E-Article

Radiating despite a Lack of Character: Ecological Divergence among Closely Related, Morphologically Similar Honeyeaters (Aves: Meliphagidae) Co-occurring in Arid Australian Environments

Eliot T. Miller,[1,2,3,4,*] Sarah K. Wagner,[4,5] Luke J. Harmon,[3,6] and Robert E. Ricklefs[1]

1. Harris World Ecology Center and Department of Biology, University of Missouri, St. Louis, Missouri 63121;   2. Department of Biological Sciences, Macquarie University, Sydney, New South Wales 2109, Australia;   3. Department of Biological Sciences, University of Idaho, Moscow, Idaho 83844;   4. Cornell Lab of Ornithology, Cornell University, Ithaca, New York 14950;   5. Ecology and Evolutionary Biology Department, University of Colorado, Boulder, Colorado 80309;   6. Institute for Bioinformatics and Evolutionary Studies (IBEST), University of Idaho, Moscow, Idaho 83844

ABSTRACT: Quantifying the relationship between form and function can inform use of morphology as a surrogate for ecology. How the strength of this relationship varies continentally can inform understanding of evolutionary radiations; for example, does the relationship break down when certain lineages invade and diversify in novel habitats? The 75 species of Australian honeyeaters (Meliphagidae) are morphologically and ecologically diverse, with species feeding on nectar, insects, fruit, and other resources. We investigated Meliphagidae ecomorphology and community structure by (1) quantifying the concordance between morphology and ecology (foraging behavior), (2) estimating rates of trait evolution in relation to the packing of ecological space, and (3) comparing phylogenetic and trait community structure across the broad environmental gradients of the continent. We found that morphology explained 37% of the variance in ecology (and 62% vice versa), and we uncovered well-known bivariate relationships among the multivariate ecomorphological data. Ecological trait diversity declined less rapidly than phylogenetic diversity along a gradient of decreasing precipitation. We employ a new method (trait fields) and extend another (phylogenetic fields) to show that while species in phylogenetically clustered, arid-environment assemblages are similar morphologically, they are as varied in foraging behavior as those from more diverse assemblages. Thus, although closely related and similar morphologically, these arid-adapted species have diverged in ecological space to a similar degree as their mesic counterparts.

Keywords: community assembly, ecomorphology, functional traits, interspecific competition, phylogenetic community structure, phylogenetic niche conservatism.

* Corresponding author; e-mail: eliot.isaac@gmail.com.

Introduction

Birds fly, whales swim, cheetahs run, and amoebae ooze (not very fast) via cellular extension. In organismal biology, the connection between form and function is intuitive, generally accepted, and often well supported quantitatively (Miles and Ricklefs 1984; Miles et al. 1987; Saunders and Barclay 1992; Ricklefs and Miles 1994; Fitzpatrick et al. 2004; Leisler and Schulze-Hagen 2011). The connection between a species' morphology and its ecology (its performance and resource use) has often led to the use of morphology as a surrogate for ecology. While ecological measures can be difficult to obtain and variable across time (Lovette and Holmes 1995) and space (Suryan et al. 2000), morphology can be measured easily and is assumed to integrate ecological relationships over the life span of the individual and to reflect past selective pressures on the population.

For a variety of reasons, ecology and morphology might also show discordant signals across a large sample of taxa. While we expect concordance between morphology and ecology among phylogenetically closely related species, some authors have concluded that, at a broader level, ". . . the strong influence of phylogeny within the trophic relationships of an assemblage negate[s] the value of an ecomorphological analysis" (Douglas and Matthews 1992, p. 220). Similar ecologies can be realized through dissimilar morphologies, and a single morphology can serve varied purposes (Wainwright 2007). Caterpillars and giraffes both feed on leaves, and while many kingfishers (Aves: Alcedinidae) feed on fish, others take almost entirely terrestrial prey, including large insects, amphibians, and reptiles. Evo-

lutionary constraints at multiple levels shape how species adapt to their environments (Arnold 1992; Futuyma 2010). For instance, beak size may not be free to evolve toward a given adaptive peak because it may be subject to conflicting selective pressures (Schluter 1996; Bright et al. 2016). The ancestral state of a population also can influence which local adaptive peak a population settles on (Hansen and Houle 2008), and a given resource might be exploited by organisms sitting on several adaptive peaks, as in the case of caterpillars and giraffes feeding on the same leaves. Finally, interspecific competition may influence the positions of adaptive peaks in the ecological landscape.

While competition may drive phenotypic divergence, environmental pressures push species within local assemblages to resemble each other, either through evolutionary convergence or habitat filtering. This spectrum of possible community assembly processes has motivated studies on phylogenetic community structure (Webb et al. 2002; Cavender-Bares et al. 2009), a proxy approach that uses evolutionary relationships to indicate ecological similarity. An arguably more direct approach to analyzing community assembly makes use of functional traits (McGill et al. 2006). This approach presumes that functional (often morphological) traits adequately represent species' ecologies. In plants, the use of functional traits has generally proven well-founded in comparisons across assemblages; for instance, the leaves of rainforest plants tend to be thinner than those of arid-adapted plants (Wright et al. 2004; Zanne et al. 2014). Again in plants, limited support for correspondence between ecology and morphological/physiological traits has been found within assemblages in more focused ecophysiological assessments (Cavender-Bares et al. 2004a, 2004b; Lambers and Poorter 2004). Based on such support, many authors have recently compared arrays of functional traits in local plant assemblages around the globe (Kraft and Ackerly 2010; Cornwell et al. 2014). However, the difficulty of obtaining more direct ecological measurements in plants has hindered our ability to determine whether community functional trait patterns generally indicate community assembly processes.

The dearth of ecological measurements for birds has likewise hampered direct assessment of broadscale community assembly patterns. Even from a morphological perspective, few recent studies have employed functional trait approaches to characterize bird assemblages (Luther 2009; Gómez et al. 2010; Ricklefs 2011, 2012; Jønsson et al. 2012; Dehling et al. 2014; Tobias et al. 2014; Weinstein et al. 2014), although this area of research has early roots (Schoener 1965; Karr and James 1975; Ricklefs and Travis 1980; Keast and Recher 1997).

Limited phylogenetic diversity in a setting with abundant ecological opportunity may initiate a period of adaptive radiation, as apparent, for example, among the Hawaiian honeycreepers (Aves: Fringillidae) or Galapagos finches (Aves: Thraupidae; Lack 1947; Schluter 2000; Lovette et al.

2002). While authors have differed on what constitutes an adaptive radiation (Givnish and Sytsma 2000; Schluter 2000; Givnish 2015), the general phenomenon of evolutionary diversification given ecological opportunity might characterize many lineages not traditionally recognized as being adaptive radiations. In such lineages, we might expect to see increased rates of trait evolution compared to related lineages that have diversified in environments with a larger suite of potential competitors. Thus, environmental pressures in combination with climatic phylogenetic niche conservatism might lead to a loss of phylogenetic diversity, followed by a subsequent radiation in ecomorphological space by the lineages able to colonize these ecologically open areas, particularly if those areas have natural barriers to gene flow.

The Australian honeyeaters (Meliphagidae) comprise a clade of 75 species of passerine birds distributed across the continent, with at least one species found in almost every habitat type. Honeyeater species vary from large-bodied generalists such as the yellow wattlebird (*Anthochaera paradoxa*, >160 g) to small, decurved-billed nectarivores such as the red-headed myzomela (*Myzomela erythrocephala*, 7–8 g) and from stout-billed, ground-foraging insectivores such as the gibberbird (*Ashbyia lovensis*) to habitual frugivores such as the painted honeyeater (*Grantiella picta*; Higgins et al. 2001). Among Australian honeyeaters, a strong pattern of increasing phylogenetic clustering follows a gradient of decreasing precipitation, as mesic-adapted lineages drop out toward the arid interior of the continent (Miller et al. 2013). Yet, Meliphagidae species richness does not decline precipitously along this precipitation gradient, a fact that Miller et al. (2013) attributed, in part, to ecological opportunity and strong selective pressure to adapt to the newly opened desert habitats as Australia underwent dramatic aridification from the Miocene onward.

In this article, we address how evolution and ecology interact to determine trait diversity of honeyeater assemblages in Australia. We hypothesize that although only a limited set of honeyeater lineages has colonized the arid interior, these species have evolved ecologically to fill similar niches to their mesic counterparts. To test this hypothesis, we explore the distribution of morphological and ecological traits within honeyeater assemblages along gradients of climate and phylogenetic community structure. Finding that ecological trait disparity does not parallel phylogenetic diversity across local assemblages, we consider whether ecological opportunity has triggered increased rates of evolution in patterns of resource use in these arid-adapted species. We collected and employed two large, near-comprehensive data sets summarizing the morphological and ecological diversity of the Australian Meliphagidae to test the prediction that ecology and morphology are strongly related across the family (crown age ~20 Ma), reflecting the biological axiom that form reflects function. We used the intersection of

these data sets, detailed Australian honeyeater distributional data (Miller et al. 2013), and a time-calibrated phylogeny of the Meliphagidae to address our hypothesis that arid-zone lineages evolved rapidly in trait space to fill novel desert habitats.

Methods

Morphological Data Collection and Processing

We used digital calipers and photograph analysis (ImageJ; Schneider et al. 2012) to assemble a set of linear measurements on museum specimens (figs. A1, A2; figs. A1–A4 are available online): culmen length from front of the nares to bill tip; culmen length from base (kinetic hinge) of the bill to tip; exposed maxilla and bill chord (ImageJ); bill width and depth at both the nares (respiratory openings in the beak) and at the base; wing chord (length from carpal joint to longest primary wing feather); length of the longest secondary wing feather; tarsus, hind-toe, and mid-toe lengths; and tail and total body lengths. Whenever possible, we measured at least three males and three females of each species/subspecies. We used ImageJ and spread-wing specimens to quantify total wing area; the length (along the axis of the wing) and width (widest point perpendicular to the wing axis) of the spread wing; and the lengths of the longest primary, the longest secondary, and the outermost/first secondary feather.

We used the wing measurements to calculate the hand-wing index (see supplemental PDF, available online), which is a proxy for a wing's aspect ratio, that is, a measure of its shape, from rounded to pointed, generally associated with maneuverability versus long-distance flight and strong dispersal (Claramunt et al. 2012). We also calculated a bill curvature index, the quotient of the maxilla length over its chord (Rico-Guevara and Araya-Salas 2014), and a bill length index, 100 × (bill length from base − bill length from nares)/ bill length from base. Large values of the bill length index correspond to species where most of the length of the bill is proximal to the nares (e.g., yellow wattlebird, *Anthochaera paradoxa*), while small values correspond to species where most of the length is distal to the nares (e.g., eastern spinebill, *Acanthorhynchus tenuirostris*). We calculated bill width and depth indexes in a similar fashion (using the width/ depth at the base vs. the nares). Here, large values correspond to bills whose width (white-gaped honeyeater, *Stomiopera unicolor*) or depth (orange chat, *Epthianura aurifrons*) tapers considerably from base to tip. These indexes provide some indication of bill shape; many Tyrannidae flycatchers, for instance, have bills that are wide near the base and taper considerably toward the tip.

When available, we used the mass of the bird at the time of collection as recorded on the specimen tag (37% of spec-imens). When no value was provided, we used the best information available to assign an approximate mass to each specimen. Specifically, if the sex of the specimen was known and a large sample of sex-specific, subspecies-specific masses was available (Higgins et al. 2001), we used that mass (59% of specimens). Otherwise, we used the next higher level of specificity, for example, the sex-specific average mass across all subspecies of that species, and so on. In this way, we as-signed a mass to all specimens. We were unable to measure any specimens of the range-restricted Eungella honeyeater (*Bolemoreus hindwoodi*) and excluded it from morphologi-cal analyses.
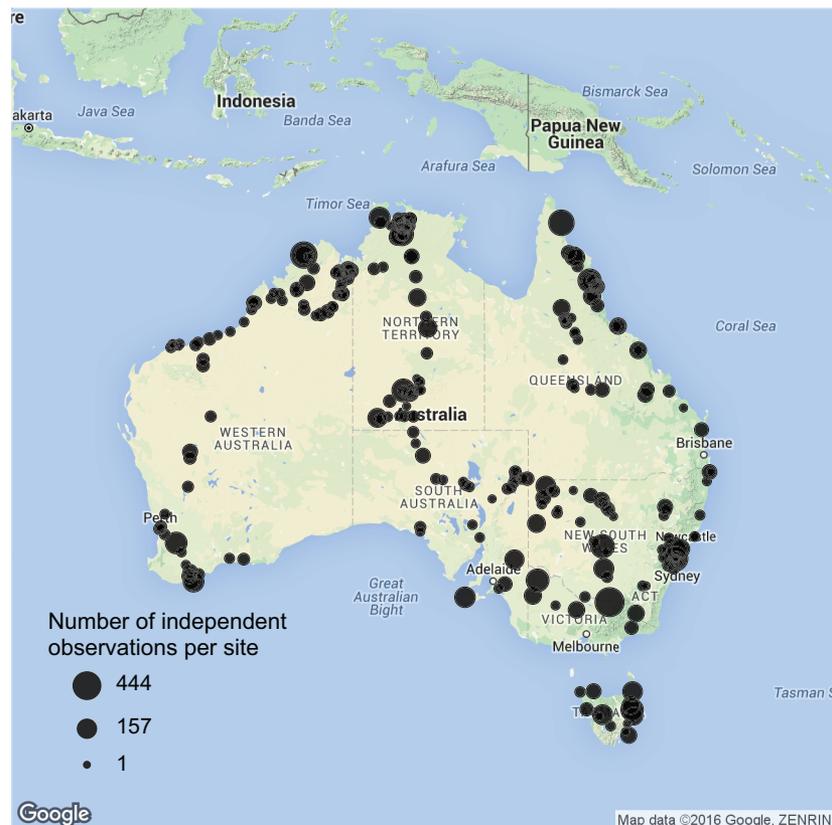
Ecological Data Collection and Processing

Collection of ecological information, primarily foraging behavior, followed protocols of Miller and Wagner (2015), which were based on standardized methods (Remsen and Robinson 1990). Between July 2009 and May 2014, we spent 295 field days throughout continental Australia, Kangaroo Island, and Tasmania (fig. 1). When not driving between sites, we spent the daylight hours walking transects record-ing foraging movements, substrates, and food items. For each observation, we recorded the time, the location, the substrate on which the bird foraged, the attack maneuver employed, whether the bird was hanging during the maneuver, the height of the foraging bird, the height of the surrounding canopy, the distance of the bird from the trunk, and the density of foliage around the foraging bird. Additional de-tails are provided in the supplemental PDF.

If the first observed foraging maneuver initially drew our attention to an individual bird, we discarded the observa-tion to minimize bias. Otherwise, if we located a bird, for instance, by its vocalizations, we recorded the first maneu-ver we saw. We endeavored to record only one observation per individual per day. To better understand individual var-iation in foraging behavior, in some cases we did record multiple observations from single birds. However, we con-sidered such series of observations as collectively represent-ing a single data point. We chose 20 independent observa-tions as the minimum required for analysis of a species' niche. We did not meet this requirement for the elusive gray hon-eyeater (*Conopophila whitei*) and, therefore, excluded it from ecological analyses.

Collection of Meliphagidae Assemblage and Climate Data

We used the species distribution data set from Miller et al. (2013). This taxonomically and spatially cleaned data set contains 2,273,404 localized observations of individuals across all Meliphagidae species. The data were downloaded and concatenated from eBird (Sullivan et al. 2009) and the At-las of Living Australia (http://www.ala.org.au/). We defined

Figure 1: Map of Australia, showing the locations where the 9,595 foraging observations for this study were made. The size of the circle corresponds to the number of independent observations that were recorded at that site.

assemblages as the species occurring within 100 × 100-km grid cells. In many parts of Australia, it is a reasonable assumption that all species in a grid cell could interact ecologically. For instance, while collecting foraging data, we occasionally recorded a species list for the area. On average, we observed a mean of 40% of the bird species recorded from a given grid cell each day ($n = 27$, $SD = 16\%$, $max = 100\%$, $min = 21\%$). We ran analyses using both the presence-absence community data matrix (CDM) and the relative abundance CDM, which, to the extent that our assessment of abundance can be relied on, can reduce the influence of vagrants and provide added biological detail on the effects of habitat filtering and competitive exclusion.

We used the mean annual temperature (MAT) and mean annual precipitation (MAP) layers from WorldClim (http://www.worldclim.org/bioclim), as summarized in Miller et al. (2013), to quantify variation in climate across the continent.

Definition and Summary of Multivariate Trait Spaces

We log transformed all morphological measurements (but not the composite indexes) and then calculated species'

averages for all morphological and ecological measures. For ecological measures, species' traits refer to mean average foraging height, proportion of attacks that were gleans, proportion of attacks that were on flowers, and so on.

We used the R (R Development Core Team 2016) package phytools (Revell 2012) to ordinate each data set separately with a phylogenetic correlation matrix-principal components analysis (pPCA; Revell 2009), that is, a PCA where the expected degree of covariance among evolutionary changes in species' traits is incorporated into the calculation of PC axes and scores. We used the maximum-likelihood optimized value of λ here. To visualize how the Meliphagidae explored these trait spaces, we used a color-coded phylomorphospace approach (Miller et al. 2013), based on an updated, time-calibrated version of the Meliphagidae phylogeny for all analyses (Joseph et al. 2014), with nine species inserted manually with addTaxa (Mast et al. 2015).

To quantify the phylogenetic signal in species' morphological and ecological traits, we used the R package geomorph (Adams 2014). This approach incorporates the multivariate nature of these data and, instead of calculating a separate value per trait or PCA, outputs a single K value

(Blomberg et al. 2003) that reflects the overall phylogenetic signal of all of the species' traits simultaneously.

Concordance of Morphology and Ecology

To examine the degree to which morphology predicts species' ecologies, and vice versa, we used a phylogenetic canonical correlation analysis (pCCA; Revell and Harrison 2008). We interpreted the initial phytools results with custom scripts that calculate the phylogenetic generalized least squares (PGLS) correlation coefficients of the raw trait variables with species' positions along the derived ecological and morphological canonical axes. We then used these correlation coefficients to calculate redundancy indexes (Stewart and Love 1968) with the candisc package. These indexes provide a measure of the amount of variance in the ecological data set that can be explained with the morphological data set, and vice versa. Many of the ecological variables are zero skewed, reflecting the paucity of certain foraging behaviors, thus we repeated these analyses excluding the most zero-skewed behaviors. Because results were qualitatively identical with either ecological data set, we do not discuss results from the reduced ecological data set in detail.

Calculation of Phylogenetic Diversity and Trait Disparity

We used several approaches to quantify phylogenetic and trait community structure (table 1). For brevity, and in keeping with previous work (e.g., Harmon et al. 2003), we frequently refer to these as phylogenetic diversity and trait disparity, respectively. However, we emphasize that we do not address total community phylogenetic diversity (Faith 1996) or total community trait space (Cornwell et al. 2006); in this article, we focus on mean distances between collections of species in phylogenetic and trait space.

Phylogenetic and trait structure are usually calculated at the level of communities (sites in a CDM), and we do so here. However, to more directly test our prediction that species from phylogenetically clustered arid-environment assemblages have evolved through trait space at a faster rate than those from less phylogenetically clustered assemblages, we developed a method to quantify how different a species is,

phylogenetically or in trait space, from the numerous species it occurs with across its range. Building on the work of Villalobos et al. (2013), we extended the phylogenetic field concept to include standardized effect sizes (SES) and abundance weighting. For each species, a phylogenetic/trait field describes the average properties of local assemblages in which that species occurs. For instance, species with large trait field SES values occur in assemblages with species that are more evenly arrayed across trait space than expected under a null model. Functions to calculate phylogenetic and trait fields have been included in the metricTester package (Miller et al. 2016a).

Whether calculated at the assemblage or species level, measures of phylogenetic or trait structure consist of the metric used to calculate structure and, optionally, a null model used to standardize the metrics. In our study, we employed four metrics: mean pairwise phylogenetic distance (MPD), interspecific abundance-weighted MPD (MPD_{inter}), mean nearest taxon distance (MNTD), and abundance-weighted MNTD ($MNTD_{AW}$). We standardized these metrics against distributions of 10,000 values obtained from randomizations generated with each of two null models: a richness null model, which maintained observed species richness but not occurrence frequencies or dispersal probabilities, and a dispersal null model (Miller 2016), where assemblage species richness, individual species' occurrence frequencies, and total CDM abundance (i.e., total number of individuals in the CDM) were approximately maintained and species were settled with a probability proportional to their relative abundance in nearby cells. These simulated communities were then used to derive expected structure metrics, which were in turn used to calculate the SES values, defined as the difference between the observed metric and the mean of the simulated metrics, divided by the standard deviation. Because (1) MPD focuses on trait/phylogenetic distances between all species in an assemblage, as opposed to just those between near neighbors, (2) MPD was recently shown to have superior statistical performance to MNTD (Miller et al. 2016a), (3) abundance-weighting the metric might likewise enable the detection of more subtle shifts in structure, and (4) the dispersal null model better accounts for the biology inherent in our continental-scale

Table 1: Abbreviations for the 12 ways in which phylogenetic and trait community structure were quantified in this study

Method	Phylogenetic and trait community structure method abbreviation			
Unstandardized	MPD	MPD_{inter}	MNTD	$MNTD_{AW}$
Standardized with richness null model	$SES_{richness}$ MPD	$SES_{richness}$ MPD_{inter}	$SES_{richness}$ MNTD	$SES_{richness}$ $MNTD_{AW}$
Standardized with dispersal null model	$SES_{dispersal}$ MPD	$SES_{dispersal}$ MPD_{inter}	$SES_{dispersal}$ MNTD	$SES_{dispersal}$ $MNTD_{AW}$

Note: Only results that employed $SES_{dispersal}$ MPD_{inter} are shown in the main text. All other phylogenetic and trait community structure results are in the supplementary materials. MPD = mean pairwise phylogenetic distance; MPD_{inter} = interspecific abundance-weighted MPD; MNTD = mean nearest taxon distance; $MNTD_{AW}$ = abundance-weighted MNTD; SES = standardized effect sizes.

study, all results presented in the main text employ SES$_{dispersal}$ MPD$_{inter}$ (table 1). However, results from all other approaches are presented in the supplemental PDF.

All metrics we employed require a matrix summarizing pairwise distances between all study taxa. In the case of phylogenetic community structure, this is simply the length of phylogenetic branches separating taxa. In the case of trait community structure, we used species' positions in multivariate trait space as derived from the pPCA ordinations to calculate pairwise Euclidean distances. Finally, the dispersal null model we used (Miller 2016) requires a matrix summarizing pairwise distances between each site in the CDM. For this, we used great circle distances between sites, as calculated with the haversine formula, and modeled the probability of species dispersing from one site to another as proportional to the reciprocal of the distance between the two.

Species-Based Measures of Trait Evolution

To calculate species-specific rates of trait evolution, we built on functions from convevol (Stayton 2015) to calculate the distance evolved along the inferred evolutionary branches of each species through multivariate trait space from the inferred root. The resulting values represent the total distance evolved by a given species (and its ancestors) from the most recent common ancestor (crown node) of the honeyeaters. Thus, large values reflect species that are deduced to have undergone notable phenotypic shifts over their evolutionary history. We then input these into a trait-diversification analysis in BAMM, version 2.5.0 (Rabosky 2014; Rabosky et al. 2014), and took the tip-averaged rates of trait evolution as our measure of rate of trait evolution away from the root of the Meliphagidae. This method tests whether certain species, such as those from arid environments, have evolved through multivariate trait space at a faster rate than others.

Correlating Patterns of Trait Evolution, Trait Community Structure, and Climate

We quantified how Meliphagidae trait disparity varies along the broad environmental gradients of continental Australia. To this end, we used ordinary least squares regression to compare the standardized morphological and ecological trait structure scores from each grid cell with their underlying MAT and MAP values. Because variables alternate between *X*- and *Y*-axes in our paneled correlation plots, we employed Pearson's correlation coefficients therein to summarize relationships.

We explored rates of trait evolution and their potential drivers by using PGLS regressions to test whether rates of morphological or ecological trait evolution from the BAMM analysis (described above) were correlated with a species' phylogenetic field. This approach asks whether species from phylogenetically clustered assemblages have exhibited in-creased rates of trait evolution, but it considers species individually and does not consider whether the co-occurring species are evenly partitioning trait space (e.g., it is possible that all species in an assemblage could have evolved quickly toward the same trait combination). Thus, we also used PGLS to compare species' trait fields to their phylogenetic fields and with their mean climate regimes. This approach more directly compares how a species partitions niche space among its potential competitors as a function of the phylogenetic neighborhood or climate it finds itself in. For example, if species in phylogenetically clustered assemblages were widely separated in trait space, then, despite close phylogenetic relationship, such species might substantially partition niche space with their potential competitors. For visual purposes, we again employ Pearson's correlation coefficients as opposed to PGLS slopes in our paneled plots.
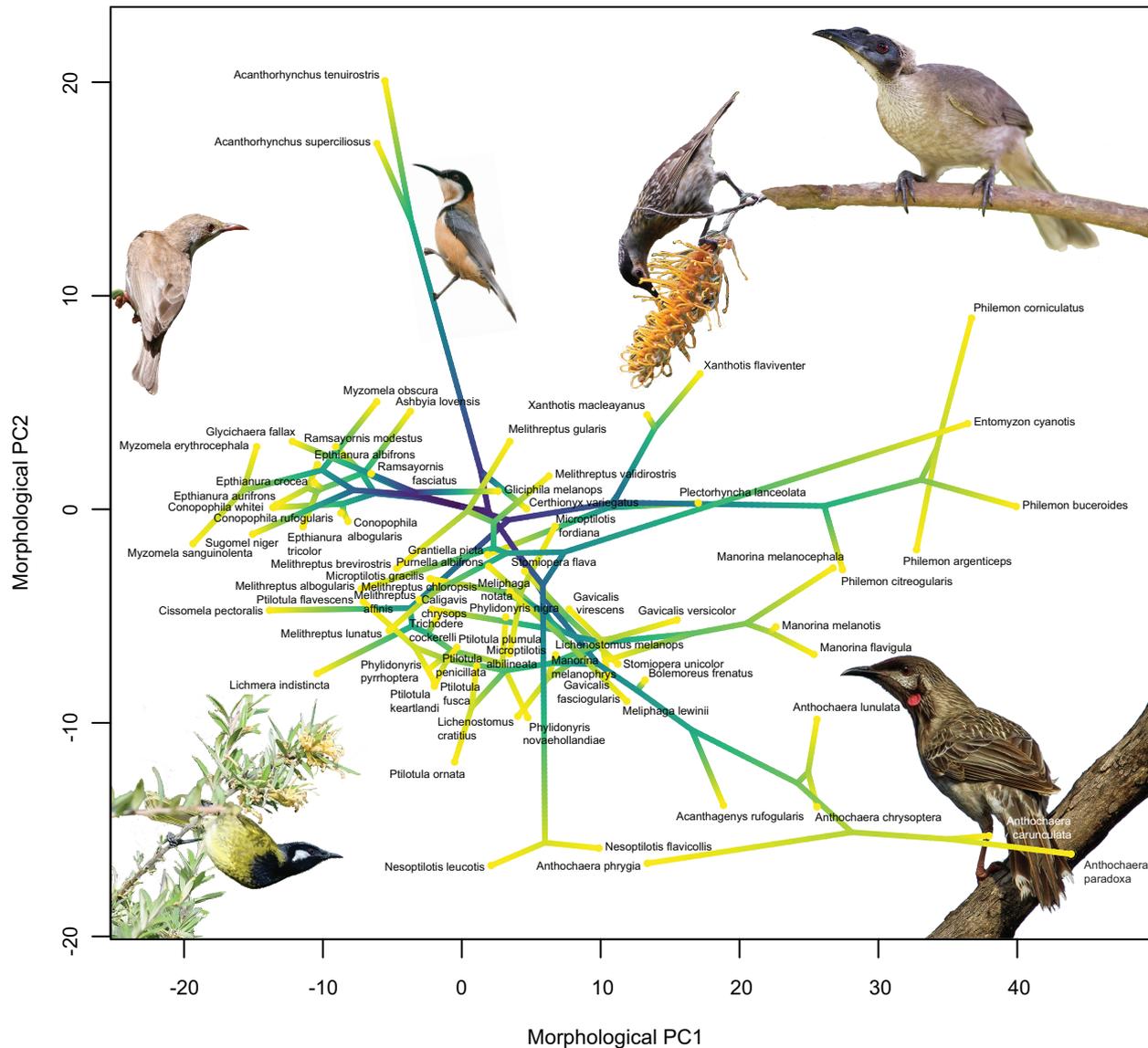
Results

Summary of the Data Sets

We measured 710 specimens of 74 of 75 Australian Meliphagidae species, although we did not take the complete set of measurements on each specimen. Sample sizes range from 1 for the range-restricted white-lined honeyeater (*Microptilotis albilineata*) to 36 for the white-plumed honeyeater (*Ptilotula penicillata*). The species-averaged data set is deposited in the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.r82jg (Miller et al. 2016*b*).

We collected 9,595 foraging observations across 74 species of Australian honeyeater. After accounting for serial observations, the data set contains 7,302 independent observations. The most-observed species was the brown honeyeater (*Lichmera indistincta*; $n = 459$). The least-observed species was the green-backed honeyeater (*Glycichaera fallax*; $n = 20$). The one individual observed of the gray honeyeater (*Conopophila whitei*) was excluded from analysis. The species-averaged data set provides detailed, quantitative measures of the foraging ecology of a large continental radiation of vertebrates and is available from Dryad: http://dx.doi.org/10.5061/dryad.r82jg (Miller et al. 2016*b*).

Multivariate Trait Spaces

The first three axes (out of 15) from the morphological PCA captured 79% of the variance in the data set. The first described differences in overall body size. The second described an axis of variation from species with long bills (e.g., both *Acanthorhynchus* species; fig. 2) to those with nares positioned toward the middle of the bill, and bills whose depth and width taper considerably over their length (e.g., both *Nesoptilotis* species). The third axis separated species with long, pointed wings and decurved bills (e.g.,

Figure 2: Phylomorphospace showing the first two axes from the phylogenetic correlation matrix-principal components analysis on the morphological data. Time since the root (∼20 Ma) is colored from blue to yellow. The first axis represents a general size axis, with larger species on the right. From top to bottom, the second axis separates species with long bills from those with bills that taper considerably over their length in depth and width. These first two axes account for 70% of the variance in the data set. In clockwise order from the top-right corner, photographs, slightly modified from originals, are of noisy friarbird (*Philemon corniculatus* by J. J. Harrison, CC BY 3.0), red wattlebird (*Anthochaera carunculata* by Patrick Kavanagh, CC BY 2.0), white-eared honeyeater (*Nesoptilotis leucotis* by David Cook, CC BY-NC 2.0), brown-backed honeyeater (*Ramsayornis modestus* by Bryan Suson), eastern spinebill (*Acanthorhynchus tenuirostris* by Mark Walters, CC BY 2.0), and Macleay's honeyeater (*Xanthotis macleayanus* by Bryan Suson).

regent, *Anthochaera phrygia*, and pied honeyeaters, *Certhionyx variegatus*) from those with bills whose depth and width taper considerably over their length. Multivariate *K* for the morphological data set was 0.863 (*P* = .001 that *K* differs from 0), emphasizing that species show a strong tendency to resemble their relatives (fig. 2).

Of the 29 axes from the ecological pPCA, the first three described 40% of the variance in the data set (the first 10

described 78%). The first principal component described an axis of variation from highly nectarivorous species that, when not foraging on flowers, tended to sally strike for flying invertebrates, to species that gleaned frequently from leaves and branches. The second PC axis distinguished species that foraged relatively high in the canopy among dense foliage, from species that foraged more in the open and took food from the ground. The third PC axis differentiated spe-

cies that foraged on hanging bark and branches and employed two rare foraging maneuvers, pulling and gaping (whereby the bill is inserted into a substrate, such as a rolled leaf or under bark, and levered up to pry open the substrate), from those that foraged in dense foliage and gleaned from leaves near the tips of branches. Multivariate K for the ecological data set was 0.471 ($P = .002$), emphasizing that while many species resemble their relatives in foraging behavior, others have become differentiated by evolution across considerable ecological distances (fig. 3).

Canonical Correlation Analysis

The first four axes of the pCCA were statistically significant (table A1; tables A1, A2 are available online). Collectively, the morphological data set explained 37% of the variance in the ecological data set. The ecological data set explained 62% of the variance in the morphological data set. Proportions of variance explained were 39% and 41%, respectively, with the reduced ecological data set. The first canonical variate described an axis ranging from species with decurved bills and pointed wings that are highly nectarivorous and regularly sally strike for aerial invertebrates to those with long tarsi and toes, wide and deep bills, and heavy mass that glean, forage on the ground and on branches, and employ pecking and sally pouncing (table A2). The second canonical axis separated species with long bills and tarsi that frequent flowers with long corollas and often take insects in aerial pursuits from those that have short tarsi, pointed wings, and hang while foraging in tall canopies. The third described a trade-off between species with bills that taper considerably in depth and that forage on branches to those with deep, decurved bills that forage high in the canopy, often from hanging bark, and glean fruits. The fourth described an axis ranging from species whose bills taper considerably in depth that employ pecking maneuvers and forage on the ground, well away from trees, to species with long tails, overall long body length, pointed wings, and a considerable portion of their bill proximal to the nares that forage relatively high in the available canopy, often on branches and on flowers with long corollas, and that often hang to do so (table A2).

Assemblage-Level Trait Community Structure and Phylogenetic and Climate Correlates

The mean pairwise distances between species in morphological space did not deviate beyond expectations for most Meliphagidae assemblages (i.e., their SES were between -1.96 and 1.96; fig. 4) given the dispersal null model, which simulated realistic assembly processes. Morphological trait disparity decreased slightly along a gradient of increasing temperature ($r^2 = 0.04$, $P < .001$, $n = 695$) and increased

slightly along a gradient of increasing precipitation ($r^2 = 0.32$, $P < .001$, $n = 695$). Thus, the coldest, wettest sites contained species that were most evenly spread in morphological trait space, although this pattern was weak.

As with morphological disparity, most Meliphagidae assemblages were not significantly structured in ecological space; however, mean ecological $\text{SES}_{\text{dispersal}}$ $\text{MPD}_{\text{inter}}$ was significantly shifted toward weak clustering in foraging space (mean $= -0.23$, Wilcoxon test $P < .01$; fig. 4, centermost panel). Ecological trait disparity decreased along a gradient of increasing temperature ($r^2 = 0.20$, $P < .001$, $n = 695$) and marginally decreased along a gradient of increasing precipitation ($r^2 = 0.01$, $P = .04$, $n = 695$). Thus, the coldest sites tended to contain species that were most evenly spread in ecological trait space, although we emphasize that the overriding signal here was the absence of a strong pattern; ecological trait disparity showed little variation across the broad environmental gradients of the Australian continent.

In short, Meliphagidae trait disparity does not closely parallel phylogenetic diversity (fig. 4, left column). Only weak positive correlations exist between morphological trait disparity and phylogenetic diversity ($r^2 = 0.30$, $P < .001$, $n = 695$) and between ecological trait disparity and phylogenetic diversity ($r^2 = 0.01$, $P = .005$, $n = 695$).
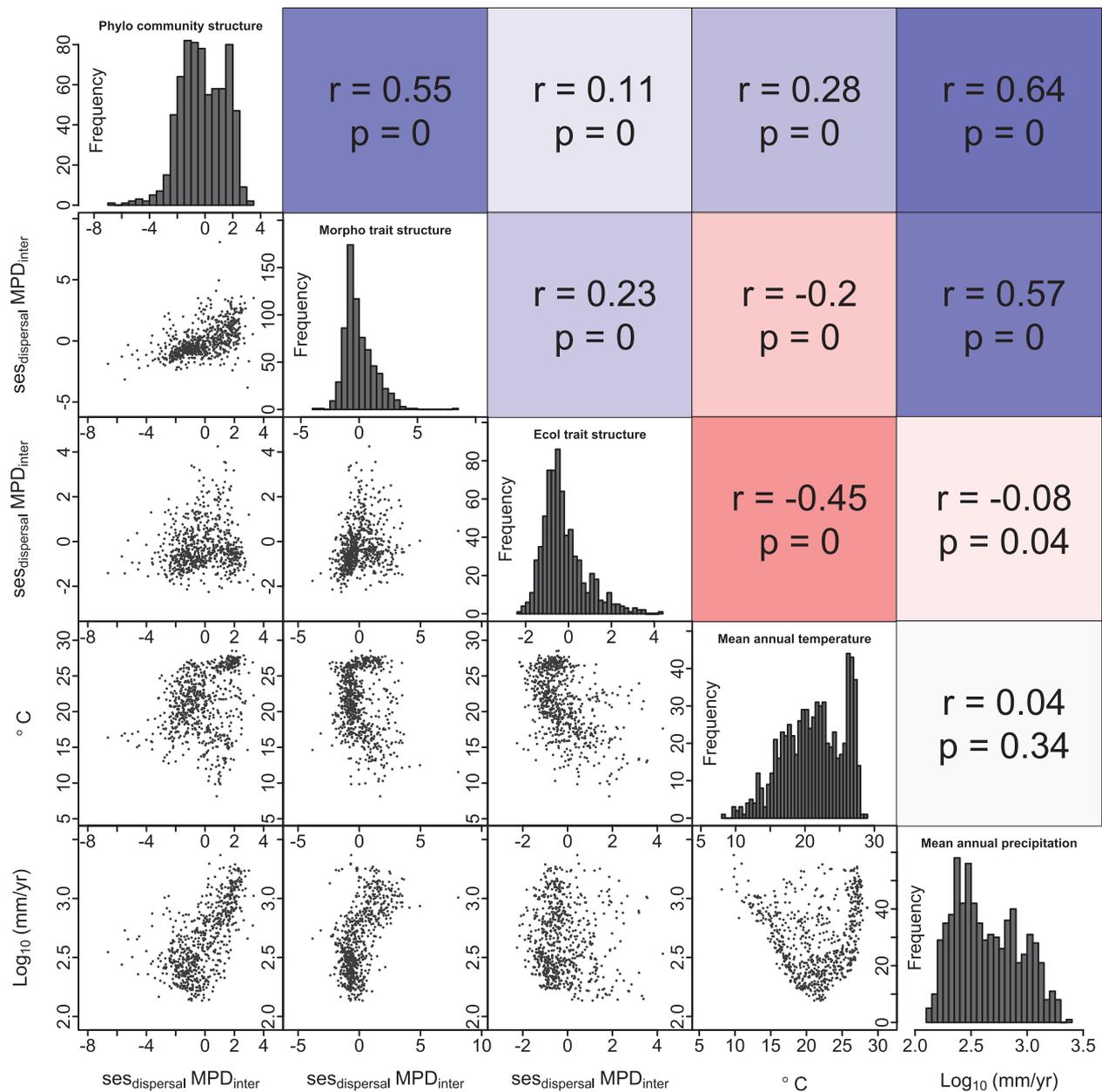
Rates of Trait Evolution

Considering distance evolved through trait space, the estimated sample size for all BAMM runs exceeded the recommended minimum of 200 (minimum used $= 495$) for both the potential number of shifts and the log likelihood.

For morphological traits, the single best shift configuration (frequency of occurrence 29%) included three increases from the background rate of evolution: in the wattlebird clade (*Anthochaera*, including the former *Xanthomyza* but excluding *Acanthagenys*), on the branch leading to the blue-faced honeyeater *Entomyzon cyanotis*), and in the friarbird clade (*Philemon*). Another 23% of runs localized the *Anthochaera* shift two nodes deeper in time, in the clade that also includes spiny-cheeked (*Acanthagenys rufogularis*) and bridled honeyeaters (*Bolemoreus frenatus*; *Bolemoreus hindwoodi* was not sampled). A few samples from the credible shift set also considered the miner clade (*Manorina*) to have diverged morphologically at a slightly elevated rate. All other likely shift configurations were variations on this general theme; that is, they included increases in the rates of evolution of branches leading toward larger-bodied species. Tip-averaged rates of morphological trait evolution are summarized in figure A3.

For ecological traits, the single best shift configuration included no abrupt shifts in the rate of trait evolution, and a phylogeny-wide rate of trait evolution that declined

Figure 3: Phylomorphospace showing the first two axes from the phylogenetic correlation matrix-principal components analysis on the ecological data. Time since the root (∼20 myr) is colored from blue to yellow. From left to right, the first axis separates highly nectarivorous species that, when not foraging on flowers, tend to sally strike for aerial invertebrates to species that glean frequently from leaves and branches. From top to bottom, the second axis separates species that forage more in the open and take food from the ground from those that forage relatively high in the canopy among dense foliage. These first two axes account for 30% of the variance in the ecological data set. Note that the distorted *Y*-axis scale underestimates the extreme ecological position occupied by the chats. Photographs, slightly modified from the originals, are chosen to illustrate behaviors rather than the species themselves. *Clockwise from top right*, gray-fronted honeyeater (*Ptilotula plumula* by Tom Johnson/Macaulay Library 37354101) sally striking for an insect, Macleay's honeyeater (*Xanthotis macleayanus* by Bryan Suson) probing an exposed *Grevillea pteridifolia* flower, blue-faced honeyeater (*Entomyzon cyanotis* by Bryan Suson) probing a branch, brown-headed honeyeater (*Melithreptus brevirostris* by Julie Clark/Macaulay Library 26267081) hanging from a leaf in dense vegetation, bell miner (*Manorina melanophrys* by Michael Dawes, CC BY-NC 2.0) gleaning lerp (a sugary protective coating around a psyllid), and white-fronted chat (*Epthianura albifrons* by David Cook, CC BY-NC 2.0) perched on a wire in open country.

over time (frequency of occurrence 63%), suggesting that ecological space was filled relatively early in the evolution of the group (fig. A4). However, 6% of runs did include an increase in the rate of evolution of the strong-billed honeyeater (*Melithreptus validirostris*) + brown-headed honeyeater (*Melithreptus brevirostris*) + black-chinned honeyeater (*Melithreptus gularis*) clade (=*Eidopsarus*; Toon et al. 2010), 6% localized that shift on the strong-billed

Figure 4: Paneled correlation plot showing the relationships between dispersal null model-standardized interspecific abundance-weighted mean pairwise phylogenetic distance (MPD_{inter}) for phylogenetic and ecological and morphological trait community structure as measured at the assemblage level and between mean annual temperature and precipitation. The histograms in the diagonal panels of the plot portray the distribution of the indicated variable. The titles of the histograms also denote the subject of the *X*-axis of each column and the *Y*-axis of each row for the lower triangle scatterplot panels. Units are indicated along the outer axes of the plot. The upper triangle panels summarize the Pearson's correlation coefficient and the significance of the relationship, both numerically and in color, where bright red indicates a strong negative correlation, and bright blue indicates a strong positive correlation ($n = 695$; note that main text results use results from ordinary least squares regressions). Code used to produce these plots is available as an R package, https://github.com/eliotmiller/corrplotter.

branch, and 2% placed the increase in rate of evolution one node deeper, on the clade that also included white-throated honeyeater (*Melithreptus albogularis*). These seven *Melithreptus* species, particularly those of the *Eidopsarus* subgenus, frequently probe branches and are notably less nectarivorous than most other Meliphagidae. Another rate shift configuration observed in 2% of runs included three increases: one on the *Eidopsarus* clade, one on the *Anthochaera*

clade (including *Xanthomyza* and excluding *Acanthagenys*), and one in the chat clade (*Epthianura* + *Ashbyia*).

Phylogenetic and Trait Fields

Species tended to occur in overdispersed phylogenetic fields (fig. 5). Mean $SES_{dispersal}$ MPD_{inter} was 2.86 (Wilcoxon signed rank test that $\mu = 0$, $P = .01$). The same was true of species' morphological trait fields, where mean $SES_{dispersal}$ MPD_{inter} was 3.05 ($P = .002$). There was a nonsignificant trend for species to occur in ecologically clustered communities ($SES_{dispersal}MPD_{inter} = -0.55$, $P = .13$). Additional field results, including both those calculated with MNTD and those standardized with the richness null model, are presented in the supplemental PDF.

Potential Drivers of Rates of Trait Evolution and Variation in Trait Fields

As noted above, little variation was found in species' rates of trait evolution; these rates were not related to species' phylogenetic fields. However, species in colder climates tend to have diversified ecologically at an increased rate (PGLS pseudo-$r^2 = 0.06$, $P = .05$, $n = 74$).

Species' standardized morphological trait fields were closely correlated with their phylogenetic fields. Species from less phylogenetically clustered assemblages tended to occur in assemblages that were less clustered in morphological trait space (PGLS pseudo-$r^2 = 0.52$, $P < .001$, $n = 74$). Species' standardized phylogenetic and ecological trait fields were also positively correlated, though less strongly (PGLS pseudo-$r^2 = 0.002$, $P = .84$, $n = 74$; abundance weighted $r^2 = 0.07$, $P = .02$, $n = 74$). When species' raw (i.e., unstandardized), unweighted ecological trait fields were compared to their raw, unweighted phylogenetic fields, species from the most phylogenetically clustered assemblages tended to occur in assemblages that were the least clustered in ecological trait space; these species not only tended to be dissimilar from the species they co-occur with, but they tended to occupy positions on the periphery of ecological space.
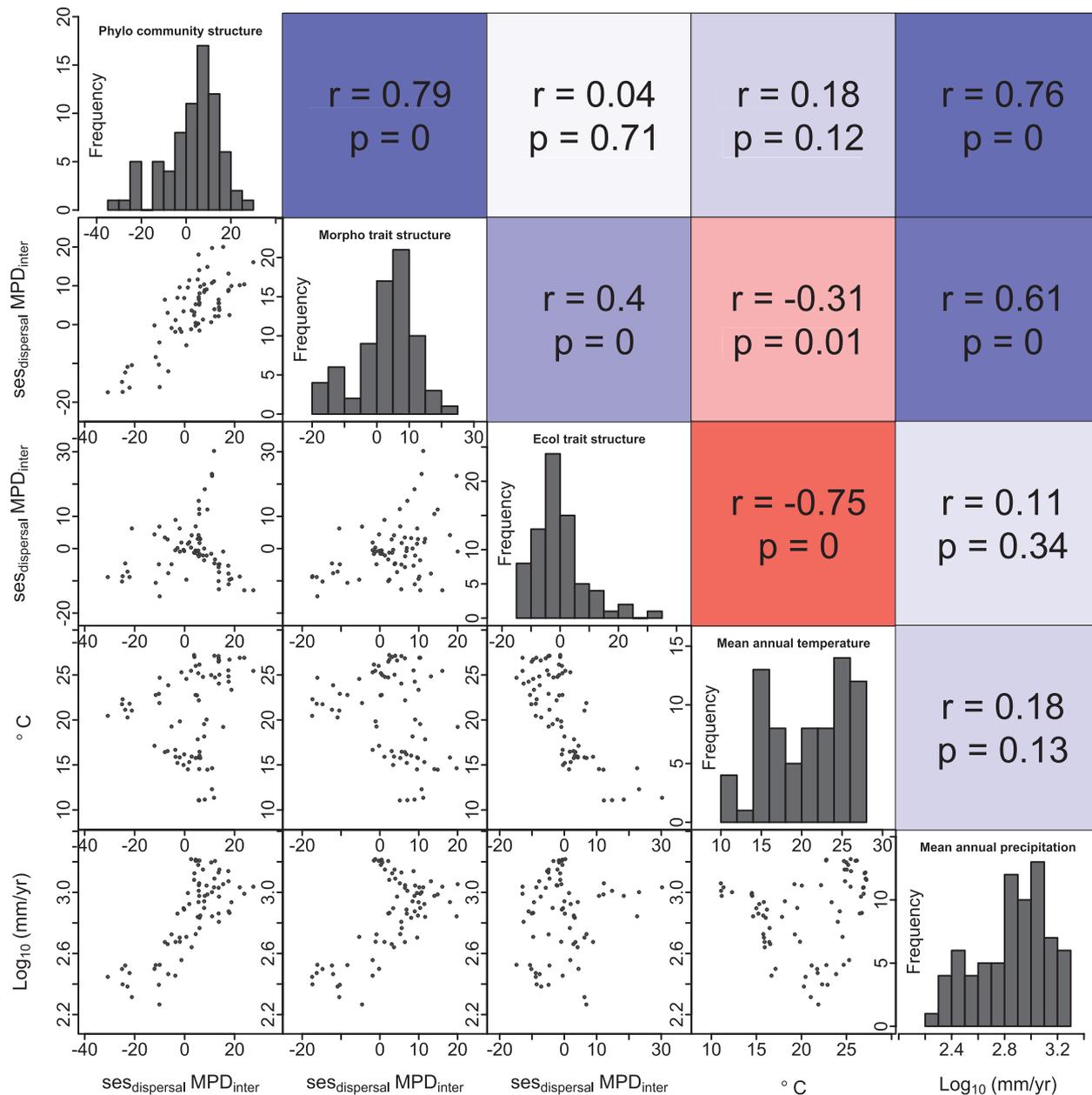
Discussion

The Meliphagidae, or honeyeaters, are a diverse family of passerines distributed predominantly in Australia, New Guinea, and the Pacific Islands. They occupy a wide range of ecological regions, with at least one species occurring almost everywhere in Australia, including Tasmania, which has four endemic species. Most species take some nectar, but some are highly frugivorous, and others are dedicated insectivores (Higgins et al. 2001). Owing to the ease of observing honeyeaters, and a history of interest in these species in Australia, their foraging behavior has been studied

in some detail (Recher 1971; Ford and Paton 1976*a*; Paton 1980; Pyke 1980; Ford and Paton 1982; Recher et al. 1985; Ford 1990).

Given the diversity of resource acquisition strategies in the honeyeaters, whether well-defined ecomorphological relationships would emerge from our analysis was unclear. For instance, small-fruit-eating passerines cannot always be distinguished from insectivores by external morphological characters. Moreover, owing to patchy resources, unpredictable flowering phenology, and many short-corolla, generalist-accessible flowers, the Australian honeyeaters are considered uniquely unspecialized in their floral preferences when compared to groups like the hummingbirds (Paton and Ford 1977; Stiles 1981). Despite this, our expectation that morphology predicts ecology in the group was borne out by the phylogenetic canonical correlation analysis (pCCA). Results from the pCCA provide numerous insights into ecomorphological relationships within the honeyeaters, and we discuss some of these below.

As noted above, honeyeaters are considered unspecialized in their floral preferences (Paton and Ford 1977). However, after many hours in the field, we knew this to be an overstatement, with certain species such as the eastern spinebill (*Acanthorhynchus tenuirostris*) showing marked bill-flower matching (fig. 6; indeed, Paton and Ford allude to potentially higher floral specificity in this and a few other species). Results from the pCCA clearly show a data-set-wide correspondence between the length of species' bills and the flowers they visit. Matching between honeyeaters and particular floral resources extends beyond specialized species such as spinebills (E. T. Miller and S. K. Wagner, personal observation), and additional investigation into honeyeater-plant networks is warranted. Nevertheless, the overall degree of matching does appear decidedly lower than that in hummingbirds. Nectar is generally abundant in Australia (Orians and Milewski 2007). For instance, some clearly ornithophilous flowers (e.g., *Grevillea speciosa*; fig. 6) have distinct slits in the base of the floral tube, rendering nectar readily available to even such short-billed species such as the brown-headed honeyeater (*Melithreptus brevirostris* [fig. 3, inset], although presumably they are not efficient pollinators). Indeed, the most important nectar resources across Australia are probably the cuplike flowers of *Eucalyptus* (Woinarski et al. 2000).

Among hummingbirds, long bills are associated with feeding on flowers with long corollas (Snow and Snow 1980), while among flycatchers, long bills are associated with aerial attacks on invertebrates (Fitzpatrick et al. 2004). Though this may seem like phenotypic convergence toward dramatically different ecologies, in the honeyeaters, we found a close relationship between a high proportion of nectarivory, frequent aerial attacks, and long bills. That some of the most nectarivorous honeyeaters regularly hawk (make

Figure 5: Paneled correlation plot showing the relationships between dispersal null model-standardized interspecific abundance-weighted mean pairwise phylogenetic distance (MPD_{inter}) for phylogenetic and ecological and morphological trait fields (species level) and between mean annual temperature and precipitation. The histograms in the diagonal panels of the plot portray the distribution of the indicated variable. The titles of the histograms also denote the subject of the *X*-axis of each column and the *Y*-axis of each row for the lower triangle scatterplot panels. Units are indicated along the outer axes of the plot. The upper triangle panels of the plot summarize the Pearson's correlation coefficient and the significance of the relationship, both numerically and in color, where bright red indicates a strong negative correlation, and bright blue indicates a strong positive correlation ($n = 73$; the intersection of the morphological and ecological trait data sets). Code to produce these plots is available as an R package, https://github.com/eliotmiller/corrplotter.

aerial attacks for flying invertebrates) is well known (Recher and Abbott 1970). Preliminary analyses suggested such species obtain a surfeit of calories in the form of nectar and that these energetically costly maneuvers are used to sup-

plement to their otherwise protein-poor primary food resource (Ford and Paton 1976*b*). These studies, however, were limited to four species. The continental, cross-season, 74-species, data-set-wide trend found here suggests the ex-

Figure 6: Eastern spinebill (*Acanthorhynchus tenuirostris*) hanging upside-down to probe a *Grevillea tripartita tripartita*. Pollen daubed on the spinebill's forehead by the pollen presenter is clearly visible. Many *Grevillea* species have long tubular corollas and a clear morphological matching between long-billed honeyeater species such as the spinebill, yet owing to a slit in the floral tube, many species are also readily accessed by short-billed species such as the brown-headed honeyeater (*Melithreptus brevirostris*). Photo by Margaret Leggoe.

istence of a more fundamental axis of variation (Westoby et al. 2002), from species that move steadily through foliage, gleaning invertebrates, and occasionally taking some nectar to those that take much nectar but occasionally perform energetically costly hawking maneuvers in pursuit of protein. Hummingbirds are also well known to supplement their diet with flying invertebrates, particularly when they are feeding to provision growing offspring; indeed, their beaks actually deform to facilitate aerial insect capture (Yanega and Rubega 2004).

Species on the periphery of ecological trait space, which drove patterns of assemblage structure, mostly were well-known ecological eccentrics. However, at least according to our measurements, these species were not notably deviant in morphospace but were often outliers in ecomorphological relationships. Thus, the morphology of the painted honeyeater (*Grantiella picta*), a species that foraged on fruit 47% of the time in our data (almost twice as frequently as the next most frugivorous species), resembles that of Gilbert's honeyeater (*Melithreptus chloropsis*), a species that we never observed to eat fruit. And chats in the genera *Epthianura* and *Ashbyia*, long considered a separate family due to their idiosyncratic, open-country foraging behavior, differ little in gross morphology from *Conopophila*, *Ramsayornis*, and *Glycichaera*. Finally, the ecologically unique genus *Melithreptus*,

including the nuthatch-like strong-billed honeyeater (*Melithreptus validirostris*), overlaps in morphospace with other genera. Thus, morphology was a good predictor of ecology, but the relationship was imperfect, and some species, particularly those from arid regions and the endemic honeyeaters of Tasmania, foraged in strikingly distinctive ways given conserved morphologies.

Our morphological measures did not capture any aspects of internal morphology, which might further distinguish species in relation to their foraging ecology (Ricklefs 1996); chats, for instance, have lost most of the bristles on their brush-tipped tongues (Parker 1973). Another internal morphological character with clear ecological ramifications is a unique jaw articulation in some species, particularly the strong-billed honeyeater, other *Melithreptus*, and the black-eared and yellow-throated miners (*Manorina melanotis* and *Manorina flavigula*; Bock and Morioka 1971). This articulation, concealed in traditionally prepared specimens, was postulated to facilitate raising the maxilla when force was applied to it, allowing the tongue to be moistened with saliva and then extruded from the bill. However, Bock and Morioka were unsure of how birds used this morphology, and, while they cited Keast (1968), they apparently did not notice his report therein of what we call gaping, that is, using the bill to pry apart foraging substrates (Remsen and Robinson 1990) by the strong-billed honeyeater. Others have discussed the potential use of this articulation in *Melithreptus* (Willoughby 2005), but in general its behavioral associations remain poorly studied. In our data set, the correlation between the articulation and gaping was quite clear. The species that most frequently employed gaping was the strong-billed honeyeater. Three other species of *Melithreptus* also used the technique, as did black-eared and yellow-throated miners. However, the sister to *Melithreptus*, the blue-faced honeyeater (*Entomyzon cyanotis*) also employed gaping occasionally, as did both species of *Stomiopera*, particularly the white-gaped honeyeater (*Stomiopera unicolor*). Bock and Morioka (1971) examined jaws of blue-faced honeyeaters, finding them to be devoid of the articulation. They also examined an unspecified number of species of *Meliphaga* sensu lato (to which *Stomiopera* previously belonged), and similarly found no sign of the jaw gaping morphology. Whether they studied *Stomiopera* skeletons is unclear. It seems likely that careful study of *Stomiopera* will reveal jaw articulations similar to those seen in *Melithreptus* and *Manorina*.

Meliphagidae assemblages are only weakly structured in ecological trait space, and ecological space filling does not vary notably along the Australian precipitation gradient. In other words, the average distance between species in trait space does not covary with precipitation. Ecological trait disparity is higher in colder regions of Australia, but this signal is driven in large part by Tasmanian honeyeater assemblages, the constituents of which deviate markedly from one

another in foraging behavior (presumably divergence after island colonization; e.g., Reynolds et al. 2016). This lack of ecological trait community structure along the Australian precipitation gradient stands in stark contrast to patterns of phylogenetic and morphological trait community structure, where the arid interior is inhabited by closely related (Miller et al. 2013), morphologically similar assemblages of honeyeaters (see also Pigot et al. 2016). These birds, perhaps in conjunction with shorter time-scale competitive exclusion processes, have diversified to fill local trait spaces comparable to more mesic assemblages.

How did arid-zone honeyeaters accomplish this impressive filling of trait space? According to our BAMM analysis, species from phylogenetically clustered assemblages do not appear to have evolved any faster through ecological or morphological trait space. Of course, evolutionary rates are distinct from directions. Species in phylogenetically clustered assemblages might have exhibited divergent directional evolution away from potential competitors. Comparing species' phylogenetic fields and their trait fields provides indirect evidence of this possibility. As one would expect, species' phylogenetic and morphological trait fields were positively related. That is, species that occur in the most phylogenetically overdispersed assemblages also occur in the most morphologically overdispersed assemblages. Yet, this relationship was only weakly manifested from an ecological perspective. Thus, after accounting for variation in species richness and for dispersal limitation, species from phylogenetically clustered assemblages are nearly as evenly arrayed ecologically as species from much more phylogenetically diverse assemblages (fig. 5). And, when unstandardized by the expected standard deviation among null model communities, the relationship between species' ecological trait fields and phylogenetic fields was actually strongly negative. This suggests that despite close phylogenetic relationships and a tendency toward similar morphologies, the species from arid regions have diverged in ecology to a degree that they are, on average, nearly as different from their competitors in foraging ecology as are those species that co-occur in mesic areas.

Our results are based on an ecological space that is defined by species' foraging traits. A potentially more informative approach would define the ecological space a priori, with independent measures of local resource availability. By simulating community assembly where the settled species are drawn from ecologically similar sites, our dispersal null model goes part of the way toward addressing this shortcoming (Miller 2016). Previous ecomorphological studies have included comparatively small numbers of species (e.g., Saunders and Barclay 1992), phylogenetically disparate/uneven comparisons (e.g., Douglas and Matthews 1992), single-site comparisons (e.g., Miles and Ricklefs 1984), and, owing to the difficulty of obtaining quantitative resource-use mea-

sures, fairly gross descriptors of species' ecology (e.g., Pap et al. 2015). We avoided these issues by examining ecomorphological relationships in a phylogenetic context across a large clade over continental spatial scales. Our approach admittedly has spatiotemporal limitations, and we hope that citizen scientists may ultimately help to contribute sufficient data to address these questions over even larger scales.

Based on the results shown here, we conclude that honeyeater species in the arid interior, those in phylogenetically clustered assemblages, have not evolved any faster through trait space than species in more mesic environments. Instead, they have diverged from each other so as to partition trait space to an equivalent degree to that seen in more mesic areas. Morphology predicts ecology in the Australian Meliphagidae. However, the relationships show marked flexibility. Certain lineages, such as the chats, forage in radically different ways from their relatives, exploiting entirely divergent resources with fairly conserved morphologies. Thus, community assembly and trait diversification in the honeyeaters reflects a combination of adaptation—both to local habitats and in response to the presence of competitors—and constraint as a result of past evolutionary history.

Literature Cited

Adams, D. C. 2014. A generalized *K* statistic for estimating phylogenetic signal from shape and other high-dimensional multivariate data. Systematic Biology 63:685–697.

Arnold, S. J. 1992. Constraints on phenotypic evolution. American Naturalist 140(suppl.):S85–S107.

Blomberg, S. P., T. Garland Jr., and A. R. Ives. 2003. Testing for phylogenetic signal in comparative data: behavioral traits are more labile. Evolution 57:717–745.

Bock, W. J., and H. Morioka. 1971. Morphology and evolution of the ectethmoid-mandibular articulation in the Meliphagidae (Aves). Journal of Morphology 135:13–50.

Bright, J. A., J. Marugán-Lobón, S. N. Cobb, and E. J. Rayfield. 2016. The shapes of bird beaks are highly controlled by nondietary factors. Proceedings of the National Academy of Sciences of the USA 113: 5352–5357.

Cavender-Bares, J., D. D. Ackerly, D. A. Baum, and F. A. Bazzaz. 2004a. Phylogenetic overdispersion in Floridian oak communities. American Naturalist 163:823–843.

Cavender-Bares, J., K. Kitajima, and F. A. Bazzaz. 2004b. Multiple trait associations in relation to habitat differentiation among 17 Floridian oak species. Ecological Monographs 74:635–662.

Cavender-Bares, J., K. H. Kozak, P. V. A. Fine, and S. W. Kembel. 2009. The merging of community ecology and phylogenetic biology. Ecology Letters 12:693–715.

Claramunt, S., E. P. Derryberry, J. V. Remsen, and R. T. Brumfield. 2012. High dispersal ability inhibits speciation in a continental radiation of passerine birds. Proceedings of the Royal Society B 279: 1567–1574.

Cornwell, W. K., D. W. Schwilk, and D. D. Ackerly. 2006. A trait-based test for habitat filtering: convex hull volume. Ecology 87: 1465–1471.

Cornwell, W. K., M. Westoby, D. S. Falster, R. G. FitzJohn, B. C. O'Meara, M. W. Pennell, D. J. McGlinn, et al. 2014. Functional distinctiveness of major plant lineages. Journal of Ecology 102:345–356.

Dehling, D. M., S. A. Fritz, T. Töpfer, M. Päckert, P. Estler, K. Böhning-Gaese, and M. Schleuning. 2014. Functional and phylogenetic diversity and assemblage structure of frugivorous birds along an elevational gradient in the tropical Andes. Ecography 37:1047–1055.

Douglas, M. E., and W. J. Matthews. 1992. Does morphology predict ecology? hypothesis testing within a freshwater stream fish assemblage. Oikos 65:213–224.

Faith, D. P. 1996. Conservation priorities and phylogenetic pattern. Conservation Biology 10:1286–1289.

Fitzpatrick, J. W., J. M. Bates, K. S. Bostwick, I. C. Caballero, B. M. Clock, A. Farnsworth, P. A. Hosner, et al. 2004. Family Tyrannidae (tyrant-flycatchers). Pages 170–462 in Handbook of the birds of the world. Vol. 9. Lynx, Barcelona.

Ford, H. A. 1990. Relationships between distribution, abundance and foraging specialization in Australian landbirds. Ornis Scandinavica 21:133–138.

Ford, H. A., and D. C. Paton. 1976a. Resource partitioning and competition in honeyeaters of the genus *Meliphaga*. Australian Journal of Ecology 1:281–287.

———. 1976b. The value of insects and nectar to honeyeaters. Emu 76:83–84.

———. 1982. Partitioning of nectar sources in an Australian honeyeater community. Australian Journal of Ecology 7:149–159.

Futuyma, D. J. 2010. Evolutionary constraint and ecological consequences. Evolution 64:1865–1884.

Givnish, T. J. 2015. Adaptive radiation versus "radiation" and "explosive diversification": why conceptual distinctions are fundamental to understanding evolution. New Phytologist 207:297–303.

Givnish, T. J., and K. J. Sytsma. 2000. Molecular evolution and adaptive radiation. Cambridge University Press, Cambridge.

Gómez, J. P., G. A. Bravo, R. T. Brumfield, J. G. Tello, and C. D. Cadena. 2010. A phylogenetic approach to disentangling the role of competition and habitat filtering in community assembly of Neotropical forest birds. Journal of Animal Ecology 79:1181–1192.

Hansen, T. F., and D. Houle. 2008. Measuring and comparing evolvability and constraint in multivariate characters. Journal of Evolutionary Biology 21:1201–1219.

Harmon, L. J., J. A. Schulte, A. Larson, and J. B. Losos. 2003. Tempo and mode of evolutionary radiation in iguanian lizards. Science 301:961–964.

Higgins, P. J., J. M. Peter, and W. K. Steele. 2001. Handbook of Australian, New Zealand and Antarctic birds. Vol. 5. Tyrant-flycatchers to chats. Oxford University Press, Melbourne.

Jønsson, K. A., P.-H. Fabre, S. A. Fritz, R. S. Etienne, R. E. Ricklefs, T. B. Jørgensen, J. Fjeldså, et al. 2012. Ecological and evolutionary determinants for the adaptive radiation of the Madagascan vangas. Proceedings of the National Academy of Sciences of the USA 109: 6620–6625.

Joseph, L., A. Toon, Á. S. Nyári, N. W. Longmore, K. Rowe, T. Haryoko, J. Trueman, and J. L. Gardner. 2014. A new synthesis of the molecular systematics and biogeography of honeyeaters (Passeriformes: Meliphagidae) highlights biogeographical and ecological complexity of a spectacular avian radiation. Zoologica Scripta 43:235–248.

Karr, J. R., and F. C. James. 1975. Ecomorphological configurations and convergent evolution in species and communities. Pages 258–291 in M. L. Cody and J. M. Diamond, eds. Ecology and evolution of communities. Belknap, Cambridge, MA.

Keast, A. 1968. Competitive interactions and the evolution of ecological niches as illustrated by the Australian honeyeater genus *Melithreptus* (Meliphagidae). Evolution 22:762–784.

Keast, A., and H. F. Recher. 1997. The adaptive zone of the genus *Gerygone* (Acanthizidae) as shown by morphology and feeding habits. Emu 97:1–17.

Kembel, S. W., P. D. Cowan, M. R. Helmus, W. K. Cornwell, H. Morlon, D. D. Ackerly, S. P. Blomberg, and C. O. Webb. 2010. Picante: R tools for integrating phylogenies and ecology. Bioinformatics 26:1463–1464.

Kraft, N. J. B., and D. D. Ackerly. 2010. Functional trait and phylogenetic tests of community assembly across spatial scales in an Amazonian forest. Ecological Monographs 80:401–422.

Lack, D. 1947. Darwin's finches. Cambridge University Press, Cambridge.

Lambers, H., and H. Poorter. 2004. Inherent variation in growth rate between higher plants: a search for physiological causes and ecological consequences. Advances in Ecological Research 34:283–362.

Leisler, B., and K. Schulze-Hagen. 2011. The reed warblers: diversity in a uniform bird family. KNNV, Zeist, Netherlands.

Lovette, I. J., E. Bermingham, and R. E. Ricklefs. 2002. Clade-specific morphological diversification and adaptive radiation in Hawaiian songbirds. Proceedings of the Royal Society B 269:37–42.

Lovette, I. J., and R. T. Holmes. 1995. Foraging behavior of American redstarts in breeding and wintering habitats: implications for relative food availability. Condor 97:782–791.

Luther, D. 2009. The influence of the acoustic community on songs of birds in a Neotropical rain forest. Behavioral Ecology 20:864–871.

Mast, A. R., P. M. Olde, R. O. Makinson, E. Jones, A. Kubes, E. T. Miller, and P. H. Weston. 2015. Paraphyly changes understanding of timing and tempo of diversification in subtribe Hakeinae (Proteaceae), a giant Australian plant radiation. American Journal of Botany 102:1634–1646.

McGill, B. J., B. J. Enquist, E. Weiher, and M. Westoby. 2006. Rebuilding community ecology from functional traits. Trends in Ecology and Evolution 21:178–185.

Miles, D. B., and R. E. Ricklefs. 1984. The correlation between ecology and morphology in deciduous forest Passerine birds. Ecology 65:1629–1640.

Miles, D. B., R. E. Ricklefs, and J. Travis. 1987. Concordance of ecomorphological relationships in three assemblages of passerine birds. American Naturalist 129:347–364.

Miller, E. 2016. A new dispersal-informed null model for community ecology shows strong performance. bioRxiv 46524.

Miller, E. T., D. R. Farine, and C. H. Trisos. 2016a. Phylogenetic community structure metrics and null models: a review with new methods and software. Ecography, http://dx.doi.org/10.1111/ecog.02070.

Miller, E. T., and S. K. Wagner. 2015. The ecology of the Australian sandstone *Meliphaga* honeyeater species. Australian Field Ornithology 32:38–52.

Miller, E. T., S. K. Wagner, L. J. Harmon, and R. E. Ricklefs. 2016b. Data from: Radiating despite a lack of character: ecological divergence among closely related, morphologically similar honeyeaters (Aves: Meliphagidae) co-occurring in arid Australian environments. American Naturalist, Dryad Digital Repository, http://dx.doi.org/10.5061/dryad.r82jg.

Miller, E. T., A. E. Zanne, and R. E. Ricklefs. 2013. Niche conservatism constrains Australian honeyeater assemblages in stressful environments. Ecology Letters 16:1186–1194.

Orians, G. H., and A. V. Milewski. 2007. Ecology of Australia: the effects of nutrient-poor soils and intense fires. Biological Reviews 82:393–423.

Pap, P. L., G. Osváth, K. Sándor, O. Vincze, L. Bărbos, A. Marton, R. L. Nudds, and C. I. Vágási. 2015. Interspecific variation in the structural properties of flight feathers in birds indicates adaptation to flight requirements and habitat. Functional Ecology 29:746–757.

Parker, S. A. 1973. The tongues of *Ephthianura* and *Ashbyia*. Emu 73:19–20.

Paton, D. C. 1980. The importance of manna, honeydew and lerp in the diets of honeyeaters. Emu 80:213–226.

Paton, D. C., and H. A. Ford. 1977. Pollination by birds of native plants in South Australia. Emu 77:73–85.

Pennycuick, C. J. 2008. Modelling the flying bird. Academic Press, Burlington, MA.

Pigot, A. L., C. H. Trisos, and J. A. Tobias. 2016. Functional traits reveal the expansion and packing of ecological niche space underlying an elevational diversity gradient in passerine birds. Proceedings of the Royal Society B 283, http://dx.doi.org/10.1098/rspb.2015.2013.

Pyke, G. H. 1980. The foraging behaviour of Australian honeyeaters: a review and some comparisons with hummingbirds. Australian Journal of Ecology 5:343–369.

R Development Core Team. 2016. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. http://www.R-project.org.

Rabosky, D. L. 2014. Automatic detection of key innovations, rate shifts, and diversity-dependence on phylogenetic trees. PLoS ONE 9:e89543.

Rabosky, D. L., M. Grundler, C. Anderson, P. Title, J. J. Shi, J. W. Brown, H. Huang, and J. G. Larson. 2014. BAMMtools: an R package for the analysis of evolutionary dynamics on phylogenetic trees. Methods in Ecology and Evolution 5:701–707.

Recher, H. F. 1971. Sharing of habitat by three congeneric honeyeaters. Emu 71:147–152.

Recher, H. F., and I. J. Abbott. 1970. The possible ecological significance of hawking by honeyeaters and its relation to nectar feeding. Emu 70:90.

Recher, H. F., R. T. Holmes, M. Schulz, J. Shields, and R. Kavanagh. 1985. Foraging patterns of breeding birds in eucalypt forest and woodland of southeastern Australia. Australian Journal of Ecology 10:399–419.

Remsen, J. V., and S. K. Robinson. 1990. A classification scheme for foraging behavior of birds in terrestrial habitats. Studies in Avian Biology 13:144–160.

Revell, L. J. 2009. Size-correction and principal components for interspecific comparative studies. Evolution 63:3258–3268.

———. 2012. phytools: an R package for phylogenetic comparative biology (and other things). Methods in Ecology and Evolution 3:217–223.

Revell, L. J., and A. S. Harrison. 2008. PCCA: a program for phylogenetic canonical correlation analysis. Bioinformatics 24:1018–1020.

Reynolds, R. G., D. C. Collar, S. A. Pasachnik, M. L. Niemiller, A. R. Puente-Rolón, and L. J. Revell. 2016. Ecological specialization and morphological diversification in Greater Antillean boas. Evolution 70:1882–1895.

Ricklefs, R. E. 1996. Morphometry of the digestive tracts of some passerine birds. Condor 98:279–292.

———. 2011. Applying a regional community concept to forest birds of eastern North America. Proceedings of the National Academy of Sciences of the USA 108:2300–2305.

———. 2012. Species richness and morphological diversity of passerine birds. Proceedings of the National Academy of Sciences of the USA 109:14482–14487.

Ricklefs, R. E., and D. B. Miles. 1994. Ecological and evolutionary inferences from morphology: an ecological perspective. Pages 13–41 *in* P. C. Wainwright and S. M. Reilly, eds. Ecological morphology: integrative organismal biology. University of Chicago Press, Chicago.

Ricklefs, R. E., and J. Travis. 1980. A morphological approach to the study of avian community organization. Auk 97:321–338.

Rico-Guevara, A., and M. Araya-Salas. 2014. Bills as daggers? a test for sexually dimorphic weapons in a lekking hummingbird. Behavioral Ecology 26:21–29.

Saunders, M. B., and R. M. R. Barclay. 1992. Ecomorphology of insectivorous bats: a test of predictions using two morphologically similar species. Ecology 73:1335–1345.

Schluter, D. 1996. Adaptive radiation along genetic lines of least resistance. Evolution 50:1766–1774.

———. 2000. The ecology of adaptive radiation. Oxford University Press, New York.

Schneider, C. A., W. S. Rasband, and K. W. Eliceiri. 2012. NIH Image to ImageJ: 25 years of image analysis. Nature Methods 9:671–675.

Schoener, T. W. 1965. The evolution of bill size differences among sympatric congeneric species of birds. Evolution 19:189–213.

Snow, D. W., and B. K. Snow. 1980. Relationships between hummingbirds and flowers in the Andes of Columbia. Bulletin of the British Museum of Natural History 38:105–139.

Stayton, C. T. 2015. The definition, recognition, and interpretation of convergent evolution, and two new measures for quantifying and assessing the significance of convergence. Evolution 69:2140–2153.

Stewart, D., and W. Love. 1968. A general canonical correlation index. Psychological Bulletin 70:160–163.

Stiles, F. G. 1981. Geographical aspects of bird-flower coevolution, with particular reference to Central America. Annals of the Missouri Botanical Garden 68:323–351.

Sullivan, B. L., C. L. Wood, M. J. Iliff, R. E. Bonney, D. Fink, and S. Kelling. 2009. eBird: a citizen-based bird observation network in the biological sciences. Biological Conservation 142:2282–2292.

Suryan, R. M., D. B. Irons, and J. Benson. 2000. Prey switching and variable foraging strategies of black-legged Kittiwakes and the effect on reproductive success. Condor 102:374–384.

Tobias, J. A., R. Planqué, D. L. Cram, and N. Seddon. 2014. Species interactions and the structure of complex communication networks. Proceedings of the National Academy of Sciences of the USA 111:1020–1025.

Toon, A., J. M. Hughes, and L. Joseph. 2010. Multilocus analysis of honeyeaters (Aves: Meliphagidae) highlights spatio-temporal heterogeneity in the influence of biogeographic barriers in the Australian monsoonal zone. Molecular Ecology 19:2980–2994.

Villalobos, F., T. F. Rangel, and J. A. F. Diniz-Filho. 2013. Phylogenetic fields of species: cross-species patterns of phylogenetic structure and geographical coexistence. Proceedings of the Royal Society B 280:20122570.

Wainwright, P. C. 2007. Functional versus morphological diversity in macroevolution. Annual Review of Ecology, Evolution, and Systematics 38:381–401.

Webb, C. O., D. D. Ackerly, M. A. McPeek, and M. J. Donoghue. 2002. Phylogenies and community ecology. Annual Review of Ecology and Systematics 33:475–505.

Weinstein, B. G., B. Tinoco, J. L. Parra, L. M. Brown, J. A. McGuire, F. G. Stiles, and C. H. Graham. 2014. Taxonomic, phylogenetic, and trait beta diversity in South American hummingbirds. American Naturalist 184:211–224.

Westoby, M., D. S. Falster, A. T. Moles, P. A. Vesk, and I. J. Wright. 2002. Plant ecological strategies: some leading dimensions of variation between species. Annual Review of Ecology, Evolution, and Systematics 33:125–159.

Willoughby, N. 2005. Comparative ecology, and conservation, of the *Melithreptus* genus in the Southern Mount Lofty Ranges, South Australia. PhD diss. University of Adelaide.

Woinarski, J. C. Z., G. Connors, and D. C. Franklin. 2000. Thinking honeyeater: nectar maps for the Northern Territory, Australia. Pacific Conservation Biology 6:61–80.

Wright, I. J., P. B. Reich, M. Westoby, D. D. Ackerly, Z. Baruch, F. Bongers, J. Cavender-Bares, et al. 2004. The worldwide leaf economics spectrum. Nature 428:821–827.

Yanega, G. M., and M. A. Rubega. 2004. Feeding mechanisms: hummingbird jaw bends to aid insect capture. Nature 428:615–615.

Zanne, A. E., D. C. Tank, W. K. Cornwell, J. M. Eastman, S. A. Smith, R. G. FitzJohn, D. J. McGlinn, et al. 2014. Three keys to the radiation of angiosperms into freezing environments. Nature 506:89–92.

Associate Editor: David C. Collar
Editor: Judith L. Bronstein

Left, Sarah Wagner is crouched observing and recording foraging honeyeaters in the monsoon forests of northern Australia. Eliot Miller captured the image in the field while the two of them were collecting the quantitative foraging measurements that enabled the researchers' investigation of niche partitioning in these species. *Right*, one of Eliot Miller and Sarah Wagner's campsites, 40 km north of Broken Hill, New South Wales, Australia. This was one of the few areas the team found good numbers of pied honeyeaters (*Certhionyx variegatus*). They spent a day and a half here studying their foraging behavior before driving further inland. Photo credits: Eliot T. Miller.