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Research article

Tracking phenological distributions and interaction potential across life stages

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Climate change is shifting the phenological timing, duration, and temporal overlap of interacting species in natural communities, reshaping temporal interaction networks worldwide. Despite much recent progress in documenting these phenological shifts, little is known about how the phenologies of species interactions are tracked across different life history stages. Here we analyze four key phenological traits and the pairwise interaction potential of nine amphibian species for the adult (calling/breeding) and subsequent larval (tadpole) stage at eight different sites over six years. We found few strong correlations among phenological traits within species, but the strength of these correlations varied across species. As a consequence, phenological trait combinations of both stages varied substantially across species without clear signs of multidimensional clustering, indicating a distinct and diverse range of species-specific phenological strategies. Despite this considerable variation in the phenologies across species, the temporal overlap between species was largely preserved through the two life history stages. Further, we also detected significant correlations among the duration and temporal overlap of interactions with other species across stages in five species, demonstrating that temporal patterns of species interactions are mirrored across life history stages. For these species, these results indicate a strong tracking of phenologies and species interactions across life history stages even in species with complex life cycles where stages occupy completely different environments. This suggests that phenological shifts in one stage can impact the temporal dynamics and structure of interaction networks across developmental stages.

Keywords: amphibians, community structure, competition, ontogeny, phenological synchrony

Introduction

Global climate change is altering the timing and duration of life history events (phenology) across biomes (Walther 2002, Parmesan and Yohe 2003, Root et al. 2003, Burkle et al. 2013). While much progress has been made in documenting these

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phenological shifts, previous studies typically focus on a single life stage. Consequently, little is known about how climate-driven phenological shifts in one life history stage are linked to the phenologies of subsequent life history stages (Haefner and Edson 1984, Moll and Brown 2008, Yang and Rudolf 2010). Even less is known about how the timing and duration of interspecific interactions are related across life stages. Yet, phenological shifts in one stage could propagate across stages leading to a substantial reshuffling of the entire interaction network (Clausen and Clausen 2013, Carter et al. 2018, Rudolf 2018) and thereby influence critical ecosystem processes (Suttle et al. 2007, Both et al. 2009, Abraham et al. 2010, Visser and Gienapp 2019). In contrast, if the timing of interactions within life stages are largely uncorrelated, shifts in one stage would have a relatively smaller and more localized effect on temporal community structure. Studying how phenologies and the temporal coordination of species interactions are linked across life stages is therefore essential to fully understanding how any phenological shift affects populations and communities.

How phenological patterns are related across stages likely depends on several factors. Changes in environmental conditions typically alter the phenology (e.g. first appearance, duration, and/or peak abundance) of individuals (Blankenhorn 1972, Kudo and Ida 2013, Post 2019, Visser and Gienapp 2019), and these changes may cause shifts in phenology and demographic rates of individuals in a subsequent stage (Moll and Brown 2008, Miller et al. 2018). In the simplest case, we might expect a phenological shift similar in direction and magnitude to that of the previous stage. For instance, earlier hatching likely results in earlier metamorphosis and earlier peak breeding may result in earlier peak offspring abundance, indicating a 'tracking' of phenological shifts across stages. However, each stage is also affected by the environmental conditions it currently experiences. If conditions change differently across stages or if phenological shifts in one stage alter conditions individuals experience in subsequent stages, this could weaken or even counteract signals of phenological tracking across stages (Rasmussen and Rudolf 2015, Carter and Rudolf 2019). For instance, early hatching might not result in earlier timing of metamorphosis if it is also associated with slower developmental rates, perhaps resulting from colder temperatures experienced by early arriving individuals. If such stage specific factors are strong enough, some or most phenological patterns may not be correlated across stages. But given the power of climate change to modify abiotic conditions experienced by stages across habitats, phenological shifts may be tracked across life history stages in species with complex life cycles (Both et al. 2009, Yang 2020).

The tracking of phenologies across stages becomes particularly important in the larger context of species interactions. In many communities, species interact across multiple stages (Moll and Brown 2008, Yang and Rudolf 2010). Phenological shifts can strongly determine the outcome of species interactions, e.g. by changing the temporal overlap of species (Dayton and Fitzgerald 2001, Carter et al. 2018, Rudolf 2018, Post 2019). If shifts in the timing and duration of phenologies are tracked between stages, shifts in the degree of temporal overlap between species may similarly be mirrored. This may be especially likely when it can be beneficial to maintain interaction levels among competitors, predators and prey, or mutualists across stages (Orizaola et al. 2013). Mirroring shifts in temporal overlap may also benefit species that jockey with each other to take advantage of priority effects, since shifting timing as early as possible to reduce competition at the outset of a life history event is a sound strategy for multiple stages (Alford and Wilbur 1985, Rasmussen and Rudolf 2014, Post 2019). It may be also beneficial to mirror shifts in previous stages to maintain favorable or escape unfavorable interactions (Dayton and Fitzgerald 2001, Orizaola et al. 2013, Rasmussen and Rudolf 2016). If this mirroring is beneficial to multiple species in temporally structured communities, we may expect shifts in temporal overlap to be correlated among life history stages. Lack of correlation in temporal overlap between stages would indicate that the nature of the biotic interactions and the composition of interaction networks for each stage have diverged, rendering each stage's phenological responses to shifting biotic factors highly dissimilar. A lack of a correlation would also make it difficult to infer the impact of phenological shifts in single stages on overall community dynamics. However, if interactions are well correlated across stages, we could infer community-wide changes to specific phenological traits, including phenology-mediated interactions, by simply focusing on surveying the earliest and or most easily observable life stages.

Here we analyzed phenological records of two life stages of 12 amphibian species from eight pond communities to determine how phenological patterns at the population and community level are linked across different life history stages. Specifically, we 1) quantified and compared phenological patterns and strategies across species, and 2) asked how timing, duration, and temporal overlap of phenologies are related across adult and tadpole stages within species. Finally, we tested 3) how phenological shifts in species interactions are correlated between life history stages.

Material and methods

Study system

Studying the phenology of amphibian communities has several advantages and permits a highly sensitive and reliable approach to linking phenological distributions to competitive interactions. First, timing and duration of amphibian phenophases (life history stages) respond to tractable climatic cues like rainfall, temperature, and air pressure, but which cues are most important varies across species (Blankenhorn 1972, Pechmann et al. 1989, Kopp and Eterovick 2006, Saenz et al. 2006). Between-year fluctuations in weather thus precipitate some of the strongest species-specific phenological shifts of any taxa (Blaustein et al. 2001, Oseen and Wassersug 2002, Saenz et al. 2006, Parmesan 2007). Secondly, amphibian species exhibit diverse life history strategies, the phenologies of fall and winter-breeding amphibians are distinct from those of summer or spring-breeding species (Saenz et al. 2006, Parmesan 2007, Hocking et al. 2008). Finally, spatial competition among amphibians of different species is known to occur locally in multiple life history stages. Adults calling during the breeding phenophase produce audio interference that can interfere with heterospecifics' search for potential mates (Schwartz 1987). Larvae and adults also compete over common resources such as food and space, yet the two stages experience different selective pressures between their distinct habitats and differ in which season they are most active (Alford and Richards 1999, Dayton and Fitzgerald 2001).

Data collection

We collected data on tadpole abundance and adult calling activity of 12 amphibian species over six years in eight ponds in southeast Texas. We obtained estimates of tadpole abundance from funnel traps that were placed underwater in each pond and checked weekly. Two traps were deployed at each pond for the entire study, regardless of size of pond. Traps were placed in the littoral zone of each pond, where tadpoles tend to concentrate (Porej and Hetherington 2005). The traps were placed in shallow water so that the tops of the traps were exposed out of the water to allow any accidental bycatch species to reach the water surface to breathe. The entrance to the traps were always completely under the water's surface. Abundances of all species were recorded and individuals returned to ponds, so recapturing individuals later was possible. We tracked adult calling activity and estimate abundance from audio recorders installed at each pond that recorded amphibian calling for one minute at six timestamps (21:00, 22:00, 23:00, 00:00, 01:00 and 02:00) each day in accordance with the times when species were actively calling (Bridges et al 2000). Manual processing of audio data involved using a sonogram reference to identify the number of calling species in a 1 min period. Up to five individuals were distinguishable from each minute-long recording, so the maximum number of individuals was bounded at 30, in line with the procedure outlined in Saenz et al. (2006). We summed observations of adults across all six recording times in a day to acquire measurements of total abundance for each day from May 2000 to December 2015. The weekly observations of funnel trap count data for tadpoles spanned May 2001 through December 2006, therefore this range was analyzed for both data types. Using six years of data has been shown to accurately capture typical phenological dynamics (Brown et al. 2016), but long-term trends are out of the question given that perceived declines may represent between-year fluctuations or site-selection bias (Blaustein et al. 1994, Bridges et al. 2000, Fournier et al. 2019). We obtained records of 12 species of amphibians (*Hyla versicolor*, *Hyla cineria*, *Bufo valliceps*, *Bufo woodhouseii*, *Rana catesbeiana*, *Rana clamitans*, *Rana sphenocephala*, *Gastrophryne carolinensis*, *Pseudacris crucifer*, *Pseudacris triseriata*, *Acris crepitans* and *Rana palustris*). However, some rare species (*H. cineria*, *G. carolinensis*, *P. triseriata*, *A. crepitans* and *R. palustris*), with fewer than 15 days of observation across all ponds and years, were not included in our analysis of among-species phenological dynamics. In this community, the average larval duration preceding metamorphosis typically ranges from 20 to 35 days (*B. valliceps, G. carolinensis, H. versicolor*), 55 to 70 days (*A. crepitans*, *H. cinerea*, *P. trisereata, R. sphenocephala*), and 90 days (*P. crucifer, R. clamitans*), with *R. catesbeina* having a duration of 365 days (see Fig. 14 in Saenz 2004). However, tadpole larval period can be strongly influenced by biotic and abiotic factors and thus can be much shorter or longer depending on specific environmental conditions. Climatic metadata, specifically records of temperature, rainfall, and photoperiod length for each pond, could not be included because we did not track among-site abiotic data. Therefore, we could not investigate correlations between phenological shifts in interactions and climatic changes.

The eights ponds are divided equally between two neighboring national forests in southeast Texas, with four located in Stephen F. Austin Experimental Forest (SFA), a disjunct unit of the Angelina National Forest under the control of the Southern Research Station, and four in the Davy Crockett National Forest (DC) (see Fig. 1 of Perez et al. 2021 for a map). Ponds in DC were built in 1992 with surface area ranging from 900 to 2000 m^2 and with a maximum depth of 2.5 m, while SFA ponds were built in 2000 and range in surface area from 500 to 600 m^2 with a maximum depth of 1 m (Saenz et al. 2006). Ponds in both forests support diverse communities, including many aquatic invertebrates, but only the larger DC forest ponds can support fish such as mosquitofish, green sunfish, and largemouth bass. There was not a significant difference in weather conditions among both forest types (temperature: $p = 0.155$, mean ± SEM 19.08 ± 8 C° at DC, 18.09 ± 8 C° at SFA; rainfall: $p = 0.212$, mean ± SEM, 103.8 ± 26 cm $year^{-1}$ at DC, 104.2 ± 29 cm $year^{-1}$ at SFA), nor did these metrics shift significantly between years (temperature: $p = 0.777$, $R^2 = 0.034$, rainfall: $p = 0.401$, $R^2 = 0.013$). Within years, total rainfall levels differed by at most 91 cm between areas (in 2002, SFA saw 141 cm and DC had 50 cm). Thus, we did not include 'forest' as a predictor in our final model (without any loss in model performances). The ponds represented eight independent experimental units because an average distance of 17 km between ponds made the dispersal of juveniles or adults between ponds highly unlikely within a season.

The shape of each species' phenological distribution is highly unique, creating large variation in the potential for between-species interactions (Fig. 1a). Out of nine species with sufficient observations to apply smoothers, six displayed one distinct larval activity peak in the spring or summer (Fig. 1a). We also detected the bimodal life histories of *R. sphenocephala*, *R. catesbeina* and *R. clamitans*, which showed two distinct activity peaks separated from each other in time, with a primary peak in the spring and summer, for the first two, and a secondary peak in the fall for all three. These peaks were preceded by similar adult calling peaks in most species, but *R. catesbeina* and *R. clamitans* demonstrated a singular, broad, and cryptic peak over several spring and summer months,

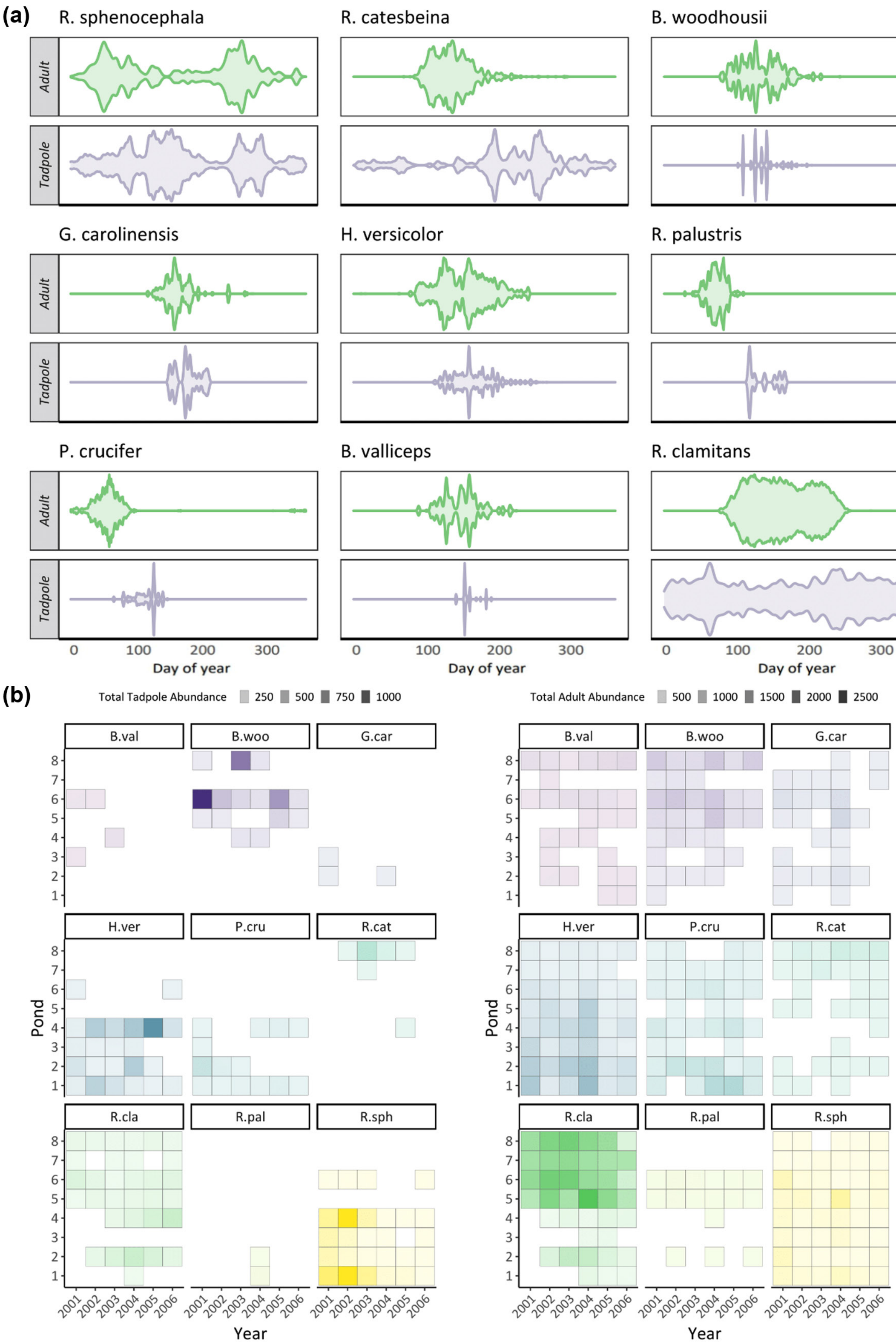

Figure 1. Typical phenological distributions of adult and tadpole members of each of nine species, across six years and eight ponds. (a) Violin plots showing the abundance pooled across all years and ponds within a given life stage of different amphibian species over the course of a year. (b) Presence/absence of tadpoles in each year and pond, shaded by total abundance (total tadpoles captured in traps at each site). Ponds 1–4 belong to DC Forest, while 5–8 belong to SFA Forest.

reflecting a highly flexible life history strategy that can yield multiple cohorts and the possibility of recovering tadpoles throughout the entire year. Larvae of *R. clamitans* and *R. sphenocephala* overwinter in ponds due to relatively warm year-round temperatures (Saenz 2004). Adults of all species do not enter a period of diapause or dormancy during the year, given the mild winters of the study region. Differential preferences in habitat choice among species caused some not to co-occur in the same forests, *H. versicolor* and *R. sphenocephala* tadpoles were common at SFA but rarely observed in DC ponds, while the opposite was true for *R. clamitans* (Fig. 1b). Pond 7 was removed from analysis of phenological traits due to extremely low tadpole abundance over the years.

Response variables

We worked with time series count data of 12 species covering ~six years for each of the eight ponds. Temporal resolution differed between adult calling data and tadpole data, since calling observations were made daily in contrast to the weekly checks of funnel traps. Thus, we converted daily adult calling data to a weekly time scale to match the tadpole sampling scale. We found that weekly resolution still showed the same general patterns and provided sufficient temporal resolution for model-fitting without significantly affecting model diagnostics. We analyzed four metrics of phenological traits for each species and stage in every pond and year where they were observed. These 'single-species metrics' were first day and median day of observation, temporal range, and integrated phenophase area. We used Julian day of the year (1–365) rather than the calendar date to calculate these metrics. This allowed us to directly compare years, ponds, and species on the same temporal scale. First day was defined as the day when an individual of a given species and stage was first observed at a given pond in a year. We chose to use absolute first date rather than another metric (e.g. third day of observation, 5% quantile) since these other metrics seriously truncated our tadpole distributions, many of which were quite narrow and were calculated on a sensitive, weekly grain. Median day represents the day when 50% of the total abundance of each stage of a species was reached in a given year and pond. These two traits captured the timing of phenologies, while the temporal range metric targeted their duration. The temporal range metric (duration) represented the total number of days in a year when at least one individual of a species was observed. For adults, daily observations allowed us to calculate a sensitive days-duration metric. However, tadpoles were sampled on a weekly basis, thus duration measures were in increments of seven days (weekly measures of observation were multiplied by seven). No species in our system can complete development in under 12 days, however, in some extreme cases duration may be underestimated or overestimated. If tadpoles were only observed during one sampling period but not after, we assumed that they were present for 1.5 weeks (10.5 days) since we do not know whether they reached metamorphosis right after the first trap check or right before the second. This assumption did not bias our duration results since all measurements of larval duration were standardized to the same scale. We calculated phenophase area by integrating under a Lowess-smoothed curve ($f = 1/50$, $iter = 3$, $delta = 4$) of the count time series data in a given year and pond. Lowess smoothing was done following Carter et al. (2018) using the *Lowess* and *integrate.xy* functions from 'sfsmisc' in R (Maechler et al. 2016). This metric represents the duration of a phenophase weighted by abundance of individuals in a given life history stage.

Measuring pairwise temporal overlap of species phenologies provides a holistic, community-level assay of phenological interaction potential across years and ponds that is more accurate and powerful than single trait metrics to measure the duration of species' co-occurrence (Carter et al. 2018, Post 2019). We calculated the area of temporal overlap between Lowess-smoothed phenological curves of all possible species-pairs for each pond and year and derived a metric, the proportional overlap, for both species in each pair. Proportional overlap is calculated as the overlap area divided by total the area under the phenology curve of a given focal species ($A_{overlap}/A_{focal}$) and represents how much of a focal species' overall distribution is accounted for by the area of overlap between both species and fits a zero-one inflated beta distribution. An overlap of 1 means that the entirety of a focal species' distribution overlaps with the other species, often implying that the focal species distribution is small and contained within the other species' distribution. One hundred and sixty-four species pairs showed non-zero temporal overlap with 20 having complete overlap. In 18 of those 164 cases, two species co-occurred on the same day, but those days were not consecutive. The integration function interpreted non-consecutive days of co-occurrence as zero temporal overlap. However, since these species still co-occurred, we did not eliminate these apparent observations of zero overlap from analysis. Additionally, a metric of 'median difference' was calculated to account for differences in the timing of peak abundance between species pairs. For this, the median days of observation for the species in a pair were subtracted and then standardized by the total day range of the focal species.

The phenologies of some species spanned the winter season, December through January, bridging two years. Thus, a year with a cutoff of day 365 did not capture the full phenological distributions of both the tadpoles and adults of these species. We rescaled the data so that the time periods analyzed contained the full distributions of both adults and tadpoles for one cycle. These 'relative years' began with the first date of adults calling and ended either 380 days from that point or on the last day of tadpole observation prior to the onset of a new adult calling period. We only considered instances where both tadpoles and adults of a species were found in a given year. As a result, some species had relative year metrics for the entire year range, while others had only two relative years, each relative year potentially disjunct in time from the other by several years.

The same procedure was used to capture relative interaction envelopes that contained the full distributions of both species in a pair. The left bound of this interaction envelope was set as the first day of adult calling for the earlier-calling species in the pair. The right bound was set as the last day of tadpole observation for the later-hatching species, ending this relative interaction envelope before the initiation of another adult breeding peak for the earlier-calling species in the pair.

Phenological metrics such as duration of phenophase, interaction potential, and median day of tadpole observation were calculated relative to the day of first adult calls. However, as these metrics required the presence of both tadpoles and adults in a given year and pond, sample size was reduced relative to data considering only tadpole interactions: from $n = 129$ to $n = 76$ in the case of single species metrics and from $n = 164$ to $n = 88$ for species pairs.

Single-species metrics

We first examined the factors that drive the differences in phenological distributions among species to understand patterns in phenology between species and stages. To handle unequal variance across species, we fit linear models with generalized least squares (GLS) ('nlme' R package, Pinheiro et al. 2023) to investigate the influence of species identity, site, and year on single species phenological metrics for both tadpoles and adults. We fit separate models for first date, median date, and day range, log-transforming the first date response variable and weighting variance by species identity. We fit a second set of models to combined adult and tadpole data to test for an interaction between species and stage identity on the same single-species metrics. Models and corresponding error structures were selected based on diagnostic residual plots, as well as Cooks-distance measurements, pseudo-R-squared calculations, and AIC comparisons. We used the *Anova* function in 'car' R package (Fox et al. 2022) to determine significance of predictors. Significant predictors would indicate that timing and duration of each stage depends on some combination of differences between sites, years and the inherent life histories of species. The likelihood-ratio test was applied and estimated marginal means (*emmeans* function from 'emmeans' R package, Lenth et al. 2023) were calculated for all models to compare typical timing and duration between species, ponds, and years.

We conducted non-metric dimensional scaling (NMDS) to determine whether species showed distinct phenology strategies. We used the median date, first date, and days duration variables averaged across all ponds and standardized to the (0,1) interval by subtracting the mean of each trait from each individual observation and dividing by the range of the trait. We then applied the *metaMDS* function from the 'vegan' R package (Oksanen et al. 2022) and set it to three dimensions (three dimensions showed the lowest stress measurements) and plotted the coordinates for each species. This cohesive approach combined the information on timing and duration we had on both adults and tadpoles, therefore we expected any clusters to represent overarching differences in phenological strategies for breeding and hatching. We included vector loadings for each trait used in ordination to determine which traits were important to creating phenological differences among species.

Consistencies in phenological patterns across stages

Correlation coefficients between the phenological traits of each stage were calculated using repeated measures correlation coefficients in the 'rmcorr' R package (Bakdash and Marusich 2022) , controlling for the species' identity and using the built-in bootstrapping method to calculate confidence intervals (set to 100 resamples). We used GLMs to test whether adult phenology traits predict tadpole phenology traits, with a given response tadpole metric as dependent variable and same metric for adults as predictor, along with species and pond identity and the breeding period being considered (all predictors were fixed effects). We only included species with at least five non-zero observations in both stages in the same pond and year to acquire power for an interaction in these models: *H. versicolor*, *R. sphenocephala*, *B. woodhousii*, *R. clamitans* and *P. crucifer*. Relative median date, duration, and area for tadpoles were log-transformed to improve model performance, but we did not fit a model to the first day of observation, as the relative first day for adults was always 1 and thus no variability existed in that predictor. Interaction effects between adult metrics and species identity on tadpole metrics were initially included in GLM models but did not significantly determine any metric or help improve model performance and thus were dropped for final analysis. To test whether variation in the timing and duration of adults affects the same phenological traits in tadpoles, we used the *Anova* (type 2) function in 'car' package (Fox et al. 2022) to assess the correlation of phenology metrics between stages. Linear relationships for main effects and species-specific effects between adult and tadpole metrics were calculated and compared in post hoc contrasts using the *emtrends* function from'emmeans' R package (Lenth et al. 2023). A significant correlation between timing or duration of the two stages would indicate that shifts in adult timing and duration are tracked in tadpole phenologies.

Correlations in temporal overlap between species and stages

To determine what factors explain the interaction potential, or temporal overlap, between species within each stage we fit a beta regression to proportional overlap between species pairs. This was done separately for tadpoles and adult stages using the *betareg* function in the 'betareg' R package (Zeileis et al. 2021). Since proportional overlap data contained both zeros and ones , we applied a transformation recommended for zero-one-inflated beta distributions in 'betareg' (Douma and Weedon 2019): $\frac{y(n-1)+.5}{n}$. We did not include year in this model because only six years of data were available and we therefore did not expect fluctuations among years to help explain species interactions. The final model included tadpole (or adult) proportional overlap, the identity of the species pair, and the pond, and the difference between median date of observation for the two species. Including median difference accounted for differences in timing between species. We used the *joint.tests* function to assess the significance of predictors, and calculated marginal means. A model was also fit to combined adult and tadpole data to test for differences in interaction potential based on stage, with the same checking process applied. A significant interaction would indicate marked differentiation in the interactions between species in each stage.

Temporal patterns of interspecific interactions across stages

We modeled how tadpole and adult interaction potential, or temporal overlap, is correlated. We fit a beta regression similar to the one described in section 'Consistencies in phenological patterns across stages' ('betareg' R package Zeilieis et al. 2021) to non-zero observations (with the same transformation from Douma and Weedon (2019) described in section 'Consistencies in phenological patterns across stages') of the 10 species pairs with enough power (at least five observations) for a potential pair-specific relationship between overlap in age classes. We included adult proportional overlap, pair, and site identity as fixed effects. An interaction term between adult overlap and pair identity reduced model performance and did not significantly determine variation in tadpole overlap. Therefore, simple species-pair-specific slopes were calculated between adult and tadpole overlap to approximate the relationship between overlap in stages for each species pair. We used the *lr.test* and *Anova* functions to estimate the significance of model terms and *cplot* ('effects' R package) to plot model predictions. Predicted values were estimated on the scale of the response and compared to raw data. A significant relationship between overlap in the two age classes would indicate that tadpoles track shifts in the interspecific interactions between adults.

Results

Phenological strategies across species

Our multivariate ordination analysis combining both adult and tadpole phenology revealed a diversity of phenological strategies driven by differences in timing and duration (Fig. 2). While our data did not allow a full phylogenetic cluster analysis, a visual inspection of NMDS plot (Fig. 2) showed no clear phylogenetic signal. For instance, the two *Bufo* species clustered tightly, but the four *Rana* species are spread across the NMDS plane. Instead, species identity was a significant predictor for all phenological traits (Table 1). First and median day of species occurance differed significantly across all species in both stages, with the first species appearing in late winter (16

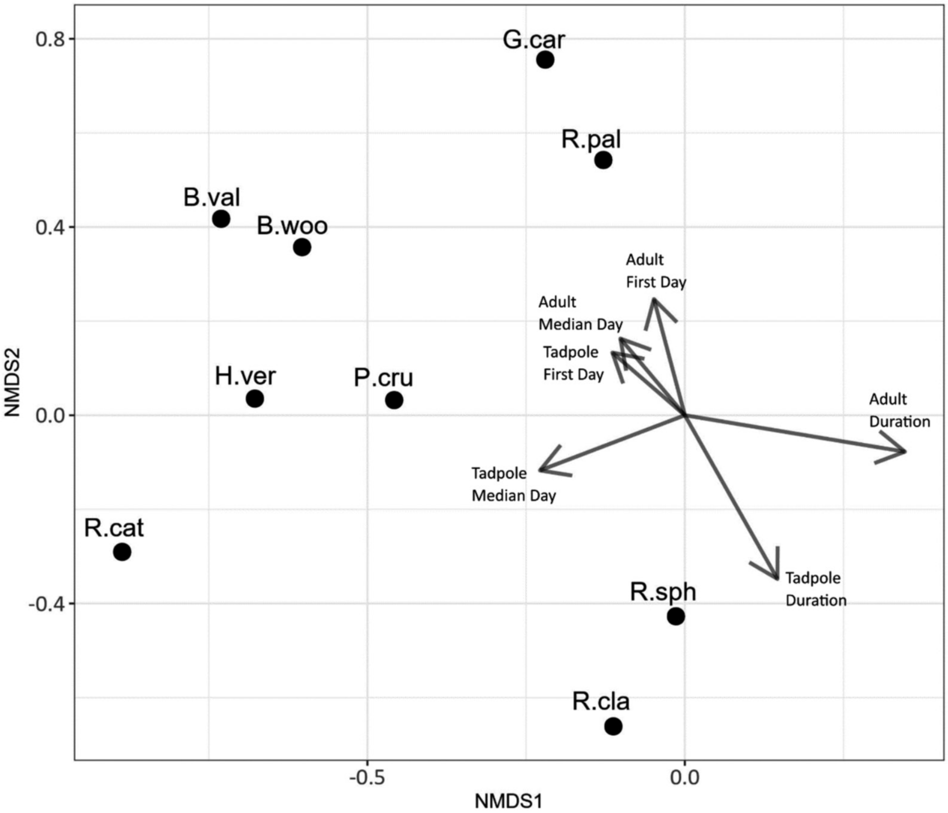

Figure 2. NMDS ordination plot showing species specific combination six phenological metrics across adult and tadpole stage. Points represent loadings for each species, and vector arrows are labeled by variable, with length indicating relative influence over clustering.

Table 1. Results of ANOVA for each of three phenological traits (first and median day of observation, days duration) for both adults and tadpoles. In each of the first three rows, Wald χ^2 statistics are listed for the species, pond, and year model terms. The presence of asterisks denotes the significance of terms in explaining variability (***=significance to the p=0.001 level, ** to the .01 level, and * to the .05 level). On the bottom row, the model R^2 values are listed, using the Nagelkerke metric.

Term	DF	Adult first day	Adult median day	Adult duration	Tadpole first day	Tadpole median day	Tadpole duration
Phenological trait model results							
Species	8	756.66***	844.07***	167.21***	156.88***	216.74***	118.00***
Pond	7	13.18	4.21	26.56***	1.6e+08**	14.02	66.84***
Year	5	22.3***	48.58***	2.15	3.62e+07	6.51e+07***	11.76*
Model RSQ	n/a	0.729	0.673	0.466	0.432	0.695	0.594

January adults, 26 March tadpoles) and last species appearing in early summer (14 May adults, 1 July tadpoles) (Fig. 3b-c, Supporting information). Our post hoc analysis indicates distinct guilds of species active in late winter versus summer, with spring species overlapping with both of these extreme seasonal guilds (Fig. 3a). Species also differed significantly in the length of phenophases. *Rana clamitans* and *R. sphenocephala* had by far the longest mean duration of the ten species analyzed in both tadpoles and adults, with 99.9 ± 17.3 and 31.9 ± 17.2 days in tadpoles and 101.7 ± 9.9 and 47.2 ± 3.01 days in adults (Supporting information). In contrast, species like *B. valliceps*, *P. crucifer* and *G. carolinensis* had very short phenophases, lasting only 6–11 and 9–11 days for adults and tadpoles, respectively (Supporting information). Few strong correlations among phenological traits were observed both across and within species, but the strength of these correlations varied across species (Supporting information). Overall, these analyses reveal a diverse but distinct range of phenological strategies with species specific combinations of phenological traits.

Phenological traits across stages

The timing and duration of the adult calling and tadpole life history events significantly differ between stages ($p=0.008$ for median day, $p < 0.001$ for first day, $p < 0.001$ for duration), but the rank order of these metrics was highly conserved between stages (Fig. 3). While the differences between stages simply reflects the inherent temporal separation of the calling and larval phases, the similarities in order of emergence across stages and species reveal a temporal consistency in the phenologies across stages. Indeed, we found that when accounting for species specific differences, the duration of the adult calling phenophase significantly predicted larval phenophase duration with a positive log-linear relationship between both metrics ($p=0.020$, $R^2=0.608$) (Fig. 4, Supporting information). A shift in the duration of adults which impacts the temporal overlap between species may therefore be mirrored in tadpoles. We observed a weaker positive relationship ($p=0.085$, $R^2=0.531$) for the integrated phenophase areas between stages, and we found no significant correlations between the timing of adult and tadpole median abundance ($p=0.607$, $R^2=0.379$). A closer inspection of correlation across traits and stages also revealed that the first day of calling in the adult stage of a given species was negatively correlated with duration of the following tadpole stage (except for *R. clamitans*), suggesting that a delay in onset of breeding activity in a given year may be partially offset by a shortening of the larval phenophase for most species (Supporting information).

Temporal overlap between species and stages

The potential for interspecific competition varied between sites, species pairs, and years, but was correlated between adult and tadpole communities. The degree of proportional temporal overlap significantly differed based on species pair in tadpoles ($p < 0.0001$, $R^2=0.509$) and in adults ($p=0.039$, $R^2=0.608$) and this difference in overlap could be explained by differences in median timing between pairs ($p=0.048$ for tadpoles, $p < 0.001$ for adults). Critically, stage identity did not significantly determine levels of interaction potential ($p=0.121$), indicating that interaction potential between species pairs was largely preserved across the two life history stages. The overlap in phenologies of species pairs was correlated between adult and tadpole stages, indicating that phenological shifts in competitive interactions are mirrored across life history stages. We found highly significant, positive correlation between adult and tadpole interaction potential ($p < 0.001$, $R^2=0.593$) visible in Fig. 5. Importantly, this relationship emerges after accounting for species identities, indicating that the interaction of a given species pairs are tracked across stages over time and space. Diverse pair specific correlations between the overlap of the two stages contributed to this positive trend (Supporting information). Species-pair identity significantly determined levels of tadpole interaction potential ($p < 0.001$), but more data are required to assess a potential interaction between adult overlap and species pair identity. These results indicate that the degree of temporal overlap is maintained between stages, and similar shifts to temporal overlap occur in both adults and tadpoles.

Discussion

Phenological shifts are an important community-level biomarker of the effects of climate change (Parmesan and Yohe 2003, Root et al. 2003, Brown et al. 2016, Post 2019), but little is known about how phenological patterns and species interactions are related across life history stages, especially in species with complex life histories (Haefner and Edson 1984, Moll and Brown 2008). Here we found that although species displayed a diverse set of phenological strategies, shifts in the timing and duration of phenologies were correlated across adult and tadpole stages. Consequently, shifts in temporal overlap of pairwise competitive interactions were also mirrored between stages. Overall, these results indicate a strong tracking of phenologies and species interactions across life history stages and suggest that phenological shifts in one stage can impact the temporal dynamics and structure of interaction networks across developmental stages.

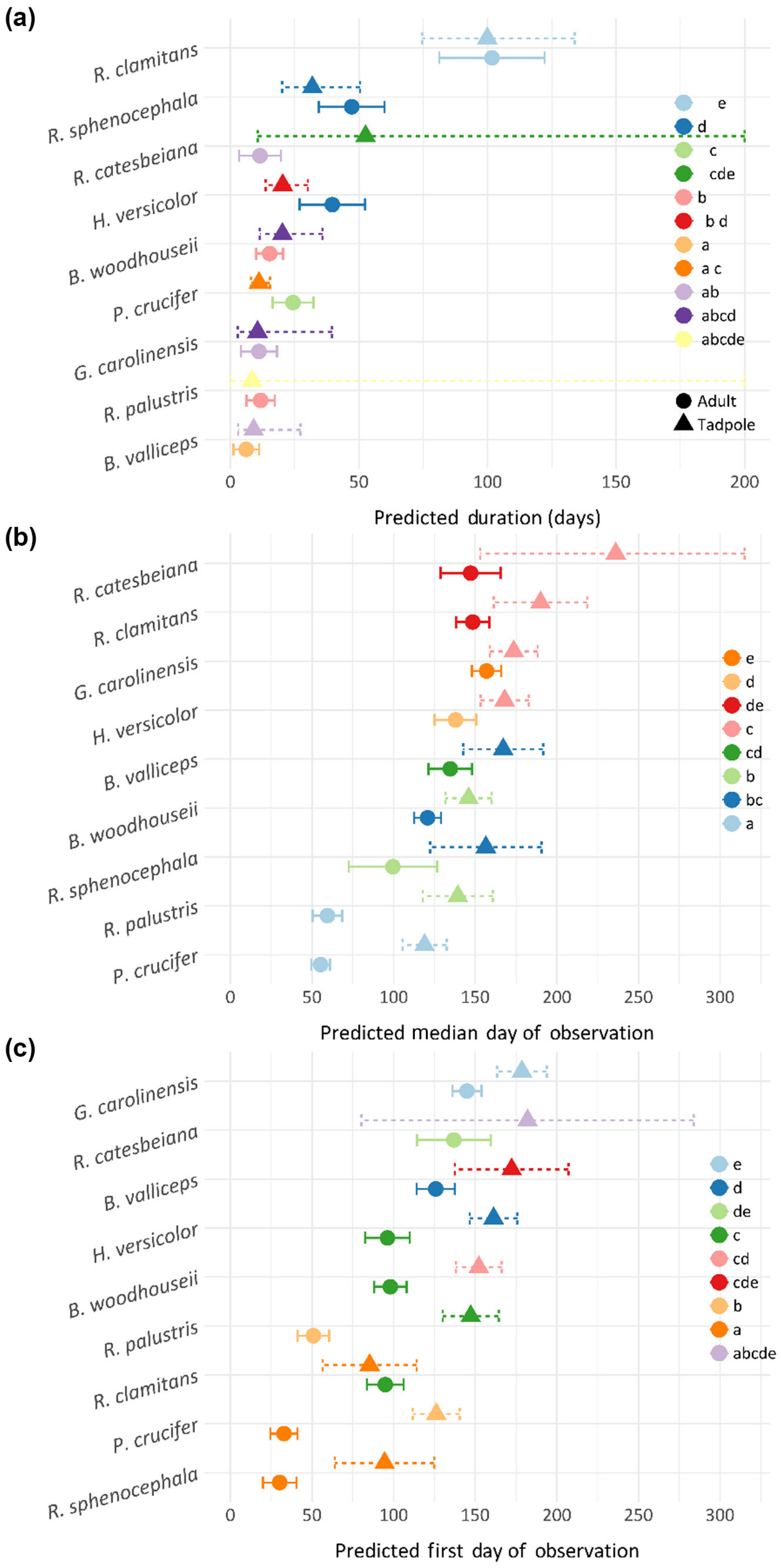

Figure 3. Phenology metrics across nine different species for adults and tadpole stage. Symbols indicate mean (a) duration of stage specific phenophase, (b) median day of observation, and (c) first day of observation. Whiskers indicate 95% CI. Values were estimated from respective general linear models and account for pond and year specific effects. Shape and line type distinguish tadpole and adult stages. Species with same colors do not significantly differ from each other for a given stage. Note that larval durations represents estimates from weekly samples and thus may underestimate larval periods in species with very short phenophases.

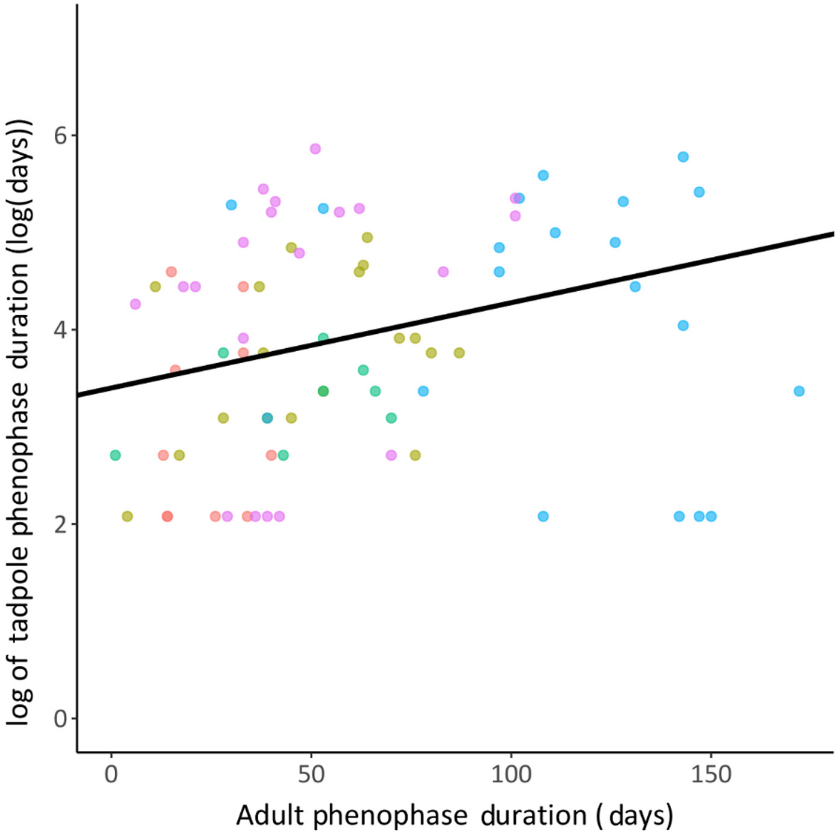

Figure 4. Relationship between adult and log-transformed tadpole phenophase duration ($p = 0.020$, $R^2 = 0.608$). Colored points represent individual observations of each of five species analyzed, and black line indicates GLM predicted relationship after accounting for relative year, pond, and species specific effects.

Phenological strategies

Phenological strategies represent the evolution of the cuing of life history events in response to selective pressures, including the intensity of competition and the availability of resources (Monasterio and Sarmiento 1976, Sauer et al. 2003, Post 2019). We found that species in our communities exhibit a range of phenological strategies without clear clustering. Species became active at different times of the year, without clear seasonal clustering, except that fall was a period of low activity. Across species, phenological traits like length of phenophase were also not clearly linked to a particular season. For instance, the length of tadpole period could be very short in species that reproduced in either winter or summer, or species that breed at the same time of year could have long or very short phenophases. The differences in phenological strategy we observed represent a combination of previously described, seasonally structured 'explosive versus prolonged' life history strategies and eco-evolutionary responses to biotic factors and the environment (Trochet et al. 2007, López et al. 2011, Hartel et al. 2007).

The duration of a phenophase was especially important to distinguishing phenological strategies of species (Fig. 2), and species durations ranged from species with very short phenophases of a few weeks in both stages to species where each stage was present for many months. Long phenophases have been previously identified as a strategy for increasing temporal overlap with resource phenology (Olliff-Yang et al. 2020). Patterns in length of a phenophase may also distinguish seasonal specialists, which occur in a narrow range of sites and temporally variable abiotic conditions, from generalists like *R. clamitans* (Fig. 1a) (Vignoli et al. 2007). Despite all this diversity, the typical rank order of timing and duration within each community was highly conserved between adults and tadpoles (Fig. 3). Past studies of adult and tadpole communities have observed similar 'temporal nestedness' resulting, in part, from species-specific phenological strategies that minimize competition and promote synchrony with environmental conditions (Sazima and Eterovick 2000, Vignoli et al. 2007, López et al. 2011). Our results indicate that a phenological shift in one stage has the potential to impact the timing, duration, and interactions of a subsequent stage.

Phenological tracking across stages

The timing and density of adult reproduction affects the fitness of offspring (Matsushima and Kawata 2005), while hatching duration and intraspecific synchrony can determine adult recruitment rates (Rasmussen and Rudolf 2015, Carter and Rudolf 2022). Yet correlations among the phenologies of life stages are poorly understood because coarse grain data often reduces the tractability of phenological traits (Moll and Brown 2008, Carter et al. 2018). We observed phenological

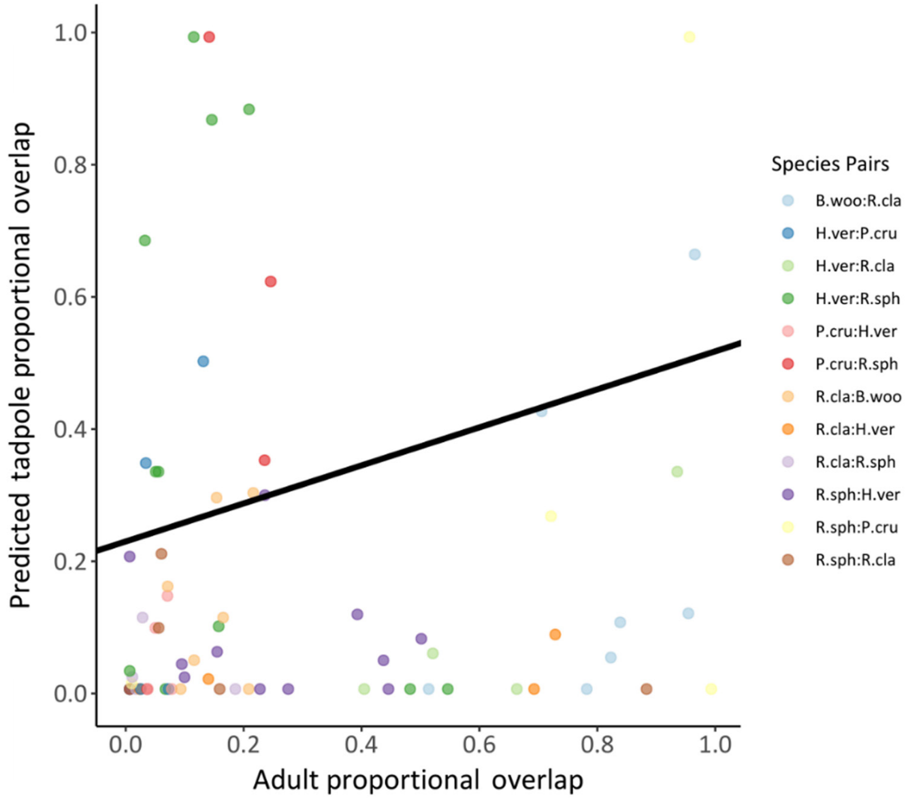

Figure 5. Model results from a beta regression of tadpole and adult proportional overlap ($p < 0.001$, $R^2 = 0.593$). Colored points are raw data points that correspond to unique observations of temporal overlap for a given species, pond, and year. The black trend line represents the significant overall trend predicted by the beta regression model. Note that this relationship also accounts for other effects (e.g. pond and species pair-specific effects) which are not shown in the raw data.

tracking (i.e. positive correlations) between the durations of adult and tadpole phenologies, but not in metrics of timing. This difference could be driven by several non-exclusive factors. First appearance and median abundance represents a single metric statistic, and thus are much more sensitive to variation (e.g. temperature, rainfall, food availability) across sites and years, weakening statistical power to pick up shifts and correlations across the two stages (Carter et al. 2018). In contrast, duration and integrated area are more holistic metrics that focus on the entire distribution of phenologies. Consequently, they tend to have more statistical power to pick up temporal trends and shifts in phenologies and will be less sensitive to environmental variation (Carter et al. 2018). In addition, differences in phenological patterns, including within-cohort synchrony and voltinism can also weaken this relationship (Raczyński et al. 2022). In species such as *R. sphenocephala*, an extended larval period can result in overlapping tadpole cohorts that can mask bimodal calling patterns in adults. Both factors could also explain why we observed few significant differences among the timing of species' median abundance (Carter et al. 2018).

The significant correlation of duration of the adult and tadpole phenophases (and slightly weaker correlation for integrated phenological area) indicate that phenological shifts are tracked between age classes (Fig. 4). Furthermore, the duration of shifts in adults corresponded with similar shifts in tadpoles. This phenological tracking of duration from adults to tadpoles may further impact synchrony and fitness during metamorphosis, by maintaining density and intraspecific competition from reproduction to hatching (Rudolf and Rödel 2007, Yang and Rudolf 2010). With springs beginning earlier, breeding adults that compete or exploit priority effects in early spring and summer may respond by expanding their durations, potentially impacting the competitive dynamics of offspring, or by increasing the number of clutches produced in a year (Morrison and Hero 2003, Post 2019, Olliff-Yang et al. 2020).

Phenological dynamics of interspecific interactions

At the community level, the relative timing of phenologies and their overlap determines the potential of species to interact (Carter et al. 2018, Rudolf 2018, Sazima and Eterovick 2000). Given the differences in phenologies across species, it is not surprising that temporal overlap between species pairs varied substantially with species identity (Supporting information). However, despite the large variation and stage specific differences in the duration of phenologies, the temporal overlap of species pairs was largely preserved across both life stages. Species that never called at the same time were also much less likely to co-occur as tadpoles and when species pairs did overlap in time, both stages had similar (± 20%) mean levels of temporal overlap. Importantly, this analysis isolates the correlations of stage specific interaction potential of species pairs across time (different years) and space (different breeding sites). Thus, these relationships do not simply emerge because species belong to the same seasonal 'guild' but reflect true tempo-spatial co-variance. Although this portion of our analysis was limited to five species, these results show the potential of biotic interactions to be conserved across two temporally separate life history events in two very different habitats. Overall, this suggests that phenological shifts in one stage can alter species interactions in subsequent stages.

Further research is necessary to determine whether the strength of the correlation between the temporal overlap of multiple stages varies significantly among species with differential phenological strategies. For example, phenological tracking could be a valuable strategy for species which call and hatch in the summer, a period with many species overlapping in time and jockeying to exploit priority effects (Alford and Wilbur 1985). A species like *R. clamitans* could benefit relatively less from phenological tracking, since although they call in the summer, larvae remain in ponds year-round. Phenological tracking could be much more important for species like *P. triseriata* which are seasonal (late winter) specialists and are relatively weak interspecific competitors (Rudolf and Singh 2013, Rudolf 2018). However, identifying such relationships requires longer time series and data on how key resources and other important biotic and abiotic conditions change over time to elucidate windows of opportunity for each species (Visser and Gienapp 2019, Kharouba and Wolkovich 2020). Our analysis was limited to 6 years; adequate to capture typical phenological dynamics, but not long enough to accurately detail long-term trends in abundance, climate, and phenological traits (Visser and Both 2005). Only five species had sufficient records for modeling patterns of temporal overlap. More data could reveal such trends and inform restorative efforts to amphibian ecosystems as well as further corroborate the importance of species-specific slopes in determining the strength of correlations between tadpole and adult phenologies (Marsh and Trenham 2001).

Conclusion

In the coming decades climate-driven shifts will only increase in magnitude and non-stationarity, yielding new stable states from which a return to equilibrium conditions will be impossible (Todd et al. 2010, CaraDonna et al. 2014, Wolkovich et al. 2014). In addition, global amphibian population declines due to disease and habitat loss increasingly prevent forming clear images of aquatic communities (Blaustein et al. 1994, Alford and Richards 1999, Bury 1999, Stuart et al. 2004, Grant et al. 2016). Therefore, a crucial future direction of this work is to integrate understandings of shifts in community structure with predictive modeling of community change globally and to develop new technologies for assessing the temporal dynamics of interactions (Wolkovich et al. 2014, Post 2019, Yang 2020). Determining how shifts in competitive interactions throughout complex life histories impact interaction networks, population dynamics, and community assembly will provide key insights into how climate change re-directs ecosystem processes (Abraham et al. 2010, Yang and Rudolf 2010, Visser and Gienapp 2019). As our ability to capture finer pictures of the interaction networks of communities grows, so will the importance of considering the connections between the phenology and interactions of the multiple habitats composing an ecosystem (Both et al. 2009, Yang and Rudolf 2010, Thackeray et al. 2016, Yang 2020). Determining which factors influence the phenological shifts of interactions, including testing critical assumptions of phenological hypotheses, is still a major goal of future research (Visser and Gienapp 2019, Kharouba and Wolkovich 2020). But the trophic and spatial impacts of phenological shifts may in fact be much broader than previously understood, especially when considering organisms which separate their life history stages via long distance dispersal and migration (Moll and Brown 2008, Clausen and Clausen 2013, Carter et al. 2018). In the search for the community-level mechanisms and demographic consequences of phenological shifts, this study can serve as a homing beacon as to the temporal and ecological scope of how shifts in competitive interactions shape community structure.

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Author contributions

Calvin M. Carroll: Formal analysis (lead); Methodology (equal); Software (equal); Validation (equal); Visualization (lead); Writing – original draft (lead); Writing – review and editing (equal). **Daniel Saenz**: Conceptualization (equal); Data curation (equal); Investigation (equal); Methodology (equal); Writing – review and editing (equal). **Volker H. W. Rudolf**: Conceptualization (equal); Data curation (equal); Funding acquisition (equal); Investigation (equal); Methodology (equal); Project administration (equal); Supervision (equal); Writing – review and editing (equal).

Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.25338/B8G92P (Carroll et al. 2023).

Supporting information

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

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