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Foraging ecology of insectivorous birds in a mixed forest of Hong Kong

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ABSTRACT

In a mixed forest in Hong Kong, the foraging ecology of nine species of insectivorous birds was studied. Leaves and branches of diameters smaller than 2 cm were the most frequently searched microhabitats. Gleaning was the most frequently used foraging method. Apart from Blue-winged Minla and Japanese White-eye, no two species used similar proportions of vertical strata and microhabitats at the same time. Bird species using similar proportion of microhabitats were foraging in different proportion of vertical strata. This niche segregation enabled the bird species to coexist in the same habitat. Velvet-fronted Nuthatch differed from other species by its more frequent use of branches of diameters larger than 2 cm and tree trunks. This might be one of the reasons why this exotic species successfully established a breeding population in the study area.

1. Introduction

Foraging ecology of forest birds had been intensively studied in other parts of the world, e.g., North America and Australia, in the 1980s and 1990s. Foraging niches of birds in forest habitats can be separated by using different vertical strata, microhabitats and food resources [1–5]. Foraging tactics used by birds in a habitat are affected by vegetation structure [6–8]. However, little is known about the foraging ecology of forest birds in the South China region. Foraging ecology of forest birds has only been studied at Ding Hu Shan National Nature Reserve in South China and the study only covered breeding season (May–July) [9]. The primary aim of this study was to determine the uses of microhabitats and foraging tactics of common insectivorous bird species in the largest secondary forest of Hong Kong – Tai Po Kau nature reserve. I also compared foraging niches of the common species in the study area to understand how they could coexist in the same habitat, which is a question central in ecology [10–12].

2. Study area and methods

2.1. Study area

The study area was a 40 year-old mixed forest with a continuous canopy at 100–200 m a.s.l. in Tai Po Kau Nature Reserve (22°25′N, 114°11′E), Hong Kong Special Administrative Region of China. This reserve is the largest contiguous forest area in Hong Kong, covering 460 hm^2. The mean annual temperature of the nature reserve is 22.9 °C, mean annual relative humidity is 78.7% and mean annual rainfall is 2900 mm. Wet and dry seasons are marked, with the dry season between November and February and the wet season between March and October. The forest canopy of the study area was made up of native trees and planted exotic species reaching heights of 18–22 m. Native tree species included Short-flowered Machilus *Machilus breviflora*, Red Machilus *M. thunbergii*, Chestnut Oak *Castanopsis fissa* while exotic tree species included Acacia *Acacia confusa* and Brisbane Box *Lophostemon confertus*. The understorey was dominated by Wild Coffee *Psychotria asiatica*, Asiatic Ardisia *Ardisia quinquegona*, Chinese Quinine *Dichroa febrifuga* and Lamb of Tartary *Cibotium barometz*.

2.2. Survey methods

A forest trail of 5 km through the study area was walked in each survey. Birds seen scanning for prey from vantage points were considered to be foraging birds. I used 10 × 42 binoculars to observe foraging birds in the study area. For each foraging bird, I recorded the microhabitat being searched, its height above the ground at the moment of observation, and the foraging method used (if any). The foraging heights were estimated using pre-measured references on the forest trail. A total of 108 surveys were carried out between March 2001 and August 2002.

2.3. Classification of microhabitats and foraging methods

Microhabitats were classified into the following categories: surface and underneath of branch, surface and underneath of leaves, trunk, dead structures (including leaves, branches, tree holes), floral parts, climbers, understorey plants and litter on the ground. Diameter of branches was estimated to the nearest centimeters using the length of the observed bird species from literatures as reference. The surface and underneath of branches were defined

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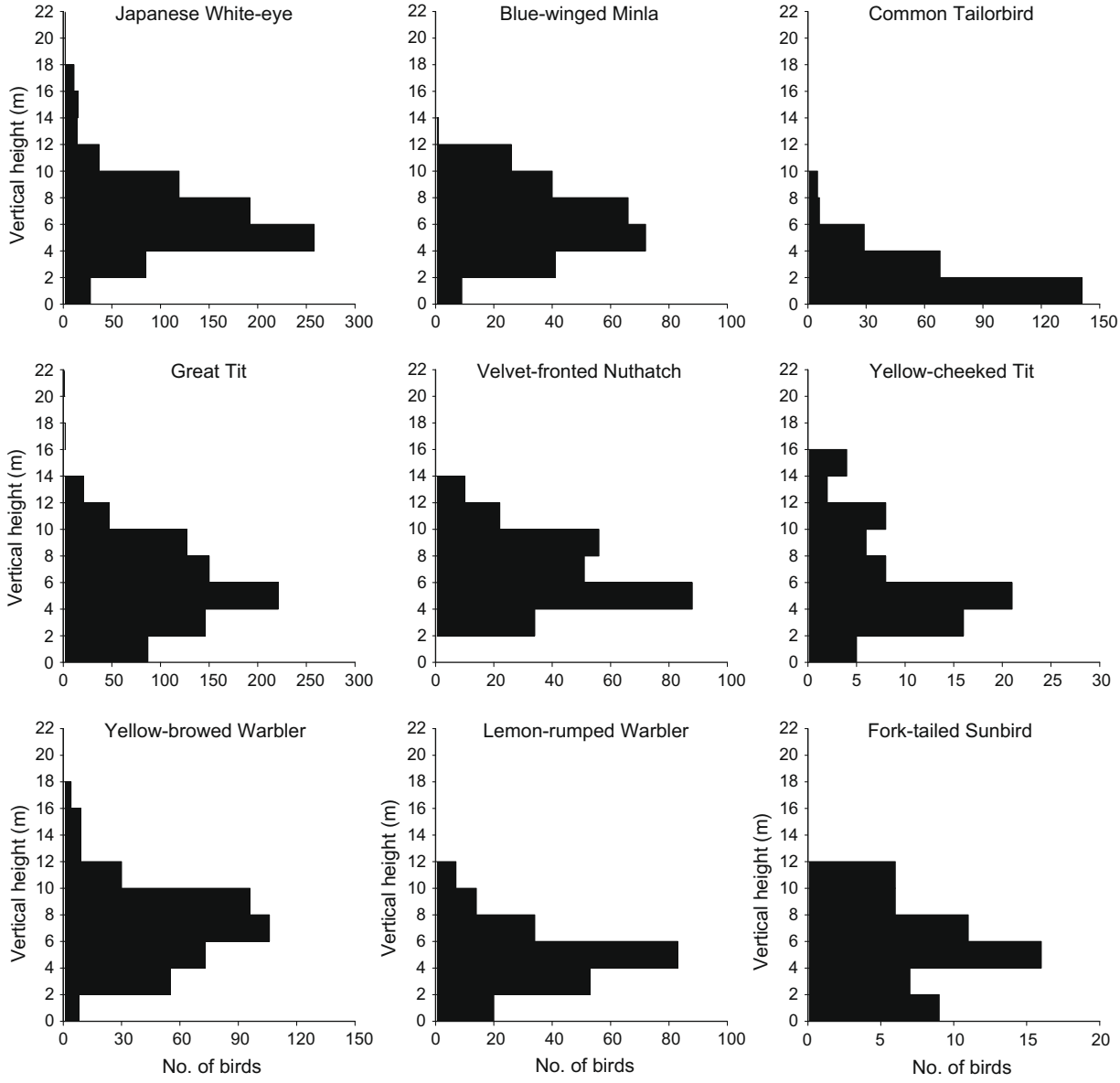

Fig. 1. Vertical distributions of the nine species.

as the parts of the branches above and below a horizontal line dividing the branches into two halves.

Six categories of foraging methods were classified: gleaning – capturing a prey from the surface of the substrate the bird is perching; hovering – maintaining an airborne position by flapping wings and spreading tail, to find prey on the underneath of a substrate; hanging – capturing a prey from another substrate surface (below the one the bird is perching) by a bird hanging upside down; sallying – capturing or pursuing a flying prey on wing; probing – seizing prey from bark crevices, floral parts or other concealed microhabitats; stretching – capturing a prey from another substrate (not the one the bird is perching) by stretching the body but without taking off. Captured preys will be identified and size estimated as far as possible.

2.4. Comparison of foraging niches

The vertical strata (11 columns) and microhabitats (11 columns) of the nine species (9 rows) were listed as a 9 rows × 22 columns matrix for Principal Components Analysis (PCA) of foraging microhabitat utilization.

Chi-sq Test was used to investigate niche overlap between common residents, and between common residents and winter visitors. The uses of vertical feeding strata were compared. The uses of microhabitats of species occupying similar vertical feeding strata were then compared. When residents and winter visitors were compared, the observations of residents between November and March were analysed. Uses of microhabitats of species using different vertical feeding strata were also compared to investigate the separation of ecological niches by uses of different vertical strata. The p-value of all statistical tests was 0.05.

3. Results

3.1. Vertical stratification

A total of 3422 foraging birds and 37 species were observed during the study, which included tits, white-eyes, leaf warblers, minlas, tailorbirds, nuthatches, babblers and flycatchers. There

Table 1
Frequency of search of microhabitats by each species (% of total birds observed).

Microhabitats		JWE	GT	YCT	VFN	CTB	BWM	FTSB	YBW	LRW
Leaf	Surface	355 (48.7)	190 (24.7)	13 (17.3)	0 (0.0)	65 (27.4)	106 (41.7)	13 (25.0)	153 (39.4)	94 (45.0)
	Underneath	189 (25.9)	105 (13.7)	12 (16.0)	0 (0.0)	60 (25.3)	62 (24.4)	19 (36.5)	124 (32.1)	82 (39.2)
Branch (diameter < 2 cm)	Surface	125 (17.1)	335 (43.6)	23 (30.7)	27 (10.5)	59 (24.9)	67 (26.4)	19 (36.5)	4 (1.0)	3 (1.4)
	Underneath	6 (0.8)	19 (2.5)	1 (1.3)	17 (6.6)	0 (0.0)	2 (0.8)	0 (0.0)	84 (21.8)	18 (8.6)
Branch (diameter > 2 cm)	Surface	11 (1.5)	51 (6.6)	10 (13.3)	100 (38.8)	6 (2.5)	6 (2.4)	0 (0.0)	1 (0.3)	0 (0.0)
	Underneath	0 (0.0)	3 (0.4)	2 (2.7)	49 (19.0)	0 (0.0)	1 (0.4)	0 (0.0)	0 (0.0)	0 (0.0)
Trunk		0 (0.0)	17 (2.2)	1 (1.3)	56 (21.7)	1 (0.4)	1 (0.4)	0 (0.0)	0 (0.0)	1 (0.5)
Dead (leaves, branches, tree holes)		18 (2.5)	33 (4.3)	4 (5.3)	6 (2.3)	8 (3.4)	1 (0.4)	0 (0.0)	13 (3.4)	2 (1.0)
Buds, floral parts		16 (2.2)	4 (0.5)	1 (1.3)	0 (0.0)	1 (0.4)	1 (0.4)	0 (0.0)	1 (0.3)	2 (1.0)
Climber		9 (1.2)	11 (1.4)	8 (10.7)	3 (1.2)	10 (4.2)	7 (2.8)	1 (1.9)	7 (1.8)	7 (3.3)
Understorey plants and litter		0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	27 (11.4)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)

JWE = Japanese White-eye, GT = Great Tit, VFN = velvet-fronted Nuthatch, CTB = Common Tailorbird, BWM = Blue-winged Minla, YCT = Yellow-cheeked Tit, FTSB = Fork-tailed Sunbird, YBW = Yellow-browed Warbler, LRW = Lemon-rumped Warbler.

Table 2
Foraging methods (% of total bird observed).

Species	Glean	Hover	Hang	Sally	Stretch	Probe
Japanese White-eye	43.6	6.1	30.1	4.3	11.0	4.9
Great Tit	48.1	3.8	24.0	12.5	2.9	8.7
Yellow-cheeked Tit	35.3	0.0	47.1	0.0	17.6	0.0
Velvet Fronted Nuthatch	33.0	0.0	0.0	0.0	0.0	67.0
Blue-winged Minla	80.0	0.0	12.5	0.0	7.5	0.0
Common Tailorbird	56.1	4.9	4.9	2.4	24.4	7.3
Fork-tailed Sunbird	6.3	75.0	0.0	12.5	0.0	6.2
Yellow-browed Warbler	52.5	20.8	4.2	19.2	3.3	0.0
Lemon-rumped Warbler	35.2	41.9	1.9	21.2	0.0	0.0

Table 3
Preys and their frequency.

Prey types	Frequency
Unidentified	669
Caterpillar	30
Spider	6
Hemipteran	5
Coleopteran	2
Lepidopteran	1
Isopteran	1
Dipteran	1

were nine species with more than 50 birds observed: Japanese White-eye *Zosterops japonica*, Great Tit *Parus major*, Yellow-cheeked Tit *Parus spilonotus*, Yellow-browed Warbler *Phylloscopus inornatus*, Lemon-rumped Warbler *Phylloscopus proregulus*, Velvet-fronted Nuthatch *Sitta frontalis*, Blue-winged Minla *Minla cyanouroptera*, Common Tailorbird *Orthotomus sutorius* and Fork-tailed Sunbird *Aethopyga christinae*. According to local and regional studies on feeding ecology, these species mainly feed on insects and other small invertebrates [13,14]. Yellow-browed Warbler and Lemon-rumped Warbler are winter visitors, which are present in Hong Kong mainly between November and March. Velvet-fronted Nuthatch and Blue-winged Minla are recently introduced species, and Hong Kong is outside their native distribution ranges [15].

The vertical distributions of the nine species are shown in Fig. 1. Birds utilized height between 0 and 22 m. Japanese White-eyes and Great Tits were the only species utilizing the 20–22 m vertical stratum. All species except Yellow-browed Warbler and Common Tailorbird showed peak occurrence in the 4–6 m vertical stratum. Common Tailorbird made heavy use of the 0–2 m vertical stratum, while Velvet-fronted Nuthatch avoided this stratum completely.

3.2. Microhabitat uses

Leaf was the most frequently searched microhabitat by all species except Great Tit and Velvet-fronted Nuthatch. The substratum most frequently searched by Great Tit and Velvet-fronted Nuthatch were branches with diameters smaller than 2 cm and bigger than 2 cm respectively. Great Tit also searched leaves considerably, but Velvet-fronted Nuthatch was not observed searching leaf. Velvet-fronted Nuthatch is the only species that searched on trunk and underside of branches of diameter larger than 2 cm considerably (see Table 1).

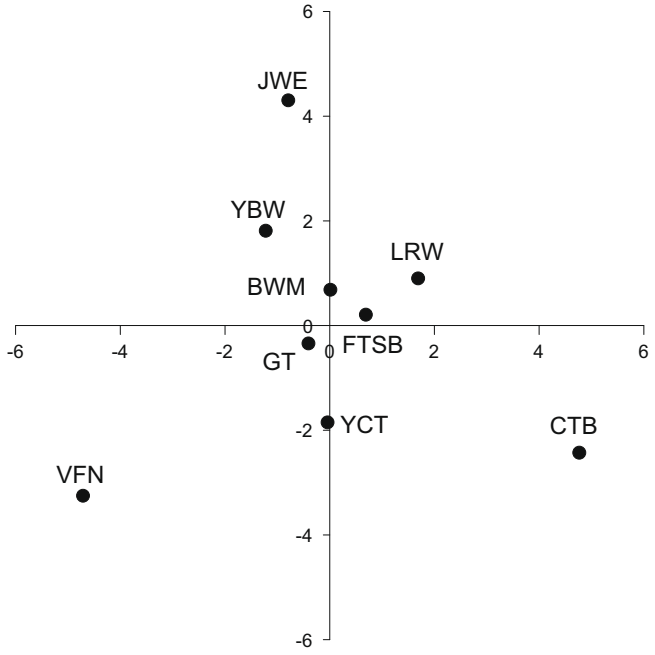

Fig. 2. Two-dimensional ordination of nine species of birds.

3.3. Foraging methods and preys

The foraging method gleaning was used the most frequently by five species, including Japanese White-eye, Great Tit, Blue-winged Minla, Common Tailorbird and Yellow-browed Warbler (Table 2). The foraging method hovering was used the most frequently by Fork-tailed Sunbird and Lemon-rumped Warbler. The foraging methods used most frequently by Velvet-fronted Nuthatch and Yellow-cheeked Tit were probing and hanging, respectively.

There were a total of 715 observations of preys catching (Table 3). Most of these preys (65.6%) were captured from leaves. Identifiable preys only made up 6.4% of total feeding observations,

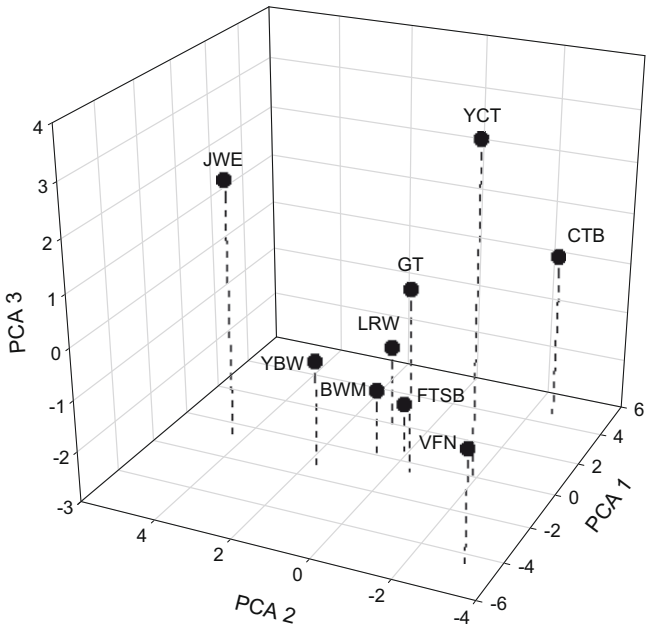

Fig. 3. Three-dimensional ordination of nine species of birds.

and most were records of Great Tit (32.6% of total observations) and Yellow-browed Warbler (21.7%).

3.4. Potential niche overlap

The first three components accounted for 28.7%, 24.5% and 15% respectively, or a total of 68.2% of the variation. The foraging microhabitat utilization ordination (Figs. 2 and 3) showed that Common Tailorbird and Velvet-fronted Nuthatch occupied niches very different from other species. Velvet-fronted Nuthatch made use of the underneath of branches and the surface of trunks much more frequently than any other species. Common Tailorbird made use of the forest understorey much more frequently than any other species. Despite of belonging to the same genus and having similar morphology, Yellow-browed Warbler and Lemon-rumped Warbler did not show higher similarity in their niches as expected when compared to other species in the study area.

The Chi-sq Test analyses of uses of vertical strata between common residents, and between common residents and winter visitors are shown in Tables 4a and 4b. Some species showed similar uses of vertical strata, e.g., Japanese White-eye and Velvet-fronted Nuthatch, Blue-winged Minla and Fork-tailed Sunbird. Apart from Blue-winged Minla and Japanese White-eye, none of these species showed similar uses of microhabitats (Tables 5a and 5b). In fact, some species using different proportion of vertical strata used similar proportion of microhabitats (Tables 6a and 6b). This phenomenon, however, was only observed between residents and winter visitors, e.g., Yellow-browed Warbler and Fork-tailed Sunbird, Yel-

Table 4b
Comparison of uses of vertical strata between residents and winter visitors.

Species	YBW	LRW
JWE	$\chi^2 = 12.81$, $p = 0.1187$	$\chi^2 = 17.12$, $p = 0.0088$
GT	$\chi^2 = 22.23$, $p = 0.0045$	$\chi^2 = 11.37$, $p = 0.0775$
VFN	$\chi^2 = 38.67$, $p < 0.0001$	$\chi^2 = 17.92$, $p = 0.003$
CTB	$\chi^2 = 121.19$, $p < 0.0001$	$\chi^2 = 82.5$, $p < 0.0001$
YCT	$\chi^2 = 18.83$, $p = 0.0185$	$\chi^2 = 14.42$, $p = 0.0442$
FTSB	$\chi^2 = 78.82$, $p < 0.0001$	$\chi^2 = 67.99$, $p < 0.0001$
BWM	$\chi^2 = 18$, $p = 0.0212$	$\chi^2 = 7.38$, $p = 0.1938$
LRW	$\chi^2 = 35.5$, $p < 0.0001$	–

Table 5a
Comparison of uses of microhabitats between residents using similar vertical strata.

Species	JWE	GT	VFN	FTSB
GT	$\chi^2 = 33.3$, $p < 0.0001$			
VFN	$\chi^2 = 158$, $p < 0.0001$			
YCT	–	$\chi^2 = 17.5$, $p = 0.041$		
FTSB	–	$\chi^2 = 25.4$, $p = 0.0006$	–	
BWM	$\chi^2 = 7.1$, $p = 0.3102$	$\chi^2 = 22.2$, $p = 0.0023$	$\chi^2 = 152.8$, $p < 0.0001$	$\chi^2 = 10.2$, $p = 0.0375$

Table 5b
Comparison of uses of microhabitats between residents and winter visitors using similar vertical strata.

Species	YBW	LRW
JWE	$\chi^2 = 38.3$, $p = 0.0082$	–
GT	–	$\chi^2 = 89$, $p < 0.0001$
BWM	–	$\chi^2 = 17.6$, $p = 0.0075$

Table 4a
Comparison of uses of vertical strata.

Species	JWE	GT	VFN	CTB	YCT	FTSB
GT	$\chi^2 = 9.64$, $p = 0.2914$					
VFN	$\chi^2 = 9.27$, $p = 0.3198$	$\chi^2 = 13.31$, $p = 0.0384$				
CTB	$\chi^2 = 101.84$, $p < 0.0001$	$\chi^2 = 70.31$, $p < 0.0001$	$\chi^2 = 112$, $p < 0.0001$			
YCT	$\chi^2 = 20.23$, $p = 0.0095$	$\chi^2 = 12.15$, $p = 0.0957$	$\chi^2 = 23.09$, $p = 0.0016$	$\chi^2 = 75.24$, $p < 0.0001$		
FTSB	$\chi^2 = 16.28$, $p = 0.0385$	$\chi^2 = 7.41$, $p = 0.2848$	$\chi^2 = 23.45$, $p = 0.0007$	$\chi^2 = 66.15$, $p < 0.0001$	$\chi^2 = 16.4$, $p = 0.0022$	
BWM	$\chi^2 = 6.86$, $p = 0.5516$	$\chi^2 = 8.69$, $p = 0.1917$	$\chi^2 = 8.75$, $p = 0.1875$	$\chi^2 = 97.37$, $p < 0.0001$	$\chi^2 = 17.23$, $p = 0.0159$	$\chi^2 = 11.04$, $p = 0.0506$

Table 6a
Comparison of uses of microhabitats by species using different vertical strata.

Species	JWE	GT	VFN	CTB	YCT
GT	–				
VFN	–	$\chi^2 = 118.17$, $p < 0.0001$			
CTB	$\chi^2 = 22.4$, $p = 0.0022$	$\chi^2 = 28.39$, $p = 0.0004$	$\chi^2 = 149.2$, $p < 0.0001$		
YCT	$\chi^2 = 43.6$, $p < 0.0001$	–	$\chi^2 = 100.4$, $p < 0.0001$	$\chi^2 = 32.1$, $p = 0.0004$	
FTSB	$\chi^2 = 21$, $p = 0.0018$	–	$\chi^2 = 161.7$, $p < 0.0001$	$\chi^2 = 22.2$, $p = 0.0011$	$\chi^2 = 40.1$, $p < 0.0001$
BWM	–	–	–	$\chi^2 = 17.6$, $p = 0.0072$	$\chi^2 = 35.21$, $p = 0.0001$

Table 6b
Comparison of uses of microhabitats between residents and winter visitors using different vertical strata.

Species	YBW	LRW
JWE	–	$\chi^2 = 43$, $p < 0.0001$
GT	$\chi^2 = 86.3$, $p < 0.0001$	–
VFN	$\chi^2 = 169.8$, $p < 0.0001$	$\chi^2 = 178$, $p < 0.0001$
CTB	$\chi^2 = 50.5$, $p < 0.0001$	$\chi^2 = 41.4$, $p < 0.0001$
BWM	$\chi^2 = 10.3$, $p = 0.07$	–
YCT	$\chi^2 = 46.3$, $p < 0.0001$	$\chi^2 = 60.1$, $p < 0.0001$
FTSB	$\chi^2 = 6.7$, $p = 0.2478$	$\chi^2 = 12.71$, $p = 0.0479$
LRW	$\chi^2 = 9.9$, $p = 0.1271$	–

low-browed Warbler and Lemon-rumped Warbler, and Fork-tailed Sunbird and Lemon-rumped Warbler. Resident species using different proportion of vertical strata also used different proportion of microhabitats.

4. Discussion

Apart from Velvet-fronted Nuthatch, the observed species mainly searched leaves for preys. This might be related to the largest surface area of leaf among the studied microhabitats. However, leaf contains the bulk of photosynthetic product and nutrient. This may lead to higher abundance of herbivorous invertebrates on leaves, and in turn attracted more birds to forage. The second hypothesis was more probable as most preys were captured from leaves. Branches of diameter smaller than 2 cm was the second most frequently searched microhabitat and this might be due to the proximity to leaves. These hypotheses need further study to reveal the distribution pattern of these fauna on trees.

Lack [16] suggested that the ecological niches of birds can be separated from each other by distribution range, habitat uses and feeding niches. Vertical foraging strata and microhabitat are considered the important habitat parameters partitioning feeding niches of birds in forest [17–20]. Apart from Blue-winged Minla and Japanese White-eye, no two species in the study area used similar combinations of vertical strata and microhabitats at the same time (Tables 5a–6b). Bird species used similar proportion of microhabitats were foraging in different vertical strata, and hence could exploit food resources not used by others. This niche segregation could reduce inter-specific competition, so that different species could coexist in the study area. This finding is consistent with those from other parts of the world [1–8].

Gause's Law of competitive exclusion states that two species occupying the same niches will not coexist forever. Statistic analysis showed that Blue-winged Minla and Japanese White-eye used similar proportion of vertical strata and microhabitats in the study area. Change in of the bird community of the study area in the last 10 years was studied by Kwok [21]. Blue-winged Minla is an exotic forest specialist species and its mean density increased by 12 times in the last decade. Japanese White-eye is a habitat generalist and its density dropped by 13% in the last 10 years. Blue-winged Minla might be substituting Japanese White-eye in the study area. Substitution of bird species prefer open canopy by those favor close canopy as forest age increases have been reported in many studies [22–24].

The foraging niche ordination provided explanation to the success establishment of the exotic species Velvet-fronted Nuthatch in the study area. This species established breeding population in Tai Po Kau nature reserve in the last decade [25]. The success establishment of Velvet-fronted Nuthatch was related to its capability to use microhabitats that are under-exploited by other species. It was the only species foraging on branches of diameter larger than 2 cm and tree trunk in high frequency. This species possess big toes and long claws and is able to cling to tree trunk and underside and vertical sides of big branches, and forage on these microhabitats [26].

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