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Independent evolution of the sexes promotes amphibian diversification

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Classic ecological theory predicts that the evolution of sexual dimorphism constrains diversification by limiting morphospace available for speciation. Alternatively, sexual selection may lead to the evolution of reproductive isolation and increased diversification. We test contrasting predictions of these hypotheses by examining the relationship between sexual dimorphism and diversification in amphibians. Our analysis shows that the evolution of sexual size dimorphism (SSD) is associated with increased diversification and speciation, contrary to the ecological theory. Further, this result is unlikely to be explained by traditional sexual selection models because variation in amphibian SSD is unlikely to be driven entirely by sexual selection. We suggest that relaxing a central assumption of classic ecological models—that the sexes share a common adaptive landscape—leads to the alternative hypothesis that independent evolution of the sexes may promote diversification. Once the constraints of sexual conflict are relaxed, the sexes can explore morphospace that would otherwise be inaccessible. Consistent with this novel hypothesis, the evolution of SSD in amphibians is associated with reduced current extinction threat status, and an historical reduction in extinction rate. Our work reconciles conflicting predictions from ecological and evolutionary theory and illustrates that the ability of the sexes to evolve independently is associated with a spectacular vertebrate radiation.

1. Introduction

The role of sexual dimorphism in adaptive radiation is uncertain. Ecological theory predicts that sexual dimorphism in ecologically relevant traits may limit diversification during adaptive radiation if sexually dimorphic species occupy a greater volume of morphospace and thus limit ecological opportunity for speciation [1–3]. Similarly, disruptive selection created by intraspecific resource competition can lead to the evolution of sexual dimorphism and a relaxation of selection for lineage divergence [4]. These ecological predictions are in contrast to sexual selection theory, which generally predicts a positive association between sexual dimorphism and speciation, when sexual dimorphism indicates a history of sexual selection. Sexual selection can promote reproductive isolation [5], therefore cementing speciation, and increase the rate of adaptation to a novel environment [6,7]. In addition, sexual selection in one sex combined with an intersexual genetic correlation can produce a correlated peak shift in the sex under indirect selection [8,9]. Although sexual selection is often expected to lead to increased extinction rates [10,11], empirical examples are equivocal [12,13]. Thus, ecological and evolutionary theory makes opposing predictions for the role of sexual dimorphism in macroevolutionary diversification. Reconciling these alternative views of sexual dimorphism is a major obstacle in the study of organismal diversity, yet has received little attention.

Here, we examine the relationship between sexual size dimorphism (SSD) and diversity dynamics across the Amphibia, a large and highly diverse vertebrate clade. Modern amphibians diverged from related tetrapods in the Carboniferous over 300 Ma [14]. Despite these ancient origins, over 80% of the extant amphibian diversity arose in or after the Late Cretaceous, less than 100 Ma [15]. This recent diversification includes some of the most exceptional known vertebrate radiations. For example, the hyloid frog genus *Pristimantis*, which is less than 50 Myr old [14,16], is the most speciose vertebrate genus ([16]; $n = 458$, [17]). Despite recent high net diversification and a poor fossil record, time-calibrated molecular phylogenies suggest background extinction rates have been high throughout the history of the amphibian diversification [15,18]. Today, amphibians are undergoing a mass extinction driven by climate change, pathogens and habitat loss [19].

Further, extant amphibians exhibit a remarkable degree of variation in sexual dimorphism, particularly in body size [20]. SSD in amphibians is on average female-biased (females larger) but varies considerably across species and clades [20,21]. Critically, much of this variation in SSD appears to be driven by direct selection on female size, more so than male size [20], suggesting SSD is not simply a proxy for the strength of sexual selection. Moreover, because amphibians exhibit markedly conserved body shape within orders, SSD may summarize sexual divergence in life history and ecology. Thus, SSD is a simple univariate measure that captures a degree of multivariate ecologically relevant divergence between the sexes. If SSD reflects ecological divergence between the sexes, classic ecological theory would predict a trade-off between diversification and the evolution of SSD during the process of amphibian diversification.

2. Material and methods

(a) Data acquisition

Body size data were obtained from a dataset of male and female average body lengths of 1139 amphibian species compiled from the literature [20]. (Data available on the Dryad Digital Repository, http://dx.doi.org/10.5061/dryad.24251.) SSD was calculated as larger sex/smaller sex -1, arbitrarily set negative for male-larger species [22]. Species' average body size was calculated as the log-transformed average of male and female size. We calculated mean values for as many non-nested monophyletic families and subfamilies as possible ($n = 49$). We obtained the approximate latitudinal midpoint for species in our dataset from the IUCN Red List database of species range maps, accessed through Amphibiaweb (http://amphibiaweb.org/). We transformed raw latitudes to their absolute values prior to analysis. The numbers of known species in each of the 49 clades in our dataset were obtained from the Amphibian Species of the World v. 5.6 database [17]. The taxonomy of this database coincides with recent phylogenetic hypotheses [17,23]. We obtained extinction risk for all species in our dataset for which assessments had been made from the IUCN Red List (http://www.iucnredlist.org/) [24].

Our phylogenetic hypothesis for both our clade-level and species-level analysis is taken from a recent amphibian phylogeny [23]. We used penalized maximum likelihood to date this tree; we used fossil calibration points compiled by Wiens [25] to set known minimum ages for these nodes, with the addition of a minimum age constraint of 93.9 Ma for the Caecilidae crown group based on Cretaceous fossil evidence [26]. Rather than place an age constraint on the root to estimate the crown age of the tree, we fixed the crown to the 306 Ma estimate from Pyron's hybrid fossil/molecular Bayesian analysis, where this date was estimated using data from other tetrapods [14]. Thus, all nodes with the exception of the crown were estimated; generous maximum age constraints were placed on nodes with minimum age constraints (necessary in 'chronos' in APE [27] in R to avoid fixing the node at the minimum age). We used a strict clock model because this has been shown to provide robust branch length estimates [28]. From this tree and the clade species richness data, we estimated diversification rates ($\lambda = b - d$) for each clade for which we had sufficient data (see above; maximum likelihood (ML) diversification rates could not be fitted for clades with fewer than three extant species) using maximum-likelihood birth–death models [29] accounting for incomplete taxon sampling in Diversitree [30] in R. Our estimates of clade age were similar ($r = 0.86$) to another chronogram [18] recently estimated using similar procedures and the same molecular phylogeny, although our estimates of stem age were younger for many clades (electronic supplementary material, table S7). To assess the sensitivity of our results to the estimated divergence times, we repeated our entire data analysis using Pyron & Wiens' [18] chronogram. We present the full results of this analysis in the electronic supplementary material, but present results from both analyses below wherever inconsistency arose. Our full dataset and dated phylogeny are available on Dryad (doi:10.5061/dryad.j7090), and clade-level summary statistics are presented in electronic supplementary material, table S7.

(b) Statistical analysis: phylogenetic mixed models

We used a series of phylogenetic generalized linear mixed models [31] to assess the effects of SSD and other predictors on clade diversification rate, clade species richness and extinction risk at the species level. We choose to model both diversification rate and species richness because although diversification rate can be a meaningless estimator if clade diversity dynamics are at an ecologically imposed equilibrium [32], amphibian diversification may violate this equilibrium assumption [15,33].

Our model with diversification rate as the dependent variable included clade average body size, SSD and clade average latitude as independent variables. We did not include clade age in this model because it is mathematically confounded with the diversification rate λ. We treated the residual error as exponentially distributed [34] and excluded one outlier clade (Hyperoliidae, $b-d = 0.82$) whose estimate of diversification rate was 6 s.d. from the mean. Including this clade did not affect our conclusions (see electronic supplementary material). We repeated this analysis with species richness (N) as the dependent variable and assumed a geometric error distribution [34]. To account for differences in clade age, we included stem age as a fixed effect. We modelled an overdispersion parameter in both models to allow for the possibility of unexplained (by the fixed effects and macroevolutionary model) variance in the response [31]. We set a lower bound of 0 for the phylogenetic variance component.

IUCN extinction risk is an ordinal, categorical estimate of extinction threat that represents an underlying continuous latent variable (the unknown true extinction risk). Thus, we used a linear model with multinomial error and a cumulative probit link function to assess the effect of species SSD, average body size, lineage age (the terminal edge length from the dated tree) and species latitudinal midpoint on the probability of transitioning to a higher extinction threat category, accounting for phylogeny ($n = 708$ species for which we had phylogenetic, dimorphism and IUCN data). An overdispersion parameter is not estimable in multinomial mixed models, so no R-side random effects were modelled. As a caveat, IUCN extinction risk estimates are influenced by data availability and may thus be taxonomically skewed. However, in amphibians, where most new and poorly described species are in the tropics, including latitude as a covariate in analyses of IUCN extinction risk may in part control for any taxonomic skew in extinction risk.

Fixed effect parameter estimates in tables are based on analyses with the independent variables standardized to unit variance to make effect sizes comparable across variables in a model. All models were fit using residual maximum pseudo-likelihood in the GLIMMIX procedure in SAS v. 9.3 (SAS Institute, Cary, NC, USA). Example SAS code to fit phylogenetic mixed models is provided in the electronic supplementary material.

(c) Statistical analysis: joint analysis of dimorphism and diversification

Although the clade-level analysis of diversification described above can indicate if shifts in dimorphism across amphibian clades have been associated with changes in diversification, recent advances in comparative methods allow the direct estimation of trait-dependent diversification on a species-level phylogeny [35,36]. We fit maximum-likelihood models of SSD-dependent diversification using QuaSSE [35] in the Diversitree package [30] in R using the dated amphibian phylogeny (see above). This approach allows speciation and extinction rates to vary as any specified function of a quantitative trait. We fit candidate models that allowed speciation rate to be constant, or vary in a linear, sigmoidal or Gaussian ('hump-shaped') manner with SSD, accounting for incomplete taxon sampling ($n = 759$ species from the phylogeny for which we had dimorphism data). For each candidate speciation function, we fit a model with extinction either as constant or a linear function of SSD. Although it is possible to fit complicated extinction functions using the QuaSSE approach, recovering relationships between traits and extinction on molecular phylogenies is tenuous, and at best only general patterns can sometimes be recovered [35]. For each candidate combination of speciation and extinction, we allowed for the possibility of a directional bias in phenotypic evolution through time. We ranked the fitted models by AIC.

Although the QuaSSE analysis (and clade diversification rate estimates) account for incomplete taxon sampling, this sampling is assumed to be random with respect to the quantitative trait of interest. We found only weak evidence for a relationship between mean SSD and clade sampling fraction in our dataset ($r = -0.25$, $p = 0.08$, with outlier dropped), suggesting that non-random sampling of species with respect to SSD is unlikely to affect our conclusions. It is, however, unclear exactly how sensitive QuaSSE analyses are to deviations from non-random sampling. To ensure that our general conclusions were robust to among-clade variation in taxon sampling, we repeated the clade-level phylogenetic mixed models incorporating sampling fraction as a weight term in the analysis, using the weight statement in proc GLIMMIX, which gives less weight to poorly sampled clades. Conclusions remain unchanged (electronic supplementary material, table S6), suggesting our results are robust to variation in taxon sampling. Further, we note that because coverage of diverse clades in both the phylogeny and our body size dataset is poor in comparison to species-depauperate clades, among-clade disparity in diversification is likely underestimated (conclusions should be conservative). Additionally, there is no evidence in amphibians that SSD is at all related to taxonomic decisions associated with the assignment of species status.

3. Results

SSD is a significant predictor of diversification rate and species richness across amphibian clades (figure 1 and table 1). Parameter estimates indicate that species richness was an increasing function of average SSD (phylogenetic generalized mixed model: $F_{1,44} = 6.37$, $p = 0.0153$; figure 1*a* and; table 1*a*), accounting for latitude ($F_{1,44} = 2.64$, $p = 0.1115$; figure 1*a* and table 1*a*), body size ($F_{1,44} = 1.07$, $p = 0.3062$) and stem age ($F_{1,44} = 2.99$, $p = 0.0909$), and the same result is obtained regardless of the dated phylogeny used (electronic supplementary material, table S2). Diversification rate was also an increasing function of average SSD ($F_{1,42} = 8.24$, $p = 0.0064$; figure 1*b* and table 1*b*) accounting for latitude ($F_{1,42} = 3.17$, $p = 0.0821$) and body size ($F_{1,42} = 0.4$, $p = 0.53$). However, the strength of this effect was sensitive to the details of the estimation of clade-specific rates. Although SSD was still significantly positively correlated with ML birth–death diversification rate estimated with Pyron & Wiens' species-level dating scheme [18] in a univariate analysis ($F_{1,44} = 5.46$, $p = 0.024$; electronic supplementary material, table S3*b*), including latitude and body size in the model reduced the relative effect of SSD ($F_{1,42} = 1.22$, $p = 0.275$; electronic supplementary material, table S3*a*). Conversely, SSD remained a significant predictor of diversification in a multiple regression when ML rates were estimated using species richness and Pyron & Wiens' stem age estimates [18] (i.e. $\ln(N)/t$; $F_{1,42} = 7.17$, $p = 0.01$; electronic supplementary material, table S3*c*). Thus, although SSD was generally a positive predictor of diversification rate, the relative contributions of SSD, latitude and body size in part depends on the divergence times and estimation procedure used to estimate clade-specific diversification rates.

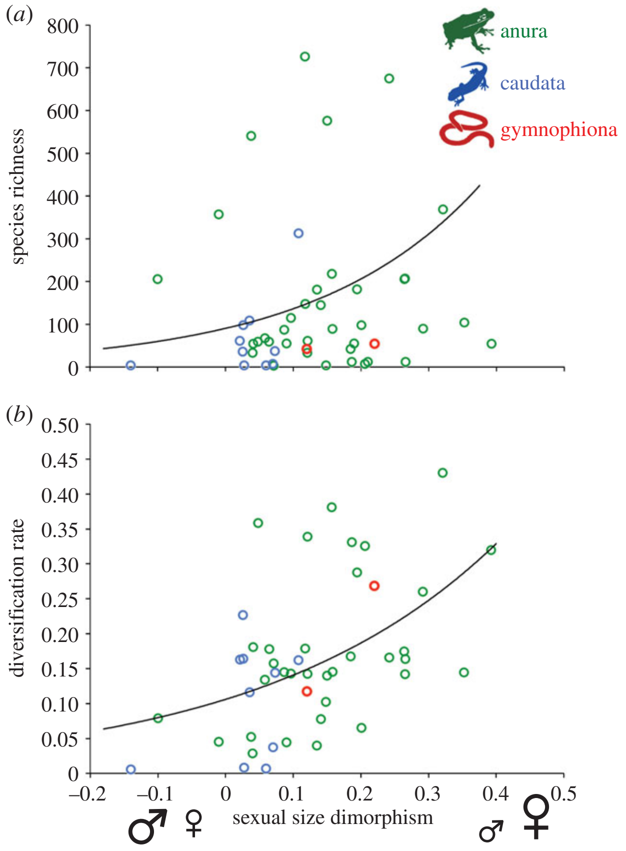

Figure 1. Sexual dimorphism predicts diversification across amphibian clades. Sexual dimorphism predicts (*a*) species richness and (*b*) diversification rate across amphibian clades. Regression lines are the predicted values while holding other fixed effects constant, from phylogenetic generalized mixed models with (*a*) geometric or (*b*) exponential error structure.

Across species, SSD is a significant predictor of current extinction risk (figure 2). Parameter estimates indicate that SSD is negatively associated with the probability of a transition to higher extinction threat level across species (phylogenetic generalized mixed model: $F_{1,700} = 16.44$, $p < 0.0001$; figure 2 and table 2), accounting for latitude ($F_{1,700} = 16.28$, $p < 0.0001$), body size ($F_{1,700} = 3.64$, $p = 0.0569$) and time since speciation ($F_{1,700} = 4.20$, $p = 0.0407$). These results are robust to differences in the dating scheme of the phylogeny used in the analysis (electronic supplementary material, table S4).

A joint analysis of the evolution of dimorphism and diversification on the phylogeny [35] provides unequivocal support for a relationship between SSD and diversification; all models

Table 1. Parameter estimates from models of diversification across clades with (*a*) species richness and (*b*) diversification rate as dependent variables. Estimates in tables are regression coefficients for fixed effects, or the random phylogenetic variance component σ^2_{A} and dispersion parameter from phylogenetic generalized mixed models with either (*a*) geometric or (*b*) exponential error structure. Independent variables were standardized to unit variance to make effects comparable across independent variables within a model. *p*-values are from Wald *F*-tests, and a likelihood ratio test for σ^2_{A}.

effect	estimate	s.e.	*p*-value
(*a*)			
sexual dimorphism	0.4415	0.175	0.0153*
latitude	−0.3581	0.2205	0.1115
lineage age	−0.3817	0.2208	0.0909
body size	−0.191	0.1845	0.3062
intercept	38.787	14.2163	0.0091**
random: σ^2_{A}	0.1509	0.4272	0.6709
random: dispersion	1.1251	0.3035	—
response: species richness; error d.f. = 44			
(*b*)			
sexual dimorphism	0.3027	0.1055	0.0064**
latitude	−0.2043	0.1147	0.0821
body size	−0.06562	0.1038	0.5307
intercept	−1.8797	0.09885	<0.0001***
random: σ^2_{A}	0	—	1
random: dispersion	0.4482	0.0978	—
response: diversification rate; error d.f. = 42			

Statistical significance at $^*\alpha = 0.05$, $^{**}\alpha = 0.01$, $^{***}\alpha = 0.0001$.

with dimorphism as a predictor of diversification had AIC values at least 33.6 units below a constant rate model (table 3, divergence times estimated in this study; electronic supplementary material, table S5, alternative dating scheme). A single top-ranked model was clearly favoured over the candidate set using our divergence time estimates (table 3), indicating a Gaussian ('hump-shaped') relationship between SSD and speciation rate with a peak at a moderate value of dimorphism (0.177) significantly greater than both 0 (i.e. sexual monomorphism, $\Delta\log L = 423.7$, $p \approx 0$; figure 3) and the modal value of SSD ($\Delta\log L = 103.6$, $p \approx 0$; figure 3). This model also indicated a negative relationship between SSD and extinction rate, and thus an overall positive relationship between SSD and net diversification rate (speciation—extinction, figure 3*b*). These parameter estimates were generally robust to divergence times used; fitting this model to Pyron & Wiens' [18] dated tree recovered the same overall pattern between SSD, speciation and extinction (electronic supplementary material, figure S3). However, relative to other models in the candidate set, a sigmoidal relationship between SSD and speciation with constant extinction had greatest support using this dating scheme (electronic supplementary material, table S5). This model indicates a positive, saturating relationship between SSD and diversification rate that is similar in overall shape to that estimated using our divergence time estimates. Taken together, these results provide unanimous support for SSD as a positive predictor of diversification rate through an increase in speciation, with additional support for a negative relationship between SSD and extinction rate that depends to a degree on the dating scheme used.

4. Discussion

We show that SSD is positively associated with net diversification and diversification rate across amphibian clades and negatively associated with extinction risk across species. Further, the evolution of sexual dimorphism is associated with both increased speciation and reduced extinction across the phylogeny. SSD is generally a stronger and more consistent predictor of diversification and extinction than body size and was a more consistent predictor of net diversification than latitude across our analyses (tables 1 and 2). Because latitudinal variation in diversification has played a key role in generating the global distribution of extant amphibian species richness [18], our work illustrates that the evolution of SSD can influence diversification jointly with latitude, as reflected in their similar effect sizes in several of our analyses (tables 1 and 2; electronic supplementary material, S1–S4). In amphibians, the pattern of lineage accumulation through the past 300 Myr suggests that both high speciation and extinction rates have contributed to turnover responsible for generating patterns of extant diversity [15,18]. Our results indicate two roles for the evolution of SSD in this diversification. First, the association between SSD and both historical and current extinction risk (figures 2 and 3) suggests that reduced extinction in dimorphic species has contributed to historical diversity dynamics that correspond with current global patterns of amphibian decline and extinction, although the relative support for an historical role for SSD-dependent extinction depended on the divergence time estimates used. Second, the fact that the most diverse clades are recent in origin [33] suggests that SSD is also associated with increased speciation, which is corroborated by our consistent estimates of a positive relationship between SSD and speciation. Thus, our results suggest that the evolution of female-biased SSD has been associated with both elevated speciation, as well as an ongoing history of reduced extinction. These data conflict with the ecological hypotheses for the role of sexual dimorphism in diversification. Although the observed relationship between SSD and clade diversification and speciation is consistent with predictions of sexual selection theory, past work suggests that sexual selection may fail to explain variation in SSD in amphibians because divergence in female size is a more important contributor to SSD than male size divergence [20]. Further, sexual selection theory generally predicts a positive relationship between dimorphism and extinction, opposite to the negative relationship between dimorphism and extinction illustrated here. Thus, the patterns of dimorphism-dependent diversification that we have observed in amphibians are unlikely to be explained entirely by sexual selection.

We propose that relaxing an unrealistic assumption of traditional ecological hypotheses—that males and females share a common set of adaptive zones in phenotype space—leads to an alternative hypothesis that independent evolution of

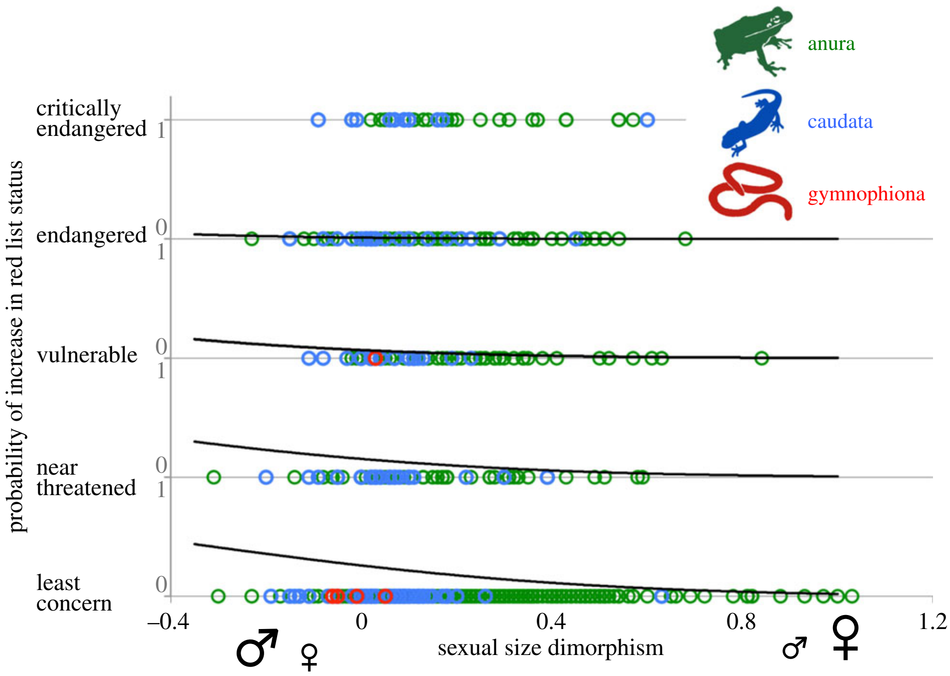

Figure 2. Sexual dimorphism reduces IUCN extinction status across 708 amphibian species. Accounting for phylogeny, body size, lineage age and latitude, the probability of transitioning to a higher extinction risk status decreases with the degree of female-biased SSD, based on a phylogenetic generalized linear mixed model with multinomial error and cumulative probit link. Black lines indicate predicted probabilities while holding other fixed effects constant.

Table 2. Parameter estimates from model of IUCN extinction risk across 708 amphibian species. Estimates are regression coefficients for fixed effects, or the random phylogenetic variance component σ^2_{A} from a phylogenetic generalized mixed model with multinomial error structure. Independent variables were standardized to unit variance to make effects comparable across independent variables within the model. *p*-values are from Wald *F*-tests for fixed effects, and a likelihood ratio test for σ^2_{A}.

effect	estimate	s.e.	*p*-value
sexual dimorphism	−0.2648	0.06531	<0.0001***
latitude	−0.3468	0.08596	<0.0001***
lineage age	−0.1203	0.05867	0.0407*
body size	0.1283	0.06725	0.0569
intercept 5	5.1335	2.1989	0.0198*
intercept 4	5.8927	2.2	0.0076**
intercept 3	6.3658	2.2012	0.0039**
intercept 2	6.739	2.2021	0.0023**
random: σ^2_{A}	4.462	1.1617	<0.0001***

Statistical significance at $^*\alpha = 0.05$, $^{**}\alpha = 0.01$, $^{***}\alpha = 0.0001$.

the sexes may promote diversification into otherwise inaccessible adaptive zones. A key assumption of the ecological theory of sexual dimorphism is that points in phenotype space that represent a natural selection peak in population mean fitness of one sex would, for example, also maximize mean fitness for the other sex of another species. Yet recent empirical evidence from lizards [2], stickleback [37] and stick insects [38] demonstrates that large regions of ecologically relevant morphospace in adaptive radiations of all scales can be sex-specific. In other words, ecological opportunity is sex-specific. In fact, the prevalence of sexually antagonistic selection [39] implies that there are regions of the adaptive landscape that are sex-specific, and thus inaccessible for a sexually monomorphic lineage where males and females are constrained from evolving independently, for example through intersexual genetic correlations [40]. In addition, the sexes themselves are defined by divergent life-history strategies of gamete investment that are expected to lead to sexual conflict over divergent optima for many traits [41] (see the electronic supplementary material). The ability of a lineage to sexually diverge can be seen then as an innovation, rather than a constraint, which allows exploration of this sex-specific morphospace, thereby promoting diversification. Distinct from evolutionary genetic models that rely on intersexual genetic correlations to produce sexually correlated peak shifts [8,9], relaxing constraints on the independent evolution of the sexes may allow a lineage to diversify into sex-specific adaptive zones.

If the ability of the sexes to evolve independently promotes diversification into sex-specific adaptive zones, then we expect that dimorphism, which is both an index of past sexually antagonistic selection and the ability of the sexes to genetically diverge in response, will covary positively (i) with net diversification and (ii) with the rate of diversification, because diversification is expected to be rapid during the colonization of novel adaptive zones [5,42], and (iii) sexual dimorphism should be associated with reduced extinction risk, because sexually monomorphic species should be maladapted if a component of adaptation is sex-specific [40]. All of these predictions are consistent with the results of our analysis of diversification in amphibians, and the latter is distinct from predictions of traditional sexual selection theory.

Amphibians exhibit the greatest diversity of reproductive modes among vertebrates, and comparative analyses indicate repeated evolution of direct development (a female-limited trait) in anurans [43], suggesting the presence of sex-specific adaptive zones. In addition, amphibians are

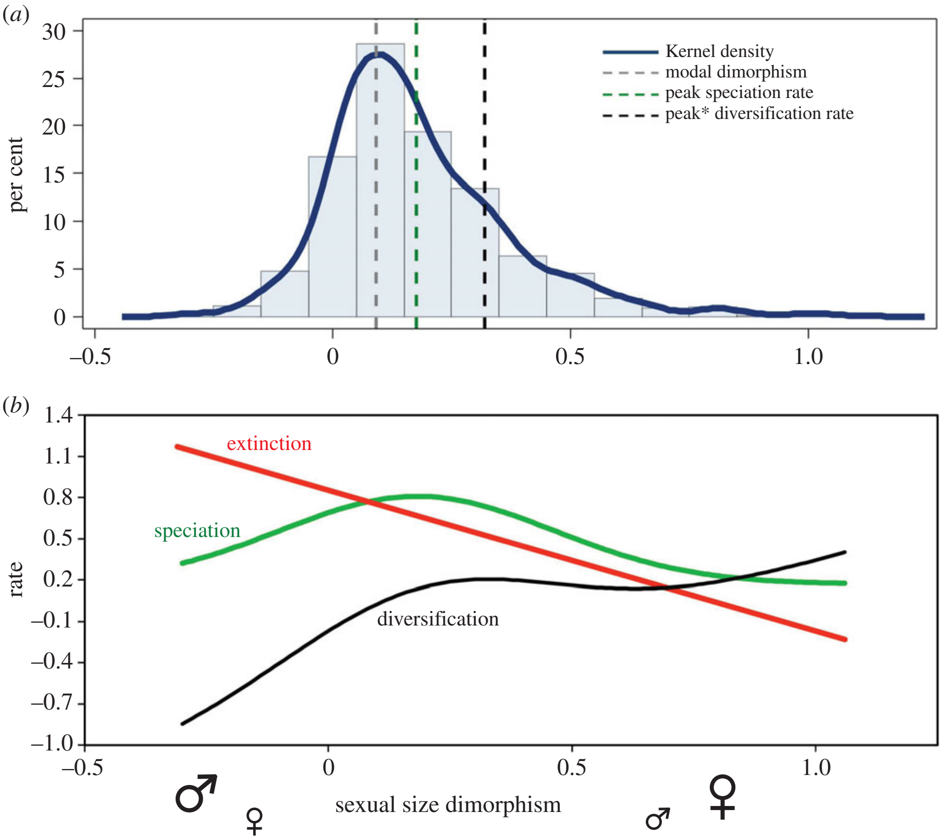

Figure 3. Sexual dimorphism predicts diversification in joint analysis of phenotypic evolution and diversification. (*a*) Distribution of SSD in amphibians. Peak speciation and rate and diversification rate from top-ranked diversification model occur at values of SSD greater than both zero and the modal value of the distribution of amphibian SSD. (*b*) Maximum-likelihood estimates of the relationship between SSD and speciation and extinction, from the top-ranked QuaSSE diversfication model. A combination of a hump-shaped relationship with speciation, centred on an intermediate value of dimorphism, and a negative relationship between extinction and dimorphism contribute to an overall increasing relationship between SSD and diversification rate (speciation—extinction). Asterisk denotes local peak within 95% of the phenotypic distribution (i.e. excluding increase at the extreme SSD values).

Table 3. Model rankings from joint phylogenetic analysis of dimorphism and diversification. Candidate models where fitted using the QuaSSE program in R. k = number of parameters in model; trend is whether (1) or not (0) random walk evolution of dimorphism was modelled with an overall trend through time.

speciation function	extinction function	trend	*k*	log likelihood	AIC	ΔAIC
Gaussian	linear	1	8	−775.5	1567.1	0
Gaussian	linear	0	7	−847.2	1708.4	141.3
Gaussian	constant	0	6	−859.2	1730.5	163.4
Gaussian	constant	1	7	−858.6	1731.2	164.1
sigmoidal	constant	1	7	−891.3	1796.7	229.6
sigmoidal	constant	0	6	−900.4	1812.8	245.7
linear	linear	1	6	−904.3	1820.6	253.5
linear	linear	0	5	−920.4	1850.8	283.7
sigmoidal	linear	0	7	−934.2	1882.4	315.3
sigmoidal	linear	1	8	−938.8	1893.6	326.5
linear	constant	1	5	−944.7	1899.4	332.3
linear	constant	0	4	−946	1899.9	332.8
constant	constant	0	3	−963.8	1933.5	366.4

characterized by high sex chromosome turnover [44], consistent with an hypothesis of pervasive sexually antagonistic selection [45] that would be expected if a large component of ecological opportunity is sex-specific. The wide variation in genetic sex-determining mechanisms and chromosome heteromorphy present in amphibians also suggests variation in the degree of genetic constraint on the evolution of sexual dimorphism [46], consistent with our hypothesis that relaxing constraints on the evolution of dimorphism may promote diversification, as is our estimate of a phyletic trend in opposition (−0.0324) to dimorphism-dependent cladogenesis in our top-ranked diversification model.

Our interpretation rests on two main assumptions. First, we have assumed that female-biased SSD is not simply a proxy for the strength of sexual selection. This assumption is supported by comparative analysis of body size variation in amphibians [20], but this comparative work cannot completely exclude the possibility that larger female size correlates with variance in male reproductive success for some unforeseen reason. Yet even if this assumption is violated, the evolution of sexual dimorphism must still be associated with an increase in ecological opportunity in order to predict diversification; this is in fact an underappreciated implicit assumption of a large body of work examining the role of sexual selection in diversification. Concomitantly, the assumption adopted by many past comparative studies, that sexual dimorphism in a single trait captures variation in the strength of total sexual selection, is likely to be violated in across-taxa comparisons. Regardless, we emphasize that our hypothesis of sex-specific ecological opportunity is not exclusive of the action of sexual selection; sexual selection and sex-specific ecological divergence may often act simultaneously [8]. A second assumption of our hypothesis is that the extent of ecological opportunity available to a sexually dimorphic lineage outweighs any loss owing to increased niche width in dimorphic species. Although formal development of the ideas presented here may inform the validity of this assumption, we see this as a largely empirical issue that may depend on the shape of the adaptive landscape on which a particular lineage is evolving. Theory suggests that sexual divergence can occur jointly with lineage divergence under some conditions of multivariate ecological opportunity [37]. Further, the ubiquity of sexually antagonistic selection in the wild [39] supports the assumption that sex-specific adaptive zones are commonplace.

Our new focus on the role of sex-specific ecological opportunity in adaptive radiation is not meant to be a singular explanation. In reality, the different models that integrate sexual dimorphism and diversification may each play a role at some point in a given radiation. For example, the scale of the radiation under question may in part determine the processes at play. Our work examined global patterns of amphibian diversification over hundreds of millions of years. At finer scales, competition may play a significant role, as suggested in *Anolis* lizards where dimorphism decreases with species richness across the Caribbean islands [1–3]. Incorporating time and ecological opportunity explicitly [47] may be informative to integrating these multiple hypotheses and approaches to the joint study of the evolution of the sexes and adaptive diversification.

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References

1. Schoener TW. 1977 Competition and the niche. In *Biology of the reptilia* (eds C Gans, DW Tinkle), pp. 35–136. New York, NY: Academic Press.
2. Butler M, Sawyer SA, Losos JB. 2007 Sexual dimorphism and adaptive radiation in *Anolis* lizards. *Nature* **447**, 202–205. (doi:10.1038/nature05774)
3. Losos JB. 2009 *Lizards in an evolutionary tree: ecology and adaptive radiation of anoles*. Berkeley, CA: University of California Press.
4. Bolnick DI, Doebeli M. 2003 Sexual dimorphism and adaptive speciation: two sides of the same ecological coin. *Evolution* **57**, 2433–2449. (doi:10.1111/j.0014-3820.2003.tb01489.x)
5. Schluter D. 2000 *The ecology of adaptive radiation*, p. 288. Oxford, UK: Oxford University Press.
6. Lorch PD, Proulx S, Rowe L, Day T. 2003 Condition-dependent sexual selection can accelerate adaptation. *Evol. Ecol. Res.* **5**, 867–881.
7. Agrawal AF. 2001 Sexual selection and the maintenance of sexual reproduction. *Nature* **411**, 692–695. (doi:10.1038/35079590)
8. Bonduriansky R. 2011 Sexual selection and sexual conflict as engines of ecological diversification. *Am. Nat.* **178**, 729–745. (doi:10.1086/662665)
9. Lande R, Kirkpatrick M. 1988 Ecological speciation by sexual selection. *J. Theor. Biol.* **133**, 85–98. (doi:10.1016/S0022-5193(88)80026-2)
10. Kokko H, Brooks R. 2003 Sexy to die for? Sexual selection and the risk of extinction. *Ann. Zool. Fennici* **40**, 207–219.
11. Darwin C. 1871 *The descent of man and selection in relation to sex*, p. 2. London, UK: J. Murray.
12. Morrow EH, Pitcher TE. 2003 Sexual selection and the risk of extinction in birds. *Proc. R. Soc. Lond. B* **270**, 1793–1799. (doi:10.1098/rspb.2003.2441)
13. Morrow EH, Fricke C. 2004 Sexual selection and the risk of extinction in mammals. *Proc. R. Soc. Lond. B* **271**, 2395–2401. (doi:10.1098/rspb.2004.2888)
14. Pyron RA. 2011 Divergence time estimation using fossils as terminal taxa and the origins of Lissamphibia. *Syst. Biol.* **60**, 466–481. (doi:10.1093/sysbio/syr047)
15. Roelants K, Gower DJ, Wilkinson M, Loader SP, Biju SD, Guillaume K, Moriau L, Bossuyt F. 2007 Global patterns of diversification and the history of modern amphibians. *Proc. Natl Acad. Sci. USA* **104**, 887–892. (doi:10.1073/pnas.0608378104)
16. Heinicke MP, Duellman WE, Hedges SB. 2007 Major Carribean and Central American frog faunas originated by ancient oceanic dispersal. *Proc. Natl Acad. Sci. USA* **104**, 10 092–10 097. (doi:10.1073/pnas.0611051104)
17. Frost DR. 2013 *Amphibian species of the world: an online reference, v. 5.6*. New York, NY: American Museum of Natural History. See http://research.amnh.org/vz/herpetology/amphibia/ (accessed 9 January 2013).
18. Pyron RA, Wiens JJ. 2013 Large-scale phylogenetic analyses reveal the causes of high tropical amphibian diversity. *Proc. R. Soc. B* **280**, 20131622. (doi:10.1098/rspb.2013.1622)
19. Stuart SN, Chanson JS, Cox NA, Young BE, Rodrigues AL, Fischman DL, Waller RW. 2004 Status and trends of amphibian declines and extinctions worldwide. *Science* **306**, 1783–1786. (doi:10.1126/science.1103538)
20. De Lisle SP, Rowe L. 2013 Correlated evolution of allometry and sexual dimorphism across higher taxa. *Am. Nat.* **182**, 630–639. (doi:10.1086/673282)
21. Shine R. 1979 Sexual selection and sexual dimorphism in the Amphibia. *Copeia* **2**, 297–306. (doi:10.2307/1443418)
22. Lovich JE, Gibbons JW. 1992 A review of the techniques for quantifying sexual size dimorphism. *Growth Dev. Ageing* **56**, 269–281.
23. Pyron RA, Wiens JJ. 2011 A large-scale phylogeny of Amphibia including over 2,800 species, and a revised classification of extant frogs, salamanders, and caecilians. *Mol. Phylogenet. Evol.* **61**, 543–583. (doi:10.1016/j.ympev.2011.06.012)
24. IUCN. 2013 IUCN Red List of Threatened Species, v. 2013.1. See http://www.iucnredlist.org/.
25. Wiens JJ. 2011 Re-evolution of lost mandibular teeth in frogs after more than 200 million years, and re-evaluating Dollo's law. *Evolution* **65**, 1283–1296. (doi:10.1111/j.1558-5646.2011.01221.x)
26. Evans SE, Milner AR, Werner C. 1996 Sirenid salamanders and a gymnophione amphibian from the Cretaceous of Sudan. *Paleontology* **39**, 77–95.

27. Paradis E, Claude J, Strimmer K. 2004 APE: analyses of phylogenetics and evolution in R language. *Bioinformatics* **20**, 289–290. (doi:10.1093/bioinformatics/btg412)
28. Paradis E. 2013 Molecular dating of phylogenies by likelihood methods: a comparison of models and a new information criterion. *Mol. Phylogenet. Evol.* **67**, 436–444. (doi:10.1016/j.ympev.2013.02.008)
29. Nee S, May RM, Harvey PH. 1994 The reconstructed evolutionary process. *Phil. Trans. R. Soc. Lond. B* **344**, 305–311. (doi:10.1098/rstb.1994.0068)
30. FitzJohn RG. 2012 Diversitree: comparative phylogenetic analyses of diversification in R. *Methods Ecol. Evol.* **3**, 1084–1092. (doi:10.1111/j.2041-210X.2012.00234.x)
31. Hadfield JD, Nakagawa S. 2010 General quantitative genetic methods for comparative biology: phylogenies, taxonomies, meta-analysis and multi-trait models for continuous and categorical characters. *J. Evol. Biol.* **23**, 494–508. (doi:10.1111/j.1420-9101.2009.01915.x)
32. Rabosky DL. 2009 Ecological limits and diversification rate: alternative paradigms to explain the variation in species richness among clades and regions. *Ecol. Lett.* **12**, 735–743. (doi:10.1111/j.1461-0248.2009.01333.x)
33. Rabosky DL, Slater GJ, Alfaro ME. 2012 Clade age and species richness are decoupled across the Eukaryotic tree of life. *PLoS Biol.* **10**, e1001381. (doi:10.1371/journal.pbio.1001381)
34. Ricklefs RE. 2007 Estimating diversification rates from phylogenetic information. *Trends Ecol. Evol.* **22**, 601–610. (doi:10.1016/j.tree.2007.06.013)
35. FitzJohn RG. 2010 Quantitative traits and diversification. *Syst. Biol.* **59**, 619–633. (doi:10.1093/sysbio/syq053)
36. Maddison WP, Midford PE, Otto SP. 2007 Estimating a binary character's effect on speciation and extinction. *Syst. Biol.* **56**, 701–710. (doi:10.1080/10635150701607033)
37. Cooper IA, Gilman RT, Boughman JW. 2011 Sexual dimorphism and speciation on two ecological coins: patterns from nature and theoretical predictions. *Evolution* **65**, 2553–2571. (doi:10.1111/j.1558-5646.2011.01332.x)
38. Roy D, Seehausen O, Nosil P. 2013 Sexual dimorphism dominates divergent host plant use in stick insect morphoogy. *BMC Evol. Biol.* **13**, 135. (doi:10.1186/1471-2148-13-135)
39. Cox RM, Calsbeek R. 2009 Sexually antagonistic selection, sexual dimorphism, and the resolution of intralocus sexual conflict. *Am. Nat.* **173**, 176–187. (doi:10.1086/595841)
40. Lande R. 1980 Sexual dimorphism, sexual selection, and adaptation in polygenic characters. *Evolution* **34**, 292–305. (doi:10.2307/2407393)
41. Shärer L, Rowe L, Arnqvist G. 2012 Anisogamy, chance and the evolution of the sex roles. *Trends Ecol. Evol.* **27**, 260–264. (doi:10.1016/j.tree.2011.12.006)
42. Simpson GG. 1953 *The major features of evolution*. New York, NY: Columbia University Press.
43. Gomez-Mestre I, Pyron RA, Wiens JJ. 2012 Phylogenetic analyses reveal unexpected patterns in the evolution of reproductive modes in frogs. *Evolution* **66**, 3687–3700. (doi:10.1111/j.1558-5646.2012.01715.x)
44. Evans BJ, Pyron RA, Wiens JJ. 2012 Polyploidization and sex chromosome evolution in amphibians. In *Polyploidy and genome evolution* (eds PS Soltis, DE Soltis), pp. 385–410. Heigelberg, Germany: Springer.
45. van Doorn GS, Kirkpatrick M. 2007 Turnover of sex chromosomes induced by sexual conflict. *Nature* **449**, 909–912. (doi:10.1038/nature06178)
46. Rice WR. 1984 Sex-chromosomes and the evolution of sexual dimorphism. *Evolution* **38**, 735–742. (doi:10.2307/2408385)
47. Mahler DL, Revell LJ, Glor RE, Losos JB. 2010 Ecological opportunity and the rate of morphological evolution in the diversification of greater Antillean anoles. *Evolution* **64**, 2731–2745. (doi:10.1111/j.1558-5646.2010.01026.x)