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RESEARCH ARTICLE

A global analysis of viviparity in squamates highlights its prevalence in cold climates

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Abstract

Aim: Viviparity has evolved more times in squamates than in any other vertebrate group; therefore, squamates offer an excellent model system in which to study the patterns, drivers and implications of reproductive mode evolution. Based on current species distributions, we examined three selective forces hypothesized to drive the evolution of squamate viviparity (cold climate, variable climate and hypoxic conditions) and tested whether viviparity is associated with larger body size.

Location: Global.

Time period: Present day.

Taxon: Squamata.

Methods: We compiled a dataset of 9061 squamate species, including their distributions, elevation, climate, body mass and reproductive modes. We applied species-level and assemblage-level approaches for predicting reproductive mode, both globally and within biogeographical realms. We tested the relationships of temperature, interannual and intra-annual climatic variation, elevation (as a proxy for hypoxic conditions) and body mass with reproductive mode, using path analyses to account for correlations among the environmental predictors.

Results: Viviparity was strongly associated with cold climates at both species and assemblage levels, despite the prevalence of viviparity in some warm climates. Viviparity was not clearly correlated with climatic variability or elevation. The probability of being viviparous exhibited a weak positive correlation with body size.

Conclusions: Although phylogenetic history is important, potentially explaining the occurrence of viviparous species in regions that are warm at present, current global squamate distribution is characterized by a higher relative abundance of viviparity in cold environments, supporting the prediction of the "cold-climate" hypothesis. The roles of climatic variation and hypoxia are less important and not straightforward. Elevation probably exerts various selective pressures and influences the prevalence of viviparity primarily through its effect on temperature rather than on oxygen concentration.

KEYWORDS
biogeography, body size, climatic variability, cold climate, elevation, global analysis, reproduction, squamates, structural equation modelling, viviparity

1 | INTRODUCTION

The diversity of reproductive strategies across the vertebrate tree of life is vast. Such versatility in life history has facilitated their successful expansion across various types of environments world-wide (e.g., Conaway, 1971; Laugen et al., 2003; Prado et al., 2005; Schwimmer & Haim, 2009; Shine & Brown, 2008). For instance, the evolution of shelled (cleidoic) eggs promoted the expansion of tetrapods into terrestrial habitats (D'Alba et al., 2021), and the retention of eggs inside the body of the parent significantly improved embryo survivability (Sadleir, 1973; Shine, 2014). Live-bearing [viviparity, herein used to include ovoviviparity (i.e., retention of eggs *in utero* almost until hatching)] evolved across all major vertebrate clades, except archelosaurs (birds, crocodilians and turtles; Blackburn, 2015a; Shine, 2005; but see Kuchling & Hofmeyr, 2022). Viviparity is widespread in squamates (observed in *c*. 20% of lizard and snake species; Meiri et al., 2021; and see below). Pyron and Burbrink (2014) made the controversial suggestion that viviparity is ancestral in squamates, with multiple subsequent reversals to oviparity. This hypothesis has been strongly disputed because reversal to oviparity requires re-evolution of lost reproductive traits, such as the eggshell, which are exceedingly difficult to regain once lost (e.g., Griffith et al., 2015; Lee & Shine, 1998; Pincheira-Donoso et al., 2013; Tinkle & Gibbons, 1977). It should be noted that such a reversal is nevertheless possible; it was shown in *Eryx jayakari* (Lynch & Wagner, 2010) and was recently suggested for the family Liolaemidae (Esquerré et al., 2019). Viviparity is thought to have emerged on >100 independent phylogenetic occasions from an oviparous ancestor, with a few inferred reversals to oviparity (Blackburn, 1999, 2015a, 2015b; Esquerré et al., 2019; Griffith et al., 2015; Lee & Shine, 1998; Shine, 1985, 2015; Wright et al., 2015). The prevalence of both oviparity and viviparity in many squamate clades and the multiple origins of viviparity make squamates an excellent model in which to study the selective forces behind the evolution and biogeography of reproductive modes.

The association of viviparity with cold climates is widely addressed in the literature and is mostly examined in view of the "cold-climate" hypothesis (Shine, 2014). This "cold-climate" hypothesis claims that viviparity is selected for in cold regions because uterine retention of embryos shields them better from the deleterious effects of low temperatures in comparison to exposed eggs (Guillette, 1993; Packard, 1966; Packard et al., 1977; Shine, 1983, 2014; Tinkle & Gibbons, 1977). Lack of thermal insulation of the egg, exacerbated by the scarcity of protected nesting sites in cold regions, can result in prolonged development and increased risk of death from hypothermia (Neill, 1964). Lengthy development can increase susceptibility to predation and the risk of missing the warm, more plentiful season, with the resources it provides (Tinkle & Gibbons, 1977). Although viviparous species make up a small proportion of squamates in warm regions, they predominate at high latitudes and elevations (Feldman et al., 2015; Greene, 1970; Ma et al., 2018; Pincheira-Donoso et al., 2013; Tinkle & Gibbons, 1977; and see below). Among closely related species that differ in reproductive mode, shifts to viviparity are associated with cooler environments (Cruz et al., 2022; Feldman et al., 2015; Guillette et al., 1980; Shine, 1987; Shine & Bull, 1979).

Unpredictable climate is another potential driver of viviparity in squamates (Tinkle & Gibbons, 1977), and its link with reproductive mode is generally made through the "climatic predictability" and the "maternal manipulation" hypotheses (e.g., Cruz et al., 2022; Feldman et al., 2015; Shine, 2002, 2014). The "climatic predictability" hypothesis emphasizes the occurrence of unpredictable environmental events (e.g., sporadic heatwaves, cold spells or shifting onset of seasons; Tinkle & Gibbons, 1977) as drivers of viviparity. Viviparous species are not restricted to cold climates and are diverse in several warm regions, particularly in the Neotropics (Feldman et al., 2015; Tinkle & Gibbons, 1977). Unpredictable, irregular climatic events (e.g., heatwaves and cold spells, floods and droughts), could put oviparous taxa, with eggs that remain where they were laid, at a selective disadvantage (e.g., Moreno & Møller, 2011; Shine, 1985; Tinkle & Gibbons, 1977). Viviparous mothers, in contrast, can avoid some of these perils behaviourally, conferring a selective advantage on their offspring, as emphasized by both the "climatic predictability" hypothesis and the "maternal manipulation" hypothesis (the latter suggesting viviparity to be beneficial in various suboptimal conditions, such as being too cold, too warm or too variable; Cruz et al., 2022; Shine, 2014). Despite its theoretical plausibility, the "climatic predictability" hypothesis has rarely been evaluated directly, and when it was, it generally received no empirical support (Feldman et al., 2015; Shine, 2002, 2014; Watson et al., 2014). To test the predictions of this hypothesis properly, it is crucial to identify relevant measures of environmental unpredictability. To date, the most commonly used proxy for unpredictability is intra-annual seasonality, often defined as the variation in temperature and precipitation within an annual cycle (e.g., Feldman et al., 2015; Horreo et al., 2021; Shine, 2014; Watson et al., 2014). However, highly seasonal climates can have highly predictable temperatures and precipitation for species with a relatively long life span (e.g., Khavrus & Shelevytsky, 2012; Markham, 1970). For example, warm, dry summers and cool, wet winters make Mediterranean climates both seasonal and predictable (Mooney, 1988). A more important aspect of climatic variability, to which an evolutionary lineage might conceivably respond in an adaptive manner, is the variation among, as opposed to within, annual cycles (Meiri et al., 2008). Interannual variation is greatly affected by extreme climatic events, such as El Niño and La Niña (e.g., pronounced temperature anomalies, blizzards and droughts), leading to less predictable climatic patterns in the long run (McPhillips et al., 2018; Moreno & Møller, 2011). Interannual variation could impose strong selection pressures on organisms (e.g., Grant et al., 2017; Hoffmann & Sgró, 2011; Marrot et al., 2017; Moreno & Møller, 2011; Williams et al., 2016). Reptiles can maintain their homeostasis behaviourally, for instance by changing their body temperatures (by basking or hiding in more insulated places; Le Henanff et al., 2013; Neill, 1964; Pettersen et al., 2022) or by swimming or climbing to safety when a site is flooded owing to extreme precipitation. Such tactics, however, are unavailable

to eggs. Although oviparous females might adjust their nesting behaviour to protect their eggs from unfavourable environmental conditions (e.g., Aubret et al., 2003; Harlow & Grigg, 1984; Peñalver-Alcázar et al., 2015; Shine, 2005), overall, parental care is rare in squamates (Doody et al., 2009; Reynolds et al., 2002). Accordingly, embryo survival in unpredictable environmental conditions could be expected to be higher in viviparous species.

Recently, another explanation, aside from cold climate, was suggested for the relative prevalence of viviparous species at high elevations. With an increase in elevation, the atmospheric pressure and the partial pressure of oxygen decline (Körner, 2007). Hypoxia (i.e., low oxygen partial pressure) has a significant impact on animal respiration (Körner, 2007). It can have particularly negative effects, such as retarded growth and depressed metabolism, on embryonic development of oviparous species and on fitness-related hatchling phenotypes, such as reduced body mass and slower locomotion (Cordero et al., 2017; Kam, 1993; Souchet et al., 2020). According to the "hypoxia" hypothesis, viviparity can buffer the embryo from reduced oxygen availability at high elevations because the partial pressure of oxygen in the mother's bloodstream is higher than that in the environment of exposed eggs (Pincheira-Donoso et al., 2017; Watson & Cox, 2021). Indeed, retaining embryos *in utero* can provide multiple fitness benefits, optimizing offspring body size, limb length, locomotion speed, etc. (e.g., Ji et al., 2007; Li et al., 2009; Shine, 1995, 2004, 2005; Webb et al., 2006). These benefits of uterine retention emphasize the advantage of viviparity over oviparity in extreme and, particularly, oxygen-poor environments.

However, viviparity physically burdens the gravid female, for instance, impeding movement speed and agility (Qualls & Shine, 1995; Shine, 1980; Tinkle & Gibbons, 1977). It also restricts the ability of females to reproduce again for the duration of pregnancy, resulting in a significantly lower rate of reproduction (Meiri et al., 2012). Body size is found to be positively correlated with locomotion speed (Schmidt-Nielsen, 1984; Sinervo & Huey, 1990), thereby potentially mitigating the negative impact of carrying embryos on a female's speed and the consequent reduction in her ability to evade predators (Shine, 1980; Shine & Bull, 1979; Sinervo et al., 1991; Tinkle & Gibbons, 1977). In squamates, the relative brood mass (i.e., the mass of the embryos relative to the mass of the mother) declines with increasing adult size (Meiri et al., 2021). Thus, larger gravid females might be relatively less burdened and able to move faster than smaller gravid females, resulting in lower predation risk. Additionally, the higher diversity of potential food items available for larger individuals, together with lower energetic cost per unit body mass, enable the female to reduce foraging frequency and therefore to be less exposed to predators, which are also fewer for larger individuals (Rivas & Burghardt, 2001). This is especially important in viviparous reproduction, because predation of a gravid female would also eliminate her embryos, whereas predation of an oviparous female will usually not cause a loss of her clutch. Neill (1964) concluded that the transition to viviparity in snakes has been accomplished most often in large-bodied species. Therefore, one might expect to observe viviparity in larger species more often than in smaller ones.

Here, we tested most of the common selective forces hypothesized to drive the evolution of viviparity (e.g., Pincheira-Donoso et al., 2017; Shine, 2014; Watson & Cox, 2021), in addition to the relationship of reproductive mode to body size. Specifically, we tested the predictions that viviparity will be associated with the following factors: (1) cold climates; (2) unpredictable climates; (3) high elevations (a proxy for hypoxic conditions); and (4) large adult body sizes. Given that environmental factors can be intercorrelated, we used path analysis to account for such correlations in the prediction of reproductive mode. We included interannual climatic variation as a predictor, which has not been assessed before. We fitted models to examine the contributions of elevation and climatic variables to the relative abundances of viviparous species within equal-area grid cells (assemblage-level analyses) and to reproductive modes of individual species within their ranges (species-level analyses), globally and in biogeographical realms. Our assemblage-level analyses focused on the proportion of viviparous species of all squamates in a grid cell. They tested whether environmental conditions acted as filters that favoured species with one reproductive mode over another. Our species-level analyses addressed individual species, incorporating species-specific traits, such as adult body mass (representing body size) and phylogenetic affiliation, alongside data on the environmental/climatic niche of the species. Our dataset of >9000 species included *c*. 83% of extant non-marine squamate species, making this the largest-scale study of the selective forces for squamate viviparity to date.

2 | METHODS

2.1 | Data collection

We compiled a dataset for 9061 of the 10,954 extant non-marine squamate species (following the taxonomy in the August 2020 checklist of The Reptile Database; Uetz et al., 2021), including data on reproductive mode, body size, climate and elevation in their respective ranges. Species range maps are extent of occurrence (EOO) maps from an updated version of Roll et al.'s (2017) reptile-distribution data (internally known as GARD 1.7; http://www.gardinitiative.org/). We downloaded elevation data at a resolution of 3 arc-sec from EarthEnv-DEM90 (Robinson et al., 2014), using the R programming environment v.4.1 (R Core Team, 2022). We used the raster layer of these elevation data to subset the EOO maps of 6272 species to create suitable elevation range maps, based on literature records (i.e., not derived from the EOO maps themselves) on the elevational range at which species have been observed (minimum and maximum values). Of these 6272 species, we used elevational observations for 4573 species from the literature (Supporting Information Appendix S1), and we phylogenetically imputed elevation for 1699 species lacking such data, using the "picante" R package (Kembel et al., 2010), based on the dichotomous version of the phylogenetic tree made by Tonini et al. (2016). For the 2789 species for which elevational observation data were

lacking and which were impossible to phylogenetically impute (i.e., not represented in the tree), we used the EOO ranges directly (we also performed sensitivity analyses excluding species lacking elevational data).

We also extracted data on five climatic variables (per species range and per grid-cell; see below): mean annual temperature (BIO1; henceforth "temperature"; in degrees Celsius), intra-annual temperature variation (BIO4; "temperature seasonality"; standard deviation ×100), intra-annual variation in total precipitation (BIO15; "precipitation seasonality"; coefficient of variation ×100), interannual variation in mean temperature ("interannual temperature variation"; coefficient of variation ×100) and interannual variation in total precipitation ("interannual precipitation variation"; coefficient of variation ×100). We extracted the first three climatic variables from an updated version (CHELSA v.2.1; for the years 1981–2010) of the work by Karger et al. (2017), at a resolution of 30 arc-sec, and the other two (interannual variability) from an updated version of ERA5 [Copernicus Climate Change Service (C3S), 2017; for the years 1979–2020], at a resolution of 15 arc-min, using Google Earth Engine (Gorelick et al., 2017).

We defined both ovoviviparous and viviparous species as viviparous, because ovoviviparity and viviparity have practically the same function in relationship to our hypotheses (i.e., retaining embryos *in utero* until development is complete). We took data on reproductive mode for 7142 species from the studies by Feldman et al. (2015), Meiri (2018) and Meiri et al. (2021). We imputed parity mode for 1919 additional species (392 snakes, of which 315 are scolecophidians, all coded as oviparous; 1500 lizards; and 27 amphisbaenians), representing 21% of the 9061 species in our dataset. To do so, we used the "picante" R package (Kembel et al., 2010) and the dichotomous phylogenetic tree produced by Tonini et al. (2016), imputing reproductive mode only for species with ≥95% statistical support for the imputation outcome ($n = 744$). We complemented these by imputing the reproductive mode of 1175 species absent from the phylogenetic tree, only for species belonging to families that met the following three criteria: (1) a consistent reproductive mode (either oviparous or viviparous) across all family members with a known datum; (2) ≥30% (in families with ≥19 species) or 50% of the species in the family (for families with 7–18 species) have published data on reproductive mode; and (3) the family consists of at least seven species. We also treated the four members of the subfamily Boinae with unknown mode as viviparous, because all 29 species with data are viviparous. Furthermore, given that most blind snakes are believed to be oviparous (Lillywhite, 2014), we considered all members of the family Typhlopidae as oviparous despite having data for only 14.7% of 258 species (all oviparous, except the ovoviviparous *Argyrophis muelleri*; Das, 2011). All 391 squamate species meeting the criteria for both phylogenetic and manual imputation were imputed identically by the two methods, attesting to the robustness of the method (we also performed sensitivity analyses excluding imputation). We excluded species with mixed reproductive mode ($n = 18$) from the analyses but present some descriptive statistics that include them. Nevertheless, because the distributions of oviparous and viviparous populations of *Zootoca vivipara* are well known, we included it in the assemblage-level analyses (but not in the species-level analyses) as two "species" with different distributions and reproductive modes.

2.2 | Species-level data

We calculated mean values for elevation and the five climatic variables across each species range, using the "exact_extract" function in the "exactextractr" R package (Baston, 2021). Additionally, we collected data on the maximal body mass of species from the studies by Feldman et al. (2016) and Meiri et al. (2021). For each species, we recorded the biogeographical realms in which it occurs, according to Olson et al. (2001), by intersecting the EOO with the realms.

2.3 | Assemblage-level data

We created gridded maps of the number of viviparous species divided by total species richness (excluding species with mixed or unknown reproductive mode) on an equal-area Behrmann projection, with a cell size of *c*. 96.5 km×96.5 km (*c*. 1°×1° at the equator). We calculated mean values for elevation and the five climatic variables for each cell as described for species above.

2.4 | Statistical analyses

To analyse the relationship between reproductive mode and the predictor variables at both assemblage and species levels, we used path analysis, a special case of structural equation modelling, using the "lavaan" (Rosseel, 2012) and "phylopath" (van der Bijl, 2018) R packages. Structural equation models enable the covariation among variables to be accounted for by testing both direct and indirect effects of the various predictors on the response variable (Grace, 2006). We included indirect effects in our models based on a preliminary Pearson's correlation test among the predictors, including only correlations >.3 as a rule of thumb (for model structures, see Supporting Information Figure S1). To reduce heteroscedasticity and normalize residual distributions, we $\log_{10}$-transformed all explanatory variables before analyses.

We conducted analyses both at a global scale and separately within six biogeographical realms (Australasia, the Palaearctic, the Nearctic, the Neotropics, the Afrotropics and Indomalaya; Olson et al., 2001) to test whether correlates of viviparity are universal across regions. We did not perform analyses for Oceania (but present descriptive statistics for it) because it consists of small islands, each constituting <50% of a 9309.6 km^2 grid cell, in a relatively constant, warm climate (making Oceania irrelevant for testing the predictions of climatic hypotheses). To check that imputation of reproductive mode did not impact the results, we performed additional analyses excluding species with imputed reproductive mode. We standardized parameter estimates and their errors for convenient comparison

across analyses. Further information on analytical methods is provided in the Supporting Information (R script in Appendix S1).

2.5 | Species-level analyses

The response variable in our species-level analyses was the probability of a species being viviparous (coded as "1", vs. "0" for oviparous). Given that each species was assigned a binary reproductive mode, we fitted models assuming a binomial distribution. Our predictor variables included the five climatic variables, elevation and maximum body mass. We scored species for all realms in which a species had ≥20% of its distribution. A few (254; i.e., 3%) of the species occurred in more than one realm and were analysed in both those realms. To account for phylogenetic dependence, we used the most complete time-calibrated phylogenetic tree available for squamates (Tonini et al., 2016), including 8444 of the species in our dataset. Using the "define_model_set" and "phylo_path" functions in the "phylopath" package, we built a structural equation model including both direct and indirect effects of climate, elevation and body mass on the probability of being viviparous (Supporting Information Figure S1a). To test whether polytomies affected the results, we performed sensitivity analyses including only dichotomous relationships in the phylogenetic tree (for 4349 species with reproductive mode data and 5180 species with imputed data). We also repeated these analyses excluding species lacking elevational data.

2.6 | Assemblage-level analyses

We conducted assemblage-level analyses for 13,636 grid cells covering the distributions of our 9044 species (after exclusion of all species with mixed modes of reproduction, except for *Z. vivipara*, which we treated as oviparous for the grid cells in which egg-laying populations occur and as viviparous for the grid cells where females give birth to live young). Our response variable in these analyses was the proportion of viviparous species out of the total species richness with known reproductive mode in each cell. Explanatory variables were elevation and the five climatic variables. Given that the response variable was in the form of proportions, we applied "logit" transformation on the response variable. Given that "logit" transformation cannot handle zeros, we rescaled the response variable before applying it, by applying the transformation: $y' = [y(N-1)+½]/N$, where y is the original response variable, and N is the total number of grid cells used for the analysis (Smithson & Verkuilen, 2006).

We calculated Moran's *I* to test for spatial autocorrelation, using the "Moran.I" function in the "ape" package (Dormann et al., 2007; Paradis et al., 2004). Moran's *I* was significantly higher than zero. We therefore corrected our models for spatial autocorrelation in the following manner. First, we built structural equation models using the "sem" function of the "lavaan" package (Rosseel, 2012), including both direct and indirect effects of climate and elevation on the proportion of viviparity (Supporting Information Figure S1b). Second, we recalculated the standard errors and *p*-values based on geographical distances, using the "lavSpatialCorrect" function, by Jarrett Byrnes (https://github.com/jebyrnes/spatial_correction_lavaan). To verify that residency of species on islands did not affect squamate life history, we conducted an additional analysis focusing on only the 12,321 non-insular grid cells (or 12,273 cells excluding species with imputed reproductive mode). We also repeated these analyses excluding the 4488 species lacking elevational data.

3 | RESULTS

Our dataset comprised 9061 species, of which 7589 are oviparous, 1454 are viviparous, and 18 have bimodal reproduction (Table 1; Supporting Information Appendix S1). The major clades Gekkota, Scolecophidia and Laterata are predominantly oviparous (>98% of species), whereas the clades Anguiformes and Scincomorpha have the highest proportion of viviparous species (>30%) followed by alethinophidian snakes (22.9%; Table 2).

3.1 | Species-level analyses

Our global-scale model included significant effects ($p < .05$) for all the predictors of the probability of being viviparous, except variation in interannual precipitation (Figure 1a; Supporting Information Table S1). The model explained 78% of the variation in the probability of being viviparous. Temperature had a moderate negative correlation with viviparity (standardized estimate: −.46 ± .07), and elevation, temperature seasonality and interannual variation had weak negative effects (−.12 ± .03, −.08 ± .04 and −.09 ± .03, respectively). In contrast, precipitation seasonality, interannual precipitation variation and body mass had weak positive effects (.08 ± .03, .05 ± .03 and .12 ± .04, respectively; Figure 1a; Supporting Information Table S1). All sensitivity analyses yielded qualitatively similar results (Supporting Information Table S2). The significance of the effects of predictors and their direction, however, varied among realms, with notably stronger effects of temperature in Australasia, the Nearctic and the Neotropics (Figure 2a; Supporting Information Table S1).

3.2 | Assemblage-level analyses

Our assemblage-level dataset comprised 13,636 grid cells including 1–184 species (0–120 oviparous and 0–25 viviparous species per cell; Figure 4). Species richness decreased with temperature in both oviparous and viviparous species, but the slope for oviparous species was much steeper (Figure 3). The proportion of viviparous species generally increased with absolute latitude (Figure 4), especially in the Palaearctic, Nearctic and Australasia.

The global-scale model included significant effects ($p < .001$) for all the predictors of the proportion of viviparity except elevation. It explained 43% of the variation in the proportion of viviparity. Mean

TABLE 1 Descriptive statistics for the geography of squamate mode of reproduction

Region	Number of species	Number of oviparous species	Number of viviparous species	Number of grid cells	Temperature (°C, mean ± *SD*)	Number of viviparous species per grid cell (mean ± *SD*; range)	Proportion (%) of viviparity per grid cell (mean ± *SD*; range)
Global	9045	7590	1455	13,636	17.2 ± 10.1	4.5 ± 4.8 (0–25)	26.3 ± 29.9 (0–100)
Afrotropical	1825	1595	230	2448	24.3 ± 3.4	3.0 ± 2.7 (0–17)	7.7 ± 9.8 (0–100)
Australasia	1490	1225	265	1289	22.4 ± 4.5	5.0 ± 3.9 (0–22)	18.7 ± 23.0 (0–100)
Indomalaya	1768	1546	222	1119	24.5 ± 3.3	5.3 ± 3.5 (0–21)	12.0 ± 9.9 (0–100)
Nearctic	456	323	133	1277	10.4 ± 6.6	5.5 ± 4.2 (0–18)	50.6 ± 28.6 (0–100)
Neotropical	3187	2606	581	2278	22.1 ± 5.6	10.7 ± 6.6 (0–25)	18.4 ± 15.1 (0–100)
Oceania	51	47	4	132	26.5 ± 0.9	0.1 ± 0.3 (0–2)	0.5 ± 2.4 (0–18)
Palaearctic	919	803	116	5093	10.0 ± 10.6	1.9 ± 1.5 (0–10)	38.4 ± 36.3 (0–100)

Note: The total number of species and of oviparous and viviparous species are presented, globally and for each realm. Oviparous and viviparous populations of *Zootoca vivipara* are counted here as two species with different reproductive modes. For each realm, we also present: number of cells; temperature annual mean and standard deviation; number of viviparous species per grid cell (mean, standard deviation and range); and proportion (as a percentage) of viviparous species out of total species richness per grid cell (mean, standard deviation and range). Reproductive mode was imputed for 1919 species.

annual temperature was by far the strongest predictor (−.49 ± .01; Figure 1b; Supporting Information Table S3) and was negatively correlated with the proportion of viviparity globally and across realms, except Indomalaya (Figure 2b; Supporting Information Table S3). The proportion of viviparity exhibited a weak positive correlation with interannual variation in temperature and a weak negative correlation with interannual variation in precipitation (.23 ± .01 and −.16 ± .01, respectively; Figure 1b; Supporting Information Table S3). The relationship with seasonality metrics was very weakly negative (Figure 1b; Supporting Information Table S3). The predictors and their effects varied across realms, with the effects of temperature being somewhat weaker in warmer realms (Figure 2b; Supporting Information Table S3). Elevation had no significant global effect on the proportion of viviparity, weak negative effects in the Palaearctic and Nearctic realms, and weak to moderate positive effects in warmer realms (Figure 2b; Supporting Information Table S3). All sensitivity analyses yielded qualitatively similar results (see Supporting Information Table S4).

4 | DISCUSSION

4.1 | Cold climate

We found strong to moderate support for the prediction of the "cold-climate" hypothesis. Low environmental temperature emerged as a main driver of squamate viviparity. Temperature was the strongest predictor of viviparity at both the species and assemblage levels. Most of the (few) species that inhabit the coldest climates are viviparous (Figure 3): 71 of the 100 species inhabiting ranges with the coldest mean temperatures (≤4.8°C) are viviparous, three have mixed reproductive modes, and 26 are oviparous (Supporting Information Table S5). Furthermore, temperature is correlated with latitude (e.g., Supporting Information Figure S2), and it is noteworthy that of the 58 species with latitudinal centroids >45° (in either hemisphere) in our dataset, 44 are viviparous (75.9%), one has a mixed reproductive mode [*Z. vivipara* (Lacertidae), with oviparous populations only at the southern edges of its range, around latitude 46° N (Horreo et al., 2018)], and only 13 are oviparous. Likewise, 66 of the 100 species inhabiting ranges with the highest latitudinal centroids are viviparous, one has a mixed reproductive mode, and 33 are oviparous (the null for this is 19% based on all our squamate species with reproductive status). These observations accord with our modelled predictions that viviparous species generally tend to dominate the squamate faunas of cold areas, whereas oviparous species dominate in warmer regions.

We show that viviparity is associated with cold climates at the global scale. Accordingly, realms that are mainly tropical and subtropical (Olson et al., 2001) present, on average, weaker effects of temperature on reproductive mode. Although the "cold-climate" hypothesis proposes an increase in the adaptive value of viviparity in cold climates, the number of viviparous species is greatest in the generally warmer tropical regions (Table 1; Figure 4). The

TABLE 2 Descriptive statistics for squamate mode of reproduction across major clades

Clade	Number of species	Number oviparous	Number viviparous	Proportion viviparous (%)
Acrodonta	555	507	48	8.6
Alethinophidia	2780	2143	636	22.9
Anguiformes	176	106	70	39.8
Anomalepididae	19	19	0	0
Dibamia	10	10	0	0
Gekkota	1861	1843	18	1.0
Laterata	779	767	11	1.4
Pleurodonta	1115	911	203	18.2
Scincomorpha	1358	876	467	34.8
Scolecophidia	408	407	1	0.2

Note: The total number of species and of oviparous and viviparous species are presented for each clade. The proportion of viviparous species out of total species richness of each clade is presented as a percentage. These numbers include imputed values for 1919 species.

occurrence of viviparous species in such climates might be the result of dispersal after viviparity evolved in cold climates (e.g., Fenwick et al., 2012; Klein et al., 2021). Alternatively, some viviparous populations might be relicts, remaining in a place they occupied during colder periods, such as during Pleistocene glaciations (Kupriyanova et al., 2017; Odierna et al., 2004; Renssen & Vandenberghe, 2003; Stute et al., 1995). Hence, viviparous lineages might have retained viviparity owing to the extreme difficulty of re-evolving oviparity, given the complexity of evolutionary steps required to re-evolve the shelled egg (Blackburn, 2015b; Griffith et al., 2015; King & Lee, 2015; Lambert & Wiens, 2013; Lee & Shine, 1998; Pincheira-Donoso et al., 2013; Shine, 2015; Wright et al., 2015). For example, species of the diverse genus *Liolaemus* (Liolaemidae) most probably evolved viviparity at high elevations in the Andes, later dispersing to the warmer adjacent lowlands and maintaining this reproductive mode (Esquerré et al., 2019; Pincheira-Donoso et al., 2013; Schulte et al., 2000). Likewise, pit vipers (Viperidae: Crotalinae) were shown to diversify, along with other viviparous viperid lineages, in the wake of the Eocene–Oligocene glaciation, while diversification of oviparous lineages was suppressed (Lynch, 2009). Subsequently, multiple viviparous lineages dispersed into and diversified in tropical regions [e.g., the Neotropical genus *Bothrops*, the Afrotropical genus *Bitis* and the Indomalayan genus *Tropidolaemus* (Alencar et al., 2016; Fenwick et al., 2012; Klein et al., 2021; Lynch, 2009)].

Tropical biomes are generally the warmest and most productive, with a long period of thermally suitable conditions for reproduction each year (Tejero-Cicuéndez et al., 2022). In such conditions, selective pressures on reproductive mode might be weaker than in colder or less productive environments (Lambert & Wiens, 2013). For instance, oviparous species richness declines much more rapidly towards lower temperatures than that of viviparous taxa, suggesting stronger selection against oviparity at cold temperatures (Figure 3). Productive environments, in turn, can contain enough vacant niches, food and shelter for the dispersing viviparous lineages to thrive (Tejero-Cicuéndez et al., 2022). Therefore, such environments are not expected to impose significant costs on the gravid female. Thus, even if at a disadvantage compared with oviparous species, owing to generally lower reproductive frequency (Meiri et al., 2012), viviparous species appear to be able to establish and maintain substantial populations in warm regions.

A noteworthy case that allows examination of the effects of climatic pressures on reproductive mode in consistently cooling conditions is the Australasian squamate fauna, which is dominated by endemic post-Eocene radiations (Oliver & Hugall, 2017; Skipwith et al., 2019). The major Australasian lineages were likely to be oviparous at the time when they evolved or colonized Australasia. Subsequently, viviparity evolved multiple times in three families: at least twice in the Elapidae; >12 times in the Scincidae, following three independent colonization events; and once in the Diplodactylidae, which are geckos of Gondwanan origin (Blackburn, 1982, 1999; Sanders et al., 2008; Skipwith et al., 2019). Since the beginning of these colonizations and during the Cenozoic in general, there were no dramatic decreases in temperature in Australia (Martin, 2006). New Zealand, in contrast, being generally warm at the time of the first skink (Scincidae) arrival (i.e., post-Eocene until early Miocene; Chapple & Hitchmough, 2016), underwent a profound cooling during the Pliocene and Pleistocene, especially in areas of mountain uplifting *c*. 5–2 Ma (Winkworth et al., 2005). Viviparous New Zealand lineages are thought to have evolved before this mountain uplifting (Skipwith et al., 2019) and never dispersed into mainland Australia (Chapple & Hitchmough, 2016). Consequently, under the "cold-climate" hypothesis, one would expect few occurrences of viviparous species in currently warm climates in Australasia. Our species-level model results for Australasia show the strongest association between probability of being viviparous and low temperatures (Figure 2a). Temperature showed a similar trend for the proportion of viviparous species in the assemblage-based model (Figure 2b). Overall, Australasia demonstrated similar patterns to the global analysis, supporting the prediction of the "cold-climate" hypothesis.

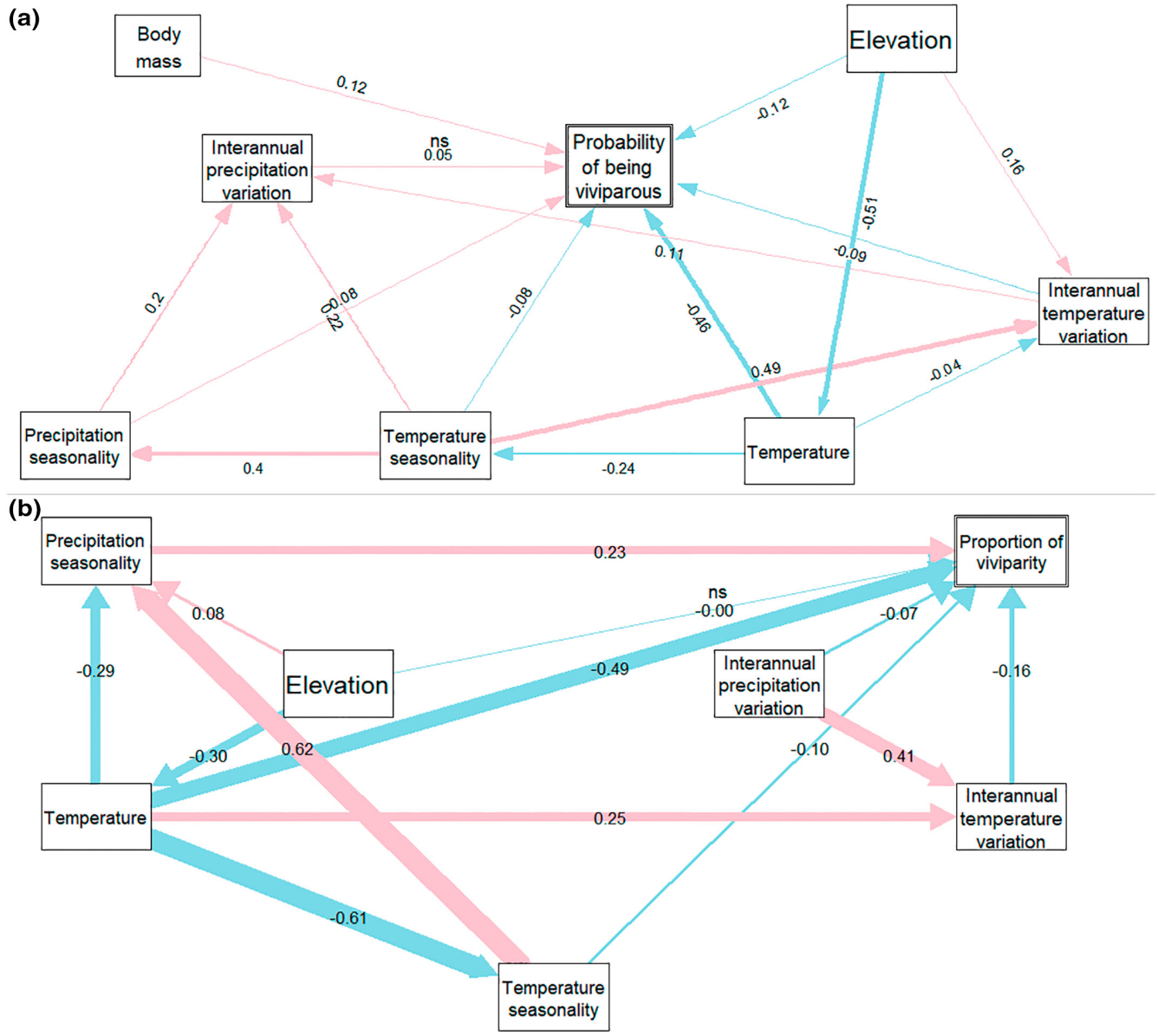

FIGURE 1 Results of global-scale path analyses for correlations among (a) environmental variables, body mass and the probability of being viviparous (species-level analysis) and (b) environmental variables and the proportion of viviparous species (assemblage-level analysis). All relationships are significant ($p < .05$) except those marked with "ns". The standardized correlation estimates appear along the lines between variable pairs. Line widths indicate the strength of the correlation, and line colours indicate the direction of the correlation (light blue = negative; pink = positive). For more details, see the Supporting Information (Table S1).

4.2 | Climatic variability

The role of climatic variability is less clear than the effect of cold temperatures. At the assemblage level, the proportion of viviparity was positively correlated with interannual temperature variation, but negatively correlated with interannual precipitation variation. Interannual variation probably represents climatic predictability because, unlike seasonality, it does not vary periodically and is, therefore, difficult to adapt to directly (Grant et al., 2017; Moreno & Møller, 2011). Therefore, climatic suitability for incubation during the same calendric period would vary, leaving behavioural flexibility of the gravid mother as a better mechanism to ensure survival of embryos (e.g., Hoffmann & Sgró, 2011; Moreno & Møller, 2011). However, we obtained the opposite result at the species level (i.e., viviparity was associated with low interannual temperature variation). Despite the methodological distinction among the two types of analyses (proportion of viviparity within grid cells vs. binary reproductive mode within species ranges), the effects were weak in both analyses. This might suggest that the true effects for climatic variation are negligible.

Seasonal climates can be as predictable as non-seasonal ones (e.g., Khavrus & Shelevytsky, 2012; Markham, 1970). Therefore, an animal might be able evolutionarily to adjust its life-history traits, including reproductive mode, to the seasonal patterns of its habitat. Accordingly, the main selective force imposed by climatic seasonality might not be

FIGURE 2 Standardized estimates (on *x*-axis) of predictors of (a) the probability of being viviparous (species-level path analyses) and (b) the proportion of viviparous species (assemblage-level path analyses), both globally and across six biogeographical realms (on *y*-axis). The predictors are colour coded (see key above the plot). The "0" red dashed vertical line represents a border, indicating no correlation between the probability of being viviparous and a given predictor. ***$p < .001$; **$p < .01$; *$p < .05$; "."$p < .1$.

the climate per se, but rather the limited duration of the season best fitted for reproduction (Shine, 2014), hence potentially favouring a reproductive strategy that maximizes the number of offspring. However, the present evidence indicates no such trade-off, because oviparous and viviparous species have similar reproductive outputs in seasonal environments (Meiri et al., 2020). Thus, seasonality is not expected to have a relationship with reproductive mode, and we found that it does not have strong or consistent effects. Intra-annual temperature variation was negatively correlated with both the proportion of viviparity and the probability of being viviparous. This contradicts the predictions of the "climatic predictability" and the "maternal manipulation" hypotheses, both of which predict that viviparous species will inhabit climatically more variable habitats (e.g., Feldman et al., 2015; Horreo et al., 2021; Watson et al., 2014). We argue, however, that seasonality cannot be equated to climatic predictability.

Importantly, temperature variation, either intra-annual (seasonal) or interannual, is negatively associated with mean annual temperature (Figure 1a,b), which weakens their effects on reproductive mode distribution. For example, of the 100 species with the highest interannual temperature variation in their ranges, only 23% are viviparous (48% of which occur in the coldest areas), 2% have bimodal reproduction, and 75% are oviparous (Supporting Information Table S5). This is close to the global distribution of reproductive modes (*c.* 19, <1 and *c.* 81%, respectively). Our findings suggest that climatic variation probably

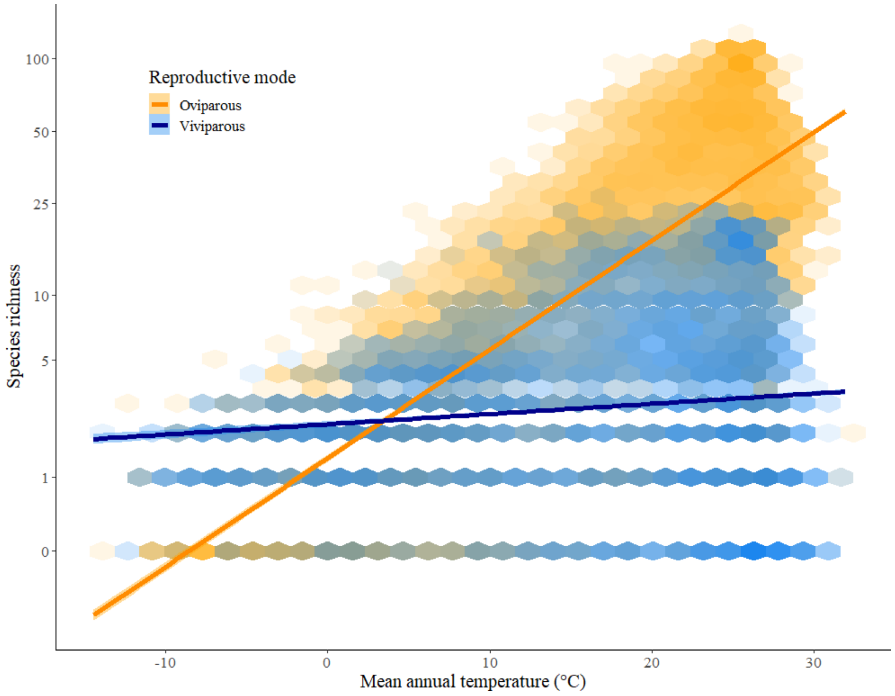

FIGURE 3 Species richness distributions of oviparous (orange) and viviparous (blue) squamate species across temperature annual means. Hexagons represent the count of grid cells, with fitted linear regression. Hexagons representing a higher number of cells are darker. The slopes are calculated by ordinary least squares. The *y*-axis is $\log_{10}$-transformed. The regression slope of oviparous species is much steeper than that of viviparous species.

affects reproductive mode mainly through mean annual temperature, with relatively low marginal impact.

4.3 | Elevation

Our results do not support a role for high elevation in selecting for viviparity except via its relationship with temperature. Elevation showed a weak negative correlation with the probability of being viviparous and was not correlated with the proportion of viviparity globally. Thus, we fail to support the prediction of the "hypoxia" hypothesis, according to which viviparity more strongly characterizes high-elevation faunas than temperature alone would suggest. At the realm scale, elevation was positively correlated with the proportion of viviparity in warmer realms (the Neotropics, the Afrotropics and Indomalaya), but negatively so in the colder realms (Supporting Information Table S1). Investigation of the relationship of elevation with temperature might reveal the reason for such results. Elevation exhibited a moderately negative correlation with temperature globally, but much more strongly so in the warmer realms (Supporting Information Table S1). This suggests that elevation does not have an independent role in driving the evolution of viviparity. Although live-bearing at high elevations (and in other hypoxic environments) is suggested to be beneficial, putatively because it increases embryonic oxygen supply (Pincheira-Donoso et al., 2017; Watson & Cox, 2021), the embryonic development and hatchling phenotypes of some oviparous species are little affected by hypoxia (e.g., Du et al., 2010; Li et al., 2020). Furthermore, high elevation might select for viviparity in warm regions for other reasons, such as extreme temperature fluctuations and dry conditions, and might impose lower costs on the gravid female owing to lower competition and predation pressures (Fox et al., 1994; Hodges, 2004).

4.4 | Body size

Our species-level analyses indicated that large-sized squamates are only slightly more likely to be viviparous. The small effect size emphasizes the difficulty of distinguishing between ecological and phylogeny-related factors (Westoby et al., 1995), because phylogenetic affinities can constrain both ecophysiological (e.g., viviparity) and morphological traits (e.g., body size) for a species. Hence, although our results are in line with the prediction that viviparity will evolve in larger (rather than smaller)-bodied species, further tests of the relationship of viviparity to species traits are required.

5 | CONCLUSIONS

Our study provides strong support for the prediction of the long-held "cold-climate" hypothesis, which asserts that viviparity is advantageous in cold climates. Accounting for the relationship between temperature and elevation, we show that elevation is not associated with viviparity globally, and we suggest that elevation could represent varied selective pressures in different environments. One way or another, we found no support for the predictions of the "hypoxia" hypothesis. Our results for climatic variability were incongruous within and between assemblage-level and species-level analyses and provide neither strong support nor a clear refutation of the predictions of the "climatic predictability" and the "maternal manipulation" hypotheses. The results of our species-level analyses show only a weak association between large body size and viviparity, which might not be sufficient to support the hypothesis that viviparity evolves in species with larger body size. Phylogeny imposes constraints on traits such as reproductive mode and body size, resulting in viviparous species occupying environments other than

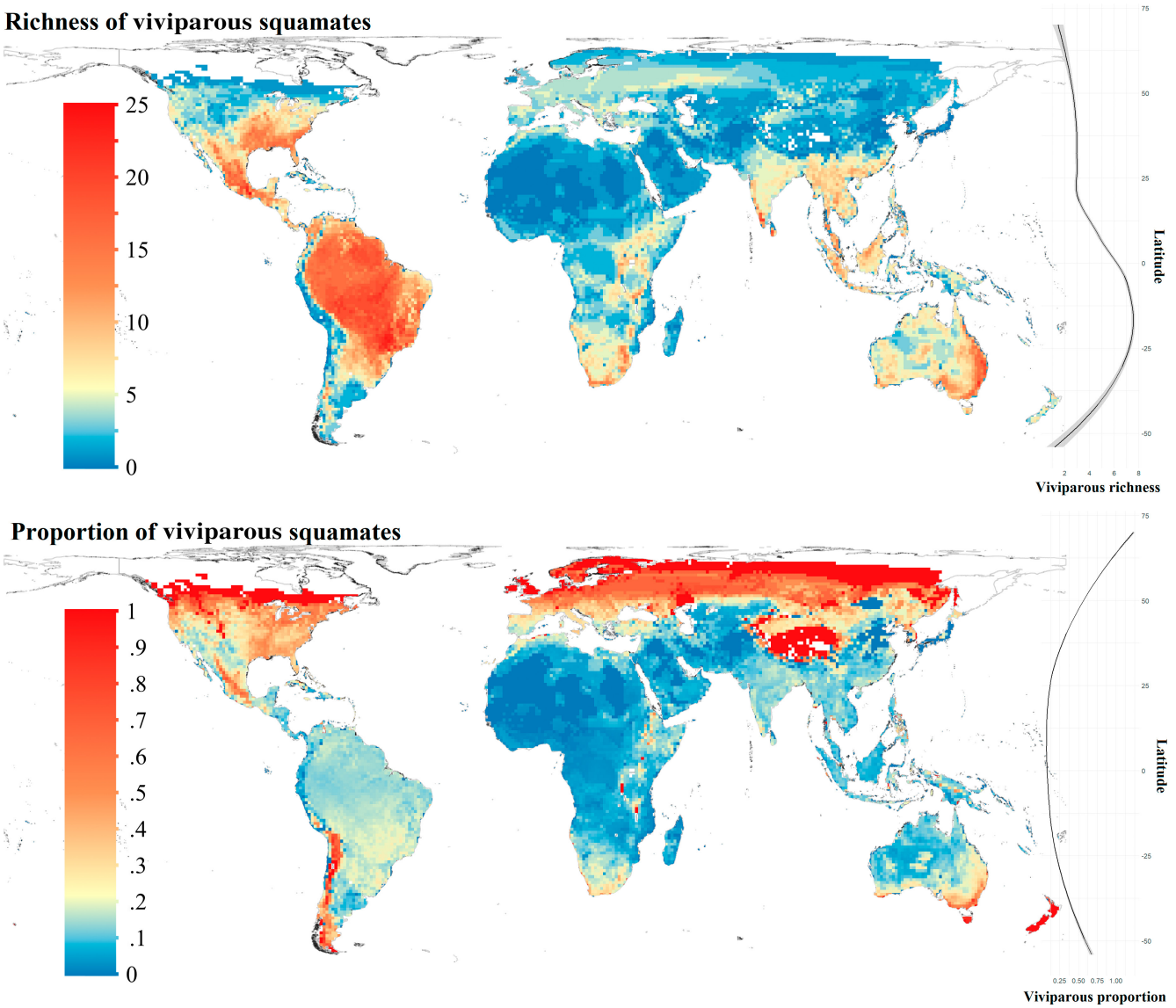

FIGURE 4 Top left: Richness of viviparous squamate species in equal-area Behrmann projection grid cells (9309.6 km^2). Top right: A "loess" curve of latitudinal variation in richness of viviparous squamate species (curve and 95% confidence interval). Bottom left: Proportion of viviparous squamate species in grid cells. Bottom right: A "loess" curve of latitudinal variation in proportion of viviparous squamate species (curve and 95% confidence interval). White areas lack squamates.

only those in which viviparity arose. Consequently, current species distributions might not fully reflect the conditions in which evolution of viviparity took place. It also should be noted that the factors driving the evolution of viviparity might vary between clades and include species-specific traits (e.g., habitat use).

In conclusion, our findings highlight the complexity of processes potentially underlying the evolution of viviparity and provide compelling opportunities for future research, but they also provide clear support for low temperatures as selecting for viviparity in squamates.

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CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available in the Supporting Information of this article at: https://doi.org/10.5061/dryad.kd51c5b6m.

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BIOSKETCH

Anna Zimin is a PhD student interested in the macroecology, biogeography and conservation of squamates.

SUPPORTING INFORMATION

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

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