Ecological opportunity and ecomorphological convergence in Australasian robins (Petroicidae)

Vicente García-Navas¹, Marta Rodríguez-Rey² and Les Christidis^{3,4}

¹Department of Integrative Ecology, Estación Biológica de Doñana (EBD-CSIC), Seville, Spain

²Department of Biosciences, Swansea University, Swansea, Wales, United Kingdom

³National Marine Science Centre, Southern Cross University, Coffs Harbour, NSW, Australia

⁴School of BioSciences, University of Melbourne, Parkville, Victoria, Australia

Corresponding author: Vicente García-Navas, Department of Integrative Ecology, Estación Biológica de Doñana (EBD-CSIC), Avenida Américo Vespucio 26, Seville E-41092, Spain.
Email: vicente.garcianavas@gmail.com

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Abstract

Ecological theories of adaptive radiation predict that ecological opportunity (EO) stimulates cladogenesis through entry into a novel environment and/or release of competition pressures.

Due to its dynamic paleoclimatic and geological history, the Australo-Papuan region constitutes an opportune scenario to study patterns of diversification in relation to the colonization of new ecological niches. Here, we employ a comparative framework using the Australasian robins (Petroicidae) as a model system to test whether the diversification of this bird family fulfils a niche-filling process as predicted by the EO model, and to test whether the observed morphological similarity is described by a pattern of phylogenetic niche conservatism (PNC) or convergence. Although we detected an early-burst, we did not find a slowdown in speciation or morphological evolution as expected in a niche-filling scenario. Divergence in tarsus length and tail length (PC1) was consistent with a multi-peak model, in which PC1 represents a convergent trait among distantly related clades sharing the same foraging strategy. Our study thus shows that convergence rather than PNC seems to explain the existence of morphological similarity across independent lineages in the Petroicidae. We also found a low level of PNC regarding annual variations in temperature and precipitation, which is in agreement with the hypothesis that diversification within the Petroicidae involved repeated radiations. We suggest two non-mutually exclusive hypotheses to explain the overall lack of density-dependent cladogenesis. First, the extreme spatial and temporal heterogeneity of this region may have generated a pattern of repeated ecological opportunity over time and, second, this family may not yet have reached equilibrium diversity.

Keywords: adaptation, Australia, evolutionary radiation, morphology, phenotypic evolution.

Ecological opportunity (EO), defined as “a prospective, lineage-specific characteristic of an environment that contains both niche availability, allowing a population to persist in the environment, and niche discordance, causing diversifying selection within the lineage” (*sensu* Wellborn and Langerhans 2015), has long been evoked as a prerequisite for adaptation. When ancestral species colonize a new environment with abundant, underexploited resources (i.e. free from potential competitors) and/or novel microclimate, it is expected these favorable conditions facilitate an early-burst of lineage diversification and morphological evolution driven by EO (Hughes and Eastwood 2006, Mahler et al. 2010, Yoder et al. 2010, Algar and Mahler 2016, Norman and Christidis 2016). As ecological space becomes saturated, speciation and morphological evolution rates slow down (“niche-filling” hypothesis) (Harmon et al. 2003, Seehausen 2006, Phillimore and Price 2008, López-Fernández et al. 2013). Under this model, speciation rates show a density-dependent pattern, with an increase in species richness mirrored by a corresponding decline in the speciation rate (Rabosky and Lovette 2008, Rabosky 2013). Such a pattern seems to hold true for radiations confined to small geographic areas (e.g. Harmon et al. 2003, Rabosky 2009). However, it is not clear if clades of organisms with high dispersal potential (e.g. those that successfully expand their ranges across extensive continental land masses) exhibit density-dependent diversification rates (see e.g. Liedtke et al. 2016 and references therein).

Geologic and climatic changes can generate novel environments stimulating speciation and act as the impetus for adaptive radiation (Stroud and Losos 2016). However, in this regard, several authors have suggested that evolutionary adaptation to novel climates is relatively uncommon, and that descendant species tend to remain in an environment similar to that of their ancestors (Miller et al. 2013, reviewed in Wiens and Graham 2005). This argument has often been used to define the term “phylogenetic niche conservatism” (PNC) which implies that some processes constrain divergence among closely related species, resulting in closer ecological niches than expected from phylogenetic relationships (Losos 2008, Wiens et al. 2010).

Due to its complex tectonic history Australia provides an ideal scenario for studying how species have responded to new climate opportunities in the recent past (Henderson and Johnson 2016). The Australian climate is characterized by a strong contrast in precipitation between the interior of the continent, in which desert and dry shrubland communities dominate, and the coastal areas in which tropical and temperate forests constitute the more abundant habitat type (Crisp et al. 2004, Hill 2004, Martin 2006). This pattern is the result of the aridification process that caused expansion of the central Australian arid zone ca. 15 millions of years ago (Ma). Australian fossil record shows that, coinciding

with the tectonic isolation of the continent, the aseasonal-wet biome gave way to drier and more seasonal habitats (Byrne et al. 2008). Thus, precipitation is the main environmental driver in this region and, accordingly, previous studies have shown that water availability has a strong influence on observed ecological patterns (e.g. bird richness: Hawkins et al. 2005).

The Australasian robins (Aves: Passeriformes: Petroicidae) constitute an early branching lineage in the passeridan radiation (Barker et al. 2004) and consist of 49 species (Dickinson and Christidis 2014) of small to medium-sized insectivorous birds of relatively homogeneous size and shape. They occur in Australia, New Guinea, Tanimbar (Lesser Sundas), New Zealand and several South Pacific Islands (Boles 2007) and a complex biogeographical history may have involved repeated radiations within and across Australia and New Guinea (Loynes et al. 2009, Christidis et al. 2011). The Petroicidae diverged from other oscine passerines in the Eocene, approximately 45 Ma (Ericson et al. 2014), but recent estimates of this node from fossil-calibrated phylogenomic datasets suggest a much younger age for the oscines and passeridans (Moyle et al. 2016). Nevertheless, it seems to be clear that this family arose when the Australian continent was much wetter than it is today and was largely covered by Gondwanan rainforests, which are nowadays restricted to eastern Australia. The extensive aridification process that started in the Oligocene led to the progressive proliferation of new arid environments, which would have provided substantial EO for lineages capable of colonizing novel and open habitats (Rix et al. 2015). In this regard, some robins exhibit behavioural traits (cooperative breeding, food-hoarding) that have been associated with climatic uncertainty, constituting a ‘bet-hedging’ strategy to cope with short-temporal resource fluctuations under more stressful environmental conditions (Rubenstein and Lovette 2007, Menzies and Burns 2008).

The Petroicidae exhibit little phenotypic diversity compared to other Australasian bird families (e.g. with most species being rotund and stocky). The main variation among species involves differing proportions of body parts (legs, bill) in relation to their life-history (e.g. foraging strategy; Boles 2007). In the genus *Petroica* closely related species are sympatric, which is an uncommon circumstance within Australian (Christidis and Norman 2010) and Palearctic (Drovestki et al. 2013, Voelker et al. 2015) songbirds. As is the case of North American wood warblers (Parulidae), some *Petroica* robins share breeding ranges and exhibit behavioural niche differentiation, in which co-occurring species differ in subtle aspects of their foraging behaviour (Recher et al 2002, Lovette and Hochachka 2006). Because of their limited morphological disparity and high levels of intrageneric sympatry, this family is ideal for the study of evolutionary processes that underlie relationships between morphology and ecology. Phenotypic

similarity among independent lineages can arise as consequence of either PNC or convergent evolution (Cooper et al. 2010, Wiens et al. 2010, Losos 2011). Although evidence is accumulating in favor of both mechanisms, the evolutionary underpinnings of phenotypic similarity in vertebrates are still poorly understood (Muschick et al. 2012, Bravo et al. 2014).

The present study uses morphological and ecological data within a comparative framework to test whether the Petroicidae diversified in an adaptive radiation and, if so, whether it was triggered by the emergence of new adaptive zones (novel climates and/or isolated areas). We performed our study at two scales: i) at a large scale (i.e., by considering the entire Australo-Papuan region) and ii) at local scale (only considering the Australian mainland). When considering the complete distribution, we expect that colonization of new areas (New Guinea and surrounding islands) would be associated with a signature of early rapid diversification and low subclade morphological disparity. Likewise, within Australia, we expect that novel climatic environments would have spurred radiation in this taxonomic group, whose members can be found in a wide range of habitats, from wet rainforests to arid scrublands. Also, we tested whether phenotypic similarity in this family is due to PNC or to convergent evolution.

Methods

Taxonomic considerations

We followed the taxonomic classification proposed by Christidis et al. (2011) according to which the Petroicidae comprises six subfamilies: (i) Eopsaltriinae (comprising *Tregellasia*, *Eopsaltria*, *Gennaeodryas*, *Melanodryas*, *Peneothello*, *Poecilodryas*, *Heteromyias*, *Quoyornis* and *Plesiodryas*; (ii) Pachycephalopsinae comprising *Pachycephalopsis*; (iii) Microecinae comprising *Microeca*, *Kempiella*, *Devioeca*, *Monachella* and *Criptomicroeca*; (iv) Petrocinae comprising *Petroica* and *Eugerygone*; (v) Drymodinae comprising *Drymodes*; and (vi) Amalocichlinae comprising *Amalocichla*. *Amalocichla* and *Drymodes* were placed in the Turdidae by earlier taxonomists because of their largely terrestrial life-style and associated morphology (thrush-like body form) (Schodde and Mason 1999, Boles 2007). Boles (2007) argued that both *Amalocichla* species “possibly do not belong with present family” (p. 439, Boles 2007) based on morphological and behavioral traits, but Norman et al. (2009) showed by means of genetic data that *Amalocichla* is the sister taxon to the remaining members of the Petroicidae. Although the current placement of *Amalocichla* in the Petroicidae has been widely accepted, we opted for excluding these two species from our dataset. The two species of *Amalocichla* (also called New Guinean thrushes)

are ground-dwelling birds with an aberrant morphology in comparison with the remaining robin species, which are rather homogeneous in body proportions (see Fig. S1). The inclusion of these two *outlier* species may blur our analyses aimed to study the evolutionary processes that underlie relationships between ecology and phenotype in a morphologically conserved group. Thus, beyond taxonomic considerations, for the purposes of the present study we considered it appropriate to focus only on species exhibiting a relatively uniform body form and similar habits (the first five subfamilies listed above). *Petroica boodang* and *Heteromyias cinereifrons*, and the recently recognised species *Petroica longipes*, *Melanodryas westralensis* and *Drymodes beccarii* (Dickinson and Christidis 2014) are not included in the most complete molecular phylogeny of extant bird species (Jetz et al. 2012) from which we obtained our set of phylogenetic trees (see below), thus preventing its inclusion in the present study. In total, our study comprised 42 of the 49 currently recognized Petroicidae species (Dickinson and Christidis 2014).

Phylogeny

BirdTree project (Jetz et al. 2012) constituted the first attempt to produce a complete phylogenetic tree of avian taxa based on a robust Bayesian phylogenetic framework, a useful tool for evolutionary biologists aiming at conducting comparative studies. We used the BirdTree online platform (<<http://birdtree.org>>) to generate a subset of 1000 ultrametric, fully resolved Markov chain Monte Carlo (MCMC) trees for the 42 Petroicidae species included in this study using the Hackett et al. (2008) backbone phylogeny (9993 OTUs) (see Rubolini et al. 2015 for more details). From this sample of candidate trees, we obtained the Maximum Clade Credibility (MCC) tree (i.e., the tree with the maximum product of posterior clade probabilities) by using the “MaxCladeCred” function of the R package *phangorn* (Schliep 2011). We repeated the same procedure for the set of 19 species inhabiting the Australian continent and Tasmania.

It should be noted that the Jetz et al.’ phylogeny suffer from several drawbacks as it does not include sequence data for some species, whose position in the tree was randomly simulated.

Yet, the obtained chrono-phylogenetic tree was consistent with the topology provided by Christidis et al. (2011) (which included 37 of the 49 species), with the exception of the placement of *Eopsaltria flaviventris*, which was placed in a new monotypic genus (*Cryptomicroeca*), by Christidis et al. (2011), and *Monachella muelleriana*. At this point, we must also note that dating should be treated with caution as our calibrations are based on age estimates provided by Jetz et al. (2012), however these divergence-time estimates were in line with the Ericson et al (2014)’ time-scale, which is based on seven nuclear genes, five passerines fossils, and an updated interpretation of the New Zealand-Antarctica split.

Morphological and ecological data

We compiled information on body size, bill size, wing length, tarsus length, and tail length (mean values for males of the nominal species) from the literature, mainly from the *Handbook of Australian, New Zealand and Antarctic Birds* (Higgins and Peter 2002) and the *Handbook of New Guinea Birds* (Rand and Gilliard 1967). These morphological traits are strongly associated with behavioural and ecological characteristics like diet or dispersal capacity. Bill size is tightly associated with foraging behaviour and prey size, whereas wing length has a strong influence on dispersal ability (Fitzpatrick 1985). Tarsus length has a strong influence on substrate utilization and perch types, and tail length has been shown to correlate with specific foraging movements, due to its aerodynamic properties in terms of maneuverability and balance (Fitzpatrick 1985, Thomas 1997). From the size-corrected values of this set of morphological traits (i.e. relative wing length, relative tarsus length, relative tail length and relative bill size), we performed a principal component analyses (PCA) in order to obtain an uncorrelated set of variables. The first three axes explained ~87% of the variation (PC1 = 38.9%; PC2 = 26.0%, and PC3 = 22.2%) and were used in subsequent analyses. The highest morphological loadings from PC1 were relative tarsus length and relative tail length (positively loaded: 0.729 and 0.841, respectively), whereas corrected-size differences in wing size accounted for variation explained by PC2 (factor loading: 0.938). The third PC axis (PC3) was dominated by relative bill size (factor loading: -0.796). Body size was log-transformed prior to analyses as recommended by Münkemüller et al. (2015).

The principal foraging technique used by most robins is ground-pouncing (i.e. capturing prey by pouncing from a perch to the ground). However, some species capture their prey in flight, either by catching aerial insects (“hawking”) or by making sally-strikes to glean items from the canopy, whereas the two *Drymodes* species forage almost exclusively on the ground (thrush-like lifestyle). Hence, we divided robin species into three main categories according to their foraging behaviour: i) “ground”, ii) “ground-pouncing” and iii) “sallying”. Information on this variable was compiled from the literature (Higgins and Peter 2002, Boles 2007, Antos et al. 2008) and species accounts published online in specialized websites (e.g. New Zealand Bird Online, <<http://nzbirdsonline.org.nz>>).

We quantified two abiotic axes (mean temperature and mean precipitation at species’ localities) of the climate niche for the 42 species included in this study. We compiled species distribution records of Petrocidae family from the eBird Database (Sullivan et al. 2009; available at <<http://ebird.org>>), Global Biodiversity Information Facility (GBIF, <<http://gbif.org>>) and the Atlas of Living Australia

(<http://ala.org.au>). We deleted non-georeferenced and duplicate records after checking that all them had the same projection and datum in R 3.3.2. We plotted the data for visual inspection of erroneous and poorly georeferenced records. We obtained a total of 406,133 records, with an average of 8,829 data point per species, ranging from 1 (*Petroica archboldi*) to 720 (*Melanodryas cucullata*) occupied grid cells. Subsequently, we extracted mean annual temperature and mean annual precipitation (Bio1 and Bio12, respectively) from WorldClim database (available at <http://worldclim.org/bioclim>) for a 100×100 km resolution grid in which we calculated the mean value of both abiotic variables (mean temperature and mean precipitation) for each grid cell using QGIS (QGIS Development Team 2016). These two variables have been used in similar studies to define the climate niche of birds (Miller et al. 2013). Because of the ability for birds to undertake local movements, they are able to avoid extreme temporal conditions as maximum temperatures in the warmest month or minimum precipitation in the driest month. Therefore, we consider that the two climate niche proxies employed (i.e. mean values) are more appropriate for the aims of our study.

Diversification analyses

We first generated a lineage-through-time (LTT) plot, and calculated the lineage diversification index - (LDI), which indicates the deviation of the empirical LTT pattern from the expectation under a constant-rate pure-birth (PB) process (Harmon et al. 2003). For the observed LTT plot, we calculated the 95% confidence interval from our sample of trees (1000 trees). The LTT plot is expected to form a straight line when the number of lineages is plotted on a logarithmic scale and diversification rates are constant through time (null-model; $\lambda = 0.5$, $\mu = 0$). Under this process, the number of species increases monotonically and exponentially. If diversification rates decrease through time, the observed plot is expected to lie above the straight line, whereas the opposite is expected if diversification rates increase through time (Harmon et al. 2003). We tested for deviations from a PB process by calculating the gamma statistic (γ ; Pybus and Harvey 2000) in the R package *laser* (Rabosky 2006). Negative values of γ indicate that the nodes are closer to the root than expected, implying a deceleration in the rate of diversification; positive values of γ indicate a bias towards the tips of the tree and denote acceleration in the diversification rate towards the present. A deceleration in diversification rate is inferred when $\gamma \leq -1.645$ (one-tailed test at $\alpha=0.05$), which is interpreted as evidence for the existence of an early-burst of diversification (Harmon et al. 2003). As four species are not included in our phylogeny, we used the Monte Carlo constant-rate (MCCR) test to account for incomplete sampling. We performed these

analyses on the MCC tree as well as on our set of 1000 trees randomly sampled from the posterior distribution of the MCMC search in order to account for phylogenetic uncertainty.

Subsequently, we fitted likelihood models for diversification rates onto the MCC tree and our sample of trees using the *laser* package. We examined two constant-rate models (1 and 2) and three variable-rate models (3-5): (1) a pure-birth (PB) model; (2) a birth-death (BD) model; (3) an exponential diversity-dependent (DDX) model; (4) a logistic diversity-dependent (DDL) speciation rate model and (5) a BD variable-rate model with the speciation rate r_1 shifting to r_2 at a time t (yule2rate). The fit of the models was compared using the Akaike information criterion (AIC) (Burnham and Anderson 2002). If EO or niche availability facilitates speciation of Australasian robins, we would expect: (i) a decline in the diversification rates through time; and (ii) a better fit of density-dependent models in comparison with continuous-decline models. However, if EO remains high due to other factors (high extinction rates, periodic changes in climatic conditions), then this expectation would not hold (see e.g. Schweizer et al. 2014).

Morphological disparity analyses

We compared morphological disparity simulated under a Brownian Motion (BM) model with observed disparity among and within subclades relative to total disparity at all time steps across our phylogenetic tree by means of disparity-through-time (DTT) plots. Disparity values near 0 imply that most of the phenotypic variation is partitioned among subclades, whereas values ≥ 1 indicate that subclades have independently evolved to occupy similar places of morphological space. In order to quantify such a difference, we computed the morphological disparity index (MDI) of Harmon et al. (2003), which represents the sum of the areas between the curve describing the morphological disparity of the trait, and the curve describing the disparity under the null hypothesis of BM (1000 simulations). In this way, where lineages have shifted into novel environments early in their evolutionary radiation and descendent species maintain conserved ancestral traits (PNC), we would expect a larger body size variation among subclades (negative MDI values). In contrast, where niche conservatism is weak, we would expect more variation in body size among species within subclades (positive MDI values). We computed DTT analysis for all morphological traits (body size, PC1, PC2 and PC3) using the *geiger* package in R (Harmon et al. 2008).

Testing for PNC versus convergent evolution

We projected morphological traits on a phylomorphospace using the R package *phytools* (Revell 2012) in order to visualize patterns of phenotypic change in the context of the phylogeny and gain insights into the evolutionary history of morphospace occupation (Sidlauskas 2008). Subsequently, in order to characterize and test PNC and convergent ecomorphological evolution, we performed four different and complementary analyses: phylogenetic signal, model comparison analyses, the node-height test, and the Wheatsheaf index (Cooper et al. 2010, Wiens et al. 2010, Arbuckle et al. 2014, Münkemüller et al. 2015). First, we calculated Pagel's lambda (λ) (Pagel 1999) and Blomberg's K statistic (Blomberg et al. 2003) in *phytools* (Revell 2012) to determine the strength of phylogenetic signal in our data. Pagel's lambda (λ) varies between 0 (no phylogenetic signal) to 1 (strong phylogenetic signal). Values of Blomberg's K between 0 and 1 are interpreted the same as λ , whereas values of K higher than 1 indicate that species traits are more similar than expected under BM (i.e. niche retention), which may result from constraints or stabilizing selection.

Secondly, we examined whether the morphological traits evolved under a Brownian Motion (BM) model (whereby traits evolve up the phylogeny via random walk, with no preferred direction; i.e. neutral drift, Felsenstein 1985); an early-burst (EB) model (which predicts a slowdown in the rates of phenotypic evolution over time, Blomberg et al. 2003); or an Ornstein-Uhlenbeck (OU) model (an extension of BM where an additional term describes attraction towards an optimal value, Hansen 1997, Butler and King 2004). Complementarily, when considering all species (i.e. the entire phylogeny), we were able to model a more complex OU model. We assessed the fit of a multi-peak OU model (OUM) with separate random walk variances for “ground species”, “ground-pouncing species” and “sallying species” selective regimes (σ^2) and one global selection parameter (α). To integrate uncertainty in tree topology, branch lengths and the evolutionary history of foraging behaviour, we fit the OUM model to the stochastic character-mapped reconstructions (SIMMAP; Bollback 2006) generated in *phytools* for a sample of 100 trees obtained from the posterior distribution of the Bayesian analysis. Models were run using the R package *OUwie* (Beaulieu and O'Meara 2014) and compared by using the sample size corrected Akaike's Information Criterion (AICc).

Thirdly, we applied a node-height test in order to examine whether patterns of phenotypic divergence fit a niche-filling model, as might be expected during evolutionary radiations (Freckleton and Harvey 2006). We calculated phylogenetic independent contrasts (PICs) for each morphological trait and correlated the absolute value of the PIC to the height of the nodes from which they were generated. A negative correlation between both (PICs ~ node height) is predicted when evolution follows a niche-

filling model, because as niches become filled with increasing species number the differences, among the niches of ancestors and descendants become progressively smaller (Freckleton and Harvey 2006).

Lastly, to quantify the strength of convergence within the two main foraging categories (ground-pouncing and sallying) we implemented the Wheatsheaf index (w) using the R package *windex* (Arbuckle and Minter 2014). This index primarily relies on phylogenetic relatedness and morphological similarity to estimate pull towards an adaptive peak. Higher scores represent a large distance across an adaptive landscape towards the phenotypic optimum as well as close proximity between focal species (i.e. those belonging to a niche for which the traits are hypothesized to converge). For more details about this method, see Arbuckle et al. (2014).

Climatic disparity analyses and ecological correlates of phenotypic evolution

We calculated Pagel's λ and Blomberg's K statistic to test for the existence of PNC in species' environmental niches. We also compared support for different models of evolution (EB, OU, and BM) in a similar way as described above. We then examined associations between morphology and abiotic factors (temperature, precipitation) independent of similarity due to phylogeny by means of Phylogenetic Generalized Least Squares (PGLS) (Grafen 1989). We implemented the PGLS models using the MCC tree to determine whether an independent trait predicts values of other dependent traits (morphological PC axes) while controlling for the non-independence of points due to phylogenetic relationships. The most appropriate value of the scaling-parameter λ (which determines the tempo and mode of trait evolution) was estimated by ML using the *caper* package in R (Orme et al. 2012). We used variation partitioning to distinguish between the phylogenetic (subfamily), ecological (foraging strategy) and spatial (biogeographical region) sources of variance in morphological traits as implemented in the R package *vegan* (Oksanen 2015). Finally, we used the phylogenetic-ANOVA ("phylANOVA" function in *phytools*) to test for differences in morphological traits among foraging categories. We also performed an ML estimation of ancestral character states for this discrete variable to reconstruct its evolutionary history through time using the *ape* library (Paradis et al. 2004) in R.

Results

Patterns of lineage diversification

We found an early-burst of diversification from 40 to 35 Mya followed by a much slower (and relatively constant) diversification rate to the present. The LTT plot followed a straight line from the late Oligocene, after an early period in which the rate of accumulation of new lineages was rapid (Fig. 1; see also Fig. S2). The results of the MCCR analysis suggest that lineage accumulation over time in Petroicidae does not differ from the pattern expected under the null PB model of constant rate diversification ($\gamma_{\text{MCC}} = -1.249$, $p = 0.124$). When the constant-rate test was performed on the set of 1000 chronograms, we obtained a similar γ value (mean $\gamma_{1000} = -1.201$, $p = 0.11$). The one-tailed test yielded a statistically significant result in 11.6% (116/1000) of cases. When restricting our analyses to Australia, we again found no evidence of a decelerating lineage accumulation rate toward present times based on the γ statistic over 1000 trees drawn from the post-burn in set (mean $\gamma_{1000} = -0.772$, $p > 0.05$ in all cases). We obtained a similar result when this analysis was performed on the MCC tree ($\gamma_{\text{MCC}} = -0.370$, $p = 0.71$).

The maximum-likelihood analyses of lineage diversification based on five candidate models identified the yule2rates model as the best descriptor of the estimated pattern of evolutionary diversification of Petroicidae regardless, of the employed method (MCC tree or 1000 trees from the posterior distribution) (see Table 1). In both cases, the difference in AICc (ΔAICc) between this model and the second most supported model was > 2 units (Table 1). These results suggest that a diversity-dependent model (consistent with a niche-filling process) can be ruled out.

Morphological diversification over time

Body size and relative wing size (PC2) disparity primarily accumulated late in the history of the group within subclades (Table 2; Fig. 1). PC3 and PC1 showed a more constant pattern over time (Fig. 1). We obtained positive MDI values for all morphological traits, which indicate a constant or accelerating rate of trait diversification (Table 2). That is, overall disparity is distributed within subclades rather than among them. We obtained very similar results (positive MDI values, i.e. values larger than that expected from a BM model) for the set of Australian species (Table 2).

Convergent evolution

The phylomorphospace reveals that ground-pouncing species, irrespective of the subfamily to which they belong, generally cluster together, suggesting the existence of moderate convergent evolution (Fig. 2). Sallying species showed a wider distribution across the morphospace (Fig. 2). When grouped by subfamily, we found that Petroicinae occupy a smaller region of the morphospace compared with Eopsaltriinae indicating that the former subfamily shows a less disparate morphology (Fig. 2).

Both body size and PC1 showed a strong phylogenetic signal (body size: $\lambda = 0.809$, $p < 0.001$, $K = 0.608$, $p = 0.001$; PC1: $\lambda = 0.962$, $p < 0.001$, $K = 0.631$, $p < 0.001$) whereas both PC2 and PC3 did not show phylogenetic signal (PC2: $\lambda = 0.032$, $p = 0.75$, $K = 0.193$, $p = 0.75$; PC3: $\lambda = 0.377$, $p = 0.14$, $K = 0.355$, $p = 0.04$). Regardless of the analyzed dataset (all species or only those from Australia), we found that PC2 and PC3 followed an OU model (but the OUM also provided a good fit), suggesting that diversification of wing and bill has remained constrained by selection (Table 2). Body size evolution across the entire phylogeny also followed an OU model, but not when restricting our analyses to the Australian species, wherein the BM model received more support. Model fitting for PC1 revealed substantial support for the multi-peak OUM model of evolution (Table 2). It suggests the existence of different adaptive optima among foraging strategies ($\theta_{\text{ground}} = 2.85 \pm 0.49$; $\theta_{\text{ground-pouncing}} = 0.09 \pm 0.14$; $\theta_{\text{sallying}} = -0.56 \pm 0.19$).

We found a significant positive relationship between node height and PICs of PC2 ($b = 0.041$, $R^2 = 0.27$, $F_{1,39} = 15.5$, $p < 0.001$) indicating that the rate of wing evolution has increased rather than decreased through time in Australasian robins. The node-height test yielded positive, but not significant relationships for the remaining variables (body size: $p = 0.85$; PC1: $p = 0.47$; PC3: $p = 0.18$). For the Australian subset, we found significant positive relationships between node height and PICs of PC2 and PC3 (PC2: $b = 0.051$, $R^2 = 0.38$, $F_{1,16} = 11.47$, $p < 0.01$; PC3: $b = 0.069$, $R^2 = 0.20$, $F_{1,16} = 5.15$, $p = 0.037$). Body size and PC1 showed no significant correlation (both p -values > 0.5).

The Wheatsheaf index confirmed that convergence in terms of tail length and tarsus length (PC1) within ground-pouncing species was significantly different from what would be

expected under a random distribution, suggesting a high strength of selection on these traits ($w = 1.19$, $p = 0.021$, 95%CI = 1.13-1.29; see Fig. S3). The Wheatsheaf test did not yield significant results for the other traits examined (PC2 and PC3; Table S2). We did not find evidence for convergent evolution within sallying foragers (Table S2).

Climatic disparity and ecological correlates of phenotypic evolution

We found a significant phylogenetic signal for temperature when analyzing the entire data set

($\lambda = 0.419$, $p < 0.01$) but not when restricting our analyses to the Australian group ($\lambda = 0.184$, $p = 0.58$).

The phylogenetic signal for precipitation was not significant in either case (all species: $\lambda \sim 0$, $p \sim 1$; Australian species: $\lambda \sim 0$, $p \sim 1$). Closely related species exhibit very different profiles in terms of precipitation which is due to the existence of large differences in distribution range within clades (Figs. 3 and 4). As expected according to the obtained measures of phylogenetic signal, the comparisons of model fit based on the AICc indicated that the OU model was the best-fitting model for precipitation (AICc; EB: 711.20, OU: 698.59, BM: 708.88) whereas temperature fitted the BM model (AICc; EB: 454.16, OU: 453.69, BM: 451.83). The OU model was the most supported model in both cases when restricting our analyses to Australia (results not shown).

Robin body size declined as mean temperature increased (PGLS, $F_{1,40} = 9.97$, $p = 0.003$). PC1 showed a significant inverse correlation with mean temperature (PGLS, $F_{1,40} = 5.28$, $p = 0.03$; Fig. S4) and a non-significant trend to decrease with precipitation (PGLS, $F_{1,40} = 2.84$, $p = 0.09$; Fig. 4) suggesting that more arid environments favor ground-based foraging strategies and thus, a morphology of longer legs adapted to this life-style. In fact, we observed a preponderance of sallying and “hawking” as (canopy-based) foraging strategy in species inhabiting wetter environments (New Guinea region) whereas in drier areas (Australian continent) perch-and-pounce hunters (i.e. ground-foraging species) are more frequent (see Fig. 2 and 3; see also Fig. S5). The relationship between PC1 and precipitation become statistically significant when restricting our analyses to Australia (PGLS, $F_{1,17} = 418.6$, $p < 0.001$). As the foraging strategy largely varied among regions, we conducted variation partitioning in order to disentangle the relative influence of these factors on PC1. Variance partitioning showed that variation in PC1 is better explained by foraging mode (adj. R^2 : 15.4%) rather than by geographic region (8.8%) or subfamily (6.3%). The remaining size-corrected morphological variables (PC2 and PC3) did not correlate significantly with temperature or precipitation (all p -values > 0.20).

Results from ancestral reconstruction analyses are displayed in Figure 5. We were able to support the ancestral node of the tree as being of ground-pouncing behaviour (see Fig. 5). PC1 varied significantly among foraging categories (PhylANOVA, $F_{2,39} = 20.94$, $p < 0.001$). There was no significant effect of foraging behaviour on the remaining morphological variables (PC2 and PC3, both p -values > 0.25)

Discussion

Lineage diversification through time

The Petroicidae show signs of an early adaptive radiation (early-burst), but we found no evidence of the slowdown in speciation rate predicted under the ecological opportunity (EO) paradigm. Instead, we found that the tempo of lineage accumulation in the Petroicidae was nearly constant through time after an initial period of increased cladogenesis (Fig. 1). Fritz et al. (2012) also found that island radiations, including New Guinea, with moderate dispersal abilities are prone to show constant diversification rates through time. Colonization of new areas could provide new ecological opportunities for dispersing lineages, allowing the maintenance of a constant rate of diversification (e.g. Burbrink et al. 2012). The observed within clade disparity in terms of distribution range (Fig. 5) suggests that the colonization of new environments from the source area did not occur in one wave. Consequently, it has been proposed that the complex biogeographic history of this group may involve multiple repeated radiations both within, and across Australia and New Guinea (Christidis et al. 2011) which is consistent with the probable existence of intermittent land bridges during the Miocene and late Pliocene (Langford et al. 1995). Dispersal into Australia from the Pacific may have also complicated the picture in the genus *Petroica*, which includes a large number of subspecies formed during the Plio-Pleistocene (see Kearns et al. 2015, 2016). Such a complex biogeographical history may have generated a continuous supply of new opportunities for this group, thereby making it hard to find a signature of density-dependent diversification in this radiation. Under an iterative radiation scenario, lineages evolve to take advantage of novel ecological opportunities (Norman and Christidis 2016) in form of frequent founder events, which may explain why clades tend to exhibit overlapping patterns of ecological and morphological diversity (Losos et al. 1998, Frédérich et al. 2013). Dynamic archipelagos with extreme spatial and temporal heterogeneity constitute a suitable framework for the appearance of iterative radiations. For example, the successive rising of new islands in

Southeast Asia is thought to have produced repeated ecological opportunities for *Crociodura* shrews to diversify, leading to a relatively constant rate of cladogenesis through time (Esselstyn et al. 2009). Thus, although patterns of diversification in Australasian robins are consistent with an adaptive radiation process early in their evolutionary history, several processes (new ecological opportunities linked to orogenic and climatic events) may promote continued diversification. In fact, incipient speciation in some lineages like *P. multicolor* (16 recognized subspecies) could result in a third elevated rate of diversification in the past few millions of years (Kearns et al. 2015).

Restricting our analyses to the Australian continent produced similar results. The yule2rate model was identified as the best model, which supports the existence of an early-burst of diversification typical of an initially explosive radiation. The initial rapid diversification coincides with the first signs of aridification in the Australian continent, which arose at the beginning of the Oligocene (roughly 35 Ma) (Crisp et al. 2004, Byrne et al. 2008). Although we argue that the lack of a diversity-dependent slowdown in speciation may be due to the emergence of new ecological opportunities, an alternative, but non-exclusive explanation, is that the Petroicidae may constitute a young evolutionary radiation that has not existed long enough for the net diversification rate to plateau, as would be expected under a density-dependent model (see also Burbrink et al. 2012). The obtained γ values support this hypothesis because these are expected to be less negative than the critical value of -1.645 when a clade has yet to reach its stability. However, we feel this is unlikely as the Petroicidae are one of basal lineages in the major passerine radiation Passerides (Moyle et al 2016).

Morphological disparity

In an early niche-filling scenario of adaptive radiation, phenotypic disparity is expected to be partitioned among subclades (Harmon et al. 2003). This is due to the taxa whose cladogenesis is concentrated earlier in their history being expected to fill available ecological space and leave little opportunity for subsequent ecological diversification within subclades (Harmon et al. 2003, Burbrink and Pyron 2010). Instead, we found that morphological disparity mainly was partitioned within rather than among subclades during most of the group's history, such that subclades occupied a greater than expected proportion of morphospace. The positive MDI values are noteworthy because they reveal a pattern of convergence in ecomorphological traits (see below). Extensive morphological diversification within clades coupled with divergence in resource use (microhabitat partitioning and elevational segregation) could permit the species to minimize interspecific competition by resource partitioning thus allowing speciation in

sympatry (Wellborn and Langerhans 2015, Stroud and Losos 2016). Our results contrast with those reported by Schweizer et al. (2014) in neotropical parrots (Arini), which exhibited rapid filling of size-dependent ecological space and considerable variation in size between subclades, but no signs of an early-burst of speciation. Both studies support the notion that both morphology and lineage diversification rarely present a congruent pattern. It could be due to the tempo of lineage and phenotypic diversification becoming decoupled as result of the effect of restrictions (evolutionary constraints) or biases (convergent evolution) on the course or outcome of adaptive evolution (Losos 2011, Price et al. 2016).

Convergent evolution

Our findings show that adaptive convergent evolution rather than phylogenetic niche conservatism explains the high level of phenotypic similarity present in the Petroicidae.

Different clades of Petroicidae seem to exhibit moderate adaptive convergent evolution in morphology linked to the foraging mode (i.e. microhabitat components), allowing them to coexist and exploit a larger region of ecomorphospace. Hence, foraging behaviour clearly appears to be a major driving force of morphological evolution in this family. Specifically, we detected moderate convergence in terms of length of tail and legs in those species that take prey from the ground by pouncing. These species survey the ground for prey from a perch, therefore the length of their tail must be adequate to ensure an optimal balance (Thomas 1997). Likewise, tarsus length must be large enough to allow foraging efficiently on the ground but, in turn, not too large to hinder flight capability (Leslier and Winkler 1984). Morphological adaptation to a particular niche (canopy vs. ground) may confer a fitness advantage to individuals through their performance. Our analyses revealed that the optimal size of both tail and tarsus length was different for sallying- and ground-pouncing species. Thus, life-style (i.e. foraging strategy) rather than phylogeny influences overall morphology in the Petroicidae. For example, we found that ground-pouncing species belonging to the subfamily Eopsaltriinae resemble more closely ground-pouncing species of Petroicinae than other members (sallying foragers) of Eopsaltriinae (Fig. 3). The existence of selection towards a ground-pouncing morphotype received additional support from the Wheatsheaf index test, which revealed that the strength of convergence for length of tail and legs between ground-pouncing species belonging to different clades is

substantial. Our results are in agreement with previous studies carried out in other taxonomic groups in which similar ecological associations between habitat use and morphology have been shown to explain convergent patterns of phenotypic evolution (e.g. Losos 1990, Aliabadian et al. 2012, Edwards et al. 2012, Muschick et al. 2012). Regarding the other two morphometric traits, wing length and bill size, we detected the existence of a single phenotypic optimum suggesting that the evolution of these traits is constrained by selective forces that are relatively homogeneous across taxa. This is likely given that all species are primarily insectivorous (Boles 2007) and therefore would share a similar bill morphology. Likewise, with regard to wing size, most of the Petroicidae do not exhibit any major seasonal movements and are generally regarded as being sedentary (Boles 2007). Thus, selective pressures influencing these traits are likely to be rather similar, and as result, stabilizing selection may have favored a single adaptive optimum in both cases. However, it must be interpreted with caution as results yielded no universal best fit model for these two traits; the multi-peak model also received substantial support.

Climatic disparity and ecological correlates of phenotypic evolution

Phyloclimatespace revealed that some closely related species occupy very different bioclimatic environments (Fig. 2). That is, the evolution of climatic profiles has been remarkably heterogeneous within phylogenetic groups of this family due to each of the main three clades containing a mix of taxa endemic to either Australia or New Guinea, along with taxa shared between the two. In line with this, we found a low phylogenetic signal ($\lambda < 0.5$ in both cases) for temperature and no signal for precipitation, irrespective of the employed dataset (all species or only those inhabiting Australia). These results contrast with that reported by Miller et al. (2013) who found increased phylogenetic clustering away from the ancestral environment and a significant phylogenetic signal for precipitation in honeyeaters.

Phylogenetic conservatism of climatic niches has been hypothesized to limit the dispersal of species between wet and mesic-arid environments (Wiens et al. 2013). In the Petroicidae, the lack of niche conservatism is probably associated to the pattern of multiple repeated radiations that seems to have driven the diversification of this family over time (e.g. Kearns et al 2016). Ancestral character reconstructions illustrate that Australasian robins show more pronounced evolution of climatic niches

near the present, particularly from the end of Miocene, 10 Ma (Fig. S6). Arid-adapted species tend to occupy wider geographic ranges indicating that these are species with a wide ecological tolerance (Fig. S7), whereas areas receiving an average annual precipitation of 2000 mm seem to harbor the highest number of species probably due to those constitute remnants of the habitat type from which the Petroicidae originated (see Figs. 4 and S8). The colonization of wetter environments probably coincided with changes in foraging strata; accordingly, ground-pouncing foragers were more abundant in New Guinea (61%) and canopy gleaners were the largest group in Australia (71%). It resulted in morphological differences between foraging categories in terms of tail and tarsus length, with species possessing a larger tail and larger legs associating with lower foraging strata.

Conclusions

We found increased cladogenesis in the early diversification of Petroicidae, as the EO hypothesis predicts for organisms freed from the burden of competition through the invasion of novel/unoccupied habitats. However, we found no statistical support for ecological saturation (diversity-dependence) in the speciation rates of this family, which could be linked to the way in which Petroicidae species radiated into new areas. Repeated radiations and historical processes from the Miocene onwards may have contributed to keep diversification rates roughly constant, preventing the expected diversity-dependent decline (Esselstyn et al. 2009, Derryberry et al. 2011, Liedtke et al. 2016). Our study supports the notion that the lack of any slowdown in speciation rates through time seems to be a general feature of adaptive radiations in complex and dynamic ecosystems (Schweizer et al. 2014). Thus, constant rates of diversification could be a more pervasive pattern than is commonly assumed, even in radiations experiencing an initial explosive radiation.

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FIGURE LEGENDS

Figure 1: Lineage-through-time plot (LTT) (top) and disparity-through-time (DTT) plot for morphological traits (below) in Petroicidae. In the LTT plot, the red line denotes the median number of lineages. The dotted area represents the 95% confidence interval of the number of lineages, whereas the grey line indicates the expected number of lineages under exponential growth with constant speciation and no extinction. The frequency distribution of γ values is shown in the inset. In the DTT plot, the solid lines indicate the mean subclade disparity through time for each trait based on the MCC tree, while the dashed line shows the median expected subclade disparity derived from 10,000 simulations under Brownian motion evolution. In order to illustrate the general appearance (body-form) of a robin species we randomly chose the Canary flyrobin *Devioeca papuana*.

Figure 2: Phylomorphospace projection of the first two principal components (top: PC1 vs. PC2) and the first and third component (middle: PC1 vs. PC3) of Australasian robins. Each dot represents one species (i.e. PC scores from the mean value for each species), colored according to their foraging strategy (red: ground; blue: ground-pouncing; green: sallying). Shape of the tips denotes the clade to which they belong (circles: Eopsaltriinae; squares: Petroicinae; triangles: Microecinae, diamonds: Pachycephalopsinae). PC1 scores are positively correlated with tail length and tarsus length (39% of the total variation). PC2 scores (26%) load positively with wing size, whereas PC3 scores (22%) are negatively associated to bill size. The dots are connected by lines that indicating phylogeny. Illustrations of some species representing extreme points are reproduced with permission from the *Handbook of Birds of the World* (del Hoyo et al. 2007).

Figure 3: Phylomorphospace depicting the niche spaces defined by mean annual temperature and mean annual precipitation. Each dot represents one species (i.e., PC scores from the mean value for each species), colored according to their foraging strategy (red: ground; blue: ground-pouncing; green: sallying). Shape of the tips denotes the clade to which they belong (circles: Eopsaltriinae; squares: Petroicinae; triangles: Microecinae; diamonds: Pachycephalopsinae). The dots are connected by lines that indicating phylogeny.

Figure 4. Reconstructed evolution of (left) mean annual precipitation and (right) PC1 (tail length and tarsus length) in Australasian robins. Below, mean values of these variables for each species are plotted against each other grouping by foraging strategy (red: ground, blue: ground-poucing, and green: sallying).

Figure 5. Ancestral reconstruction of foraging behaviour (“ground”; “ground-pouncing”; “sallying”) under a model of equal rates (ER) in Petroicidae. Pie charts denote the relative likelihood that an ancestor had a particular foraging strategy. Species range-size (measured as the total number of occupied 100×100 grid cells) is also represented to the right of the species names. Colors denote the region to which they belong (Australia and its offshore islands, including Tasmania: orange; West Papua/Indonesia and Papua New Guinea: black; Australo-Papua region: orange-black; New Zealand: pink; New Caledonia: yellow; and Solomon Islands archipelago: blue).

TABLE LEGENDS

Table 1: Results of the diversification models analyses based on the MCC and 1000 chronogram set. The following information is given: log-likelihood ($\ln L$), mean AIC value, difference in mean AIC scores between each model and the overall best-fit model (Δ) and parameters (r , speciation rate for multi-rate models; a , extinction rate; k , logistic; x , exponential; t , transition for rates shifts in multi-rate Yule models) for each model (PB: pure-birth model; BD: birth-death model; DDL: density-dependent logarithmic model; DDX: density-dependent exponential model; yule2rate: Yule with a shift).

	PB	BD	DDL	DDX	yule2rate
a) 1000 trees					
Parameters	$r_1 = 0.056$	$r_1 = 0.056$ $a = 0$	$r_1 = 0.097$ $k = 59.480$	$r_1 = 0.270$ $x = 0.529$	$r_1 = 0.062$ $r_2 = 0.019$ $t = 2.482$
$\ln(L)$	-41.176	-41.176	-38.969	-38.724	-35.792
AICc	84.352	86.352	81.938	81.448	77.585
ΔAIC	6.767	8.767	4.353	3.863	0
b) MCC tree					
Parameters	$r_1 = 0.053$	$r_1 = 0.053$ $a = 0$	$r_1 = 0.076$ $k = 83.998$	$r_1 = 0.199$ $x = 0.445$	$r_1 = 0.060$ $r_2 = 0.017$ $t = 3.904$
$\ln(L)$	-42.830	-42.830	-42.377	-41.216	-35.582
AICc	87.660	89.660	87.428	86.432	77.165
ΔAIC	10.495	12.495	10.263	9.267	0

Table 2: Relative likelihood in form of AICc values, number of parameters (k) and ranking for each of the three models of character evolution (BM, Brownian motion; OU, single-peak Ornstein-Uhlenbeck; OUM, multi-peak Ornstein-Uhlenbeck; EB, early-burst) evaluated for the four morphological traits for a) the entire phylogeny ($n = 42$ spp.) and b) the subset of Australian species ($n = 19$ spp.). Morphological disparity index (MDI) is also provided for each component. σ^2 is the BM rate and α denotes the selection strength ($\alpha = 0$ under the BM model). Results show that divergence in PC1 was consistent with a stabilizing selection model wherein different clades in the phylogeny evolve towards different optima (multiple-optimum OU), whereas both PC2 and PC3 have evolved according to an OU process with a single adaptive peak (note that we lacked enough power to build a multi-peak model for the smaller data set).

Trait	Model	Rank	k	$\ln(L)$	ΔAIC
a) Entire phylogeny					
Body size (MDI = 0.089)	OU = -23.45 ($\alpha = 0.037$)	1	3	15.04	0
	BM = -20.76 ($\sigma^2 = 0.002$)	2	2	12.53	2.69
	EB = -18.43	3	3	12.53	5.02
	OUM = -12.87	4	4	12.27	10.58
PC1 (MDI = 0.003)	OUM = 98.47	1	4	-43.40	0
	BM = 108.17 ($\sigma^2 = 0.039$)	2	2	-51.94	9.7
	OU = 110.47 ($\alpha = 0.041$)	3	3	-51.92	12
	EB = 110.57	4	3	-51.94	12.10
PC2 (MDI = 0.560)	OU = 124.81 ($\alpha = 2.718$)	1	3	-59.09	0
	OUM = 126.67	2	4	-57.50	1.86
	BM = 157.80 ($\sigma^2 = 0.002$)	3	2	-76.75	32.99
	EB = 160.12	4	3	-76.75	35.31
PC3 (MDI = 0.354)	OU = 123.68 ($\alpha = 0.089$)	1	3	-58.53	0
	OUM = 124.07	2	4	-56.20	0.39
	BM = 132.24 ($\sigma^2 = 0.069$)	3	2	-63.97	8.56
	EB = 134.57	4	3	-63.97	10.89
b) Australia					
Body size (MDI = -0.077)	BM = -19.98 ($\sigma^2 = 0.001$)	1	2	12.37	0
	OU = -17.19 ($\alpha = 0.004$)	2	3	12.39	2.79
	EB = -17.14	3	3	12.39	2.84
PC1 (MDI = 0.028)	OU = 54.00 ($\alpha = 0.051$)	1	3	-23.20	0
	BM = 54.85 ($\sigma^2 = 0.045$)	2	2	-25.05	0.85
	EB = 57.70	3	3	-25.05	3.70
PC2 (MDI = 0.553)	OU = 58.93 ($\alpha = 2.718$)	1	3	-30.86	0
	EB = 74.85	2	3	-41.15	15.92
	BM = 77.70 ($\sigma^2 = 0.131$)	3	2	-41.15	18.77
PC3 (MDI = 0.676)	OU = 58.38 ($\alpha = 2.718$)	1	3	-25.39	0
	BM = 66.94 ($\sigma^2 = 0.086$)	2	2	-31.09	8.56
	EB = 69.79	3	3	-31.09	11.41

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Author/s:

Garcia-Navas, V;Rodriguez-Rey, M;Christidis, L

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