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Convergent evolution across the Australian continent: ecotype diversification drives morphological convergence in two distantly related clades of Australian frogs

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Abstract

Animals from different clades but subject to similar environments often evolve similar body shapes and physiological adaptations due to convergent evolution, but this has been rarely tested at the transcontinental level and across entire classes of animal. Australia's biome diversity, isolation and aridification history provide excellent opportunities for comparative analyses on broad-scale macroevolutionary patterns. We collected morphological and environmental data on eighty-four (98%) Australian hylid frog species and categorized them into ecotypes. Using a phylogenetic framework, we tested the hypothesis that frogs from the same ecotype display similar body shape patterns: (i) across all the Australian hylids, and (ii) through comparison with a similar previous study on 127 (97%) Australian myobatrachid species. Body size and shape variation did not follow a strong phylogenetic pattern and was not tightly correlated with environment, but there was a stronger association between morphotype and ecotype. Both arboreal and aquatic frogs had long limbs, whereas limbs of fossorial species were shorter. Other terrestrial species were convergent on the more typical frog body shape. We quantified the strength of morphological convergence at two levels: (i) between fossorial myobatrachid and hylid frogs, and (ii) in each ecomorph within the hylids. We found strong convergence within ecotypes, especially in fossorial species. Ecotypes were also reflected in physiological adaptations: both arboreal and cocooned fossorial frogs tend to have higher rates of evaporative water loss. Our results illustrate how adaptation to different ecological niches plays a crucial role in morphological evolution, boosting phenotypic diversity within a clade. Despite phylogenetic conservatism, morphological adaptation to repeatedly emerging new environments can erase the signature of ancestral morphotypes, resulting in phenotypic diversification and convergence both within and between diverse clades.

Introduction

Understanding processes shaping the great morphological diversity we observe among species, and the patterns and determinants of this diversity, always has been an important area of research in evolutionary biology (Gould, 1970; LaBarbera, 1989; Blackburn & Gaston, 1994; Foote, 1997). Development of ever more refined phylogenetic hypotheses, coupled with recent analytical and technological advances, has spurred a resurgence in attempts to better understand how morphological evolution is shaped by adaptation in the context of phylogenetic history (Losos, 1990; Wainwright, 1991; Schluter, 2000; Gavrilets & Losos, 2009). One of the most powerful and fascinating aspects of these emerging approaches is the improved ability to clearly identify repeated patterns of morphological evolution across species-rich radiations. In so doing, it is possible to examine underlying selective pressures that

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might have promoted the evolution of particular morphotypes.

Gross body shape and environmental niche are often correlated (Wainwright & Reilly, 1994; Malhotra & Thorpe, 1997; Harmon *et al.*, 2005; Losos & Mahler, 2010). Different selective pressures imposed by the environment will drive diversification within a clade (Losos *et al.*, 1997), but similar selective pressures can drive optimization on the same solution multiple times, leading to convergence among species between even distantly related clades. Thus, it is common to observe convergent morphotypes in species from different lineages that share a similar ecotype (Chiba, 2004; Kawahara & Rubinoff, 2013; Ingram & Kai, 2014). Examples include locomotion in jerboas and kangaroo rats (Webster & Dawson, 2004) or lamnid sharks and tunas (Donley *et al.*, 2004), trophic functional morphology in marsupial and placental carnivores (Jones *et al.*, 2003), diet in Old World and New World rats (Ben Moshe *et al.*, 2010), hindlimb morphological adaptations of *Biziura* and true stifftail diving ducks (McCracken *et al.*, 1999), and body size and shape difference as an adaptation to environmental niche in Anoles of the Greater Antilles (Harmon *et al.*, 2005). Similarly, parallel adaptive evolution of clades that are part of the same broader radiation is relatively common (Schluter & Nagel, 1995), and it often leads to morphological convergence due to independent adaptations to the same environmental niche (Schluter, 2000; Losos, 2011; Muschick *et al.*, 2012). Morphological and behavioural convergence has emerged in similar environments of geographically isolated species pairs in many taxa, including Hawaiian web-building spiders (Blackledge & Gillespie, 2004), cave amphipods (Jones *et al.*, 1992), Caribbean anoles (Losos, 1992), and ecomorphs of cichlid fishes in lakes Malawi and Tanganyika (Kocher *et al.*, 1993; Salzburger, 2009). Conversely, it is also common that new morphotypes appear in the same lineage, as the colonization of new or vacant habitats can provide new ecological niches that might not have been present in the past (Schluter, 2000). Studies in *Anolis* lizards (Losos *et al.*, 1997), warblers (Böhning-Gaese *et al.*, 2003) and dendrobatid frogs (Graham *et al.*, 2004) demonstrate that environmental niches display a high level of evolutionary lability. Whereas habitat use can impact both species richness and phenotypic traits, phylogenetic legacy also can constrain adaptive processes (Wiens, 2015). Nevertheless, morphological adaptation to particular environments might be able to override phylogenetic conservatism – convergence can erase traces of previous morphological adaptation to an ancestral microhabitat (Moen *et al.*, 2013), sometimes even enabling species that share the same ecotype or behaviour to look morphologically more similar to each other than to their ecologically different but closely related sister clades (Serb *et al.*, 2011; Tobler & Hastings, 2011; Mahler *et al.*, 2013).

Amphibians are thought to experience more environmental constraints than most vertebrates due to permeable skin that provides low resistance to evaporative water loss in terrestrial habitats (Navas *et al.*, 2004; Buckley *et al.*, 2012). Nevertheless, they have successfully diversified into forms that can cope with an astonishingly wide array of habitat types through morphological, behavioural and physiological adaptations. Amphibians, and anurans in particular, are found across a wide range of habitats, varying greatly in temperature, aridity and elevation: from the permafrost of Alaska, to rainforest, mountainous regions, and even deserts (Feder & Burggren, 1992). Although gross morphology of anurans is thought to be conserved in the sense that they represent a highly derived vertebrate body type (Shubin & Jenkins, 1995; Lougheed *et al.*, 2006), frogs and toads generally display a tight correlation between body shape patterns and habitat use or environmental niche (Duellman, 1986; Wells, 2010; Blackburn *et al.*, 2013; Vidal-García *et al.*, 2014). Thus, convergent evolution in morphotype should be common across diverse lineages that share similar ecotypes (Moen *et al.*, 2013). This is especially conspicuous in fossorial frogs, as they display a more rotund body shape with relatively shorter and stronger limbs that provide a lower surface-to-volume ratio while helping them burrow (Emerson, 1976). Examples of this body plan are as follows: North American *Scaphiopus*, South American *Lepidobatrachus*, Australian myobatrachids *Heleioporus* and *Myobatrachus*, and European *Pelobates* (Wells, 2010). In contrast, arboreal frogs tend to display a body shape that can be spread to distribute weight along the snout–vent axis: slender bodies, long limbs, toe and finger disc pads, and extensive webbing that helps in mid-flight when jumping (Tyler, 1998). This body shape pattern is displayed in arboreal frogs from different lineages, such as the South American hylid genus *Phyllomedusa* or the African rhacophorid *Chiromantis* (Duellman, 1986).

We were interested in testing for the existence and strength of convergent evolution at the level of an entire continent, comprising many diverse habitats, and across multiple highly diverse radiations. Australia is very biome-diverse, with one of the largest arid zones in the world, a long history of isolation, and numerous discrete endemic radiations, making it a model area for broad-scale comparative analyses (Byrne *et al.*, 2008). Since at least early–mid-Miocene (~15–23 MYA), Australia has become progressively more arid, and is now dominated by arid or seasonally arid biomes, a process that has played a dominant role in the evolution of the Australia biota (Byrne *et al.*, 2008; Pepper *et al.*, 2011a, c, 2013; Pepper & Keogh, 2014). In stable environments, ecological similarities and environmental niche might be likely to be conserved in certain clades for long macroevolutionary periods of time (Wiens & Graham, 2005; Crisp *et al.*, 2009), leading to the hypothesis that some arid-adapted taxa could have diversified from an ancestor already adapted to aridity (Byrne *et al.*, 2008). On the other hand, in unstable and comparatively derived environments such as the Australian arid zone, ecological niches might be evolutionarily labile (Losos *et al.*, 2003), and the climatic changes might have driven adaptation to dry environments (Byrne *et al.*, 2008; Pepper *et al.*, 2011b). However, the idea that adaptive diversification in Australia's arid zone might lead to similar morphotypes, physiological mechanisms and behavioural adaptations in different lineages has not been tested yet. Hylid frogs, commonly referred to as 'tree' frogs, and myobatrachid or 'southern' frogs are the two largest frog radiations in Australia, together comprising almost 90% of Australian frog species (Cogger, 2014). Both groups are species-rich and ecologically diverse in that they occupy most of the available habitats in the region, including arid regions. We have shown previously with the myobatrachid frog radiation that there is a good match between environment and body shape: species in wet habitats displayed streamlined body shape and long limbs, species in arid environments have shorter limbs, and habitat generalist species display an intermediate (typical) body shape that works well in a wide variety of environments (Vidal-García *et al.*, 2014). Most morphological diversity in myobatrachids evolved early in their diversification history (Vidal-García *et al.*, 2014).

The Australian hylid radiation, like myobatrachid frogs, also has diversified into several ecotypes, making it an ideal model system in which to look for repeated morphological patterns in the same ecotype. Hylid frogs are one of the most species-rich families of anurans and include 13% of all 7380 amphibian species (*AmphibiaWeb*, 2015). The Pelodryadinae hylid lineage is the second largest radiation of the five frog families represented in Australia. It currently is comprised of two genera and 86 described species in Australia (although some still recognize only a single genus *Litoria* pending future taxonomic revision; Frost, 2014) and 176 species in the Australo-Papuan region, but there are certainly many more undescribed species, particularly in Papua (Kraus & Allison, 2004; Richards & Oliver, 2006; Oliver *et al.*, 2008; Richards *et al.*, 2009). Australian hylids occupy an extensive array of ecotypes ranging from species that are primarily fossorial, to those that are highly aquatic, and also species that occupy a wide range of terrestrial microhabitats including rocky areas, grasslands, rainforest canopy and wet sclerophyll forest litter (Cogger, 2014). All species from the Meso and South American sister clade Phyllomedusinae are highly arboreal, and it is thought that the most likely ancestral ecotype for Pelodryadinae hylid frogs was arboreal (Moen *et al.*, 2013; Bonetti & Wiens, 2014). The Australo-Papuan hylid radiation is estimated to have diverged approximately ~62 to 52 MYA from the other hylids (Moen *et al.*, 2013; Bonetti & Wiens, 2014; Pyron, 2014). The long period of isolation and enormous range of ecological opportunities in Australia might have played a role in promoting ecotype diversification of the Pelodryadinae, enabling them to evolve into forms that could occupy a wide range of novel environmental niches.

We examined morphological, environmental and physiological data of the Australian hylid frogs in a phylogenetic context and compared it to the myobatrachid frog radiation. We focused on four main questions: (i) Are there body size and shape differences among different clades and ecotypes? (ii) Do species from the same ecotype show similar morphological patterns, even across different clades and families? (iii) Are these body shape similarities due to morphological convergence and ecological adaptation, or evolutionary conservatism? (iv) Do physiological traits, such as cutaneous evaporative water loss, vary among species relative to body shape and environmental niche? To answer these questions, we examined morphological variation, evaporative water loss and habitat use in the four main ecotypes (arboreal, ground-dwelling, semi-aquatic and fossorial) across all species and lineages of Australian hylid frogs. We then compared it with morphological and environmental patterns found in the myobatrachid frog radiation using phylogenetic comparative methods.

Materials and methods

Morphological traits and physiology

We collected detailed morphometric data from 434 specimens across 84 of 86 total species of the Australian hylids from the genera *Cyclorana* and *Litoria*. Sample size was five adult individuals per species, with the exception of a few species for which we could only measure three or four specimens due to limited museum collections. A list of the species and specimens used in this study is provided in the Appendix S1. All morphological measurements were collected as per Vidal-García *et al.* (2014). We took 34 external morphological measurements to the nearest 0.1 mm with digital callipers. All measurements were taken by the same person (MVG) to ensure consistency in the data collection. We preferentially measured female frogs to avoid the potentially confounding effects of sexual size dimorphism and sexually selected male traits, but we did have to include some males for several nonsexually dimorphic species due to a lack of adult females in the collections (details on specimens in Appendix S1). Given that our primary focus was on interspecies differences, this had no impact on our results.

We gathered data on cutaneous resistance to water loss (s cm^{-1}) from the literature in order to characterize physiological adaptation to the environment (Tracy *et al.*, 2010). Values from Tracy *et al.* (2010) were adapted to match our specimens by interpolating their snout–vent length (SVL), in order to be able to use them for further analyses. Based on SVL values in the specimens used in Tracy *et al.* (2010), we estimated approximate values of cutaneous resistance to water loss for each species according to our mean SVL for each species in our morphometric data set.

We used the same 25 morphological raw variables and two morphological ratios (relative arm and leg length) from our previous study on the myobatrachid frogs (Vidal-García *et al.*, 2014) to test for morphological convergence patterns between hylids and myobatrachid frogs.

Environmental variables

We used the Atlas of Living Australia online database (Atlas of Living Australia, 2014) to obtain distribution data of each frog species, and several environmental variables that are of relevance to frogs across the full spectrum of habitat variables: annual mean evaporation, precipitation in the warmest quarter (Bio18; Hijmans *et al.*, 2005), temperature in the warmest period (Bio05; Hijmans *et al.*, 2005), soil nutrient status, annual mean moisture index, topographic slope and mean net primary productivity (NPP), and the best five independent terrestrial layers (precipitation in the driest quarter: Bio17; seasonality of precipitation: Bio15; seasonality of radiation: Bio23; radiation in the warmest quarter: Bio26; moisture on the highest quarter: Bio32). In total, we assembled 12 environmental variables for 10 × 10 km blocks in the Universal Transverse Mercator coordinate system (UTM) centred on the location of each museum record. We manually added all records from Queensland Museum, because they are not currently included in the Atlas of Living Australia, so that we could plot the whole geographic distribution of each species across Australia. We gathered this information for every Australian hylid species, resulting in 105 630 records. We then calculated mean values for all the environmental variables based on the whole geographic distribution of each species, as a measure of niche position. To calculate it, we used each UTM just once to avoid a biased ecological data set due to duplicated records for the same location. We also gathered data on ecological habits or ecotypes of each species by summarizing qualitative traits on their natural ecology and microhabitat preferences from Cogger (2014), Tyler (1998), Barker *et al.* (1995) and Anstis (2013). Based on this, we categorized each species into one of four ecotypes: (i) arboreal, (ii) semi-aquatic, (iii) ground-dwelling or (iv) fossorial.

Statistical analyses

After the evaluation of the data obtained for all 34 morphological variables, nine were excluded because they were difficult to measure accurately (i.e. shoulder width and forearm width), were absent in some species (i.e. tympanic membrane), or were highly correlated with other measurements and, thus, overrepresented in our data set (i.e. toe and finger length). Body weight also proved difficult to measure accurately because of the number of gravid females and was also discarded from further analysis. This left a total of 25 morphological variables for detailed analysis (Table S1). To quantify body size and shape differences among species and genera, we evaluated the 25 linear measurements with principal component analysis (PCA), and the 12 environmental variables were also first evaluated using PCA. That allowed us to reduce the multidimensionality of the data and look at the morphological and ecological differences between species and clades more clearly. In the raw morphological data set, the first principal component (PCraw 1) is highly correlated with body size, whereas the second (PCraw 2) and the third (PCraw 3) represent body shape. We also evaluated the impact on our results of first correcting for size variation. We did this by replicating our PCA on size-corrected morphological data (PCAcorr; 24 linear measurements corrected by taking residuals with body size – SVL). As very few measurements were missing from individuals, we calculated standard principal components with imputation of missing values to include all the specimens in both PCAs. We used linear regression analyses to test for any correlation between each principal component of the raw morphological data set and the environmental data set. We also examined the distribution of burrowing behaviour (burrowing, no burrowing) and ecotype (fossorial, ground-dwelling, aquatic, arboreal) for each species as it related to body size/shape and habitat.

To incorporate phylogenetic history into our analysis of morphological change, we used the mitochondrial (12S and 16S) data for Australian hylid frogs published in Rosauer *et al.* (2009) to generate a Bayesian phylogenetic tree. These data also were incorporated into the assessment of the phylogenetic history of the world's amphibians by Pyron & Wiens (2011) and amphibian biogeography (Pyron, 2014), and the topologies presented for Australian hylids in these three papers were highly consistent. Our aim was simply to generate a usable topology with branch lengths rather than inferring phylogeny; therefore, we used the aligned sequences made available from Pyron's (2014) paper and constrained our analyses to make sure that the resultant topology did not differ from previously published phylogenetic analyses. The phylogeny was then pruned to obtain subtrees suitable for each of the analyses, using the R package *ape* (Paradis *et al.*, 2004). The genus *Litoria*, as currently understood, is species-rich and also taxonomically problematic in that it includes a vast array of morphological and ecological diversity. Pending taxonomic revision, to improve our analyses of morphological evolution we divided *Litoria* into 20 species groups based on a combination of genetic and morphological distinctiveness and also used the grouping '*Cyclorana*' for an additional group of morphologically distinct hylids [see Frost (2014) for summary of current state of the taxonomy; Fig. 1]. We calculated Pagel's lambda (λ) (Pagel, 1999; Freckleton *et al.*, 2002) and Blomberg's *K*-statistic (Blomberg *et al.*, 2003) with the R package *phytools* (Revell, 2012), and the *K*-statistic's generalization for multivariate data (K_{mult}; Adams, 2014a) with geomorph (Adams *et al.*, 2014), to determine the strength of phylogenetic signal in our data. Pagel's lambda and the *P*-value from *K* and K_{mult} statistics evaluate the magnitude of phylogenetic signal in certain variables (or sets of variables), whereas the *K* and K_{mult} statistics assess the fit of a Brownian motion (BM) evolutionary model of trait evolution (Pagel, 1999; Freckleton *et al.*, 2002; Blomberg *et al.*, 2003). Univariate tests for phylogenetic signal (Pagel's lambda and Blomberg's *K*) were performed for ten relevant variables: morphology PCraw 1, morphology PCraw 2, morphology PCraw 3, SVL, morphology PCcorr 1, morphology PCcorr 2, relative arm length (arm length/SVL ratio), relative leg length (leg length/SVL ratio), relative webbing (webbing 4th–5th toe/SVL), shape ('pointiness') of the snout (eye–snout length/eye span), environmental PC 1 and environmental PC 2. We performed the tests for Pagel's lambda taking the standard error (SE) within species into account in all morphological variables. We evaluated the magnitude of phylogenetic signal in multivariate data (K_{mult}) in the 25 raw and 24 size-corrected morphological variables, and the 12 environmental variables. As we obtained lower *K* and K_{mult} values than expected under a BM model of trait evolution (see Table S4), we assessed the fit of different alternative models of trait evolution (Ornstein–Uhlenbeck, Early Burst and a white – non-phylogenetic – model) with the sample size-corrected Akaike's Information Criterion (AICc; Burnham & Anderson, 2002), using *geiger* (Harmon *et al.*, 2008). We performed phylogenetic generalized least squares (PGLS) regression analyses to test whether the phylogenetic relationships affected the covariance between different variables: relative arm length, relative leg length, relative webbing and relative naris–snout length) and the principal components for both the morphological and the environmental data set. We also performed the PGLS generalization for multivariate data with the 25 raw and the 24 size-corrected morphological variables (Adams, 2014b). All PGLS analyses for univariate data were performed with the R package *caper* (Orme *et al.*, 2013), and with the function procD.pgls in *geomorph* for multivariate data (Adams *et al.*, 2014).

To help facilitate comparisons with the Australian myobatrachid frogs, we used the phylogenetic framework previously employed for Australian myobatrachid frogs in Vidal-García *et al.* (2014). We estimated ancestral states in Australian hylids and myobatrachids for several morphologically continuous variables that showed most of the body shape variation among all species (relative leg length, relative arm length, foot shape, head shape, among others) and ecotypes, to visualize morphological convergence between different clades and ecotypes, using the R packages *ape* (Paradis *et al.*, 2004) and *phytools* (Revell, 2012). To assess the strength of morphological convergence in each ecotype, we applied the Wheatsheaf index (Arbuckle *et al.*, 2014) using phylogenetic relatedness and morphological similarity data. We used it at two different levels: (i) all different ecomorphs within the Australian hylids (as several different ecotypes can even be found within the same clade; Fig. 2), and (ii) between fossorial hylids and myobatrachids, to detect both the strength of convergent evolution on fossorial ecomorphs and which morphological traits are most important for burrowing behaviour. To obtain the variance–covariance matrices necessary for these analyses (derived from both the Australian hylid phylogeny, and the phylogeny including Australian hylids and myobatrachids), we used the R package *ape* (Paradis *et al.*, 2004).

Results

In the raw morphological data set, the first three principal components (eigenvectors) accounted for a total of 93.02% of the overall variation, with PCraw 1, PCraw 2 and PCraw 3 explaining 88.76%, 4.257% and 2% of the variance, respectively (Table S1). As expected, PCraw 1 was highly correlated with body size (SVL, $r^2 = 0.966$, $P < 0.0001$), so we treated it as an estimate of absolute body size. Absolute adult body size (SVL) differed greatly among species, ranging from 14.85 to 132.84 mm. The average SVL of the smallest species was only 15.39 ± 0.45 mm (*Litoria microbelos*), whereas the largest was 103.03 ± 4.37 mm (*Litoria splendida*). Both PCraw 2 and PCraw 3 represented body shape: PCraw 2 was highly correlated with overall foot shape and especially degree of foot webbing ($r^2 = 0.609$, $P < 0.0001$) and PCraw 3 was correlated with head shape, in particular pointiness of the snout (naris–snout distance, $r^2 = 0.217$, $P < 0.0001$). Overall body shape differed greatly among species, but subtly among different clades (raw morphological PCraw 2 and PCraw 3; Fig. 1). In morphological PCraw 2, the fossorial genus *Cyclorana*, and especially *Cyclorana novaehollandiae*, displayed the most extreme negative loadings (small feet, lack of webbing), whereas some *Litoria* species (such as the aquatic frog *Litoria castanea* or *L. dahlii*) displayed the most positive values (large feet, extensive toe webbing) (Fig. 1). In morphological PCraw 3, *Cyclorana alboguttata* and *Litoria nasuta* displayed the most positive values (pointy snout), whereas *L. splendida* displayed

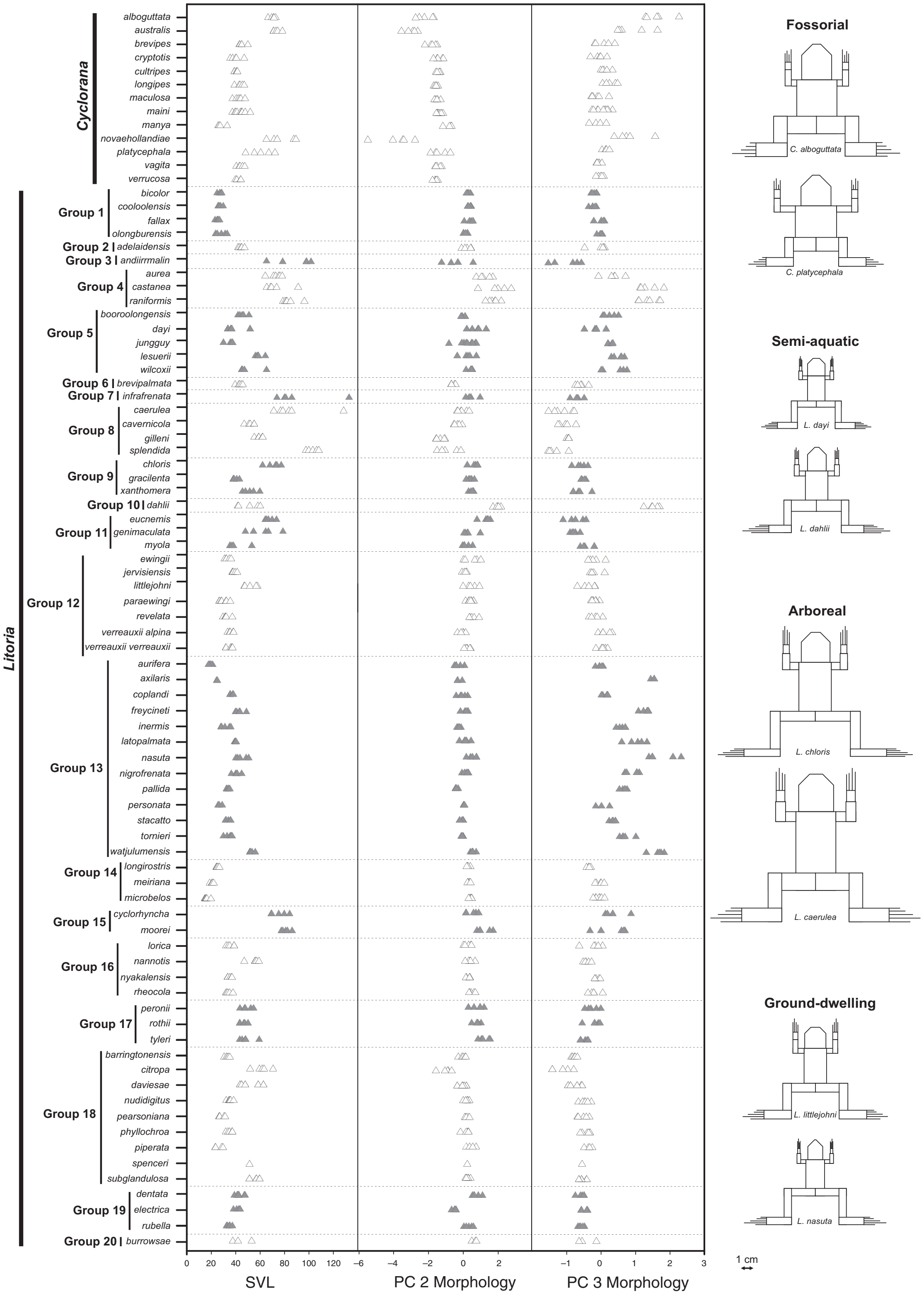

Fig. 1 Scatterplot by species of snout–vent length (SVL), and PC 2 and PC 3 from the morphological data set. *Litoria* species are grouped by phylogenetic clades. The representative drawings summarize mean measurements and body shape patterns displayed by two species from each ecotype.

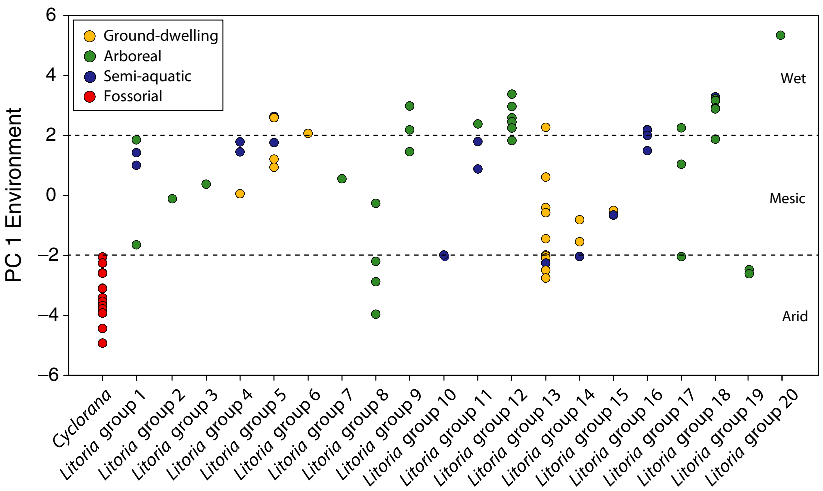

Fig. 2 Summary of mean PC 1 values of the environmental data set for each species showing the environmental breadth displayed in each clade.

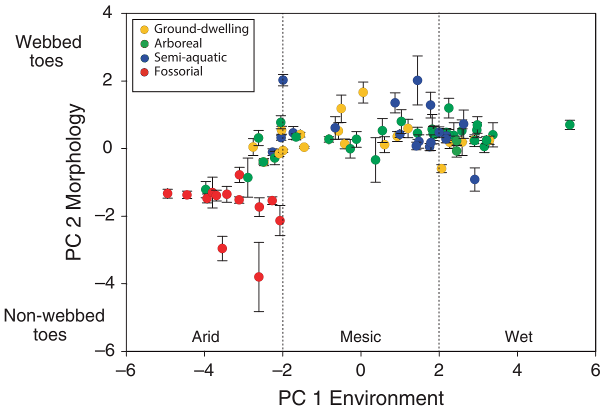

Fig. 3 Scatterplot of mean values ± SD for PC 1 of the environmental data set and PC 2 of the morphological data set by species.

the most negative values (blunt snout) (Fig. 1). The first five principal components from the size-corrected morphological data set accounted for a total 75.19% of the overall shape variation, with PCcorr 1 and PCcorr 2 explaining 32.96% and 18.31% of the variance (Table S2, Fig. S2). PCcorr 1 was highly correlated with foot, tibial and femur length ($r^2 = 0.8306$, $P < 0.0001$; $r^2 = 0.7711$, $P < 0.0001$; and $r^2 = 0.769$, $P < 0.0001$, respectively), whereas most variation in PCcorr 2 was explained by head shape (head width: $r^2 = 0.6628$, $P < 0.0001$; mouth width: $r^2 = 0.6589$, $P < 0.0001$; and head length: $r^2 = 0.5392$, $P < 0.0001$).

In the environmental data set, the first two principal components accounted for 75.55% of the overall variation. PCenv 1 explained 50.70% of the variance and PCenv 2 an additional 24.84% (Table S3). PCenv 1 was highly correlated with moisture [annual mean climatic moisture index (CMI): Bio28, $r^2 = 0.906$, $P < 0.0001$], mean NPP ($r^2 = 0.865$, $P < 0.0001$) and precipitation in the driest quarter (Bio17, $r^2 = 0.835$, $P < 0.0001$). The annual mean CMI depicts the relationship between plant water demand and available precipitation (Willmott & Feddema, 1992) and thus is directly proportional to NPP ($r^2 = 0.742$, $P < 0.0001$). Therefore, we interpreted PCenv 1 as an estimate of 'habitat humidity'. As the CMI indicator ranges from −1 to +1 (Willmott & Feddema, 1992), we interpolated this scale to PCenv 1 so as to define the ecological niche of each species. There was a strong relationship between the distribution of burrowing behaviour and occupation of arid environments (Fig. 2), with significant ecological differences between fossorial and the other ecotypes ($t_{45.56} = 11.722$, $P < 0.0001$). Most species across the various phylogenetic groups occupy mesic and wet environments rather than arid, although a number of species have adapted to arid conditions, including both fossorial species such as *Cyclorana*, and arboreal species, such as *L. gilleni*, *L. splendida* and *L. caerulea* ($r^2 = 0.776$, $P < 0.0001$; Litoria group 8; Fig. 2). Environmental PCenv 2 was correlated with radiation seasonality (Bio 23; Hijmans *et al.*, 2005), which corresponds to a latitudinal gradient and a general association with biomes.

We found a strong phylogenetic signal in all tested variables (and multivariate sets) with estimated λ values equivalent to 1, and significant P-values for the K and K_{mult} statistics, except for relative arm length (Table S4), that displayed marginally lower and nonsignificant values. K and K_{mult} had lower values than those expected under a BM evolution model, and this was supported by better fit of the alternative models of trait evolution for most variables (Table S5). An Ornstein–Uhlenbeck model (with a single optimum) showed the best fit for several variables, and PCA variables were generally best fitted by the white (nonphylogenetic) model (Table S5). There was no relationship between body size (SVL) and environmental niche

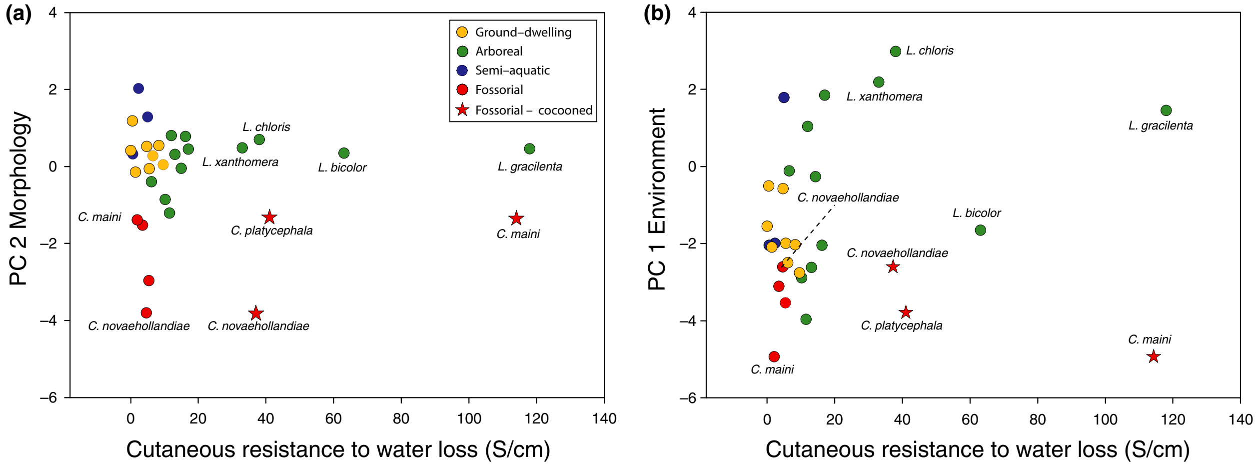

Fig. 4 (a) Scatterplot of mean values per species for cutaneous resistance to water loss (S cm^{-1}) and PC 2 of the morphological data set by species. (b) Scatterplot of mean values per species for cutaneous resistance to water loss (S cm^{-1}) and PC 1 of the environmental data set by species. Only species with cutaneous resistance data from Tracy *et al.* (2010) are depicted.

(environmental PCenv 1, $r^2 = 0.0036$, $P = 0.4745$), and this was consistent following phylogenetic correction with PGLS ($r^2 = 0.0005$). There was a weak relationship between environmental niche and morphological PCraw 2 ($r^2 = 0.2250$, $P < 0.0001$; Fig. 3) and PCraw 3 ($r^2 = 0.061$, $P < 0.0001$), but this relationship did not persist following phylogenetic correction for morphological PCraw 2 ($r^2 = 0.0537$) or all the 24 size-corrected morphological variables ($r^2 = 0.0046$; Fig. S2). No relationship was found between the 25 raw variables and the ecotype ($r^2 = 0.0559$), or between the 24 size-corrected morphological variables and ecotype ($r^2 = 0.1290$). On the other hand, cutaneous resistance to water loss (s cm^{-1}) did not display a correlation with morphology (phylogenetic and size-corrected morphological variables; $r^2 = 0.0162$), whereas it separated the four ecotypes very well with phylogenetic correction ($r^2 = 0.5297$): aquatic, ground-dwelling and noncocooned fossorial species displayed the lowest values, whereas arboreal and cocooned fossorial frogs had highest cutaneous resistance (Fig. 4a). Cutaneous resistance in fossorial species was also higher in more arid regions, although it did not follow a specific trend in arboreal frogs (Fig. 4b).

Despite substantial overlap in the biplot of relative arm length (humerus length + forearm length + hand length) and relative leg length (femur length + tibial length + foot length) among ground-dwelling, arboreal and semi-aquatic species, there is some similarity between some arboreal and semi-aquatic species, and conspicuous differences in fossorial species, which occupied a different region of the morphospace (Fig. 5). Morphological patterns found in fossorial hylids also were consistent with those found on the myobatrachid burrowing species: there were clearer differences among fossorial hylid species and the other ecotypes, than with myobatrachid fossorial species (Fig. 5). Even though myobatrachid frogs are morphologically quite divergent from Australian hylids, *Cyclorana* species occupied similar regions on the morphospace plot as the myobatrachid backward burrowers. Limb ratio (relative arm length/relative leg length) similarities between fossorial species of both families are conspicuous when plotting ancestral state estimation analyses: most hylid species and internal nodes of the hylids display relatively low ratio-values, whereas most myobatrachid backward burrowers and *Cyclorana* species exhibit higher values (Fig. S1). Ancestral state estimation analyses on current ecotype states suggest that Australian hylids have experienced multiple shifts in ecotype over their evolutionary history (Fig. S1).

We used the Wheatsheaf index to further evaluate this potential morphological convergence between fossorial frogs in the two families and obtained positive values when assessing the strength of the morphological convergence: Wheatsheaf index results were significant for most of the variables in fossorial species in Australian hylids and myobatrachids (Table S6). The arboreal ancestral ecotype of the Pelodryadinae suggests different ecotypes have evolved independently, and perhaps multiple times, within the Australian hylids (Moen *et al.*, 2013; Pyron, 2014; Bonetti & Wiens, 2014; Fig. 2). This allowed us to test for the convergence strength among different ecomorphs within the Australian hylids (except for the fossorial *Cyclorana* due to the monophyletic origin of this ecomorph). Both arboreal and aquatic ecotypes displayed significant results in most of the variables when the Wheatsheaf index was applied, showing a strong morphological convergence in these ecomorphs (Table S7). On the other hand, terrestrial species did not display as much morphological convergence.

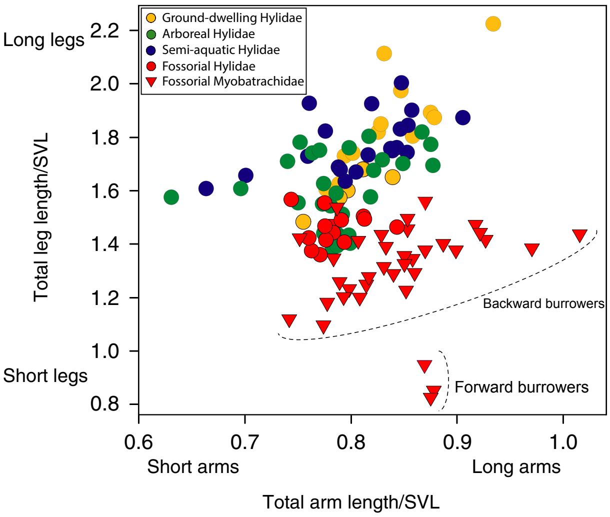

Fig. 5 Scatterplot of the ratio of relative arm length [arm length/snout–vent length (SVL)] to relative leg length (leg length/SVL). The means are displayed for each species.

Discussion

We examined morphological variation, habitat use and cutaneous resistance to water loss across all lineages and species of Australian hylid frogs to test for morphological convergence in ecotype. At a broad level, we found that morphotype matches ecotype, especially in the more extreme arboreal and fossorial ecotypes, which suggests that adaptation to different ecological niches plays a crucial role in shaping morphological diversity. Correlation between body shape and ecotype found in hylids was similar to patterns displayed by the myobatrachid frog family (Vidal-García *et al.*, 2014), showing morphological convergence of relative limb length on each ecotype in these two frog radiations. Fossorial backward-burrowing hylids resembled backward-burrowing myobatrachids, suggesting that ecology can erase ancestral morphotypes and drive convergence of phenotypes between different radiations. Cutaneous resistance to water loss also was related to ecotype, reaching its maximum values in arboreal species and cocooned fossorial frogs. We discuss each of our four main aims in turn.

Are there body size and shape differences among different clades and ecotypes?

The ancestor of the Pelodryadinae is thought to be arboreal and their sister group, the Phyllomedusinae, is exclusively arboreal (Moen *et al.*, 2013; Bonetti & Wiens, 2014; Pyron, 2014), yet the Australo-Papuan Pelodryadinae radiation has diversified into three novel ecotypes: ground-dwelling, semi-aquatic and fossorial, even shifting to a different ecotype more than once. Morphological differences among Australian hylids did not display a strong phylogenetic signal at a broad scale: certain body shapes have evolved multiple times within certain clades. Conversely, they did have a strong phylogenetic signal at a finer scale: species subtly conform to particular shapes within ecotypes, and this is especially conspicuous between the fossorial genus *Cyclorana* and species from the other ecotypes. This stresses the importance of certain environmental adaptations in shaping morphological patterns. Small-bodied species are more likely to be present in seasonal or cooler environments (Mousseau, 1997; Olalla-Tárraga & Rodríguez, 2007), whereas larger bodied species might be more common in areas with lower water availability (Ashton *et al.*, 2000), but we did not find any match between body size and environment or ecotype within *Litoria*. Australia is highly environmentally diverse, offering a wide variety of ecological niches, which might have played an important role in the ecological diversification of Australian hylids. Diversification rates in amphibians also might be higher than in other tetrapod radiations (Alfaro *et al.*, 2009; Rabosky, 2009a, b), which means adaptation to different ecologies may erase the imprint of past adaptation to an ancestral ecology (Moen *et al.*, 2013). Nevertheless, environmental niche evolution from one ancestral ecotype to several novel ecotypes might not be an unusual diversity of adaptive forms (Losos & Miles, 2002), and indeed, closely related species that display different ecologies and occupy different microhabitats are common in adaptive radiations (Schluter, 2000).

Do species from the same ecotype show similar morphological patterns, even across different clades and families?

Body shape patterns roughly matched each ecotype, and this correlation was strongest in the fossorial *Cyclorana* spp., which display nonwebbed feet, more pointed snouts and proportionally shorter limbs. This morphotype also was observed in all codistributed backward-burrowing myobatrachid frog species: body shape patterns among fossorial species from different families were strikingly similar when compared to closely related species from different ecotypes. Morphological convergence is not only shared between Australian fossorial frogs, but among most backwards burrowers, such as several species of bufonids, leptodactylids, microhylids, pelobatids and ranids (Wells, 2010). Semi-aquatic and arboreal hylid species displayed relatively longer limbs, which is thought to be linked with locomotive correlates (Emerson, 1985; Marsh, 1994; Jorgensen & Reilly, 2013). Semi-aquatic hylid species occupied a very small region of the morphospace, which might be explained by strong selective pressure for adaptations to aquatic life and improved swimming abilities. There was some morphological variation within arboreal species, which could be partly correlated with environmental variables, degree of arboreality and which part of the canopy they occupy (Manzano *et al.*, 2008). Some species, such as *Litoria xanthomera* or *L. chloris*, display long fore and hind limbs, big finger and toe pads, and extensive foot and hand webbing that helps them jump from the highest parts of the tree canopy. Conversely, other semi-arboreal species that occupy lower parts of the canopy display less extreme disc pads, degree of webbing and limb ratios, as they might not need to travel as vertically. Ground-dwelling hylid frogs did not show a well-defined morphological pattern although some of the most extreme jumping terrestrial frogs from *Litoria* group 13 (which includes the striped rocket frog *L. nasuta* and the Watjulum frog *L. watjulumensis*) displayed some of the largest ratios of hindlimbs to SVL. Interestingly, ecotypes were usually not conserved within and across *Litoria* lineages, which suggests that the particular ecotype of each species might be due to a combination of their phylogenetic history combined with their particular microhabitat resources and niche (Moen *et al.*, 2013). The transition from an arboreal/aquatic hylid ancestor to the fossorial *Cyclorana* spp. likely took place approximately 11–14 MYA, based on our ancestral state reconstruction of ecotypes in Australian hylids. This broadly corresponds with estimated time frames for the intensification of arid conditions in Australia (Byrne *et al.*, 2008). Adaptive responses to increasing aridity of Australia's environments and ecotype transitions also are observed in several other taxa that are highly dependent on water availability, such as diving beetles, amphipods, isopods and geckos (Leys *et al.*, 2003; Cooper *et al.*, 2007, 2008; Byrne *et al.*, 2008; Oliver & Bauer, 2011). Furthermore, a certain degree of phenotypic similarity would be predictable among species-rich radiations that are closely related or have diversified from two different, but morphologically similar, ancestors (Ingram & Mahler, 2013). Despite the tight correlation between ecology and phenotype, there might be other factors facilitating adaptation to each ecotype: species with a more generalized or conserved body shape pattern might display a wider array of behavioural tactics than other species, such as physiological mechanisms, and the selection of microhabitat shelter sites (Heatwole, 1961; Seebacher & Alford, 2002; Smith *et al.*, 2003).

Do physiological traits, such as cutaneous evaporative water loss, vary among species relative to body shape and environmental niche?

Most amphibians also rely on other behaviour to adapt to arid environments and reduce the evaporative water loss, such as burrowing or adopting certain body postures that protect vascularized ventral skin (Shoemaker *et al.*, 1992; Toledo & Jared, 1993; Tyler, 1998). Some frog species, such as *Cyclorana*, burrow and form cocoons of stratum corneum that encases the whole body, to avoid desiccation in arid environments. Other physiological mechanisms involve the secretion of substances (mucus, vasotocin, oxytocin, other hormones) that influence the cutaneous resistance of the skin to water (Toledo & Jared, 1993). Some arboreal frogs have the ability to change their cutaneous resistance potentials according to the air moisture. *Phyllomedusa* and some *Litoria* species (such as *L. caerulea*) spread lipid secretions all over the body surface to reduce water loss (Toledo & Jared, 1993). Cutaneous resistance of hylid frog species (Tracy *et al.*, 2010) was highly variable among species, and we did not find any clear phylogenetic, morphological or environmental correlation. Nevertheless, there was a correlation between ecotype and resistance to evaporative water loss, with arboreal species displaying the highest resistance to water loss, and aquatic and fossorial the lowest. Fossorial frogs also display the ability to change their water loss potential due to cocoon formation, coupled with their body shape (Bentley & Yorio, 1979; Withers, 1998). The high disparity shown in cutaneous resistance data between cocooned and noncocooned specimens of *Cyclorana maini* and *Cyclorana platycephala* stresses the importance of their burrowing behaviour and cocoon formation to avoid dehydration once the soil around their burrows presents low water potentials. Arboreal hylid species, such as *L. gracilenta*, *L. splendida* or *L. infrafrenata*, might avoid excessive water loss by high cutaneous resistance, coupled with postural changes that protect their ventral surfaces (Tyler, 1998). This is supported by previous studies, as most of the frogs that display elevated values are arboreal frogs (Tracy & Christian, 2005), mainly in the families Hylidae, Rhacophoridae and Hyperoliidae. Certain clades or species within these lineages usually differ widely in cutaneous resistance to water loss (Young *et al.*, 2005; Tracy *et al.*, 2010). Physiological responses also might be coupled with body shape, as a more rounded body shape might be advantageous in arid environments as it also helps minimize the water loss by increasing the volume–surface area ratio (Vidal-García *et al.*, 2014). Adaptation to a certain environmental niche could be achieved through correlated evolution of morphological and physiological traits (Emerson & Arnold, 1989; Bauwens *et al.*, 1995). Furthermore, ecological niche establishment could be constrained by physiological and morphological characteristics, especially if their interaction can determine performance capacities, enabling or hindering adaptation to certain environments (Losos, 1990; Garland & Losos, 1994).

Are body shape similarities due to morphological convergence and ecological adaptation, or evolutionary conservatism?

Diversification into different ecotypes is usually followed by morphological specialization (Wainwright, 2007), but it may not be the only component, and there could be adaptive processes at other levels. Mechanical or environmental convergence also may foster morphological convergence if the starting body shape patterns were similar (Alfaro *et al.*, 2004; Wainwright, 2007). Convergence has been widely demonstrated in related clades that have dispersed to, or been isolated in, geographically distinct areas such as different islands, lakes, or even continents where the establishment of new ecotypes specialists occurs due to ecological opportunities and a lack of niche competitors (Losos, 1996; Schluter, 2000; Wiens *et al.*, 2006; Ingram & Mahler, 2013). Several tetrapod taxa display striking morphological convergence among phylogenetically distant clades: felids and linsangs (Gaubert & Veron, 2003), *Draco* and *Anolis* lizards (Ord & Klomp, 2014), and grebes and loons (Van Tuinen *et al.*, 2001). Convergent ecomorphs might be relatively common in species-rich community assemblages as the number of species would surpass the number of available niches (Scheffer & van Nes, 2006; Miller & Powell, 2010). That would be the case for cichlid communities in Tanganyika Lake (Muschick *et al.*, 2012), Caribbean *Anolis* lizards (Mahler *et al.*, 2013), and coral reef damselfishes (Frédérich *et al.*, 2013). Thus, convergent evolution might be a common and recurrent event in lineages that live in labile landscapes (Stayton, 2008; Hansen, 2012; Mahler *et al.*, 2013).

On the other hand, morphological convergence patterns in sympatric clades are less common as resident species could constraint establishment opportunities in certain niches, hindering diversification of similar morphotypes (Muschick *et al.*, 2012; Ingram & Mahler, 2013). Although our results suggest a tendency for morphological convergence between hylid and myobatrachid species sharing the same ecotype, the body shape pattern of fossorial ecotype hylids resembles, but does not completely match, the one present in myobatrachid backward burrowers. That would not be surprising, as morphological convergence between distantly related clades could be masked by phylogenetic legacy. Furthermore, different lineages also can take different paths through the morphospace even if they are exposed to the very same selection histories (Foote, 1994; Wainwright, 2007). Dissimilar morphological diversification across a radiation could be driven by an unequal amount of morphological change among clades or have arisen as a consequence of the directionality of morphological change (Sidlauskas, 2008). Different clades also may have displayed slightly different adaptive responses to the same selection pressures due to their phylogenetic legacy (Alfaro *et al.*, 2005; Ord & Klomp, 2014), thus affecting the degree of morphological convergence.

Despite the long evolutionary history of amphibians, most of extant frog lineages display a proportionally late diversity (Roelants *et al.*, 2007). The Pelodryadinae hylids of Australia and New Guinea are an old radiation (~61 to 52 MY) (Roelants *et al.*, 2007; Pyron, 2014), but are probably still younger than the myobatrachid frog radiation, which is endemic to Australo-Papua (J.S. Keogh, D. Moore, P. Byrne & J.D. Roberts, unpublished). When novel hylid ecotypes appeared in Australia, the myobatrachid backward burrowers already may have occupied those ecological niches. Thus, morphological evolution within the Pelodryadinae might have been driven by adaptation to a more limited number of environmental niches and ecotypes. It is not surprising that the fossorial *Cyclorana* spp. evolved from an arboreal ancestor, as other Australian arid-adapted tetrapods also diversified from mesic or even tropical ancestors (Chapple & Keogh, 2004; Joseph *et al.*, 2006; Hugall *et al.*, 2008; Sanders *et al.*, 2008). Furthermore, the Pelodryadinae ancestor was solely arboreal, so hylid species from novel ecotypes might still resemble their arboreal ancestor (Moen *et al.*, 2013). Differences in the phylogenetic legacy of myobatrachids and hylids, and differences in ancestral ecotypes, could have influenced their morphological diversification and the level of convergence shown between the two radiations. Certain evolutionary conservatism seems to be quite common in anuran amphibians (Bossuyt & Milinkovitch, 2000; Roelants *et al.*, 2007; Vidal-García *et al.*, 2014). For example, the 'typical' or most generalized anuran morphology displayed in most ground-dwelling frogs is ubiquitous right across many anuran clades worldwide (Shubin & Jenkins, 1995; Jenkins & Shubin, 1998; Austin *et al.*, 2002).

In summary, our study suggests that ecotype diversification has played an important role in shaping morphological traits in Australian hylid frogs. Despite the fact that the 'typical' frog body shape pattern is the most common in species that occupy a wide range of ecological niches, morphotype usually matches ecotype. This is especially noticeable in the case of fossorial frogs, as their body shape is constrained by water balance restrictions imposed by arid microhabitats and their burrowing performance. Cutaneous evaporative water loss is correlated with body shape patterns and especially with fossorial and arboreal ecotypes. Our results also suggest that there is morphological convergence among different taxa that share the same ecotype. Aridification of Australia in the last 15 MY has driven environmental change, diversification opportunities and ecological adaptation. Despite the different evolutionary history of Australian hylids and Australo-Papuan myobatrachids, they display quite similar morphologies when sharing the same ecotype. Thus, although morphology is usually constrained by phylogenetic legacy, environmental correlates and niche conservatism also play an important role in shaping body shape patterns, driving morphological convergence between distantly related clades and shaping diversification within radiations.

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Supporting information

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Codes of the specimens per species.

Figure S1 Ancestral state estimation of ecotypes and relative limb length ratios: relative arm length (arm length/SVL) to relative leg length (leg length/SVL), across Australian hylid species. This figure was generated using the R packages *ape* and *phytools*.

Figure S2 Scatterplot of PC 1 and PC 2 values of the size-corrected morphological data set displaying shape differences among the four ecotypes: ground-dwelling, arboreal, semi-aquatic and fossorial. 95% confidence interval ellipses are shown for each ecotype.

Figure S3 (a) Scatterplot of PC 1 values of the size-corrected morphological data set and PC 1 of the environmental data set displaying relative leg length differences among ecotypes across an environmental gradient. (b) Scatterplot of PC 2 values of the size-corrected morphological data set and PC 1 of the environmental data set displaying relative head size differences among the four ecotypes in arid-to-wet environments.

Table S1 PCA loadings for the morphological dataset, using 25 raw variables.

Table S2 PCA loadings for the morphological dataset corrected by body size (SVL).

Table S3 PCA loadings for the environmental dataset.

Table S4 Summary of phylogenetic signal tests.

Table S5 Statistic support of evolutionary models fit for selected morphological and environmental variables based on AICc values using *geiger*.

Table S6 Wheatsheaf indices, with 95% confidence intervals (lower and upper bounds) and *P*-values for each group of variables in the Fossorial ecotype in both hylids (75 total species included, 13 fossorial) and myobatrachids (116 total sp. included, 36 fossorial).

Table S7 Wheatsheaf indices, with 95% confidence intervals (lower and upper bounds) and *P*-values for each group of variables in the hylids (75 total species included – 13 fossorial, 15 semi-aquatic, 17 terrestrial and 30 arboreal).

Data deposited at Dryad: doi:10.5061/dryad.p36kh

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