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E-ARTICLE

Exploring Conditions That Strengthen or Weaken the Ecological and Evolutionary Consequences of Phenological Synchrony

Shannon K. Carter* and Volker H. W. Rudolf

Department of Biosciences, Program in Ecology and Evolutionary Biology, Rice University, Houston, Texas 77005

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ABSTRACT: Climate change–driven phenological shifts alter the temporal distributions of natural populations and communities, but we have little understanding of how these shifts affect natural populations. Using agent-based models, we show that the interaction of within-population synchrony (individual variation in timing) and timing of interspecific interactions shapes ecological and evolutionary dynamics of populations within a seasonal cycle. Low-synchrony populations had lower survival and biomass but relatively stronger individuals. These effects were surprisingly robust and did not require size-based competitive asymmetries. However, reducing population synchrony could either negatively or positively affect population demography depending on whether the phenology of the focal species was advanced or delayed relative to its competitor. Furthermore, selection for earlier hatching increased when the interspecific competitor arrived earlier and when population synchrony was high. These results emphasize the importance of variation in the phenology of individuals within populations to better understand species interactions and predict ecological and evolutionary outcomes of phenological shifts.

Keywords: phenology, phenological synchrony, agent-based model, population demography, species interactions, competition.

Introduction

The dynamics of natural communities are driven by the interactions within and among comprising populations. Strength of competition is usually assumed to simply scale with density, but composition of individuals can also play a strong role because individuals can vary greatly in size, competitive ability, and other demographic traits (Polis 1984; Bolnick et al. 2011). These traits can influence other members of the community directly by influencing pairwise interaction outcomes (Crumrine 2005; Petchey et al. 2008; Carter et al. 2018*b*) and indirectly by affecting density/numeric effects (Carter and Rudolf 2019). To further complicate things, individuals' performances are influenced by other members of the community, including intra- and interspecific competitors (Roughgarden 1983). Thus, the individual composition of populations and community dynamics are inherently linked.

Variation in the seasonal timing of life history events (e.g., phenology) within a population is a key factor governing per capita differences among individuals. In seasonal communities, most interactions occur among growing individuals and are initiated by relative phenologies (e.g., date of reproduction, hatching, germination; Yang and Rudolf 2010; Rudolf 2019). Individuals that differ in their phenology also typically differ in the environmental conditions they have encountered and in age, which is often linked to size, competitive ability, or other traits (Miller-Rushing et al. 2010; Rasmussen and Rudolf 2015; Carter and Rudolf 2019). Importantly, climate change alters the temporal distributions of natural populations and communities (CaraDonna et al. 2014; Carter et al. 2018*a*), emphasizing the need for a clear framework for predicting what conditions/systems are likely to strengthen or weaken effects of temporal shifts in natural communities.

One way in which the temporal distribution of a phenological event (hereafter, "phenological synchrony") can affect ecological interactions is by increasing age-dependent per capita effects (i.e., differences in relative competitive ability of older vs. younger individuals in a population; Peters 1983). Low-synchrony populations (high variation in individual timing around the mean) are composed of individuals with a wide range of ages compared with highly synchronized populations. Since older individuals in low-synchrony populations have more time to grow, they are likely to be larger (fig. 1*a*). This could lead to competitive asymmetry (i.e., differences in per capita effects across individuals), whereby few strong (early-arriving) individuals monopolize resources (Rasmussen and Rudolf 2015; Carter and Rudolf 2019). For example, resources are

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* Corresponding author; email: skcarter25@gmail.com.

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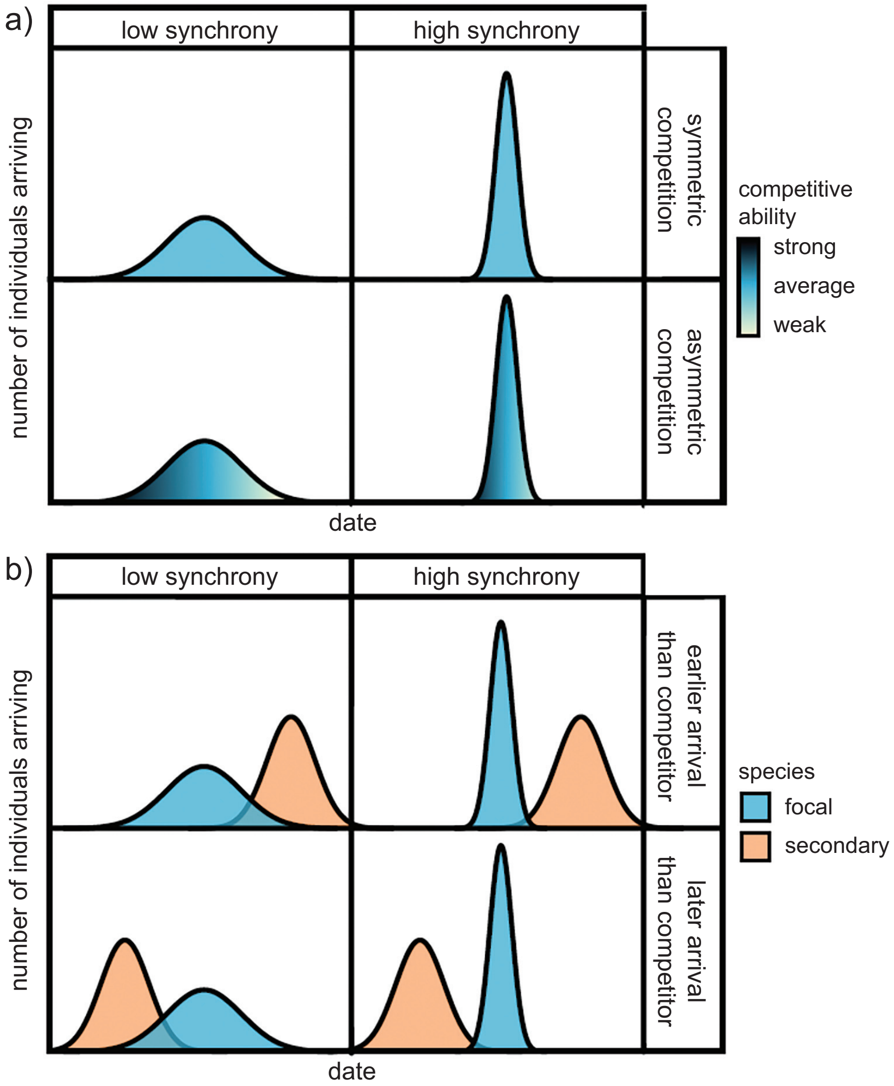

Figure 1: Conceptual framework illustrating different factors that could strengthen or weaken the effect of phenological synchrony. Panel *a* shows that competitive asymmetry and synchrony will interact to affect the proportion and relative competitive ability of early- versus late-arriving competitors. Panel *b* shows that in a community context, the presence and timing of a heterospecific competitor could strengthen or weaken the advantage of early arrival and therefore the competitive asymmetries between individuals in a population.

disproportionately captured by stronger (often larger) competitors: tall plants receive more light (Weiner 1990), and large animals control larger territories (Robertson 1996; Young 2004) and consume more resources (Hamrin and Persson 1986; Englund 1991; French and Smith 2005; Bassar et al. 2013). Recent studies have proposed that size-mediated competitive asymmetry is the key mechanism linking phenological synchrony to population-level patterns (e.g., survival, mean per capita mass) and species interactions (Rasmussen and Rudolf 2015; Carter and Rudolf 2019). However, these empirical studies have been unable to track individuals over time, making it impossible to compare the performance of early versus late individuals and therefore demonstrate the underlying mechanisms and role of competitive asymmetry. Furthermore, in nature intraspecific competition spans a continuum from highly symmetric to highly asymmetric per capita effects (Nicholson 1954; Hassell 1975; Peters 1983; Schwinning 1996; Weiner et al. 2001). For instance, in some cases resources are evenly allocated to all individuals (symmetric competition). This includes belowground root competition in plants (Gerry and Wilson 1995; Cahill and Casper 2000) and resource competition among nonhierarchical social or aggregate groups (Isbell 1991; Lima et al. 1999; Etienne et al. 2002). In species where individuals are competitively equal across ages, the effect of synchrony could be weaker or even absent compared with a species in which consumption rates scale with size. The ecological and evolutionary effects of phenological synchrony could therefore depend on how the per capita effect of individuals scales with age and size differences among individuals. However, because previous studies have generally been confined to a single fixed relationship between age/size and competitive ability, the connection between the consequences of phenological synchrony and competitive asymmetry remains poorly understood.

The picture is further complicated because community context can modify the effects of phenological synchrony and its interaction with intraspecific competitive asymmetry (fig. 1*b*). For example, if early individuals arrive before heterospecific competitors, this low-competition context should allow them to grow more and strengthen their competitive advantage over later (conspecific and heterospecific) arrivers (Dash and Hota 1980; Levitan 1988; Schram et al. 2006; Rudolf 2018; Rudolf and McCrory 2018). This increase in competitive asymmetry has been shown to decrease population survival but increase average size of surviving individuals (Carter and Rudolf 2019). In contrast, if early individuals arrive after heterospecific competitors, the resulting increase in interspecific competition could decrease the advantage that early arrivers have over later-arriving conspecifics, resulting in a more symmetric population with higher survival but overall weaker/smaller individuals. The timing (relative phenology) of interspecific interactions could therefore alter the consequences of population synchrony by either equalizing or strengthening differences in the intra- and interspecific competitive abilities of individuals. These changes in relative fitness within populations should also alter selection on timing of phenology and thus the potential of populations to adaptively shift their phenology in response to climate change. Phenological synchrony therefore likely determines both how the population experiences and responds to the environment and how the population affects the environment, but processes and outcomes are difficult to intuit or pull out empirically given the complex feedbacks.

Here we develop an agent-based model to (1) measure the effects of phenological synchrony on population vital rates, relative fitness, and competitive interactions; (2) determine mechanisms (e.g., individual differences in timing and competitive ability) driving effects of phenological synchrony; and (3) explore how size-mediated competitive asymmetry and competitive context can strengthen or weaken these mechanisms. This approach allowed us to link intra- and interspecific variation in phenologies to population demographic rates, quantify natural selection, and identify the underlying mechanisms across different ecological contexts, thereby providing a holistic understanding of how phenological shifts will influence populations and communities.

Methods

Model Overview

We constructed an agent-based model in NetLogo to examine how phenological synchrony affects resource competition and explore how these effects change across different ecological contexts (Wilensky 1999). An agent-based model is appropriate for this question because the actions of individuals govern the dynamics of the system: size/age differences among individuals determine consumption rates, resource drawdown, and interactions among individuals (Tisue and Wilensky 2004; Railsback and Grimm 2019). Agent-based models have been successfully used to model and study ecological dynamics of animal and plant cohorts (Trebitz 1991; DeAngelis et al. 1993; DeAngelis and Gross 2018). Here we expand these models in several new ways that explore the ecological and evolutionary consequences of phenological synchrony and competitive asymmetry across different community contexts.

Our general approach was to evaluate the response of key demographic rates (proportion survival, biomass export, developmental period, individual growth rates, and individual body size) across a gradient of phenological synchrony. Phenological synchrony in this case refers to the amount of individual variation around the mean date of a phenological event that signifies arrival to a new environment or resource niche (e.g., hatching, migratory arrival, metamorphosis). To explore the effects of synchrony across different ecological contexts, we then varied (1) scaling ratio between body size and consumption rate (competitive asymmetry), (2) mean timing relative to a heterospecific resource competitor, and (3) relative competitive strength with heterospecific competitor (competitive dominance).

Model Description

Our model simulated the arrival of a consumer population (meant generally as any phenological event bringing a population to a new resource), its consumption of a limited resource, growth, and survival to the subsequent phenological event (again, meant generally to represent any life history event that removes individuals from this resource, such as metamorphosis, switch to reproductive stage, change in habitat or resource use, or migration). A single generation was modeled. This generic life cycle can represent a diversity of systems. For instance, it could reflect the life cycle of invertebrates (e.g., dung beetle, fruit fly), vertebrates (e.g., amphibians), or plants (e.g., annual desert plants) exploiting a temporary resource. Details of parameters and their relations used in simulations can be seen in table 1 and figure 2, and a verbal overview follows. Note that any of the functions or parameters can easily be modified to simulate other systems.

Table 1: Model parameters

Parameter	Description	Value(s) and explanation
σ	Standard deviation of phenological arrival (i.e., [inverse of] phenological synchrony)	Adjusted as an explanatory variable; tested values 0 (high synchrony) to 30 (low synchrony) at intervals of 3
a	Scaling ratio between size and consumption rate (i.e., competitive asymmetry)	Adjusted as an explanatory variable; tested values 0, .5, 1; for $a = 0$, size-dependent maintenance cost was removed; for the heterospecific competition model, a was fixed at .5
μ	Mean date of phenological arrival	Fixed at 40—earliest mean possible such that with $\sigma = 30$, the earliest individuals had an arrival date greater than 0; for the heterospecific competition model, μ of the competitor was fixed at 60, and μ of the focal species was 45 (early arrival), 60, 75 (late arrival)
i	Intercept of relationship between size and consumption; baseline feeding amount (number of units)	Fixed at 3—sensitivity tests showed no qualitative differences for $i = 2, 4$ (fig. S1); for 2 consumer model, to make secondary species competitively dominant, i was set to 4 with sensitivity tests for $i = 3, 5$ (fig. S5)
d	Amount of growth per patch consumed	Fixed at .05—sensitivity analyses showed no qualitative differences for $d = .045, .055$ (figs. S2, S6)
t	Time step; 1 unit approximates 1 day	. . .
m	Constant time-independent mortality rate	Fixed at .0017—calculated by average mortality per time step
w	Minimum threshold size for advancement to next phenological stage	Fixed at 6—sensitivity analyses showed no qualitative differences for $w = 5, 7$ (figs. S3, S7)
p	Resource unit; p_a refers to number of units that are available for consumption, and p_{tot} refers to the total number of resource units initially in the environment	p_{tot} is fixed at 9,801 to generate resource competition yielding intermediate survival; p_a is dynamic property depending on resource drawdown by consumers
f	Number of units consumed by a focal individual in a single time step	Dynamic property related to the individual's size and resource availability
s	Current size of individual	Dynamic property related to the individual's consumption
g	Growth rate over the last 5 time steps	Dynamic property measuring change in size over the previous 5 time steps; sensitivity analyses showed no qualitative differences for considering recent growth over the last 3 or 7 time steps (figs. S4, S8)

In the model, arrival timing of individuals is governed by a normal distribution, with standard deviation (σ) around the mean (μ) representing phenological synchrony. We tested a uniform distribution as well, which produced the same qualitative results. The effect of phenological synchrony was tested across a range from $\sigma = 0$ (highest synchrony) to $\sigma = 30$ (lowest synchrony) at intervals of 3. Individuals took on average 100 days to develop, which is nearly equivalent to the range of arrival timing for the case with lowest synchrony. The number of consumers was fixed at 80, which facilitated an amount of competition to support intermediate survival. The resource was nonrenewable and temporary—reaching peak abundance when the consumers arrived and depleted only by consumption. This decision was based on the temporary systems we worked in and the data we had to compare/validate our model, but more generally, it reflects most temporary systems (e.g., temporary ponds, rotting fruit, or host of parasites) or any systems driven by resource pulses or where consumption rates substantially exceed renewal rates of the resource. All individuals enter the environment at the same size, arbitrarily defined as one.

On arrival, individuals consume and grow. At each time step (which roughly equates a day) an individual consumes a number of resource units, f, related to resource availability, instantaneous size, and the size-consumption scaling relationship, a. When $a = 0$, consumption rates are independent of the size of individuals (all individuals have same consumption rates). In contrast, when $a > 0$, consumption rates scale positively with size, and larger individuals consume more resources than smaller individuals. In the model, we varied a, testing three different scenarios ranging from perfectly symmetrical intraspecific competition ($a = 0$; all individuals consume at the same rate regardless of size/age), as commonly seen with underground plant competition (Gerry and Wilson 1995; Cahill and Casper 2000) or resource allocation among social groups (Isbell 1991; Lima et al. 1999; Etienne et al. 2002), to strong asymmetrical competition ($a = 1$; larger individuals consume at a higher rate than small individuals), such as aboveground

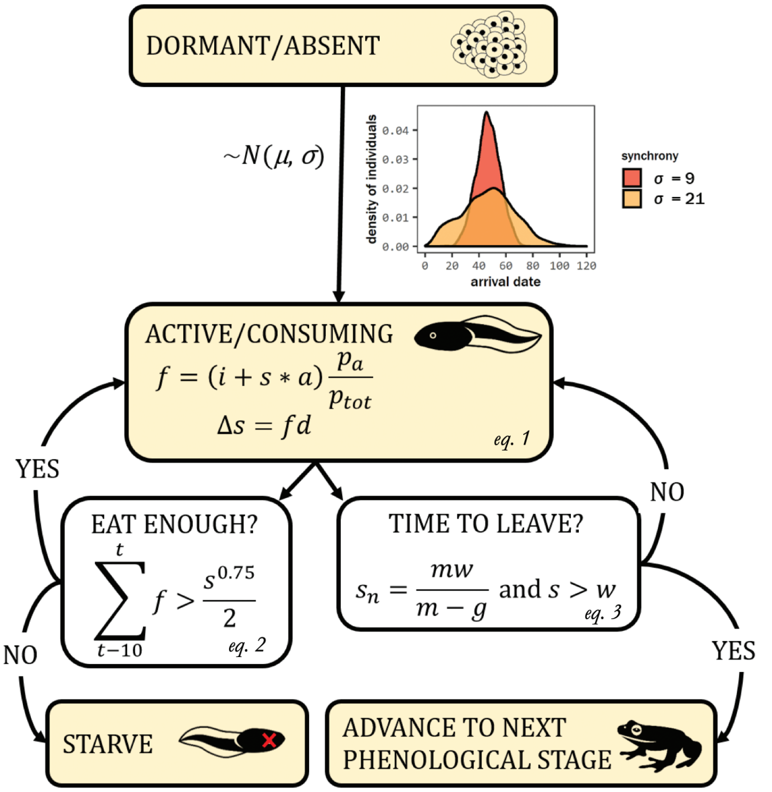

Figure 2: Schematic of different states of individuals in the model and relationships between them. Yellow boxes indicate different stages of individuals, and white boxes indicate relationships that govern transitions between different stages. The model describes a generic system where individuals start interacting with their environment when they become active (e.g., hatch, emerge from dormancy, germinate). When individuals become active naturally varies across individuals, and this variation follows a general distribution (N, with a given mean [μ] and variance [σ]). Populations can vary along a spectrum from high phenological synchrony (low variation across individuals) to low synchrony (high variance). Once individuals become active, they consume (and thus compete for) a shared depletable resource (e.g., algae or nitrogen; eq. [1]). Individuals starve if they do not consume enough to meet basic metabolic needs (eq. [2]). Once individuals have reached a certain minimum size threshold ($s > w$), they constantly evaluate their current stage and recent growth rates to determine the optimal time for advancing to the next phenological stage (e.g., metamorphosis, initiate reproduction, or dormancy; eq. [3]). See “Methods” and table 1 for detailed model and parameter descriptions, but note that the individual model components and functions of the model can be adjusted to reflect the details of a wide range of animal and plant systems.

competition in plants (Weiner 1990) and resource competition in size-structured populations (Hamrin and Persson 1986; Englund 1991; Bassar et al. 2013). We also simulated an intermediate case ($a = 0.5$) between these two extremes. Individuals die by starvation if they do not consume enough resources in recent history to support size-scaled basal metabolism ($s^{0.75}$; Reichle 1968; West et al. 1997; White and Seymour 2003). For cases where $a = 0$, since consumption did not increase with size, we removed the scaling of maintenance cost with size. In these cases, we simulated a fixed (size-independent) starvation threshold of 2, which was roughly equivalent to the average of the starvation threshold across sizes for $a = 0.5$ and $a = 1.0$.

We followed the optimality model approach of Day and Rowe (2002; their eq. [7]) to determine when individuals move on to the next phenological stage. The full model is explained in detail in Day and Rowe (2002). Briefly, we assume that individuals need to reach a minimum size w before they can advance to the next stage (Day and Rowe 2002; Rudolf and Rödel 2007). After they reach the threshold, individuals evaluate at each time step whether conditions for transition to the next stage are met, based on a trade-off between their current size, s; current growth rate, g; mortality, m; and minimum size, w (fig. 2, eq. [3]). If the conditions are met, individuals advance to the next phenological stage (e.g., metamorphosis, change in resource use, migration; see fig. S1 for examples of the relationship between growth trajectories and timing of metamorphosis).

To test the role of ecological context, a heterospecific consumer was added, with different arrival means relative to the focal species. Arrival phenology of this heterospecific competitor was fixed at mean 60 with standard deviation of

5. The phenological mean of the focal species was adjusted relative to the heterospecific consumer to be earlier than the competitor ($\mu = 45$), same time as the competitor ($\mu = 60$), or later than the competitor ($\mu = 75$). These mean arrival times were tested across the same range of synchrony outlined above (from 0 to 30 at intervals of 3). For all cases in the two-species model, we used weak competitive asymmetry ($a = 0.5$) for both species. Additionally, we made the heterospecific competitor a stronger competitor than the focal species (consuming on average one more resource patch per time step) to strengthen effects of mean arrival timing.

Selection Analysis

To elucidate the potential evolutionary consequences of phenological synchrony and timing of interactions and understand how phenological synchrony itself might change over time, we calculated relative fitness of individuals and selection gradients across different ecological scenarios. Since our model focuses on the early life stage of organisms and does not specifically include reproduction, we focused on traits that are closely (positively) correlated with lifetime fitness: survival and mass at metamorphosis. The latter is typically (but not always) positively correlated with future reproductive output and survival in many systems. Following previous work (Weis et al. 2015; De Lisle and Svensson 2017), we relativized fitness and standardized arrival date to zero mean and unit variance within each population. We pooled all simulations for a given ecological scenario, since by design all variation between replicates is due to sampling error alone. We then used standard generalized linear models (GLMs) to calculate selection (i.e., partial regression) coefficients. In the single-species scenario, we used relative arrival time (i.e., percentile), population synchrony, and competitive asymmetry as predictors. The same model was used in the two-species scenario but with arrival time instead of competitive asymmetry as fixed predictor. We analyzed survival using a GLM with logit link and binomial distributed error and back-transformed coefficients to obtain standard selection coefficients (Janzen and Stern 1998). We analyzed only mass data of survivors, which was normally distributed and thus analyzed with standard Gaussian error distribution. Simulations with perfect synchrony ($\sigma = 0$) were excluded from the analyses because relative hatching time is the same for all individuals. All analyses were carried out in R using the lme4 package (Bates et al. 2015).

Sensitivity Analysis

One of the main goals of this study was to evaluate different systems/conditions that strengthen or weaken the ecological effects of phenological synchrony. Thus, we avoided setting parameters from reference literature for particular systems to maintain as much generality in the model's parameters as possible. Instead, we reduced the number of parameters as much as possible, and for those we set, we performed rigorous sensitivity analyses. For perturbations of parameters i, d, w, and g, we adjusted plus or minus ≥10% and compared quantitative and qualitative results with the chosen model. Recent growth rate, g, was an emergent property of individual resource consumption. Thus, we did not perturb g per se but instead adjusted the time interval considered "recent" growth. In some cases, perturbations changed quantitative results, but qualitative patterns were robust to these perturbations (figs. S1–S8). The few cases that produced qualitative changes in results are detailed in "Discussion."

Results

Effect of Synchrony and Size-Based Competitive Asymmetry on Demographic Traits

Phenological synchrony had strong effects on all five demographic rates we measured, and the magnitude of these effects was contingent on competitive asymmetry. Generally, increasing competitive asymmetry strengthened the effects of phenological synchrony: synchrony mattered most for populations with strong asymmetric competition, with vital rates differing by as much as 42% across a range of phenological synchronies (fig. 3). However, even with perfectly symmetric competition (consumption rates of all individuals equal, regardless of age or size), vital rates changed significantly with synchrony (7%–14% difference across the range of synchrony), suggesting that age- and size-dependent differences in competitive ability are not required for synchrony effects. We also found that synchrony usually had nonlinear effects (i.e., small changes in synchrony had large effects when synchrony was high but small effects when synchrony was already low). This decline is likely because in treatments with lowest synchrony ($\sigma \cong 24$–30), individuals are spread so thinly across time that all densities are low (i.e., zero to two individuals arriving per time step).

Survival, Biomass, and Body Size. Survival decreased as synchrony decreased, with late arrivers failing to complete development. Those that survived, the early arrivers, grew to greater size. However, the increase in size did not compensate for the decrease in numbers, so the total biomass export fell with decreasing synchrony. The pattern for biomass qualitatively matched survival, but effect sizes for biomass were roughly half (fig. 3). The smaller effect size for biomass versus survival can be explained by differences in per capita body size. Body size of surviving individuals generally increased as populations became less synchronized. So reductions in survival at low synchrony were partially

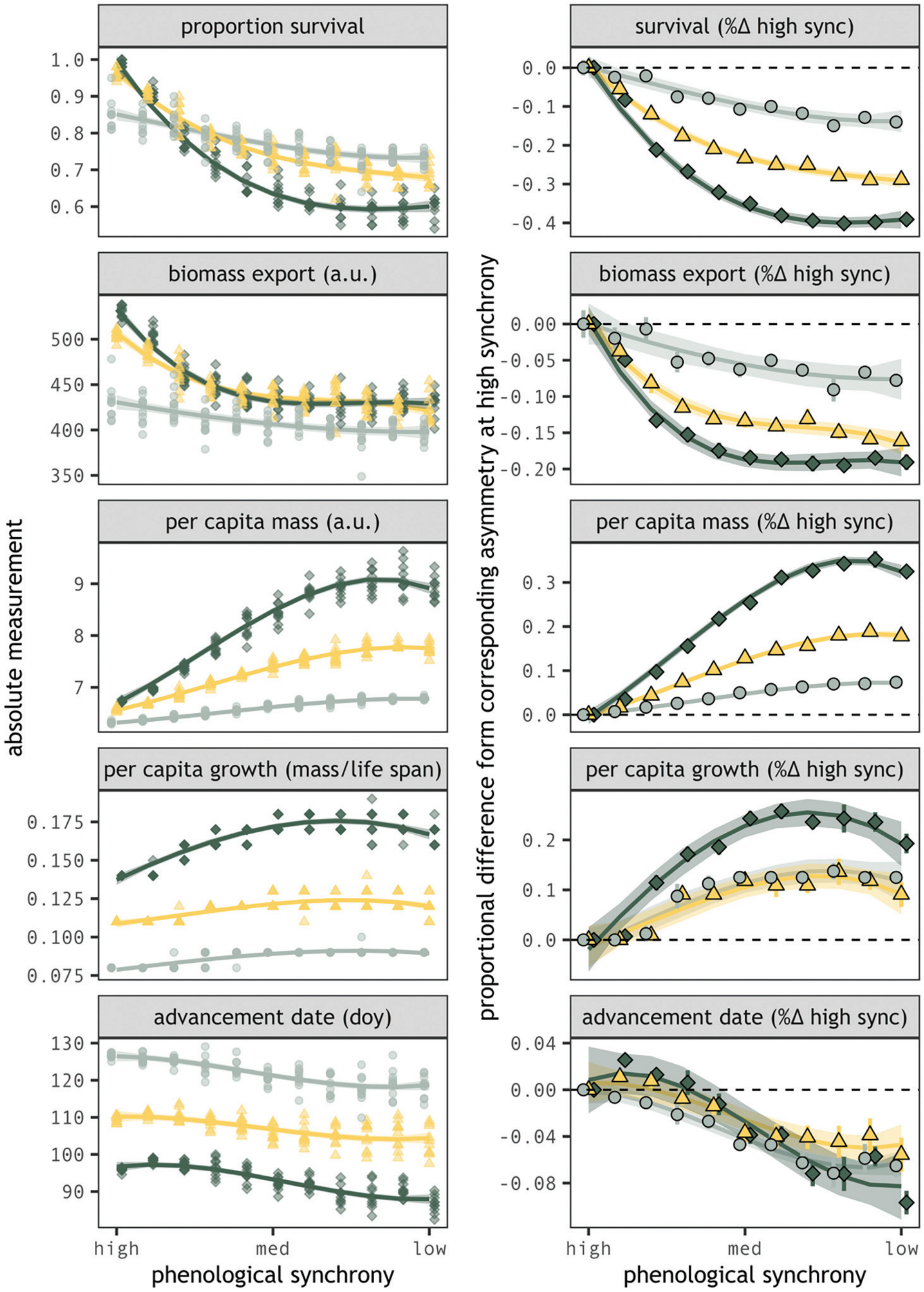

Figure 3: Effects of phenological synchrony and size-dependent competitive ability (asymmetry) on vital rates of a consumer population. The left panel shows absolute data from 10 simulation replicates. The right panel shows results proportionally scaled to high synchrony, which served as a control to allow a baseline for interpreting the effects of asymmetry in per capita competition. To scale our results for a particular vital rate, we took the absolute value, subtracted the value for the same asymmetry treatment in the case with highest synchrony, and divided by the absolute value. Rows represent different vital rates. Gray circles represent no asymmetry (uniform competitive ability for all individuals), yellow triangles represent weak size-based competitive asymmetry, and green diamonds represent strong asymmetry. a.u. = arbitrary units.

counterbalanced by larger average body sizes, thereby reducing differences in biomass.

All three of these effects were amplified by increasing size-based competitive asymmetry. For instance, survival was up to four times lower at lowest synchrony in populations with strong competitive asymmetry compared with populations with competitive symmetry. This difference arose because at high synchrony, a higher proportion of resources went to individuals that ended up dying, relative to low-synchrony populations where resources were more strongly allocated toward those individuals that survived (compare growth rates of dead individuals across synchrony levels; fig. 4).

Growth Rates and Timing of Advancement to Next Phenological Stage. Low phenological synchrony and strong competitive asymmetry both increased mean somatic growth rates and advanced transition to the next phenological stage. With competitive symmetry, growth rates were on average 9.1% higher in low-synchrony populations relative to high-synchrony populations. With size-mediated competitive asymmetry, this difference increased to 12.5% for populations with weak competitive asymmetry and to 21.4% for populations with high competitive asymmetry (fig. 3).

This pattern is predominantly driven by how resources were divided across individuals, as indicated by individual growth rates. At high synchrony, there was little difference between growth rates of early- and late-arriving individuals and those that survived or died. However, at low synchrony, early individuals grew much faster and survived, while latecomers had much lower growth rates and many died (fig. 4). This difference in growth rates between survivors (early arrivers) and nonsurvivors (late arrivers) was enhanced by competitive asymmetry: the fastest-growing (early-arriving) individuals grew even faster (>2 times) compared with populations with competitive symmetry because of the positive feedback between growth rate and competitive ability. Additionally, late arrival resulted in slow growers that did not survive. Thus, two mechanisms, acceleration of growth rates and death of slow growers, jointly elevated mean population growth rates. The same mechanisms also advanced the next phenological stage to an earlier mean date for populations with highly asymmetric competition and low synchrony relative to populations with symmetric competition and high synchrony.

Overall, our results were robust to the specific parameters/assumptions we used (figs. S1–S8). The only condition where qualitative results varied was when we reduced parameters related to feeding efficiency (i, p, w) for symmetric competition populations (compare gray lines on survival and biomass panels across variable perturbations for figs. S1–S4). In these cases, survival and biomass followed an opposite relationship with synchrony: survival/biomass increased as populations became less synchronized. This is because for high-synchrony populations without size-dependent competition, resources were evenly distributed among individuals. If resources were plentiful enough to support survival, this led to high survival and small individuals, but if resources depleted before individuals satisfied the minimum size requirement to advance (as was the case when we reduced resource efficiency), there was a mass die-off.

Selection on Phenology. Relative hatching time was negatively related to relative fitness of individuals for both survival and mass (fig. 5). However, this relationship was contingent on phenological synchrony and competitive asymmetry (two-way and three-way interactions in table S1). The relative fitness advantage of individuals that hatched first increased with lower synchrony, and this effect was strengthened in populations with higher competitive asymmetry. Overall, this suggests that selection strongly favors early hatching, especially in systems with low synchrony and high competitive asymmetry.

Effects of Synchrony and Relative Timing on Species Interactions

When a heterospecific competitor was present, demographic rates and selection were driven by the interaction of phenological patterns within and across species. While later arrival relative to the interspecific competitor generally resulted in reduced performance of a population and individuals (fig. 6), this effect was contingent on the phenological synchrony within populations. At high within-population synchrony levels, species that arrived early or at the same time as their competitor had much higher survival than late-arriving populations, but this difference became negligible at low synchrony levels. This interaction was driven by the contrasting effects of population synchrony. When the focal species arrived before or at the same mean arrival time as the competitor, reducing synchrony decreased survival. However, the opposite was true when the focal species arrived on average after the competitor: here low-synchrony populations had higher survival relative to high-synchrony populations. These opposing effects of population synchrony can be explained by differences in the fate of individuals. The cost of arriving late was reduced at low synchrony because not all individuals arrived after the heterospecific competitor in low-synchrony populations; the earliest individuals were arriving concomitantly or earlier than heterospecific competitors. For the heterospecific competitor, patterns were generally weaker

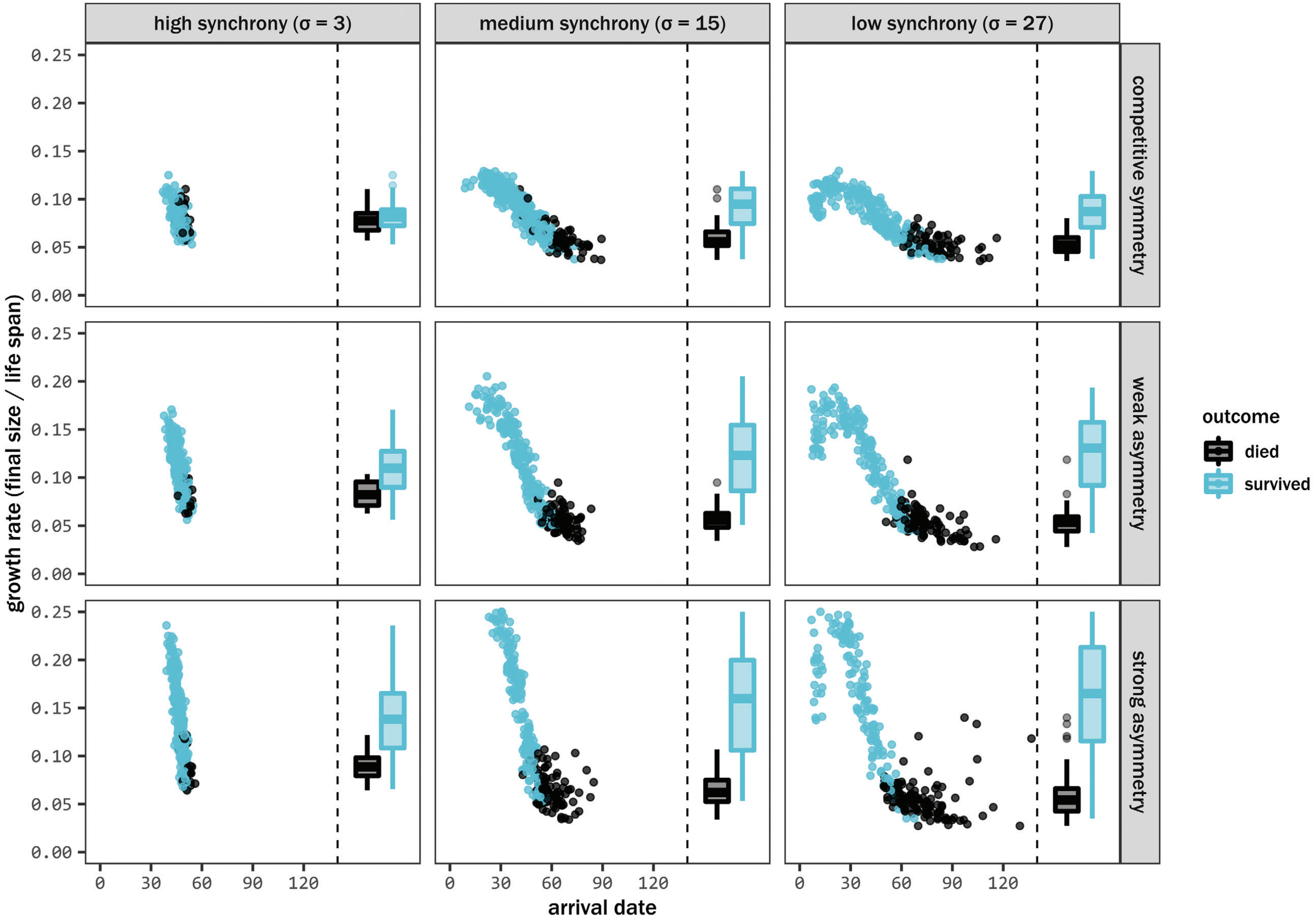

Figure 4: Growth rates for individuals based on their arrival date for populations with different arrival phenological synchronies (columns) and competitive asymmetries (rows). Blue points signify individuals that survived, and black points signify individuals that died. Boxplots show median and variation in growth rates for individuals across arrival dates and are placed in an arbitrary position on the *x*-axis. All simulations are based on moderate size-based competitive asymmetry ($a = 0.5$).

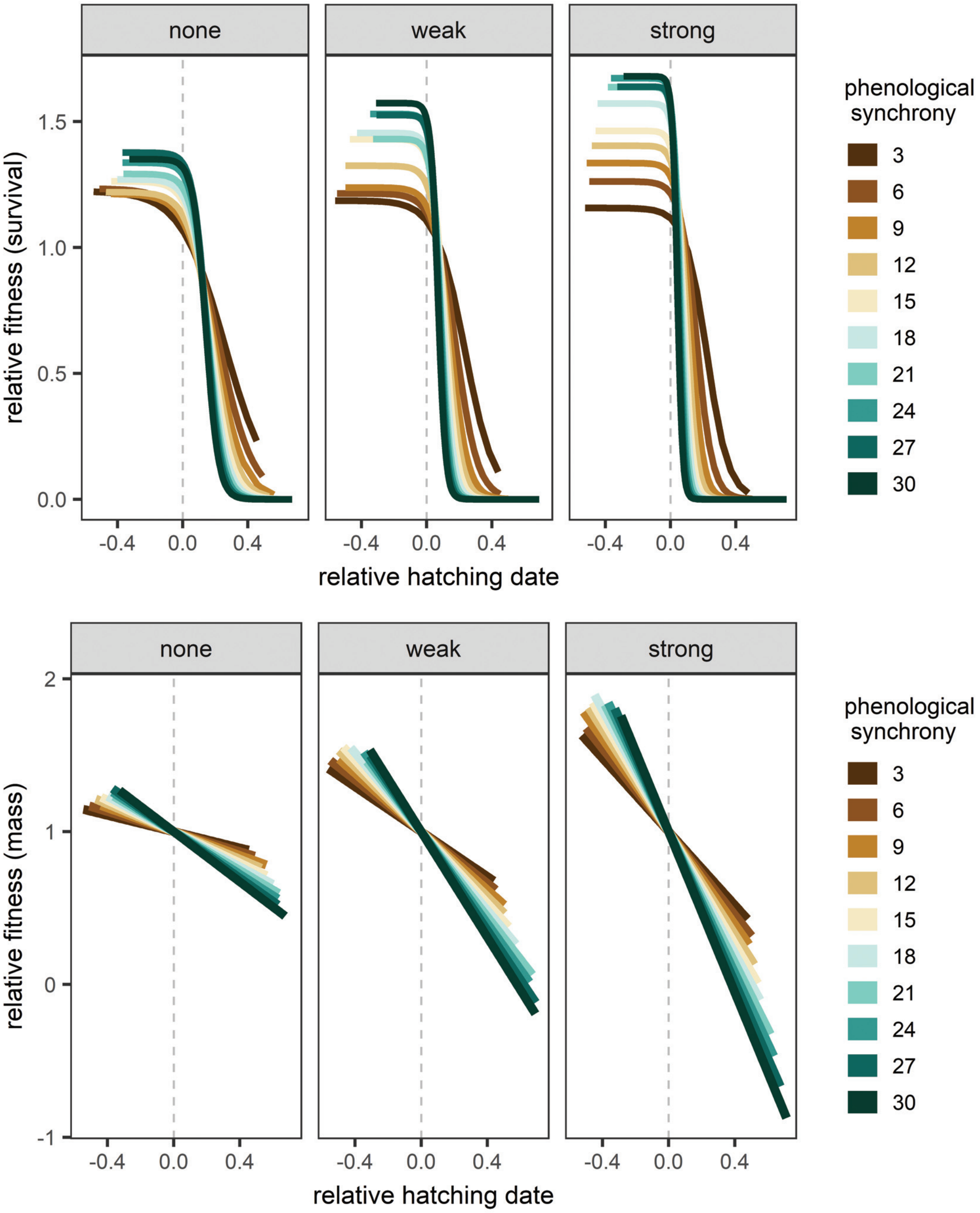

Figure 5: Effects of phenological synchrony and size-dependent competitive ability (asymmetry) on selection gradients across hatching dates of individuals using survival or mass (at metamorphosis) as fitness proxy. Panel headings (rows) indicate respective strength (none, weak, or strong) of competitive asymmetry. Phenological synchrony indicates level of variation in hatching dates within populations, ranging from high synchrony (3 = low variation) to low synchrony (30 = high variation).

in the opposite direction (fig. S10), so we focus our discussion of the results on the focal species.

Survival, Biomass, and Body Size. Low-synchrony populations that arrived at the same time as or before their competitor had lower survival (31.2% and 30.0%, respectively) and biomass export, although biomass decreased more in the latter scenario (6.4% same vs. 17.5% earlier arrival). However, when populations arrived later then their competitor, survival and biomass increased substantially

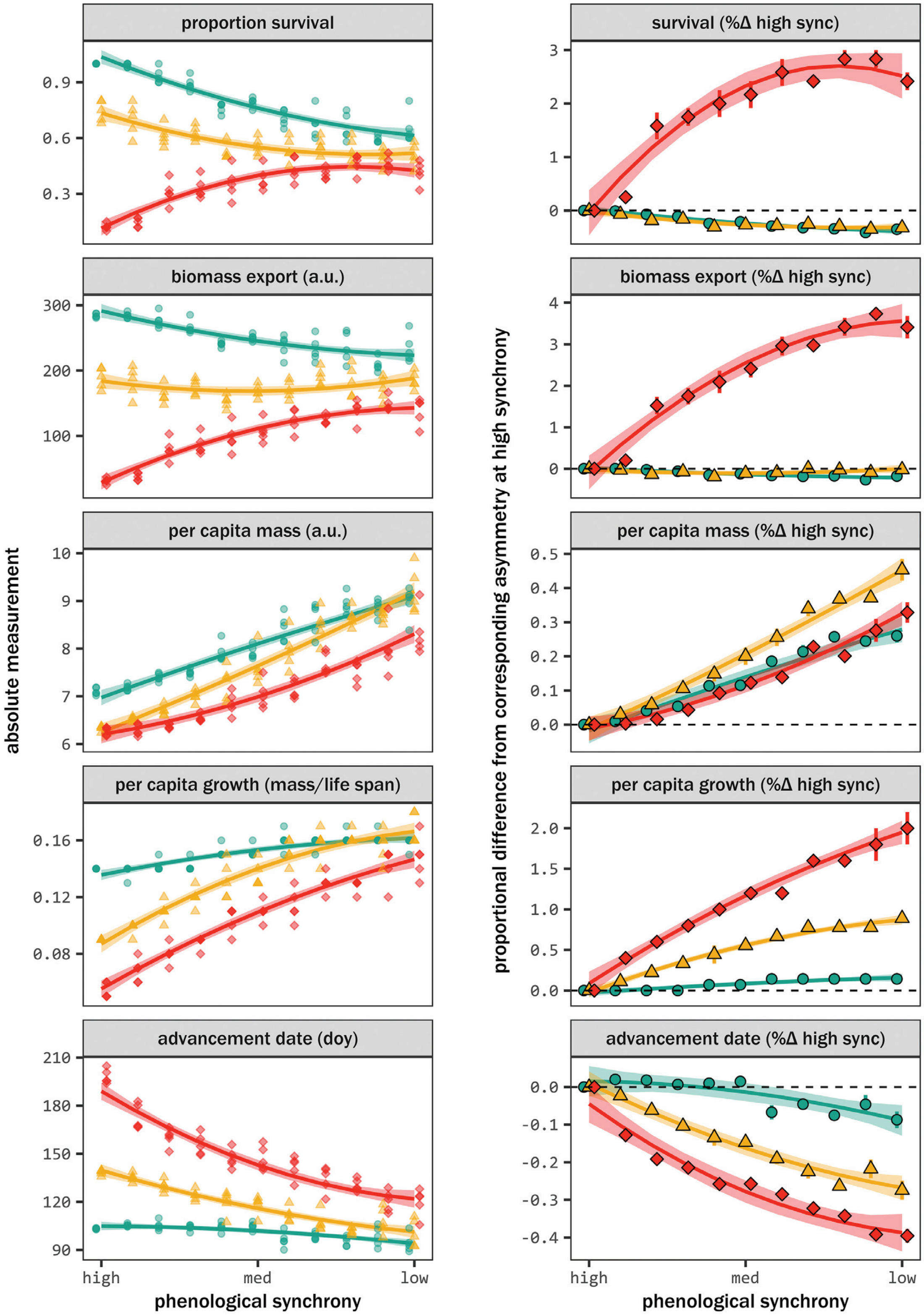

Figure 6: Effects of phenological synchrony and relative mean arrival relative to heterospecific competitor (community context) on vital rates of a consumer population. The left panel shows absolute data from 10 simulation replicates. The right panel shows results proportionally scaled to high synchrony, which served as a control to allow a baseline for interpreting how the effect of synchrony changes in different community contexts. To scale our results for a particular vital rate, we took the absolute value, subtracted the value for the same mean arrival treatment in the case with highest synchrony, and divided by the absolute value. Rows represent different vital rates. Green circles represent early arrival relative to competitor, yellow triangles represent same arrival as competitor, and red diamonds represent later arrival than competitor. a.u. = arbitrary units.

as populations became less synchronized, and this effect was stronger in magnitude (356% increase for survival and 554% increase for biomass). Note that this pattern is also counter to the pattern in single-population simulations (fig. 3). This positive effect of low population synchrony was driven by the fact that individuals of low-synchrony populations were sufficiently spread temporally that some individuals arrived before the heterospecific competitors. The early individuals survived, increasing the survival relative to high-synchrony populations where all individuals arrived after the heterospecific competitor when resources were already depleted.

For all arrival scenarios, average per capita biomass increased as populations became less synchronized. Therefore, at the individual level, effects of synchrony were the same across community contexts, but population-level effects were different. The magnitude of this trend was equal for populations arriving at the same time as or after the competitor (35.8% increase) but less for populations arriving before the competitor (18.1%; although these populations had a higher average per capita mass across the range of population synchronies). Overall, these results demonstrate that the effects of population synchrony have to be considered in a community context and depend on the relative timing of interspecific interactions.

Growth Rates and Timing of Advancement to Next Phenological Stage. The effect of population synchrony and relative timing of interactions can be explained by the survival and growth rates of individuals. For populations that arrived at the same time as or after the heterospecific competitor, individuals grew on average faster and advanced to the next phenological stage earlier as populations became less synchronized (figs. 6, 7). This pattern was not matched for early-arriving populations, which had high mean growth rates and early phenological advancement across the range of phenological synchronies. Mean growth rates of low-synchrony populations were 200% higher relative to high synchrony for late-arriving populations, but that increase was only 60% for populations arriving at the same time as the competitor and only 6.7% for populations arriving before the competitor. Thus, differences in population demography are driven by a feedback between traits of individuals and differences in the environmental conditions they experience.

Selection on Phenology. Individuals that hatched earlier than their conspecifics had generally higher relative fitness, but the fitness difference was contingent on both phenological synchrony and timing relative to the heterospecific competitor (fig. 8; table S2). For mass, the qualitative fitness difference pattern was similar across arrival time, but fitness differences increased with reduced phenological synchrony and the later the focal species arrive relative to its competitor, indicating that both strengthen selection on early hatching. In contrast, the effect of phenological synchrony on survival-based relative fitness was reversed for populations that arrived later than the competitor: here the relative fitness advantage of early hatching was highest at low synchrony. This selection pattern is consistent with the contrasting effect of synchrony on survival (fig. 6), where decreasing synchrony increased survival rates in populations that hatched late but decreased survival in populations that hatched at the same time or earlier.

Discussion

Differences in seasonal timing of offspring emergence is a key driver of intraspecific variation, but we still have a surprisingly limited understanding of when and how this temporal variation influences populations and communities. Here we show that phenological synchrony within populations is an important driver of population demography, natural selection, and interspecific competition. Consistent with previous studies, decreasing synchrony altered intraspecific competition and thereby negatively affected all population-level rates and increased strength of selection. Contrary to predictions, size-mediated competitive asymmetry was not necessary for these effects to arise. Furthermore, the ecological and evolutionary effects of phenological synchrony were contingent on the community context; they could be weakened or even reversed depending on the relative timing of the onset of heterospecific competition. Overall, these results emphasize the key role of phenological synchrony in mediating the dynamics and structure of populations and communities and how they will respond to phenological shifts.

Synchrony and Population Demography

When individuals differ in their phenologies, they usually experience different environments. As a consequence, changing phenological synchrony of populations frequently also increases trait differences, and this should influence interactions among individuals and demographic rates (Łomnicki 2009; Rasmussen and Rudolf 2015; Weis et al. 2015; Snyder and Ellner 2016; Carter and Rudolf 2019). Consistent with this prediction, we show that changes in synchrony can alter population-level demographic traits. For instance, relative to high-synchrony populations, low-synchrony populations have lower average survival, but surviving individuals grow faster and reach a larger size. These results are consistent with patterns observed in different animal and plant systems. For instance, the relative emergence times of seedlings strongly determines their individual performance (Ross and Harper 1972). Similarly,

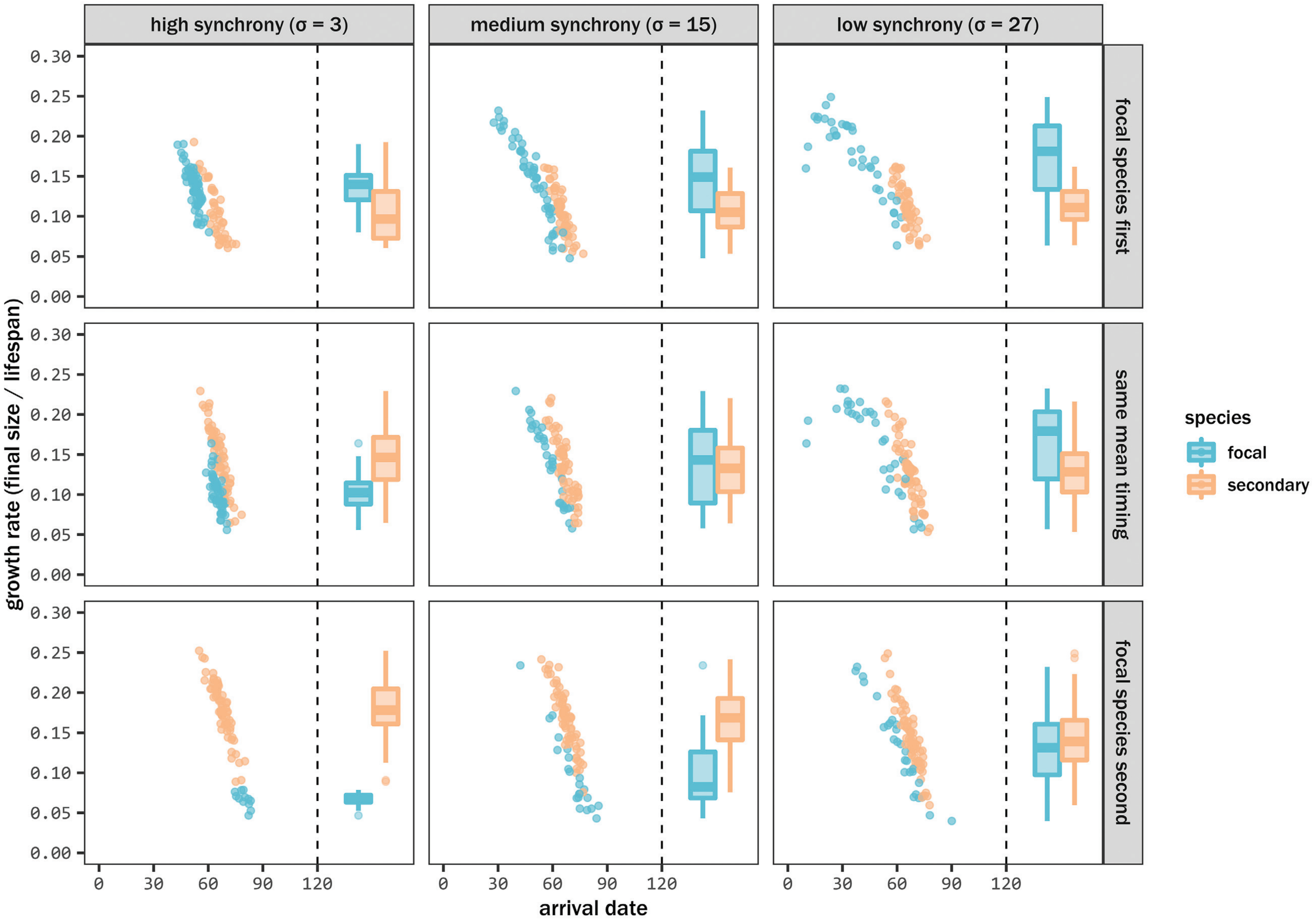

Figure 7: Growth rates for individuals of two competing species based on their arrival date for population phenologies. Phenological synchrony (columns) and mean (rows) of the focal species were adjusted relative to the secondary species. Focal species is shown in teal, and secondary species is shown in orange. Only surviving individuals are shown. Boxplots show median and variation in growth rates for individuals across arrival dates and are placed in an arbitrary position on the *x*-axis.

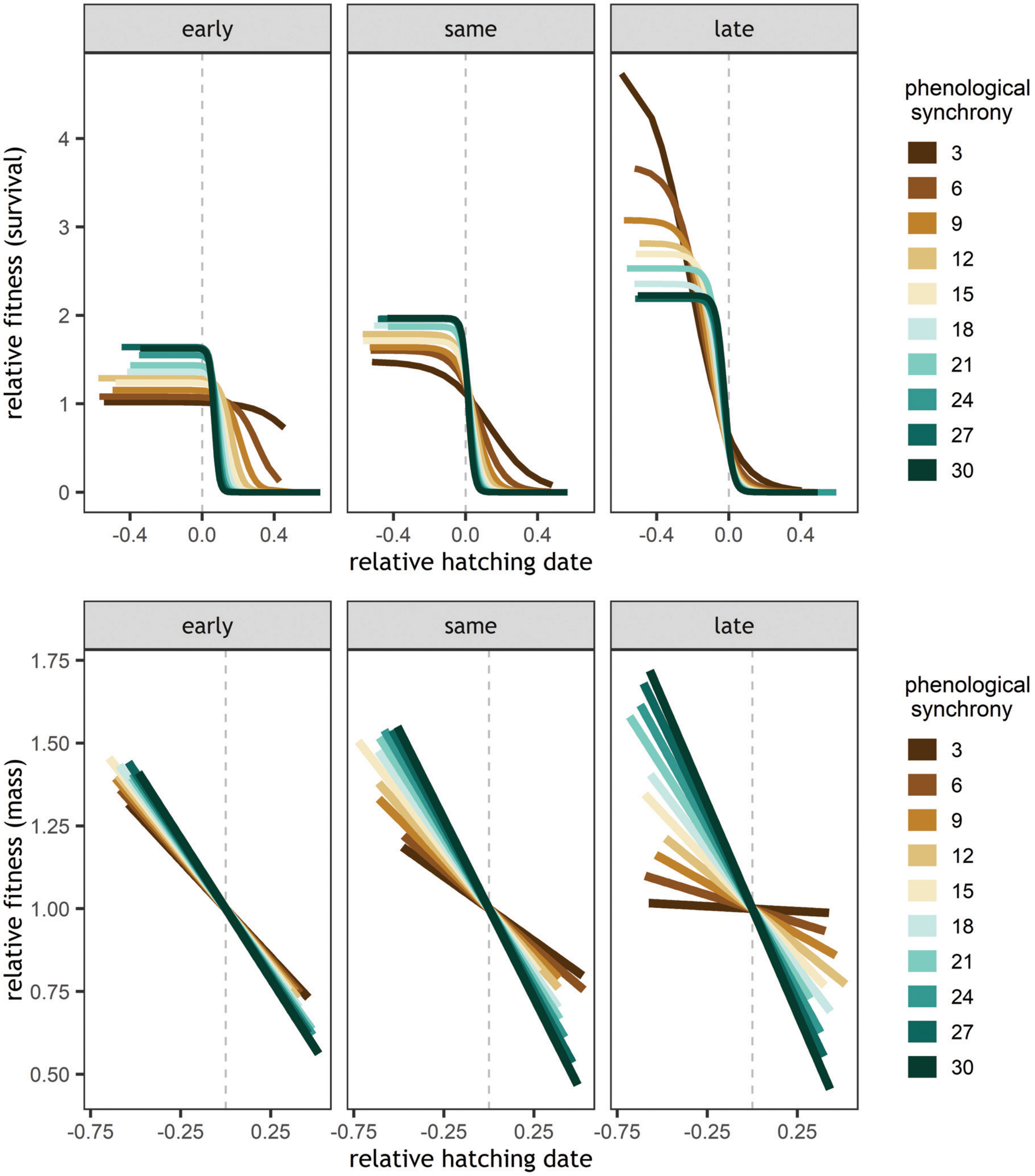

Figure 8: Effects of phenological synchrony and mean arrival relative to heterospecific competitor on selection gradients across hatching dates of individuals using survival or mass (at metamorphosis) as fitness proxy. Panel headings (rows) indicate timing relative to heterospecific competitor. Phenological synchrony indicates level of variation in hatching dates within populations, ranging from high synchrony (3 = low variation) to low synchrony (30 = high variation).

studies of natural populations and models of fish cohorts found that individuals hatching earlier or at a larger size performed better than later-hatching individuals (Trebitz 1991; DeAngelis et al. 1993; Scheffer et al. 1995). Finally, results also closely match empirical patterns in recent tadpole synchrony experiments, including relationships between hatching synchrony and synchrony of timing of metamorphosis (Rasmussen and Rudolf 2015; Carter and Rudolf 2019). Overall, this confirms that our model is a useful tool to predict dynamics in natural systems.

Recent studies suggest that the effects of phenological variation should be largely driven by differences in per capita competitive abilities of early versus late individuals (Rasmussen and Rudolf 2015; Carter and Rudolf 2019). However, testing this prediction has remained elusive because it is difficult to manipulate this relationship empirically while keeping other conditions constant, and previous models have assumed a single fixed relationship between size and per capita effects (Trebitz 1991; DeAngelis et al. 1993; Scheffer et al. 1995). Here we overcome this limitation by explicitly manipulating the relationship between per capita competitive ability and size. We found that size-dependent competitive differences can strongly amplify the demographic consequences of phenological synchrony because of a positive feedback between growth and competitive advantage of early arrivers (Rudolf 2018). However, size-mediated differences in per capita effects were not necessary for synchrony effects to occur. While this may seem surprising, it is important to keep in mind that differences in arrival time alone still alter an individual's traits and the conditions it experiences. Early arrivers of low-synchrony populations experience lower conspecific densities and have more time to eat and grow, giving them a disproportionate share of resources. This suggests that phenological synchrony should influence population demographic rates in most natural systems, but the magnitude of this effect varies depending on how per capita effects scale with size/age of individuals.

Synchrony and Timing of Interspecific Interaction

Phenology varies within and between species, and our results emphasize that we need to consider both to predict the effects of changes on population and community dynamics. When the focal species arrived early or at the same time as the competitor, survival decreased as populations became less synchronized, but the opposite was true when the focal species arrived after the heterospecific competitor. This reversal of synchrony effects can be explained by how the timing of interspecific interactions influences the consequences of intraspecific variation in phenology. The temporal spread of low-synchrony populations meant that even though the focal population arrived on average later than the competing species, some individuals arrived earlier. These earlier individuals gained a size-mediated competitive advantage and thus were more likely to survive, which led to higher survival at the population level. This scenario is a poster child for situations where population dynamics are almost completely driven by the "lucky" few individuals that happened to hatch early and do well early in life (Snyder and Ellner 2016). More generally, this demonstrates that low-synchrony populations spread individuals across more varied conditions, some of which are likely to be better (e.g., earlier arrival than competitors) and some worse (e.g., later arrival than competitor). On the other hand, the temporal clustering of individuals in high-synchrony populations means that all individuals are subject to the same conditions. This is beneficial when conditions are good but costly when mean timing aligns with unfavorable conditions. Interestingly, this also implies that low population synchrony could serve as a buffer against the negative effects of shifts in phenologies of interspecific competitors, which is consistent with a recent empirical study (Carter and Rudolf 2019). Therefore, considering phenological synchrony is key to understanding how natural populations and communities will respond to climate change–driven phenological shifts.

Selection on Phenology. Low phenological synchrony is often interpreted as a way of temporal niche partitioning that can reduce intraspecific competition because of lower conspecific densities (Post 2019). In contrast, we found that even without a size-mediated competition, early-arriving individuals have a fitness advantage that increased with higher levels of phenological asynchrony. Assuming all else is equal, this should select for early arrival and high phenological synchrony, which would increase overall density of the population but reduce per capita growth and developmental rates of individuals in the absence of interspecific competition. These results suggest that selection clearly favors early arrival (under most scenarios) and should thus reduce phenological variation in the absence of other factors. This pattern holds true even in the presence of interspecific competition, unless all individuals arrive after a competitor. This is consistent with previous theory (Carothers and Jaksić 1984; Loreau 1992) and indicates that the concept of partitioning time to reduce competition cannot explain intraspecific variation in phenology when individuals compete for (and deplete) a shared resource. Yet phenological variation is ubiquitous in natural populations. We currently have poor understanding of whether these are transitory states or what maintains this variation. Several mechanisms could facilitate this variation, including temporal variation of resources or, as in our case, temporal variation in timing of interspecific interactions. However, we first need a better understanding of the genetics underlying phenological variation to fully predict when and how phenologies and phenological synchrony will evolve. Once these processes are known, they could be integrated in our modeling framework and combined with existing models (e.g., Rudolf 2019) to examine effects on long-term ecological and evolutionary dynamics of populations and communities. Continuing to develop such a genetic framework will be critical as we aim to predict the outcomes of climate change on natural ecosystems.

Future Directions. Climate change is altering phenologies at the individual and community scales, and our model is a critical step toward understanding conditions that modify the effects of phenological shifts. Although our model was robust to specific parameter assumptions and able to predict general patterns observed in natural systems, we could not include processes that currently lack sufficient data to guide model development. For example, we modeled only one generation because we simply know too little about transitions/links between phenologies of subsequent life cycle stages. However, consistent with recent empirical work, our results show that timing of the next phenological stage can change according to synchrony: early individuals of low-synchrony populations grow quickly, leading to a relatively early mean phenology of the next stage. It is possible that early phenology could be beneficial in the next stage because it allows priority access to resources (Alford and Wilbur 1985; Lawler and Morin 1993). On the other hand, early phenology can have negative outcomes, for example, if necessary seasonal resources are not yet present (Visser et al. 1998), the environment is too harsh (Vitasse and Rebetez 2018; Vitasse et al. 2018), timing does not align with mutualists (Kudo et al. 2004; Burkle et al. 2013; Kudo and Ida 2013), or there is mate limitation (Bonner et al. 2019). An important step for future studies will be measuring phenology of natural populations across seasons to understand how within-season outcomes play out across phenological stages and years.

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Statement of Authorship

S.K.C. and V.H.W.R. conceptualized the research, S.K.C. performed the analysis with review and feedback from V.H.W.R., and S.K.C. and V.H.W.R. jointly wrote and edited the manuscript.

Data and Code Availability

Data and code for this project are available on Zenodo (https://doi.org/10.5281/zenodo.6547161; Carter 2022) and GitHub (https://github.com/shannonkcarter/phenology_abm_repo).

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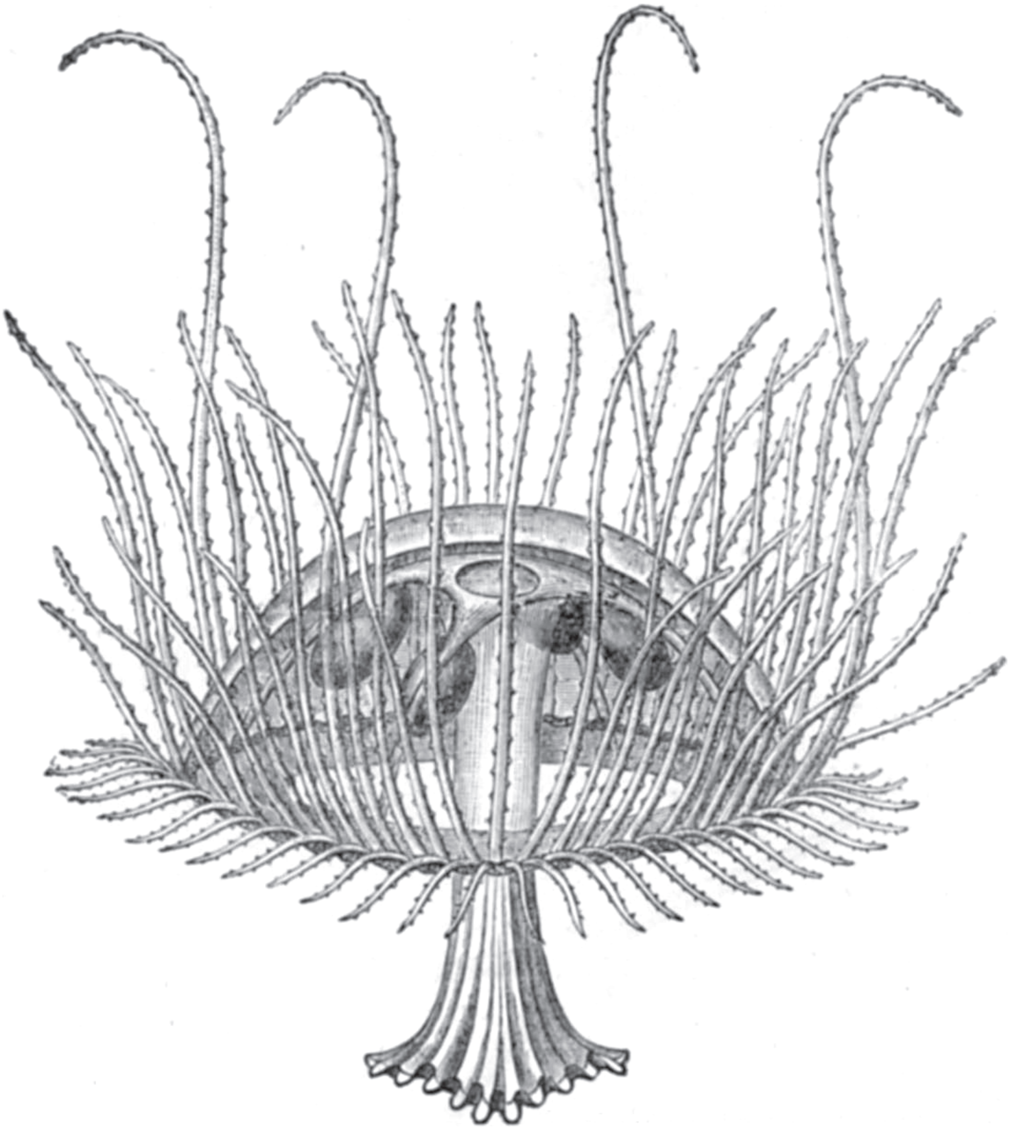

“The effect of poisons is discussed at length, particularly the effects of a change from salt water to fresh, as illustrated by the fresh-water Medusa, *Limnocodium sowerbii* (printed *sorbii*), of the tank in Regents Park [figured]. It appears that a much less profound physiological change would be required to transmute a marine jelly-fish into a jelly-fish adapted to inhabit brine, than would be required to enable it to inhabit fresh water.” From the review of Romanes’ *Researches on the Nervous Systems of Jelly and Star-Fish* (*The American Naturalist*, 1885, 19:1188–1199).