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Avian diversity and abundance across years: consistent patterns in forests but not grasslands on Viti Levu, Fiji

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ABSTRACT

Context. Habitat loss is a global problem and in Fiji >50% of the land area once covered by forests has been converted to grasslands and agricultural land. About 99% of Fiji's endemic biodiversity and 80% of the land bird species have been identified as forest species. **Aims.** In this study, we compare forest and grassland sites and test for consistency in avian diversity, abundance, foraging guild, and distribution status (endemic, native, introduced to Fiji) over a 5-year period (2016–2020). **Methods.** We surveyed bird communities using the point count method with a 100 m radius and 7-min observation period per site. **Key results.** A one-way analysis of similarities (ANOSIM) analysis showed significant differences in species composition and bird abundance between the forested habitats and grassland habitats. A general linear model test showed significant differences in foraging guild composition and distribution status between forested and grassland habitats. There were no significant differences between the three forested sites (primary montane forest, secondary old-growth forest, old-growth mahogany plantations with regenerating native species), while grassland sites had stronger annual change in species composition. **Implications.** Forest cover, irrespective of whether these forests are of primary or secondary nature, therefore plays an important role in maintaining the native and endemic land bird species and other biodiversity in oceanic island ecosystems such as Viti Levu Island, Fiji.

Keywords: avian biodiversity, aves, community assemblage, foraging guild, forests, grasslands, introduced species, Pacific Islands, primary forest, secondary forest, species richness, vegetation structure, woodlands.

Introduction

Globally, biodiversity is declining at a rapid rate and two of the main drivers behind this decline are introduced (exotic alien) species and habitat loss, both of which are a result of human related activities (Birdlife International 2018; Bongaarts 2019; Soares *et al.* 2020). Birds comprise more than 11 000 species globally, with 40% being threatened due to declining populations and 183 species confirmed to have gone extinct in the past 500 years (Birdlife International 2018). Tropical forests are highly biodiverse ecosystems, containing 15 of the 25 global hotspots for biodiversity (Brooks *et al.* 2002; Birdlife International 2018; Şekercioğlu *et al.* 2019). Tropical oceanic island ecosystems are particularly important biodiversity hotspots, as they support a high number of endemic species with often small population sizes over relatively small geographic areas (Kier *et al.* 2009). Concurrently, birds and other taxa on oceanic islands have extremely high extinction risk with record-level local and species extinction and population decline (Steadman 1995; Brooks *et al.* 2002; Xu *et al.* 2017). Added to this biodiversity crisis is the relative lack of research into functional ecology in tropical systems compared with temperate areas (Clarke *et al.* 2017), and a paucity of long-term monitoring for species diversity and the distribution of functional foraging guilds (Birdlife International 2018; Domisch *et al.* 2019).

Long-term data sets on avian abundance and diversity can provide clues about potential threats or threatening processes, which is useful information for conservation managers.

Several studies have found greater avian diversity and abundance associated with seasonal peaks in resource abundance and breeding onset (Clunie 1984; Watling 2001; Naikatini 2009; Almazán-Núñez *et al.* 2018; Kopij 2019). Avian surveys have increasingly documented patterns of avian decline, especially in island ecosystems that must contend with a suite of factors such as habitat loss, introduced predators, and introduced pathogens (Steadman 1993; Innes *et al.* 2009; Dvorak *et al.* 2012; Koop *et al.* 2016). Habitat loss is a key threatening process (Xu *et al.* 2017), as is climate change (Şekercioğlu *et al.* 2012), which is predicted to impact high-elevation species in particular (Birrell *et al.* 2020). Therefore, habitat cover types such as forest or grassland and elevation are additional valuable sources of information to interpret patterns of decline or increase from avian surveys (McCain 2009; Mueller-Dombois *et al.* 2012; Ferger *et al.* 2014; Sam *et al.* 2019). Understanding differences in the annual consistency of species or foraging guild composition in different habitat types and/or at different elevation ranges provides essential baseline information about potential changes that may guide management decisions and helps to frame testable hypotheses for the occurrence of such patterns.

The relative composition of different foraging guilds in different habitat cover types is a window through which to understand community structure (Verner 1984; Nally 1994; Korňan and Kropil 2014). There is a breadth of knowledge about the different composition of avian foraging guilds in different ecosystems including coastal systems, arid/grassland systems, and woodland systems (Vale *et al.* 1982; Nally 1994). For example, foliage gleaners (insectivores) may be most dominant and show higher diversity in forested habitat cover types, generalist feeders are common in desert-shrub habitat cover types, and ground-seed feeders (granivores) are dominant in grassland habitat cover types (Vale *et al.* 1982; Nally 1994; Somasundaram and Vijayan 2008; Bett *et al.* 2016; Howland *et al.* 2016; Ehlers Smith *et al.* 2018; Kopij 2019). Seasonal shifts in the prevalence of foraging guilds may also be observed such as, in an arid grassland habitat cover type in India, insectivores were dominant during the winter season and omnivores were dominant during summer (Varun and Dutta 2020). The number of avian foraging guilds varies but is often between five and nine per ecosystem (Taylor *et al.* 2017; Chatterjee *et al.* 2020). The guild structure and composition in an ecosystem is a product of the physical structure of the system, geographic location, resource availability and the ability of birds to exploit the available resources (Vale *et al.* 1982; Nally 1994; Chatterjee *et al.* 2020). The high bird species richness and guild diversity in forested habitats has been shown to be related to the heterogeneity of the vegetation structure and the plant guilds present (Cubley *et al.* 2020).

The Fijian archipelago has approximately 500 named islands and islets of which about 100 are inhabited, and a range of terrestrial habitat types such as grasslands and forests spanning elevational gradients from 0 to 1323 m.a.s.l. (Derrick *et al.* 1965; Smith 1979). There are nine principal vegetation types recognised in Fiji: lowland rainforest, upland rainforest, cloud forest, dry forest, *Talasiga* vegetation, freshwater-wetland vegetation, mangrove forest and scrub, coastal strand vegetation and small island vegetation (Mueller-Dombois and Fosberg 1998). Fiji harbours 108 native bird species, of which 61% are land birds, 28% seabirds and 11% migrant shorebirds (Birdlife Datazone 2017). Of the 66 native land bird species, 52% are endemic to Fiji, 11% are threatened with extinction and one species has been confirmed to have gone extinct from Fiji (Watling 2001; Birdlife Datazone 2017).

Viti Levu island is the largest island in the Fijian archipelago with an area of 10 338 km^2 (Smith 1979), which is approximately 57% of the total landmass for Fiji, with eight of nine principal vegetation types described for Fiji found on Viti Levu. Therefore, it is a good system to begin research into how habitat cover type affects avian diversity and foraging guild composition on Fiji. Furthermore, 49 (74%) of the 66 native land bird species are extant on Viti Levu island. The habitat associations for some of these native and endemic species have briefly been discussed by Gorman (1975) and Reid *et al.* (2019) including some observations and records (Clunie 1984; Watling 2001; Tabudravu 2009) but patterns of occurrence in different habitat types across years has never been quantitatively analysed. To better manage the extant avifauna in forest and anthropogenically modified grasslands in Fiji, we urgently need comparative data on patterns of avian diversity and abundance between habitat types.

In the Fijian archipelago, there is still a gap in knowledge about the number of guilds, guild structure, species diversity and community assemblage in the different terrestrial habitats, which this study aimed to address. We used bird point count data collected from forest and grassland habitat cover types on Viti Levu, Fiji and asked if avian species diversity and community assemblage differ across years and habitat cover types. Reid *et al.* (2019) carried out a short-term study during July in 2016 and found consistency of point count data across survey days. We compared (1) avian species diversity and community composition, (2) the proportion of different foraging guilds (insectivore, nectarivore, granivore, frugivore, omnivore), and (3) the distribution status (endemic, native, introduced) at the species level and the individual level across habitats. We predicted that the diversity of avian species would be greatest in the least-disturbed primary high-elevation forest, followed by the secondary mid-elevation forest and, mahogany plantation low-elevation forest, and be lowest in grasslands. As the grasslands and forests are composed of different vegetation communities and exhibit different plant phenology, we expected that the percentage of species per foraging guild would differ across different habitat cover types. Finally, we predicted that the primary high-elevation forest would sustain the most endemic species and we predicted comparable proportions of endemic and native species in the secondary mid-elevation and mahogany plantation low-elevation forest (see also Reid *et al.* 2019). Grasslands, which have been heavily modified by human activity, were predicted to support more introduced species (Reid *et al.* 2019). One overarching aim of this study was to assess whether avian forest communities and grassland communities show consistent patterns across several years.

Materials and methods

Our study was carried out on the island of Viti Levu, Fiji from 2016 to 2020 during the month of July, coinciding with the breeding season from June to November (Watling 2001; Naikatini 2009). A total of 174 point count stations were surveyed in three forest habitat cover types and two grassland habitat cover types: high-elevation forest (–17°40′55.9″S, 177°32′30.4″E), mid-elevation forest (–17°40′86.0″S, 177°32′38.2″E), low-elevation forest (–18°3′16.8″S, 178°27′41.1″E), mid-elevation grassland (–17°40′21.4″S, 177°32′40.0″E), and low-elevation grassland (–18°4′38.9″S, 177°24′12.9″E) (Fig. 1). Table 1 shows the number of point surveys per study site. The number of sampling stations in each habitat cover type was based on a previous study in Fiji whereby a minimum of five stations was sufficient to record 95% of the bird diversity in a forest habitat (Naikatini 2009). In this study, we noted all birds seen or heard at every survey point (Naikatini 2009; Reid *et al.* 2019).

Description of the study sites

Mt Koroyanitu national heritage park

Three study sites are located within the general area of this national park including high-elevation forest, mid-elevation forest and mid-elevation grassland. The Mt Koroyanitu National Heritage Park, unlike reserves managed by the Ministry of Forestry, uses a community-based management

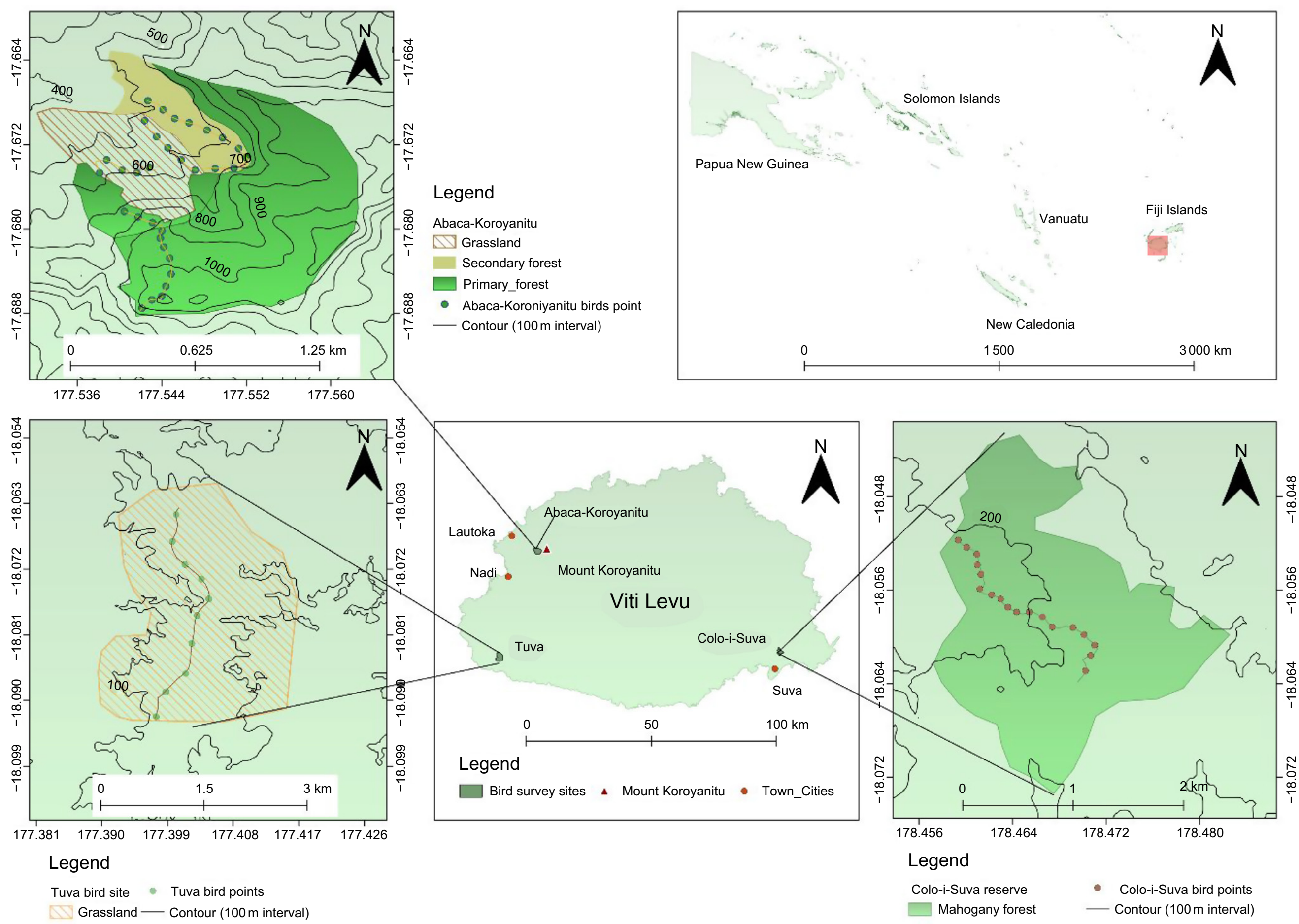

Fig. 1. A map of Viti Levu Island showing the four study sites. The Abaca-Koroyanitu study sites contain three habitat types: secondary mid-elevation forest, primary high-elevation forest, and mid-elevation grassland. The Tuva site contains the lowland grassland habitat, and the Colo-i-Suva site contains the lowland mahogany forest habitat.

Table 1. A summary of the number of sampling stations, total number of birds, total number of species, and average number of birds per sampling station recorded during the 5 years (2016–2020) in the different habitat cover types: high-elevation primary forest (Forest-High), mid-elevation secondary forest (Forest-Mid), low-elevation mahogany forest (Forest-Low), mid-elevation grassland (Grassland-Mid), and low-elevation grassland (Grassland-Low).

	Forest – High	Forest – Mid	Forest – Low	Grassland – Mid	Grassland – Low
Total #sampling stations	42	41	48	27	16
2016	6	7	7	4	na
2017	9	7	15	4	na
2018	8	7	9	5	na
2019	9	10	8	7	7
2020	10	10	9	7	9
Total #birds	595	933	808	915	169
% Endemic	65	74	67	48	20
% Native	34	24	31	22	36
% Introduced	1	2	2	47	44
Total #species	27	31	30	19	12
% Endemic	48	55	53	47	33
% Native	48	35	40	32	42
% Introduced	4	10	7	21	25
Average #birds/station	14	17	17	25	11

na, not applicable.

approach which was initiated in 1990 by the iTaukei Land Trust Board, Fiji Pine Limited and Ministry of Forestry (Thaman 1996; Waqaisavou 1997; Malani 2002). It covers an area of 25 000 ha with 700 documented plant species, 11 of which are endemic to the park (Thaman 1996). The park was set up with the main purposes being conservation and eco-tourism (Thaman 1996; Waqaisavou 1997; Malani 2002).

The high-elevation forest at 1000 m.a.s.l. was located along the track to Mt. Batilamu. The vegetation type is montane rain forest which is still intact or in primary state with *Agathis macrophylla* (Araucariaceae) being the dominant tree species (Anderson *et al.* 2018).

The mid-elevation forest at 500 m.a.s.l. was located along the Savuione waterfall track. The forest is secondary regrowth due to shifting subsistence agriculture and traditional tree removal practices (Reid *et al.* 2019). The dominant tree species include native trees such as *Pterocimbium oceanicum* (Sterculiaceae), *Bischofia javanica* (Phyllanthaceae), *Syzygium malaccense* (Myrtaceae), *Vitex vitilevuense* (Verbenaceae) and *Dendrocnide harveyi* (Urticaceae) (Keppel *et al.* 2022).

The mid-elevation grassland habitat at 500 m.a.s.l. was located between the Abaca Nase lodge and Mt. Batilamu. It is a degraded lowland vegetation type, that developed as a result of constant burning and human activities like subsistence agriculture over a long period of time (Latham 1983). The grassland habitat is dominated by introduced grass (Poaceae) species such as *Pennisetum polystachyon*, *Sporobolus elongatus* and *Panicum maximum*, with patches of the native reed *Miscanthus floridulus* that had once dominated this vegetation type (Ash 1992; Mueller-Dombois and Fosberg 1998).

Colo-i-Suva forest park

The low-elevation forest sampled at this site was at 100 m.a.s.l. The park was established in 1963, with an area of 92 ha and it is part of the Colo-i-Suva Forest Reserve which was established in 1953 covering an area of 369.5 ha (Waqaisavou 1997; Tuiwawa *et al.* 2018). Initially established as a mahogany plantation which has never been logged, it is now a conservation area and used for recreational and educational purposes and is open to the public (Malani 2002; Tuiwawa and Keppel 2012). About 50 000 people visit the park annually which includes the local public, school field trips and tourists (Tuiwawa *et al.* 2018). The introduced Mahogany (*Swietenia macrophylla*) is the dominant tree species but regenerating populations of native plant species in the Colo-i-Suva Forest Reserve have been observed and documented (Tuiwawa and Keppel 2012; Tuiwawa *et al.* 2018; Reid *et al.* 2019).

Tuva grassland

This low-elevation grassland occurs at 100 m.a.s.l., in the Tuva river watershed. This is a degraded catchment with 65% of the area being non-forested, 26% being covered with Pine (*Pinus caribaea*) plantation and only 9% being still covered with secondary forest (Government of Fiji and United

Nations Development Programme 2015; Institute of Applied Sciences 2019). It is one of the six designated sites in Fiji for the United Nations Development Programme (UNDP) Ridge to Reef Project for rehabilitation and reforestation activities (Government of Fiji and United Nations Development Programme 2015). The non-forested areas of the catchment are covered with grassland habitats similar to those in Abaca and are dominated by introduced grass species such as *Pennisetum polystachyon*.

Bird surveys

We conducted bird surveys at 174 point count stations and followed similar methods as in Reid *et al.* (2019). The point count method was used to determine the presence of birds in the area; this method has been recommended for forested habitats and used globally including the Pacific and Fiji in the past (Fancy 1997; Fancy *et al.* 1999; Jackson and Jit 2007; Naikatini 2009; O'Connor *et al.* 2010; Reid *et al.* 2019). The sampling stations were separated by 200 m to prevent any double counting of birds. At each site, all the birds detected visually and audibly were recorded. The location (GPS coordinates) of each station, time of survey and the estimated distance of each bird detected from the point count station, within 100 m radius, were also recorded. Seven minute counts were conducted in the early morning hours between 0630 and 0930 hours, following a 3-min rest and preparation period after arriving at each sampling station. The bird surveys were led by two experienced field ornithologists during 2016, 2017, 2018 (AN, SK) and only AN during 2019 and 2020 with assistance during all years from four undergraduate students noting calling directions (each student monitored a 90° field of view). The large team size monitoring a 360° field of view, reduced the possibility of double counting. All species were identified by AN and SK using the bird field guide book by Watling (2001) as reference.

The foraging guilds, distribution and conservation status categories

Each species was categorised according to its feeding guild, distribution status and conservation status. We used Watling (2001) to determine the foraging guilds and distribution status categories and the Birdlife Datazone (2017) to assign conservation categories to each species. For foraging guild, each species was categorised as either nectarivore, insectivore, frugivore, omnivore, granivore or carnivore. For the distribution status each species was categorised as either native, endemic or introduced species. Of the 57 land birds of Viti Levu Island, there are 16 insectivore, 13 omnivore, 10 carnivore, eight frugivore, five nectarivore, and five granivore species (Watling 2001). For distribution status of the 57 land bird species, there are 29 native, 20 endemic, and eight introduced species (Watling 2001; Birdlife Datazone 2017). For conservation status of the 57 land bird species, Birdlife Datazone (2017) lists one Extinct (*Hypotaenidia poeciloptera*), one Critically Endangered (*Charmosyna amabilis*), one Endangered (*Megalurulus rufus*), two Vulnerable (*Alopecoenas stairi*, *Erythrura kleinschmidti*), two Near Threatened (*Clytorhynchus nigrogularis*, *Prosopeia personata*), and the remaining 50 species as Least Concern (LC) (Table 2).

Statistical analysis

Prior to the statistical analysis, we transformed our data and expressed them as percentage of foraging guilds (insectivore, nectarivore, frugivore, granivore and omnivore) and distribution or geographic range status (endemic, native and introduced) at each site for each year. This was done both at the species (species richness) and individual (total individuals) level. To test for similarities in species composition among the five different survey sites over the 5 years, we used multivariate analysis of similarities (ANOSIM) for statistical analysis and non-metric multidimensional scaling (nMDS) for graphing purposes using the PAST 4.01 software (Hammer *et al.* 2001). The ANOSIM test is a non-parametric test looking at similarities between two or more tested samples (Clarke 1993). We assessed similarity in species composition between the different habitat cover types using the Jaccard similarity index (accounts for species presence versus absence only) and the Bray–Curtis similarity index (accounts for the quantity of different species) to create a dissimilarity matrix between sites. We then used nMDS to present the data in a scatter plot. To test the effects of the different habitat cover types on the foraging guilds (insectivore, nectarivore, frugivore, granivore and omnivore) and distribution/geographic range status (endemic, native and introduced) over the different years, we used General Linear Model (GLM) Multivariate Analysis in the IBM SPSS Statistics software (version 22, IBM Corp 2013). In the multivariate analysis we used habitat as the fixed variable, year was the covariate, and foraging guild and distribution status were the dependent variables.

Results

Avian diversity, abundance and conservation status

We counted 3421 birds including 34 species of birds and 22 bird families across 174 sampling stations (Tables 1, 2). Sixty-one percent (n = 2097) of all birds counted were endemic, 28% (n = 943) were native and 11% (n = 374) were introduced. At the species level 50% (n = 17) of the recorded species were endemic, 13% (n = 13) were native and 12% (n = 4) were introduced (Table 2). The

Table 2. Bird list for species seen or heard in high-elevation primary forest (F-H), mid-elevation secondary forest (F-M), low-elevation mahogany forest (F-L), mid-elevation grassland (G-M) and low-elevation grassland (G-L) surveyed in July, 2016, 2017, 2018, 2019, 2020 on Viti Levu Island, Fiji.

	Scientific name	Common name	Family	IUCN	Status	F-H	F-M	F-L	G-M	G-L
1	*Circus approximans*	Swamp Harrier	Accipitridae	LC	E					
2	*Accipiter rufitorques*	Fiji Goshawk	Accipitridae	LC	N					
3	*Todiramphus chloris*	Collared Kingfisher	Alcedinidae	LC	N	8	7	7	0	1
4	*Anas superciliosa*	Pacific Black Duck	Anatidae	LC	N					
5	*Dendrocygna arcuata*	Wandering Whistling-duck	Anatidae	LC	N					
6	*Aerodramus spodiopygius*	White-rumped Swiftlet	Apodidae	LC	N	0	6	14	103	0
7	*Butorides striata*	Green-backed Heron	Ardeidae	LC	N					
8	*Egretta sacra*	Pacific Reef-egret	Ardeidae	LC	N					
9	*Egretta novaehollandiae*	White-faced Heron	Ardeidae	LC	N					
10	*Artamus mentalis*	Fiji Woodswallow	Artamidae	LC	E	1	0	3	3	7
11	*Lalage maculosa*	Polynesian Triller	Campephagidae	LC	N	28	36	21	7	14
12	*Ducula pacific*	Pacific Imperial-pigeon	Columbidae	LC	N					
13	*Ducula latrans*	Barking Imperial-pigeon	Columbidae	LC	E	66	52	92	0	0
14	*Chrysoena luteovirens*	Golden Dove	Columbidae	LC	E	19	14	19	2	0
15	*Ptilinopus perousii*	Many-coloured Fruit-dove	Columbidae	LC	N	18	11	11	0	0
16	*Columba vitiensis*	Metallic Pigeon	Columbidae	LC	N	25	6	15	0	3
17	*Columba livia*	Rock Dove	Columbidae	LC	I					
18	*Alopecoenas stairi*	Shy Ground-dove	Columbidae	VU	N	0	3	0	0	0
19	*Streptopelia chinensis*	Spotted Dove	Columbidae	LC	I	1	0	0	2	0
20	*Cacomantis flabelliformis*	Fan-tailed Cuckoo	Cuculidae	LC	N	7	5	11	0	0
21	*Erythrura pealii*	Fiji Parrotfinch	Estrildidae	LC	E	2	0	1	338	9
22	*Lonchura oryzivora*	Java Sparrow	Estrildidae	LC	I					
23	*Erythrura kleinschmidti*	Pink-billed Parrotfinch	Estrildidae	VU	E					
24	*Amandava amandava*	Red Avadavat	Estrildidae	LC	I	0	0	0	256	23
25	*Falco peregrinus*	Peregrine Falcon	Falconidae	LC	N					
26	*Hirundo tahitica*	Pacific Swallow	Hirundinidae	LC	N					
27	*Megalurulus rufus*	Long-legged Thicketbird	Locustellidae	EN	E	0	1	0	0	0
28	*Gymnomyza brunneirostris*	Giant Honeyeater	Meliphagidae	LC	E	30	23	15	0	0
29	*Foulehaio procerior*	Kikau	Meliphagidae	LC	E	207	95	34	19	14
30	*Myzomela jugularis*	Orange-breasted Myzomela	Meliphagidae	LC	N	14	10	42	9	4
31	*Clytorhynchus nigrogularis*	Black-throated Shrikebill	Monarchidae	NT	E	2	0	1	0	0
32	*Myiagra castaneigularis*	Chestnut-throated Flycatcher	Monarchidae	LC	E	12	3	23	0	0
33	*Clytorhynchus vitiensis*	Fiji Shrikebill	Monarchidae	LC	N	21	9	10	1	0
34	*Mayrornis lessoni*	Slaty Monarch	Monarchidae	LC	N	22	15	24	0	0
35	*Myiagra vanikorensis*	Vanikoro Flycatcher	Monarchidae	LC	N	32	15	44	10	2
36	*Pachycephala vitiensis*	Fiji Whistler	Pachycephalidae	LC	E	12	5	39	0	0
37	*Petroica pusilla*	Pacific Robin	Petroicidae	LC	N	20	19	9	2	1
38	*Coturnix ypsilophora*	Brown Quail	Phasianidae	LC	I					
39	*Phigys solitarius*	Collared Lory	Psittacidae	LC	E	26	3	15	1	0
40	*Prosopeia personata*	Masked Shining-parrot	Psittacidae	NT	E	46	18	93	0	0
41	*Charmosyna amabilis*	Red-throated Lorikeet	Psittacidae	CR	E					
42	*Pycnonotus cafer*	Red-vented Bulbul	Pycnonotidae	LC	I	10	5	6	17	38
43	*Hypotaenidia poeciloptera*	Bar-winged Rail	Rallidae	EX	N					

(*Continued on next page*)

Table 2. (*Continued*).

	Scientific name	Common name	Family	IUCN	Status	F-H	F-M	F-L	G-M	G-L
44	*Hypotaenidia philippensis*	Buff-banded Rail	Rallidae	LC	N					
45	*Porphyrio porphyrio*	Purple Swamphen	Rallidae	LC	N					
46	*Zapornia tabuensis*	Spotless Crake	Rallidae	LC	N					
47	*Amaurornis cinerea*	White-browed Crake	Rallidae	LC	N					
48	*Rhipidura layardi*	Fiji Streaked Fantail	Rhipiduridae	LC	E	21	8	11	3	0
49	*Horornis ruficapilla*	Fiji Bush-warbler	Scotocercidae	LC	E	89	83	105	13	0
50	*Acridotheres tristics*	Common Mynah	Sturnidae	LC	I					
51	*Acridotheres fuscus*	Jungle Mynah	Sturnidae	LC	I	5	0	6	2	20
52	*Aplonis tabuensis*	Polynesian Starling	Sturnidae	LC	N	4	2	11	0	0
53	*Turdus poliocephalus*	Island Thrush	Turdidae	LC	N	8	22	16	0	0
54	*Tyto alba*	Common Barn-owl	Tytonidae	LC	N					
55	*Tyto longimembris*	Eastern Grass-owl	Tytonidae	LC	N					
56	*Zosterops lateralis*	Silvereye	Zosteropidae	LC	N	40	61	59	68	32
57	*Zosterops explorator*	Fiji White-eye	Zosteropidae	LC	E	112	46	36	67	0

The distribution status is shown as Endemic (E), Native (N) or Introduced (I) (Watling 2001). The conservation status based on the IUCN Red List is shown as Least Concern (LC), Near Threatened (NT), Vulnerable (VU), Endangered (EN), Critically Endangered (CR) or Extinct (EX) (Birdlife International 2018). Numerical values indicate the total number of individuals that were detected during the 5 years of survey. The table lists all 57 bird species that occur on Viti Levu; rows without numbers indicate species not observed within 100 m of the point count station.

mid-elevation forest supported the most species and the lowland grassland recorded the least number of species (Table 1, Fig. 2). The mid-elevation grassland had the most birds per sampling station and the lowland grassland recorded the least number of birds per sampling station (Table 1, Fig. 3).

Community composition (species and abundance) across the sites

There was a significant difference in the bird species composition between the five sites based on a one-way ANOSIM, using presence/absence ($R = 0.5678$, $P = 0.0001$) and the Jaccard similarity index. There was also a significant difference in the bird abundance data between different habitat types ($R = 0.4716$, $P = 0.0001$) using the Bray–Curtis similarity index. The pairwise comparison tests showed significant differences between the forested versus the grassland sites (Table 3). The scatter plots based on nMDS showed that the three forest sites clustered together, suggesting similar distribution patterns for species composition when compared to the two grassland sites (Fig. 4). The number of birds across habitat cover types also followed a similar distribution pattern (Fig. 5).

Avian foraging guild composition (insectivore, nectarivore, granivore, frugivore, omnivore) across sites

There was a significant effect of habitat cover type on the relative proportion of birds per foraging guild, and no significant effect of year, which we tested using GLM one-way MANCOVA ($F_{(15,\ 30.768)} = 4.781$, $P = 0.001$, Wilks' $\Lambda = 0.036$, partial $\eta^2 = 0.000$) (Fig. 5, Tables 4, 5). Similarly, there was a significant effect of habitat cover type on the number of birds per foraging guild and no significant effect of year ($F_{(15,\ 30.768)} = 3.065$, $P = 0.004$, Wilks' $\Lambda = 0.080$, partial $\eta^2 = 0.004$) (Fig. 5, Tables 4, 5).

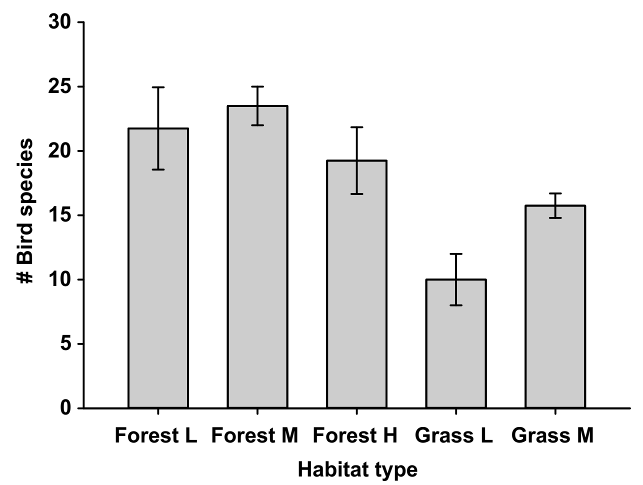

Fig. 2. The average (± s.e.) number of bird species recorded during bird surveys across 5 years (2016–2020) in lowland mahogany plantation forest (Forest L, 100 m.a.s.l., $N = 48$ sampling stations), mid-elevation secondary forest (Forest M, 500 m.a.s.l., $N = 41$ sampling stations), high-elevation primary forest (Forest H, 1000 m.a.s.l., $N = 42$ sampling stations), mid-elevation grassland (Grass M, 500 m.a.s.l., $N = 27$ sampling stations) and during 2 years (2019, 2020) in a lowland grassland (Grass L, 100 m.a.s.l., $N = 16$ sampling stations).

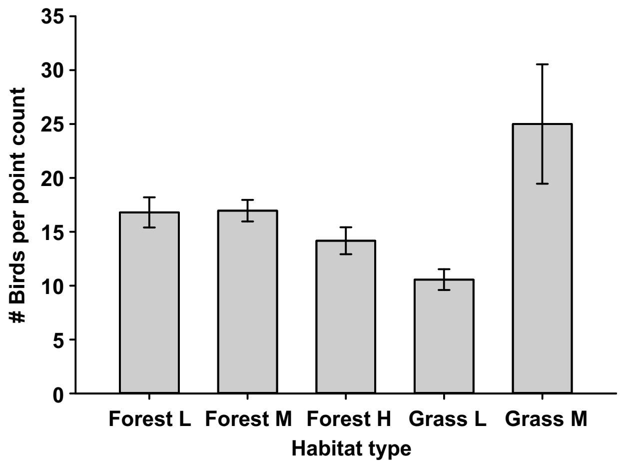

Fig. 3. The average (± s.e.) number of birds per point count during bird surveys across 5 years (2016–2020) in lowland mahogany plantation forest (Forest L, 100 m.a.s.l., *N* = 48 sampling stations), mid-elevation secondary forest (Forest M, 500 m.a.s.l., *N* = 41 sampling stations), high-elevation primary forest (Forest H, 1000 m.a.s.l., *N* = 42 sampling stations), mid-elevation grassland (Grass M, 500 m.a.s.l., *N* = 27 sampling stations) and during 2 years (2019, 2020) in lowland grassland (Grass L, 100 m.a.s.l., *N* = 16 sampling stations).

Table 3. Statistical results shown as *P*-values for the pairwise comparison from a one-way ANOSIM Jaccard test (number of species) and one-way ANOSIM Bray–Curtis test (number of individuals) for birds recorded in five habitat cover types: primary high-elevation forest (Forest H), secondary mid-elevation forest (Forest M), lowland mahogany plantation forest (Forest L), mid-elevation grassland (Grass M) and lowland grassland (Grass L), across Viti Levu Island.

	Forest M	Forest H	Forest L	Grass M	Grass L
Jaccard (species) pairwise summary					
Forest M		0.079	0.241	0.009	0.044
Forest H	0.079		0.887	0.007	0.047
Forest L	0.241	0.887		0.008	0.047
Grass M	0.009	0.007	0.008		0.098
Grass L	0.044	0.047	0.047	0.098	
Bray–Curtis (abundance) pairwise summary					
Forest M		0.310	0.072	0.007	0.043
Forest H	0.310		0.071	0.009	0.046
Forest L	0.072	0.071		0.008	0.048
Grass M	0.007	0.009	0.008		0.332
Grass L	0.043	0.046	0.048	0.332	

The study was performed over five survey years (2016–2020). The *P*-values have been corrected using the Bonferroni method.

In general, forests supported more insectivores and grasslands supported more granivores, and this pattern was stable across years (Fig. 6).

Avian distribution status (endemic, native, introduced) across sites

There was a significant effect of habitat cover type on the number of species per 'distribution status' and no significant effect of year, which we tested using GLM one-way MANCOVA ($F_{(9,\ 2.054)} = 4.309$, $P = 0.002$, Wilks' $\Lambda = 0.085$, partial $\eta^2 = 0.561$) (Tables 6, 7). Similarly, there was a significant effect of habitat type on the number of birds per 'distribution status' and no significant effect of year ($F_{(9,22.054\ \ 3)} = 5.121$, $P = 0.01$, Wilks' $\Lambda = 0.064$, partial $\eta^2 = 0.600$) (Tables 6, 7). The forests supported comparable diversity and number of endemic and native birds, but grasslands supported more introduced species, and this pattern was consistent across years.

Discusssion

There were similarities in avian species diversity, number of birds, and proportion of foraging guilds across the 5 years in all three forest habitats irrespective of elevation (range 100–1100 m.a.s.l.), and different species diversity, number of birds, and foraging guilds in the two grassland sites (range 100–500 m.a.s.l.). The forest habitat cover types had 27–31 species on average and the grassland sites 12–19 species. In general, the number of birds per year was more stable and ranged from 11 to 17 birds per sampling station in forest habitat cover types and from 10 to 27 birds per sampling station in grassland habitat cover types. Both forests and grasslands had comparable diversity and abundance of endemic and native birds, but grasslands had more introduced species, and this pattern was consistent across the 5 years.

Our initial objective tested for diversity and community composition for which we predicted that species diversity and avian abundance would be highest in high-elevation primary forest, followed by mid-elevation secondary forest and lowland plantation forest, respectively, and lowest in the modified grassland habitats. This assumption was based on studies that have shown plant and invertebrate diversity to be highest in primary forest systems and lowest in modified or degraded systems (Barlow *et al.* 2007; Kormos *et al.* 2017; Neoh *et al.* 2017; Sayer *et al.* 2017). In contrast to this prediction, we found comparable species diversity across the three forest habitats (Fig. 2). We also found lower species diversity in the grasslands compared with the forest habitats. Our study therefore corroborated the prediction that forests have higher species diversity than grasslands but did not find differences among forest types related to elevation. One factor that has been widely described as being significant for avian diversity globally is forest cover, with greater diversity in areas with greater forest cover (Jayapal *et al.* 2009; Newmark *et al.* 2010). Tropical tree diversity and other terrestrial biodiversity

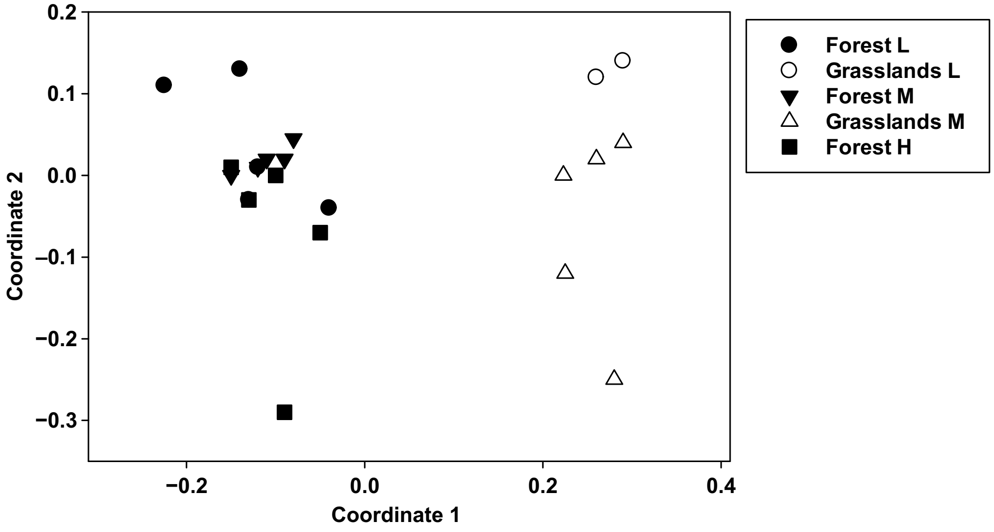

Fig. 4. Bird species composition similarity across forest and grassland sites on Viti Levu island. Data are shown using nMDS Jaccard similarity index scatter plot for the percentage number of species detected at each site: three forest sites (Forest L = low elevation, Forest M = mid elevation, Forest H = high elevation) sampled during 2016–2020, and two grassland sites (Grasslands M = mid elevation, Grasslands L = low elevation). Grassland sites differed from forest sites in avian species composition.

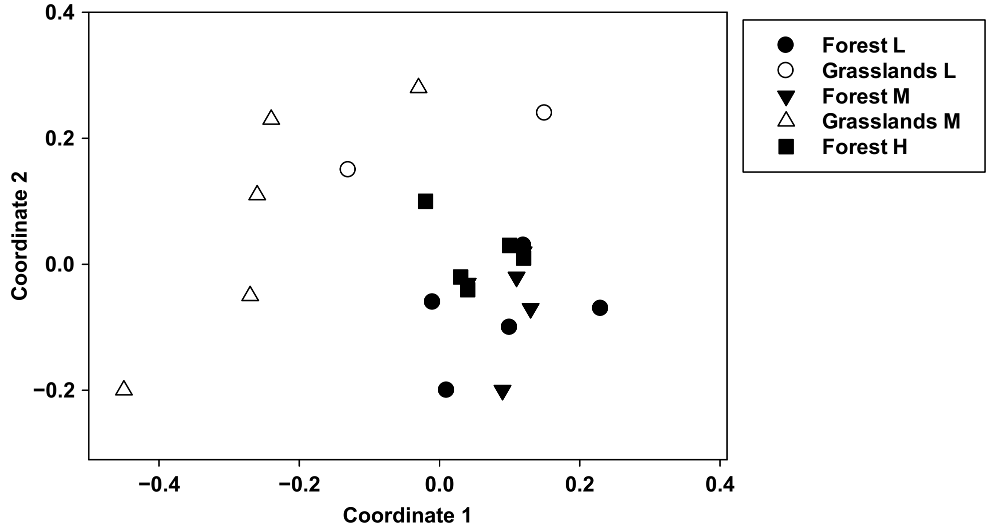

Fig. 5. Bird abundance composition similarity across forest and grassland sites on Viti Levu island. Data are shown using nMDS Bray–Curtis similarity index scatter plot for the percentage of birds detected at each site: three forest sites (Forest L = low elevation, Forest M = mid elevation, Forest H = high elevation) sampled during 2016–2020, and two grassland sites (Grasslands M = mid-elevation grassland sampled during 2016–2020; Grasslands L = lowland grassland sampled during 2019–2020). Grassland sites differed from forest sites in bird assemblage composition.

generally tends to decrease with increasing elevation (Diamond 1988; Givnish 1999; Lomolino 2001). Species diversity tends be the highest around mid-elevation along an elevation gradient, a phenomenon known as the mid-domain effect (Colwell and Lees 2000), which has also been observed for Coleoptera in Fiji where diversity was highest at mid-elevations on Viti Levu Island (Waqa-Sakiti *et al.* 2018). Similarly, high avian diversity in mid-elevation forest was observed in the Pacific island of Mauna Loa, Hawaii, where it was interpreted to be the result of vegetation structure (Mueller-Dombois *et al.* 2012), and at Mt. Wilhelm, Papua New Guinea (Sam *et al.* 2020). Although vegetation studies carried out in Fiji show that tree species diversity is highest in primary tropical

Table 4. Statistical results using general linear model multivariate analysis with *F*-values and *P*-values for the effect of habitat cover type (fixed factor) and year (covariate) on foraging guild (insectivores, nectarivores, frugivores, granivores, omnivores) (dependent factor) analysed at the species level (number of species) and individual level (number of birds).

Factor	Dependent	d.f.	Sum squared	Mean squared	*F*-value	*P*-value
Number of species (species)						
Year (covariate)	Insectivores	1	11.99	11.99	0.28	0.602
	Nectarivores	1	2.21	2.21	0.15	0.702
	Frugivores	1	6.72	6.72	0.49	0.495
	Granivores	1	12.88	12.88	1.42	0.253
	Omnivores	1	35.53	35.53	0.88	0.363
Habitat (independent)	Insectivores	3	1157.19	385.73	9.15	0.001
	Nectarivores	3	25.21	8.40	0.58	0.638
	Frugivores	3	783.49	261.16	19.02	0.000
	Granivores	3	1019.40	339.80	37.32	0.000
	Omnivores	3	1070.44	356.81	8.84	0.001
Number of birds (individuals)						
Year (covariate)	Insectivores	1	93.33	93.33	1.20	0.291
	Nectarivores	1	30.10	30.10	0.43	0.523
	Frugivores	1	84.10	84.10	0.84	0.375
	Granivores	1	190.97	190.97	0.80	0.386
	Omnivores	1	110.22	110.22	0.76	0.398
Habitat (independent)	Insectivores	3	892.71	297.57	3.81	0.033
	Nectarivores	3	1274.76	424.92	6.03	0.007
	Frugivores	3	1870.97	623.66	6.21	0.006
	Granivores	3	4720.69	1573.56	6.58	0.005
	Omnivores	3	519.72	173.24	1.19	0.348

The study was performed over five survey years (2016–2020) across five habitat cover types. At the species level, foraging guild composition differed significantly across habitats but not years, with the exception of nectarivores. At the individual level, foraging guild composition differed significantly across habitats but not years, with the exception of omnivores.
d.f., degrees of freedom.

Table 5. Tukey's pairwise comparison between the habitat cover types: grassland mid-elevation (Grassland M), high-elevation primary forest (Forest H), mid-elevation secondary forest (Forest M), low-elevation mahogany plantation (Forest L), in relation to the number of species and number of birds recorded for the different foraging guilds (insectivore, nectarivore, frugivore, granivore, omnivore) over the 5 years of survey (2016–2020).

Status habitats	Insectivore				Nectarivore				Frugivore				Granivore				Omnivore			
	Grass.	H	M	L	Grass.	H	M	L	Grass.	H	M	L	Grass.	H	M	L	Grass.	H	M	L
Number of species (species diversity)																				
Grassland M		0.003	0.002	0.000		0.909	0.270	0.915		0.000	0.000	0.000		0.000	0.000	0.000		0.010	0.000	0.000
Forest H	0.003		0.897	0.193	0.909		0.320	0.993	0.000		0.565	0.670	0.000		0.415	0.481	0.010		0.154	0.159
Forest M	0.002	0.897		0.237	0.270	0.320		0.316	0.000	0.565		0.322	0.000	0.415		0.910	0.000	0.154		0.984
Forest L	0.000	0.193	0.237		0.915	0.993	0.316		0.000	0.670	0.322		0.000	0.481	0.910		0.000	0.159	0.984	
Number of individuals (relative abundance)																				
Grassland M		0.039	0.400	0.008		0.027	0.001	0.359		0.039	0.018	0.001		0.002	0.003	0.002		0.615	0.321	0.091
Forest H	0.039		0.184	0.423	0.027		0.156	0.151	0.039		0.690	0.062	0.002		0.904	0.958	0.615		0.615	0.215
Forest M	0.400	0.184		0.043	0.001	0.156		0.009	0.018	0.690		0.128	0.003	0.904		0.946	0.321	0.615		0.447
Forest L	0.008	0.423	0.043		0.359	0.151	0.009		0.001	0.062	0.128		0.002	0.958	0.946		0.091	0.215	0.447	

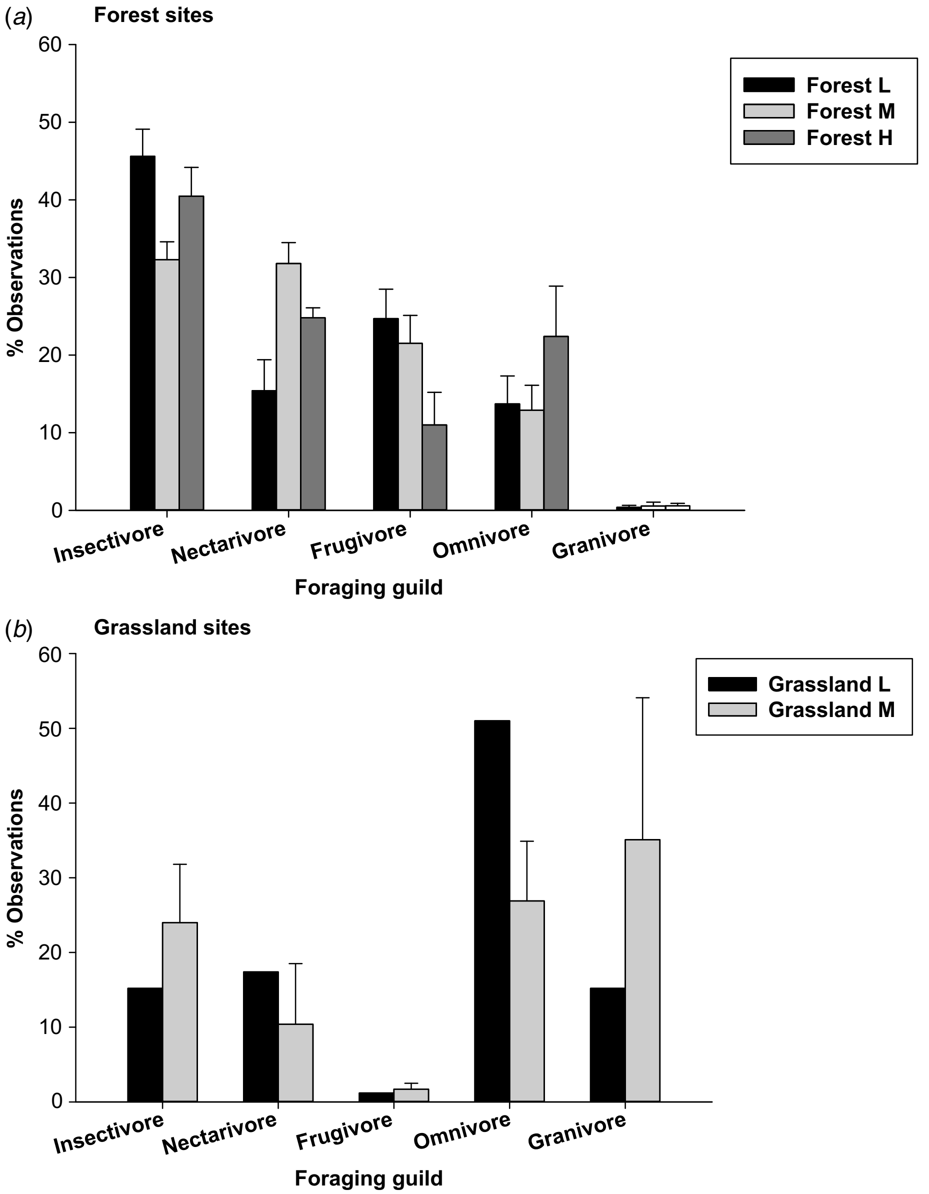

Fig. 6. The annual percentage (mean ± s.e.) of birds observed per foraging guild (insectivores, nectarivores, frugivores, granivores, omnivores) in (*a*) the three forest sites (Forest L = low elevation, Forest M = mid elevation, Forest H = high elevation) (sampled during 2016–2020), and (*b*) the two grassland sites (Grassland M = mid-elevation grassland sampled during 2016–2020; Grassland L = lowland grassland sampled during 2019–2020).

rainforest systems, studies on plant diversity in Fiji have failed to find significant differences among different elevations (Ash 1992). Our finding that species diversity was comparable in the forest habitats could indicate strong niche specialisation of the forest birds. Further research is needed, however, to identify the association between plant diversity and forest structure and cover, which is not known for Viti Levu.

For our second objective, we tested for the proportion of different foraging guilds (insectivore, nectarivore, granivore, frugivore, omnivore) in the four different habitat cover types. We predicted that the percentage of species per foraging guild will differ across cover types due to the different vegetation structure and plant community. Insectivores recorded the highest species diversity in all the habitats, and it was the most common guild recorded in all the habitats except for grassland, where granivores were more abundant (Fig. 6). Grassland sites often contain many seed heads and can sustain large groups of birds in a small area, which is congruent with our observation of more granivore species in the grasslands. Granivores often form large flocks while foraging in open grassland areas and this increases feeding

Table 6. Statistical results using general linear model multivariate analysis with *F*-values and *P*-values for the effect of habitat cover type (fixed factor) and year (covariate) on distribution status (endemic, native, introduced) (dependent factor) at the species level (number of species) and individual level (number of birds).

Fixed	Dependent	d.f.	Sum squared	Mean squared	*F*-value	*P*-value
Number of species (species)						
Year (covariate)	Endemic	1	106.6	106.60	3.40	0.085
	Native	1	21.46	21.46	1.03	0.327
	Introduced	1	29.76	29.76	1.67	0.214
Habitat (fixed)	Endemic	3	325.77	108.59	3.46	0.043
	Native	3	324.53	108.18	5.18	0.012
	Introduced	3	1163.71	387.90	21.96	0.001
Number of birds (individuals)						
Year (covariate)	Endemic	1	21.90	21.90	0.14	0.712
	Native	1	108.24	108.24	0.51	0.487
	Introduced	1	33.12	33.12	0.86	0.368
Habitat (fixed)	Endemic	3	4265.2	1421.72	9.17	0.001
	Native	3	690.94	230.31	1.08	0.387
	Introduced	3	2011.75	670.58	17.48	0.001

The study was performed over five survey years (2016–2020) across five habitat cover types. At the species level, the proportion of endemic, native and introduced species differed significantly across the different habitat cover types. At the individual level, the proportion of endemic and introduced species differed significantly across the different habitat cover types but not the number of native birds.
d.f., degrees of freedom.

Table 7. Results of Tukey's pairwise comparison showing *P*-values for the habitat cover type comparisons: Grassland mid-elevation (Grassland M), high-elevation primary forest (Forest H), mid-elevation secondary forest (Forest M), low-elevation mahogany plantation (Forest L), in relation to the number of species and number of birds recorded for the different distribution status (endemic, native, introduced) over the 5 years of survey (2016–2020).

Status habitats	Endemic				Native				Introduced			
	Grass.	H	M	L	Grass.	H	M	L	Grass.	H	M	L
Number of species (species diversity)												
Grassland M		0.480	0.013	0.016		0.002	0.063	0.013		0.000	0.000	0.000
Forest H	0.480		0.512	0.588	0.002		0.086	0.351	0.000		0.351	0.756
Forest M	0.013	0.512		0.907	0.063	0.096		0.427	0.000	0.351		0.527
Forest L	0.016	0.588	0.907		0.013	0.351	0.427		0.000	0.756	0.527	
Number of individuals (relative abundance)												
Grassland		0.005	0.000	0.001		0.803	0.139	0.273		0.000	0.000	0.000
Forest H	0.005		0.155	0.314	0.803		0.210	0.391	0.000		0.944	0.992
Forest M	0.000	0.155		0.654	0.139	0.210		0.676	0.000	0.944		0.936
Forest L	0.001	0.314	0.654		0.273	0.391	0.676		0.000	0.992	0.936	

efficiency and safety (Perea *et al.* 2014). Forest birds were mostly insectivores and frugivores, which tend to defend territories for invertebrate consumption, flowers and fruits (Stamps 1994). Such differences in search behaviour for food resources, foraging guild and territory defence behaviour could explain our observation of varying abundances of birds in the two habitat types. The high diversity and abundance of insectivores in forest habitats has been linked to forest structure and has been observed, for example, in Papua New Guinea (Sam *et al.* 2019; Sam *et al.* 2020), in Tanzania (Ferger *et al.* 2014) and India (Jayapal *et al.* 2009). The diversity and number of the phytophagous guilds (frugivores, nectarivores) have been observed to be influenced by food availability and not forest structure alone (Jayapal *et al.* 2009). This could have affected nectarivore and frugivore diversity observed in the five study sites but remains to be investigated in the future.

Lastly, we tested for distribution status (native, endemic, introduced) focusing on species diversity and abundance of birds across the different habitat cover types. We found similar results compared with two earlier studies in Fiji by Gorman (1975) and Reid *et al*. (2019) who also found evidence that endemic bird species tend to prefer forested habitats; and grasslands contained the greatest number of introduced birds and introduced species. Apart from the grassland habitat, all the three forested habitats (primary, secondary and plantation forest) showed no significant difference in the diversity and abundance of endemic, native and introduced species. These results agree with the 'vegetation structure theory' (Hurlbert 2004; Ferger *et al.* 2014), which posits that diversity and abundance are primarily determined by vegetation structure. However, this should be explored in more detail in future studies as we did not specifically compare food availability, climatic conditions, or vegetation structures in this study. The fact that 80% of breeding land birds in Fiji are forest species (Gorman 1975; Birdlife International 2006) suggests that the ancestors of Fijian birds would have arrived and evolved in a forest dominated ecosystem or perhaps chosen forested habitats. Furthermore, the fact that there was no significant difference between the three forest cover types despite differences in disturbance status, elevation, tree species composition and climatic conditions would also suggest that most of the forest species in Fiji are generalists occupying a wide range of forest habitats, which has been observed in other island ecosystems (MacArthur and Wilson 1967; Lack 1973).

Conclusion

The main findings of this study show stability and consistency across 5 years in Fiji's forest bird communities, irrespective of differences in forest type, forest age or elevation. However, such consistency was lacking in grasslands. Given that most of Fiji's forests have been degraded, the finding that the age of the forest was not a strong predictor for avian species diversity or abundance is a positive sign for bird conservation in Fiji. It suggests that secondary forests have great value for native Fijian birds and that reforestation and improved habitat connectivity should be effective tools to sustain Fiji's forest birds. We conclude that, for Fiji, there is evidence for stable avian community structure in forests that is maintained across years and is not strongly influenced by elevation, while grasslands have a more variable avian community composition.

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