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How important is aerial leaf litter for insectivorous birds foraging in a Malaysian tropical forest?



Mohammad Saiful Mansor^{a, *}, Fasihah Zarifah Rozali^b,
Nurul Ashikin Abdullah^c, Shukor Md Nor^a, Rosli Ramli^c

^a School of Environmental and Natural Resource Sciences, Faculty of Science and Technology, Universiti Kebangsaan Malaysia, Bangi, Selangor, Malaysia

^b School of Biological Sciences, Universiti Sains Malaysia, Pulau Pinang, Malaysia

^c Institute of Biological Sciences, Faculty of Science, University of Malaya, Kuala Lumpur, Malaysia

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ABSTRACT

Aerial leaf litter is a vital resource for insectivorous birds in tropical forests, particularly those that rely on dietary litter-dependent arthropods. The present study quantified and determined aerial-leaf litter selection patterns of specialist and regular dead-leaf users. In total, 486 observation sessions were conducted in a lowland tropical forest from February 2014 to September 2015. At least two 'specialist' species (over 75% of the observations) and seven 'regular users' species (25–74% of the observations) were found foraging for arthropods among aerial curled dead leaves within the aboveground vertical vegetation layers. These species belonged to four genera of the family Timaliidae and Pellorneidae: *Cyanoderma*, *Stachyris*, *Pellorneum*, and *Malacopteron*. The chestnut-winged babbler (*Cyanoderma erythropterum*) and the black-throated babbler (*Stachyris nigricollis*) were two species that heavily exploited the aerial leaf litter, accounting for 89% and 76% of the observations, respectively. The present study indicates that aerial leaf litter could serve as a vital foraging resource for most gleaning forest babblers in Malaysian rainforests. Moreover, niche separation among these dead-leaf foragers occurred due to their differing vertical strata preferences. The variations in body and bill sizes among the studied species suggest that they consume various arthropod sizes and taxonomic groups. A morphological analysis identified Hymenoptera, Coleoptera, and Arachnida as the dominant litter-dependent arthropods, and a molecular analysis revealed the presence of additional insect groups in the aerial leaf litter (e.g. Diptera and Lepidoptera). This study highlights the importance of maintaining undergrowth vegetation that can intercept aerial leaf litter to provide important foraging opportunities for forest bird species.

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1. Introduction

Aerial leaf litter represents a critical microhabitat in tropical forests (Gradwohl and Greenberg, 1980, 1982; Rosenberg, 1990). This substrate is known as aerial/arboreal/hanging leaf litter, which consists of dead leaves trapped by understory plants. This substrate offers a protected microclimate away from hot and dry environments (providing moisture) and is an

* Corresponding author.

E-mail address: msaifulmansor@gmail.com (M.S. Mansor).

ideal microhabitat for the daytime roosts of many litter-dependent arthropod and microarthropod groups (Greenberg, 1987; Turner and Foster, 2009; Trentini et al., 2018). Certain tree species have a tendency to self-retain dead leaves (Yoshida and Hijii, 2006), and many understory plants capture high quantities of tree canopy leaf litter before it reaches the ground (Dearden and Wardle, 2008; Silver et al., 2014). Canopy litter is often caught within many vegetation strata from the top of the canopy to near the ground, where vegetation is often sufficiently dense to prevent falling leaf litter from reaching the ground (Remsen and Parker, 1984).

Variation in bird species richness between tropical forests and other climates can be explained by the variation in available resources that provide foraging opportunities for birds. For instance, aerial leaf litter in Neotropical regions harbors many arthropod groups that serve as food for numerous understory insectivorous birds (Remsen and Parker, 1984; Rosenberg, 1997; Vargas et al., 2011). In temperate regions, the worm-eating warbler (*Helminthos vermivorus*) appears to heavily utilize aerial leaf litter and even vagrant individuals in California foraged at aerial dead leaves (Remsen and Parker, 1984). Some warbler species also feed on arthropods in aerial leaf litter at their wintering grounds (Lack and Lack, 1972; Morton, 1980). The adoption of this type of behavior by many dead-leaf foragers may be the consequence of a long-term evolutionary process that defines how communities are structured. The falling of canopy leaves is presumably frequent in the tropics and much less seasonal than in temperate regions (Cizungu et al., 2014; da Silva et al., 2018). Therefore, dead leaves suspended in the vegetation appear to be available year-round in most areas, which suggests the potential importance of this substrate in tropical regions.

Dead curled leaves suspended in understory plants may hold significantly more arthropods than live green leaves (Gradwohl and Greenberg, 1980, 1982; Rosenberg, 1990; Leme, 2001). The abundance and diversity of arthropods in aerial leaf litter may be unique and/or significantly divergent from those in ground leaf litter (Bird et al., 2004; Yoshida and Hijii, 2006; Fagan et al., 2006; Roswag et al., 2015) or other substrates. These microhabitats are assumed to be an important aspect of niche separation from live-leaf forager species. Furthermore, aerial leaf litter may decay more slowly than ground litter, which may result in more shelter and higher arthropod availability in aerial strata than on the ground (Iverson et al., 2018). Litter-dependent arthropods can be rapidly harvested by dead-leaf foragers, but the rate of recolonization by arthropods is high (Gradwohl and Greenberg, 1982; Rosenberg, 1993). Limited and patchily distributed aerial leaf litter may increase birds' activity budget (Remsen and Parker, 1984); thus, birds may be sensitive to reductions of such substrates in managed landscapes.

Most studies of the impact of habitat disturbance on biodiversity have not discriminated among the effects of that disturbance on different foraging microhabitats of various species, such as tree bark, branches, the forest floor, and clusters of hanging dead leaves. Such heterogeneity in foraging substrates is crucial for many forest birds, which may be restricted entirely to feeding in a single microhabitat. Foraging specialization by tropical forest birds on particular microhabitat types contributes to high bird species diversity (Sillett, 1994), and the higher number of specialist species in tropical forest communities may reflect the continuity of these resources. In Neotropical regions, curled dead leaves are searched by many bird species, including species highly specialized for foraging on this substrate as well as other foliage-gleaner birds that occasionally utilize aerial litter (Remsen and Parker, 1984; Tarbox et al., 2018).

Forestry practices in tropical forests, such as selective logging and canopy and understory clear-cutting (Dupuy and Chazdon, 2008), may result in marked decreases in the abundance of hanging dead leaves, thereby decreasing the available food resources for many dead-leaf foragers (Styring et al., 2016; Mansor et al., 2018). The historical practices in fragmented tropical forest limit the microhabitat availability, which highly impacted the species richness of specialized forest birds (Rosenvold et al., 2011; Bregman et al., 2014). Information on the habitat requirements of bird species, for example, information on their reliance on certain microhabitats, may aid in identifying the species most sensitive to the effects of forestry practices (Fox et al., 2010). Such information can possibly be used to enhance the conservation planning of bird assemblages in managed landscapes. As such, obtaining this information is an important first step in planning for the maintenance of complex ecological networks in tropical ecosystems.

Although aerial litter provides shelter for many arthropods and foraging opportunities for birds, little research has been conducted on the importance of this substrate as sources for many tropical insectivorous birds. In the tropics, the year-round availability of fruits (Lambert, 1991) and the abundance of large arthropods (Jedlicka et al., 2006) and ants (Fayle et al., 2010) contributes significantly to bird species richness there. However, bird specialization on aerial leaf litter has not been studied extensively in Southeast Asia. Previous studies have revealed the use of aerial leaf litter by many insectivorous birds in Malaysia (Styring et al., 2016; Mansor and Ramli, 2017); however, none have focused on the ability of aerial leaf litter to provide food sources for various bird species. Therefore, the objective of the present study is to document the contribution of aerial leaf litter to tropical bird species diversity by (1) determining the degree of foraging substrate specialization among tropical bird species in Malaysia, and (2) investigating the types of arthropod groups that occur within aerial leaf litter using both morphological and molecular next-generation sequencing.

2. Methods

2.1. Study area

The study was conducted in the Krau Wildlife Reserve in the Bukit Rengit area of Pahang state, central Peninsular Malaysia (Fig. 1). This reserve is a second largest protected area in Peninsular Malaysia after Taman Negara, with a size of approximately

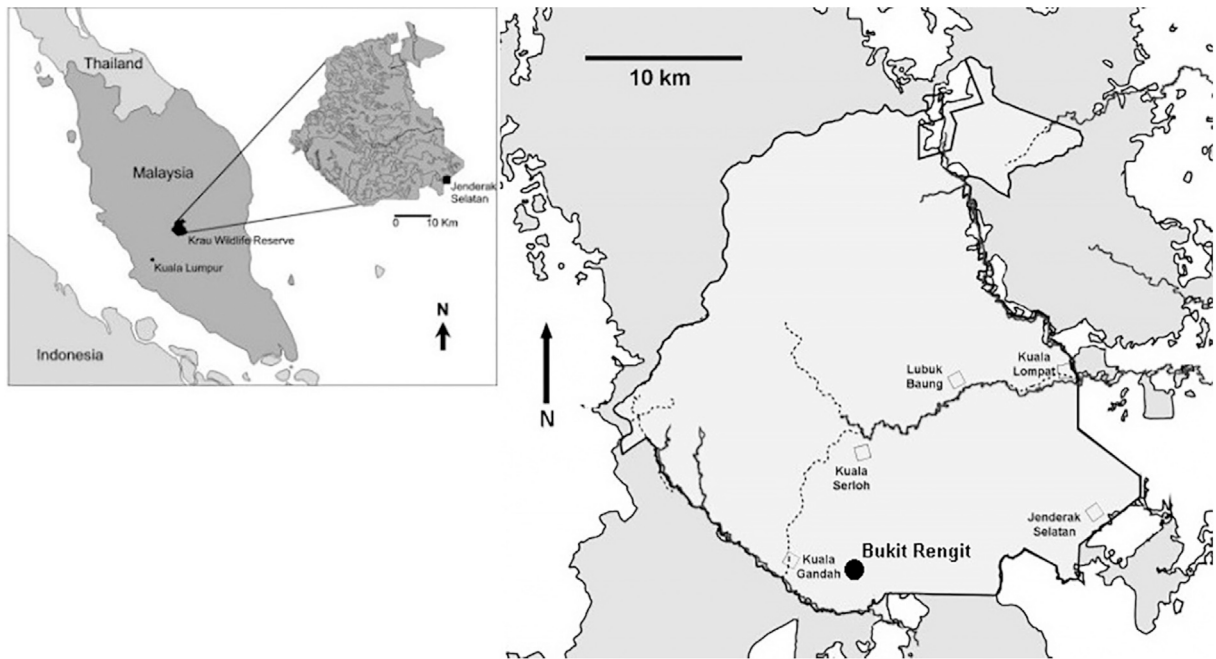


Fig. 1. Map of Krau Wildlife Reserve, Pahang, central Peninsular Malaysia. The reserve is represented by light grey, forest areas surrounding the reserve by dark grey, and non-forest areas by white. Map adapted from Zakaria et al. (2014).

624 km² and an elevation ranging from 50 m at Kuala Lompat to over 2000 m at the summit of Gunung Benom. The reserve consists of a large area of old-growth lowland and hill dipterocarp forests forest (Clark, 1996), with associated dominant tree species including *Dipterocarpus cornutus*, *D. baudi*, *D. grandiflorus*, *Hopea sangal*, *Shorea acuminata*, *S. ovalis*, *S. leprosula*, *S. cutisii*, *Anisoptera laevis*, and *Vatica cuspidata* (Yusof and Sorenson, 2000). The climate is tropical with daily temperature variation between 23 °C and 33 °C, and a mean annual rainfall of roughly 2000 mm. Maximum rainfall occurs in September–December and March–May.

2.2. Foraging observations

Birds were located visually and randomly along several forest trails, and followed opportunistically. Data were collected between February 2014 and September 2015, for 10 days/month for a period of 20 months. Birds were observed throughout the day, between 0730 and 1830 h. Observations of each foraging bird were made using 10 × 42 binoculars, recorded by voice recorder, and later transcribed onto data spreadsheets. The following foraging data of each encountered foraging bird were recorded: 1) foraging height, defined as the level from which a food item is taken estimated in 2 m intervals; and 2) foraging substrate, defined as the precise substrate from which a food item was taken (Remsen and Robinson, 1990).

Dead-leaf foragers were defined in the field and grouped into three categories based on their degree of specialization, following Remsen and Parker (1984): (i) specialist species, which search in aerial leaf litter in more than 75% of recorded observations; (ii) regular users, which search in aerial leaf litter in 25–75% of recorded observations; and (iii) occasional users, which search less than 25% of total observations in dead-leaves. In addition to an examination of the existing literature, incidental and opportunistic observations were used to compare birds' actual preferred microhabitats.

2.3. Aerial leaf litter arthropods

Two types of aerial leaf litter were identified as foraging sites by the majority of dead-leaf foragers: dead leaves clustered in small palms and curled dead leaves suspended on vegetation, both of which were collected and pooled for arthropod sampling. Aerial leaf litter ($n = 100$) was collected 1–2 m above the ground, along several forest trails by a distance of 10 m intervals and placed into plastic containers. Only partial clusters of aerial leaf litter were collected in order to minimise disturbance. Arthropods were separated from the leaves using a sieve, and Winkler extraction was then performed for 72 h in the laboratory, with arthropods being subsequently preserved in 99.8% ethanol.

All preserved samples were morphologically examined under a Leica ZOOM 2000 stereomicroscope (Leica Microsystems Inc., IL, USA) following the guidelines and identification keys provided by Triplehorn and Johnson (2005) and Whitaker and

Castor (2010). The arthropods were identified to the lowest possible taxonomic level, generally to order but sometimes to family and genus levels.

2.4. DNA extraction, PCR amplification and sequencing

Fragments of arthropods and remaining leaf litter were pooled for DNA extraction using the NucleoSpin® Soil (Macherey-Nagel GmbH & Co., Düren, Germany). All extraction steps were performed according to the manufacturer's protocol. A 286 base-pair length fragment of the mitochondrial DNA cytochrome *c* oxidase subunit I barcode region (COI) was amplified from each DNA extract using the forward primer LCO1490 (5'-GTCAACAAATCATAAAGATATTGG-3') and the reverse primer HCO1777 (5'-ACTTATATTGTTTATACGAGGAA-3') (Brown et al., 2012). Amplification was performed in a final volume of 50 µl containing 25 µl of NEXpro™ e-PCR Master Mix (NEX Diagnostics, Gyeonggi-do, South Korea), 10 pmol of each forward and reverse primer, and 2.0 µl of genomic DNA. PCR was done using Applied Biosystems Veriti 96-Well Thermal Cycler (Applied Biosystems Inc., CA, U.S.A.). After an initial denaturing step at 94 °C for 2 min 30 s, amplification proceeded for 35 cycles at 94 °C for 30 s, 44 °C for 30 s, 72 °C for 45 s and a final extension at 72 °C for 10 min. Amplicons were extracted from 2% agarose gels and purified using the AxyPrep DNA Gel Extraction Kit (Axygen Biosciences, CA, U.S.A.), following the manufacturer's protocols and quantified using QuantiFluor™ -ST (Promega, WI, U.S.A.). The primer set was modified by the addition of Illumina primer sequence and Illumina's Nextera overhang adaptors on the 5' ends. Sample libraries were normalized, pooled in equimolar and sequenced on MiSeq (2 × 250/300 bp) Desktop Sequencer (Illumina, CA, U.S.A.), following the standard protocols.

2.5. Data and statistical analyses

Amplicon sequences obtained from the Illumina MiSeq were filtered and collapsed into unique haplotypes (singletons removed) and the clustered into Operational Taxonomic Units (OTUs) using the USEARCH v8.1.1861 (Edgar, 2013). All OTU sequences were aligned and queried through the GenBank (<http://www.ncbi.nlm.nih.gov/>) or Biodiversity of Life Database (BOLD) (<http://www.boldsystems.org/>; Ratnasingham and Hebert, 2007). A sequence that has at least 98% similarity to any other reference sequence was considered identified to species level (King et al., 2015). Sequences were identified to higher taxonomic levels when they could not be clearly matched to a single species, most likely because sequences of particular species were not contained in the databases (Handl et al., 2011; Ishak et al., 2011). We considered individual insects to be matched to an order when similarity exceeded 85%; to a family when similarity exceeded 90%; and to genus when similarity exceeded 95%.

One-way analysis of variance (ANOVA) was used to examine differences in foraging strata among studied bird species as expressed as the percentage of the six height categories (Krüger et al., 2012). The analysis was performed using the software package PAleontological Statistics (PAST, version 2.17c; Hammer et al., 2001).

3. Results

In total, 486 independent observations were conducted on two specialist species, seven 'regular users' species, and some incidental observations of occasional dead-leaf forager species (Table 1). The specialist and regular dead-leaf foragers were members of the family Timaliidae and Pellorneidae belonged to four genera: *Cyanoderma* (one species), *Stachyris* (three species), *Pellorneum* (three species), and *Malacopteron* (two species). These species were observed foraging by either gleaning in small palm clustered leaf litter or on curled leaves suspended in vegetation and other microhabitats (e.g. live green leaves, small branches, and ground leaf litter). Aerial leaf litter ($n = 202$) represented over half (57%) of all the utilized substrates by specialists and regular dead-leaf users.

Species that were identified as occasional users were the buff-necked woodpecker (*Meiglyptes tukki*), hairy-backed bulbul (*Tricholestes criniger*), red-eyed bulbul (*Pycnonotus brunneus*), and rufous-winged philentoma (*Philentoma pyrhoptera*). There were few observations of occasional dead-leaf foragers; however, the species we observed have been shown in previous work to vary in preferred microhabitat (i.e. bark and live green leaves) (Wells, 1999, 2007; Robson, 2008). In the present study, the buff-necked woodpecker was observed peck-foraging in tree bark, the hairy-backed bulbul and the red-eyed bulbul were mostly seen gleaning live green leaves, and the rufous-winged philentoma predominantly sally foraged on live green leaves.

With the exception of the black-capped babbler (*Pellorneum capistratum*), a ground forager, all of the specialists and regular users foraged between 0.5 and 10 m above the ground, with the > 0–2 m stratum being used by most species. The scaly-crowned babbler (*Malacopteron cinereum*), rufous-crowned babbler (*M. magnum*) and chestnut-rumped babbler (*Stachyris maculata*) exhibited partitioning from the other dead-leaf foragers, as evidenced from their foraging height preferences (Table 1).

3.1. Aerial leaf-litter arthropods

Morphological analysis revealed the arthropod groups found in aerial leaf litter consisted primarily of Coleoptera, Hymenoptera, and Arachnida, accounting for 42%, 16%, and 13%, respectively, of the observed arthropods (Table 2). All of the

Table 1

Foraging substrate and foraging height variables utilized by specialists, regular and occasional dead-leaf users.

Species	Foraging substrate (%)				Trunk	Twig (fruit)	Air	Foraging height (mean ± SD)
	Live green-leaf	Branch	Aerial leaf litter	Floor leaf litter				
Specialists								
Chestnut-winged babbler (<i>Cyanoderma erythropterus</i>), n = 64	10.94	0.00	89.06	0.00	0.00	0.00	0.00	2.41 ± 1.47 m
Black-throated babbler (<i>Stachyris nigricollis</i>), n = 37	16.22	8.11	75.68	0.00	0.00	0.00	0.00	1.68 ± 0.85 m
Regular users								
Chestnut-rumped babbler (<i>S. maculata</i>), n = 31	0.00	32.26	67.74	0.00	0.00	0.00	0.00	6.45 ± 2.72 m
Grey-throated babbler (<i>S. nigriceps</i>), n = 36	55.55	0.00	44.44	0.00	0.00	0.00	0.00	1.31 ± 0.47 m
Short-tailed babbler (<i>Pellorneum malaccense</i>), n = 30	43.34	0.00	50.00	6.67	0.00	0.00	0.00	0.93 ± 0.78 m
Ferruginous babbler (<i>P. bicolor</i>), n = 39	53.84	0.00	46.15	0.00	0.00	0.00	0.00	1.13 ± 0.52 m
Black-capped babbler (<i>P. capistratum</i>), n = 36	11.11	0.00	44.44	44.44	0.00	0.00	0.00	0.61 ± 0.77 m
Rufous-crowned babbler (<i>Malacopteron magnum</i>), n = 39	51.28	0.00	48.72	0.00	0.00	0.00	0.00	6.13 ± 2.02 m
Scaly-crowned babbler (<i>M. cinereum</i>), n = 42	71.43	0.00	28.57	0.00	0.00	0.00	0.00	5.14 ± 2.15 m
Occasional users								
Buff-necked woodpecker (<i>Meiglyptes tukki</i>), n = 32	0.00	25.00	9.38	0.00	65.62	0.00	0.00	7.75 ± 4.30 m
Red-eyed bulbul (<i>Pycnonotus brunneus</i>), n = 30	23.33	0.00	6.67	0.00	0.00	70.00	0.00	9.87 ± 1.48 m
Hairy-backed bulbul (<i>Tricholestes criniger</i>), n = 34	76.47	0.00	8.82	0.00	0.00	14.71	0.00	5.79 ± 1.75 m
Rufous-winged philentoma (<i>Philentoma pyrhoptera</i>), n = 36	66.67	11.11	11.11	0.00	0.00	0.00	11.11	5.81 ± 1.04 m

Table 2

List of arthropod taxa found in the aerial leaf litter based on morphological analysis.

Class	Order	Family	Taxa grouping
ARACHNIDA	Acari Araneae		Acari morphosp.
			Araneae morphosp. 1
			Araneae morphosp. 2
			Araneae morphosp. 3
CHILOPODA			Chilopoda morphosp. 1
			Chilopoda morphosp. 2
INSECTA	Hymenoptera	Formicidae	<i>Polyrhachis</i> sp. 1
			<i>Polyrhachis</i> sp. 2
			<i>Tetramorium</i> sp.
			Formicidae morphosp. 1
			Formicidae morphosp. 2
			Coleoptera morphosp. 1
			Coleoptera morphosp. 2
			Coleoptera morphosp. 3
			Coleoptera morphosp. 4
			Coleoptera morphosp. 5
	Coleoptera		Coleoptera morphosp. 6
			Coleoptera morphosp. 7
			Coleoptera morphosp. 8
			Coleoptera morphosp. 9
			Coleoptera morphosp. 10
			Coleoptera morphosp. 11
			Coleoptera morphosp. 12
			Coleoptera morphosp. 13
	Blattodea		Blattodea morphosp. 1
			Blattodea morphosp. 2
			Blattodea morphosp. 3
	Orthoptera		Orthoptera morphosp. 1
			Orthoptera morphosp. 2
	Mantodea		Mantodea morphosp.
	Hemiptera		Hemiptera morphosp.

arthropods were identified to order; some hymenopterans were further identified to genus: *Polyrhachis* and *Tetramorium*. Other arthropod groups included Blattodea (10%), Orthoptera (6%), Chilopoda (6%), Mantodea (3%), and Hemiptera (3%) (Fig. 2).

The analysis of 48,496 paired-end reads sequenced using the Illumina MiSeq platform resulted in the detection of 39 distinct arthropod OTUs among the aerial leaf litter samples. The assigned OTUs were divided into four arthropod classes: Arachnida, Chilopoda, Collembola, and Insecta (Fig. 2). Thirty-four OTUs represented insects belonging to 19 families in six orders (Coleoptera, Hymenoptera, Diptera, Lepidoptera, Hemiptera, and Orthoptera) (Table 3). The 11 Coleoptera OTUs represented six families (Brachyceridae, Carabidae, Chrysomelidae, Curculionidae, Melyridae, and Staphylinidae), one sub-family (Harpalinae) and one species (*Xyleborus volvulus*). Hymenoptera, Diptera, and Lepidoptera were each represented by

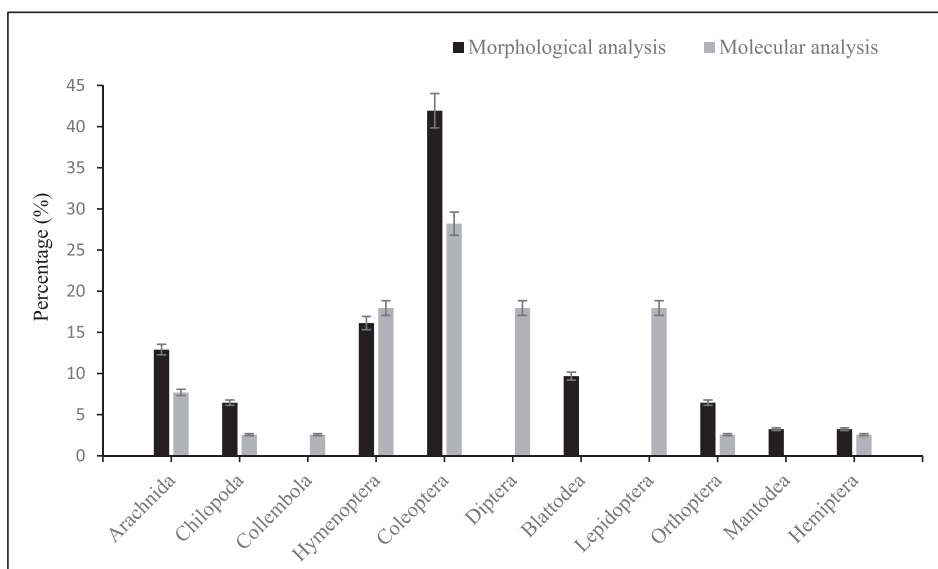


Fig. 2. The overall distribution (with standard error) of arthropod groups occur within aerial leaf litter identified by morphological and molecular analysis.

Table 3

List of arthropod taxa found in the aerial leaf litter based on molecular analysis. OTU sequences from aerial leaf litter arthropods and remaining leaf litter identified to order, family, genus and species level by comparison to reference sequences in the Genbank and BOLD. Taxa are named according to best BLASTn matches.

Class	Order	Family	Taxa grouping	Similarity
ARACHNIDA	Araneae	Nephilidae	<i>Nephila antipodiana</i>	98%
			Araneae sp.	90%
CHILOPODA	Scolopendromorpha	Salticidae	Salticidae sp.	91%
			Scolopendromorpha sp.	88%
COLLEMBOLA	Entomobryomorpha	Paronellidae	Paronellidae sp.	92%
			Brachyceridae sp.	92%
INSECTA	Coleoptera	Carabidae	Harpalinae sp. 1	98%
			Harpalinae sp. 2	99%
			Carabidae sp.	91%
		Chrysomelidae	Chrysomelidae sp. 1	93%
			Chrysomelidae sp. 2	91%
		Curculionidae	<i>Xyleborus volvulus</i>	98%
			Coleoptera sp. 1	90%
			Coleoptera sp. 2	89%
		Melyridae	Melyridae sp.	92%
	Hymenoptera	Staphylinidae	Staphylinidae sp.	91%
		Formicidae	<i>Polyrhachis</i> sp.	97%
			<i>Tetramorium</i> sp.	96%
			<i>Technomyrmex</i> sp.	96%
			Formicidae sp. 1	93%
			Formicidae sp. 2	92%
		Eulophidae	Eulophidae sp.	91%
	Diptera	Ichneumonidae	Ichneumonidae sp.	92%
		Cecidomyiidae	Cecidomyiidae sp.	91%
		Ceratopogonidae	Ceratopogonidae sp.	92%
		Empididae	Empididae sp.	92%
		Muscidae	Muscidae sp.	94%
		Mycetophilidae	Mycetophilidae sp.	91%
	Lepidoptera		Diptera sp. 1	90%
			Diptera sp. 2	88%
		Erebidae	<i>Zale</i> sp.	96%
			Erebidae sp.	95%
		Lycaenidae	Lycaenidae sp.	90%
		Saturniidae	Saturniidae sp.	93%
		Tortricidae	Tortricidae sp.	94%
			Lepidoptera sp. 1	90%
	Hemiptera		Lepidoptera sp. 2	88%
		Cicadellidae	Cicadellidae sp.	91%
Orthoptera			Orthoptera sp.	89%

seven OTUs. The Hymenoptera OTUs represented three genera (*Polyrhachis*, *Tetramorium*, and *Technomyrmex*) and three families, and the Lepidoptera OTUs represented one genus (*Zale* sp.) and four families. Diptera and Hemiptera OTUs were only identified to the family level, whereas the Orthoptera was identified to the order level. The analysis also identified three arachnid OTUs representing two families (Nephilidae and Salticidae) and one species (*Nephila antipodiana*). The remaining OTUs were identified as Collembola (Paronellidae) and Chilopoda (Scolopendromorpha).

4. Discussion

All of the observed dead-leaf specialists and regular users were members of the family Timaliidae and Pellorneidae, a diverse family of insectivorous birds from tropical Asia. Utilising this resource may require specialized strategies not exhibited by non-dead-leaf foragers. This specialized behavior are also exhibited by other species in Sundaland (Styring et al., 2016; Mansor and Ramli, 2017) and other tropical regions (Remsen and Parker, 1984; Vargas et al., 2011; Tarbox et al., 2018). Many of the babblers may have adaptations for foraging in dead leaves including bill morphology, plumage color and social structure. Such morphological adaptations that correspond to specialized attack maneuvers are very crucial for birds to forage on particular substrates (Mansor and Sah, 2012).

Litter-dependent arthropods can be rapidly harvested by dead-leaf foragers, but the rate of recolonization by arthropods is high (Rosenberg, 1993). For this reason, the slender bills of primary dead leaf foragers are very important because they allow foraging without disrupting the curled dead leaves that provide suitable habitats for litter-dependent arthropods. Most babblers have slender or mid-stout bills (Mansor and Ramli, 2017) that are very useful for extracting prey without damaging dead leaves. Furthermore, subtle morphological differences in plumage color appear to occur between dead-leaf foragers and live-leaf foragers. Most dead-leaf foragers in present study are brownish, rufous, and grayish in color (possibly mimicking the color of dead leaves). Most of the dead-leaf specialist taxa in South America (primarily *Epinecrophylla*, *Philydor* and *Automolus*) are brown birds (Remsen and Parker, 1984) that are superficially similar morphologically to the babblers. This color camouflage allows them to blend in with the microhabitat may help birds reduce their predation risk (Gluckman and Cardoso, 2010).

Foraging on curled dead leaves may expose birds to predators due to the noisy foraging process. Some species occasionally insert their entire heads within the litter to explore large curled dead leaves (Morton, 1980), leaving them even more exposed to predators. This exposure likely explains why most dead-leaf foragers such as babblers join mixed-species flocks (Rosenberg, 1997; Sridhar et al., 2009). Participation in mixed-species flocks might allow birds to benefit from the reduced need for antipredator vigilance, allowing them to devote more time and effort to foraging (Greenberg, 2000; Sridhar et al., 2009). Heterogeneous-member flocking can decrease predation risk through alarm calling (Goodale and Kotagama, 2005), thereby increasing bird species fitness (Jullien and Clobert, 2000). Joining mixed-species flocks to explore aerial leaf litter more thoroughly through acrobatic maneuvers (e.g. stretching, hanging, and probing) as shown in study babblers (Mansor and Ramli, 2017) may also provide benefits for these species compared to live-leaf gleaners (Remsen and Parker, 1984). In addition, the short and weak rictal bristles of most babblers allow them to forage on curled dead leaves without producing excess noise, further reducing their predation risk. Although some babblers occurred in mixed-species flocks in the present study, most occurred as single individuals, in pairs, or in very small conspecific groups. Laggards in flocks, such as spending long times exploiting the aerial leaf litter, may fail to catch up with the overall flock, leading to them being left behind (Kotagama and Goodale, 2004).

The present study revealed that the different species of sympatric dead-leaf foragers utilized different foraging strata, ranging from 0.61 to 6.45 m ($F_{5,48} = 3.703$; $p = 0.014$). The hypothesis that foraging height is an important factor in shaping bird species assemblages was suggested by MacArthur and MacArthur (1961) and has been widely tested and supported (Mansor and Sah, 2012; Freeman, 2014; Hamer et al., 2015). Variation in the carbon isotope values of insects between upper and lower vegetation zones (Roswag et al., 2015) suggest variation in the distribution of insect groups among vegetation layers. In addition, different habitat strata may support unique groups and distributions of insects (Gokula and Vijayan, 2000). Different prey groups were believed to be taken by different groups of height-partitioned birds (Mansor et al., 2018).

The various body sizes of sympatric dead-leaf foragers may facilitate their coexistence through variation in prey selection (Radford and Du Plessis, 2003). Both specialist and regular dead-leaf forager species in the present study differ slightly in mean body weight, which ranges from 13.95 g to 28.85 g. It is expected that larger birds consume larger prey items (Recher et al., 2002), which may allow few species to overlap in certain foraging niche. For instance, larger babblers (e.g. the black-throated babbler) were observed feeding on larger prey items than were the smaller babblers (e.g. chestnut-winged babbler) in Malaysia (Mansor et al., 2018). Such partitioning between residents and migrants was also documented in the Neotropics; resident species frequently feed on larger arthropods, whereas migrant species mostly feed on small hard-bodied arthropods (Poulin and Lefebvre, 1996). However, most birds display specialized morphological traits related to specific feeding strategies to enable efficient foraging in certain microhabitats, which results in niche partitioning (Luther and Greenberg, 2011; Mansor and Sah, 2012).

The present study revealed that aerial leaf litter provides a suitable habitat for numerous arthropod groups, such as coleopterans, hymenopterans, dipterans, lepidopterans, blattodeans, and arachnids. This finding differs to some extent from work in Panama (Gradwohl and Greenberg, 1982) and Peru (Rosenberg, 1993) that found coleopterans, roaches, orthopterans, and spiders were the dominant taxa in aerial leaf litter, thus revealing that litter-dependent arthropods may vary across regions. Alternatively, the difference between studies might reflect the capability of next-generation sequencing platforms to

amplify the DNA of soft-bodied litter-dependent arthropods (e.g. the larval stages of Diptera and Lepidoptera) and microarthropods (e.g. Collembola), which were not evident in earlier studies that depended upon morphologically-based identification. The preference of many coleopterans for arboreal curled dead leaves as daytime roosts (Greenberg, 1987) may help explain their high numbers. In contrast to Rosenberg (1993), the present study revealed Hymenoptera as abundant in aerial leaf litter. Aerial leaf litter is also used as a nesting site by many arboreal tropical ant species (Longino and Nadkarni, 1990). Spiders that hunt arthropods roost in aerial leaf litter (Gradwohl and Greenberg, 1982), which may partially explain the high number of spiders encountered in this substrate.

Aerial dead-leaf foragers may require more time and energy to search and extract prey due to the patchy distribution of this substrate relative to live green leaves (Remsen and Parker, 1984). This patchiness would increase the average travelling time between foraging substrates. The ability of dead-leaf specialists to manipulate and consume large litter-dependent arthropods (Rosenberg, 1993) would help maintain their foraging fitness. Arthropod biomass can be greater in aerial leaf litter than in live leaves due to its larger body sizes in the former than on the latter, as well as differences in arthropod taxonomic groups (Rosenberg, 1997). Large arthropods from aerial leaf litter were observed to be consumed by babblers, which typically spent more than 3 min foraging among the same cluster of curled dead leaves. Therefore, effectively defending an area with numerous clusters of curled dead leaves could guarantee sufficient year-round food resources. Most resident birds foraging on aerial leaf litter are known to actively defend their territories even against conspecifics (Powell, 1979; Munn and Terborgh, 1979).

4.1. Implications for conservation and management

We found that all of the dead-leaf specialists and regular users in lowland Malaysian rainforests were members of the family Timaliidae and Pellorneidae. Among babbler species observed in this study, the chestnut-winged babbler and the black-throated babbler exhibited the strongest association with aerial leaf litter (over 75% of recorded observations). This finding suggests a high dependence of these species on aerial leaf litter and their greater potential vulnerability to disturbance that reduces understory vegetation needed to capture fallen canopy leaves in lowland Malaysian rainforests. Microhabitat selection in these species may limit their foraging opportunities but effectively reduce interspecific competition from live green-leaf foragers. Given this limitation, it is vital for dead-leaf foragers to have slender bills to forage without damaging curled dead leaves. Leaving such leaves intact ensures that these leaves can continue to provide long-term microhabitats for newly established litter-dependent arthropods, a food source for dead-leaf foragers. The strong association between babblers and aerial leaf litter makes these birds good indicators of the abundance of the resource (litter-dependent arthropods).

Babblers are a key Malaysian insectivorous bird group (Yong et al., 2011). They forage mostly in the understory and are very sensitive to habitat disturbance (Fimbel et al., 2001; Mansor and Ramli, 2017; Styring et al., 2018). Such sensitive bird species may be unable to adapt to the conditions generated by habitat loss and degradation. However, fragmented forests and advanced secondary forests are frequently comprised of numerous understory vegetation types that capture fallen leaves, which may encourage dead-leaf foragers to colonize degraded habitats. The understory shrubs, woody vines (DeWalt et al., 2006; Tarbox et al., 2018), ferns, small palms (Vargas et al., 2011), and rattans (Styring et al., 2016) that are abundant in advanced forest fragments are thus very useful in capturing fallen leaves. This attribute increases the probability that fragmented habitats can act as ecological traps when birds actively select poor habitats for reproduction over healthy forests, especially forest-edge species (Ries and Fagan, 2003). Although the conditions of forest fragments are degraded, their continuity and proximity to other large fragments may provide consistent resources and foraging opportunities for dead-leaf foragers.

Bird groups other than babblers were occasionally observed using aerial leaf litter in the present study as well as previous studies (Mansor and Sah, 2012). These species included the hairy-backed bulbul, the white-bellied erpornis (*Erpornis zantholeuca*), and the wintering Arctic warbler (*Phylloscopus borealis*). Therefore, the removal of understory vegetation that can intercept fallen canopy leaves can be expected to reduce foraging opportunities for both resident and migratory birds as well as live-leaf foragers. The structure of understory plants also plays a significant role in the capture of falling dead leaves. The understory shrubs, woody vines, ferns, small palms, and rattans that are abundant in tropical forests are also particularly useful in intercepting forest canopy litterfall. Both canopy and understory plant removal may alter habitat microclimates (Qiao et al., 2014; Lin et al., 2015), which is expected to disturb the abundance and composition of litter-dependent arthropods (Turner and Foster, 2009) and thereby affect dead-leaf forager assemblages (Terborgh, 1980). In addition, understory plants may play significant roles in sustaining forest ecosystems and nutrient cycling (Qiao et al., 2014; Wang et al., 2016). The present study highlights the importance of managing and conserving all vegetation layers (from the understory to the emergent layer) that can provide fallen leaves and/or capture them at various strata to ensure a continuous supply of aerial leaf litter.

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Disclosure statement

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References

- Bird, S.B., Coulson, R.N., Fisher, R.F., 2004. Changes in soil and litter arthropod abundance following tree harvesting and site preparation in a loblolly pine (*Pinus taeda* L.) plantation. *For. Ecol. Manage.* 202, 195–208.
- Bregman, T.P., Sekercioglu, C.H., Tobias, J.A., 2014. Global patterns and predictors of bird species responses to forest fragmentation: implications for ecosystem function and conservation. *Biol. Conserv.* 169, 372–383.
- Brown, D.S., Jarman, S.N., Symondson, W.O.C., 2012. Pyrosequencing of prey DNA in reptile faeces: analysis of earthworm consumption by slow worms. *Mol. Ecol. Resour.* 12, 259–266.
- Cizungu, L., Staelens, J., Huygens, D., Walangululu, J., Muhindo, D., Van Cleemput, O., Boeckx, P., 2014. Litterfall and leaf litter decomposition in a central African tropical mountain forest and Eucalyptus plantation. *For. Ecol. Manage.* 326, 109–116.
- Clark, D.B., 1996. Abolishing virginity. *J. Trop. Ecol.* 12 (5), 735–739.
- da Silva, W.B., Périco, E., Dalzochio, M.S., Santos, M., Cajiaba, R.L., 2018. Are litterfall and litter decomposition processes indicators of forest regeneration in the neotropics? Insights from a case study in the Brazilian Amazon. *For. Ecol. Manage.* 429, 189–197.
- Dearden, F.M., Wardle, D.A., 2008. The potential for forest canopy litterfall interception by a dense fern understorey, and the consequences for litter decomposition. *Oikos* 117, 83–92.
- DeWalt, S.J., Ickes, K., Nilus, R., Harms, K.E., Burslem, D.F., 2006. Liana habitat associations and community structure in a Bornean lowland tropical forest. *Plant Ecol.* 186, 203–216.
- Dupuy, J.M., Chazdon, R.L., 2008. Interacting effects of canopy gap, understorey vegetation and leaf litter on tree seedling recruitment and composition in tropical secondary forests. *For. Ecol. Manage.* 255 (11), 3716–3725.
- Edgar, R.C., 2013. UPARSE: highly accurate OTU sequences from microbial amplicon reads. *Nat. Methods* 10, 996–998.
- Fagan, L.L., Didham, R.K., Winchester, N.N., Behan-Pelletier, V., Clayton, M., Lindquist, E., Ring, R.A., 2006. An experimental assessment of biodiversity and species turnover in terrestrial vs. canopy leaf litter. *Oecologia* 147 (2), 335–347.
- Fayle, T.M., Bakker, L., Cheah, C., Ching, T.M., Davey, A., Dem, F., Earl, A., Huaimi, Y., Hyland, S., Johansson, B., Ligtermoet, E., Lim, R., Lin, L.K., Luangyotha, P., Herlander, Martins, B., Palmeirim, A.F., Paninhuan, S., Rojas, S.K., Sam, L., Sam, P.T.T., Susanto, D., Wahyudi, A., Walsh, J., Weigl, S., Craze, P.G., Jehle, R., Metcalfe, D., Trevelyan, R., 2010. A positive relationship between ant biodiversity and predatory function across a disturbance gradient in a south-east Asian rain forest. *Myrmecol. News* 14, 5–12.
- Fimbel, R.A., Grajal, A., Robinson, J.G., 2001. The Cutting Edge: Conservation Wildlife in Logged Tropical Forest. Colombia University Press, New York.
- Fox, V.L., Buehler, C.P., Byers, C.M., Drake, S.E., 2010. Forest composition, leaf litter, and songbird communities in oak- vs. maple-dominated forests in the eastern United States. *For. Ecol. Manage.* 259 (12), 2426–2432.
- Freeman, B., 2014. Sexual niche partitioning in two species of New Guinean *Pachycephala* whistlers. *J. Ornithol.* 85 (1), 23–30.
- Gluckman, T.L., Cardoso, G.C., 2010. The dual function of barred plumage in birds: camouflage and communication. *J. Evol. Biol.* 23 (11), 2501–2506.
- 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.
- Goodale, E., Kotagama, S.W., 2005. Testing the roles of species in mixed-species bird flocks of a Sri Lankan rain forest. *J. Trop. Ecol.* 21, 669–676.
- Gradwohl, J., Greenberg, R., 1980. Barro Colorado island, Panama. *Auk* 97, 385–395.
- Gradwohl, J., Greenberg, R., 1982. The effect of a single species of avian predator on the arthropods of aerial leaf litter. *Ecology* 63 (2), 581–583.
- Greenberg, R., 1987. Seasonal foraging specialization in the worm-eating warbler. *Condor* 89, 158–168.
- Greenberg, R., 2000. Birds of many feathers: the formation and structure of mixed-species flocks of forest birds. In: Boinski, S., Gerber, P.A. (Eds.), *On the Move: How and Why Animals Travel in Groups*. University of Chicago Press, Chicago, pp. 521–558.
- Hamer, K.C., Newton, R.J., Edwards, F.A., Benedict, 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.
- Handl, S., Dowd, S.E., Garcia-Mazcorro, J.F., Steiner, J.M., Suchodolski, J.S., 2011. Massive parallel 16S rRNA gene pyrosequencing reveals highly diverse fecal bacterial and fungal communities in healthy dogs and cats. *FEMS Microbiol. Ecol.* 76 (2), 301–310.
- Ishak, H.D., Plowes, R., Sen, R., Kellner, K., Meyer, E., Estrada, D.A., Dowd, S.E., Mueller, U.G., 2011. Bacterial diversity in *Solenopsis invicta* and *Solenopsis geminata* ant colonies characterized by 16S amplicon 454 pyrosequencing. *Microb. Ecol.* 61 (4), 821–831.
- Iverson, L.R., Peters, M.P., Bartig, J.L., Rebbeck, J., Hutchinson, T.F., Matthews, S.N., Stout, S., 2018. Spatial modeling and inventories for prioritizing investment into oak-hickory restoration. *For. Ecol. Manage.* 424, 355–366.
- Jedlicka, J.A., Greenberg, R., Perfecto, I., Philpott, S.M., Dietsch, T.V., 2006. Seasonal shift in the foraging niche of a tropical avian resident: resource competition at work? *J. Trop. Ecol.* 22, 385–395.
- Jullien, M., Clobert, J., 2000. The survival value of flocking in neotropical birds: reality or fiction? *Ecology* 81, 3416–3430.
- King, R.A., Symondson, W.O.C., Thomas, R.J., 2015. Molecular analysis of faecal samples from birds to identify potential crop pests and useful biocontrol agents in natural areas. *Bull. Entomol. Res.* 105 (3), 261–272.
- Kotagama, S.W., Goodale, E., 2004. The composition and spatial organization of mixed-species flocks in a Sri Lankan rainforest. *Forktail* 20, 63–70.
- Krüger, F., Harms, I., Fichtner, A., Wolz, I., Sommer, R.S., 2012. High trophic similarity in the sympatric North European trawling bat species *Myotis daubentonii* and *Myotis dasycneme*. *Acta Chiropterol.* 14 (2), 347–356.
- Lack, D., Lack, P., 1972. Wintering warblers in Jamaica. *Living Bird*, 11, 129–153.
- Lambert, F.R., 1991. Keystone characteristics of bird-dispersed *Ficus* in a Malaysian lowland rain forest. *J. Ecol.* 79, 793–809.
- Leme, A., 2001. Foraging patterns and resource use in four sympatric species of antwrens. *J. Field Ornithol.* 72, 221–227.
- Lin, N., Bartsch, N., Heinrichs, S., Vor, T., 2015. Long-term effects of canopy opening and liming on leaf litter production, and on leaf litter and fine-root decomposition in a European beech (*Fagus sylvatica* L.) forest. *For. Ecol. Manage.* 338, 183–190.
- Longino, J.T., Nadkarni, N.M., 1990. A comparison of ground and canopy leaf litter ants (Hymenoptera: Formicidae) in a neotropical montane forest. *Psyche* 97, 81–93.

- Luther, D., Greenberg, R., 2011. The island syndrome in coastal wetland ecosystems: convergent evolution of large bills in mangrove passerines. *Auk* 128, 201–204.
- MacArthur, R.H., MacArthur, J.W., 1961. On bird species diversity. *Ecology* 42 (3), 594–598.
- Mansor, M.S., Abdullah, N.A., Halim, M.R.A., Nor, S.Md, Ramli, R., 2018. Diet of tropical insectivorous birds in lowland Malaysian rainforest. *J. Nat. Hist.* 52 (35–36), 2301–2316.
- Mansor, M.S., Ramli, R., 2017. Foraging niche segregation in Malaysian babblers (Family: Timaliidae). *PLoS One* 12 (3), e0172836.
- Mansor, M.S., Sah, S.A.M., 2012. Foraging patterns reveal niche separation in tropical insectivorous birds. *Acta Ornithol* 47 (1), 27–36.
- Morton, E.S., 1980. Adaptations to seasonal changes by migrant land birds in the Panama canal zone. In: Keast, A., Morton, E.S. (Eds.), *Migrant Birds in the Neotropics: Ecology, Behavior, Distribution, and Conservation*. Smithsonian Institution Press, Washington DC, pp. 437–453.
- Munn, C.A., Terborgh, J.W., 1979. Multi-species territoriality in Neotropical foraging flocks. *Condor* 81 (4), 338–347.
- Poulin, B., Lefebvre, G., 1996. Dietary relationships of migrant and resident birds from a humid forest in Central Panama. *Auk* 113 (2), 277–287.
- Powell, G.V., 1979. Structure and dynamics of interspecific flocks in neotropical mid-elevation forest. *Auk* 96, 375–390.
- Qiao, Y., Miao, S., Silva, L.C.R., Horwath, W.R., 2014. Understory species regulate litter decomposition and accumulation of C and N in forest soils: a long-term dual-isotope experiment. *For. Ecol. Manage.* 329, 318–327.
- Radford, A.N., Du Plessis, M.A., 2003. Bill dimorphism and foraging niche partitioning in the Green Woodhoopoe. *J. Anim. Ecol.* 72 (2), 258–269.
- Ratnasingham, S., Hebert, P.D.N., 2007. BOLD: the barcode of Life data system. *Mol. Ecol. Notes* 7, 355–364. www.barcodinglife.org.
- Recher, H.F., Davis, J.W.E., Calver, M.C., 2002. Comparative foraging ecology of five species of ground-pouncing birds in western Australian woodlands with comments on species decline. *Ornithol. Sci.* 1 (1), 29–40.
- Remsen Jr., J.V., Parker III, T.A., 1984. Arboreal dead-leaf-searching birds of the Neotropics. *Condor* 86, 36–41.
- Remsen Jr., J.V., Robinson, S.K., 1990. A classification scheme for foraging behavior in terrestrial habitats. *Stud. Avian Biol.* 13 (13), 144–160.
- Ries, L., Fagan, W.F., 2003. Habitat edges as a potential ecological trap for an insect predator. *Ecol. Entomol.* 28 (5), 567–572.
- Robson, C., 2008. *A Field Guide to the Birds of South-East Asia*. New Holland Publishers, London.
- Rosenberg, K.V., 1990. Dead-leaf foraging specialization in tropical forest birds: measuring resource availability and use. *Stud. Avian Biol.* 13, 360–368.
- Rosenberg, K.V., 1993. Diet selection in Amazonian antwrens: consequences of substrate specialization. *Auk* 110 (2), 361–375.
- Rosenberg, K.V., 1997. Ecology of dead-leaf foraging specialists and their contribution to Amazonian bird diversity. *Ornithol. Monogr.* 48, 673–700.
- Rosenvald, R., Lohmus, A., Kraut, A., Remm, L., 2011. Bird communities in hemiboreal old-growth forests: the roles of food supply, stand structure, and site type. *For. Ecol. Manage.* 262 (8), 1541–1550.
- 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.
- Sillett, T.S., 1994. Foraging ecology of epiphyte-searching insectivorous birds in Costa Rica. *Condor* 96, 863–877.
- Silver, W.L., Hall, S.J., González, G., 2014. Differential effects of canopy trimming and litter deposition on litterfall and nutrient dynamics in a wet subtropical forest. *For. Ecol. Manage.* 332, 47–55.
- Sridhar, H., Beauchamp, G., Shanker, K., 2009. Why do birds participate in mixed-species foraging flocks? A large-scale synthesis. *Anim. Behav.* 78, 337–347.
- 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.
- Styring, A.R., Unggang, J., Jukie, A., Tateh, O., Megom, N., Sheldon, F.H., 2018. Bird community structure in native forest fragments and *Acacia mangium* plantations in Borneo. *Wilson J. Ornithol.* 130 (1), 112–130.
- Tarbox, B.C., Robinson, S.K., Loiselle, B., Flory, S.L., 2018. Foraging ecology and flocking behavior of insectivorous forest birds inform management of Andean silvopastures for conservation. *Condor* 120 (4), 787–802.
- Terborgh, J., 1980. Causes of tropical species diversity. *Proc. XVII. Int. Ornithol. Congr.* 955–961.
- Trentini, C.P., Villagra, M., Gómez Pámies, D., Bernava Laborde, V., Bedano, J.C., Campanello, P.I., 2018. Effect of nitrogen addition and litter removal on understory vegetation, soil mesofauna, and litter decomposition in loblolly pine plantations in subtropical Argentina. *For. Ecol. Manage.* 429, 133–142.
- Triplehorn, C.A., Johnson, N.F., 2005. *Borror and DeLong's Introduction to the Study of Insects*, seventh ed. Thomson Brooks/Cole, California.
- Turner, E.C., Foster, W.A., 2009. The impact of forest conversion to oil palm on arthropod abundance and biomass in Sabah, Malaysia. *J. Trop. Ecol.* 25, 23–30.
- Vargas, L.E., Sánchez, N.V., Avalos, G., 2011. Forest structure and territory size relationship in the neotropical understory insectivore *Henicorhina leucosticta*. *J. Trop. Ecol.* 27 (1), 65–72.
- Wang, F.C., Fang, X.M., Ding, Z.Q., Wan, S.Z., Chen, F.S., 2016. Effects of understory plant root growth into the litter layer on the leaf litter decomposition of two woody species in a subtropical forest. *For. Ecol. Manage.* 364, 39–45.
- Wells, D.R., 1999. *The Birds of the Thai-Malay Peninsula. Volume I: Non-passerines*. Academic Press, London.
- Wells, D.R., 2007. *The Birds of the Thai-Malay Peninsula. Volume II: Passerines*. Christopher Helm, London.
- Whitaker, J.O., Castor, L., 2010. Identification of insect parts found in bat Guano. In: Kunz, T.H., Parsons, S. (Eds.), *Ecological and Behavioural Methods for the Study of Bats*, second ed. Johns Hopkins University Press, Baltimore (MD), pp. 567–592.
- Yong, D.L., Qie, L., Sodhi, N.S., Koh, L.P., Peh, K.S., Lee, T.M., Lim, H.C., Lim, S.L.H., 2011. Do insectivorous bird communities decline on land-bridge forest islands in Peninsular Malaysia? *J. Trop. Ecol.* 27 (1), 1–4.
- Yoshida, T., Hijii, N., 2006. Spatiotemporal distribution of aboveground litter in a *Cryptomeria japonica* plantation. *J. For. Res.* 11, 419–426.
- 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.