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Testing for adaptive radiation: A new approach applied to Madagascar frogs*

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Adaptive radiation is a key topic at the intersection of ecology and evolutionary biology. Yet the definition and identification of adaptive radiation both remain contentious. Here, we introduce a new approach for identifying adaptive radiations that combines key aspects of two widely used definitions. Our approach compares evolutionary rates in morphology, performance, and diversification between the candidate radiation and other clades. We then apply this approach to a putative adaptive radiation of frogs from Madagascar (Mantellidae). We present new data on morphology and performance from mantellid frogs, then compare rates of diversification and multivariate evolution of size, shape, and performance between mantellids and other frogs. We find that mantellids potentially pass our test for accelerated rates of evolution for shape, but not for size, performance, or diversification. Our results demonstrate that clades can have accelerated phenotypic evolution without rapid diversification (dubbed "adaptive non-radiation"). We also highlight general issues in testing for adaptive radiation, including taxon sampling and the problem of including another adaptive radiation among the comparison clades. Finally, we suggest that similar tests should be conducted on other putative adaptive radiations on Madagascar, comparing their evolutionary rates to those of related clades outside Madagascar. Based on our results, we speculate that older Madagascar clades may show evolutionary patterns more similar to those on a continent than an island.

KEY WORDS: comparative methods, diversification, Mantellidae, morphological evolution, locomotor performance, phylogeny.

Adaptive radiation is a seminal topic in ecology and evolutionary biology. Yet, despite its undeniable importance, the definition and identification of adaptive radiation remain highly contentious (Givnish 1997, 2015; Olson and Arroyo-Santos 2009; Glor 2010; Hernández-Hernández 2019; Gillespie et al. 2020). Here, we first briefly review how adaptive radiation has been defined and present our view of the concept. We then introduce a new phylogenetic approach for identifying adaptive radiations based on this view and apply this approach to new data from a putative adaptive radiation of frogs from Madagascar.

We suggest that much of the disagreement over definitions of adaptive radiation can be reduced to two major debates. First, are adaptive radiations defined by internal criteria (based solely on patterns occurring within the putative radiation) or by external criteria (comparing the putative radiation to other groups)? Second, are diversification rates (rates of species accumulation, or speciation minus extinction) relevant to identifying adaptive radiations? Two foundational works, both built on the concepts of Simpson (1953), illustrate these debates. In his now-classic book, Schluter (2000) gave four criteria for defining adaptive radiation: (1) common ancestry (i.e., the radiation is a clade), (2) correlations between phenotypes and environments among species, (3) evidence that the phenotypic traits have utility, and (4) rapid speciation. Importantly, many authors currently consider this to be the most widely accepted definition of adaptive radiation

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(Gillespie et al. 2020). In contrast, Losos and Miles (2002) suggested that adaptive radiations should exhibit exceptionally large disparity in ecologically relevant morphological traits relative to other clades. Thus, under Schluter's (2000) criteria, adaptive radiations can be defined by internal criteria alone, and rapid speciation is included. In contrast, following Losos and Miles (2002), adaptive radiation can only be identified by comparing the radiation to other clades (i.e., external criteria), and diversification rates are not considered. These two works helped to stimulate the recent explosion of research on adaptive radiation. But given their divergent criteria for defining adaptive radiations, it is unsurprising that there is now little consensus about how adaptive radiations should be identified (e.g., Glor 2010; Givnish 2015; Hernández-Hernández 2019; Gillespie et al. 2020).

More surprisingly, many studies have largely abandoned these criteria altogether in favor of other approaches (reviews in Olson and Arroyo-Santos 2009; Givnish 2015). Recently, many papers have identified adaptive radiations based exclusively on declining diversification rates within clades over time (reviewed in Moen and Morlon 2014; Givnish 2015; Martin and Richards 2019). If rates decline from rapid to slow (i.e., rather than slow to slower), this pattern of slowing rates is potentially consistent with initially rapid speciation, a key component of adaptive radiation (Simpson 1953; Schluter 2000; Gavrilets and Vose 2005). Yet the actual causes of this pattern of slowing diversification are debated and include non-adaptive processes and methodological artifacts (Moen and Morlon 2014). Perhaps most importantly, focusing only on declining speciation rates disregards the "adaptive" component of adaptive radiation (Fig. 1; Givnish 1997, 2015; Rundell and Price 2009; Czekanski-Moir and Rundell 2019). Similarly, analyses of declining rates of phenotypic evolution over time have also been used to test for adaptive radiation. This pattern of declining rates, often called the early burst model (Harmon et al. 2010), is based on the idea that phenotypic rates may decline as niches are progressively filled during adaptive radiation (Simpson 1953). Yet such early bursts seem to be quite rare overall and are even absent in some iconic radiations (Harmon et al. 2010; Hopkins and Smith 2015; Slater 2015; Slater and Friscia 2019). Furthermore, these declines may also have other explanations and need not indicate a fast initial rate.

Here, we propose a novel framework to test for adaptive radiation (Figs. 1 and 2). Our approach follows the idea that adaptive radiations show exceptional phenotypic divergence relative to other clades (Losos and Miles 2002), with phenotypic variation that is linked to function and ecology (Simpson 1953; Schluter 2000). We also test for accelerated net diversification rates relative to other clades, in accordance with the long-standing idea that adaptive radiations are associated with rapid species proliferation (Simpson 1953). Thus, consistent with these classic works, we consider adaptive radiations to be clades with rates of diversification and phenotypic evolution that are significantly accelerated relative to other clades, where the phenotypic variables are linked to ecology. We include rates of phenotypic divergence, rather than simply accumulated disparity (as in Losos and Miles 2002). Our approach has similarities to others that tested for accelerated rates (e.g., Poe et al. 2018; Nürk et al. 2019). We build on those approaches by generating predictions for rate differences among groups using simulations.

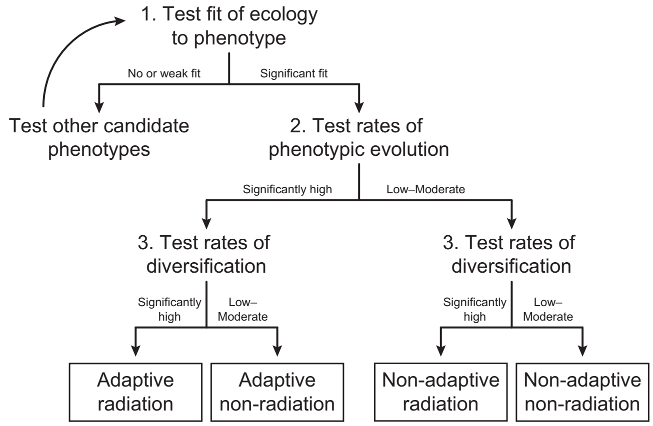

Figure 1. **Flow chart showing our overall framework for identifying adaptive radiations relative to other patterns. This framework follows the definition of Losos and Miles (2002) and Schluter's (2000) four criteria for defining adaptive radiation. The analyses are focused on a clade (first criterion) that is the candidate adaptive radiation, compared to closely related clades. First, one tests the fit of phenotype to ecology (second criterion) and ideally morphology to performance (third criterion) within the clade. These analyses address whether there has been an adaptive component to phenotypic evolution in the clade, and which variables show the adaptive fit. Note that one would not need to show such a fit to conclude either of the non-adaptive scenarios in the bottom right. Second, one tests whether there has been accelerated rates of evolution in the ecologically relevant phenotypic variable in the clade (relative to other clades), following from the idea of exceptional phenotypic diversity in Losos and Miles (2002). Third, diversification rates are tested to assess whether there was rapid proliferation of species in the clade (following Schluter's fourth criterion), relative to other clades. The possible outcomes are then classified based on the patterns of diversification and phenotypic evolution, including adaptive radiation, adaptive non-radiation (coined here), non-adaptive radiation (Gittenberger 1991), and non-adaptive non-radiation (also coined here).**

Our method is agnostic about the causes of adaptive radiation (e.g., ecological opportunity): we follow previous authors and focus on identifying adaptive radiations as a first step, and not simultaneously trying to identify the causative processes. Furthermore, the processes that contribute to adaptive radiations (e.g., ecology-driven speciation, ecological opportunity) could be widespread in clades that are not actually adaptive radiations.

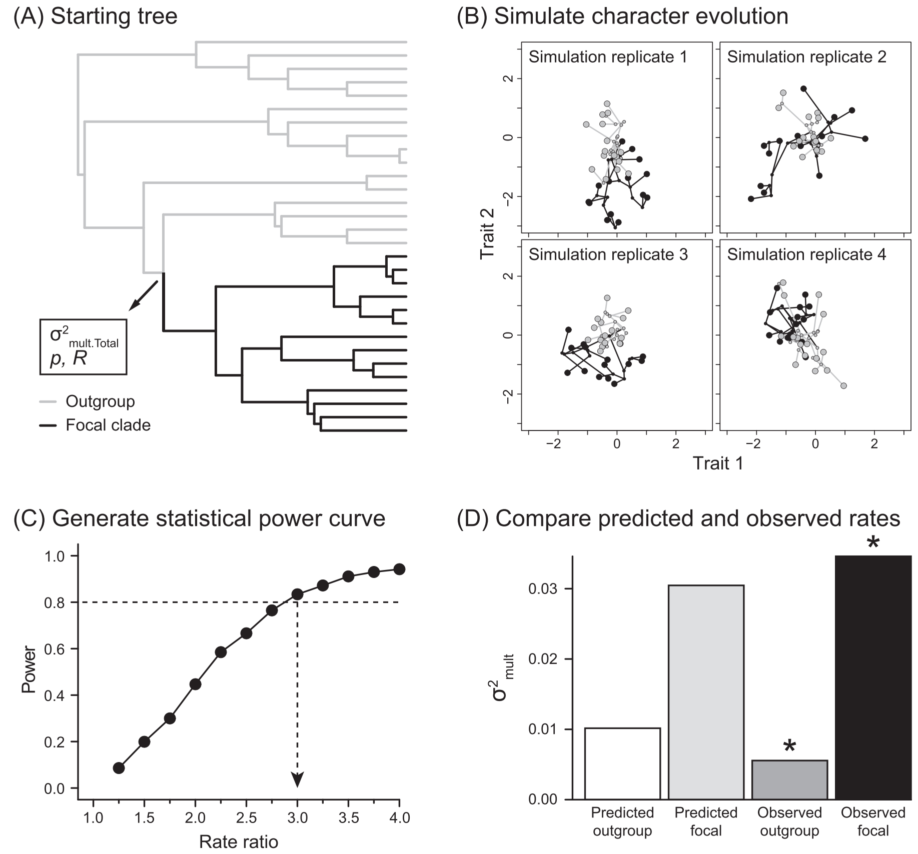

Figure 2. Flow chart used to test for significantly elevated rates of phenotypic evolution in adaptive radiations (and other clades). In (A), a candidate adaptive radiation (AR) is identified (black) and is part of a larger clade (gray), considered the "outgroup" for comparing rates of phenotypic evolution (the outgroup need not be monophyletic). From the empirical data, one estimates an overall rate of multivariate evolution across the entire tree ($\sigma^2_{mult.Total}$) for a set number of traits (*p*) and calculates an average trait correlation (*R*). These values are then used in simulations of various rate ratios between the candidate AR and the outgroup taxa (B). For visualization of potential trait simulation outcomes, we plot phylomorphospaces of four two-trait simulation replicates in which the candidate AR had a σ^2_{mult} three times higher than the outgroup. Phylomorphospaces were plotted in *phytools* (Revell 2012), with internal nodes taking their simulated values. Next, to generate a power curve for different rate ratios (C), multivariate rates of evolution are statistically compared (Adams 2014b) between the candidate AR and outgroup for each simulation replicate for each rate ratio; the proportion of significant results across simulation replicates at a given rate ratio indicates the power of the test at that ratio. Here, we simulated rate ratios from 1.25 to 4.0 at an interval of 0.25, with 1000 replicates per rate ratio. We next choose our predicted ratio as the lowest rate ratio that gives a power value of 0.80 (Fig. S1), the standard value for high power (Cohen 1992). In (D), we give the comparison of predicted and observed results. In this particular case, we see that the observed difference in rates (rate ratio of 6.22) is more extreme than the predicted difference, consistent with a significant result using Adams's (2014b) method ($P < 0.001$). Asterisks indicate a significant difference. The tree in (A) and "observed" rates in (D) were randomly simulated for illustrative purposes.

Therefore, we do not think that focusing on processes alone can solve the problem of identifying adaptive radiations.

Our approach also differs from many previous ones by analyzing rates of evolution in functional performance data. Performance data are a key link between ecology, morphology, and fitness (Arnold 1983). They also bridge Schluter's (2000) criteria of phenotype-environment correlation (typically linking morphology and ecology) and trait utility (i.e., the morphology impacts fitness). Although performance data are critical for assessing adaptation (e.g., Losos 1990; Irschick et al. 2008), these data are seldom analyzed in macroevolutionary studies (Price and Schmitz 2016; Muñoz and Price 2019). Previous studies of adaptive radiation have not analyzed and compared rates of performance evolution.

We apply this new approach to an endemic frog clade from Madagascar (Mantellidae). Madagascar may harbor several adaptive radiations, including clades of beetles (Wirta et al. 2008; Moore and Robertson 2014), frogs (including mantellids; Bossuyt and Milinkovitch 2000; Scantlebury 2013; Wollenberg Valero et al. 2017), birds (Jønsson et al. 2012; Reddy et al. 2012), lizards (Scantlebury 2013), snakes (Burbrink et al. 2019), and mammals (including lemurs; Poux et al. 2005; but see Poux et al.

2008; Herrera 2017). Many groups are predicted to have radiated on Madagascar because the ecological opportunity offered by colonizing new places (e.g., an island) is thought to spur adaptive radiation (Wagner et al. 2012; Stroud and Losos 2016; Burress and Tan 2017). However, many studies have only tested declining diversification rates over time (e.g., Poux et al. 2005; Reddy et al. 2012; Scantlebury 2013). Thus, these tests have ignored the crucial adaptive aspects of adaptive radiation: evolution in ecology, morphology, and performance. Moreover, nearly all tests of Malagasy adaptive radiations have been internal, without comparing these clades to those in other regions.

The anuran family Mantellidae is often described as an adaptive radiation, given its high species richness, ecological diversity, and endemicity to Madagascar and nearby islands (e.g., Bossuyt and Milinkovitch 2000; Andreone et al. 2002). However, only one study explicitly analyzed its phenotypic evolution (Wollenberg Valero et al. 2017), and none compared mantellid evolutionary rates to those of other frog clades. Here, we present new data on the morphology and performance of mantellid frogs to test for adaptive radiation in this clade. We combine these data with matched morphological and performance data for clades from other regions, testing whether evolutionary rates in Mantellidae are elevated relative to other clades (Fig. 2). We then conduct similar comparisons of diversification rates.

Surprisingly, our results suggest that Mantellidae is not an adaptive radiation based on our definition, because the group shows accelerated phenotypic evolution but not significantly accelerated diversification. We suggest that this overall pattern (dubbed an "adaptive non-radiation") is relatively neglected but potentially widespread in the study of adaptive radiation. Our results call into question whether other Malagasy groups are actually adaptive radiations, especially given the lack of comparison of these groups to those in other regions for both diversification rates and phenotypic rates. Lastly, we discuss the importance of taxon sampling in tests of adaptive radiation and demonstrate the overall robustness of our analyses to its effects.

Materials and Methods

FIELDWORK AND DATA COLLECTION

We briefly summarize all our methods here and give full details in Supporting Information S1. Collecting and animal care permits are noted in the Acknowledgements. In Madagascar, we collected morphological and performance data from 241 individuals across 36 species, including 25 mantellid species. We combined these data with those of Moen et al. (2013) to total 80 species across four continents (Fig. 3). For morphology-only analyses (see below), we added data from Moen et al. (2016) for a total of 217 species across 12 global locations. All raw (intraspecific) data are posted to Dryad (Supporting Information S2), as well as species means for all taxa (Supporting Information S3). We show that our taxon sampling is adequate in Supporting Information S1.

We collected data on peak jumping, swimming, and clinging performance following Moen et al. (2013). All three variables are relevant to microhabitat use (Moen et al. 2013). While anurans are well recognized as jumping organisms (Gans and Parsons 1966; Jenkins and Shubin 1998; Pough et al. 2015; Mendoza et al. 2020), most of the species studied here swim in water at least occasionally (e.g., for breeding; Glaw and Vences 2007; Moen 2019). Moreover, many species studied here climb (Glaw and Vences 2007; Moen et al. 2013), which is facilitated by adhesion. Some anurans use other behaviors (e.g., burrowing, walking; Emerson 1976; Reynaga et al. 2018), but they are relatively rare compared to the three behaviors we quantified (Duellman and Trueb 1986; Emerson 1988; Buttimer et al. 2020). Importantly, these three behaviors could be elicited from all species.

We recorded jumps and swims with a high-speed camera. We analyzed each video to extract peak velocity, used the peak velocity across videos for each individual as raw data, then calculated species means across individuals. We measured adhesive performance by placing frogs on a rotating non-stick pan, recording the angle at which frogs lost adhesion, and using the maximum angle as data (Emerson 1991). Peak performance should generally better reflect past selection than other measures of performance (e.g., average performance; Losos et al. 2002). It is also the most ecologically relevant aspect of performance for anurans, given that most species are sit-and-wait predators (Duellman and Trueb 1986; Wells 2007) that avoid their own depredation by first hiding and then using burst performance to escape when predators approach (Heinen and Hammond 1997; Bulbert et al. 2015). We give additional justification for analyzing peak performance in Supporting Information S1.

We collected morphological data from individuals used in performance trials (methods followed Moen et al. 2013, 2016). Based on previous work in anurans (Moen and Wiens 2009; Moen et al. 2013), our nine body-shape variables combine those important in locomotion (e.g., leg length, muscle mass), microhabitat use (e.g., foot webbing, adhesive disks), and diet (e.g., head/mouth width). We also included body size (snout-to-vent length: SVL), given the general importance of size in adaptive radiation (e.g., Harmon et al. 2010).

We also assigned microhabitat states to species to test the fit of morphology and performance to ecology. Adult anurans use a diversity of microhabitats (Duellman and Trueb 1986; Bossuyt and Milinkovitch 2000; Moen et al. 2013, 2016; Pough et al. 2015). These have been classified into eight categories (Moen and Wiens 2017): aquatic (lives almost entirely in water), arboreal (found above the ground on trees or other vegetation), burrowing (digs its own burrows, spending most of its life underground), terrestrial (found on the ground and/or in leaf litter), and

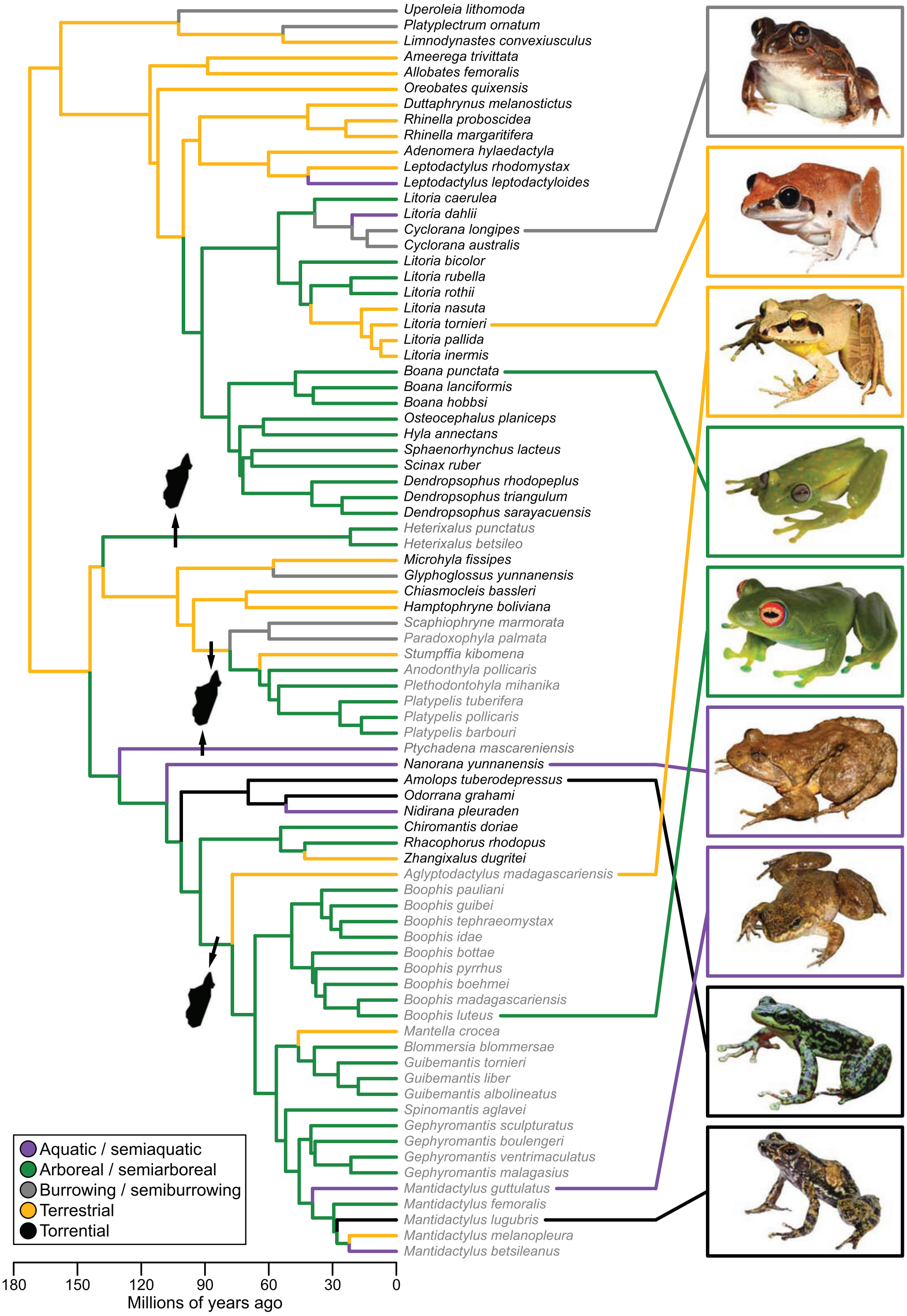

Figure 3. Evolution of ecomorphs on the 80-species phylogeny used here. Topology and branch lengths are a summary from the posterior distribution from Jetz and Pyron (2018), as described in the main text. All clade posterior probabilities were 1.0, save for the node subtending *Boana hobbsi* and *B. lanciformis*, which was 0.686. Gray names indicate species from Madagascar, with the bottommost set of species in Mantellidae. The four separate colonization events of the island represented by our sampled species are indicated by arrows on the branches (Vences et al. 2003, 2004). Ecomorph colors follow the lumped categories indicated in Supporting Information S1. Internal branches are colored following maximum-likelihood ancestral-state estimation (Schluter et al. 1997) assuming equal transition rates among states (the optimal model for this dataset). We compared models of ecomorph state transitions and estimated ancestral states in *diversitree* version 0.9-13 (FitzJohn 2012). The photos of *Amolops* and *Nanorana* were taken by Jing Che and are used here with permission. All other photos were taken by DSM.

torrential (lives along fast-flowing streams on vegetation and wet rocks, often near waterfalls). Three more categories (semiaquatic, semiarboreal, and semiburrowing) characterize species whose ecology represents some time on the ground (i.e., terrestrial) with time in other microhabitats. These latter categories focus more on the non-terrestrial aspect because that part of a species's ecology is more likely to be reflected in its morphology and performance (e.g., a frog that spends time both on the ground and in bushes or trees will need to be able to climb, unlike strictly terrestrial species). These categories fit many previous descriptions of microhabitat use in anurans (Pough et al. 2015), including those used for Malagasy frogs (Glaw and Vences 2007). We describe microhabitat assignment in more depth in Supporting Information S1.

Comparative analyses used a consensus of Bayesian trees from Jetz and Pyron (2018; Fig. 3). This represents the most comprehensive (in terms of taxonomic coverage and sequence data) estimate of anuran phylogeny published to date. We also ran a subset of analyses on 1000 trees from their posterior distribution. Additional details on the phylogeny are in Supporting Information S1, and consensus trees for 217 and 80 species are available as Supporting Information S4 and S5. We also explored an alternative tree for the diversification analyses (Feng et al. 2017).

DATA ANALYSIS

Size standardization

We standardized all variables to body size in order to analyze shape (morphology) and performance (Gomes et al. 2009; Astley 2016). We recognize that many methods can be used to standardize data to size (Klingenberg 2016; Price et al. 2019). However, previous analyses of a subset of these data show that many different methods (e.g., ratios, phylogeny-based and standard residuals) give nearly identical results in downstream comparative analyses (Moen 2019). Here, we conducted phylogenetic regressions of each (natural-logged) variable on a measure of (natural-logged) body size (Revell 2009), using the R package *phytools* version 0.6.99 (Revell 2012). We then used the residuals of these regressions as data for comparative analyses. These data are available as Supporting Information S6.

Testing the fit of body shape and performance to ecology

Two key criteria of adaptive radiation are that phenotypes correlate with ecology and that phenotypes have utility (Schluter 2000). For the first criterion, we tested the fit of shape and performance to microhabitat. For the second, we tested for covariation between shape and performance.

We tested relationships between microhabitat and morphology and performance using Q-mode multivariate phylogenetic generalized least-squares (Adams 2014a) in the R package *geomorph* version 3.1.3 (Adams and Otárola-Castillo 2013). We tested the effect of ecology on morphology and performance, and whether that effect differed in Mantellidae, using 999 permutations to test for statistical significance. To visualize body-shape differences among ecomorphs, we conducted phylogenetic principal components analysis (Revell 2009) on the covariance matrix of our nine body-shape variables (i.e., size-standardized regression residuals), using *phytools*.

Second, to test overall relationships between the nine body-shape and three performance variables, we conducted two-block partial least-squares analysis (2B-PLS; Rohlf and Corti 2000) to test covariation between these two sets of variables. To account for phylogeny we used phylogenetic transformation, where one projects phenotypic data into a multivariate space of phylogenetically uncorrelated variables (Garland and Ives 2000; Adams 2014b). For these 2B-PLS analyses, we used custom-written functions in R (R Core Team 2020) from Moen et al. (2013), included here in Supporting Information S11. We analyzed the 25 mantellid species alone and then analyzed the remaining 55 non-mantellid species. These analyses allowed us to test whether mantellids showed similar form-function relationships as in other anurans.

Comparing rates of phenotypic evolution

We compared rates of evolution between Mantellidae and other frog clades for body size, body shape, and performance variables. Previous studies of adaptive radiation have also compared rates across clades (e.g., Poe et al. 2018; Nürk et al. 2019), but our approach differs in three key ways. First, we included performance data, which are crucial for linking morphology to ecology (see Introduction). Second, we estimated rates of multivariate phenotypic evolution. Third, we derived expected differences in rates of evolution between a candidate adaptive radiation and its outgroup based on power analyses that incorporated observed phylogeny size (i.e., species sampled), number of traits, and trait correlations. We use "outgroup" here to refer to the single set of all sampled species outside the candidate adaptive radiation (regardless of whether the outgroup taxa form a monophyletic group or not; Fig. 2).

We used the multivariate approach of Adams (2014b) to compare rates of phenotypic evolution. This method calculates a single Brownian-motion (BM) rate for multiple characters that accounts for their correlation. BM is a relatively simple model of evolution, but its use avoids statistical problems associated with other models in the multivariate framework used here (Adams and Collyer 2018, 2019). We recognize that BM models of trait evolution (e.g., stochastic change proceeding at a constant rate) might be considered inconsistent with some models of adaptive radiation (e.g., an early burst of trait evolution). However, BM is also consistent with adaptive evolution (e.g., stabilizing selection with different optima, punctuated change) and does not require neutral evolution or genetic drift (Hansen and Martins 1996; O'Meara et al. 2006; Harmon et al. 2010). In Supporting Information S1, we give further justification for our use of BM, and we show that our data are largely consistent with this model. We recognize that future work will undoubtedly improve upon the specific methods utilized here. Our overall framework (Figs. 1 and 2) can easily incorporate new or alternative methods (e.g., for estimating rates) as they become available (see Discussion).

We conducted three main tests to compare groups, following the outline in Figure 2. These tests only differed in identities of the comparison groups. In all tests, we compared the multivariate rate for a focal group (e.g., Mantellidae) and the outgroup (e.g., other frogs), as in Figure 2A. We then conducted 999 parametric simulations to test statistical significance. In each simulation replicate, trait evolution is simulated under the global estimated rate for the two groups combined. Next, rates are estimated for the two groups from the simulated data, given that the estimated rate from each group will randomly differ due to stochasticity in the simulations. Lastly, a ratio of the larger estimated rate to the smaller estimated rate is calculated for each simulation replicate. The resulting distribution of rate ratios provides a null distribution of the differences in rates between the two groups. The frequency with which the observed rate ratio is larger than these null ratios is the *P*-value. We performed these analyses with *geomorph*. Our main tests used the consensus tree. We describe results from a distribution of trees in Supporting Information S1. Our R code is provided in Supporting Information S7.

In our first main test, we compared rates in mantellids to those in other frogs. We used our 80-species phylogeny to separately compare rates for size, shape, and performance. We also compared size and shape rates between these groups in our larger morphological dataset (217 species) to address effects of taxon sampling. We conducted power simulations (following Adams and Collyer 2018) to determine a predicted rate ratio between groups, which was the minimum ratio with statistical power of 0.80 (Fig. 2C). This is a standard threshold for high power (Cohen 1992). Thus, if an adaptive radiation showed this rate ratio (compared to outgroups), 80% of tests would show that the radiation has a significantly higher rate. Full details are provided in Supporting Information S1.

Our test of adaptive radiation in the focal group might be misled if other putative adaptive radiations are included in the set of outgroup taxa for comparison. Among the current outgroup taxa, Pelodryadinae (a subfamily of Hylidae from Australia) has diversified in microhabitat, morphology, and performance on a large island with few other frog groups (Moen et al. 2013; Vidal-Garcia and Keogh 2015). It also shows rates of diversification and body-size evolution that are significantly higher than other clades of Hylidae (Wiens et al. 2011). Therefore, Pelodryadinae may itself be an adaptive radiation, and including it in tests of accelerated rates for Mantellidae might be problematic. Our second and third main tests assessed this possibility in two ways. First, we compared Mantellidae to all other frogs while excluding the 11 pelodryadine species (i.e., 69 species included). Second, we compared Mantellidae and Pelodryadinae (i.e., two potential adaptive radiations) together to all other frogs, to see if collectively they had elevated rates. We note that other anuran groups have been called adaptive radiations (e.g., Setiadi et al. 2011; Blackburn et al. 2013; Rivera et al. 2017), but our sampling locations did not include members of these groups. Moreover, the cophyline microhylid frogs of Madagascar show the species and ecological diversity typical of adaptive radiations (Andreone et al. 2005; Scherz et al. 2016). However, we did not formally test this group since relatively few were sampled (6 species). Furthermore, few ecotypes were sampled (five of six species arboreal; two total ecotypes of four possible; Scherz et al. 2016) and so they should not affect our test of Mantellidae.

We also explored the sensitivity of this multivariate rate method (Adams 2014b) to taxon sampling. This was important given that most results showed no support for elevated rates in Mantellidae, yet more extensive morphological sampling showed some support (see Results). We give full details of these power simulations in Supporting Information S1.

Comparing diversification rates

We used the estimator of Magallón and Sanderson (2001) to calculate net diversification rates, which only requires species richness and ages of clades (see Supporting Information S1 for justification for this approach). For richness, we first used species diversity of all 54 currently recognized frog families from AmphibiaWeb (2020). This source lists 229 described species for Mantellidae. We also considered the projected richness of 409 species (Perl et al. 2014). We extracted stem and crown ages of families from the consensus tree (Jetz and Pyron 2018). We also used stem ages from a more recent phylogeny (Feng et al. 2017) that has somewhat younger ages, but fewer families sampled (44 of 54). We assumed three relative extinction fractions ($\epsilon = 0.0$, 0.5, 0.9), following standard practice. Note that these fractions do not assume constant extinction rates among clades. We also calculated diversification rates using the birth-death estimators of Nee et al. (1994), which use branch-length distributions to estimate rates. In Supporting Information S1 we describe and justify all methods for estimating diversification rates.

To compare mantellid rates to other families, we used phylogenetic ANOVA (Garland et al. 1993) with *phytools*. We assessed statistical significance with 1000 simulations on the consensus tree, pruned to the family level (Supporting Information S8). All methods for estimating net diversification rates gave

Table 1. Fit between microhabitat, body shape, and performance based on Q-mode multivariate PGLS analyses. Microhabitat alone best explains variation in performance and body shape, with little evidence for mantellids being distinctive. Both analyses were conducted on the 80-species dataset to be comparable.

Phenotype	Factor	R^2	F	Z	P
Performance	Microhabitat	0.127	2.768	1.574	0.037
	Mantellidae	0.010	0.909	0.516	0.342
	Micro + Mantellidae	0.047	1.360	0.666	0.248
Body shape	Microhabitat	0.441	14.938	3.706	0.001
	Mantellidae	0.015	1.989	0.853	0.170
	Micro + Mantellidae	0.019	0.087	0.232	0.483

R^2 is the proportion of variation in the response variables explained by each factor. F is the F-ratio of the factor. Z is the standardized effect size (Z-score). P is the probability that those factors explain variation in the response variables by chance, as assessed by 999 permutations of the original dataset across the phylogeny.

qualitatively identical results (Table S6), so our main results focused on described species richness, the most comprehensive tree (Jetz and Pyron 2018), and the most accurate clade ages (stem ages; Sanderson 1996). Relevant diversification data are in Supporting Information S9.

Results

PHENOTYPE-ECOLOGY RELATIONSHIPS

Across all frogs, we found a significant fit between microhabitat and body shape ($P = 0.001$; Table 1), and between microhabitat and performance ($P = 0.037$). Separate factors for Mantellidae and an interaction between microhabitat and being in Mantellidae were insignificant in both analyses (Table 1), meaning ecomorphological relationships in Mantellidae fit those found across other anurans. Figure 4 shows how ecomorphs cluster in performance and shape space. Arboreal and terrestrial species are broadly distributed in jumping and swimming velocity, but arboreal species have higher clinging performance. Torrential and aquatic ecomorphs have high swimming velocity and poor clinging ability. Burrowing species have low values for all performance variables (though burrowing performance itself was not assessed).

In terms of morphology (Fig. 4), arboreal and torrential species have large toe and finger tips (i.e., enlarged pads) and often large foot-webbing area. Aquatic species have extensive webbing and small digit tips. Burrowing species are most distinguished by enlarged metatarsal tubercles (used for digging; Emerson 1976). Terrestrial species are distributed across morphological phylogenetic PC space. In general, species associated with different microhabitats show high performance at tasks related to those microhabitats (arboreal: clinging; aquatic: swimming) and modified morphologies related to increased performance (expanded toepads for clinging, webbing for swimming, and tubercles for digging).

Based on 2B-PLS, body shape and performance in Mantellidae significantly covaried in two of three possible dimensions (Table S1), with correlations of 0.710 and 0.444 between shape and performance axes on those dimensions (Fig. 4E). Additional analyses on all other species showed similar relationships between variables, but with all three dimensions significant (Table S2). Vector correlations of the 2B-PLS weights in mantellids versus those of other frogs were 0.888 and 0.765 for dimensions 1 and 2, respectively, showing similarity in the two significant axes across taxa.

PHENOTYPIC RATE COMPARISONS

Using the main dataset of 80 species, Mantellidae had higher evolutionary rates than other frogs for body size and shape, but neither was statistically significant (size: $P = 0.164$; shape: $P = 0.794$; Table 2; Fig. 5A,B). In performance, mantellid rates were actually lower than in other frogs (Table 2; Fig. 5C). Additional analyses on the 217-species dataset showed stronger support for higher shape rates (but not size) in Mantellidae (Table 2), though not statistically significant.

Excluding Pelodryadinae from the 80-species analyses, the ratio of rates in mantellids to other frogs increased for all three trait types, but differences were still insignificant (size: $P = 0.079$; shape: $P = 0.819$; performance: $P = 0.535$; Table 2). However, the 217-species dataset showed significantly elevated rates of shape evolution in Mantellidae when Pelodryadinae was excluded (Table 2). Additional analyses (Table S4) showed higher rates in all three trait types when comparing Mantellidae + Pelodryadinae to other frogs, but results were not significant. Results across the posterior distribution of phylogenies were similar (Table S3).

We assessed why mantellids showed stronger results for shape in the 217-species dataset than the 80-species dataset. Pelodryadinae alone (11 species here) had significantly high rates for shape and performance in the 80-species dataset (Table S5),

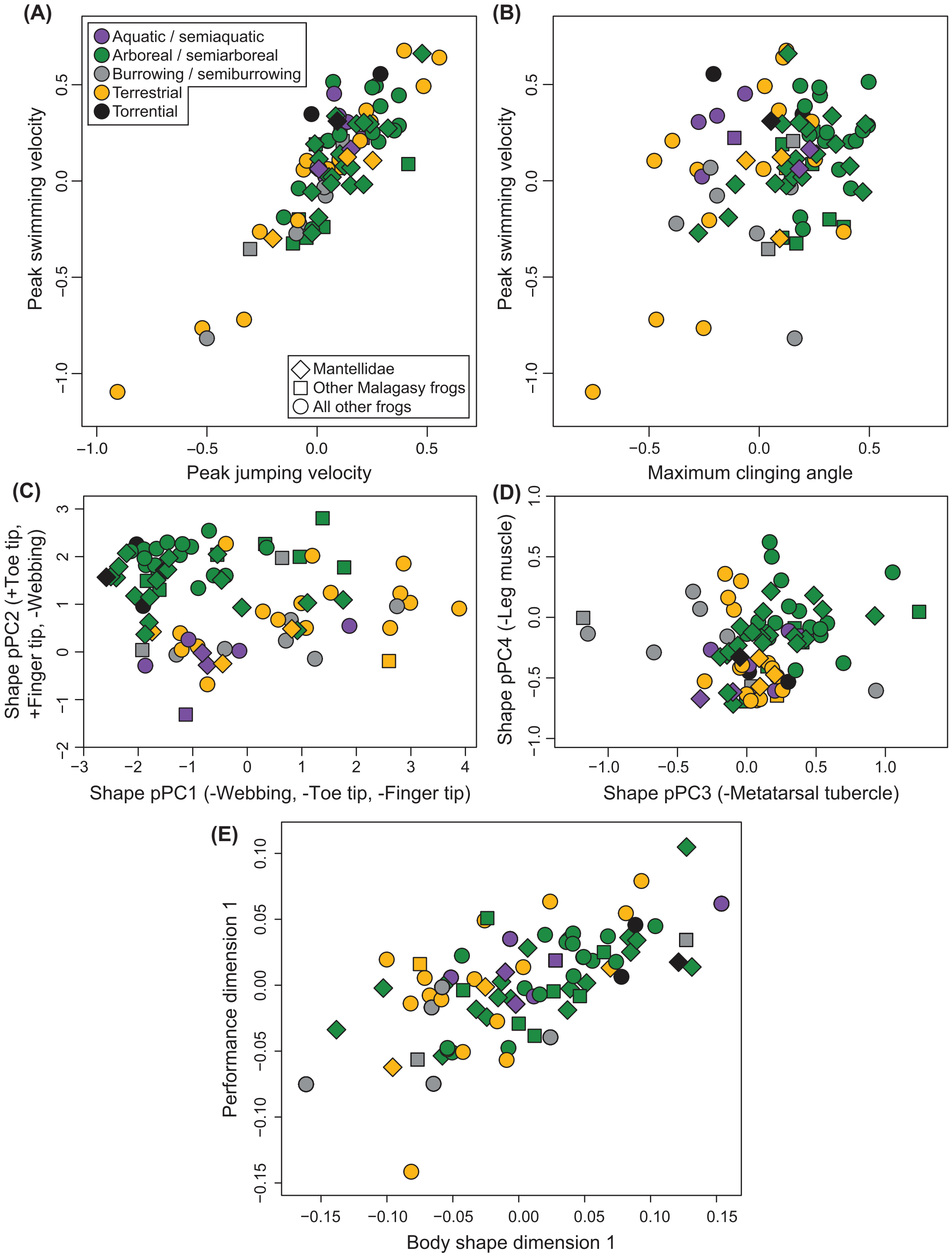

Figure 4. Visualization of differences in performance (A,B), body shape (C,D), and covariance between performance and shape (E) among frog ecomorphs. Symbol colors indicate microhabitat use (i.e., ecomorph), following the lumped categories indicated in Supporting Information S1. Symbol shape indicates the frog group. Performance data are shown as residuals of phylogenetic regressions of each variable on snout-to-vent length (SVL) and thus have no units. Body-shape data are from the 80-species sample for which we also had performance data. They are shown as the first four axes of a phylogenetic principal components analysis (pPCA) on morphological residuals, with those residuals obtained as for performance data. These first four pPCA axes encompassed 96.5% of the total morphological variation in body shape (Supporting Information S1: Table S7). In (E), axes are the latent variables from the first dimension of a two-block partial least-squares analysis. These latent variables are linear combinations of our nine body-shape and three performance variables, chosen such that the new latent variables show maximum covariation (Rohlf and Corti 2000). While we analyzed Mantellidae and non-mantellid frogs in two separate analyses (Tables S1 and S2), here we analyzed them together to produce the figure, given similar results.

Table 2. Results of evolutionary rate comparisons between Mantellidae and other anurans. Results are from the (A) 80-species complete dataset (25 mantellids; 55 other anurans), (B) 217-species morphological dataset (36 mantellids; 181 other anurans), (C) 69-species complete dataset without Pelodryadinae, and (D) 206-species morphological dataset without Pelodryadinae. All results are from analyses on the maximum clade credibility (MCC) tree.

Comparison	Trait type	Overall σ^2	Mantellidae σ^2	Other σ^2	σ^2 ratio	P
(A) With Pelodryadinae, 80-species tree	Body size	0.00201	0.00272	0.00169	1.605	0.164
	Body shape	0.00395	0.00406	0.00390	1.042	0.793
	Performance	0.00078	0.00060	0.00087	0.695	0.129
(B) With Pelodryadinae, 217-species tree	Body size	0.00237	0.00239	0.00236	1.013	0.958
	Body shape	0.00345	0.00404	0.00333	1.212	0.061
(C) Without Pelodryadinae, 69-species tree	Body size	0.00194	0.00272	0.00149	1.819	0.097
	Body shape	0.00369	0.00407	0.00347	1.171	0.304
	Performance	0.00066	0.00060	0.00070	0.861	0.535
(D) Without Pelodryadinae, 206-species tree	Body size	0.00236	0.00239	0.00235	1.016	0.940
	Body shape	0.00328	0.00404	0.00312	1.294	0.015

"Overall σ^2" represents the rate estimated for the entire tree (without specifying groups). For each comparison, "σ^2 ratio" represents the ratio of the mantellid rate to the other rate, and *P* reflects the probability of obtaining that ratio or one more extreme if both groups had the same rate. Note that this *P*-value may include the possibility that mantellids have lower rates than other frogs (e.g., in performance on 80- and 69-species trees).

suggesting that sampling 25 mantellid species should be sufficient to obtain significant results. When comparing mantellid results from 80- and 217-species trees, we found that shape rates for mantellids were similar across both datasets, whereas other frogs showed higher rates in the 80-species sample and lower rates in the 217-species sample. Our power simulations showed that this lower rate ratio in the 80-species sample may thus have compromised statistical power more than tree size per se (Fig. S1; full results in Supporting Information S1).

DIVERSIFICATION RATES

Mantellid diversification rates were unexceptional compared to other frog families. Based on described mantellid richness and stem-age estimates, their diversification rates were not significantly higher ($\epsilon_{0.0}$: $P = 0.328$; $\epsilon_{0.5}$: $P = 0.268$; $\epsilon_{0.9}$: $P = 0.244$). Results were similar using projected mantellid richness, crown-group ages, alternative diversification-rate methods, and family ages from an alternative phylogeny (Table S6).

Discussion

We developed an approach to identify adaptive radiations, based on the idea that they show elevated rates of ecologically relevant phenotypic evolution and diversification. Our approach applies existing comparative tools to compare the pace of evolution in a candidate adaptive radiation relative to other clades (Figs. 1 and 2). We applied this approach to a putative adaptive radiation of frogs from Madagascar. Although previous authors have considered mantellid frogs to be an adaptive radiation (Bossuyt and Milinkovitch 2000; Wollenberg Valero et al. 2017), our approach reveals a more mixed pattern. Mantellids showed significantly accelerated rates of evolution in body shape (under certain sampling schemes) but not in size, performance, or diversification. Importantly, their lack of accelerated net diversification rates means that they fail our overall test for adaptive radiation (Fig. 1).

In the sections that follow, we discuss how our approach can be generalized and how phylogenetic scale and taxon sampling affect tests of adaptive radiation. We also discuss why mantellids largely show unexceptional rates of evolution. We finish by addressing the general pattern of rapid morphological evolution that is decoupled from rapid diversification.

GENERALIZING THE APPROACH

We describe two unresolved issues when applying our approach, though neither is unique to our approach. First, what traits should be used? In our study, we characterized overall morphology (size and shape) and performance variables relevant to microhabitat use. However, many other variables could have been included (e.g., life history, physiology, diet), including some that are broadly important in anuran diversification (e.g., climatic niche; Moen and Wiens 2017) and others that show impressive variation in mantellids (e.g., larval ecomorphology; Wollenberg Valero et al. 2017). Indeed, different variables may be important at different stages of adaptive radiation (Streelman and Danley 2003), and focusing on the wrong trait could lead to the wrong answer with any approach. As a guiding principle, we suggest that the most relevant variables will depend on the group, and they should span the major ecological and morphological variation in the clade. Another consideration is whether the ecological and morphological variables help drive rapid speciation, which should

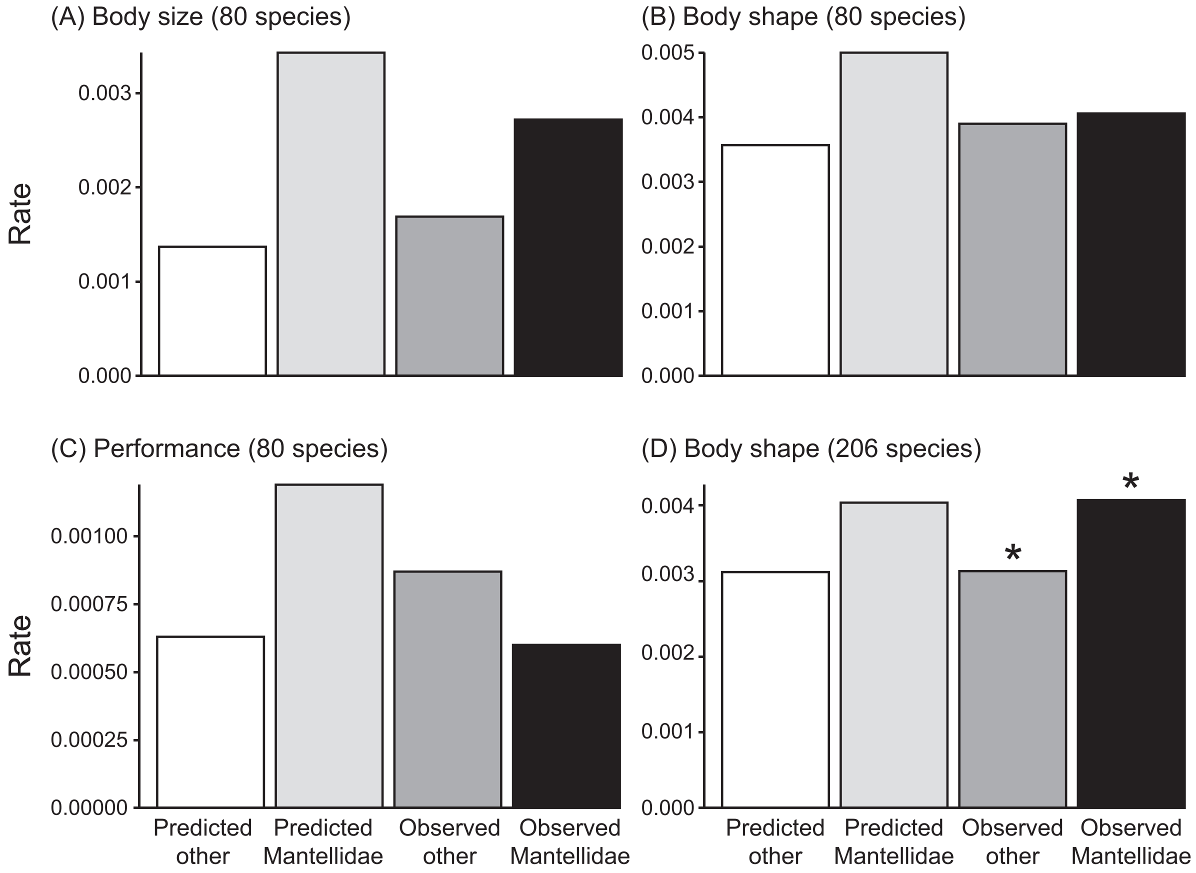

Figure 5. Predicted and observed rates between Mantellidae and other frogs, as tested on the 80-species phylogeny (A–C) and the 206-species phylogeny without Pelodryadinae (D). In each panel, the first two bars indicate the predicted differences between Mantellidae and other frogs if Mantellidae were an adaptive radiation, determined as in Figure 2. The second two bars indicate the observed rates for these two groups (Table 2). In each panel, adaptive radiation would be supported if the observed mantellid rates were at least as high, and the other-frog rates were as low or lower, than their predicted rates. This does not occur in (A–C). We thus show (D) to demonstrate a significant result, as this was the only test in which mantellids showed significantly high rates of evolution (Table 2). Rates in (A) are in units of $\ln(\text{mm})^2$ per million years, whereas those in (B–D) are unitless because they are multivariate rates from data that were standardized to body size using regression residuals. Asterisks indicate a significant difference.

make them particularly relevant (e.g., Schluter 2000). Utilizing this consideration should help reduce spurious correlations between accelerated diversification and phenotypic evolution.

Second, what if results are significant for some traits, but not others? How many traits are necessary for a clade to be considered an adaptive radiation? We suggest that significantly accelerated rates in any ecological or morphological trait can qualify a clade as an adaptive radiation, especially if that trait is linked to rapid diversification. However, we consider accelerated diversification rates alone to be insufficient, as have other authors (e.g., Schluter 2000; Losos and Mahler 2010; Givnish 2015). Importantly, no definition of adaptive radiation requires that all tested traits show exceptional diversity or accelerated rates relative to other clades. Minimally, we suggest that an adaptive radiation should have increased net diversification rates and increased rates of evolution in at least one ecologically relevant phenotypic trait.

We note that a random association of high rates of phenotypic evolution with high rates of diversification could mislead our method. In other words, if the accelerated ecological and phenotypic change were not causally related to the high net diversification rate, our method could suggest a clade was an adaptive radiation even if it were not (Simpson 1953; Schluter 2000; Givnish 2015). However, we do not expect this situation to occur frequently. Moreover, our method should not be construed as an end to research: positive test results should stimulate additional studies to probe the processes underlying the links between ecology, morphology, performance, and diversification within the radiation. Our method is based on the idea that increased rates of phenotypic evolution and diversification are key signatures of adaptive radiation, and it is especially relevant to comparing a putative adaptive radiation to other clades.

We also note that our general approach (Figs. 1 and 2) is not necessarily tied to any of the specific analytical methods applied here. For example, we performed multivariate analyses using a BM model (as strongly recommended by Adams and Collyer 2018, 2019), but analyses of single traits and alternative models could be applied to test for accelerated rates in a candidate adaptive radiation (Clavel et al. 2019). Similarly, alternative methods could be used to estimate diversification rates (Morlon 2014).

TAXON SAMPLING AND TESTS OF ADAPTIVE RADIATION

Our results highlight the importance of taxon sampling, an issue rarely discussed in studies of adaptive radiation. One aspect of taxon sampling is that the outgroup taxa for our comparative analyses included at least one adaptive radiation, the pelodryadine hylids. Like mantellids, pelodryadines radiated in relative isolation and evolved all major frog ecomorphs (Moen et al. 2013; Vidal-Garcia and Keogh 2015). Despite our limited sampling of pelodryadines (11 species), they showed significantly accelerated rates for shape and performance (in contrast to mantellids, with 25 species; Table S5). Furthermore, using stem ages from the consensus tree of Jetz and Pyron (2018), pelodryadines have significantly higher net diversification rates than other family-level clades ($\epsilon_{0.0}$: $r = 0.081$, $P = 0.023$; $\epsilon_{0.5}$: $r = 0.071$, $P = 0.025$; $\epsilon_{0.9}$: $r = 0.047$, $P = 0.031$). Ultimately, Pelodryadinae passed our tests for adaptive radiation, even though it was not the focus of this study.

Importantly, when we compared mantellids to other frogs, pelodryadines increased the inferred rates in other frogs, making the rates in mantellids less exceptional. Thus, including an adaptive radiation in the comparison group could potentially compromise tests of the candidate clade. This potential challenge in identifying adaptive radiations is not unique to our method, as the risk exists for any method that uses external criteria. We demonstrated how to address this issue by excluding pelodryadines and by testing pelodryadines and mantellids together relative to other frogs. Yet, doing so depended on prior knowledge about pelodryadines (e.g., Moen et al. 2013). Thus, identifying and removing adaptive radiations among the outgroup taxa may be difficult in practice. Another approach might be to visualize rates across the phylogeny and look for clades with accelerated rates, rather than testing candidate adaptive radiations selected a priori (as done here). We did not implement that method here because it has only been developed for single phenotypic characters (Eastman et al. 2011; Revell et al. 2012; Castiglione et al. 2018). However, instead of the multivariate approach used here, one could test relevant phenotypic variables individually to find accelerated rates, though correlated traits may show similar results.

We also acknowledge that even our best phenotypic sampling represented a tiny fraction of all the relevant species. There are >200 described mantellid species and >7000 other frog species (AmphibiaWeb 2020), whereas our best sampling included only 217 frog species total. Nevertheless, we found significant results that made sense in light of patterns of ecomorph evolution and diversification rates (e.g., Pelodryadinae is an adaptive radiation). Although some results may change as more species are included, representative sampling of clades and ecomorphs might be more important than the proportion of species sampled. To test whether our ecomorph sampling in Mantellidae represented the whole family well, we estimated the frequencies of ecomorph states for a large sample of mantellid species (Moen and Wiens 2017) and confirmed that these roughly matched those among our sampled species. First, the 217-species dataset included all seven ecomorphs found in Mantellidae. A chi-square test of proportions (Sokal and Rohlf 1995) showed that we sampled these seven ecomorphs in roughly similar proportions to those seen across the whole family ($P = 0.087$, where $P < 0.05$ would indicate significantly different proportions). The 80-species dataset had only five of seven ecomorphs. However, ecomorph proportions in this dataset were more similar to those for the entire family ($P = 0.239$), despite missing burrowing and aquatic taxa. These two ecomorphs may be overrepresented in the 217-species data, given their rarity in the family (0.7 and 1.3% of all taxa, respectively; Moen and Wiens 2017).

More generally, taxon sampling that is limited and random should not bias phenotypic rate estimates for a clade. To test this proposition, we simulated trait evolution on our full 3449-species maximum clade credibility tree from Jetz and Pyron (2018), then randomly subsampled taxa to reflect our sampling here (e.g., 25 mantellids and 55 outgroup species, which corresponds to 13 and 1.7% of these groups, respectively, in the full tree). We then assessed parameter estimation accuracy, Type I error rates, and statistical power under a range of simulation scenarios, including differing number of traits, trait correlation, and tree size (full details of simulations in Supporting Information S1). Under all simulation conditions, we found no parameter-estimation bias due to subsampling taxa (Fig. S2). Statistical power was identical to our estimates based on simulating along the smaller analysis trees (i.e., 80- and 217-species trees), and Type I error rates were centered around 5%, as expected (Fig. S3). These results suggest that our sampling did not mislead our overall inferences. This finding is encouraging, because large groups like anurans (>7300 species) will rarely have more than a small percentage of species sampled, given the difficulty of collecting phenotypic data (particularly functional performance data) from many species. Nonetheless, we think that a broader assessment of the effect of sampling on rates of evolution would be a valuable direction for future work.

Another unresolved sampling question is how far “out” the outgroup comparisons should go. Our sampling here emphasized neobatrachian frogs, the clade including mantellids and >95% of frog species (AmphibiaWeb 2020). But it did not extend beyond frogs. Including outgroup taxa that are too distant risks including confounding factors (e.g., frogs and their sister group, salamanders, have radically different morphologies; Pough et al. 2015). Yet, including only the sister group to mantellids (Rhacophoridae) would have limited our statistical power and thus biased our analyses against finding mantellids to be an adaptive radiation. We do not have a "one-size-fits-all" solution to this problem, but we caution other researchers to carefully consider how their outgroup sampling might influence their results.

CRITERIA FOR TESTING ADAPTIVE RADIATION

We acknowledge that some readers might disagree with our criteria for what constitutes an adaptive radiation. First, conclusions based on internal criteria may differ from those based on external comparisons to other groups. For example, rates of morphological evolution decline over time within mantellids (Wollenberg Valero et al. 2017), a pattern often attributed to adaptive radiation. Yet, most of our analyses showed that rates of mantellid phenotypic evolution are unexceptional compared to other clades. More broadly, the comparison of candidate adaptive radiations to other clades relates to another important question: whether adaptive radiations are ubiquitous or rare. Across the Tree of Life, some clades show exceptional evolution in terms of rapid diversification rates and diverse phenotypes (i.e., many classic adaptive radiations), whereas others do not (Simpson 1953; Schluter 2000; Losos and Mahler 2010; Wagner et al. 2012; Martin and Richards 2019). To understand the processes underlying this pattern, one must first identify these exceptional clades, and this can only be done comparatively. Therefore we favor including external criteria over the exclusive use of internal criteria for defining adaptive radiations (as in Losos and Miles 2002).

Second, requiring rapid diversification for adaptive radiation is even more contentious (e.g., Olson and Arroyo-Santos 2009; Glor 2010; Givnish 2015). Some of this disagreement may be based on the idea that including diversification rates leads one to ignore all other variables (e.g., Givnish 2015). Excluding diversification only to encourage inclusion of ecological and morphological data is unnecessary, as we demonstrate with our framework (Fig. 1). Moreover, diversification rates have been a crucial component of definitions of adaptive radiation throughout the concept's history (Hernández-Hernández 2019), including some of the most definitive treatments (Simpson 1953; Schluter 2000). Thus, we consider accelerated diversification rates to be necessary, but insufficient by themselves, to support adaptive radiation.

Third, our approach emphasizes differences in overall rates among clades, rather than changes in rates over time. We recognize that this contrasts with some conceptualizations of Simpson's (1953) model of adaptive radiation (e.g., early burst; Harmon et al. 2010). However, using our approach, rates need not be constant within clades over time (see Supporting Information S1). Moreover, finding a pattern of declining rates of phenotypic evolution over time can be very sensitive to taxonomic or temporal scale (Hopkins and Smith 2015; Slater and Friscia 2019). Using our approach, clades with periods of rapid phenotypic change or diversification should have faster overall rates than clades that do not have such periods, all else being equal. Importantly, a pattern of declining rates over time does not necessarily indicate that the initial rates were rapid: rates could start slow relative to other clades and then become even slower over time. This possibility underscores the importance of comparisons among clades. We also emphasize again that there are many possible explanations for declining rates that do not involve ecological opportunity or adaptive radation (Moen and Morlon 2014).

WHY ARE MANTELLIDS NOT AN ADAPTIVE RADIATION?

We suggest that the most straightforward explanation for why mantellid frogs do not appear to be an adaptive radiation is that they are not a young clade, leading to moderate rates of diversification and phenotypic evolution. Although they show accelerated shape evolution (in one analysis), they lack significantly elevated net diversification rates. Mantellidae is an island radiation that evolved a diversity of microhabitat-based ecomorphs (Bossuyt and Milinkovitch 2000; Moen et al. 2016). These ecomorphs encompass almost all those seen in frogs (e.g., aquatic, arboreal, burrowing, terrestrial; Moen and Wiens 2017). Moreover, some types evolved repeatedly within the family (Fig. 3). The family also shows remarkable ecomorphological diversity in tadpoles (Wollenberg Valero et al. 2017), which we did not analyze here. In contrast, many anuran families are more uniform in ecomorph composition (Moen and Wiens 2017), including the sister clade of Mantellidae, Rhacophoridae, which is mostly arboreal. However, mantellid frogs may show modest (not fast) evolutionary rates for diversification, morphology, and performance simply because the family is not young. Mantellidae includes hundreds of species (many sharing the same ecomorph type) and is similar in age to other families (Feng et al. 2017), both factors that can lead to lower rates of diversification and phenotypic evolution. Surprisingly, Mantellidae's sister family, Rhacophoridae, has nearly twice as many species (AmphibiaWeb 2020), despite showing limited ecomorph diversity (Moen and Wiens 2017). Why these two clades of identical (stem) age differ so strikingly in ecological and species diversity remains unclear.

More generally, we suggest that some diverse clades with a long residence time in Madagascar (like mantellids) might mirror slower continental radiations instead of rapid island radiations. Previous authors have suggested that Madagascar might resemble a continent more than an island in terms of geology and diversification (e.g., de Wit 2003; Raxworthy et al. 2008; Vences et al. 2009). However, we support this suggestion for the first time with a comparison of evolutionary rates between Madagascar clades and continental clades, including rates of phenotypic evolution.

WHAT DO YOU CALL CLADES WITH RAPID PHENOTYPIC EVOLUTION BUT WITHOUT ACCELERATED DIVERSIFICATION RATES?

There has been considerable discussion in the literature contrasting adaptive radiations with non-adaptive radiations (e.g., Gittenberger 1991; Givnish 1997; Rundell and Price 2009; Czekanski-Moir and Rundell 2019). Non-adaptive radiations are often characterized as rapidly diversifying clades with limited ecological divergence. Here, mantellids show the opposite pattern: accelerated shape evolution but unexceptional diversification rates. To our knowledge, there is no specific name for this pattern. Some authors consider accelerated phenotypic evolution alone to represent adaptive radiation (Givnish 1997, 2015; Rundell and Price 2009), but this view is controversial (Sanderson 1998; Schluter 2000; Martin and Richards 2019; Gillespie et al. 2020). Simões et al. (2016) proposed “disparification” for clades with high morphological variation relative to their sister clades. Yet, this term is not focused on rates and therefore includes clades with morphological diversity that accumulated slowly over time (and it does not address diversification).

We suggest that the pattern of rapid phenotypic rates without rapid lineage diversification can be called “adaptive non-radiation”, with “non-radiation” referring to the lack of rapid diversification (Fig. 1). Gittenberger (1991) originally defined “radiation” as a large clade, and Mantellidae is relatively large (229 described species; AmphibiaWeb 2020). Yet Gittenberger later (2004) restricted “radiation” to refer to rapid diversification. We prefer this more recent definition, and our usage here parallels that for “non-adaptive radiation” (Rundell and Price 2009; Czekanski-Moir and Rundell 2019).

This pattern of adaptive non-radiation can arise when ecological divergence within a clade fails to drive rapid diversification. We suspect that many clades fit this pattern, and we do not claim that the pattern itself is novel or unique to our study. For example, Adams et al. (2009) found decoupled rates of diversification and morphological evolution in salamanders, with some clades (e.g., *Eurycea*) showing rapid morphological change but unexceptional net diversification rates. Many other studies have found decoupled rates of diversification and morphological evolution (e.g., Cantalapiedra et al. 2017; Crouch and Ricklefs 2019; Folk et al. 2019) but have not emphasized (or named) this pattern of adaptive non-radiation.

Conclusions

In this study, we developed an approach to test for adaptive radiations based on the idea that adaptive radiations show elevated rates of diversification and phenotypic evolution relative to other clades. We then applied this approach to a clade of frogs from Madagascar (Mantellidae). Our results show that mantellid frogs are not an adaptive radiation under our definition, since they do not show accelerated net diversification rates. We do find some support for accelerated shape evolution in Mantellidae. Although some authors have emphasized that there can be rapid diversification without significant ecological change (non-adaptive radiation; Gittenberger 1991, 2004; Givnish 1997; Rundell and Price 2009), our results illustrate that clades can have rapid phenotypic change unaccompanied by rapid diversification (here called adaptive non-radiation). Our results also show how tests for adaptive radiation can depend critically on taxon sampling, particularly when other adaptive radiations occur in the clades used for comparison. Yet, our simulations show that limited taxon sampling alone need not bias estimates of phenotypic rates. Finally, we show that a “classic” adaptive radiation in Madagascar (mantellid frogs) does not appear to be one, particularly when comparing their diversification rates to other clades. We suggest that other putative Malagasy adaptive radiations should also be re-examined, especially those postulated primarily based on declining rates over time and without including phenotypic data or comparison to other clades.

AUTHOR CONTRIBUTIONS

D.S.M. and J.J.W. conceived the study. All authors conducted fieldwork and collected performance data. D.S.M. collected morphological data and conducted data analysis. D.S.M. and J.J.W. drafted the paper. All authors discussed the results and provided input on the manuscript.

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DATA ARCHIVING

Data and code associated with this paper (Supporting Information S2–S14) are available on Dryad (https://doi.org/10.5061/dryad.z08kprr9s; Moen et al. 2021).

CONFLICT OF INTEREST

The authors have declared no conflict of interest.

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Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Supporting information S1. Supplementary methods and results. Supporting information files S2–S14 can be accessed on Dryad (Moen et al. 2021).
Figure S1. Results of power simulations of multivariate evolutionary rate comparisons at our two different tree sizes.
Figure S2. The effect of subsampling clades on parameter estimation when comparing rates of continuous trait evolution.
Figure S3. Type I error and power estimates for subsampling simulations.
Table S1. Results of two-block partial least-squares analysis of the relationship between body shape and performance in Mantellidae (25 species).
Table S2. Results of two-block partial least-squares analysis of the relationship between body shape and performance in non-mantellid frogs (55 species).
Table S3. Evolutionary rate comparisons of Mantellidae and other anurans across a posterior distribution of 1000 trees.
Table S4. Results of evolutionary rate comparisons when grouping Mantellidae and Pelodryadinae together and comparing their shared rate to the background rate of other anurans, as assessed on the 80-species complete-data phylogeny.
Table S5. Evolutionary rate comparisons between Pelodryadinae and other anurans (including Mantellidae) on the 80-species phylogeny.
Table S6. Results from all diversification-rate analyses.
Table S7. Results of phylogenetic principal components analysis of body-shape residuals.
Table S8. Maximum-likelihood estimates of λ and its support region of values for all individual traits and trees.
Table S9. Results of evolutionary model-fitting to the traits and trees of this study.