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RESEARCH ARTICLE

Foraging Strategy and Guild Structure of Avifauna in Sikkim, Eastern Himalaya, India

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Abstract Understanding resource preference and use pattern in avian community will add a significant value in conservation and management of birds as well as forest restoration and landscape management in the region. We studied the foraging behaviour of 26 bird species at three resource dimensions—foraging height, foraging substrate and foraging method—in a sub-tropical forest in East district of Sikkim, Eastern Himalaya, India during August 2018 to April 2019. Most bird species utilized 0–5 m height category, whereas on the basis of foraging substrate, twigs were used by majority of the species for foraging. Similarly, wood gleaning method was used by maximum species of birds for feeding. Niche width was highest in Blue Whistling Thrush *Myophonus caeruleus* and lowest in Spotted Dove *Stigmatopella chinensis*. On the other hand, niche overlap was found to be highest between pair of Green-crowned Warbler *Seicerus burkii* and Grey-hooded Warbler *Phylloscopus xanthoschistos*, whereas some of the pairs showed complete niche segregation. Bird species showing higher overlap in one dimension were found to be showing no or lesser overlap in another dimension. Specialization was found to be higher in foraging substrate followed by foraging method and foraging height. In all three dimensions, important specialist species were identified during the study that called for conservation efforts.

Keywords Birds · Foraging height · Foraging method · Foraging substrate · Niche breadth and Niche overlap

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Introduction

Foraging is the most important activity undertaken by animals for their survival and successful reproduction. Studies on foraging behaviour take into consideration the way species obtain food, the types of food taken, the foraging substrates exploited and the vertical heights at which different species forage (Somasundaram and Vijayan 2008). Some species are generalist and they forage at all heights and on a variety of substrates with various feeding techniques while others show varying degree of specialization and are called specialists (Recher 1989; Gokula and Vijayan 2000; Elafri et al. 2017). The generalists often exhibit niche overlap which either leads to competition or coexistence. Specialists, on the other hand, become vulnerable as they are unable to cope with changes in their habitat (Somasundaram and Vijayan 2008). "Guilds" defined as a group of species that uses same resources in a similar way (Root 1967) are recognized as natural ecological units of a community and guild structure (primarily focussing on foraging guilds) are considered as an important aspect in understanding the structure of bird communities (Hawkins 1989; Wiens 1989; Paszkowski and Tonn 2006). Hence, niche characteristics and guild structure are significant indicators of niche partitioning of a community (Simberloff and Dayan 1991; Chatterjee et al. 2020). Moreover, vegetation structures have been considered as the main catalyst influencing the foraging strategy of the species as diverse vegetation types will provide higher niche breadth for bird species thereby reducing competition and facilitating co-existence (Prache and Delagarde 2011).

Research on foraging ecology of birds gained its importance in the 1960s and many studies on various aspects of foraging have been undertaken since then (Perrins and Birkhead 1983; Wiens 1989). In Madagascar, East

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Africa, species using same foraging technique and location were found to be differed by at least one resource dimension such as the foraging height (Eguchi et al. 1993). Similarly, comparative study on foraging ecology of five Australian robins in woodland of Western Australia recorded differences in habitat use, structure of the ground, substrates use, foraging manoeuvres, foraging height and prey attack with wide range of overlap in all foraging dimensions between species (Recher et al. 2002). Birds belonging to different feeding guilds also differ in foraging strategies, for example, insectivorous birds needed longer time duration for foraging compared to other species (Stanton et al. 2016).

In India, studies on foraging behaviour of birds are scanty and few available literatures are mostly from the Western Ghats. Maximum niche overlap was found in usage of heights followed by foraging substrates and methods among birds of thorn forest in Madumalai wildlife sanctuary, Tamil Nadu, India (Gokula and Vijayan 2000). Similar results were obtained from Montane rain forest of the Western Ghats of Karnataka, Kerala and Tamil Nadu in Southern India (upto a range of 1000 m elevation) where foraging substrates and methods followed by vertical strata were the most important factors that separated bird communities into different foraging guilds (Somasundaram and Vijayan 2008). Niche overlap was highest in foraging height and lowest in foraging method in oak forest of Kumaon region in Central Himalaya. Further, bird species showed higher specialization in foraging substrate followed by foraging method and foraging height (Sultana and Hussain 2010). Warblers of North-West Himalaya showed niche contraction because of lower species richness in the region, whereas in South-East Himalaya, species showed larger niche breadth due to higher species richness (Harihar and Price 2014). Niche segregation is also influenced by coexistence of species as recorded in Himalayan river birds in Central Nepal (Buckton and Ormerod 2008).

Himalaya with its high topographic variation of landscapes and microclimatic conditions harbour a diverse range of biodiversity within itself. Its varying altitudes ranging from 300 to $>$ 8000 m and vegetation types starting from tropical semi-deciduous forest to alpine meadows provides suitable habitat for a vast array of avian diversity (Acharya et al. 2011; Chandra et al. 2018). Further, bird diversity is higher in the Eastern Himalaya as compared to the Western part of the Himalaya due to its more unique vegetation types and habitat heterogeneity (Price et al. 2003). Hence, study focussing on understanding resource preference and use pattern in avian community will add a significant value in conservation and management of birds as well as forest restoration and landscape management in the region (Gabbe et al. 2002). Further, it helps to explain partitioning of available resources, niche overlap, competition and coexistence among species in the habitat (Somasundaram and Vijayan 2008). However, despite such importance, no studies have been conducted in the Eastern Himalayan regions to assess the foraging behaviour of birds in any ecosystem type. Hence, the present study addresses this gap with the two major objectives: (1) To understand the foraging behaviour of birds in different forest patches in Sikkim, Eastern Himalaya, and (2) To understand the interspecific competition and niche overlap between the species in the study area.

Materials and Methods

Study Area

Sikkim, with an small geographical area (7096 km^2), is an Eastern Himalayan state of India. The region comprises a variety of ecological zones with elevation extending from 300 to 8500 m resulting into the development of six distinct vegetation types (Haribal 1992; Rawat and Tambe 2011; Acharya and Sharma 2013). With such diverse vegetation types and climatic conditions, Sikkim is rich in avifauna that comprises of around 580 bird species ($\sim$ 45% of total Indian birds) including many globally threatened and Eastern Himalayan endemic species (Acharya and Vijayan 2010, 2011; Acharya and Sharma 2013). The present study was undertaken in three different locations around Gangtok in the East district of Sikkim, namely Deorali, ICAR Tadong and 7th mile Samdur. These sites were located in the tropical moist and broadleaved vegetation within an elevation range between 1300 and 1500 m (Table 1, Fig. 1). The study site falls under an endemic bird area and a part of the Himalayan biodiversity hotspot, one among the 36 globally significant biodiversity regions (Stattersfield 1998; Mittermeier et al. 2011; Marchese 2015).

Sampling Methodology

Foraging behaviour of birds were studied using the standard transect method (Somasundaram and Vijayan 2008). A transect of 1 km length was laid in each study site accounting for a total of three transects in the study area. The birds were observed during the morning hours (06:00 to 10:00 Hrs) when feeding activity was at its peak and foraging observations in detail were made using binoculars whenever a bird was seen feeding. The birds were identified in the field with the help of standard field guide for Indian birds (Grimmett et al. 2011). The field study was conducted for the period of nine months during August 2018 to April 2019. Based on field observations only those

Table 1 Details of study sites located in East Sikkim, Eastern Himalaya

Sl. No	Study sites	Transects	Latitude	Longitude	Elevation (m)
1	7th mile, Samdur	Transect I	27° 18′ 27″ N	88° 35′ 19″ E	1068
2	ICAR Tadong	Transect II	27° 19′ 33.6″ N	88° 36′ 7.78″ E	1326
3	Deorali	Transect III	27° 19′ 2.9″ N	88° 36′ 22.4″ E	1443

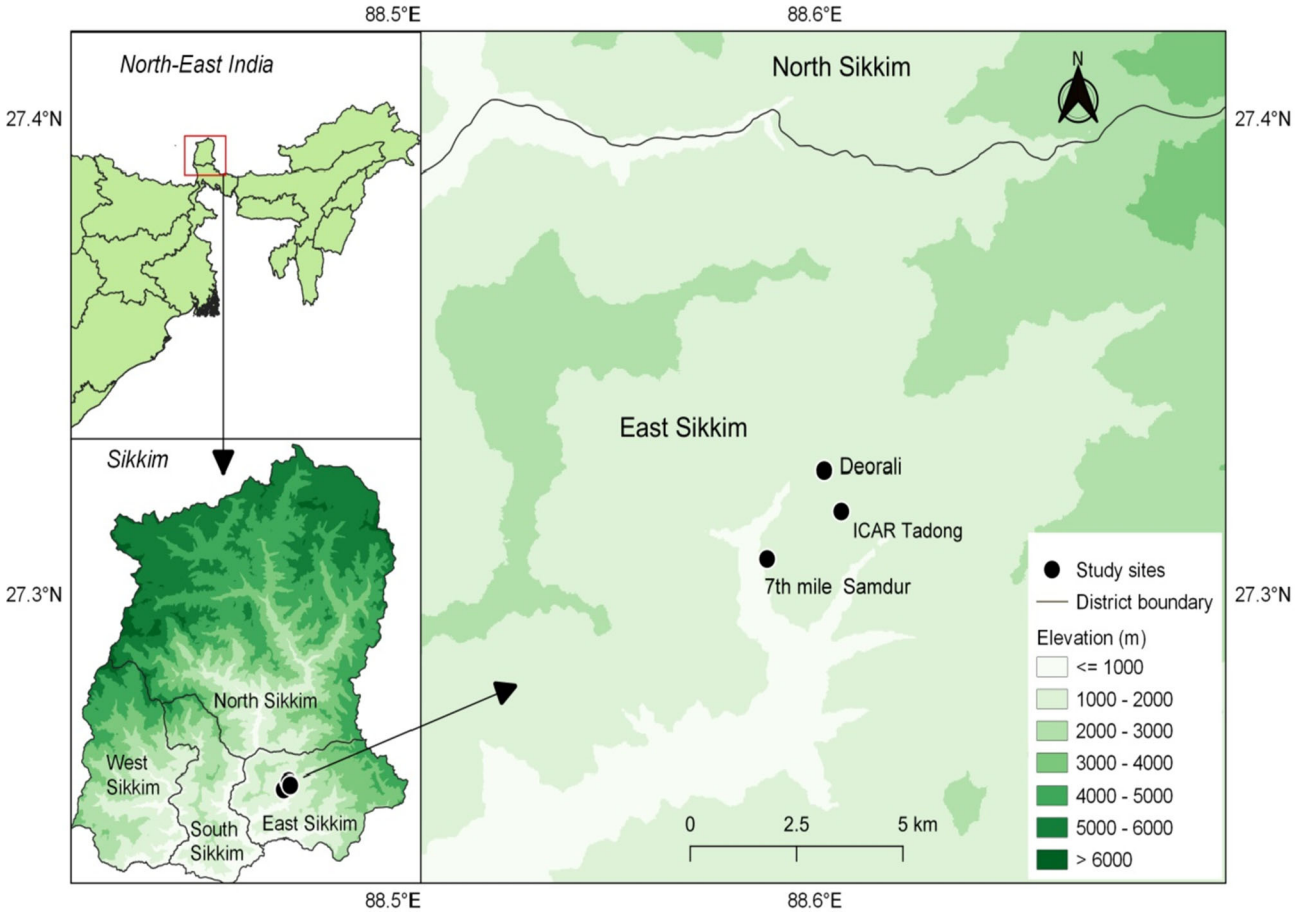

Fig. 1 Map of study sites located in Sikkim, Eastern Himalaya

birds with more than nine observations were considered for further analysis because some of the species had limited observation which can lead to inaccurate estimation of guild characteristics such as niche overlap and niche breadth, as well as identification of specialist and generalist species in the study area (Gokula and Vijayan 2000). During the study following observations were made and noted while walking along the transects:

Foraging substrate: The substrates were classified into six categories following standard method as described by Gokula and Vijayan (2000): (a) ground (debris, litter and grass), (b) trunk/main branches (main axes of trees), (c) foliage (leaves including leaf-blades and petioles), (d) twigs (small branches to which leaves were attached) (e) flower and fruits, (f) air, and (g) nectar/seed/fruit.

Foraging height: The foraging height were assigned to five vertical height categories viz., 0 m, 0–5 m, 5–10 m, 10–15 m and $>$ 15 m following Acharya and Vijayan (2017).

Foraging method: Foraging methods were primarily classified into four categories: (a) glean: when a standing bird picks a stationary food from its substrate, (b) probe: only bird's beak penetrates through the substrate to locate concealed food items, (c) pounce: when a flying bird grabs a stationary food item as it lands on the substrate and, (d) sally: when a bird fly into the air to catch a flying prey. The methods were further classified into sallying, pouncing, foliage-gleaning, wood-gleaning, ground animal-exploiting (carnivore), nectar gleaning, fruit-gleaning and grain or seed gleaning.

Data Analyses

Based on the field observation, the following indices were derived for each species from the pooled data of all the sites.

Niche Breadth

Niche breadth along any single resource category (i.e. foraging height, foraging substrate or foraging method) was calculated using the standard Simpson's index of diversity (Pianka 1973):

$$\text{Simpson's index } (\beta) \;=\; 1/\sum^{n} \text{pi}^2$$

where pi represented the proportion of ith substrate (or height category or method used). β varies from 1 to n on the basis of pi value.

Niche Overlap

Niche overlap of all possible combination of pairs for birds observed during the study was calculated as follows (Pianka 1973):

$$\text{Oab} = \sum \text{pia} \cdot \text{pib} / \sqrt{\sum \text{pia}^2 \cdot \sum \text{pib}^2}$$

where Oab is the overlap value between two species, pia and pib are the proportions of the ith resources used by species a and b respectively. The above equation provided overlap values for one pair of species that ranges from 0 to 1 reflecting no overlap to complete niche overlap between the pair of species.

Finally, hierarchical cluster analysis was performed using all three resource categories to understand the guild structure of avian community. Cluster analysis was done in SPSS software version 18.0 using between group linkages and Euclidean distance coefficients. Additionally, different bar plots were drawn for species richness in three resource categories using "ggplot2" package in R version 3.1.4. One-way analysis of variance (ANOVA) was used to find out whether the species significantly varied in different height categories, substrate used and foraging methods adopted.

Results

A total of 618 individuals representing 42 species of birds were recorded during the present study. However, only 565 observations belonging to 26 species (with > 9 observations) were selected for the analysis (see "Appendix 1" for species details).

Foraging Height

Most of the bird species were found using more than one height categories for foraging. Among the five height categories, majority of the species were found to utilize 0–5 m (23 species) followed by 5–10 m (21 species), 10–15 m (11 species) and > 15 m (3 species) (Fig. 2). The number of bird species significantly varied among different height categories ($F = 10.470$; $p < 0.001$). Two species (Green-crowned Warbler *Seicerus burkii* and Green-tailed Sunbird *Aethopyga nipalensis*) were solely dependent on 0–5 m height, whereas Spotted Dove used only ground level for feeding activities (Table 2).

Foraging Substrate

Among the set of substrates, maximum species used twigs for foraging and only one species (Spangled Drongo *Dicrurus hottentottus*) used air as foraging substrate (Fig. 3). The number of bird species significantly varied in each substrate categories ($F = 8.266$; $p < 0.001$). Among all the species, Chestnut-bellied Nuthatch *Sitta cinnamoventris* and Lesser Yellownape *Picus chlorolophus* were found to exclusively rely on trunk for foraging, whereas, none of the remaining substrates were found exclusively utilized by any other bird species (Table 3).

Foraging Method

The birds in the study area used eight types of foraging techniques namely, foliage gleaning, pouncing, sallying, wood gleaning, ground carnivore, nectar gleaning, fruit gleaning and grain gleaning. While the majority of bird species (22) used wood gleaning for foraging, sallying was used by only one species (Fig. 4). There was a significant variation in species among different foraging method

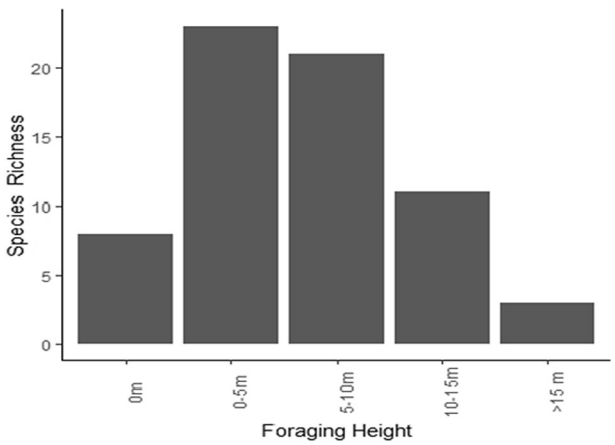

Fig. 2 Foraging height utilization by bird species in Sikkim, Eastern Himalaya

Table 2 Percent use of various foraging height by birds in Sikkim, Eastern Himalaya

Name of species	Foraging height utilization (%)				
	0 m	0–5 m	5–10 m	10–15 m	> 15 m
Blue Whistling Thrush	35.3	35.3	17.6	11.8	0
Blue-winged Siva	0	33.3	66.7	0	0
Chestnut-bellied Nuthatch	0	10	60	30	0
Common Green Magpie	0	20	80	0	0
Common Tailorbird	20	60	20	0	0
Great Barbet	0	11.1	33.3	55.6	0
Green-backed Tit	0	50.5	23.7	25.8	0
Green-crowned Warbler	0	**100**	0	0	0
Green-tailed Sunbird	0	**100**	0	0	0
Grey- headed Canary Flycatcher	0	30	70	0	0
Grey-backed Shrike	0	60	40	0	0
Grey Treepie	9.5	19	66.7	4.76	0
Grey-hooded Warbler	0	81.8	18.2	0	0
Lesser Yellownape	0	18.2	54.5	18.2	9.1
Red-vented Bulbul	2	34	20	44	0
Red-tailed Minla	0	44.7	39.5	15.8	0
Red-billed Leothrix	86.7	13.3	0	0	0
Rufous Sibia	0	41.4	58.6	0	0
Rufous-Vented Yuhina	68.2	31.8	0	0	0
Short-billed Minivet	0	0	30	70	0
Spangled Drongo	0	18.2	54.5	18.2	9.1
Spotted Dove	**100**	0	0	0	0
Velvet-fronted Nuthatch	0	45.8	50	4.2	0
Whiskered Yuhina	0	88.2	11.8	0	0
White-crested Laughingthrush	25	36.1	38.9	0	0
Yellow-bellied Warbler	0	67.6	32.4	0	0

Bold indicates the species with 100% exclussiveness in one particular resource category

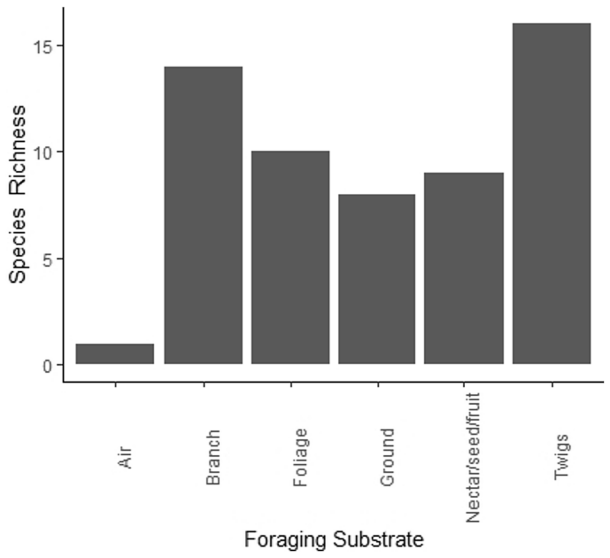

Fig. 3 Foraging substrate utilised by bird species in Sikkim, Eastern Himalaya

categories (F = 13.557; $p < 0.001$). Two species (Chestnut-bellied Nuthatch and Lesser Yellownape) exclusively used wood gleaning method, whereas Green-tailed Sunbird and Spotted Dove used only nectar gleaning and grain gleaning method respectively (Table 4).

Niche Breadth

Considering all three categories (foraging height, foraging substrate and foraging method), bird species having the largest niche width was Blue Whistling Thrush (3.18), indicating its dependency on more than one height category, substrate and foraging method. Other species with wider niche breadth were Grey Treepie *Dendrocitta formosae* (3.01) followed by Red-vented Bulbul *Pycnonotus cafer* (2.7), Common Tailorbird *Orthotomus sutorius* (2.6), White-crested Laughingthrush *Garrulax leucolophus* (2.4) and Red-tailed Minla *Minla ignotincta* (2.2). On the other hand, species with smaller niche width were Spotted Dove (1.0) followed by Green-tailed Sunbird (1.1), Whiskered Yuhina *Yuhina flavicollis* (1.2), Chestnut-bellied Nuthatch

Table 3 Percent use of various foraging substrate by birds in Sikkim, Eastern Himalaya

Name of species	Foraging substrate use (%)						
	Ground	Twigs	Branch	Trunk	Nectar/seed/fruit	Foliage	Air
Blue Whistling Thrush	29.4	5.88	41.2	0	23.5	0	0
Blue-winged Siva	0	33.3	0	0	0	66.6	0
Chestnut-bellied Nuthatch	0	0	0	**100**	0	0	0
Common Green Magpie	0	0	60	0	0	40	0
Common Tailorbird	20	50	0	0	30	0	0
Great Barbet	0	0	0	0	**100**	0	0
Green-backed Tit	0	55.6	17.5	0	0	26.8	0
Green-crowned Warbler	0	14.2	0	0	21.4	64.2	0
Green-tailed Sunbird	0	0	0	0	**100**	0	0
Grey-headed Canary Flycatcher	0	30	70	0	0	0	0
Grey-backed Shrike	0	0	80	0	0	20	0
Grey Treepie	9.52	14.2	38.1	0	33.3	4.76	0
Grey-hooded Warbler	0	36.3	0	0	0	63.6	0
Lesser Yellownape	0	0	0	**100**	0	0	0
Red-vented Bulbul	0	20	80	0	0	0	0
Red-tailed Minla	4	42	34	0	4	16	0
Red-billed Leothrix	0	31.5	57.9	0	0	10.5	0
Rufous Sibia	86.6	13.3	0	0	0	0	0
Rufous-Vented Yuhina	0	0	17.2	0	82.7	0	0
Short-billed Minivet	77.2	9.09	13.6	0	0	0	0
Spangled Drongo	0	0	0	0	72.72	0	27.3
Spotted Dove	100	0	0	0	0	0	0
Velvet-fronted Nuthatch	0	0	20.8	79.2	0	0	0
Whiskered Yuhina	0	88.2	11.8	0	0	0	0
White-crested Laughingthrush	22.2	55.5	22.2	0	0	0	0
Yellow-bellied Warbler	0	32.4	0	0	0	67.5	0

Bold indicates the species with 100% exclussiveness in one particular resource category

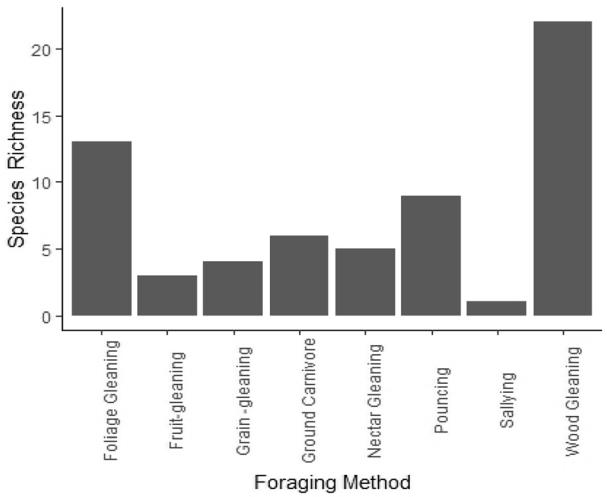

Fig. 4 Foraging method used by bird species in Sikkim, Eastern Himalaya

(1.3) and Red-billed Leiothrix *Leiothrix lutea* (1.3) indicating specialist nature of these birds (Table 5). Most of the species were generalist in all the resource dimensions considered in this study. However, some species were specialist in atleast one dimension; for e.g., Spotted Dove obtained food from the ground, Green-tailed Sunbird and Lesser Yellownape were specialised in substrate selection, Velvet-fronted Nuthatch *Sitta frontalis* and Chestnut-bellied Nuthatch preferred specific foraging methods (Table 5).

Niche Overlap

The niche overlap was highest in foraging height category followed by foraging method and substrate use.

Foraging Height

Based on pairwise niche overlap of bird species in foraging height, maximum overlap was found between Green-crowned Warbler and Grey-hooded Warbler(0.99) as well as Green-tailed Sunbird and Green-crowned Warbler (0.99). Velvet-fronted Nuthatch and Red-billed Leiothrix

Table 4 Percent use of different foraging methods by birds in Sikkim, Eastern Himalaya

Name of species	Foraging methods exploitation (%)							
	Foliage gleaning	Pouncing	Salliying	Wood gleaning	Ground carnivore	Nectar gleaning	Fruit gleaning	Grain gleaning
Blue Whistling Thrush	0	0	0	47.1	29.4	0	11.7	11.7
Blue-winged Siva	66.6	0	0	33.3	0	0	0	0
Chestnut-bellied Nuthatch	0	0	0	**100**	0	0	0	0
Common Green Magpie	50	0	0	50	0	0	0	0
Common Tailorbird	20	0	0	50	20	10	0	0
Great Barbet	0	5.5	0	0	0	0	61.1	33.3
Green-backed Tit	32.9	3.1	0	63.9	0	0	0	0
Green-crowned Warbler	50	14.2	0	28.6	0	7.1	0	0
Green-tailed Sunbird	0	0	0	0	0	**100**	0	0
Grey-headed Canary Flycatcher	0	20	0	80	0	0	0	0
Grey-backed Shrike	20	10	0	70	0	0	0	0
Grey Treepie	5.2	0	0	57.8	10.6	0	0	26.3
Grey-hooded Warbler	54.5	18.1	0	27.2	0	0	0	0
Lesser Yellownape	0	0	0	**100**	0	0	0	0
Red-vented Bulbul	22	0	0	64	4	0	6	4
Red-tailed Minla	26.3	5.26	0	68.4	0	0	0	0
Red-billed Leothrix	86.6	0	0	13.3	0	0	0	0
RufousSibia	0	0	0	13.7	0	86.2	0	0
Rufous-Vented Yuhina	0	10	0	90	0	0	0	0
Short-billed Minivet	0	0	0	36.3	63.6	0	0	0
Spangled Drongo	0	0	9.1	0	0	90.9	0	0
Spotted Dove	0	0	0	0	0	0	0	**100**
Velvet-fronted Nuthatch	0	0	0	**100**	0	0	0	0
Whiskered Yuhina	5.9	0	0	94.1	0	0	0	0
White-crested Laughingthrush	0	0	0	58.3	41.6	0	0	0
Yellow-bellied Warbler	62.1	5.4	0	32.4	0	0	0	0

Bold indicates the species with 100% exclussiveness in one particular resource category

showed least niche overlap (0.1) between the species pairs, whereas there was no overlap of niches between Spotted Dove and Lesser Yellownape ("Appendix 2").

Hierarchical cluster analysis of niche overlap based on foraging height showed maximum species using wide range of heights for foraging. On the basis of foraging height used, the bird species were divided into two major groups: first group (Red-billed Leiothrix, Rufous-vented Yuhina *Yuhina occipitalis* and Spotted Dove) foraged frequently at or near ground level and, second group consists of the species that foraged at different heights above the ground. Further, species foraging above the ground were sub-divided into sub-canopy and canopy feeder. Canopy feeders includes species such as Lesser Yellownape, Spangled Drongo, Grey Treepie, Chestnut-bellied Nuthatch, whereas Green-crowned Warbler and Blue-winged Siva *Actinodura cyanouroptera* represented sub-canopy feeders (Fig. 5).

Foraging Method

Species pair such as Blue-winged Siva and Yellow-bellied Warbler *Abroscopus superciliaris*, Short-billed Minivet *Pericrocotus brevirostris* and Chestnut-bellied Nuthatch, Whiskered Yuhina and Chestnut-bellied Nuthatch, Red-tailed Minla and Green-backed Tit *Parus monticolus*, Velvet-fronted Nuthatch and Chestnut-bellied Nuthatch, Green-tailed Sunbird and Spangled Drongo, showed higher overlap in foraging method. Species pairs such as Blue-winged Siva and Great Barbet *Megalaima virens*, Chestnut-bellied Nuthatch and Green-tailed Sunbird showed

Table 5 Niche width of birds based on foraging height, foraging substrate and foraging method in Sikkim, Eastern Himalaya

Name of species	Foraging height	Foraging substrate	Foraging method	Mean
Blue Whistling Thrush	3.4	3.17	2.97	3.18
Blue-winged Siva	1.8	1.8	1.8	1.8
Chestnut-bellied Nuthatch	2.17	1	1	1.39
Common Green Magpie	1.47	1.92	2	1.79
Common Tailorbird	2.27	2.63	2.94	2.6
Great Barbet	2.31	1	2.05	1.78
Grey-headed Canary Flycatcher	1.72	1.72	1.47	1.63
Green-backed Tit	2.64	1.47	1.85	1.98
Green-tailed Sunbird	1.35	1	1	1.11
Green-crowned Warbler	1.52	1.61	2.8	1.97
Grey-backed Shrike	1.92	1.47	1.85	1.74
Grey Treepie	3.17	3.47	2.39	3.01
Grey-hooded Warbler	1.42	1.86	2.46	1.91
Lesser Yellownape	2.68	1	1	1.56
Short-billed Minivet	2.86	1.47	1.21	1.84
Red-vented Bulbul	2.86	3.11	2.15	2.7
Red-tailed Minla	2.62	2.24	1.85	2.23
Red-billed Leothrix	1.3	1.3	1.3	1.3
Rufous Sibia	1.94	1.39	1.3	1.54
Rufous-Vented Yuhina	1.76	1.6	1.8	1.72
Spangled Drongo	2.75	1.65	1.1	1.83
Spotted Dove	1	1	1	1
Velvet-fronted Nuthatch	2.16	1.49	1	1.55
Whiskered Yuhina	1.26	1.26	1.12	1.21
White-crested Laughingthrush	**2.9**	2.45	1.94	2.43
Yellow-bellied Warbler	1.7	1.78	2.02	1.83

Bold indicates the species with 100% exclussiveness in one particular resource category

complete niche separation in foraging method used ("Appendix 3").

On the basis of hierarchical cluster analysis, bird species were divided into two major groups. First group consisted of species using fruit gleaning, grain gleaning and nectar gleaning method for foraging, whereas second group was represented by insectivorous birds which used foliage gleaning, pouncing, wood gleaning and ground carnivore methods for food exploitation (Fig. 6).

Foraging Substrate

Chestnut-bellied Nuthatch and Lesser Yellownape showed complete niche overlap as both species used only trunk as a substrate to obtain their food. On the contrary, Blue Whistling Thrush and Grey-headed Canary Flycatcher *Culicicapa ceylonensis* showed lowest niche overlap (0.01). There was a complete niche segregation among some species pairs such as Lesser Yellownape and Blue Whistling Thrush, and Rufous-vented Yuhina and Rufous Sibia *Heterophasia capistrata* ("Appendix 4").

Hierarchical cluster analysis divided the observed species into six broad groups. The first group comprised of nectarivorous, granivorous and frugivorous species, while second group consists of ground forager birds. Bird species such as Lesser Yellownape, Velvet-fronted Nuthatch and Chestnut-bellied Nuthatch were found using trunk for foraging and formed the third group. The remaining three group consists of generalist species that used more than one type of substrate for foraging. Among these species, foliage and twigs feeders formed the first group, twigs, branch and foliage users represented second group whereas, branch, foliage, twigs and ground forager formed the third group (Fig. 7).

Discussion

The study examines the foraging strategies, niche breadth and niche overlap in bird community in a sub-tropical forest patch in Sikkim, Eastern Himalaya, one of the most diverse birdlife regions of the world. The study adds to our

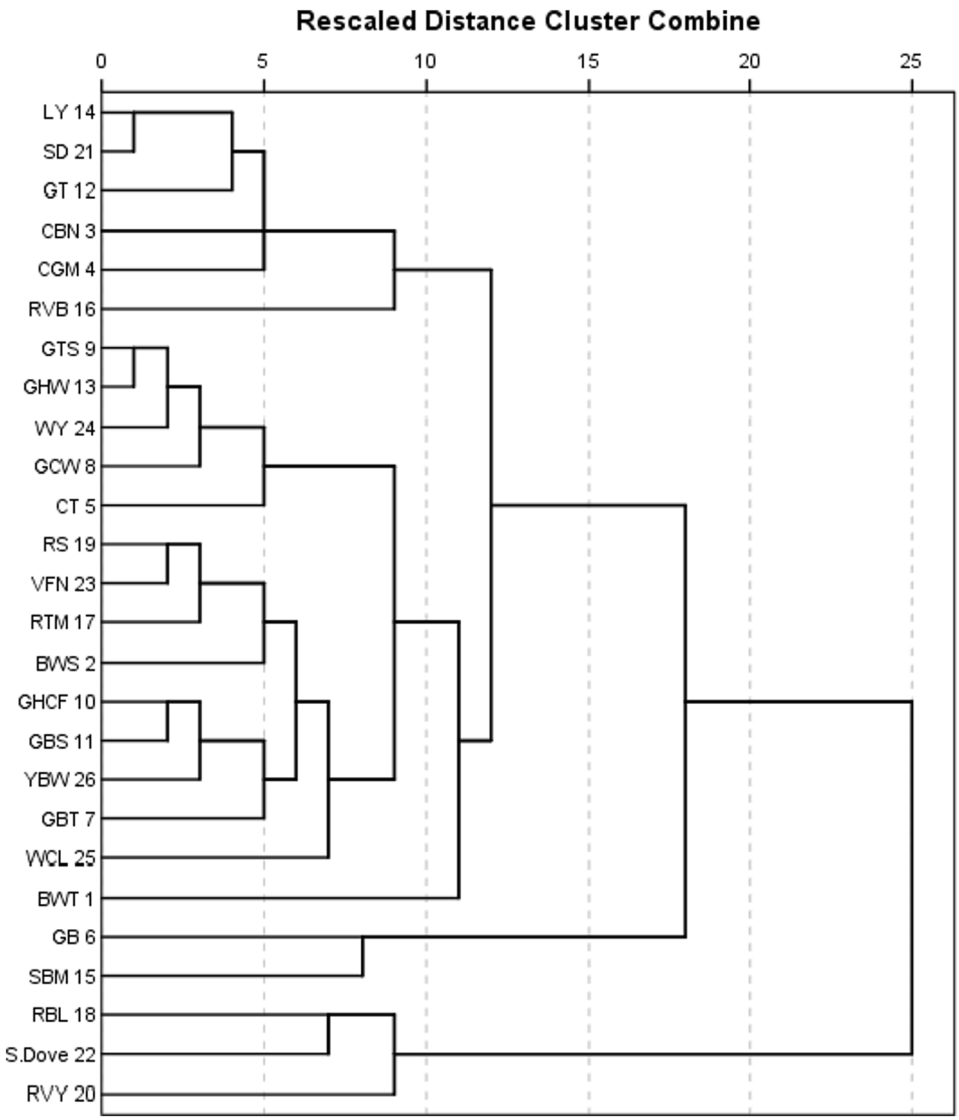

Fig. 5 Interspecific relationship (niche overlap) of bird species based on usage of foraging height in Sikkim, Eastern Himalaya (bird names are in abbreviation and the details are given in "Appendix 2")

understanding on foraging technique and co-existence of species among different bird species.

Foraging height categories 0–5 m and 5–10 m along with twigs (foraging substrate) was the most preferred resource categories used by the birds in the study area. The result indicates the preference of majority of species (65.39%) to mid-canopy or canopy as their foraging stratum (Ali 1962; Ali and Ripley 2002). Similarly, maximum bird species used wood gleaning as the preferred foraging method during feeding. This can be attributed to the fact that gleaning is associated with insectivorous birds (Gokula and Vijayan 2000) and most of the birds (76.93%) recorded during the study were insectivorous species (Ali 1962; Ali and Ripley 2002; Rajashekara and Venkatesha 2015). Further, the study found narrower niche breadth in foraging substrate and method, and wider in foraging height indicating more specialization within foraging substrate and foraging method with less foraging height preference (Somasundaram and Vijayan 2008). Studies have recorded that both foraging substrate and method used by the birds are the main factors effecting the partitioning of resources within the ecosystem (Liordos 2010; Perez-Crespo et al. 2013). Most species were found to be foraging on wide range of heights but segregated themselves in either substrate or methods used. While many species used all height categories but, in some cases, species got separated based on height i.e. ground forager and the above ground forager (Gokula and Vijayan 2000; Sultana and Hussain 2010).

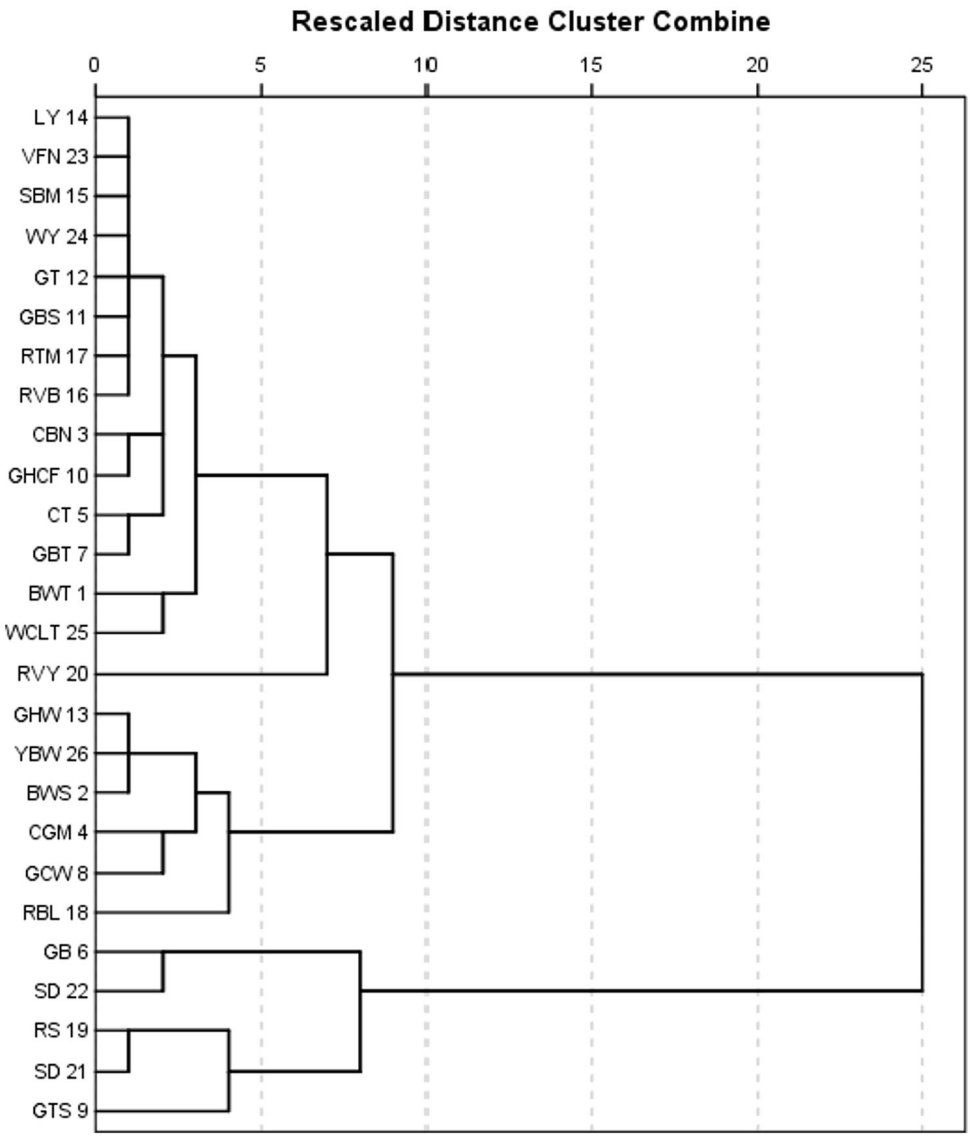

Fig. 6 Interspecific relationship (niche overlap) of bird species based on exploitation of foraging method in Sikkim, Eastern Himalaya (bird names are abbreviation and the details are given in "Appendix 2")

The presence of different substrates or microhabitats above the ground further reduces the competition between species and facilitate their coexistence (Acharya and Vijayan 2017).

Most of the species recorded in this study were generalist in all three resource dimensions considered. Two species (Green-tailed Sunbird and Spotted Dove) are specialist in three resource categories and remaining species are specialist in at least one resource dimension. This trend indicates the unstable nature of the environment and habitat degradation in the area, and probably linked to the general global process of habitat homogenization (McKinney and Lockwood et al. 1999; Olden et al. 2004; Rajashekara and Venkatesha 2017a). The habitat heterogeneity favours the habitat specialist in the region, and the existence of birds and usage of microhabitats are also dependent on human disturbance factors (Rajashekara and Venkatesha 2017a; b) because our study sites were located near the urban area. Previous studies have highlighted that the generalist species are more prone to competitions, whereas specialist are more susceptible to changes in the environmental conditions (Sol et al. 2002; Devictor et al. 2008; Clavel et al. 2011; Büchi and Vuilleumier 2014; Rajashekara and Venkatesha 2017a). Specializations occur in areas or habitats with low species richness, rich resources and areas with restricted and stable habitat (Gokula and Vijayan 2000; Harihar and Price 2014; Nielsen et al. 2019). On the other hand, generalist species thrive in relatively disturbed

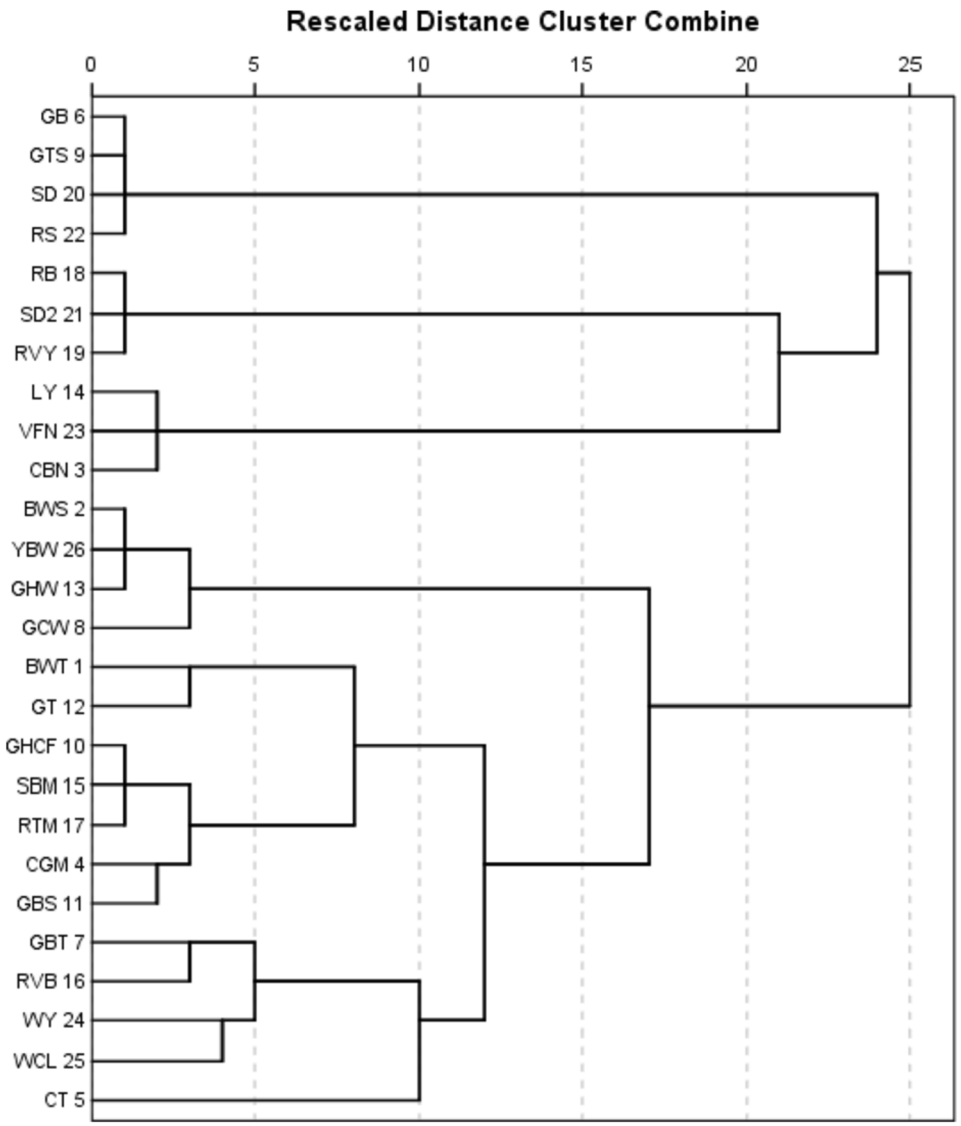

Fig. 7 Interspecific relationship (niche overlap) of bird species based on utilization of foraging substrate in Sikkim, Eastern Himalaya (bird names are in abbreviation and the details are given in "Appendix 2")

habitat and are able to exploit varied resources (Julliard et al. 2006). High disturbed areas tend to have higher threat levels and harbour low species diversity compared to low disturbed area (Rajashekara and Venkatesha 2015, 2017a,). However regardless of various disturbances many urban areas provides food sources and roosting site to support various feeding guilds (Rajashekara and Venkatesha 2015, 2017a). The availability of variety of food sources and safe habitats are major factor determining the occurrence and abundance of bird population in urban regions (Rajashekara and Venkatesha 2015). Since substrate determines prey type, specialization is more commonly observed in foraging substrate. Birds display specialized morphological adaptation to feed on specific prey or food materials and, hence generally exploit particular substrate for food acquisition (Perrins and Birkhead 1983; Wiens 1989).

The differences in resource utilization pattern reduces competition between species leading to coexistence. In the present study, foraging substrate was the prime resource dimension responsible for the determination of foraging guild followed by methods used and foraging height. Niche overlap determines the degree of competition with higher value of overlap leading to increased competition between species by reducing the exclusive niche of each species and, therefore, supports more species as compared to the one with lower niche overlap (Klopfer and MacArthur 1961; Wiens 1989; Anthwal et al. 2008). The species with

higher niche overlap display various other behavioural strategies in order to reduce competition. For example, species with higher niche overlap such as Green-crowned Warbler and Grey-hooded Warbler forage quickly, moved to another patch/site rapidly and thereby avoided competition. Further, Red-billed Leothrix and Spotted Dove mainly foraged on ground (higher mean niche overlap in foraging height and foraging substrate) but differed in their food type and methods used. Similarly, Red-billed Leiothrix is insectivorous and depend on ground carnivore method but Spotted Dove feeds on grain and use grain gleaning method. Hence, species with high mean overlap in one dimension such as height avoided competition by specializing in another dimension such as substrate (Sultana and Hussain 2010). High overlap in foraging height can also be attributed to clumped distribution of specific food item such as insects, fruits, seeds and flower at certain vertical heights (Acharya and Vijayan 2017). Low overlap in foraging method and foraging substrate are influenced by the role of morphology in determination of foraging method and foraging substrate. Hence, variation in niche overlap can be attributed to morphology and distribution of resources available in the ecosystem (Alatalo 1982; Hodgkison et al. 2004).

Morphology has a great importance in determining substrate selection and method used by organisms (Robinson et al. 1982; Hodgkison et al. 2004). Species having similar guild are mostly closely related taxonomically with similar morphological features (Begon and Townsend 2021). However, researchers have also argued that morphology alone does not determines the foraging pattern of birds (Ricklefs and Travis 1980; Hutto 1981). Foraging behaviour is also determined by abundance, types and distribution of available resources in the habitat (Recher and Davis 1998; Korňan et al. 2013). Some studies have recorded seasonal and temporal variation in foraging behaviour (Murakami 2002; Powell et al. 2015) but the present short-term study did not correlate the seasonal and temporal changes in morphology due to time and logistical issues. Hence, a detailed study is necessary to determine the effect of seasonal and temporal changes in foraging behaviour and role of morphology in determining foraging behaviour of birds.

The guild structure and community characteristics of bird species are an important ecological indicators of habitat quality and heterogeneity and, therefore, aids in assessing conservation requirements of species and its habitat (Canterburry et al. 2000). The present study recorded maximum species as generalists with lower niche breadth and relatively higher niche overlap leading to increased competition among species. Such strategy resulted in resource partitioning among the bird species resulting in the determination of the diversity of co-existing species (MacArthur 1958). Similarly, seven bird species were identified as specialist in at least one of the three resource dimensions. With gradual degradation of habitat in the study area due to various natural as well as anthropogenic activities, the specialists which are unable to adapt to the changing environment are at great risk of local extinction. The study highlighted the importance of small forest patches around urban areas for retention of avifauna but long term study involving larger spatial and temporal dimensions are necessary to understand the resource utilization pattern by birds. The knowledge on the specialist and generalist species and their foraging strategy can aid in designing appropriate conservation plans. Therefore, conservation measures are required for the specialist species in the area by protecting their habitat and associated resources with the involvement of all relevant stakeholders.

Appendix 1

Bird species recorded with total number of observations in Sikkim, Eastern Himalaya (species selected for studying foraging behaviour are given in bold font, "S" is used to denote specialist species in at least one of the resource dimensions

Sl. no	Name of species	Scientific name	Migratory status	Total no. of observations
1	Black-chinned Yuhina	*Yuhina nigrimenta*	R	6
2	**Blue Whistling Thrush**	*Myophonus caeruleus*	R	17
3	Blue-throated Barbet	*Megalaima asiatica*	R	2
4	**Blue-winged Siva**	*Siva cyanouroptera*	AIM	12
5	Blyth's Leaf Warbler	*Phylloscopus reguloides*	AIM	4
6	Chestnut-winged Cuckoo	*Clamator coromandus*	SV	5
7	**Chestnut-bellied Nuthatch (S)**	*Sitta(castanea) cinnamoventris*	R	10
8	**Common Green Magpie**	*Cissa chinensis*	R	10
9	**Common Tailorbird**	*Orthotomus sutorius*	R	10
10	**Great Barbet (S)**	*Megalaima virens*	R	18
11	**Green-backed Tit**	*Parus monticolus*	AIM	97
12	**Green-crowned Warbler (S)**	*Seicerus burkii*	AIM	14
13	**Grey- headed Canary Flycatcher**	*Culicicapa ceylonensis*	AIM	10
14	**Green-tailed Sunbird (S)**	*Aethopyga nipalensis*	R	13
15	**Grey-backed Shrike**	*Lanius tephronotus*	SV	10
16	**Grey Treepie**	*Dendrocitta formosae*	R	21
17	Grey-headed Woodpecker	*Picus canus*	R	1
18	**Grey-hooded Warbler**	*Phylloscopus xanthoschistos*	AIM	11
19	Himalayan Bulbul	*Pycnonotus leucogenys*	AIM	7
20	Lesser Necklaced Laughingthrush	*Garrulax monileger*	R	3
21	**Lesser Yellownape (S)**	*Picus chlorolophus*	R	11
22	Long-tailed Sibia	*Heterophasia picaoides*	R	1
23	IndianWhite-eye	*Zosterops palpebrosus*	R	2
24	Pygmy Blue Flycatcher	*Muscicapella hodgsoni*	R	1
25	**Red-vented Bulbul**	*Pycnonotus cafer*	R	50
26	**Red-billed Leothrix**	*Leiothrix lutea*	AIM	15
27	**Red-tailed Minla**	*Minla ignotincta*	AIM	38
28	**Rufous Sibia**	*Heterophasia capistrata*	R	29
29	**Rufous-vented Yuhina**	*Yuhina occipitalis*	AIM	22
30	Rufous-breasted Accentor	*Prunella strophiata*	R	3
32	**Spangled Drongo**	*Dicrurus hottentottus*	R	11
33	**Spotted Dove (S)**	*Stigmatopella chinensis*	M	11
34	**Short-billed Minivet**	*Pericrocotus brevirostris*	AIM	11
34	Tickell's Leaf Warbler	*Phylloscopus affinis*	SV	4
35	**Velvet-fronted Nuthatch (S)**	*Sitta frontalis*	R	24
36	Verditer Flycatcher	*Eumyias thalassinus*	AIM	2
37	**Whiskered Yuhina**	*Yuhina flavicollis*	AIM	17
38	**White-crested Laughingthrush**	*Garrulax leucolophus*	R	36
39	White-browed Shrike-babbler	*Pteruthius flaviscapis*	R	2
40	White-rumped Munia	*Lonchura striata*	R	3
41	White-tailed Robin	*Myiomela leucura*	R	7
42	**Yellow-bellied Warbler**	*Abroscopus superciliaris*	AIM	37

Migratory status—*R* Resident, *AIM* Altitudinal migrant, *SV* Summer visitor

Appendix 2

Niche overlap in foraging height for bird species pair in Sikkim, Eastern Himalaya

Name	BWT	BWS	CBN	CGM	CT	GB	GBT	GCW	GTS	GHCF	GBS	GT	GHW	LY	SBM	RVB	RTM	RBL	RS	RVY	SD	SD2	VFN	WY	WCLT	YBW
BWT	1	0.58	0.48	0.47	0.88	0.46	0.75	0.72	0.70	0.56	0.72	0.71	0.71	0.55	0.33	0.67	0.74	0.74	0.64	0.86	0.55	0.65	0.69	0.69	0.89	0.73
BWS	0.58	1	0.86	0.98	0.67	0.53	0.71	0.68	0.60	0.91	0.87	0.88	0.63	0.93	0.35	0.56	0.90	0.07	0.99	0.19	0.93	0.00	0.96	0.56	0.87	0.79
CBN	0.48	0.86	1	0.89	0.40	0.85	0.65	0.38	0.30	0.67	0.61	0.96	0.34	0.97	0.76	0.71	0.79	0.02	0.81	0.06	0.97	0.00	0.78	0.26	0.68	0.52
CGM	0.47	0.98	0.89	1	0.51	0.53	0.57	0.50	0.41	0.80	0.74	0.86	0.45	0.94	0.38	0.47	0.80	0.04	0.93	0.10	0.94	0.00	0.88	0.37	0.79	0.64
CT	0.88	0.67	0.40	0.51	1	0.31	0.86	0.95	0.94	0.89	0.92	0.62	0.95	0.54	0.12	0.63	0.85	0.44	0.77	0.66	0.54	0.30	0.83	0.94	0.89	0.95
GB	0.46	0.53	0.85	0.53	0.31	1	0.87	0.30	0.26	0.45	0.42	0.84	0.28	0.76	0.98	0.90	0.66	0.03	0.51	0.07	0.76	0.66	0.54	0.23	0.44	0.37
GBT	0.75	0.71	0.65	0.57	0.86	0.69	1	0.90	0.88	0.88	0.90	0.79	0.89	0.72	0.54	0.92	0.95	0.12	0.79	0.35	0.72	0.00	0.86	0.87	0.76	0.91
GCW	0.72	0.68	0.38	0.50	0.95	0.30	0.90	1	0.90	0.92	0.95	0.56	1.00	0.53	0.11	0.65	0.87	0.15	0.78	0.41	0.53	0.00	0.85	0.99	0.77	0.77
GTS	0.70	0.60	0.30	0.41	0.94	0.26	0.88	0.99	1	0.88	0.92	0.49	1.00	0.45	0.07	0.63	0.83	0.15	0.71	0.42	0.45	0.00	0.80	0.99	0.72	0.96
GHCF	0.71	0.91	0.67	0.80	0.89	0.45	0.88	0.92	0.88	1	0.99	0.78	0.90	0.79	0.25	0.66	0.97	0.12	0.96	0.33	0.79	0.00	0.99	0.86	0.89	0.97
GBS	0.72	0.87	0.61	0.74	0.92	0.42	0.90	0.95	0.92	0.99	1	0.74	0.93	0.74	0.22	0.67	0.96	0.13	0.93	0.35	0.74	0.00	0.97	0.90	0.88	0.99
GT	0.71	0.88	0.96	0.86	0.62	0.84	0.79	0.56	0.49	0.78	0.74	1	0.52	0.96	0.73	0.81	0.89	0.23	0.86	0.31	0.96	0.18	0.86	0.46	0.83	0.67
GHW	0.71	0.63	0.34	0.45	0.95	0.28	0.89	1.00	1.00	0.90	0.93	0.52	1	0.49	0.09	0.63	0.85	0.15	0.74	0.41	0.49	0.00	0.82	1.00	0.74	0.97
LY	0.55	0.93	0.97	0.94	0.54	0.76	0.72	0.53	0.45	0.79	0.74	0.96	0.49	1	0.63	0.70	0.86	0.05	0.90	0.13	0.99	0	0.88	0.41	0.78	0.66
SBM	0.33	0.35	0.76	0.38	0.12	0.98	0.54	0.11	0.07	0.25	0.22	0.73	0.09	0.63	1	0.82	0.49	0.00	0.32	0.00	0.63	0.00	0.35	0.05	0.26	0.17
RVB	0.67	0.56	0.71	0.47	0.63	0.90	0.92	0.65	0.63	0.66	0.67	0.81	0.63	0.70	0.82	1	0.82	0.12	0.61	0.27	0.70	0.03	0.68	0.61	0.59	0.66
RTM	0.74	0.90	0.79	0.80	0.85	0.66	0.95	0.87	0.83	0.97	0.96	0.89	0.85	0.86	0.49	0.82	1	0.11	0.94	0.31	0.86	0	0.98	0.80	0.87	0.93
RBL	0.74	0.07	0.02	0.04	0.44	0.03	0.12	0.15	0.15	0.12	0.13	0.23	0.15	0.05	0.00	0.12	0.11	1	0.09	0.96	0.05	0.99	0.10	0.15	0.51	0.14
RS	0.64	0.99	0.81	0.93	0.77	0.51	0.79	0.78	0.71	0.96	0.93	0.86	0.74	0.90	0.32	0.61	0.94	0.09	1	0.24	0.90	0	0.99	0.68	0.90	0.87
RVY	0.86	0.19	0.06	0.10	0.66	0.07	0.35	0.41	0.42	0.33	0.35	0.31	0.41	0.13	0.00	0.27	0.31	0.96	0.24	1	0.13	0.91	0.29	0.42	0.48	0.38
SD	0.55	0.93	0.97	0.94	0.54	0.76	0.72	0.53	0.45	0.79	0.74	0.96	0.49	0.99	0.63	0.70	0.86	0.05	0.90	0.13	1	0	0.88	0.41	0.78	0.66
SD2	0.65	0.00	0.00	0.00	0.30	0.66	0.00	0.00	0	0.00	0.00	0.18	0.00	0.00	0.00	0.03	0.00	0.99	0.00	0.91	0	1	0	0	0.43	0
VFN	0.69	0.96	0.78	0.88	0.83	0.54	0.86	0.85	0.80	0.99	0.97	0.86	0.82	0.88	0.35	0.68	0.98	0.10	0.99	0.29	0.88	0	1	0.77	0.90	0.93
WY	0.69	0.56	0.26	0.37	0.94	0.23	0.87	0.99	1.00	0.86	0.90	0.46	1.00	0.41	0.05	0.61	0.80	0.15	0.68	0.42	0.41	0	0.77	1	0.70	0.95
WCLT	0.89	0.87	0.68	0.79	0.89	0.44	0.76	0.77	0.72	0.89	0.88	0.83	0.74	0.78	0.26	0.59	0.87	0.51	0.90	0.48	0.78	0.43	0.90	0.70	1	0.84
YBW	0.73	0.79	0.52	0.64	0.95	0.37	0.91	0.77	0.96	0.97	0.99	0.67	0.97	0.66	0.17	0.66	0.93	0.14	0.87	0.38	0.66	0	0.93	0.95	0.84	1

BWT Blue Whistling Thrush, *BWS* Blue-winged Siva, *CBN* Chestnut-bellied Nuthatch, *CGM* Common Green Magpie, *CT* Common Tailorbird, *GB* Great Barbet, *GBT* Green-backed Tit, *GCW* Green-crowned Warbler, *GTS* Green-tailed Sunbird, *GHCF* Grey-headed Canary Flycatcher, *GBS* Grey-backed Shrike, *GT* Grey Treepie, *GHW* Grey-hooded Warbler, *LY* Lesser Yellownape, *SBM* Short-billed Minivet, *RVB* Red-vented Bulbul, *RTM* Red-tailed Minla, *RBL* Red-billed Leothrix, *RS* Rufous Sibia, *RVY* Rufous-vented Yuhina, *SD* Spangled Drongo, *SD2* Spotted Dove, *VFN* Velvet-fronted Nuthatch, *WY* Whiskered Yuhina, *WCLT* White-crested Laughingthrush, *YBW* Yellow-bellied Warbler

Appendix 3

Niche overlap in foraging method for bird species pair in Sikkim, Eastern Himalaya

Name	BWT	BWS	CBN	CGM	CT	GB	GBT	GCW	GTS	GHCF	GBS	GT	GHW	LY	SBM	RVB	RTM	RBL	RS	RVY	SD	SD2	VFN	WY	WCLT	YBW
BWT	1	0.81	0.57	0.57	0.87	0.27	0.72	0.39	0	0.79	0.77	0.89	0.35	0.81	0.81	0.82	0.76	0.12	0.13	0.84	0.00	0.20	0.81	0.81	0.96	0.37
BWS	0.81	1	0.45	0.95	0.95	0	0.81	0.96	0.75	0.43	0.67	0.47	0.96	0.45	0.44	0.71	0.74	0.95	0.07	0.22	0.00	0.00	0.45	0.50	0.36	0.99
CBN	0.57	0.45	1	0.71	0.86	0	0.89	0.48	0	0.97	0.95	0.90	0.43	0.99	0.99	0.94	0.93	0.15	0.16	0.50	0.00	0.00	0.99	1.00	0.81	0.46
CGM	0.57	0.95	0.71	1	0.85	0	0.95	0.93	0	0.69	0.87	0.69	0.91	0.71	0.70	0.89	0.91	0.81	0.11	0.35	0.00	0.00	0.71	0.75	0.58	0.95
CT	0.87	0.95	0.86	0.85	1	0	0.92	0.72	0.17	0.83	0.91	0.85	0.66	0.86	0.85	0.94	0.92	0.47	0.30	0.72	0.17	0.00	0.86	0.88	0.90	0.70
GB	0.27	0.00	0.00	0.00	0	1	0.00	0.02	0	0.02	0.01	0.19	0.02	0.00	0.01	0.11	0.01	0.00	0.00	0.00	0.00	0.48	0.00	0.00	0.00	0.01
GBT	0.72	0.81	0.89	0.95	0.92	0.00	1	0.82	0	0.87	0.98	0.83	0.79	0.89	0.89	0.98	0.99	0.59	0.14	0.44	0.00	0.00	0.89	0.91	0.72	0.82
GCW	0.39	0.96	0.48	0.93	0.72	0.02	0.82	1	0.12	0.52	0.72	0.50	0.99	0.48	0.50	0.72	0.76	0.90	0.19	0.24	0.12	0.00	0.48	0.53	0.39	0.98
GTS	0.00	0.75	0.00	0.00	0.17	0.00	0	0.12	1	0	0.00	0.00	0.00	0.00	0.00	0	0	0	0.99	0.00	1.00	0.00	0.00	0.00	0.00	0.00
GHCF	0.79	0.43	0.97	0.69	0.83	0.02	0.87	0.52	0	1	0.96	0.87	0.49	0.97	0.99	0.91	0.92	0.15	0.15	0.48	0.00	0.00	0.97	0.97	0.79	0.47
GBS	0.77	0.67	0.95	0.87	0.91	0.01	0.98	0.72	0.87	0.96	1	0.87	0.68	0.95	0.96	0.98	0.99	0.41	0.15	0.47	0.00	0.00	0.95	0.97	0.78	0.69
GT	0.89	0.47	0.90	0.69	0.85	0.19	0.83	0.50	0.69	0.87	0.87	1	0.45	0.90	0.89	0.90	0.86	0.22	0.14	0.59	0.00	0.41	0.90	0.90	0.82	0.48
GHW	0.35	0.96	0.43	0.91	0.66	0.02	0.79	0.99	0.91	0.49	0.68	0.45	1	0.43	0.46	0.68	0.73	0.91	0.07	0.21	0.00	0.00	0.43	0.48	0.35	0.98
LY	0.81	0.45	1.00	0.71	0.86	0.00	0.89	0.48	0.71	0.97	0.95	0.90	0.43	1	0.99	0.94	0.93	0.15	0.16	0.50	0.00	0.00	0.99	1.00	0.81	0.46
SBM	0.81	0.44	0.99	0.70	0.85	0.01	0.89	0.50	0.70	0.99	0.96	0.89	0.46	0.99	1	0.93	0.93	0.15	0.16	0.49	0.00	0.00	0.99	0.99	0.81	0.47
RVB	0.82	0.71	0.94	0.89	0.94	0.11	0.98	0.72	0.89	0.91	0.98	0.90	0.68	0.94	0.93	1	0.99	0.46	0.15	0.52	0.00	0.06	0.94	0.96	0.80	0.72
RTM	0.76	0.74	0.93	0.91	0.92	0.01	0.99	0.76	0.91	0.92	0.99	0.86	0.73	0.93	0.93	0.99	1	0.50	0.15	0.46	0.00	0.00	0.93	0.95	0.76	0.75
RBL	0.12	0.95	0.15	0.81	0.47	0.00	0.59	0.90	0.81	0.15	0.41	0.22	0.91	0.15	0.15	0.46	0.50	1	0.02	0.08	0.00	0.00	0.15	0.21	0.12	0.94
RS	0.13	0.07	0.16	0.11	0.30	0.00	0.14	0.19	0.11	0.15	0.15	0.14	0.07	0.16	0.16	0.15	0.15	0.02	1	0.08	0.98	0.00	0.16	0.16	0.13	0.07
RVY	0.84	0.22	0.50	0.35	0.72	0.00	0.44	0.24	0.35	0.48	0.47	0.59	0.21	0.50	0.49	0.52	0.46	0.08	0.08	1	0.00	0.00	0.50	0.50	0.91	0.23
SD	0.00	0.00	0.00	0.00	0.17	0.00	0.00	0.12	0	0	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.98	0.00	1	0.00	0.00	0.00	0.00	0.00
SD2	0.20	0.00	0.00	0.00	0.00	0.48	0.00	0.00	0	0	0.00	0.41	0.00	0.00	0.00	0.06	0.00	0.00	0.00	0.00	0.00	1	0.00	0.00	0.00	0.00
VFN	0.81	0.45	0.99	0.71	0.86	0.00	0.89	0.48	0.71	0.97	0.95	0.90	0.43	0.99	0.99	0.94	0.93	0.15	0.16	0.50	0.00	0.00	1	1.00	0.81	0.46
WY	0.81	0.50	0.98	0.75	0.88	0.00	0.91	0.53	0.75	0.97	0.97	0.90	0.48	0.99	0.99	0.96	0.95	0.21	0.16	0.50	0.00	0.00	0.99	1	0.81	0.52
WCLT	0.96	0.36	0.81	0.58	0.90	0.00	0.72	0.39	0.58	0.79	0.78	0.82	0.35	0.81	0.81	0.80	0.76	0.12	0.13	0.91	0.00	0.00	0.81	0.81	1	0.38
YBW	0.37	0.99	0.46	0.95	0.70	0.01	0.82	0.98	0.95	0.47	0.69	0.48	0.98	0.46	0.47	0.72	0.75	0.94	0.07	0.23	0.00	0.00	0.46	0.52	0.38	1

BWT Blue Whistling Thrush, *BWS* Blue-winged Siva, *CBN* Chestnut-bellied Nuthatch, *CGM* Common Green Magpie, *CT* Common Tailorbird, *GB* Great Barbet, *GBT* Green-backed Tit, *GCW* Green-crowned Warbler, *GTS* Green-tailed Sunbird, *GHCF* Grey-headed Canary Flycatcher, *GBS* Grey-backed Shrike, *GT* Grey Treepie, *GHW* Grey-hooded Warbler, *LY* Lesser Yellownape, *SBM* Short-billed Minivet, *RVB* Red-vented Bulbul, *RTM* Red-tailed Minla, *RBL* Red-billed Leothrix, *RS* Rufous Sibia, *RVY* Rufous-vented Yuhina, *SD* Spangled Drongo, *SD2* Spotted Dove, *VFN* Velvet-fronted Nuthatch, *WY* Whiskered Yuhina, *WCLT* White-crested Laughingthrush, *YBW* Yellow-bellied Warbler

Appendix 4

Niche overlap in foraging substrate for each species pair in Sikkim, Eastern Himalaya

Name	BWT	BWS	CBN	CT	GB	GBT	GCW	GTS	GHCF	GBS	GT	GHW	LY	SBM	RVB	RTM	RBL	RS	RVY	SD	SD2	VFN	WY	WCLT	YBW
BWT	1	0.05	0	0.46	0.42	0.29	0.10	0.42	0.72	0.71	0.90	0.05	0	0.74	0.58	0.69	0.53	0.65	0.39	0.52	0.56	0.19	0.20	0.53	0.05
BWS	0.05	1	0	0.36	0.00	0.76	0.90	0.00	0.18	0.22	0.20	1.00	0	0.11	0.58	0.35	0.07	0.05	0.00	0.00	0.00	0.00	0.44	0.39	1.00
CBN	0.00	0	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.97	0.00	0.64	0.00
CGM	0.61	0.50	0	0.00	0.00	0.46	0.54	0.00	0.94	0.94	0.64	0.48	0	0.81	0.66	0.81	0.00	0.14	0.00	0.00	0.17	0.21	0.11	0.29	0.50
CT	0.46	0.36	0	1	0.49	0.17	0.17	0.49	0.32	0.00	0.58	0.40	0	0.20	0.66	0.38	0.44	0.41	0.46	0.32	0.48	0.00	0.80	0.82	0.35
GB	0.42	0.00	0	0.49	1	0.00	0.22	0.99	0.00	0.00	0.62	0.00	0	0.00	0.07	0.00	0.00	0.00	0.94	0.00	0.98	0.00	0.00	0.00	0.00
GBT	0.29	0.76	0	0.17	0.00	1	0.47	0.00	0.59	0.37	0.46	0.79	0	0.47	0.92	0.71	0.13	0.15	0.00	0.00	0.06	0.07	0.90	0.85	0.75
GCW	0.10	0.90	0	0.17	0.22	0.47	1	0.22	0.02	0.24	0.25	0.88	0	0.02	0.35	0.19	0.01	0.01	0.21	0.00	0.22	0.00	0.07	0.07	0.91
GTS	0.42	0.00	0	0.49	0.99	0.00	0.22	1	0.03	0.00	0.62	0.00	0	0.00	0.07	0.00	0.00	0.00	0.94	0.00	0.98	0.00	0.00	0.00	0.00
GHCF	0.72	0.18	0	0.32	0.00	0.59	0.02	0.03	1	0.94	0.76	0.20	0	0.99	0.84	0.98	0.06	0.20	0.00	0.00	0.19	0.23	0.51	0.66	0.10
GBS	0.71	0.22	0	0.00	0.00	0.37	0.24	0.00	0.94	1	0.71	0.21	0	0.94	0.65	0.88	0.00	0.17	0.00	0.00	0.20	0.25	0.13	0.34	0.22
GT	0.90	0.20	0	0.58	0.62	0.46	0.25	0.62	0.76	0.71	1	0.21	0	0.75	0.71	0.76	0.22	0.33	0.58	0.18	0.75	0.18	0.36	0.54	0.20
GHW	0.05	1.00	0	0.40	0.00	0.79	0.88	0.00	0.20	0.21	0.21	1	0	0.12	0.61	0.37	0.08	0.06	0.00	0.00	0.00	0.00	0.49	0.43	1.00
LY	0.00	0.00	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.97	0.00	0.00	0.00
SBM	0.74	0.11	0	0.20	0.00	0.47	0.02	0.00	0.99	0.94	0.75	0.12	0	1	0.76	0.96	0.04	0.20	0.00	0.00	0.20	0.25	0.37	0.55	0.10
RVB	0.58	0.58	0	0.66	0.07	0.92	0.35	0.07	0.84	0.65	0.71	0.61	0	0.76	1	0.92	0.18	0.26	0.07	0.07	0.19	0.15	0.81	0.88	0.58
RTM	0.69	0.35	0	0.38	0.00	0.71	0.19	0.00	0.98	0.88	0.76	0.37	0	0.96	0.92	1	0.07	0.20	0.00	0.00	0.18	0.22	0.58	0.71	0.35
RBL	0.53	0.07	0	0.44	0.00	0.13	0.01	0.00	0.06	0.00	0.22	0.08	0	0.04	0.18	0.07	1	0.98	0.00	0.99	0.00	0.00	0.15	0.48	0.07
RS	0.65	0.05	0	0.41	0.00	0.15	0.01	0.00	0.20	0.17	0.33	0.06	0	0.20	0.26	0.20	0.98	1	0	0.98	0.04	0.04	0.14	0.50	0.05
RVY	0.39	0.00	0	0.46	0.94	0.00	0.21	0.94	0.00	0.00	0.58	0.00	0	0	0.07	0.00	0.00	0	1	0	0.92	0.00	0.00	0.00	0.00
SD	0.52	0.00	0	0.32	0.00	0.00	0.00	0.00	0.00	0.00	0.18	0.00	0	0	0.07	0.00	0.99	0.98	0	1	0	0	0	0.35	0
SD2	0.56	0.00	0	0.48	0.98	0.06	0.22	0.98	0.19	0.20	0.75	0.00	0	0.20	0.19	0.18	0.00	0.04	0.92	0	1	0.05	0.03	0.07	0.00
VFN	0.19	0.00	0.97	0.00	0.00	0.07	0.00	0.00	0.23	0.25	0.18	0.00	0.97	0.25	0.15	0.22	0.00	0.04	0	0	0.05	1	0.03	0.09	0.00
WY	0.20	0.44	0.00	0.80	0.00	0.90	0.07	0.00	0.51	0.13	0.36	0.49	0	0.37	0.81	0.58	0.15	0.14	0	0	0.03	0.03	1	0.91	0.43
WCLT	0.53	0.39	0.64	0.82	0.00	0.85	0.07	0.00	0.66	0.34	0.54	0.43	0	0.55	0.88	0.71	0.48	0.50	0	0.35	0.07	0.09	0.91	1	0.38
YBW	0.05	0.99	0	0.35	0.00	0.75	0.91	0.00	0.10	0.22	0.20	1.00	0	0.10	0.58	0.35	0.07	0.05	0	0	0.00	0.00	0.43	0.377	1

BWT Blue Whistling Thrush, *BWS* Blue-winged Siva, *CBN* Chestnut-bellied Nuthatch, *CGM* Common Green Magpie, *CT* Common Tailorbird, *GB* Great Barbet, *GBT* Green-backed Tit, *GCW* Green-crowned Warbler, *GTS* Green-tailed Sunbird, *GHCF* Grey-headed Canary Flycatcher, *GBS* Grey-backed Shrike, *GT* Grey Treepie,*GHW* Grey-hooded Warbler, *LY* Lesser Yellownape, *SBM* Short-billed Minivet, *RVB* Red-vented Bulbul, *RTM* Red-tailed Minla, *RBL* Red-billed Leothrix, *RS* Rufous Sibia, *RVY* Rufous-vented Yuhina, *SD* Spangled Drongo, *SD2* Spotted Dove, *VFN* Velvet-fronted Nuthatch, *WY* Whiskered Yuhina, *WCLT* White-crested Laughingthrush, *YBW* Yellow-bellied Warbler

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Declarations

Conflict of interest On behalf of all authors, the corresponding author states that there is no conflict of interest.

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