



Foraging behaviour of songbirds in woodlands and forests in eastern Australia: resource partitioning and guild structure

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ABSTRACT

One of the major questions in ecology is how species share their ecological space and what enables them to coexist. Partitioning of foraging niches should facilitate local coexistence. Thus, detailed data on foraging ecology are needed to provide insight into the assembly of communities. To this end, we quantified foraging behaviour of songbirds (Passeriformes) on 21 sites in woodlands and open forests of eastern Australia along a 3000 km long latitudinal transect spanning from the tropics to southern temperate regions. We obtained 5894 prey attacks by 2624 individuals from 112 species. Birds foraged mostly by gleaning (53.4% of attacks) on leaves (51.3%) in the outer part of crown (41.4%) and in medium foliage density (40.8%). Birds foraged along the whole vertical extent of vegetation, but individual species concentrated their foraging into particular strata. In the 41 best sampled species (minimum of 30 attacks recorded), we identified foraging guilds defined first by the foraging substrate and then by the foraging method. Specialisation on foraging substrate was positively correlated with specialisation on method. The organisation of guilds, patterns of substrate and method used across species, and species specialisation were similar to previous local-scale studies from eucalypt woodlands and forests, and from forests in northern temperate regions in Europe and North America. Thus, using our own data and comparisons with previous studies, we confirm a general pattern of foraging guild organisation of woodland and forest songbirds outside the tropics.

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Community assembly; ecological isolation; foraging method; foraging substrate; functional diversity

Introduction

How species share their ecological space and what enables them to coexist in space and time is a major question of ecology (MacArthur 1958; Lack 1971; Ricklefs and Schluter 1993). One of the ways species can coexist in the long term is by occupying different ecological niches (MacArthur and Levins 1967); divergent niches reduce competition and facilitate species coexistence (Schoener 1986). Species can differentiate their niches on the basis of their preferences for particular habitats or in terms of their foraging behaviour (MacArthur 1958; Lack 1971). Although progress has been previously made using local-scale datasets (reviewed in Schoener 1974; Ross 1986), large-scale data are needed to provide a robust insight into niche partitioning across habitats and clades (Comte *et al.* 2016; Gainsbury and Meiri 2017; Miller *et al.* 2017).

Birds are an ideal group to study these questions and studies of foraging behaviour in birds have a long tradition (Hartley 1953; MacArthur 1958; reviewed in Morrison *et al.* 1990). The authors usually describe the foraging behaviour of birds in terms of preferred food,

foraging height, substrate and the way birds collect the food (i.e. foraging method; reviewed in Remsen and Robinson 1990). However, the majority of published studies limited their effort to a few bird communities on a single site or across a limited spatial extent (e.g. Recher *et al.* 1985; Ford *et al.* 1986), while others compared a few sites on different continents (Holmes and Recher 1986; Terborgh and Robinson 1986; Marra and Remsen 1997; Korňan *et al.* 2013). The limited spatial replication and extent of most studies prevented the quantification of typical foraging strategies of species that would be valid throughout the species' distribution. This lack of spatial replication hampered these studies in identifying general patterns in foraging behaviour of species across large geographical scales. Yet, such studies could provide important insights into the evolution of foraging strategies in birds (Miller *et al.* 2017).

Here, we present analyses of foraging behaviour in 21 bird communities of eucalypt woodlands and open-forests across a large geographical gradient in eastern Australia. On the basis of 5894 prey attacks by 112 species of songbirds (Passeriformes), we 1)

identify general patterns in the use of foraging methods and substrates across all the sampled communities along the 3000 km long transect, 2) cluster 41 well-sampled species based on their foraging strategies into foraging guilds, 3) describe the relationship between foraging behaviour and canopy height across the 21 sites, and 4) compare our results with previous studies of foraging behaviour in similar habitats in Australia.

Study area and methods

Study areas

We worked at 21 sites during the austral breeding season from September to December in 2016 and 2017 (Table S1). Similar seasonal timing means that our sampling is standardised in terms of seasonal effects, but also that we cannot take seasonal differences in foraging behaviour into account (e.g. Recher and Davis 2014; Recher 2016). All sites were located in eucalypt woodlands and open-forests of eastern Australia (Johnson 2006; Figure S1). We selected habitats with native vegetation within protected areas (mostly National Parks) and without any agricultural activity (Table S1). At each site, we delimited three transects (Figure S2). Each transect was 2 km long and 50 m wide (10 ha) and was divided into two sides – right and left, each 25 m wide, divided by a path or a narrow forest road along which we walked. We placed the transects such that they were representative of local vegetation and had homogeneous vegetation cover, with three spatial replicates at each site. Transects were usually at least 1 km apart. In general, it was not easy to find sites and transects with desired characteristics and thus our site selection was influenced by convenience (availability of sites, access to sites, availability of paths or small roads). In spite of these problems, we achieved a large-scale coverage of eucalypt woodlands and open-forests across eastern Australia (Figure S1).

In order to measure canopy height at each site, we used a systematic sampling design by placing 10 points (200 m apart) along each transect (Figure S2). At each point, we delimited a semi-circle with the radius of 25 m (area ca. 980 m²) with alternating left and right direction from the transect. Canopy height was estimated by measuring three highest trees in each sampling semi-circle, always taking three measurements of a given tree by a laser range-finder (Nikon Forestry) and recording their average. Thus, in total, we measured 90 trees at each site (3 transects x 10 points x 3 trees).

Foraging behaviour

Each transect was walked twice by two observers with 0–3 days between the two sessions. The two observers worked on different sides of the transect and swapped sides between the two sessions. We started observations shortly after dawn and walked along the transect with roughly constant speed for 4 h, thus standardising observation effort. We limited observations to days without rain and strong wind. We recorded foraging behaviour of all passerines (Passeriformes) with the exception of individuals foraging high above the canopy ('aerial foragers'), which were mostly swallows and martins (Hirundinidae) and woodswallows (Artamidae), although woodswallows also forage on vegetation and the ground. We constantly and systematically scanned all vegetation for birds. We thus aimed to minimise bias introduced by locating only singing or otherwise conspicuous individuals. We located most of the birds by sight without using auditory cues ($n = 1959$), while 188 birds were detected due to singing and 470 due to vocalising (usually contact voices among members of a group). Once we located a bird, we counted to five before recording its behaviour to avoid bias towards recording conspicuous behaviours. If it did not forage within 1 min, we left it and continued searching for another bird. We were interested in patterns of resource partitioning, and thus did not record the process of searching for food, but only an event of actually procuring or attempting to procure food (*prey attack*). First records of prey attacks might sometimes differ from subsequent ones (Recher and GebSKI 1990) and thus sampling more prey attacks from the same individual could be useful. On the other hand, this could lead to underestimating uncertainties in quantifying foraging behaviour (Hejl *et al.* 1990). We thus compromised and for each individual recorded at most three prey attacks (mean = 2.25 attacks per individual bird, $n = 2624$ individual birds). For each prey attack, we recorded bird species (or genus, if species identification was impossible), foraging method and substrate, foraging height, height of the plant the bird foraged on, distance from the plant stem and foliage density around the foraging bird.

In terms of behaviour, we recognised eight types of *foraging methods* used by birds for attacking the prey that we adapted from previous studies of foraging in Australian birds (e.g. Recher *et al.* 1985; Ford *et al.* 1986):

- (a) *Gleaning* – moving on/through the substrate and taking prey from its surface; prey is taken while the bird is on the substrate (e.g. many thornbills, Acanthizidae and honeyeaters, Meliphagidae)

- (b) *Hang-gleaning* – gleaning while the bird is hanging upside-down (e.g. Striated Thornbill, *Acanthiza lineata* and Silvereye, *Zosterops lateralis*)
- (c) *Snatching* – moving on/through the substrate and making short flights to take the prey from nearby substrates; prey is taken while the bird is in the air (e.g. Rufous Whistler, *Pachycephala rufiventris*)
- (d) *Hover-snatching* – snatching while the bird stays in the air (hovers) when taking the prey from a substrate (e.g. Weebill, *Smicrornis brevirostris*)
- (e) *Probing* – extracting food from/within thick or deep substrate, such as soil, litter or flowers (e.g. flower-feeding honeyeaters)
- (f) *Manipulation* – includes a variety of methods such as scratching, digging and tearing to expose the prey (e.g. Crested Shrike-Tit, *Falcunculus frontatus* and Australo-Papuan babblers, Pomatostomidae)
- (g) *Pouncing* – direct flight from a perch to the site where the prey is taken (usually ground), whereby the bird lands and takes the prey; it may continue flying afterwards (e.g. butcherbirds, Cracticidae and Australasian robins, Petroicidae)
- (h) *Flycatching* (same as Hawking or Sallying) – flying from a substrate to take a flying prey, whereby both the foraging bird and prey are in the air (e.g. monarch flycatchers, Monarchidae or fantails, Rhipiduridae)

We recognised eight categories of *substrate*: ground (including all ground covers, e.g. bare ground, litter, grass), leaf (all types and sizes), bark (on trunks, branches and twigs), bud (unopened leaf or flower), flower (any size or type), fruit (including dry and fleshy fruits), air (open space), and other (includes special substrates, such as spider webs). *Plant height* and *foraging height* of each prey attack was measured by a laser rangefinder (Nikon Forestry). When we recorded more than one prey attack of the same individual, we estimated the average height of all of them. When the bird foraged on a shrub or a tree, we distinguished the following four categories of *distance from stem* – directly on the stem, inner half of the shrub/tree crown, outer half of the crown, and on the outer edge of the crown. Finally, we recognised three categories of the *foliage density* around the foraging bird – low (including zero), medium and high.

Data analyses

For each site, we summarised the total number of prey attacks recorded in the field, mean foraging height, and the percentage of foraging methods and substrates used.

For these calculations, we used all records of prey attacks of all individuals. To visualise the clustering of species into foraging guilds we constructed dendrograms based on proportions of methods and substrates used by individual species. Various authors recommend between 30 and 70 records to reliably describe the foraging behaviour of a given species, depending on the criterion of reliability used (Morrison 1984; Brennan and Morrison 1990; Recher and GebSKI 1990). In this study, only species with a minimum of 30 prey attacks recorded were included in analyses of foraging guilds and specialisation ($n = 41$ species). We used Bray–Curtis distance for the calculation of the dissimilarity matrix (the *vegdist* function in the *vegan* package, Oksanen *et al.* 2017) and three different clustering algorithms: complete, ward.D2, and average (the *hclust* function in the *stats* package, R Core Team 2016). We selected Bray–Curtis distance, because it is recommended for proportional data (Borcard *et al.* 2011). Since all three clustering methods gave similar results, we arbitrarily chose ward.D2 for presentation.

For each of the 41 best sampled species we also calculated Levins' index of specialisation (Krebs 1999) based on the proportions of foraging methods and substrates used (Tables S2 and S3):

$$B = 1/\sum p_i^2$$

where p_i is the proportional use of the category i . Then, we standardised the index to vary between 0 and 1, which made it independent of the number of categories:

$$B_A = 1 - (B - 1)/(n - 1)$$

where B is the unstandardised index for each species and n is the number of categories that is constant across all species (it is 8 for both foraging method and substrate). Higher values of the modified Levins' index indicate higher specialisation (i.e. less even use of categories by a given species, see Krebs 1999). We quantified the repeatability of species specialisation for the foraging method and substrate across four community wide studies conducted in eucalypt woodlands and forests (this study; Recher *et al.* 1985; Ford *et al.* 1986; Recher and Davis 1998). For this calculation, we included only species that were studied in at least two of the four studies. Repeatability then shows how similar the specialisation of individual species was across the 2–4 estimates included. We used the intra-class correlation coefficient calculated in the ICC package (Wolak *et al.* 2012) for the R software (R Core Team 2016).

Lastly, we calculated the occurrence of species across our 21 sites. We used presence-absence and the total number of individuals recorded (abundance hereafter), across all six transect monitoring sessions (three transects x two

monitoring sessions at each site). To visualise species occurrence across sites, we constructed heat maps based on presence-absence and abundance matrices. Similar sites (in terms of species composition) and species (in terms of site occupancy) were clustered together. We used the Gower distance for presence-absence data and Bray–Curtis distance for abundance data, while the *hclust* function (method = complete) of R (R Core Team 2016) was used for clustering in both cases.

Results

Foraging behaviour across sites

Together we recorded 5894 prey attacks from 2624 individual birds at our 21 sites. We identified 2605 individuals to the level of species (the remaining 19 individuals to genus), with a total of 112 species recorded. Overall, the most frequently used methods were gleaning, probing and snatching (42.0%, 24.7% and 12.0%, respectively; Figure 1, Tables S4 and S5) and the most frequently used substrates

for collecting food were leaf, flower and bark (51.3%, 22.1% and 17.4%, respectively; Figure 1, Tables S4 and S5). These three methods and substrates represented 78.7% and 90.9%, respectively, of the prey attacks recorded. Moreover, if we aggregate hang-gleaning with gleaning due to their similarity, the proportion of (hang-)gleaning increases to 53.4%, while the total sum of the three most common methods increases to 90.2%. The majority of prey attacks were recorded in the outer part of vegetation (41.4%) and the least on the plant's stem (7.4%; Figure S3). Birds made prey attacks most often in medium foliage density (40.8%; Figure S4).

Species foraging strategies

In terms of the most frequently used foraging methods and substrates, our results were similar to previous studies conducted in eucalypt woodlands and forests in southern Australia (Recher *et al.* 1985; Ford *et al.* 1986; Recher and Davis 1998; Table S5). The results were similar whether they were calculated based on

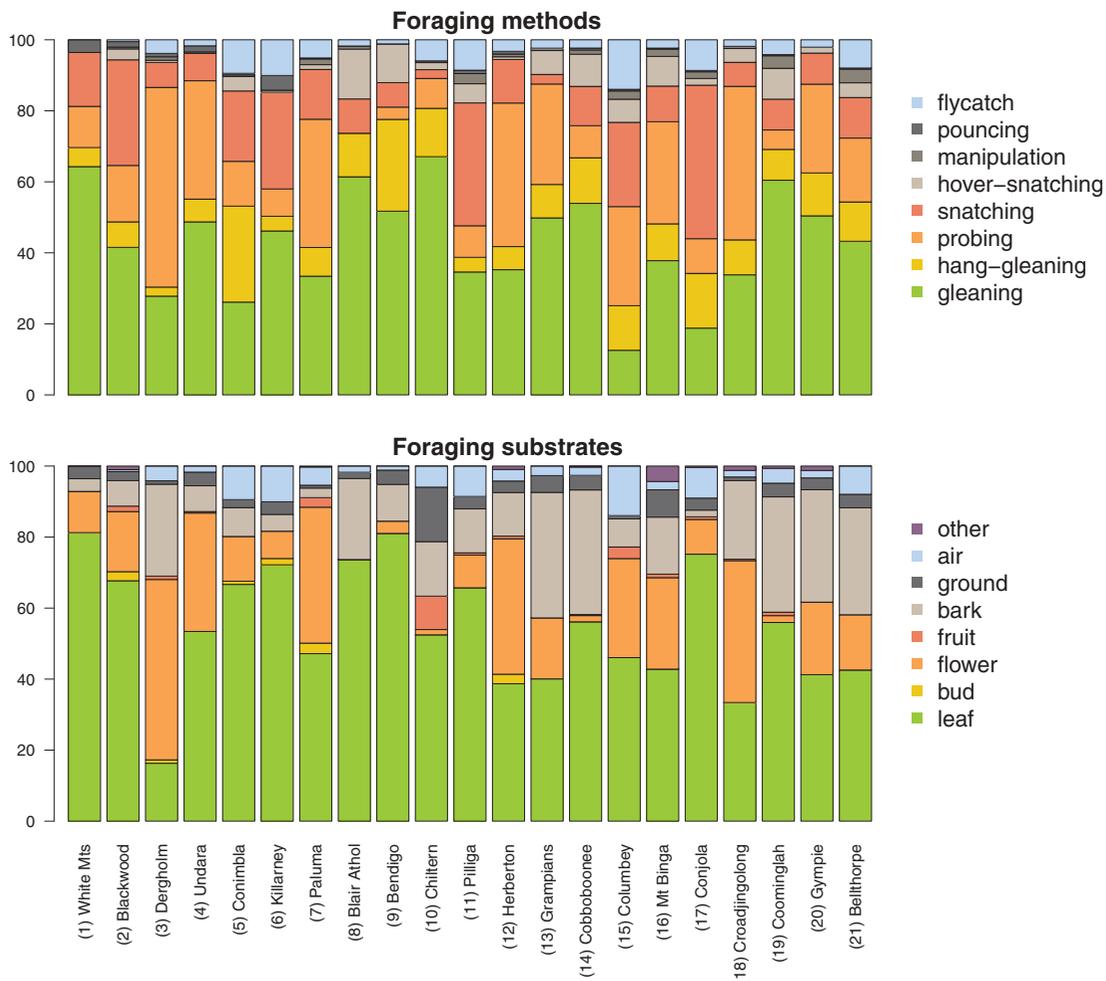


Figure 1. Proportions of foraging methods and substrates used by all species at our 21 sites showing site-to-site variability in the foraging strategies used. Sites are ordered by mean canopy height (from lowest to highest; canopy heights in Table S4).

weighted or unweighted averages (Table S5). Overall, most species in all four studies considered here foraged by gleaning from leaves, with the exception of Dryandra woodland in south-western Australia, where species foraged most frequently on the ground (Recher and Davis 1998).

The specialisation on the method and substrate was positively correlated across our 41 species (Pearson's $r = 0.47$, regression slope [se] = 0.43 [0.13], $p = 0.002$, $R_{sq} = 0.22$). Species were more specialised on substrate than on the foraging method (Figure 2). The specialisation on the method and substrate was also positively correlated in other studies in eucalypt woodlands and forests (Ford *et al.* 1986: Pearson's $r = 0.61$, regression slope [se] = 0.43 [0.10], $p < 0.001$, $R_{sq} = 0.37$; Recher *et al.* 1985: Pearson's $r = 0.57$, regression slope [se] = 0.29 [0.07], $p < 0.001$, $R_{sq} = 0.33$; Recher and Davis 1998: Pearson's $r = 0.61$, regression slope [se] = 0.57 [0.14], $p < 0.001$, $R_{sq} = 0.37$).

However, unlike in our study, species were in general more specialised on the foraging method than on substrate (Figure 2). Species with low specialisation in both foraging method and substrate belonged most often to Australasian robins (Petroicidae; Figure 2). Repeatability across the four studies was moderate for specialisation on both the foraging method (ICC = 0.37) and substrate (ICC = 0.37; $n = 37$ species with 2–4 estimates of the specialisation taken from this study, Recher *et al.* 1985; Ford *et al.* 1986; Recher and Davis 1998).

Foraging guilds

For each of the 41 best sampled species (Table S6), we obtained prey attack records from multiple sites (mean = 7.9 sites), which ensured that species typical behaviour was not biased by local conditions at one atypical site. The 41 species analysed clustered into distinct guilds

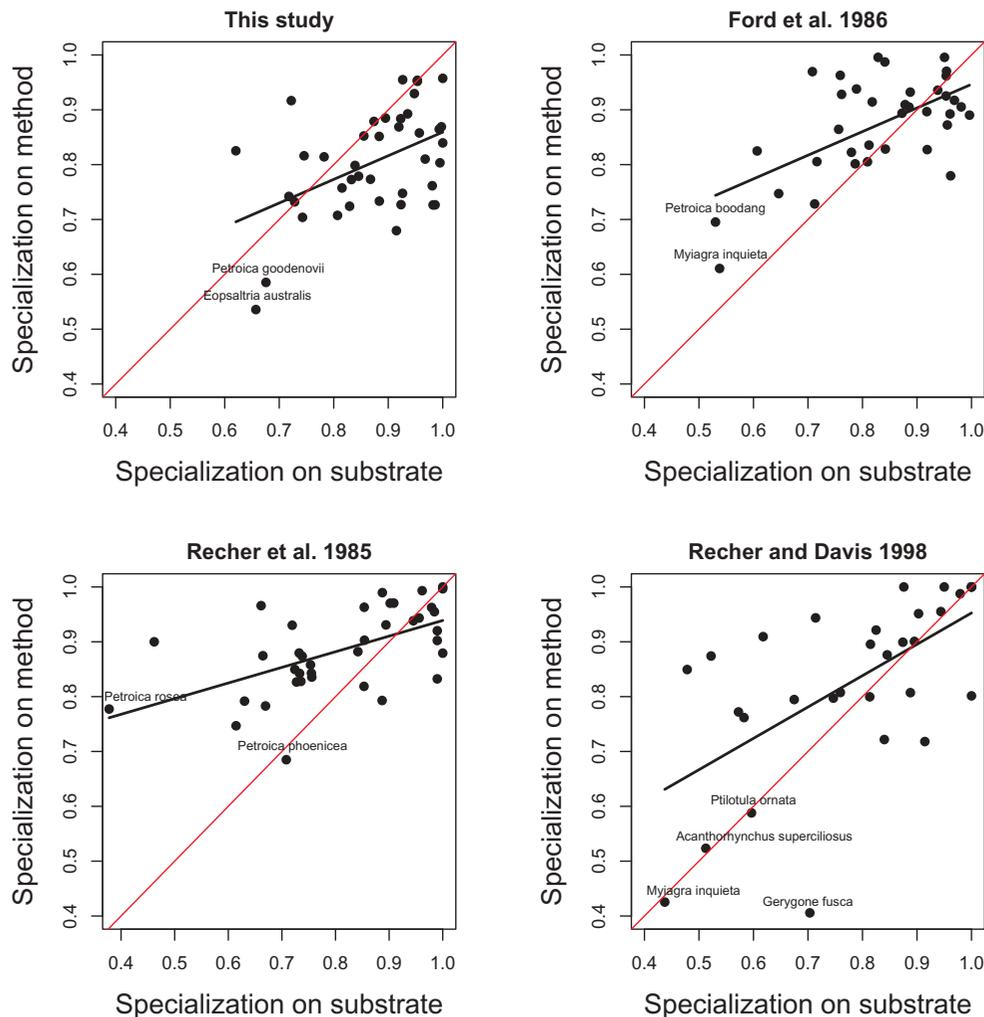


Figure 2. The relationship between the specialisation on foraging method and substrate in this study and three previous studies conducted in southern Australia. Specialisation is quantified using the Levins' index, where high values mean high specialisation (see Methods). The black line is a linear regression line, while the red line is a 1:1 line for reference (species falling on that line have the same specialisation on both method and substrate).

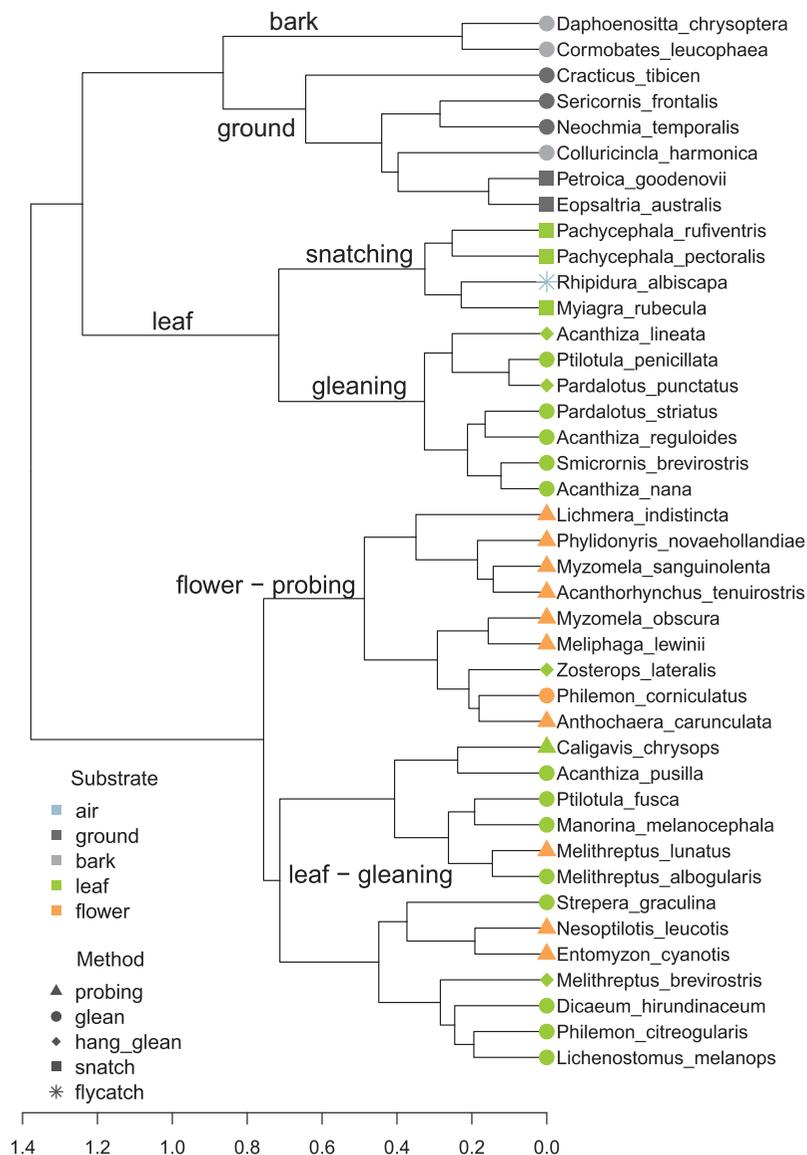


Figure 3. Dendrogram showing the similarity in foraging behaviour among 41 bird species with at least 30 prey attacks recorded based on their use of foraging substrates and methods. These species were sampled at our 21 sites across eastern Australia, so their observations do not come from one locality. The colour and shape of the symbol represent the substrate and method the most commonly used by each species. We used the Bray–Curtis distance (the scale below the figure) to calculate the dissimilarity matrix and the method ‘ward.D2’ (in the *hclust* function) to create the dendrogram.

(Figure 3). However, the number of delimited guilds could vary depending on how finely we define them. We suggest that five guilds can be delimited according to the most often used foraging substrate: bark, ground, flower and two groups of species foraging on leaves (Figure 3). These guilds could be further characterised by the foraging method: species in the bark and ground guilds used mostly gleaning, but also snatching, while the flower-feeding guild used mostly probing. In the two guilds foraging on leaves, one was characterised by gleaning while the other could be subdivided into the subgroups characterised by snatching vs. gleaning (Figure 3).

Canopy height and foraging behaviour

Average foraging height increased with canopy height across the sites (Pearson’s $r = 0.91$, $p < 0.001$, $n = 21$). Individual birds tended to forage across the whole vertical gradient irrespective of canopy height (Figure S5) and, accordingly, the standard deviation of foraging height increased with canopy height across the sites (Pearson’s $r = 0.93$, $p < 0.001$, $n = 21$). Foraging height of individual birds also increased with the height of the particular plant individual the bird foraged on (Pearson’s $r = 0.86$, $p < 0.001$, $n = 2356$; Figure S5) and birds used the whole height of the plant up to 10–

15 m. In taller trees, birds concentrated their foraging efforts in the canopy higher up the tree (Figure S5). Despite the whole community covering the whole height of vegetation, species partitioned foraging height and concentrated their foraging on different vertical strata of the vegetation (Figure 4).

Foraging behaviour of birds tended to change with changing canopy height, especially in terms of substrates used. With increasing canopy height, the proportion of foraging on leaves decreased, although not statistically significantly (Pearson's $r = -0.32$, $p = 0.157$,

$n = 21$), whereas the proportion of foraging on bark significantly increased (Pearson's $r = 0.59$, $p = 0.005$, $n = 21$; Figure 1). Out of the three most common foraging methods, we found the strongest relationship between canopy height and the proportion of snatching, but it was not statistically significant (Pearson's $r = -0.16$, $p = 0.502$, $n = 21$; Figure 1). With increasing canopy height, birds foraged more frequently in the inner part of the canopy (Pearson's $r = 0.59$, $p = 0.005$, $n = 21$) and in foliage with low density (Pearson's $r = 0.75$, $p < 0.001$, $n = 21$).

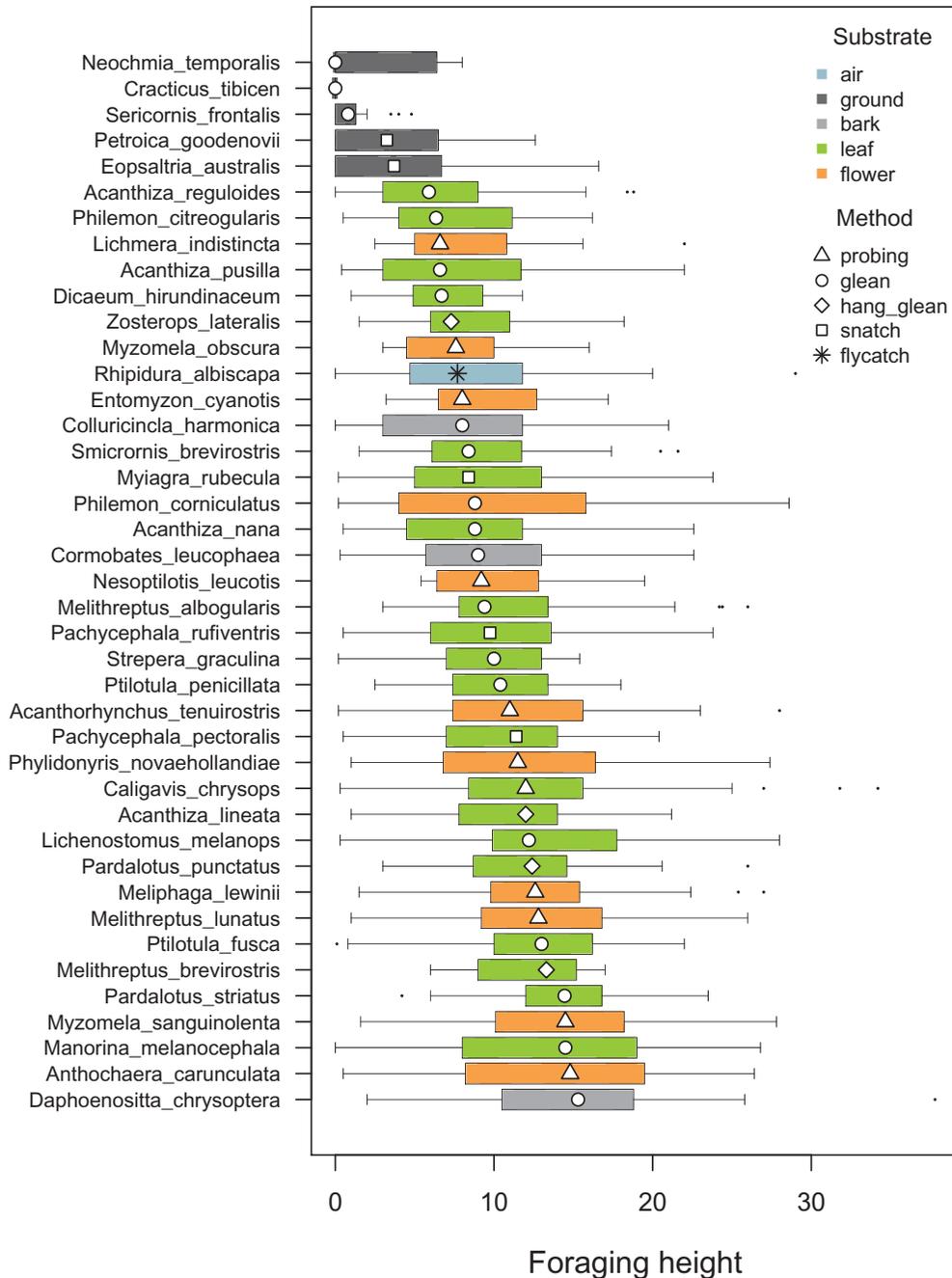


Figure 4. Median foraging heights of the 41 passerine species with at least 30 foraging records obtained during the whole study. Symbols are medians while boxes are quartiles. Species are sorted by increasing median foraging height (from top to bottom).

Discussion

Foraging methods, substrates and specialisation

Gleaning was a dominant foraging method, being most frequently used by 20 of the 41 species analysed. Hang-gleaning was most frequently used in four species out of the 41 species. Probing was a specialised method typically used by honeyeaters (11 species; Meliphagidae) taking nectar. Snatching was used most often by five species, including whistlers (*Pachycephala*) and Australasian robins (*Eopsaltria*, *Petroica*; Table S2). Gleaning, probing and snatching were the most common foraging methods recorded by Ford *et al.* (1986) in a eucalypt woodland in north-eastern New South Wales (accounting for 85.6% of foraging records) and by Recher *et al.* (1985) in woodlands and open-forests in south-eastern New South Wales (accounting for 78.9% of foraging records; see Table S5). In terms of substrates, birds foraged most frequently from leaves and bark, which together accounted for 65.4% (Recher *et al.* 1985), 68.8% (this study) and 77.8% (Ford *et al.* 1986) of all prey attacks, respectively (Table S5). In contrast to all the above-mentioned studies, a study from eucalypt woodlands in south-western Australia (Recher and Davis 1998) showed that besides gleaning and probing from leaves and bark, pouncing onto the ground was unusually important (40.2% of all foraging records were on the ground; Table S5).

Differences among studies can be accounted for by at least two factors. First, some studies were conducted during the whole year (Ford *et al.* 1986), while others were conducted during spring only (Recher *et al.* 1985; Recher and Davis 1997). Similarly, this study was conducted during austral spring when trees at several sites were in bloom, with a relatively high proportion of probing from flowers (e.g. Croajingolong, Dergholm, Herberton, Paluma; see Figure 1). Second, vegetation structure might be responsible. For example, in a study of the mulga *Acacia aneura* habitat with canopy cover less than 20%, songbirds foraged mostly by gleaning/pecking (84.2% of foraging records) from the ground (63.8% of records; Recher and Davis 1997). Thus, although the overall functional structure of this community was a scaled-down version of eucalypt forest avifauna, the prevalence of ground foraging was apparent. This could be caused by the relative paucity of taller vegetation compared to eucalypt woodlands and forests and by the fact that mulga has low canopy cover and often grows as a monoculture with little or no mid-storey and often no understorey. Similarly, the proportion of foraging on bark increased with increasing canopy height in this study (see Figure 1), probably because larger, taller trees have more bark. Both these examples suggest that increased substrate availability can lead to its more

intense utilisation by birds in the local community (Gilmore 1985).

As in previous studies, species highly specialised on the foraging method were also highly specialised on substrate, and vice versa (Figure 2; Ford 1990). The least specialised species belonged to Australasian Robins (Petroicidae) and this was consistent across studies. Finally, repeatability of specialisation across studies was only moderate (0.37 for both foraging method and substrate), suggesting that geographic and seasonal flexibility in foraging behaviour is present. Indeed, geographic variability in foraging behaviour has been documented by previous studies, and it seems to be driven by vegetation structure, floristics and food availability (e.g. Recher *et al.* 2002; Recher and Davis 2014; Recher 2018).

Foraging guilds and niche partitioning

We identified a similar guild structure to that of previous studies, while species composition across studies differed. This shows that guild structure is conservative between structurally similar habitats (Mac Nally 1994). Moreover, the same guild structure (first substrate, then method) was revealed in forests of the temperate North America and Europe (Holmes *et al.* 1979; Korňan and Adamík 2007; Korňan *et al.* 2013) and a high-altitude forest of India (Somasundaram and Vijayan 2008). By contrast, foraging strategies of birds in tropical forests of New Guinea and Malaysia were first partitioned by foraging height and only then by foraging behaviour (Bell 1983; Mansor and Mohd Sah 2012), while height and behaviour were comparable in importance in delimiting guilds in Australian wet tropical forests (Crome 1978; Frith 1984).

Related species that are morphologically similar and live in the same broad region often differ in habitat affinities, foraging behaviour, and food (Lack 1971), as shown in classical studies on titmice in Europe (former *Parus*; Hartley 1953) and wood warblers in North America (*Setophaga*; MacArthur 1958). Accordingly, species from several genera were widely separated on dendrograms constructed based on foraging substrate and method (e.g. *Acanthiza* thornbills [Figure 3]), which showed that they had different foraging ecologies. These foraging differences could facilitate their local coexistence, as suggested previously for several genera of passerines in Australia (e.g. *Acanthiza*, Bell 1985; Recher 1989, *Rhipidura*; Cameron 1985, *Gerygone*; Keast and Recher 1997, and *Melithreptus*; Keast 1968; reviewed in Ford 1985, 1989).

We identified several pairs of ecologically similar species in terms of foraging substrate and method, as evidenced by their proximity on the dendrogram

(Figure 3). Consequently, we might ask what are the ecological differences facilitating their coexistence. First, Eastern Yellow Robin *Eopsaltria australis* and Red-capped Robin *Petroica goodenovii* both foraged mostly by snatching and from the ground, used similar foraging height (Figure 4), and co-occurred frequently on our 2-km transects (Figures S6 and S7). However, Eastern Yellow Robins tend to use moister microhabitats as compared to Red-capped Robins and thus are unlikely to co-occupy the same microhabitats and overlap territories. Moreover, these two species were the most generalist out of the 41 songbird species with enough data (Figure 2, Tables S2, S3 and S6). This could enable them to switch their foraging strategies depending on the particular environmental context (Recher *et al.* 2002). Moreover, Eastern Yellow Robin is roughly twice as large as Red-capped Robin (Table S6) and thus might take at least partially different prey (Vézina 1985). Second, an interesting case is Weebill *Smicrornis brevirostris* and Yellow Thornbill *Acanthiza nana*, which both forage almost exclusively from leaves (ca. 95% of prey attacks). Moreover, they often co-occur (Figures S6 and S7), forage at similar heights (Figure 4), have virtually the same body mass and beak length (Table S6), and take similar food based on stomach analyses and foraging observations (Woinarski 1985). However, they use a variety of foraging methods, including gleaning (46–51%), hang-gleaning (10–11%), snatching (20–33%), and hover-snatching (10–18%, Table S2; Woinarski 1985), which might enable them to switch foraging methods in response to locally co-occurring species (Recher 1989). Third, another example of ecologically similar species is Rufous Whistler and Golden Whistler (*Pachycephala pectoralis*) that both forage predominantly by snatching from leaves at similar heights (Figures 3 and 4; Mac Nally 2000). They also have very similar body mass and beak length (Table S6), which suggests similar food. However, although co-occurring on our 2-km transects (Figures S6 and S7) and elsewhere in Australia (Mac Nally 2000), microhabitat segregation on a fine spatial scale could facilitate coexistence of these two species. On our transects, Golden Whistler occurred in moister microhabitats with more understorey compared to Rufous Whistler that was more generalist in habitat preferences (the latter species occurred as the only species on all 21 sites, Figure S6).

In conclusion, we showed that i) gleaning from leaves was the principal method of foraging, ii) specialisation on foraging substrate and method correlated positively, iii) repeatability of specialisation across studies was moderate, and iv) guild structure was

delimited first by foraging substrate and then by foraging method, as in previous studies from Australia, North America, Europe and India.

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Data availability statement

All supporting data can be found as Supplemental Online Material attached to this manuscript.

Data deposition

All supporting data can be found as Supplemental Online Material attached to this manuscript.

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Geolocation information

Eastern Australia: longitude from 141.14°E to 152.70°E; latitude from 17.33°S to 38.15°S.

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