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A century of avifaunal turnover in a small tropical rainforest fragment

Navjot S. Sodhi[1,*], Tien Ming Lee[1], Lian Pin Koh[1,†] and Robert R. Dunn[2,‡]

[1] Department of Biological Sciences, National University of Singapore, 14 Science Drive 4, Singapore 117543, Republic of Singapore
[2] Department of Environmental Biology, Curtin University of Technology, GPO Box U1987 Perth, Western Australia 6845, Australia

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Abstract

Despite the alarming rate of tropical deforestation, the long-term conservation value of forest fragments remains poorly understood. We report on the avifaunal turnover in an isolated 4 ha tropical forest fragment in Singapore (i.e. Singapore Botanic Gardens rainforest fragment (SBGRF)) between 1898 and 1998. Over 100 years, the SBGRF lost 18 (49%) species and gained 20 species. More forest-dependent species (3) were lost from the SBGRF than survived (1) or colonised it (no species). Conversely, significantly more introduced species (4) colonised the fragment than were previously recorded (1 species). Significantly more nectarivores survived (8 species) or colonised (9 species) than were lost (two species). In essence, while the avian species richness in the SBGRF remained relatively constant after a century, its species composition underwent significant changes. The avian species composition in the SBGRF in 1998 appeared to be more similar to that of the contemporary smaller and younger Singaporean secondary forest patches than to either the larger and older forest reserves or to the SBGRF 100 years ago. Our study suggests that small isolated tropical forest fragments may have limited long-term conservation value for native forest bird species.

INTRODUCTION

Tropical humid forests are vanishing at an alarming rate across the world, primarily from large-scale anthropogenic disturbances such as logging, infrastructure building and agriculture (Laurance, 1999; Achard *et al*., 2002; Geist & Lambin, 2002). Such deforestation results in catastrophic consequences for tropical biotas (e.g. Brook, Sodhi & Ng, 2003*a*; Sodhi *et al*., 2004*a*). Although the negative impacts of forest fragmentation, one of the consequences of deforestation, have been widely documented (e.g. local extinctions: Turner, 1996), recent research shows that even small forest fragments (e.g. < 100 ha) may continue to serve important ecological (e.g. as reservoirs for seeds; Turner & Corlett, 1996) and perhaps social (e.g. Kong *et al*., 1999) functions. However, the long-term (i.e. > 50 years) patterns and processes of faunal extinctions in tropical forest fragments remain poorly understood due to the paucity of empirical data (Sodhi, Liow & Bazzaz, 2004*b*).

Here, we investigate the temporal turnover (i.e. the losses and gains) in the avifaunal species of a 4 ha rainforest fragment over a century from 1898 to 1998 in a highly urbanised tropical landscape (i.e. Singapore), which has lost more than 95% of its native forests and 67% of its forest bird species (Castelletta, Sodhi & Subaraj, 2000). We examine potential spatial scale effects in local species extinctions by comparing the avifaunal losses from this forest fragment with those from the entire island of Singapore. We also determine how unique the bird community in this fragment would have been for Singapore had there been no turnover over the 100 years by comparing its avifaunal community with those of other existing Singaporean fragments. Furthermore, we examine potential ecological selectivity in the species extirpations by comparing species characteristics (e.g. body size) between birds that have been lost from this forest fragment and those that have survived or colonised it. Lastly, we compare turnover of the avifaunal community, over the similar period, with those of the vascular plant community in the same fragment (Turner *et al*., 1996). Our study of the avifauna of the Singapore Botanic Gardens over a 100-year period provides unique and valuable insights into the long-term feasibility of conserving biodiversity in small forest fragments in deforested tropical regions.

*All correspondence to: Dr Navjot S. Sodhi. Tel: 65-6874-2700; Fax: 65-6779-2486; E-mail: dbsns@nus.edu.sg
†Current address: Department of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ 08544-1003, USA.
‡Current address: Department of Ecology and Evolutionary Biology, University of Tennessee, 1416 Circle Drive, 569 Dabney Hall, Knoxville, TN 37996-1610, USA.

METHODS AND MATERIALS

Our study site, the Singapore Botanic Gardens (SBG), is located in the Republic of Singapore (103°50′E, 1°20′N: Fig. 1), a tiny island state ($540\ km^2$) 1.4 km

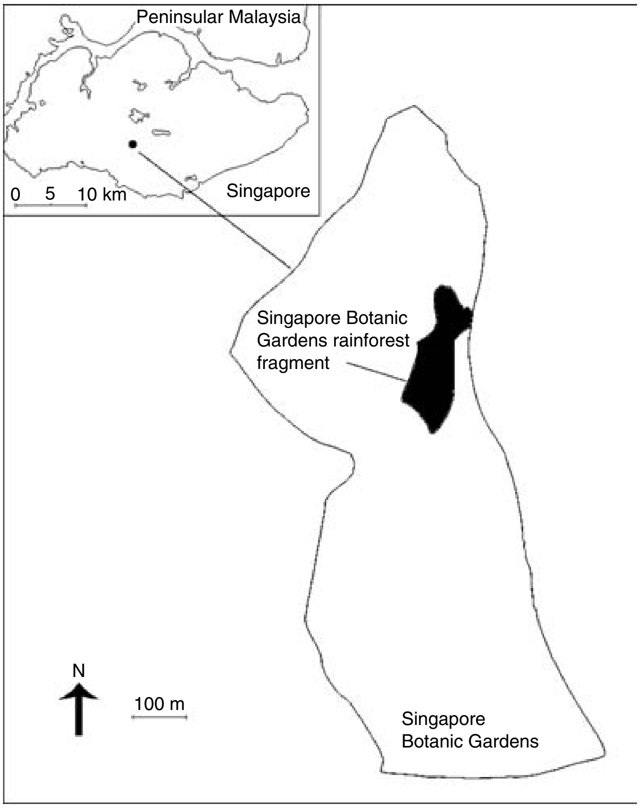

Fig. 1. Map showing the location of the Singapore Botanic Gardens rainforest fragment (SBGRF) in the Singapore Botanic Gardens.

south of Peninsular Malaysia. The island has an equatorial climate with high mean annual temperature (30 °C) and daily humidity (90%) and a mean annual rainfall of 2000 mm (Corlett, 1992). Heavy deforestation in Singapore commenced shortly after 1819, during which the predominant tropical lowland rainforests were cleared, initially for cultivation and subsequently for urbanisation (Corlett, 1992). Currently, 2400 ha of forest (about 5% of the island's surface) remain on the island, of which less than 10% is primary forest.

The SBG was established at its current location in 1859 (Burkill, 1918). The garden contains a 4 ha lowland tropical rainforest fragment, hereafter referred to as the Singapore Botanic Gardens rainforest fragment, SBGRF, which was isolated between 140–174 years ago (Turner *et al*., 1996). This forest fragment remains intact and is currently located 3 km away from the nearest old growth forest (Central Catchment Nature Reserve) in Singapore.

We obtained our historical checklist of bird species in the SBG from Ridley (1898; available on request). H. N. Ridley became the first director of the SBG in 1888 and published his observations of the birds of the SBG in 1898. From his detailed reports of the breeding activities of both resident and migratory birds in the SBG, it is clear that his observation period must have been over the course of at least several months. Ridley's checklist of birds probably included those observed in the SBGRF (e.g. green broadbill: see Table 1 for scientific names of recorded bird species), as well as other areas within the SBG. Because our study is concerned only with the avifauna of the SBGRF, we modified Ridley's checklist of birds (hereafter referred to as the 1898 survey) by excluding open habitat species that were unlikely to have been found in the SBGRF (i.e. paddyfield pipit, *Anthus rufulus*; peaceful dove, *Geopelia striata*; white-headed munia, *Lonchura maja*; Java sparrow, *Padda oryzivora*; and Eurasian tree sparrow, *Passer montanus*). None of these species was listed in the recent survey of the SBGRF. The contemporary avifaunal checklist of the SBGRF was obtained from a recent study (Castelletta, Thiollay & Sodhi, 2005), in which the rainforest fragment was surveyed 11 times (bimonthly) between June 1997 and June 1999 by an experienced observer until sampling saturation was reached (hereafter referred to as the 1998 survey: see Fig. 2 in Castelletta *et al*., 2005). To investigate the turnover in the avifaunal community over a century, bird species in the SBGRF were classified into one of three categories: 'extinct' represents species present only in the 1898 survey; 'survivor' represents species present in both the 1898 and 1998 surveys; while 'coloniser' represents species present only in the 1998 survey.

To examine potential spatial scale effects in local species extinctions, we compared the proportion of bird species that were extinguished from the SBGRF with the proportion of bird species that were extinguished from the whole island using data in Castelletta *et al*. (2000), despite the fact that the data were from different time periods. To compare the avifaunal species composition of the SBGRF in 1998 with that of 1898 and with those of other existing primary and secondary forest fragments and with abandoned plantations (hereafter referred to as forest patches) surveyed in a recent study (Castelletta *et al*., 2005), we carried out non-metric multidimensional scaling (NMS) to ordinate sample units (i.e. forest patches) in species space (McCune & Grace, 2002). The NMS was performed using the 'autopilot (slow and thorough)' mode in PC-ORD Version 4.14 (McCune & Mefford, 1999) with Sorensen distance as a dissimilarity measure. Sample scores for forest patches were plotted to show their relative dissimilarity in species composition along two axes of the final optimum two-dimensional ordination space. Species scores (calculated by weighted averaging of each species in each sample unit) were also plotted to illustrate their association with forest patches.

To examine potential ecological selectivity in species extinctions in the SBGRF, we compared mean body size, habitat specialisation (i.e. forest versus non-forest-dependent), origin (i.e. native versus introduced) and feeding guild (i.e. carnivore, frugivore, insectivore, nectarivore and granivore) among the three categories of birds (i.e. extinct, survivor and coloniser). We defined 'forest-dependent birds' as species that have been observed exclusively in the primary and secondary forests and 'non-forest-dependent birds' as species that have been recorded in other habitat types. Definitions of all species characteristics were based on Robson (2002). Waterbird, nocturnal and migratory species were excluded from all our analyses. Each variable was tested for normality prior to any statistical analysis. All statistical analyses were performed using Minitab Version 13.2 (Minitab Inc., 2000).

RESULTS

Of the 37 species recorded in 1898, 18 (49%) were extirpated from the SBGRF by 1998 (Table 1). Extinct forest-dependent birds included the rhinoceros hornbill, green broadbill and emerald dove. Nineteen (51%) species persisted in the forest fragment, including the changeable hawk eagle, hill myna and greater racket-tailed drongo (Table 1). Twenty additional species colonised the SBGRF during this same time period, including the coppersmith barbet, white-vented myna and house crow (Table 1). The proportion of resident bird community lost from the SBGRF appeared to be similar to the inferred bird extinction estimate for the whole Singapore Island over a 183-year period (59%: Brook *et al*., 2003*a*). Furthermore, despite the small sample size, the proportion of forest-dependent species extirpated (75%: 3 out of 4 species) seemed to broadly correspond with that observed from the entire island since 1819 (67%: Castelletta *et al*., 2000).

The distance between two forest patches in the ordination of their sample scores shows the relative dissimilarity in their species compositions (Fig. 2(a)). Current avian species composition (1998 survey) of the SBGRF appeared to be more similar to that from young secondary forest fragments and abandoned plantations (27–102 ha) than to those from old secondary forest fragments (58–935 ha: Fig. 2(a)). The bird community of the SBGRF in 1898 differed from that of all existing forest patches (Fig. 2(a)).

The mean body size of birds did not differ significantly among the three categories (ANOVA, $F = 0.59$, $P = 0.56$). Three forest-dependent species were lost from the SBGRF whereas only one survived and none colonised it (Likelihood ratio $\chi^2 = 4.91$, $P = 0.09$). Significantly more introduced species (4) colonised the fragment than were previously recorded (no species: Likelihood ratio $\chi^2 = 8.95$, $P = 0.01$). The proportions of carnivores, frugivores, granivores and insectivores did not differ significantly among the categories ($P > 0.10$). However, significantly more nectarivores survived in or colonised the SBGRF than were lost (Pearson $\chi^2 = 5.88$, $P = 0.05$).

DISCUSSION

Since the Singapore Botanic Gardens Rainforest Fragment (SBGRF) may have been isolated a few decades (34–68 years) prior to Ridley's (1898) survey, it is highly probable that the extinctions of some sensitive bird species proceeded undetected. Indeed, we know from other studies that 100-ha fragments can lose one half of their species in less than 15 years (Ferraz *et al*., 2003), suggesting that the avifaunal community in the SBGRF might have experienced much higher extinction rates within the first few decades of its isolation. In addition, the potential impact of changes to the landscape surrounding the SBGRF (e.g. urbanisation: Lim & Sodhi, 2004) on bird richness remains unknown due to the lack of relevant land-use data over the last century. Therefore, in essence, we may be documenting the species turnover in the SBGRF bird community after an initial relaxation with the most sensitive species already extinct.

Nevertheless, given the above limitations and small sample size (i.e. one fragment), several conservation implications can be drawn from our study. Of the 18 bird species lost from the SBGRF, only five species (e.g. the rhinoceros hornbill) represented local extinctions from the entire island of Singapore (Table 1; Castelletta *et al*., 2000). The other species lost from the SBGRF survive in other parts of Singapore, suggesting their loss is not due solely to island-scale pressures, but more so as a result from the local effects occurring at the fragment-level. The impact of extinction-causing mechanisms appears to vary across spatial scales (for a review, see Fahrig, 2003), resulting in the observed differences in extinction patterns. For example, negative edge effects are likely to be more pronounced in small fragments such as the SBGRF than in larger forests in Singapore. In addition, inter-fragment migration may have prevented the extirpation of some species from the whole of Singapore (i.e. the rescue effect: Brown & Kodric-Brown, 1977).

While acknowledging that Ridley (1889) may have missed some species, the general trend of avifaunal turnover in the SBGRF is towards the loss of native forest species and the gain of introduced species. Introduced species in the SBGRF represent almost 20% of all individuals in the fragment (Castelletta *et al*., 2005). However, most of the colonisers were, in fact, native species (80%: 16 out of 20 colonisers). This contrasts with colonisation patterns in other tropical forest fragments such as the Bogor Botanic Gardens (84 ha, in Java), where only one colonisation by a native species (the black-crowned night heron, *Nycticorax nycticorax*) was noted in 50 years (Diamond, Bishop & van Balen, 1987). Likewise, there was a near absence of recolonisation by native species in the neotropical Barro Colorado Island (Robinson, 1999). The recolonisation rates of native species in forest isolates are probably dependent on factors such as the type of isolation (i.e. forest fragment versus island) and the characteristics of the surrounding matrices.

Our ordination results show large differences between the species composition of the SBGRF in 1898 and 1998, as well as differences between SBGRF 1898 and other contemporary forest patches. These differences are due to two shifts in the bird community. First, five species in the SBGRF 1898 are now locally extinct from bird communities in Singapore (Table 1, Fig. 2(b)). Second, there is a growing number of introduced species and the disappearance of forest-dependent species from the SBGRF over a century (Fig. 2(b)).The SBGRF would have been much more valuable for conservation if no species turnover had occurred over the 100 year period.

Although the loss of forest birds in the SBGRF suggests that the fragment has declined ecologically over time, the colonisation by some forest edge species (e.g. the striped tit babbler) does suggest it may play some role in conservation. Hopes of the SBGRF retaining even

Table 1. Summary information of bird species recorded in the Singapore Botanic Gardens rainforest fragment

Scientific name	Common name	Category	Mean body size (cm)	Habitat specialisation	Origin	Feeding guild				
						CAR	FRU	GRA	INS	NEC
Acridotheres javanicus	White-vented myna	Coloniser	26.00	0	1	0	1	0	1	1
Acridotheres tritis	Common myna	Coloniser	25.75	0	0	0	1	0	1	1
Aegithina tiphia	Common iora	Survivor	13.25	0	0	0	0	0	1	0
Aethopyga siparaja	Crimson sunbird	Survivor	12.25	0	0	0	0	0	1	1
Alcedo meninting	Blue-eared kingfisher	Extinct	16.00	0	0	1	0	0	0	0
Anthreptes malacensis	Brown-throated sunbird	Survivor	14.00	0	0	0	0	0	1	1
Aplonis panayensis	Asian glossy starling	Survivor	20.25	0	0	0	1	0	1	1
Apus affinis	House swift	Survivor	14.50	0	0	0	0	0	1	0
Arachnothera longirostra	Little spiderhunter	Extinct	16.25	0	0	0	0	0	1	1
Buceros rhinoceros	Rhinoceros hornbill	Extinct*	106.50	1	0	0	1	0	0	0
Cacatua goffini	Tanimbar corella	Coloniser	32.00	0	1	1	1	1	0	1
Cacomantis merulinus	Plaintive cuckoo	Extinct	22.50	0	0	0	1	0	1	0
Calyptomena viridis	Green broadbill	Extinct*	16.00	1	0	0	1	0	1	0
Celeus brachyurus	Rufous woodpecker	Extinct	25.00	0	0	0	0	0	1	0
Centropus bengalensis	Lesser coucal	Extinct	38.00	0	0	1	0	0	1	0
Centropus sinensis	Greater coucal	Coloniser	50.00	0	0	1	0	0	1	0
Chalcophaps indica	Emerald dove	Extinct	25.00	1	0	0	1	0	0	0
Chrysococcyx xanthorhynchus	Violet cuckoo	Coloniser	16.75	0	0	0	1	0	1	0
Collocalia fuciphaga	Edible-nest swiftlet	Extinct*	13.00	0	0	0	0	0	1	0
Columba livia	Rock pigeon	Coloniser	33.00	0	1	0	1	0	0	0
Copsychus saularis	Oriental magpie robin	Survivor	20.00	0	0	0	0	0	1	0
Corvus macrorhynchos	Large-billed crow	Survivor	53.50	0	0	1	0	0	1	0
Corvus splendens	House crow	Coloniser	41.50	0	1	1	1	0	1	0
Coturnix chinensis	Blue-breasted quail	Extinct*	14.00	0	0	1	1	1	1	0
Cypsiurus balasiensis	Asian palm swift	Survivor	11.50	0	0	0	0	0	1	0
Dendrocopos moluccensis	Sunda pygmy woodpecker	Extinct	12.75	0	0	0	1	0	1	0
Dicaeum cruentatum	Scarlet-backed flowerpecker	Coloniser	8.75	0	0	0	1	0	1	1
Dicaeum trigonostigma	Orange-bellied flowerpecker	Coloniser	9.00	0	0	0	1	0	1	1
Dicrurus paradiseus	Greater racket-tailed drongo	Survivor	33.25	0	0	1	0	0	1	1
Dinopium javanense	Common flameback	Extinct	29.00	0	0	0	1	0	1	0
Eudynamys scolopacea	Asian koel	Coloniser	42.00	0	0	0	1	0	1	0
Eurystomus orientalis	Dollarbird	Survivor	29.50	0	0	1	0	0	1	0
Gracula religiosa	Hill myna	Survivor	29.00	0	0	0	1	0	1	1
Halcyon pileata	Black-capped kingfisher	Extinct	30.25	0	0	1	0	0	0	0
Halcyon smyrnensis	White-throated kingfisher	Survivor	28.50	0	0	1	0	0	0	0
Haliaeetus leucogaster	White-bellied sea eagle	Extinct	77.50	0	0	1	0	0	0	0
Haliastur indus	Brahminy kite	Extinct	48.00	0	0	1	0	0	1	0
Hemiprocne longipennis	Grey-rumped treeswift	Coloniser	19.75	0	0	0	0	0	1	0
Hirundo tahitica	Pacific swallow	Coloniser	13.50	0	0	0	0	0	1	0
Loriculus galgulus	Blue-crowned hanging parrot	Coloniser	13.25	0	0	1	1	1	0	1
Macronous gularis	Striped tit babbler	Coloniser	13.25	0	0	0	1	1	1	1
Malacocincla abbotti	Abbott's babbler	Coloniser	15.75	0	0	0	1	1	1	1
Megalaima haemacephala	Coppersmith barbet	Coloniser	17.00	0	0	0	1	0	0	0
Merops viridis	Blue-throated bee-eater	Coloniser	23.00	0	0	0	0	0	1	0
Oriolus chinensis	Black-naped oriole	Survivor	26.00	0	0	0	1	0	1	0
Orthotomus atrogularis	Dark-necked tailorbird	Coloniser	11.25	0	0	0	1	1	1	1
Orthotomus ruficeps	Ashy tailorbird	Extinct	11.50	0	0	0	1	1	1	1
Picus miniaceus	Banded woodpecker	Coloniser	26.25	0	0	0	1	0	1	0
Psittacula longicauda	Long-tailed parakeet	Survivor	41.00	0	0	0	1	1	0	1
Pycnonotus goiavier	Yellow-vented bulbul	Survivor	20.25	0	0	0	1	0	1	1
Pycnonotus plumosus	Olive-winged bulbul	Survivor	20.25	0	0	0	1	0	1	1
Spizaetus cirrhatus	Changeable hawk eagle	Survivor	68.00	1	0	1	0	0	0	0
Streptopelia chinensis	Spotted dove	Survivor	30.50	0	0	0	1	0	0	0
Surniculus lugubris	Drongo cuckoo	Extinct	24.50	0	0	0	1	0	1	0
Todiramphus chloris	Collared kingfisher	Coloniser	25.00	0	0	1	0	0	0	0
Treron vernans	Pink-necked green pigeon	Survivor	29.25	0	0	0	1	0	0	0
Turnix suscitator	Barred buttonquail	Extinct*	16.25	0	0	0	0	1	1	0

For habitat specialisation: 1, represents forest-dependent species; 0, represents non-forest-dependent species.
For origin: 1, represents introduced species; 0, represents native species.
For feeding guild: 1, represents the classification of the species as carnivore (CAR), frugivore (FRU), granivore (GRA), insectivore (INS) or nectarivore (NEC). Feeding guild categories are not mutually exclusive.
* indicates actual local extinction from the entire island of Singapore.

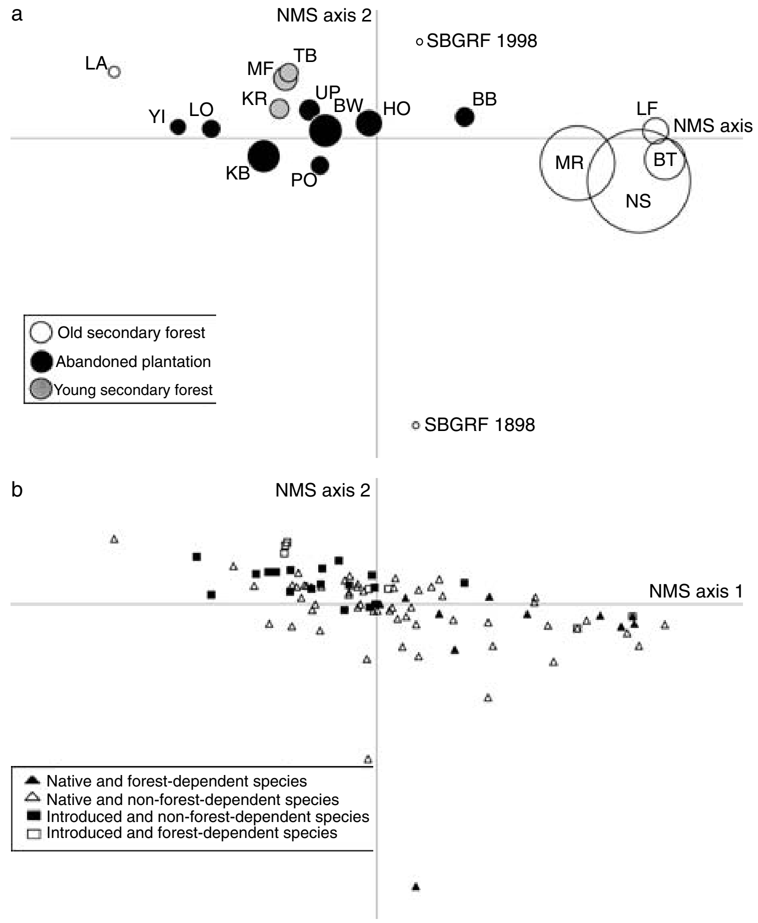

Fig. 2. Non-metric multidimensional scaling (NMS) ordination of sample scores (a) and species scores (b) in species space. The coefficients of determination (R^2) for the correlations between ordination distances and distances in the original *n*-dimensional space are 0.338 and 0.576 for axis 1 and axis 2, respectively. Samples include the Singapore Botanic Gardens rainforest fragment (SBGRF 1898 and SBGRF 1998), Bukit Timah Nature Reserve (BT), Nee Soon Forest (NS), MacRitchie (MR), Lornie Forest (LF), Bukit Batok Nature Park (BB), Bukit Batok West Wood (BW), Poyan Wood (PO), Khatib Bongsu (KB), Holland Wood (HO), Yishun Park (YI), Kent Ridge Park (KR), Ulu Pandan Canal (UP), Mount Faber Park (MF), Labrador Park (LA), Loyang Wood (LO) and Telok Blangah Hill Park (TB). Bubble size reflects the relative areas of the forest fragments.

these forest edge species are dampened, however, by the influx of introduced potential nest predators (e.g. the house crow), which may jeopardise their survival (Wong, Sodhi & Turner, 1998; Sodhi *et al*., 2003). Consequently, the invasion of introduced species is also indicative of possible deterioration of habitat quality (e.g. Kennedy *et al*., 2002; Fig. 2(b)). Indeed, our study revealed that introduced and non-forest-dependent species seemed to be more closely associated with the smaller and less matured forest patches than larger and more matured ones, whereas native and forest-dependent species appeared to show the opposing trend (Castelletta *et al*., 2005; Fig. 2(b)). Furthermore, the relatively abundant introduced bird community (20%; see below) in the SBGRF may facilitate the introduction of invasive plants through seed dispersal. This may result in the homogenisation of the plant community, further diminishing the habitat quality of the SBGRF.

Large-bodied species are particularly extinction-prone due to factors such as low population sizes, low reproductive rates and high food requirements (Sodhi *et al*., 2004*b*). However, the influence of body size on the extinction-proneness of birds has not been conclusively documented (e.g. Renjifo, 1999). In our study, the lack of body size effect on the extinction probability of birds could be due to the loss of particularly sensitive and/or large species prior to 1898. As such, body size effects on extinction probability might be less evident after the initial stages of species extinctions (Sodhi *et al*., 2004*b*).

The proportions of most feeding guilds, except the nectarivores, did not change through time, suggesting that some degree of compensation might be occurring across the foraging niches (e.g. the asian koel possibly replaced the drongo cuckoo: see Table 1). Nevertheless, even changes in species composition within feeding guilds may have ecological impacts. For example, the replacement of large-gaped frugivores (e.g. the green broadbill) by small-gaped species (e.g. the coppersmith barbet) may affect the dispersal of larger seeds. The higher proportion of nectarivores observed in the extant species (i.e. 'survivors' and 'colonisers') were probably due to the availability of more flowering ornamental plant species in the SBGRF now than in the past (Turner *et al*., 1996).

The proportion of vascular plant species loss (51%: Turner *et al.*, 1996) in the SBGRF over a similar time period was nearly identical to the proportion of its avian species loss (49%). The proportion of introduced flora in this fragment increased five-fold from 4% (i.e. 19 out of 467 species in the 1890s) to 20% (i.e. 80 out of 394 species in 1994; including a few deliberately planted species). This trend paralleled the increase in introduced bird species. The influx of introduced bird and vascular plant species may reflect the deterioration in quality of the SBGRF over time (e.g. Laurance *et al.*, 2002). Other more poorly studied taxa in the SBGRF have probably suffered similar levels of extirpation and compositional change (see Brook *et al.*, 2003*a*).

While the avian species richness in the SBGRF remained relatively constant after a century, its species composition underwent significant changes. Such small isolated tropical forest fragments may have limited long-term viability and conservation value for native forest bird (and possibly plant) species. The long-term effects of fragmentation on ecological processes such as seed dispersal within forest fragments remain to be investigated. Nevertheless, the conservation potential of such existing forest fragments may be enhanced by augmenting their size through reforestation practices (e.g. Sodhi *et al.*, 2004*b*), improving their connectivity through linkage to neighbouring fragments or continuous forests (e.g. Castelletta *et al.*, 2005) and eradicating introduced species (e.g. Brook *et al.*, 2003*b*).

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