

LETTER

Niche conservatism constrains Australian honeyeater assemblages in stressful environments

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Abstract

The hypothesis of phylogenetic niche conservatism proposes that most extant members of a clade remain in ancestral environments because expansion into new ecological space imposes a selectional load on a population. A prediction that follows is that local assemblages contain increasingly phylogenetically clustered subsets of species with increasing difference from the ancestral environment of a clade. We test this in Australian Meliphagidae, a continental radiation of birds that originated in wet, subtropical environments, but subsequently spread to drier environments as Australia became more arid during the late Cenozoic. We find local assemblages are increasingly phylogenetically clustered along a gradient of decreasing precipitation. The pattern is less clear along a temperature gradient. We develop a novel phyloclimatespace to visualise the expansion of some lineages into drier habitats. Although few species extend into arid regions, those that do occupy larger ranges and thus local species richness does not decline predictably with precipitation.

Keywords

Arid zone, Australia, biodiversity gradients, community assembly, Meliphagidae, phyloclimatespace, phylogenetic clustering, phylogenetic niche conservatism, phylogenetic structure, range size.

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INTRODUCTION

Phylogenetic conservatism of the niche, here defined broadly as the climate envelope within which a species occurs, has been invoked as a possible explanation for latitudinal gradients in species richness (Darlington 1959; Latham & Ricklefs 1993; Wiens & Donoghue 2004; Hawkins *et al.* 2005; Jablonski *et al.* 2006). This hypothesis predicts that evolutionary adaptation to novel climates is rare, and descendant species remain within climate space similar to that of their ancestors. Accordingly, as climate differs increasingly from the ancestral state of a particular clade, those species able to persist should belong to decreasing subsets of evolutionary lineages that have acquired adaptations to these different conditions. Thus, one expects to find increasing phylogenetic clustering in community structure along a gradient from ancestral to derived climate space.

Although phylogenetic community structure is often seen to shift along climate gradients, empirical evidence demonstrating the importance of phylogenetic niche conservatism in generating latitudinal diversity gradients has been mixed (Algar *et al.* 2009; Hortal *et al.* 2011; Parra *et al.* 2011). Indeed, phylogenetic niche conservatism, and the resulting predicted phylogenetic clustering away from the environment of initial radiation, need have no clear bearing on regional and local species richness patterns. Lineages that exhibit large shifts in climatic niche space might diversify more rapidly (Olalla-Tárraga *et al.* 2011) or have larger range sizes in novel habitats.

Across many regions of the world, the predominant environmental gradient reflects variation in temperature (Hawkins *et al.* 2005). In Australia, however, where the interior of the continent has

become exceedingly arid compared to coastal areas over the past 20 Mya (Appendix S1), precipitation is the primary environmental driver. The north-south temperature gradient in Australia is less pronounced than present in northern hemisphere continents, owing to infrequency of freezing at higher latitudes in Australia, and in keeping with the trend of lower temperature seasonality in the southern hemisphere (Greenwood & Wing 1995; additional citations Appendix S1). Hawkins *et al.* (2005) demonstrated strong influences of water availability on bird richness patterns in Australia. Moreover, the continent has drifted equatorward coincident with a general cooling of the globe, leading to complex temperature changes over time (Appendix S1). Thus, the overall influence of temperature on the evolution of its biota is arguably less clear than that of the strong, directional trend in precipitation during this time. We focus on precipitation here, but also report temperature results.

The Australian Meliphagidae, or honeyeaters, comprise an abundant and widespread group of 75 bird species. At least one species can be found almost anywhere on the continent, and they are varied ecologically, from largely nectarivorous to almost entirely insectivorous (Higgins *et al.* 2001). The Meliphagidae diverged from other basal oscine passerines in the Eocene, approximately 45 Mya (Jönsson *et al.* 2011), when Australia was breaking away from Antarctica and what remained of Gondwana (Appendix S1). The family thus arose in a generally warm, wet world, on a continent that was much wetter than it is today; Meliphagidae likely originated in the wet forests that were widespread in Australia at that time (Appendix S1). The northward movement of the continent led to extensive aridification, which intensified in the mid- to late-Miocene, 5–15 Mya (Appendix S1). The new arid climate space would have provided

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substantial ecological opportunity for lineages that could adapt to the novel, physiologically stressful, open-vegetation environments. Because Meliphagidae are speciose, form a dominant part of Australian avian assemblages, span a range of climatic and ecological niches, radiated largely *in situ*, and face few dispersal limits within the continent, the family is an ideal taxon for analysis of evolution in climate space. Importantly, a recent molecular phylogeny is available (Nyári & Joseph 2011).

In this paper, we address the role of phylogenetic niche conservatism in the evolutionary radiation of Australian Meliphagidae. We develop a phylogenetic space approach for visualising evolution through climate space, and use it to inform interpretation of patterns of phylogenetic community structure. We predict that evolution into new climate space is infrequent, and that local assemblages are composed of increasingly related species along a gradient of decreasing precipitation as compared to the ancestral climate of Meliphagidae. Because temperature has fluctuated throughout the evolution of this group, and in absolute terms the modern temperature gradient in Australia spans neither a notable portion of the global range in temperatures to which birds are subjected nor the range of temperatures to which the clade is thought to have been subjected over time, we do not expect to see clear results with respect to temperature. Nevertheless, *a priori*, we also predict that Meliphagidae assemblages should be increasingly phylogenetically clustered along a gradient away from the ancestral temperature regime. Despite these predicted relationships, and the linkage in the literature between these ideas and diversity gradients, we would not necessarily expect to see a strong relationship between climate and species richness, as species' range sizes and the diversification rates of particular lineages, among other factors, are also relevant. To address this potential disconnect, we explore species' range sizes, occupancy of suitable climate space, and species richness in local assemblages as functions of climate.

METHODS

Geographical data assembly

We obtained all sight and specimen records of Meliphagidae in Australia from the Global Biodiversity Information Facility (<http://www.gbif.org/>, $n = 37\,462$), eBird (Sullivan *et al.* 2009, $n = 28\,056$), and the Atlas of Living Australia (<http://www.ala.org.au/>, $n = 2\,296\,074$). We filtered the three databases in R (R Development Core Team 2011) to eliminate duplicate or non-georeferenced records, which left $n = 2\,273\,404$.

We generated a list of unique taxon names in this database ($n = 385$), determined their modern taxonomic interpretation (Toon *et al.* 2010; Nyári & Joseph 2011), and cleaned all names accordingly. Some of the taxa do not occur in Australia, and were therefore either incorrectly identified or poorly georeferenced. We discarded these, which left $n = 2\,269\,088$ across 75 species (minimum $n = 130$, *Meliphaga fordiana*; maximum $n = 230\,992$, *Anthochaera carunculata*). We cleaned this initial database by visually inspecting all records on a species-by-species basis to eliminate poorly georeferenced points ($n = 3075$). The resulting point distributions were similar to, but more detailed than, available range maps. The final data set consisted of 2 269 088 unique records, because some of these records are associated with counts of multiple individuals, it contained 3 259 066 individuals total.

Climate data assembly

We described the climate niche of each species and grid cell with WorldClim layers (<http://www.worldclim.org/bioclim>). We divided Australia, including Tasmania, into equal-area grid cells ('local assemblages') of 100×100 km and summarised the mean of each layer for each grid cell. To determine the effect of spatial scale on our analyses (Cavender-Bares *et al.* 2006), we did the same for cells of 50×50 and 200×200 km. After exploring interrelationships among the 19 WorldClim variables, we chose to use mean annual temperature (MAT) and mean annual precipitation (MAP) to describe climate; these variables are uncorrelated in Australia ($r^2 = 0.001$). We used MAT instead of maximum, minimum or diurnal range in temperature for two reasons: (1) these were strongly correlated with MAP (r^2 greater than or equal to 0.21) and (2) many honeyeater species are nomadic, and temperature extremes may not be as biologically relevant if birds migrate or undertake local movements to avoid the harshest conditions (Higgins *et al.* 2001). We used the \log_{10} of MAP because the distribution of precipitation is strongly right-skewed in Australia, and much interesting species turnover occurs among arid and semi-arid grid cells; the distribution of \log_{10} MAP is close to normal (Shapiro–Wilk test, unlogged MAP $W = 0.83$, \log_{10} MAP $W = 0.96$; the value of a normal distribution equals 1).

We defined the centre of each species' climatic niche as the mean MAT and MAP of unique grid cells in which the species occurred.

Community data matrix assembly and manipulation

For each grid cell, we used a split-apply-combine strategy (Wickham 2011) to generate two forms of spatially referenced data matrices (Webb *et al.* 2008), where species' abundances were calculated either as (1) the total number of records per species per grid or (2) the total number of individuals per species per grid. Since results were qualitatively similar for both matrices, and not all records were associated with count data, we report results only on the more conservative number of records.

Not all grid cells were evenly sampled. To account for this, we used rarefaction in the R package *vegan* (Oksanen *et al.* 2012) to restrict our analyses to grid cells for which at least 90% of the species were estimated to have been sampled (Chao 1987), and from which at least as many records existed as there were species in the most species-rich grid cell. Thus, in addition to cuts based on rarefaction, we excluded grid cells with fewer than 32, 33, and 36 unique records at the 50×50 km, 100×100 km and 200×200 km scales respectively. In total, these cuts removed 15, 22 and 43% of the original 50, 100 and 200 km grid cells, respectively, more or less evenly distributed throughout the continent (Appendix S5). Although it made no qualitative difference to results, to ensure all Meliphagidae were represented in the final matrix, we included a grid cell estimated to have had 84% of its species recorded, as otherwise *Lichenostomus hindwoodi* would have been excluded.

Range size was quantified as the number of grid cells in which a species occurred. We calculated each species' proportion of suitable climate space occupied as the number of grid cells occupied divided by the number of grid cells available within the range of climate space bounded by the 5 and 95% quantiles of its distribution in climate space. This was done separately for MAT and MAP. We regressed species richness, range size and the proportion of grid

cells occupied against MAP and MAT, accounting for potential spatial autocorrelation in species richness (Appendix S2).

Defining assemblages over a given scale is necessary in macroecological studies; we justify the scale we chose for this study in the following. First, Australia is relatively homogeneous topographically. Second, because we focus on phylogenetic niche conservatism, and the role it may have in mediating species occurrence patterns, whether the species in a grid cell interact is not critical. Third, in a separate study, ETM travelled extensively and studied the behaviour of all Australian Meliphagidae species. Both these observations and those of others (Higgins *et al.* 2001 and references therein) support the high vagility of these species. During this work, ETM occasionally recorded all birds seen during a single morning of travel by foot. From these lists, we conclude it is likely to observe a considerable portion of a grid cell's constituent Meliphagidae species at a single time and place ($n = 27$ mornings, mean proportion of species = $0.40 \pm \text{SD } 0.16$, range = $0.16\text{--}1$). Finally, results were qualitatively similar across the 16-fold range in scale discussed above.

Assembly of the phylogeny

We used a modified version of a recently published phylogeny (Nyári & Joseph 2011). This tree, created from nuclear (Fib5) and mitochondrial (ND2) genes, was associated with branch lengths, but lacked nine of the 75 Australian species. We added these species manually, in one case (*Manorina*) incorporating molecular information available in GenBank (www.ncbi.nlm.nih.gov/genbank) to infer intrageneric relationships, and in another case (*Melithreptus*) incorporating more recent phylogenetic information (Toon *et al.* 2010). We assumed *Conopophila whitei* to be sister to *C. rufogularis/albogularis*, and *Xanthotis macleayanus* to be sister to *X. flaviventer*. We specified branch lengths from these new taxa to their nearest node by choosing biogeographically similar comparisons and assigning the new taxa the average branch lengths of their relevant comparisons. For instance, *X. flaviventer*, missing from the original phylogeny, was added to the terminal branch of its sister at a depth equal to the mean distance separating *C. rufogularis/albogularis*, *Meliphaga fordiana/albilineata*, *Ramsayornis fasciatus/modestus* and *Phylidonyris nigra/novaeollandiae*. Branch lengths used in phylogenetic analyses (except the ancestral state reconstruction with priors, see below) represent uncorrected genetic distances, though in figures we have scaled the phylogeny using a penalised likelihood approach (Sanderson 2002) to facilitate visualization.

Phylogenetic signal in climate niche

To test our hypothesis of phylogenetic niche conservatism in species' environmental niches, we assumed a drift (Brownian motion) model of evolution (Cooper *et al.* 2010) and calculated Pagel's λ (Pagel 1999) using the R package *phytools* (Revell 2012). This metric has recently been shown to perform well among those describing phylogenetic signal (Münkemüller *et al.* 2012). In practice, λ ranges from zero to one, where $\lambda = 1$ denotes that the trait in question is consistent with an underlying Brownian model of evolution. A P -value for λ is calculated with a likelihood ratio test, where the observed λ is compared to a trait distribution having no phylogenetic signal (Revell 2012). We ran this analysis with both the non-ultrametric and ultrametric (Sanderson 2002) form of the tree. Because results were qualitatively similar, we report only those for the non-ultrametric phylogeny (see also Litsios & Salamin 2012). Results of analyses using

Blomberg's K (Blomberg *et al.* 2003) in the R package *picante* (Kembel *et al.* 2010) yielded similar results, and we do not report those here.

Ancestral state reconstruction

We reconstructed ancestral climate states using two approaches. First, we used restricted maximum likelihood (REML) ancestral state reconstruction (Schluter *et al.* 1997), as implemented in the R package *ape* (Paradis *et al.* 2004) to infer the most likely MAT and $\log_{10}(\text{MAP})$ climate values for the ancestor of modern Meliphagidae, assuming a Brownian model of evolution. This function returned similar results using least squares (Felsenstein 1985), maximum likelihood and REML.

Second, because the first approach does not consider the geologically and palynologically corroborated decrease in precipitation over the course of Meliphagidae evolution (Appendix S1), we used a Bayesian approach (Slater *et al.* 2012), where we fit models of evolution to species' current climate niches after placing priors on the root state. Our priors (mean MAP 1250 ± 275 SD mm yr⁻¹, mean MAT 19 ± 1.5 SD °C) are based on published literature (Appendix S1) and expert opinion (pers. comm. D. R. Greenwood, S. McLoughlin). We reconstructed ancestral precipitation based on the common logarithms of species' MAP values. The two alternatives we considered were Brownian and directional trend models of evolution. The latter is a Brownian model that incorporates an additional parameter, M , describing the expected value of the trait, in this case climatic niche, through time (Slater *et al.* 2012). The R function used, *fitContinuousMCMC*, will be incorporated in future versions of *geiger* (Harmon *et al.* 2008). We ran 10^7 generations of each model, sampling every 100 generations, and discarded the first 10^4 generations as burn-in. Number of generations needed was determined by repeated runs and comparisons of effective sample size with Tracer (<http://beast.bio.ed.ac.uk/Tracer>). We compared the fit of these different models with Akaike's information criterion for MCMC samples, using *fitContinuousMCMC* functions.

Phyloclimatespace

We visualised Meliphagidae exploration of climate space using an approach similar to a phylomorphospace (Sidlauskas 2008). In our case, our axes described the MAT and MAP of the extant taxa or the internal nodes as inferred by REML ancestral state reconstruction. Tips and internal nodes were plotted on this climate space, and the resulting points connected according to the underlying phylogeny. The branches were coloured by assigning all extant taxa a colour state of red. We divided the remaining nodes into four quantiles corresponding to distance from the root in the ultrametric tree, and assigned nodes colours as a function of their respective quantile (where blue was closest to the root). We used the R package *plotrix* (Lemon 2006) to colour branches by blending colours between two nodes according to a walk through RGB colour space.

We further explored a visual trend in the resulting figure by plotting the precipitation midpoint of each evolutionary vector (i.e. a branch from either an internal node to another such node or to an extant taxon) as a function of its angle through climate space.

Phylogenetic community structure

We used *picante* to calculate the mean phylogenetic pairwise distance (MPD) among the members of each grid cell (Webb 2000). This

index is not weighted by abundance. MPD increases with phylogenetic over-dispersion (or evenness, larger phylogenetic distances among the members of an assemblage) and decreases with clustering (shorter phylogenetic distances).

Abundance-weighted MPD is defined as the average phylogenetic distance between two randomly chosen individuals from the assemblage (Webb *et al.* 2008). It incorporates intraspecific phylogenetic distances of zero (assuming each taxon is represented by a single branch). However, our prediction that phylogenetic clustering increases away from ancestral environments concerns interspecific phylogenetic distances. By setting the diagonal element of the relative weight matrix used in the calculation of traditional abundance-weighted MPD equal to zero, we modified it to reflect only interspecific phylogenetic distances. We refer to this as interspecific abundance-weighted MPD, and its appropriate interpretation is the average phylogenetic distance among heterospecific individuals. Alternatively, it can be thought of as the MPD among species, where all distances are weighted by the number of individuals of each co-occurring species. Interspecific abundance-weighted MPD is particularly useful here in that it downweights the influence of vagrants on MPD scores.

We regressed both forms of MPD for each grid cell against the corresponding MAT and MAP value to test the prediction that phylogenetic clustering increases with distance from the ancestral climate. Because spatial autocorrelation is a potentially confounding issue of such analyses, we used spatial eigenvector mapping and variation partitioning to separate the components of spatial and environmental influences on the response variables (Appendix S2).

Though null models have been developed to explore the statistical significance of any given assemblage's phylogenetic structure (Kembel 2009), these standardise an observed score to a given set of assumptions. Our prediction was directly concerned with phylogenetic distances irrespective of species richness; we were interested in the relationship of raw MPD scores to climate. Accordingly, we developed null expectations of MPD under four scenarios (Appendix S3). We used the null expectations to calculate the 97.5 and 2.5% quantiles of the distribution of the metric at each value of species richness observed in the original data set. A given grid cell was considered 'overdispersed' or 'clustered' if the observed MPD score was greater or less than, respectively, the confidence intervals of the simulated scores at the corresponding richness (a two-tailed test).

RESULTS

Phylogenetic signal in environmental niche

Significant phylogenetic signal was observed in species' climate traits. For precipitation, $\lambda = 0.595$ ($P = 0.01$), and for temperature, $\lambda = 0.616$ ($P = 0.0005$). Thus, the observed phylogenetic trait distribution differed significantly from that expected given a star phylogeny (Revell 2012).

Ancestral state reconstruction

Our first method of reconstruction (REML) placed the ancestor of the Meliphagidae in an environment that received 748.6 mm yr⁻¹ precipitation (Fig. 1, 95% CI = 447.5–1252.6, residual log-likelihood = 19.3), with a MAT of 21.1 °C (95% CI = 10.8–31.5 °C, residual log-likelihood = -518.4, subject to the known limitations

of such reconstructions; Cunningham *et al.* 1998; Ané 2008; Slater *et al.* 2012; Appendix S4). This is moist by current Australian standards, and is at the upper range of precipitation that supports temperate woodland vegetation (Appendix S1).

Our second method, a Bayesian approach with a prior placed on the root (Slater *et al.* 2012), found, for MAP, highest support for a trend model of evolution with negative M , the parameter describing the expected value through time (on a log₁₀ scale, mean = -0.21, 95% highest probability density = -0.48–0.05; due to the penalised likelihood smoothing approach, all tip to root distances equal 1). For MAT, a trend model of evolution was also best supported (mean $M = 2.20$, 95% HPD = -3.23–7.97). In neither case was the trend model strongly supported over a stationary Brownian model. For MAP, Akaike's difference score (dAIC) of the Brownian model was 2.45. For MAT, dAIC was 3.53. We therefore calculated the ancestral state at the root as the weighted average of these two models, based on the Akaike weights. We used kernel density estimates (Rosenblatt 1956), and calculated the HPD with the R package *bdrcde*. With this approach, the ancestral Meliphagidae were inferred to come from an environment characterised by mode MAP of 1205 mm yr⁻¹ (95% HPD = 829–1779 mm yr⁻¹) and mode MAT of 19.3 °C (95% HPD = 16.2–22.0 °C). Inferred MAT is

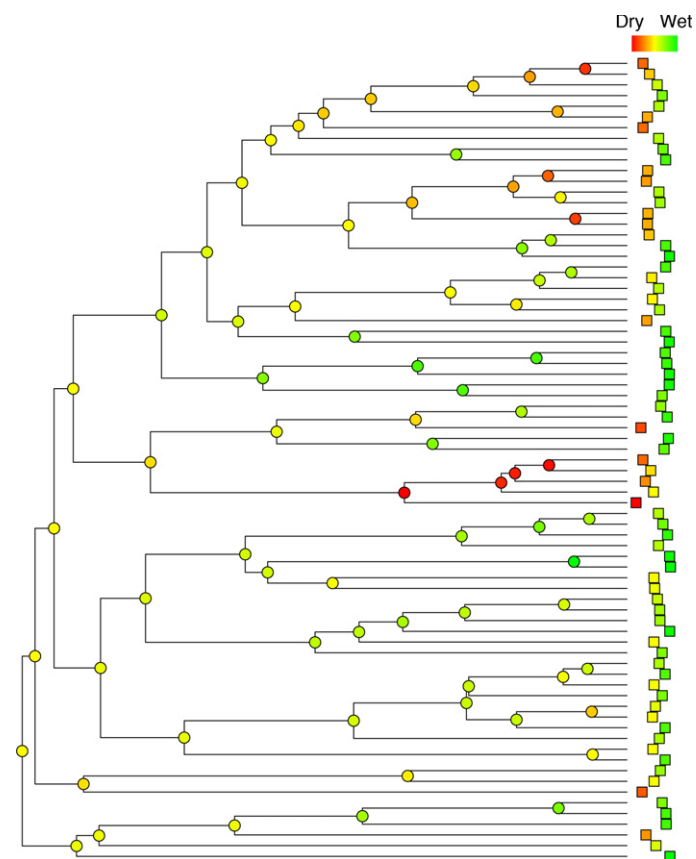


Figure 1 The Australian Meliphagidae phylogeny with mean annual precipitation depicted both across the tips and at the internal nodes (reconstructed with Brownian model of evolution and no trend). These values are represented both by the colour of the circles (internal nodes) and the squares (extant taxa) and, in the case of the extant taxa, by the distance of the squares from the tips of the phylogeny. Distances are proportional to the mean annual precipitation experienced by a given taxon. Colours range from red (taxa inhabiting driest areas) to orange to green (wettest areas). Observed $\lambda = 0.595$ ($P = 0.01$).

therefore approximately in the middle of current Australian temperature range, while the inferred MAP is much wetter than most of modern Australia (dashed lines Fig. 3).

Phyloclimatespace

Few lineages shifted out of the ancestral precipitation regime to invade the arid zone of Australia (Fig. 2a). In contrast, at moderate to high precipitation, evolution across broad ranges of temperature was frequent. Moving progressively from areas of high to low precipitation, we found that the orientation of evolutionary vectors in climate space narrowed significantly, with the lineages evolving towards drier climates remaining within narrow temperature ranges, and that lineages already in arid areas tended to evolve towards even drier climates (Fig. 2b).

Phylogenetic community structure

Local Meliphagidae assemblages were increasingly phylogenetically clustered along a gradient of decreasing precipitation from the inferred ancestral state of the Meliphagidae, whether measured in non-abundance-weighted (Fig. 3a, $r^2 = 0.496$, $P < 0.0001$, $n = 695$) or interspecific abundance-weighted MPD (Fig. 3c, $r^2 = 0.716$, $P < 0.0001$, $n = 695$). Honeyeaters that co-occur in drier areas are more closely related to each other than are species in wetter areas. Results were consistent across a 16-fold range in grid area; linear

regressions of MPD against MAP were significant both at the 50×50 km (non-abundance-weighted $r^2 = 0.474$, $P < 0.0001$, $n = 1851$, interspecific abundance-weighted $r^2 = 0.648$, $P < 0.0001$, $n = 1851$) and the 200×200 km scales (non-abundance-weighted $r^2 = 0.558$, $P < 0.0001$, $n = 214$, interspecific abundance-weighted $r^2 = 0.753$, $P < 0.0001$, $n = 214$; see also Lanier *et al.* 2013). These results remained consistent after accounting for spatial autocorrelation; adjusted r^2 values after removal of spatial nuisance parameters for both forms of MPD at the 100 km scale were 0.496 and 0.716 respectively (Appendix S2).

The phylogenetic structure of Meliphagidae assemblages was poorly related to the temperature gradient in Australia. This was true irrespective of whether measured in non-abundance-weighted (Fig. 3b, $r^2 = 0.006$, $P = 0.039$, $n = 695$) or interspecific abundance-weighted MPD (Fig. 3d, $r^2 = 0.015$, $P = 0.001$, $n = 695$), and held across both changes in scale and after accounting for spatial autocorrelation (Appendix S2).

For non-abundance-weighted MPD, the assemblages of 40 of 695 total grid cells exhibited closer phylogenetic relationships than 97.5% of the richness null expectations at the corresponding species richness. Of these, 33 also exhibited significant phylogenetic clustering according to the frequency null expectations. The assemblages of seven grid cells were significantly overdispersed according to frequency null expectations, one of which was also considered overdispersed according to the richness null (Figs 3a,b and S3.2). For interspecific abundance-weighted MPD, 137 assemblages were con-

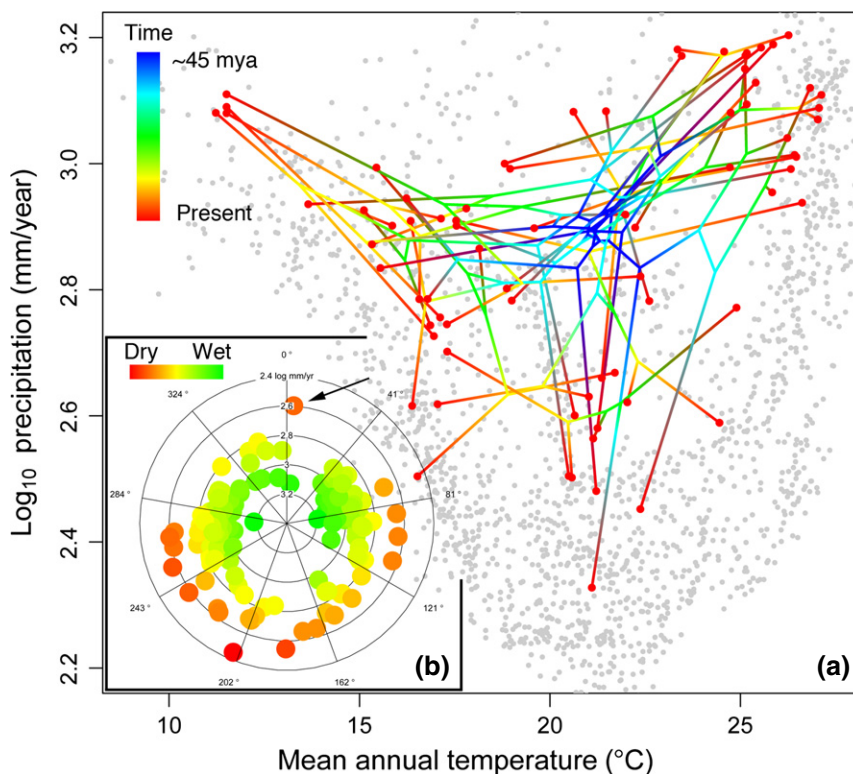


Figure 2 Meliphagidae evolution through climate space. (a) Extant taxa plotted as red points, positioned according to current climate niche. These are connected by the underlying phylogeny, with internal nodes placed with respect to inferred ancestral states (REML method). Colours in this panel represent distance of node from root (i.e. \pm proportional to time). Grey points show modern range of Australian climate. The four species in the top left corner are Tasmanian endemics. (b) Precipitation midpoint of each vector as a function of angle through climate space. Like Fig. 1, colour in this panel represents precipitation, and the axis is inverted, such that lineages that evolved through wet climate space are plotted closest to origin. There is a tendency for lineages already in dry areas (outer ring of polar graph) not to evolve towards wetter climates (i.e. \pm towards 0°). Outlier vector in this respect (small arrow) is discussed in Appendix S7.

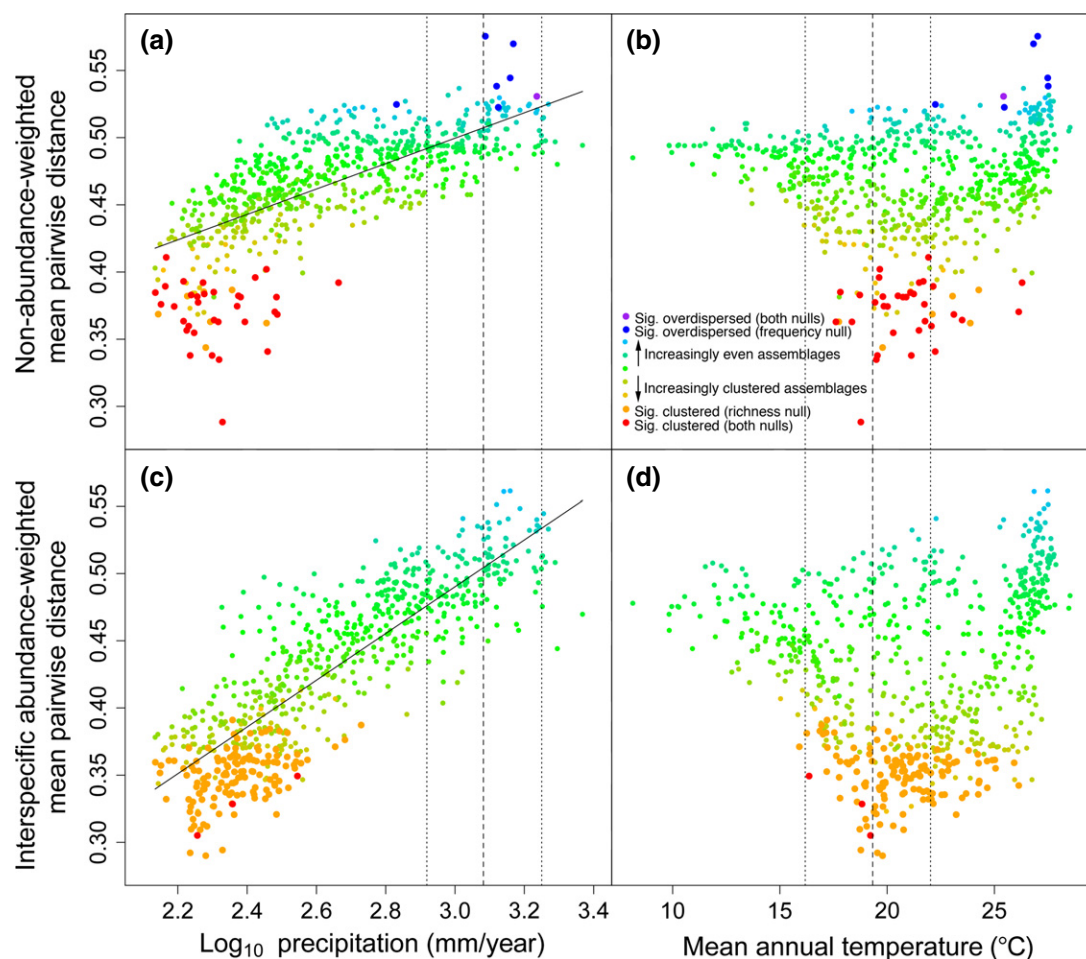


Figure 3 MPD as a function of climate. Points represent 100×100 km grids. Nonsignificant points coloured according to position between upper and lower confidence intervals (Appendix S3). Larger points deviate beyond one or more null model. Dashed lines represent inferred mode and 95% highest probability distribution for ancestral state at root (Bayesian approach with priors). Solid lines are ordinary least squares regressions. (a) Non-abundance-weighted MPD as function of \log_{10} of MAP. Phylogenetic distances among assemblage members increase with precipitation ($r^2 = 0.496$, $P < 0.0001$, $n = 695$). (b) Non-abundance-weighted MPD as function of MAT. Phylogenetic distances are poorly related to temperature ($r^2 = 0.006$, $P = 0.039$, $n = 695$). (c) Interspecific abundance-weighted MPD as function of \log_{10} of MAP ($r^2 = 0.716$, $P < 0.0001$, $n = 695$). (d) Interspecific abundance-weighted MPD as function of MAT ($r^2 = 0.015$, $P = 0.001$, $n = 695$).

sidered significantly clustered according to the richness null, but only 3 of these were significantly clustered using the frequency null (Figs 3c,d and S3.3).

Species richness

Species richness was positively correlated with MAP (Fig. 4a, Appendix S2, $r^2 = 0.245$, $P < 0.0001$, $n = 695$), as predicted by many hypotheses for the latitudinal diversity gradient and, since the ancestral state of the clade was inferred to have been an area of high precipitation, also in accordance with phylogenetic niche conservatism. It was, however, either weakly negatively correlated with MAT (Fig. 4b, $r^2 = 0.094$, $P < 0.0001$, $n = 695$) or, if spatial autocorrelation was accounted for, uncorrelated (Appendix S2). Regardless, neither climate variable explained much variation in species richness.

Range sizes

Range size was inversely related to MAP, such that species in arid areas occupy larger ranges than do species in wetter areas (Fig. 4c,

$r^2 = 0.374$, $P < 0.0001$, $n = 75$). Range size was not related to MAT (Fig. 4d, $r^2 = 0.0004$, $P = 0.872$, $n = 75$). Moreover, species in arid areas occupy a larger proportion of available habitat space than do species in wetter areas (with respect to precipitation, $r^2 = 0.18$, $P = 0.0001$, $n = 75$, Fig. S6A; with respect to temperature $r^2 = 0.258$, $P < 0.0001$, $n = 75$, Fig. S6C). There was a weak but significant negative relationship between per cent of occupied temperature space and species' mean temperature niches ($r^2 = 0.056$, $P = 0.041$, $n = 75$, Fig. S6D).

DISCUSSION

Phylogenetic niche conservatism predicts descendant species remain in environmental space similar to that of their ancestors, with infrequent shifts into new climates (Latham & Ricklefs 1993; Wiens & Donoghue 2004). Accordingly, one expects increased phylogenetic clustering with increasing distance from the ancestral environment of a clade. For the Australian Meliphagidae, a diverse bird group distributed continent-wide, but believed to have originated in an area of high precipitation (Jonsson *et al.* 2011; Appendix S1; this

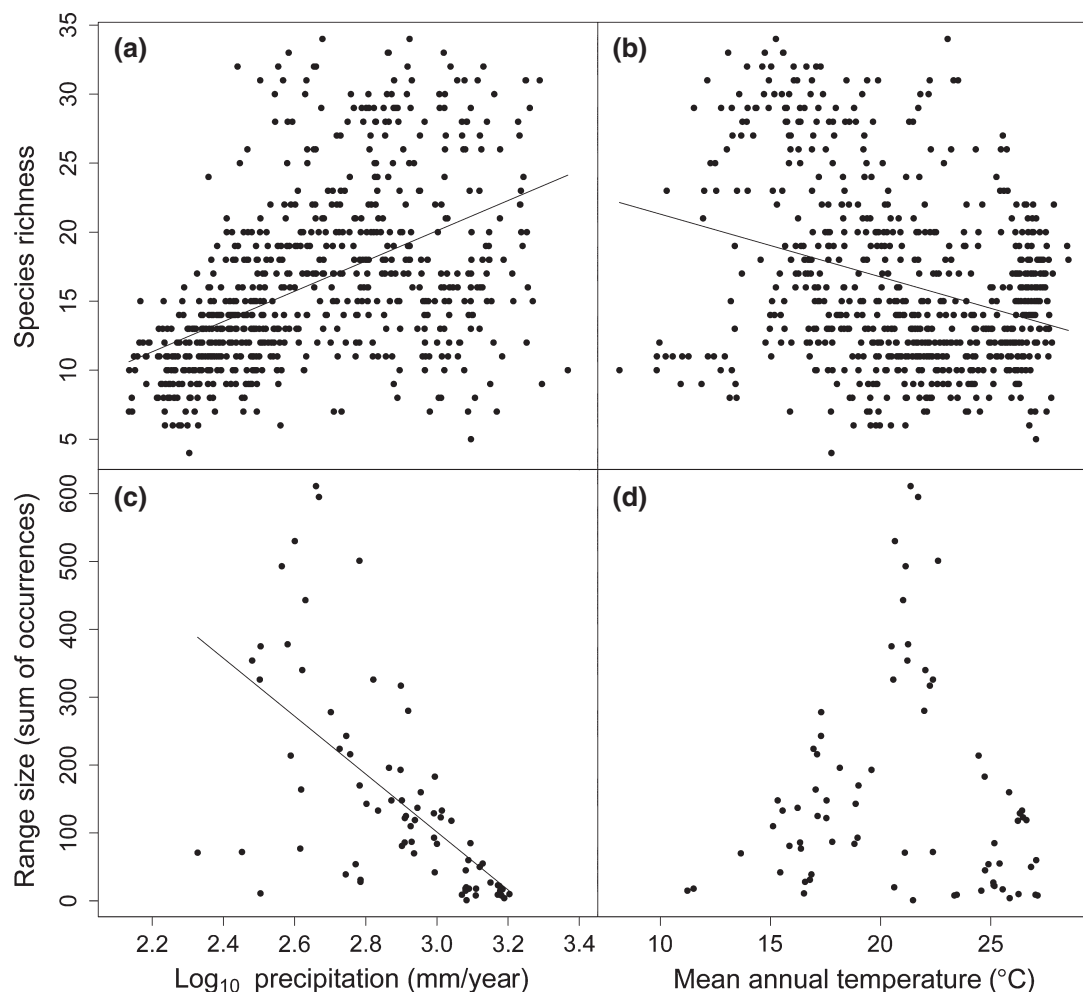


Figure 4 (a) Species richness per 100×100 grid cell as a function of MAP. More species are found in wetter areas, but little variation in species richness is explained by MAP ($r^2 = 0.245$, $P < 0.0001$, $n = 695$). (b) Species richness as function of MAT ($r^2 = 0.094$, $P < 0.0001$, $n = 695$). (c) Species range sizes (sum of grid cells in which a species occurs) as function of MAP ($r^2 = 0.374$, $P < 0.0001$, $n = 75$). Points in this and next panel represent individual species. The three outlying species with small range sizes in arid regions are *Asbybia lovensis*, *Manorina melanotis* and *C. whitei*. The first two are habitat specialists with restricted ranges, while the third occurs widely throughout inland Australia but is rarely observed. (d) Species range sizes as function of MAT ($r^2 = 0.0004$, $P = 0.87$, $n = 75$).

study), we predicted increased phylogenetic clustering in increasingly arid climates. This was strongly supported; variation among assemblages in MAP explains much variation in phylogenetic community structure at a continental scale. We also predicted increased phylogenetic clustering away from the ancestral MAT of the clade. This was not supported, and may be related to fluctuating temperatures in Australia during Meliphagidae evolution, and the small extant temperature gradient in Australia (Appendix S1).

Our phyloclimatespace approach offers additional insight into the Australian Meliphagidae radiation. Shifts into novel climate space were rare; radiation into and within arid climates was particularly infrequent. In general, few lineages are characterised by long branches, which would suggest dramatic niche shifts. Evolution across broad swathes of Australian temperature regimes was evident among lineages inhabiting moist climates. Lineages that had moved into semi-arid habitats were the source of lineages that radiated into even more arid climates and, in keeping with the trend model of evolution being best supported, there appears to be a strong directionality to the evolution of these lineages. This is best seen in the winnowing of the distribution of evolutionary vectors in arid areas

(Fig. 2b). Finally, few lineages evolved towards both hotter and drier habitats, and of these, none terminated in hot deserts. Because water availability decreases with increasing temperature, the adaptive load imposed on a population by a shift towards lower precipitation might be offset by parallel evolution to a lower temperature regime. In future studies, such questions might be better addressed by an analysis that considers species' entire climate envelopes or, ideally, their physiological tolerances (Vieites *et al.* 2009).

Despite strong support found here and by others (Algar *et al.* 2009; Hortal *et al.* 2011; Kooyman *et al.* 2011; Parra *et al.* 2011) for the phylogenetic niche conservatism hypothesis, i.e. increased phylogenetic clustering away from ancestral environments, species richness of Australian Meliphagidae declines only slightly with decreasing precipitation (Fig. 4a). This could have resulted from rapid diversification of the few lineages adapted to arid climates, although this does not seem to be the case (Fig. 2a). Rather, arid-adapted species tend to occupy larger geographical ranges (Fig. 4c) and a greater proportion of available climate space (Fig. S6) than mesic-restricted species.

Radiation into arid climates has been infrequent, but the increased phylogenetic clustering in these areas cannot be attributed to any

single clade. Instead, a few such clades within the Meliphagidae have entirely or partly radiated into dry areas. In total, 34 unique species occur in various combinations in significantly phylogenetically clustered assemblages. Of these, the Australian chats, long considered a separate family (Epthianuridae, Appendix S7), comprise one notable example. The *Ptilotula* clade (Nyári & Joseph 2011) of six species is another. The majority of these significantly clustered sites were located in the arid interior (Appendix S5).

Significantly overdispersed assemblages of species (Figs 3 and S3.2) might be interpreted as evidence for competitive exclusion, but we caution against this for three reasons: (1) we have not directly assessed competition among these species (Mayfield & Levine 2010), (2) seven (or one, depending on the null) significant sites is fewer than we would expect by chance (2.5%) to be significantly overdispersed and (3) the lack of significantly overdispersed sites when MPD is abundance-weighted suggests that vagrant and/or rare species might have influenced the non-abundance-weighted results.

Increased phylogenetic clustering away from an ancestral climate might be expected of a rapidly diversifying taxon with poor dispersal, irrespective of phylogenetic niche conservatism. However, the Australian Meliphagidae are highly mobile, and many species engage in migrations and/or nomadic movements (Higgins *et al.* 2001). Moreover, after correction for spatial autocorrelation, the results remained significant (Appendix S2). The strong pattern observed here seems unlikely to be the product of geographical inertia. Indeed, many Meliphagidae lineages likely underwent range shifts as the continent drifted northwards and the climate changed with it. Accordingly, phylogenetic clustering in arid-zone Meliphagidae represents the effect of an increasingly relevant habitat filter in drier areas. Numerous physiological adaptations for aridity have been documented in the Meliphagidae and other passerines (Williams & Main 1977; Maclean 1996; Tieleman 2005). In Australia, some arid areas are also among the warmest on the continent, which compounds physiological stresses (Maclean 1996; McKechnie & Wolf 2010). An alternative potential basis for this phylogenetic clustering, by no means mutually exclusive, is the lower productivity of arid regions (Boelman *et al.* 2003), combined with phylogenetically conserved differences in abilities to procure sufficient resources in such areas.

The Meliphagidae arose when Australia was much wetter than it is today, and was largely covered by Gondwanan forests (Appendix S1). As the continent drifted northwards, it experienced extensive aridification. A few clades have yielded lineages that invaded novel arid habitats, producing phylogenetic clustering in these areas. Such evolutionary shifts were presumably facilitated by ecophysiological adaptations to the new climates (Maclean 1996) and, perhaps, foraging adaptations associated with different vegetation structure and food resource characteristics of these new areas. Although phylogenetic niche conservatism may bear a complex relationship to patterns of local and regional species richness (Algar *et al.* 2009), it can clearly govern aspects of diversification, species' distributions and community assembly processes along strong gradients of environmental conditions.

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AUTHORSHIP

ETM collected, prepared and analysed the data. AEZ and RER provided input on the design and implementation of the study from start to finish. ETM wrote the manuscript, and all authors contributed substantially to revisions.

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