

Shifts in phenological mean and synchrony interact to shape competitive outcomes

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Abstract. Climate change-induced phenological shifts are ubiquitous and have the potential to disrupt natural communities by changing the timing of species interactions. Shifts in first and/or mean phenological date are well documented, but recent studies indicate that shifts in synchrony (individual variation around these metrics) can be just as common. However, we know little about how both types of phenological shifts interact to affect species interactions and communities. Here, we experimentally manipulated the hatching phenologies of two competing species of larval amphibians to address this conceptual gap. Specifically, we manipulated the relative mean hatching time (early, same, or late relative to competitor) and population synchrony (high, medium, or low levels of variation around the mean) in a full 3×3 factorial design to measure independent and interactive effects of phenological mean and population phenological synchrony on competitive outcomes. Our results indicate that phenological synchrony within a population strongly influences intraspecific competition by changing the density of individuals and relative strength of early- vs. late-arriving individuals. Individuals from high-synchrony populations competed symmetrically, whereas individuals from low-synchrony populations competed asymmetrically. At the community scale, shifts in population phenological synchrony interact with shifts in phenological mean to affect key demographic rates (survival, biomass export, per capita mass, and emergence timing) strongly. Furthermore, changes in mean timing of species interactions altered phenological synchrony within a population at the next life stage, and phenological synchrony at one life stage altered the mean timing of the next life stage. Thus, shifts in phenological synchrony within populations cannot only alter species interactions, but species interactions in turn can also drive shifts in phenology.

Key words: amphibians; competition; phenological shifts; phenology; species interactions; synchrony; timing

INTRODUCTION

Phenologies, the seasonal timing of life-history events, play an important role in driving the dynamics of natural systems because they determine when an individual enters an environment, and in turn, the individual's stage and size when interacting with other members of the community (Yang and Rudolf 2010, Thackeray et al. 2016). Phenological shifts in spring life-history events are a common response to climate change across diverse taxa, and it is a major goal to understand how these temporal shifts will impact species interactions in natural communities (Parmesan and Yohe 2003, Root et al. 2003, Menzel et al. 2006). To address this issue, previous research has predominantly focused on measuring shifts in the first or mean occurrence of a phenological event in natural populations. These studies have consistently found that, across varied taxa, the timing of first and mean spring life-

history events advance in time to match the earlier onset of spring due to climate change (Parmesan 2007, Taylor 2008, Vitasse et al. 2018). Because different species vary in the magnitude of phenological response, interacting species frequently become mismatched in time, which can change interaction strength and disrupt natural communities (Renner and Zohner 2018, Rudolf 2018, Rudolf and McCrory 2018). However, individuals within a species vary in their timing, creating a distribution of phenologies for a given life-history event at the population level (hereafter phenological synchrony; Miller-Rushing et al. 2010, Rasmussen and Rudolf 2015). Importantly, the shape of this phenological distribution can change among years and is closely tied to changing weather patterns, including climate change (Wolkovich et al. 2014, Carter et al. 2018). As a result, shifts in a population's phenological synchrony can occur with equal or greater frequency relative to shifts in first or mean phenological events (CaraDonna et al. 2014, Carter et al. 2018), but the consequences of shifts in synchrony for species interactions and regulation of communities remain poorly understood.

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The importance of phenological synchrony for the regulation of natural populations becomes apparent when we consider how synchrony affects both the density of interacting individuals and per capita interaction strength. Increasing the synchrony of a phenological event within a population increases the average density of interacting individuals (Loe et al. 2005, Koenig et al. 2015). Although this numerical effect should increase intraspecific competition, phenological synchrony can also alter how much per-capita effects vary among individuals, that is, competitive symmetry (Rudolf and Rasmussen 2013, Rasmussen and Rudolf 2015). Offspring that hatch at the same time will have similar sizes and thus have similar (symmetric) competitive abilities, whereas offspring that hatch earlier are typically competitively dominant over smaller conspecifics that hatch later (Rudolf and Singh 2013, Rasmussen et al. 2014). Therefore, a low-synchrony population should result in a low-density population where individuals compete asymmetrically, whereas a high-synchrony population should result in a high-density population where individuals compete symmetrically (Henson and Cushing 1996).

The picture is further complicated when we consider the role of population phenological synchrony in a community context. Research on priority effects provides a

strong foundation for understanding how relative mean phenological events affect species interactions (Tilman 1988, Fukami 2010), but little is known about the role of synchrony, or how these two aspects of phenology might interact (Fig. 1, Rasmussen and Rudolf 2016). Considering two competing species, at least three major outcomes are possible. First, there may be no effect of synchrony. Effects of population synchrony may be overwhelmed by stronger effects of relative mean arrival (i.e., an early arriver benefits from priority access to the resource). In this case, mean phenological events of populations are sufficient to predict outcomes, meaning synchrony can be ignored and outcomes across any column in Fig. 1 would be identical. Second, mean and synchrony may have additive effects. Previous work has shown higher survival for high-synchrony populations relative to low-synchrony populations (Rasmussen and Rudolf 2015). If the effects of mean and synchrony are additive, we would then expect to see higher survival of high-synchrony populations across a range of relative arrival times (e.g., survival of the orange population would increase moving down columns and across rows to the left in Fig. 1).

Finally, synchrony and mean might have interactive effects on competitive outcomes. Phenological synchrony affects the proportion of individuals experiencing

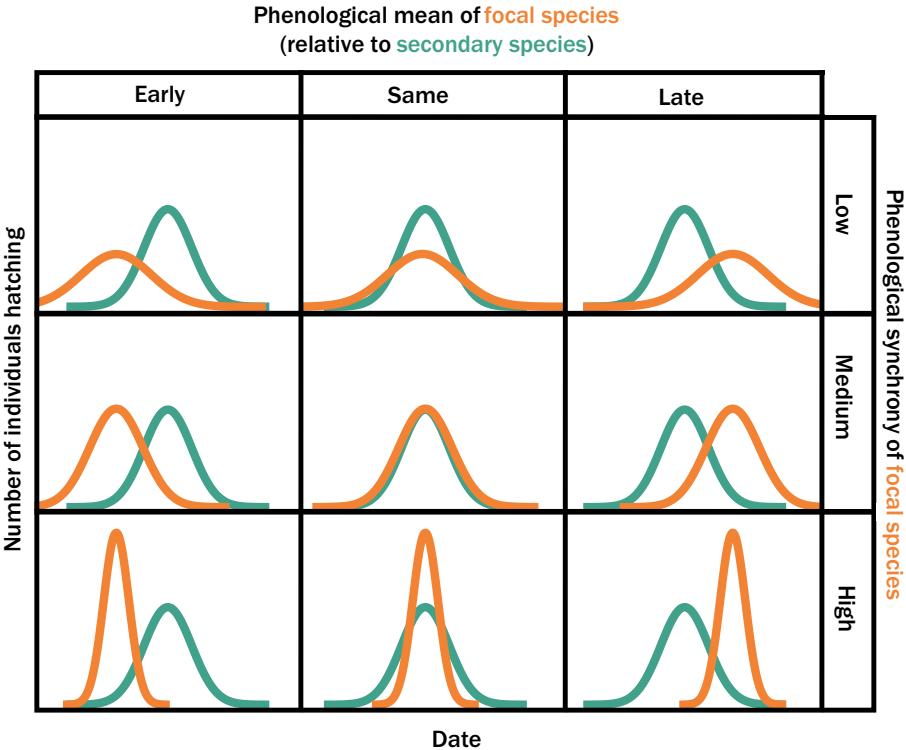


FIG. 1. Conceptual illustration of potential phenological shifts between two interacting species. For simplicity, we have designated a secondary species (represented in teal, *Rana* in our experiment) and adjusted the phenology of the focal species (represented in orange, *Hyla* in our experiment) relative to it. Columns show differences in phenological mean between the two species and rows show differences in phenological synchrony of the focal species. With concomitant shifts in phenological mean and synchrony, it is difficult to intuit net effects on population demography and species interactions.

different conditions (compare top and bottom rows of Fig. 1). In a high-synchrony population, all individuals experience the same conditions, which could be good (e.g., early arrival relative to competitor as shown in Fig. 1, or alternatively, favorable environmental conditions) or bad (e.g., late arrival relative to competitor, or harsh environmental conditions). Alternatively, low-synchrony populations spread individuals across good and bad conditions, akin to bet hedging (Wilbur et al. 2006, Tarazona et al. 2017, Rocha et al. 2018, Shima et al. 2018). Therefore, differences in synchrony could strongly affect the outcome of shifts in mean phenology—a high-synchrony population might be more sensitive to shifts in phenological mean because all individuals shift to experience a new condition, whereas low synchrony might be more robust to shifts in phenological mean. Because the interplay between phenological mean and phenological synchrony is difficult to intuit, we need empirical data to give expectations for how these concomitant types of shifts are likely to affect natural systems.

The interaction between relative mean difference in phenologies and population phenological synchrony also has the potential to carry over to affect synchrony for subsequent phenological events. In the absence of interspecific competition, per capita differences among individuals in low synchrony populations should result in higher survival of the earliest individuals if competition is strong (Rasmussen et al. 2014), potentially skewing the distribution of the next phenological stage to be clustered around an early event. However, if competition is low, or if individuals are not plastic in their development rates, a population's synchrony may be maintained from one phenological stage to the next. By altering the density and/or size differences among individuals within a population, shifts in mean phenologies of an interspecific competitor can therefore also modify the intraspecific drivers that increase or decrease phenological synchrony in a focal population. If true, this would imply that shifts in timing of interspecific interactions could be an important but overlooked driver of variation in phenological synchrony of later life-history events, but this remains to be tested.

Here, we evaluate the effects of phenological shifts in a community context. Specifically, we use a mesocosm experiment to examine how different metrics (mean and synchrony) of phenology affect the outcome of competition between two competing amphibian species. Specifically, we altered the order of arrival (i.e., mean hatching date) between the two species and the phenological synchrony of one of the two species. This system allowed us to ask: (1) What are the independent and interactive effects of phenological mean and phenological synchrony on population demography and competitive interactions? (2) Does a population's phenological synchrony change across phenological stages?

METHODS

Study system

We studied the gray tree frog (*Hyla versicolor* or *Dryophytes versicolor*, hereafter *Hyla*) and its competitor the Southern Leopard frog (*Rana sphenoccephala* or *Lithobates sphenoccephalus*, hereafter *Rana*) to determine effects of mean and synchrony of hatching phenology on the performance of *Hyla*. We chose *Hyla* as the focal species because it develops more quickly, enabling us to capture the full period of its emergence and therefore track phenological synchrony across phenological stages. The two species are an ideal system for several reasons. First, they commonly co-occur throughout the southeastern United States and are resource competitors, both in larval and adult stages (Alford and Wilbur 1985). Second, both species show significant variation in the duration and seasonal timing of breeding (Carter et al. 2018), so we expect larval offspring to overlap at different times based on year-specific weather conditions. Third, we are able to delay egg hatching in both species, allowing us to manipulate phenology experimentally. Finally, amphibians exhibit a strong but highly variable phenological response relative to other taxa (Parmesan 2006, Todd et al. 2010) and are declining globally (Bury 1999, Stuart et al. 2004), suggesting they should be a high priority for examining consequences of phenological shifts.

Experimental system and design

Egg clutches of *Hyla* and *Rana* were collected from Davy Crockett National Forest on 30 March 2018. Initially, all clutches were maintained at 15°C to slow development. Then, 1–2 d prior to introduction to the experiment, batches of eggs were moved to warmer conditions (25°C) to induce hatching. This allowed us to introduce tadpole hatchlings of the same size (Gosner stage 25; ~2.1 mm snout-to-vent length (SVL) for *Hyla* and ~4.4 mm SVL for *Rana*) on different days. These temperatures are well within the range both species would experience in ephemeral ponds in nature, and developmental assays have shown few negative side effects on performance for tadpoles reared at these temperatures (Moore 1939, Rudolf and Singh 2013, Rasmussen and Rudolf 2016). The experiment was a full 3 (phenological synchrony) × 3 (phenological mean) factorial design. In addition, we had single-species controls manipulating synchrony only, which allowed us to separate the intraspecific effects of synchrony from the competitive effects of arrival order. To create our phenological synchrony treatments, we manipulated the variation in hatching date for *Hyla* around a mean hatching date, 15 April 2018. For high-synchrony treatments, all 45 *Hyla* individuals hatched on 15 April. For medium-synchrony treatments, hatching occurred on 3 d from 12 April–18 April. For low-synchrony

treatments, hatching occurred on 5 d from 9 April–21 April. For medium- and low-synchrony treatments, the 45 *Hyla* individuals were equally divided among the three and five introductions, respectively. To create the phenological mean treatments, we manipulated the hatching date of *Rana* to occur early (9 April), at the same time (15 April), or late (21 April) relative to the mean hatching date of *Hyla*. All *Rana* individuals for a given treatment hatched on a single day (conceptual schematic of treatments in Fig. 1 and detailed schedule in Appendix S1: Fig. S1). Control (i.e., no interspecific competition) populations lacked *Rana*. For both species, a subset of individuals was photographed and measured before each introduction, which confirmed that individual body sizes (for a given species) were the same across all introductions (Appendix S1: Fig. S2). There were six replicates per competition treatment and two replicates of control populations, for a total of 60 experimental units.

After eggs hatched in lab, they were added to 360-L cattle tank mesocosms that closely imitate the small ephemeral ponds in which these tadpoles develop in nature. Each mesocosm contained 45 *Hyla* individuals and 30 *Rana* individuals. Mesocosms were kept in ambient conditions in an open field in Houston, Texas. One week prior to the first tadpole additions (2 April), we filled mesocosms with dechlorinated water and immediately covered each mesocosm with 60% shade cloth to prevent external colonization. Five days prior to the first tadpole introductions (4 April), we added 400 mL concentrated phytoplankton and zooplankton inoculate and 4 L of dried leaf litter collected from margins of local ponds. These additions are aimed to recreate key aspects of natural pond conditions, providing food and habitat structure for the developing tadpoles. After tadpole hatchlings were added (9 April–21 April), mesocosms were monitored daily to collect newly emerged *Hyla* froglets (hereafter, metamorphs). Because *Rana* development time is much slower, their emergence was not captured. Metamorphs were weighed in the lab and then released. The experiment ended 14 September 2018, at which point emergence rate had declined substantially to very low levels (only 1–2 metamorphs collected across all 60 mesocosms each day), so we were confident we captured the full emergence period for *Hyla* (Appendix S1: Fig. S3). At the conclusion of the experiment (18 September–20 September), mesocosms were emptied and all remaining tadpoles (mostly *Rana*) were removed. Tadpoles removed were photographed, measured (head width and SVL), and released. At this point, 22 *Hyla* (out of 2,700 initially added) and 283 *Rana* (out of 1,620 initially added) were collected from the mesocosms. For *Hyla*, these remaining individuals were equally distributed across all treatments ($\chi^2_{11} = 16.19$, $P = 0.13$). We recorded the number of remaining *Rana* individuals in each mesocosm, but because *Rana* face high mortality when emerging, we suspect these

measurements are misleading and do not consider them in our analysis (Appendix S1: Fig. S4, S5).

We used five response variables to quantify the effect of phenological mean and synchrony on key demographic rates of *Hyla*: (1) proportional survival (number of metamorphs collected divided by 45 hatchlings initially added), (2) total biomass export (cumulative mass of all metamorphs emerged from a mesocosm), (3) mean per capita mass (the individual masses of all metamorphs from a mesocosm), (4) mean emergence date (the date of emergence for each individual from a mesocosm), and (5) standard deviation of emergence date. Together, these five variables give us a picture of per capita and numeric consequences of phenological mean and synchrony on *Hyla* populations. The 22 *Hyla* tadpoles collected at the end of the experiment were not included in these analyses because the mass values of tadpoles and metamorphs are not comparable and these individuals did not have an emergence date. Lacking reliable estimates for four of the five response variables, we chose to omit *Hyla* tadpoles collected at the end of the experiment from all analyses.

Statistical analyses

All analyses were performed in the R statistical computing environment (R Development Core Team 2017). We ran linear and generalized linear mixed models using the “lme4” package (Bates et al. 2015) to analyze the independent and interactive effects of variation in *Hyla*’s mean hatching date relative to that of the competitor *Rana* (categorical predictor with three levels: early, same, late) and phenological synchrony (categorical predictor with three levels: high, medium, low) on the five response variables detailed above. All response variables were scaled relative to the appropriate single-species controls by subtraction. For example, considering survival, we subtracted the proportion survival for low-synchrony control from the proportion survival for each low-synchrony treatment (early, same, and late relative to *Rana*). This approach allowed us to partition the effects of phenological synchrony between population and community scales (i.e., intraspecific vs. interspecific competition). For all response variables except per capita mass, this scaling method did not change the qualitative pattern of the results (e.g., compare Fig. 3 and Appendix S1: Fig. S6). In the case of per capita mass, we take special care to interpret the results. All models were tested with multiple error structures and selected based on fit with the data, which was normal error structure for all variables. For the standard deviation of emergence-time model, assumption of equal variances across treatments was not met, so this model was reformulated in the “nlme” package to account for unequal variance in phenological synchrony (Pinheiro et al. 2018). For all models, we included spatial block as a random effect and analyzed significance of fixed effects and their

interactions with analysis-of-variance tests with the “car” package (Fox and Weisberg 2011).

RESULTS

Controls—*intraspecific competition*

Control populations of *Hyla* (lacking interspecific competitor *Rana*) tested the effects of phenological synchrony on five key demographic response variables: proportion survival, biomass export, mean per capita mass, mean time to emergence, and standard deviation of time to emergence. For these populations, proportion survival of *Hyla* was lowest in low-synchrony populations ($58 \pm 3\%$), highest in medium-synchrony populations ($69 \pm 3\%$), and intermediate in high-synchrony populations ($62 \pm 22\%$; Fig. 2A). *Hyla* total biomass export (i.e., cumulative mass of all *Hyla* individuals that survived to emergence within a mesocosm) was similar across synchrony treatments (ranging from $5,035 \pm 1,678$ mg at high synchrony to $6,127 \pm 775$ mg at low synchrony; Fig. 2B). Mean per capita *Hyla* body mass decreased as hatching became more synchronized—individuals from low-synchrony populations were 237 ± 54 mg, whereas those from high-synchrony populations were 177 ± 42 mg (Fig. 2C). Time to emergence increased as hatching became more synchronized—individuals from low-synchrony populations took on average 33 ± 10 d to emerge, and individuals from high-synchrony populations took 56 ± 24 d to emerge (Fig. 2D). Synchrony of timing at hatching was not maintained in the next phenological stage (measured as the standard deviation of individuals’ time to emergence). In fact, synchrony at hatching was reversed at the emergence stage. Populations that hatched highly synchronized had more variation in emergence (standard deviation of emergence 15.1 ± 5.6 d), whereas populations that hatched with low synchrony emerged more highly synchronized (standard deviation of emergence 10.3 ± 0.8 d; Fig. 3, Fig. 2E).

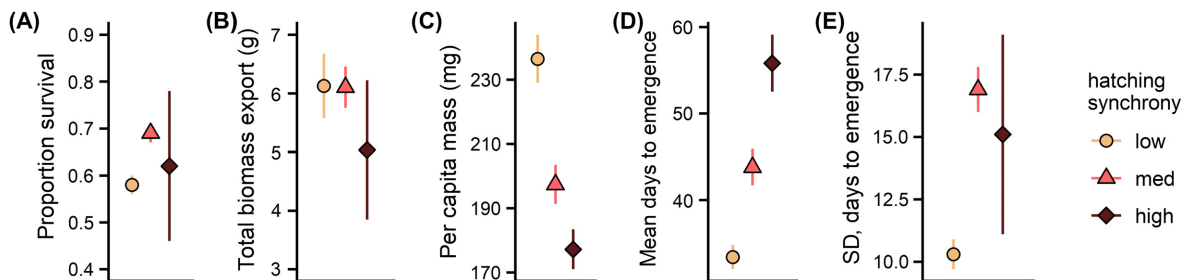


FIG. 2. Responses of populations of *Hyla* to experimental manipulations of hatching synchrony. These plots show control treatments, without interspecific competition. (A) Proportion of tadpoles that survived to emergence, (B) total biomass export (i.e., cumulative mass of all tadpoles that survived to emergence), (C) average per capita mass of all metamorphs, (D) average number of days from mean hatching time to emergence, (E) standard deviation in time to emergence for all individuals. Points represent means ± 1 standard error (from two replicates).

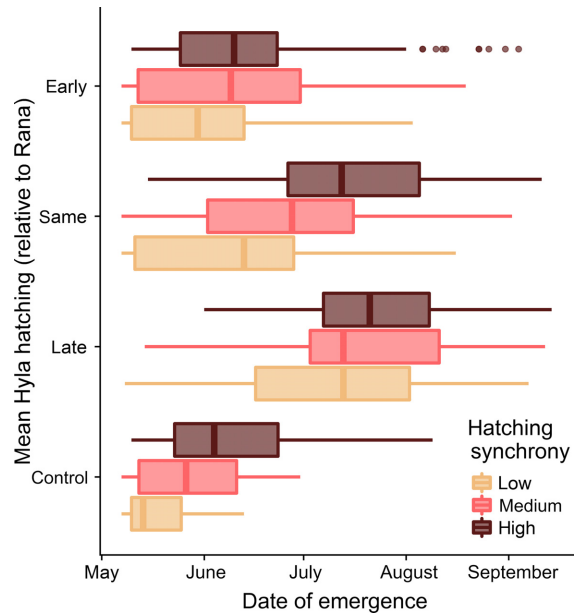


FIG. 3. Box plot showing emergence timing of individual *Hyla* tadpoles for different manipulations of mean and synchrony in hatching timing.

Experimental treatments—*interspecific competition*

Survival.—The strength of interspecific competition (i.e., *Hyla* survival relative to competitor-free control) was driven by mean hatching date relative to competitor, and the interaction between mean and synchrony, but not by synchrony independently (Fig. 4A; mean: $\chi^2_{2, 51} = 30.4$, $P < 0.0001$, synchrony: $\chi^2_{2, 51} = 3.15$, $P = 0.21$, mean * synchrony: $\chi^2_{4, 51} = 11.7$, $P = 0.02$). Thus, the effect of mean hatching time on *Hyla* survival depended on *Hyla* synchrony. For low- and medium-synchrony populations, *Hyla* survival declined as they hatched later relative to *Rana*, as expected (for low-synchrony populations, survival was $56 \pm 6\%$ when arriving early, $49 \pm 7\%$ when arriving at the

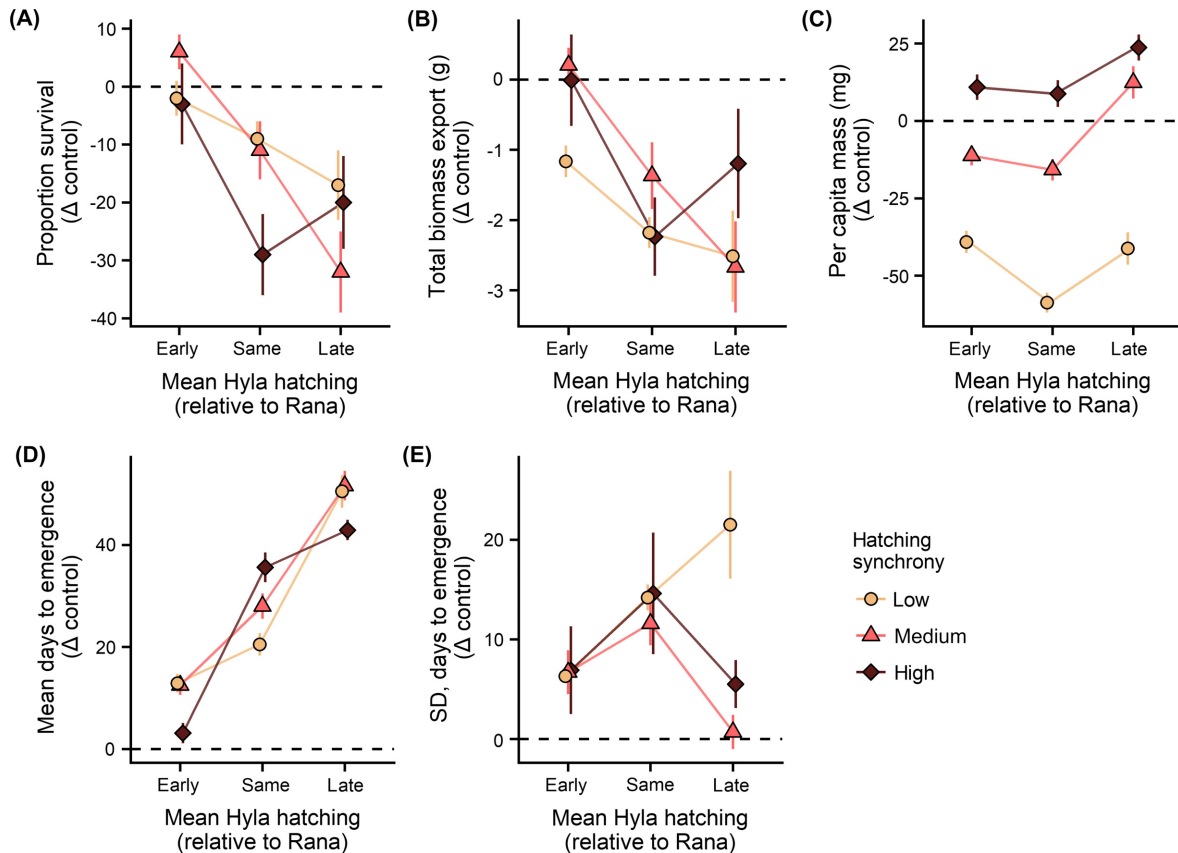


FIG. 4. Responses of populations of *Hyla* to experimental manipulations of mean and synchrony of hatching timing. All points are scaled by subtraction relative to the control value for a particular synchrony treatment and variable (control baseline represented by dashed black line). (A) Proportion of *Hyla* tadpoles that survived to emergence, (B) total biomass export (i.e., cumulative mass of all *Hyla* tadpoles that survived to emergence), (C) average per capita mass of all *Hyla* metamorphs, (D) average number of days from mean hatching time to emergence, (E) standard deviation in time to emergence for all *Hyla* individuals. Points represent means $\pm$ 1 standard error (from six replicates).

same time, and $41 \pm 16\%$ when arriving late; for medium-synchrony treatments, survival was $75 \pm 7\%$ when arriving early, $58 \pm 13\%$ when arriving at the same time and $37 \pm 17\%$ when arriving late). However, high-synchrony populations followed a different pattern—survival was lowest when *Hyla* and *Rana* had the same mean hatching date ($33 \pm 16\%$) and higher when either species hatched first ($59 \pm 17\%$ when *Hyla* arrived first, $43 \pm 18\%$ when *Rana* arrived first). Synchrony had the strongest effect when competitors hatched at the same time, with the proportion of survival ranging from $33 \pm 16\%$ at high synchrony to $58 \pm 13\%$ at medium synchrony. In contrast, synchrony had very little impact on survival when *Hyla* hatched late relative to *Rana*. In these cases, survival was equally low across the three synchrony levels, ranging from $37 \pm 17\%$ at medium synchrony to $43 \pm 18\%$ at high synchrony, suggesting that strong competition made synchrony less important. Compared with competitor-free controls, *Hyla* survival was equal when they hatched before *Rana* (survival of all

synchrony treatment populations within 6% of the appropriate single population controls), but survival was always lower than that of controls when *Hyla* hatched at the same time as or after arrival (survival 9–29% lower than controls for same arrival and 17–32% lower for late arrival). This suggests that interspecific competition between *Hyla* and *Rana* is negligible when *Hyla* hatches first.

Biomass export.—The competitive effect (i.e., *Hyla* biomass relative to competitor-free controls) depended only on mean hatching time relative to competitor, but not on phenological synchrony or the interaction between them (Fig. 4B; mean: $\chi^2_{2, 51} = 21.6$, $P < 0.0001$, synchrony: $\chi^2_{2, 51} = 4.14$, $P = 0.13$, mean * synchrony: $\chi^2_{4, 51} = 6.4$, $P = 0.17$). The effect of mean hatching on biomass closely matched that on survival, with a decline in biomass as *Hyla* hatches later relative to *Rana* for low- and medium-synchrony populations, but resulted in a U-shaped relationship for high-synchrony populations. However, although mean and synchrony had synergistic effects on

proportion survival, no significant interaction was detected for biomass. Similar to survival, biomass for mesocosms with competition closely matched single-species control values when *Hyla* hatched before *Rana*, but were much lower when the species hatched at the same time or when *Hyla* hatched after *Rana*, indicating that *Hyla* largely escaped competition with *Rana* when it hatched early.

Per capita mass.—The competitive effect (i.e., average *Hyla* mass relative to competitor-free controls) depended on both mean hatching date and hatching synchrony, but not on the interaction between them (Fig. 4C; mean: $\chi^2_{2, 51} = 7.85$, $P = 0.02$, synchrony: $\chi^2_{2, 51} = 120$, $P < 0.0001$, mean * synchrony: $\chi^2_{4, 51} = 2.42$, $P = 0.66$). The effect of mean was the same across synchrony levels: individual *Hyla* that hatched at the same time as competitor *Rana* were smaller on average than those that hatched before or after their competitor (186–197 mg for early hatching, 178–186 mg for the same hatching time, 195–209 mg for late hatching). The competitive effect of synchrony on *Hyla* body mass was large. Individuals from low-synchrony *Hyla* populations experiencing interspecific competition were much smaller than individuals from low-synchrony *Hyla* populations without interspecific competition. On the other hand, individuals from high-synchrony *Hyla* populations with interspecific competition were slightly larger than individuals from high-synchrony *Hyla* populations without interspecific competition.

Emergence phenology (mean, variance, and distribution).—The competitive effect (i.e., average *Hyla* emergence time relative to competitive free controls) depended significantly on mean hatching relative to that of the competitor *Rana*, with *Hyla* taking longer to develop when they hatch later than *Rana*. Hatching synchrony independently did not have a significant effect on time to emergence, but did interact with mean (Fig. 4D; mean: $\chi^2_{2, 51} = 101$, $P < 0.0001$, synchrony: $\chi^2_{2, 51} = 0.84$, $P = 0.66$, mean * synchrony: $\chi^2_{4, 51} = 10.1$, $P = 0.038$). Emergence times for the three synchrony levels for any given hatching order were similar; however, the shape of mean relationship was different for each synchrony: high synchrony was concave down, medium synchrony was linear, and low synchrony was concave up. Taken together, this indicates that hatching synchrony mediates the effect of mean hatching. For high-synchrony populations, there is a cost in development time for arriving at the same time (91 ± 28 d) vs. early (59 ± 25 d), but no additional cost if late (99 ± 22 d). On the other hand, for low-synchrony populations, hatching earlier or at the same time as competitor results in the same development time (46 ± 22 d for early, 54 ± 25 d for same), but there is a cost when hatching late (84 ± 34 d).

Standard deviation of emergence time depended on mean hatching relative to *Rana*, hatching synchrony, and the interaction between synchrony and mean

(Fig. 4E; mean: $\chi^2_{2, 51} = 9.34$, $P = 0.0094$, synchrony: $\chi^2_{2, 51} = 12.4$, $P = 0.0020$, mean * synchrony: $\chi^2_{4, 51} = 18.6$, $P = 0.00096$). For medium- and high-synchrony populations, standard deviation of emergence was hump-shaped: highest when hatching coincided with interspecific competitor *Rana*, and lower when either species hatched first. For *Hyla* populations that hatched with low synchrony, standard deviation of emergence increased as *Hyla* hatched later relative to *Rana*. Across all treatments, synchrony of emergence was much lower than synchrony in hatching. Although hatching spanned at most a 13-d window, the average duration of the emergence period was 98 ± 27 d. Commonly, emergence distributions had a bimodal shape, indicating two distinct cohorts of *Hyla* metamorphs arising from one cohort of *Hyla* hatchlings (Appendix S1: Fig. S7).

DISCUSSION

Climate change drives phenological shifts across taxa, and it is critical that we understand how this temporal restructuring affects species interactions and, in turn, natural communities (Parmesan and Yohe 2003, Miller-Rushing et al. 2010, Yang and Rudolf 2010). Shifts in first and mean phenological dates are well documented, and recent work has shown that shifts in synchrony (individual variation around these metrics) can be just as common (CaraDonna et al. 2014, Carter et al. 2018). However, we know little about how both types of phenological shifts interact to affect species interactions and natural communities. Using an empirical system, we found that shifts in phenological synchrony could have similar or even stronger effects than shifts in mean phenologies. Furthermore, effects of these two aspects of phenology were often synergistic. Therefore, making meaningful predictions about how phenological shifts will disrupt species interactions necessitates broadening our view of phenology to include phenological synchrony.

Effects of phenological synchrony on intraspecific competition

The outcomes of intraspecific competition depend on the abundance of individuals and their per capita composition (Werner and Gilliam 1984). Phenological synchrony can affect both because it affects the density and size structure of a population at any given point in time (Rasmussen and Rudolf 2015). We expect low-synchrony populations to have low density and much variation between individuals in size and thus competitive ability. This should lead to asymmetric competition where relatively few individuals can monopolize a limiting resource. High-synchrony populations should have higher densities and little variation in body size among individuals, leading to symmetric competition where resources are divided more evenly amongst competitively

equal individuals (Henson and Cushing 1996, Rasmussen and Rudolf 2015). Our results support these expectations. Compared with high-synchrony populations, populations that hatched with low synchrony had lower survival, but surviving individuals were larger and developed quickly.

Effects of phenological shifts on interspecific competition

Phenologies play a key role in shaping interspecific interactions because they define when and for how long species are present in their environment and able to interact with other members of the community (Anderson et al. 2015, Kharoub et al. 2018, Renner and Zohner 2018). Considering resource competitors, it is well known that order of arrival can strongly affect the interaction via size-mediated priority effects (Sutherland and Karlson 1977, Rasmussen et al. 2014, Rudolf 2018). In contrast, virtually nothing is known about if or how phenological synchrony within populations can change this relationship. In the simplest case, population synchrony could be unimportant. Alternatively, population synchrony could interact additively or synergistically with differences in species' mean phenologies. It is difficult to intuit which case is most likely, and only one study has tested the outcomes of these concomitant shifts (Rasmussen and Rudolf 2016). Mean hatching time affected all five attributes of *Hyla* we measured in our study. Although this emphasizes the importance of shifts in the mean timing of phenologies for species interactions, the effects of population synchrony were often just as strong, and for three of these attributes, population synchrony modified the effect of changes in mean arrival time (and vice versa). Only for one response were effects of mean and synchrony additive.

These interactive effects of population synchrony and differences in mean phenology between species likely arise because changing population synchrony alters competitive asymmetry within populations (intraspecific effects) and how individuals experience interspecific competition. As expected with size-mediated priority effects (Yang and Rudolf 2010, Rasmussen et al. 2014), survival generally decreased as *Hyla* arrived later relative to its competitor. However, the rate of decline differed based on synchrony: compared with medium- and high-synchrony populations, low-synchrony populations did slightly worse in the best scenarios (early arrival) but slightly better in the worst scenarios (late arrival). This makes intuitive sense, because individuals in high-synchrony populations all experienced either favorable conditions (reduced interspecific competition with relative early arrival) or unfavorable conditions (increased interspecific competition with relative late arrival). In contrast, in low-synchrony populations, only early-hatching individuals would experience reduced interspecific competition with late arrival of the interspecific competitor. However, early arrival of the interspecific competitor should reduce competitive asymmetry within

a low-synchrony population by reducing the growth rate and survival of early-hatching individuals (Morin 1986, Gimnig et al. 2002, Couret et al. 2014). This would reduce the negative effect of early hatchlings on later-hatching conspecifics and could thereby at least partially compensate for the negative effect of interspecific competition.

This mechanism is consistent with the concurrent changes in total biomass. Qualitatively, biomass followed a very similar pattern to survival, but unlike survival, there was no significant interaction between mean and synchrony treatments for biomass. Even though we did not detect a significant effect of synchrony on biomass, this is likely because effects of population synchrony on individual mass and survival counteracted each other. At the population scale, compensatory dynamics between survival and individual mass led to relatively uniform biomass across population synchrony treatments. In a community context, compensatory dynamics (i.e., when survival was low, individuals tended to be larger) buffered biomass across different ecological contexts, thereby reducing differences between synchrony treatments. These complex interactions between species' mean phenologies and phenological synchrony within populations indicate that predicting the outcomes of mean phenological shifts on species interactions requires consideration of distribution of phenologies within populations.

Overall, the results indicate maintenance of low phenological synchrony within populations as a bet-hedging strategy. Bet-hedging life-history strategies increase fitness in unpredictable environments (Tarazona et al. 2017, Rocha et al. 2018, Shima et al. 2018), and our results show individual variation in hatching could buffer survival across good and bad conditions. By "putting all their eggs in one basket," highly synchronized populations run a great risk of mistiming because all individuals are affected. In good scenarios, survival was highest, but when populations arrived at the same time or late relative to their competitor, all individuals faced strong competition and survival was low. Similarly, when highly synchronized populations mistime events (e.g., migratory birds arriving before their food, alpine flowers blooming before a snowfall, insect swarms emerging before spring green up), fitness costs are high (Both et al. 2006, Inouye 2008, Mayor et al. 2017).

The relationships of phenologies across life stages

Organisms go through a series of life-history stages during a year, but we rarely pay attention to whether and how the phenological patterns are preserved or change across life-history events and what the underlying mechanisms are. In our study, we found that phenological patterns were not preserved across stages (hatching vs. emergence), but instead changed: differences in intra- and interspecific competition caused by differences in hatching phenology carried over to affect the phenology of the next ontogenetic stage, emergence.

In cases without interspecific competition, we saw a complete reversal of synchrony from hatching to emergence: populations that hatched with low synchrony emerged with high synchrony and vice versa. We attribute this to strong size-mediated priority effects, which gave early-arriving individuals an advantage in low-synchrony populations, generated a bias in survival, and led to synchronous and early-emergence phenology. High hatching synchrony shifted to low-emergence synchrony because high intraspecific competition prolonged the interaction period and slowed individuals' growth. Adding interspecific competition complicated this by modifying the drivers—density and per capita differences in size—that caused these shifts. When the interspecific competitor arrived early, density/competition was higher and the advantage of early arrival was reduced. In general, interspecific competition increased mean and variation in emergence phenology, but the magnitude of these changes depended on initial phenology conditions (i.e., at hatching). Together, this provides clear experimental evidence that not only can phenological shifts affect species interactions, but species interactions can in turn drive phenological shifts.

This feedback between species interactions and phenology is likely to be seen in systems where competition is high and organisms' development rates are plastic. Because strong competition drove phenological shifts across ontogeny, we only expect it to happen when resources are limited to some extent. Further, it requires individuals to be plastic in their development rates. Consistent with many species that utilize ephemeral habitats, emergence timing was highly plastic (ranging from 22 to 152 d), which strengthened the advantage of early individuals (Newman 1992, Blanckenhorn 1998, Denver et al. 1998). In more stable environments, development times are generally less flexible or even fixed, and in these cases, we would not expect phenological shifts across ontogeny to be as strong (DeWitt et al. 1998). It would be possible to test whether competition drives phenological shifts in other natural populations without conducting manipulative experiments by measuring the phenological synchrony of natural populations at different phenological stages. It remains largely unknown what mechanisms determine phenology (either mean or synchrony) across ontogenetic stages and years. Data on phenological synchrony across ontogenetic stages could help determine these mechanisms and therefore predict which species are likely to shift.

CONCLUSIONS

Phenological shifts are a well-documented response to climate change, and it is time to start linking these patterns to expected impacts in natural communities. We show that this requires expanding our typical treatment of phenology to include not just first or mean events, but also variation around these metrics within populations. Changes in phenological synchrony within

populations are just as likely to alter ecological interactions as changes in phenological mean, and the effects are likely to be synergistic. Importantly, our study also reveals a feedback loop between phenology and ecological interactions: Shifts in phenology can alter the mechanisms driving the outcome of interactions, but the same changes in mechanisms and outcome of interactions can in turn alter phenological patterns in the next life stage. Together, this highlights the need to integrate multiple aspects of phenological patterns with species interactions to understand and predict the effect of phenological shifts on natural communities.

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DATA AVAILABILITY

Data and scripts are available from the Dryad Data Repository: <https://doi.org/10.5061/dryad.69325t8>