

LETTER

Shifts in phenological distributions reshape interaction potential in natural communities

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Abstract

Climate change has changed the phenologies of species worldwide, but it remains unclear how these phenological changes will affect species interactions and the structure of natural communities. Using a novel approach to analyse long-term data of 66 amphibian species pairs across eight communities, we demonstrate that phenological shifts can significantly alter the interaction potential of coexisting competitors. Importantly, these changes in interaction potential were mediated by non-uniform, species-specific shifts in entire phenological distributions and consequently could not be captured by metrics traditionally used to quantify phenological shifts. Ultimately, these non-uniform shifts in phenological distributions increased the interaction potential for 25% of species pairs (and did not reduce interaction potential for any species pair), altering temporal community structure and potentially increasing interspecific competition. These results demonstrate the potential of phenological shifts to reshape temporal structure of natural communities, emphasising the importance of considering entire phenological distributions of natural populations.

Keywords

Amphibians, climate change, interaction potential, phenology, species interactions, temporal overlap.

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INTRODUCTION

Global changes in climate have led to significant spatiotemporal restructuring of natural communities around the world (Parmesan & Yohe 2003; Menzel *et al.* 2006; Chen *et al.* 2011). Changes in the seasonal timing of species life-history events (phenological shifts) are among the best-documented of these ecological responses to climate change (Fitter & Fitter 2002; Walther *et al.* 2002; Parmesan & Yohe 2003; Brown *et al.* 2016). Species tend to advance their timing in response to warming temperatures, but there is substantial variation in the rate and even direction of shifts across co-occurring species (Dunn & Winkler 1999; Root *et al.* 2003; Parmesan 2007; Thackeray *et al.* 2016), and these species-specific phenological responses can alter the timing of species interactions (Edwards & Richardson 2004; Clausen & Clausen 2013; Kudo & Ida 2013). Given the importance of biotic interactions in structuring natural communities and ecosystem processes, these phenology-driven changes are expected to have profound ecological effects (Kudo *et al.* 2004; Memmott *et al.* 2007; Both *et al.* 2009; Yang & Rudolf 2010).

An important consequence of phenological shifts is their potential to alter the temporal overlap and therefore interaction potential between species within a community (Visser & Both 2005; Burkle *et al.* 2013; CaraDonna *et al.* 2014). Simply construed, temporal overlap is the period of time when two individuals are present in a given phenological stage and can interact with each other. However, individuals vary in their phenologies, comprising a distribution of phenologies at the population level. To accurately determine interaction potential between two populations, we therefore need to consider the phenological distributions of both populations and how they

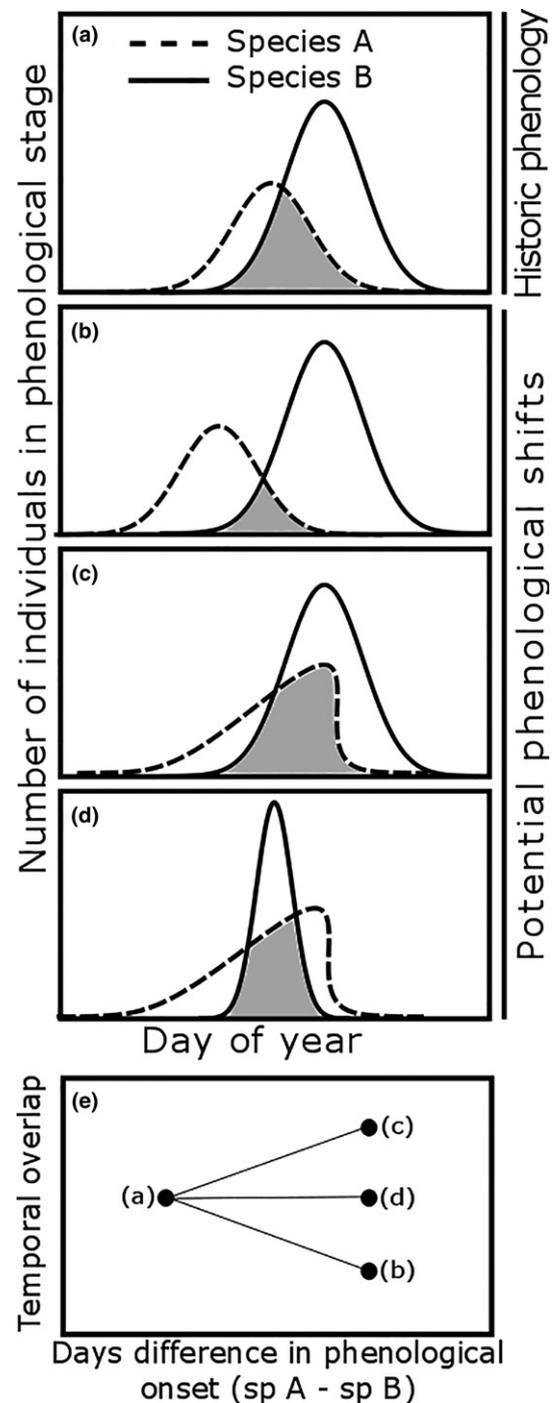
intersect with one another. For example consider a population A that overlaps with population B for a 15-day period. The encounter probability, and thus interaction potential, between the two populations will clearly be much greater if 80% of population A's individuals are present during that period than if only 5% are present. However, to date, most phenological research has summarised a population's phenology into a single metric (e.g. first flowering date, seasonal peak abundance) and rarely considers entire phenological distributions (but see CaraDonna *et al.* 2014). As a consequence, we know very little about the phenological distributions of species and how they change over time. Yet, this knowledge is key for determining how phenology shapes temporal overlap of species and predicting how species interactions will be affected by climate change (Miller-Rushing *et al.* 2010; CaraDonna *et al.* 2014; Rasmussen & Rudolf 2015).

Phenology-driven changes in temporal overlap could be caused by one of two major types of phenological shifts, outlined in Figure 1. First, the shape of both distributions can stay uniform but shift forward or backward in time (compare Fig. 1a and b). Alternatively, the shape of either one (Fig. 1c) or both (Fig. 1d) distributions can shift non-uniformly (e.g. first, peak and last phenological event do not shift at an equal rate across years). Importantly, in the latter case, single metrics will be uninformative for describing changes in temporal overlap, and instead it will be necessary to consider the whole phenological distribution. We can test which type of shift is responsible for changes in overlap (and therefore whether or not summary metrics are reliable) by leveraging a simple statistical property: if distributions are similar and uniform across time, then temporal patterns can be well approximated using a single metric. Therefore, if distributions of species

Figure 1 Conceptual representation of temporal overlap of two species under historical conditions (a) and three hypothetical phenological shifts (b–d). Each of the shift scenarios shows an equal advancement of first phenological date for species A, whereas species B first date remains constant. (b) a shift in which species A's phenology advances relative to species B, but the distributions ('shape') remains constant (c) Species B's phenology remains unchanged but the distribution of species A changes (e.g. first event advances faster than peak or last) (d) The distributions of both species change, but species A and B change differently. (e) compares the historical case of (a) to each shift scenario to demonstrate how the correlation between difference in first phenological date and temporal overlap depends on phenological distributions of each species. Scenario (b) supports the hypothesis that increasing difference in start date decreases temporal overlap and therefore a single metric can be used to predict change in temporal overlap. However, in cases (c) and (d), first phenological date is positively correlated and uncorrelated with temporal overlap, respectively. In these cases, the whole phenological distribution would need to be considered to predict change in temporal overlap.

pairs shift uniformly (Fig. 1b), we expect a negative correlation between difference in start date and temporal overlap (as time between phenological onset increases, overlap decreases) (Fig. 1e). However, if phenological distributions for either or both species change differentially (the case in Fig. 1c and d), there would be no correlation or potentially even a positive correlation between difference in start date and temporal overlap (Fig. 1e). In the examples presented in Figure 1, median dates would more predictably correlate to temporal overlap, but median dates can also be misleading, especially when considering bimodal or multimodal distributions. For example even if two populations have the same median phenological date, temporal overlap can be very low if one population has a bimodal distribution and the other has a unimodal distribution that falls between the peaks of the bimodal distribution. In these cases, single phenological metrics would poorly represent the phenological distribution and therefore over- or under-estimate corresponding changes in temporal overlap. Using the clear predictions in this novel conceptual framework, we can test how the temporal overlap of species changes over time and identify the underlying mechanisms.

Here, we use this whole-population approach to test if and how phenological shifts alter interaction potential of species in natural communities. Specifically, we analysed a unique long-term abundance-based amphibian calling phenology dataset to map precise phenological distributions of individual species within and across multiple communities over time (see Fig. 2 for an example). This is an apt system for linking phenological shifts to species interactions because these amphibians can compete locally in a number of ways: through vocal interference and/or for resources both directly as adults and indirectly through their offspring (Alford & Wilbur 1985; Schwartz 1987; Morin *et al.* 1990). This system allowed us to assess: (1) Do phenological shifts cause long-term trends in the interaction potential among competitors? (2) Are changes in interaction potential caused by uniform or non-uniform phenological shifts? We found phenological shifts increase the interaction potential of competitors over time, due to a predominance of non-uniform shifts in phenological distributions.



MATERIALS AND METHODS

Study system and dataset

Amphibians are an apt system for studying phenology for several key reasons. First, their reproduction is timed by a suite of climate cues, including temperature, precipitation and air pressure (Blankenhorn 1972; Pechmann *et al.* 1989); thus their phenological distribution is largely determined by year-specific weather conditions (Díaz-Paniagua 1992; Saenz *et al.* 2006). Second, different species respond to different environmental

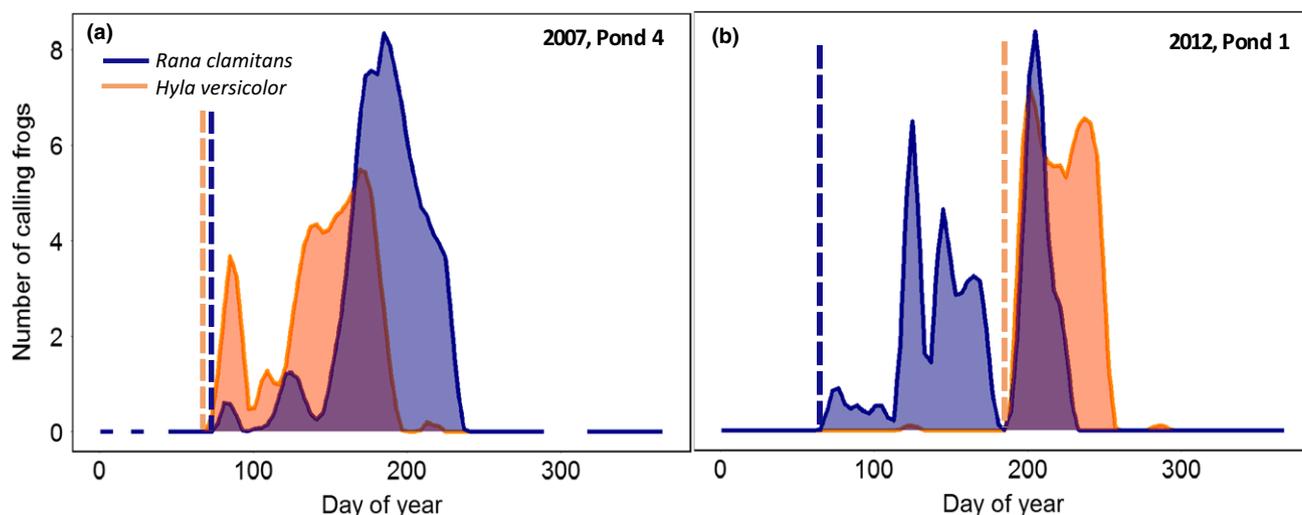


Figure 2 Phenological distributions and temporal overlap for *R. clamitans* and *H. versicolor* in two contexts. These phenological distributions were made for each pairwise combination of the 12 amphibians in each of the eight ponds and each of the 15 years in the dataset, resulting in 2,010 plots. In this example, temporal overlap between *R. clamitans* and *H. versicolor* (indicated by the area of intersection between the two curves) is equal in the two contexts, but in (a) the species start calling on the same day, whereas in (b) the onset of their calling periods is separated by 160 days. Dashed lines mark the first day of calling.

cues, and thus are expected to show different phenological responses, which could temporally restructure the community (Oseen & Wassersug 2002; Saenz *et al.* 2006). Finally, amphibians exhibit a strong but highly variable phenological response relative to other taxa (Forchhammer *et al.* 1998; Blaustein *et al.* 2001; Parmesan 2007; Todd *et al.* 2010), and are declining globally (Blaustein *et al.* 1994; Bury 1999; Stuart *et al.* 2004; Grant *et al.* 2016), suggesting they should be a high priority for examining causes and consequences of phenological shifts.

We analysed high-resolution amphibian calling data (coincident with breeding phenology) collected from audio recorders installed at eight ponds in northeast Texas. Ponds ranged in area from 35 m² to 1720 m² with an average of 380 m². Maximum depth of the ponds ranged from 1.5 to 4.0 m. The farthest ponds were separated by 34 km and the average distance between ponds was 17 km. The recorders collected calling data six times a day (9:00 pm, 10:00 pm, 11:00 pm, 12:00am, 1:00am, 2:00am) for a 1-min interval from May 2000 to December 2015. This sampling protocol encompasses the peak daily calling time for all species in this community, and sampling six times per day increased probability that all species vocalising at a pond were detected (Bridges *et al.* 2000; Saenz *et al.* 2006). Recordings were processed manually with sonogram reference, and number of calling individuals for 12 species (*Hyla versicolor*, *Hyla cineria*, *Bufo valliceps*, *Bufo woodhouseii*, *Rana catesbeiana*, *Rana clamitans*, *Rana sphenoccephala*, *Gastrophryne carolinensis*, *Pseudacris crucifer*, *Pseudacris triseriata*, *Acris crepitans* and *Rana palustris*) were recorded. Importantly, these 12 species all compete locally in a number of ways. For example acoustic interference between heterospecifics can make calls more difficult for females to distinguish and localise (Jones 1966; Schwartz 1987). In addition, both adults and their tadpole offspring can compete locally for common resources (Alford & Wilbur 1985).

The eight ponds are clustered at two distinct sites – Davy Crockett National Forest (DC) and Stephen F. Austin Experimental Forest (SFA) – which vary in some key ways. The ponds in SFA are on average smaller and unable to support fish, whereas those in DC are large enough to support fish communities (most commonly mosquitofish, green sunfish and largemouth bass). Furthermore, despite being separated by < 30 km, the sites can differ significantly in daily and annual average weather conditions. DC was on average 0.5–1.0 °C warmer every year than SFA (See Fig. S1). Annual rainfall total for the two sites averaged through the 15-year period were equal (mean ± SEM; 103.8 ± 26 cm/year at DC, 104.2 ± 29 cm/year at SFA), but within a year, they differed by as much as 91 cm (in 2002, SFA had 141 cm precipitation and DC had 50 cm) (see Figure S2). These eight ponds constitute eight independent units since it is extremely unlikely for an individual frog or toad to call at multiple ponds in a single year (Alford & Richards 1999; Marsh & Trenham 2001). Juvenile amphibians can disperse up to 15 km, but breeding adults show strong site fidelity through their lifespan, and therefore for a single individual to call at multiple ponds would be a very rare event (Sinsch 1990).

Data processing and analysis

We quantified phenological distributions for each species in each year and pond by smoothing scatter plots of number of calls over time using the lowess function ($f = 1/50$, $iter = 3$, $\delta = 4$) in the stats package of R version 3.2.2 (sample plots in Fig. 2). These lowess settings showed variation on a 2–3 day scale, but smoothed within-day noise. Sensitivity analyses with different values for the lowess settings gave qualitatively similar results. For each species in each pond and year, we estimated three values: first, median and last calling date. We defined first calling date as the day when five

cumulative calls had been recorded to exclude individual early calling outliers unrepresentative of the bulk of the population's phenology. Likewise, last calling date represented the day of year when all but five of the year's calls had been recorded. Sensitivity analysis indicated that results were qualitatively similar using smaller or larger calling buffers. Median calling date was the day of year on which 50% of the year's calls had been recorded.

To link phenology to temporal overlap, we did pairwise comparisons of the phenological distributions for competing species (resulting in 15 years \times 8 ponds \times 66 species pairs = 7920 comparisons). From these pairwise comparisons, we estimated three values: temporal overlap, days-difference in first calling date and days-difference in median calling date. For temporal overlap, we calculated the integrated area of intersection between lowess distribution curves. We standardised temporal overlap by dividing the area of intersection by the total area under the curve of the focal species' phenological distribution. This approach thus accounts for the period of overlap (temporal coexistence) but weighs it by the abundance of the focal species during a given time period, giving us a standardised metric for encounter probability within a given year. For days-difference in first and median calling date, we simply subtracted the first (or median) calling date of the focal species minus the first (or median) calling date of the secondary species and standardised by dividing by the total length of the calling period for the focal species. Species pairs that did not sufficiently overlap (co-occurred in ≤ 15 of the 120 year-ponds) were excluded, leaving 48 species pairs for analysis. From the 5760 unique year-pond comparisons represented by these 48 species pairs, we excluded any year-ponds in which one or both species did not call, leaving us with 2010 unique comparisons for analysis.

Long-term trends in interaction potential (Q1)

To test for long-term trends in interaction potential (Q1), we fit linear mixed effect models using the lmer function in the lmerTest package of R. Temporal overlap between two species was predicted by year with pond as a random effect for all species pairs (Table S1). Pond was included as a random effect to account for potential correlations of calling behaviours within a given pond, but ponds are distant enough from each other that they are uncorrelated, independent units. To compare ability of single metrics vs. distributions to measure phenological shifts, we repeated the analysis but with difference in first calling date between the two species as a dependent variable.

Testing uniformity of phenological distributions (Q2)

To test for uniformity of phenological distributions across time and space (Q2), we used two methods. First, we quantified variation in the median and duration of calling periods for all 12 species. Second, we fit linear mixed effect models using the lmer function. Temporal overlap between two species was predicted by days-difference in single phenological metrics (e.g. first/median calling date for species A – first/median calling date for species B; see Fig. 1e for predictions) across years for

each species pair with pond as a random effect (Table S4). Again here we included pond as a random effect to account for potential repeated measures of calling within a pond.

RESULTS

Long-term trends in interaction potential (Q1)

Temporal overlap, and thus the interaction potential of species pairs, significantly increased over the 15-year period for 25% (12/48) of species pairs tested (Fig. 3a, Table S1) and never significantly decreased for any species pair. A subset of the species pairs that increased temporal overlap and two pairs that showed no trend in temporal overlap also showed significant decrease in distance between single metrics (first and/or median), though the detections of these trends was much lower (only 10% or 5/48 species pairs for first calling date and 8% or 4/48 species pairs for median calling date; Fig. 3b, Table S1). The trend for first date, median date and overlap were consistent, with first and median dates always moving closer together and temporal overlap always increasing, which all suggest that species phenologies are growing more similar over time. Notably, only one species (*Gastrophryne carolinensis*) showed a significant shift in first or median calling date, advancing 2.3 ± 0.72 days per year in first calling and 1.5 ± 0.67 days per year in median calling. Remaining trends for single species summarised in Table S2.

Testing uniformity of phenological distributions (Q2)

Phenological distributions were in general highly non-uniform across years and ponds, and species differed in how uniform their distributions were year-to-year. Of the 12 amphibian species, *Rana sphenoecephala*'s phenological distribution was most non-uniform – the duration of its calling period ranged from 2 to 325 days long (mean \pm SEM; 177 ± 90 days; Fig. 4), with a median calling date ranging from February 5–October 31 (mean \pm SEM; June 9 ± 89 days; Fig. 5). *Rana palustris* had the most uniform distribution, though still demonstrated significant variation: its calling period ranged from 2 to 37 days long (mean \pm SEM; 14 ± 10 days; Fig. 4) with median calling date ranging from February 15–March 25 (mean \pm SEM; March 10 ± 11 days; Fig. 5). Because of the difference in shape and uniformity of phenological distributions between these two species across space and time, temporal overlap spanned the entire possible range from 0% to 100%. The phenological distributions for the remaining 10 species were more consistent than *R. sphenoecephala* but less consistent than *R. palustris* (summary of each species phenology in Figures 4 & 5 and Table S3).

Temporal overlap was rarely correlated with difference in phenological metrics, indicating that phenological distributions were non-uniform across species and changed shape substantially over time. Out of 48 species pairs examined, only 14% (7/48) showed a significant relationship ($P < 0.05$) between difference in first calling date (e.g. between species A and B) and temporal overlap (Fig. 6a, Table S4). This does not include adjusted alpha levels for multiple comparisons, so the proportion of significant results is hardly more than we

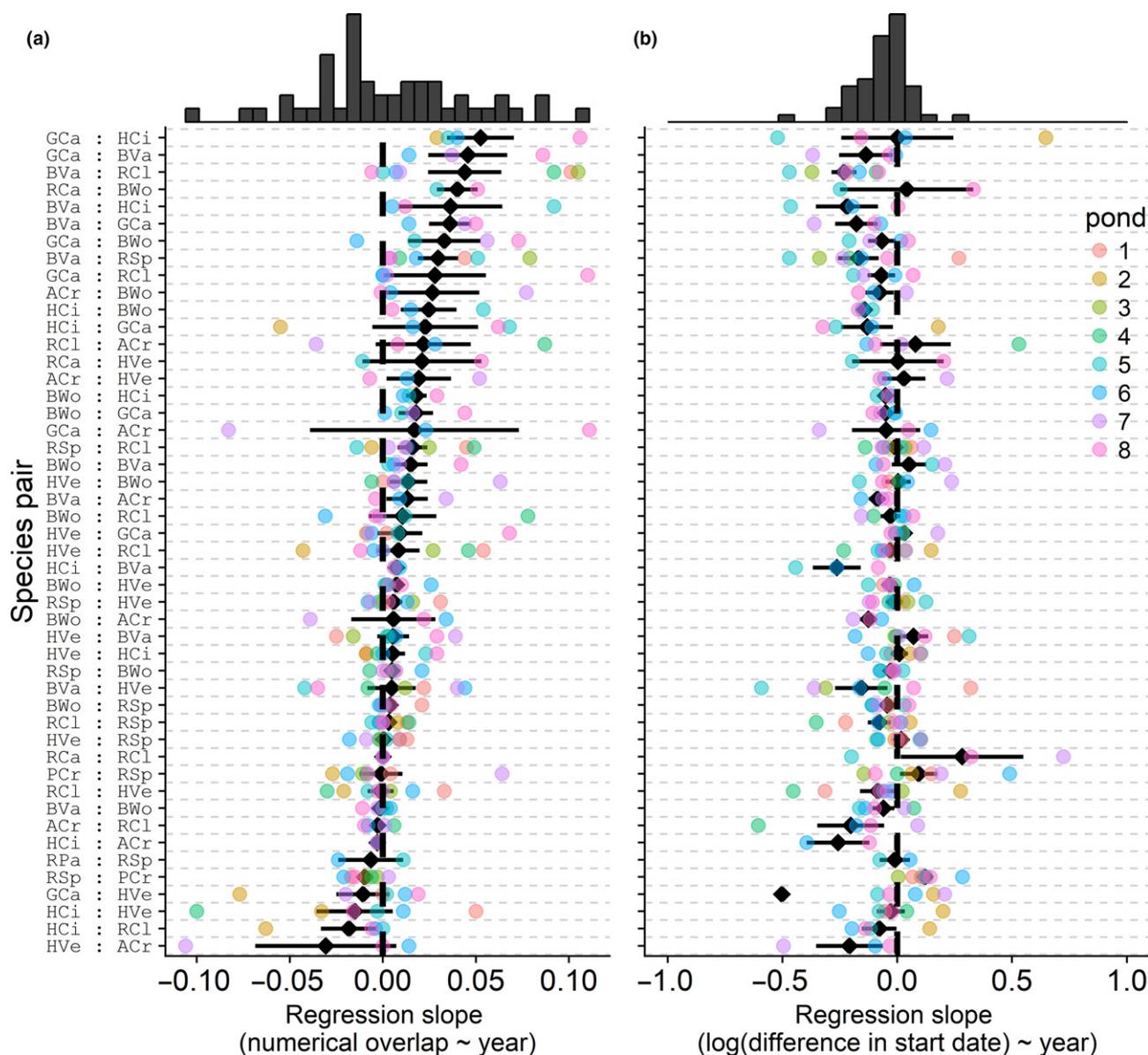


Figure 3 Linear regression coefficients for models of shifting phenological metrics over the 15 year study period (a, using difference in start date; b, using difference in temporal overlap) for 48 pairs of competing amphibians. Coloured dots represent overlap at one of eight ponds regressed through years and black diamonds represent averages of all ponds ± 1 SE. Marginal histogram represents the distribution of all regression coefficients. For difference in calling onset (a), a *negative* regression coefficient indicates phenologies converging over time. For temporal overlap (b), a *positive* regression coefficient indicates phenologies converging over time. First phenological dates got significantly closer for 5/48 species pairs. Temporal overlap became significantly greater for 12/48 species pairs.

would expect by chance. Furthermore, among the seven significant correlations, three were negative (expected for uniform shifts – increasing difference in start date associated with decrease in temporal overlap Fig. 1b) and four were positive (opposite of expectation – increasing difference in start date associated with increase in temporal overlap, Fig. 1c), further suggesting that many of the significant relationships were driven by chance. Importantly, none of the significant negative correlations were for species pairs that showed a significant change in temporal overlap, indicating that these changes in overlap were driven by non-uniform shifts in distributions. Difference in median calling date was somewhat better at

predicting overlap, with 23% (11/48) of regressions indicating a significant relationship, with 10 negative slopes and 1 positive (Fig. 6b, Table S4). Together this indicates that relative timing of single metrics mostly failed to describe temporal overlap between species because of significant non-uniformity in the distribution of phenologies across years in this system (i.e. as represented in Fig. 1c, d). Figure 2 provides an extreme example of our raw data exemplifying the incongruence between phenological onset and temporal overlap. Importantly, the results also indicate that the change in interaction potential over time (Fig. 3) was driven by non-uniform shifts in the phenological distributions of species.

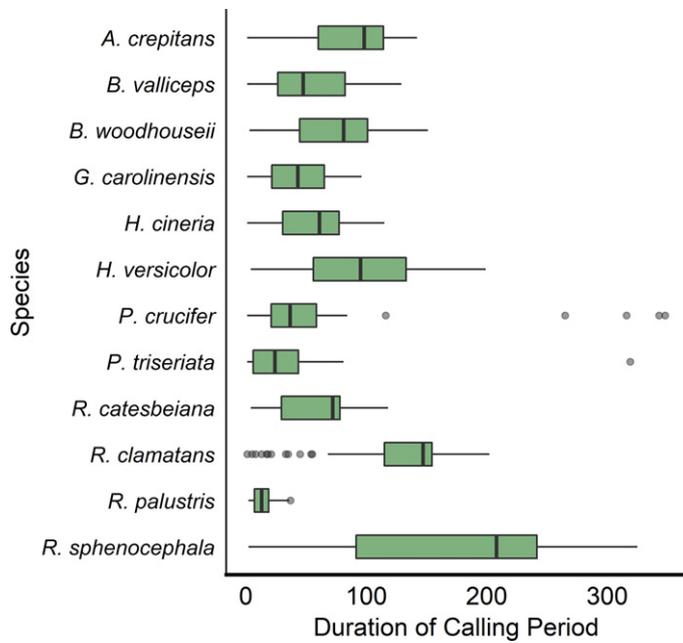


Figure 4 Variation in the length of calling periods for each species, pooling across all eight ponds and all 15 years.

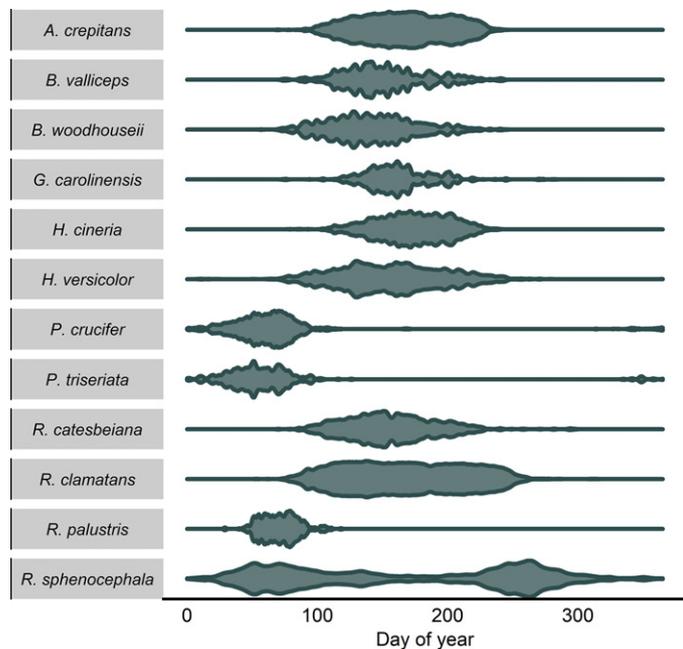


Figure 5 Seasonal calling windows for each species. Width of the bubble represents probability of calling on that day, pooling all eight ponds across all 15 years.

DISCUSSION

Phenological shifts are among the best-documented ecological responses to climate change, yet we currently know little about how these shifts affect species interactions (Parmesan & Yohe 2003; Brown *et al.* 2016). While previous studies have provided important evidence documenting phenological shifts, they

typically do not consider all individuals in a population or interacting populations, making it difficult to link phenological shifts to species interactions (Visser & Both 2005; Yang & Rudolf 2010). By accounting for a population’s whole phenological distribution, we demonstrate that phenological shifts increase the interaction potential between 25% of competitors in this community. Convergence of these competitors’ phenologies over time suggests that strength of competition is likely increasing in this system. Importantly, by taking a novel approach of correlating single phenological metrics with temporal overlap, we show that these shifts are driven primarily by changes in the ‘shape’ of phenological distributions. Because of the predominance of non-uniform phenological shifts, changes in interaction potential could not be detected with single metrics (e.g. first or median calling date). Overall, these results indicate that phenological shifts can fundamentally restructure natural communities and emphasise the need to consider whole population phenology to reliably detect these changes.

Directional shifts in the relative phenologies of interacting species over time could either increase or decrease the potential for species interactions and thus have important long-term consequences for community structure and species coexistence (Suttle *et al.* 2007). We observed clear restructuring of temporal overlap of species in our amphibian communities. In our system, temporal overlap significantly increased for 25% of competitor pairs over the 15-year period. In this system, amphibians can compete locally via acoustic interference and resource competition (both directly as adults and indirectly through their tadpole offspring) (Jones 1966; Alford & Wilbur 1985; Schwartz 1987). Previous studies suggest that interspecific competition increases when hatching phenologies converge; thus, regardless of the underlying mechanism, the convergence in phenologies of competitors in our system could increase the strength of interspecific competition (Alford & Wilbur 1985; Morin *et al.* 1990). This could cause long-term changes in abundance and potentially persistence of amphibians and significantly impact community stability and resilience (Suttle *et al.* 2007).

The significant convergence of phenologies in our study emphasises that considering the whole distribution of phenologies allows detection of phenological trends over shorter time series. Current methods rely on single metrics because this data is easier to attain and may be the only data available for many systems (Miller-Rushing *et al.* 2008). However, these metrics represent only a single or few individuals, and thus are highly sensitive to outliers and may misrepresent the bulk of the population. As a consequence, long time series data are needed to detect trends using single metrics, but such long-term datasets are rare, especially for animals. In addition, single metrics cannot capture changes in the distribution of phenologies and thus miss important phenological shifts. For instance a population’s first day of flowering may advance faster or slower than peak flowering date (CaraDonna *et al.* 2014). Our results show that a whole population approach substantially increases our ability to detect phenological trends over shorter time scales and capture important changes in community structure that would be missed otherwise. Only one species showed a shift in phenological first or median over time (*G. carolinensis*; advancing 2.3 ± 0.72 days per year in

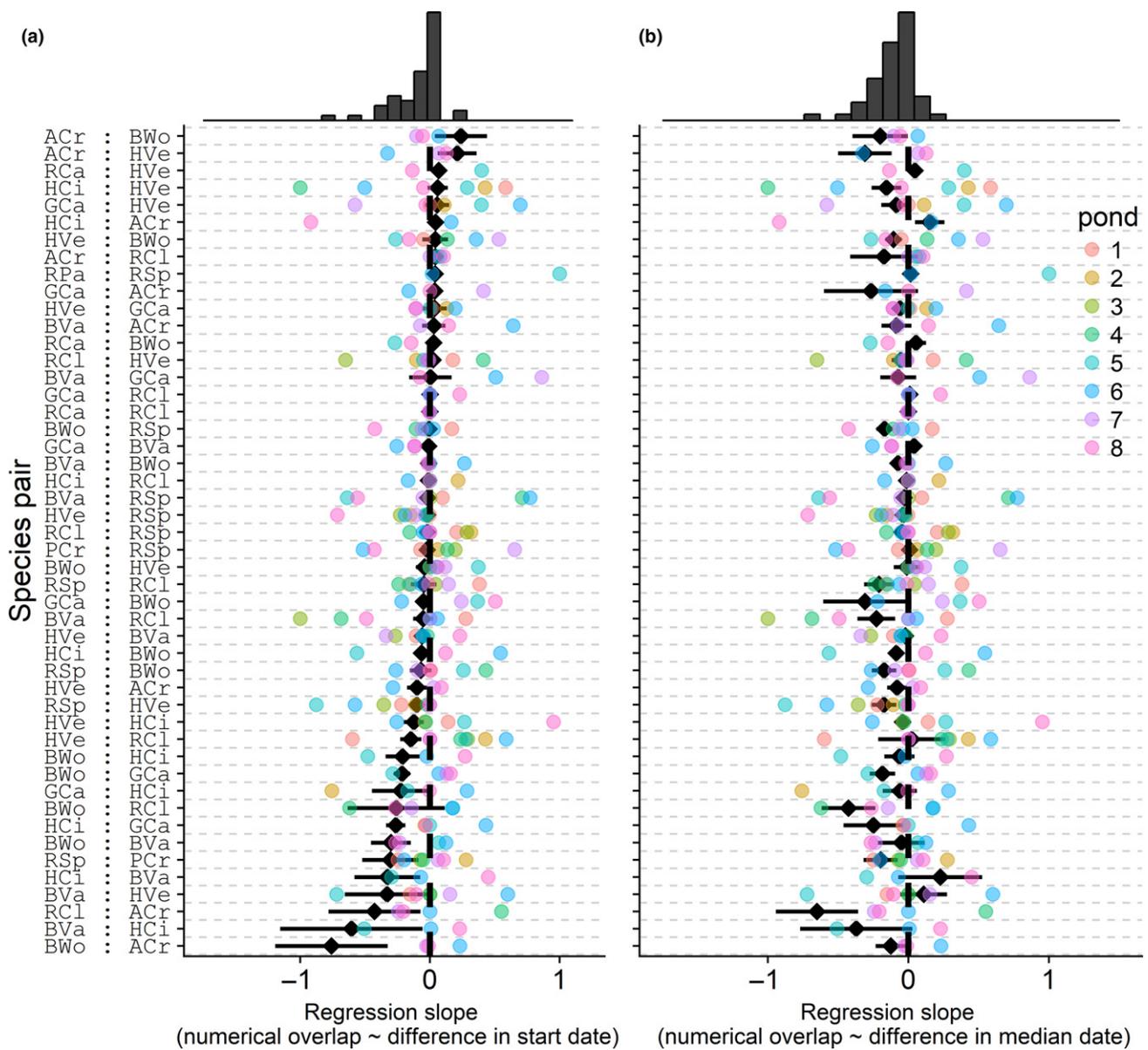


Figure 6 Linear regression coefficients for models of temporal overlap predicted by single metrics, (a) difference in start date, (b) difference in median date, for 48 pairs of competing amphibians (letters represent first initial of genus and first and second letter of species name; focal species listed first). Coloured dots represent temporal overlap for one of eight ponds regressed across years and black diamonds represent averages of all ponds \pm 1 SE. Marginal histogram represents the distribution of all regression coefficients. A negative regression slope indicates that relative timing of start or median accurately summarise temporal overlap, whereas a 0 or positive slope indicates these metrics poorly summarise temporal overlap.

first calling date and 1.54 ± 0.67 days per year in median calling date; see Table S2). However, we observed an increase in temporal overlap for 25% of species when considering pairwise interactions. So by relying on single metrics, we would underestimate the prevalence of phenological shifts in this system and would not predict any changes in temporal community overlap. Overall, because they are more robust to outliers, median phenological dates proved marginally better than start dates at correlating predictably with temporal overlap. However, calculating a population’s median phenological date requires data on the whole population, in which case it is more accurate to consider the full distribution. Collecting the high temporal resolution data necessary to describe

phenological distributions remains a challenge in many systems but may be more feasible with advances in citizen science, remote sensing, and eDNA. These approaches allow wide-scale sampling over time without overly burdening any single researcher.

Changes in interaction potential over time can be driven by different types of phenological shifts (Fig. 1). In our study, shifts in interaction potential were clearly driven by non-uniform shifts in the population-level distribution of phenologies, both within a species across space and time and across species (Fig. 1c and d). Across species, non-uniform shifts arise when species respond differentially to environmental change. Species in our dataset occupy a range of seasonal niches, and we

already know that their breeding phenologies are triggered by different abiotic factors (Dayton & Fitzgerald 2001; Kopp & Eterovick 2006; Saenz *et al.* 2006). For instance some species' calling phenologies are strongly associated with rainfall (e.g. *B. valliceps*, *B. woodhousii*, *H. versicolor*, *G. carolinensis*), whereas others more strongly rely on temperature cues (*P. crucifer*, *P. triseriata* and *R. palustris*) (Saenz *et al.* 2006). Therefore, a population's phenological distribution in a given year and place is shaped by an interaction between that species' life-history strategy, season-specific weather conditions and long-term climate trends. Consequently, it is not surprising that we detected non-uniform shifts in phenological responses of species in our system and no simple climatic drivers of these shifts (Figs S3 and S4).

Our unique dataset indicates that phenologies can vary across communities within a given year. While we found general trends for species pairs to increase overlap across sites, there was considerable variation in this pattern across our different ponds. Consistent with many phenological studies, we relied on local weather stations which covered two regional sites, each encompassing four ponds. Ponds within each site can experience different weather conditions (e.g. rainfall can be spatially very patchy) and differences in local conditions could further modify local pond specific microclimate. Such site-specific variation in microclimates would not be captured in regional weather patterns and could further help explain why we found no clear climatic drivers of phenological shifts in our system (Figs S3 and S4). It is important to note that the climate data we used are comparable in quality and scale to that used in many other phenology studies. However, our use of multiple replicate communities revealed that simple regional climate predictors are not strong enough to capture variation across space, a conclusion that is impossible to make if only considering one replicate community or several highly clustered communities. A goal of future phenology studies should be to measure more fine-scale, site-level climate data to link climatic factors to phenological patterns across local and regional geographical scales.

Phenological distributions might be more uniform across time and space if phenology is determined by a more consistent cue (e.g. photoperiod), and/or if populations are composed of the same individuals year-to-year (e.g. perennial plants). In these less variable systems, it may take longer to see non-uniform shifts in species' phenological distributions. However, even if a particular species' phenological distribution is very uniform over time, in a community context there will be many species with varied life histories and seasonal niches. It is highly unlikely that each population's phenological distribution will be uniform across time, and therefore we can expect to see changes in temporal overlap that would go undetected by considering only single metric summaries. For instance in long-lived perennial plants, a system much more predictable than our amphibian system, species differ substantially in the rate at which first, peak and last flowering dates change over time, indicating that phenological distributions change over time (CaraDonna *et al.* 2014). Therefore, non-uniform shifts in phenological distributions are unlikely to be unique to amphibians and instead are bound to occur in a wide range of plant and animal systems.

Now that phenological responses to climate change have been well-documented, the crucial next step is to understand and predict the consequences of this pattern. Our study clearly indicates that because phenological distributions change non-uniformly, we need to expand on traditional single metric approaches and instead consider the entire distribution of phenological events represented in a population. In this system, shifts in the shapes of phenological distributions caused long-term changes in interaction potential that could not be detected with phenological summary metrics. Important next steps in phenology research will be to first identify which factors determine shifts in species' phenological distributions, and then determine whether systematic patterns could be used to extrapolate and predict phenological changes across taxa and ecosystems. In addition, we need experimental studies that determine how changes in the distributions are linked to outcomes of species interactions. Combining both research venues will then allow us to create a mechanistic framework to link climate-mediated changes in phenologies to the structure and dynamics of natural communities.

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The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS

DS collected and processed the data, SKC analysed the data and SKC and VHWR designed the research and wrote the paper.

DATA ACCESSIBILITY

The data supporting the results will be archived in Dryad.

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