Bursts of morphological and lineage diversification in modern dasyurids, a "classic" adaptive radiation

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The Australasian marsupial family Dasyuridae exhibits one of the most spectacular species-level diversity of any marsupial group. The existence of such exceptional species and phenotypic diversity is commonly attributed to ecological opportunity (EO). According to the EO hypothesis, organisms freed from the burden of competition may undergo an initial burst in diversification and morphological evolution. Subsequently, as accessible niches become occupied, rates of diversification should slow through time. We examined dynamics of lineage and phenotypic diversification in order to test whether Dasyuridae diversified in a classic adaptive radiation. We found that patterns of both lineage diversification and phenotypic (body mass) disparity exhibited an early burst (EB) as predicted by the EO model. Three historical events may have spurred this radiation: the extinction of thylacinids, the emergence of the New Guinean cordillera, and the spread of arid habitats as evidenced by the existence of phylogenetic clustering in these regions. In contrast to previous studies carried out in continent-wide systems, our results support a niche-filling scenario with an EB signal strong enough to be detected. This study shows that the Dasyuridae diversification fully conforms to the postulates of the EO hypothesis and thus, it constitutes a "classic" adaptive radiation.

Running head: Diversification in dasyurid marsupials.

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INTRODUCTION

Australia and nearby islands have been exemplary subjects for studies of radiations of endemic biota throughout the last century (see e.g., Mayr 1942). In fact, some Australian radiations - mainly marsupials- inspired the seminal work of George G. Simpson, who coined the term "ecological opportunity" to define an environment previously occupied by organisms for some reason competitively inferior to its new inhabitants, and is nowadays considered one of the most influential evolutionary biologists (Simpson 1944, 1953). Ecological opportunity is nowadays defined as any event that could make niche space available, including emergence of new environments, mass extinctions and key innovations that allows species to interact with the environment in a novel way (i.e. new niche dimensions) (Stroud & Losos 2016). According to the ecological opportunity (EO) hypothesis, the colonization of a novel or initially underexploited adaptive zone is expected to lead to an early-burst of lineage diversification and morphological evolution indicating that lineages are taking advantage of a niche space free of competitors (Schluter 2000, Yoder *et al*. 2010). Subsequently, this is usually followed by a density-dependent slowdown in the rate of speciation and phenotypic diversification as a result of increased competition as ecological niches become filled (Seehausen 2006, Phillimore & Price 2008, Rabosky & Lovette 2008). However, some authors have pointed out that this pattern, the classic model of adaptive radiation, may be relatively uncommon in comparative data (reviewed in Harmon *et al*. 2010; see also Venditti *et al*. 2011).

Although a relatively high proportion of studies of EO have been conducted in oceanic islands (e.g., Caribbean Basin islands and Hawaiian archipelago; Gillespie 2004, Mahler *et al*. 2010) or islands *sensu lato* (mainland "lake" archipelagos; e.g., Wagner *et al*. 2012), during the last five years the representation of continent-scale studies in the literature of adaptive radiations has increased substantially (Bravo *et al*. 2014, Schweizer *et al*. 2014, Liedtke *et al*. 2016). Due to their larger size, continents are in general more stable over time than islands and consequently it has been suggested that the emergence of EO should be *a priori* less frequent in mainland systems (Pinto *et al*. 2008). To date, evidence in favor of the EO hypothesis from continental radiations is mixed. Some authors claim bursts of lineage and morphological diversification, frequently linked to the colonization of an underexploited area (Schenk *et al*.

2013, Price *et al*. 2014), others have found a lack of signal attributable to the more complex geographic and climatic histories of continents (Liedtke *et al*. 2016, Maestri *et al*. 2017).

Australia provides a very suitable scenario for studying diversification at a continental scale. The progressive expansion of the Australian arid zone during the past 25 millions of years appears to have spurred diversification in a number of plant and animal clades (reviewed in Byrne *et al*. 2008). In fact, despite of its apparent topographic homogeneity, the Australian arid region holds some of the most species-rich terrestrial vertebrate communities known including that of sphenomorphine skinks (Rabosky *et al*. 2003), and the world's most diverse radiation of subterranean diving beetles (Leys *et al*. 2003). In this regard, there is increasing evidence that opportunities for speciation may have been great in this area (Crisp *et al*. 2004, Hugall *et al*. 2008, Catullo & Keogh 2014) suggesting a possible link between aridification and diversification rates in several taxonomic groups. However, diversification rates have been rigorously evaluated (for example, by means of lineage-through-time plots) in only a handful of studies (see e.g., Rabosky *et al*. 2007), due to the fact that most of the data sets currently available for arid-zone biota suffer from several drawbacks (mainly deficiencies in taxon sampling and fossil calibration points), thus preventing the implementation of this type of analyses (Byrne *et al*. 2008).

Dasyuridae is a family of marsupials comprising two subfamilies (Dasyurinae, Sminthopsinae) and four tribes (Dasyurini, Phascogalini, Sminthopsini and Planigalini). It constitutes the principal radiation of insecto-carnivorous mammals within Australasia. Of the 75 described species, 52 are restricted to Australia and 14 to New Guinea and surrounding islands; two species are present on both sides of Torres Strait. Many dasyurids are small (7-30 g) and mouse-like but the group also contains the larger cat-sized quolls (*Dasyurus* spp., up to 7 kg.), as well as the Tasmanian devil (*Sarcophilus harrisii*), which at ~10 kg represent the largest extant species. Dasyurids are found in habitats ranging from montane rainforests to nearly rainless deserts of inland Australia, and most of biogeographic associations (i.e., Eremaean species, Torresian species, etc.) are represented within the four tribes, a feature characteristic of Australo-Papuan radiations (e.g., Christidis *et al*. 2011). The existence of this striking within-clade disparity in terms of biogeography suggests that the colonization of arid environments

from mesic habitats did not occur in one wave (i.e., multiple independent evolution) (Westerman *et al*. 2016).

In this study, we used a time-calibrated phylogeny, data on body mass and community phylogenetics to test for macro-evolutionary patterns predicted by the EO hypothesis in modern dasyurids. According to the EO model, organisms freed from the burden of competition, such as through the colonization of a novel or underexploited environment, should experience an ecological "release" characterized by increased cladogenesis (early phase) followed by a progressive slowdown in diversification rate (late phase) (Schluter 2000, Harmon *et al*. 2010). We tested for the existence of this temporal pattern in this iconic marsupial radiation. Regarding phenotypic diversification, predictions of EO are fundamentally expected to apply to traits that are correlated with ecological niches (Schluter 2000). Therefore, we tested whether morphological disparity is partitioned among rather than within subclades using one morphological trait that is strongly associated with niche: body mass (Fisher *et al*. 2011). Body mass is a key trait in dasyurids as well as in other mammals, as it influences fitness through its effects on reproduction (larger males have priority access to females; Kraaijeveld-Smit *et al*. 2003, Fisher & Cockburn 2006) and survival (Körtner & Geiser 2009). If the radiation of a lineage has been adaptive, it is expected that the diversification dynamics of both the lineage and the phenotype show signal of diversity-dependent diversification (niche-filling) over time. Thus, both diversity dimensions should exhibit similar patterns (Schluter 2000). In addition, we tested for a relationship between body mass and the two main environmental variables, temperature and precipitation, which vary markedly across the distribution range of this group. The existence of a phenotype-environment correlation is one of the four criteria that have been suggested to be necessary for adaptive radiations to take place (Schluter 2000). The three remaining are: common ancestry, trait utility (experimental or theoretical tests of performance or fitness of a trait in its corresponding environment) and rapid bursts of speciation. The two phylogenetic criteria, *viz*. common ancestry and rapid speciation, are examined using the molecular data (see above). Finally, we tested for the existence of phylogenetic structure (underdispersion or "clustering"), which might be indicative of *in situ* diversification. Specifically, the presence of phylogenetic clustering in environments different from the zone

colonized by the most recent common ancestor has been previously interpreted as evidence for the existence of a burst in diversification rate upon entering a new area (Cardillo 2011).

MATERIAL AND METHODS

Data set

Our study comprised 68 out of extant 75 dasyurid species (i.e., 91% of extant species). The following seven species were excluded from the present study since these were not included in the phylogenetic study (Westerman *et al*. 2016, see more below) in which this study is based on: *Phascolosorex doriae*, *Sminthopsis boullangerensis* (a species of dunnart found only on Boullanger Island and formerly considered a subspecies of *S. griseoventer*), *A. adustus*, *A. subtropicus*, *A. mysticus*, *A. argentus* and *Antechinus arktos*. The last five species belong to the Australian dusky Antechinus complex and some of them have been recently described (*A. mysticus*: Baker *et al*. 2012; *A. argentus*: Baker *et al*. 2013; *A. arktos*: Baker *et al*. 2014).

The fossil record for this family includes *Barinya wangala* (Wroe 2003), the currently oldest recognized dasyurid dating back from the middle Miocene and which has been placed in its own subfamily, Barinyainae. The remaining putative extinct dasyurids have never been described and their placement within Dasyuridae remains unclear and controversial (summarized in Black *et al*. 2012).

Phylogeny and divergence time estimates

Analyses conducted here are based on the phylogenetic estimate and associated divergence times presented in a recent study (Westerman *et al*. 2016). In this study, Westerman and colleagues reassessed the phylogenetic relationships of 68 of 75 living dasyurids species using a large molecular database comprising published and novel sequences for eight nuclear genes [*breast cancer early onset gene 1* (*BRCA1*), *apolipoprotein B gene* (*ApoB*), *recombination activating gene 1* (*RAG1*), *von Willibrand Factor gene* (*vWF*), *embryonic globin gene intron 1* (*ε-globin*), *protamine P1* (*protP1*), *interphotoreceptor binding protein* (*IRBP*) and *beta fibrinogen intron* (*bfib7*)] and seven mitochondrial genes [*cytb*, *12S rRNA*, *tRNA valine plus 16S*

154 *rRNA*, *nicotinamide dehydrogenase* (*NADH*) *genes 1* and *2*, and *cytochrome oxidase genes* (*COI*
155 and *COII*)] to yield a total DNA sequence database of over 17 kb. Divergence time estimates
156 were performed using BEAST v.1.8 (Drummond *et al*. 2006) with the uncorrelated lognormal
157 relaxed molecular clock (see Westerman *et al*. 2016 for more details). Our present analyses
158 were performed using the maximum clade credibility (MCC) tree provided in that study. In
159 addition, we used a set of 1 000 trees randomly sampled from the posterior distribution of the
160 Markov chain Monte Carlo (MCMC) search in order to account for phylogenetic uncertainty.
161
162 *Morphological and ecological data*
163 We compiled data on average adult body mass (g) from the literature (both primary sources and
164 summary publications; e.g., Van Dyck *et al*. 2013) for each species. Body mass and body length
165 (size) are strongly correlated ($r^2 = 0.96$, $p<0.001$). We obtained similar results when using body
166 length as focal trait and thus, for the sake of brevity, we only report results for body mass. Body
167 mass was log-transformed prior to analyses.
168
169 *Diversification analyses*
170 To visualize the pattern of diversification we constructed a lineage-through-time (LTT) plot,
171 which illustrates the deviation of the empirical LTT pattern from the expectation under a
172 constant-rate pure-birth process (Harmon *et al*. 2003). For the empirical LTT plot, we calculated
173 the 95% confidence interval (CI) from our sample of trees (1 000 trees). We determined the
174 extent to which branching events in our phylogeny depart from those expected under a constant-
175 rate process by computing the gamma (γ) statistic (Pybus & Harvey 2000) in the R package
176 *laser* (Rabosky 2006). A deceleration in diversification rate is inferred when $\gamma \leq -1.645$, which
177 is interpreted as evidence for the existence of an early-burst of diversification (Harmon *et al*.
178 2003). We assessed γ by using the Monte Carlo constant-rate (MCCR) test, as this approach
179 allows accounting for incomplete sampling. We performed these analyses on the MCC tree as
180 well as on our set of 1 000 trees randomly sampled from the posterior distribution of the
181 Markov chain Monte Carlo (MCMC) search in order to account for phylogenetic uncertainty.
182 To further test for temporal slowdowns in diversification rate consistent with adaptive radiation,

we applied a model-fitting strategy in *laser*. We compared the fit of two-constant rate models (1 and 2) and three variable -rate models (3-5): (1) a pure-birth (PB) or Yule model; (2) a birth-death (BD) model; (3) an exponential diversity-dependent (DDX) model, which models the speciation rate as a function of the number of extant lineages at any time point and may be increasing or decreasing; (4) a logistic diversity-dependent (DDL) speciation rate model, in which the number of lineages increases until reaching a *k* limit analogous to the 'carrying capacity' parameter of population ecology, and (5) a BD variable-rate model with the speciation rate r_1 shifting to r_2 at a time *t* (yule-2-rate). Model-fit was compared using the bias-corrected version of the Akaike Information Criterion (AICc). In order to test for constancy of diversification rates, we computed the ΔAICrc statistics: AICrc = AIC_{H0}-AIC_{H1}, where AIC_{H0} is the AIC score of the best rate-constant model and AIC_{H1} is the AIC score of the best rate-variable model. This model comparison was performed using the function "fitdAICrc" in *laser*. When $\Delta AIC_{RC} > 0$, then the best of the rate-variable models is also the best model for the observed diversification pattern; when $\Delta AIC_{RC} < 0$, the best rate-constant model would be favored (Rabosky & Lovette 2008).

In addition, we examined changes in rates of diversification across the MCC tree by means of Bayesian Analysis of Macroevolutionary Mixtures (BAMM v.2.5; Rabosky *et al*. 2014). This approach uses reversible-jump Markov chain Monte Carlo (rjMCMC) to fit models with one or more diversification regimes to subsets of the tree. We ran four chains of 100 000 000 generations each, sampled every 50 000 generations. The first 10 000 000 generations were discarded as burn-in. We set starting parameters priors with the setBAMMpriors function in the R package *BAMMtools* (Rabosky *et al*. 2017). We identified a credible set of distinct shift configurations that account for 95% of the probability of the data.

Morphological disparification

First, we tested for phylogenetic signal in body mass using Blomberg's *K* statistic (Blomberg *et al*. 2003) as implemented in the R package *phytools* (Revell 2012). Values of *K* near 1 indicate a strong phylogenetic signal, whereas values near 0 denote a decoupling of phylogenetic and phenotypic divergence. *K* values > 1 indicate that some factor is causing closely related species

212 to be more ecologically similar than would be expected under random walk (i.e. niche
213 retention).

214 Subsequently, we tested the EO prediction of an early-burst in morphological trait
215 divergence, leading to proportionately greater disparity than expected under a BM model early
216 in group' evolutionary history, and a lower proportion of phenotypic variation partitioned within
217 subclades by means of disparity-through-time (DTT) plots (Harmon *et al*. 2003). DTT plots
218 illustrate relative subclade disparity, that is, mean squared pairwise Euclidean distances between
219 all species in morphospace in each subclade whose ancestral lineages were present at that time,
220 relative to the disparity of the entire taxon (Harmon *et al*. 2003). In order to quantify such a
221 difference, we computed the morphological disparity index (MDI), which represents the sum of
222 the areas between the curve describing the average disparity of the trait and the curve describing
223 the expected disparity under a null model of BM (1 000 simulated datasets). A negative MDI
224 score would indicate that early subclade disparity was lower (and among subclade disparity
225 higher) than expected under BM, which is consistent with that predicted by the EO model
226 (Harmon *et al*. 2003). We carried out DTT analysis for body mass and size using the *geiger*
227 package (Harmon *et al*. 2008).

228 We also tested the EO prediction of a decline in the rate of phenotypic evolution
229 through time by means of two complementary methods: by using the node height test
230 (Freckleton & Harvey 2006), and by using a model-based approach that assessed which models
231 of trait evolution provides a better fit to our data. First, we calculated phylogenetic independent
232 contrasts (PICs) for each morphological trait and correlated the absolute value of the PIC to the
233 height of the nodes from which they were generated. A negative correlation is predicted when
234 evolution follows a niche-filling model, because as niches become filled with increasing species
235 number the differences among the niches of ancestors and descendants become progressively
236 smaller (Freckleton & Harvey 2006). Secondly, we quantified the tempo and mode of trait
237 diversification by fitting three alternative models that describe different evolutionary patterns:
238 (i) the Brownian motion model (BM, which describes a random walk of trait evolution along
239 branches in the phylogeny), (ii) the early-burst or "niche-filling" model (EB, where rates
240 exponentially decrease over time under the assumption that niches are saturated by

accumulating species within lineages), and (iii) the Ornstein-Uhlenbeck model (OU, which assumes that selection pulls the trait values around an adaptive optimum, i.e. "bounded" evolution). Models were run using *geiger* and their goodness-of-fit were compared using AICc and AIC weights (AICw). In addition, we tested for increasing or decreasing evolutionary rates using Pagel's delta, δ. When $\delta > 1$ it implies that evolutionary change is concentrated towards the tips (i.e., accelerated trait rates) and $\delta < 1$ towards the root (i.e. slowed trait rates). In a further step, we tested for trait-dependent diversification related to body mass in the dasyurids using BAMM. According to the EB model, trait evolution slows at the same pace across the entire clade (Slater & Pennell 2014). We tested for congruence between rates of lineage and phenotypic diversification resulting from EO (Price *et al*. 2016).

Lastly, we tested for the existence of a relationship between body mass and two environmental variables: mean annual temperature and annual precipitation. We extracted mean annual temperature and mean annual precipitation layers (*BIO1* and *BIO12*, respectively) from WorldClim database (Hijmans *et al*. 2005) for a 100×100 km resolution grid in which we calculated the average value of both abiotic variables for each grid cell using QGIS (QGIS Development Team 2016). Thereby, we obtained mean values of temperature and precipitation for each dasyurid species. We then examined associations between phenotype (body mass) and environmental factors (temperature, precipitation) independent of similarity due to phylogeny by means of Phylogenetic Generalized Least Squares (PGLS) implemented in the *caper* package (Orme *et al*. 2012).

Phylogenetic species clustering

We employed a community phylogenetics approach (Kembel 2009) to depict the phylogenetic structure of species assemblages. A pattern of phylogenetic clustering might indicate in-situ speciation whereas a pattern of phylogenetic over-dispersion might indicate either extensive regional competitive exclusion or multiple allopatric speciation (Cardillo 2011, Mazel *et al*. 2016). To that end, we divided the observed geographic ranges into seven biogeographic regions based on Fox & Archer 1984: (1) Eremaean region, (2) south-western temperate (SW), (3) non-tropical east (NTE) or Bassian region, (4) monsoon or Torresian region, (5) Irian region

(remnant rainforests), (6) New Guinea, and (7) Tasmania. Dasyurid species were coded as present (=1) or absent (=0) in each region (species were allowed to occur in multiple regions) based on distribution data available from the International Union for Conservation of Nature (the IUCN Red List of Threatened Species; www.iucnredlist.org) that were checked against distribution maps provided in the Atlas of Living Australia (www.ala.org.au) and Global Biodiversity Information Facility (GBIF, www.gbif.org). For each biogeographic region, we calculated mean pairwise distance (MPD) and mean nearest taxon distance (MNTD) (Webb *et al*. 2002) using the R package *picante* (Kembel *et al*. 2010). MPD and MNTD increase with phylogenetic evenness (larger phylogenetic distances among species of an assemblage) and decreases with clustering (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 clustering and over-dispersion. Meanwhile, MNTD is the branch length distance between each species and its closest relative in a community and thus, this measure is more sensitive to patterns of clustering and over-dispersion closer to the tips of the tree. 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 null distribution under a "independentswap" model. We obtained very similar results when considering alternative null models (results not shown). Differences in patterns of clustering and overdispersion at shallow (MNTD) and deeper (MPD) levels in the phylogeny might indicate support for a niche-filling scenario (Cardillo 2011, Lv *et al*. 2016).

RESULTS

Diversification

The LTT analysis for Dasyuridae revealed a decline in diversification toward the present (Fig. 1a). Around 16-17 Ma diversification rates tend to decrease through time and most modern dasyurid genera and species already existed before the latest Miocene. The obtained gamma statistic (γ_{MCC} = -6.445, p <0.001) indicated that the internal nodes are closer to the root than

299 expected under the pure-birth model (i.e. early rapid diversification), rejecting the null
300 hypothesis of a constant-rate of cladogenesis over time. When the constant-rate test was
301 performed on the set of 1000 chronograms, we obtained a rather similar γ value (γ_{1000} = -5.568).
302 The one-tailed test yielded a statistically significant result in 90.9% (909/1000) of cases.
303 Consistent with the LTT analysis, results of the birth-death likelihood analysis indicate that
304 DDL (logistic-density dependent model) was the best-fitting model in both cases (Table 1),
305 which suggests that Dasyuridae diversification has tended to decline over time as a function of
306 accumulating species. The DDL model provided a better fit than the preferred rate-constant
307 (PB) model (ΔAICrc = 45.86). Yet, the yule-2-rate model also received substantial support from
308 the data (Table 1).
309 The BAMM analyses detected no rate shift; none of the branches were associated with a
310 speciation-extinction rate slowdown.
311
312 *Morphological disparity*
313 We found a significant phylogenetic signal for body mass (K = 1.44, p = 0.001). The obtained K
314 value indicates that longer braches (old lineages) contribute proportionally more to trait
315 evolution, which supports the EB model (Hernández *et al*. 2013). Relative disparity of body
316 mass was lower than expected under Brownian motion (Fig. 1b), but this departure was non-
317 significant (p = 0.117). The negative MDI value (MDI = -0.225) indicates that disparity tends to
318 be distributed among subclades. Consistent with the EO hypothesis, we found a significant
319 negative relationship between node height and contrast values, which indicates that the rate of
320 body mass evolution decreased as the number of species increased (estimate: -0.055 ± 0.023, t =
321 -2.36, d.f. = 65, p = 0.02; Fig. 1c). Maximum likelihood model fitting results for body mass
322 indicate that the EB model was the best model (ΔAICc > 4; Table 2). Mean values for r, the
323 parameter from the EB model that describes the rate at which trait evolution slows through time,
324 were moderately high (r_{MCC} = -0.115; r_{1000} = -0.111) in comparison with the r estimates
325 provided in [10] (r = -0.007, range: -0.15 to 0). Accordingly, the obtained delta value (δ =
326 0.273) indicates that the rates of body mass evolution have slowed over time.

We further investigated the temporal rate dynamics and rate heterogeneity of body mass evolution using BAMM. Five distinct configurations emerged after we identified a 95% credible set of distinct shift configurations: no shifts (posterior probability [PP] = 0.50) and one shift- located in the Dasyurus clade- for the remaining four configurations (PP = 0.26, 0.13, 0.04 and 0.03; see Supporting Information). Thus, in congruence with the pattern of lineage diversification, there was no evidence overall for a rate shift in body mass evolution.

When exploring the existence of a phenotype-environment correlation, we found a significant negative association between body mass and mean annual temperature (PGLS; $F_{1,66}$ = 7.65, p <0.007; Fig. 3). The relationship between body mass and annual precipitation was not significant (p >0.5).

Phylogenetic species clustering

We found a significant pattern of phylogenetic clustering irrespective of the employed measure (MPD or MNTD) for the assemblage of species inhabiting New Guinea (Table 3). According to the obtained MPD values, the Eremaean assemblage also shows a significant pattern of underdispersion across the whole phylogeny (Table 2). On the contrary, both the NTE and Torresian region have small MNTD values because, within these regions, each species has a close relative in the assemblage, but the MPD values does not differ significantly from the null model because the distance matrix contains both very large and very small distances (see Fig. 2) and the average of these is almost equal to the overall average edge length (Table 3). We obtained almost identical results when combining NTE and Tasmania, and the Australian rainforests (Irian region) and New Guinea into two single categories (see Supporting Information).

DISCUSSION

The ecological theory of adaptive radiation predicts accelerated rates of speciation associated with divergence in ecologically relevant phenotypic traits like body size/mass (e.g. Schluter 2000, Losos 2010). This phenomenon may arise if a trait changes more rapidly in some species

than others in response to selective pressures. This change may facilitate rapid access to underexploited ecological niches or increased reproductive isolation, thereby boosting the speciation rate. Our results provide compelling evidence for the existence of congruent bursts of lineage and morphological diversification in the dasyurid radiation, meeting thus the predicted pattern of adaptive diversification shaped by ecological opportunity (EO).

Lineage diversification in modern dasyurids

According to the EO model, organisms freed from the burden of competition, such as through the invasion of a novel or underexploited habitat, should experience a "release" characterized by increased cladogenesis (accelerated speciation rates and decreased extinction rates) and associated phenotypic diversification. Subsequently, clades should show a slowdown in speciation toward the present as niche space became saturated (Schluter 2000). Our results support this hypothesis; we found that the model that predicts a density-dependent decline in diversification rates (DDL model) provided the best approximation to the observed pattern of lineage accumulation through time. This result suggests that the tempo of dasyurid diversification may be mediated by ecological interactions among relatives. Limited ecological opportunity emerging from increased intraspecific competition and shortage of available ecological niches may explain the existence of diversity-dependent diversification in this radiation (Rabosky & Lovette 2008, Phillimore & Price 2008). Although this pattern of reduced speciation rates following a burst in diversity has also been detected in studies at continental scale (Burbrink & Pyron 2009), most evidence comes from studies carried out in geographically confined regions (lakes: Seehausen 2006, Wagner *et al*. 2012, islands: Harmon *et al*. 2003), where once niches are filled, diversification rate can only decline. By contrast, in vast continental regions, organisms may encounter new ecological opportunities successively, and the colonization of these underexploited zones may suppose the maintenance of a constant-rate of diversification (Derryberry *et al*. 2011). Regarding this, it should be noted that although Australia is considered by definition a continent, its reduced size in comparison with other landmasses (e.g. Eurasia, Africa, North America) and its climatic characteristics (predominance

of arid and semi-arid regions) make it a kind of "big island", which may explain that Australian radiations are more similar to those found in islands than to other continental ones.

In agreement with that predicted by the density-dependent model, our findings suggest that this evolutionary radiation has existed long enough for the net diversification rate to plateau (Weir 2006, Rabosky & Lovette 2008, Rabosky 2013). Alternatively the slowdown in diversification could be explained with the simple assumption that speciation takes time rather than occurs instantaneously (protracted speciation). That is, speciation events that initiated in the recent past may not have completed yet, so they do not count towards the total number of extant species at the present (Etienne & Rosindell 2012, Moen & Morlon 2014). Frequent peripatric speciation could also lead to diversification slowdowns without niche differentiation (Pigot *et al*. 2010). Under this model, one species with a wide geographic range gives rise to many small-ranged species that are unlikely to further speciate, leading to a linear increase in species over time ("geography of diversification"; Moen & Morlon 2014). This hypothesis is plausible since closely related species of dasyurids rarely show range overlap. Thus, the role of geography in explaining diversification slowdowns deserves to be explored in further studies. On the other hand, although the DDL model provided the best fit to our data, the yule-2-rate also received substantial support suggesting the possible existence of a sudden change in the rate of diversification. That abrupt shift could have been occurred about 16 millions of years ago, once niches become filled (see Fig. 1a).

Morphological disparity: strong support for the EB model

To the best of our knowledge, ours is the first study providing evidence for the existence of an EB pattern across an entire family using the three main approaches for detecting early bursts of trait evolution in comparative datasets: disparity-through-time (DTT) analysis (Harmon *et al*. 2003), the node height test (Freckleton & Harvey 2006), and maximum-likelihood (ML) (Harmon *et al*. 2010). Of these three methods, the most conservative and less frequently employed is ML. For example, Harmon and colleagues (2010) carried out an extensive analysis on a large number of comparative datasets (including some clades that are traditionally considered textbook examples of adaptive radiation like Galápagos finches or *Anolis* lizards)

412 and they found that only one out of the forty-nine clades analyzed supported the EB model
413 using ML, concluding that it may be due to either the absence of "classic" adaptive radiations or
414 the ephemerality of the EB signal. Regarding this latter, Slater & Pennell (2014) argued that the
415 EB model has received little support in the literature as it cannot be easily detected with
416 phylogenetic comparative data rather to the absence of this pattern in nature. In fact, a few
417 authors have found support for decelerating rates of evolution in certain clades (Burbrink &
418 Pyron 2009, Derryberry *et al*. 2011) but, interestingly, none of these studies employed a ML
419 approach to do so. Our results are certainly striking as they provide evidence that early bursts of
420 phenotypic evolution are completely identifiable in moderately sized phylogenies (50-100 taxa)
421 using ML model fitting when a series of circumstances are met. Regarding this, it is worth
422 mentioning that although Cooper & Purvis (2010) reported that the inferred rate of body mass
423 (not size) evolution in the Tasmanian devil was exceptionally high (see also Venditti *et al*.
424 2011), our results remained similar when excluding this comparatively large species from our
425 data set (i.e. strong support for the EB model; Akaike weights, EB: 0.96, OU: 0.01, BM: 0.03).
426 Thus, the detected burst is not attributable to an explosive increase confined to one branch
427 (Tasmanian devil). In other words, our results are not driven by a single unusual datum.
428
429 *Phenotype-environment correlation*
430 By definition, adaptive radiations generally involve phenotypic diversification along one or
431 more ecological dimensions of specialization (Schluter 2000, Yader *et al*. 2010). The existence
432 of a phenotype-environment correlation is one of the four criteria employed by Schluter (2000)
433 to define a radiation as adaptive. Here, we have shown that the dasyurid radiation seems to meet
434 that criterion. We found a negative correlation between body mass and annual temperature,
435 suggesting that dasyurid species may have reduced their body size to adapt to warmer
436 environments (Rodríguez *et al*. 2006, Gohli & Voje 2016). The higher surface area-to-volume
437 ratio of smaller animals (e.g. dunnarts) in hot and dry climates facilitates body heat loss through
438 the skin and thus, helps cool the body (e.g. Brown & Lee 1969). Furthermore, body mass has
439 been shown to be associated with daily torpor, a strategy to reduce energy expenditure during
440 the winter period (Geiser & Baudinette 1990). As daily torpor lowers daily energy and water

requirements, it may be crucial for survival and reproduction of dasyurid species in the arid zone (Holloway & Geiser 1996, Körtner & Geiser 2009). Thus, a lower body mass may consistently confer fitness benefits, which is in agreement with the Schluter' third criterion: trait utility. Yet, experimental tests are necessary to confirm this hypothesis. In addition, the existence of adaptive diversification in relation to habitat use is also certainly plausible in the radiation of Dasyuridae according to the observed ecological disparity: some species are entirely terrestrial (e.g. *Sminthopsis* spp.), other species are semi-arboreal (e.g. *Antechinus stuartii*, *A. bellus*) and some others (e.g. *Murexia longicaudata*, *Phascogale tapoatafa*) are arboreal specialists. Thus, adaptation to distinctive structural habitats may explain the remarkable phenotypic differences that can be found among dasyurid species. For example, semi- or arboreal species like the spotted-tailed quoll *Dasyurus maculatus* have a well-developed hallux and limb ratios indicative of a slow-running and an arboreal life-style. This toe tends to be reduced or absent in more terrestrial species like the eastern quoll *D. viverrinus*, which is adapted to the open grasslands and exhibits a low femur/metatarsal ratio indicating faster running speeds (Jones & Stoddart 1998). Habitat partitioning (both vertical and horizontal) would reduce competition for food among sympatric species as it has been shown in dasyurid communities (Jones 1997). This suggests that competition, both intra- and interfamily (see above), seems to be an important force behind this adaptive radiation and it has influenced size relationships among species. In fact, character displacement has been demonstrated for this guild (Jones & Barmute 2000), which constitutes evidence of competition operating on an evolutionary time scale. Further studies using morphological measurements (e.g. limb size, tail length) from museum specimens would provide insight into the association between phenotype and habitat use, and other ecomorphological relationships in this family.

Phylogenetic species clustering

The arid zone (Eremaean region) showed "basal" clustering as expected taking into account that basal lineages in each of the dasyurid tribes are comprised of arid taxa -reflecting that the rise of modern dasyurids is linked to the colonization of more xeric-arid environments- and that MPD is more strongly influenced by the basal structure of the phylogenetic tree. This pattern suggests

that arid lineages underwent a rapid niche-filling radiation, with rates of diversification slowing in more recent times as expected under density-dependent models of speciation (see also Cardillo 2011). In the NTE and Torresian region, MNTD values suggested phylogenetic structuring which were not evident from MPD values. This pattern of "terminal" clustering reflects a relatively high proportion of sympatric congeners in disparate clades, which might be promoted by niche partitioning via fine-scale habitat preferences. The MNTD measures solely the nearest phylogenetic neighbor for each species and thus, it seems to be a better index of potential competition in a given assemblage (Mazel *et al*. 2016). The New Guinean assemblage showed both "basal" and "terminal" clustering probably due to its more recent origin. Our results suggest that the niche-filling process (rapid radiation and subsequent slowdown) occurred primarily in the arid region, which has been frequently regarded as biodiversity engine ("species pump"; Byrne *et al*. 2008). In fact, the arid region harbors a higher diversity (24 species) than any other region (Fig. 2). This finding is in agreement with previous studies showing rapid diversification in Australian arid environments (Rabosky *et al*. 2007, Powney *et al*. 2010). The greatest species richness observed in the Eremaean region, as opposed to the zone from which dasyurids originated (sclerophyll and woodlands habitats; Krajewski *et al*. 2000a), suggests the existence of a burst in diversification rate upon colonizing this previously unexploited environment (Schweizer *et al*. 2014, Lv *et al*. 2016).

Major features of an exceptional radiation

So, what makes this radiation special? Why does the radiation of dasyurid marsupials retain the EB signal in both lineage and trait data? Probably, the most important feature is the elevated synchronicity of this radiation. The four tribes exhibit major cladogenic events from the early to middle Miocene (23-15 Ma) and before the end of this epoch most modern dasyurid genera and species, including those from New Guinea, were already in existence (Westerman *et al*. 2016, Krajewski *et al*. 2000a). Most splits in each of the four dasyurid subfamilies appear to coincide with two historical episodes: the spread of more open woodland-grassland habitats during the early-mid Miocene and the waves of dispersal into proto-New Guinean islands (Black *et al*. 2012). On the other hand, the rise of modern dasyurids has often been claimed to be associated

with the climate-driven extinction of archaic thylacinids and bandicoots, which dominated the insectivourous-carnivorous niche during the late Oligocene to middle Miocene and whose ecological role was occupied by the smaller dasyurids during the latter half of the Neogene (Krajewski *et al*. 2000b, Wroe 2003). Hence, a relaxation of interspecific competition (due to the progressive decline in thylacinid diversity) in conjunction with the availability of new underexploited areas appears to underlie this rapid and explosive radiation. It is likely that these factors led to an EB signal too strong to be eroded by later processes.

Conclusions

In this study we provide one of the clearest examples of "classic" adaptive radiation described so far for a mammal group. In fact, the Dasyuridae fulfills at least three of the four criteria for adaptive radiation (*sensu* Schluter 2000). Both diversification and morphological disparity analyses provided strong evidence for the role of EO as the main stimulus for the emergence of exceptionally diverse clades (Glor 2010, Losos 2010, Stroud & Losos 2016). Our results show that both lineage diversification and body size disparity showed the same pattern of slowdown toward the recent. Such a congruent pattern -the core prediction from adaptive radiation theory- is hardly ever found, especially in analyses without the fossil record (Slater & Pennell 2014, Slater 2015a,b). The existence of phylogenetic clustering in several regions supports the idea of a multiple explosive radiation of species as main characteristic of the diversification process in this family. This study constitutes an exception to the common assumption that constant-rate lineage and trait diversification is the most pervasive model in continent-scale radiations (Tran 2014, Alhajeri *et al*. 2016, Liedtke *et al*. 2016). Overall, our findings indicate that some radiations in nature resemble perfectly a niche-filling scenario as predicted by the EO theory.

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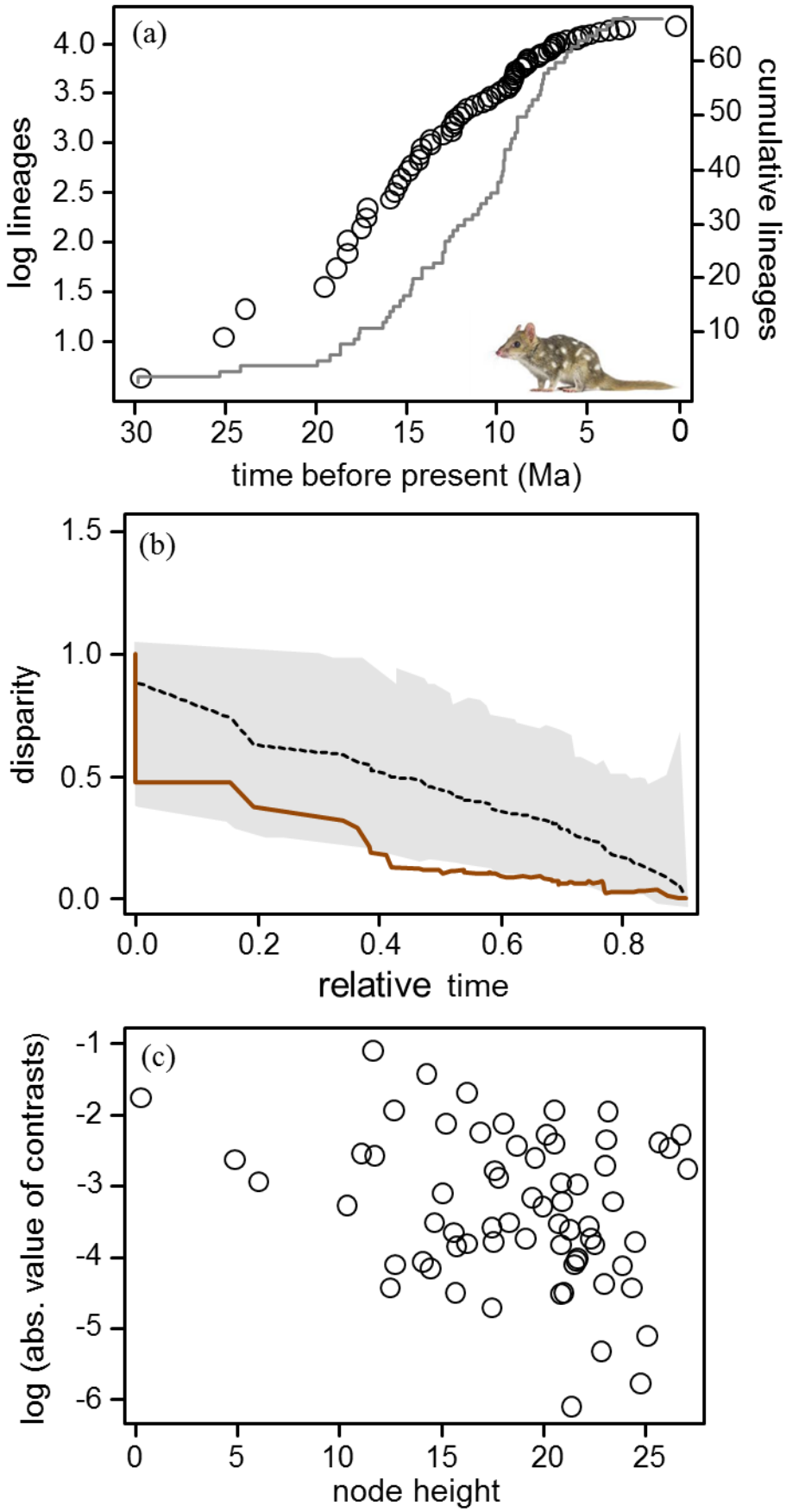
Figure captions

Figure 1 (a) Lineage-through-time (LTT) plot for dasyurids represented in form of log-transformed lineage number (circles) and number of cumulative species (solid line). (b) Disparity-through-time (DTT) plot for body mass. The solid line is the observed disparity and the dashed line is the mean expected disparity derived from 10,000 simulations under Brownian motion evolution. The grey area represents the 95% confidence interval. (c) Node height test (NHT) plot showing absolute body mass (abs) contrasts against node height.

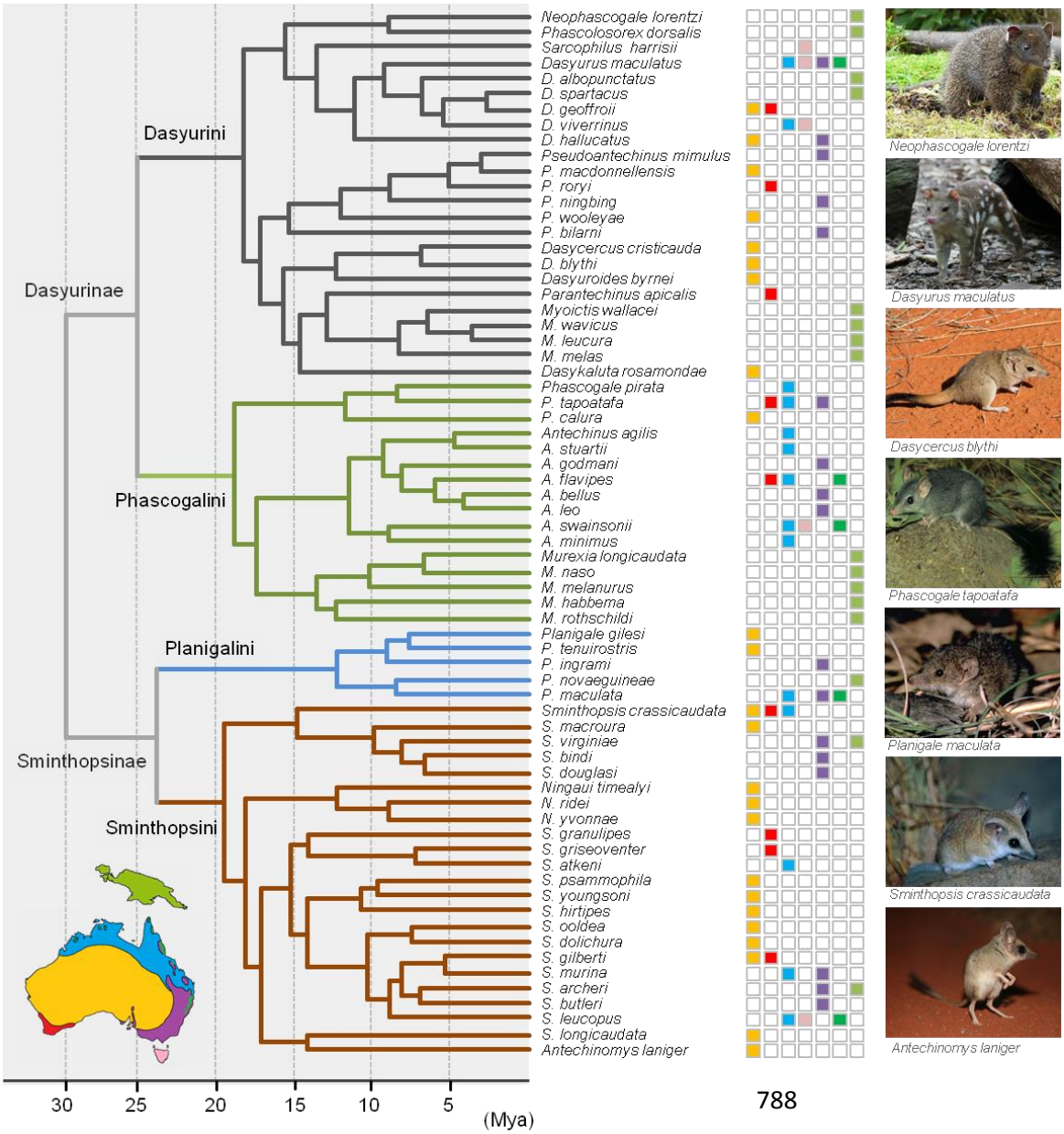
Figure 2 The biogreographic regions inhabited by dasyurid species, mapped onto a Bayesian phylogeny (MCC tree). Colour of the branches indicates the four different tribes. Colour coding of the grid located at the right of the tips corresponds to the seven biogeographic regions (orange: Eremaean; red: SW; purple: Bassian; pink: Tasmania; blue: Torresian; dark green: Irian; light green: New Guinea). Photographs: Creative Commons and David Nelson.

Figure 3 Relationship between body mass and mean annual temperature in dasyurids represented in the form of (a) standardized phylogenetic independent contrasts (PIC) and (b) raw data.

765 Figure 1


(a)
log lineages
cumulative lineages
time before present (Ma)
(b)
disparity
relative time
(c)
log (abs. value of contrasts)
node height

787 Figure 2



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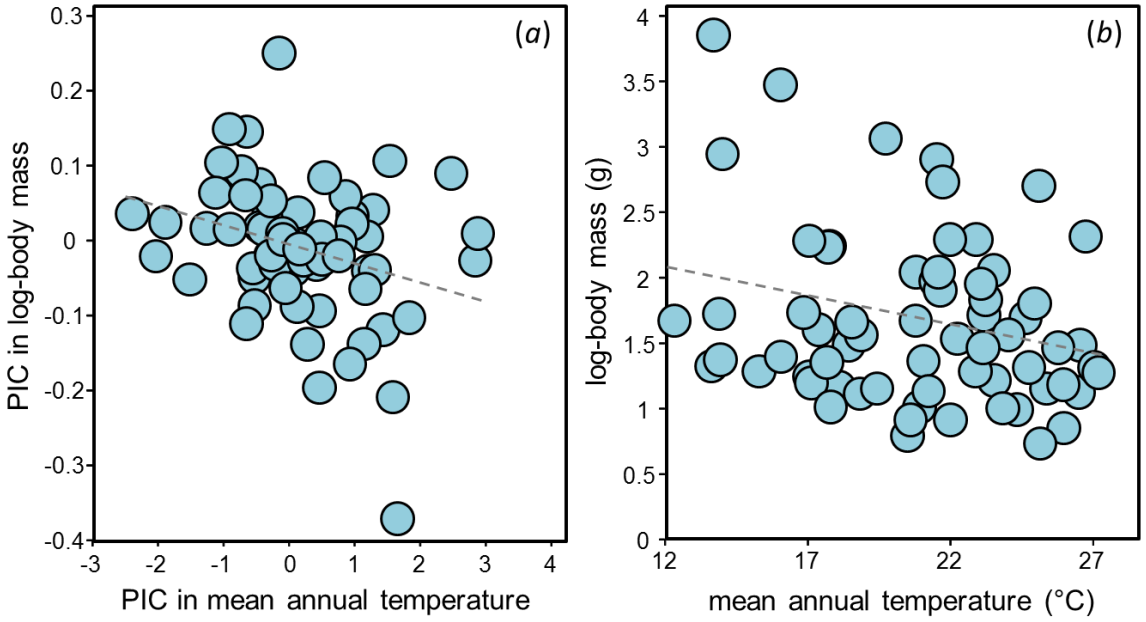
790

Figure 3


(a)
PIC in log-body mass
PIC in mean annual temperature
0.3
0.2
0.1
0
-0.1
-0.2
-0.3
-0.4
-3
-2
-1
0
1
2
3
4
(b)
log-body mass (g)
mean annual temperature (°C)
4
3.5
3
2.5
2
1.5
1
0.5
0
12
17
22
27

795 **Table 1** Results of the birth-death likelihood (BDL) analysis based on a) the Bayesian MCC
796 tree, and b) a set of 1000 trees randomly sampled from the posterior distribution of the MCMC
797 search. The following information is given: log-likelihood (ln *L*), mean AIC value, difference in
798 mean AIC scores between each model and the overall best-fit model (Δ) and parameters (*r* = net
799 diversification rate in form of speciation events per million years; *a* = extinction fraction; *k* =
800 carrying capacity; *x* = magnitude of the rate change as a function of *Nt*) for each model (PB:
801 pure-birth model; BD: birth-death model; DDL: density-dependent logarithmic model; DDX:
802 density-dependent exponential model; yule2rate: Yule model with a shift).

	PB	**BD**	**DDL**	**DDX**	**yule2rate**[2]
b) MCC tree					
Parameters	r_1 = 0.084	r_1 = 0.084 a = 0	r_1 = 0.298 k^1 = 69.930	r_1 = 0.548 x^1 = 0.526	r_1 = 0.120 r_2 = 0.008 t = 3.710
ln(*L*)	-11.344	-11.344	12.586	-2.613	12.043
ΔAIC	45.860	47.860	0	30.397	3.085
a) 1000 trees					
Parameters	r_1 = 0.089	r_1 = 0.089 a = 0	r_1 = 0.310 k^1 = 70.118	r_1 = 0.592 x^1 = 0.532	r_1 = 0.123 r_2 = 0.009 t = 3.227
ln(*L*)	-7.494	-7.494	15.634	1.255	16.037
ΔAIC	44.256	46.256	0	28.757	1.194

803 [1] More complex variants of the Yule model, that is, models assuming constant speciation rates within
804 more than two intervals (Yule3rate, Yule4rate, Yule5rate) did not provide a better fit (lower AICc
805 values) than the best model (DDL) and therefore, these are not reported.
806

807 **Table 2** Relative fit of three alternative models ("niche-filling" or early-burst, EB; Ornstein-
808 Uhlenbeck, OU; Brownian motion, BM) to body mass of Dasyurinae. Values obtained from the
809 MCC tree and values summarized across 1000 chronograms randomly sampled from the
810 posterior distribution of the BEAST MCMC analysis are shown.

811

812

813

	EB	**OU**	**BM**
(a) MCC tree			
ln(*L*)	-17.887	-22.812	-22.812
ΔAICc	0	9.849	7.658
AIC_w	0.971	0.007	0.021
(b) 1000 trees			
ln(*L*)	-18.475	-22.405	-22.405
ΔAICc	0	7.859	5.669
AIC_w	0.873	0.036	0.089

Table 3 Community phylogenetic results for the seven biogeographic regions. *N* is the number of taxa occurring in each region. Observed values, randomized values (null model), *z*-values for the observed value based on the randomization tests and *p*-values were calculated for both measures: mean pairwise distance (MPD) and mean nearest taxon distance (MNTD). Significant values are indicated in bold.

	N	**Observed**	**Random.**	***z*-value**	***p*-value**
(a) MPD					
Eremaean	24	45.81	47.23	-2.46	**0.029**
SW	9	45.28	43.85	0.87	0.821
NTE	14	44.52	45.79	-1.19	0.114
Tasmania	5	36.77	39.54	-0.94	0.157
Torresian	17	46.87	46.38	0.56	0.684
Irian	5	42.06	39.57	0.88	0.823
New Guinea	16	43.01	46.20	-3.33	**0.008**
(b) MNTD					
Eremaean	24	22.71	22.29	0.27	0.617
SW	9	33.99	29.35	1.30	0.914
NTE	14	21.23	25.80	-1.81	**0.044**
Tasmania	5	34.69	35.99	-0.18	0.405
Torresian	17	18.72	24.32	-2.68	**0.006**
Irian	5	38.30	35.83	0.44	0.608
New Guinea	16	20.63	24.86	-1.92	**0.036**