper M (2002) A solution to the problem of separation in logistic regression. *Stat Med* 21:2409–2419
- Ikin K, Barton PS, Blanchard W, Crane M, Stein J, Lindenmayer DB (2019) Avian functional responses to landscape recovery. *Proc R Soc B* 286:20190114
- Kopecky M, Macek M (2015) Vegetation resurvey is robust to plot location uncertainty. *Divers Distrib* 21:322–330
- Lewis SL, Edwards DP, Galbraith D (2015) Increasing human dominance of tropical forests. *Science* 349:827–832
- Lim KS (2019) Birds of bukit timah nature reserve. *Singapore Gardens' Bull Singap* 71(Suppl. 1):185–208
- Liu D, Semenchuk P, Essl F et al (2023) The impact of land use on non-native species incidence and number in local assemblages worldwide. *Nat Commun* 14(1):2090
- Maire E, Grenouillet G, Brosse S, Villéger S (2015) How many dimensions are needed to accurately assess functional diversity? A pragmatic approach for assessing the quality of functional spaces. *Glob Ecol Biogeogr* 24(6):728–740
- Mariano-Neto E, Santos RAS (2023) Changes in the functional diversity of birds due to habitat loss in the Brazil atlantic forest. *Frontiers Glob Change* 6:1041268
- Myers N, Mittermeier RA, Mittermeier CG, da Fonseca GAB, Kent J (2000) Biodiversity hotspots for conservation priorities. *Nature* 403:853–858



- Nature Society (Singapore), 2022. Checklist of the birds of Singapore. <https://www.nss.org.sg/report/a1947d2e-8nss-bird-checklist-2022.pdf>. Accessed 9 November 2023
- Oksanen J, Blanchet FG, Friendly M, Kindt R, Legendre P, McGlinn D, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Stevens MHH, Szoecs E, Wagner H (2020) *vegan*: Community Ecology Package. R package version 2.5–7. <https://CRAN.R-project.org/package=vegan>. Accessed 9 November 2023
- Oliveira H, dos Anjos L (2022) Silent changes in functionally stable bird communities of a large protected tropical forest monitored over 10 years. *Biol Conserv* 265:109407
- Peng J, Yang Y (2022) On Improvability of model selection by model averaging. *J Econometrics* 229(2):246–262
- Pillay R, Michelle Venter M, Aragon-Osejo J, González-del-Pliego P, Hansen AJ, Watson JEM, Venter O (2021) Tropical forests are home to over half of the world's vertebrate species. *Frontier Ecol Env* 20(1):10–15
- Pillay R, Watson JEM, Hansen AJ, Jantz PA, Aragon-Osejo J, Armenteras D, Atkinson SC, Burns P, Ervin J, Goetz SJ, González-Del-Pliego P, Robinson NP, Supples C, Virnig ALS, Williams BA, Venter O (2022) Humid tropical vertebrates are at lower risk of extinction and population decline in forests with higher structural integrity. *Nat Ecol Conserv* 6(12):1840–1849
- Primack RB, Miller-Rushing AJ, Miller TK (2022) Was Henry David Thoreau a good naturalist? An approach for assessing data from historical natural history records. *BioScience* 72(10):1018–1027. <https://doi.org/10.1093/biosci/biac063>
- R Core Team (2021) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>. Accessed 9 November 2023
- Ramírez-Delgado JP, Di Marco M, Watson JEM, Johnson CJ, Rondinini C, Corredor Llano X, Arias M, Venter O (2022) Matrix condition mediates the effects of habitat fragmentation on species extinction risk. *Nat Commun* 13:595
- Ridley HN (1898) Birds in the botanic gardens, Singapore. *J Straits Branch R Asiatic Soc* 31:73–89
- Ripple WJ, Wolf C, Newsome TM, Hoffman M, Wirsing AJ, McCauley DJ (2017) Extinction risk is most acute for the world's largest and smallest vertebrates. *Proc Natl Acad Sci USA* 114(40):10678–10683
- Riva F, Martin CJ, Millard K, Fahrig L (2022) Loss of the world's smallest forests. *Glob Change Biol* 28:7164–7166
- Rosenburg DK, Noon BR, Meslow EC (1997) Biological Corridors: Form. Funct Efficacy *Biosci* 47(10):677–687
- Schleuter D, Daufresne M, Massol F, Argillier C (2010) A user's Guide to Functional Diversity Indices. *Ecol Mono* 80(3):469–484
- Sekercioglu CH (2006) Increasing awareness of avian ecological function. *Trends Ecol Evol* 21:464–471
- Sekercioglu CH (2007) Conservation ecology: Area trumps mobility in fragment bird extinctions. *Curr Biol* 17(8):R283–R286
- Sodhi NS, Liow LH, Bazzaz FA (2004a) Avian extinctions from tropical and subtropical forests. *Annu Rev Ecol Syst* 35:323–345
- Sodhi NS, Koh LP, Brook BW, Ng PKL (2004b) Southeast Asian biodiversity: an impending disaster. *Trends Ecol Evol* 19:654–660
- Sodhi NS, Lee TM, Koh LP, Dunn RR (2005) A century of avifaunal turnover in a small tropical rainforest fragment. *Anim Conserv* 8:217–222
- Sodhi NS, Lee TM, Koh LP, Prawiradilaga DM (2006) Long-term avifaunal impoverishment in an isolated tropical woodlot. *Conserv Biol* 20(3):772–779
- Song X-P, Hansen MC, Stehman SV, Potapov PV, Tyukavina A, Vermote EF, Townshend JR (2018) Global land change from 1982 to 2016. *Nature* 560:639–643
- Stouffer PC, Jirinec V, Rutt CL, Bierregaard RO Jr, Hernández-Palma A, Johnson EI, Midway SR, Powell LL, Wolfe JD, Lovejoy TE (2020) Long-term change in the avifauna of undisturbed Amazonian rainforest: ground-foraging birds disappear and the baseline shifts. *Ecol Lett* 24:186–195
- Taubert F, Fischer R, Groeneveld J et al (2018) Global patterns of tropical forest fragmentation. *Nature* 554:519–522
- Taylor PD, Fahrig L, Henein K, Merriam G (1993) Connectivity is a vital element of landscape structure. *Oikos* 68:571–573
- Tews J, Brose U, Grimm V, Tielbörger K, Wichmann MC, Schwager M, Jeltsch F (2004) Animal species diversity driven by habitat heterogeneity/diversity: The importance of keystone structures. *J Biogeogr* 31(1):79–92
- Tingley MW, Beissinger SR (2009) Detecting range shifts from historical species occurrences: New perspectives on old data. *Trends Ecol Evol* 24:625–633



- Tinsley B (2009) Gardens of perpetual summer: the Singapore Botanic Gardens. National Parks Board, Singapore
- Tobias JA, Sheard C, Pigot AL, Devenish AJM, Yang J, Sayol F et al (2022) AVONET: morphological, ecological and geographical data for all birds. *Ecol Lett* 25:581–597
- Tulloch AIT, Barnes MD, Ringma J, Fuller RA, Watson JEM (2016) Understanding the importance of small patches of habitat for conservation. *J Appl Ecol* 53:418–429
- Turner IM, Corlett RT (1996) The conservation value of small isolated fragments of lowland tropical rain forest. *Trends Ecol Evol* 11:330–334
- Turner IM, Chua KS, Ong JSY, Soong BC, Tan HTW (1996) A century of plant species loss from an isolated fragment of lowland tropical rain forest. *Conserv Biol* 10:1229–1244
- Uezu A, Metzger JP, Vielliard JME (2005) Effects of structural and functional connectivity and patch size on the abundance of seven Atlantic Forest bird species. *Biol Conserv* 123:507–519
- Volenc ZM, Dobson AP (2020) Conservation value of small reserves. *Conserv Biol* 34:66–79
- Walker BH (1992) Biodiversity and ecological redundancy. *Conserv Biol* 6(1):18–23
- Wells DR (1999) *The Birds of the Thai-Malay Peninsula (Vol. 1: Non-Passerines)*. Academic Press, Cambridge
- Wells DR (2009) *The Birds of the Thai-Malay Peninsula (Vol. 2: Passerines)*. Bloomsbury Publishing, London
- Wilson EO (1988) *Biodiversity*. National Academy Press, Washington, DC
- Wintle BA, Kujala H, Whitehead A, Cameron A, Veloz S, Kukkala A, Moilanen A, Gordon A, Lentin PE, Cadenhead NCR, Bekessy SA (2019) Global synthesis of conservation studies reveals the importance of small habitat patches for biodiversity. *Proc Natl Acad Sci USA* 116(3):909–914
- Wong JSY, Soh MCK, Low BW, Er KBH (2022) Tropical bird communities benefit from regular-shaped and naturalised urban green spaces with water bodies. *Landsc Urban Plan* 231:10644
- Wright SJ (2005) Tropical forests in a changing environment. *Trends Ecol Evol* 20:553–560
- Yee ATK, Corlett R, Liew SC, Tan HTW (2011) The vegetation of Singapore – an updated map. *Gardens' Bull Singap* 63:205–212
- Yee ATK, Chong KY, Seah WW, Lua HK, Yang S (2019) *Vegetation of Singapore*. Flor Singap 1:47–70
- Yong DL, Lim KC, Lee TK (2017) *A Naturalist's Guide to the Birds of Singapore*, 3rd edn. John Beaufoy Publishing, United Kingdom
- Zambrano J, Garzon-Lopez CX, Yeager L, Fortunel C, Cordeiro NJ, Beckman NG (2019) The effects of habitat loss and fragmentation on plant functional traits and functional diversity: what do we know so far? *Oecologia* 191(3):505–518

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