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Foraging ecology and occurrence of 7 sympatric babbler species (Timaliidae) in the lowland rainforest of Borneo and peninsular Malaysia

Alison R. STYRING[a,*], Roslina RAGAI[b], Mohamed ZAKARIA[c], and Frederick H. SHELDON[d]

[a]The Evergreen State College, Olympia, Washington, 98505, USA, [b]Grand Perfect Sdn. Bhd., ParkCity Commerce Square, 97000 Bintulu, Sarawak, Malaysia, [c]Department of Forest Management, Faculty of Forestry, Universiti Putra Malaysia, Serdang, Selangor, Malaysia, and [d]Museum of Natural Science and Department of Biological Sciences, Louisiana State University, Baton Rouge, Louisiana, USA 70803.

*Address correspondence to Alison R Styring. E-mail: styringa@evergreen.edu

Abstract

Understanding foraging strategies of birds is essential to understanding mechanisms of their community assembly. To provide such information on a key Southeast Asian rainforest family, the babblers (Timaliidae), we evaluated foraging behavior and abundance in 7 morphologically and behaviorally similar sympatric species (*Cyanoderma erythropterum*, *C. rufifrons*, *Stachyris maculata*, *S. nigricollis*, *S. poliocephala*, *Macronus ptilosus*, and *Mixornis gularis*) in 5 habitats defined by structural complexity: (1) continuous native rainforest, (2) logged native rainforest fragments, (3) mature industrial tree plantation, (4) young industrial plantation, and (5) oil palm plantation. Enough data were obtained to compare abundance in all 7 species and foraging behavior in 5. All species were common in forest fragments and mature industrial tree plantations and less so in continuous rainforest and young industrial plantations; only *M. gularis* occurred in oil palm. In terms of foraging, *M. gularis* was the greatest generalist; *C. rufifrons* foraged mainly on live leaves in the forest midstory; and *S. maculata*, *C. erythropterum*, and *M. ptilosus* foraged mainly on dead leaves suspended in understory vegetation at significantly different heights. The dead-leaf substrate depends on a rich supply of falling leaves and extensive understory structure, conditions most common in native forest and old industrial plantations, and less so in mature forest, young plantations, and oil palm. Because of the importance of foraging data to understanding and managing biodiversity, we encourage the development of foraging fields in eBird (ebird.org), so that birdwatchers may help collect these relatively rare data.

Key words: Brunei, dead leaves, logged forest, plantation, Sabah, Sarawak.

A major focus of evolutionary biology is to explain community assembly in terms of phylogenetic history and current ecological interactions (Ricklefs 1987; Webb et al. 2002; Hubbell 2005; Johnson and Stinchcombe 2007). For tropical forests, knowledge of historical sources of taxa and ecological maintenance of communities is especially important not only to understanding of the causes of biodiversity (Mittelbach et al. 2007), but also to managing wildlife as these forests shrink from human disturbance (Wilson 2005; Sodhi and Brook 2006).

In ornithology, ecologists have attempted to explain the coexistence of large numbers of tropical bird species in terms of niche partitioning for more than 50 years (MacArthur 1964; Cody 1974; Diamond 1975; Grant 1986), and the introduction of an historical perspective into community ecology began effectively about 20 years go (Richman and Price 1992; Harvey et al. 1994), when phylogenetic estimates became reliable (Sheldon and Whittingham 1997). We now have a rich body of phylogenetic information on tropical bird groups with which to judge

evolutionary history (e.g., in Southeast Asia: Hosner et al. 2010; Jønsson et al. 2010; Moyle et al. 2011, 2012; Alström et al. 2013; den Tex and Leonard 2013) and should be in a position in terms of ecological and phylogenetic information, and theoretical development, to improve substantially our understanding of the origination, assembly, and maintenance of tropical bird communities (Webb et al. 2002; Ricklefs and Bermingham 2008; Graham et al. 2009; Ricklefs and Jønsson 2014; Smith et al. 2014).

Knowledge of foraging ecology is particularly important to understanding niche partitioning in bird communities (Lack 1971; Robinson and Holmes 1982; Grant 1986; Price 1991). However, in Southeast Asian rainforests, apart from hornbills and woodpeckers, whose foraging ecology is reasonably well known (Leighton 1982; Poonswad 1998; Styring et al. 2002; Lammertink 2004; Styring and Zakaria 2004b; Kinnaird and O'Brien 2007), only a handful of comparative foraging studies exist. In Sundaland, such studies have been restricted to Peninsular Malaysia, Singapore, and Borneo. Lambert (1989a, 1989b) examined foraging in fig trees by pigeons, barbets, bulbuls, flowerpeckers, and other frugivores. A few researchers have examined the contents of stomachs (Wong 1986), feces (Yap et al. 2007), or boluses (Lourie and Thompkins 2000), or have analyzed stable isotope variation (Edwards et al. 2013), in attempts to understand bird diet within or among communities. Only 4 studies have studied community-wide foraging directly by observing what birds actually do. Two of these examined phylogenetically disparate taxa in mangroves (Noske 1995; Sodhi et al. 1997), and 2 examined foraging microhabitats in closely related, sympatric, rainforest insectivores (Soh 2001; Mansor and Sah 2012). The latter 2 studies are expected to be most informative in terms of resource partitioning because closely related species share recent phylogenetic history and are relatively similar in morphology, behavior, and physiology (Peterson et al. 1999). Thus, such species most likely employ different foraging strategies to reduce competition (Lack 1971; Price 1991; Naoki 2007).

To further our understanding of niche partitioning in understory insectivorous bird communities in insular Southeast Asia, we collected foraging data on 7 species of babblers (Timaliidae) from various types of native and plantation forests in Peninsular Malaysia and Borneo. These species were: chestnut-winged babbler *Cyanoderma erythropterum*, rufous-fronted babbler *Cyanoderma rufifrons*, chestnut-rumped babbler *Stachyris maculata*, black-throated babbler *Stachyris nigricollis*, gray-headed babbler *Stachyris poliocephala*, fluffy-backed tit-babbler *Macronus ptilosus*, and striped tit-babbler *Mixornis gularis* (classification from Moyle et al. 2012). *Mixornis gularis* in this case included *M. bornensis*, a subjective synonym for the geographic variant inhabiting Borneo (Collar and Robson 2007; Lim et al. 2011). Of the 7 species, 2—*M. gularis* (sensu lato) and *C. rufifrons*—are widespread in Southeast Asia. The other 5 are restricted to Borneo, Sumatra, the Malay Peninsula, and some intervening islands (Sheldon et al. 2015). All are members of a single clade (Timaliinae), but the species are not particularly closely related to one another within that clade (Moyle et al. 2012). Instead, they are dispersed throughout the subfamily such that no 2 are sister species. Despite their phylogenetic dispersion, the 7 species are remarkably similar to one another in plumage, voice, and social behavior, and they are sympatric in secondary, disturbed primary, and some plantation forests of Borneo, Sumatra, and the Malay Peninsula (Van Marle and Voous 1988; Smythies 1999; Wells 2007).

Most of these babblers appear to be sensitive to extensive forest disturbance or replacement by plantations. Of the 7 species, 3 have been listed as "near threatened" (*M. ptilosus*, *S. maculata*, and *S. nigricollis*) by the IUCN (2013). These 3 were extirpated from Singapore by deforestation and development during the first half of the 20th century (Castelletta et al. 2000). Only one, *M. gularis*, occurs in oil palm *Eleais guineensis* or in rubber *Hevea brasiliensis* plantations where the understory has been cleared (Peh et al. 2006; Sheldon et al. 2010). Another, *S. poliocephala*, is notably rare or uncommon in some secondary forests (Peh et al. 2005; Sheldon et al. 2010; Styring et al. 2011). All of the species, except *C. erythropterum* and *M. gularis*, occur in low numbers in industrial plantations, i.e., plantations that produce pulp, chip, and inexpensive wood products from trees such as mangium *Acacia mangium* and Albizia *Paraserianthes falcataria* (Sheldon et al. 2010; Styring et al. 2011).

Variation in the occurrence of these highly similar species suggested they require different microhabitats for survival. Discovery of these differences should provide insight into how the birds avoid competition and should aid analyses of babbler phylogenetic community assembly in Southeast Asia. Understanding the species' microhabitat differences would also help wildlife managers design or maintain forested areas for these birds in cities like Singapore and in exotic tree plantations that are sweeping the region.

The objectives for this study were specifically: (1) to examine the foraging behaviors of the 7 babbler species described above with the aim of identifying key foraging preferences in each species and potentially important microhabitats, and (2) to estimate abundances of each species in large tracts of native forest, in native forest fragments, and in plantation habitats.

Materials and Methods

Study sites

Research was conducted at 4 sites: Sungai Lalang Forest Reserve, Selangor, Peninsular Malaysia; Tasek Merimbun Heritage Park, Brunei; and Sabah Softwoods, Sabah, and Sarawak Planted Forest, Sarawak, in Malaysian Borneo (Figure 1). Sungai Lalang Forest Reserve (SLFR; 3°4′ N, 101°50′ E, ~100–800 m above sea level; hereafter m.a.s.l.) is ~16,000 ha of forest reserve that consists mostly of selectively logged native forest and primary forest reserves. Forest types at SLFR ranged from lowland to hill dipterocarp forest. Surveys at SLFR were conducted in July–August 1999, February–April 2000, and June–July 2000 at 3 sites: a 260 ha area of forest
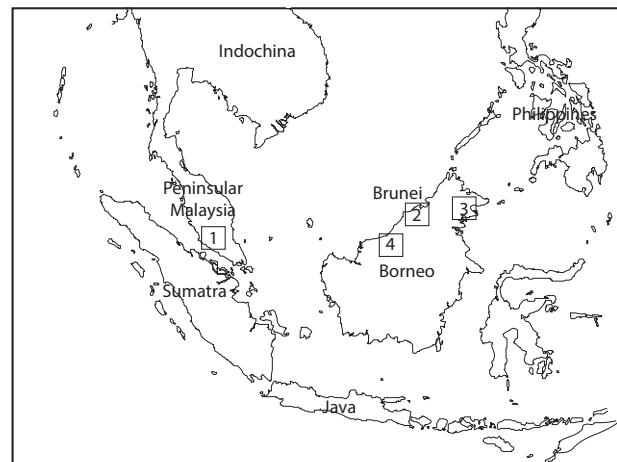
Figure 1. Study sites. (1) Sungai Lalang Forest Reserve, Selangor, Malaysia (SLFR); (2) Taske Merimbun Heritage Park, Brunei (TMHP); (3) Sabah Softwoods, Sabah, Malaysia (SS); and (4) Sarawak Planted Forest, Sarawak, Malaysia (SPF).

that had been selectively logged in 1993 (180–230 m.a.s.l.), a 387 ha area of forest that had been selectively logged in 1990 (100–250 m.a.s.l.), and a 82 ha Virgin Jungle Reserve that had never been logged (130–250 m.a.s.l.). Tasek Merimbun Heritage Park (TMHP; 4°35′ N, 114°40′ E, ~ 20 m.a.s.l.) is a ~ 7,800 ha reserve that consists mainly of primary lowland peat swamp and dipterocarp forest. Work at TMHP was conducted in June 1999. Sabah Softwoods (SS; 4°37′ N, 117°44′ E, ~ 300 m.a.s.l.) is a ~ 60,000 ha tree plantation consisting of mangium, Albizia, and other industrial species, oil palm, and logged native forest (; Sheldon et al. 2010; Sheldon and Styring 2011; Styring et al. 2011). Surveys were conducted at SS in June–July 2005 in recently established (<5 years) and mature (≥ 5 years) mangium, mature Albizia, 10-year-old oil palm, and logged native forest. Sarawak Planted Forest (SPF; 2°56′ N, 113°07′ E, ~ 50 m.a.s.l.) is a ~ 500,000 ha of mixed-use area that consists of ~ 200,000 ha of industrial tree plantation (primarily mangium), 2 permanent reserves of old-growth forest (~ 20,000 ha each), a ~ 25,000 ha wildlife corridor that consists of logged native forest, and native customary rights land (Stuebing 2005). Surveys were conducted at SPF in July–August 2006, August 2008, August 2010, and March–April 2011 in young and old mangium, logged native forest, and old-growth forest (Sheldon and Styring 2011; Styring et al. 2011).

Research at SLFR was a collaborative effort to understand forest recovery after selective logging (Styring and Zakaria 2004a; Haneda et al. 2005; Zakaria et al. 2005), whereas research at the three Bornean sites focused primarily on differences in rainforest bird diversity among native forest, industrial tree plantation, and oil palm (Sheldon et al. 2010; Styring et al. 2011). Both purposes allowed copious opportunities to observe babbler foraging under a variety of habitat circumstances. Although the spatial distribution of study sites was relatively broad, all observations came from areas that were historically considered lowland rainforest. For our foraging observations, habitat was categorized into 5 broad types: (1) continuous native forest (logged and unlogged; tracts at least 50 in size), (2) native forest fragments (tracts < 15 ha in size), (3) mature exotic tree plantation (≥ 5 years old), (4) young exotic tree plantation (< 5 years old) and (5) oil palm (≥ 10 years old, Table 1).

Abundance data

Point counts were conducted at all sites except TMHP along transects at each site. At each point, a 3-minute survey was conducted using distance sampling (Buckland et al. 2001). Each bird seen or heard was recorded and its distance measured with a laser rangefinder. Duration of the observation period was established at SLFR to obtain a "snapshot" estimate of bird densities and to avoid positive bias in density estimates (Buckland 2006). All surveys were conducted between 0600 and 0900 h. At SS, transects were 1000 m long and surveyed one time each: 4 in oil palm ($n = 80$ surveys), 5 in

young industrial plantation ($n = 100$), 18 in old industrial plantation ($n = 360$), and 6 in continuous native forest ($n = 120$); totaling 33 km surveyed. At SPF, transects were 1,000 m (except in small fragments) and surveyed one time each: 10 in young industrial plantation ($n = 200$), 24 in old industrial plantation ($n = 480$), 28 in continuous native forest ($n = 560$), and 14 in small fragments of native forest. Because the fragments at SPF were small (ranging in size from 2–14 ha), 1000 m transects were not always possible; transects ranged from 200 m in very small (2 ha) fragments to 1000 m in the largest (14 ha) fragments. Total transect length surveyed across the 14 fragments was 4.4 km ($n = 30$), and total transect length surveyed at SPF was 66.4 km. Points were spaced between 50–200 m apart along transects (50 m prior to 2006 and 200 m thereafter). Distance between points increased after 2006 when initial analyses indicated a 95% detection radius of 100 m (Styring et al. 2011). Observational records were filtered so that all detections of babblers were a minimum of 150 m apart.

Foraging data

Foraging data were collected at SLFR, TMHP, and SPF by ARS, and at SPF by RR and FHS. No foraging observations were made at SS. Foraging individuals were observed across 20 km of transects at SPF. At SLFR, transects ranged from 1200 m to 2000 m, and each was surveyed twice: 4 in recently logged forest, 5 in older logged forest, and 4 in unlogged forest; totaling 17.4 km. Foraging birds were observed along 16 transects, ranging from 500 m to 1,900 m in length and totaling 20 km. At THMP, 4 transects were surveyed 1–4 times each over a period of 1 month. These transects ranged from 900 m to 1,500 m in length and totaled 4.7 km.

Foraging observations began at the end of the dawn chorus (~ 0700 h), when birds were actively searching for food and light was adequate for observations. Surveys ended at ~ 1100 h. Foraging individuals were first detected either by sight or sound, and their behavior was documented using the methods of Remsen and Robinson (1988). Data collected included: (1) height (estimated with rangefinder or clinometer) above ground; (2) foraging substrate—dead leaf, suspended dead leaf, live leaf, liana, rattan, palm, dead wood (dead liana/rattan, dead branch), loose bark; and (3) attack maneuver (probe, hang down, glean, and reach). An individual bird was observed until it successfully acquired a food item (determined either by the observation of the food or by eating behavior). Foraging observations were recorded once per individual per species per transect per survey to ensure independence. Individuals observed on a given transect may have been observed in separate surveys, but given the high frequency of target species detection (on most surveys target species were detected at least twice) compared to the low rate of foraging observations (few foraging birds were observed per transect-survey), the probability of observing any one individual more than once was small. Moreover, repeated surveys of transects were

Table 1. Study sites and types of data collected

Study site	Continuous native forest	Native forest fragment	Old plantation	Young plantation	Oil Palm
Sungai Lalang Forest Reserve	Point counts, foraging, habitat	na	na	na	na
Tasek Merimbun Heritage Park	Foraging	na	na	na	na
Sabah Softwoods	Point counts, habitat	na	Point counts, habitat	Point counts, habitat	Point counts, habitat
Sarawak Planted forests	Point counts, foraging, habitat	point counts	Point counts, foraging, habitat	Point counts, foraging, habitat	Point counts, foraging, habitat

often temporally spaced by 5–12 months, further reducing the likelihood of repeat observations. Even with this low probability, every effort was made to assure independence in observations by spacing transects as far apart as possible and traversing them in different directions (e.g., from N to S on 1 day and S to N on another).

Habitat data

Habitat data were collected at 3 survey sites (SLFR, SS, and SPF), but sampling approach and variables collected differed somewhat between SLFR, where surveyed habitat was within established 3 ha forest monitoring plots in each forest type, and SS/SPF, where habitat surveys were conducted at the location of each point count. (Styring and Zakaria 2004a; Sheldon et al. 2010; Styring et al. 2011). In most respects, data for habitats are comparable among sites by including such common variables as number of forest layers (maximum of 3: herbaceous, shrub, and canopy), presence/absence of an herbaceous layer, presence/absence of a shrub layer, canopy height, and percentage canopy cover (Table 2).

Data analysis

To examine differences across habitat types, bird density was estimated using Distance 6.0 (Thomas et al. 2006). The Distance method estimates abundance based on the detection function from a sample of observations. Therefore, differences in detection associated with any factor (including habitat) that might influence detectability can be modeled into the estimates of density and abundance. Estimates are accurate if (1) all individuals at distance zero are detected, (2) movement of individuals being surveyed is random (i.e., observers do not affect bird movements), and (3) distances are accurate (Thomas et al. 2002). To meet these assumptions, observers approached points quietly and waited for several minutes before beginning a survey, measured distances with tilt-compensated laser rangefinders, and focused attention near point zero during the survey period. Density analyses were run independently for each species and data were stratified by habitat category (Table 1). We selected the half-normal key function with a cosine expansion as the most suitable model for the survey data based on visual inspection of histogram plots of detection

probability over distance and quantile-quantile corresponding to the fit of our data to the model. Cosine adjustments were made sequentially and evaluated using Aikake's Information Criterion (AIC) (Thomas et al. 2010).

To compare foraging behavior among species and to visualize substrate preferences, correspondence analysis was performed on substrates and attack maneuvers in JMP 9 (SAS 2010). This kind of analysis is particularly effective for depicting variation in foraging data (Miles 1990; Naoki 2007). Foraging height was compared among species using Analysis of Variance, and post-hoc comparisons were made using Tukey's Honestly Significant Differences in JMP 9 (SAS 2010). All means expressed in the results include associated variation expressed as $\pm$ standard deviation (SD) of the mean.

Because of the different approaches to collecting habitat data among sites, a detailed analysis of the relationships of foraging behavior or avian densities and habitat is beyond the power of inference of the dataset. However, comparisons of the habitat variables (Table 2) were made using descriptive statistics (mean $\pm$ SD) to look for any consistent patterns among the assigned habitat categories (Table 3).

Results

Habitats

General characteristics of the 5 forest categories were as follows. Canopy height: Native forest (SS, SPF, SLFR) ranged in canopy height from 17.8 ± 6.9 m in recently logged forest to 27.0 ± 3.9 m in $\sim$20-year-old logged forest. This range overlapped the height in unlogged forest sites: mean canopy height from 18.7 ± 7.2 m at SLFR to 28.1 ± 7.1 m in an old-growth forest preserve at SPF. It also overlapped the height in mature mangium and Albizia: mean height 17.3 ± 2.2 m in 5-year mangium to 29.0 ± 4.0 m in 8[+]-year-old Albizia. Younger mangium plantation and mature oil palm were substantially shorter, ranging from 8.5 ± 1.6 m in 2-year-old mangium to 9.4 ± 1.5 m in 10-year-old oil palm (Table 3). Habitat complexity: Native forest had the highest habitat complexity in terms of number of forest layers and canopy height (Figures 2 and 3). Older groves of industrial tree plantation also had high levels of habitat

Table 2. Habitat variables compared among 3 study sites: Sungai Lalang Forest Reserve, Sabah Softwoods, and Sarawak Planted Forests

Variable	Measurement
Number of forest layers	Estimated by determining presence or absence of (1) an herbaceous layer, (2) a shrub layer, and (3) a canopy layer
Herbaceous layer	Scored based on presence (score=1) or absence (score=2) of herbaceous vegetation within the sampling area
Shrub layer	Scored based on presence (score=1) or absence (score=2) of shrubby vegetation within the sampling area
Canopy height	Estimated with clinometer (SLFR) or laser rangefinder (SS&SPF)*
Canopy cover	Scored on a scale of 0–4: 0 = None; 1 = 0–25%; 2 = 25–50%; 3 = 50–75%; 4 = 75–100% at random location within plot

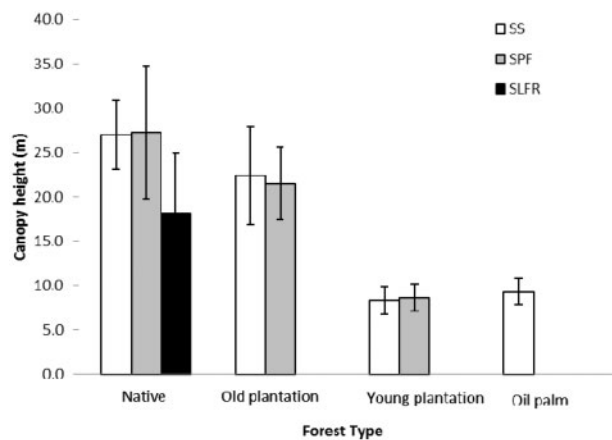*SLFR = Sungai Lalang Forest Reserve, SPF = Sarawak Planted Forests, and SS = Sabah Softwoods.

Table 3. Means and standard deviations of habitat variables collected at 3 study sites

	Native forest			Old plantation		Young plantation		Oil palm
	SLFR	SPF	SS	SPF	SS	SPF	SS	SS
Number of forest layers	3.0 ± 0.2	2.9 ± 0.03	3.0 ± 0.0	2.2 ± 0.4	1.8 ± 0.7	1.1 ± 0.3	1.0 ± 0.0	1.0 ± 0.0
Herbaceous layer	1.0 ± 0.1	1.0 ± 0.1	1.0 ± 0.0	1.0 ± 0.1	1.0 ± 0.0	0.9 ± 0.3	1.0 ± 0.0	1.0 ± 0.0
Shrub layer	1.0 ± 0.2	1.0 ± 0.1	0.5 ± 0.5	1.0 ± 0.1	1.0 ± 0.1	0.1 ± 0.3	0.5 ± 0.5	0.1 ± 0.3
Canopy height (m)	18.1 ± 6.8	27.3 ± 7.5	27.0 ± 3.9	21.5 ± 4.1	22.4 ± 5.5	8.6 ± 1.5	8.3 ± 1.5	9.3 ± 1.5
Canopy % cover	2.8 ± 0.9	2.9 ± 1.2	2.5 ± 0.6	2.8 ± 0.9	2.3 ± 0.6	3.0 ± 0.8	1.7 ± 0.8	2.4 ± 0.5

SLFR = Sungai Lalang Forest Reserve, SPF = Sarawak Planted Forests, and SS = Sabah Softwoods.
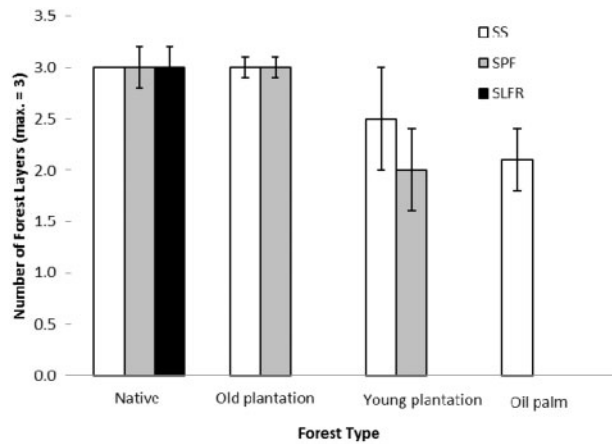
Figure 2. Average number of forest layers (± 1 SD) by forest type and field site. SS = Sabah Softwoods, SPF = Sarawak Planted Forests, and SLFR = Sungai Lalang Forest Reserve.

Figure 3. Mean canopy height (± 1 SD) by forest type and field site. SS = Sabah Softwoods, SPF = Sarawak Planted Forests, and SLFR = Sungai Lalang Forest Reserve.

complexity and a diverse array of native shrubs and trees in the understory. Young plantation and oil palm (even mature oil palm) were structurally simpler, with only 2 distinct layers.

Bird occurrence

As a whole, the species compared in this study were most abundant in moderately disturbed habitats (Table 4). Most of the species were abundant in logged native forest fragments and older industrial tree groves. They were less abundant in large areas of primary and mature logged forest and young industrial plantation. Only one taxon, *M. gularis,* was observed in mature oil palm plantation.

Foraging ecology

A total of 190 independent foraging observations were made of the 7 target species. *Cyanoderma erythropterum* was seen foraging much more frequently than the other species ($n = 101$). It was not the most common species encountered in our surveys (Table 4), but it was easier to observe than more common species, such as *Mixornis gularis*, which were almost always detected audibly. *Stachyris nigricollis* and *Stachyris poliocephala* were observed foraging only a few times ($n = 3$ and $n = 2$, respectively), although

detected audibly numerous times. Consequently, we include them in the analysis of abundance but not foraging.

Live leaves, dead leaves at ground level, and suspended dead leaves constituted the main foraging substrates of the 5 remaining species (Figure 4). Correspondence analysis of substrate preference resulted in 2 axes that explained 98% of the variation in the substrate data (Figure 5). The combination of foraging frequency, correspondence analysis, and foraging height (Figure 6) revealed several patterns. *Mixornis gularis* displayed the most general foraging behavior, feeding on live leaves in trees (48% of the observations), dead leaves on the ground (29%), and suspended dead leaves (19%). In contrast, 3 species foraged much more frequently on a single substrate type. The first 2, *C. erythropterum* and *S. maculata*, were similar in foraging, concentrating mainly on suspended dead leaves in tangles of liana, rattan, *Macaranga*, and live palm: *C. erythropterum* (75%) and *Stachyris maculata* (67%). However, they foraged at different heights (Figure 6), with *S. maculata* significantly higher (10.7 ± 4 .8 m) than *C. erythropterum* (6.1 ± 4.2 m). The third species with a single substrate preference, *Cyanoderma rufifrons*, foraged primarily on live leaves (65%). *Macronus ptilosus* had a distinctly different foraging preference than the other 4 species. It foraged in dead leaves and dead palm fronds (38%) and stayed lower to the ground (1.4 ± 1.6 m). It was often observed foraging on dead leaves that collected in the bases of living and dead Bertam palms (*Eugeissona spp.*).

Analysis of attack maneuvers resulted in 2 axes that explained 99% of the variation in the data (Figure 7). Of the species that foraged on dead leaves, *S. maculata* probed substantially more than other species (52% of observations) and obtained items frequently by gleaning (24%) and hanging (16%). *Cyanoderma erythropterum* obtained items primarily by gleaning (48%), probing (28%), and hanging (18%). *Macronus ptilosus* primarily gleaned (50%), but also probed (21%) and reached (29%). Of the 2 "live leaf" foragers, both *C. rufifrons* and *M. gularis* primarily gleaned food items (77% and 63%, respectively). *Cyanoderma rufifrons* also hung down (24%). *Mixornis gularis*' second-most frequently used maneuver was reaching (29%).

Discussion

Foraging patterns and habitats

The birds compared in this article are remarkably alike in song, plumage, sociality, and habitat (Smythies 1999; Sheldon et al. 2001; Wells 2007). Most have songs based on the same theme, described as "huh-huh-huh…," "poop-poop-poop…," etc., in different frequency-ranges and with variable cadences. Most species engage in duets; males making the characteristic vocalizations and others (females?) answering with harsh, nasal "churring" sounds. Most of the species have a similar reddish brown dorsal coloration and are striped or dark ventrally. Four species have bluish skin on the head (*M. gularis, M. ptilosus, C. erythropterum,* and *S. maculata*), which they appear to display while calling. All of the species are highly social and some may be cooperative breeders. With the exception of *S. poliocephala,* all the species forage in small to large intraspecific groups (from 3 to 18 individuals), and most attend mixed-species flocks. All are common in logged or secondary forest.

As expected from competition theory (Diamond 1975; Karr 1980), these babblers employ largely different foraging strategies and substrates, despite their similarities in other respects. *Cyanoderma erythropterum, S. maculata,* and *M. ptilosus* appear to concentrate on dead and curled leaves, which serve as hiding and nesting sites for

Table 4. Density estimates (individuals/ha) of select babblers across native and plantation forest habitats from 3 sites in Malaysia (SLFR, SPF, SS)

Species	n	CNF	NFF	MP	YP	OP
Mixornis gularis	761	3.2 (19.6)	5.3 (23.9)	11.4 (20.4)	14.4 (22.0)	14.5 (20.6)
Macronus ptilosus[a]	240	1.9 (22.1)	3.2 (27.7)	3.6 (22.1)	2.3 (22.2)	–
Cyanoderma erythropterum	350	5.4 (16.1)	5.5 (17.0)	6.6 (11.7)	2.9 (11.4)	–
Cyanoderma rufifrons	103	4.7 (22.5)	–	3.6 (20.6)	4.7 (21.8)	–
Stachyris maculata[a]	158	4.3 (12.7)	3.6 (21.1)	6.1 (12.6)	3.6 (18.5)	–
Stachyris nigricollis[a]	118	1.7 (10.9)	2.8 (13.1)	2.8 (12.8)	1.9 (11.3)	–
Stachyris poliocephala	23	8.2 (18.3)	–	14.7 (24.2)	–	–

Numbers in parenthesis are the percent coefficient of variation for each estimate. N = number of detections; CNF = continuous native forest (logged and unlogged); NFF = native forest fragment (all of these were logged forest); MP = mature plantation (> 5 years old); YP = young plantation (< 5 years old); and OP = oil palm.
[a]Near-threatened listing by IUCN (2013).
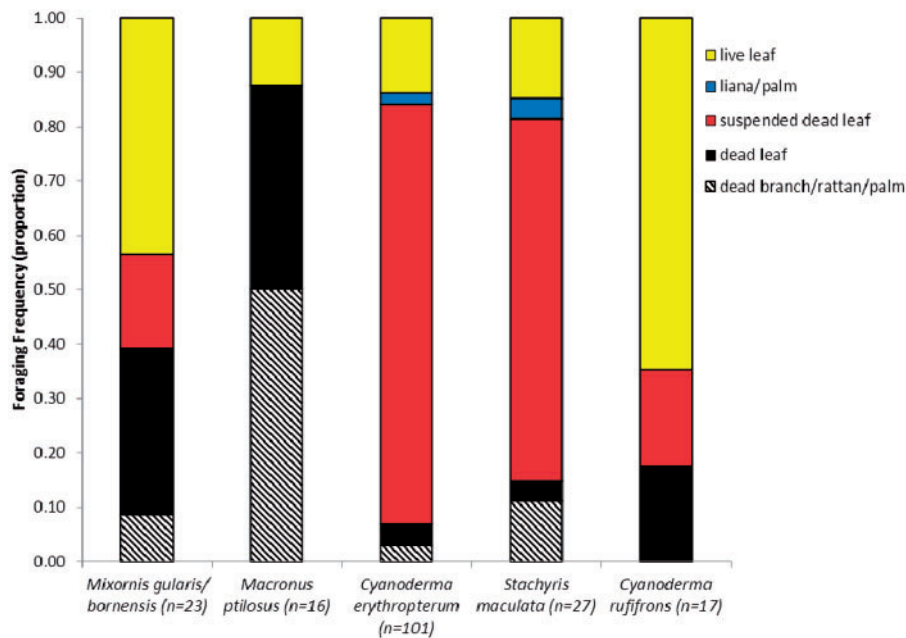
Figure 4. Stacked bar chart of proportional foraging frequency on specified substrates by 5 timaliine babbler species commonly found in lowland habitats in Peninsular Malaysia and Borneo

arthropods. *Cyanoderma erythropterum* and *S. maculata* search leaves suspended in vine and liana tangles, with *S. maculata* concentrating at sites higher in the understory than *C. erythropterum*. *Macronus ptilosus* spends a large proportion of its time foraging among dead leaves on the ground, but mainly concentrates on leaf clusters collected in the bases of Bertam palms, rattans, dead palms, and dead wood. Other researchers have noted the tendency of *C. erythropterum* and *S. maculata* to forage in dead leaves, but the foraging of *M. ptilosus* has not been previously characterized (Smythies 1999; Wells 2007). Dead leaves contain more arthropod prey than living leaves (Greenberg 1987; Thiollay 1988; Rosenberg 1990; Leme 2001), but are also more patchily distributed and presumably require more time and energy to find and extract food from than green leaves (Robinson and Holmes 1982; Gradwohl and Greenberg 1982, 1984; Remsen and Parker 1984; Rosenberg 1993).

Perhaps as a result of their dead-leaf strategy, *C. erythropterum*, *S. maculata*, and *M. ptilosus* occur in greatest abundance in regenerating logged forest and older plantation groves, where greater light penetration encourages the development of a thicker understory (Wong 1985;

Denslow et al. 1986; Lambert 1992; Mitra and Sheldon 1993; Sheldon et al. 2010; Styring et al. 2011) and where leaf litter is expected to be substantial (Edwards et al. 2009; Stratford and Stouffer 2013). In these habitats, opportunities for capture of falling leaves by understory vegetation is enhanced by the copious development of lianas, vines, and shrubs (DeWalt et al. 2003, 2006). *Cyanoderma erythropterum*, *S. maculata*, and *M. ptilosus* are also common in habitats that we did not investigate in this study, including pole forests growing on ultrabasic soils, bamboo thickets, and river edges (FHS personal observation; Sheldon et al. 2001), as would be expected of dead leaf foragers (Rosenberg 1990, 1993). On the other hand, these birds are not as abundant in actively managed habitats in which the understory is denuded, such as oil palm, manicured rubber, young industrial tree groves, and rehabilitated logged forest (Peh et al. 2006; Edwards et al. 2009; Sheldon et al. 2010; Li et al. 2013). Nor are they as abundant in mature rainforest (except *C. erythropterum*; Table 1). Possible reasons are that the understory in mature forest is more open, causing appropriate microhabitats to be more widely spaced, and that competition from even more specialized insectivores is expected to be greater.
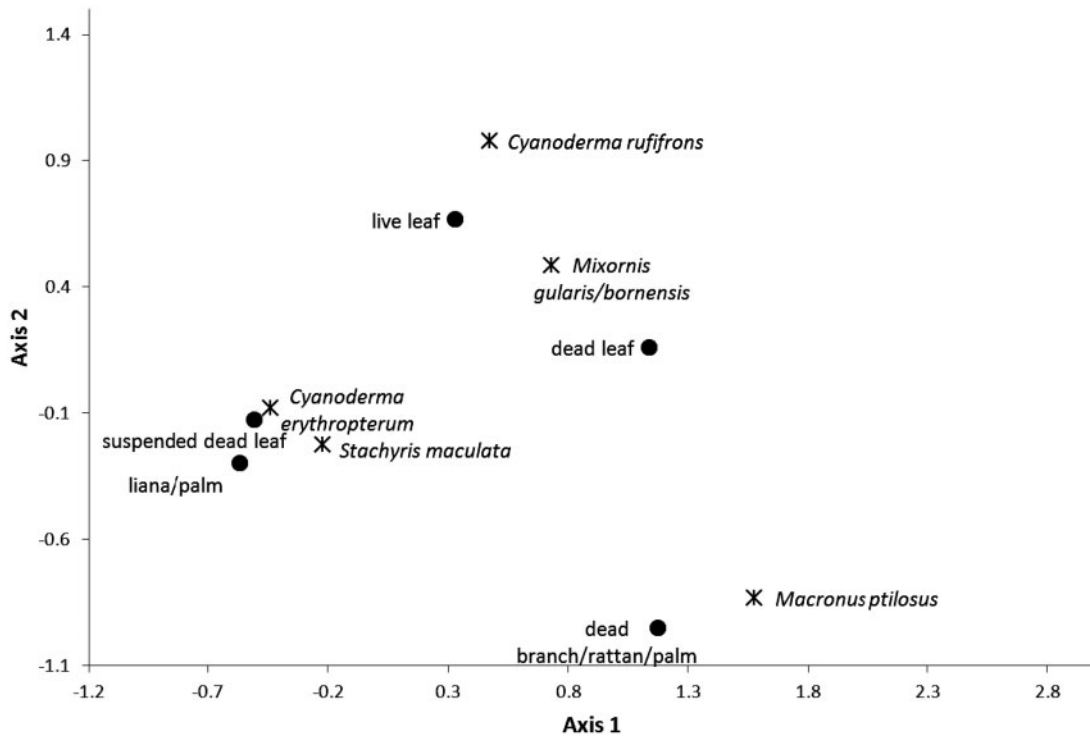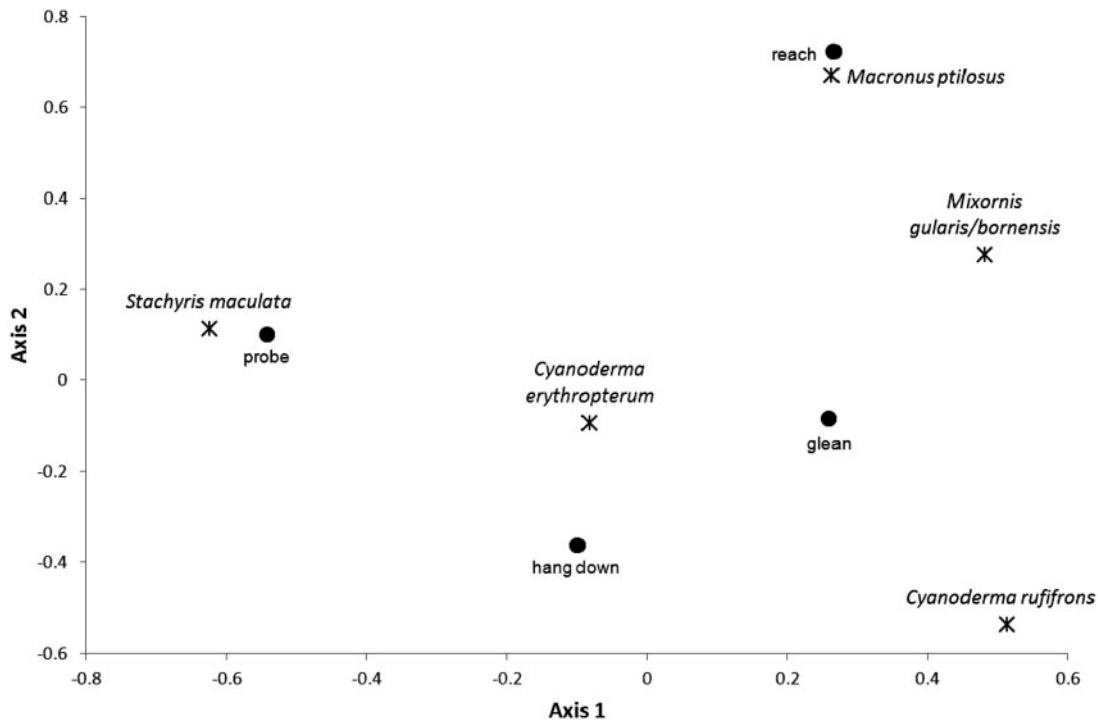
Figure 5. Correspondence analysis of substrate preferences of 5 species of timaliine babblers. The first 2 axes explain 98% of the variation in the data (axis 1 = 67.4%, axis 2 = 30.6%).
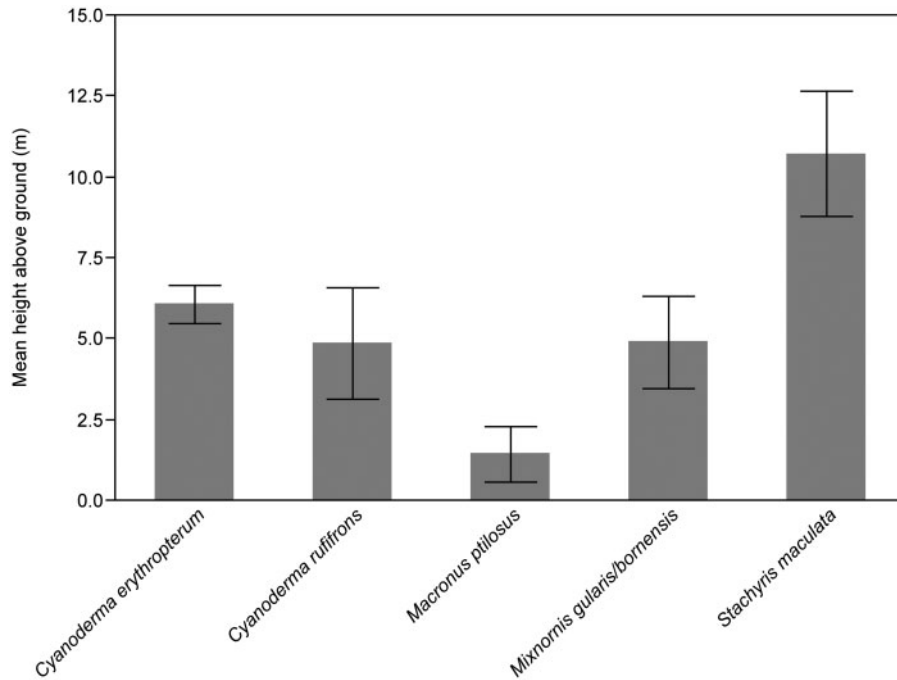
Figure 6. Average foraging height of 5 species of timaliine babblers. Error bars represent 95% confidence intervals. ANOVA results ($F_{4,170}$ = 15.2, $P < 0.001$), Tukey's HSD comparisons indicate that *S. maculata* forages at significantly greater heights than all other species ($P < 0.001$ in all cases). *Macronus ptilosus* forages significantly lower to the ground ($P < 0.04$ in all cases) than all but one other species *C. rufifrons*.

In contrast to the dead-leaf specialists, *Cyanoderma rufifrons* foraged primarily on green leaves and was most abundant in forest types with copious green leaves, including native forest and young and old industrial tree plantations (but not oil palm). Its foraging habits have not been recorded previously, except that this species is believed to spend more time in the canopy than the other babblers we examined (Sheldon et al. 2001; Teesdale 1972a, 1972b). In our study, however, we did not find it at greater height than the other species (Figure 4).

Figure 7. Correspondence analysis of attack maneuvers in 5 species of timaliine babblers. The first 2 axes explain 99% of the variation in the data (axis 1 = 60.1%, axis 2 = 39.8%).

Stachyris nigricollis and *S. poliocephala* were observed feeding only a few times in our study. However, when observed, they were foraging on dead leaves. *Stachyris nigricollis* was once seen probing into a suspended dead leaf 7 m high and twice gleaning dead leaves collected at the base of a rattan. Two *S. poliocephala* were observed gleaning suspended dead leaves at a height of 3 m. The use of dead leaves by *S. poliocephala* in Borneo was previously noted by Norman (1964).

Mixornis gularis was the greatest generalist of the group. It fed on the widest variety of substrates (Figure 2) and was common in the widest variety of disturbed forest and plantation habitats (Smythies 1999; Wells 2007; Mansor and Sah 2012). *Mixornis gularis*' eurytopy explains its ubiquity in much of Southeast Asia and why it is the only babbler that inhabits oil palm per se (Peh et al. 2006; Sheldon et al. 2010). (Some other babblers occur in oil palm, but only under certain circumstances: e.g., White-chested Babbler (*Trichatoma rostratum*), a river-edge specialist, will follow wooded streams into oil palm.)

The foraging patterns of *C. erythropterum* and *M. gularis* were previously studied by Mansor and Sah (2012), working in Perak, northern Peninsular Malaysia. Although they used different survey techniques, their results were similar to ours. They found *M. gularis* to be a leaf gleaner, concentrating on the underside of leaves, and that *C. erythropterum* "consistently used dead tree parts", which included dead branches and curled up dead leaves. They found that both species occurred mainly in forest of intermediate foliage density. The only apparent differences between their findings and ours were in foraging heights of *C. erythropterum* and *M. gularis*. In their study, foraging heights of *C. erythropterum* were between 0 m and 4 m ($n = 99$) compared to our mean foraging height of 6.1 m (95% CI = 5.3–6.9 m; $n = 101$). They found *M. gularis* to forage at > 6 m in 89% of observations (with 43% occurring 10–12 m; $n = 65$), whereas we found that *M. gularis* foraged at a mean height of 5.2 m (95% CI = 3.5–6.8 m; $n = 23$; Figure 4).

Phylogenetic issues

Although remarkably similar in many respects, the 7 sympatric babblers of this study are distinct phylogenetically (Webb et al. 2002). They are in the Timaliinae, but no 2 are sister species, and they occur in clades spread across the subfamily. Even congeners are not particularly closely related. All the species are cladistically separated from one another by species that occur elsewhere in Southeast Asia or by congeners on the same land mass that inhabit distinctly different habitats. Specifically, the 3 *Stachyris* species—*S. nigricollis*, *S. maculata,* and *S. poliocephala*—are each members of different clades within the genus. Two other *Stachyris* species occur in Peninsular Malaysia and Borneo, white-necked babbler *S. leucotis* and gray-throated babbler *S. nigriceps*, but the former is restricted to steep slopes in mature forest, and the latter is montane. Two *Stachyridopsis* species occur on the Malay Peninsula, *S. rufifrons* and *S. chrysaea* (the Golden Babbler), but *S. chrysaea* is montane. *Cyanoderma rufifrons* and *C. erythropterum* are the only *Cyanoderma* species to occur in Borneo and Peninsular Malaysia. The only other timaliine species in Borneo or Peninsular Malaysia are scimitar babblers (*Pomatorhinus*), and these differ markedly in bill shape and feeding methods from our study species (Smythies 1999; Wells 2007).

The diverse relationships and distinct foraging microhabitats of these babblers suggest that both dispersal and competition have played strong roles in their evolution. In describing the interplay of phylogeny and ecology, Webb et al. (2002, p. 478) noted: "…phylogenetic overdispersion (repulsion) can result either when closely related taxa with the most similar niche-use are being locally excluded (phenotypically repulsed), such that there is minimum niche overlap of coexisting species, or when distantly related taxa have converged on similar niche-use and are phenotypically attracted." This case seems to fall somewhat in between these 2 extremes. A quantitative examination of these issues must await the

collection of foraging data on the numerous other babblers that are sympatric with our study species, including members of *Malacopteron, Malacocincla, Napothera, Ptilocichla, Kenopia, Trichastoma*, and *Pellorneum*.

Conservation

The industrial plantation sites where we worked (SS and SPF) were part of large landscapes with substantial areas of native forest nearby. Moreover, the relaxed management style in both these plantations facilitated the development of complex understories with microhabitats appropriate for our study species. Undergrowth was intensively managed by cutting only during the first few years after planting to allow saplings to develop. Thereafter, the groves were left to grow without further management. Because industrial trees grow rapidly and allow substantial light penetration, uncleared plantation understories become a layered forest with a distinct midstory by 5–7 years, and the ground level develops into a thick and tangled jungle (Mitra and Sheldon 1993; Sheldon et al. 2010; Styring et al. 2011). Also, at SPF, there were numerous small native forest fragments within the plantation along streams that provided additional habitat for all the species we examined and may have been important as refuges when industrial tree plots were cropped.

The situation is different in oil palm. The only babbler species we observed using oil palm extensively was *M. gularis*. The understory of mature oil palm is naturally dark and largely devoid of vegetation because the dense canopy prevents light penetration and understory plants are cleared by cutting and the use of herbicides. Thus, the oil palm we examined lacked the falling leaves and structural complexity required as foraging substrates by all but one of the babblers studied. It also lacks foraging and nesting substrates for most other forest birds, resulting in an unusually depauperate avifauna, as reported many times (Danielsen and Heegaard 1995; Koh and Gan 2007; Peh et al. 2006; Edwards et al. 2010; Sheldon et al. 2010; Azhar et al. 2011, 2013).

A lack of understory complexity and consequently reduced bird species diversity is characteristic of all carefully managed plantations. Rubber, for example, is often cleared of vegetation, which seriously reduces its bird species richness (Phommexay et al. 2011; Li et al. 2013). However, when a healthy understory is allowed to develop, rubber plantations may support a relatively wide variety of bird species (Aratrakorn et al. 2006; Beukema et al. 2007; Najera and Simonetti 2010). In all cases of plantation management, if understory structure is allowed to persist it improves bird diversity within the plantation, and likely improves the use of plantations as a matrix for birds to move between native forest fragments (Renjifo 2001; Sekercioğlu et al. 2002; Azhar et al. 2011, 2013).

Future foraging studies and citizen science

One reason for the dearth of foraging studies in Southeast Asia is that obtaining foraging data for rainforest birds takes an unusually large effort in terms of time. It can be difficult to accumulate data for even a single species that is adequate to determine its foraging patterns, let alone for a group or community of species. Thus, academics, who are under great pressure to produce research publications and grants quickly, generally cannot afford to undertake such studies. At the same time, knowledge of foraging behaviors and microhabitat preferences is essential to understanding the evolution of rainforest birds and to managing their habitats for conservation.

One solution to this problem is to obtain foraging data from birdwatchers. The success of eBird demonstrates the power of citizen science in contributing to our understanding of avian biology and increasing scientific literacy in non-scientists (La Sorte et al. 2013, 2015). Development of a citizen-science effort to observe foraging behavior would be enhanced substantially by the addition of foraging fields to eBird's database, which in a short time would accumulate copious data. In the meantime, birdwatchers need to be made aware of the need for such ecological data and should be encouraged to collect it appropriately.

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