Climate Ecology as a Driver of Global Breeding Periods in Anurans

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Abstract

Climate can have profound effects on reproductive behavior and physiology, especially in ectothermic animals. In amphibians, the evolution of breeding period due to climate has received little attention despite its direct connection to fitness and relevance to conservation. We used phylogenetic comparative methods to analyze a global dataset of frog breeding periods, climate, body size, and microhabitat for 497 species (41 of 54 families). We found support for the hypothesis that breeding periods are longer in the warmer, wetter, aseasonal tropics and shorter in the colder, dryer, seasonal temperate zone. However, this latitudinal reproduction gradient is more complex than expected; the effect of climate depends on body size. Additionally, breeding periods were similar across microhabitats. Overall, our model describes ~20% of variation in breeding periods and these results are robust to phylogenetic uncertainty. Our results set within an eco-physiology framework have broad implications for more targeted priorities in amphibian conservation.

Introduction

Climate change is increasingly threatening global biodiversity with increasing extinctions as environments are altered (Arneth *et al.* 2020; Bellard *et al.* 2012; Thomas *et al.* 2004; Urban 2015). While climate change is a growing problem in the present, its past effects have molded the behavior and physiology of species still around today. Thus, by studying coevolution between organisms and the environment, we can better understand how climate change will differentially affect species survival. Importantly, evolutionary biology is taking a key role in conservation biology (Zizka *et al.* 2021), with climate change and anthropogenic impacts at the heart of these studies. As successful reproduction is necessary for survival and fitness, studies of the ecology and evolution of reproductive traits are needed to understand the effects of climate change on species reproductive success. For example, climate change has led to shifting clutch sizes, offspring sizes, and breeding season start times in vertebrates (Bronson 2009; Padilla Perez and Angilletta 2022; Pankhurst and Munday 2011; Telemeco *et al.* 2013; Todd *et al.* 2011; Visser *et al.* 2004). However, limited natural history observations across many species and vertebrate groups has stalled research that would help us better understand how climate impacts various reproductive behaviors. Therefore, ideal model systems for learning how climate affects reproductive behaviors and success include groups with abundant natural history observations and whose reproduction is tied to particular environments.

Anurans (frogs and toads) are an ecologically and taxonomically diverse ectotherm group (>7,400 species; AmphibiaWeb 2022) whose reproduction and development is generally dependent on water availability during breeding. Their iconic calling behavior used for reproduction has made them a prime target for natural history studies, making their reproductive behaviors reasonably well-known. Anurans inhabit a wide array of habitats around the world

including tropical rainforests, arid deserts, temperate forests, freezing tundras, and more. These habitats are used differently by various species which specialize in aquatic, terrestrial, fossorial (underground), or arboreal (above ground) microhabitats (Moen & Wiens 2017). Studies of amphibian reproduction and climate are dominated by advancements in our understanding of reproductive modes (e.g., Gomez-Mestre *et al.* 2012) or reproductive timing (Beattie 1985; Benard 2015; Neveu 2009; Reading 2003; Todd *et al.* 2011; While and Uller 2014). Comparatively little is known about the relationship between climate and breeding period (sensu Wells 1977), the duration of breeding within a population, which is unique from the duration of breeding across populations of a single species. This is despite the stunning contrast of tropical species that breed year-round to explosive-breeding species that limit reproduction to only a few days or weeks of the year (Wells 1977). Common knowledge in herpetology says there exists a latitudinal gradient in breeding periods, where tropical amphibians breed for generally longer periods compared to temperate amphibians (Wells 2007). However, the precise role of climate on breeding periods has yet to be identified across the phylogeny of anurans and further study is necessary given widespread amphibian declines (Campbell Grant *et al.* 2020; Fisher and Garner 2020).

If climate has an effect on breeding periods, we can expect physiology to play a central role since frogs are especially sensitive to the environment as ectotherms and are reliant on water for reproduction. Natural selection has likely led to physiological changes such that populations maximize their reproductive investment leading to longer breeding periods in the context of specific climate exposure or microhabitat use (Huey *et al.* 2012; Williams *et al.* 2008). Thus, climate is tied to physiological and reproductive traits to the extent that individuals experience changes in regional climate and atmospheric conditions during the breeding period while in water or on land. These links have been shown previously, where body temperature is correlated with substrate temperature and air temperature in the toad *Bufo canorus* (Cunningham 1963). Both temperature and water are known breeding cues in frogs and warmer

temperatures likely lead to longer breeding periods due to greater food supply, reproductive investment, and egg formation in frogs (Girish and Saidapur 2000; Lardner and Loman 2003; Rastogi *et al.* 1983). Additionally, since reproduction in anurans is generally tied to water, we can expect increased water availability to result in longer breeding periods. These abiotic variables can also interact, as higher temperatures in drier environments may lead to increased rates of water loss. From this perspective, larger-bodied species with lower surface area:volume (SA:V) ratios may benefit from lower rates of water loss relative to smaller species. Alternatively, larger-bodied species may be at a disadvantage in sub-optimal environments due to greater resource demand and limited area for water or heat exchange. Species body size likely influences the effect climate has on breeding period due to trade-offs between reproduction and physiological performance over the course of the breeding period. Knowledge of how climate and body size interact to influence anuran breeding periods is unknown but is likely to allow for more targeted conservation efforts.

The goal of this study is to identify how ecological factors are related to reproduction (breeding periods) in anurans on a global scale. Specifically, we test (H1) whether longer breeding periods are the result of warmer, wetter climates, (H2) whether differences in body size significantly alter the way climate influences breeding periods, (H3) whether species with different non-breeding microhabitat preferences exhibit differences in breeding period, and (H4) whether climate differs significantly between species microhabitat and geographical (temperate and tropical) zones. Here, we provide the first quantitative assessment of the latitudinal gradient of reproduction in anurans, including climatic and possible physiological drivers.

Material and Methods

Climate data

We obtained coordinate data for 497 species representing 41 of 54 anuran families from GBIF.org (GBIF.org 2021a,b,c,d) accessed 3 October 2021. These queries were for presence coordinate data for non-fossil native observations lacking geospatial issues. We cleaned the data by removing coordinates points with >100km uncertainty or outside land boundaries of a high resolution (1:10m) world countries map using the R v4.2.1 (R Core Team 2021) package *rworldxtra* v1.01 (South 2012). We also removed coordinates incorrectly associated with and within 100m of biodiversity collections outside of the natural range of the species. Additionally, we removed *Corythomantis greeningi* since its coordinates mapped to a continent far outside its natural range. We restricted data for the invasive Cane Toad (*Rhinella marina*) to its naturally occurring range from southern United States to South America (AmphibiaWeb 2021). Next, we removed species with less than 3 unique observations from the dataset and retained only unique coordinates for each species to minimize the effects of spatial autocorrelation. Lastly, we removed data outside the spatial 95% Confidence Interval for each species distribution with a minimum of 30 occurrences using the median absolute deviation (mad) method (Huber 1981). This resulted in a final coordinate dataset of 822,953 observations (mean = 1,656 observations per species) after removing species without behavior or body size (see below) or missing from the phylogeny of Jetz and Pyron (2018). Data cleaning was performed using the *CoordinateCleaner* package v2.0-20 (Zizka *et al.* 2019).

We extracted seven variables from each coordinate using the WorldClim 2.1 (Fick & Hijmans 2017) and envirem (Title & Bemmels 2018) databases at 30 seconds (~1km^2) resolution. Our data included variables affecting temperature and water availability and covering all possible breeding period values (0–365 days). The final dataset included annual mean temperature, temperature seasonality, annual precipitation, precipitation seasonality, annual

potential evapotranspiration (PET), PET seasonality, and topographic wetness. Topographic wetness is the land's ability to retain water obtained from estimates of upslope incurrent areas and local slope, which is correlated to vascular plant species richness and soil moisture (see Sørensen *et al.* 2005). We calculated species means for each climate variable to analyze the dataset in a phylogenetic comparative framework.

Behavior data

We collected species means of breeding period (sensu Wells 1977) for each species in this study. To obtain species means, we collected approximate start and end dates for breeding periods from the primary literature or AmphibiaWeb (2022) and averaged all available breeding period data for individual populations. We then calculated the difference in calendar days between the start and end dates, assuming 365 calendar days. Since some dates were reported as qualitative data (e.g., "May", or "early May"), we ascribed values of either the first or last day of the month when breeding periods were reported as starting or ending on a specific month without a specific date given. When breeding periods were reported as the "early" or "late" parts of a month, we matched this to the end of the 1st week and 3rd week, respectively. Rarely, breeding periods were reported as specific seasons (e.g., "Summer" or "wet season") and we defined these as the number of days corresponding to each season and country. Populations from species which are explosive breeders are typically associated with breeding periods lasting only a few days to weeks, but never more than a month (Wells 1977). Since we never observed published data reporting explosive breeding over a period longer than 2 weeks, we conservatively assigned a period of 2 weeks to species whose only description of the breeding period was "explosive breeding".

Body size, habitat, and phylogenetic data

We collected maximum male body sizes (snout-vent length) and habitat data for every species in this study from the primary literature and other datasets (AmphibiaWeb 2022; IUCN 2022; Moen and Wiens 2017; Womack and Bell 2020). Species were assigned to microhabitat categories following Moen and Wiens (2017) and included: (1) aquatic, (2) arboreal, (3) burrowing, (4) terrestrial, and (5) torrential. We also included partial categories such as: (6) semi-arboreal, (7) semi-aquatic, and (8) semi-burrowing. Finally, we calculated phylogenetic covariance matrices from the consensus tree of Jetz and Pyron (2018) to incorporate evolutionary history as weights in phylogenetic regression. Additionally, we used 1,000 samples from the pseudoposterior distribution of trees from Jetz and Pyron (2018) to assess models in terms of phylogenetic uncertainty (see below).

Statistical analysis and visualization

All analyses were performed in R. We used *ggtree* v3.4.0 (Yu 2020; Yu *et al.* 2018; Yu *et al.* 2017) to plot average species breeding periods and temperate-tropical geographical zones. We analyzed the data using phylogenetic generalized least squares (PGLS; Grafen 1989; Martins & Hansen 1997) implemented through *RRPP* v1.3.0 (Collyer and Adams 2018, 2019). Notably, *RRPP* uses a residual randomized permutation procedure to fit models, evaluate significance, and calculate effect sizes for model terms. We used 9,999 iterations for significance testing in all models. We estimated phylogenetic covariance matrices using *ape* v5.6-2 (Paradis & Schliep 2019).

We scaled each climate variable and performed a principal component analysis (PCA) to avoid collinearity issues in our models. To test our hypotheses, we used phylogenetic multiple regression to examine the relationship of breeding period, all 7 principal components (PCs), and body size. To account for allometry of body size and since the natural logarithm of surface area-

to-volume ratio is expected to scale linearly with the natural logarithm of body size (Castro *et al.* 2021; Klein *et al.* 2016; Santini *et al.* 2018), we used the natural logarithm of body size in our models. Additionally, we fit a phylogenetic ANCOVA model which included interactions between each PC and body size. We also used ANOVA to test whether adding these interactions resulted in a significant improvement in model performance. To aid in interpretation of these models, we used phylogenetic regression to determine the relationship between breeding period and each individual climate variable. We determined the effects of phylogenetic uncertainty in our models by rerunning the ANCOVA model once each for 1,000 trees from the pseudoposterior distribution of Jetz and Pyron (2018), following Baken *et al.* (2021). From these analyses we obtained one distribution of 1,000 Z-scores per model term and visualized the proportion of trees under which terms were not significant. We plotted these distributions using ggridges v0.5.3 (Wilke 2021).

We used phylogenetic ANOVA to test whether breeding periods differ between microhabitat categories, followed by evaluation of pairwise comparisons. We controlled for Type I error rates due to multiple comparisons using the Sidak-like step-down procedure, which is more powerful than the Sidak and Bonferroni methods (Holland & Copenhaver 1987), using *mutoss* v0.1-12 (MuToss Coding Team *et al.* 2017). We used a phylogenetic factorial MANCOVA to determine how climate (all 7 PC's) differs among microhabitats and temperate/tropical zones. Finally, we visualized these data by plotting conver hulls for groupings of microhabitat and geographical zone using *geomorph* v4.0.4 (Adams *et al.* 2021; Baken *et al.* 2021b).

Results

Frog breeding periods follow a latitudinal gradient

We examined phylogenetic patterns of average breeding period (mean = 148 days, range = 1–365 days, std. error = 4.5 days) and geographical zone (temperate/tropical) (Fig. 1) and found species with longer breeding periods tend to live in tropical regions, whereas temperate species breed for shorter periods. However, this pattern has several exceptions, such as temperate species with long breeding periods and tropical species with very short breeding periods. Overall, temperate species breed for an average of 127.8 days (median = 107 days, range = 1–365 days, std. error = 5.87 days) and tropical species breed for an average of 167.3 days (median = 181 days, range = 5–365 days, std. error = 6.52 days). Climate principal components (PCs) 1–3 explained 90% of data variance (Table 1; SI 1). We found variable loadings for PC1 to be similar to known latitudinal climate differences and determined PC1 was highly correlated (r = -0.94) with the absolute value of median latitude for each species (SI 1).

Climate and body size impact breeding periods

As body size can play a large role in thermal physiology and desiccation, we compared model fits between two models with and without interactions between climate and body size (snout-vent length). Indeed, including body size substantially improved model fit (F = 2.40, p = 0.0082; Table 2). Overall, this model explained 18% of variation in breeding periods.

We next describe this model in the context of phylogenetic uncertainty and given the individual effects of each climate variable (see SI 1). We found larger species from the tropics (high scores on PC1) tend to exhibit longer breeding periods relative to smaller species and the magnitude of this effect can be up to 60-90 days. However, this pattern reverses in the temperate zone where relatively smaller species exhibit longer breeding periods (Fig. 2A). For

example, *Rana pretiosa* (median latitude = 42.60) can be 14mm larger than *Rana macrocnemis* (median latitude = 45.33) but exhibit a breeding period 48 days shorter (61-13=48 days). This effect was due to latitudinal differences in temperature, temperature seasonality, precipitation, and potential evapotranspiration (PET) seasonality, each showing similar effects when analyzed individually (SI 1 Table 1). Since PET did not have a significant individual effect on breeding periods, it likely does not affect breeding periods although it loads highly onto PC1; we do not interpret PET further for any PC. The effect of PC1 was robust to phylogenetic uncertainty and significant in 89.7% of surveyed trees while its combined effect with body size was supported in 64.2% of trees (Fig. 3). Independent of latitude (PC1), we found a significant impact of PC2 and body size on breeding periods (Fig. 2B). Specifically, we found that relatively larger species breed for longer periods in rainy environments with low topographic wetness (high values for PC2) and smaller species breed for longer periods in environments with little rain but high topographic wetness. Although topographic wetness had no individual effect on breeding periods, it did exhibit a significant impact when paired with body size. This trend showed moderate support across surveyed phylogenies with significance of PC2 and the interaction with size supported in 0.714% and 0.704% of trees, respectively (Fig. 3). Additionally, we found support for a size-independent role of PC3, where species living regions with low precipitation seasonality (PC3) exhibit longer breeding periods (Fig. 2C). This pattern was significant in 87.9% of surveyed trees compared to only 31.4% of trees when taking size into account (Fig. 3). Finally, we also found a size-independent effect of PC7 associated with warmer temperatures, independent of temperature effects of other PC's, where longer breeding periods are associated with warmer temperatures. This pattern was supported in 66.9% of surveyed phylogenetic histories.

Breeding periods are not different between microhabitats

The microhabitats species occupy can have different effects on breeding period depending on differences in temperature and moisture within temperate or tropical regions. Therefore, we tested whether anuran species with different microhabitat preferences exhibit differences in breeding periods. We initially found support for this relationship, where species from various microhabitats have different breeding periods ($F = 4.09$, $p = 0.0062$). However, pairwise differences between microhabitats were not significant after accounting for multiple comparisons (see SI 1 Table 2). In contrast to our expectation, we found large overlap in breeding periods across microhabitat categories (Fig. 4A), including a wide breeding period range associated with burrowing and semi-burrowing species. Semi-arboreal species had the greatest proportion of species with a long breeding period. We next used a factorial MANCOVA used examine climatic differences corresponding to combinations of microhabitat and geographical zone (i.e., their interaction; $F = 2.05$, $r^2 = 0.02$, $Z = 2.27$, $p = 0.0124$), but none of these were significant after correcting for multiple comparisons (see SI 1 Table 3). Finally, we found significant climate differences among microhabitats ($F = 7.01$, $r^2 = 0.08$, $Z = 3.77$, $p = 0.0001$; Fig. 4B) and between temperate and tropical zones ($F = 87.46$, $r^2 = 0.14$, $Z = 8.93$, $p = 0.0001$) but we did not find pairwise differences in the former after accounting for geographical zone (see SI 1 Table 4).

Discussion

This study documents the evolution of reproductive behavior associated with climate in one of the largest vertebrate groups. Here we present the first quantitative evidence, to our knowledge, of the latitudinal gradient of breeding period in anurans and its relationship to climate. Our overall findings support longer breeding periods where frogs invest more time into reproduction in warmer and wetter habitats with little seasonality. We also discovered that the

time invested into reproduction, within the context of particular climates, is influenced by body size. We discuss our results in the context of physiology and reproduction and suggest how this new information can guide conservation management priorities of anurans in different climates.

Body size played an important role in determining how climate affects breeding periods. This is likely due to its effect on physiological processes such as regulating body temperature and water loss, where larger frogs are better at maintaining body temperatures and are slower to dessicate (Castro *et al.* 2021; Klein *et al.* 2016; Santini *et al.* 2018; Tracy *et al.* 2010). The size-dependent effect of climate on anuran reproduction is most notable when comparing 1) temperate versus tropical environments, and 2) regions with high rainfall and limited propensity to hold water versus regions with low rainfall and high topographic water retention. These results are consistent with our hypothesis that larger body sizes are associated with greater resource demands and limited area for water and heat exchange, resulting in shorter breeding periods in environments with little rain, cooler temperatures, and low topographic water retention. High temperature seasonality and high potential evapotranspiration seasonality also seem to shorten breeding periods in larger species, possibly due to their combined effect and this may be due to meeting physiological demands in relatively unpredictable environments. Interestingly, environments which shorten breeding periods in larger species seem to be less detrimental to smaller species, possibly due to their lower resource demand and relatively greater area for water and heat exchange. Furthermore, larger-bodied species may be at a disadvantage in cool and dry environments because the amount of energy used for maintaining homeostasis (hydration) may limit the amount of reproductive investment females are able to make, since egg formation is energetically costly for females. This seems likely, given that we know larger frog species exhibit greater reproductive investment in the form of forming larger clutches and larger eggs (Prado & Haddad 2005; Silva *et al.* 2020). Body size is also correlated with reproductive investment in seasonally breeding endotherms like lagomorphs, whose body size is correlated with neonatal mass, gestation time, and maternal reproductive effort (Swihart

1984). Temperature and water preferences and limits can evolve in a correlated fashion (Bonetti and Wiens 2014; Guevara-Molina *et al.* 2020; Köhler *et al.* 2011) and likely involve underexplored molecular and morphological traits associated with the skin and body size in amphibians (Finn *et al.* 2014; Shibata *et al.* 2014; Tracy *et al.* 2010). How temperature and water limits have shaped anuran breeding physiology is unclear and is an area that needs more research.

Ecology, in addition to physiology, plays an important role in determining breeding periods. Our results suggest seasonal environments present the challenge of overcoming unreliable cues for reproduction, similar to findings at shorter ecological scales (Todd *et al.* 2011). Here, we found size-dependent patterns, themselves independent of latitude, where breeding periods in smaller species decline in rainier environments with lower topographic wetness. These qualities are characteristic of high-altitude rainforests, or cloud forests, such as those found in Central and South America, which hold much of the world's anuran diversity (Cortés *et al.* 2008; Duellman 1988; Giaretta *et al.* 1999). One explanation for this pattern is that cloud forests exhibit relatively rapid local drainage of water resources necessary for prolonged amphibian reproduction. Another possible explanation is that areas with low topographic wetness and correspondingly low vascular plant species richness (Sørensen *et al.* 2005) presents a challenge for prolonged breeding periods in smaller species by limiting protection from canopy cover or reproductive opportunities associated with leaf- or phytotelma-breeding species (Donnelly and Guyer 1994; Poelman *et al.* 2013; Schulte *et al.* 2010). Predation risk may also differ between small and large species, where larger species are less reliant on canopy cover due to their large size reducing predation pressure (Nakazawa *et al.* 2013), resulting in longer breeding periods. Future research investigating the role of plant diversity and predator-prey relationships in anurans seems likely to explain this variability in amphibian reproduction.

Microhabitat use across and within species undoubtedly plays a critical role in how animals experience broader regional climates and together they define climate exposure (Huey *et al.* 2012; Williams *et al.* 2008). While ambient and body temperatures are connected (Cunningham 1963), water stream and air temperatures are also correlated to atmospheric temperatures in both warmer and colder climatic zones (Erickson and Stefan 1996; Mohseni and Stefan 1999; Pilgrim *et al.* 1995). However, support for our hypothesis of differences in breeding periods between species occupying different microhabitats was lacking. Instead, we found a minority of burrowing species exhibit explosive breeding (extremely short breeding periods) and an overabundance of semi-arboreal species which breed for longer periods. The latter is likely related to radiations of small semi-arboreal frogs in the tropics of Central and South America, one of the most diverse regions of the world. Perhaps unsurprisingly, we did not find discernible climatic differences between microhabitats. This could reflect a low correlation between regional climate and ambient conditions within microhabitats (e.g., a burrow). However, such a strong role of microhabitat buffering seems unlikely if we expect, for example, microhabitats within a temperate desert to resemble each other more closely than microhabitats within a tropical rainforest. Instead, the lack of breeding period differences among microhabitats most likely reflects the ecological breadth of frog communities and global convergent evolution of microhabitat use across anurans (Moen *et al.* 2015). Further study of the relationships between microhabitat, reproductive traits, and climate would likely result in additional model improvements and better predictions of breeding period. For example, previous work found decreased fecundity in anurans was associated with warmer winters within species (Benard 2015; Neveu 2009; Reading 2003) and warm, wet climates across terrestrial egg-laying species (Gomez-Mestre *et al.* 2012). Notably, species in seasonal environments may have evolved larger clutches in response to shorter breeding periods (Sheridan 2009). Future research will continue to disentangle the relationships between behaviors, the environment, and further investigate the role of life history in determining the effect of climate on reproductive ecology.

Unfortunately, we still know very little about the life histories of many frogs. A sustained push for deeper understanding of life history diversity is necessary for identifying causal mechanisms related to eco-evolutionary patterns.

Adaptation to changing climates is a key part of amphibian evolutionary history and should be centered in future amphibian conservation efforts. Previous research has shown conclusive evidence of adaptation to changing climates over ecological timescales (<40 yrs.; Beattie 1985; Benard 2015; Freidenburg and Skelly 2004; Neveu 2009; Reading 2003; Skelly and Freidenburg 2008; Skelly *et al.* 2007; Todd *et al.* 2011). This work, along with previous studies on breeding start date (Beattie 1985; Ulloa *et al.* 2019; While and Uller 2014), identify both water and temperature as important environmental cues for the start of the breeding period. Associated neuroendocrine systems, thermal preferences, and critical thermal limits seem to show flexibility in responding to changing climate, but this might change as the effects of climate change become more severe. Huey *et al.* (2012) provide a model used to assess extinction vulnerability over time, which can be affected by behavioral thermoregulation, acclimation, and adaptation. Unfortunately, most anuran species live in warm, dry environments and these same species exhibit narrow climatic niche breadths (Bonetti & Wiens 2014) which can restrict dispersal (Chejanovski & Wiens 2014). The current study shows how species with restricted breeding periods living in the cold, dry, and seasonal environments may be less tolerant of climate change. Within the temperate zone, larger frogs with greater resource demands may be particularly vulnerable, while smaller frogs are most vulnerable in the tropics. Independent of latitude differences, we also found larger species may be vulnerable in areas receiving little rain. Without physiological adaptation to climate change, frogs might mistime their reproduction and be faced with either extinction, or potentially speciation through temporal isolation of reproduction. This might be one of the possible mechanisms linking diversification rates and rates of climatic niche change in anurans (Moen & Wiens 2017).

Amphibians are facing unprecedented threats due to climate change from the lens of eco-physiology. Notably, climate change seems to amplify the current amphibian chytrid fungus epidemic due to size-related osmoregulatory costs (Wu *et al.* 2018). Given the several factors contributing to growing extinction risks faced by frogs and toads, an attempt to maintain reproductive fitness by maximizing breeding duration seems critical. Overall, our research suggests a regional-based approach toward conserving species' flexibility in the timing and period of breeding. There are multiple factors impacting amphibian breeding periods but regional climate has a noticeable average effect on breeding periods worldwide. Extinction risks due to the mistiming of reproduction or shortened breeding periods might be highest in smaller tropical species which are common in tropical lowlands. Species living in tropical lowlands along with those living in cloud forests have both been identified as being under threat of extinction (von May *et al.* 2019; Meza-Parral and Pineda 2015; Murrieta-Galindo *et al.* 2013; Ponce-Reyes *et al.* 2013). Further research is needed to understand the neuroendocrine cues used for timing reproduction in frogs, thermal preferences, and the role of molecular or morphological adaptations related to water and heat stress. Without this research, future temperature instability will increase extinction risk without either dispersal to suitable habitats or the ability to acclimate and adapt to their changing environment (Huey *et al.* 2012). Perhaps the existence of tropical explosive breeders shows capacity for adaptation and persistence in the face of climate change. For example, species faced with limited breeding periods may also adapt to produce more eggs (Sheridan 2009) and habitat shifts associated with thermal preference and choosing egg-laying sites may help mitigate negative thermal climatic effects on tadpoles (Pintanel *et al.* 2022; Todd *et al.* 2011). Amphibians have much to benefit from dedicated conservation efforts to protect large and diverse landscapes allowing dispersal, protecting plant diversity, and preserving a thermally-diverse range of habitat options. Similar efforts have been successful in partially restoring amphibian diversity in cloud forests (Díaz-García *et al.* 2020). Future research

might seek to combine environmental, behavioral, and physiological data to assess extinction risk and habitat suitability (Greenberg and Palen 2021; Griffis-Kyle 2016; Huey 1991).

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Tables

Table 1. PCA summary and loadings of climate variables. PCA based on means for 497 species. Cumulative proportion of variance is given in parentheses next to PC heading. Loadings with a magnitude >=0.30 are in bold. Asterisks indicate variables with a significant individual effect on breeding periods and carets indicate variables with a significant interaction with body size (see SI).

Variable	PC1 (52)	PC2 (76)	PC3 (90)	PC4 (94)	PC5 (97)	PC6 (99)	PC7 (100)
Annual Mean Temperature*^	**0.47**	-0.28	0.08	-0.02	0.24	0.15	**0.78**
Temperature Seasonality*^	**-0.47**	-0.14	-0.09	**0.44**	0.25	**0.70**	0.04
Annual Precipitation*^	**0.38**	**0.38**	0.13	**0.75**	0.27	-0.21	-0.14
Precipitation Seasonality*^	0.15	-0.26	**-0.90**	0.23	-0.16	-0.15	0.00

Annual Potential Evapotranspiration (PET)	**0.42**	**-0.4**	0.00	-0.23	**0.47**	0.21	**-0.59**
PET Seasonality*^	**-0.45**	-0.28	0.01	0.02	**0.59**	**-0.60**	0.11
Topographic Wetness^	0.01	**-0.67**	**0.40**	**0.37**	**-0.47**	-0.15	-0.10

Table 2. Model summary of the effects of climate and body size on breeding periods in 497 frog species. Climate shown as PC's. Body size is snout-vent length (SVL) in mm. Breeding periods are species means. *Df* = degrees of freedom, *SS* = sum of squares, *MS* = mean square, *Rsq* = coefficient of determination, *F* = *F*-statistic, *Z* = standardized effect size (*Z*-score), and *P* = *p*-value. Rows with significant terms ($p < 0.05$) are in bold.

Term	***Df***	***SS***	***MS***	***Rsq***	***F***	***Z***	***P***
PC1	**1**	**6279.32**	**6279.32**	**0.05**	**26.34**	**3.69**	**1e-04**
PC2	**1**	**2443.75**	**2443.75**	**0.02**	**10.25**	**2.59**	**0.0017**
PC3	**1**	**6756.84**	**6756.84**	**0.05**	**28.34**	**3.83**	**1e-04**
PC4	1	22.69	22.69	0	0.10	-0.71	0.7519
PC5	1	734.96	734.96	0.01	3.08	1.39	0.0810
PC6	1	601.68	601.68	0	2.52	1.22	0.1152
PC7	**1**	**1643.48**	**1643.48**	**0.01**	**6.89**	**2.12**	**0.0096**
SVL	**1**	**1058.17**	**1058.17**	**0.01**	**4.44**	**1.71**	**0.0389**
PC1:SVL	**1**	**1555.92**	**1555.92**	**0.01**	**6.53**	**2.07**	**0.0115**

PC2:SVL	**1**	**2228.56**	**2228.56**	**0.02**	**9.35**	**2.49**	**0.0020**
PC3:SVL	1	831.79	831.79	0.01	3.49	1.51	0.0599
PC4:SVL	1	0.12	0.12	0	0	-2.05	0.9812
PC5:SVL	1	30.6	30.6	0	0.13	-0.62	0.7241
PC6:SVL	1	57.72	57.72	0	0.24	-0.32	0.6277
PC7:SVL	1	103.47	103.47	0	0.43	0.02	0.5090
Residuals	481	114677.84	238.42	0.82	NA	NA	NA
Total	496	139026.91	NA	NA	NA	NA	NA

Figure Legends

Figure 1. Phylogenetic differences in average breeding period and geographic region across 497 species of frogs. A. Phylogeny of 497 species with breeding period and region mapped at the tips. Node labels identify the 4 highest-sampled families in our dataset. Inner ring shows tropical versus temperate regions. The tropical zone is shown in red and the temperate zone is shown in blue. Outer ring shows the breeding period. Species with shorter breeding periods are shown in lighter colors while species with longer breeding periods are shown in darker colors. **B.** Boxplot showing differences in breeding period between temperate (N = 237) and tropical (N = 260) species. Temperate species breed for an average of 127.8 days (median = 107 days, range = 1–365 days, std. error = 5.87 days) and tropical species breed for an average of 167.3 days (median = 181 days, range = 5–365 days, std. error = 6.52 days). Combined, anurans breed for a mean of 148 days (range = 1–365 days, std. error = 4.5 days).

Figure 2. Climate and body size (snout-vent length) influence breeding periods in 497 frog species. All relationships are significant at $p < 0.0115$. Regression lines for A,B represent effects at 10th and 90th percentiles of body size (snout-vent length; 24 and 80 mm). **A.** High scores on PC1 represent warm, rainy areas with low temperature and annual potential evapotranspiration seasonality and are

correlated with latitude. Larger species have longer breeding periods in the tropics; smaller species have longer breeding periods in the temperate zone. Combined effects of PC1 and body size yield *Rsq* = 0.07. **B**. High PC2 scores are regions with relatively higher annual precipitation but low topographic wetness. Larger species have longer breeding periods in rainy climates with low topographic wetness. Smaller species have longer breeding periods in less rainy climates with high topographic wetness. The combined effect of PC2 and body size yields *Rsq* = 0.05 **C**. High PC3 scores are regions with relatively lower precipitation seasonality but higher topographic wetness. Regression line shown in red. Longer breeding periods are common in areas with lower precipitation seasonality and higher topographic wetness. *Rsq* = 0.05. **D.** Density plot showing the distribution of raw (untransformed) body sizes of species used in this study.

Figure 3. Effect of phylogenetic uncertainty on effect sizes (z-scores) relating climate and body size to breeding periods. Z-scores for each model term calculated from 1,000 trees of the pseudoposterior distribution of Jetz and Pyron (2018). PC's are climate variables; SVL is snout-vent length. Vertical line denotes the Z = 1.645 significance cutoff for empirically generated Z-scores. Values to the right of distributions indicate percent of significant Z-scores per distribution. Red highlights portions of the density within the 10th percentile.

Figure 4. Breeding period and climate differences between microhabitats across 497 frog species. A. Average breeding periods do not differ between microhabitats; most ranges overlap. semi-arboreal species stand out in having the greatest proportion of species with longer breeding periods. **B.** Scatterplot of first two PCA axes corresponding to climate variables. Polygon outlines encase species in microhabitats corresponding in color. PC1 is correlated with absolute latitude (*r* = -0.94). Temperate species denoted by circles and encased in solid lines. Tropical species denoted by triangles and encased in dashed lines.

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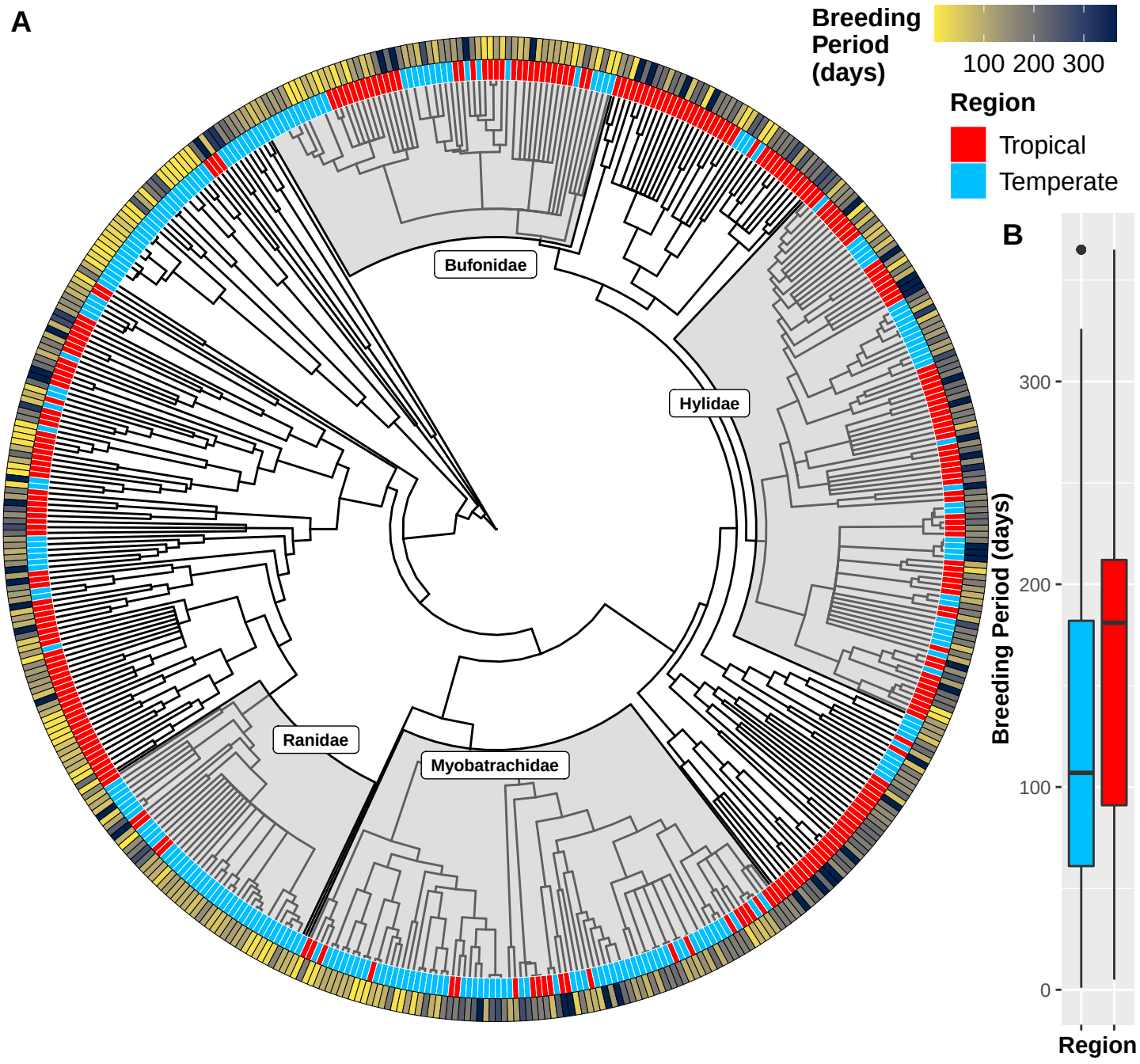
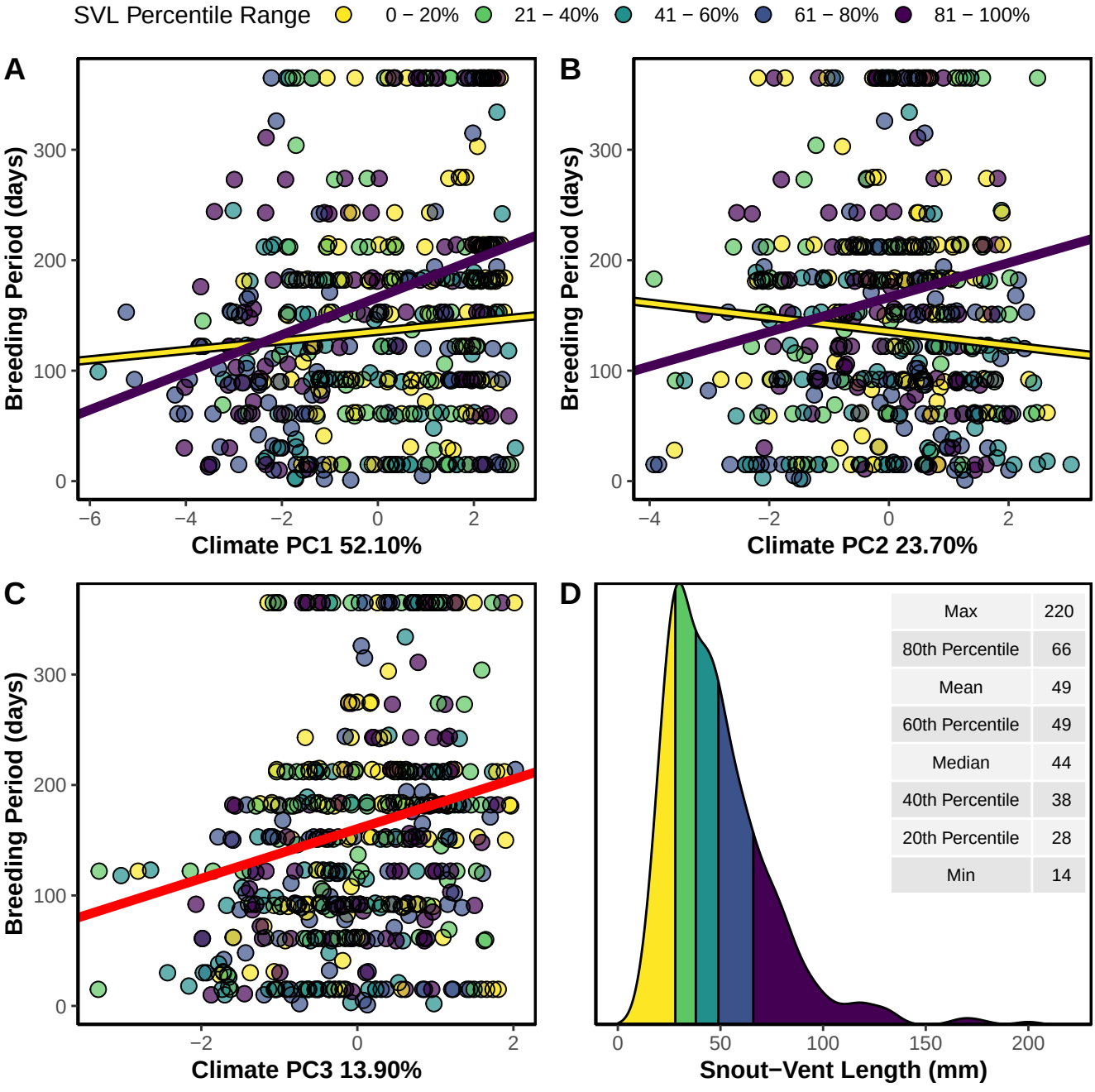
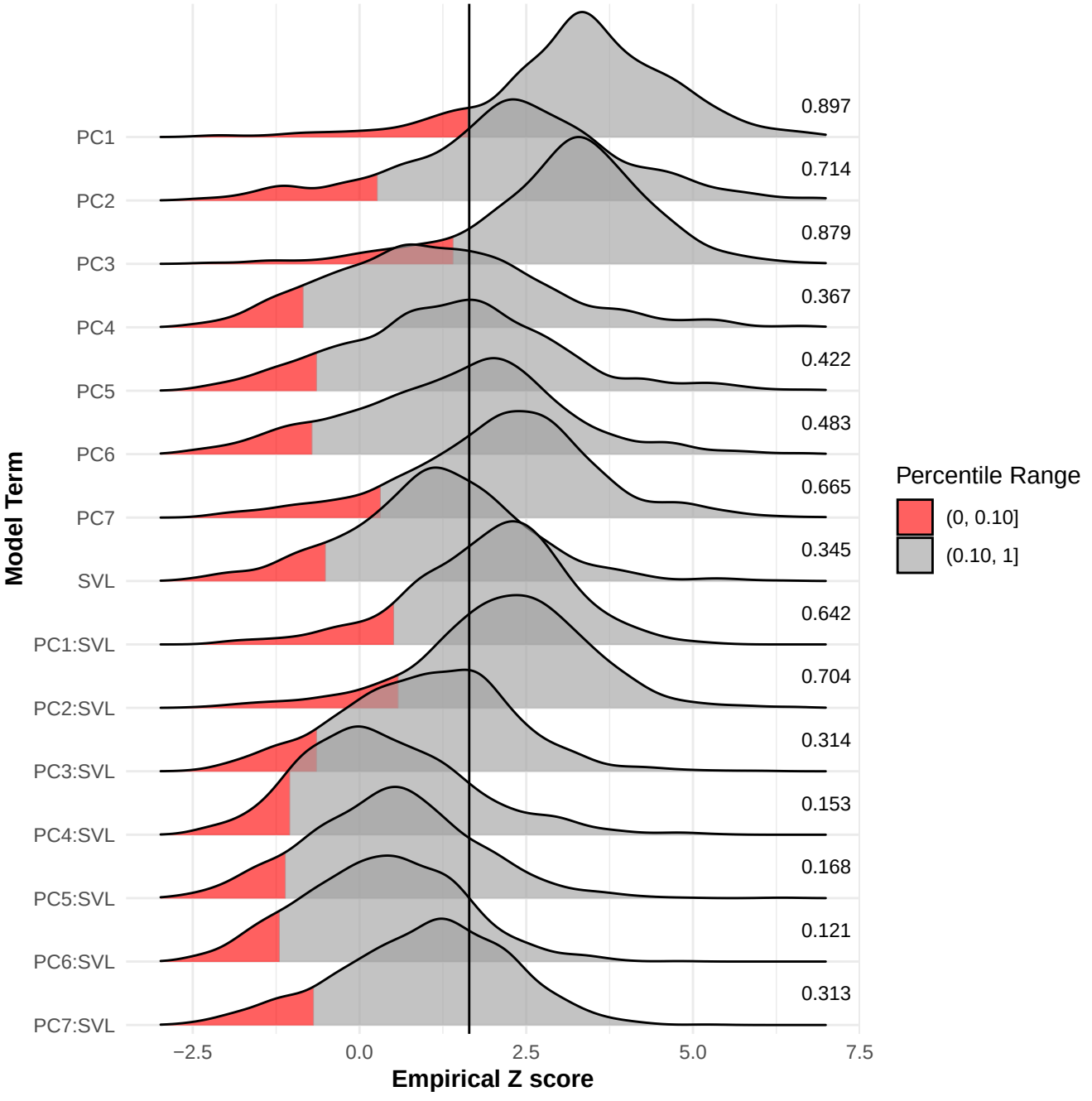
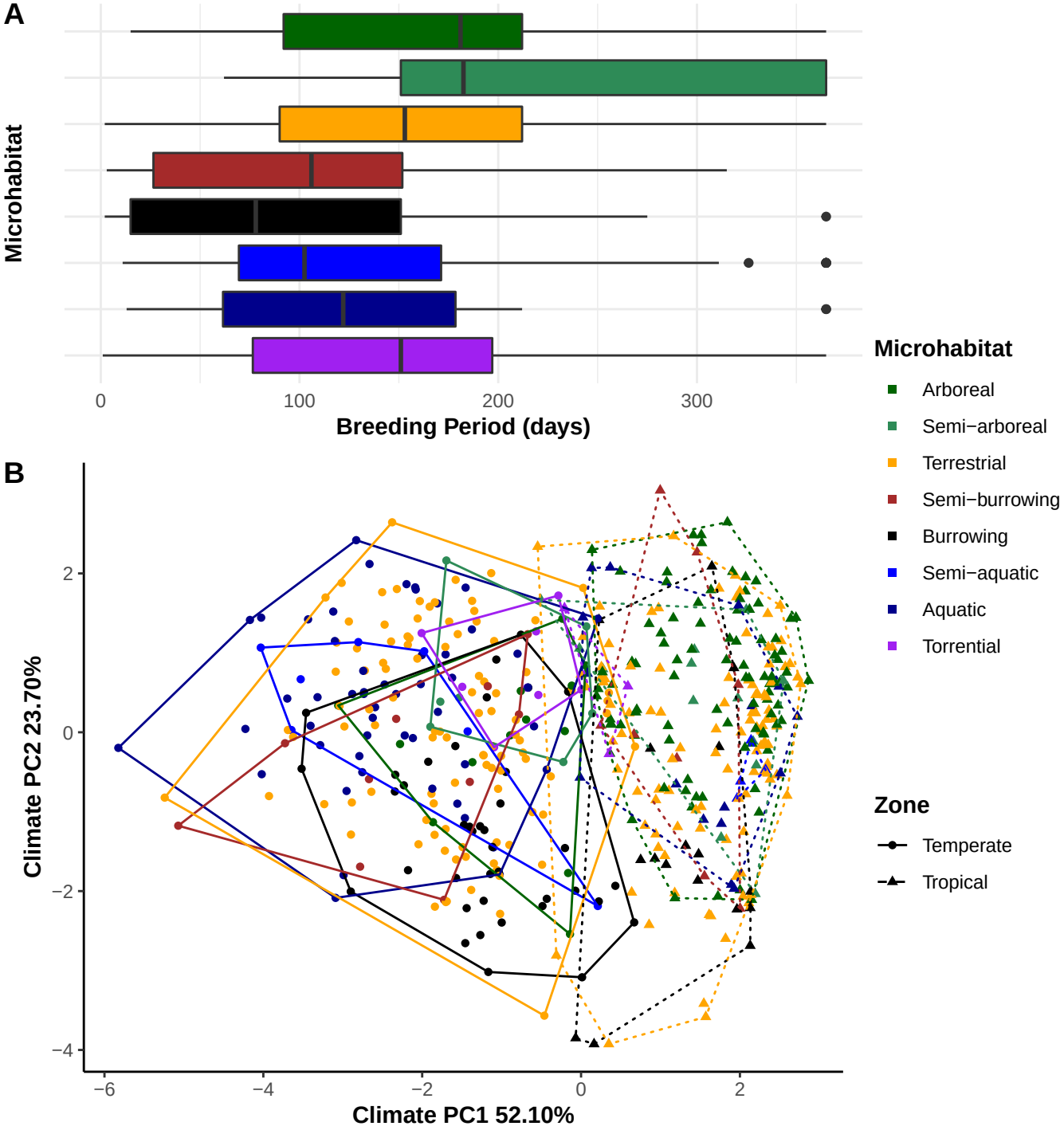

A
Breeding Period (days)
100 200 300
Region
Tropical
Temperate
Bufonidae
Hylidae
Ranidae
Myobatrachidae
B
Breeding Period (days)
300
200
100
0
Region


SVL Percentile Range
0 – 20%
21 – 40%
41 – 60%
61 – 80%
81 – 100%
A
Breeding Period (days)
Climate PC1 52.10%
B
Breeding Period (days)
Climate PC2 23.70%
C
Breeding Period (days)
Climate PC3 13.90%
D
Snout−Vent Length (mm)
Max 220
80th Percentile 66
Mean 49
60th Percentile 49
Median 44
40th Percentile 38
20th Percentile 28
Min 14


Model Term
PC1
PC2
PC3
PC4
PC5
PC6
PC7
SVL
PC1:SVL
PC2:SVL
PC3:SVL
PC4:SVL
PC5:SVL
PC6:SVL
PC7:SVL
0.897
0.714
0.879
0.367
0.422
0.483
0.665
0.345
0.642
0.704
0.314
0.153
0.168
0.121
0.313
−2.5
0.0
2.5
5.0
7.5
Empirical Z score
Percentile Range
(0, 0.10]
(0.10, 1]


A
Microhabitat
0
100
200
300
Breeding Period (days)
B
Climate PC2 23.70%
2
0
−2
−4
−6
−4
−2
0
2
Climate PC1 52.10%
Microhabitat
Arboreal
Semi−arboreal
Terrestrial
Semi−burrowing
Burrowing
Semi−aquatic
Aquatic
Torrential
Zone
Temperate
Tropical