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The multiple origins of sexual size dimorphism in global amphibians

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Abstract

Aim: Body size explains most of the variation in fitness within animal populations and is therefore under constant selection from ecological and reproductive pressures, which often promote its evolution in sex-specific directions, leading to sexual size dimorphism (SSD). Several hypotheses have been proposed to explain the vast diversity of SSD across species. These hypotheses emphasize: (a) the mate competition benefits to larger male size (sexual selection); (b) the benefits of larger female size for fecundity (fecundity selection); (c) the simultaneous benefits of niche divergence for males and females to reduce intersexual competition for ecological resources (natural selection); and (d) the underlying impact of geographical variation in climatic pressures expected to shape large-scale patterns of SSD in synergy with the above selection pressures (e.g., intensification of fecundity selection as breeding seasons shorten). Based on a new, global-scale amphibian dataset, we address the shortage of large-scale, integrative tests of these four hypotheses.

Location: Global.

Time period: Extant.

Major taxa studied: Class Amphibia.

Methods: Using a > 3,500 species dataset spanning body size, ecological, life-history, geographical and climatic data, we performed phylogenetic linear models to address the sexual, fecundity, ecological and climatic hypotheses of SSD.

Results: Evolution of SSD is discordant between anurans and salamanders. Anuran SSD is shaped by climate (male-biased SSD increases with temperature seasonality) and by nesting site. In salamanders, SSD converges across species that occupy the same types of microhabitats ("ecodimorphs"), whereas reproductive or climatic pressures have no effects on their SSD. These contrasts are associated with latitudinal gradients of SSD in anurans, but not in salamanders.

Main conclusions: Amphibian SSD is driven by ecological and climatic pressures, whereas no roles for sexual or fecundity selection were detected. We show that macroevolutionary processes determined by different forms of selection lead to latitudinal patterns of trait diversity, and the lack of them.

KEYWORDS
amphibians, climate, fecundity selection, life histories, natural selection, sexual selection

1 | INTRODUCTION

The optimization of sex-specific reproductive and ecological performance is rarely achieved by conspecific males and females of similar body size (Andersson, 1994; Fairbairn et al., 2007). Therefore, disruptive selection often drives males and females to evolve different body sizes to enhance their sex-specific fitness (Bondurianský & Rowe, 2005; Butler et al., 2007; Fairbairn, 2007; Pincheira-Donoso & Hunt, 2017; Shine, 1989). This leads to sexual size dimorphism (SSD), one of the most widespread forms of intraspecific adaptive evolution across the animal tree of life (Bolnick & Doebeli, 2003; Fairbairn et al., 2007).

A range of hypotheses have been suggested to explain the evolution of SSD. Traditionally, SSD has been attributed to sexual selection driving larger male body size; when mating success in males is positively correlated with their body size during contests with other males and female choice, male-biased SSD is predicted (Andersson, 1994; Darwin, 1871; Rosenthal, 2017). Alternatively, fecundity selection theory predicts that SSD is female biased in species where fitness increases with larger brood size (transient fecundity) attained by larger female size (Darwin, 1874; Fairbairn et al., 2007; Nali et al., 2014; Pincheira-Donoso & Hunt, 2017). However, this prediction has been questioned because it ignores the prevalent and simultaneous effects of sexual selection for larger (or smaller) male size (Pincheira-Donoso & Hunt, 2017). Therefore, larger females that cause female-biased SSD can evolve driven by mechanisms other than fecundity selection, and female-biased SSD is not necessarily correlated with the strength of fecundity selection (Cox et al., 2003; Pincheira-Donoso & Hunt, 2017; Woolbright, 1983; Zamudio, 1998). A more recent hypothesis (the "niche divergence hypothesis"), that intersexual competition for ecological resources creates natural selection that drives divergence between males and females, has increasingly gained support (Bolnick & Doebeli, 2003; Pincheira-Donoso et al., 2018; Shine, 1989). According to this hypothesis, the intensity of intraspecific ecological competition is mitigated by disruptive natural selection driving males and females into different regions of the niche space (Bolnick & Doebeli, 2003; Butler et al., 2007; Meiri et al., 2014; Pincheira-Donoso et al., 2018; Shine, 1989; Slatkin, 1984; Temeles et al., 2000). Likewise, sex-specific natural selection arising from intrinsic differences in reproductive roles exposes males and females to different ecological pressures within their shared environments (Losos et al., 2003; Shine, 1989). Therefore, this ecological SSD hypothesis makes no predictions about whether males or females are larger, given that either sex can benefit from a larger size (Pincheira-Donoso et al., 2018).

A potential implication of the idea that SSD can be the outcome of different forms of selection is that the macroevolutionary pathways underlying the divergence between the sexes within lineages can influence the geographical patterns of distributions of this trait at large spatial scales. For example, the niche space occupied by sexes undergoing divergence by natural selection can saturate the ecological opportunity required for speciation during adaptive radiation (Bolnick & Doebeli, 2003; Butler et al., 2007; Pincheira-Donoso et al., 2018). Therefore, ecological SSD could mirror the outcome of adaptive radiation when character displacement partitions niche space within an area. Across geographical space, this process might inhibit the evolution of macroecological patterns if the same set of resources (e.g., microhabitats) are available in different geographical areas. In contrast, climatic constraints (e.g., length of breeding season) responsible for the intensity of fecundity and sexual selection (Andersson, 1994; Cox et al., 2003; Pincheira-Donoso & Tregenza, 2011) are more likely to create latitudinal patterns of SSD (Pincheira-Donoso & Hunt, 2017).

Although some studies conducted across vertebrates and invertebrates have implemented large-scale approaches to address some of the multiple predictions described above (Amarello et al., 2010; Blanckenhorn et al., 2006; Cox et al., 2003; Dunham et al., 2013; Joos et al., 2017; Michael et al., 2014; Tarr et al., 2019), truly integrative analyses remain anecdotal. The only global-scale studies to date have investigated the relationships between environmental pressures (climate and ecology) and SSD and have revealed contradictory findings. An analysis on global turtles showed significant effects of climate and habitat use on SSD (Agha et al., 2018), whereas a study on birds failed to identify any global predictors of SSD (Friedman & Remes, 2016). Despite these efforts, no global-scale studies exist that investigate the predicted effects of sexual selection, fecundity selection and natural selection and the environmental influences of climate as drivers of SSD, thus preventing wider interpretations about the role of these mechanisms in the evolution of sexual dimorphism.

We created the largest global dataset on SSD for a tetrapod Class, spanning 3,500+ amphibian species (43% of their living diversity). Using phylogenetic analyses based on multiple proxies of all three forms of selection and climate, we test the hypotheses that: (a) male-biased SSD evolves in species where the outcome of competition over mates is influenced by fighting among males, relative to species where male–male aggression is absent (Andersson, 1994; Shine, 1979); (b) fecundity selection promotes larger clutch sizes, attained by evolution of larger female size, leading to the prediction that female-biased SSD increases as a function of increasing fecundity (Darwin, 1874); (c) different microhabitat structures within habitats create different opportunities for ecological divergence between the sexes, which leads to the prediction that patterns of SSD should converge among species that occupy similar microhabitats, regardless of geographical location and phylogenetic affiliation (Agha et al., 2018; Butler et al., 2007; Losos et al., 2003; Pincheira-Donoso et al., 2009; Shine, 1989); and (d) climatic gradients, through their effects on multiple fitness-relevant traits (e.g., life-history traits), shape variation of SSD at large geographical scales. Also, fecundity selection for larger broods intensifies as opportunities for reproduction decline towards more seasonal climates, leading to the further prediction that female-biased SSD increases with increasing seasonality and thus, towards higher latitudes (Cox et al., 2003; Nali et al., 2014; Pincheira-Donoso & Tregenza, 2011).

2 | METHODS

2.1 | Species data

We created a dataset spanning SSD and multiple sexual, reproductive, ecological and climatic candidate predictors across a sample of 3,506 amphibian species from all three living orders (Anura or "anurans", Caudata or "salamanders", and Gymnophiona or "caecilians"). The taxonomy follows Frost (2020). The data were collected predominantly from the primary literature, including articles and monographic books, and from field/museum observations (Supporting Information Table S1, Appendix S1). To collate SSD data, we recorded the maximum body size of adult males and females separately (Supporting Information Table S2). Species for which only young or one individual per sex is known were excluded. For anurans and salamanders, we used the snout–vent length (SVL; this is measured as the snout-to-urostyle length in anurans and the snout-to-edge of cloacae in salamanders) because this is the most widely used body size proxy in these groups (Duellman & Trueb, 1994; Wells, 2007). For caecilians, we used total body length because this is widely documented and is often the only documented proxy for size (Pincheira-Donoso et al., 2019). However, most records of body size available for caecilians focus on one overall measure per species or on one of the sexes only. Thus, although multiple patterns of SSD are reported for all three amphibian orders, many analyses were restricted to anurans and salamanders to reduce the risk of non-credible statistical results obtained from caecilians. The SSD for each species was calculated with the formula $\ln(SVL_{Male}/SVL_{Female})$, an intuitive measure that returns negative values for species where females are the larger sex and positive values when males are larger, which has also been shown to perform with robust statistical power (Fairbairn, 2007; Smith, 1999). Species for which male and female body size is the same (SSD = 0) were considered sexually monomorphic. This dataset is part of the Global Amphibian Biodiversity Project (GABiP, at www.amphibianbiodiversity.org) initiative.

2.2 | Sexual and fecundity data

To address the roles of sexual selection and fecundity selection as drivers of SSD, we used a dataset spanning mating and life-history traits (Supporting Information Table S1). Measures of sexual selection are particularly difficult to obtain unless a species has undergone systematic behavioural observations. In addition, many traits known to play key roles in mate competition among (mostly male) amphibians, such as chemical and acoustic signals, are not necessarily correlated with body size (Andersson, 1994; Duellman & Trueb, 1994; Norris & Lopez, 2011; Wells, 2007). In contrast, male–male competition is widely known to create sexual selection for larger male body size (Andersson, 1994; Clutton-Brock, 1988; Shine, 1979), serving as a key proxy for sexual selection. Male–male competition has been documented extensively

as a form of mating competition among amphibians (Duellman & Trueb, 1994; Mathis et al., 1995; Sparreboom, 2014; Sullivan et al., 1995; Wells, 2007), and many observations have shown that larger males are more aggressive during the breeding season and more successful when engaging in contests (Camp, 1999; Houck, 1988; Sparreboom, 2014; Sullivan et al., 1995; Wells, 2007). Therefore, we used male intrasexual aggressive behaviour as a proxy for sexual selection on male size. Data on male–male contests were taken from sources that describe direct agonistic encounters between individuals, whereas inferential observations, such as males avoiding a site when encountering another male, or bite scars in the skin (e.g., Mathis et al., 1995; Sparreboom, 2014), were excluded. Likewise, male traits that have been assumed to be proxies for male combat, such as tusks and spines (Shine, 1979), were also treated as inferential proxies for male fights because they often evolve to optimize functions such as foraging, amplexus and interspecific defence (Duellman & Trueb, 1994; Han & Fu, 2013; Wells, 2007). No evidence for male contests in a species can be attributable to either lack of the behaviour or lack of observation of the behaviour when it exists (Han & Fu, 2013). Thus, we limited our sexual selection analyses to comparisons between species in which fighting exists against species where extensive behavioural observations that have reported, for example, nest building, female searching, satellite behaviour or mating calls, have failed to observe male contests (Han & Fu, 2013; Sparreboom, 2014). These species were assumed to lack male fighting.

To address the role of fecundity selection, we analysed transient fecundity (brood size) and nesting site preference as factors expected to influence reproductive output (Duellman & Trueb, 1994; Wells, 2007). To estimate transient fecundity, we obtained the median value calculated from the range of brood sizes recorded per species, often reported as the maximum and minimum. When different sources provided different ranges of brood size for the same species, we obtained the median brood size per study and then calculated a single average value for that given species across sources. For hynobiid salamanders that lay eggs into two sacks, clutch size values were not recorded when authors failed to indicate whether the reported number of eggs referred to one or to both sacks combined. We also excluded records of broods that were inferred (rather than observed) to have been laid by a particular species or when the clutch was suspected to be communal. For nesting site data, each species was assigned to one of five categories depending on whether eggs are laid in water (which only includes water bodies in the ground), on the ground (terrestrial sites), in burrows (cavities, under trunks), in vegetation (bushes and trees, including the use of small accumulations of water in flowers or between leaves) or in the parental body (gastric or skin-brooder species). These data are based on observations of individuals occupying those nesting sites. Species for which the nesting site was speculated (e.g., based on close relatives) were excluded. Likewise, all species for which different literature sources reported conflicting records were excluded (Supporting Information Table S1).

2.3 | Ecological data

To investigate the role of ecological pressures on SSD, we used a dataset consisting of two key components of a species niche from which natural selection arises: preference for microhabitat type and diel activity period (Supporting Information Table S1). For the microhabitat data, each species was assigned to one of five categories based on their preference for aquatic (strict water-divers), semi-aquatic (species that depend on intermittent contact with water bodies, e.g., swamp-dwellers, species permanently exposed to waterfall showers), terrestrial (predominantly ground-dwellers), vegetation (species that perch on bushes or trees) or underground ("fossorial"; species that, except for breeding seasons, live underground, including both burrows and caves) microhabitat types. For diel activity period data, species were classed as nocturnal, diurnal, cathemeral (active during day and night) or crepuscular (active only in twilight). Records based on inferences stemming from the ecology of closely related species were excluded.

2.4 | Environmental data

To address the role of climate on SSD (Agha et al., 2018; Pincheira-Donoso & Hunt, 2017; Tarr et al., 2019), we created an environmental dataset with multiple predictors obtained using geographical range maps for all the amphibian species for which distributional data are available at the International Union for Conservation of Nature (IUCN) archive (www.iucnredlist.org). This dataset consists of mean annual temperature (averaged across the 12 months of the year, in degrees Celsius), temperature seasonality (calculated as the standard deviation of the annual mean temperature × 100, in degrees Celsius), mean annual precipitation (the average amount of rainfall, measured in millimetres per year) and precipitation seasonality (coefficient of variation of monthly precipitation across the year). These environmental predictors were obtained from the WorldClim 2 (www.worldclim.org/version2) archive (Fick & Hijmans, 2017; Hijmans et al., 2005) and are expressed at a spatial resolution of 2.5 arc-min (~5 km at the equator). In addition, we added the concentration of atmospheric oxygen as a fifth predictor. Spatial declines in oxygen levels have been shown to create strong selection on life-history traits, primarily exerting constraints on success rates of embryo development (Andrews, 2002; Lambert & Wiens, 2013; Pincheira-Donoso et al., 2017; Wells, 2007). To obtain oxygen levels, we followed the protocol described by Pincheira-Donoso et al. (2017), by first estimating air pressure from the distributional range of each species, using the hypsometric equation $p = P_0 \times (1 - 0.0065 \times h/T + 0.0065 \times h + 273.15)^{-5.257}$ (Seinfeld & Pandis, 2016), where P is the atmospheric pressure (in hectopascals), P_0 represents atmospheric pressure at sea level (1,013.25 hPa or 1 atm), h indicates the elevation above sea level (in metres), and T indicates environmental temperature (in degrees Celsius). Using atmospheric pressure (P), we calculated the proportion of available atmospheric oxygen relative to the baseline 100% availability of oxygen at sea level with the formula:

Oxygen = $(P/P_0) \times 100$ (Pincheira-Donoso et al., 2017; Seinfeld & Pandis, 2016). We assigned each species a single value per predictor (Supporting Information Table S1), calculated as the average of all values obtained for each variable by dividing the geographical range of each species into 2.5 arc min grid cells (*c.* 5 km × 5 km) using ArcGIS 10.2 (www.esri.com). Finally, we included latitude (midpoint, in degrees from the Equator) extracted from each individual map as a further predictor to test for geographical gradients of SSD.

2.5 | Statistical and phylogenetic analyses

We performed phylogenetically controlled linear models [phylogenetic linearized least squares (PGLS)] to investigate the evolution of SSD as a function of the above-described predictors. All phylogenetic regression models used Jetz and Pyron's (2018) phylogenetic tree for 7,238 amphibian species, from which we extracted all species for which data were available (Supporting Information Table S1). Before any analyses, we investigated the allometric influence of body size on SSD. This relationship, termed Rensch's rule, states that the magnitude of SSD increases with increasing body size in species in which males are larger, whereas SSD decreases with increasing body size in species in which females are larger (Abouheif & Fairbairn, 1997; Blanckenhorn, Dixon, et al., 2007; Fairbairn, 1997; Pincheira-Donoso & Tregenza, 2011). To test for Rensch's rule across amphibians, we used major axis regressions (RMA, model II). This technique offers a suitable approach to test the null hypothesis of isometry $\beta = 1.0$ (Blanckenhorn, Dixon, et al., 2007; Fairbairn, 1997; Sokal & Rohlf, 1995). When the logarithm of male body size is plotted on the *y* axis and the logarithm of female body size on the *x* axis, an allometric association consistent with Rensch's rule occurs when variance in *x* is less than in *y*, and thus, when a hyperallometric or positive allometric relationship is observed (Fairbairn, 1997). Standard errors (*SE*) and 95% confidence intervals calculated on error in both *x* and *y* for major axis (MA) slopes are obtained (Blanckenhorn et al., 2007). To control for phylogenetic effects on SSD, we performed the RMA analyses based on phylogenetic independent contrasts (PICs) of male and female body size, obtained using the R package "ape" (Paradis et al., 2004).

We then designed multiple PGLS models that separately address the sexual, fecundity, ecological and climatic hypotheses of SSD. For the sexual selection tests, we created PGLS models that compare levels of SSD between species for which male–male fights are known and species in which they have not been observed. In addition to these analyses, we created frequency distribution plots that show the distribution of species according to their SSD around a reference line that indicates sexual monomorphism (SSD = 0). These plots are designed to show whether the frequency of species without male–male competition tends to show female-biased SSD (left of the zero reference line) relative to the group in which fights exist, which are predicted to be biased towards a higher frequency of species with male-biased SSD. To test for a role of fecundity selection, we first addressed the core

prediction that increases in brood size are a function of increasing female body size (Darwin, 1874; Pincheira-Donoso & Hunt, 2017). The test of this prediction is crucial to make robust interpretations subsequently about the relationship between fecundity and SSD, because this association offers more direct evidence of fecundity selection (Cox et al., 2003; Pincheira-Donoso & Tregenza, 2011). Given the strong positive relationship observed between body size and brood size (see Results), our tests of fecundity selection were performed by regressing SSD on clutch size, with control for female body size, to establish the role of variance in reproductive output on intersexual size divergence (see multivariate climatic analyses described in the next paragraph for a further test of the prediction of fecundity selection that increasing fecundity is selected for towards more seasonal environments). Finally, to test the ecological hypothesis of SSD (Butler et al., 2007; Pincheira-Donoso et al., 2018; Shine, 1989), we created two sets of alternative models. First, we addressed the question of whether microhabitat-specific natural selection drives convergent evolution of SSD across species that occupy the same microhabitat types, regardless of their phylogenetic affiliation (Butler et al., 2007; Losos et al., 2003; Pincheira-Donoso et al., 2009). This hypothesis predicts "ecomorphological" SSD (which we term "ecodimorphs"), and thus, divergent patterns of SSD among species that occupy different microhabitats (Butler et al., 2007). This analysis consisted of phylogenetic ANOVAs quantifying whether variation in SSD differs among the above microhabitat categories, as factors (aquatic, semi-aquatic, terrestrial, vegetation and fossorial). Second, we performed similar analyses to test whether SSD is predicted across diel activity categories, based on the same adaptive principles described for microhabitat-driven convergence.

Finally, we created PGLS models to investigate large-scale patterns of SSD across climatic and geographical space. We first tested for the role of climate on SSD, performing a series of phylogenetic multiple regressions of SSD on all five climatic predictors described above to determine the exclusive role of environmental pressures on intersexual size divergence. The same multiple regressions were repeated with brood size added to the above climatic predictors in the models, in order to investigate further whether climate influences SSD once the role of fecundity on SSD is controlled for, given that fecundity selection is expected to intensify as the opportunities for reproduction are compromised towards environments with shorter breeding seasons (Cox et al., 2007; Fitch, 1981; Pincheira-Donoso & Hunt, 2017; Pincheira-Donoso & Tregenza, 2011). This test is crucial because it complements the conclusions that can be drawn from the fecundity selection tests presented in the previous paragraph. In addition to the climatic analyses, we investigated the expression of latitudinal gradients by regressing SSD on latitude, which is a widely used core geographical predictor to identify biodiversity patterns in macroecology. Importantly, given that latitude is not a mechanistic predictor in itself (rather, multiple selection agents, such as climate, vary with latitude), it was treated independently from the climatic drivers above. Given the loss of statistical power resulting from the differences in sample sizes across the whole range of explanatory

variables described thus far, a full model confronting all hypotheses based on the inclusion of all predictors was not possible.

All the above analyses were performed for anurans and salamanders separately to establish lineage-specific patterns of SSD evolution (sample sizes for caecilians were often too low to enable us to perform analyses independently). These two orders differ in multiple core features (e.g., body plan, life histories, distribution, genome size), and thus, their responses to selection are expected to differ. In all regressions, continuous predictors were $\log_{10}$-transformed to meet assumptions about normality and homogeneity of variance. For every model, we tested the significance of the value of Pagel's λ, which measures the influence of shared evolutionary history on the divergence of regression residuals among species (Pagel, 1999). All phylogenetic linear models were performed using the packages "ape" (Paradis et al., 2004), "nlme" (Pinheiro et al., 2018) and "caper" (Orme et al., 2012) implemented in R (R Development Core Team, 2017). For the phylogenetic tree with variation of values of SSD through time along the branches (shown in Figure 1), we used a maximum-likelihood phylogenetic reconstruction implemented in the package "phytools" (Revell, 2012). For the hexagon density scatter plots presented in Figure 5c,d, we used the approach described by Roll et al. (2017).

To reinforce the inference from our climatic PGLS models, we performed model-averaging analyses using the Akaike information criterion (AIC) and Akaike model weights to reduce the whole set of models (Burnham & Anderson, 2002), adopting a dredging approach that retains a confidence subset of regression models that lie within six AIC units of the most informative model. This approach removes the set of models that have spurious parameter estimates owing to poor model fit above the chosen AIC threshold (Harrison et al., 2018; Richards, 2005). The importance of each explanatory variable was judged according to AIC-weighted mean effect sizes averaged across the subset of regression models, and are presented as AIC-weighted slope estimates ± 95% confidence intervals to estimate the significance of the effect of each predictor on SSD. Model-averaging analyses were performed using the R package "MuMIn" (Barton, 2017).

3 | RESULTS

SSD varied extensively across orders, families and species (Figures 1 and 2). Female-biased SSD strongly prevailed in all three amphibian orders (Figure 2). In anurans, SSD was female biased in 90.8% of species, male-biased in 7.5%, and monomorphism was observed in 1.7% of species. In salamanders, 79.2% of species showed female-biased SSD and 19.1% male-biased SSD, and 1.8% were monomorphic (SSD = 0). In caecilians, SSD was observed to be female biased in 81.3% of species and male biased in 18.8%, and no monomorphic species were observed (Figure 2). Anurans showed by far the widest range of variation in SSD (Figure 2). Regarding allometric effects of body size on SSD (Rensch's rule), our phylogenetic analyses consistently rejected this pattern. The
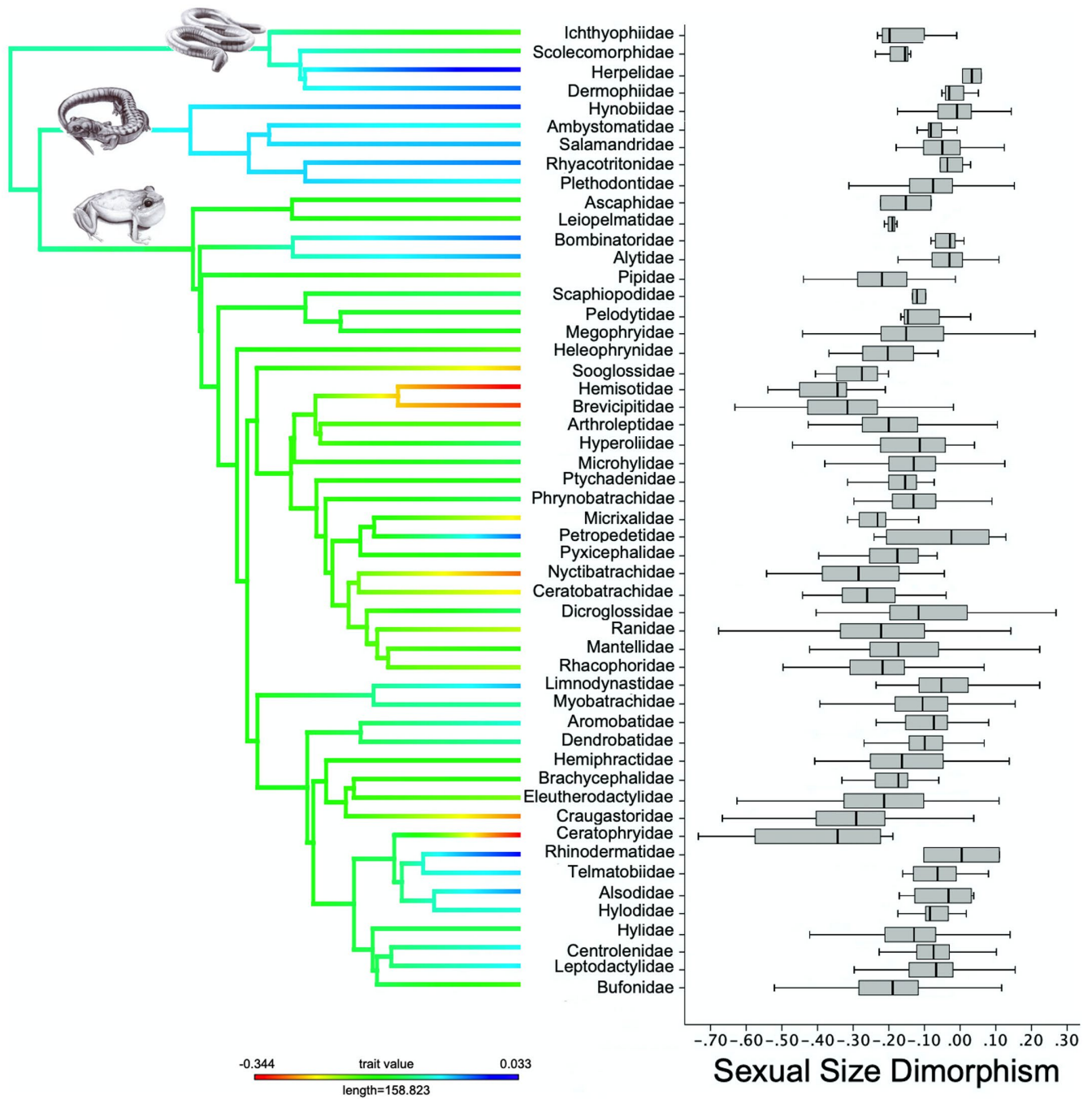
FIGURE 1 Phylogenetic patterns of sexual size dimorphism (SSD) across families of living amphibians. The tree shows the distribution of median SSD across species per family along the branches, and the bar below provides the colour codes for levels of both male- (positive) and female-biased (negative) SSD. The predominant tendency is for female-biased SSD, with the most extreme cases of female-biased SSD being observed among anurans (Ceratophryidae, Craugastoridae, Ranidae, etc.). See Methods for details about SSD calculations

slopes of RMA regressions were not significantly different from one for anurans (PICs: slope = 1.002 ± 0.004, intercept = −0.001, 95% confidence interval = 0.981–1.024, ordinary least square, OLS slope = 0.93 ± 0.01, n = 1,264) or for salamanders (PICs: slope = 0.989 ± 0.017, intercept = −0.001, 95% confidence interval = 0.941–1.041, OLS slope = 0.95 ± 0.02, n = 147). No test was possible for caecilians.

3.1 | Sexual selection on SSD

Our analyses consistently failed to identify a relationship between male contests and SSD. Frequency distributions revealed that the tendencies for female- and male-biased SSD were qualitatively identical when making comparisons between species with and without male–male competition in both anurans and salamanders (Figure 4a–d).

FIGURE 2 Patterns of sexual size dimorphism (SSD) across orders of amphibians. The same tendencies for predominant female-biased SSD observed across families are observed when the frequency distribution (a; black vertical lines indicate sexual size monomorphism) and (taxonomic) order-level median (and quartile distribution) of SSD (b) are plotted. See Methods for details about SSD calculations
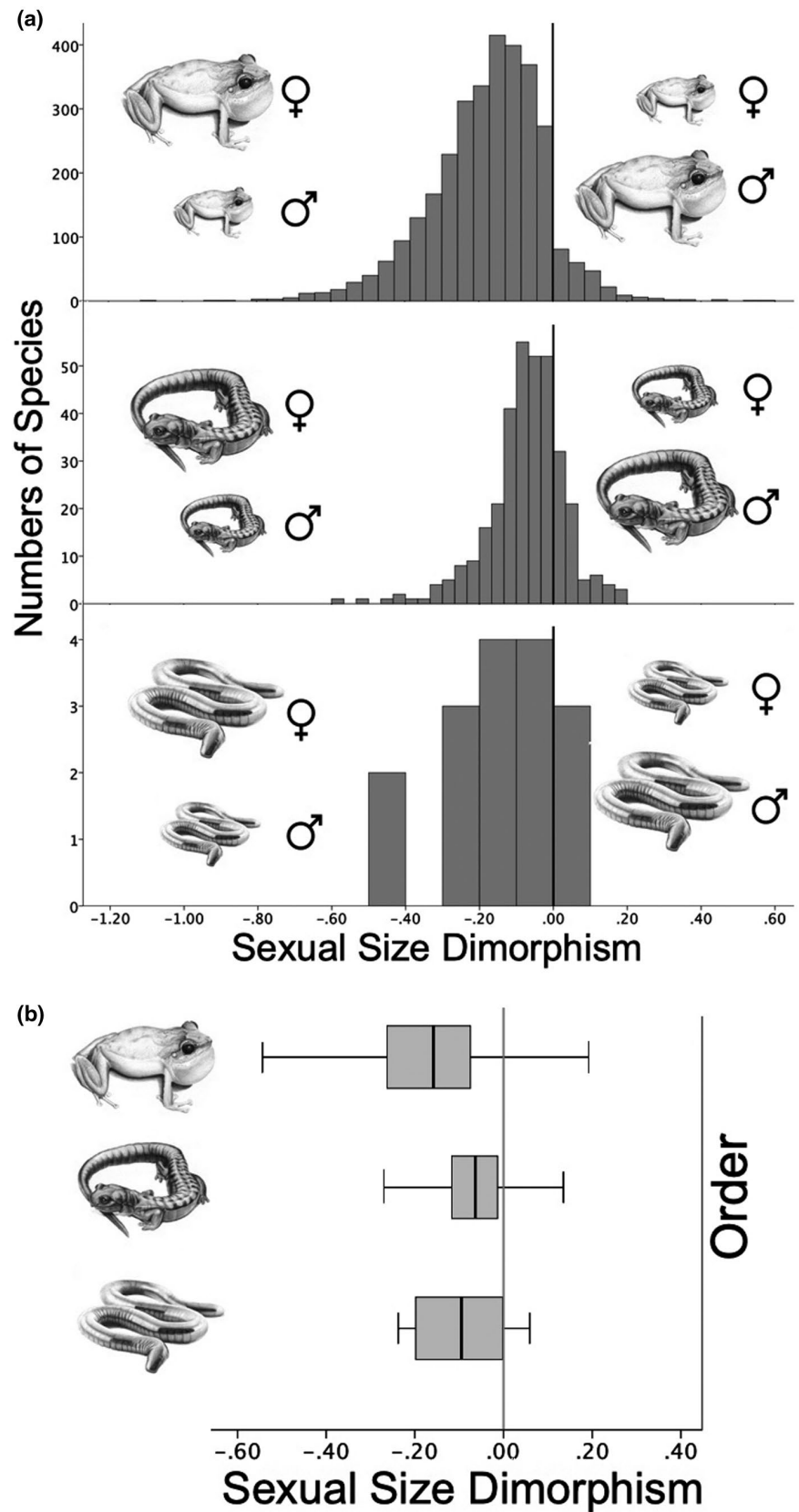
Phylogenetic analyses confirmed this finding, showing that no differences existed in the direction and magnitude of SSD between species in which males engaged in fights over access to females, relative to species in which male contests were absent (Table 1; Figure 4e,f).

3.2 | Fecundity selection on SSD

Our analyses showed that increases in brood size were strongly associated with larger female body size in anurans and salamanders

TABLE 1 Relationships between proxies of sexual, fecundity and natural selection and the global diversity of sexual size dimorphism across amphibians

Models	λ	n	R^2	F (d.f.)	t	Estimate	p
Fecundity selection							
Fecundity ~ SVL							
Anurans	.838	1,441	.29	588.6 (1, 1,439)	24.26	1.831	**< .001**
Salamanders	.812	151	.062	9.89 (1, 149)	3.145	0.909	**< .01**
SSD ~ fecundity[*]							
Anurans	.71	1,441	–	0.01 (1, 1,438)	−0.09	−0.0003	.926
Salamanders	.64	151	–	0.078 (1, 148)	−0.28	−0.0017	.781
SSD ~ nesting site							
Anurans[a]	.714	970	–	8.68 (1, 968)	2.946	0.014	**.003**
Anurans[b]	.697	970	–	8.65 (1, 968)	−2.941	−0.012	**.003**
Salamanders[a]	.871	91	–	3.00 (1, 89)	1.733	0.022	.087
Salamanders[b]	.049	91	–	3.27 (1, 89)	1.807	0.013	.074
Sexual selection							
Male–male competition							
Anurans	.701	621	–	0.15 (1, 619)	0.389	0.005	.697
Salamanders	.9	74	–	0.016 (1, 72)	−0.127	−0.003	.899
Natural selection							
SSD ~ microhabitat							
Anurans[a]	.626	2,349	–	0.53 (1, 2,347)	0.729	0.002	.466
Anurans[b]	.606	2,349	–	0.32 (1, 2,347)	−0.569	−0.002	.569
Salamanders[a]	.630	270	–	4.73 (1, 268)	2.175	0.012	**.03**
Salamanders[b]	.597	270	–	8.30 (1, 268)	−2.881	−0.013	**< .01**
SSD ~ diel activity							
Anurans	.680	1635	–	1.66 (2, 1,633)	1.290	0.006	.197
Salamanders	.399	160	–	1.67 (2, 158)	−1.292	−0.013	.198

Note.: SSD = sexual size dimorphism; SVL = snout–vent length. All analyses have been performed separately for anurans and salamanders. Caecilians have been excluded because of small sample sizes. Fecundity refers to transient fecundity (i.e., brood size). Phylogenetic analyses of nesting site and microhabitats as predictors have been performed twice for each order: (a) with SSD treated as a measure of male- (positive values) and female-biased (negative values) dimorphism; and (b) with SSD treated as a measure of the absolute magnitude of the difference in size between the sexes, where all values are treated as positive. Most models showed significant phylogenetic signal, estimated using Pagel's λ (Pagel, 1999); see main text for details. Significant results in boldface.

[a]Female-biased SSD as negative values and male-biased SSD as positive values.

[b]SSD as a measure of the absolute magnitude of differences in body size.

[*]Results from an analysis of covariance with body size added as a covariate. Estimate and *t*-value were obtained from phylogenetic linearized least squares (PGLS).

(Table 1; Figure 3a; the same tendency was observed, but not tested, in caecilians). However, the prediction that female-biased SSD increases as a function of increasing brood size (controlling for body size) was rejected by our analyses across all amphibians (Table 1; Figure 3b). In contrast, we found that SSD in anurans differed significantly among species that selected different nesting sites. Although anuran species that lay eggs in burrows had a tendency for greater degrees of SSD (treated as an absolute magnitude of difference in body size between the sexes), species that lay their eggs on leaves in bushes and trees showed a drastic decrease in SSD (Figure 4i). No such association between SSD and nesting site was observed in salamanders (Table 1), although the greatest extent of SSD was

observed among plant egg-layers (Figure 4j), which entirely opposed the pattern observed in anurans.

3.3 | Natural selection on SSD

Analyses investigating the effects of ecological pressures revealed similar degrees of SSD across salamander species that occupy the same types of microhabitats, once their phylogenetic origin was controlled for (Table 1). The fossorial salamanders had the lowest degree of SSD, whereas species that occupy vegetation had the largest difference in body size between the sexes (Figure 4h).
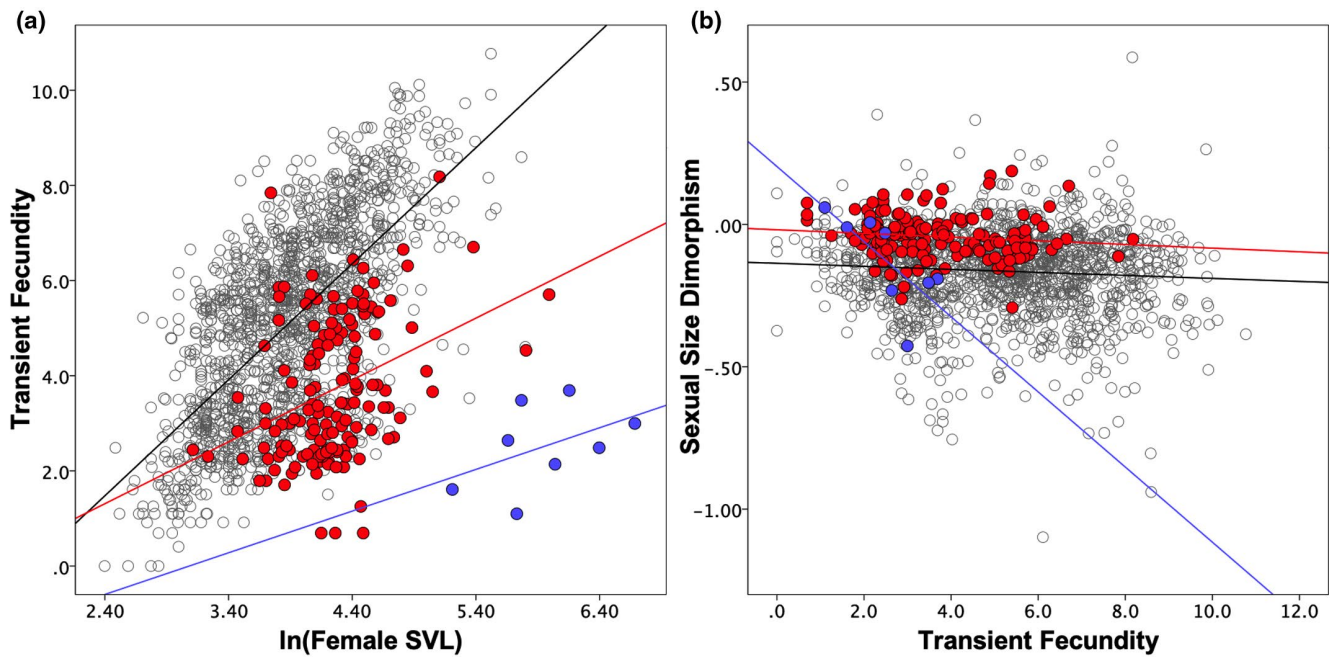
FIGURE 3 The relationships between transient fecundity (brood size) and (interspecific and intersexual) variation in body size. (a) The analyses show that increasing clutch size in all three amphibian orders (grey = anurans; red = salamanders; blue = caecilians) is a strong function of increasing female body size (SVL = snout–vent legth). (b) There is a (lack of significant) relationship between fecundity and sexual size dimorphism (SSD) for the same three groups (and colour codes)

This finding remained consistent both when distinctions between female-based and male-biased SSD were incorporated into the analyses and when SSD was treated as an absolute value of the difference in size between the sexes (Table 1). In contrast, our analyses failed to detect an effect of microhabitat on the SSD of anurans (Table 1; Figure 4g). These observations were not affected when SSD was treated as a magnitude from female- to male-biased differences or as an absolute measure of magnitude only (Table 1).

3.4 | Macroecological patterns of SSD through climate and geography

Analyses on the role of climatic factors identified temperature seasonality as the only significant predictor of spatial variation in SSD in anurans; males increased in size more relative to females as thermal seasonality increased (Table 2; Figure 5c). Likewise, the model containing brood size added to all five climatic predictors revealed exactly the same relationship (Table 2), whereas the remaining predictors had no effects. The model-averaging analyses using the same sets of predictors strongly confirmed temperature seasonality as the only driver of anuran SSD, with and without brood size included (Table 2). In contrast, the same analyses performed on salamanders failed to identify a role for climate on SSD (Table 2; Figure 5d).

The geographical analyses of SSD were consistent with these findings. No latitudinal gradients (based on absolute values of latitude, ignoring whether the gradient was south or north) of SSD were

observed in salamanders globally (Table 2; Figure 5b), whereas we observed a significant increase in SSD with increasing latitude in anurans globally (i.e., males increased more in size relative to females with increasing latitude; Table 2; Figure 5a). Intriguingly, the spatial patterns shown in Figure 5a,b suggested that the latitudinal gradients of SSD might differ among geographical regions of the world, particularly within anurans. A further set of analyses, investigating the geographical patterns of anuran SSD within regions separately, confirmed the same positive association between SSD and latitude within the Americas ($n = 1,366$, $\lambda = .58$, $R^2 = .01$, estimate = 0.001, $F_{1,1,364} = 8.07$, $p < .01$; Figure 5a; although distinctive patterns between North and South America existed: female-biased SSD increased with latitude in the former and male-biased SSD in the latter) and the Eurasian region ($n = 377$, $\lambda = .62$, $R^2 = .03$, estimate = 0.003, $F_{1,375} = 10.97$, $p = .001$; Figure 5a). Interestingly, however, the latitudinal gradient of anuran SSD was reversed in Africa, where female size increased more relative to male size with increasing latitude ($n = 349$, $\lambda = .54$, $R^2 = .02$, estimate = −0.002, $F_{1,347} = 5.51$, $p = .02$; Figure 5a). The same region-specific analyses performed in salamanders showed no relationships between SSD and latitude, consistent with the global model.

4 | DISCUSSION

Our study reveals the distinctive factors driving the evolution of sexual size dimorphism across amphibian orders. In anurans, SSD is associated with climatic gradients in temperature seasonality (a phenomenon that shapes latitudinal gradients of SSD) and

with nesting site occupation. These findings provide global-scale evidence suggesting that selection for divergence between the sexes is significantly influenced by variation in the length of the

breeding season (Cox et al., 2003; Pincheira-Donoso & Hunt, 2017; Pincheira-Donoso & Tregenza, 2011) and by the constraints that nesting structures exert on reproduction (Nali et al., 2014). These
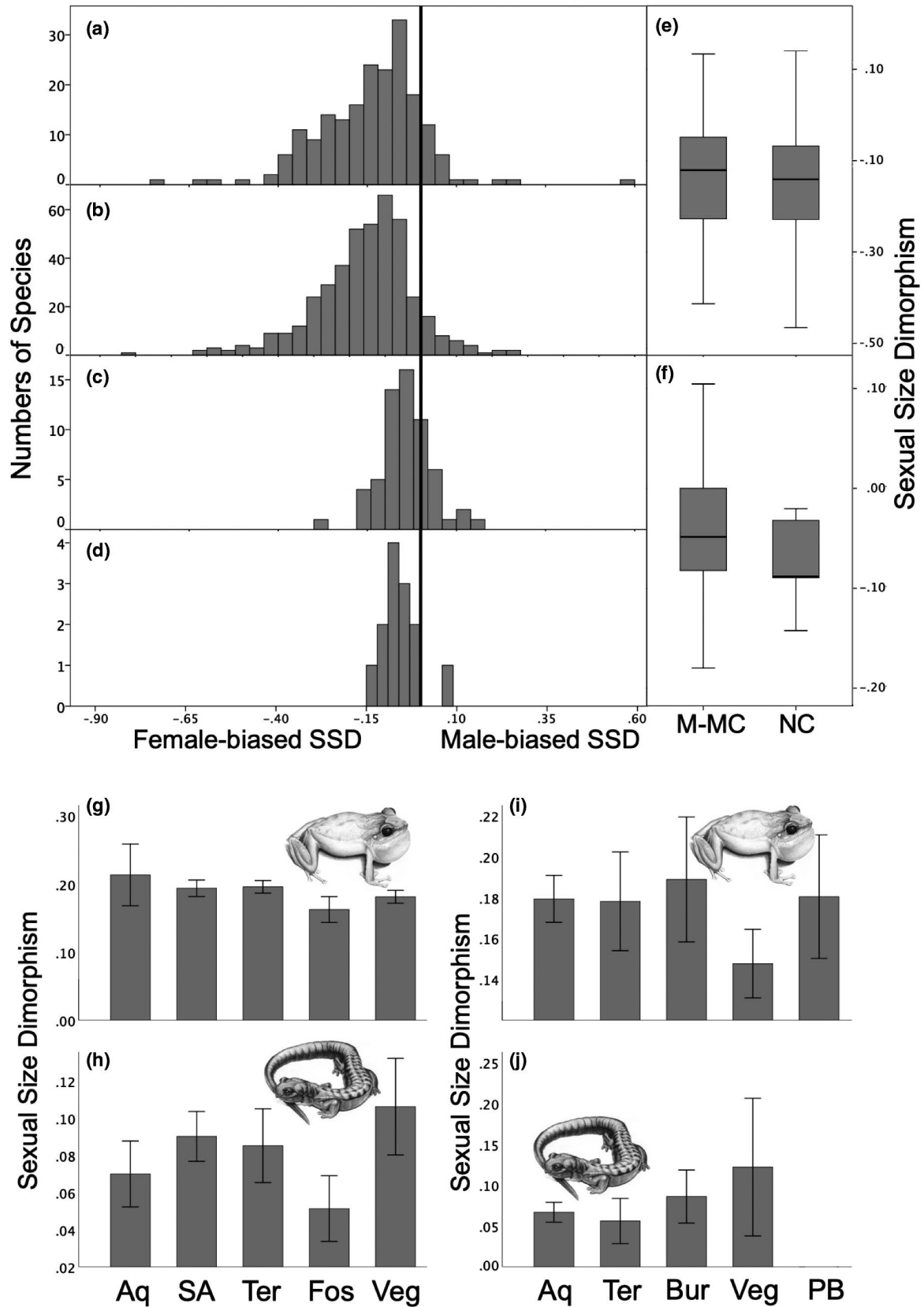
FIGURE 4 Effects of ecological pressures, but not sexual selection, on amphibian sexual size dimorphism (SSD). (a–d) Frequency distributions of SSD show that the frequency of anuran (a,b) and salamander (c,d) species with male-biased SSD (to the right of the black vertical line that indicates sexual size monomorphism) is not higher in species in which access to mates is mediated by male–male combats (a,c) relative to species in which no male combat exists (b,d). (e,f) These findings are confirmed by the boxplots, which show that the magnitude of SSD is qualitatively identical for species with (M-MC) and without (NC) male–male combat in both anurans (e) and salamanders (f). (g,h) Bar plots, in contrast, show the significant influence of microhabitat use (Aq = aquatic; Fos = fossorial; SA = semi-aquatic; Ter = terrestrial; Veg = bushes and trees) on the variation of SSD among salamanders (h) and the lack of significant effects in anurans (g). (i,j) The opposite effects are observed for the relationship between SSD and nesting site (Aq = aquatic; Bur = burrows; PB = parents' body; Ter = terrestrial; Veg = bushes and trees), which has a significant influence in anurans (i), but not in salamanders (j). In these plots (g–j), SSD is treated as an absolute measure of the magnitude of SSD, regardless of whether females or males are the larger sex

two sources of selection on SSD are likely to operate synergistically. In fact, although our analyses failed to identify a relationship between increasing fecundity and female-biased SSD, in contrast to previous studies conducted on frogs (e.g., Han & Fu, 2013), we found strong evidence that larger females produce larger broods and a tendency for brood size to increase with increasing latitude (as shown by the negative association between fecundity and SSD; see Table 2). These findings are consistent with fecundity selection theory, which predicts the evolution of larger broods mediated by larger females towards environments where reproductive opportunities are reduced, mostly regions with shorter breeding seasons (Pincheira-Donoso & Hunt, 2017). At the same time, this evidence reinforces the view that a link between the intensification of fecundity selection and female-biased SSD is incidental, rather than general, and dependent on the action of multiple other sources of selection on body size, such as male-specific sexual selection for larger body size (Nali et al., 2014; Pincheira-Donoso & Hunt, 2017; Zamudio, 1998). In contrast, variation in SSD in salamanders is associated with use of microhabitat types. This link suggests a role for natural selection in driving convergent evolution in SSD. Importantly, our analyses failed to identify a role for male–male competition-mediated sexual selection in the evolution of SSD across all amphibian clades, as previously observed in anurans (Han & Fu, 2013; Nali et al., 2014).

Why anurans and salamanders have followed such discordant routes in the evolution of SSD remains an open question. The answer might be linked to their contrasting life-history features and biogeographical patterns. Given the strong effects of climate on fecundity (Jetz et al., 2008; Pincheira-Donoso & Hunt, 2017), the evolution of the truly global distribution of anurans is expected to have exposed these amphibians to a much wider range of climatic pressures, leading to a much wider range of life-history adaptations to these demands, such as their extreme interspecific variation in clutch size (between one and > 80,000 eggs). In contrast, the global geographical range of salamanders is considerably more restricted than in anurans (Pough et al., 2015; Sparreboom, 2014), leading to a much narrower range of climatic pressures that are likely to influence selection on life-history traits (e.g., their narrow variation in clutch size from two to < 3,800 eggs). Nonetheless, a concrete explanation for the association between SSD and microhabitat occupation in salamanders would be unnecessarily speculative at present.

A range of further evolutionary contrasts between anurans and salamanders is likely to predispose their processes of diversification

to follow alternative trajectories, which might contribute to explain their distinct patterns of SSD. In addition to differences in fecundity, fertilization is external in *c.* 90% of anuran species, whereas *c.* 90% of salamanders have internal fertilization via spermatophores (Duellman & Trueb, 1994; Pough et al., 2004; Wells, 2007). Also, although genome size in anurans is roughly comparable with that of most tetrapods, the exceptionally large genomes of salamanders can be ≤ 10 times the size of the next-largest tetrapod genomes (Canapa et al., 2015; Kapusta et al., 2017; Liedtke et al., 2018). These differences are expected to influence how selection shapes both lineages. For example, climate is thought to affect the evolution of genome size in anurans (but not in salamanders), which has been hypothesized to be caused by the life-history contrasts between these groups (Liedtke et al., 2018). Therefore, the answer to their different patterns of evolution might derive from many factors (Nali et al., 2014).

4.1 | The influence of macroevolution on macroecological patterns of biodiversity

The contrasting patterns of SSD observed between anurans and salamanders suggest that the different forms of selection associated with intersexual divergence within each order might play a role in their configuration of global patterns of SSD distribution. When the evolution of a trait is shaped by selection from factors that vary geographically (e.g., climate), a macroecological pattern of trait variation can be expected. This is the case for anurans, in which SSD varies according to latitudinal gradients associated with geographical gradients in temperature seasonality. Many other components of biodiversity conform to this process. For example, the evolution of life-history traits associated with fecundity (e.g., clutch size, egg size, parity) can be shaped strongly by selection from the climate (Jetz et al., 2008; Meiri et al., 2020; Pincheira-Donoso & Hunt, 2017; Pincheira-Donoso et al., 2013; Shine, 2005). Thus, the configuration of geographical gradients in the variation of these climate-sensitive traits is expected (Pincheira-Donoso & Hunt, 2017; Tarr et al., 2019).

In contrast, when selection arises from interspecific competition over finite resources that promote mitigation of conflicts via niche partitioning at the local scale (e.g., character displacement), macroecological patterns are expected to be superseded by within-assemblage diversification of the trait. This is the case for interspecific diversity of SSD in salamanders, which seems to

TABLE 2 Climatic and geographical drivers of amphibian sexual size dimorphism

Models	n	λ	R^2	F	t	p	Slope	95% CI
		PGLS					**Model-averaging analyses**	
SSD ~ predictors								
Anurans								
(a) MRM	2,649	.626	.01	4.52	–	**< .001**	–	–
Annual temperature	–	–	–	–	1.20	.229	–	–
Temperature seasonality	–	–	–	–	3.62	**< .001**	**0.039**	**(0.0214, 0.0585)**
Annual precipitation	–	–	–	–	0.84	.399	–	–
Precipitation seasonality	–	–	–	–	0.72	.473	–	–
Oxygen	–	–	–	–	−1.79	.073	−0.035	(−0.0890, 0.0199)
(b) Latitude	2,709	.614	.002	5.73	2.39	**.02**	–	–
Salamanders								
(a) MRM	290	.616	.003	0.187	–	.967	–	–
Annual temperature	–	–	–	–	0.54	.588	–	–
Temperature seasonality	–	–	–	–	0.78	.435	–	–
Annual precipitation	–	–	–	–	0.07	.943	–	–
Precipitation seasonality	–	–	–	–	−0.15	.884	–	–
Oxygen	–	–	–	–	−0.60	.549	−0.013	(−0.1239, 0.0986)
(b) Latitude	298	.651	.0001	0.032	−0.18	.857	–	–
SSD ~ Fec + predictors								
Anurans								
MRM	1,356	.704	.03	6.14	–	**< .001**	–	–
Fecundity	–	–	–	–	−4.78	**< .001**	**−0.014**	**(−0.0191, −0.0082)**
Annual temperature	–	–	–	–	0.85	.397	–	–
Temperature seasonality	–	–	–	–	2.97	**.003**	**0.051**	**(0.0269, 0.0751)**
Annual precipitation	–	–	–	–	−0.57	.570	–	–
Precipitation seasonality	–	–	–	–	0.01	.991	–	–
Oxygen	–	–	–	–	−1.34	.180	−0.050	(−0.1316, 0.0306)
Salamanders								
MRM	141	.192	.04	0.87	–	.517	–	–
Fecundity	–	–	–	–	−1.31	.194	–	–
Annual temperature	–	–	–	–	1.44	.153	–	–
Temperature seasonality	–	–	–	–	0.53	.596	–	–
Annual precipitation	–	–	–	–	0.24	.811	–	–
Precipitation seasonality	–	–	–	–	−1.48	.140	–	–
Oxygen	–	–	–	–	−0.55	.585	0.025	(−0.1046, 0.1552)

Note: All phylogenetic analyses (PGLS) were performed separately for anurans and salamanders (caecilians are excluded because of small sample sizes). Environmental analyses are based on MRMs with mean annual temperature, temperature seasonality, mean annual precipitation, precipitation seasonality and oxygen concentrations as predictors. Geographical analyses include only latitude as a predictor. The bottom subsection of the table shows the same MRM analyses controlling for Fec. For each MRM, we report the slope and 95% CI of the drivers returned by model-averaging analyses given their threshold ΔAIC < 6 (drivers with ΔAIC > 6 are not shown). Among these returned predictors, significant predictors are shown in bold. Most models showed a significant phylogenetic signal.

ΔAIC = change in Akaike information criterion; CI = confidence interval; Fec = transient fecundity; MRM = multiple regression model; PGLS = phylogenetic linearized least squares; SSD = sexual size dimorphism.

be partitioned by the adaptation of species to different microhabitat structures at local scales. Thus, if the same array of ecological resources subject to interspecific competition that are available within an area (e.g., a suite of microhabitat types) are available at

different locations along a geographical gradient, multiple replicated sets of "ecodimorphs" across regions are expected to evolve, eroding a geographical signal (Butler et al., 2007; Pincheira-Donoso et al., 2018). This scenario is observed among replicated
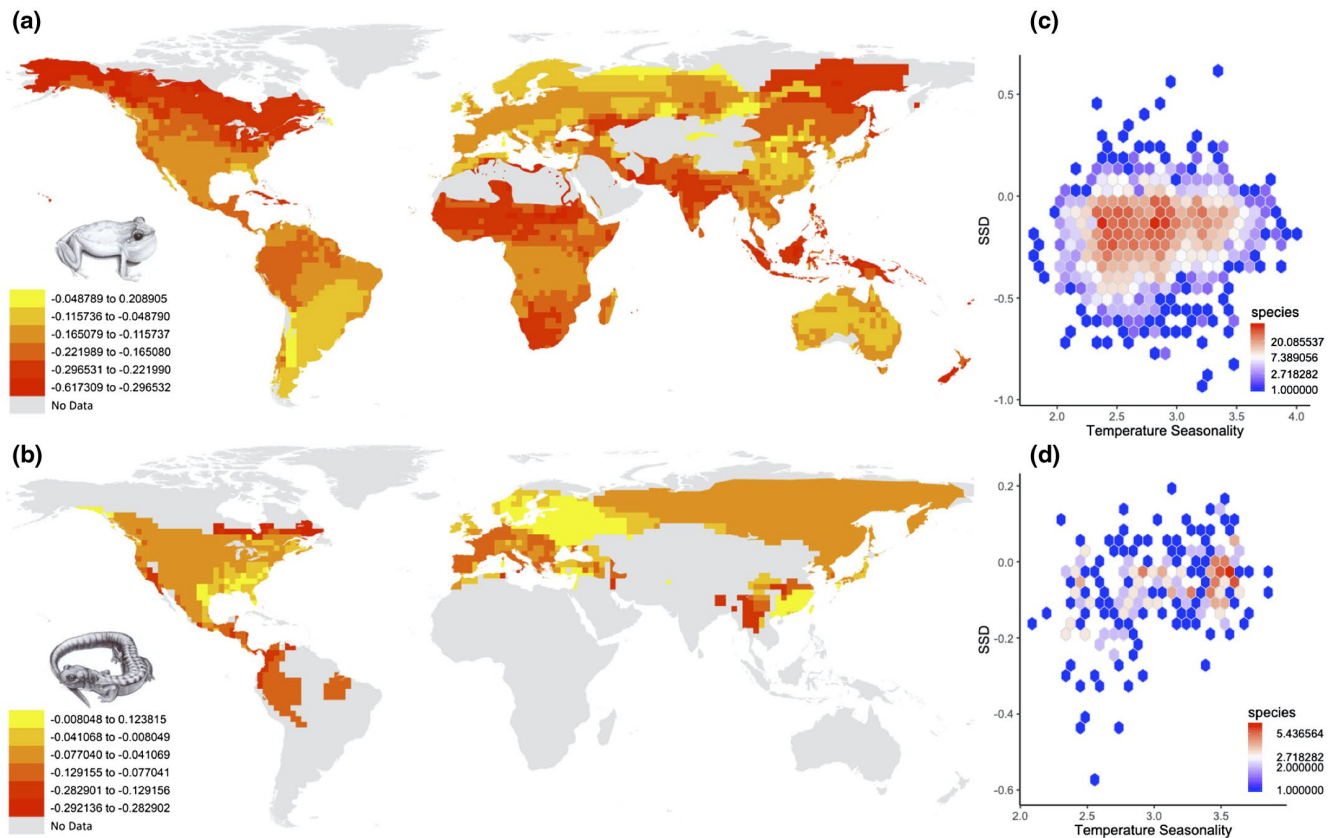
FIGURE 5 Global distribution of median sexual size dimorphism (SSD) in amphibians. (a,b) Maps show the distributional patterns of SSD separately for anurans (a) and salamanders (b), with grid cell sizes of 2° × 2°. (c,d) Hexagon density scatter plots showing the effects of thermal seasonality on the magnitude of SSD among grid cells in anurans (c) and salamanders (d). The distributional patterns of SSD for caecilians are not shown because of the limited availability of data

community structures of, for example, anole lizards across the Caribbean, which have diversified extensively within islands, without a macroecological signature of trait variation through geographical space (Losos, 2009). Consequently, we expect that processes of diversification driven by competition over limited resources (predominantly adaptive radiations) are more likely to prevent the evolution of large-scale geographical patterns of trait diversity, whereas processes shaped by geographically varying selection shape macroecological patterns. Our global analyses on amphibians support these expectations.

DATA AVAILABILITY STATEMENT

All the datasets used in this study are available as supplementary material to the main article and will be made open access at the GABiP initiative's repository at http://www.amphibianbiodiversity.org upon publication.

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BIOSKETCH

Daniel Pincheira-Donoso is interested in the links between evolutionary theory and large-scale patterns of biodiversity. His research investigates the ecological sources of natural selection that drive the origin, distribution and extinction of biodiversity at broad spatial and temporal scales.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.