Zimin Anna (Orcid ID: 0000-0001-6210-6976)

Zimin Sean V. (Orcid ID: 0000-0003-1782-608X)

Barki Goni (Orcid ID: 0000-0002-1366-5066)

de Oliveira Caetano Gabriel Henrique (Orcid ID: 0000-0003-4472-5663)

Chapple David (Orcid ID: 0000-0002-7720-6280)

Itescu Yuval (Orcid ID: 0000-0002-6301-7112)

Novosolov Maria (Orcid ID: 0000-0002-4034-3441)

Meiri Shai (Orcid ID: 0000-0003-3839-6330)

Zimin Anna (Orcid ID: 0000-0001-6210-6976)

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

Anna Zimin[1*], Sean V. Zimin[2], Richard Shine[3], Luciano Avila[4], Aaron Bauer[5], Monika Böhm[6], Rafe Brown[7], Goni Barki[8,35], Gabriel Henrique de Oliveira Caetano[8], Fernando Castro Herrera[9], David G. Chapple[10], Laurent Chirio[11], Guarino R. Colli[12], Tiffany M. Doan[13], Frank Glaw[14], L. Lee Grismer[15], Yuval Itescu[16,17], Fred Kraus[18], Matthew LeBreton[19], Marcio Martins[20], Mariana Morando[4], Gopal Murali[8], Zoltán T. Nagy[21], Maria Novosolov[22], Paul Oliver[23,24], Paulo Passos[25], Olivier S. G. Pauwels[26], Daniel Pincheira-Donoso[27], Marco Antonio Ribeiro-Junior[1], Glenn Shea[28,29], Reid Tingley[10], Omar Torres-Carvajal[30], Jean-François Trape[31], Peter Uetz[32], Philipp Wagner[5,33], Uri Roll[8,a] & Shai Meiri[1,34,a]

[1]School of Zoology, Tel Aviv University, Tel Aviv, Israel,

[2]Department of Life Sciences, Ben-Gurion University of the Negev, Beer Sheva, Israel,

[3]Department of Biological Sciences, Macquarie University, Sydney, Australia,

[4]Instituto Patagónico para el Estudio de los Ecosistemas Continentales, Consejo Nacional de Investigaciones, Científicas y Técnicas (IPEEC-CONICET), Puerto Madryn, Chubut, Argentina,

[5]Villanova University, Villanova, Pennsylvania, USA,

[6]Global Center for Species Survival. Indianapolis Zoological Society, Indianapolis, Indiana, USA,

[7]Department of Ecology & Evolutionary Biology, & Biodiversity Institute, University of Kansas, Lawrence, Kansas, USA,

[8]Mitrani Department of Desert Ecology, The Jacob Blaustein Institutes for Desert Research, Ben-Gurion University of the Negev, Midreshet Ben-Gurion, Israel,

[9]Universidad del Valle, Cali, Valle del Cauca, Colombia,

[10]Monash University, Melbourne, Victoria, Australia,

[11]Muséum National d'Histoire Naturelle, Paris, France,

[12]Departamento de Zoologia, Universidade de Brasília, Brasília, Distrito Federal, Brazil,

[13]New College of Florida, Sarasota, Florida, USA,

[14]Zoologische Staatssammlung München (ZSM-SNSB), Munich, Germany,

[15]Department of Biology, La Sierra University, Riverside, California, USA,

[16]Leibniz-Institute of Freshwater Ecology and Inland Fisheries (IGB), Berlin, Germany,

[17]Institute of Biology, Freie Universität Berlin, Berlin, Germany,

[18]Department of Ecology & Evolutionary Biology, University of Michigan, Ann Arbor, Michigan, USA,

[19]Mosaic, Yaounde, Cameroon,

[20]Departamento de Ecologia, Instituto de Biociências, Universidade de São Paulo, São Paulo, São Paulo, Brazil,

[21]Independent researcher,

[22]Globe University of Copenhagen, Copenhagen, Denmark,

[23]Biodiversity and Geosciences Program, Queensland Museum, South Brisbane, Queensland, Australia,

[24]Centre for Planetary Health and Food Security, Griffith University, Brisbane, Queensland, Australia,

[25]Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil,

[26]Royal Belgian Institute of Natural Sciences, Brussels, Belgium,

[27]School of Biological Sciences, Queen's University Belfast, Belfast, UK,

[28]University of Sydney, Sydney, New South Wales, Australia,

[29]Australian Museum Research Institute, The Australian Museum, Sydney, New South Wales, Australia,

[30]Pontificia Universidad Católica del Ecuador, Quito, Ecuador,

[31]Institut de Recherche pour le Développement, Dakar, Senegal,

[32]Virginia Commonwealth University, Richmond, Virginia, USA,

[33]Allwetterzoo Münster, Münster, Germany,

[34]The Steinhardt Museum of Natural History, Tel Aviv University, Tel Aviv, Israel,

[35]Albert Katz International School for Desert Studies, The Jacob Blaustein Institutes for Desert Research, Ben-Gurion University of the Negev, Midreshet Ben-Gurion, Israel,

[a]equal contribution

* corresponding author: Anna Zimin <annazimin@mail.tau.ac.il>,

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

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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 to study the patterns, drivers, and implications of reproductive mode evolution. Based on current species distributions we examined three selective forces hypothesized to drive squamate viviparity evolution: (1) cold climate, (2) variable climate, and (3) hypoxic conditions, and tested whether viviparity is associated with larger body size.

Location: Global

Taxon: Squamata

Methods: We compiled a dataset of 9,061 squamate species including their distributions, elevation, climate, body mass, and reproductive modes. We applied species-level and assemblage-level approaches for predicting reproductive mode, 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, employing 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 was weakly positively correlated with body size.

Conclusions: Although phylogenetic history is important, potentially explaining the occurrence of viviparous species in presently warm regions, 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 of 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.

Introduction

The diversity of reproductive strategies across the vertebrate tree of life is vast. Such life history versatility has facilitated their successful expansion across various types of environments worldwide (e.g., Conaway, 1971; Laugen et al., 2003; Prado et al., 2005; Shine & Brown, 2008; Schwimmer & Haim, 2009). 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 parent's body significantly improved embryo survivability (Sadleir, 1973; Shine, 2014). Live-bearing [viviparity, herein used as including ovoviviparity (i.e., retention of eggs *in utero* almost until hatching)] evolved across all major vertebrate clades, except archelosaurs (birds, crocodilians and turtles; Shine, 2005; Blackburn, 2015a; but see Kuchling & Hofmeyr, 2022). Viviparity is widespread in squamates (observed in ~20% of lizard and snake species; Meiri et al., 2021, and see below). Pyron & Burbrink (2014) controversially suggested 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., Tinkle & Gibbons, 1977; Lee & Shine, 1998; Pincheira-Donoso et al., 2013; Griffith et al., 2015). 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 in over 100 independent phylogenetic occasions from an oviparous ancestor, with a few inferred reversals to oviparity (Shine, 1985, 2015; Lee & Shine, 1998; Blackburn, 1999, 2015a, 2015b; Griffith et al., 2015; Wright et al., 2015; Esquerré et al., 2019). The prevalence of both oviparity and viviparity in many squamate clades, and the multiple origins of viviparity, make squamates an excellent model 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 compared to exposed eggs (Packard, 1966; Packard et al., 1977; Tinkle & Gibbons, 1977;

Shine, 1983, 2014; Guillette, 1993). 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). Indeed, while viviparous species comprise a small proportion of squamates in warm regions, they predominate in high latitudes and altitudes (Greene, 1970; Tinkle & Gibbons, 1977; Pincheira-Donoso et al., 2013; Feldman et al., 2015; Ma et al., 2018 and see below). Amongst closely related species that differ in reproductive mode, shifts to viviparity are associated with cooler environments (Shine & Bull, 1979; Guillette et al., 1980; Shine, 1987; Feldman et al., 2015; Cruz et al., 2022).

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., Shine, 2002, 2014; Feldman et al., 2015; Cruz et al., 2022). 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 (Tinkle & Gibbons, 1977; Feldman et al., 2015). 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., Tinkle & Gibbons, 1977; Shine, 1985; Moreno & Møller, 2011). Viviparous mothers, on the other hand, can behaviourally avoid some of these perils, 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, e.g., being too cold, too warm or too variable; Shine, 2014; Cruz et al., 2022). Despite its theoretical plausibility, the 'climatic-predictability' hypothesis has rarely been directly evaluated, and when it did, it generally received no empirical support (Shine, 2002, 2014; Watson et al., 2014; Feldman et al., 2015). To properly test the predictions of this hypothesis, 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., Shine, 2014; Watson et al., 2014; Feldman et al., 2015; Horreo et al., 2021). However, highly seasonal climates can have highly predictable temperatures and precipitation for species with a relatively long life span (e.g., Markham, 1970; Khavrus & Shelevytsky, 2012). 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 conceivably might adaptively respond, 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 (Moreno & Møller, 2011; McPhillips et al., 2018). Interannual variation could impose strong selection pressures on organisms (e.g., Hoffmann & Sgró, 2011; Moreno & Møller, 2011; Williams et al., 2016; Grant et al., 2017; Marrot, Garant, & Charmantier, 2017). Reptiles can behaviourally maintain their homeostasis, e.g., by changing their body temperatures (by basking or hiding in more insulated places; Neill, 1964; Le Henanff et al., 2013; Pettersen et al., 2021), or by swimming or climbing to safety when a site is flooded due 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., Harlow & Grigg, 1984; Aubret et al., 2003; Shine, 2005; Peñalver-Alcázar et al., 2015), overall parental care is rare in squamates (Reynolds et al., 2002; Doody et al., 2009). 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 to the relative prevalence of viviparous species at high altitudes. As the elevation rises, 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 on embryo development of oviparous species – such as retarded growth and depressed metabolism – and on fitness-related hatchling phenotypes, such as reduced body mass and slower locomotion (Kam, 1993; Cordero et al., 2017; 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., Shine, 1995, 2004, 2005; Webb, Shine, & Christian, 2006; Ji, Lin, Lin, Qiu, & Du, 2007; Li, Qu, Hu, & Ji, 2009). 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 (Tinkle & Gibbons, 1977; Shine, 1980; Qualls & Shine, 1995). It also restricts females' ability 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 predator-evasion ability (Tinkle & Gibbons, 1977; Shine & Bull, 1979; Shine, 1980; Sinervo et al., 1991). In squamates, the relative brood mass (i.e., the mass of the embryos relative to the female's mass) declines with increasing adult size (Meiri et al., 2021). Thus, larger gravid females may be relatively less burdened and able to move faster than can 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 lower foraging frequency and so 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 eliminate her embryos as well, while 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., Shine, 2014; Pincheira-Donoso et al., 2017; Watson & Cox, 2021), and the relationship of reproductive mode with body size. Specifically, we tested the predictions that viviparity will be associated with (1) cold climates, (2) unpredictable climates, (3) high elevations (a proxy for hypoxic conditions), and (4) large adult body sizes.

Because 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 previously assessed. 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 focus on the proportion of viviparous species of all squamates in a grid cell. They test whether environmental conditions act as filters that favour species with one reproductive mode over another. Our species-level analyses address individual species, incorporating species-specific traits such as adult body mass (representing body size) and phylogenetic affiliation, alongside data on the species' environmental/climatic niche. Our dataset of over 9,000 species includes ~83% of extant non-marine squamate species, making this the largest-scale study of the selective forces for squamate viviparity to date.

Methods

Data collection

We compiled a dataset for 9,061 out of 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 R programming environment v4.1 (R Core Team, 2022). We used the raster layer of these elevation data to subset the EOO maps of 6,272 species to create suitable elevation range maps, based on literature records (i.e., not derived from the EOO maps themselves) on elevational range at which species have been observed (minimum and maximum values). Of these 6,272 species, we used elevational observations for 4,573 species from the literature (Appendix S1 in the Supporting information), and we phylogenetically imputed

elevation for 1,699 species lacking such data, using 'picante' R package (Kembel et al., 2010), based on the dichotomous version of the phylogenetic tree made by Tonini et al. (Tonini et al., 2016). For the 2,789 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 perform sensitivity analyses excluding species lacking elevational data). We further extracted data on five climatic variables (per species range and per grid-cell – see below): mean annual temperature (BIO1; henceforth 'temperature'; °C), 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 2.1; for the years 1981–2010) of Karger et al. (2017), at a resolution of 30 arc-seconds, 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-minutes, 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 relation to our hypotheses (i.e., retaining embryos *in utero* until development is complete). We took data on reproductive mode for 7,142 species from Feldman et al. (2015), Meiri (2018), and Meiri et al. (2021). We imputed parity mode for 1,919 additional species (392 snakes, of which 315 are scolecophidians, all coded as oviparous; 1,500 lizards and 27 amphisbaenians), representing 21% of the 9,061 species in our dataset. To do so, we employed the 'picante' R package (Kembel et al., 2010) and the dichotomous phylogenetic tree by Tonini et al. (Tonini et al., 2016), imputing reproductive mode only for species with at least 95% statistical support for the imputation outcome (n = 744). We complemented these by imputing the reproductive mode of 1,175 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) At least 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; (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, since most blind snakes are believed to be oviparous (Lillywhite, 2014), we considered all members of the family Typhlopidae as oviparous despite only having data for 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 perform 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.

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 species maximal body mass from 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. (Olson et al., 2001), by intersecting the EOO with the realms.

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 ~96.5×96.5 km (approximately 1°×1° at the equator). We calculated mean values for elevation and the five climatic variables for each cell as described for species above.

Statistical analyses

To analyse the relationship between reproductive mode and the predictor variables at both assemblage and species levels, we employed path analysis, a private case of Structural Equation Modelling, using the 'lavaan' (Rosseel, 2012) and 'phylopath' (van der Bijl, 2018) R packages. Structural equation models enable accounting for covariation among variables 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 above 0.3 as a rule of thumb (see Figure S1 for model structures). To reduce heteroscedasticity and normalize residual distributions, we $\log_{10}$ transformed all explanatory variables prior to analyses.

We conducted analyses both at a global scale and separately within six biogeographic realms (Australasia, the Palearctic, 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 less than 50% of a 9,309.6 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 supplementary R script (Appendix S1).

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). Because 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. Few (254, i.e., 3%) of the species occurred in more than one realm and were analysed in both the realms they occur. To account for phylogenetic dependence we used the most complete time-calibrated phylogenetic tree available for squamates (Tonini et al., 2016), including 8,444 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 (Figure S1a). To test whether polytomies affected the results, we performed sensitivity analyses including only dichotomous relations in the phylogenetic tree (for 4,349 species with reproductive mode data and 5,180 species with imputed data). We also repeated these analyses excluding species lacking elevational data.

Assemblage-level analyses

We conducted assemblage-level analyses for 13,636 grid cells, which cover the distributions of our 9,044 species (after exclusion of all species with mixed reproduction mode, except *Zootoca vivipara* which we treated as oviparous in the grid cells egg-laying populations occur in, and as viviparous in 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. Because the response variable is in the form of proportions, we applied 'logit' transformation on the response variable. As 'logit' transformation cannot handle zeros, we rescaled the response variable prior to applying it, by applying the transformation: $y' = [y(N-1) + \frac{1}{2}]/N$, 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 (Paradis et al., 2004; Dormann et al., 2007). 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 (Figure S1b). Second, we recalculated the standard errors and p-values based on geographic distances, using the "lavSpatialCorrect" function, by Jarrett Byrnes (https://github.com/jebyrnes/spatial_correction_lavaan). To verify that species' island residency did not affect squamate life history, we conducted an additional analysis focusing only on the 12,321 non-insular grid cells (or 12,273 cells excluding species with imputed reproductive mode). We also repeated these analyses excluding the 4,488 species lacking elevational data.

Results

Our dataset comprised 9,061 species, of which 7,589 are oviparous, 1,454 are viviparous, and 18 have bimodal reproduction (Table 1; 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).

Species-level analyses

Our global-scale model included significant effects ($p < 0.05$) for all the predictors of the probability of being viviparous, except variation in interannual precipitation (Figure 1a; Table S1 in Supporting Information). The model explained 78% of the variation in the probability of being viviparous. Temperature had a moderate negative correlation with viviparity (standardized estimate: -0.46 ± 0.07), while elevation, temperature seasonality, and interannual variation had weak negative effects (-0.12 ± 0.03, -0.08 ± 0.04, and -0.09 ± 0.03, respectively). On the other hand, precipitation seasonality, interannual precipitation variation, and body mass had weak positive effects (0.08 ± 0.03, 0.05 ± 0.03, and 0.12 ± 0.04, respectively; Figure 1a; Table S1). All sensitivity analyses yielded qualitatively similar results (Table S2). The significance of the predictors' effects and their direction, however, varied among realms, with notably stronger effects of temperature in Australasia, the Nearctic and the Neotropics (Figure 2a; Table S1).

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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 Palearctic, Nearctic, and Australasia.

The global-scale model included significant effects ($p < 0.001$) for all the predictors of viviparity proportion except elevation. It explained 43% of the variation in the proportion of viviparity. Mean annual temperature was by far the strongest predictor (-0.49 ± 0.01; Figure 1b; Table S3) and was negatively correlated with the proportion of viviparity globally and across realms, except Indomalaya (Figure 2b; Table S3). The proportion of viviparity was weakly positively correlated with interannual temperature variation and weakly negatively correlated with interannual precipitation variation (0.23 ± 0.01 and -0.16 ± 0.01, respectively; Figure 1b; Table S3). The relationship with seasonality metrics was very weakly negative (Figure 1b; Table S3). The predictors and their effects varied across realms, with the effects of temperature being somewhat weaker in warmer realms (Figure 2b, 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, Table S3). All sensitivity analyses yielded qualitatively similar results (see Table S4).

Discussion

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 ($\leq 4.8°C$) are viviparous, three have mixed reproductive mode and 26 are oviparous (Table S5). Furthermore, temperature is correlated with latitude (e.g., Figure S2), and it is noteworthy that of the 58 species with latitudinal centroids above 45º (in either hemisphere) in our dataset, 44 are viviparous (75.9%), one has a mixed reproductive mode [*Zootoca vivipara* (Lacertidae), with oviparous populations only at the southern edges of its range – around latitude 46 ºN (Horreo et al., 2018)], and only 13 are oviparous. Similarly, 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 actual number of viviparous species is greatest in the generally warmer tropical regions (Table 1; Figure 4). The occurrence of viviparous species in such climates may 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 may be relicts, remaining in a place they occupied during colder periods, e.g., during Pleistocene glaciations (Stute et al., 1995; Renssen & Vandenberghe, 2003; Odierna et al., 2004; Kupriyanova et al., 2017). Hence, viviparous lineages might have retained viviparity due to the extreme difficulty to re-evolve oviparity given the complexity of evolutionary steps required to re-evolve the shelled egg (Lee & Shine, 1998; Lambert & Wiens, 2013; Pincheira-Donoso et al., 2013; Blackburn, 2015b; Griffith et al., 2015; King & Lee, 2015; Shine, 2015; Wright et al., 2015). For example, species of the diverse genus *Liolaemus* (Liolaemidae) most likely evolved viviparity at high elevations in the Andes, later dispersing to the warmer adjacent lowlands and maintaining this reproductive mode (Schulte et al., 2000; Pincheira-Donoso et al., 2013; Esquerré et al., 2019). Similarly, 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* (Lynch, 2009; Fenwick et al., 2012; Alencar et al., 2016; Klein et al., 2021)].

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). Under such conditions, selective pressures on reproductive mode may 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 to oviparous species, due 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 to examine 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 oviparous during the time they evolved, or colonized Australasia. Viviparity subsequently evolved multiple times in three families: at least twice in the Elapidae, over a dozen times in the Scincidae – following three independent colonization events, and once in the Diplodactylidae – 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, on the other hand, 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 about 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 indeed 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.

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, hence, difficult to directly adapt to (Moreno & Møller, 2011; Grant et al., 2017). 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 may suggest that the true effects for climatic variation are negligible.

Seasonal climates can be as predictable as non-seasonal ones (e.g., Markham, 1970; Khavrus & Shelevytsky, 2012). Therefore, an animal might be able to evolutionarily 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 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 number of offspring. However, the current evidence indicates no such trade-off, as 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 indeed we found it does not have strong or consistent effects. Intra-annual temperature variation was negatively correlated with both proportion of viviparity and the probability of being viviparous. This contradicts the predictions of the 'climatic-predictability' and the 'maternal manipulation' hypotheses, both predicting that viviparous species will inhabit climatically more variable habitats (e.g., Watson et al., 2014; Feldman et al., 2015; Horreo et al., 2021). We argue, however, that seasonality cannot be equated with 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 (Table S5). This is close to the global distribution of reproductive modes (~19%, <1%, and ~81% respectively). Our findings suggest that climatic variation probably affects reproductive mode mainly through mean annual temperature, with relatively low marginal impact.

Elevation

Our results do not support a role for high elevations in selecting for viviparity except via its relationship with temperature. Elevation was weakly negatively correlated with the probability of being viviparous, and 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 (Table

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S1). Investigating elevation's relationship with temperature might reveal the reason for such results. Elevation was moderately negatively correlated with temperature globally, but much more strongly so in the warmer realms (Table S1). This suggests that elevation does not have an independent role in driving the evolution of viviparity. Even though live-bearing at high elevations (and other hypoxic environments) is suggested to be beneficial, because it putatively increases embryo 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, Thompson, & Shine, 2010; Li et al., 2020). Furthermore, high elevation may select for viviparity in warm regions for other reasons, such as extreme temperature fluctuations and dry conditions, and impose lower costs on the gravid female due to lower competition and predation pressures (Fox et al., 1994; Hodges, 2004).

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), as 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 with species traits are required.

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 the other, we found no support for the predictions of the 'hypoxia' hypothesis. Our results for climatic variability were incongruous within and between assemblage-

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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 just those in which viviparity arose. Consequently, current species distributions may not fully reflect the conditions under 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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Tables and Figures

Table 1. Descriptive statistics for the geography of squamate reproduction mode.

Region	No. species	No. oviparous species	No. viviparous species	No. grid cells	Temperature (°C, mean±SE)	No. viviparous spp. per grid cell (mean±SE; range)	Proportion (%) viviparity per grid cell (mean±SE; range)
Global	9,045	7,590	1,455	13,636	17.2±10.1	4.5±4.8 (0-25)	26.3±29.9 (0-100)
Afrotropical	1,825	1,595	230	2,448	24.3±3.4	3.0±2.7 (0-17)	7.7±9.8 (0-100)
Australasia	1,490	1,225	265	1,289	22.4±4.5	5.0±3.9 (0-22)	18.7±23.0 (0-100)
Indomalaya	1,768	1,546	222	1,119	24.5±3.3	5.3±3.5 (0-21)	12.0±9.9 (0-100)
Nearctic	456	323	133	1,277	10.4±6.6	5.5±4.2 (0-18)	50.6±28.6 (0-100)
Neotropical	3,187	2,606	581	2,278	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)
Palearctic	919	803	116	5,093	10.0±10.6	1.9±1.5 (0-10)	38.4±36.3 (0-100)

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 (in percent) of viviparous species out of total species richness per grid cell (mean, standard deviation, and range). Reproductive mode was imputed for 1,919 species.

Table 2. Descriptive statistics for squamate reproduction mode across major clades.

Clade	No. species	No. oviparous	No. viviparous	Proportion viviparous
Acrodonta	555	507	48	8.6%
Alethinophidia	2,780	2,143	636	22.9%
Anguiformes	176	106	70	39.8%
Anomalepididae	19	19	0	0%
Dibamia	10	10	0	0%
Gekkota	1,861	1,843	18	1.0%
Laterata	779	767	11	1.4%
Pleurodonta	1,115	911	203	18.2%
Scincomorpha	1,358	876	467	34.8%
Scolecophidia	408	407	1	0.2%

The total number of species, and of oviparous and viviparous species are presented for each clade. Proportion of viviparous species out of total species richness of each clade is presented as a percentage. These numbers include imputed values for 1,919 species.
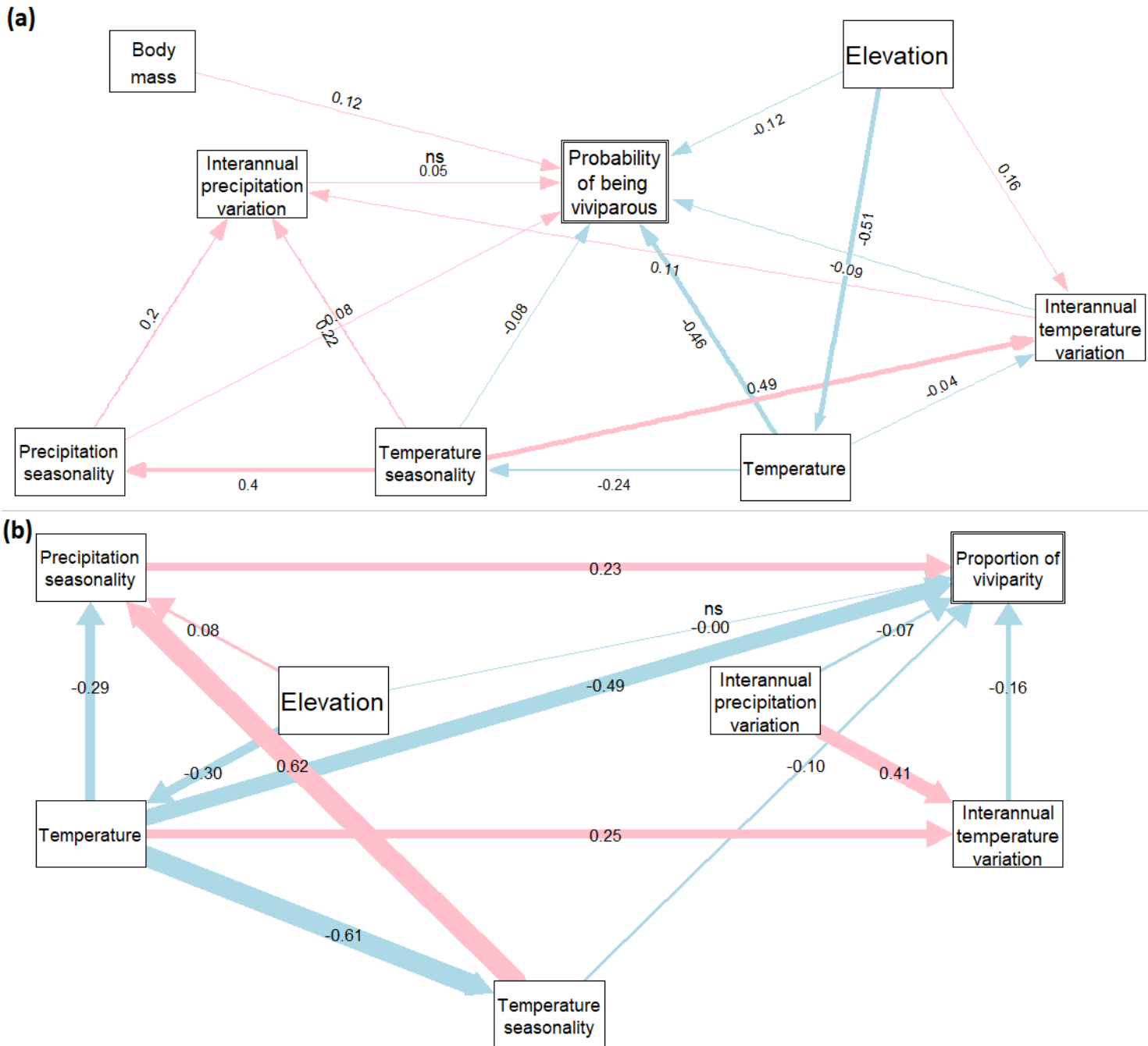
Figure 1. Global-scale path analyses' results for correlations among (a) environmental variables, body mass and the probability of being viviparous (species-level analysis); (b) environmental variables and proportion of viviparous (assemblage-level analysis). All relationships are significant (p < 0.05) except those marked with "ns". The standardized correlation estimates appear along the lines between variable pairs. Line widths indicate the strength of the correlation, while line colours indicate the direction of the correlation (light-blue = negative; pink = positive). For more details see Table S1.
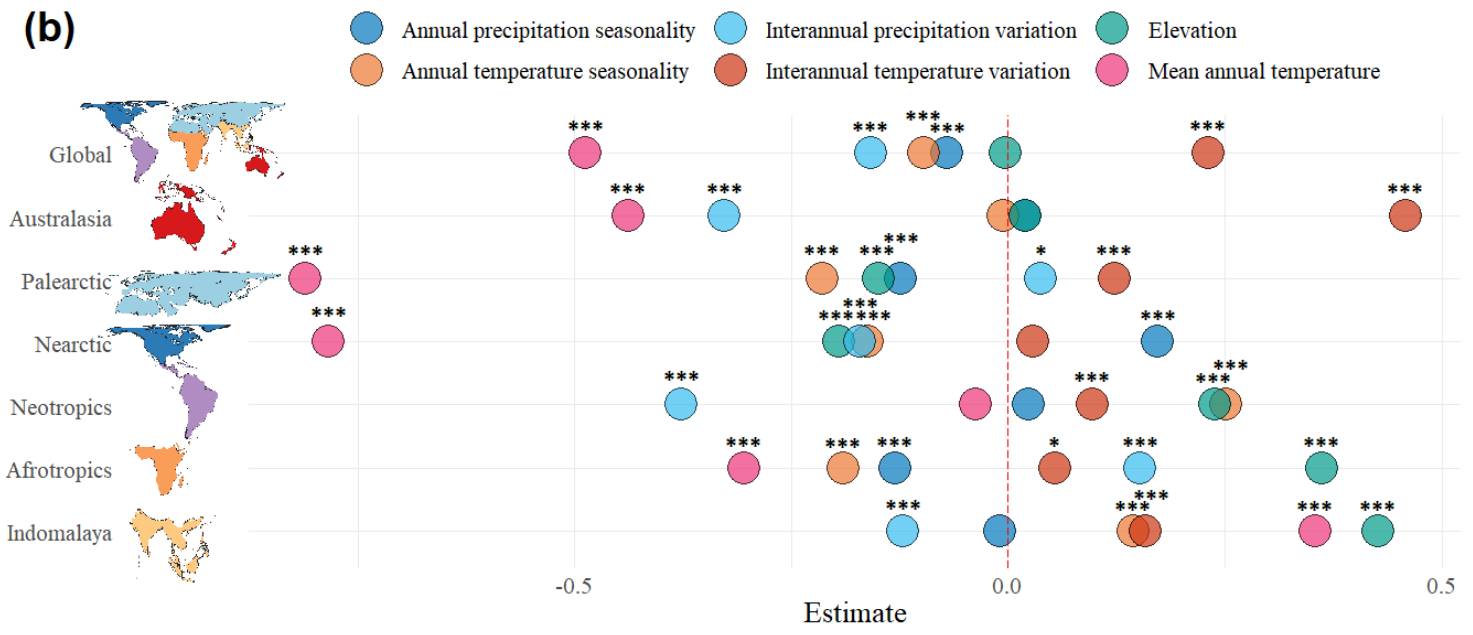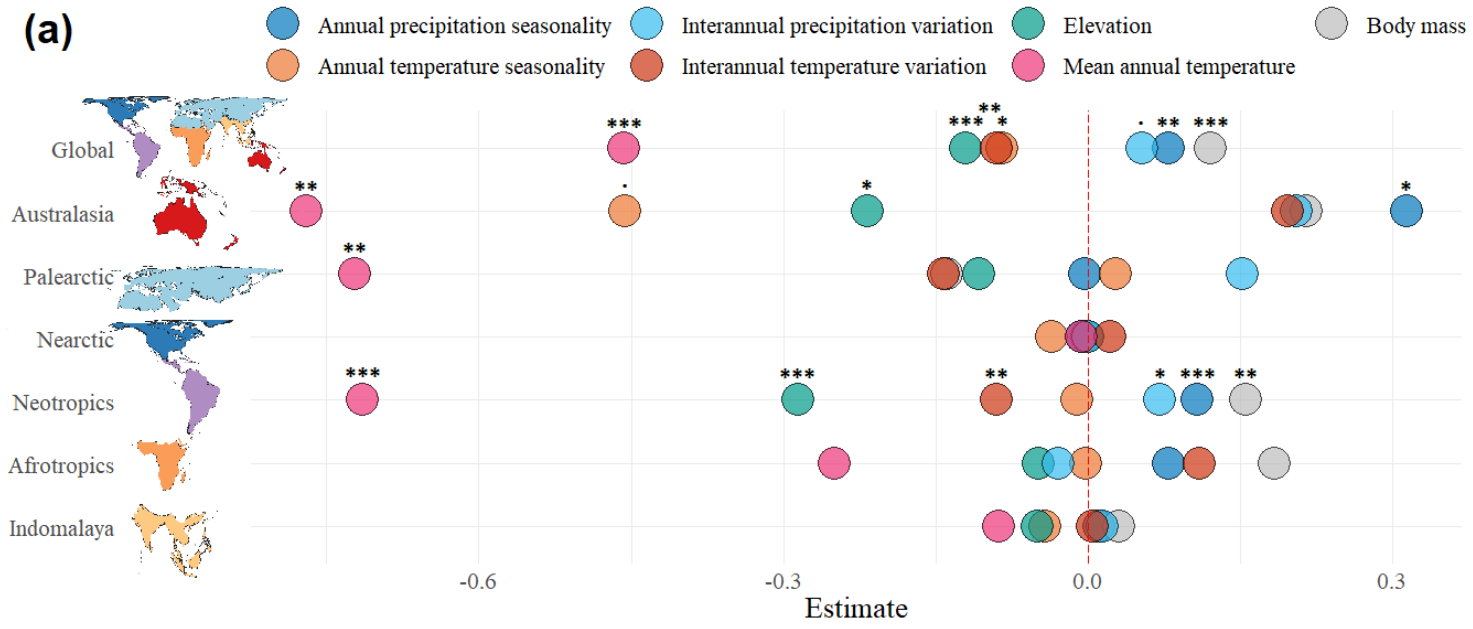
Figure 2. Standardized estimates (on x axis) of predictors of (a) the probability of being viviparous (species-level path analyses); (b) proportion of viviparous species (assemblage-level path analyses); globally and across six biogeographic realms (on y axis). The predictors are colour coded (see legend above the plot). "0" red horizontal line represents a border, indicating no correlation between probability of being viviparous and a given predictor. Significance levels coding: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1.
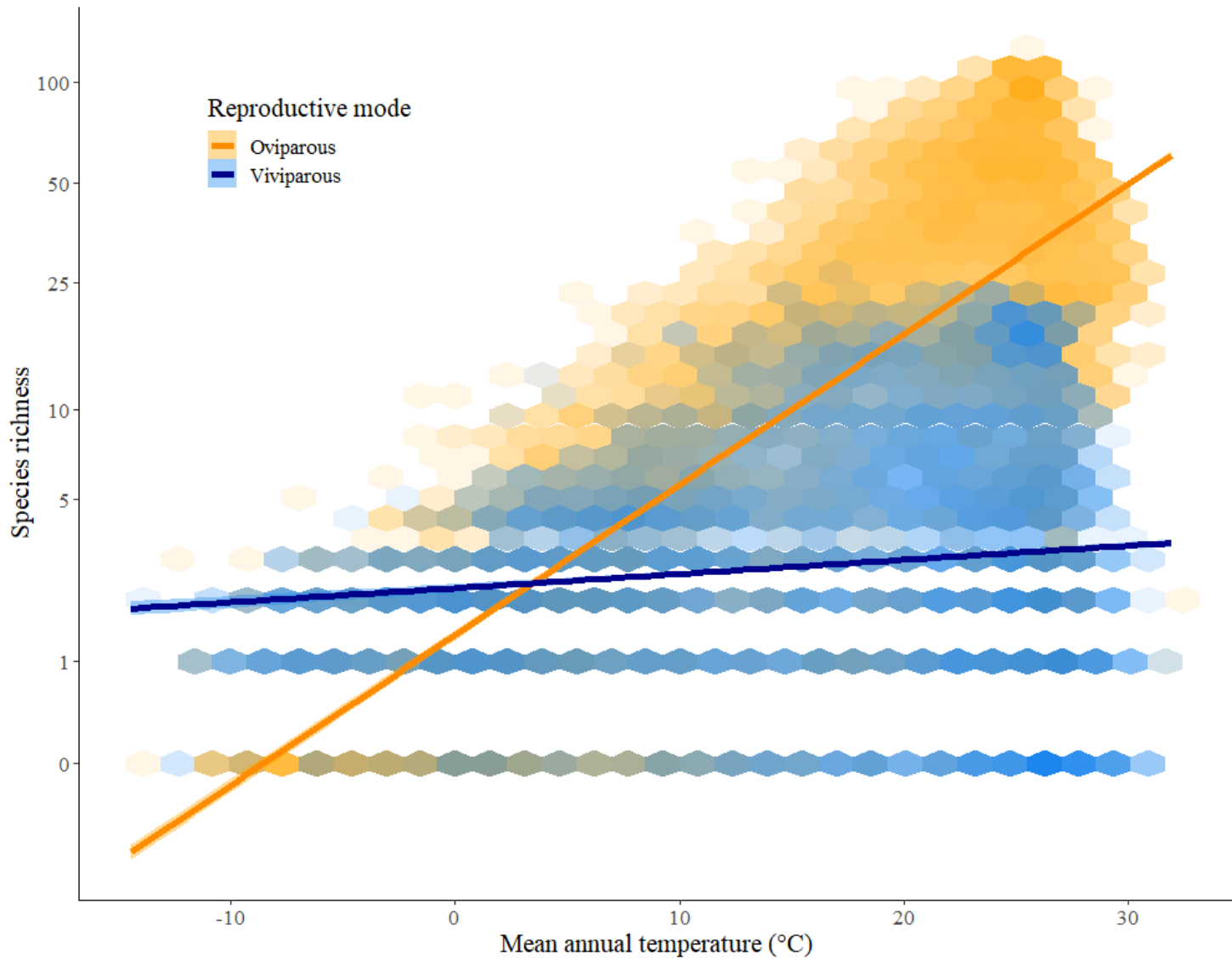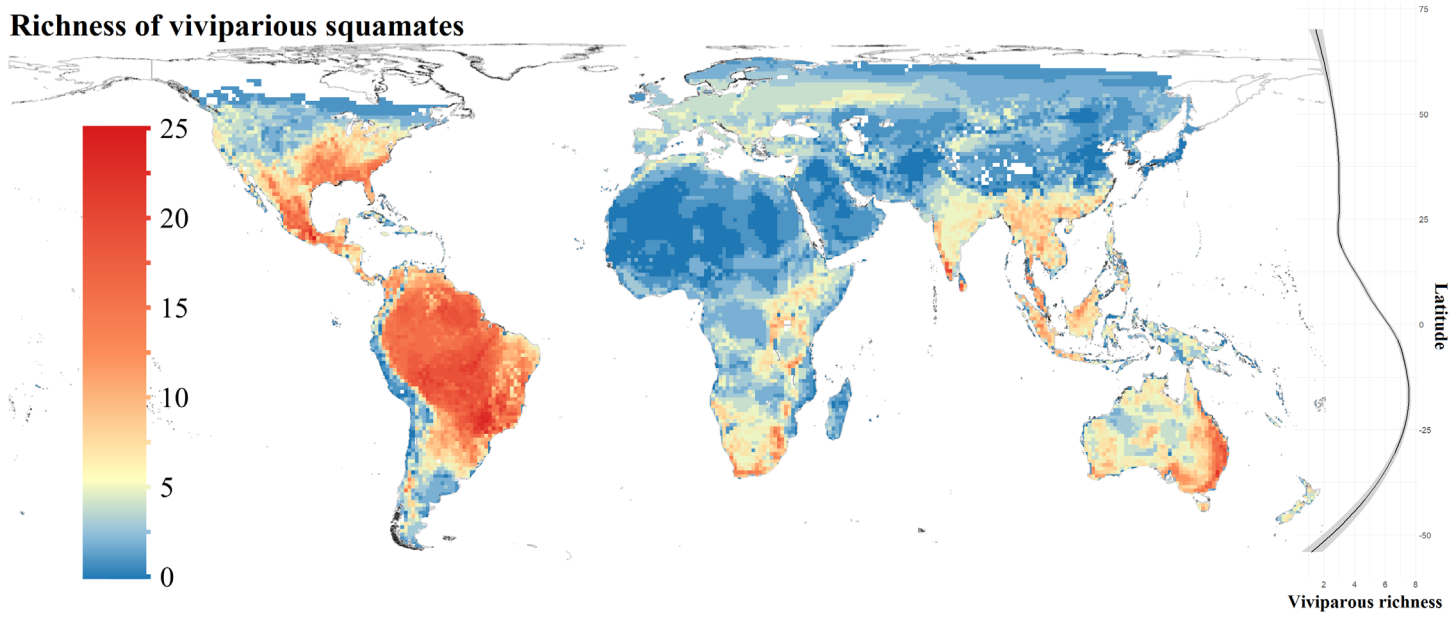
Figure 3. Species richness distributions of oviparous (orange) and viviparous (blue) squamate species across temperature annual means. Hexagons represent count of grid cells, with fitted linear regression. Hexagons representing higher number of cells are darker. The slopes are calculated by ordinary least squares. The y axis is log10 transformed. The regression slope of oviparous species is much steeper than that of viviparous species.
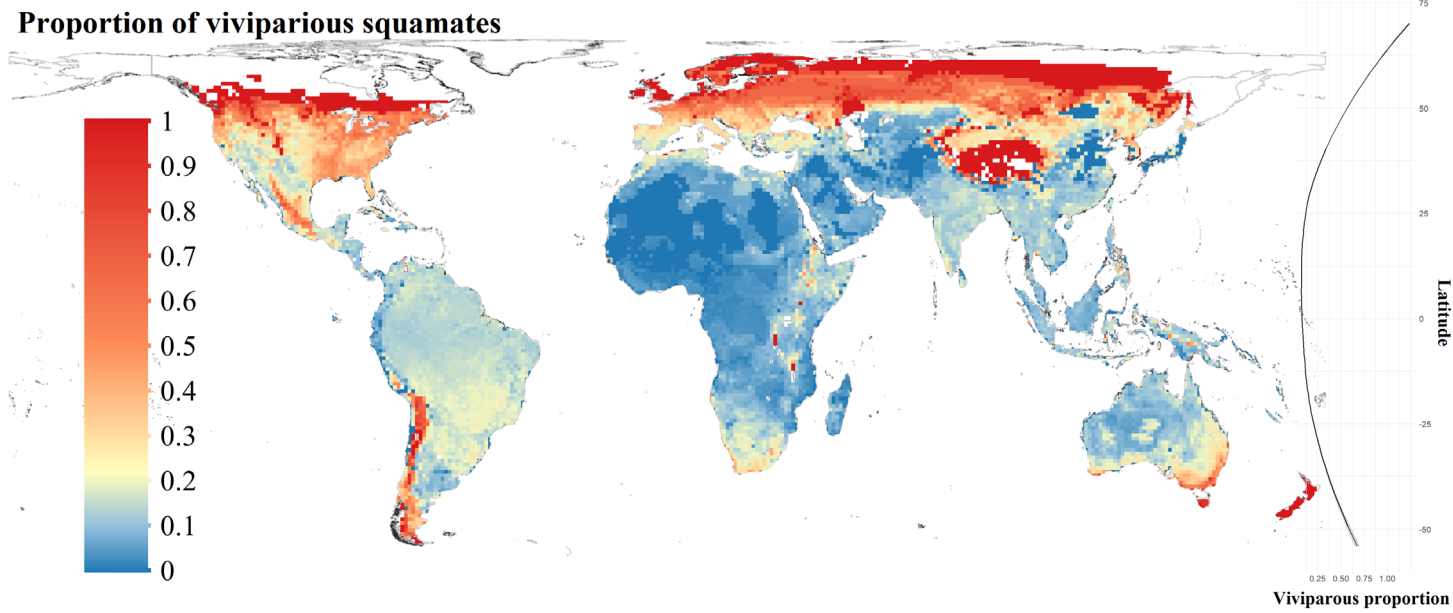
Figure 4. Top left: richness of viviparous squamate species in equal-area Behrmann projection grid cells (9,309.6 km²). Top right: a "Loess" curve of latitudinal variation in richness of viviparous squamate species (curve and 95% CI). Bottom left: proportion of viviparous squamate species in grid cells. Bottom right: a "Loess" curve of latitudinal variation in proportion of viviparous squamate species (curve and 95% CI). White areas lack squamates.

Data Availability Statement

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

Appendix S1. datasets for species-level and assemblage-level analyses in 'xlsx' and 'RData' formats, and R Markdown script for analyses and plots.

Supporting figures and tables

Figure S1. Structural equation model structure, including relations among predictors of reproductive mode.

Figure S2. Mean annual temperature across absolute latitudes.

Table S1. Standardized estimates for the species-level analyses showing relationships between probability of being viviparous and environmental variables and body mass.

Table S2. Standardized estimates for the species-level global-scale sensitivity analyses showing relationships between probability of being viviparous and environmental variables and body mass.

Table S3. Standardized estimates for the assemblage-level analyses showing relationships between proportion of viviparity and environmental variables in grid cells.

Table S4. Standardized estimates for the assemblage-level global-scale sensitivity analyses showing relationships between proportion of viviparity and environmental variables in grid cells.

Table S5. Percentage of viviparity among species with extreme environmental conditions in their geographic ranges.