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Current and lagged climate affects phenology across diverse taxonomic groups

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The timing of life events (phenology) can be influenced by climate. Studies from around the world tell us that climate cues and species' responses can vary greatly. If variation in climate effects on phenology is strong within a single ecosystem, climate change could lead to ecological disruption, but detailed data from diverse taxa within a single ecosystem are rare. We collated first sighting and median activity within a high-elevation environment for plants, insects, birds, mammals and an amphibian across 45 years (1975–2020). We related 10 812 phenological events to climate data to determine the relative importance of climate effects on species' phenologies. We demonstrate significant variation in climate-phenology linkage across taxa in a single ecosystem. Both current and prior climate predicted changes in phenology. Taxa responded to some cues similarly, such as snowmelt date and spring temperatures; other cues affected phenology differently. For example, prior summer precipitation had no effect on most plants, delayed first activity of some insects, but advanced activity of the amphibian, some mammals, and birds. Comparing phenological responses of taxa at a single location, we find that important cues often differ among taxa, suggesting that changes to climate may disrupt synchrony of timing among taxa.

1. Introduction

Climate can strongly influence phenology (the timing of life-history events) by speeding up or delaying events such as emergence, peak activity and reproduction [1]. In turn, phenology can influence individual fitness [2,3], species interactions [4,5] and ecosystem function [6]. Shifts in climate may alter phenology and consequently organismal fitness by exposing organisms to unfavorable abiotic environments and through altering the strength of species interactions

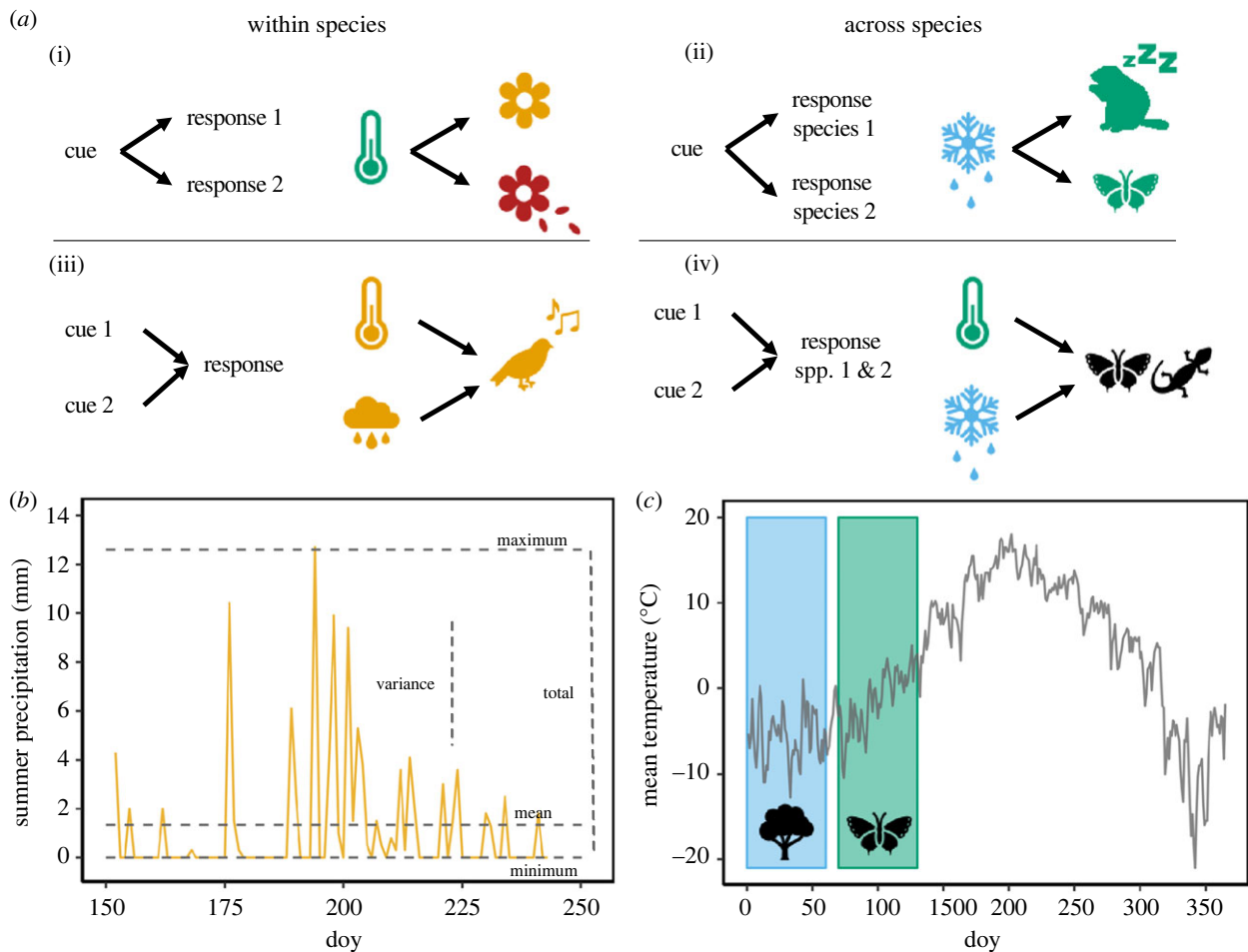


Figure 1. Potential phenological responses to climate. Colours represent the season in which a cue or response occurs: green = spring, yellow = summer, red = fall and blue = winter. (a) Both within and across species, one cue might lead to multiple responses, or several cues might lead to a single response. Examples of one cue influencing several responses are A1) temperature cueing both flower and fruiting timing within the same species or A2) snowmelt date cueing first day of activity of small mammals and insects. Examples of several cues leading to a single response are A3) temperature and precipitation jointly initiating bird song or A4) first activity of insects responding to temperature while first activity of salamanders responds to precipitation. For a particular cue such as precipitation, species may respond to (b) different aspects of the cue e.g. mean, minimum, maximum, variance or growing season total or (c) the season in which the cue occurs, such as winter temperature cueing tree flowering whereas spring temperature cues butterfly activity.

(phenological mismatch). For example, earlier snowmelt may cue earlier formation of flower buds that may then face higher frost mortality [7–9], pollen limitation may increase when plants flower before pollinators are active [10–12], or herbivorous insects may hatch prior to budburst [13] (but see [14]).

Understanding how climate change influences phenology is challenging for several reasons. First, the many potential climate cues are not changing synchronously [15]. Second, phenology itself is multivariate, including diverse events such as growth, reproduction and dispersal, and features such as activity initiation, median activity, and activity duration. All of these phenological events and features can change at different rates and be affected by different climate cues [16]. Despite the rise in studies examining the effects of climate on phenology, we still have a relatively narrow view of the diversity of phenological responses to highly multi-dimensional climate as most studies focus on one or a few climate cues, phenological responses and taxonomic groups (but see [17–19]).

To understand how climate may influence assemblages of organisms we need to recognize the diversity of climate cues that affect phenology (figure 1a). In many temperate and montane environments, snowmelt is an important phenological cue

[20–23] and perhaps the simplest of climate cues, occurring only once in most seasons. Temperature and precipitation are more complex; they can be measured in many biologically relevant ways (e.g. mean, minimum, maximum, total amount, frequency) and occur in multiple seasons (figure 1b). Aspects of both temperature and precipitation can affect phenology (e.g. [17,24]), and can change at different rates (e.g. spring climate is shifting more than fall climate in most temperate areas [15]). Organisms can also experience these diverse climate cues in both current and prior years [25]. Multivariate climate space, the suite of acceptable climatic conditions for a given species, has been used in conservation biology for species distribution models [26] or prioritizing areas to protect [27,28]. Multivariate climate space could be used in phenological models to explore the relative importance of different cues in explaining phenological variation among species, or phenological syndromes.

The interaction between individual species' phenologies and climate can be complex. A single phenological event may be driven by several climate cues, and different phenological events in a species' life may be driven by different cues (figure 1a). For example, in small mammals that hibernate, spring emergence is often driven by snowmelt date, whereas hibernation initiation can be driven by photoperiod [29,30].

While warmer temperatures are well-known to advance phenological events for many taxa, the magnitude of change, or the number of days advanced per unit time, can differ among phenological events [31]. For example, plant flowering and fruiting may both advance in response to higher temperatures, but flowering may advance more rapidly [32,33].

Phenological responses to climate can vary greatly among species; species can respond to different climate cues, different aspects of a given cue, or to the same cue in different ways [34,35] (figure 1*a*). For example, in an arid environment, first flowering of low-elevation plant species was cued by precipitation whereas high-elevation plant species were cued by temperature [36]. Even when species respond to the same cue of ‘temperature’, they might respond to different aspects of temperature—one species may respond to the average, another to the maximum [37], or species may respond differently to the average temperatures of different seasons, such as spring and summer [38,39] (figure 1*c*). Species may also respond to the same cue but with different magnitudes, such that one species is advancing at a faster rate than another. This is often seen across trophic levels, with plants advancing faster in response to hotter temperatures than primary or secondary consumers [19,40,41]. If species with strong interactions are using different climate cues or climate cues from different seasons, this may lead to temporal mismatch as seasons are shifting at different rates with global climate change [15,25].

Past climatic cues can be important because organisms use them in predictive processes [25]. For example, a cue experienced at one time, t , might inform an organism of breeding conditions or food availability at a later time [39,42] or influence its ability to respond to later cues. To understand phenological activity at time t , we should consider both current cues and cues at $t - x$, where x indicates an earlier timeframe. This timeframe can range from weeks to years prior to a given phenological event [43–46]. Prior weather can be a good phenological predictor, such as in Arctic ungulates where fall temperature determines conception timing and thus spring parturition date [44,47–49]. Fall weather can also predict flowering times for fruit trees and other angiosperms in the following spring [50,51]. Prior weather may also be important in predicting phenology of shorter-lived mammals and insects, as weather in one season can affect conditions in the next; winter snowfall can affect summer water availability [52], or fall temperatures and frost can affect pre-hibernation food supply and subsequent spring survival [53–55]. In migrating birds, spring arrival time is often dependent on the weather at wintering and stopover locations [56]. Although we know prior climate *can* matter for phenology, few studies have compared the importance of prior versus current climate.

Studies from around the world demonstrate that climate cues and species’ responses can vary greatly, but detailed data from diverse taxa and several climate predictors within a single ecosystem are rare (but see [35]). Thus, we know little about how diverse climate-phenology interactions are among potentially interacting species and the potential for ecological disruptions. To understand how multiple aspects of phenology of different taxa respond to the effects of several climate predictors, we used systematically collected first sighting and median activity data from a single high-elevation ecosystem for 30 plant, 13 insect, 16 bird, 2 mammal and 1 amphibian species representing 10 812 phenological events across 45 years (1975–2020; see electronic supplementary material, figure S1 for species names) combined with climatic

data. We asked (*Aim 1*) which climate cues are important across taxa, (*Aim 2*) whether climatic cues from the prior growing season (or even longer ago) are good phenological predictors, (*Aim 3*) whether the magnitude and direction of response to climate cues differ among taxa and (*Aim 4*) whether climate responses reveal cross-taxon phenological syndromes for species in one location.

2. Methods

(a) Study location

We studied the phenological responses of plants, insects, mammals, amphibians and birds near the Rocky Mountain Biological Laboratory (RMBL) in Colorado, USA (38.96°N, –106.99°W). Data were collected from approximately 2945 m above sea-level up to 3414 m (for amphibians). This seasonal montane habitat typically has a persistent snowpack from November through May.

(b) Climate data

Climate data were obtained from the Crested Butte Weather Station (Station USC00051959) and by resident billy barr at the RMBL [57,58]. We use the subscript t to indicate a cue from the current growing season, where the growing season starts in spring, and $t - 1$ to indicate a prior cue (electronic supplementary material, figure S2). We refer to $t - 1$ cues as ‘lagged’, and address in our discussion how this definition relates to previous uses of ‘lags’ in relationships between climate and phenology. We defined spring as 1 March to 31 May, summer as 1 June to 31 August, fall as 1 September to 30 November, and winter as 1 December to 28 February. Current season cues included snowmelt (first date of bare ground in a permanent 1 × 1 m plot at the RMBL) and average spring temperature. Lagged cues ($t - 1$) were average summer and fall temperatures (°C) and cumulative summer and fall precipitation (mm). Several cues included data from current and prior growing season months (t and $t - 1$; electronic supplementary material, figure S2): average winter temperature (°C), cumulative winter and spring snow precipitation (snow water equivalent, mm), and a cold severity index. Cold severity index is calculated from September through May and integrates three components: total snowfall, duration of snow cover and temperature. Due to the insulating properties of snow, average temperatures $\leq 0^\circ\text{C}$ are summed when the snowpack depth is ≤ 30 cm (adapted from [59,60]). High cold severity index values indicate cold temperatures with low snow cover and a later snowmelt date. About a third of dates were missing snow depth; missing data were interpolated using the R package ‘forecast’ [61]. See electronic supplementary material, 1 for details on climate data collection and choice of cues included in our analyses. To generate results that are comparable across taxa, we scaled all climate data with a z-score transformation prior to analysis.

(c) Phenology data

Researchers at the Rocky Mountain Biological Laboratory have collected phenological data on a variety of taxonomic groups since 1975. Data on first sightings each year were available for plants, insects, mammals, amphibians and birds, whereas median activity data were available only for plants, insects and mammals. Plant first sighting was the first flowering day for each species and median activity was the median date between first and last flower. Insect first sighting was observation of first egg or first adult emergence, depending on the species. Median insect activity was the day of maximum abundance during the season; note that first sighting and median activity data were available for different sets of insect species. Mammal first sighting was first pup emergence and median activity was the day of maximum pup emergence. Because female

hibernating squirrels typically initiate reproduction within days of emergence from hibernation [30] and have fixed periods of gestation and lactation [62], pup emergence is also a useful proxy for hibernation emergence phenology. Amphibian first sightings included first egg, day of hatching, and first adult sighting. Bird first sightings were spring arrival dates. We checked the correlation between first and median activity in plants and mammals (the two groups for which we had both sets of data) and found that they were positively correlated (electronic supplementary material, figure S3). Thus our first sighting data are informative for more than demonstrating outliers [63]. All data were collected using best practices and protocols approved by the appropriate agencies. Full details on the methods for gathering phenology data are in electronic supplementary material, 1.

(d) Population size

Because population size can influence estimates of first phenological activity [64], we initially included scaled prior population size ($t - 1$) in models for taxa where estimates of population size were available (mammals, butterflies and solitary bees). Preliminary analysis demonstrated that prior years' population size was not a significant phenological predictor (electronic supplementary material, table S1), so was dropped from subsequent analyses.

(e) Analyses

We first tested whether climate factors changed over time with linear regression. To examine which climate cues are most often important for different taxa and whether climatic cues from the prior growing season are good phenological predictors (Aim 1, Aim 2), we used linear models followed by backward stepwise selection for first, median, or both first and median phenological events of each species. Analyses were conducted in R v. 4.1.2 [65]. We checked variance inflation factors using the package 'car' [66] and removed co-linear climate factors with variance inflation factors greater than five [67]. For plants only, we ran mixed-effects models with 'plot' as a random factor to account for repeated observations across permanent plots. Linear models and stepwise selection were conducted using the package 'stats' [65] and model results were extracted using the package 'broom' [68]. Mixed effect models were run using 'lme4' and stepwise selection was conducted via 'lmerTest' [69,70].

To check whether climate from more than 1 year prior affected phenology (Aim 2) we ran separate mixed-effects models for plants, mammals, and amphibians containing climate cues lagged 1 year, and another model containing climate cues lagged both one and 2 years, with species (plants, mammals) or event (because amphibians had multiple first events) as random factors. Due to sample size limits, we were unable to run models including climate cues lagged both 1 and 2 years for individual species. These models were followed with backward stepwise model selection. If a cue was dropped from the 1-year lag model, we did not include it in the model with 1- and 2-year lags. We did not test insects as individuals do not live longer than a year and thus weather greater than 1 year ago was unlikely to affect the current generation, as grandmaternal effects have not been documented for phenology. We were not able to run a 1- and 2-year lagged model for birds, as our proxy for migration distance varied by species and species would be used in the model as a random factor.

To test how the magnitude and direction of response to climate cues differs among taxa (Aim 3) we ran the same linear models as for Aim 1, but without stepwise selection. Retaining all climate cues allowed us to test whether taxonomic groups had differential responses to specific cues (β slope or direction). Due to high variance inflation factors we dropped cumulative summer precipitation ($t - 1$), cumulative winter-spring precipitation and cold severity index ($t - 1$) from median insect analyses; we dropped the same variables from plant and mammal median analyses to

allow comparison across taxa. To test for differences in taxonomic responses to climate cues, we ran a generalized linear model for each climate cue with β as the response and taxonomic group as the predictor. We weighted the analysis by the square root of the number of years of data for each species to account for differences in sample size and thus precision of estimates. Generalized linear models were run using the 'stats' package and followed by pairwise comparison with Bonferroni p -value adjustment using the 'emmeans' package [65,71]. For average spring temperature and snowmelt date—the two cues that we predicted *a priori* to affect all taxa—we tested whether the response rate differed between producers (plants) and consumers (all other species) by comparing their rates of phenological change using Welch's t -tests.

Migrating birds are often affected both by temperatures at their wintering and breeding grounds, so we explored whether the arrival phenology of birds was explained by migration distance [72]. We used hand-wing index as a proxy for migration distance ([73], electronic supplementary material, table S2) and constructed a linear model with hand-wing index and local climate cues as predictors, then used backward stepwise model selection to investigate which cues were associated with bird arrival phenology.

We do not emphasize phenological advances over time because for most species (plants and insects), the annual initiation of data collection began earlier over time as access to the field site has become possible earlier in the season. Change in the timing of first phenological events over time could thus be confounded with the significantly advancing initiation of data collection (electronic supplementary material, figure S4).

Different species, regardless of their taxonomic group, could show similar combinations of sensitivities to the same climate factors (phenological syndromes). For example, one phenology strategy may be responding to snowmelt date and spring temperatures, whereas a different strategy would be responding to prior fall temperatures and winter-spring precipitation. These phenological syndromes would be revealed as distinct clusters of species' points on an ordination (Aim 4). We ran principal component analyses (PCA) for the estimated regression coefficients for each species' first and median phenological events. For each PCA, we created a matrix of the regression coefficients from the full models from Aim 3. We conducted the PCA with a variance-covariance matrix using 'FactoMineR', and checked PCA dimensions via scree plots using 'factoextra' [74,75].

3. Results

(a) Summer and fall are getting warmer

Since 1975, average summer temperature at the RMBL has increased by 0.4°C each decade while fall temperature has increased by 0.2°C per decade (electronic supplementary material, figure S5). No other climatic cues showed significant directional change over the study period (electronic supplementary material, figure S5), although snowmelt date did trend earlier by 2.4 days per decade (electronic supplementary material, figure S5). Additionally, first and median phenology for plants and insects significantly advanced over time (electronic supplementary material, figure S6), although for some species this result could be due to advancing data collection dates (electronic supplementary material, figure S4)

(b) Snowmelt date and spring temperature were important phenological cues for all taxa (Aim 1)

Snowmelt date affected all taxonomic groups; in years with earlier snowmelt, first activity advanced significantly across all

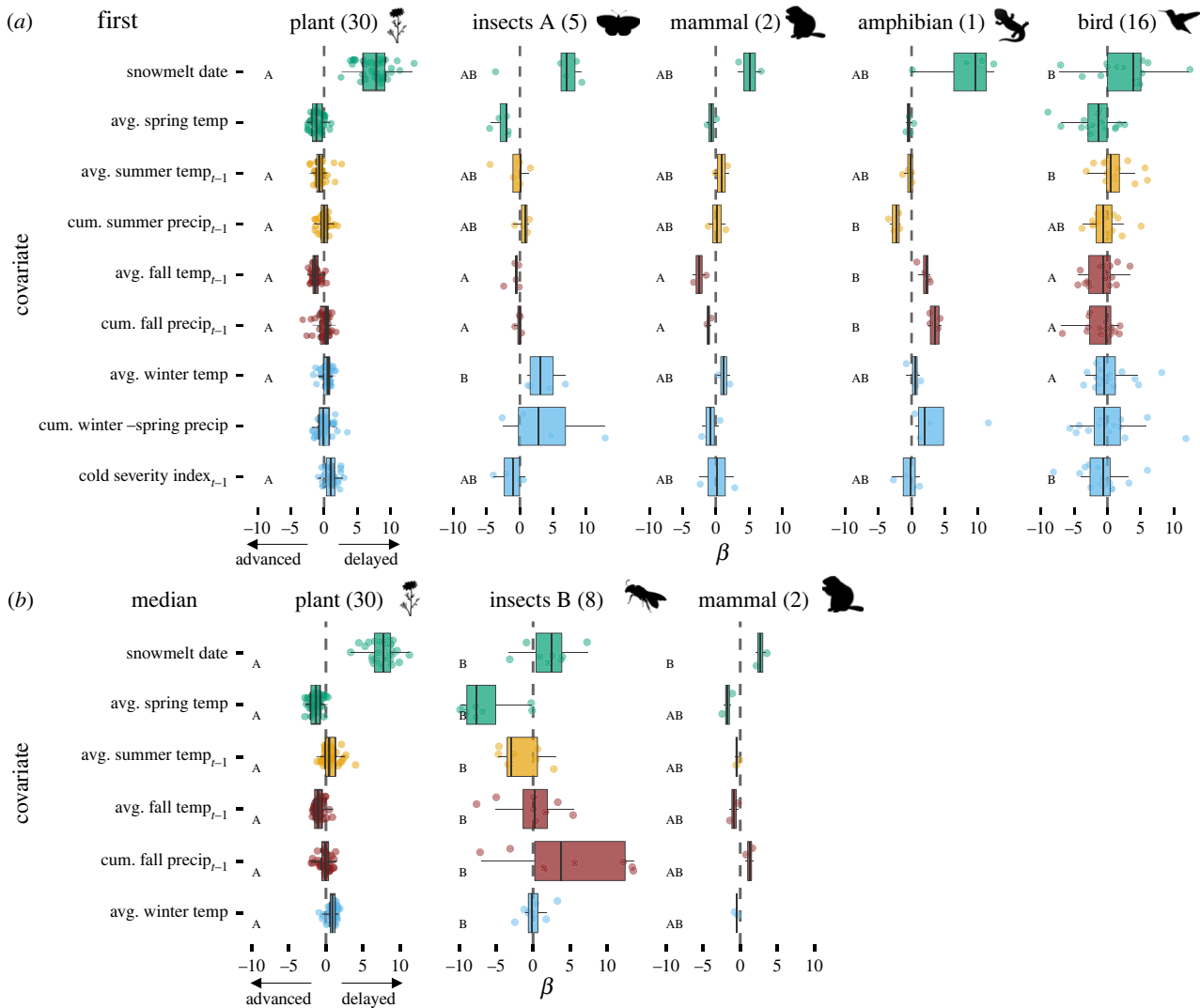


Figure 2. Estimated regression coefficients (β) from best-fit multiple linear regressions of environmental correlates on (a) first and (b) median emergence or sighting dates of plant, insect, mammal, amphibian and bird species at the RMBL. Each point represents a separate species or life stage. Parentheses next to taxa show the number of species used. Information on first and median phenology were available for different insect species (see *Methods*); we denote the groups with A and B. Subscripts next to covariates indicate either the year of sampling (t), or the year prior to sampling ($t - 1$) as a test for lagged effects of climate on phenology metrics. See electronic supplementary material, figure S2 for lagged timeframes and *Methods* for calculation of cold severity index. Different letters next to boxplots represent significant differences in pairwise comparisons across taxonomic groups ($p < 0.05$). Absence of letters next to boxplots for a climate cue indicates lack of significantly different responses across taxonomic groups. Points to the left of zero indicate advances in phenology and those to the right indicate delays. Colours denote the season of a given weather variable: green = spring, yellow = summer, red = fall and blue = winter.

taxa (figures 2 and electronic supplementary material, figure S7, tables S3–S7). However, snowmelt date was dropped from models of all eight insect species for which we had median activity data, indicating snowmelt is not as important to wasp and fly (Hymenoptera and Diptera) median activity. Most bird species arrived earlier in years when snowmelt date was earlier ($\beta = 3.6$, $t = 4.4$, $p < 0.001$) except red-winged blackbird (*Agelaius phoeniceus*) and Steller's jay (*Cyanocitta stelleri*), which arrived later in years with early snowmelt (electronic supplementary material, table S7). Hand-wing index (proxy for migration distance) was an important predictor of bird arrival, with a higher hand-wing index (longer migration) delaying bird arrival date ($\beta = 5.4$, $t = 6.97$, $p < 0.001$).

Prior research in many temperate habitats has shown that average spring temperature is important for the phenology of plants and animals [22,24,29,76]. Similarly, in our study as average spring temperature increased, first and median phenological activity were significantly earlier for most taxa (figure 2

and electronic supplementary material, figure S7, tables S3–S8). However, mammals followed a different pattern—spring temperature was not retained as a cue predicting first activity but was retained for one species as a cue predicting median pup births (electronic supplementary material, table S5). Although plants overall advanced their phenology with higher spring temperatures, early season species such as spring beauty (*Claytonia lanceolata*) significantly delayed first flowering with higher average spring temperature (electronic supplementary material, table S3).

(c) Climate cues from prior growing seasons were good predictors of phenology (Aim 2)

Cumulative summer and fall precipitation and fall temperature were important phenological cues across taxonomic groups, influencing firsts and medians. Some climate cues with lags of up to 2 years influenced plant and amphibian

phenology, but not mammal phenology. Contrary to the effect of a wet fall 1 year prior, a wetter fall 2 years prior advanced spring amphibian activity ($\beta_{t-2} = -1.6$, $t_{1,93} = -2.5$, $p = 0.02$). A hotter summer both 1 and 2 years prior advanced first and median plant phenology ($\beta_{t-2} = -0.8$, $t_{1,9088} = -6.6$, $p < 0.01$ and $\beta_{t-2} = -0.7$, $t_{1,9088} = -5.9$, $p < 0.01$). By contrast, while a cold winter 1 year prior advanced first and median plant phenology ($\beta_{t-2} = 0.2$, $t_{1,9088} = 2.6$, $p < 0.01$ and $\beta_{t-2} = 0.6$, $t_{1,9088} = 6.2$, $p < 0.01$), a cold winter 2 years prior delayed first and median plant phenology ($\beta_{t-2} = -0.5$, $t_{1,9088} = -4.7$, $p < 0.01$ and $\beta_{t-2} = -1.1$, $t_{1,9088} = -9.8$, $p < 0.01$).

(d) The magnitude and direction of response to some climate cues differed among taxa (Aim 3)

Earlier snowmelt advanced plant flowering more than snowmelt advanced events for other taxa (figure 2, tables S9–S13), advancing plant phenology 2 days for each day consumers advanced (first: $t = -3.53$, d.f. = 34.5, $p = 0.001$; median: $t = -3.58$, d.f. = 10.3, $p = 0.01$). Spring temperatures shifted producer and consumer first phenological events similarly ($t = -1.36$, d.f. = 32.7, $p = 0.18$), although consumer median phenology advanced almost 4 days for each day producers advanced with warmer average spring temperatures ($t = -2.68$, d.f. = 9.2, $p = 0.02$). While warmer summers advanced phenology of most taxonomic groups, spring bird arrivals were delayed by warmer summers the prior year (figure 2 & electronic supplementary material, figure S7, table S13). For plants, warmer summers in the prior year advanced first and median flowering for early season species but delayed first and median flowering for several late-season species including tall larkspur (*Delphinium barbeyi*), tall bluebells (*Mertensia ciliata*) and ballhead sandwort (*Eremogone congesta*; figure 2; electronic supplementary material, table S9).

Higher cumulative summer and fall precipitation provoked variable responses across and within taxonomic groups. A wetter prior summer advanced spring first flowering of all but three plant species, whereas a wetter fall delayed late-season plant species but advanced earlier season plants (figure 2, electronic supplementary material, table S9). Wetter summers delayed subsequent spring activity of burying beetles (*Nicrophorus investigator*), while advancing first activity of both Gillette's checkerspot butterfly (*Euphydryas gillettii*) and Mormon fritillary (*Speyeria mormonia*) (figure 2; electronic supplementary material, table S10). The two mammals had opposite responses to prior summer precipitation—more precipitation advanced yellow-bellied marmot (*Marmota flaviventris*) spring pup births but delayed median pup births of golden-mantled ground squirrels (*Callospermophilus lateralis*; figure 2; electronic supplementary material, table S11). Median births of golden-mantled ground squirrels were also delayed by a wetter prior fall. Arizona tiger salamanders' (*Ambystoma mavortium nebulosum*) spring phenology advanced with a wetter prior summer but was delayed by a wetter fall (figure 2; electronic supplementary material, table S12).

Most taxa responded to warmer fall temperatures by advancing first and median activity the following growing season. However, warmer fall temperatures delayed both the egg-laying date and first sighting of female paedomorphic Arizona tiger salamanders (electronic supplementary material, table S12).

Taxonomic groups responded differently to cumulative winter-spring precipitation, which delayed first activity of

some species and advanced phenology of others (figure 2). A wetter winter and spring advanced phenology of early season plants and birds with intermediate hand-wing indexes, such as the American Robin (*Turdus migratorius*), while delaying phenology of mid-season plants and birds with lower hand-wing indexes (electronic supplementary material, tables S9, S13). A similar pattern was seen in response to cold severity index, plants had a more negative response to cold temperatures with little snow insulation, while the same conditions were associated with advanced spring arrival of most bird species (electronic supplementary material, tables S9, S13).

Warmer winter temperatures strongly delayed first activity of some insects, including burying beetle (*Nicrophorus investigator*), Mormon fritillary (*Speyeria mormonia*), Gillette's checkerspot butterfly (*Euphydryas gillettii*) and flies (*Delia* spp.), but advanced median activity of solitary bees that overwinter as pupae including *Lasioglossum nigrum* and *Panurginus cressoniellus* (electronic supplementary material, table S10).

(e) Multivariate climate syndromes for species' first and median events (Aim 4)

When phenological sensitivities (β in figure 2) were examined in multivariate climate space we found no evidence for climate response syndromes. The distribution of taxa within climate-response space for first and median activity did not show strong clustering. However, the climate spaces did highlight a few broad patterns. The first two axes of the PCA using first activity for each species explained 75.2% of the variation in the data (figure 3, electronic supplementary material, figure S8), even though climate cues did not have high pairwise correlations. Winter cues dominated both axes, with variation in species' sensitivities to snowmelt date explaining substantial variation in both axes. Differing responses to cumulative winter-spring precipitation explained additional variation in PC1, while responses to average winter temperature and cold severity index explained additional variation in PC2 (electronic supplementary material, table S14). Plant and bird first activity were more broadly distributed along PC2, indicating greater heterogeneity among species in these groups in the influence of average winter temperature and cold severity index (figure 3).

The first two axes from the median activity PCA explained 83.5% of the variance in the data (figure 3; electronic supplementary material, figure S8). Species' responses to prior fall precipitation dominated PC1, whereas sensitivities to snowmelt date and average spring temperature explained variation in PC2 (electronic supplementary material, table S14). Thus, the responses of taxonomic groups and species (figure 3) can be largely reduced to variation along two axes, despite no evidence of clear cross-taxa syndromes. Plants and insects separated in climate-response space—sensitivities to snowmelt date and average spring temperature explained most variation in median plant phenology responses to climate while insect sensitivities were more variable among species with prior fall temperature and precipitation explaining more variation in median insect phenology sensitivities (figure 3).

4. Discussion

Even for species found in the same local area, we found more climate drivers of phenology than previous studies have

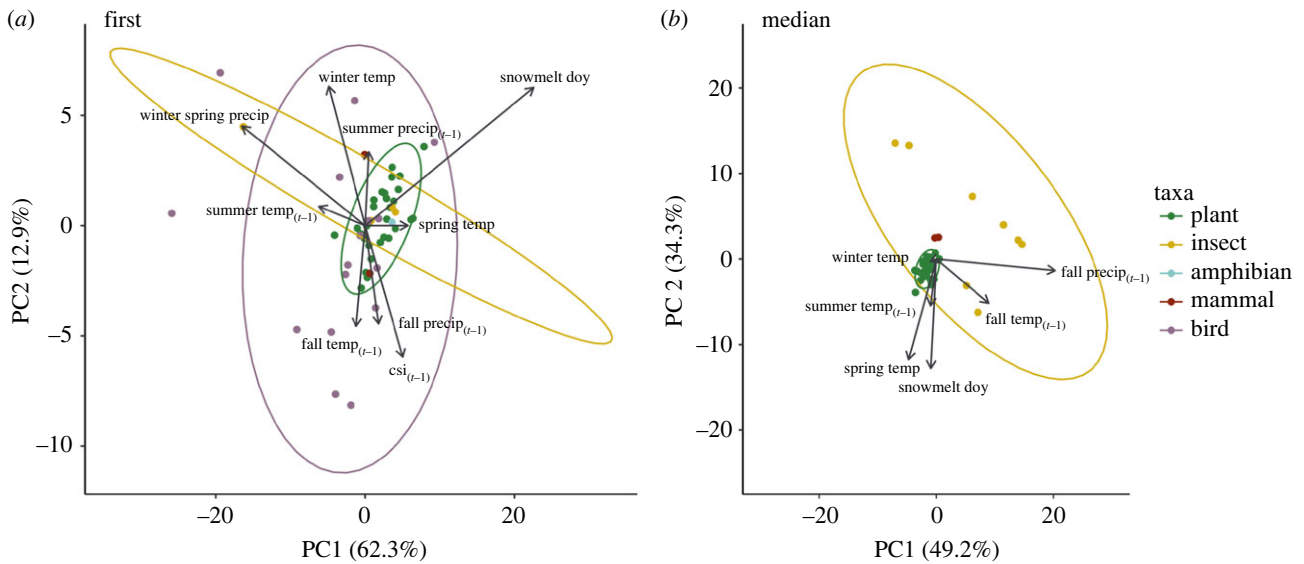


Figure 3. Principal components analysis ordination of (a) first and (b) median emergence or sighting dates of plant, insect, mammal, amphibian and bird species at the RMBL. Each point represents estimated regression coefficients for a species or life stage. Vectors indicate the direction and magnitude of correlations of climatic cues determining phenology (electronic supplementary material, table S13). Ellipses are the 95% confidence interval surrounding the centroid for each taxon's phenology. Too few points were available to calculate 95% ellipses for amphibian first activity or mammal first and median activity.

considered and found that the most important cues often differ among taxonomic groups. Taxonomic groups responded to some cues similarly, for example earlier snowmelt and warmer spring temperatures advanced phenology of almost all groups. Other cues resulted in different effects across groups, e.g. prior summer precipitation delayed first activity of some insects but advanced activity of some vertebrates. Even within taxonomic groups, different species responded to different suites of cues, or to the same cue in different ways (electronic supplementary material, table S8). We even observed that the same cue can have contrasting effects based on life stage within a single species (electronic supplementary material, table S8) [77]. Across groups, prior-season climatic cues ($t - 1$) were good phenological predictors and retained in models for all taxa. Finally, the multivariate climate-response spaces showed that variation in first and median phenological activity was driven by complex combinations of climate cues, emphasizing the importance of examining which cues are driving a species' entire phenological distribution. No clear phenological response syndromes were identified, suggesting mismatches in timing between species may occur going forward as cues result in variable responses within and between species. Testing for biologically important mismatches will require authors to identify closely interacting species and consider their full phenological responses to diverse climate cues.

Prior-season climate cues ($t - 1$) effectively predicted phenology for many taxa and suggested possible mechanisms underlying phenological responses. For example, a warmer fall advanced phenology the following spring for plants, insects and mammals. This earlier spring activity may have been fueled by an extended growing season, which allows organisms to gather more energy prior to senescence, hibernation or diapause. In plants, additional energy is gained via continued photosynthesis [54,78], whereas mammals intake more food during the extended pre-hibernation period [79]. As a caveat, longer growing seasons can affect the success of organisms not only through shifting phenology but also via altering predation risk [55,80] or other factors. In

another example, a higher cold severity index (cold temperatures with little insulating snow) delayed plant, insect and mammal phenology the following spring. In plants, this delay may be due to root damage from increased freeze-thaw cycles [81]. In other taxa, delays may be due to organisms directing more energy toward maintaining basal metabolic rate, thus delaying reproductive phenology [82–84]. These alternative hypotheses suggest directions for future work on links between physiological mechanisms and species' responses to shifts in climate.

It can be difficult to know how far back to look for climate predictors of an organism's phenology. Some cues can prompt responses within a day, such as plants flowering immediately post-snowmelt [85,86], other cues prompt responses within a month or two, such as warm spring weather stimulating insect emergence [39,87], and still other responses occur across seasons, such as fall temperature determining conception timing, and thus spring birth of arctic ungulates [44,47–49]. Cues can also accumulate over time and interact with organisms' physiological demands; for example, a warm winter combined with a warm spring delays first flower of some plant species, because they have not met their vernalization-chilling requirements [88,89]. In our study, climate data with a lag of up to 1 year affected phenology for some species in every taxonomic group. Additionally, like Mulder *et al.* [90], we found climate from up to 2 years prior can affect phenology of plants and amphibians. Thus, examining a range of the prior year's cues for phenology of short-lived organisms, and lags longer than a year for long-lived organisms, may provide a more accurate assessment of how climate influences phenology. Such extended lag times may be more common at high altitudes or latitudes, where growing seasons are short. For example, alpine bistort (*Polygonum viviparum*) has a 4-year preformation period for leaves and inflorescences [91], and the Arctic woolly bear moth (*Gynaephora groenlandica*) has a caterpillar stage lasting up to 13 years [92].

Understanding the importance of prior climate for phenology is complicated by the fact that authors do not always clearly identify the timeframe of the climate data

they use in analyses (but see [35,39]), using the term ‘lag’ to refer to a range of different times between climate and phenological events. It makes sense that spring phenology would be analysed using climate data from the prior calendar year and/or growing season, as much of the weather from the current growing season would occur after the phenological event in question. Until authors consistently identify the timeframe for all climate cues in their work, it will be difficult to determine the relative importance of climate at different timeframes prior to a phenological event across phenological datasets. We used seasonal climate cues as predictors because our goal was to synthesize phenology across a several taxonomic groups. If a smaller climate window is driving species’ phenology, e.g. temperature during a two-week period, we may have underestimated the true slopes of species in response to climate factors. If that is the case, our results are conservative and species may be responding more strongly to climate than we predicted, further emphasizing the possibility of temporal mismatches between species. If researchers are studying a species or group with a known window of climate dependence, that window should be used, and the timeframe stated when analysing climate impacts on phenology [93].

Multidimensional climate-response space showed that more of species’ variation in climate sensitivities (β in figure 3) was explained by one axis for first events than for median events. That the most important climate factors differed between phenological firsts and medians emphasizes the value of considering full phenological distributions (i.e. firsts, medians, lasts, etc.) when data are available [16]. Taxonomic groups were not separated in climate-response space, nor were there signs of cross-taxa phenological response syndromes (distinct clusters of points in PCA space). However, taxa overlapped less in PCA space for sensitivities of median activity, with cumulative prior fall precipitation ($t - 1$) driving variation among sensitivities for median insect and mammal activity and winter and spring cues driving a tight cluster of responses by median plant flowering. The large ellipses for insects in both PCAs could be due to the variation in their natural histories, or because the species we used overwinter in a variety of stages (eggs, larvae, pupae, adults) and overwintering stage may determine how cues affect phenology, or because our time series for several insects were short which could lead to imprecise slope estimates. Although our failure to see cluster of phenological syndromes could have been due to imprecise slope estimates, by examining multiple drivers of variation in phenology, we show that predicting future phenology based solely on a single cue could result in relatively poor predictions.

Producers and consumers are responding to climate drivers at different rates, which creates the potential for ecologically important phenological mismatches and altered species interactions. Earlier snowmelt advanced phenology across taxa, however, plants advanced their phenology faster than consumers in response to earlier snowmelt (figure 1). We found a different pattern in response to warmer spring temperatures, as median consumer phenology shifted faster than producer phenology. If snowmelt keeps advancing and springs continue to warm, this may lead to increased phenological mismatch, as seen in other systems [3,94,95]. To know whether mismatches could affect populations requires looking at the demographic consequences of altered phenology for species we know are interacting [96,97]. A mismatch is possible for golden-mantled ground squirrels; in years with early springs, pups are born

later in the sequence of plant phenology so some plants are senescing when pups are born, leading to altered food availability [62]. This results in pups that gain mass at half the average rate and have delayed reproductive maturation, affecting population size the following year [62]. Moving forward, as new long-term phenological and demographic datasets become available, we encourage researchers to compare datasets from interacting taxa in the same environment and subject to the same climate shifts as data documenting demographic consequences of phenological mismatches remain rare (but see [98–100]).

5. Conclusion

Although most taxonomic groups in our study responded similarly to a few environmental cues, such as snowmelt, within a single ecosystem we found significant variation within and among taxa and phenological events in which cues are most important and how species respond. Our results suggest that diagnosing the potential for climate change to advance or delay phenology, or to cause mismatches, requires considering a wide range of potential drivers and responses including cues from up to 2 years prior. The diversity of responses to multiple climate cues that we found in a single location might suggest a high potential for phenological mismatches, but mismatches might also fail to materialize if conflicting cues counteract each other. Determining whether diverse phenological responses to climate increase or decrease the chances for ecological disruption will be challenging but important future work. Our results highlight the importance of considering the complexity of climate when studying an organism’s phenological changes in response to climate, and the advantage of conducting place-based long-term research on a variety of organisms.

Data accessibility. We commit to public data access for scientific reproducibility and transparency. Our data and R scripts are available on Open Science Framework: <https://doi.org/10.17605/OSF.IO/VTFNR> [101].

The data are provided in electronic supplementary material [102].

Authors’ contributions. R.M.P.: conceptualization, data curation, formal analysis, visualization, writing—original draft, writing—review and editing; R.M.D.: conceptualization, data curation, formal analysis, writing—review and editing; D.T.B.: data curation, investigation, writing—review and editing; C.L.B.: data curation, investigation, writing—review and editing; A.K.B.: data curation, investigation, writing—review and editing; D.W.I.: data curation, investigation, writing—review and editing; R.E.I.: data curation, investigation, writing—review and editing; J.G.A.M.: data curation, investigation, writing—review and editing; R.J.S.: data curation, investigation, writing—review and editing; D.H.V.V.: data curation, investigation, writing—review and editing; C.P.W.: data curation, investigation, writing—review and editing; H.H.W.: data curation, investigation, writing—review and editing; B.D.I.: conceptualization, data curation, formal analysis, investigation, writing—original draft, writing—review and editing; N.U.: conceptualization, formal analysis, investigation, writing—original draft, writing—review and editing.

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