

RESEARCH ARTICLE

Grasshopper species' seasonal timing underlies shifts in phenological overlap in response to climate gradients, variability and change

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Abstract

1. Species with different life histories and communities that vary in their seasonal constraints tend to shift their phenology (seasonal timing) differentially in response to climate warming.
2. We investigate how these variable phenological shifts aggregate to influence phenological overlap within communities. Phenological advancements of later season species and extended durations of early season species may increase phenological overlap, with implications for species' interactions such as resource competition.
3. We leverage extensive historic (1958–1960) and recent (2006–2015) weekly survey data for communities of grasshoppers along a montane elevation gradient to assess the impact of climate on shifts in the phenology and abundance distributions of species. We then examine how these responses are influenced by the seasonal timing of species and elevation, and how in aggregate they influence degrees of phenological overlap within communities.
4. In warmer years, abundance distributions shift earlier in the season and become broader. Total abundance responds variably among species and we do not detect a significant response across species. Shifts in abundance distributions are not strongly shaped by species' seasonal timing or sites of variable elevations. The area of phenological overlap increases in warmer years due to shifts in the relative seasonal timing of compared species. Species that overwinter as nymphs increasingly overlap with later season species that advance their phenology. The days of phenological overlap also increase in warm years but the response varies across sites of variable elevation. Our phenological overlap metric based on comparing single events—the dates of peak abundance—does not shift significantly with warming.
5. Phenological shifts are more complex than shifts in single dates such as first occurrence. As abundance distributions shift earlier and become broader in warm years, phenological overlap increases. Our analysis suggests that overall grasshopper abundance is relatively robust to climate and associated phenological shifts but we find that increased overlap can decrease abundance, potentially by strengthening species interactions such as resource competition.

KEYWORDS

abundance, climate change, community, insect, montane, phenology, species interactions, synchrony

1 | INTRODUCTION

Recent climate change has led to substantial shifts in the seasonal timing (phenology) of life-history events in terrestrial and aquatic ecosystems (Cohen et al., 2018; Menzel et al., 2006; Parmesan, 2006). Differences in the response of organisms to changing environmental conditions have, however, led to significant variation in the magnitude of these temporal shifts. In turn, these varied responses in the timing of events, such as in hatching, flowering, development and migration, may result in the temporal reassembly of communities that could impact both the opportunity for and the strength of interactions between species (Tylianakis et al., 2008; Visser & Both, 2005; Yang & Rudolf, 2010). The fitness implications of these varied phenological shifts are complex and often depend on their community context (Forrest & Miller-Rushing, 2010). Understanding the factors that influence these differential shifts and predicting the nature and impacts of community reassembly presents a challenge (Diez et al., 2012; Pau et al., 2011).

A recent synthesis found pronounced (6.1 days per decade difference in phenological shifts among interacting species) and temporally accelerating shifts in phenological synchrony among pairs of interacting species (Kharouba et al., 2018). Contrary to expectations, however, this synthesis found no consistent tendency towards more or less synchrony and highlighted conceptual and methodological challenges in our ability to predict the direction and implications of phenological mismatches. Varied phenological responses leading to changes in the synchrony between species may result from differences in the exposure of these organisms to environmental conditions and from differences in life-history traits (seasonal timing, trophic position, body sizes and thermal physiologies) that influence their sensitivities and population level responses to the changing conditions (Chmura et al., 2018; Diamond et al., 2011; Rudolf & Singh, 2013; Thackeray et al., 2016). The relative importance of these underlying mechanisms may in turn vary along spatial gradients (Chmura et al., 2018; Diez et al., 2012; Pau et al., 2011). Although phenological studies are dominated by plants (CaraDonna et al., 2014; Fitter & Fitter, 2002; Wolkovich et al., 2012), studies of other groups such as insects (Altermatt, 2010; Diamond et al., 2011), birds (Cotton, 2003), amphibians (Carter et al., 2018; Rasmussen & Rudolf, 2016) and of whole communities (Kharouba et al., 2018; Ovaskainen et al., 2013; Thackeray et al., 2016) are helping to address the drives of variability in phenological responses.

Methodologically, consensus metrics for quantifying phenological overlap have yet to emerge from the limited number of studies addressing phenological synchrony and mismatches within communities. However, such studies suggest that metrics should be more integrative than comparing the relative shifts in single timepoints, such

as first or peak observation, between species (Brown et al., 2016; CaraDonna et al., 2014; Diez et al., 2012; Fleming & Partridge, 1984; Inouye et al., 2019; but see Ramakers et al., 2020). The importance of moving beyond single timepoints is revealed by studies comparing multiple metrics. A long-term study of alpine flowering (CaraDonna et al., 2014), for example, found that first, peak and last flowering often shift independently of one another. Exclusively considering first flowering would result in underestimating the number of species exhibiting phenological shifts and overestimating the magnitude of the shifts (CaraDonna et al., 2014). Likewise, Carter et al. (2018) used abundance distributions to document shifts across the seasonal cycle of amphibians that would not be reflected in single timepoint metrics. In sum, to better understand the fitness and cascading ecological impacts of phenological synchrony and mismatches on organisms and communities, it is essential that we understand the environmental and organismal mechanisms that explain the differential responses of organisms, and that we develop methods for predicting and quantifying these patterns (Chmura et al., 2018; Diez et al., 2012).

Insects provide excellent opportunities to investigate the impacts of variable phenological shifts and synchrony because species and populations may differ in their developmental responses to changing environmental conditions and cues (Hodkinson, 2005). While many species exhibit temperature controls on phenology, some additionally or alternatively use photoperiod cues (Valtonen et al., 2011). Along spatial gradients, insect responses to changing environmental factors and cues can also vary due to both plasticity and genetic differences, potentially resulting from adaptation to local conditions (Berner et al., 2004; Dingle et al., 1990; Tauber & Tauber, 1981). In this study, we leverage extensive historic (1958–1960) and recent (2006–2015) survey data for communities of grasshoppers along a montane elevation gradient to assess whether climate variability and change lead to different phenological and abundance distribution (including position, breadth and scale) shifts across species and populations. We then examine whether different phenological responses alter the temporal synchrony and overlap of communities.

Examining herbivorous grasshoppers allows us to focus on a guild of functionally similar species that are likely to compete for resources (Ritchie & Tilman, 1992). Grasshoppers also substantially influence ecosystem processes including nutrient cycling and primary productivity (Belovsky & Slade, 2018). The grasshoppers in the surveys encompass both variation in species' life-history traits, which affords the opportunity to isolate the mechanisms underlying phenological synchrony, and environmental variation along the elevation gradient. Life-history differences among the grasshoppers include the temperature dependence of their performance, consumption and development. As higher elevation sites along

gradients are associated with a more limited growing season and may also experience differential warming trends and variability (McGuire et al., 2012), gradients allow us to explore changing community level synchrony associated with locally adapted populations and to differing warming patterns. Shifts in synchrony are likely to alter competitive interactions among species, fitness associated with life-history strategies, and thus population dynamics and community composition. These shifts are likely to influence higher trophic levels and ecosystem processes.

We examine how community level synchrony shifts between cool and warm years using surveys conducted weekly from spring to late summer. The surveys assess the developmental progression of species, their population sizes and seasonal windows of occurrence. We use the availability of growing degree days (GDDs) to quantify season warmth in a manner relevant to available developmental time (Cayton et al., 2015; Hodgson et al., 2011) and we compare phenological shifts among univoltine (single annual generation) species that differ in seasonal timing and dispersal traits (and thus gene flow and the potential for local adaptation). We hypothesize that species' seasonal timing and elevation will influence relative shifts in phenology and phenological overlap (see review in Chmura et al., 2018).

1.1 | Seasonal timing

Early season species tend to exhibit the strongest developmental plasticity to capitalize on warm years (Pau et al., 2011; Wolkovich et al., 2012, 2014). As warming has led to montane grasshoppers that hatch earlier in the season advancing their development more than species that hatch later in season (Nufio & Buckley, 2019), it is expected that warming may lead to a decrease in the phenological overlap of early and late species. Alternately, constraints on the advancement of early season species, such as in their responses to snowmelt and plant phenology, may result in later season species advancing their phenology more and increasing phenological overlap. Later season species are exposed to warmer average temperatures and a great proportion of temperatures that exceed lower temperature thresholds, which may accelerate their phenology more and increase phenological overlap. Additionally, early season species may have a greater potential to extend their phenology in warm years.

1.2 | Elevation

Although many proposed mechanisms predict that warming temperatures will lead to greater phenological shifts at higher elevations where seasonal constraints may be greatest, studies do not always support this expectation or may even find no effect of elevation (Chmura et al., 2018; Hodgkinson, 2005). As is the case across many mountain ranges, warming is more pronounced at higher elevations in our study system (McGuire et al., 2012;

Pepin et al., 2015). In turn, previous studies along this gradient show that high elevation populations exhibit more pronounced developmental plasticity (including phenological delays) and countergradient variation such that they require fewer GDDs for development (Buckley et al., 2015; Conover & Schultz, 1995; Nufio & Buckley, 2019). We predict that more pronounced warming coupled with physiologically more responsive populations will result in greater phenological or abundance changes at higher elevations. Given variation among species in responses, we predict that changes in phenological synchrony should be most pronounced at higher elevation sites. However, we note that because our dataset only includes a single site at each elevation, it is possible that any site effects are a result of some other attribute besides elevation that differs between sites.

We investigate how temperature and elevation influence shifts in phenology and phenological overlap through two primary analyses. First, we examine how season warmth shifts abundance distributions across species and elevations. We then examine how these shifts may impact phenological overlap. We analyse historic and recent survey data together according to the assumption, supported by previous analyses (Nufio & Buckley, 2019), that phenological responses to climate warming over recent decades have been analogous to responses to climate variability during the resurvey period. This assumes plastic responses without evolutionary changes. We test the following expectations:

1. *Abundance distributions*—Warming will result in broader abundance distributions that shift earlier. Broader distributions may be enabled by lengthening the thermally suitable period. These shifts will be particularly pronounced for early season species at high elevations due to the mechanisms discussed above. The expected relationship between abundance and season warmth is ambiguous. Reduced phenological overlap may reduce resource competition and increase abundance, but thermal opportunity and stress may also influence abundance. In turn, the relationship between season warmth and abundance changes may be species and elevation dependent.
2. *Phenological overlap*—We expect that warm years will increase pairwise overlap among species that differ in seasonal timing, which will result in increases in community phenological overlap (average pairwise overlap among all grasshopper species). Specifically, we expect extended seasons of early season species and phenological advancements of late season species to result in increased overlap between these two groups. Additionally, increases in phenological overlap may reduce abundance if species are competing for resources.

2 | MATERIALS AND METHODS

Weekly survey data from 1958 to 1960 were assembled from field notebooks as part of the Gordon Alexander Project. Weekly resurveys were conducted between 2006 and 2015

(Nufio et al., 2010) following the original protocol, consisting of 1 person-hours of sweep netting (divided among one to three surveyors) and 0.5 person-hours of searching for adults and juveniles that may have been missed by sweep netting (Alexander & Hilliard, 1969). Weekly data for each site consist of counts of species by developmental stage (instar numbers and adults) and sex. Developmental stage (five juvenile instars and adults for most species) can be readily assessed for field-collected grasshoppers. We include juveniles in our estimates of abundance distributions (weighted by development stage, see abundance distributions section) to provide a comprehensive assessment of potential interactions. Our dataset includes 66,400 individuals recorded in 645 surveys.

We examine four prairie, montane or subalpine sites along the 40th N parallel in Boulder County, CO: Chautauqua Mesa (1,752 m, 40.00N, 105.28W), A1 (2,195 m, 40.01N, 105.37W), B1 (2,591 m, 40.02N, 105.43W), C1 (3,048 m, 40.03N, 105.55W; see Niwot Ridge Long Term Ecological Research). The sites are all grassy meadows, with similar plant communities but somewhat denser vegetation at the lower elevation sites. Grasshopper eggs are deposited as pods just below the surface in areas with exposed soil. We include all species that were observed for at least 4 years at a single site. We coarsely group the species based on their overwintering stage and seasonal timing. Three 'nymphal diapausing' species (*Arphia conspersa*, *Xanthippus corallipes* and *Eritettix simplex*) overwinter as nymphs and thus reach adulthood exceptionally early in the season. These species may exhibit earlier activity in warm years due to release from cold-induced mortality risk in addition to accelerated development. We classify the remaining species, which overwinter as eggs, as either early season (*Aeropedellus clavatus*, *Melanoplus boulderensis*) or late season (*Hesperotettix viridis*, *Melanoplus confusus*, *Melanoplus bivittatus*, *Melanoplus dawsoni*, *Cratyledes neglectus*, *Camnula pellucida*, *Melanoplus fasciatus*, *Melanoplus sanguinipes* and *Chloealtis abdominalis*) species according to their average phenology across years (species listed in approximately ascending order of seasonal timing). We refer to two egg diapausing species as early season species to be consistent with previous studies that did not include nymphal diapausing species (Buckley et al., 2015; Nufio & Buckley, 2019). All species are univoltine, but we note that the nymphal diapausing species lay eggs sufficiently early in the season (May–early June) and that these eggs hatch late in the season, which leads their juveniles to overlap with late season species. While many species are generalists, consuming both grasses and forbs, the nymphal diapausers along with *A. clavatus*, *C. abdominalis* and *C. pellucida* primarily feed on grasses and sedges.

We note that species in our analyses differ in dispersal ability (due to wing length differences) and lower rates of gene flow may result in a greater degree of local adaptation (Kawecki & Ebert, 2004; Slatyer et al., 2020; Wagner & Liebherr, 1992). *Chloealtis abdominalis*, *M. dawsoni*, *M. boulderensis* and *A. clavatus* have short wings and are least dispersive. Some other species have longer wings, but tend to be poor fliers (*M. bivittatus*, *H. viridis*, as well as females of *X. corallipes*

and *E. simplex*). Earlier season species tend to be poor fliers due to short wings, complicating addressing the role of dispersal.

2.1 | Climate data and metrics

We used a compilation of daily maximum and minimum temperature data from weather stations at our study sites from 1953 to 2008 (McGuire et al., 2012). Some missing data were interpolated using data from other stations as detailed in McGuire et al. (2012). We extended the temperature record from 2008 to 2015 using the same weather stations as in McGuire et al. (2012). The weather stations at the 2,195, 2,591 and 3,048 m sites are maintained by the Niwot Ridge Long-Term Ecological Research program. For the 1,752 m site, we used a nearby National Oceanic and Atmospheric Administration (NOAA) weather station [Cooperative Observer Network (COOP) ID 50848, 1,671 m, 39.99N, 105.27W]. We used an additional COOP weather station at Gross Reservoir to fill in some missing data as described below (COOP ID 52629, 2,423 m, 39.94N, 105.35W).

We used the technique from McGuire et al. (2012) for infilling data gaps of more than a month to reconstruct temperature data missing due to instrument failures: the 2,591 m site in 2009 and the 2,195 m site in 2009 and 2010. We used data from the NOAA and 3,048 m weather stations to predict temperatures at the 2,195 m site. We used data from the NOAA, Gross Reservoir and 3,048 m weather stations to predict temperatures at the 2,591 m site. We established linear regression relationships between the station missing data and the other stations for daily temperatures using data from 2005 to 2008. We constructed regressions separately for minimum and maximum temperatures. We filled each missing data point using the weighted average of the two or three predicted values. The weight was determined by the r^2 values of the regressions for each of the two sites. All r^2 values were >0.8 . We additionally used the R function `na.approx` in the `zoo` package to linearly interpolate additional missing data for the 2,591 m site in 2012, the 3,048 m site in 2013 and 2015 and the 2,195 m site in 2010. We restricted this interpolation to gaps of at most 5 days.

We used the daily maximum and minimum temperature data to calculate GDDs available for development as the accumulated product of time and temperature between the lower and upper developmental temperatures (LDT and UDT respectively). The calculation employed a single-sine approximation (Allen, 1976) based on daily minimum and maximum temperatures and a fixed spacing of 12 hr between temperature minima and maxima.

We calculated degree days based on air temperature rather than estimated body temperatures to avoid assumptions regarding thermoregulatory behaviour, radiation, windspeed and soil temperatures. We used a LDT of 12.0°C, which was determined to provide a good empirical fit to the data (Nufio et al., 2010). We estimated cumulative GDDs as the sum of degree days across the approximate developmental period [day of year (doy) 60–243, March

through August]. We additionally considered shorter periods (e.g. months, early season, mid season, months before each species' mean ordinal date) and found our results to be qualitatively insensitive to the time period chosen. Our estimations of GDDs are intended as an approximate translation of environmental temperature into physiological time but are not specific to populations or species.

2.2 | Abundance distributions

We first examine changes in abundance distributions across the season in response to climate variability. We focus on whether responses to climate variability differ across elevations and species with distinct seasonal timing. We use the abundance of both juveniles and adults, weighted by their development stage ($1/6 = 1\text{st}$ instar to $1 = \text{adult}$). Including juveniles allows for a smoother abundance distribution. If resource use is proportional to size, weighing abundance by development stage may better capture the strength of potential interactions between species. We focus on GDDs as a physiologically relevant metric of climate variability because it strongly predicts the timing of phenological events in insects (Cayton et al., 2015; Nufio & Buckley, 2019; van Asch & Visser, 2007).

We quantify the abundance distributions for each species, at each site, in each year using three metrics: (a) the ordinal date of the first survey when cumulative abundance exceeded 15% of seasonal abundance; (b) the breadth (days) between the 15th and 85th quantiles of seasonal abundance; and (c) the total seasonal abundance. We chose the 15th and 85th quantiles to minimize sampling biases associated with detecting rare early and late individuals. For this analysis and those below, we use linear mixed-effect models fit using restricted maximum likelihood (lmer function in the R *LME4* package) to examine how the metrics change as a function of seasonal GDDs, site, seasonal timing and their interactions. Our past analyses of environmental and physiological elevational clines suggest strong effects of elevation for the system (Nufio & Buckley, 2019). However, we analyse site as a categorical variable given that we have data for only four sites. We analyse seasonal timing (1: nymphal diapausers, 2: early season, 3: late season) as an ordered factor. We account for species as a random variable that influences the intercept of the relationship rather than analysing species independently or including species as a factor because we are particularly interested in seasonal timing. We analyse the following model for each abundance distribution metric: $\text{metric} \sim \text{GDDs} + \text{seasonal timing} + \text{site} + \text{GDDs:timing} + \text{GDDs:site} + 1|\text{species:year}$, where year is nested in species. We use the *r.squaredGLMM* function from *MuMIn* to estimate marginal pseudo- R^2 values, indicating the proportion of variance accounted for by fixed factors, for the top model in each case (Nakagawa & Schielzeth, 2013). We did not account for phylogenetic relatedness because many of the species are closely related and we were unable to readily resolve

the phylogeny based on genetic sequences. The focal species are in the family Acrididae and distributed among the sub-families Gomphocerinae, Melanoplinae (including six species from the *Melanoplus* genus) and Oedipodinae.

2.3 | Phenological overlap

We next quantify the extent of phenological overlap for each species pair at each site in each season and examine how this metric corresponds to season warmth (seasonal GDDs). For each species, we fit a loess curve (using the R function *loess*) to abundance as a function of ordinal date. We used the loess curves to provide a continuous abundance estimate across days. We focus on three metrics accounting for different aspects of phenological overlap between pairs of species. First, we examine the area of overlap normalized to (divided by) the total area of the two species, which yields a proportion. Second, we examine the duration (number of days) of overlap. Third, we examine the number of days difference in the peaks of the abundance distributions. We examined additional, similar metrics based on overlap area or days of overlap as well as metrics such as Pianka's index, which represents the proportion of individuals of two species that overlap in phenology and ranges from 0 to 1 (Fleming & Partridge, 1984). We focus on the metrics above, rather than the additional metrics, as findings were qualitatively similar across metrics. The overlap metrics are symmetric, so we dropped repeated combinations of focal and compared species.

We use linear mixed-effect models fit using restricted maximum likelihood (lmer function in the R *LME4* package) to examine how the metrics change as a function of seasonal GDDs, relative species timing (categorical variable: nymphal_nymphal, nymphal_early, nymphal_late, early_early, early_late, late_late), site and their interactions and account for the species combination as a random variable: $\text{overlap} \sim \text{GDDs} + \text{timing} + \text{site} + \text{GDDs:timing} + \text{GDDs:site} + \text{timing:site} + 1|\text{species combination}$. Next, we average pairwise phenological overlap across communities at each elevation for each year. We use linear models to examine how this community phenological overlap varies as a function of seasonal GDDs, site and their interaction.

We assess whether phenological overlap influences total season abundance. This tests the hypothesis that increases in phenological overlap increase resource competition, resulting in lower total abundance. Abundance may also relate to phenological overlap via, for example, extended seasons. However, we confirmed results were similar when using the maximum observed abundance during a single survey. We estimated average overlap across species annually for each site and focal species. We use linear mixed-effect models fit using restricted maximum likelihood (lmer function in the R *LME4* package) to examine how the log total abundance changes as a function of phenological overlap, seasonal timing of the focal species and their interaction. We accounted for the focal species as a random variable: $\text{abundance} \sim \text{overlap} + \text{timing} + \text{overlap:timing} + 1|\text{focal species}$.

3 | RESULTS

3.1 | Abundance distributions

Seasonal abundance distributions vary across species and sites, which differ in elevation, and respond differentially to season warmth (Figure 1). The day corresponding to the 15th percentile of the abundance distribution occurs earlier in warm seasons (estimate $\pm$ SE = -0.040 ± 0.015 , $t = -2.7$, $p < 0.007$, other coefficients: Table S1, ANOVA: Table 1, model $r^2 = 0.63$, Figure 2,

model fits: Figure S1). The breadth of the abundance distribution increases in warm seasons (estimate $\pm$ SE = 0.038 ± 0.015 , $t = 2.6$, $p < 0.01$, other coefficients: Table S1, ANOVA: Table 1, model $r^2 = 0.16$, Figure 2). Total abundance responds variably to season warmth among species and we do not detect significant responses to season warmth across species (ANOVA: Table 1, model $r^2 = 0.07$, Figure 2). Contrary to our expectations, we do not observe any significant interactions between species timing or sites, which differ in elevation, and season warmth (ANOVA: Table 1).

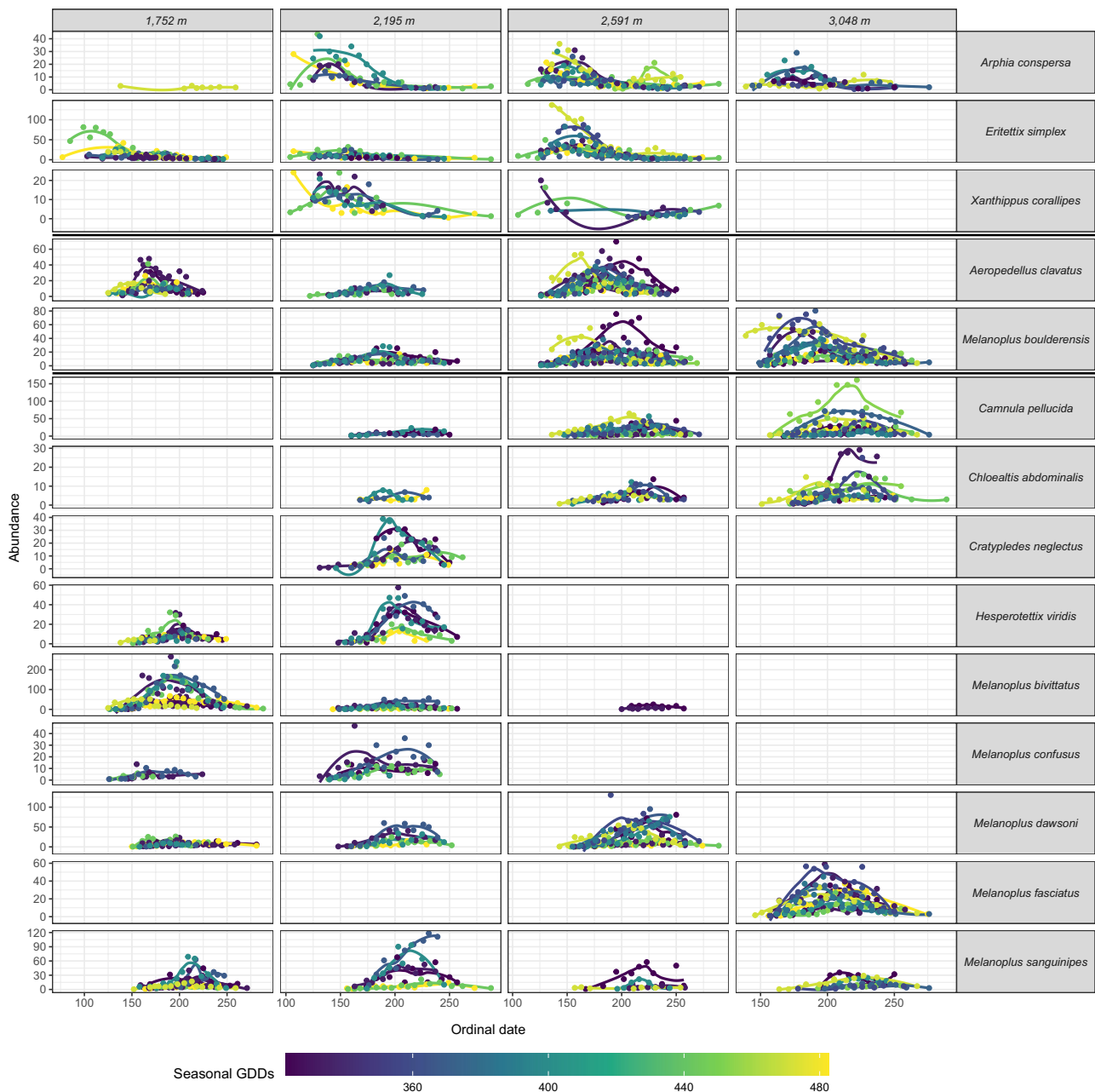
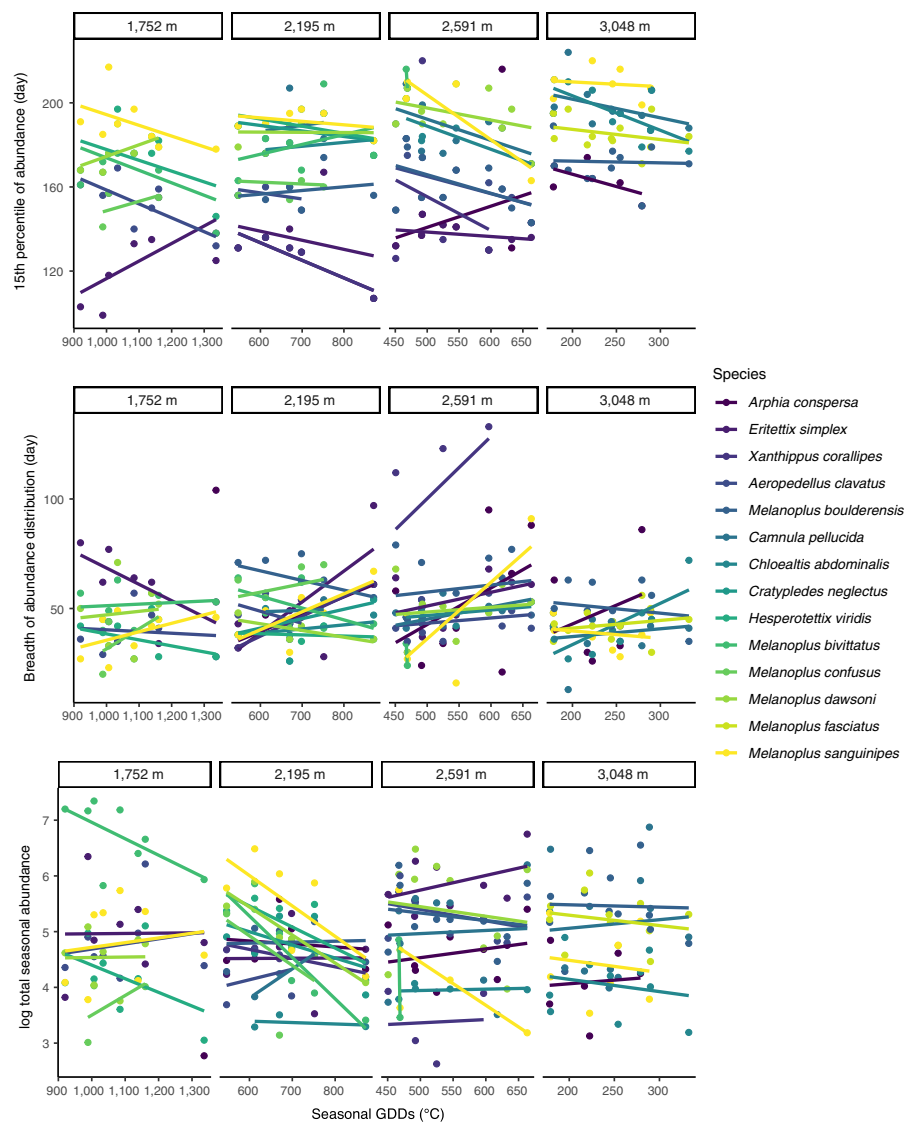


FIGURE 1 Across sites (columns left to right: low to high elevation), abundance distributions (note different scales) across the season vary as a function of seasonal warmth (seasonal GDDs averaged across the elevation gradients by year, colour). We include surveys during 1958–1960 and 2006–2015. The abundance distributions include juveniles weighted by their developmental stage ($1/6 = 1$ st instar, $1 =$ one adult) and are fit with loess curves. Species are ordered by seasonal timing (top to bottom: early to late season). The black lines separate nymphal diapausing, early and late season species

TABLE 1 ANOVA results examining how the metrics describing the position, breadth and area of the abundance distributions shift in response to seasonal growing degree days (GDDs, °C), species' seasonal timing (1: nymphal diapausers, 2: early season, 3: late season), site and their interactions (** $p < 0.001$; * $p < 0.05$)

	Ordinal date of 15th quantile				Breadth of abundance distribution			Total number of individuals		
	NumDF	DenDF	F value	Pr(>F)	DenDF	F value	Pr(>F)	DenDF	F value	Pr(>F)
GDDs	1	218	7.5	0.01*	190	6.7	0.01*	183	1.2	0.27
Species timing	2	235	29.7	3.2×10^{-12} ***	237	1.8	0.16	236	4.1	0.02*
Site	3	153	1.6	0.2	213	0.4	0.73	218	1.2	0.31
GDDs:species timing	2	157	1	0.37	228	2.8	0.06	234	2.1	0.13
GDDs:site	3	156	1.8	0.15	211	1.3	0.26	216	0.9	0.43

FIGURE 2 The position, breadth and area of the abundance distribution (top to bottom) exhibit variable responses to site elevations (columns). Species are ordered by seasonal timing (early to late). The lines indicate linear smooths for each species



3.2 | Phenological overlap

Do phenological shifts associated with warm years alter phenological overlap among members of the grasshopper communities? The area of phenological overlap responds significantly to season warmth (estimate $\pm$ SE = 0.00015 ± 0.000071), but the relationship depends

on the relative timing of the species (other coefficients: Table S2, ANOVA: Table 2, model $r^2 = 0.47$, Figure 3, model fits: Figure S2). For focal species that are nymphal diapausers, warm years tend to decrease the area of overlap with other nymphal diapausers but to increase overlap with early and late season species across elevations (Figure S2). Phenological overlap among the two early season

TABLE 2 ANOVA results examining how the three overlap metrics respond to seasonal growing degree days (GDDs, °C), the seasonal timing of the focal and compared species (1: nymphal diapausers, 2: early season, 3: late season), site and their interactions (** $p < 0.001$; * $p < 0.01$; * $p < 0.05$)

	Overlapping area (proportion)				Days of overlap			Days difference in peak abundance		
	NumDF	DenDF	F value	Pr(>F)	DenDF	F value	Pr(>F)	DenDF	F value	Pr(>F)
GDDs	1	497	4.7	0.03*	488	7.2	0.01**	535	0.5	0.47
Species timing	5	555	12.3	0***	544	3	0.01**	574	2.9	0.01**
Elevation	3	511	3.6	0.01**	506	4.4	0***	548	1.5	0.23
GDDs:timing	5	500	6.3	0***	493	0.9	0.48	537	0.7	0.62
GDDs:elevation	3	500	2.1	0.1	494	4.9	0***	539	1.2	0.3
Timing:elevation	11	493	3.7	0***	435	2.1	0.02*	474	2.3	0.01**

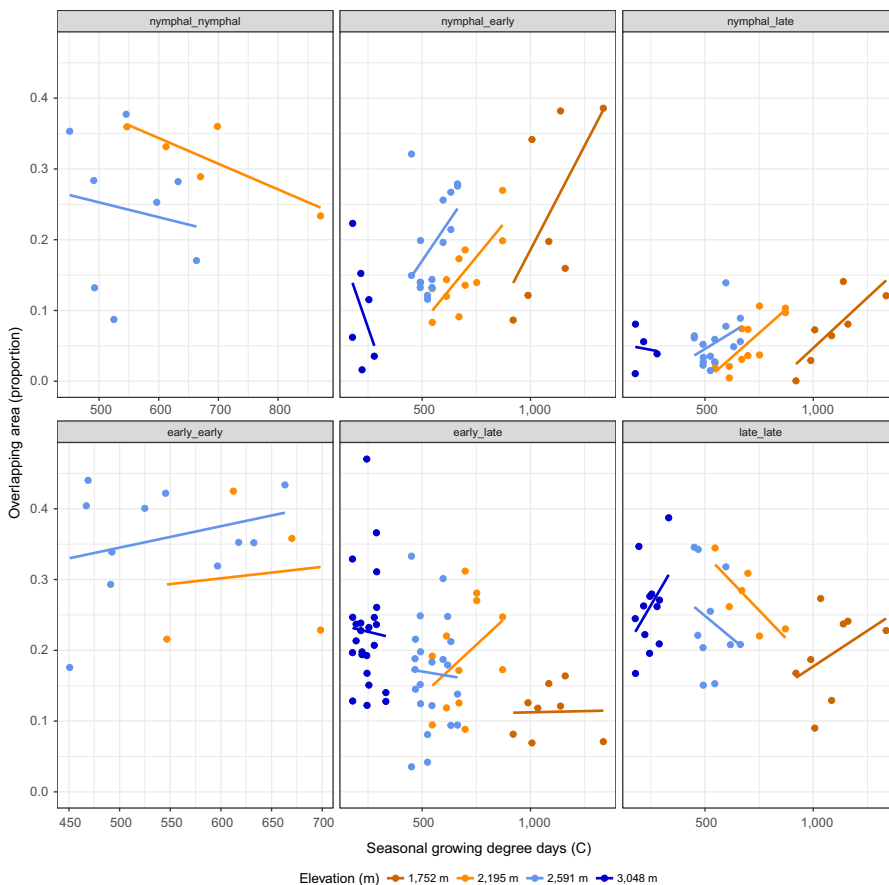


FIGURE 3 Pairwise seasonal phenological overlap (the area of overlap divided by the total area of the two species seasonal abundance distributions) varies as a function of seasonal GDDs (°C). We average pairwise overlap across seasonal timing of the focal and compared species for plotting. Sites of differing elevation are depicted with colour. Each dot represents a year and the lines indicate linear smooths for each species

species increases in warm years. Phenological overlap between early and late season species and among late season species does not shift significantly in response to season warmth.

The days of phenological overlap likewise responds significantly to season warmth (estimate $\pm$ SE = 0.039 ± 0.015 , ANOVA: Table 2, model $r^2 = 0.47$, Figure S3). However, conversely to the area of overlap, the shift in days of overlap with season warmth varies with site but not the species' timing (ANOVA: Table 2). The days of overlap increases significantly with season warmth at site elevations other than 2,591 m, where responses to warm years are variable (Table S2). The days difference in peak abundance does not shift significantly in response to season warmth (estimate $\pm$ SE = -0.013 ± 0.019) but

does vary significantly between species with different timing, which interacts significantly with site (ANOVA: Table 2, model $r^2 = 0.45$, Figure S4).

We find mixed support for the response of phenological overlap to season warmth varying with species' timing or site. We do find that phenological overlap tends to be greater at higher elevation sites (2,591 and 3,048 m) regardless of season warmth. When pairwise species overlap is averaged across communities (Figure S5, Table S3), this community phenological overlap increases in warm years when quantified as days of overlap (ANOVA: GDDs $F_{[1,29]} = 4.9$, $p = 0.03$; site $F_{[3,29]} = 3.4$, $p = 0.03$; GDDs $\times$ site $F_{[3,29]} = 0.6$, $p = 0.62$, $r^2 = 0.13$) but not area of overlap (ANOVA: GDDs $F_{[1,29]} = 2.2$,

$p = 0.16$; elevation $F_{[3,29]} = 2.1$, $p = 0.12$; GDDs $\times$ site $F_{[3,29]} = 0.3$, $p = 0.82$, $r^2 = 0.23$) or the days difference in peak abundance (ANOVA: GDDs $F_{[1,29]} = 0.7$, $p = 0.42$; site $F_{[3,29]} = 4.7$, $p = 0.008$; GDDs $\times$ site $F_{[3,29]} = 0.7$, $p = 0.56$, $r^2 = 0.01$). This highlights that changes in overlap depend on relative seasonal timing.

Is there evidence of phenological overlap influencing abundance? The relationship between all overlap metrics and the log of maximum abundance is weak ($r^2 = 0.05$ – 0.09), but each analysis suggests that nymphal diapausing species are more abundant when there is increased phenological overlap. Two of the metrics indicate that later season species are less abundant when there is increased phenological overlap. Abundance is influenced by a significant interaction between species timing and the overlapping area (ANOVA: overlap $F = 0.53$, $p = 0.47$, focal timing $F = 5.3$, $p = 0.008$, overlap $\times$ focal timing $F = 7.2$, $p = 0.001$, $r^2 = 0.08$, Figure 4) as well as days difference in peak abundance (ANOVA: overlap $F = 0.01$, $p = 0.92$, focal timing $F = 2.5$, $p = 0.09$, overlap $\times$ focal timing $F = 4.1$, $p = 0.02$, $r^2 = 0.05$, Figure S6) but there is no significant main effect of overlap. Abundance increases with the days of overlap with the

steepest slope occurring for nymphal diapausing species (ANOVA: overlap $F = 21.9$, $p < 0.001$, focal timing $F = 0.68$, $p = 0.51$, overlap $\times$ focal timing $F = 0.8$, $p = 0.45$, $r^2 = 0.09$, Figure S7).

4 | DISCUSSION

We find variable shifts in abundance distributions among species that are not well explained by species' seasonal timing or site elevation, contrary to our predictions. As species shift their phenologies differentially in warm years, phenological overlap among species tends to increase, which may increase resource competition and the potential for more frequent interactions between species. Broader abundance distributions coupled with phenological advancements of later season species tends to increase phenological overlap. In general, species at higher elevation sites (2,591 and 3,048 m) are associated with higher average levels of phenological overlap than lower elevation sites, consistent with species in the more highly seasonal environments being more temporally (seasonally) constrained

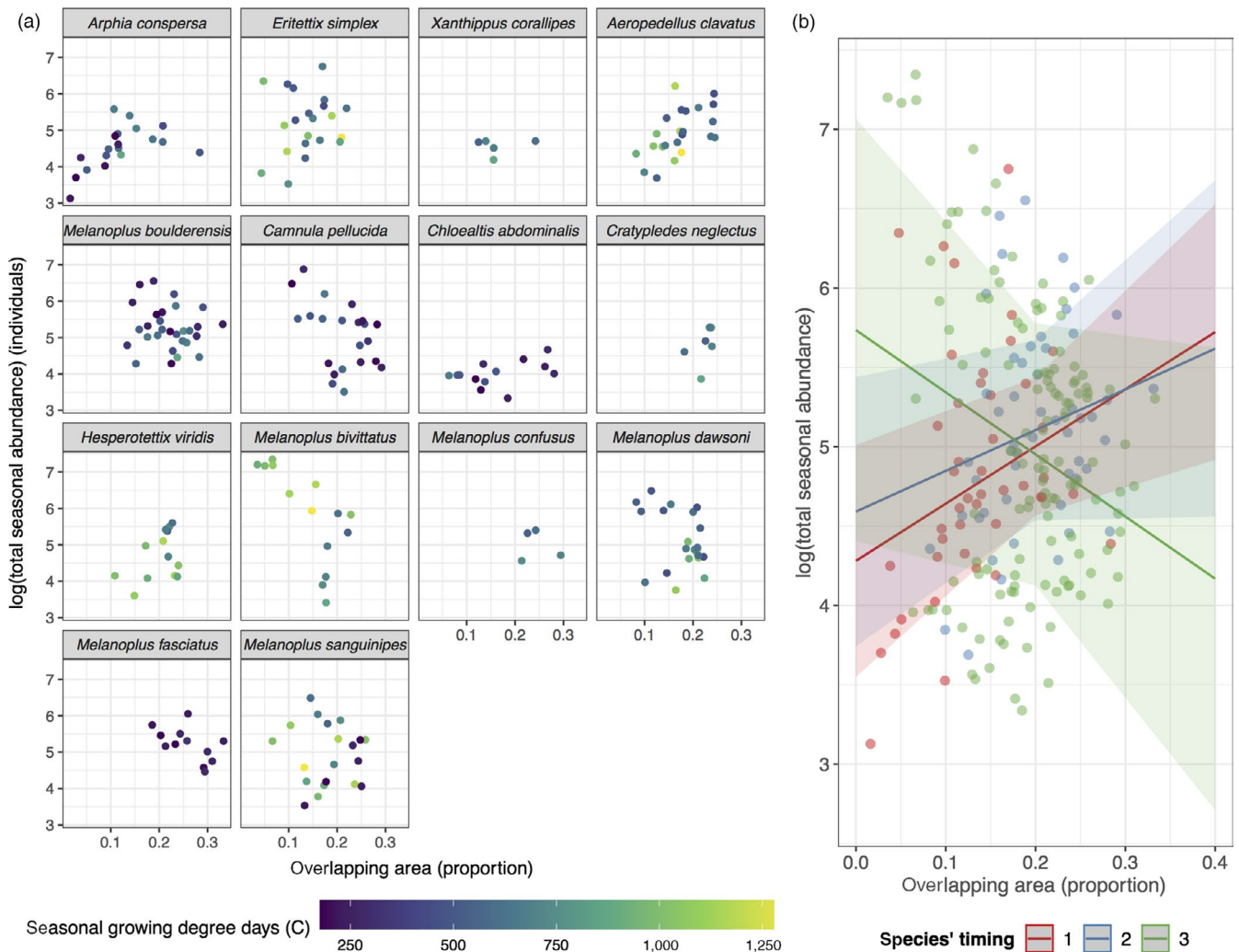


FIGURE 4 (a) Total seasonal abundance responds variably to phenological overlap (overlapping area) and season warmth (colour) across species (arranged by seasonal timing, top left to bottom right: early to late season). (b) We depict model fits describing how the relationship between abundance and overlap differs based on species' timing

by the timing of snow melt and the initiation of the first frost events (Marr, 1961). High elevations have a strong potential to experience increases in phenological overlap given they often experience the strongest warming (Pepin et al., 2015).

Phenological variability among species generally increases with climate warming (Diez et al., 2012; Pearse et al., 2017). This phenological variability can emerge from differences in the exposure of species to environmental conditions and cues and species attributes that lead to differential sensitivities to these shifting factors (Chmura et al., 2018; Theobald et al., 2017). In this system, variability in phenological shifts among species resulted in the most apparent changes in overlap occurring among species with distinct seasonal timing. Warm years reduced the area of phenological overlap *among* earlier season species but increased overlap *between* earlier and late season species (but this finding is not consistent across overlap metrics, see Section 3). As in a previous study on amphibians (Carter et al., 2018), this variability in phenological responses resulted in a significant increase in the temporal overlap of species, which led to community level changes in area of overlap, days of overlap, and, to a lesser extent, days difference in abundance peaks between species. Shifts in timing and phenological duration suggest the potential for widespread increases in community overlap (Roy & Sparks, 2000; Sherry et al., 2007).

Species' diverse shifts in peak phenology, abundance and duration are consistent with other studies finding phylogenetic conservatism in first appearance date (Davies et al., 2013) but not in other phenology metrics such as duration (CaraDonna & Inouye, 2015). Increases in phenological duration with warming (Diez et al., 2012) suggest the potential for widespread increases in phenological overlap. Shifts in phenological overlap are likely to be particularly pronounced in systems with temporally dynamic interactions such as plant–pollinator interactions (CaraDonna et al., 2017; Ogilvie et al., 2017). Phenological variability can also emerge from local climate differences and differential sensitivities to multiple environmental attributes among species (Theobald et al., 2017). Different phenological cues (environmental attribute and duration) among trophic levels can contribute to reshaping communities (Ovaskainen et al., 2013).

Our finding of a positive relationship between season warmth and area or days of phenological overlap but not days difference in peak abundance supports findings that integrative metrics of phenological overlap are needed. Increases in phenological overlap result from phenological shifts towards earlier and broader abundance distributions. We find that phenological shifts among nymphal diapausing species are a driver of shifts in phenological overlap (Figure S2). Shifts in the phenology of nymphal diapausing species may result from the ability to capitalize on plentiful, early-emerging vegetation before other species reach adulthood or from greater survivorship of individuals early in the season.

We find less support for our predictions that species' timing and site elevation influence phenological shifts in this analysis based on abundance compared to our previous analysis based on developmental trajectories (Nufio & Buckley, 2019). Although abundance is likely the most ecologically relevant metric, it responds to more factors than does development and can thus exhibit variable responses

to warming. Our analysis suggests that increased phenological overlap may correspond to increased abundance of nymphal diapausing species and either constant or reduced abundance in later species. The relationship is intriguing, but we are unable to resolve its directionality: increased phenological overlap may increase resource competition and reduce abundance. However, greater abundance, particularly that associated with broader abundance distributions may alternatively increase phenological overlap.

The accumulation of studies such as ours that compare species with differing life histories (seasonal timing), and consequently differences in environmental exposure and sensitivity, should help decipher the underlying mechanisms of phenological shifts (Chmura et al., 2018). Confirmation of underlying mechanisms will require methods such as predictive phenological modelling and manipulative experiments (Rafferty et al., 2013). Documenting abundance and including juvenile development stages may provide a more comprehensive understanding of changes in community structure than oft-employed metrics such as first occurrence. The variability in season warmth across the resurvey period points to the need to consider multiple years of data in examinations of phenological shifts. Our analysis highlights how climate change may alter community interactions via increasing phenological overlap. Increased phenological overlap is likely to be a common occurrence of warming even if the abundance shifts of particular species are variable and difficult to predict.

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AUTHORS' CONTRIBUTIONS

All authors designed the study and edited the manuscript. C.R.N. collected the data; L.B.B. led the analyses and manuscript writing; S.I.G. assembled the data and conducted analyses.

DATA AVAILABILITY STATEMENT

Data are available in Dryad Digital Repository <https://doi.org/10.5061/dryad.9ghx3ffgb> (Nufio et al. 2021). Maintained data are also available from the Niwot Ridge LTER (<https://nwt.lternet.edu/data-catalog/>).

R code is available at <https://github.com/lbuckley/HopperPhenology> and archived at <https://zenodo.org/record/4429198#.YCKYoWaNp8> (Buckley, 2021).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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