Chapter 6

FORAGING BEHAVIOR, GUILD STRUCTURE, AND SPECIES DIVERSITY IN AUSTRALIAN PASSERINES

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ABSTRACT

Bird species partition ecological space due to divergent foraging behavior and substrate use. The volume of ecological

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space (potential number of niches) increases with vegetation complexity. At the same time, foraging behavior might be constrained by phylogenetically conserved morphology. Thus, relationships between foraging behavior, morphology, phylogeny, and vegetation complexity might shed critical light on resource partitioning and species coexistence in communities. Australia is an ideal place to investigate these issues because it hosts an ancient, autochthonous radiation of passerines. We studied foraging strategies in passerines in woodlands and forests of eastern Australia along a 3,000 km long latitudinal transect spanning from the tropics to southern temperate regions. We obtained 5,894 prey attacks, recorded 9,223 individual birds, and quantified vegetation complexity on 63 line transects. In addition, we extracted data on >47,000 foraging records from published literature. Using cluster analysis, we quantified guild structure in 91 species across Australia with at least 30 foraging records each. We identified distinct guilds based on foraging substrates and behaviors that contained phylogenetically unrelated species (convergent behavioral evolution). We further showed that foraging behavior was partially predicted by morphology, which in turn was closely tied to phylogeny (high phylogenetic signal). Foraging behavior was phylogenetically more labile, allowing for faster adaptation and switching between foraging guilds. In local communities, the number of individuals, species richness, and morphological and behavioral diversity all increased with vegetation complexity (indexed by canopy height). Overall, our results show that on a continental scale, passerine birds evolved repeatable foraging guilds and guild membership was little constrained by morphology or phylogeny. Sampling from these guilds to local communities was then predicted by the volume of ecological space dictated by vegetation complexity. To sum up, we demonstrate an interplay between phylogenetic conservatism, behavioral flexibility, and ecological opportunity in shaping species richness and functional diversity from regional avifaunas to local communities.

INTRODUCTION

One of the fundamental patterns in natural history is that co-occurring species differ in morphology, physiology, and behavior. This is true for both regional spatial scales (e.g., on continents) and local communities. How these differences originate and whether they

facilitate species coexistence is not well understood. However, understanding these issues is fundamental, because unequal distribution of species diversity on Earth is among the big questions of ecology and evolution. This problem has two parts: first, the evolution of differences during the history of the clade and, second, their impact on species ecological roles and assembly in local communities. Here, we address these questions using Australian passerine birds as a model system.

During clade diversification, trait divergence happens even without selection for specific ecological roles due to "neutral" trait evolution (as in Brownian motion models; Blomberg, Garland, and Ives 2003). Moreover, adaptive radiation into divergent ecological roles has been amply documented, especially in archipelagoes and isolated ancient lakes, in plants, invertebrates, fishes, and birds (Schluter 2000; Grant and Grant 2008; Ronco et al. 2021). However, even on continental scales, we can observe repeatable evolution of ecological roles in whole classes of animals, which is usually tied to the evolution of specific morphologies and lifestyles (McGhee 2011; Pigot et al. 2020). Nevertheless, unlike in island-like settings, we are unsure whether ecological opportunity and species interactions play any role (Stroud and Losos 2016). The reason is that continents have been "full of species" most of the time, and it is not easy to imagine an adaptive radiation into an occupied ecological space across a continent, unless rare events of radical climate change or mass extinction have occurred. Climate change might make available a continent hitherto devoid of high biodiversity (think of today's Antarctica), while mass extinctions create new ecological opportunity (Maor et al. 2017; Lowery and Fraass 2019). To make a progress in our understanding of continental-scale evolution of ecological roles (i.e., species morpho/eco-types), we need a robust quantification of these roles and their links to phylogeny and morphology. Here, we attempt such a quantification on a model case of foraging behavior in Australian passerines.

Foraging behavior and related morphologies have always been at the forefront of ecological and evolutionary research. Prime examples include Darwin's finches of the Galapagos islands (Grant 1986), honeycreepers of Hawai'i (Pratt 2005), vangas of Madagascar (Jønsson et al. 2012; Reddy et al. 2012), *Anolis* lizards of the Lesser

Antilles (Losos 2009), labrid fishes of coral reefs (Burress and Wainwright 2019; Gajdzik, Aguilar-Medrano, and Frédérich 2019), and cichlid fishes of large African lakes (Seehausen 2006). The reason why foraging behavior is so important is that it provides a direct link to resource partitioning (Lack 1971; Schoener 1974). Resource partitioning has the strongest relevance in local species assemblages and, accordingly, the study of foraging behavior and ecomorphology of communities provided early examples of niche partitioning (MacArthur 1958; Pianka 1969; 1973; Holmes, Bonney, and Pacala 1979; Ricklefs and Travis 1980; Miles and Ricklefs 1984; Miles, Ricklefs, and Travis 1987; Ford 1989). However, what happens in the local community is not the whole story: the composition of communities is shaped by species available in the regional species pool (Mittelbach and Schemske 2015).

Regional species pool influences the functional diversity of local species assemblages by constraining functional types of species that can become members of these assemblages (Ricklefs and Schluter 1993; Mittelbach and McGill 2019). This regional-local dynamics is shaped by available niches, with more niches providing ecological space for more and diverse species (Ricklefs 2010). The volume of the ecological space might for example increase with increasing vegetation complexity. The link between vegetation complexity and diversity was classically demonstrated for bird species richness (MacArthur and MacArthur 1961; Recher 1969; Karr and Roth 1971). It has recently been extended for functional diversity, although these studies focused on coarse spatial grain and used species range maps and remotely sensed environmental variables (Remeš and Harmáčková 2018; Feng et al. 2020). Studies linking multiple aspects of functional diversity in local communities to vegetation complexity measured on the ground are mostly lacking (but see Vollstädt et al. 2017). Yet, they are critical for deeper understanding of the role ecological opportunity plays in shaping species assembly and coexistence.

Here we study foraging behavior and morphology of 91 passerine species in Australia across spatial scales, from continental to local. First, we delimit foraging guilds based on foraging methods and substrates, relate them to phylogeny and morphology, and analyze the correlations between behavior and morphology. In this way, we shed

light on the evolution of behavioral and morphological diversity on a regional (i.e., continental) scale. Second, we analyze the structure of local passerine assemblages and link their diversity and disparity to vegetation complexity. In this way, we illuminate links between regional processes of diversification and adaptation, and local processes of community assembly and species coexistence.

METHODS

Field Work

We worked at 21 sites during the austral breeding season from September to December in 2016 and 2017 (Figure 1). Similar seasonal timing means that our sampling was standardized across sites in terms of seasonal effects, but also that we cannot take seasonal differences in foraging behavior within sites into account. All sites were located in eucalypt woodlands and open forests of eastern Australia. We thus limited the habitat breadth that we investigated by avoiding i) shrubby and grassland vegetation in more arid parts of Australia, and ii) rainforests due to their thick vegetation, which precludes easy observation of foraging birds and thus requires much more intensive sampling than was possible in our study. We selected habitats with native vegetation, within protected areas (mostly National Parks), and without any agricultural activity including grazing by livestock. At each of 21 sites, we delimited three transects, ending up with 63 transects in total. Each transect was 2 km long and 50 m wide (10 ha) and was divided into two 25m wide sides – right and left – that were divided by the path or 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 1).
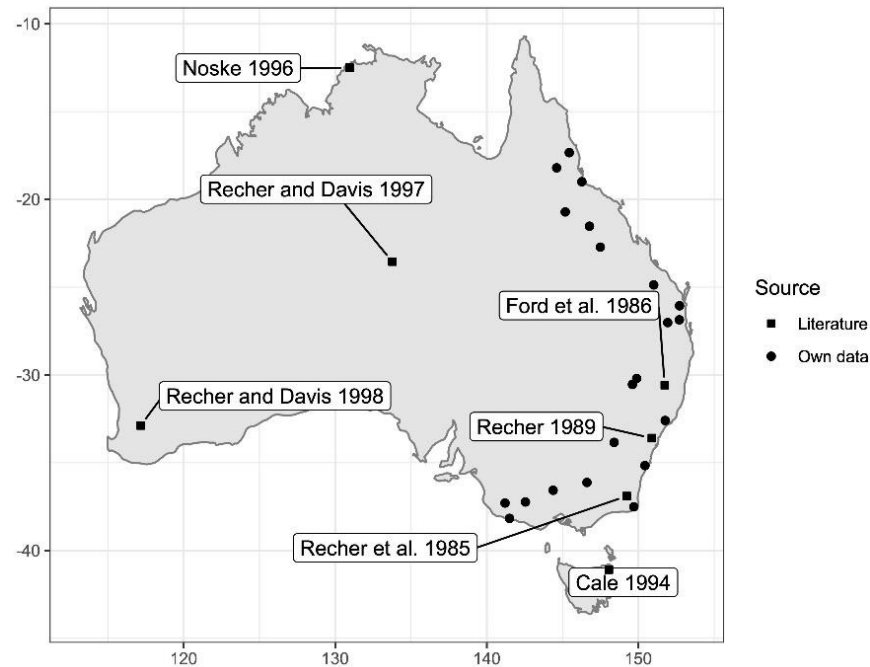
Figure 1. Map of Australia with the location of our 21 study sites ("Own data") and seven study sites of published studies ("Literature").

Vegetation Data

In order to quantify vegetation structure at each transect, we used a systematic sampling design by placing 10 points (200 m apart) along the transect. At each point, we delimited a semi-circle with the radius of 25 m (area ca. 0.1 ha or 1,000 m^2) with alternating left and right direction from the transect. Thus, the area surveyed for vegetation structure was ca. 1 ha (i.e., 10,000 m^2) on each transects and 63 ha in total. At each point, we recorded vegetation cover in five *height strata* (0–1 m, 1.1–2.0 m, 2.1–5 m, 5.1–10 m, >10 m) and vegetation cover and height of four *vegetation strata* (herbaceous, shrub, subcanopy, and canopy). Height strata were delimited by a priori selected height bands, while vegetation strata were determined by major vertical vegetation layers typical of woodlands and forests. Thus, for vegetation

strata, besides cover we also had to measure the height of individual strata. The height of the herbaceous stratum was estimated visually, while the height of shrub, subcanopy, and canopy strata was measured by taking three measurements by a laser rangefinder (Nikon Forestry). Vegetation cover of each height or vegetation stratum was estimated by eye on the scale ranging from 0 (no vegetation) to 10 (fully covered). The estimate was done independently by two observers who then converged on a consensus estimate.

We calculated four indices of vegetation complexity for every site: 1) summed vegetation coverage of height strata, 2) summed vegetation coverage of vegetation strata, 3) average canopy height (m), and 4) canopy coverage (%). These four variables were highly correlated ($r > 0.77$; except the correlation between canopy height and canopy coverage where $r = 0.52$). This collinearity was confirmed by a PCA analysis run on all vegetation characteristics. The first PC axis explained 48% of variability, correlated positively with most vegetation characteristics, and correlated also well with other vegetation metrics ($r > 0.72$). We used canopy height in further analyses, because it reliably expressed overall vegetation volume and has been recently used in numerous studies of animal diversity (Coops et al. 2018; Feng et al. 2020; Gouveia et al. 2014; Remeš and Harmáčková 2018; Roll, Geffen, and Yom-Tov 2015).

Behavioral Data

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 standardizing observation effort. We limited observations to days without rain and strong wind. We recorded all passerines (Passeriformes) detected on the transect. Moreover, we also recorded the bird's foraging behavior with the exception of individuals foraging high above the canopy ("aerial foragers"). These were mostly swallows and martins (Hirundinidae) and woodswallows (Artamidae). We constantly and systematically

scanned all vegetation for birds. We thus aimed to minimize 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 vocalizing (usually contact voices among members of a group). Once we located a bird, we counted to five before recording its behavior to avoid bias towards recording conspicuous behaviors. 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 observed prey attacks might sometimes differ from subsequent ones (Recher and Gebski 1990) and thus sampling more prey attacks from the same individual can be useful. On the other hand, this could lead to underestimating uncertainties in quantifying foraging behavior (Hejl and Verner 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 behavior, we recognized eight types of *foraging methods* used by birds for attacking the prey that we adapted from previous studies of foraging in Australian birds (Recher et al. 1985; Ford, Noske, and Bridges 1986):

1. *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)
2. *Hang-gleaning* – gleaning while the bird is hanging upside-down (e.g., Striated Thornbill, *Acanthiza lineata* and Silvereye, *Zosterops lateralis*)
3. *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*)

4. *Hover-snatching* – snatching while the bird stays in the air (hovers) when taking the prey from a substrate (e.g., Weebill, *Smicrornis brevirostris*)
5. *Probing* – extracting food from/within thick or deep substrate, such as soil, litter or flowers (e.g., flower-feeding honeyeaters and bark-feeding treecreepers, Climacteridae)
6. *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)
7. *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 some Australasian robins, Petroicidae)
8. *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 and fantails, Rhipiduridae).

We recognized eight main categories and 17 fine categories (i.e., subcategories) of foraging *substrates* from which the birds collected food (subcategories are in parentheses):

1. *Ground* (three subcategories: *bare ground*, *leaf litter*, *grass*)
2. *Leaf* (two subcategories: *small leaves* – any dimension below 10 cm, *large leaves*)
3. *Bark* (four subcategories: *twig* – bears leaves at the end of a branch, *small branch* – diameter below 10 cm, *large branch*, *trunk* – vertical stem supporting a shrub or a tree)
4. *Bud* (unopened leaf or flower; no subcategories)
5. *Flower* (any size or type; no subcategories)
6. *Fruit* (including dry and fleshy fruits; no subcategories)
7. *Air* (four subcategories: *above trees* – but not high in the sky, *between trees* – between canopies of shrubs and trees, *within trees* – within a canopy, *over ground* – below 1 m high)

8. *Other* (includes special substrates such as spider webs; no subcategories).

Table 1. Summary of data from published studies and our own field data on foraging behavior in Australian passerine birds. Only species with at least 30 foraging records were included (n = 91 unique species across the studies). Figure 1 shows the location of study sites

Location	Species	Foraging records	Habitat	Citation
Northern Australia	13	796	Mangroves	Noske 1996
New South Wales	36	9,512	Eucalypt woodland	Ford et al. 1986
New South Wales	5*	5,155	Eucalypt woodland	Recher 1989
South-East Australia	38	25,447	Eucalypt woodland and forest	Recher et al. 1985
South-West Australia	31	3,051	Wandoo eucalypt forest	Recher and Davis 1998
Central Australia	21	2,572	Mulga (*Acacia aneura*) shrubland	Recher and Davis 1997
Tasmania	12	1,032	Mature sclerophyll forest	Cale 1994
Eastern Australia	41	5,894	Eucalypt woodlands and forests	This chapter

* Only thornbills and allies (Acanthizidae) were studied.

We also extracted data on the foraging behavior of Australian passerines from published literature. In seven studies, it was possible to align the categories of foraging behavior and substrate selection with our categories, and thus they could be used for comparison. However, we had to reduce the number of categories to six for foraging methods (we merged gleaning with hang-gleaning and probing with manipulation, respectively) and foraging substrates (we merged fruit and bud into other substrates). We were thus able to cover various habitats and geographic regions in Australia (Table 1, Figure 1). On the other hand, we were not able to include several studies that used the categories of foraging behavior not comparable to ours. This precluded us from including data from wet forests of north-eastern Australia (Crome 1978; Frith 1984).

Morphology and Phylogeny

We obtained morphological measurements for the 91 species with at least 30 foraging records in museum collections. We visited collections of Natural History Museum in Tring (UK), American Museum of Natural History in New York City (USA), and Australian National Wildlife Collection in Canberra (Australia). We measured beak length, width and depth, wing length, tarsus length, and tail length in at least three males and three females per species. We took body mass from the Handbook of Australian, New Zealand, and Antarctic Birds (Higgins et al. 2006). We used these morphological measurements together with detailed field-based foraging data to analyze the relationship between morphology and foraging behavior.

We obtained the phylogeny for our species from a publicly available archive birdtree.org (Jetz et al. 2014). We downloaded 1000 phylogenies using the Hackett constraint and version 2 of the database. We calculated one Bayesian maximum credibility tree using TreeAnnotator (Drummond et al. 2012) and used this tree in all subsequent analyses.

Statistical Analyses

Using all data for all 91 species, we reconstructed guild structure across Australian passerines using the cluster analysis. We used Bray-Curtis distance for the calculation of the dissimilarity matrix (the *vegdist* function in the *vegan* package; Oksanen et al. 2020) and three different clustering algorithms: average (equivalent to UPGMA), complete, and ward.D2 (the *hclust* function in the *stats* package; R-Core-Team 2020). We selected Bray-Curtis distance, because it is recommended for proportional data (Borcard, Gillet, and Legendre 2018). We evaluated how well the dendrograms represented data by correlating the original distance matrix with the distance matrix obtained from the dendrogram itself (so called Shepard diagram; Borcard, Gillet, and Legendre 2018). The original distance matrix was best represented by the average (i.e., UPGMA) clustering method (i.e., it had the highest correlation coefficient, $r = 0.77$) and thus we used it for further presentation. We

also reconstructed a distance matrix and dendrogram based on morphological similarity using the Euclidean distance (on log10-transformed traits) and the complete clustering method (selected using the Shepard diagram, see above). We visualized the relationships between foraging behavior and phylogeny using co-dendrograms implemented in the *tanglegram* function of the *dendextend* package (Galili 2015).

We analyzed relationships between distance matrices from phylogenies and behavioral and morphological traits using Mantel tests implemented in the *ecodist* package (Goslee and Urban 2007). To quantify relationships between foraging behavior and morphology in more detail, we used phylogeny-adjusted canonical correlations fit using the *phyl.cca* function of the *phytools* package (Revell 2012). We analyzed all the 91 species (7 morphological traits) and fit the phylogeny-adjusted canonical correlations separately for foraging method and foraging substrates. We also performed resampling analyses to quantify how the strength of correlation between foraging behavior and morphology changed with the number of traits used. To do so, we used resampling without replacement, where we randomly selected from two to the maximum number of traits and fit the correlation on this selection. We repeated this resampling 50 times for each combination of the number of traits analyzed. Furthermore, we quantified the phylogenetic signal in morphological and foraging traits using the *K* statistic of Blomberg, Garland, and Ives (2003). *K* values closer to zero correspond to a random or convergent pattern of evolution. *K* values of 1 correspond to a Brownian motion process, which implies some degree of phylogenetic signal or conservatism, while *K* values greater than 1 indicate strong phylogenetic signal and conservatism of traits.

For each transect (n = 63), we calculated total abundance (the number of individuals observed), species richness (the number of passerine species observed), and behavioral and morphological functional diversity. To calculate behavioral functional diversity, we calculated Shannon index on behavioral categories (n = 25, where n = 8 for foraging methods and n = 17 for foraging substrates). This index is commonly used in community ecology and takes into account both the number of categories and the distribution of observations among

the categories (i.e., their evenness; Krebs 1999). To calculate morphological functional diversity, we used the hypervolume method of Blonder et al. (2018) applied to seven morphological traits. This method has the advantage of taking into account bird abundances and allowing for holes in morphological hyperspace (Blonder 2016). We analyzed the relationships between these community characteristics and vegetation structure (indexed by canopy height, see above) using linear mixed-effects models fit in the *lme* function of the *nlme* package (Pinheiro et al. 2021). We used the transect as a sampling unit (n = 63), with the site as a random effect (n = 21). We fit only the random intercept for sites. Canopy height was log10-transformed and all variables were scaled to enable comparison of parameter estimates.

RESULTS AND DISCUSSION

We obtained 5,894 prey attacks and recorded 9,223 individual birds across all 63 study transects in eastern Australia. We also extracted 47,525 foraging records from published studies (Table 1). The most frequently used foraging method was gleaning, because it was a dominant strategy in all but one study (mean across all studies = 55.9%; mean across studies where gleaning was dominant = 59.0%, Figure 2). The only exception was a study from mangroves (Noske 1996), where the dominant strategy was probing (53.6%) followed by gleaning (34.3%). In terms of the most frequently used foraging substrate, the situation was more varied. Leaves were the dominant substrate in four studies (mean = 56.4%; Figure 2; Recher et al. 1985; Ford, Noske, and Bridges 1986; Recher 1989; this chapter), all of which were conducted in eucalypt woodlands and forests of eastern Australia (Figure 1). Ground was the dominant substrate in two studies (mean = 52.3%; Recher and Davis 1997; 1998), while the two remaining studies had either bark (37.0%; Cale 1994) or flowers (56.3%; Noske 1996) as the dominant substrate.
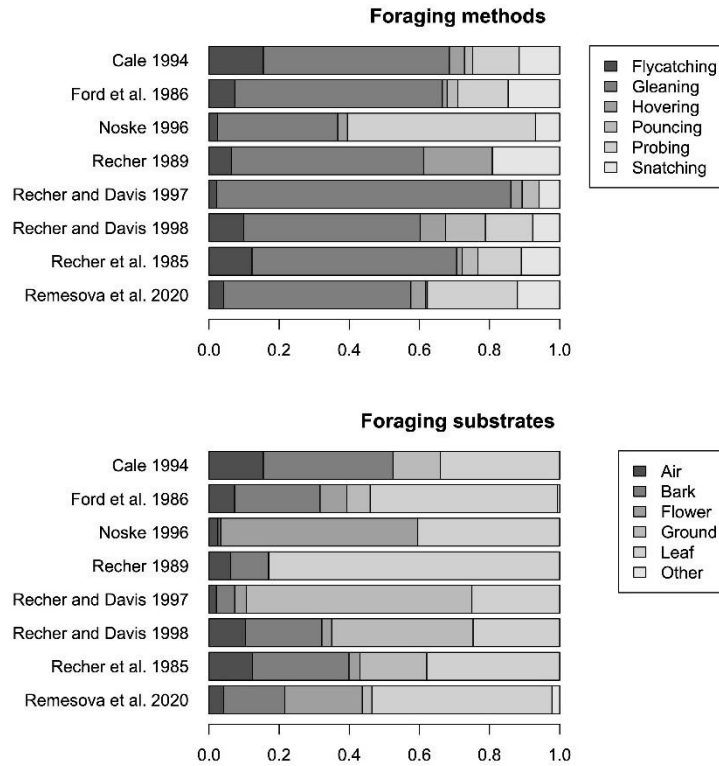
Foraging methods

Foraging substrates

Figure 2. The proportional dominance of foraging methods and substrates across the studies.

Foraging Guild Structure in Australian Passerines

Using cluster analysis, we quantified guild structure in 91 species with at least 30 foraging records each. We delimited eight guilds based on foraging behaviors and substrate use (Figure 3, Table 2). Besides seven species (one *Zoothera* thrush, one *Dicaeum* flowerpecker, two *Zosterops* white-eyes, and three estrildid finches), all species analyzed belonged to autochthonous radiations that took place either within Australia or in the Australo-Pacific region (Fjeldså, Christidis, and Ericson 2020).

Table 2. Foraging guilds of Australian passerine birds delimited based on foraging method and substrate use across Australia (n = 91 species and 53,419 foraging records). Methods and substrates in parentheses were used less often and only by some of the species in the guild. Genera without the number of species in parentheses were represented by one species only in a given guild

Guild ID	Method	Substrate	# Spp	Taxa (# spp)
1	Pouncing (Gleaning)	Ground	9	Petroicidae (7), *Rhipidura*, *Artamus*
2	Flycatching	Air	4	*Rhipidura* (2), *Myiagra*, *Artamus*
3	Snatching	Leaves	8	Petroicidae (2), *Myiagra* (2), *Pachycephala* (2), *Monarcha*, *Coracina*
4	Probing	Ground	2	*Zoothera*, *Menura*
5	Probing (Gleaning)	Flowers (Leaves)	11	Meliphagidae (11)
6	Gleaning & Probing	Bark	9	Climacteridae (3), Meliphagidae (3), *Colluricincla*, *Daphoenositta*, *Falcunculus*
7	Gleaning	Ground (Leaves)	16	Acanthizidae (5), *Malurus* (3), Estrildidae (2), *Climacteris*, *Corcorax*, *Epthianura*, *Gymnorhina*, *Pomatostomus*, *Psophodes*
8	Gleaning	Leaves	32	Acanthizidae (14), Meliphagidae (11), *Pardalotus* (2), *Zosterops* (2), *Dicaeum*, *Stagonopleura*, *Strepera*

Only two guilds were dominated by a single taxonomic family. Guild 5 (probing from flowers) was dominated by honeyeaters (Meliphagidae), while guild 8 (gleaning from leaves) was dominated by thornbills, gerygones and allies (Acanthizidae). However, otherwise the taxonomic composition of guilds was heterogeneous, and many families and genera were scattered across different guilds. For example, honeyeaters were represented also in guilds 8, 7 (gleaning from ground) and 6 (probing from bark), while thornbills in guild 7. Australasian robins (Petroicidae) were represented in guilds 1 (pouncing from ground) and 3 (snatching from leaves). The same was true for several genera, namely *Artamus*, *Myiagra*, and *Rhipidura* (Table 2). On the other hand, there were cases of conserved guild membership; for example, all three species of fairywrens (Maluridae, all in the genus *Malurus*) belonged to guild 7 (Table 2).
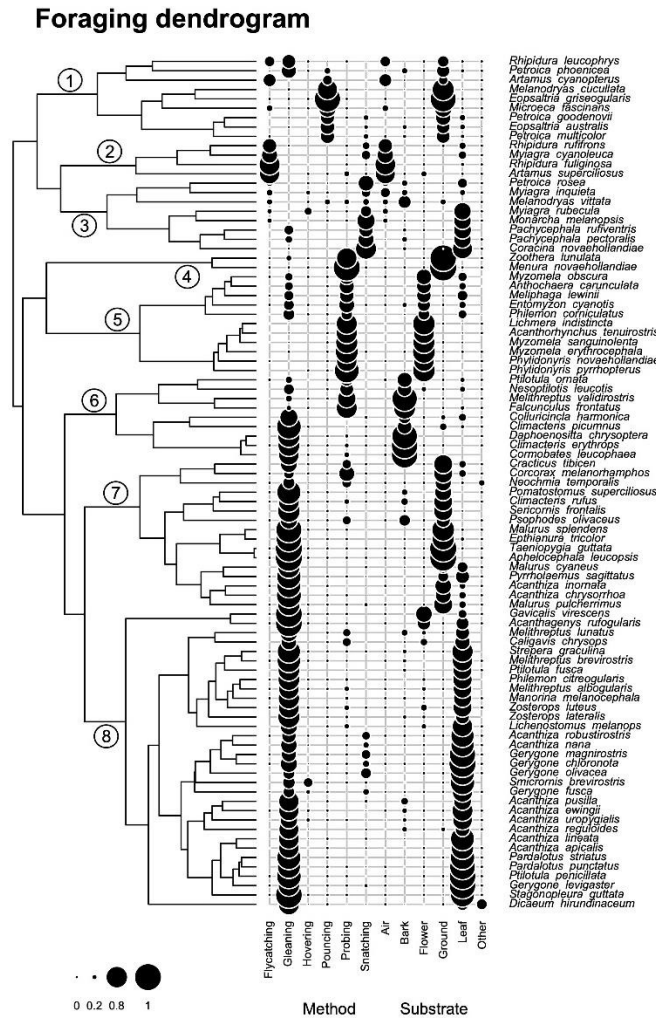
Foraging dendrogram

Figure 3. Dendrogram depicting foraging guilds of passerine birds in Australia. It was constructed based on similarity among species (Bray-Curtis distance) in foraging method (6 methods) and substrate use (6 substrates), using 53,419 foraging records across Australia. Numbers denote guilds from 1 to 8 (see Table 2). Black circles show the proportional use of foraging methods and substrates (on a non-linear scale, see the legend).

Repeated evolution of membership in foraging guilds has been demonstrated previously in various taxa. For example, New World flycatchers (Tyrannidae) represent an impressive New World radiation into a number of foraging niches, exemplified by the utilization of diverse foraging methods and substrates, including air, leaves, twigs, and ground, with correspondingly impressive ecomorphological diversity (Keast 1972; Taylor and Fitzpatrick 1980; Fitzpatrick 1985). Although much younger, ca. 22 My (Oliveros et al. 2019) or 28 My (Fjeldså, Christidis, and Ericson 2020), they are functionally equivalent to the radiation of mostly Australian lineages, best represented by the clade Meliphagoidea (or Meliphagides, ca. 28 My according to Oliveros et al. 2019 or 45 My according to Fjeldså, Christidis, and Ericson 2020), which makes a large part of species we study (50 species out of 91; Figures 3 and 4). As such, these two radiations represent parallel adaptive divergence due to exploitation of available ecological space. Similar radiations are represented by Old World sylvioid, muscicapoid, and corvoid clades (see Oliveros et al. 2019; Fjeldså, Christidis, and Ericson 2020), but their foraging behaviors and niche partitioning on the long timescales of millions of years have not been quantitatively described. The evolution into diverse ecological roles has been well documented in passerines of the Australo-Pacific region, especially in various honeyeater lineages (Keast 1968; 1985; Norman et al. 2007; Toon, Hughes, and Joseph 2010; Miller et al. 2017). In terms of local guilds, the evolution of a similar guild structure in passerine birds has been demonstrated by comparing guild structure in Australia, Europe, and North America (Korňan et al. 2013). These comparisons showed that similar guilds delimited by substrate use and foraging methods evolved independently in passerine birds of different zoogeographic regions, including Australia (Recher et al. 1985; Ford, Noske, and Bridges 1986; Ford 1989; Noske 1996; Recher and Davis 1997), North America (Holmes, Bonney, and Pacala 1979), Europe (Korňan and Adamík 2007; Korňan et al. 2013) and at least one high-altitude forest of India (Somasundaram and Vijayan 2008). Here, we confirm this observation by documenting guild structure on the largest sample of foraging records and species analyzed so far.

On the other hand, these generalizations do not extend to the tropical forests of New Guinea and Malaysia, where the foraging structure of communities is first partitioned by foraging height and only then by foraging behavior (Bell 1983; Mansor and Mohd Sah 2012), while the situation in Australian wet tropics is somewhere in between (Crome 1978; Frith 1984).

Foraging Behavior and Morphology in Relation to Phylogeny

Quite surprisingly, the correlation of the patristic distance on phylogeny with the distance matrix of foraging behavior was higher (r = 0.36, p < 0.001) than with the distance matrix of morphology (r = 0.26, p < 0.001). Although statistically significant, the correlation coefficients were in general low, because r = 0.36 means only 13% of the variability in data explained. The low correspondence between phylogeny and foraging behavior is apparent from the taxonomic structure of guilds (see above and Table 2) and can be further illustrated by crossed links in the co-dendrogram linking phylogeny and behavior (Figure 4). However, there is still some correspondence at higher level, demonstrated by bundled links that sometimes connect several species from the same genus or family to one particular guild. Nevertheless, ample crossing of connecting lines suggests that phylogeny does not constrain guild membership (Figure 4, Table 2).

Thus, independent evolution of the exploitation of ecological space takes place (see above). Our results complement previous work, demonstrating repeated evolution of niche exploitation linked to morphological evolution for example in birds (Keast 1972; Fitzpatrick 1985; Miller et al. 2017; Pigot et al. 2020) and lizards (Melville, Harmon, and Losos 2006; Losos 2009; Mahler et al. 2013).

Morphology was closely tied to phylogeny as evidenced by high values of K (Figure 5). Mean value of K for all 91 species was 1.51, indicating strong phylogenetic signal and phylogenetic conservatism of morphological traits (Blomberg, Garland, and Ives 2003).
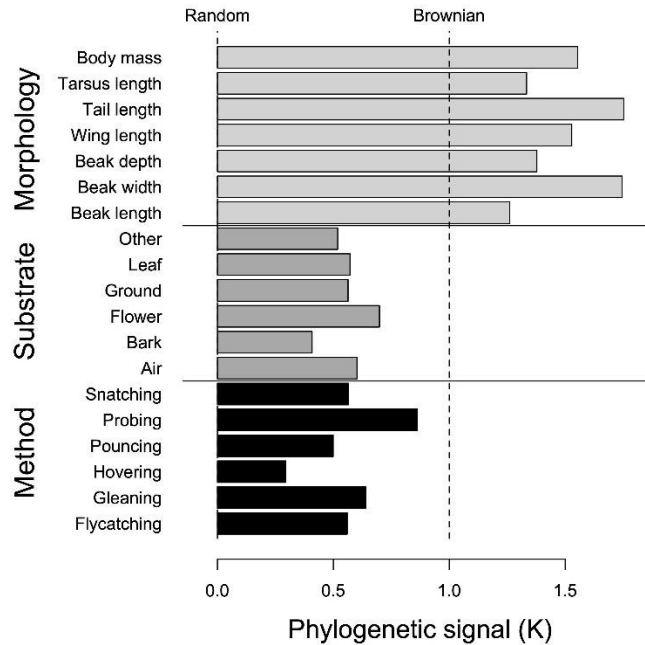
Figure 4. Co-dendrogram of the phylogeny and our behavioral dendrogram with links connecting species. In only four cases (depicted by black links) did sister species fall side by side in the behavioral dendrogram (one case each in *Acanthiza*, *Gerygone*, *Pachycephala*, and *Pardalotus*). However, certain higher structure is apparent from a "bundled" appearance of connecting lines, where the same genus/family sometimes links to the same guild or related guilds. Letters denote families, where only families with at least three species are labeled (A - Climacteridae, B - Estrildidae, C - Petroicidae, D - Monarchidae, E - Rhipiduridae, F - Maluridae, G - Acanthizidae, H - Meliphagidae), while numbers denote foraging guilds (see Figure 3, Table 2).

Figure 5. Phylogenetic signal (Blomberg's *K*) in morphological and behavioral traits in 91 species of Australian passerine birds. Morphology was phylogenetically conserved (*K* values > 1), while foraging behavior was phylogenetically labile (*K* values < 1). *K* = 1 means neutral evolution of the trait according to Brownian motion following the branching pattern of the phylogeny. *K* = 0 means trait evolution unrelated to the phylogeny (unstructured random walk).

On the contrary, behavioral traits were more phylogenetically labile (Figure 5). Mean value of *K* for foraging substrates was 0.56, while it was 0.57 for foraging methods, indicating faster or convergent evolution of behavioral traits. Bark use (*K* = 0.41) and hovering (*K* = 0.29) were relatively most phylogenetically labile, while flower use (*K* = 0.70) and probing (*K* = 0.86) were relatively most conserved. For example, substantial use of bark for foraging evolved repeatedly in several different families. It was dominant in most species of Australasian Treecreepers (Climacteridae), three species of honeyeaters (especially in the Strong-billed Honeyeater of Tasmania, *Melithreptus validirostris,* 94% of all foraging records), Crested Shrike-tit (*Falcunculus frontatus*, Falcunculidae, 81.7%), Varied Sittella (*Daphoenositta chrysoptera*, Neosittidae, 94.6%) and to a lesser extent

in the Gray Shrikethrush (*Colluricincla harmonica*, Pachycephalidae, 47.5%) and in the Dusky Robin of Tasmania (*Melanodryas vittata*, Petroicidae, 49.0%; Figure 3). On the other hand, flower use evolved only in honeyeaters (Meliphagidae, Figure 3), although by no means in all species, because honeyeaters also formed a substantial part of guild 8 (gleaning from leaves). The concentration of flower-foraging species in one taxonomic family might be explained in two complementary ways. First, flower use might need special beak morphology (Friedman et al. 2019), which might be rare to evolve. Second, the occupation of available ecological space, namely foraging from flowers, might enable fast clade diversification and full exploitation of this resource (Marki et al. 2019). Other clades might be precluded by competition from utilizing this resource in any substantial way.

Foraging Behavior in Relation to Morphology

Adjusting for phylogeny, the correlation between morphology (7 traits) and foraging methods yielded the first correlation coefficient of $r = 0.75$ (i.e., 56% of variability in data explained, $p < 0.001$). This is the correlation between the first canonical axes of the multivariate spaces of foraging methods and morphology. The first canonical axis of foraging methods had negative loadings of flycatching and positive loadings of all other behaviors (especially probing). The first morphological axis had negative loadings of beak width, wing length, and tail length, while other traits had positive loadings (especially beak length and depth). These results demonstrated that flycatching species had relatively wide, flat, and short beaks and relatively long wings and tails, while species using probing had the opposite characteristics. This agrees with previous findings for example in tyrant flycatchers (Tyrannidae), where flycatching species have also flat and wide beaks (Keast 1972; Fitzpatrick 1985). The correlation between morphology and substrate use yielded the first correlation coefficient of $r = 0.64$ (41% of variability explained, $p < 0.001$). The first canonical axis of foraging substrate use had negative loadings of air and positive loadings of all other substrates, especially flowers. The loadings or the first morphological axis were similar as above. This agrees with

previous findings of honeyeaters foraging extensively on nectar from flowers having narrow and elongated beaks (Friedman et al. 2019). Moreover, the observation that flower-exploiting hummingbirds (Trochilidae) and sunbirds (Nectariniidae) have exceptionally narrow and long beaks is also in line with our findings. Overall, we demonstrate the opposite morphological design of air-flycatching vs. flower-probing species. Our results agree with previous ecomorphological work documenting morphological convergence of distantly related species using the same foraging resources (Leisler and Winkler 1985; Pigot et al. 2020).

However, the correlation between morphology and behavior differs across studies (Ricklefs and Travis 1980; Miles and Ricklefs 1984; Miles, Ricklefs, and Travis 1987; Pigot, Trisos, and Tobias 2016; Miller et al. 2017; Friedman et al. 2019). One of the reasons might be differences in the number of morphological and ecological or behavioral traits analyzed. We thus repeated the phylogenetically-corrected canonical correlations with different numbers of traits. We used resampling without replacement, where we randomly selected from two to the maximum number of traits and fit the canonical correlation on this selection. We repeated this resampling 50 times for each combination of a given number of traits analyzed. As expected, the first correlation from the canonical correlation analysis increased with the number of behavioral and morphological traits analyzed (Figure 6). The correlation started at 0.31 for foraging methods and 0.29 for foraging substrates when two behavioral and two morphological traits were used. This means ca. 9% of variability in data explained. Clearly, two traits are too few. However, the correlation increased quite fast and reached 0.64 and 0.75 when using 12 traits together (the sum of behavioral and morphological traits). This is quite encouraging, as an achievable sampling in the field and in museum collections ensured a significant insight into the ecomorphology of the whole autochthonous radiation of passerines in Australia. In sum, we showed that foraging behavior was partially predicted by morphology, which was in turn closely tied to phylogeny (high phylogenetic signal). Foraging behavior was phylogenetically more labile, allowing for faster divergence and switching between foraging guilds.
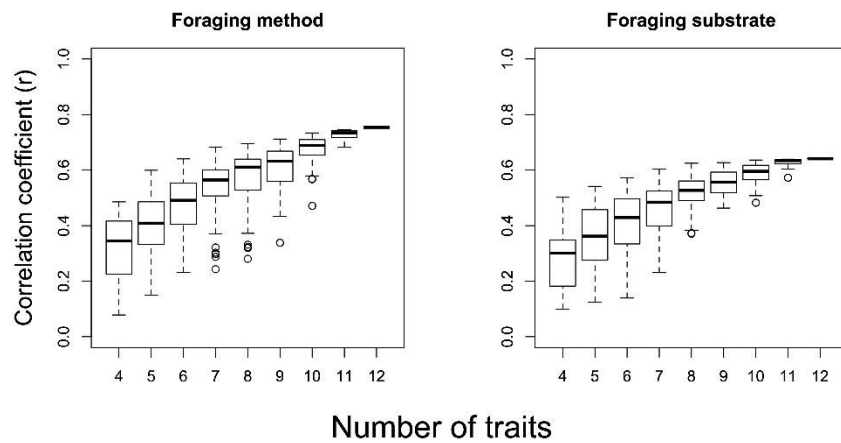
Figure 6. Correlations between foraging behavior and morphology in Australian passerine birds. Correlation coefficient is the first canonical correlation between a matrix of behavioral (max. n = 5) and morphological traits (max. n = 7). We resampled 50 times each combination of a given number of behavioral and morphological traits (from 2 to the maximum possible) and always calculated phylogenetically corrected canonical correlation. We show the summed number of behavioral and morphological traits along the horizontal axis.

Diversity in Local Communities

In local communities, total abundance (i.e., the number of individuals), species richness, and morphological and behavioral diversity all increased with vegetation complexity (indexed by canopy height; Figure 7, Table 3). The strongest was the relationship with total abundance, which makes sense in terms of more vegetation providing ecological space (food, shelter etc.) for more individuals. Higher abundance might then bring more species, in accordance with the more-individuals hypothesis (Storch, Bohdalková, and Okie 2018). Higher morphological and behavioral diversity might then follow from more species being present. Species richness and morphological diversity were the most repeatable within sites (Table 3). This probably follows from the observation that the distribution of species is highly spatially structured due to the historical legacy of cycles of allopatric speciation and secondary overlap (Warren et al. 2014). Total

abundance and behavioral diversity were less repeatable, revealing their stronger dependence on local ecological conditions.
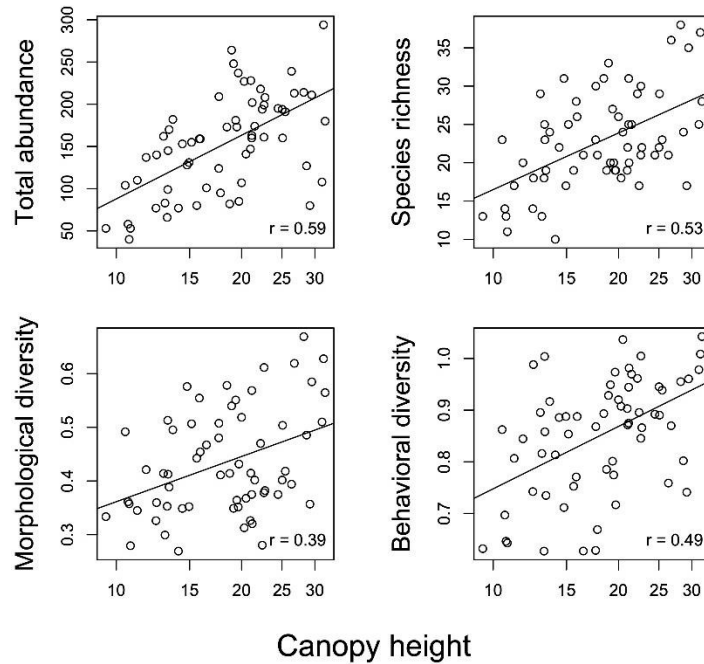

Figure 7. All aspects of passerine diversity increased with canopy height (meters) across our 63 transects (nested within 21 sites). Total abundance is the number of individuals and species richness is the number of species we recorded during the two censuses on each transect. Morphological diversity is relative volume of the 7-dimensional morphological hyperspace delimited by individuals present at a given transect. Its value is depicted as relative to the total volume of all individuals recorded across all transects. Behavioral diversity is the Shannon index calculated using foraging methods and substrates. Its value is depicted as relative to behavioral diversity of all individuals recorded. Correlation coefficients are also shown within the panels.

The interplay between regional processes driven by evolution and local processes driven by ecology are currently the focus of much research (Mittelbach and McGill 2019). In the previous sections, we showed how evolution forms repeated behavioral guilds. Here we show how members of these guilds are then sampled to local communities.

Table 3. Results of linear mixed-effects models relating passerine diversity to canopy height. Canopy height was log10-transformed, and all variables were scaled to enable comparison of parameter estimates. Denominator DF = 41. The random effect of site (always three transects per site) is equivalent to the intraclass correlation coefficient (ICC), showing how repeatable the observations on transects within sites are

Response	Estimate (SE)	F	P	ICC (%)
Total abundance	0.61 (0.137)	19.9	<0.001	43.9
Species richness	0.51 (0.147)	12.1	0.001	50.3
Morphological diversity	0.35 (0.163)	4.5	0.040	57.8
Behavioral diversity	0.47 (0.144)	10.8	0.002	37.5

Larger ecological space with more potential niches (higher canopy and thus more vegetation) enabled the coexistence of more individuals and more species with varied morphologies and foraging strategies. The critical role of vegetation volume and heterogeneity for species richness has been demonstrated by several classical studies (MacArthur and MacArthur 1961; Recher 1969; Karr and Roth 1971) and confirmed by reviews across habitats and taxa (Tews et al. 2004). Recent studies extended this reasoning to functional and phylogenetic diversity (Remeš and Harmáčková 2018; Feng et al. 2020). Our findings confirm the importance of available niches and ecological space in shaping the structure of multiple aspects of local passerine communities.

CONCLUSION

Overall, our results showed that on a continental scale, passerine birds evolved repeatable foraging guilds whose membership was little constrained by morphology or phylogeny. Sampling from these guilds to local communities was then predicted by the volume of ecological space dictated by vegetation complexity. Overall, we demonstrated an interplay between phylogenetic conservatism, behavioral flexibility, and ecological opportunity in shaping species richness and functional diversity from regional avifaunas to local communities. Similar

comprehensive studies from other continents are needed to test the generality of our findings.

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