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ORIGINAL PAPER

The Evolution of Climatic Niches and its Role in Shaping Diversity Patterns in Diprotodontid Marsupials

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Abstract

The interplay between niche conservatism and niche evolution has been suggested to play a key role in shaping the biogeographical history of a given clade. Here, we integrate climatic data associated with the distribution range of 86 diprotodontid species and their phylogenetic relationships in order to examine the evolutionary dynamics of ecological niches of Diprotodontia and explore the link between diversification, niche evolution, and trends in biodiversity over space in this iconic group. Both mean annual temperature (MAT) and annual precipitation (AP) best-fitted punctuated modes of evolution indicate that climatic niche evolution in diprotodonts is speciational. Among-clade variation in rates of climatic niche evolution was correlated with variation in rates of lineage diversification, which reinforces the view that rapid shifts in climatic niches promote speciation. We found that both climatic attributes, AP and MAT, exhibited a pattern according to which species richness progressively declined along a gradient from ancestral to derived climatic conditions and, in turn, it was negatively correlated to niche breadth. However, correlation between niche breadth and niche position was not similar for both climatic traits, as these differ with respect to the relative position of the zone colonized by the most recent common ancestor within its corresponding axis. Diprotodontia diversity decreased while phylogenetic clustering increased, suggesting that niche conservatism associated with ancestral climate probably drives most of variation in species richness in this region. Our study shows that the diversification of diprotodontid marsupials appears to have occurred against a background of moderate phylogenetic niche consevatism, which largely determines the current distribution of this group.

Keywords Australia · Diversification · Evolutionary radiation · Macroevolution · Niche conservatism

Introduction

The study of how climatic niches change over evolutionary time has attracted the interest of many ecologists during the last decade due to two main factors (e.g., Dormann et al. 2010; Peterson et al. 2011). First, this question has become even more important in a time of rapid climate change. Second, the recent development of global scale climate databases and new analytical tools facilitate research to estimate environmental conditions associated with the occurrence of a given species ("Grinnellian" niche sensu Soberón 2007) from GIS-based data. Studies to date on the evolution of climatic niches have primarily focused on two main areas: (i) determining the mode and tempo of niche evolution by fitting different evolutionary models (e.g., Schnitzler et al. 2012; Duran et al. 2013; Jara-Arancio et al. 2013; Duran and Pie 2015; Algar and Mahler 2016; Salariato and Zuloaga 2016), and (ii) assessing phylogenetic signal of the different niche dimensions and testing for the presence of phylogenetic niche conservatism (e.g., Cooper et al. 2010; Dormann et al. 2010; Miller et al. 2013). Regarding the first, assessing the tempo and mode of niche evolution can provide valuable information to unravel the process underlying species diversification and gain insight into the evolutionary story of a given clade (Losos and Ricklefs 2009). On the other hand, analyses of phylogenetic niche conservatism (PNC) are becoming increasingly common because of the importance of

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PNC as a key concept in different areas of ecology (Losos 2008; Wiens et al. 2010; reviewed in Pyron et al. 2015). Niche conservatism, defined as the tendency of closely related species to be more similar to each other in terms of niche than they are to more distant relatives, has been identified as a main cause for the existence of several spatial patterns of diversity (e.g., latitudinal gradients) and community assembly (e.g., Buckley et al. 2010; Stevens 2011). The inability of species to depart from their ancestral niche to colonize different climatic zones may be driven by several microevolutionary mechanisms including ecological competition, pleiotropy, and mainly stabilizing selection for an ecological optimum (Wiens and Graham 2005). PNC limits species' adaptation to novel abiotic conditions, so it is considered to be an important factor promoting parapatric and allopatric speciation but, in turn, may restrict species' range boundaries and make them more vulnerable to extinction (Kozak and Wiens 2006). In the opposite end, colonization of novel climate regimes (i.e., niche divergence) may reduce competition, thereby creating new ecological opportunities and allowing for the proliferation of species (e.g., Evans et al. 2009). In this vein, recent studies on birds (Title and Burns 2015; Cooney et al. 2016; Seeholzer et al. 2017) and amphibians (Kozak and Wiens 2010b; Hutter et al. 2013; but see Pyron and Wiens 2013) have shown that high rates of climatic niche evolution are associated with greater species richness and increased lineage diversification. Speciation rates may vary with climate, as warmer environments has been hypothesized to promote faster evolutionary rates due to shorter generation times, higher mutation rates, and/or faster physiological processes at higher ambient temperatures (Wiens 2011; Gillman and Wright 2014). It could explain, for instance, why some groups appear to show increased diversification in tropical regions (Rolland et al. 2014). Kinetics (i.e., the temperature dependence of evolutionary rates) thus constitutes the core of one of the hypotheses that haven been formulated to explain the existence of the latitudinal diversity gradient (Rohde 1992; reviewed in Brown 2014).

Climatic niche conservatism coupled with niche specialization can have a strong influence on broad-scale biogeographic patterns of distribution arising through restricted dispersal (Futuyma and Moreno 1988; Smith et al. 2012; Wiens et al. 2013). When climatic niches of a given lineage tend to be conserved, its geographical expansion via cladogenesis is slowed and, consequently, species differentially accumulate in space towards the ancestral area and not the geographical periphery (Kozak and Wiens 2010b). Hence, those species able to persist in an environment moderately different from the ancestral one should belong to subsets of evolutionary lineages that have acquired adaptations to these novel climatic conditions. It should lead to a higher degree of phylogenetic clustering in climatically remote areas from the ancestral environment (Miller et al. 2013). In this sense, it is expected that species occurring in more extreme or energy-demanding environments (such as deserts) tend to be more specialized to those environments. Thereby, species whose distribution comprises extreme positions of the gradient on one niche axis (e.g., annual temperature) should exhibit narrower niche breadths relative to species occurring in less extreme environments, more similar to the ancestral environment (Wiens et al. 2013). Although these hypotheses are of great interest and utility in order to better understand the current distribution of lineages, these remain poorly explored. In this regard, there is a paucity of studies exploring the connections between niche divergence, conservatism and distribution patterns across phylogenetic and geographical scales.

The Diprotodontia are the most diverse order of living marsupials, with members occupying a strikingly wide range of niches (from arboreal nectar feeders to grazers) (Flannery 1995; Van Dyck et al. 2013). They occur in Australia, New Guinea, Sulawesi and nearby islands in Indonesia, and their distribution has been hypothesized to be tightly linked to abiotic factors (climate, soil properties) rather than to biotic factors (interspecific competition) (e.g., Ritchie et al. 2009). Some species (such as the common wallaroo *Macropus robustus*) are large, mobile, and/or widely-distributed, whereas some others (e.g., the northern bettong *Bettongia tropica* or the mountain pygmy possum *Burramys parvus*) are small, with limited dispersal and/or a restricted distribution. Thus, diprotodontid marsupials constitute a suitable model to explore the interplay between climatic niche evolution and lineage diversification. Specifically, in this study, we combine phylogenetic and climatic data for extant diprotodonts using phylogenetic comparative methods to address the following questions: (i) how are diprotodontid lineages distributed in climatic space? (ii) are diprotodontid climatic niches conservative or labile? (iii) is there a relationship between climatic niche attributes and species diversification in Diprotodontia? (iv) do areas around the ancestral environment of Diprotodontia harbor a larger number of species than those whose precipitation and/or temperature regimes are away from the ancestral climatic zone? (v) do species occurring in more extreme environments tend to be more specialized to those environments and to be more closely related to each other (phylogenetic clustering) than expected?

Material and Methods

Distribution, Climatic, and Phylogenetic Data

Species distribution data were obtained from species range maps available at the International Union for Conservation of Nature database (IUCN 2017; www.iucnredlist.org). From these range maps, we described the climate niche of each species using bioclimatic WorldClim spatial variables (Hijmans et al. 2005). We divided Australia and New Guinea island into equal area grid-cells of 100 × 100 km and extracted mean annual temperature (MAT, Bio1) and annual precipitation

(AP, Bio12) for each occupied grid in QGIS (www.qgis.org). In agreement with previous studies (Miller et al. 2013; Lv et al. 2016), we chose to use MAT and AP to describe the overall climatic distribution of our species group for the sake of clarity and simplicity. These variables are uncorrelated in Australia/New Guinea ($R^2 = 0.001$).

Phylogenetic relationships among diprotodontid species were obtained from the time-calibrated tree of Mitchell et al. (2014), which constitutes the most comprehensive phylogeny of modern marsupials to date. Mitchell et al.'s phylogeny is based on a supermatrix analysis of 101 mitochondrial genomes and data from 26 nuclear loci and was time-calibrated using a set of 14 fossil-based node age constraints. This tree includes all extant genera of Diprotodontia and 68% (86/125) of modern species (Fig. 1).

Diprotodontid species with phylogenetic data ($n = 86$) were classified into biogeographic regions and geographical zones for further analyses (see 'Phylogenetic species clustering').

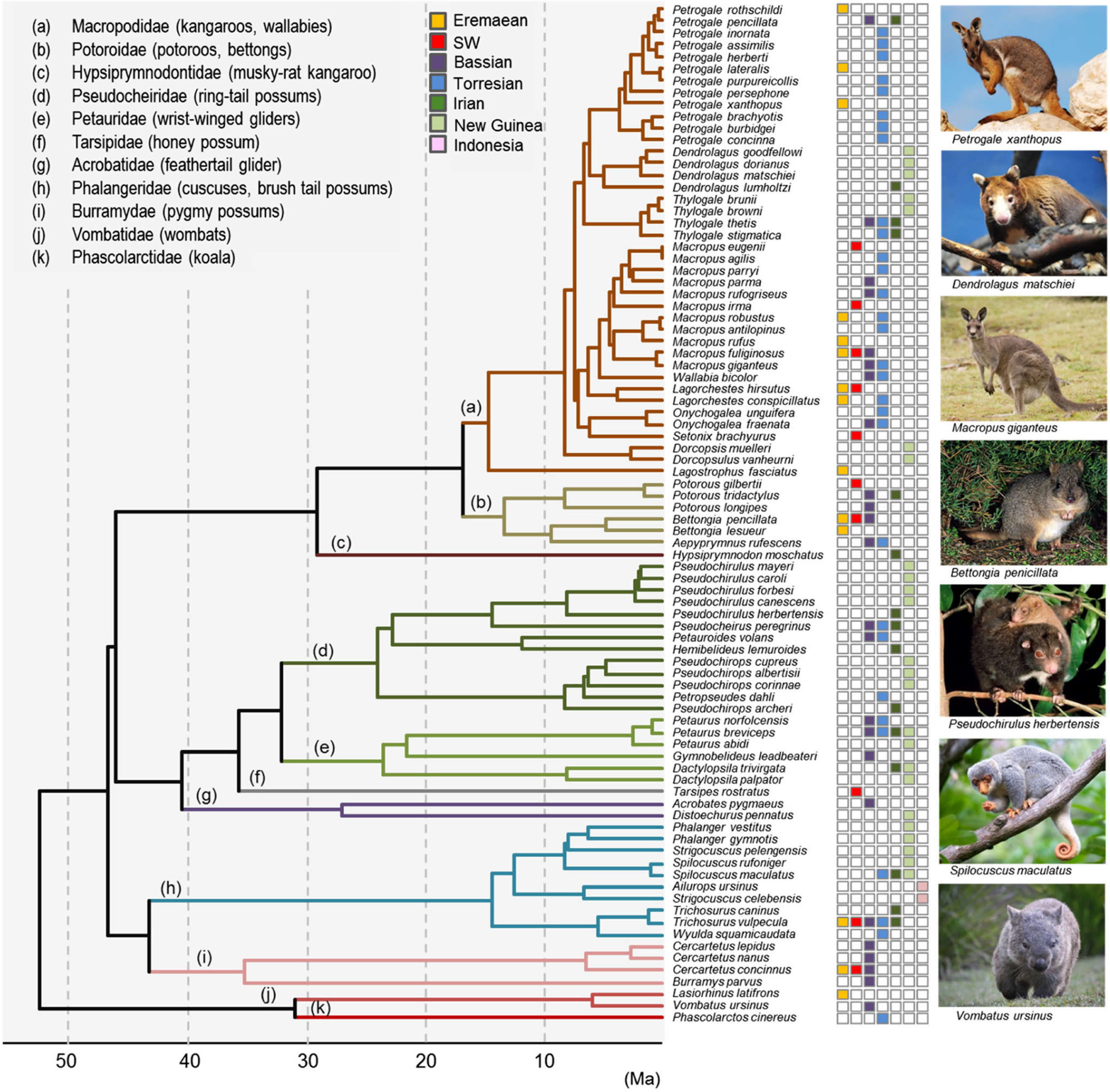


Fig. 1 Time-calibrated phylogeny for the 86 species of diprotodontid marsupials included in this study. Color of the branches indicates the eleven different families. Color coding of the grid located at the right of the tips corresponds to the seven biogeographic regions inhabited by this order (orange: Eremaean; red: Southwest; blue: Bassian; purple: Torresian; dark green: Irian; light green: New Guinea; pink: Indonesia). Photographs: Creative Commons

We identified seven biogeographic regions from the observed geographic ranges: (1) Eremaean region, (2) southwestern temperate, (3) non-tropical east or Bassian region, (4) monsoon or Torresian region, (5) Irian region (remnant rainforests), (6) New Guinea, and (7) Indonesia. Diprotodonts were coded as present (=1) or absent (=0) in each region (species were allowed to occur in multiple regions). We also discerned between "tropical," "mixed," and "temperate" species based on their latitudinal distribution range.

Ancestral State Reconstruction, Phylogenetic Signal, and Mode of Evolution

Based on MAT and AP values for each species, we reconstructed ancestral values at each node of the tree under restricted maximum likelihood (REML) estimation using the R package phytools (Revell 2012). In addition, we visualized Diprotodontia exploration of climate space by using an approach similar to a phylomorphospace ("phyloclimatespace" sensu Miller et al. 2013). We then computed two indices commonly used in phylogenetic comparative analyses to test for departures from Brownian motion (BM) and, thereby, describe the patterns of niche evolution in this group: phylogenetic signal (PS) and kappa (κ). First, we quantified the level of PS for each climatic variable using Blomberg's K (which estimates evolutionary change primarily at nodes) and Pagel's λ (which estimates lineage-specific evolutionary rates along branches) in phytools (Revell 2012). These two indices are complementary as they have different characteristics (Münkemüller et al. 2012). Pagel's lambda varies between 0 (no PS) to 1 (strong PS) and seems to be a reliable index under the assumption of a BM-like evolutionary process. On the other hand, Blomberg's K can only be used to estimate PS unambiguously when applied to traits that do not follow BM. Values of K between 0 and 1 are interpreted the same as λ, whereas values of K higher than 1 indicate that some factor is causing closely related species to be more ecologically similar than would be expected under random walk (i.e., niche retention). Second, we used κ to contrast punctuational vs. gradual niche evolution. If κ is 1, trait evolution is directly proportional to branch length ("gradual" evolution), as expected under BM. If $\kappa = 0$, trait evolution is independent of branch length ("punctuational" evolution sensu Eldredge and Gould 1972).

Although PS has been widely used in the literature to measure PNC (under the assumption that strong PS indicates PNC; e.g., Dormann et al. 2010; Olalla-Tárraga et al. 2017), several authors have pointed out that such a relationship is not straightforward and that PS constitutes an accurate predictor of PNC only under certain circumstances (Losos 2008; Cooper et al. 2010; Crisp and Cook 2012; Münkemüller et al. 2015). According to Münkemüller et al. (2015), PS should be used as a simple preliminary test that needs to be complemented with more complex analyses. Therefore, we tried to determine the type (random or conserved) of evolutionary process underlying climatic niche variation in Diprotodontia by means of model comparisons. Following Boucher et al. (2014), we fitted five alternative models: (1) the BM model in which traits evolve following a random-walk process and niche disparity accumulates roughly linearly through time (Felsenstein 1985); (2) the accelerating-decelerating (ACDC) evolution model, which relaxes the assumption of a constant rate of evolution by allowing trait change to accelerate or decelerate through time across the whole phylogeny (Blomberg et al. 2003); (3) the kappa model, which adds some degree of punctuationism to BM; (4) the Ornstein-Uhlenbeck (OU) model, which assumes niche evolution has been constrained toward a single adaptive optimum (θ) with an attraction strength proportional to the rate of adaptation (α) (Hansen 1997; Butler and King 2004); and (5) OU with strict punctuationism (OUp) where all branches of the tree are set to unity. In the OU model, α determines the influence of past history relative to current niches as well as the phylogenetic correlations between species. The inverse of the rate of adaptation is a measure of phylogenetic inertia (i.e., resistance to adaptation), which can be quantified in the form of phylogenetic half-life ($t_{1/2} = \ln(2)/\alpha$) (Hansen 1997). Phylogenetic half-life measures the time it takes for a species entering into a new niche to evolve halfway toward its new expected optimum (Hansen 1997), thus short $t_{1/2}$ values denote low PNC (Cooper et al. 2010). Support for OU or OUp would indicate the existence of constraints on niche evolution, whereas if kappa or OUp show a good fit to the data, it means that climatic niche evolution is better captured by a model of punctuated evolution (Boucher et al. 2014). Models were ran in geiger (Harmon et al. 2008) and compared by means of the corrected Akaike Information Criterion (AICc). $t_{1/2}$ values were computed using the R package mvMORPH (Clavel et al. 2015).

Diversification and Climatic Niche Evolution

We used BAMM 2.3.0 (Rabosky et al. 2014) to estimate and detect changes in the rates of climatic niche evolution. BAMM uses reversible-jump Markov chain Monte Carlo (rjMCMC) to select between models that vary in the number of evolutionary regimes (see Rabosky et al. 2013 for more details). Priors for the BAMM analysis were set using the R package BAMMtools (Rabosky et al. 2017) (poissonRatePrior = 1.0, lambdaInitPrior = 1.0, lambdaShiftPrior = 0.05). We ran the MCMC for 100,000,000 generations with four MCMC and a sampling frequency of 10,000. We checked for convergence and discarded the first 10% of samples as burn-in. We then confirmed effective sample size (ESS) > 200 using the R package coda (Plummer et al. 2006). For both climatic traits, we identified the 95% credible set of distinct rate-shift configurations (CSS) and computed the phylorate and rate-through-time plots. We then tested the correlation between the estimated diversification rate and climatic traits (AP, MAT) using Structured Rate Permutations on Phylogenies (STRAPP). This method quantifies the association between a species-level trait and the corresponding diversification rate estimates at the tips of the tree. The empirical value of the test statistic is compared to a null distribution that is generated by structured permutations of evolutionary rates across the phylogeny (Rabosky and Huang 2015). Complementarily, we used phylogenetic least-squares regressions (PGLS) to examine the relationship between diversification rates and (a) niche position, (b) clade age, and (c) clade geographic area in order to test whether higher diversification rates are associated with the position of a given genus in the climate space (e.g., warmer and drier environments), an older age ("time-for-speciation" effect; Wiens et al. 2007), and/or a larger geographic area. Diversification rates were computed using a pure-birth maximum likelihood estimator, namely lambda = ln(*N*)/*t*, where *N* is the number of extant species in a given clade and *t* is its age (based on the crown-group age obtained from our calibrated tree).

Lastly, we analyzed the relationships between diversification rates and rates of climatic niche evolution to test whether clades with more species also have higher rates of climatic niche evolution. Diprotodontid species were classified into eleven different clades corresponding to the family to which they belong (Table 1). As clades that occupy larger areas might be expected to accumulate more species and have wider climatic ranges (and thus, higher rates of climatic niche evolution), we also looked for correlations between geographic area (estimated as total number of grid cells occupied by those species comprising a given a clade) and niche evolution rates. Rates of evolution of climatic niches (AP and MAT) for each clade were estimated using the Brownian rate parameter (σ^2). In order to perform PGLS analyses, the 86-species tree was pruned so that each clade was represented by a single species. Single-species clades (Hypsiprymnodontidae, Tarsipidae, and Phascolarctidae) were omitted, so we obtained an 8-clade tree. All PGLS analyses were conducted using the caper package (Orme et al. 2012).

Diversity Gradients and Niche Specialization

We plotted species richness in relation to MAT and AP. Species richness was quantified by dividing the range of MAT and AP values across all localities for all species into 11 bands (of 2 °C each for MAT and of 500 mm each for AP) using a similar approach to that employed in Chejanovski and Wiens (2014). Regional richness for each band (e.g., from 501 to 1000 mm, or from 22.1 to 24 °C) was the number of species with values within that band. We then examined the relationship between species richness and niche breadths (see below) by averaging the niche breadths of all species coexisting in that band. The significance of such a relationship was addressed using ordinary least square (OLS) regressions as the units of analysis were climatic bands instead of species.

In addition, we tested whether species that occur in more extreme climatic conditions on a given axis are more specialized for those conditions. Accordingly, we would expect to find a higher level of specialization (i.e., narrow niches) in species inhabiting the arid region in comparison with species that occur in more mesic environments. Following Chejanovski and Wiens (2014), we calculated temperature and precipitation niche breadths by subtracting minimum from maximum values among localities for both mean annual temperature (MAT) and annual precipitation (AP). We then determined the niche

Table 1 Information on diprotodont families, including the total number of species samples in the phylogeny and those missing from the phylogeny, the clade stem-group age (in millions of years), clade area estimated as sum of occurrences (n° of 100 × 100 km grid cells), diversification rates, precipitation (AP) and temperature (MAT) midpoints along its respective evolutionary rates, and niche breadths for both climatic traits

Family	Number of taxa (missing)	Age (Ma)	Clade area (*)	Divers. rate	Mean AP (mm year^{-1})	AP rate	Mean MAT (°C)	MAT rate	AP breadth	MAT breadth
Acrobatidae	2 (0)	27.16	283	0.301	1953.88	4.172	21.40	0.247	3403.85	14.37
Burramyidae	4 (1)	35.40	233	0.602	859.76	0.706	13.58	0.349	1203.85	6.82
Hypsiprymnodontidae	1 (0)	29.36	8	0	1689.65	–	22.90	–	2406.47	3.55
Macropodidae	40 (15)	14.71	3769	1.602	1140.66	18.931	22.02	17.564	1283.98	7.46
Petauridae	6 (5)	23.74	802	0.778	2018.39	13.039	21.20	2.179	2632.71	10.35
Phalangeridae	10 (18)	14.40	913	1	2092.55	3.225	23.75	0.925	2240.90	9.28
Phascolarctidae	1 (0)	31.10	198	0	746.56	–	18.50	–	1529.43	16.52
Potoroidae	6 (5)	13.47	169	0.778	730.79	1.389	16.82	0.822	640.16	7.20
Pseudocheiridae	13 (4)	24.14	617	1.114	2290.74	8.936	22.32	0.512	2296.82	8.32
Tarsipedidae	1 (0)	35.93	50	0	510.70	–	17.16	–	863.73	5.40
Vombatidae	2 (1)	6.00	114	0.301	614.96	1.364	15.45	0.379	1124.95	7.02

(*) Range size (in km^2) and sum of occurrences were strongly correlated, so for the sake of brevity we only report the latter as index of clade area position of each species for both climatic axes. Niche position for each variable was characterized from the mean value (midpoint) across all the localities for each species. PGLS analysis was then used to examine the relationship between climatic niche breadth and niche position.

Phylogenetic Species Clustering

Phylogenetic attraction or clustering can indicate that closely related taxa share traits important for their persistence in a particular environment, which is commonly interpreted as evidence for niche conservatism (Webb et al. 2002; Cardillo 2011; Crisp and Cook 2012). Here, we examined phylogenetic clustering in MAT and AP zones (and also among the species assemblages of each biogeographic region) using the mean phylogenetic pairwise distance (MPD) and the mean nearest taxon distance (MNTD) as implemented in the R package picante (Kembel et al. 2010). MPD and MNTD increase with phylogenetic over-dispersion (i.e., larger phylogenetic distances among species of an assemblage) and decrease with under-dispersion ('clustering'; i.e., shorter phylogenetic distances). MPD is a measure of the average branch length distance among all species pairs in a given community and thus, it is thought to be more sensitive to phylogeny-wide patterns of phylogenetic under- and over-dispersion. Meanwhile, MNTD is the branch length distance between each species and its closest relative in a community and therefore, this measure is more sensitive to patterns of under- and over-dispersion closer to the tips of the tree (late radiations). Standardized effect size (z-value) was computed for both metrics by shuffling tip labels 999 times to generate a null distribution for each metric and comparing the observed value to the simulated ones (Webb et al. 2002; Kembel 2009).

The datasets used in the present study are available through the 'labarchives' repository (https://mynotebook.labarchives.com; https://doi.org/10.6070/H4P55M2M).

Results

Ancestral State Reconstruction, Phylogenetic Signal, and Mode of Evolution

We obtained a significant λ value for both climatic traits ($\lambda_{MAT} = 0.67$, $p < 0.001$; $\lambda_{AP} = 0.95$, $p < 0.001$) but Blomberg's K test yielded a significant result only for AP ($K_{MAT} = 0.06$, $p = 0.34$; $K_{AP} = 0.18$, $p = 0.01$). The obtained κ values were low ($\kappa = 0.01$) or moderately low ($\kappa = 0.26$) for MAT and AP, respectively. Accordingly, the best-fit model of evolution for AP was the kappa model, whereas for MAT the OUp model performed the best (Table 2). This indicates that climatic niche evolution in driprotodonts is speciational (= punctuated equilibria) to a lesser (AP) or greater (MAT) extent. Ancestral state reconstructions placed the ancestor of the Diprotodontia in a mesic environment characterized by mode AP of 1285 mm year^{-1} and mode MAT of 18.8 °C (Fig. 2). Within-clade variability in temperature niches was greater in comparison with that of precipitation niches, which varied much less among species belonging to the same family (Fig. 2). The time needed to move halfway (phylogenetic half-life) from the ancestral state to the inferred optimum ($\theta_{MAT} = 21.2$ °C and $\theta_{AP} = 1533.3$ mm year^{-1}) was greater for AP, which seems to be more conserved along the phylogeny than MAT ($t_{1/2}$, MAT = 0.013 Ma; AP = 6.89 Ma) (Fig. 2).

Table 2 Results of model selection for niche axes (mean annual temperature, MAT; annual precipitation, AP) in Diprotodontia

Model	MAT		AP	
	AICc	*w*AICc (rank)	AICc	*w*AICc (rank)
Brownian Motion	605.7	0 (5)	1424.7	0 (5)
ACDC	587.0	0 (4)	1411.5	0 (4)
OU	491.5	0.01 (3)	1398.2	0.01 (3)
Kappa	488.4	0.03 (2)	**1382.9**	0.93 (1)
OUp	**477.0**	0.95 (1)	1388.1	0.06 (2)

The Corrected Akaike Information Criterion, AICc, and weights, *w*AIC, with ranking position for each model (in brackets) are provided. The best fitting model for each climatic factor is shown in bold

Phyloclimatespace

Phyloclimatespace showed that the precipitation niche of most Australian species remained similar to that of the most common recent ancestor (MRCA) (Fig. 3). Only four lineages (Macropodidae, Potoroidae, Burramyidae, and Vombatidae) comprising about 14% (12/86) of the species included in this study inhabit an area with an AP <500 mm year^{-1}. In contrast, temperature niches broadly varied along branches at moderate precipitation values (i.e., nearly below the precipitation niche of the MRCA) (Fig. 3). New Guinean species remained within narrow temperature ranges, which span the current climatic space, but also within narrow precipitation ranges despite of this variable largely varies across this region (from <1000 to >3000 mm). As expected, tropical species showed narrow niche widths for MAT and wide niche widths for AP, whereas temperate species had wider niche widths for MAT and narrower niche widths for AP (Fig. 3).

Diversification and Climatic Niche Evolution

BAMM detected a significant increase in rates of niche evolution of both MAT and AP on the crown node of Macropodidae (see Fig. 2). In both cases, the posterior probability (PP) for a model with one shift was very similar ($PP_{MAT} = 0.85$, $PP_{AP} = 0.84$) while the PP for a model with a

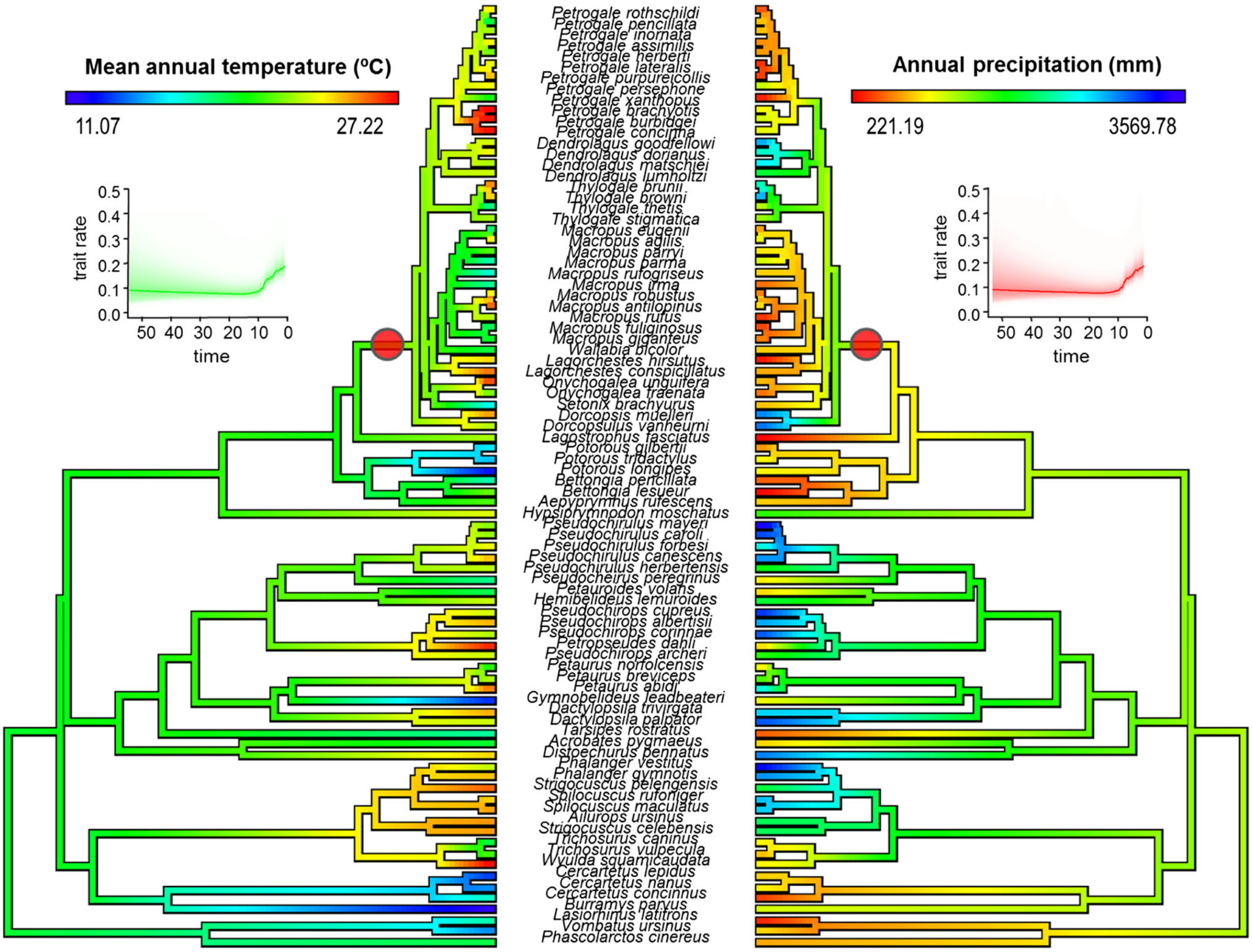


Fig. 2 Ancestral state reconstructions of mean annual temperature (MAT) and annual precipitation (AP) for Diprotodontia. The red dots represent diversification rate shift detected by BAMM analysis. The insets show how traits vary through time

single evolutionary regime was low (PP = 0.04 in both cases). We detected a shift in the diversification rate (PP = 0.85) in the same location on the tree (around 20 Ma) (Fig. S1 in ESM). Two additional configurations emerged after we identified a 95% credible set of distinct shift configurations: i) a shift located at the age in which the family Macropodidae diverged into two main clades (I: kangaroos, wallabies, wallaroos, and dorcopsises, and II: pademelons, tree-kangaroos, and rock-wallabies) (PP = 0.085), and ii) no shifts (PP = 0.041). The STRAPP results indicated no significant relationship between diversification and MAT or AP ($p > 0.5$ in both cases). Yet, we observed a marginally significant relationship between average MAT and diversification rates (PGLS; $t = 2.17$, $p = 0.07$) using PGLS regression, indicating that clades associated to warmer environments exhibit faster diversification rates. There was no significant correlation between diversification rates and AP values (PGLS; $t = 1.00$, $p = 0.35$).

In both cases (for both AP and MAT), rates of climatic niche evolution were positively related to diversification rates (PGLS; AP: $t = 2.40$, $p = 0.053$, $R^2 = 0.40$; MAT: $t = 2.72$, $p = 0.034$, $R^2 = 0.55$) (Fig. 4). That is, rapid species diversification is associated with accelerated climatic niche evolution. Among-clade variation in rates of diversification and climatic niche evolution were positively correlated with clade area (PGLS; divers. Rate vs. clade area: $t = 2.92$, $p = 0.026$, $R^2 = 0.51$; AP niche rate vs. clade area: $t = 18.05$, $p = 0.007$, $R^2 = 0.67$; MAT niche rate vs. clade area: $t = 3.94$, $p < 0.001$, $R^2 = 0.98$). On the contrary, we did not find evidence for a time-for-speciation effect as clade age and clade diversity were uncorrelated (PGLS; $t = -0.56$, $p = 0.59$). Hence, the two most speciose clades (Macropodidae and Phalangeridae) differ greatly in age and clades of similar age (e.g., Petauridae and Potoroidae) differ greatly in richness (Table 1). Clade age was neither correlated with temperature nor precipitation niche positions (both p-values >0.5). No relationship was found between the mean climatic niche breadth of the species within a clade and the clade's rate of climatic niche evolution (PGLS; AP: $t = 0.84$, $p = 0.43$; MAT: $t = -0.17$, $p = 0.87$).

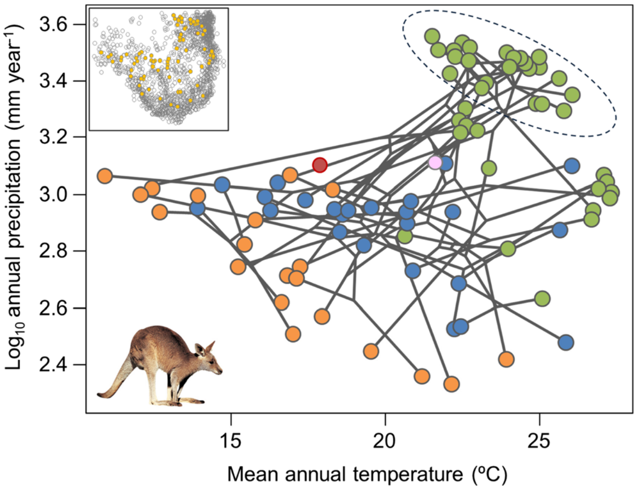


Fig. 3 Phylomorphospace of diprotodont marsupials. Dots (colored in green for "tropical" species, blue for "mixed" species, and orange for "temperate" species) represent extant species in mean annual temperature (MAT, *x*-axis) and annual precipitation (AP, *y*-axis) space. The dots are connected by lines indicating phylogeny. The red dot indicates the location in the climatic space of the MRCA whereas the pink dot indicates the inferred adaptive optima. The dotted line comprises species distributed in New Guinea and adjacent areas. The inset represents how all records of Diprotodontia species distribute over the available climatic space. We represent log-transformed values of AP instead of raw data for illustrative purposes

Diversity Gradients and Niche Specialization

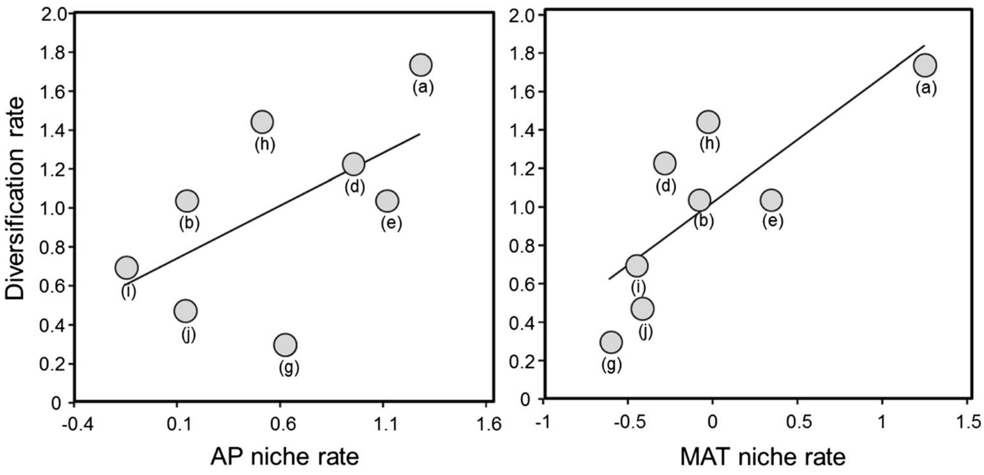
Species richness is highest in regions with AP values around 1000 mm year^{-1} and progressively decreases as environments became wetter (Fig. 5a). The zone from which the MRCA comes (1001–1500 mm year^{-1}) was the precipitation bin that contained the second highest number of species (Fig. 5a). Regarding the temperature niche, species richness correlates quadratically with MAT reaching the biodiversity maximum around 22 °C (Fig. 5b). The zone spanning from 18.1 to 20 °C (i.e., those encompassing the inferred state of the MRCA) was the third one in terms of species richness (Fig. 5b).

Temperature and precipitation niche breadths were significantly more narrow for those species from climatic zones with high species richness (see Fig. 6a, b). Species occurring in both the warmer and cooler environments (i.e., those located at both ends of the temperature continuum) tend to have narrower temperature niche breadths than those inhabiting temperate environments (i.e., intermediate MAT values) (Fig. 6c; PGLS with a quadratic effect:, $F_{1,84} = 10.62$, $p = 0.002$, $R^2 = 0.10$), whereas species at the drier end of the precipitation axis (i.e., lower AP) have more narrow niche widths (Fig. 6d; PGLS: $F_{1,84} = 112.20$, $p < 0.001$, $R^2 = 0.57$).

Phylogenetic Species Clustering

Species that inhabit the more arid areas (precipitation zones <1000 mm) are more closely related to each other than expected under the null model for MPD, while a significant or marginally significant pattern of phylogenetic community structure was detected in most regions above 2500 mm year^{-1} with MNTD (Fig. 5a; Table S1 in Electronic Supplementary Material, ESM). MPD values for the zone with the highest temperatures (28.1–30 °C) differed significantly from the null model suggesting "basal" phylogenetic clustering, whereas MNTD values were significantly negatives for the temperature zones spanning from 24.1 to 28 °C (Fig. 5b; Table S2 in ESM). We found a significant pattern of phylogenetic clustering irrespective of the employed method (MPD or MNTD) for the assemblage of species inhabiting the Bassian (monsoon) region (Table S2 in ESM). MPD values for the Eremaean (arid) region were significantly negatives but the MPD values did not differ significantly from zero. On the contrary, New Guinea exhibited a pattern of under-dispersion when this analysis was based on the mean nearest taxon distance (MNTD), but not when using the mean pairwise distance (MPD) as metric (Table S3 in ESM).

Fig. 4 Relationship between diversification rates and rates of climatic niche (MAT and AP) among the eight main clades of diprotodont marsupials. All variables were log-transformed. Significance of the relationship was analyzed using phylogenetic least-square regressions. Letters indicate clade identity according to the legend shown in Fig. 1



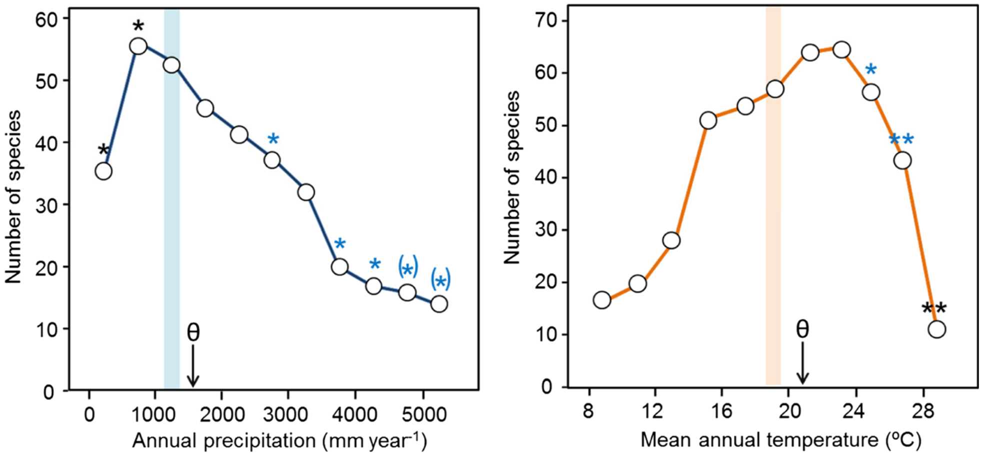


Fig. 5 Patterns of species diversity over climatic zones for diprotodont marsupials. Asterisks denote the existence of significant (** $p < 0.01$, * $p < 0.05$) or marginally significant (asterisks in brackets) phylogenetic clustering on basis on mean pairwise distance (MPD; black symbols) and mean nearest taxon distance (MNTD; blue symbols). Vertical stripes denote the location of the zone colonized by the MRCA and arrows indicate the position of the adaptive optima (θ)

Discussion

Phylogenetic Signal and Mode of Evolution

Niche evolution in Diprotodontia was inconsistent with a pattern in which traits evolve as a random walk process and niche disparity accumulates approximately linearly through time. Both climatic traits (MAT and AP) best-fitted punctuated modes of evolution (OUp and kappa, respectively) suggesting niche stasis along branches of the tree and fast niche evolution during cladogenesis events (Boucher et al. 2014). Brownian motion (BM) was not the underlying process, so we cannot

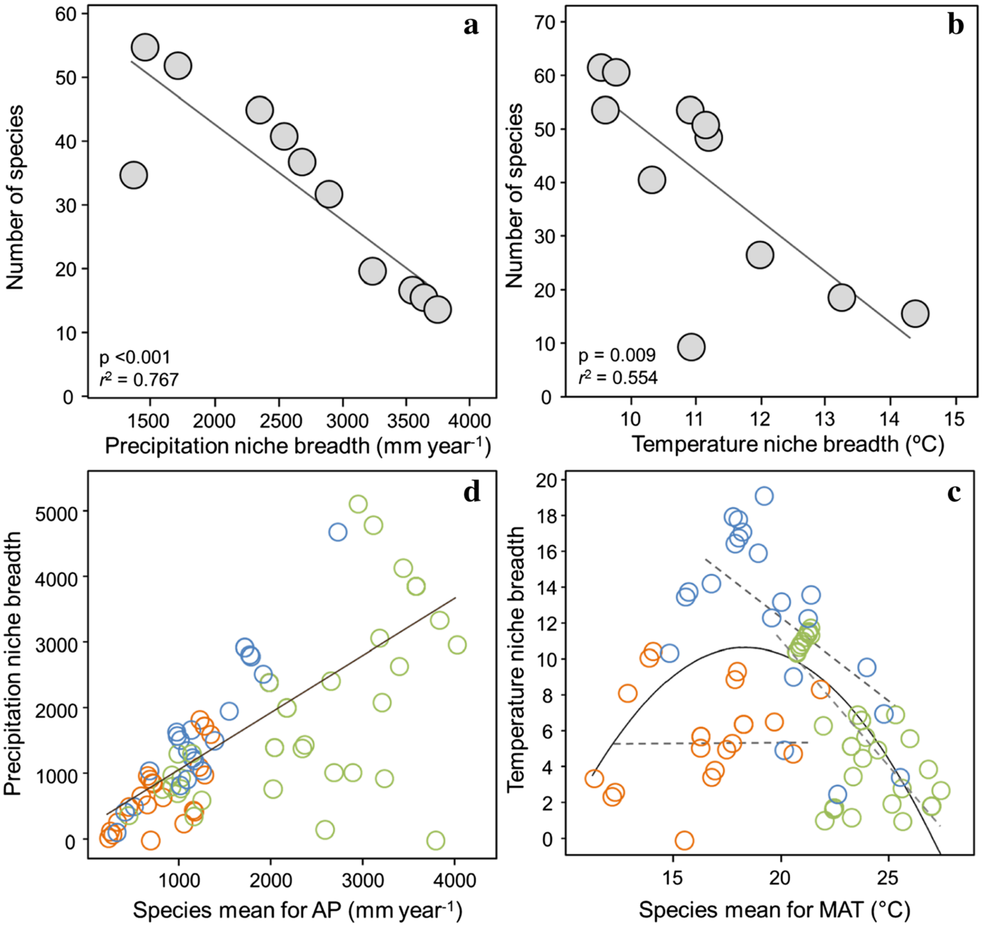


Fig. 6 Relationship between mean niche breadth and species richness per climatic band for both (**a**) precipitation and (**b**) temperature, and relationships between niche breadths and niche positions (**c**, **d**) for 86 species of diprotodonts. Niche breadths and positions were regressed using phylogenetic generalized least squares (PGLS), but the raw data are represented here for illustrative purposes differentiating between "temperate" (orange dots), "mixed" (blue dots), and "tropical" (green dots) species

interpret unambiguously the obtained values of λ to support or refute the existence of phylogenetic niche conservatism (PNC) (Revell et al. 2008; Münkemüller et al. 2012). The other index employed to measure phylogenetic signal - Blomberg's *K*- yielded low values, which implies that although there is some relationship between the degree of phylogenetic relatedness and climatic similarity, it was not significantly greater than expected under neutral drift. This result is not striking as it has been shown that when niches do not evolve according to a BM-like process, misleading patterns of PS can arise. For instance, when niches evolve under a single-peak OU model, strong constraints result in low phylogenetic signal (Ackerly 2009; Münkemüller et al. 2015). It suggests that climatic traits may fail to track phylogeny because they evolve too slowly, a pattern (phylogenetic inertia) that has been hypothesized to underlie PNC in the context of models of bounded evolution (Labra et al. 2009; Cooper et al. 2010). However, here our low phylogenetic half-values (<10 Ma in both cases) indicate that species are evolving quickly, residual phylogenetic correlations are weak and there is very little influence of the past on trait values. Thus, it is likely that species do not resemble each other more than expected under neutral drift ($K > 1$) mainly due to climatic traits do not evolve gradually. However, evidence for punctuated evolution of climatic niches does not necessarily imply rapid evolution of physiological tolerances (Boucher et al. 2014). In fact, visual inspection of diprotodonts' distribution throughout the available climate space indicates that species have barely reached the boundaries of the landscape (Fig. 7). That is, niche evolution in Diprotodontia does not appear to be bounded by geographical limitations, but by evolutionary constraints such as "habitat filtering" (see more below), which leads to pervasive stabilizing selection (Wiens 2004; Wiens et al. 2010).

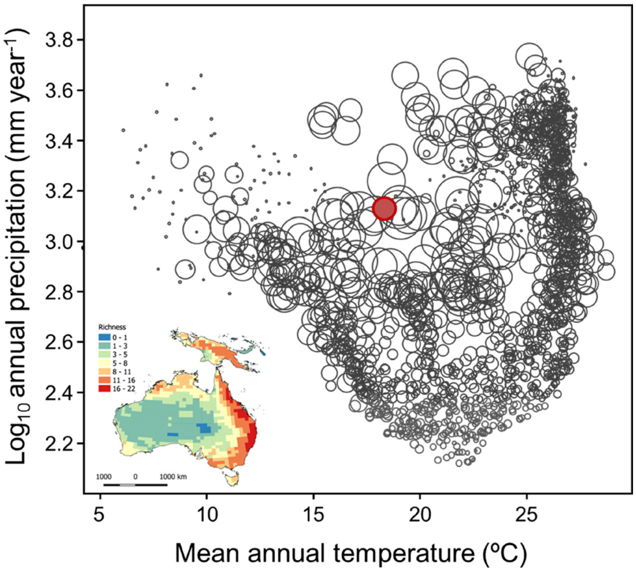


Fig. 7 Species richness in relation to annual precipitation and mean annual temperature. The size of circles is proportional to the number of species co-occurring in a given grid location within the climate space. The red dot denotes the location of the environment occupied by the MRCA. The inset shows diprotodont species richness mapped onto the distribution range if this order

Diversification and Rates of Niche Evolution

BAMM analysis indicated late increase in the rate of evolution of climatic niches during the past 10 Ma, coinciding with the rapid diversification of the kangaroo family (Fig. 2). Macropods constitute the most diverse group of the Diprotodontia order, and have successfully colonized both open (terrestrial) and wet-closed (arboreal) environments (Meredith et al. 2008). Indeed, a rapid diversification may be the most plausible hypothesis to explain the exceptional diversity of this group compared to the rest of families considering that has been relatively recent (~14 Ma). Macropods are widespread across the Australian arid region (accounting for the 64% of the species occurring in this area); it may suggests that aridity increases diversification rates as previously suggested in studies with different lineages of Australian lizards (Harmon et al. 2003; Rabosky et al. 2007; Powney et al. 2010). However, our results do not support this hypothesis; variation in precipitation did not parallel rates of lineage diversification. On the other hand, we found a marginally significant relationship between the position of a given clade in the temperature axis and its diversification rate reinforcing the notion that lineages occurring in warm environments tend to have higher speciation rates (Pyron and Burbrink 2012; Velasco et al. 2015), which according to the 'evolutionary speed' hypothesis could be due to the fact that rates of genetic evolution depend on ambient temperature (Gillman and Wright 2014). Our study also provides further support to the growing body of evidence that rapid shifts in climatic niches promote speciation, as we found that higher rates of lineage diversification were associated with higher rates of climatic niche evolution (Kozak and Wiens 2010a; Schnitzler et al. 2012; Title and Burns 2015; Seeholzer et al. 2017). Although it is difficult to determine the direction of causality underlying this correlation, the most likely hypothesis is that climatic niche evolution has an effect on the likelihood of speciation and extinction (Kozak and Wiens 2010a). The association between variation in rates of climatic niche evolution and variation in rates of lineage diversification is tightly linked to clade area because, first, it is expected that clades with larger geographic areas exhibit greater climatic niche evolution (as their species may encounter a broader range of environments and barriers that clades with more restricted ranges) and second, the colonization of new environments would in turn generate more opportunity for diversification (e.g., Stroud and Losos 2016 and references therein). However, irrespective of the underlying mechanism, it should be highlighted that clades with a lower number of species also exhibit lower rates of climatic niche evolution. It implies that these species might be less likely to shift into new environmental space in order to adapt themselves to changing conditions. Thereby reducing their evolutionary capacity to cope with global climatic change and thus, increasing their extinction risk (Bellard et al. 2012).

Ancestral State Reconstruction

Reconstruction of ancestral states indicated that the most recent common ancestor (MRCA) of present-day Diprotodontia is associated with a mesic environment with an estimated ~1300 mm annual precipitation. Subsequently, diprotodont marsupials invaded both dryer and more mesic environments. Interestingly, kangaroos and wallabies (Macropodidae) successfully colonized the Eremean region, but also experienced reversions to wet-closed habitats (*Dendrolagus* tree-kangaroos) which is contrary to the common assumption that marsupials evolved in a single direction towards open and more arid forms (Mitchell et al. 2014). It is worth mentioning that, although the availability of environments with a climate similar to that of the MRCA of Diprotodontia seems to have reduced substantially, due to the aridification process that Australia has undergone since splitting from Gondwanaland (Byrne et al. 2008), these localities are still an important reservoir for these marsupials. Most of these mesic environments comprising temperate broadleaf and mixed forests with MAT spanning from 17 to 22 °C and AP around 1300–1600 mm, are located in the Australia' East Coast (on the border between Queensland and New South Wales). This region also contains wet sclerophyllous forests and remnant rainforests (the so-called Irian elements), which leads to an increase in habitat heterogeneity that can explain its high species diversity. On the contrary, the arid region (which presently occupies more than three quarters of the continental Australia) and mostly, the western region are underexploited by diprotodont marsupials and, for example, these are not very abundant in the south-western land division of Western Australia, a region recognized globally as biodiversity hotspot (Rix et al. 2015). That is, most diprotodonts tend to avoid both very cold and dry environments probably due to physiological constraints which prevent them from inhabiting regions with these extreme climate conditions (Fig. 7).

Diversity Gradients and Niche Specialization

In contrast to expectations, the highest local diversity of diprotodonts is in temperate communities, not tropical communities. The observed negative relationship between species richness and precipitation as well as the quadratic pattern for temperature point out to a key role of niche conservatism (i.e., limiting dispersal between habitats) in shaping patterns of diversity along both climatic gradients in this group (Lv et al. 2016). As shown in Fig. 5, diprotodonts diversity decreases as climate differs increasingly from the ancestral state. In the case of AP, the position of the ancestral regime is skewed towards the dryer end of the axis; whereas for MAT there is a roughly similar distance from the point where the ancestral area is located to both ends of the axis (i.e., ancestral environment occupies an intermediate position within the current temperature range).

With regard to climatic tolerances, we also tested how occurrence in more extreme environments on a given climatic axis is related to niche breadths on that axis. We found that diprotodont species that occur at the drier end of the precipitation gradient are more specialized, whereas species that occur on the wetter end are able to tolerate a broad range of conditions. Such a positive correlation between precipitation niche breadth and AP has also been previously reported in amphibians at a global scale (Bonetti and Wiens 2014), North American lizards (Wiens et al. 2013) and Oceanian varanid lizards (Lin and Wiens 2017). Our results thus reinforce the idea that there is a general macroecological pattern according to which the strength of selection for specialization may be stronger in arid climates that under more mesic environments, which are likely less stressful (Wiens et al. 2013). On the contrary, we failed to find a negative relationship between temperature niche breadth and MAT, as reported in some of the previously mentioned studies (e.g., Bonetti and Wiens 2014; Lin and Wiens 2017). Yet, this result is product of the distribution range of diprotodonts, which encompass temperate and tropical latitudes. When analyzing each region separately, we found that niche breadth negatively correlated with MAT in species with both mixed and tropical distribution, whereas no trend was observed for those species whose distribution range is restricted to the temperate region (Fig. 5c). When considering the whole dataset, our results point out that species that occur in the most extreme positions on the MAT niche axis have narrower niche widths (that is, they are more specialized for these extreme conditions). Thus, this pattern suggests that the colonization of an environment very different to the one colonized by the ancestors might imply the loss of ability to remain in less extreme environments (i.e., environments that are more similar to the ancestral environment). In turn, this finding allows us to hypothesize that adaptation to both cooler and warmer conditions may be equally challenging and energy-demanding. In fact, it is known that some species whose temperature niches are located at opposed ends of the axis use similar mechanisms to cope with extreme conditions. For example, both arid-adapted species like the red kangaroo and montane species inhabiting the southernmost part of Victoria like *Gymnobelideus leadbeateri* resort to inactivity or daily torpor during hot and cold periods (Geiser 1994).

Phylogenetic Clustering

Some authors have postulated that similarity via inertia and drift is not enough to drive PNC (Losos 2008). Accordingly, evidence for PNC requires the existence of additional constraints preventing species to differ less than might be expected if ecological diversification had occurred in an unconstrained manner. Such coercive forces can be inferred from the way in which species are distributed across the space. Hence, our analyses of phylogenetic diversity provides evidence for PNC in climatic tolerances as only species assemblages away from the ancestral environment showed a pattern of under-dispersion (Wiens and Donoghue 2004; Hawkins et al. 2005; Miller et al. 2013). We found "basal" clustering in the dryer (AP < 1000 mm) and warmer (MAT >28 °C) environments, which suggests the existence of a "habitat filtering" effect under extreme (and energy-demanding) conditions (e.g., Cavender-Bares et al. 2009). According to this, when addressing the level of phylogenetic structure by regions, we obtained significant MPD values for the Eremean region, a similar pattern to that previously reported in dasyurid marsupials (Lanier et al. 2013; García-Navas et al. 2018) and other taxa (Miller et al. 2013). This result supports the notion that arid-zone assemblages show an overall tendency towards phylogenetic clustering probably due to specific adaptations to dry environmental conditions (low water requirements, opportunistic breeding, low metabolic rate, large home ranges) are shared by closely related species (Dawson 1995). On the contrary, as above commented, there may be no need for lineages inhabiting rainforests and montane cloud forests with 3000 mm year^{-1} to have special adaptions to survive even in wetter areas (Bonetti and Wiens 2014). Thus, the existence of "terminal" clustering in the New Guinean region would be the result of evolutionary origin or geographic inertia (i.e., no geographic structuring with respect to phylogeny). The relatively recent colonization of New Guinea-Wallacea, which is thought to have occurred about 10 Ma (Mitchell et al. 2014), and the low dispersal ability of wet-closed lineages like cuscuses and tree-kangaroos may explain the existence of phylogenetically clustered assemblages in this zone. Hence, New Guinean clades may have been prevented from exploiting dryer and more seasonal areas because of insufficient time for niche diversification and reduced mobility.

Conclusions

The emerging picture of this study is two-fold. Firstly, results from our clade-based analyses reinforce the idea that climatic niche divergence may be an important driver of rapid diversification (see also Title and Burns 2015) but, secondly, our study also provides evidence for the claim that PNC plays a relevant role in determining broad-scale diversity patterns (Miller et al. 2013; Cook et al. 2015; Morinière et al. 2016; Pie et al. 2017). Niche evolution in Diprotodontia is better captured by a model of punctuated evolution, which is in agreement with the idea that BM not should always be considered the neutral model. As there is growing evidence that BM does not provide an appropriate expectation for climatic niches (e.g., Boucher et al. 2014; Seeholzer et al. 2017), further studies focused on the evolution of realized niches should incorporate more elaborated models. These studies are paramount in order to better understand the current distribution of mammal species and predict their shift ranges in a global warming scenario.

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