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Research article

Disentangling the interrelations of body mass, egg deposition site, climate and microhabitat use in frogs and salamanders

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Amphibians exhibit a large diversity in reproductive and developmental strategies, which in turn are linked to their body size, life history and habitat. Here, we explore why terrestrial egg laying frogs are on average smaller than aquatic egg laying ones and whether this pattern also exists in salamanders. We hypothesized that egg deposition site and body mass are not linked directly across species, but that terrestrial egg layers occur in climates and use microhabitats that favor small masses. To test this, we compiled a dataset on egg deposition site (terrestrial or aquatic), development mode (biphasic with larvae or direct development without larvae), body mass, microhabitat use (water-dependent, ground-dwelling or arboreal) and climate within their distribution area (temperature, precipitation and seasonality in both) of 3091 frog and 244 salamander species. We analyzed the interrelations between these traits and environmental factors by using a cross-species approach and phylogenetic generalized least squares analysis. Body masses increased along a gradient from warm, humid and unseasonal climates to cold, dry and seasonal climates in frogs and salamanders. Terrestrial egg deposition was constrained to warm, humid and unseasonal climates only in frogs. Terrestrial eggs and an arboreal microhabitat use were linked in frogs and salamanders, and arboreal frogs were smaller than non-arboreal ones. We confirmed that frogs with terrestrial eggs had smaller average body masses than those with aquatic eggs, irrespective of their development mode, but this difference disappeared when we corrected body masses for the effects of climate and microhabitat use. In salamanders, however, egg deposition site and development mode were neither directly related to body mass, nor indirectly via the effects of climate and microhabitat use. Our results suggest that thermal and hydric environmental conditions determine the geographical distribution of body mass and reproductive strategies in amphibians and set the framework for their evolution.

Keywords: arboreality, direct development, ectotherms, energy–water conservation hypothesis, reproductive mode, terrestrial breeding



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Introduction

Animal body size varies spatially across the globe. For example, species in high latitudes are larger than species in low latitudes, which Carl Bergmann first noted in 1847. Bergmann explained this pattern by stating that large sizes increase heat conservation via low surface-to-volume ratios and allow species to live under cold ambient temperatures. Because most other life history traits of animal species strongly correlate with body size (Peters 1983), these also show spatial distributions. For example, fishes living in cooler waters typically show a larger body size, lower mortality, slower growth and later maturation than those living in warmer waters (Wang et al. 2020). Although interrelations between environmental conditions experienced by species and their life history traits have now been studied for more than a century (Bergmann 1847, Peters 1983), underlying mechanisms, e.g. of the geographical distribution of body size in ectotherms, are often still not completely understood (Slavenko et al. 2019, Caron and Pie 2024). In amphibians, our lack of knowledge is the largest, and the interrelations among life history traits and how these are affected by environmental conditions seem to be more complex than in other tetrapods (Hallmann and Griebeler 2020, Womack and Bell 2020, Henry et al. 2023, Johnson et al. 2023, Cejp and Griebeler 2024). For example, amphibian body masses, which determine most other life history traits (Cejp and Griebeler 2024), strongly depend on ambient temperature and humidity. Many species that adapted to unfavorable temperatures and humidity levels have evolved different body shapes (Castro et al. 2021), behavioral modes of thermo- and hydroregulation (Giacometti and Tattersall 2025), aestivation or hibernation (Lillywhite 2006, Costanzo 2019) and other physiological adaptations (Navas et al. 2008). Such adaptations seen in different amphibian species alter the effect of environmental conditions on their body size (Servino et al. 2022) and enable them to occupy a wide diversity of habitats of different temperatures and humidities (from fully aquatic to fully terrestrial). Amphibian habitat use is not only associated with differences in body sizes and shapes, but also with diverse types of reproduction (from aquatic eggs and larvae to viviparity; Haddad and Prado 2005). The different types of reproduction (where known) of more than 90% of frog and salamander species can be assigned to one of three distinct 'reproductive modes' (sensu Gomez-Mestre et al. 2012, Liedtke et al. 2022). These modes are based on a species' egg deposition site (aquatic versus terrestrial) and development mode (sensu Womack and Bell 2020; biphasic with a larval stage versus direct development without a larval stage). The aquatic egg layers (i.e. biphasic species that deposit aquatic eggs) form one mode. Terrestrial egg layers (i.e. species that deposit terrestrial eggs) comprise the two others, i.e. biphasic species and direct developers. Terrestrial egg layers have on average smaller body sizes than aquatic layers (Gomez-Mestre et al. 2012, Zimkus et al. 2012), but the reasons for this are unknown. Many authors suggested that direct development leads to small body sizes (Hanken and Wake 1993,

Estrada and Hedges 1996, Rittmeyer et al. 2012, Oliver et al. 2017). However, biphasic and direct developing terrestrial egg layers do not differ in their average body size, but both are smaller than aquatic layers (Gomez-Mestre et al. 2012). This observation may indicate that egg deposition site (aquatic or terrestrial) rather than development mode (biphasic or direct) determines amphibian body size.

Amphibians with terrestrial eggs (both biphasic and direct developing species) are largely restricted to tropical, warm and humid regions (Gomez-Mestre et al. 2012, Lion et al. 2019). In such environments, even very small species can thrive, as ample heat and moisture allow them to overcome the risk of heat loss and desiccation despite their high surface-to-volume ratios. Conversely, amphibians with aquatic eggs dominate in cold and dry environments, which constrain species to large sizes with low surface-to-volume ratios (Olalla-Tárraga et al. 2009, Gouveia and Correia 2016, Amado et al. 2019). Moreover, cold temperatures during egg and larval development are typically expected to result in large adults and warm temperatures in small ones (Atkinson 1994), although the heritability of intraspecific differences in growth rates between such environments is poorly studied. Thus, the size differences between terrestrial and aquatic egg layers rather could result from different climatic conditions experienced by species than from their different reproductive modes.

Some authors found that evolutionary transitions from aquatic to terrestrial egg laying went along with a transition from the use of water-dependent to water-independent microhabitats by adults (Liedtke et al. 2017, Bonett et al. 2022). Thus, the fraction of species using water-independent microhabitats should be higher in terrestrial egg layers than in aquatic layers. Most species using water-independent microhabitats are ground-dwelling (i.e. on the ground, under rocks or in leaf litter) or arboreal (i.e. typically on aboveground vegetation) and are on average smaller than water-dependent species (Wells 2007, Womack and Bell 2020). For arboreal species, small body masses are advantageous, because leaves and thin branches must support an animal's body mass, in particular when jumping from branch to branch (Astley et al. 2015, Bijma et al. 2016). Arboreal species have evolved a higher cutaneous water resistance than species using water-dependent and ground-dwelling microhabitats (Wygoda 1984, Young et al. 2005). Sustaining a high resistance to water loss reduces the risk of desiccation and allows for small body sizes in arboreal species despite their high surface-to-volume ratios (Tracy et al. 2010). All these observations suggest that not only climate, but also microhabitat use could explain the smaller body sizes in terrestrial than in aquatic egg layers, a hypothesis that has not been tested so far.

Previous studies on the interrelations between body size, reproductive mode, climate and microhabitat use have several shortcomings. Most studies focused on frogs, whereas information on salamanders is rare. Authors often used body length as a measure of body size (Gomez-Mestre et al. 2012, Slavenko and Meiri 2015, Gouveia and Correia 2016, Womack and Bell 2020). They thus ignore differences in body shapes between species, which questions any

comparison between stout, tailless frogs and elongated, tailed salamanders. Many findings on the effect of climate on body size are based on geographically limited datasets on amphibian species (Olalla-Tárraga et al. 2009, Slavenko and Meiri 2015, Amado et al. 2019, 2021). However, climatic variables correlate differently in different geographic regions (e.g. temperature and humidity correlate positively in some regions and negatively in others; Lion et al. 2019), and the effect of one climatic variable (e.g. temperature) on body size interacts with the effect of others (e.g. humidity). Thus, findings on the effects of specific climatic variables (e.g. temperature) on body size are not comparable between different regions. Finally, to the best of our knowledge, statistical tests on large-scale interspecific associations between reproductive mode and microhabitat use in frogs and salamanders, and between body mass and microhabitat in salamanders, are still lacking.

In this study, we tested whether both of the two terrestrial egg layers (i.e. the biphasic and direct developing species) have on average smaller body masses than aquatic layers (Gomez-Mestre et al. 2012) and we analyzed the respective relations of body mass and reproductive mode to climate and microhabitat use (Wells 2007, Olalla-Tárraga et al. 2009, Gomez-Mestre et al. 2012, Lion et al. 2019, Womack and Bell 2020). We explored if the climate within the species' distribution areas ('climate hypothesis'), the species' microhabitat use ('microhabitat hypothesis') or both together ('climate and microhabitat hypothesis') can explain the relation of body mass to reproductive mode. To test our three hypotheses, we established a large dataset on the body mass, egg deposition site, development mode, microhabitat use and climatic conditions in the distribution area of 3335 amphibian species. It comprises 3091 frogs, and thus more than four times more species (720 species) than the study of Gomez-Mestre et al. (2012) and it also includes 244 salamanders. Our dataset does not include caecilians and neotenic salamanders, as none of the caecilian species known has aquatic eggs, is arboreal and occurs outside the tropics (Pough et al. 2015, Liedtke et al. 2022), and neotenic salamanders do not show any of the three reproductive modes, as they are not biphasic although they have aquatic eggs. This makes both groups unsuitable to test our hypotheses.

Material and methods

Dataset

Our final dataset used to test our three hypotheses comprised 3335 amphibian species (3091 frogs and 244 salamanders), for which we had collected information on (adult) body mass or body length, reproductive mode and microhabitat use from the literature (Supporting information). To have a single value per species, we averaged mass and length values, respectively, whenever we had values from multiple sources. Finally analyzed body masses of species (in g) were mean masses of direct measurements of animals (if available in the literature; 524 species) or were calculated from the mean body length of a species (in mm; 2811 species) by applying the allometries of Santini et al. (2018) as described in Cejp and Griebeler (2024).

We log₁₀-transformed species' body masses prior to all analyses. We assigned each species to one of the three reproductive modes sensu Gomez-Mestre et al. (2012), which are 1) aquatic eggs and biphasic, larval development (Aq-L; e.g. *Bombina orientalis*, *Ichthyosaura alpestris*), 2) terrestrial eggs and biphasic, larval development (Ter-L; e.g. *Agalychnis callidryas*, *Ambystoma opacum*), and 3) terrestrial eggs and direct development without a larval stage (Ter-D; e.g. *Eleutherodactylus coqui*, *Plethodon hoffmani*). We further categorized the microhabitat of non-reproducing adults for each species as either water-dependent (strictly aquatic species and those needing water bodies), ground-dwelling (active on the ground, under rocks or in leaf litter, and independent of water bodies) or arboreal (usually active on aboveground vegetation and independent of water bodies). In amphibians, these three microhabitats are the most frequently used (Womack and Bell 2020, Pincheira-Donoso et al. 2021).

To test the 'climate hypothesis' and 'climate and microhabitat hypothesis', we established information on the climate within the distribution area for each of the 3335 species. Therefore, we downloaded polygons of distribution maps for each species from the IUCN Red List webpage (IUCN 2023) and raster maps on 19 climatic variables from the WorldClim 2.1 database (2.5 arc-min resolution; Hijmans et al. 2005, Fick and Hijmans 2017). For each of the 19 climatic variables and each species, we calculated the mean across the entire species' distribution area using the *extract* function ('terra' package ver. 1.7-65; Hijmans 2023).

Following Johnson et al. (2023), we selected mean annual temperature (BIO1, °C), annual temperature range (BIO7, °C), total annual precipitation (BIO12, mm) and precipitation seasonality (BIO15, coefficient of variation) to assess heat, humidity and seasonality within a species' distribution area. All the other 15 variables showed a high Spearman's rank correlation to at least one of these four variables across the 3335 species studied (Supporting information). These four variables, however, also correlated among each other ($0.02 < |\text{Spearman's } \rho| < 0.69$), and thus their effects on body mass can be redundant and difficult to disentangle (Gouveia and Correia 2016). To obtain independent variables on the climate experienced by each of the 3335 species, we conducted a phylogeny-informed principal component analysis (pPCA) with species' values of these four climatic variables using the function *phyl.PCA* ('phytools' package; Revell 2012). As the Kaiser–Guttman criterion (Guttman 1954) suggested the interpretation of the first two PC axes (Supporting information), we considered the PC1 and PC2 values as new climatic variables for our test of the 'climate hypothesis' and 'climate and microhabitat hypothesis'. PC1 described a gradient from cold, dry, seasonal (low mean annual temperature, low annual precipitation, high annual temperature range and high precipitation seasonality; low PC1 values) to warm, humid, unseasonal climates (high PC1 values), and PC2 described a gradient from cold climates (low mean annual temperature) with low precipitation seasonality (low PC2 values) to warm climates with high precipitation seasonality (high PC2 values) (Fig. 1). As species' PC2 values turned out

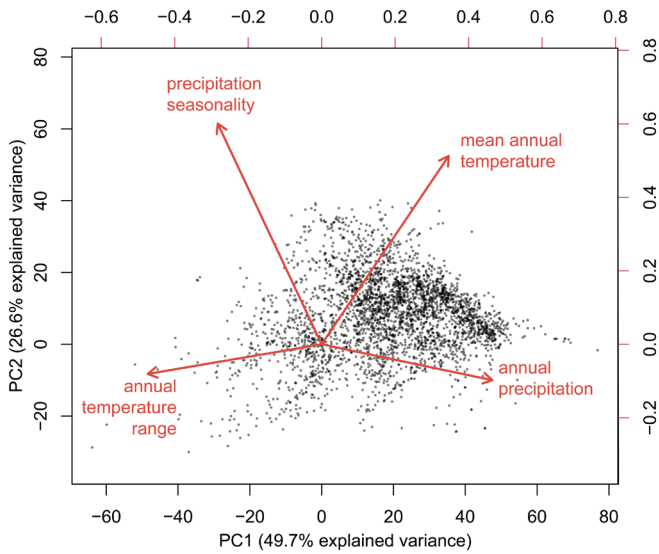


Figure 1. Biplot on the first two axes of the phylogeny-informed principal component analysis conducted with four climatic variables. Each dot represents the mean value of mean annual temperature (°C), annual temperature range (°C), annual precipitation (mm) and precipitation seasonality (coefficient of variation) in the distribution area of one of the 3335 species (3091 frogs and 244 salamanders) in our dataset. PC1 and PC2 together explain 76.2% of the total variance.

to be uninformative concerning the ‘climate hypothesis’ and ‘climate and microhabitat hypothesis’ (i.e. PC2 did not significantly correlate to body mass in frogs and salamanders; Supporting information), we hereafter report only analyses that make use of PC1 values. For analogous analyses on PC2, refer to the Supporting information.

Statistical analysis

We tested our three hypotheses for frogs and salamanders, separately, in a cross-species approach. To account for phylogenetic non-independence, we applied phylogenetic generalized least squares (PGLS) models. Therefore, we used the tree of Jetz and Pyron (2018) and pruned it to the species sample under study. All statistical analyses were done in R ver. 4.4.0 (www.r-project.org).

Tests on assumptions underlying the three hypotheses

To test whether species of reproductive modes Aq-L, Ter-L and Ter-D differed in their mean body mass and in the mean climate in their distribution areas, respectively (‘climate hypothesis’ and ‘climate and microhabitat hypothesis’; Fig. 2a), we conducted phylogeny-informed ANOVAs (pANOVAs) with reproductive mode as a predictor of body mass, and of PC1 values, respectively, following Revell and Harmon (2022). For phylogenetic correction, we applied Pagel’s λ (Pagel 1999) by converting the phylogenetic tree into a correlation structure using the function *corPagel* (‘ape’ package; Paradis et al. 2004). Then, we fitted a linear PGLS model using the function *gls* (‘nlme’ package; Pinheiro et al. 2023)

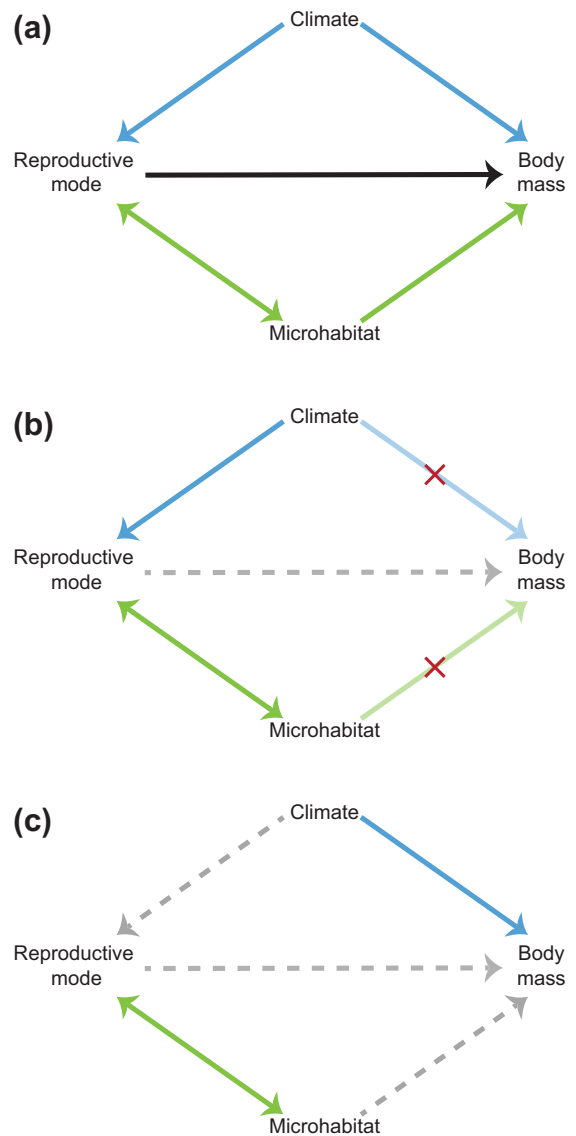


Figure 2. Graphical illustrations of our three hypotheses and the approach used for their test. Arrows indicate relations between species’ traits and presumed directions of effects. Solid arrow: the relation is confirmed statistically; dashed arrows: it is not confirmed; arrows with red crosses: the relation was controlled for (‘climate-’, ‘microhabitat-’, ‘climate- and microhabitat-corrected’ body masses). (a) Expected relations between reproductive mode and body mass, under the ‘climate hypothesis’ (blue), the ‘microhabitat hypothesis’ (green) and the ‘climate and microhabitat hypothesis’. (b) When controlling for the effect of climate, microhabitat use, or both on body mass, the indirect pathways that connect reproductive mode and body mass via climate and/or microhabitat use are closed. In this case, we expect that reproductive mode and body mass are no longer related, and thus the observed relation between reproductive mode and body mass in (a) is not causal, but an indirect consequence, as climate and/or microhabitat use link both traits. (c) In salamanders, we did not observe complete pathways that connect reproductive mode and body mass via climate and microhabitat use (Supporting information). Thus, as the relation between reproductive mode and body mass is absent in this order, we used salamanders as a ‘control group’ for checking our approach on testing the ‘climate hypothesis’, ‘microhabitat hypothesis’ and ‘climate and microhabitat hypothesis’.

to which we passed the correlation structure and then applied the *anova* function.

To test a relation between the reproductive mode and the microhabitat used by a species ('microhabitat hypothesis', 'climate and microhabitat hypothesis'; Fig. 2a), we fitted models of correlated discrete character evolution, in which microhabitat and reproductive mode evolved dependently or independently from each other (Pagel 1994; *fitPagel* function, 'phytools' package, Revell 2012), following the instructions of Revell and Harmon (2022). As these models required binary traits, we pooled ground-dwelling and arboreal species into the category 'water-independent' microhabitat, and species of modes Ter-L and Ter-D into the category 'terrestrial egg layers', as an association between the use of water-independent microhabitats and terrestrial egg laying was observed (Liedtke et al. 2017, Bonett et al. 2022). We analogously fitted evolutionary models using the microhabitat categories 'arboreal' and 'non-arboreal' (water-dependent plus ground-dwelling species), because we expected an arboreal microhabitat to affect species' body mass (Wygoda 1984, Young et al. 2005, Astley et al. 2015, Bijma et al. 2016). We assumed an association between the reproductive mode and the microhabitat used by a species, when the best model identified from its AIC value (Burnham and Anderson 2002) suggested a dependent evolution of both.

To test whether species living in warmer, more humid and less seasonal climates had on average smaller body masses than species living in cooler, drier and more seasonal climates ('climate hypothesis', 'climate and microhabitat hypothesis'; Fig. 2a), we first ran a linear PGLS model (as described above for the pANOVAs) on species' PC1 values, but significant Harvey–Collier tests (Harvey and Collier 1977; *harvtest* function, 'lmtree' package) strongly suggested non-linear relations (frogs: $t=4.06$; $p < 0.001$; salamanders: $t=8.62$, $p < 0.001$). We thus proceeded with a non-parametric approach on a potential climatic effect on species' body mass. We first binned the species' PC1 values after identifying the optimal number of bins with Knuth's algorithm (Knuth 2019; 'rebmix' package; Nagode 2015, Panić et al. 2020). We next calculated the median of the species' body masses for each PC1 bin. With these median body masses and the rank values of the respective PC1 bins, we finally conducted Spearman's rank correlation analyses. To assess the robustness of these correlations, we repeated this analysis using two other numbers of bins (i.e. the optimal number of bins \pm 50% of this number) for PC1 (Supporting information).

To test whether body mass was on average smaller in arboreal species than in water-dependent and ground-dwelling species ('microhabitat hypothesis'; Fig. 2a), we ran a pANOVA on species' body masses and microhabitat use (water-dependent, ground-dwelling or arboreal).

Test of the three hypotheses

To test the 'climate hypothesis', 'microhabitat hypothesis' and 'climate and microhabitat hypothesis', respectively, we assessed whether body masses differed on average between species of modes Aq-L, Ter-L and Ter-D, after having removed before a potential effect of climate, microhabitat or both, on their body

mass (Fig. 2b). As species' microhabitat use and climate in the distribution area (PC1 values) were highly correlated in frogs (pANOVA, $F=30.63$, $df=3088$, $p < 0.001$), and the relation between climate and body mass was not linear (above), we refrained from applying multivariate PGLS models that use climate, microhabitat or both as predictors of body mass. Instead, we calculated for each species a 'climate-corrected', 'microhabitat-corrected' and 'climate- and microhabitat-corrected' body mass. This approach accounts for both the non-linear relation between climate and body mass and the correlation between microhabitat use and climate. As a measure of a species' 'climate-corrected' body mass (of a species 'microhabitat-corrected' body mass), we calculated the deviation of a species' body mass from the median body mass of all species found in the respective PC1 bin (microhabitat category). To establish this deviation for each species, we subtracted the log₁₀-transformed median body mass of the PC1 bin (microhabitat category) a species fell into from the species' log₁₀-transformed body mass.

To establish a 'climate- and microhabitat-corrected' body mass, we took the 'climate-corrected' body mass calculated for each species and then calculated from these values the median 'climate-corrected' body mass of all water-dependent, ground-dwelling and arboreal species, respectively. Then, we subtracted the respective microhabitat-specific median body mass from the 'climate-corrected' body mass for each species. We made our test of the 'climate and microhabitat hypothesis' more robust by evaluating a second set of 'climate- and microhabitat-corrected' body masses. We calculated it by starting with the 'microhabitat-corrected' body masses that we corrected for climate.

We preferred the median body mass over the mean body mass for removing a potential effect of climate and/or microhabitat on body mass, because body size distributions are often skewed even after log transformation, and thus the median captures their central tendency better than the mean (Meiri and Thomas 2007, Slavenko and Meiri 2015, Amado et al. 2019, 2021, Servino et al. 2022).

Finally, to test our hypotheses, we ran pANOVAs on the species' reproductive modes Aq-L, Ter-L and Ter-D with their 'climate-corrected' body masses ('climate hypothesis'), 'microhabitat-corrected' body masses ('microhabitat hypothesis') and 'climate- and microhabitat-corrected' body masses ('climate and microhabitat hypothesis'). Our hypotheses were supported when differences in 'climate-corrected' body masses, 'microhabitat-corrected' body masses or 'climate- and microhabitat-corrected' body masses between terrestrial egg layers (Ter-L and Ter-D) and aquatic egg layers (Aq-L) were not significant (Fig. 2b).

Results

Tests on assumptions underlying the three hypotheses

In frogs, aquatic egg layers (Aq-L) had significantly higher average body masses than biphasic and direct developing terrestrial layers (Ter-L and Ter-D), whereas the difference in mean masses within the terrestrial layers was not significant (Table 1). In salamanders, mean body masses did not differ

Table 1. Results of phylogeny-informed ANOVAs (pANOVA) and pairwise (post hoc) t-tests conducted with species' body mass (with and without correction for climate, microhabitat or both) and three reproductive modes (Aq-L, Ter-L and Ter-D) in frogs. The 'climate-corrected' and 'climate- and microhabitat-corrected' masses use 21 bins on species' PC1 (climate) values. For 'microhabitat-corrected' body masses, we distinguished between water-dependent, ground-dwelling and arboreal microhabitats. F: F-value; t: t-value of post hoc tests; p: p-value. Significant p-values in bold. Aq-L: aquatic eggs and biphasic, larval development; Ter-L: terrestrial eggs and biphasic, larval development; Ter-D: terrestrial eggs and direct development without a larval stage.

	Body mass, $\lambda=0.91$, df=3088			Climate-corrected mass, $\lambda=0.90$, df=3088			Microhabitat-corrected mass, $\lambda=0.90$, df=3088			Climate- and microhabitat-corrected mass, $\lambda=0.89$, df=3088		
	F	t	p	F	t	p	F	t	p	F	t	p
Aq-L versus Ter-L versus Ter-D	13.03	–	< 0.001	5.62	–	0.004	4.96	–	0.007	2.47	–	0.085
Aq-L versus Ter-L	–	–4.34	< 0.001	–	–2.73	0.006	–	–2.71	0.007	–	–1.80	0.072
Aq-L versus Ter-D	–	–3.88	< 0.001	–	–2.70	0.007	–	–2.36	0.018	–	–1.80	0.073
Ter-L versus Ter-D	–	–1.80	0.072	–	–1.38	0.169	–	–1.04	0.298	–	–0.92	0.355

among species of modes Aq-L, Ter-L and Ter-D (pANOVA, $F=1.30$, $df=241$, $p=0.273$). The phylogenetic signal was high and significant in frogs ($\lambda=0.91$) and salamanders ($\lambda=0.98$). As the 'climate hypothesis', 'microhabitat hypothesis' and 'climate and microhabitat hypothesis' assumed a relation between reproductive mode and body mass, we conducted our test of these hypotheses only with frogs. Further results on salamanders are in the Supporting information.

PC1 values of frog species differed significantly between modes Aq-L, Ter-L and Ter-D. The pANOVA suggested that species of mode Aq-L have on average the lowest, of mode Ter-L intermediate and of mode Ter-D the highest PC1 values (Table 2), indicating that terrestrial egg layers live in warmer, more humid and less seasonal climates than aquatic layers.

Our evolutionary models suggested an association between terrestrial egg deposition and the use of water-independent or arboreal microhabitats for frogs. The best models identified from AIC values assumed a dependent evolution of microhabitat and reproductive mode in species, irrespective of which of the two categorizations on microhabitats (water-dependent versus water-independent or arboreal versus non-arboreal) we had applied (Supporting Information). In these models, net transition rates from a use of water-dependent to water-independent, and from a use of non-arboreal to arboreal microhabitats were higher in terrestrial egg layers (Ter-L and Ter-D) than in aquatic layers (Aq-L). The transition rates

between a terrestrial and aquatic egg deposition were independent of the microhabitats used by species (Fig. 3).

Species occurring in warmer, more humid and less seasonal climates had on average smaller body masses than species in cooler, drier and more seasonal climates (Fig. 4). The PGLS model indicated a significant decrease in body mass with increasing PC1 values ($\beta=-0.002$, $p=0.014$, $\lambda=0.91$), but the Harvey–Collier test rejected their linear relation. The median body masses of the species pooled in 21 bins (that Knuth's algorithm identified as optimal for PC1 values) correlated highly and negatively with the bins' median PC1 values (Spearman's rank correlation, $\rho=-0.88$, $p < 0.001$) and thus corroborated the PGLS model. This correlation was robust against the use of different numbers of PC1 bins (Supporting information).

The pANOVA ($F=17.55$, $df=3088$, $p < 0.001$, $\lambda=0.91$) indicated that arboreal frogs had significantly smaller average body masses than water-dependent ($t=5.13$, $p < 0.001$) and ground-dwelling species ($t=5.57$, $p < 0.001$).

Test of the three hypotheses

Contrary to our 'climate hypothesis' and 'microhabitat hypothesis', the pANOVAs revealed that frogs of mode Aq-L had significantly higher average 'climate-corrected' and 'microhabitat-corrected' body masses than frogs of modes Ter-L and Ter-D, with the biphasic and direct developing terrestrial egg layers not differing significantly from each other (Table 1). However, consistent with the 'climate and microhabitat hypothesis', the pANOVA indicated no significant differences in average 'climate- and microhabitat-corrected' body masses among species of modes Aq-L, Ter-L and Ter-D (Table 1), regardless of whether we first corrected body masses for climate and then for microhabitat or vice versa (Supporting information). Thus, climatic conditions experienced by frogs and their microhabitat use can only together explain body mass differences between terrestrial (Ter-L and Ter-D) and aquatic egg layers (Aq-L). The support of the 'climate-microhabitat hypothesis' and the rejection of the 'climate hypothesis' were robust against the use of different numbers of PC1 bins applied to calculate the 'climate- and microhabitat-corrected' and the 'climate-corrected' body masses of species (Supporting information).

Table 2. Results of phylogeny-informed ANOVAs (pANOVA) and pairwise (post hoc) t-tests on species' PC1 values and reproductive modes (Aq-L, Ter-L and Ter-D) in frogs. The phylogenetic signal in the pANOVA was $\lambda=0.91$. n: sample size; F: F-value of the pANOVA; t: t-value of phylogeny-informed post hoc tests; p: p-value. Significant p-values in bold. Aq-L: aquatic eggs and biphasic, larval development; Ter-L: terrestrial eggs and biphasic, larval development; Ter-D: terrestrial eggs and direct development without a larval stage.

	n	F	t	p
Aq-L versus Ter-L vs. Ter-D	3091	15.47	–	< 0.001
Aq-L versus Ter-L	2228	–	4.71	< 0.001
Aq-L versus Ter-D	2385	–	4.27	< 0.001
Ter-L versus Ter-D	1569	–	2.00	0.045

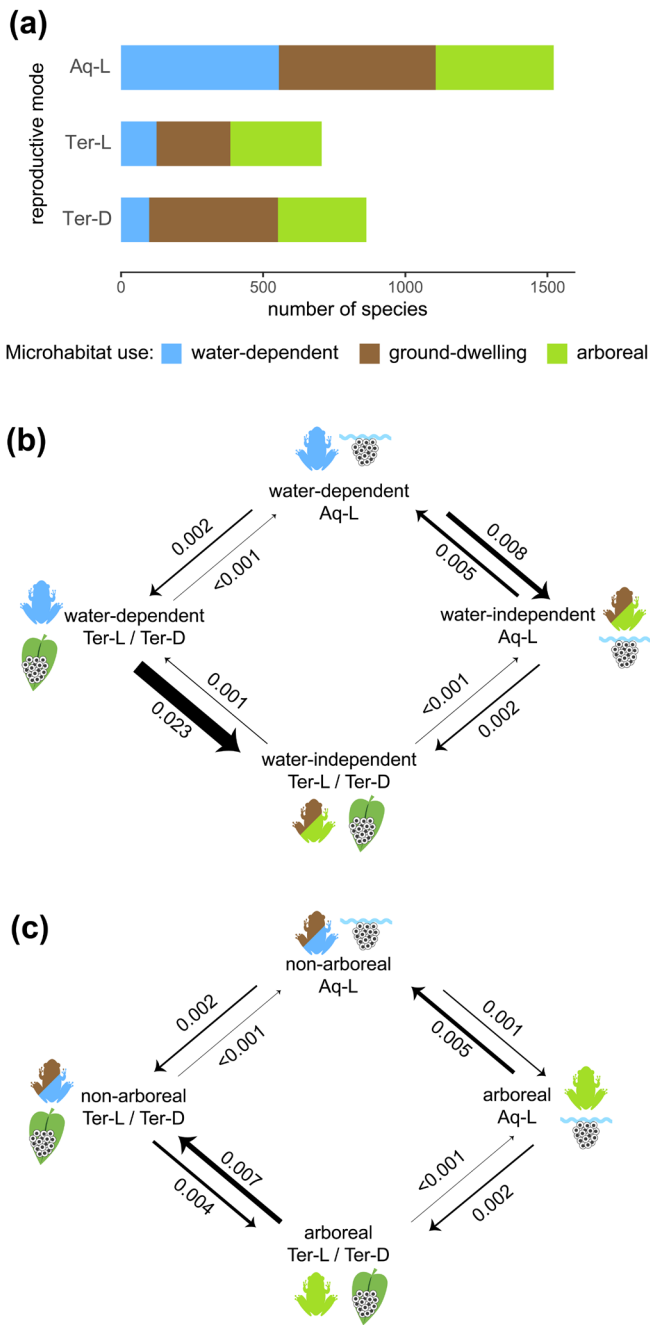


Figure 3. Results on the association of reproductive mode and microhabitat use in frogs. (a) Numbers of frog species analyzed using a water-dependent (blue), ground-dwelling (brown) or arboreal (green) microhabitat and grouped by reproductive modes (Aq-L, Ter-L and Ter-D). Best models on the evolution of microhabitat and reproductive mode in frogs, when categorizing the microhabitat used by species as water-dependent versus water-independent (b), or as arboreal versus non-arboreal (c). Numbers give the estimated transition rates. Arrow widths illustrate the values of transition rates (not to scale). Pictograms were drawn by the first author.

Discussion

In this study, we showed that warm, humid, unseasonal climates allow for terrestrial egg deposition and small body masses in frogs, whereas cold, dry and seasonal climates constrain frogs to aquatic egg deposition and large masses. Further, terrestrial egg laying facilitates the use of an arboreal microhabitat, which in turn favors small body masses. These patterns explained why terrestrial egg laying frogs were on average smaller than their aquatic egg laying counterparts. Reproductive mode and body mass were unrelated in salamanders, in which we only found significant associations between reproductive mode and microhabitat use and between climate and body mass.

Reproductive modes and body mass

We showed that aquatic egg layers (Aq-L) were on average significantly heavier than terrestrial layers (Ter-L and Ter-D) in frogs. Frog species of reproductive modes Ter-L and Ter-D did not differ significantly in their body mass. These average mass differences in frogs indicated that small body sizes are linked to terrestrial egg deposition in this order, but not to direct development, as had been suggested before (Hanken and Wake 1993, Estrada and Hedges 1996, Rittmeyer et al. 2012, Oliver et al. 2017). Conversely, for salamanders, we did not find any relation between body mass and modes Aq-L, Ter-L and Ter-D. In salamanders, however, a strong phylogenetic pattern in species' reproductive mode and body mass might hamper any test. For example, direct development (Ter-D) is found only in the family Plethodontidae, which comprises many small species (Bruce 2003, Wells 2007, Pough et al. 2015; but see e.g. *Pseudoeurycea belli*). Thus, it is difficult to disentangle whether the association of small body size and direct development is a phylogenetic or an ecological effect. As all Plethodontidae are lungless and rely completely on cutaneous respiration, small body sizes could be favored in the entire family as they increase a species' surface-to-volume ratio and respiration rate. Consequently, small body sizes of species might not be related to direct development (Wells 2007).

Differences between reproductive modes in frogs

We found that terrestrial egg laying frogs are largely restricted to warm and humid climates, which had been explained by terrestrial eggs needing heat and moisture to develop and avoid desiccation (Gomez-Mestre et al. 2012, Lion et al. 2019). In our analysis, the climate within the species' distribution areas was represented by PC1 describing a gradient from cool, dry and seasonal climates (low values) to warm, humid and unseasonal climates (high values, Fig. 1). Not only did terrestrial egg layers (Ter-L and Ter-D) have significantly higher PC1 values than aquatic egg layers (Aq-L) as expected from the 'climate hypothesis', but also direct developers (Ter-D) had higher values than biphasic species (Aq-L and Ter-L). The latter may result from longer incubation times in direct developing eggs than in eggs of biphasic species (Bradford 1990). A longer incubation time in direct developing eggs

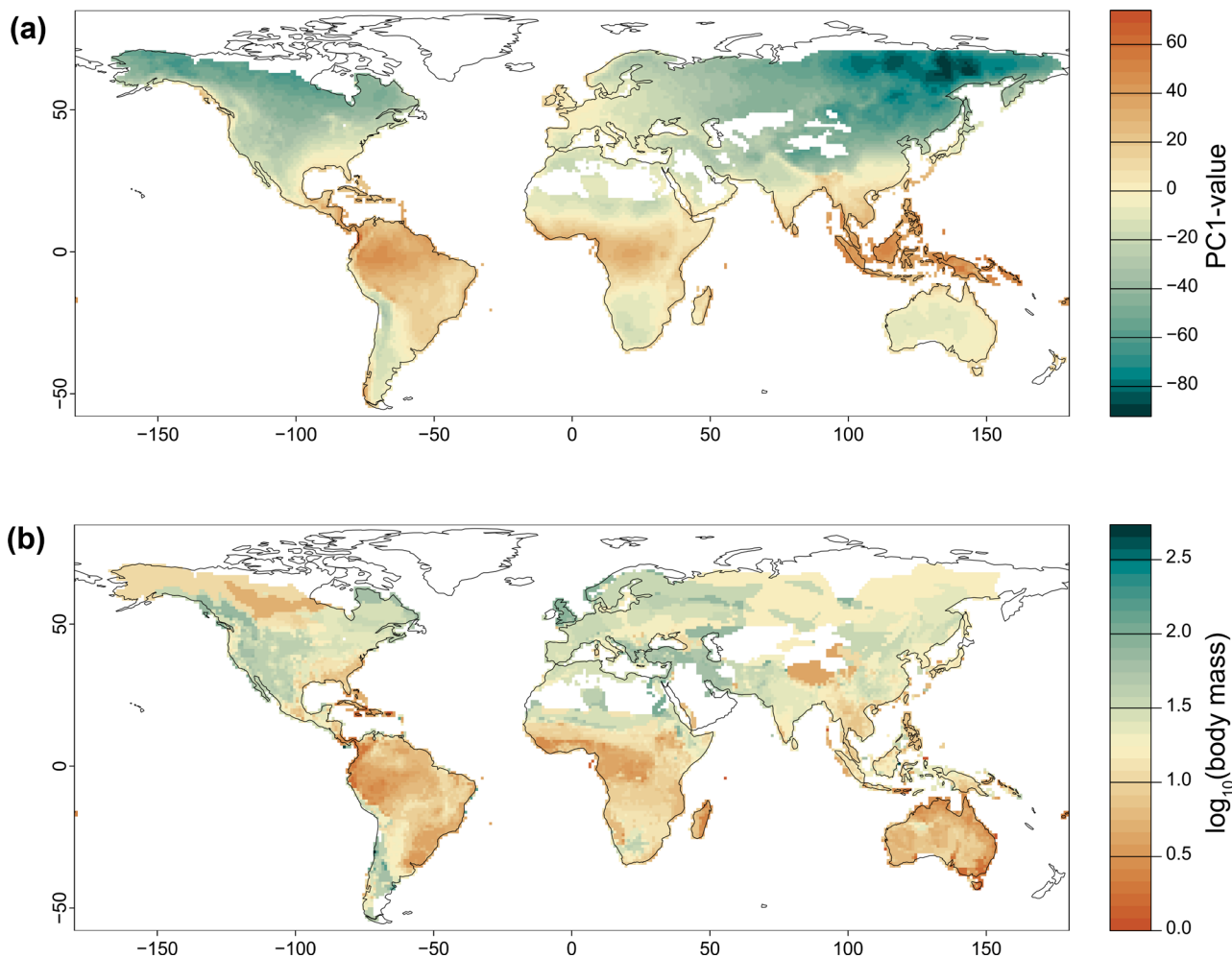


Figure 4. Global patterns of climate and body mass in frogs. (a) Geographic distribution of PC1 values established from our phylogeny-informed principal component analysis (pPCA) that was conducted with data on all 3335 amphibian species in our dataset. Large PC1 values indicate a warm and humid climate with a low seasonality across the year (high mean annual temperature, high annual precipitation, low annual temperature range and low precipitation seasonality) and small values a cool, dry and more seasonal climate. In each raster cell (resolution of 60 arcminutes), in which at least one amphibian species occurs, projections of mean values of the four climatic variables onto PC1 are shown. (b) Median log₁₀-transformed body mass of the frog species found within each raster cell. This plot is based on all 3091 frog species in our dataset.

could increase their risk of desiccation and restrict direct developers to more humid climates than biphasic species. Parental care (i.e. egg attendance) and the thickness of egg capsules could additionally affect the desiccation risk of eggs (Pough et al. 2015). Further studies should explore the thermal and hydric needs of egg development in direct developers and their potential interrelations with incubation time, parental care, egg morphology and the geographic distribution of species.

For the ‘microhabitat hypothesis’, we showed that terrestrial egg deposition and the use of water-independent and arboreal microhabitats have evolved jointly in frogs. Among terrestrial egg layers, we found higher evolutionary transition rates from water-dependent to water-independent and from non-arboreal to arboreal microhabitats than among aquatic layers (Fig. 3). This suggests that terrestrial egg deposition facilitates the use of water-independent microhabitats by

adults which goes along with physiological and behavioral adaptations that reduce evaporative water loss, e.g. the wiping of lipid secretions onto the skin (Withers et al. 1984, Lillywhite 2006). Conversely, the transition rates between terrestrial and aquatic egg deposition were independent of microhabitat use (Fig. 3), which suggests that the microhabitat used by adults is not the driver of the evolutionary transition from aquatic to terrestrial egg deposition. It might have been more likely driven by high offspring predation and high male–male competition in aquatic reproductive habitats (Touchon and Worley 2015, Zamudio et al. 2016, de Sá et al. 2020).

Patterns in body mass of frogs

We confirmed that body masses of frogs are related to climate, as is assumed by the ‘climate hypothesis’ (Fig. 4). Body mass decreased with increasing annual temperatures, annual

precipitation and decreasing seasonality of climates (PC1 values). This finding is consistent with the energy–water conservation hypothesis (Olalla-Tárraga et al. 2009); in cool and dry climates, the low surface-to-volume ratio of large amphibians is crucial to retain heat and moisture, whereas this constraint to body mass is released in warm and humid regions. In line with our findings, Moldowan et al. (2022) reported that an increase in ambient temperature (from global change) led to a decrease in body size in a spotted salamander *Ambystoma maculatum* population. We further found that, consistent with the ‘microhabitat hypothesis’, body masses of arboreal frogs were significantly smaller than masses of water-dependent and ground-dwelling species, suggesting that body mass is constrained by arboreal locomotion (Astley et al. 2015, Bijma et al. 2016). In summary, all assumptions underlying our hypotheses were met in frogs, as both small body masses and terrestrial egg deposition coincided with an arboreal microhabitat use and warm, humid and relatively unseasonal climates.

When testing each of our three hypotheses with frogs, we found that differences in body mass of terrestrial (Ter-L and Ter-D) and aquatic egg layers (Aq-L) were neither solely explained by differences in climate (‘climate hypothesis’) nor by differences in microhabitats use (‘microhabitat hypothesis’), but that they were well explained by both together (‘climate and microhabitat hypothesis’) (Table 1). On the one hand, the rejection of both the ‘climate hypothesis’ and ‘microhabitat hypothesis’ could indicate limitations of our study. First, the statistical power of our tests might increase from more accurate information on the climatic conditions experienced by species (e.g. the mean value across its distribution area might not capture the local climatic conditions in the areas in which a species is present) or from a finer resolution on microhabitat use (which, however, would decrease sample sizes). Second, although our dataset comprised 3091 frog species from 53 out of all 58 families, it still covered only approximately 34.7% of all frog species known (following Frost 2024). On the other hand, a joint effect of climate and microhabitat use reflects that species living under the same global climatic conditions (i.e. have the same average climatic conditions in their distribution area) can experience different local climatic conditions (microclimates) as they occur in different microhabitats (Gouveia and Correia 2016).

Body mass, reproductive modes, climate and microhabitat in salamanders

That we did not find body mass differences between salamanders of reproductive modes Aq-L, Ter-L and Ter-D (discussed above) enables us to check our overall approach on testing the three hypotheses and to evaluate our results on frogs (Fig. 2). In salamanders, climate did not correlate to reproductive mode, but to body mass, whereas microhabitat use was associated with reproductive mode, but not with body mass (Supporting information). Therefore, reproductive mode could not be linked indirectly to body mass through climate and/or microhabitat use in salamanders (Fig. 2c); i.e. the assumptions of our hypotheses were not met. Following

this reasoning, in salamanders, we would not expect any relation between reproductive mode and body mass, because the ‘climate hypothesis’, ‘microhabitat hypothesis’ and ‘climate and microhabitat hypothesis’ suppose that such a link must be only indirect via climate, microhabitat use or both. Thus, if we had found a link between reproductive mode and body mass in salamanders, this would have evidenced that this link is independent of climate and microhabitat use and would have disproved the reasoning of our ‘climate hypothesis’, ‘microhabitat hypothesis’ and ‘climate-microhabitat hypothesis’. On the one hand, the absence of a difference in body mass between terrestrial and aquatic egg laying salamander species emphasizes that reproductive mode and body mass are not linked directly. On the other hand, our sample on salamanders consisted of only 244 species (29.5% of all species known; Frost 2024). Thus, our analysis might have lacked the statistical power to detect significant associations and should be verified with a larger dataset. Further, the 244 species studied did not cover the complete distribution area of the order (Supporting information). All this might question whether our results are valid for salamanders in general. Nevertheless, we found a significant decrease in body mass with increasing temperature, precipitation and decreasing seasonality (PC1 values) in both frogs and salamanders (Supporting information). Conversely, previous studies reported either no correlation between body size and climate in salamanders (Johnson et al. 2023) or opposite correlations in salamanders and frogs (Slavenko and Meiri 2015). As these studies used climatic variables as independent predictors, our results suggest that our multivariate approach to model climate (pPCA) is more appropriate to infer its effect on amphibian body mass as it takes into consideration interrelations of temperature, precipitation and seasonality.

Conclusions

We demonstrated in our study that the thermal and hydric needs of adults and eggs determine the geographical distributions of body mass and reproductive modes across amphibian species. In line with the energy-water conservation hypothesis (Olalla-Tárraga et al. 2009), the frogs and salamanders studied here were on average smaller in regions of high temperature, high precipitation and low seasonality (high PC1 values) than in regions of low temperatures, low precipitation and high seasonality. In frogs, biphasic and direct developing terrestrial layers occurred only in such warm, humid and unseasonal regions, as their eggs need heat and moisture to develop (Lion et al. 2019). Further, terrestrial egg laying was common among frog and salamander species that use water-independent and arboreal microhabitats, in which adult individuals often show adaptations to reduce evaporative water loss (Lillywhite 2006, Giacometti and Tattersall 2025). These adaptations allow arboreal frogs to have smaller average body masses than water-dependent species. All this shows that the respective patterns in body mass and reproductive mode in relation to climate and microhabitat use are correlated and explain why

terrestrial egg laying frogs were on average smaller than aquatic egg layers. In salamanders, however, body mass was unrelated to reproductive mode and microhabitat use, and climate did not constrain their reproductive mode, but these results might not be well-constrained as our sample on salamander species was small (244 out of 827; Frost 2024) and did not cover their complete geographical distribution. Our study further suggests that other reproductive and life history traits will also vary geographically in frogs and salamanders, as they correlate with body mass (Hallmann and Griebeler 2020, Cejp and Griebeler 2024). For example, small, terrestrial egg layers produce rather few and relatively large eggs, while large, aquatic egg layers produce many, relatively small eggs (Gould et al. 2022). This could reflect that the minimum egg size is larger on land than in the water due to a higher desiccation risk of eggs on land than in the water. Terrestrial egg deposition is also associated with many derived traits such as diverse types of parental care, or the elimination of the larval stage through direct development (Furness et al. 2022). All this together indicates that abiotic conditions experienced by species can constrain or drive the evolution of life histories and reproductive behaviors (Pereira et al. 2017). Thus, the geographic distribution of climate sets the evolutionary framework in amphibians. Warm, humid, unseasonal regions allow for a considerable diversity in amphibian reproduction, microhabitat use and life histories, whereas in cold, dry and seasonal regions this diversity is constrained. Ongoing climate change, which threatens amphibians seriously (Foden et al. 2013), therefore might impact their evolution differently across the globe.

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Author contributions

Benjamin Cejp: Conceptualization (equal); Data curation (lead); Formal analysis (lead); Writing – original draft (equal); Writing – review and editing (equal). **Eva Maria Griebeler:** Conceptualization (equal); Supervision (lead); Writing – original draft (equal); Writing – review and editing (equal).

Data availability statement

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.9cnp5hqz0> (Cejp and Griebeler 2025).

Supporting information

The Supporting information associated with this article is available with the online version.

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