Niche separation in flycatcher-like species in the lowland rainforests of Malaysia

Mohammad Saiful Mansor[a,b,*], Rosli Ramli[a,*]

[a] Institute of Biological Sciences, Faculty of Science, University of Malaya, Kuala Lumpur, Malaysia
[b] School of Environmental and Natural Resource Sciences, Faculty of Science and Technology, Universiti Kebangsaan Malaysia, Bangi, Selangor, Malaysia

ABSTRACT

Niche theory suggests that sympatric species reduce interspecific competition through segregation of shared resources by adopting different attack manoeuvres. However, the fact that flycatcher-like bird species exclusively use the sally manoeuvre may thus challenge this view. We studied the foraging ecology of three flycatcher-like species (i.e. Paradise-flycatcher *Terpsiphone* sp., Black-naped Monarch *Hypothymis azurea*, and Rufous-winged Philentoma *Philentoma pyrhoptera*) in the Krau Wildlife Reserve in central Peninsular Malaysia. We investigated foraging preferences of each bird species and the potential niche partitioning via spatial or behavioural segregation. Foraging substrate was important parameter that effectively divided paradise-flycatcher from Black-naped Monarch and Rufous-winged Philentoma, where monarch and philentoma foraged mainly on live green leaves, while paradise-flycatcher foraged on the air. They also exhibited different foraging height preferences. Paradise-flycatcher, for instance, preferred the highest studied strata, while Black-naped Monarch foraged mostly in lower strata, and Rufous-winged Philentoma made use of the lowest strata. This study indicates that niche segregation occurs among sympatric species through foraging substrate and attack manoeuvres selection.

1. Introduction

Differences in microhabitat and resource utilization among closely-related bird species that inhabit the same geographical area have been widely reported in ornithological studies (e.g. Lara et al., 2011; Cloyed, 2014; Mansor et al., 2015; Styring et al., 2016). Coexistence of related species of similar sizes may result in specialization via fine-scale niche separation (May, 1974). Understanding how sympatric species employ unique foraging tactics from one another can assist in understanding how they co-exist in the same habitat (Robertson et al., 2013), particularly in tropical region that comprises of many species (Wells, 1976). Forest birds have adopted different ecological strategies in partitioning available resources, potentially shedding light on how birds' guilds respond to disturbances (Styring and Hussin, 2004). Habitat structure has previously been highlighted as important for forest birds as it provides many foraging opportunities (Whelan, 2001), which have subsequently shaped birds' foraging patterns (Robinson and Holmes, 1982).

Niche theory suggests that coexisting species in the same habitat will reduce interspecific competition through partitioning of shared resources (Lack, 1971; Chesson, 2000), and consequently important in structuring animal communities (Elton, 1927). Long-term competitive adaptation over evolutionary time may define the foraging strategies of a species with regards to resource exploitation. Sympatric species that adopt specific foraging tactics may result in targeting different prey items (Pulliam, 1985; Chapman and Rosenberg, 1991), consequently resulting in specialization. Specialization is associated with high foraging success based on the consistent use of selected foraging tactics over a period of time (Svanbäck and Eklöv, 2003) and morphological adaptation (Moermond, 1990). Any small differences in birds' morphological traits (e.g. wing shape and tarsus length) could mean the adoption of particular attack manoeuvres (Moermond, 1990). Birds' morphology is considered the main feature for limiting the type of attack manoeuvre they can employ that associated in substrate selection which generally leads to niche separation (Rolando and Robotti, 1985; Martin and Karr, 1990).

This study examines the foraging ecology of three flycatcher-like species (i.e., Paradise-flycatcher (*Terpsiphone* sp.), Black-naped Monarch (*Hypothymis azurea*), and Rufous-winged Philentoma (*Philentoma pyrhoptera*) that coexist in central Peninsular Malaysia by analyzing their foraging heights, foraging substrates, attack manoeuvres and foliage density use. The paradise-flycatcher, monarch,

* Corresponding authors.
  E-mail addresses: msaifulmansor@gmail.com (M.S. Mansor), rosliramli@um.edu.my (R. Ramli).

and philentoma are, however, considered sallying bird species (Wells, 2007), thus challenge the above view. These three flycatcher-like species use the sally manoeuvre for flycatching food items from one perch to another. Previously, these three species were grouped together within the family Monarchidae, generally consisting of large and robust flycatcher-like birds with bright plumage (Lekagul and Round, 1991; Fuchs et al., 2006). However, Rufous-winged Philentoma was reclassified due to their complexity and being closest relatives of the Malagasy Vangidae that consist of species from Africa and Asia (Moyle et al., 2006; Fuchs et al., 2012; Reddy et al., 2012). The former two species remain placed within the Old World Monarchidae that comprises three well-supported monophyletic clades including *Terpsiphone*, *Hypothymis* and *Trochocercus* (Pasquet et al., 2002; Fabre et al., 2012). Despite their phylogenetic dispersion, the three flycatcher-like species are having fairly similar morphology, voice and social behaviour (Wells, 2007). They show fairly similar morphology with respect to their body size, and have relatively long and slender bills with strong rictal bristles (Robson 2008; Jeyarajasingam and Pearson, 2012) that may help in aerial flycatching (Cunningham et al., 2011). Sympatric species with similar morphology are most likely employs different foraging strategies to stably coexist (Styring et al., 2016). Similarity in the usage of attack manoeuvres and frequently seen foraging together have given rise to the question of how these three flycatcher-like species partition their resources during the presence of other species in the same habitat.

Resident population of Asian Paradise-flycatcher (*Terpsiphone paradisi affinis*) is seasonally augmented by northern wintering subspecies (i.e. *T. paradisi incei*) and uncommon wintering migrant from continental Asia (i.e., Japanese Paradise-flycatcher *Terpsiphone atrocaudata*) (Wells, 2007). To avoid complication in distinguishing of these alike migratory subspecies and sister species (especially the females), we considered these birds as Paradise-flycatcher (*Terpsiphone* sp.). Previous studies have shown that the Asian Paradise-flycatcher (*Terpsiphone paradisi*) usually forages at higher levels and primarily flycatches their prey items in air, while Black-naped Monarch frequently sally on the underside of leaves (Mansor and Sah, 2012). We hypothesized that the use of attack manoeuvres and substrates by Asian Paradise-flycatcher and Black-naped Monarch are restricted by their similar morphological traits across different geographical area. In this context, differences in the use of foraging substrates to obtain food items definitely facilitate niche separation between the monarch and paradise-flycatcher. This niche partitioning allows them to stably coexist in the same geographical area (Hon-kai, 2009). However, more information is needed to gain further insight into their niche partitioning strategies, especially when the presence of other potential competitor species (such as Rufous-winged Philentoma) that occupy similar environments. Morphological similarities and sympatry of the studied species have also led us to hypothesize that these three flycatcher-like species should have different microhabitat preferences to coexist. Therefore, our study addresses the following questions: (1) how do these species forage in the wild and use vegetation to obtain their food items? and (2) how do these trophically similar species partition their resources by spatial dimensions?

2. Methods

2.1. Study area

Observations were made at Bukit Rengit area (3°35′40.02″N, 102°10′43.24″E), southern part of the Krau Wildlife Reserve, a protected area located in Pahang, central Peninsular Malaysia (Fig. 1). The reserve is the second largest protected area in Peninsular Malaysia (with an approximate size of 63,000 ha) after Taman Negara. Study sites comprised of a large area of old-growth forest (Clark, 1996) and can be considered lowland dipterocarp forest that is associated with dominant tree species including *Anisophyllea corneri*, *Mallotus penangensis*, *Gymnacranthera forbesii*, *Shorea macroptera*, *S. maxwelliana*, *S.*

lepidota, and *Elateriospermum tapos* (Nizam et al., 2006). The reserve elevation ranges from 50 m at Kuala Lompat and about 80 m at Bukit Rengit to over 2000 m at the summit of Gunung Benum (Raemaekers et al., 1980). The reserve is drained by three main river systems – Sungai Krau, Sungai Lompat and Sungai Teris. The annual mean temperature is 26 °C, and average rainfall is roughly 2000 mm, with maximum rainfall between September and December and March and May, separated by two periods of minimum rainfall (Yusof and Sorenson, 2000).

2.2. Observations on foraging strategies

Focal species were located visually and randomly along several forest trails and followed opportunistically. Observations were made for 10 days/month for a period of 20 months, from February 2014 to September 2015. Birds were observed throughout the day (from 0730 h to 1830 h) but, for the most part, the observations were conducted in the early morning and late afternoon when most forest birds are actively seeking food. Birds were observed as long as they could be kept in view, but only the initial (independent) foraging observations, first sighting of an individual bird, were used for statistical analysis to avoid problems with non-independent data. At least 30 independent observations were recorded for each bird species in order to represent the observed behaviour accurately (Morrison, 1984; MacNally, 1994). Incidental observations of focal species joining mixed-species flocks were also recorded.

The following data were noted on each foraging bird encountered, namely foraging height, foraging substrate, attack manoeuvre, and foliage density.

Foraging height - the level from which a food item is taken by birds. The height of selected trees was marked for references. This was estimated to 2 m intervals and grouped into five height categories (FH1: > 0–2 m; FH2: > 2–4 m; FH3: > 4–6 m; FH4: > 6–8 m; FH5: > 8–10 m).

Foraging substrate – the material (microhabitat) from which a food item is taken by birds. These substrates were the leaf surface, the underside of the leaf, the branches, aerial leaf litter, and air. The term 'leaf surface' is used to denote the morphological upper side of a leaf, while 'underside of the leaf' indicates the morphological underside. Attack manoeuvre – the method for how food items were taken (attacked) by birds. This manoeuvre was categorized as follows: (i) stretch – birds completely extend the legs or neck to reach food items; (ii) hover – birds maintain an airborne position by flapping wings and spreading tail; and (iii) sally – birds fly from a perch to attack a food item and then return to a perch. The terminology and strategy used to characterize attack manoeuvres follows Remsen and Robinson (1990).

Foliage density – this parameter was measured on a subjective scale from 1 to 5 in a 1-m diameter sphere around the bird. A series of numbers from 1 to 5 denoting the proportion of area covered by vegetation (e.g. leaves, bushes), ranging from 1 (covering less than 5% of the area) to 5 (covering more than 75% of the area) following an adapted approach from Braun-Blanquet (1932) covered the abundance scale as described by Allen and McLennan (1983), Allen (1993), Bowes et al. (1994), and Hurst and Allen (2007).

2.3. Statistical analyses

Correspondence analysis (CA) was performed on raw data to extract foraging patterns of focal bird species in each niche dimension. CA is effective in analysing the categorical data and detecting similarities between the rows and columns of a data matrix (Miles, 1990). A hierarchical cluster analysis using correlation coefficients was applied to group the species into distinctive guilds based on the frequency of all foraging parameters. Both analyses were performed using the PAST software package (PAleontological STatistics) ver. 2.17 (Hammer et al., 2001).
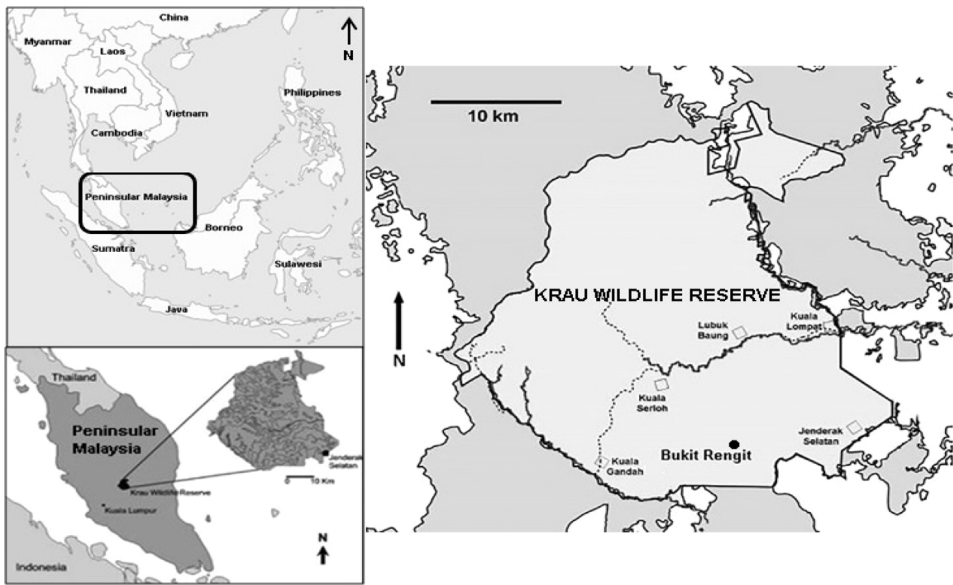
Fig. 1. Map of Krau Wildlife Reserve, Pahang, Peninsular Malaysia. The reserve is represented by light grey, forest areas surrounding the reserve by dark grey, and non-forest areas by white. Map adapted from Zakaria et al. (2014).

The 'bipartite' 2.05 (Dormann et al., 2008) package was used to calculate the following indices: (i) connectance (C), a commonly used index of coexistence analysis (Gotelli and Graves, 1996), to estimate the foraging dimensions of possible links (Dunne et al., 2002); (ii) links per species (L_x), the mean number of variables or foraging dimensions use by a species (Dorman et al., 2008); (iii) the network-level measure of specialization on particular dimension (H2′), ranging between 0 (no specialization) to 1 (complete specialization) (Dormann et al., 2008); (iv) standardized specialization index at species level (d′), a measure in the lower trophic level of a network (Blüthgen et al., 2006); and (v) niche overlap, the mean similarity in interaction patterns among species reflecting niche preferences, following Horn's index (R_o) (Horn, 1966), ranging from 0 (no common use of dimensions) to 1 (complete niche overlap). All tests were computed using R v.3.2.3 (R Core Team, 2015). This network analysis was of value for visualizing and describing the patterns within the ecological webs (Blüthgen et al., 2007).

3. Results

A total of 131 independent observation bouts were made on three flycatcher-like bird species in the study area. More than 30 independent foraging observations, ranging from 36 to 56 observations, were recorded for each focal species (Table 1). As predicted, all studied species employ the sally manoeuvre by flycatching prey items from one perch to another, but differed in the use of foraging height, foraging substrate, and foliage density. These three species occasionally had tendencies to hover (by maintaining an airborne position) through flapping their wings and spreading their tail for a very short time.

All the studied species foraged at the understory and above-ground levels, between the shrub level (> 0–2 m) and 10 m above the ground. They exhibited specific foraging height preferences. Paradise-flycatcher, for instance preferred the highest studied strata (> 8–10 m), while monarch foraged mostly in the lower strata (> 6–8 m), and philentoma favoured the lowest strata (> 4–6 m). Certain species prefer particular foraging heights while totally avoiding individual strata. For example, paradise-flycatcher completely avoided the lowest strata (> 0–4 m), while monarch did not utilize the highest strata (> 8–10 m), and philentoma never made use of the lowest (> 0–2 m) and highest strata (> 8–10 m). The results also indicated that all three focal species foraged over a broad range of substrates, from live green leaves to aerial

Table 1
Foraging height, foraging substrate, attack manoeuvre, and foliage density variables utilised by flycatcher-like species. Data are given as percentages (%).

Foraging parameter		Paradise-flycatcher, n = 39	Black-naped Monarch, n = 56	Rufous-winged Philentoma, n = 36
Foraging height	> 0–2	0.00	7.14	0.00
	> 2–4	0.00	7.14	11.11
	> 4–6	15.38	14.29	77.78
	> 6–8	7.69	71.43	11.11
	> 8–10	76.92	0.00	0.00
Foraging substrate	Leaf (surface)	0.00	7.14	44.44
	Leaf (underside)	7.69	89.29	22.22
	Branch	7.69	3.57	11.11
	Aerial leaf-litter	0.00	0.00	11.11
	Air	84.62	0.00	11.11
Attack manoeuvre	Stretch	0.00	3.57	0.00
	Hover	7.69	17.86	11.11
	Sally	92.31	78.57	88.89
Foliage density	Scale 1	46.15	7.14	33.33
	Scale 2	30.77	7.14	11.11
	Scale 3	23.08	32.14	33.33
	Scale 4	0.00	53.57	22.22
	Scale 5	0.00	0.00	0.00

dead leaves, tree branches, and air. Paradise-flycatcher foraged mostly in the air (85%) while both monarch and philentoma preferred live green leaves, particularly on the underside of the leaf and leaf surface. Paradise-flycatcher foraged mostly in rather open vegetation (1 on this scale; 46%) but occasionally used lowest-intermediate foliage (2 on this scale; 31%) and intermediate-density foliage (3 on this scale; 23%). Monarch preferred the highest-density foliage (4 on this scale; 54%) but sometimes also utilized intermediate-highest foliage (3 on this scale; 32%) while philentoma showed variation in the use of foliage density (scale 1 and scale 3; both 33%).

The correspondence analysis (CA) of the three flycatcher-like species yielded two foraging dimensions. Dimension one accounted for 66% of the data variation that was weighted on the foraging
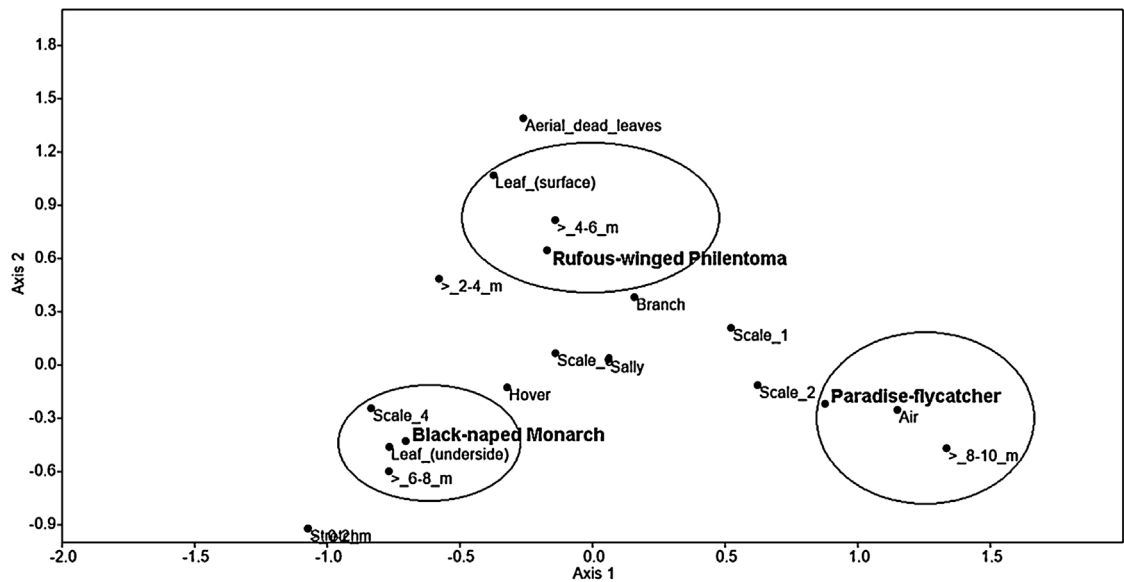
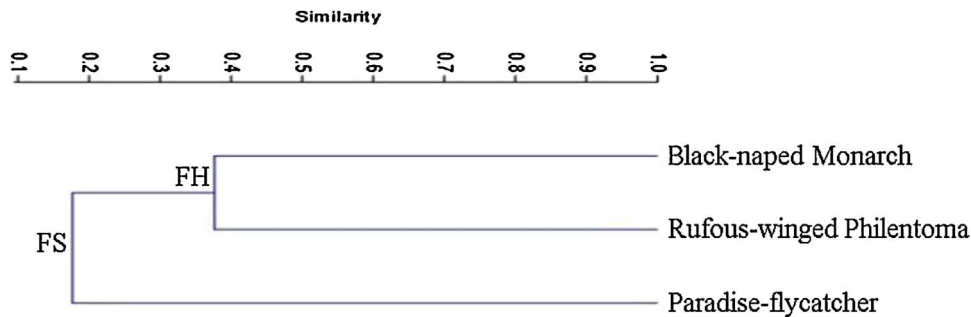**Fig. 2.** Distribution of the three flycatcher-like species based on correspondence analysis.

Fig. 3. Interspecific relationships of the three flycatcher-like species, based on cluster analysis of foraging variables (Legend: FS = foraging substrate; FH = foraging height).

substrate parameter, whereas dimension two described 33% of the data variation that was weighted on foraging height. CA plotting illustrated the distribution of studied flycatchers, reflecting their spatial variables selection (Fig. 2). Niche separation among these species is clearly explained by the cluster analysis (Fig. 3). The analysis was consistent with the CA results and effectively divided paradise-flycatcher from monarch and philentoma based on foraging substrate preferences, where both monarch and philentoma foraged mainly on live green leaves, while paradise-flycatcher foraged in the air. At the terminal branches, foraging height was a useful parameter for subdividing the substrate-preference groups into more specific groups.

Social network analysis showed that the studied species segregated their foraging niche mostly via foraging height and substrate but overlapped significantly with regards to the use of attack manoeuvres and slightly for foliage density (Table 2; see R_o). Relatively high niche overlap (R_o) was found in the use of the foliage density and attack manoeuvre parameters by the birds, ranging from 0.65 to 0.89. Both foraging height and substrate exhibited the lowest niche overlap,

ultimately suggesting that these flycatcher-like species were specialized in their vertical strata and substrate preferences while foraging. Such findings are fairly consistent with the results of the network level of specialization (H_2'), where both foraging height and substrate showed the highest specialization in the use of foraging parameters between the studied species, while the foliage density parameter was less specialized. Attack manoeuvre had the lowest value of specialization but was not considered a generalist because all focal species predominantly used the same method (i.e. sallying). At the species level of specialization (d'), all flycatcher-like species were specialized in the use of foraging height and substrate (Table 3). All species were also quite specialized in the use of foliage density except philentoma. The d' value for attack manoeuvre was not calculated because all flycatcher-like species adopted a sallying manoeuvre and had very high niche overlap (Table 2). Connectance showed the greatest value in the use of foliage density, indicating that all species demonstrating flexibility for this dimension. The mean number of links (L_x) per species value of 1.25, 1.38, 1.57, and 1.67 in bird-foraging parameters that used interactions can be interpreted as one species uses, on average, 25%, 28%, 39% and

Table 2
Indices of network analysis within the flycatcher-like species assemblages.

Parameter	C	H_2'	R_o	L_x
Foraging height	0.67	0.58	0.32	1.25
Substrate	0.73	0.61	0.34	1.38
Attack manoeuvre	0.78	0.08	0.89	1.67
Foliage density	0.92	0.22	0.65	1.57

C = connectance; H_2' = specialization of network level; R_o = niche overlap; L_x = links per species.

Table 3
Specialization index for each bird species (d') on three foraging parameters.

Parameter/Species	Paradise-flycatcher	Black-naped Monarch	Rufous-winged Philentoma
Foraging height	0.58	0.53	0.48
Substrate	0.66	0.59	0.31
Foliage density	0.35	0.24	0.02

56% of the available vertical strata, substrate, foliage density and attack manoeuvres, respectively.

4. Discussion

As expected, the three sympatric flycatcher-like species employed similar sally manoeuvres but partitioned their resources by having unique foraging dimensions, i.e. foraging substrate and vertical strata. We found that paradise-flycatcher were predominantly seen foraging in the air, while both monarch and philentoma were observed foraging mainly on live green leaves, particularly on underside of the leaf and leaf surface, respectively. High specialization values ($H_2' = 0.61$) in foraging substrate dimensions fostered niche separation among these species, and was indicative of coexistence of these sally birds in the same habitat. An abundance of ecological niches provided by the complex vegetation structure of the investigated lowland tropical rainforest supported the idea of high bird species diversity and suggested specialization in the use of resources. This was in line with the results of the cluster analysis, where the foraging substrate was present at the base of the cluster diagram and subdivided these three species into substrate-preference groups (live green leaves). PC1 was also weighed on foraging substrate and explained the largest amount of data variation, therefore underscoring the importance of this variable.

Different foraging niche preferences in locating prey items among ecologically similar bird species allow their coexistence (Morrison and With, 1987; Weimerskirch et al., 2009). Uniqueness in the use of foraging substrates and the associated morphological traits that make foraging in those places more conducive and efficient lead to specialization. Having long wings and tail allowed paradise-flycatcher to use the air as the most optimal place for flycatching. Smaller wings and tails determined that monarch and philentoma foraged more effectively in dense vegetation cover and sallying (occasionally hovering) on live green leaves. This is in agreement with previous work that showed paradise-flycatcher foraged in the air while monarch did on the undersides of leaves (Mansor and Sah, 2012), thus revealed specialization of foraging substrate that associated with attack manoeuvre selection across different geographical area. In addition, a slightly large body size (e.g. tail and wings) and long tail streamers in males may prohibit paradise-flycatcher from foraging on live green leaves that have dense vegetation cover. Although this niche separation occurred to partition resources among species, more research is necessary to reveal the type of prey items taken by the birds from the foraging substrates.

Foraging height was also different among the studied flycatcher-like species. Low niche overlap ($R_o = 0.32$) in foraging height provides better opportunities for birds to discover prey items in different vertical strata, thus reducing interspecific competition among species. This parameter was also important for subdividing substrate-preference groups in the cluster analysis and selected as the second dimension in CA. The hypothesis that height dimensions are a significant factor of bird species assemblage was suggested by MacArthur and MacArthur (1961) and has been widely tested to date (Hsieh and Chen, 2011; Freeman, 2014; Hamer et al., 2015). Various carbon isotope values of insects between upper and lower vegetation (Roswag et al., 2015) have indicated different insect group distributions, hence we assumed different prey items were taken by height-partitioned birds. Unique habitat strata may also support a number of groups and distributions of insects (Gokula and Vijayan, 2000).

Different vegetation cover use by the studied species must be related to substrate preferences. Paradise-flycatcher foraged mostly in the air, thus preferring open areas, whereas monarch foraged mostly on live green leaves, favouring dense cover. Philentoma exhibited variation in the use of foliage density and was observed to feature the lowest network-level measure of specialization ($H_2' = 0.22$), potentially reflecting their proclivity to forage on the leaf surface or in the air that is entirely avoided by monarch. Generalization of philentoma may provide broader foraging opportunities, especially when food is scarce (Terraube et al., 2011), and this could also help in reducing niche overlap at the intrapopulation level (Quevedo et al., 2009). Easier prey detection in open areas from enhanced light penetration (Barbaro et al., 2014) and abundance of insects in dense vegetation cover likely explains why philentoma prefers varying foliage density, therefore rendering them more generalist. In addition, different foliage cover preferences exhibited by bird species could possibly be related to the habitat structure and their antipredator strategies (Suhonen, 1993; Griesser and Nystrand, 2009).

Present study indicates that niche segregation occurs among sympatric species, through foraging height and substrate selection, thus following Gause's law of competitive exclusion, which states that two species occupying the same niche will not stably coexist (Hardin, 1960). Although these sympatric flycatcher-like species that use similar sally manoeuvres, they may have distinctive types of sally manoeuvre that requires more investigation. All aerial manoeuvres, such as leap, sally-strike, sally-glide, sally-pounce, flutter-chase, flush-pursue, and screen (Remsen and Robinson, 1990), if available, should be examined separately. For example, some birds may utilize the flush-pursue manoeuvre (to flush prey items from a substrate and then chase the falling or flying prey) tend to have noticeable wings, tail spots, or stripes that are useful for scaring the prey (Remsen and Robinson, 1990). Flush-pursue manoeuvre efficiency may increase with the extent of white in the plumage and plumage variation, which is related to evolutionary processes (Mumme, 2002). Distinguishing these sally manoeuvres may be difficult in the field especially focusing more than one species, though we believe it is valuable as each method involves essentially different tactics that may be significant to niche separation. Presence of northern wintering subspecies (i.e. *T. paradisi incei*) and closest-related species (i.e. *T. atrocaudata*) that feed in the same vegetation stratum with resident *T. paradisi affinis* (Wells, 2007) should also be noted in future research as present study were mostly done outside the migratory season.

References

Allen, R.B., McLennan, M.J., 1983. Indigenous Forest Survey Manual: Two Inventory Methods. FRI Bulletin No. 48, New Zealand. Forest Research Institute, Rotorua.

Allen, R.B., 1993. A Permanent Plot Method for Monitoring Changes in Indigenous Forests Manaaki Whenua-Landcare Research. Christchurch, New Zealand.

Barbaro, L., Giffard, B., Charbonnier, Y., van Halder, I., Brockerhoff, E.G., 2014. Bird functional diversity enhances insectivory at forest edges: a transcontinental experiment. Divers. Distrib. 20 (2), 149–159.

Blüthgen, N., Menzel, F., Blüthgen, N., 2006. Measuring specialization in species interaction networks. BMC Ecol. 6, 9.

Blüthgen, N., Menzel, F., Hovestadt, T., Fiala, B., Blüthgen, N., 2007. Specialization, constraints, and conflicting interests in mutualistic networks. Curr. Biol. 17 (4), 341–346.

Bowes, G.G., Thomas, A.G., Peschken, D.P., Douglas, D.W., Spurr, D.T., 1994. Habitats occupied by scentless chamomile (*Matricaria pertorata* Merat) in Saskatchewan. Can. J. Plant Sci. 74, 383–386.

Braun-Blanquet, J., 1932. In: Fuller, G.D., Conard, H.S. (Eds.), Plant Sociology. McGraw Hill Book Company, London.

Chapman, A., Rosenberg, K.V., 1991. Diets of four sympatric Amazonian woodcreepers (Dendrocolaptidae). Condor 93 (4), 904–915.

Chesson, P., 2000. Mechanisms of maintenance of species diversity. Annu. Rev. Ecol. Syst. 1, 343–366.

Clark, D.B., 1996. Abolishing virginity. J. Trop. Ecol. 12 (5), 735–739.

Cloyed, C.S., 2014. Forest structure affects resource partitioning between pygmy and

white-breasted nuthatches. Coevol 2 (1), 26–30.

Dormann, C.F., Gruber, B., Fründ, J., 2008. Introducing the bipartite package: analysing ecological networks. R News 8 (2), 8–11.

Dunne, J.A., Williams, R.J., Martinez, N.D., 2002. Food-web structure and network theory: the role of connectance and size. Proc. Natl. Acad. Sci. U. S. A. 99 (20), 12917–12922.

Elton, C., 1927. Animal Ecology. University of Chicago Press, Chicago, U.S.A.

Fabre, P.H., Irestedt, M., Fjeldså, J., Bristol, R., Groombridge, J.J., Irham, M., Jønsson, K.A., 2012. Dynamic colonization exchanges between continents and islands drive diversification in paradise-flycatchers (Terpsiphone, Monarchidae). J. Biogeogr. 39 (10), 1900–1918.

Freeman, B., 2014. Sexual niche partitioning in two species of New Guinean Pachycephala whistlers. J. Ornithol. 85 (1), 23–30.

Fuchs, J., Fjeldså, J., Pasquet, E., 2006. An ancient African radiation of corvoid birds (Aves: passeriformes) detected by mitochondrial and nuclear sequence data. Zool. Scr. 35 (4), 375–385.

Fuchs, J., Irestedt, M., Fjeldså, J., Couloux, A., Pasquet, E., Bowie, R.C.K., 2012. Molecular phylogeny of African bush-shrikes and allies: tracing the biogeographic history of an explosive radiation of corvoid birds. Mol. Phylogenet. Evol. 64 (1), 93–105.

Gokula, V., Vijayan, L., 2000. Foraging pattern of birds during the breeding season in thorn forest of Mudumalai wildlife sanctuary, Tamil Nadu, Southern India. Trop. Ecol. 41 (2), 195–208.

Gotelli, N.J., Graves, G.R., 1996. Null Models in Ecology. Smithsonian Institution Press, Washington.

Griesser, M., Nystrand, M., 2009. Vigilance and predation of a forest-living bird species depend on large-scale habitat structure. Behav. Ecol. 20 (4), 709–715.

Hamer, K.C., Newton, R.J., Edwards, F.A., Benedick, S., Bottrell, S.H., Edwards, D.P., 2015. Impacts of selective logging on insectivorous birds in Borneo The importance of trophic position, body size and foraging height. Biol. Conserv. 188, 82–88.

Hammer, Ø., Harper, D.A., Ryan, P.D., 2001. PAST: Paleontological Statistics Software, package for education and data analysis. Palaeontol. Electron. 4 (1), 1–9.

Hardin, G., 1960. The competitive exclusion principle. Science 131, 1292–1297.

Horn, H.S., 1966. Measurement of overlap in comparative ecological studies. Am. Nat. 100, 419–424.

Hsieh, F.S., Chen, C.C., 2011. Does niche-overlap facilitate mixed-species flocking in birds? J. Ornithol. 152, 955–963.

Hurst, J.M., Allen, R.B., 2007. A Permanent Plot Method for Monitoring Indigenous Forests: Field Protocols. Manaaki Whenua–Landcare Research. Christchurch, New Zealand.

Jeyarajasingam, A., Pearson, A., 2012. A Field Guide to the Birds of Peninsular Malaysia and Singapore. Oxford University Press.

Lack, D., 1971. Ecological Isolation in Birds. Blackwell Scientific Publications, London, U.K.

Lara, C., Martínez-García, V., Ortiz-Pulido, R., Bravo-Cadena, J., Loranca, S., Córdoba-Aguilar, A., 2011. Temporal-spatial segregation among hummingbirds foraging on honeydew in a temperate forest in Mexico. Curr. Zool. 57 (1), 56–62.

Lekagul, B., Round, P.D., 1991. Birds of Thailand. Saha Karn Bhaet Co., Bangkok, Thailand.

MacArthur, R.H., MacArthur, J.W., 1961. On bird species diversity. Ecology 42 (3), 594–598.

MacNally, R.M., 1994. Habitat-specific guild structure of forest birds in south-eastern Australia: a regional scale perspective. J. Anim. Ecol. 63, 988–1001.

Mansor, M.S., Sah, S.A.M., 2012. Foraging patterns reveal niche separation in tropical insectivorous birds. Acta Ornithol. 47 (1), 27–36.

Mansor, M.S., Ramli, R., Sah, S.A.M., 2015. The foraging tactics of chestnut-winged babbler (Stachyris erythroptera) and Abbott's Babbler (Malacocincla abbotti) in a lowland rainforest, Malaysia. Sains Malaysi. 44 (5), 687–692.

Martin, T.E., Karr, J.R., 1990. Behavioral plasticity of foraging maneuvers of migratory warblers: multiple selection periods for niches. Stud. Avian Biol. 13, 353–359.

May, R.M., 1974. On the theory of niche overlap. Theor. Popul. Biol. 5 (3), 297–332.

Miles, D.B., 1990. A comparison of three multivariate tech- niques for the analysis of avian foraging data. Stud. Avian Biol. 13, 295–308.

Moermond, T.C., 1990. A functional approach to foraging: morphology, behaviour and the capacity to exploit. Stud. Avian Biol. 13, 427–430.

Morrison, M.L., With, K.A., 1987. Interseasonal and intersexual resource partitioning in hairy and white-headed woodpeckers. Auk 104, 225–233.

Morrison, M.L., 1984. Influence of sample size and sampling design on analysis of avian foraging behavior. Condor 86, 146–150.

Moyle, R.G., Cracraft, J., Lakim, M., Nais, J., Sheldon, F.H., 2006. Reconsideration of the phylogenetic relationships of the enigmatic Bornean Bristlehead (Pityriasis gymnocephala). Mol. Phylogenet. Evol. 39 (3), 893–898.

Mumme, R.L., 2002. Scare tactics in a neotropical warbler: white tail feathers enhance flush-pursuit foraging performance in the slate-throated redstart (Myioborus miniatus). Auk 119 (4), 1024–1035.

Nizam, M.S., Fakhrul-Hatta, M., Latiff, A., 2006. Diversity and tree species community in the Krau wildlife reserve, Pahang, Malaysia. Malays. Appl. Biol. 35 (2), 81–85.

Pasquet, E., Cibois, A., Baillon, F., Erard, C., 2002. What are African monarchs (Aves, Passeriformes)? A phylogenetic analysis of mitochondrial genes. Comptes Rendus Biologies de l'Academie des Sciences 325, 107–118.

Pulliam, H.R., 1985. Foraging efficiency, resource partitioning, and the coexistence of sparrow species. Ecology 66, 1829–1836.

Quevedo, M., Svanbäck, R., Eklöav, P., 2009. Intrapopulation niche partitioning in a generalist predator limits food web connectivity. Ecology 90 (8), 2263–2274.

R Core Team, 2015. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Raemaekers, J.J., Aldrich-Blake, F.P.G., Payne, J., 1980. Malayan forest primates: ten years' study in tropical rain forest. In: Chivers, D.J. (Ed.), The Forest. Plenum Press, New York, pp. 29–62.

Reddy, S., Driskell, A., Rabosky, D.L., Hackett, S.J., Schulenberg, T.S., 2012. Diversification and the adaptive radiation of the vangas of Madagascar. Proc. R. Soc. B 279, 2062–2071.

Remsen Jr., J.V., Robinson, S.K., 1990. A classification scheme for foraging behavior of birds in terrestrial habitats. Stud. Avian Biol. 13, 144–160.

Robertson, O.J., McAlpine, C., House, A., Maron, M., 2013. Influence of interspecific competition and landscape structure on spatial homogenization of avian assemblages. PLoS One 8 (5), e65299.

Robinson, S.K., Holmes, R.T., 1982. Foraging behavior of forest birds: the relationships among search tactics, diet, and habitat structure. Ecology 63 (6), 1918–1931.

Robson, C., 2008. A Field Guide to the Birds of South-east Asia. New Holland Publishers, London, U.K.

Rolando, A., Robotti, C.A., 1985. Foraging niches of tits and associated species in northwestern Italy. Ital. J. Zool. 52 (3–4), 281–297.

Roswag, A., Becker, N.I., Encarnação, J.A., 2015. Importance of multi-dimensional analyses of resource partitioning in highly mobile species assemblages. Popul. Ecol. 57 (4), 601–611.

Styring, A.R., Hussin, M.Z., 2004. Foraging ecology of woodpeckers in lowland Malaysian rain forests. J. Trop. Ecol. 20 (5), 487–494.

Styring, A.R., Ragai, R., Zakaria, M., Sheldon, F.H., 2016. Foraging ecology and occurrence of 7 sympatric babbler species (Timaliidae) in the lowland rainforest of Borneo and peninsular Malaysia. Curr. Zool. 62 (4), 345–355.

Suhonen, J., 1993. Predation risk influences the use of foraging sites by tits. Ecology 29 (4), 342–370.

Svanbäck, R., Eklöv, P., 2003. Morphology dependent foraging efficiency in perch: a trade-off for ecological specialisation? Oikos 102 (2), 273–284.

Terraube, J., Arroyo, B., Madders, M., Mougeot, F., 2011. Diet specialisation and foraging efficiency under fluctuating vole abundance: a comparison between generalist and specialist avian predators. Oikos 120 (2), 234–244.

Weimerskirch, H., Shaffer, S., Tremblay, Y., Costa, D., Gadenne, H., Kato, A., Ropert-Coudert, Y., Sato, K., Aurioles, D., 2009. Species- and sex-specific differences in foraging behaviour and foraging zones in blue-footed and brown boobies in the Gulf of California. Mar. Ecol. Prog. Ser. 391, 267–278.

Wells, D.R., 1976. Resident birds. In: In: Lord Medway, Wells, D.R. (Eds.), Birds of the Malay Peninsula, vol. 5. Witherby, London, and University Malaya Press, Kuala Lumpur, pp. 1–33.

Wells, D.R., 2007. The birds of the thai-Malay peninsula. The Passerine, vol. 2 Christopher Helm, London, U.K.

Whelan, C.J., 2001. Foliage structure influences foraging of insectivorous forest birds: an experimental study. Ecology 82 (1), 219–231.

Yusof, E., Sorenson, K.W., 2000. Krau Wildlife Reserve: protected area management experiences. J. Wild. Parks 18, 3–13.

Zakaria, N., Senawi, J., Musa, F.H., Belabut, D., Onn, C.K., Md Nor, S., Ahmad, N., 2014. Species composition of amphibians and reptiles in Krau wildlife reserve, Pahang, peninsular Malaysia. Check List 10, 335–343.