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Foraging guild structure and niche characteristics of waterbirds wintering in selected sub-Himalayan wetlands of India

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ABSTRACT

Guild structure and niche characteristics are important indicators of quantitative niche partitioning of a community. In the present study the niche structure was analyzed to determine whether resource partitioning reflected coexistence or exclusion of different waterbird species in relevant guilds at sub-Himalayan terai-dooars wetlands. Trophic guild structure and niche organization in wintering waterbirds were studied to understand why some species were rare and some were abundant and what possibly determined the diversity and abundance of multi-species waterbird communities. Two trophic components of niche partitioning, namely foraging habitat and foraging techniques, were considered in the present study. Cluster analyses based on foraging habitats and foraging techniques (i.e., two dimensions) provided bi-dimensional foraging guilds. Waterbirds precisely formed five distinct guilds, namely, medium and shallow water generalists, stalking waders, pecking waders, mud picking wader and divers. Further, a much higher diversity of waterbirds was observed from shallow and medium water habitats than deep waters which could be the outcome of higher net available trophic energy. Potential competitive interactions within intra-guild members were possibly minimized by using varied feeding techniques. The present study pointed out that the specialist guild members showed comparatively higher intra-guild niche overlap, whereas generalist guild members showed much lower niche overlap. Results indicated that waterbird communities were influenced mostly by trophic resources at a site and the birds' ability to exploit them. Waterbird guild structures and niche characteristics thus provide important ecological indicators of the ability of wetlands to support a range of species. Further, information on guild structures and niche characteristics are surely important for monitoring the biotic health of sub-Himalayan wetlands that would be important to work out effective wetland conservation strategies.

1. Introduction

Wetlands are critical foraging areas for many waterbird species. The relatively high productivity of wetlands often enables the coexistence of several waterbird species using similar food resources (Hafner et al., 1986; Weller, 1999). The food choice of the waterbirds varies not only between species but may also be different between breeding and foraging grounds. Resource partitioning by these birds usually involves a combination of differences in foraging habitat use, food preference and feeding techniques (Pöysã, 1983; Poysa, 1984; MacNally, 1994; Polla et al., 2018).

The guild concept (Grinnell, 1917; Root, 1967) has always been extremely helpful in understanding and portraying the structure of bird communities with the major emphasis being on foraging guilds (Wiens, 1989; Paszkowski and William, 2006). Guilds (Simberloff and Dayan, 1991) are considered as natural 'ecological units' occurring in various communities forming the 'building blocks' of each community (Hawkins and Mohon, 1989). Root (1967) defined guild as being 'a group of species that exploits the same class of environmental resources in a similar way' and categorized that 'this term groups together species, without regard to taxonomic positions, that overlap significantly in their niche requirements' (Jaksić and Medel, 1990). The composition of guilds differs between sites and is correlated both with habitat features and with the methods used by animals to exploit the resources (Holmes and Robinson, 1988). Simberloff and Dayan (1991) consider that guild structure and niche characteristics are important indicators of

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quantitative niche partitioning of a community.

Waterbirds have various morphological and behavioural adaptations for foraging, which enable them to make optimal use of the food resources available. This may be through differences in bill shape, neck and tarsus length that allow them to forage at various water depths and different areas of the wetland (Ntiamoa-Baidu et al., 1998; Elphick, 2008). If the resources are related to food and nutrition, the guild is termed as a foraging guild. Foraging habitat and feeding strategies of waterbirds are important to study to understand resource partitioning (Pöysã, 1983; Weller, 1999; Gatto and Quintana, 2008; Liordos, 2010; Pérez-Crespo et al., 2013) and optimal utilization of available resources. Canterbury et al. (2000) elaborate that guild structures and community characteristics of birds could serve as important ecological indicators of habitat quality and heterogeneity. Thereby, in the present study, the guilds are characterized to extract information about possible interactions caused by interspecific resource partitioning in the waterbird community.

Wetlands from the foothills of the Himalayas up to the vast shoreline of India not only provided wintering sites for large numbers of ducks and waders but were also important staging areas for waterbirds migrating further south to Australia and New Zealand (Silvius and Parish, 1987). An urgent need was felt for serious research works and conservation of small yet potentially important waterbird wintering grounds and staging sites in the tropics. However, there have been only a few detailed studies of resource partitioning, feeding guilds and factors influencing the diversity and abundance of waterbirds at the wetlands of India and neighboring south-east Asian countries. Chettri et al. (2001, 2002, 2005) studied the relationships between bird community attributes—including migratory groups and feeding guilds—and vegetation variables. Borges and Shanbhag (2008) studied an important wetland situated on the Central Asian Indian migratory flyway and reported that waterbirds partitioned the available resources, although a considerable niche overlap existed on the wintering ground. Feeding guilds of waterbirds of Gharana Wetland Reserve of Jammu were reported by Pandora and Sahi (2014) and by Anthal and Sahi (2017). These studies pointed out the feeding habitats and foraging resources of the foothills of the northern Himalayas. Two more recently published works from southern West Bengal with a mention of feeding guilds without scientific testing of hypotheses were by Datta (2016) and Khan et al. (2016). Habitat heterogeneity, fragmentation, anthropogenic interactions, and vegetation structure influenced the waterbird community structure (Pérez-García et al., 2014). A holistic approach is particularly important for identifying the physical, chemical and biological factors affecting the structure of the ecosystems. Knowledge of the functional mechanisms involved in maintaining species diversity is needed from the management standpoint to conserve a wide array of species using a site or series of sites. To date, the foraging guilds of the inland wetlands of India have received little attention, especially from the wetlands of Himalayan foothills of eastern India. Thereby, we tested three hypotheses: i) species which use a wider range of feeding techniques than others also utilize a wider range of habitats; ii) specialist feeding guilds occupy a relatively narrow niche with little overlap with other guilds and iii) that generalist feeders are more abundant than specialist feeders.

2. Material and methods

2.1. Study areas

Three wetlands chosen as study sites were all low-lying (< 125 m asl), with flat topography (< 10% slope), and were located within the ecologically sensitive “Indo-Burma biodiversity hotspot” of the Central Himalayas Biogeographical Zone (Fig. 1, Appendix 1). These sub-Himalayan wetlands are important as staging and wintering areas for waterbirds migrating along the East Asian-Australasian Flyway (EAAF) and are associated to two important Endemic Bird Areas (EBAs), namely Eastern Himalayan and Assam Plains EBAs. One of these three wetlands (Nararthali wetland) was located inside Buxa Tiger Reserve and National Park in the Assam Plains Endemic Bird Area (EBA 131) and the other two prominent wetlands (namely Rasomati wetland, a protected forest and Rasik Beel wetland complex under National Wetland Conservation Programme) were included under Assam-Sylhet plains Wetland Region (W14) (Kumar et al.,2005). Many rivers that originated in the Himalayas crisscrossed this region and their depositions formed the flood plain landmass over a long geological time (Rudra, 2012). With time, these rivers changed their courses and formed oxbow lakes, a type of lentic freshwater wetlands (wetland type code 1102; ISRO, 2011). Three such lakes of varied dimensions and recognised as important wintering and staging sites for migratory waterbirds at the Himalayan foothills (commonly known as terai and dooars) were chosen for the present study (Appendix 1). A Garmin eTrex 30 GPS was used to record the coordinates and altitude of the study sites.

2.2. Bird density and abundance calculation

Intensive field observations were made and the obtained data were used for calculation of waterbird density and abundance. Field observations were conducted twice in a month (preferably in second and last week) during the wintering months (October through March) to record waterbird numbers and distribution at the each of the study sites over three successive winters, from winter 2012/13 to winter 2014/15 inclusive. October through March was considered the best period for studying wintering and as well as resident birds in the sub-Himalayan region (Koskimies and Pöysä, 1989; Salewski et al., 2003; Mazumdar et al., 2007). The counts were made along line transects (following Hutto et al., 1986; Bibby et al., 1992; Buckland et al., 1993), by a group of three trained observers at three specific time intervals (06:00–07:00, 12:00–13:00 and 17:00–18:00 hrs) during the day. All sides of each wetland were approachable and were surveyed during each sampling session, by walking along a transect length of 1 km and counting all birds seen on land or water within 50 m of the transect, using a True-Plus 360 Laser range finder. Time and weather conditions at the start of each sampling session were also recorded. Flying birds were recorded separately. We also conducted random binocular point-counts of the populations of birds to obtain a more-robust area-wise estimate (Bibby et al., 1992; Gopal, 1995; Chatterjee et al., 2013, 2017) and species identification. A Nikon Fieldscope (25–75 × 82 ED), Bushnell Equinox Z (4.5 × 40) Night Vision and Nikon Action (10 × 50) binoculars were used for spotting t he characteristics of the birds in sight. Areas covered by the circular binocular field at different distances, namely at 10, 20, 30, 40, 50 and 100 m, were calculated for each binocular used by each observer by averaging three measurements of ground-cover on an open field for each of the six selected distances. At twenty sampling points on the shoreline, at an interval of 100 m, we recorded the total number and number of individuals per species at each of the sampling spots randomly chosen at five different sighting distances ranging from 10 to 100 m. Binocular-field counts of three separate trained observers at three specific time intervals, as mentioned above, included all avian species, either resting on the bank or reeds or wandering on the bank. The raw count data of all measures were averaged month-wise to obtain representative data and used as population size per unit area (Gibbons and Gregory, 2006). We followed Ali and Ripley (1987), Grimmett et al. (2011) and Kazmierczak and van Perlo (2000) for avifauna identification and nomenclature.

2.3. Water depth and vegetation structure

Waterbird foraging habitats were categorized according to water depth, associated types of available vegetation and vegetation species in the present study. Average water depth was measured from shore to shore at an interval of 1 m along two transects–one along the width and

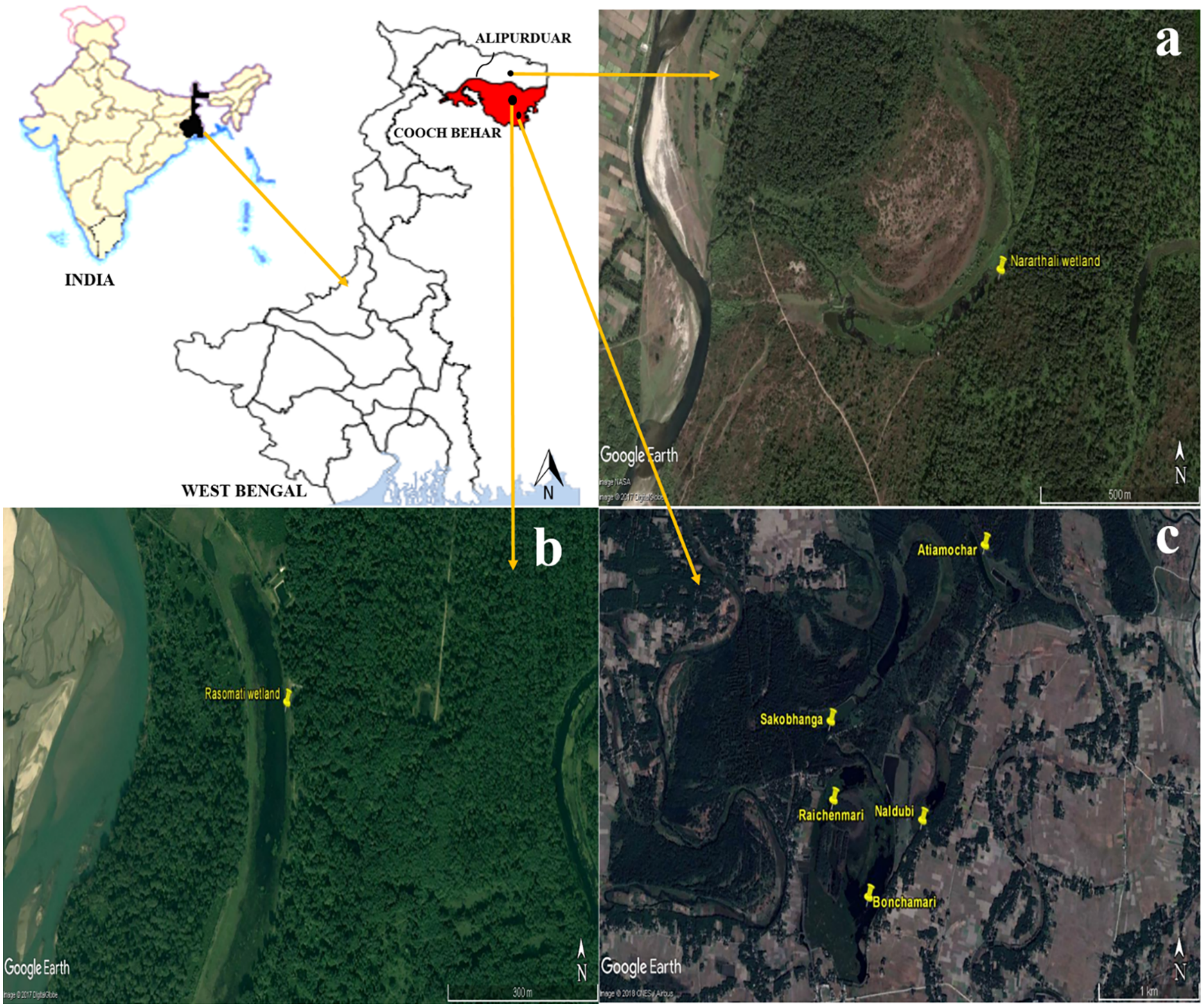

Fig. 1. Map of Study sites; (a) Nararthali wetland, (b) Rasomati wetland and (c) Rasik Beel Wetland Complex (Raichenmari-Sakobhanga wetland, Bochamari wetland and Atiamochar-Naldubi wetland) at sub-Himalayan region of northern part of West Bengal, India.

one along the length of the water body representing the shallow (< 30 cm), medium (30–60 cm) and deep portions (> 60 cm). Depths were measured from a boat using a weight and a string marked in centimeter. Three such transects, 1 m apart from each other, were used to record the depths for calculating the depth-wise final average. Vegetation sampling was also made at the points of depth recording along the transect lines. Vegetation technique was carried out following Paszkowski and William (2006). Sampling of submersed vegetation was conducted once in a month during the first week of August and September for each sampling year before the waterbird arrival. An iron anchor of 60 cm high with three re-curved hooks, tied to a strong nylon rope was used for hauling out submersed vegetation. To sample marginal vegetation, 10 or 15 quadrates [1 × 1 square meter (m^2) each], depending on the size of the wetland, were laid. 10 or 15 such 2x2 m^2 quadrates, made up of thin bamboo sticks with thermocol blocks (2 cm^3) at the nodes were used for sampling floating vegetation. Aquatic macrophytes and filamentous algae, in each case, were identified. The extent of floating vegetation (especially *Eichhornia crassipes*) covering the wetland was calculated from aerial observation (made from watchtowers), plotted on graph paper, for each month in each year of the study.

2.4. Foraging guilds of waterbirds

Waterbirds were assigned into a particular guild based upon the way the species obtained food items, the type of food consumed, the foraging habitat used and the depth in the water where the species foraged (MacNally, 1983, 1994). Only the first observation on each individual of a particular species was taken into consideration (initial observation method of Liordos, 2010) and scan sampling (Martin and Bateson, 1993) technique was employed from selected vantage observation points, nearest safe approachable distance from each habitat type. A Nikon Fieldscope (25–75 × 82 ED), Bushnell Equinox Z (4.5 × 40) Night Vision and Nikon Action (10 × 50) binoculars were used to scan all the details of the behavior of the species in the field at each habitat type for a fixed time period (7 am–10 am, and 2 pm–5 pm) and on 4 random days of observation during each of the wintering months. The species identity, foraging habitat and foraging technique were recorded for each individual of a particular waterbird species in consultation with the works of Ali and Ripley (1968, 1969a,b). The water depth where the foraging could take place was determined using morphometric data like beak length, head length, neck length, femur, tibiotarsus and tarsometatarsus lengths of the bird species (Pöysä, 1983; Ntiamoa-Baidu et al., 1998; Green, 1998) using museum specimens and published data. In case of wading birds, the exposed vertical leg length was used to estimate the water depth. For diving ducks and other divers, the most frequent feeding depth was the weighted mean of the water depths in the habitats they used following the methodology described by Pöysä (1983). Available bird specimens in the Zoological Survey of India (ZSI), Kolkata and Bengal Natural History Museum (BNHM), Darjeeling, India, were studied to collect morphometric data (Appendix 2 and 3).

Only the initial behavior was recorded because (i) in the wetlands under observation all birds had equal opportunity to be located owing to lack of any visual hindrance and the proximity to the observer (ii) to avoid any temporal 'autocorrelation' coming out of sequential consecutive observations on the same individual (Morrison, 1984; Hej et al., 1990). Subsequently, the data-set was arranged in three matrices (Gatto and Quintana, 2008; Liordos, 2010; Pérez-Crespo et al., 2013): one for foraging habitat (27 species × 9 habitat variable), a second for foraging technique (27 species × 9 feeding technique) and the third combining the previous two matrices (27 species × 81 possible combinations of variables for foraging habitat and foraging technique, i.e., bi-dimensional). Out of 81 possible combinations (9 habitats × 9 techniques), combinations were considered feasible on omitting unrealistic combinations such as muddy shore-diving and grassy meadow–upending). Only species with at least 30 recorded foraging behaviors (i.e. foraging habitat and foraging technique) were included for analysis. Each row of the matrix depicted a particular species. Each column represented a resource or foraging categories (in terms of habitat, technique or breadth combined). Each entry in a cell of a matrix represented the count of individual in a particular state of foraging habitat or foraging technique applied. Thereafter, these matrix entries were tabulated as proportional values by summation of counts (row) and then dividing each resource utilization count (which are the entry in an original matrix) by its total (row total). The one-dimensional (habitat and technique) and bi-dimensional matrices were subsequently tabulated for niche breadth, niche overlap and also for assignment of guilds and to calculate foraging depth using the foraging technique. Waterbird foraging habitats were categorized according to Pöysã (1983), MacNally (1983, 1994), Liordos (2010) and Pérez-Crespo et al. (2013) considering the water depth and type of available vegetation (Table 1).

2.5. Waterbirds foraging behaviour

Feeding behaviors were characterized by the foraging techniques used by the waterbirds. The following categories were identified from previous studies (Pöysã, 1983; Liordos, 2010; Pérez-Crespo et al., 2013) which we used while categorizing our field observations on birds' feeding behaviour

- Diving: The bird becomes invisible to the observer on diving into the water.
- Striking: A feeding technique, in which a bird suddenly strikes into its prey using its beak and neck after a stalking movement.
- Beak submerged: When the birds forage by dipping the beak, partly or in full, into the water.
- Head submerged: When the birds forage by dipping the head including the beak in water. In this case, the eyes too were underwater while foraging.
- Neck submerged: This was a feeding technique where the birds foraged by dipping the neck in water, fully or partly.
- Upending: Upending or 'tipping' was a feeding technique where the bird was partially submerged in a vertical position while foraging with its tail and legs were above the water surface.
- Filtering/Gleaning: The bill was held in the plane of water surface submerging only the mandible to strain the water surface for gleaning/straining food items from the water surface.
- Picking from mud: When the birds foraged by picking any food items from the top of the muddy substratum. This technique also included grazing for a food item on to the mud surface.
- Pecking: When the birds foraged using tactile probing and peck-digging/pecking to detect and collect prey items from surface or sub-surface.

Table 1
Waterbird foraging habitats categorized according to water depth and associated types of available vegetation.

Foraging habitat	Depth	Nature of vegetation	Available vegetation species
Deep water with submersed vegetation (DWSV)	> 60 cm	Unanchored submersed vegetation (UASV)	*Uricularia aurea, U. bifida, U. hirta*
		Rooted submersed vegetation (RSV)	*Limnophila heterophylla, L. repens, L. sessiliflora, Hydrilla verticillata, Vallisneria natans, Ottelia alismoides*
Deep water with emergent vegetation (DWEV)	> 60 cm	Emergent vegetation (EV) with Emergent Amphibious (EAV) nature	*Scirpus juncoids, S. articulatus, S. maritimus, Cyperus stoloniferus, Bulleostylis densa, Oryza rufipogen, O. meyeriana, Paspalidium punctatum*
Medium depth with submersed vegetation (MDSV)	> 30 cm < 60 cm	UASV	*U. aurea, U. bifida, U. hirta*
		RSV	*L. heterophylla, L. repens, L. sessiliflora, H. verticillata, V. natans, O. alismoides, Hygrophila polysperma, H. phlomoides, Alternantnera paronychiodes*
Medium depth with emergent vegetation (MDEV)	> 30 cm < 60 cm	EV and EAV	*Scirpus juncoids, S. articulatus, S. maritimus, C. stoloniferus, B. densa, O. rufipogen, O. meyeriana, P. punctatum, Marsilea quadrifolia, Ipomea aquatic, I. cornea, I. hederifolia*
Medium depth with floating vegetation (MDFV)	> 30 cm < 60 cm	UASV	*U. aurea, U. bifida, U. hirta*
		RSV	*L. heterophylla, L. repens, L. sessiliflora, H. verticillata, V. natans, O. alismoides, H. polysperma, H. phlomoides, A. paronychiodes, Ceratopteris thalictroides, Aponogeten undulates, Butomopsis latifolia, Monochoria hastat, M. vaginalis*
		Free floating vegetation (FFV)	*E. cressipes, Trapa natans, Salvinia natans, Nymphoides hydrophylla, N. indica, Nymphea nouchali, N. puleiscens, N. rubra*
Shallow water with floating vegetation (SWFV)	up to 30 cm	EV and EAV	*Scirpus juncoids, S. maritimus, Cyperus stoloniferus, O. rufipogen M. quadrifolia, I. aquatic, I. hederifolia*
		UASV	*U. aurea, U. bifida, U. hirta*
		FFV	*E. cresssipes, T. natans, Lemna perpusilla, A. pheloxoroides, Pistia stratiotes, S. natans*
		Marshland vegetation (MV)	*M. quadrifolia, Luawigia adscendens, L. pubescens, Persicaria barleata*
Shallow water clear surface (SWCS)	up to 30 cm	UASV	*U. aurea, U. bifida, U. hirta*
		RSV	*L. heterophylla, L. repens, L. sessiliflora, H. verticillata, V. natans*
Grassy meadows (GM)	Up to 15 cm (where inundated)	EAV	*C. stoloniferus, O. rufipogen O. meyeriana*
		MV	*L. adscendens, L. perennis, L. octovolvis, Bracopa monnieri, Phyla nudiflora, Lasia spinosea, Amischotolype hookeri, Commelina benghalensis, Bulbostylis densa, Murdannia nudiflora, M. spirata, Arundinella benghalensis, A. intricate, Axonopus compressus, Cynodon dactylon, Digitaria ciliaris, D. sanguinalis, Eragrostis tenella, Imperata cylindrica, Panicum rupens, Paspalam conjugatum, Saccharum sponteneum, Setaria glauca, Setaria palmifolia, C. pilosus, C. rotundus, Fimbristylis miliacea, Kyllinga nemoralis*
Muddy shoreline (MS)	None	EAV and MV	*C. stoloniferus, C. pilosus, C. rotundus, L. adscendens, L. perennis, P. rupens, C. dactylon*

2.6. Niche breadth and niche overlap calculation

Both one- and two-dimensional matrices were used for the calculation of foraging niche breadth using the formula $B = 1/\Sigma p_j^2$, where, p_j = number of individuals found in or using resource state "j" (Levins, 1968). However, Standardized Niche Breadth (B_A) was later calculated (Hurlbert, 1978) using $B_A = (B - 1)/(n - 1)$; Where, B_A = Levins's standardized niche breadth; B = Levins's measure of niche breadth; n = number of possible resource states. It is often useful to standardize niche breadth to express it on a scale from 0.0 to 1.0. Foraging niche overlap between every pair of species of waterbirds & within each niche dimension was calculated using Pianka's formula (1986), $O_{jk} = (\Sigma p_{ij}\, p_{ik})\, (\Sigma p_{ij}^2\, p_{ik}^2)^{-1/2}$, where pij and pik are proportional values of utilization of resource i by species j and k, respectively. Like Standardized niche Breadth (B_A), this index was also symmetrical with values between 0 and 1. It assumed that the value of 1 denoted complete overlap between the species pair under consideration and reaching 0 when the two species were completely isolated, with no niche overlap.

2.7. Assigning a guild in the community

The cluster analysis was used for assigning a guild to the members of the waterbird community. For this purpose, original matrices (for Foraging habitat, technique and combined) were taken into account and were subjected to arcsine transformation, as suggested by Fowler and Cohen (1990), where y = arcsine $X^{0.5}$ which was used to depict proportion and to reduce Kurtosis of the distribution of a variable (Pérez-Crespo et al., 2013).

2.8. Statistical analyses

The grouping was done statistically (using STATISTICA 6.0, StatSoft Inc., 2002) based on similarities (Euclidean distances). Hierarchical cluster analysis based on avifaunal abundance were presented in the form of dendrograms to identify the avian guilds depending on the foraging techniques and foraging habitats. The single linkage method (in which the groups were organized according to the distance between their nearest members) was applied in the present study that fused the groups according to the single distance between the pairs of members in the respective set. We compared the differences in the niche overlap between five guilds analyzing post hoc with Tukey's honestly significant difference (Tukey HSD) test (level of significance at $p < 0.05$) to highlight the significant differences between the guilds observed (Winer, 1971). The Tukey's HSD tests all pairwise differences while controlling the probability of making one or more Type-I errors.

3. Results

A total of 27 species belonging to 9 families were considered for the present study. Thirteen species were winter visitor (WV) and rest were resident (R). Family Anatidae was represented by 12 species followed by family Ardeidae with 5 species, Charadriidae with 3 species, Phalacrocoracidae with 2 species and a single species each of the five families viz., Podicipedidae, Ciconiidae, Rallidae, Jacanidae, and Scolopacidae. The individual density of these waterbird species was represented in Table 2. A total of 4520 foraging observations on 27

Table 2
Mean population density, size, and percentage among total populations, foraging observations and migratory status of 27 waterbird species.

Family Name	Common Name	Scientific Name	Migratory Status	Density (ind. ha^{-1}) Mean ± SD	Population Size (ind.) Mean ± SD	Percentage among total population (%)	Foraging observations
Anatidae	Lesser Whistling-duck	*Dendrocygna javanica*	R	15.25 ± 13.27	259 ± 124	31.11	42
	Cotton Pygmy-goose	*Nettapus coromandelianus*	R	0.56 ± 0.50	12 ± 11	1.15	604
	Gadwall	*Anas strepera*	WV	2.06 ± 2.59	36 ± 26	4.21	448
	Mallard	*Anas platyrhynchos*	WV	0.15 ± 0.16	3 ± 3	0.31	95
	Indian Spot-billed Duck	*Anas poecilorhyncha*	R	1.07 ± 2.37	8 ± 15	2.19	561
	Northern Shoveler	*Anas clypeata*	WV	0.05 ± 0.07	1 ± 1	0.11	53
	Northern Pintail	*Anas acuta*	WV	0.29 ± 0.54	3 ± 4	0.59	294
	Garganey	*Anas querquedula*	WV	0.03 ± 0.04	8 ± 13	0.06	65
	Common Teal	*Anas crecca*	WV	3.02 ± 2.50	76 ± 89	6.15	268
	Red-crested Pochard	*Netta rufina*	WV	0.14 ± 0.26	2 ± 2	0.28	90
	Common Pochard	*Aythya ferina*	WV	0.18 ± 0.29	3 ± 2	0.36	156
	Ferruginous Duck	*Aythya nyroca*	WV	1.99 ± 2.68	35 ± 26	4.06	334
Podicipedidae	Little Grebe	*Tachybaptus ruficollis*	R	0.81 ± 0.93	10 ± 4	1.65	74
Ciconiidae	Lesser Adjutant	*Leptoptilos javanicus*	R	0.16 ± 0.16	2 ± 1	0.33	67
Ardeidae	Indian Pond Heron	*Ardeola grayii*	R	1.93 ± 2.18	23 ± 5	3.95	51
	Grey Heron	*Ardea cinerea*	R	0.01 ± 0.01	1 ± 1	0.02	32
	Purple Heron	*Ardea purpurea*	R	0.01 ± 0.01	1 ± 1	0.03	34
	Intermediate Egret	*Ardea intermedia*	R	0.24 ± 0.07	7 ± 5	0.48	52
	Little Egret	*Egretta garzetta*	R	0.77 ± 0.81	10 ± 3	1.57	79
Phalacrocoracidae	Little Cormorant	*Microcarbo niger*	R	1.37 ± 0.95	27 ± 10	2.80	433
	Great Cormorant	*Phalacrocorax carbo*	WV	0.07 ± 0.09	3 ± 4	0.15	103
Rallidae	Common Moorhen	*Gallinula chloropus*	R	6.53 ± 12.49	48 ± 78	13.31	121
Charadriidae	Northern Lapwing	*Vanellus vanellus*	WV	0.69 ± 0.34	32 ± 42	1.41	135
	Grey-headed Lapwing	*Vanellus cinereus*	WV	2.32 ± 1.20	104 ± 142	4.74	125
	Little Ringed Plover	*Charadrius dubius*	R	0.27 ± 0.24	5 ± 2	0.54	81
Jacanidae	Bronze-winged Jacana	*Metopidius indicus*	R	0.97 ± 0.77	18 ± 8	1.99	70
Scolopacidae	Common Sandpiper	*Actitis hypoleucos*	WV	0.34 ± 0.34	6 ± 4	0.69	53

Table 3
Extent of waterfowl foraging habitat (% of wetland area). Abbreviations are as follows: Deep water with submersed vegetation (DWSV), Deep water with emergent vegetation (DWEV), Medium depth with submersed vegetation (MDSV), Medium depth with emergent vegetation (MDEV), Medium depth with floating vegetation (MDFV), Shallow water with floating vegetation (SWFV), Shallow water clear surface (SWCS), Grassy meadows (GM) and Muddy shoreline (MS).

Waterbirds foraging habitats	Nararthali	Rasomati	Rasik Beel Wetland Complex			Mean ± SD
			Atiamochar-Naldubi	Bochamari	Raichenmari-Sakobhanga	
DWSV	7	4	8	11	14	8.80 ± 3.83
DWEV	8	2	2	4	6	4.40 ± 2.61
MDSV	10	7	10	13	14	10.80 ± 2.77
MDEV	12	16	13	6	11	11.60 ± 3.65
MDFV	15	13	11	17	17	14.60 ± 2.61
SWFV	16	19	7	29	11	16.40 ± 8.41
SWCS	8	7	26	6	8	11.00 ± 8.43
GM	9	4	1	4	5	4.60 ± 2.88
MS	15	28	22	10	14	17.80 ± 7.16

waterbird species were made (Table 2). Although we considered 9 different foraging habitats and 9 different foraging techniques resulting in 81 combinations with these two dimensions, waterbirds used only 56 foraging combinations.

Foraging habitat was presented in Table 3. Mean depth of deep water, medium water and shallow water were 122 ± 46 cm, 41 ± 17 cm and 15 ± 9 cm respectively. The percent distributions of these three categories of depth-class in the wetlands under study were 13.20 ± 5.36%, 37.00 ± 3.00% and 27.40 ± 6.58% of total habitats respectively. Exposed muddy shore also constituted a significant portion of the wetland foraging habitat. Floating, submersed and emergent vegetation were seen in deep and shallow water depths. Grassy meadow habitat was much less common in the wetlands under study.

Cluster analysis based on two niche dimensions, namely feeding habitats and feeding techniques (i.e., bi-dimensional niche space) (i.e., incorporating feeding habitats and also feeding techniques) suggested that a mean Euclidean distance of 56.94 reliably defined five species clusters (Fig. 2), which were represented as five separate guilds: medium and shallow water generalists (Guild1), stalking waders (Guild 2), pecking waders (Guild 3), mud picking waders (Guild 4), and divers (Guild 5). Guild 1 was represented by 11 waterbirds including 9 duck species along with the Common Moorhen and Bronze-winged Jacana. These utilized 35 foraging combinations among 56 observed foraging combinations (Appendix 4). Guild 2 was represented by 5 Ardeidae species (herons and egrets) and one stork. They most frequently used striking behavior (on average 89.33% of all) as feeding technique mainly from shallow water (46.5%), medium depth water (25.5%), and mud (11.0%). Indian Pond Heron and Little Egret solely used striking as feeding technique (Appendix 5). Both Guild 3 and 4 were represented by 2 species. Grey-headed and Northern Lapwings formed the Guild 3 while Little Ringed Plover and Common Sandpiper from the Guild 4. Lapwings preferably used pecking technique during feeding (81.5%), especially from grassy meadow (30.5%) and mud (27.0%) (Appendix 6). Plover and Sandpiper together on an average used picking from mud technique prevalently (78.5%) while muddy shore was the most favorable feeding habitat (52.5%) (Appendix 7). Three diving duck species, one grebe and 2 cormorant species formed the Guild 5. They mostly used a diving technique to obtain food (80.2%) from a deeper part (> 60 cm) of the wetland (85.8%). Little Cormorant exclusively used diving for utilization of food resources (Appendix 8).

Foraging niche breadth calculated based on foraging habitats (Table 4) showed that Grey Heron had the highest niche breadth

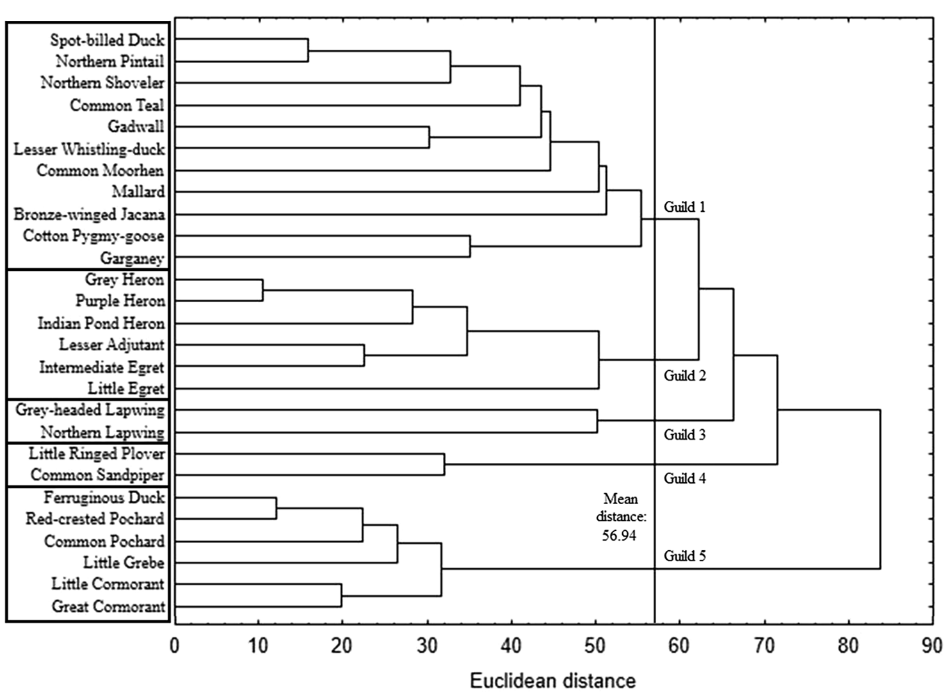

Fig. 2. Classification of the bi-dimensional foraging niches (foraging habitat and foraging technique) of waterbirds at selected sites. Guild 1: medium and shallow water generalists; Guild 2: stalking waders; Guild 3: pecking waders; Guild 4: mud picking waders, Guild 5: divers.

Table 4
Foraging niche breadth (FNB), by species and guild, of 27 waterbird species.

	FNB (B)			Levins's standardized FNB (B_A)		
	Foraging habitat (n = 9)	Foraging technique (n = 9)	Both dimension (n = 56)	Foraging habitat (n = 9)	Foraging technique (n = 9)	Both dimension (n = 56)
Guild 1: Medium and shallow water generalists						
Indian Spot-billed Duck	4.16	3.40	10.22	0.63	0.40	0.51
Northern Pintail	3.85	3.05	8.64	0.57	0.68	0.64
Northern Shoveler	3.09	4.14	6.54	0.70	0.79	0.79
Common Teal	3.53	4.63	8.05	0.51	0.91	0.54
Gadwall	3.69	3.44	8.17	0.54	0.49	0.38
Lesser Whistling-duck	3.17	3.64	5.13	0.54	0.66	0.52
Common Moorhen	1.90	2.65	4.93	0.45	0.82	0.79
Mallard	3.05	2.37	5.36	0.68	0.46	0.48
Bronze-winged Jacana	2.52	3.20	6.20	0.76	0.55	0.58
Cotton Pygmy-goose	1.87	3.05	4.15	0.43	0.68	0.31
Garganey	1.98	2.46	2.61	0.49	0.49	0.32
Mean (Guild 1)	2.98 ± 0.81	3.28 ± 0.69	6.36 ± 2.23	0.57 ± 0.11	0.63 ± 0.17	0.53 ± 0.16
Guild 2: Stalking waders						
Grey Heron	5.82	1.44	6.65	0.69	0.44	0.71
Purple Heron	5.79	1.35	7.47	0.68	0.35	0.81
Indian Pond Heron	4.51	1.00	4.56	0.70	–	0.71
Lesser Adjutant	4.09	1.45	5.74	0.62	0.22	0.59
Intermediate Egret	4.06	1.26	5.04	0.77	0.26	0.81
Little Egret	2.26	1.00	2.28	0.63	–	0.64
Mean (Guild 2)	4.42 ± 1.32	1.25 ± 0.21	5.29 ± 1.81	0.68 ± 0.05	0.32 ± 0.10	0.71 ± 0.09
Guild 3: Pecking waders						
Grey-headed Lapwing	2.03	1.46	3.29	0.34	0.23	0.38
Northern Lapwing	3.38	1.47	4.26	0.60	0.23	0.47
Mean (Guild 3)	2.71 ± 0.95	1.47 ± 0.01	3.78 ± 0.69	0.47 ± 0.18	0.23 ± 0.00	0.43 ± 0.06
Guild 4: Mud picking waders						
Little Ringed Plover	2.13	1.62	3.06	0.56	0.62	0.69
Common Sandpiper	2.24	1.30	2.35	0.41	0.30	0.27
Mean (Guild 4)	2.19 ± 0.08	1.46 ± 0.23	2.71 ± 0.50	0.49 ± 0.11	0.46 ± 0.23	0.48 ± 0.30
Guild 5: Divers						
Ferruginous Duck	2.00	1.71	2.76	0.25	0.24	0.16
Red-crested Pochard	2.24	1.53	2.77	0.41	0.18	0.16
Common Pochard	1.70	1.74	1.95	0.35	0.25	0.14
Little Grebe	2.01	1.90	3.02	0.51	0.45	0.40
Little Cormorant	1.34	1.00	1.34	0.34	–	0.34
Great Cormorant	1.37	1.38	1.48	0.12	0.38	0.10
Mean (Guild 5)	1.78 ± 0.37	1.54 ± 0.32	2.22 ± 0.73	0.33 ± 0.13	0.30 ± 0.11	0.22 ± 0.12

followed by Purple Heron. However, the lowest value of the same was recorded for Little Cormorant followed by Great Cormorant. The highest value of niche breadth based on feeding techniques was observed for Common Teal followed by Northern Shoveler. Comparable values were recorded for Lesser Whistling-duck, Gadwall and Indian Spot-billed Duck. Narrowest niche breadth based on foraging techniques was observed for Indian Pond Heron, Little Egret and Little Cormorant. Considering both feeding dimensions Indian Spot-billed Duck showed widest niche breadth whereas narrowest niche breadth showed by Little Cormorant. Based on mean values obtained from two-dimensional matrices we found that Guild 1 was characterized by a wide niche breadth and Guild 5 by narrow niche breadth. Mean niche breadth based on foraging habitat revealed the broadest breadth for Guild 2 while narrowest breadth for Guild 5. The mean value of niche breadth calculated solely on feeding techniques showed the highest niche breadth for Guild 1. However, much lower and comparable values were recorded for Guild 5, Guild 3, Guild 4 and Guild 2.

The post-hoc analysis with Tukey HSD test highlighted the significant differences between the intra-guild niche breadth based on foraging habitats and foraging techniques. Interestingly, bi-dimensional intra-guild niche breadths were significantly different for all the waterbird species occupying all the five guilds when foraging techniques were taken into account for niche breadth calculations (Appendix 9).

Mean niche overlap based on bi-dimensional foraging strategy was highest within the members of Guild 5 followed by Guild 4, Guild 2 and Guild 3. Representative avian species of Guild 1 showed least values for mean niche overlap. In Guild 1 highest pairwise niche overlap was observed between Indian Spot-billed Duck and Northern Pintail while no overlap was observed between Mallard–Garganey and Mallard–Lesser Whistling Duck (Appendix 10). Grey and Purple Heron, members of Guild 2 showed the highest value of intra-guild niche overlap. However, Little Egret showed the lowest value of niche overlap with Grey and Purple Heron within the guild. Each of Guild 3 and 4 was represented by only two species and the values of pairwise niche overlap between two species of these two guilds were 0.54 and 0.87 respectively. Comparatively higher values of niche overlaps were seen between the members of the Guild 5 (Appendix 10). Pairwise intra-guild niche overlap between of members of Guild 5 varied from 0.88 (between Common Pochard and Little Grebe) to 0.98 (between Ferruginous Duck and Red-crested Pochard). As per post-hoc analysis (Tukey HSD, at $p < 0.05$) Guild 1 was significantly differed from Guild 4 and Guild 5, whereas Guild 2 significantly differed with Guild 5 (Table 5).

4. Discussion

In the present study, the niche structure was analyzed to focus on (1) the density and variety of waterbirds in the wetlands of sub-Himalayan foothills and (2) the partitioning of foraging resources in such a community of waterbirds. In the past two decades, a good number of researchers have identified that generalist species are

Table 5
Analysis of Post-hoc with Tukey HSD test (*marked values are significant at $p < 0.05$) to highlight the significant differences in niche overlap between the guilds observed.

	Guild 1 (Medium and shallow water generalists)	Guild 2 (Stalking waders)	Guild 3 (Pecking waders)	Guild 4 (Mud picking waders)
Guild 2 (Stalking waders)	0.86931			
Guild 3 (Pecking waders)	0.07055	0.42015		
Guild 4 (Mud picking waders)	0.00672*	0.07629	0.88369	
Guild 5 (Divers)	0.00178*	0.02441*	0.62738	0.98914

replacing specialists causing functional homogenization at the community level that often deteriorated ecosystem functioning and biodiversity (Clavel et al., 2011). Therefore, studies on niche organizations and guild structure would amply serve as ecological indicators of ecosystem goods and services, and to detect and assess changing environmental conditions (Canterbury et al., 2000).

Foraging habitat exploitation and foraging techniques employed by the water birds were the prime factors influencing the partitioning of resources (Pöysã, 1983; Jaksić and Medel, 1990; Green, 1998; Gatto and Quintana, 2008; Liordos, 2010; Pérez-Crespo et al., 2013). Trophic guild structure and niche organization in wintering waterbirds at three different wetlands were studied to understand and portray the structures of waterbird communities. Cluster analyses based on both foraging habitats and foraging techniques yielded five bi-dimensional foraging guilds (Guilds 1–5). Members of the guild that employed varieties of feeding techniques were considered as generalist while other guilds that employed special foraging techniques were the specialists (Elafri et al, 2017). In our study members of the Guild 1 would be considered as a generalist as the members employed varieties of feeding techniques while Guilds 2–5 employed special foraging techniques like striking, pecking, picking and diving respectively. This observation pointed out that the diverse foraging habitats at the wetlands under study attracted diverse species of wintering waterbirds equipped with different feeding techniques. It was noted that the guilds accommodating specialists were represented by a much lower number of species (2–6) than the generalist guild (Guild 1 with 11 species). Members of specialist guilds avoided inter-guild competition by adopting more specific foraging techniques than the members of other guilds. Species like Little Cormorant and Little Egret were observed to use a simple foraging technique. Preference for the same feeding technique within the guild members of specialist guilds caused higher niche overlap. However, intra-guild competition could be minimized by utilizing different foraging depths according to the morphometric compatibility of the waterbird. Indian Spot-billed Duck, for an example of generalists, used a maximum of 7 foraging techniques; therefore, showed the highest value of two-dimensional niche breadth. The competitive interactions within intra-guild members were possibly minimized by the employment of varied feeding techniques. Members of Guild 1, i.e., medium and shallow water generalists, facilitated niche packing to accommodate more species by acquiring food resources using different foraging maneuvers. Stalking waders of varying body sizes (Indian Pond Heron to Lesser Adjutant) formed a guild (Guild 2) and exploited varied foraging resources of different depths and habitats.

Groups of species having similar ecological roles could be members of the same guild but could not be the occupants of the same niche (Root, 1967). Use of different foraging techniques at different habitats brought about comparatively wider mean bi-dimensional niche breadth for generalists than other specialist guilds. The present study pointed out that the specialist guild members showed comparatively higher values of intra-guild niche overlap (0.54–0.95) whereas the generalist guild members showed a much lower value of mean niche overlap (0.33). In trophic terms, when the competitors were absent, a given species would most probably specialize less than it would in the presence of competitors (Jørgensen et al., 2007). Jorgensen (1997) commented that when more combinations and processes were available for energy flow, the organization that was able to give the highest energy under the prevailing circumstances would be selected. Ducks preferred wetlands with rich submerged vegetation for foraging. Such higher diversity and richness of food resources like aquatic insects, mollusca, fish and amphibians that occurred in wetlands with varied water depth-classes and with intrinsic submerged vegetation accounted for subsisting greater diversity of waterbirds like dabbling ducks, diving ducks and other divers besides waders (Meerhoff et al., 2003). Clavel et al. (2011) proposed community-level specialization as an indicator of the impact of habitat and climate disturbances on biodiversity. Simberloff and Dayan (1991) reviewed the comparative analyses of communities that used functional classifications based on “feeding groups.” It was pointed out that classifying a local avifauna based on the location of the feeding site, type of food taken, and foraging method would be more indicative of local foraging resources. Our study can be a good example of how to use the presence of species from different foraging guilds as an indicator of foraging resources. The use of indicators had frequently been incorporated into policies and regulations to monitor the ecological integrity of different ecosystems including wetlands (Carignan and Marc-André, 2002). A review work by Ahmed, 2016 recorded that indicator species were to monitor ecosystem or environmental health and integrity; assess habitat restoration and assess the effects of pollution and contamination. The present study on waterbird niche organizations and guild structure at wetlands of Himalayan foothills would serve to identify and evaluate the quality of habitats in changing environmental conditions.

The most important findings were the higher number of species clustered as generalist feeders (using several foraging techniques) in comparison with specialist feeders (fewer foraging techniques), and the differences in niche overlap. Niche overlaps answered to the question of how waterbird species spatially partitioned the resources in the community. Mean niche overlap was higher within the members of the guilds than between other species. Several authors suggested that competitive interactions are more likely to occur among species of the guilds than those between other species (Pérez-Crespo et al., 2013; Elafri et al., 2017). Birand et al. (2012) commented that the species with narrower niche widths tend to be more affected by habitat fluctuation. Present work showed that as the dimension increased (comparing breadth for single trophic axis, namely foraging habitat or foraging technique with bi-dimensional, i.e., for those two axes together), niche width increased which might help specialists in waterbird community to withstand habitat perturbations within a limited range.

The congenial physico-chemical conditions of the wetlands with suitable nutrient regime harboured varieties of vegetation and associated biota (Chatterjee et al., 2017; Pal et al., 2017; Chatterjee, 2018) that provided ample prey-base for the foraging waterbirds. Fox (1981) stated that additional species are accommodated by significantly increasing mean spatial niche separation, thus decreasing mean spatial overlap (diffusing competition). Interestingly, in the present study much higher diversity of waterbirds was observed from shallow and medium water than deepwater habitats which could be the outcome of higher net available trophic energy. Liordos (2010) studied foraging guilds of wintering waterbirds in a small relatively shallow coastal wetland and reported shallow-water generalists were the most numerous. In addition to limiting access to foraging habitats, water depth also affected the net energy intake of waterbirds because foraging efficiency decreased with increasing water depth. Published works (Kushlan, 2007; Ma et al., 2010) commented that lesser net energy gain due to deep diving in contrast to higher net energy intake in shallower water depths than deep waters could encourage a higher number of species to forage in medium and shallow depths. Our observation corroborated the published works. Hattori and Mae (2001) reported that habitats with higher water depth sustained much higher density of ducks and many other diving birds. The present study pointed out that direct competition among wintering waterbirds was avoided by resource partitioning on a trophic scale which helped in structuring the community in specific trophic guilds. As was suggested by Bethke (1991), more than one niche parameter (two in our case, namely foraging habitat and foraging techniques) along relevant resource dimensions were analyzed to segregate waterfowls, minimizing niche overlap

5. Conclusion

Findings showed that wintering waterbird species at the wetlands of sub-Himalayan forested areas exploited the foraging resources in different ways. Two main ways of exploiting different trophic aspects like foraging habitat and foraging techniques were observed to establish trophic guilds in these wintering waterbirds. Some species could be identified as generalists as they employed different foraging techniques in obtaining trophic resources while other species were specialists and took resort to any specialized foraging technique. Frequently used specific foraging technique of specialists helped them to establish separate guilds allowing minimum overlap with other guilds. Generalists, on the other hand, avoided severe intra-guild competition and helped in efficient resource-partitioning and niche packing. However, food choice and acquiring techniques were more or less consistent among the wintering waterbirds, otherwise, it would be a more difficult exercise in defining a guild based on shared resources in cases of seasonal omnivory or either opportunistically or regularly changing diet. No single waterbird species, but a group of species, such as in Guild 1 – 5 for example in the present study, was indicative of foraging resources of the wetland. Diverse feeding resources may allow for more species with varied foraging techniques to exploit the resources. Clavel et al. (2011) reviewed researches on the concept of the ecological niche and species specialization and observed that niche organization was an important ecological indicator of a worldwide decline in specialist species. The present study suggested that foraging techniques would be more important for the establishment of a trophic guild than foraging habitats. Furthermore, the diversity of foraging habitats encouraged aggregation of waterbirds with varied foraging behavior or techniques, which were strongly morphology-mediated and helped to structure the wintering waterbird community at the study sites.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2019.105693.

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