

Adaptive radiation and the evolution of nectarivory in a large songbird clade

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The accumulation of exceptional ecological diversity within a lineage is a key feature of adaptive radiation resulting from diversification associated with the subdivision of previously underutilized resources. The invasion of unoccupied niche space is predicted to be a key determinant of adaptive diversification, and this process may be particularly important if the diversity of competing lineages within the area, in which the radiation unfolds, is already high. Here, we test whether the evolution of nectarivory resulted in significantly higher rates of morphological evolution, more extensive morphological disparity, and a heightened build-up of sympatric species diversity in a large adaptive radiation of passerine birds (the honeyeaters, about 190 species) that have diversified extensively throughout continental and insular settings. We find that a large increase in rates of body size evolution and general expansion in morphological space followed an ancestral shift to nectarivory, enabling the build-up of large numbers of co-occurring species that vary greatly in size, compared to related and co-distributed nonnectarivorous clades. These results strongly support the idea that evolutionary shifts into novel areas of niche space play a key role in promoting adaptive radiation in the presence of likely competing lineages.

KEY WORDS: Character displacement, key innovations, macroecology, macroevolution, morphological evolution, species richness.

Adaptive radiation describes the scenario in which lineage diversification is coupled with extensive ecological divergence into a wide variety of niches (Osborn 1902; Huxley 1942; Simpson 1953; Schlüter 2000a). Although some iconic adaptive radiations have been extensively studied by evolutionary biologists (e.g., Darwin's finches, Hawaiian honeycreepers, and Caribbean anoles), our general understanding of the factors that promote this phenomenon remain incomplete (Schlüter 2000a). Ecological opportunity in the form of new and/or underexploited resources is believed to be a common prerequisite for adaptive radiation, but this may arise in a multitude of ways. For example, ecological opportunity may emerge as a consequence of (i) the colonization

of new geographic areas, (ii) the appearance of a new resource, (iii) the extinction of competitors/predators, or (iv) as a result of the evolution of key innovations (Simpson 1953; Schlüter 2000a; Losos and Mahler 2010; Stroud and Losos 2016). Most well-studied adaptive radiations have resulted from the colonization of geographically isolated areas and are therefore likely to have unfolded in the absence of competition from closely related lineages (Losos 2010; Soulebeau et al. 2015; Stroud and Losos 2016). Much less is known about the factors facilitating adaptive radiation when the levels of species diversity among potentially competing lineages is already high. This scenario is particularly applicable to radiations occurring throughout continental settings,

where the bulk of the world's species diversity is distributed. In these instances, one important factor is thought to be the evolution of new morphological and physiological traits that allow lineages to use novel resources, and radiate free from competition with related co-occurring species (Simpson 1944; Miller 1949; Hunter 1998; Rabosky 2017).

The evolution of traits that facilitate access to previously inaccessible resources has been hypothesized to underlie the evolutionary success of many large radiations, with proposed examples including the evolution of phytophagy in insects (Mitter et al. 1988), or the pharyngeal jaw in labroid fishes (Liem 1973; Galis and Drucker 1996). Under this scenario, lineages that are able to invade unoccupied niche space are predicted to undergo increased rates of trait evolution and exhibit greater ecological disparity compared to related clades, assuming that the available resources are amenable to further subdivision (Futuyma 1998; Losos and Mahler 2010; Rabosky 2017). Moreover, such clades should also be characterized by a shift in ecological positioning relative to the background clade, as may be evidenced by the evolution of new traits (or trait combinations) that facilitate novel patterns of resource utilization (Rabosky 2017). Adaptive radiations that unfold in this way may also be expected to support higher numbers of species at smaller spatial scales, as greater ecological divergence facilitates a high degree of sympatry among the constituent taxa (Schlüter 1996). The invasion of underexploited areas of niche space through the evolution of novel traits has also been proposed to result in increased lineage diversification in some instances (Mitter et al. 1988; Slowinski and Guyer 1993; Hodges and Arnold 1995; Bond and Opell 1998). However, this hypothesis remains contentious, as the evolution of such traits may increase the overall diversification of the parent clade (thus raising its accumulated species richness), without necessarily increasing rates of lineage diversification among the innovative clade (Rabosky 2017). Empirical assessments of these predictions, and documentation of the tempo and mode by which radiations of this nature unfold, are currently limited. We address these issues by assessing the effect of an ancestral shift in diet on rates of morphological evolution, lineage diversification, and patterns of species co-occurrence within a large clade of passerine birds that has radiated extensively throughout continental and insular settings.

The infraorder Meliphagidae is a passerine radiation of approximately 290 species distributed across Australasia and the Indo-Pacific (Gardner et al. 2010; Marki et al. 2017). Australasia is thought to represent the ancestral area of songbird (oscine passerines) diversification (Barker et al. 2004; Jönsson et al. 2011; Moyle et al. 2016), thus providing a contrasting geographic setting to other studies of adaptive radiations that have predominantly assessed these trends in isolated and species depauperate island environments (Pratt 2005; Grant and Grant 2008; Losos 2009). Ecological and phenotypic diversity is particularly pronounced in

the honeyeater subclade (family Meliphagidae), which comprises about 65% (187 species) of the overall species richness of the infraorder. The honeyeaters have thus been suggested to constitute an adaptive radiation driven by the evolution of traits that allowed exploitation of a diet rich in nectar (Keast 1976, 1985). Honeyeater species possess a number of unique morphological and physiological adaptations for nectarivory, including structural modifications to the renal system for more efficient balancing of fluid intake and a brush-tipped protrusible tongue (Paton and Collins 1989; Casotti and Richardson 1992; Goldstein and Bradshaw 1998a,b). These adaptations are hypothesized to have allowed honeyeaters to successfully exploit a novel food source (nectar) and radiate into areas of ecological niche space that were previously unoccupied in this geographic setting (Keast 1976; Miller et al. 2017). Together, these factors make the honeyeaters (and the overall Meliphagidae) an ideal study system for investigating the dynamics of adaptive radiation at large geographic scales.

Here, we use empirical data to assess core, but largely untested predictions of adaptive radiation theory following the invasion of novel niche space. First, we test the prediction that following the evolution of nectarivory honeyeaters should occupy a unique and diverse part of morphological space compared to other co-distributed and closely related passerine clades. Second, we evaluate whether the macroevolutionary dynamics of trait evolution in nectarivorous lineages are decoupled from those of nonnectarivorous lineages. Finally, having established such a link, we examine whether these processes have influenced lineage diversification dynamics, geographic variation in species richness, and the functional diversity of Meliphagoid assemblages.

Materials and Methods

PHYLOGENETIC, MORPHOLOGICAL, AND ECOLOGICAL DATA

We used the recently published molecular phylogeny of the Meliphagidae by Marki et al. (2017) in all analyses. This phylogeny is almost complete at the species-level and includes 286 of 289 (99%) of the currently recognized species according to the IOC World Bird List version 6.2 (Gill and Donsker 2016). The phylogeny was calibrated using a combination of fossils and secondary calibration points, and was summarized as a maximum clade credibility (MCC) tree upon which all comparative analyses were performed, unless otherwise stated.

To quantify morphological variation among the Meliphagidae, we collected data on seven ecologically relevant traits that represent major aspects of external avian anatomy, from museum study skins. We measured tarsus length, hind toe length (including claw), wing length, Kipp's distance, and bill length, width, and depth (Table S1). Male specimens were measured where possible,

although in a few cases when these were unavailable in the respective collections, the measurements for these species were supplemented with those from females or unsexed specimens. We obtained measurements for a total of 1245 individual specimens including all but 13 taxa represented in the phylogeny (the species for which we were not able to obtain morphological data were *Acanthiza katherina*, *Amytornis ballarae* and *A. dorotheae*, *Aphelocephala pectoralis*, *Bolemoreus hindwoodi*, *Chenorhamphus campbelli*, *Lichmera monticola*, *Manorina melanotis*, *Meliphaga cinereifrons* and *M. fordiana*, *Myzomela blasii*, *Ptiloprora mayri*, *Stipiturus mallee* and *S. ruficeps*), with an average of 4.5 ± 1.9 SD specimens measured per species. In addition to the Meliphagides, we also collected morphological measurements for the majority of species within 13 families that are co-distributed with the honeyeaters (Artamidae, Campephagidae, Cinclosomatidae, Climacteridae, Corvidae, Melanocharitidae, Monarchidae, Oriolidae, Pachycephalidae, Paradisaeidae, Petroicidae, Ptilonorhynchidae, and Rhipiduridae) totaling 398 additional species (2085 specimens measured, mean per species = 5.2 ± 1.6 SD). Using ANOVA across the full morphological data set, we found that between-species variance on average accounted for 98% (range 96–99%) of the variance across all seven traits. Consequently, all subsequent analyses were performed on the log-transformed mean trait values calculated for each individual species. The MCC tree and the morphological measurements from the individual specimens have been made available on the Dryad online repository (<https://doi.org/10.5061/dryad.p936ng4>).

We discretely classified individual meliphagoid species according to whether they include nectar in their diets using information from a large database of ecological traits (Wilman et al. 2014). For species not included in the Wilman et al. (2014) diet database but present in the phylogeny ($n = 13$), we used the most frequent condition among members of the genus to represent their dietary category.

ANALYSES OF TRAIT EVOLUTION

To assess the evolutionary origins of nectarivory among the Meliphagides, we reconstructed ancestral diets using stochastic character mapping (Bollback 2006) implemented in the R package *phytools* (Revell 2012; R Core Team 2016). To do this, we first compared two models of variation in transition rates among states by computing the likelihoods of an equal-rates (ER) and an all-rates different (ARD) model to our data. Likelihood ratio tests indicated that the more complex ARD model did not represent a significantly better fit than an ER model ($d = 1.05$, $P = 0.31$) and therefore we consequently estimated 1000 stochastic character maps using the ER model. To test the hypothesis that honeyeaters occupy distinct and extended parts of morphological space relative to co-distributed clades, we used a number of different approaches. First, to compare the morphological diversity

of honeyeaters ($n = 180$ species) with that of the four remaining meliphagoid families ($n = 93$ species, herein we refer to these clades as the “background meliphagooids”), we performed a phylogenetic principal component (pPC) analysis upon the covariance matrix of the seven log-transformed variables (Revell 2009). Second, we also assessed the morphological space occupied by honeyeaters to that of a broader subset of the Australasian/Indo-Pacific avifauna that encompassed the background meliphagooids, in addition to the members of 13 further passerine families present in the region ($n = 491$ species, herein we refer to this assemblage of clades as the “regional passerines”). For this analysis, we used the species scores generated from a separate principal component analysis (PCA) of the log-transformed morphological measurements. Due to the lack of comprehensive molecular phylogeny for this wider species set, we were unable to correct for the influence of shared ancestry in this analysis. Combined, PC axes 1–4 explained 95% of the overall variance in both the phylogenetic and nonphylogenetic PCAs (Tables S2 and S3), and we thus focused our subsequent analyses and interpretations on these variables. To test whether honeyeaters occupy unique parts of morphological space compared to the background meliphagooids and the regional passerine fauna, we estimated the four dimensional hypervolumes of honeyeaters relative to related clades, using the “hypervolume” methodology (Blonder et al. 2014). We thus performed two sets of comparisons using the first four PCA axes derived from the separate pPC and PC analyses described above (honeyeaters vs. background meliphagooids, and honeyeaters vs. regional passerines). The hypervolumes were estimated using a multidimensional kernel estimation procedure, and bandwidths that were determined using the Silverman bandwidth estimator (Blonder et al. 2015). Overlap in the hypervolumes between the clades in the two sets of analyses was calculated using the Sørensen index (see Blonder et al. 2015), whereby a value of 0 indicates no overlap between the hypervolumes, and a value of 1 indicates identical hypervolumes. Finally, to further assess whether honeyeaters occupy unique parts of morphological space and to define specific traits that differentiate the groups, we performed a linear discriminant analysis upon the seven original log-transformed morphological measurements, treating the regional passerine clades as both a single class, and as multiple classes divided by family.

The invasion of novel niche space has been predicted to result in a decoupling of rates of ecomorphological evolution between the invading and noninvading clades (Rabosky 2017). To test this hypothesis, we compared the relative fit of different models of trait evolution using the R package *mvMORPH* (Clavel et al. 2015). Specifically, we compared a Brownian motion (BM) model with a single rate of trait evolution for all lineages (BM1) to a BM model with separate rates of trait evolution for nectarivorous and non-nectarivorous lineages (BMM). We fit these two models to each of the 1000 stochastic character maps. Univariate analyses were

run for each of the first four pPC axes (pPC1–4). Similarly, we also compared models of multivariate evolution (pPC1–4) across 10 evenly sampled stochastic character maps. Model support was assessed using Akaike information criterions corrected for small sample sizes (AICc) and Akaike weights. To test for the possible influence of phylogenetic uncertainty, we repeated the above analyses across a posterior distribution of 1000 Meliphagidae trees obtained from the study of Marki et al. (2017) upon which we first estimated stochastic character maps using a single simulation per tree. In addition, we also assessed finer scale lineage variation in the tempo and mode of meliphagoid morphological evolution using a variable rates model as implemented in BayesTraits version 2 (available from <http://www.evolution.rdg.ac.uk/>). This approach uses reversible-jump Markov chain Monte Carlo algorithms (rjMCMC) and two scaling mechanisms to identify rate changes along single branches and for whole clades across the phylogeny (Venditti et al. 2011). We used default priors for the phylogenetic mean (α) and Brownian variance (σ) parameters and ran a single rjMCMC chain for each of the four pPC axes for 50 million generations, sampling every 5000th generation. In addition, we ran a correlated multivariate analysis that assessed the evolutionary dynamics of all four axes simultaneously, using the same parameters. We assessed mixing and convergence of the chains, before the first 5 million generations were removed as a burn-in. BayesTraits outputs a posterior distribution of trees in which the branches are scaled by the rate of evolutionary change that best explain the distribution of the trait values at the tips. Results were summarized by (i) calculating the mean rate of trait evolution along each branch, considering the posterior distribution of trees and (ii) by calculating the posterior probability of branch or clade shifts over all samples for each node in the tree. To account for uncertainty in the precise location of rate shifts across posterior samples, we calculated the posterior probability of a rate shift as the sum of the probability of this having occurred on a focal node, or on either of the descendant nodes (following Cooney et al. 2017). In addition to BayesTraits, we also investigated another widely used framework for inferring variable rates of trait evolution across a phylogeny (BAMM version 2.5.0; Rabosky 2014; Rabosky et al. 2014a). The BAMM method attempts to identify the location and number of distinct macroevolutionary rate regimes on the phylogeny. The number of distinct regimes is modeled following a Poisson distribution, with rjMCMC used to sample different regimes that best explain the distribution of trait values at the tips of the tree. We used the R package *BAMMtools* (Rabosky et al. 2014b) to estimate the prior settings for the phenotypic rates and for the hyperprior on the Poisson rate prior. The rjMCMC chains were run for 10 million generations each, sampling every 1000th generation. Convergence and mixing of the individual chains was assessed through visual inspection and by computing effective sample sizes, with the first 10% of

samples subsequently discarded as a burn-in. We analyzed each of the four pPC axes calculated for the Meliphagidae using the MCC tree as input.

To compare model fit between alternative evolutionary methods, we used the approach outlined in Cooney et al. (2017) that builds on the methodological developments of Pennell et al. (2015) and Chira and Thomas (2016), to calculate log-likelihoods describing the relative fit of different models of continuous trait evolution to each pPC axis. These analyses were performed using the *fitContinuous* function in the R package *geiger* (Harmon et al. 2008). We thus calculated the likelihood of three single-process models (BM, Ornstein–Uhlenbeck, and early-burst) fitted to the original untransformed tree, and compared these to the likelihoods of BM models fit to the mean rate-transformed trees derived from BAMM (obtained using the function *getMeanBranchLengthTree* in *BAMMtools*) and BayesTraits. AIC values for the BAMM and BayesTraits models were calculated after attempting to penalize for the number of estimated parameters. In BAMM, each identified rate shift is associated with the estimation of three parameters that denote the phenotypic rate at the start of a shift, the shift location, and a rate parameter controlling phenotypic change through time (Rabosky et al. 2014a). Consequently, for the BAMM models, the number of parameters for which to penalize by was calculated as the sum of: $3 \times$ (the average number of rate shifts across the posterior distribution) + 1 (root state) + 2 (root processes). In BayesTraits, each rate shift is associated with the estimation of two parameters that denote the location and rate of each branch or node shift, respectively. Thus, for BayesTraits, the number of parameters for which to penalize by was calculated as the sum of: $2 \times$ (the average number of rate shifts across the posterior distribution) + 1 (root state) + 1 (background variance). As the likelihood of the BAMM and BayesTraits models are not maximized in Bayesian analyses, the AIC values are likely to be conservative estimates of the true model fit relative to the single-process models. Model comparisons (using delta AIC) suggest that BayesTraits provides a branch-length transformation that results in the most Brownian-like distribution of the tip data among the range of models tested for all pPC axes (pPC1–4, Table S4). Consequently, we focus our interpretation and discussion on the BayesTraits results (although those generated by BAMM were largely congruent, Fig. S1).

To test whether the evolution of nectarivory by honeyeaters has led to an increase in the total volume of ecomorphological space occupied by the Meliphagidae (Rabosky 2017), we assessed the accumulation of morphological disparity and the filling of morphospace through time. Using maximum likelihood in *phytools* (Revell 2012), we estimated ancestral states for each of the pPC axes using the mean rate-transformed trees from BayesTraits. We then divided the tree in time slices at 0.5 million year intervals, starting at the root, and for each time slice extracted ancestral state

estimates for all lineages present at a given time. We compared both disparity accumulation of the individual PC axes and for all axes combined, by summing the variances across all four axes. Finally, we compared the empirical accumulation of trait disparity through time, with that expected under a constant-rate BM model and a variable-rates (VR) model of trait evolution. Thus, for both null models, we simulated 500 replicate datasets for each of the pPC axes and for pPC1–4 combined, to calculate disparity through time curves.

LINEAGE DIVERSIFICATION AND SPATIAL DIVERSITY PATTERNS

The invasion of novel or unoccupied niche space may in some instances lead to a decoupling in diversification dynamics between the invading and noninvading clades (e.g., Mitter et al. 1988, but see Givnish 2015; Rabosky 2017). To test for a decoupling in the dynamics of lineage diversification between nectarivorous and nonnectarivorous lineages, we applied the hidden-state speciation and extinction framework (HiSSE; Beaulieu and O'Meara 2016). The HiSSE framework is an extension of the binary-state speciation and extinction model (BiSSE; Maddison et al. 2007) developed to circumvent issues of high type I error rates associated with this method (Rabosky and Goldberg 2015). Using HiSSE, we compared the fit of five different models of lineage diversification (see Table S5 for details of number of parameters and constraints for each model), accounting for incomplete taxon sampling (3/289 species missing). Given the difficulty in reliably estimating transition rates in these analyses (Beaulieu and O'Meara 2016) and in line with our model comparisons above, we set transition rates between diet categories to be equal across all models. Model support was assessed using AICc scores and Akaike weights, and the results were visualized using model-averaged marginal reconstructions of diet and net diversification rates.

To assess whether increased ecological dispersion among honeyeaters has led to a heightened accumulation of sympatric species diversity (Schluter 1996), we compared the geographic species richness patterns of the honeyeaters to that of the background meliphagoids. To do this, we obtained range maps from a global distributional database (Rahbek and Graves 2001; Rahbek et al. 2012), with species ranges recorded at a resolution of $1^\circ \times 1^\circ$. We then mapped the species richness of the honeyeaters and the background meliphagoids by overlaying the ranges, before summing the number of species present in each 1° grid cell. Subsequently, we assessed the range and standard deviation of the individual pPC axes throughout all grid cells among both groups. Using linear models, we regressed the grid cell values of the species richness of the honeyeaters against the background meliphagoids. Finally, we determined how the range and standard deviation of the pPC axes varied among the honeyeaters and

background meliphagoids as a function of the species richness of all grid cells. As the range can be sensitive to outlying values, we also mapped the 95% quantiles of the range in pPC1–4 to explore the robustness of our results.

Results

DIET RECONSTRUCTIONS AND MORPHOLOGICAL DIVERSITY

The ancestral estimation of the presence of nectar in the diet of the Meliphagidae is strikingly characterized by a shift from a nonnectarivorous diet to one that can incorporate nectar in the common ancestor of honeyeaters (Fig. 1A). Nectarivory has also evolved independently among the pardalotes (family Pardalotidae) and among a handful of species of Australasian warblers (family Acanthizidae) that are members of the background meliphagoids. Among honeyeaters, loss of nectarivory has occurred independently on a number of more terminal branches, such as in the largely frugivorous genera *Melipotes* and *Macgregoria*, as well as in more insectivorous genera such as *Epthianura* and *Timeliopsis*. A pPCA of the seven log-transformed morphological traits (Table S1) comparing honeyeaters against background meliphagoids showed that the first axis (pPC1) strongly reflected overall size, explaining 65.3% of the total variance in the morphological measurements (Table S2). The next three axes (pPC2–4) were related to variation in Kipp's distance (pPC2), bill depth and width (pPC3), and bill length (pPC4), together explaining 29.8% of the variance. Visual comparisons of species scores on pPC axes 1–4 highlight the great morphological disparity and distinctiveness of the honeyeaters. First, the variance of body sizes (pPC1) exhibited by honeyeaters is much greater than that of the background meliphagoids (Fig. 2A). Although differences in shape variance are less extensive, honeyeaters generally have higher values of pPC2, in part, reflecting their greater Kipp's distance values (Fig. 2A). In addition, honeyeaters largely cluster separately from the background meliphagoid groups on pPC4, which is primarily related to differences in relative bill length (Fig. 2B). Results of a second, phylogenetically uncorrected PCA comparing honeyeaters against the regional passerine fauna are largely congruent with these findings (Table S3), with honeyeaters exhibiting a high diversity of body sizes (Fig. 2C) and unique morphologies related to bill shape and length (PC3–PC4; Fig. 2D).

The four dimensional hypervolume comparisons strongly support the above findings, with the Sørensen index indicating limited morphological overlap between the honeyeaters and background meliphagoids (Fig. S2, Sørensen's index = 0.07), and between the honeyeaters and regional passerines (Fig. S3, Sørensen's index = 0.22). Moreover, honeyeaters were found to occupy a high fraction of unique morphological space relative

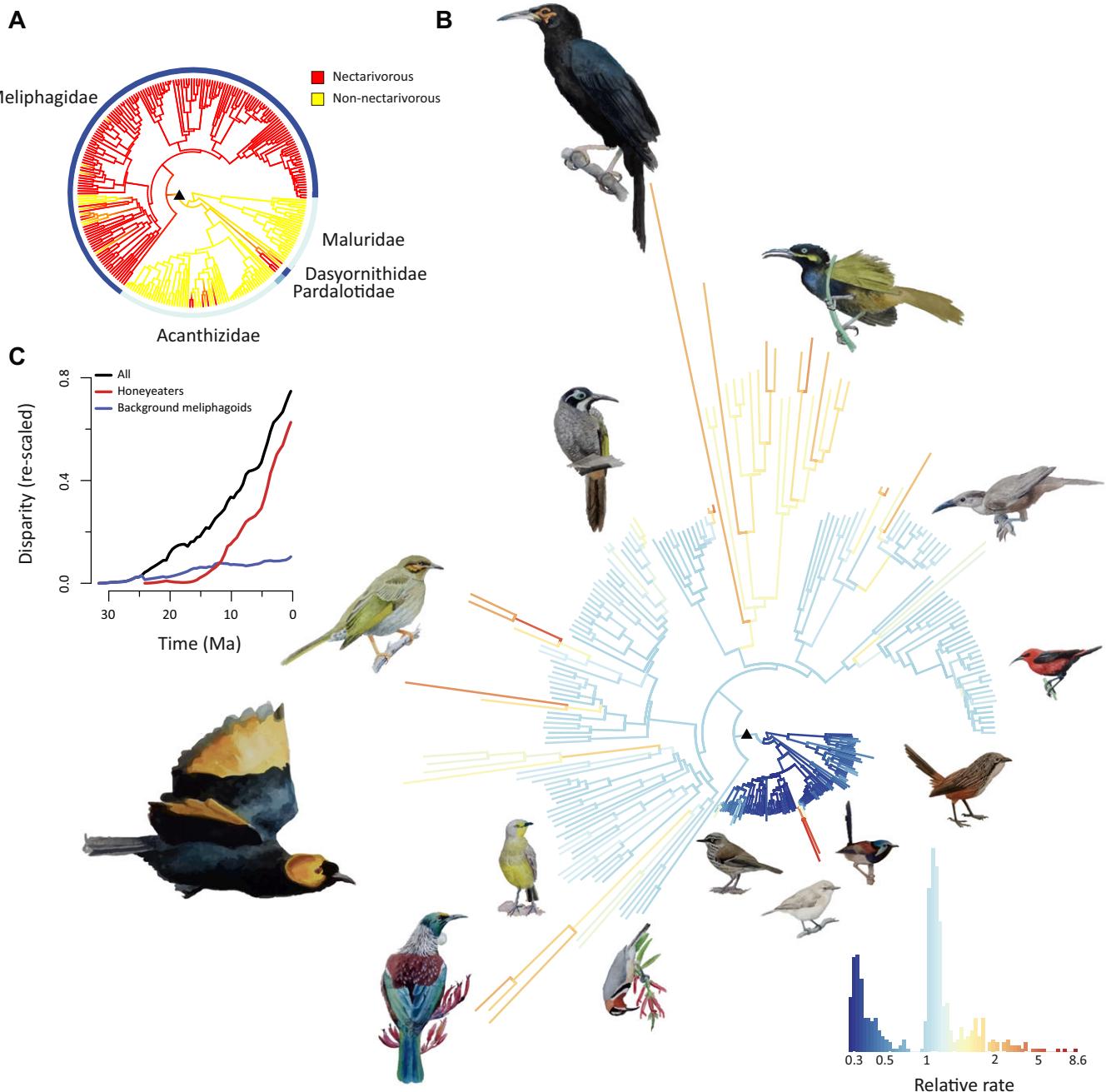


Figure 1. Diet and body size evolution among the Meliphagidae. (A) Phylogeny of the Meliphagidae with ancestral estimation of the presence (red) or absence (yellow) of nectar in the diet. Reconstructions were performed using stochastic character mapping and summarized using the *densityMap* function in the R package *phytools*. (B) The phylogeny with branch lengths scaled by the mean rate of body size (pPC1) evolution as estimated using the variable-rates model in *BayesTraits*. Branch coloring reflects the relative rate of evolution. (C) Accumulation of size disparity through time for the overall radiation (black), honeyeaters (red), and background meliphagoids (blue). The black triangles show the stem branch of honeyeaters. Illustrations are watercolors by Jon Fjeldså showing (clockwise from top) crow honeyeater (*Gymnomyza aubryana*), mao (*Gymnomyza samoensis*), Meyer's friarbird (*Philemon meyeri*), cardinal myzomela (*Myzomela cardinalis*), white-throated grasswren (*Amytornis woodwardi*), variegated fairywren (*Malurus lamberti*), large-billed gerygone (*Gerygone magnirostris*), white-browed scrubwren (*Sericornis frontalis*), western spinebill (*Acanthorhynchus superciliosus*), tui (*Prosthemadera novaeseelandiae*), gibberbird (*Ashbyia lovensis*), MacGregor's honeyeater (*Macgregoria pulchra*), orange-cheeked honeyeater (*Oreornis chrysogenys*), and Belford's melidectes (*Melidectes belfordi*).

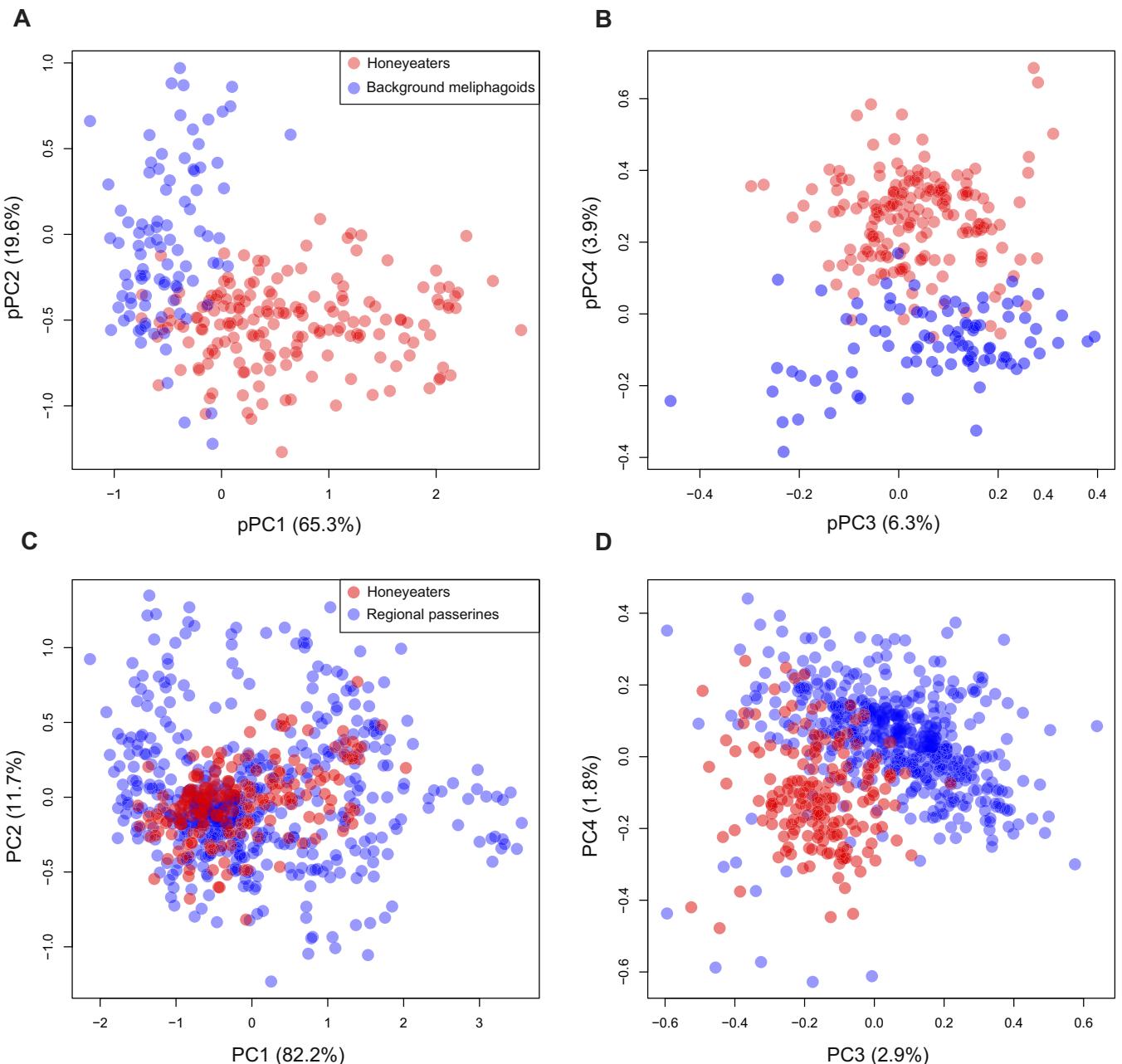


Figure 2. Morphospace of Australasian passerine birds. Morphological diversity of honeyeaters ($n = 180$ species; A and B) compared to that of the four background meliphagoid families ($n = 93$ species), as well as 13 additional Australasian passerine families ($n = 398$ species; C and D) as visualized using the four first axes of variation from a phylogenetic and standard principal component analysis, respectively. Principal components for the two sets of comparisons were generated separately.

to both background meliphagoids and to the broader regional passerine fauna (0.93 and 0.47 of the overall morphospace, respectively). A linear discriminant analysis of the seven original log-transformed measurements is in congruence with these results, illustrating that honeyeaters occupy distinct parts of morphological space relative to other regional passersines, with more than two-thirds of honeyeater species correctly classified as members of the family. Group means on the single discriminant axis

were -1.51 ± 0.93 for honeyeaters and 0.56 ± 1.03 for the remaining regional passerine species (Fig. S4). Normalized canonical coefficients separating the two groups indicate that the distinctiveness is largely driven by the comparatively long and narrow bills of the honeyeaters relative to other regional passersines (Table S6). Similar results were obtained from a comparison of honeyeaters against the regional passerine clades when these were divided by family, with 89% of honeyeaters correctly classified (Table S7).

Table 1. Comparisons of evolutionary models testing for a decoupling of rates of trait evolution between nectarivorous and nonnectarivorous lineages.

	pPC1	pPC2	pPC3	pPC4	pPC1-4
BM1					
Delta AICc	7.8 ± 1.8	8.5 ± 1.1	0.00 ± 0.00	9.1 ± 1.9	17.1 ± 3.8
AICc weight	0.03 ± 0.02	0.02 ± 0.01	0.71 ± 0.02	0.02 ± 0.02	0.00 ± 0.00
σ^2	0.022 ± 0.000	0.007 ± 0.000	0.002 ± 0.000	0.001 ± 0.000	0.032 ± 0.000
BMM					
Delta AICc	0.0 ± 0.0	0.0 ± 0.0	1.8 ± 0.2	0.0 ± 0.0	0.0 ± 0.0
AICc weight	0.97 ± 0.03	0.98 ± 0.01	0.29 ± 0.02	0.98 ± 0.02	1.00 ± 0.00
σ^2 (nectarivorous)	0.026 ± 0.000	0.005 ± 0.000	0.002 ± 0.000	0.002 ± 0.000	0.035 ± 0.000
σ^2 (nonnectarivorous)	0.014 ± 0.001	0.009 ± 0.000	0.002 ± 0.000	0.001 ± 0.000	0.026 ± 0.001

The best-fitting models are highlighted in bold. Shown are the mean and standard deviations of delta AICc values, AICc weights, and Brownian variance (σ^2) as estimated across 1000 (univariate analyses of pPC1-4) and 10 (multivariate analysis of pPC1-4) stochastic character maps accounting for the evolutionary history of diets among the Meliphagides.

MORPHOLOGICAL EVOLUTION

Comparisons of different models of trait evolution using *mvMORPH* provided strong support for a decoupling of trait diversification dynamics among nectarivorous and nonnectarivorous lineages. Models with separate rates of trait evolution (BMM) for nectarivorous and nonnectarivorous lineages represented the best-fitting model for pPC1, pPC2, pPC4, and the multivariate analysis of pPC1-4, whereas a single-rate BM (BM1) model was the best fit for pPC3 (Table 1). For pPC1, pPC4, and pPC1-4, nectarivorous lineages were found to have a higher rate of evolution than nonnectarivorous lineages. For pPC2, nectarivorous lineages were found to have a lower rate of evolution than nonnectarivorous lineages. These results were largely corroborated when phylogenetic uncertainty was accounted for (Table S8), although support for a single-rate BM (BM1) model was only marginally better than a BMM model for the analysis of pPC3.

The BayesTraits analyses of the multivariate data (pPC1-4 combined) recovered a number of rate shifts distributed across the Meliphagides (Fig. S5), including a substantial single-branch shift on the stem branch of the honeyeaters (PP = 0.73), as well as several rate shifts on more terminal branches and nodes among both honeyeaters and background meliphagoids. Deconstructing these trends among the individual pPC axes provided strong support for a clade-wide shift to higher rates of trait evolution near the base of the honeyeater clade on pPC1 (PP = 0.90; Fig. 1B; Fig. S5) and for three species of *Gerygone* among the background meliphagoids (PP = 0.83). No rates shifts in the univariate analysis of pPC2-4 were strongly supported (all PP < 0.7).

Analyzing the accumulation of morphological disparity through time, we find that disparity has steadily accumulated across the Meliphagides when considering all pPC axes congruently (Figs. S6-S8). Focusing on the individual pPC axes,

we show that this pattern is largely driven by an expansion in size disparity (pPC1) among the honeyeaters (Fig. 1C). Although body size disparity has continued to increase throughout the evolutionary history of the honeyeaters, this has not been the case for the background meliphagoid lineages, which have accumulated more limited disparity overall (Fig. 1C). Disparity accumulation on pPC2 exhibits a contrasting trend, however, with an early increase in disparity among the background meliphagoids, followed by two periods of relative stasis toward the present. Although the background meliphagoids have accumulated higher total disparity on pPC2 than the honeyeaters, both groups have continued to accumulate disparity through time on this axis. Disparity accumulation on pPC3 exhibit similar trends to that of pPC1, being characterized by continual accumulation of disparity toward the present (Figs. S6-S8). For pPC4, the disparity accumulation of the overall Meliphagides is characterized by an early expansion in disparity, followed by relative stasis, reflecting the divergence in bill morphology between the honeyeaters and the background meliphagoids. Following the occupation of unique areas of morphospace, disparity accumulation among the honeyeaters and background meliphagoids is comparatively less extensive and is dominated by a largely continuous and constant accumulation of disparity through time. Comparing the above trends to null expectations based on constant-rate (BM) and VR models suggests that disparity accumulation among meliphagoid lineages is largely consistent with a process of continuous niche expansion, with the possible exception of overall meliphagoid and background meliphagoid disparity accumulation on pPC2, and overall meliphagoid disparity accumulation on pPC4, which for both axes show signatures of slowdowns in disparity and as a consequence, niche expansion toward the present.

LINEAGE DIVERSIFICATION AND SPATIAL DIVERSITY PATTERNS

An analysis of lineage diversification dynamics using HiSSE suggested that a model with speciation rate variation associated with a hidden trait was the most strongly supported (AIC weight = 0.67, Table S5). In addition, an alternative model in which extinction rates were also free to vary between the two hidden states also received substantial support (AIC weight = 0.24). Models in which speciation rate variation was associated with diet received little support (AIC weight < 0.03). Mapping model-averaged marginal reconstructions of diet and speciation rates onto the Meliphagidae tree suggests that rates of speciation are generally high, with the exception of certain lineages that have lower rates, including the bristlebirds (*Dasyornithidae*), goldenface and fernwren (*Pachycare flavogriseum* and *Oreoscopus gutturalis*), and two species of Sulawesi honeyeaters (*Myza*) (Fig. S9).

Analyzing spatial diversity patterns, we found that honeyeaters exhibit geographic gradients of species richness that are highly correlated with the overall pattern shown by the background meliphagoid clades (Figs. 3A and 4A, $R^2 = 0.65$ where richness of either group ≥ 1). Furthermore, both groups almost completely overlap in the range of their overall distribution, with the highest levels of grid cell richness being found in eastern Australia and New Guinea (Fig. 3A). However, the absolute richness of the honeyeaters (max richness = 42, mean richness = 10.5 ± 7.5 SD) is substantially higher than that of background meliphagoids (max richness 25, mean richness = 6.9 ± 6.2 SD) across the majority of grid cells in which the groups co-occur. To assess how species richness patterns compare with those of morphological diversity, we mapped the range and standard deviation of the individual pPC axes across grid cells (Fig. 3B, C; Fig. S10). First, we find that honeyeaters have a higher diversity of body sizes (pPC1) across grid cells compared to the background meliphagoids (Fig. 3B, C), with both continental areas (e.g., eastern Australia and New Guinea) and islands (e.g., New Caledonia and Manus) standing out as areas harboring exceptional body size diversity, results that are robust to the exclusion of outliers (Fig. S11). Thus, for a given level of grid cell richness, both the range and standard deviation of body size are greater among the honeyeaters in contrast to the background meliphagoid groups (Fig. 4B, C; Fig. S12). Conversely, for pPC2, the background meliphagoid groups show a higher range and standard deviation within grid cells. For pPC3 and 4, we find that within grid cells, the honeyeaters and background meliphagoid groups overlap extensively in the range and standard deviation of the values of their co-occurring species (Fig. S10). Thus, unlike our findings for pPC1, the geographic patterns of range and standard deviation among pPC2–4 do not reflect the underlying gradients in species richness.

Discussion

The invasion of novel ecological niche space has been hypothesized to underlie the adaptive diversification of a wide range of organismal groups, but the role of this process in generating species and phenotypic diversity across large geographic scales remains poorly known. In this study, we tested key predictions of this hypothesis by analyzing the effects of an extensive shift in diet and resource use among a large continental and insular radiation of passerine birds—the honeyeaters. By explicitly analyzing these trends in a phylogenetic context that includes the honeyeaters and their closest relatives, we find strong evidence that the evolution of nectarivory represented the exploitation of underutilized ecological space that has coincided with substantial increases in the rate of morphological evolution, leading to the accumulation of extensive morphological disparity. Analyses of morphological evolution provide evidence for a clade-wide shift to substantially higher rates of body size evolution within the honeyeaters (Fig. 1B; Fig. S1; Table 1). The increase in rates of body size evolution followed a major change in diet that evolved to encompass nectar (Fig. 1A), allowing honeyeaters to enter novel regions of niche space in comparison to the regional passerine fauna with which they co-occur. However, this significant dietary shift did not lead to a decoupling (i.e., acceleration or deceleration) of the dynamics of speciation among the honeyeaters and the background meliphagoids (Fig. S9, Table S5). Conversely, analyses of spatial diversity patterns suggest that despite having converged on congruent geographic diversity patterns, honeyeaters exhibit consistently higher levels of body size diversity and species richness than their close relatives within 1° grid cells (Figs. 3 and 4). These findings suggest that a shift toward nectarivory positively influenced the capacity of the honeyeaters to accumulate high sympatric species diversity. Extensive diversification along the body size axis could enable a greater number of honeyeater species to coexist, reflecting their entry into an unoccupied adaptive zone (nectarivory) that allowed honeyeaters to radiate into vacant ecological and morphological space. Together, our findings highlight the important role that evolutionary innovation and the invasion of novel ecological niche space play in generating extensive ecological diversity and the build-up of sympatric species diversity throughout large geographic areas.

Character displacement resulting from interspecific competition for resources is believed to be the main driver of ecological and phenotypic disparification in adaptive radiation (Simpson 1953; Schlüter 2000a,b; Losos and Mahler 2010). For honeyeaters, size-related aggression and displacement within flowering trees is a well-known phenomenon and assumed driver of body size evolution (Paton and Ford 1983; Diamond et al. 1989). This hypothesis provides a possible explanation for the tight congruence between the shift toward a nectarivorous diet

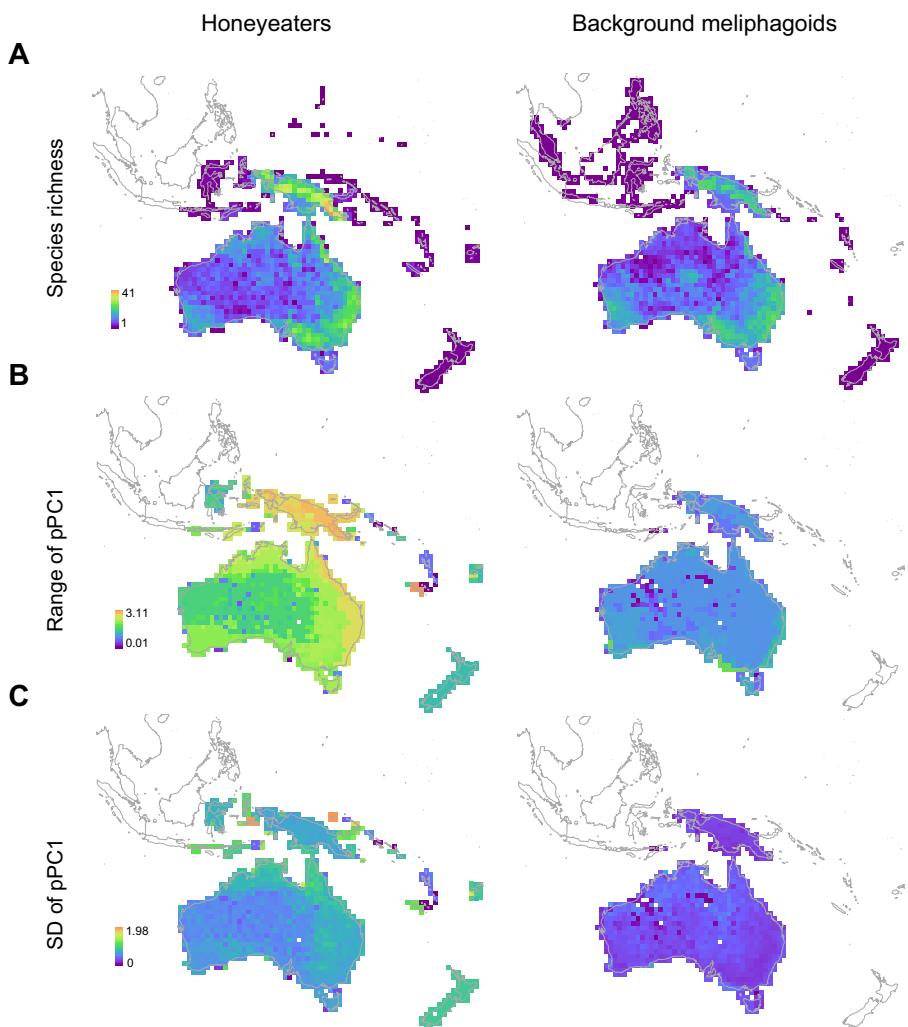


Figure 3. Spatial diversity patterns of honeyeaters compared to that of background meliphagoids in $1^\circ \times 1^\circ$ grid cells. Comparisons between honeyeaters (left) and background meliphagoids (right) for differences in species richness (A), range (B), and standard deviation (C) of pPC1.

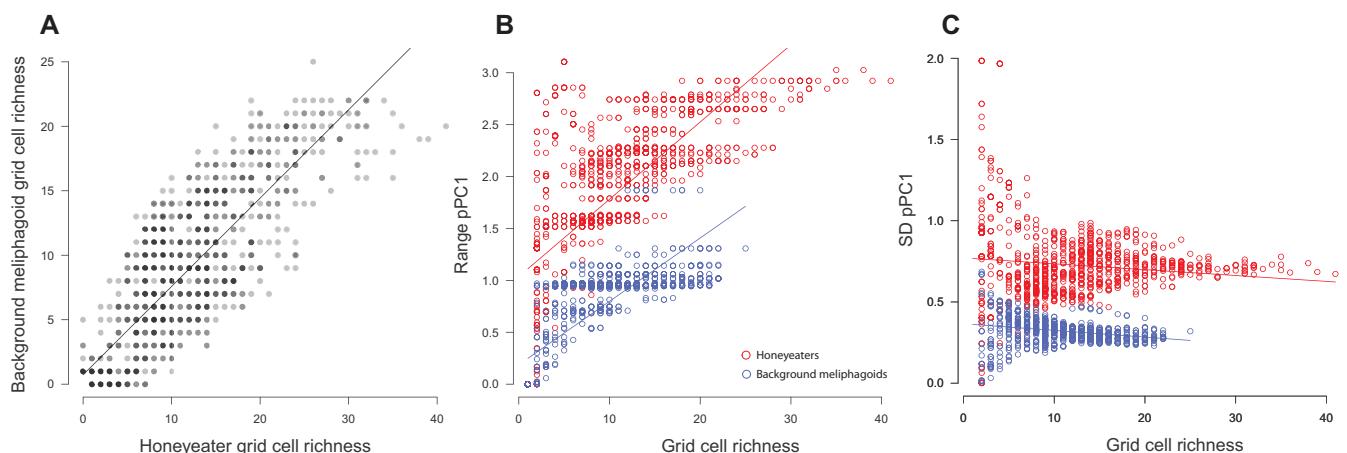


Figure 4. Results of linear models examining the relationships between spatial diversity patterns. The panels show the relationships between (A) grid cell richness of the honeyeaters and background meliphagoids, grid cell richness of both groups and their range (B), and grid cell richness of both groups and standard deviation (C) of pPC1. Points represent the values in each $1^\circ \times 1^\circ$ grid cell. Line in (A) is the 1:1 line, whereas lines in (B) and (C) are the least-squares regression fits.

and the increase in rates of body size evolution and disparity accumulation in the group. Honeyeaters are notorious for their aggressiveness, and even Alfred Russel Wallace noted how friarbirds would ferociously defend flowering trees against potential competitors (Wallace 1869). Although mimicry may be one tactic to avoid attack from larger species (Diamond 1982; Prum 2014; Jönsson et al. 2016), positive selection for smaller body size may represent another viable scenario, as small birds may be able to use resources that are inaccessible or not easily monopolized by larger birds (e.g., on small terminal twigs in outer parts of a tree), thus avoiding aggressive attacks (Diamond et al. 1989). Interestingly, our findings of rapid and extensive body size evolution among honeyeaters are in stark contrast to the two other major nectarivorous clades of birds—the hummingbirds and sunbirds—which exhibit comparatively limited body size diversity, but greater overall phenotypic specialization for interaction with their flower resources (Stiles 1981; Fleming and Muchhal 2008; Zanata et al. 2017). Fleming and Muchhal (2008) attributed the among-clade differences in nectarivory specialization and body size diversity to variation in floral resource predictability among major regions, ranging from highest in the Neotropics to comparatively low in Australia. In concordance with this hypothesis, we suggest that strong competition for a valued resource, which can be highly unpredictable in its spatial and temporal occurrence, has been the prominent driver of body size evolution among the Australasian honeyeaters. In addition to increased rates of body size evolution, the transition to a nectarivorous diet appears to have had a profound influence on bill evolution among honeyeaters. Our results thus suggest that honeyeaters have unique bill morphology (i.e., longer and narrower) compared to the background meliphagoids and other regional passerines (Fig. S4; Tables S6 and S7), whereas nectarivorous meliphagoid lineages are also found to have a higher rate of bill (pPC4) evolution than nonnectarivorous lineages (Table 1). Taken together, our results suggest that the evolution of nectarivory among honeyeaters have had important consequences for both rates of morphological evolution (i.e., body size) and morphological adaptations (i.e., bill size and shape) in this clade.

The extensive and continuous accumulation of morphological disparity among honeyeaters relative to the background meliphagoids could partly be caused by recent morphological evolution into further novel and unoccupied areas of niche-space (Simpson 1944; Slater 2015; Cooney et al. 2017). Examples of this include the genera *Macgregoria* and *Melipotes* that have transitioned to a largely fruit-based diet that is also reflected in their generally shorter and straighter bills relative to most other honeyeaters. Alternatively, this pattern could reflect the outcome of strong ecological character displacement, whereby interspecific competition among recently separated taxa selects for rapid phenotypic divergence (Brown and Wilson 1956; Schluter 2000b).

Many island species such as the two sympatric New Zealand honeyeater taxa *Prosthemadera* and *Anthornis* may represent an extreme example of this process, as they display high levels of recent body size divergence, which is also consistent with the expectation of greater character displacement among species in depauperate environments (Schluter 2000b). Thus, both character displacement and diversification into further available and unoccupied niche space are probable explanations that likely contributed to the continual accumulation of disparity in the case of honeyeaters.

Although transitions into new adaptive zones (and adaptive radiation more generally) need not always result in increased rates of lineage diversification, increases in ecological diversity of the adaptively radiating clade are predicted to facilitate the build-up of extensive sympatric species diversity (Givnish 1997; Losos and Mahler 2010; Givnish 2015; Stroud and Losos 2016; Rabosky 2017). Consistent with these predictions, we find that although there is no evidence of a decoupling of the lineage diversification dynamics among nectarivorous and nonnectarivorous meliphagoid lineages (Fig. S9; Table S5), the evolution of nectarivory appears to have influenced the build-up of extensive sympatric species richness among the predominantly nectarivorous honeyeaters. Thus, although honeyeaters and the other families within the Meliphagidae share very similar distributional extents and geographic diversity gradients (Figs. 3 and 4), honeyeaters exhibit much higher levels of species richness within the same grid cells compared to the background meliphagoids. Although honeyeaters might be expected to accumulate higher grid cell richness than the background meliphagoids due to their higher overall species diversity, this null explanation is unlikely to be sufficient in accounting for the strong correlations between grid cell richness, body-size disparity, and the trends of trait evolution. The evolution of nectarivory among the honeyeaters may thus represent an intriguing example of how evolutionary innovations may positively influence the build-up of species diversity without necessarily having direct effects on rates of lineage diversification (Rabosky 2017).

A number of nonmutually exclusive mechanisms may underlie the increased sympatric species diversity of honeyeaters, including elevated ecological diversity (Keast 1976; Miller et al. 2017), and increased dispersal capabilities. The association between sympatric species richness and body size diversity recovered here suggests either that diversity drives ecological divergence by character displacement, or alternatively, that expansion into unoccupied niche space allows more species of honeyeaters to coexist through relaxed ecological filtering. Although substantial expansion in morphological space of other regional clades may have been constrained by the presence of ecologically similar lineages, honeyeaters appear to have been able to expand more freely due to the general absence of competing

nectarivores. Although Australasia and the Indo-Pacific is inhabited by some other nectarivorous birds, including non-passerine parrots such as the lorries and lorikeets (family Psittacidae: tribe Loriinae), this group is thought to have radiated considerably later than the honeyeaters, with most of the diversification having taken place in the last 5 million years (Schweizer et al. 2015). In comparison with honeyeaters, this group is characterized by comparatively low levels of sympatric species diversity (Schweizer et al. 2015), which could suggest that the ecological diversification of lorries and lorikeets has itself been constrained by the more ecologically diverse honeyeaters. Lories and lorikeets appear to be less ecologically diverse than honeyeaters, exhibiting a comparatively reduced diversity of bill shapes and adaptation to a narrower range of habitats, dietary resources, and foraging modes. However, in the absence of detailed ecological and morphological data for the lorries and lorikeets, these hypotheses necessitate formal testing. Finally, a number of nectarivorous bats also inhabit the Australasian/Indo-Pacific region (family Pteropodidae), but as these are primarily nocturnal, direct competition with the diurnal honeyeaters is unlikely to have been pervasive.

Under a model of allopatric speciation, for character displacement to occur, genetic/reproductive differentiation must first accumulate in geographic isolation before subsequent range shifts into sympatry (Price 2008). The rate at which this process occurs is at least partly contingent on the dispersal propensity of the organisms in question, as this positively influences the rate at which lineages achieve range overlap (Pigot and Tobias 2015). A lack of positive selective pressures on factors that directly facilitate dispersal may thus help to explain why some adaptive radiations are notably species-poor (Losos and Mahler 2010; Givnish 2015). Among honeyeaters, good dispersal abilities are a well-established characteristic of many species and this is likely to have enabled frequent colonization and exchange between geographic regions (Keast 1968; Marki et al. 2017). The irregular, unpredictable, and often highly disjunct occurrence of many nectar sources may have exposed honeyeaters to significant positive selection for increased dispersal capabilities as evidenced by the major seasonal and nomadic movements of many species (Keast 1968; Pyke 1980; Wooller 1981). Our findings support this, with honeyeaters having on average longer and more projected wing tips compared to background meliphagoids, suggesting high dispersal capacity (Fig. S13; Claramunt et al. 2012). Thus, increased dispersal abilities among the many nectar-dependent honeyeaters may have been an additional factor promoting the build-up of species diversity by increasing the rates at which new populations are founded, and their subsequent transitions back into sympatry following differentiation (Pigot and Tobias 2015).

The utilization of previously inaccessible resources has been hypothesized to underlie the adaptive radiation of a wide range of organismal groups. Here, we have shown that an ancestral shift to a

nectarivorous diet is correlated with rapid body size evolution and the accumulation of extensive size disparity within the speciose radiation of Australasian honeyeaters. Importantly, our findings suggest that the rapid invasion of novel and previously unoccupied ecological space can positively affect the build-up of species and functional diversity across different spatial scales, even in the presence of related and likely competing lineages. Overall, these results highlight the important role of ecological opportunity in facilitating the generation of morphological and species diversity across large geographic areas.

AUTHOR CONTRIBUTIONS

P.Z.M. conceived the study and collected the morphological data; P.Z.M., J.D.K., and C.R.C. performed analyses; and P.Z.M., J.D.K., C.R.C., C.R., and J.F. interpreted the analyses and wrote the manuscript.

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DATA ARCHIVING

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CONFLICT OF INTEREST

The authors have no competing interest.

LITERATURE CITED

- Barker, F. K., A. Cibois, P. Schikler, J. Feinstein, and J. Cracraft. 2004. Phylogeny and diversification of the largest avian radiation. *Proc. Natl. Acad. Sci. USA* 101:11040–11045.
- Beaulieu, J. M., and B. C. O’Meara. 2016. Detecting hidden diversification shifts in models of trait-dependent speciation and extinction. *Sys. Bio.* 65:583–601.
- Blonder, B., C. Lamanna, C. Viole, and B. J. Enquist. 2014. The n-dimensional hypervolume. *Glob. Ecol. Biogeogr.* 23:595–609.
- Blonder, B., D. Nogués-Bravo, M. K. Borregaard, J. C. Donoghue, II, P. M. Jørgensen, N. J. B. Kraft, J.-P. Lessard, N. Morueta-Holme, B. Sandel, J.-C. Svensson, et al. 2015. Linking environmental filtering and

- disequilibrium to biogeography with a community climate framework. *Ecology* 96:972–985.
- Bollback, J. P. 2006. SIMMAP: Stochastic character mapping of discrete traits on phylogenies. *BMC Bioinformatics* 7:88.
- Bond, J. E., and B. D. Opell. 1998. Testing adaptive radiation and key innovation hypotheses in spiders. *Evolution* 52:403–414.
- Brown, W. L., and E. O. Wilson. 1956. Character displacement. *Syst. Zool.* 5:49–64.
- Casotti, G., and K. C. Richardson. 1992. A stereological analysis of kidney structure of honeyeater birds (Meliphagidae) inhabiting either arid or wet environments. *J. Anat.* 180:281–288.
- Chira, A. M., and G. H. Thomas. 2016. The impact of rate heterogeneity on inference of phylogenetic models of trait evolution. *J. Evol. Biol.* 29:2502–2518.
- 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. *Proc. Biol. Sci.* 279:1567–1574.
- Clavel, J., G. Escarguel, and G. Merceran. 2015. mvMORPH: An R package for fitting multivariate evolutionary models to morphometric data. *Methods Ecol. Evol.* 6:1311–1319.
- Cooney, C. R., J. A. Bright, E. J. R. Capp, A. M. Chira, E. C. Hughes, C. J. A. Moody, L. O. Nouri, Z. K. Varley, G. H. Thomas. 2017. Megaevolutionary dynamic of the adaptive radiation of birds. *Nature* 542:344–347.
- Diamond, J. M. 1982. Mimicry of friarbirds by orioles. *Auk* 99:187–196.
- Diamond, J., S. L. Pimm, M. E. Gilpin, and M. LeCroy. 1989. Rapid evolution of character displacement in myzomelid honeyeaters. *Am. Nat.* 134:675–708.
- Fleming, T. H., and N. Muchhal. 2008. Nectar-feeding bird and bat niches in two worlds: Pantropical comparisons of vertebrate pollination systems. *J. Biogeogr.* 35:764–780.
- Futuyma, D. J. 1998. Evolutionary biology. Sinauer Associates, Sunderland, MA.
- Galis, F., and E. G. Drucker. 1996. Pharyngeal biting mechanisms in centrarchid and cichlid fishes: Insights into a key evolutionary innovation. *J. Evol. Biol.* 9:641–670.
- Gardner, J. L., J. W. H. Trueman, D. Ebert, L. Joseph, and R. D. Magrath. 2010. Phylogeny and evolution of the Meliphagoidea, the largest radiation of Australasian songbirds. *Mol. Phylogenet. Evol.* 55:1087–1102.
- Gill, F., and D. Donsker. 2016. IOC World Bird List (v 6.2). <https://doi.org/10.14344/IOC>.
- Givnish, T. J. 1997. Adaptive radiation and molecular systematics: Issues and approaches. Pp. 1–54 in T. J. Givnish and K. J. Sytsma, eds. Molecular evolution and adaptive radiation. Cambridge Univ. Press, Cambridge, U.K.
- . 2015. Adaptive radiation versus ‘radiation’ and ‘explosive diversification’: Why conceptual distinctions are fundamental to understanding evolution. *New Phytol.* 207:297–303.
- Goldstein, D. L., and S. D. Bradshaw. 1998a. Regulation of water and sodium balance in the field by Australian honeyeaters (Aves: Meliphagidae). *Physiol. Zool.* 71:214–225.
- . 1998b. Renal function in red wattlebirds in response to varying fluid intake. *J. Comp. Physiol. B*, 168:265–272.
- Grant, P. R., and B. R. Grant. 2008. How and why species multiply: The radiation of Darwin’s finches. Princeton Univ. Press, Princeton, NJ.
- Harmon, L. J., J. T. Weir, C. D. Brock, R. E. Glor, and W. Challenger. 2008. GEIGER: Investigating evolutionary radiations. *Bioinformatics* 24:129–131.
- Hodges, S. A., and M. L. Arnold. 1995. Spurring plant diversification: Are floral nectar spurs a key innovation? *Proc. R. Soc. Lond. B* 262:343–348.
- Hunter, J. P. 1998. Key innovations and the ecology of macroevolution. *Trends. Ecol. Evol.* 13:31–36.
- Huxley, J. 1942. Evolution: The modern synthesis. Allen & Unwin, London, U.K.
- Jönsson, K. A., P.-H. Fabre, R. E. Ricklefs, and J. Fjeldså. 2011. Major global radiation of corvoid birds originated in the proto-Papuan archipelago. *Proc. Natl. Acad. Sci. USA* 108:2328–2333.
- Jönsson, K. A., K. Delhey, G. Sangster, P. G. P. Ericson, and M. Irestedt. 2016. The evolution of mimicry of friarbirds by orioles (Aves: Passeriformes) in Australo-Pacific archipelagos. *Proc. R. Soc. Lond. B* 283:20160409.
- Keast, A. 1968. Seasonal movements in the Australian honeyeaters (Meliphagidae) and their ecological significance. *Emu* 67:159–209.
- . 1976. The origins of adaptive zone utilizations and adaptive radiations, as illustrated by the Australian Meliphagidae. Pp. 71–82 in Proceedings of the XVI International Ornithological Congress. Canberra, Australia.
- . 1985. An introductory ecological biogeography of the Australo-Pacific Meliphagidae. *New Zeal. J. Zool.* 12:605–622.
- Liem, K. F. 1973. Evolutionary strategies and morphological innovations: Cichlid pharyngeal jaws. *Syst. Zool.* 22:425–44.
- Losos, J. B. 2009. Lizards in an evolutionary tree: Ecology and adaptive radiation of anoles. University of California Press, Berkeley, CA.
- . 2010. Adaptive radiation, ecological opportunity, and evolutionary determinism. *Am. Nat.* 175:623–639.
- Losos, J. B., and D. L. Mahler. 2010. Adaptive radiation: The interaction of ecological opportunity, adaptation, and speciation. Pp. 381–420 in Bell, M. A., D. J. Futuyma, W. F. Eanes, and J. S. Levinton, eds. Evolution since Darwin: The first 150 years. Sinauer Associates, Sunderland, MA.
- Maddison, W.P., P. E. Midford, and S. P. Otto. 2007. Estimating a binary character’s effect on speciation and extinction. *Sys. Bio.* 56:701–710.
- Marki, P. Z., K. A. Jönsson, M. Irestedt, J. M. T. Nguyen, C. Rahbek, and J. Fjeldså. 2017. Supermatrix phylogeny and biogeography of the Australasian Meliphagidae radiation (Aves: Passeriformes). *Mol. Phylogenet. Evol.* 107:516–529.
- Miller, A. H. 1949. Some ecologic and morphologic considerations in the evolution of higher taxonomic categories. Pp. 84–88 in E. Mayr and E. Schüz, eds. Ornithologie als Biologische Wissenschaft. Carl Winter, Heidelberg, Germany.
- Miller, E.T., S. K. Wagner, L. J. Harmon, and R. E. Ricklefs. 2017. Radiating despite a lack of character: Ecological divergence among closely related, morphologically similar honeyeaters (Aves: Meliphagidae) co-occurring in arid Australian environments. *Am. Nat.* 189:14–30.
- Mitter, C., B. Farrell, and B. Wiegmann. 1988. The phylogenetic study of adaptive zones: Has phytophagy promoted insect diversification? *Am. Nat.* 132:107–128.
- Moyle, R. G., C. H. Oliveros, M. J. Andersen, P. A. Hosner, B. W. Benz, J. D. Manthey, S. L. Travers, R. M. Brown, and B. C. Faircloth. 2016. Tectonic collision and uplift of Wallacea triggered the global songbird radiation. *Nat. Commun.* 7:12709.
- Osborn, H. F. 1902. The law of adaptive radiation. *Am. Nat.* 36:353–363.
- Paton, D. C. and B. G. Collins. 1989. Bills and tongues of nectar-feeding birds: A review of morphology, function and performance, with intercontinental comparisons. *Austral Ecology*, 14:473–506.
- Paton, D. C., and H. A. Ford. 1983. The influence of plant characteristics and honeyeater size on levels of pollination in Australian plants. Pp. 235–248 in Jones, C. E. and R. J. Little, eds. Handbook of experimental pollination biology. Van Nostrand-Reinhold, Princeton, NJ.
- Pennell, M. W., R. G. FitzJohn, W. K. Cornwell, and L. J. Harmon. 2015. Model adequacy and the macroevolution of angiosperm functional traits. *Am. Nat.* 186:E33–E50.

- Pigot, A. L., and J. A. Tobias. 2015. Dispersal and the transition to sympatry in vertebrates. *Proc. Biol. Sci.* 282:20141929.
- Pratt, H. D. 2005. The Hawaiian Honeycreepers: Drepanidae. Oxford Univ. Press, Oxford, U.K.
- Price, T. 2008. Speciation in birds. Roberts and Co, Boulder, CO.
- Prum, R. O. 2014. Interspecific social dominance mimicry in birds. *Zool. J. Linn. Soc.* 172:910–941.
- Pyke, G. H. 1980. The foraging behaviour of Australian honeyeaters: A review and some comparisons with hummingbirds. *Aust. J. Ecol.* 5:343–369.
- Rabosky, D. L. 2014. Automatic detection of key innovations, rate shifts, and diversity: Dependence on phylogenetic trees. *PLoS One* 9:e89543.
- . 2017. Phylogenetic tests for evolutionary innovation: The problematic link between key innovations and exceptional diversification. *Phil. Trans. R. Soc.* 372:20160417.
- Rabosky, D. L., S. C. Donnellan, M. Grundler, and I. J. Lovette. 2014a. Analysis and visualization of complex macroevolutionary dynamics: An example from Australian scincid lizards. *Syst. Bio.* 63:610–627.
- Rabosky, D. L., and E. E. Goldberg. 2015. Model inadequacy and mistaken inferences of trait-dependent speciation. *Sys. Bio.* 64:340–355.
- Rabosky, D. L., M. Grundler, C. Anderson, P. Title, J. J. Shi, J. W. Brown, H. Huang, and J. G. Larson. 2014b. BAMMtools: An R package for the analysis of evolutionary dynamics on phylogenetic trees. *Methods Ecol. Evol.* 5:701–707.
- Rahbek, C., and G. R. Graves. 2001. Multiscale assessment of patterns of avian species richness. *Proc. Natl. Acad. Sci. USA* 98:4534–4539.
- Rahbek, C., L. A. Hansen, and J. Fjeldså. 2012. One degree resolution database of the global distribution of birds. The Natural History Museum of Denmark, University of Copenhagen, Denmark. Available at <http://macroecology.ku.dk/resources/>.
- R Core Team. 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.
- 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 Ecol. Evol.* 3:217–223.
- Schlüter, D. 1996. Ecological causes of adaptive radiation. *Am. Nat.* 148:S40–S64.
- . 2000a. The ecology of adaptive radiation. Oxford Univ. Press, Oxford, U.K.
- . 2000b. Ecological character displacement in adaptive radiation. *Am. Nat.* 156:S4–S16.
- Schweizer, M., T. F. Wright, J. V. Peñalba, E. E. Schirtzinger, L. Joseph. 2015. Molecular phylogenetics suggest a New Guinean origin and frequent episodes of founder-event speciation in the nectarivorous lorries and lorikeets (Aves: Psittaciformes). *Mol. Phylogenet. Evol.* 90:34–48.
- Simpson, G. G. 1944. Tempo and mode in evolution. Columbia Univ. Press, New York, NY.
- . 1953. The major features of evolution. Columbia Univ. Press, New York, NY.
- Slater, G. J. 2015. Iterative adaptive radiations of fossil canids show no evidence for diversity-dependent trait evolution. *Proc. Natl. Acad. Sci. USA* 112:4897–4902.
- Slowinski, J. B., and C. Guyer. 1993. Testing whether certain traits have caused amplified diversification: An improved method based on a model of random speciation and extinction. *Am. Nat.* 142, 1019–1024.
- Soulebeau, A., X. Aubriot, M. Gaudeul, G. Rouhan, S. Hennequin, T. Haevermans, J.-Y. Dubuisson, and F. Jabbour. 2015. The hypothesis of adaptive radiation in evolutionary biology: Hard facts about a hazy concept. *Org. Divers. Evol.* 15:747–761.
- Stiles, F. G. 1981. Geographical aspects of bird-flower coevolution, with particular reference to Central America. *Ann. Mo. Bot. Gard.* 68:323–351.
- Stroud, J. T., and J. B. Losos. 2016. Ecological opportunity and adaptive radiation. *Annu. Rev. Ecol. Evol. Syst.* 47:507–532.
- Venditti, C., A. Meade, and M. Pagel. 2011. Multiple routes to mammalian diversity. *Nature* 479:393–396.
- Wallace, A. R. 1869. The Malay Archipelago. Dover Publication, New York, NY.
- Wilman, H., J. Belmaker, J. Simpson, C. de la Rosa, M. M. Rivadeneira, and W. Jetz. 2014. EltonTraits 1.0: Species-level foraging attributes of the world's birds and mammals. *Ecology* 95:2027.
- Wooller, R. D. 1981. Seasonal changes in a community of honeyeaters in southwestern Australia. *Emu* 81:50–51.
- Zanata, T. B., B. Dalsgaard, F. C. Passos, P. A. Cotton, J. J. Roper, P. K. Maruyama, E. Fischer, M. Schleuning, A. M. M. González, J. Vizentini-Bugoni, et al. 2017. Global patterns of interaction specialization in bird-flower networks. *J. Biogeogr.* 44:1891–1910.

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Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. Description of morphological traits measured using a calliper and taken to the nearest 0.1 mm (tarsus, hind toe and bill measurements), or using a wing ruler taken to the nearest 1 mm (wing length and Kipp's distance).

Table S2. Trait loadings and proportion of variance explained by each of the phylogenetic principal component (pPC) axes for the analysis of the Meliphagides dataset ($n = 273$ species).

Table S3. Trait loadings and proportion of variance explained by each of the principal component axes for the analysis of the full passerine dataset ($n = 671$ species).

Table S4. Comparison of model fit for different models of morphological evolution.

Table S5. Comparisons of lineage diversification models using HiSSE.

Table S6. Normalized canonical coefficients separating honeyeaters and other regional passerines on the basis of the seven original log-transformed variables.

Table S7. Classification of passerine species based on the linear discriminant analysis.

Table S8. Comparisons of evolutionary models testing for a decoupling of rates of trait evolution between nectarivorous and non-nectarivorous lineages that accounted for phylogenetic uncertainty.

Figure S1. Mean shift configurations of BAMM analysis of pPC1-4.

Figure S2. Pairwise plots showing the estimated four-dimensional pPC hypervolumes for honeyeaters (red points) and background meliphagoids (blue).

Figure S3. Pairwise plots showing the estimated four-dimensional PCA hypervolumes for honeyeaters (red points) and regional passerines (blue).

Figure S4. Distribution of discriminant scores for honeyeaters (top panel) and other regional passerines (bottom panel).

Figure S5. Results from the BayesTraits variable-rates analysis of pPC1-4.

Figure S6. Accumulation of morphological disparity through time (pPC1-4) for the Meliphagides (solid black line), with separate lines for the honeyeaters (solid red line) and background meliphagoids (solid blue line).

Figure S7. Accumulation of morphological disparity through time (pPC1-4) for the Meliphagides (solid black line), with separate lines for the honeyeaters (solid red line) and background meliphagoids (solid blue line).

Figure S8. Phenograms of morphological disparity through time (pPC1-4) for the Meliphagides with separate coloration for the honeyeaters (red) and background meliphagoids (black).

Figure S9. Model-averaged speciation rates among the Meliphagides as inferred using the hidden-state speciation and extinction (HiSSE) framework.

Figure S10. Spatial diversity patterns of honeyeaters compared to that of background meliphagoids in $1^\circ \times 1^\circ$ grid cells.

Figure S11. Spatial diversity patterns of honeyeaters compared to that of background meliphagoids in $1^\circ \times 1^\circ$ grid cells.

Figure S12. Results of linear models examining the relationships between spatial diversity patterns.

Figure S13. Relationship between pPC2 and the log-transformed Kipp's distance values.