

Community phenology of insects on oak: local differentiation along a climatic gradient

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Abstract. Climate change is advancing the onset of phenological events, with the rate of advance varying among species and trophic levels. In addition, local populations of the same species may show genetic differences in their response to seasonal cues. If populations of interacting species differ in their response, then climate change may result in geographically varying shifts in the community-level distribution of interaction strength. We explored the magnitude of trophic- and species-level responses to temperature in a tritrophic system comprising pedunculate oak, insect herbivores, and their associated parasitoids. We sampled local realizations of this community at five sites along a transect spanning fifteen degrees of latitude. Samples from each trophic level at each site were exposed to the same set of five climatic regimes during overwintering in climate chambers. We then recorded the number of days and degree-days required for oak acorns to develop and insects to emerge. In terms of dates of events, phenology differed among populations. In terms of degree-days, we found that for two species pairs, the heat sum required to develop in spring differed by an additional ~500 degree-days between trophic levels when overwintering at the highest temperature. For three species, within-population variation in the number of degree-days required for emergence was higher at warmer temperatures. Our findings suggest that changing temperatures can modify interactions within a community by altering the relative phenology of interacting species and that some interactions are more vulnerable than others to a shift in temperature. The geographic variation in the phenological response of a species suggests that there is a genetic component in determining the phenology of local populations. Such local variation blended with interspecific differences in responses makes it complex to understand how communities will respond to warmer temperatures.

Key words: climate change; community ecology; mismatch; phenology.

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INTRODUCTION

In any habitat with temporally variable resources and climatic conditions, we expect species to have evolved a phenological match to key aspects of their environment. By responding to relevant cues, organisms can track the seasons

and become active when resources and conditions are favorable. Temperature and/or photoperiod are key phenological cues for many organisms (Hanninen and Tanino 2011, Vitasse and Basler 2013, Lindestad et al. 2019). Organisms using temperature cues often depend on a series of cold days (i.e., chilling) to initiate

development. After the chilling period has ended, development is triggered by warm temperatures in spring (i.e., forcing) (Hanninen and Tanino 2011, Stålhandske et al. 2015, Tansey et al. 2017).

Within communities, species may respond differently to changes in relevant cues. Warmer spring temperatures generally advance phenology in a wide range of taxa (Roy and Sparks 2000, Menzel et al. 2006, Fu et al. 2013, Kharouba et al. 2018), but the rate of advance can differ among species (Thackeray et al. 2016, Kharouba et al. 2018). Such interspecific variation could affect the phenological synchrony between interacting species. Some general patterns have been hypothesized regarding relevant variation in phenological responses. A recent meta-analysis reported that lower trophic levels are generally more sensitive to temperature than other trophic levels (Thackeray et al. 2016)—a pattern earlier proposed by other studies (Visser and Holleman 2001, Both et al. 2009, Plard et al. 2014), and more recently supported by an analysis of patterns across the former Soviet Union (Roslin et al. 2021). Across space, different populations can be exposed to different patterns of seasonal variation, which could result in local adaptation to phenological cues. As genetic variation in phenology is common in both plants and insects (Olson et al. 2013, Vitasse et al. 2013, Stålhandske et al. 2014, Lindestad et al. 2019, Valdes et al. 2019), such population-level variation in phenological responses to warmer temperatures can be expected to be common (Delgado et al. 2020; but see Phillimore et al. 2016, Stålhandske et al. 2017). If we want to understand how species interactions will change in a warming climate, we therefore need to elucidate both the phenological response of species and trophic levels to temperature, but also the role of plasticity vs. genetic variation in determining phenology.

Phenological mismatch between trophic levels could reduce individual fitness for the higher trophic level (Visser et al. 1998, Tikkanen and Julkunen-Tiitto 2003, Edwards and Richardson 2004, Post and Forchhammer 2008, Both et al. 2009, Plard et al. 2014, Doiron et al. 2015, Burgess et al. 2018). Many herbivorous insects benefit from feeding on their host plant shortly after budburst and during leaf expansion, as young

leaves reflect a resource of higher quality than older leaves (Feeny 1970, Aide and Londono 1989, Tikkanen and Julkunen-Tiitto 2003). Similarly, it is necessary for parasitoids to match the phenology of their host. Many studies have investigated phenological synchrony in plant–herbivore (Tikkanen and Julkunen-Tiitto 2003, Schwartzberg et al. 2014, Uelmen et al. 2016) and herbivore–parasitoid interactions (Van Nouhuys and Lei 2004, Klapwijk et al. 2010, Evans et al. 2013, Meineke et al. 2014). However, most studies have focused on the synchrony between two or a few interacting species. Since species are often embedded in a more complex network of interactions, we need studies targeting a wider community to assess the community-level response to changes in phenological synchrony.

Beyond changes in the population mean of phenological events, it is important to understand how the temporal distribution of individuals within a population changes with temperature, and how this may in turn influence interspecific interactions. Changes in the shape of these distributions could extend or shorten the window of opportunity within which species can interact, and change the (relative) abundance of individuals during any time period. For instance, the phenological distribution (i.e., within-population variation in phenology) of budburst could widen as a response to warmer temperatures (Zohner et al. 2018). For herbivores synchronized with these plants, a wider phenological distribution in budburst could buffer the herbivore population against a mismatch in mean phenology with its food plant, but at the cost of having fewer food plants available at any given time. Hence, what we lack is a more general, population-based view of how communities are affected by climate change, to what extent local populations differ in their response to temperature, and how this affects interactions at the community level.

Here, we explore how geographically separated populations differ in their phenological response (i.e., in their mean phenology and phenological distribution) to temperature along a temperature gradient, and how this is reflected in the community-level synchrony among trophic levels. To this end, we focus on insects associated with pedunculate oak, *Quercus robur*. To achieve community-level manipulations of

ambient climate, we focused on the smallest oak individuals possible (acorns), on herbivores associated with abscised oak leaves, and on the parasitoids of these herbivores. In autumn, we sampled acorns and insects at five locations along a climatic gradient. We then exposed them to their local overwintering climate and up to four additional climates in climate chambers, representing the local climate of all sampling locations. In spring, we observed phenological events at each trophic level: the development of acorns (root, shoot, and leaf development) and the emergence of insects (herbivores and their parasitoids). This experiment allowed us to assess how winter climate influenced the phenological synchrony between trophic levels (plant–herbivore, herbivore–parasitoid) and the phenological distribution of species and populations. More specifically, we tested the following hypotheses:

1. Trophic levels will differ in their phenological response to temperature, so that a change in temperatures will alter the phenological synchrony between interacting species of different trophic levels.
2. Shifts in temperature will modify the phenological distribution (i.e., within-population variation in timing) of acorn development and insect emergence.
3. Populations originating from different climates will show different phenological responses to temperature.

MATERIAL AND METHODS

We sampled insect communities and acorns at five locations following a temperature gradient in Europe. The transect spanned fifteen degrees of latitude, or 2300 km (Fig. 1). We collected material at each trophic level (acorns, herbivores, and parasitoids) in the autumn of 2016 and then exposed each community to both its original overwintering regime and other temperature regimes in a common garden design (Kawecki and Ebert 2004). In the following spring, we recorded the date and the accumulated temperature required for adult insect emergence (herbivores and parasitoids) and acorn root, shoot, and leaf development.

Study system

The pedunculate oak *Q. robur* is widely distributed over temperate Europe (Eaton et al. 2016). Within populations, individuals can differ by up to a month in their phenology of both budburst and leaf senescence (Delpierre et al. 2017). As our experimental design was based on manipulating ambient temperatures in climate chambers, and as larger oaks are logistically hard to manipulate under field conditions (but see Sinclair et al. (2015) and Ekholm et al. (2020)), we decided to focus on acorns. Acorns represent the smallest stage of oaks, making them easy to use in phenology experiments while also controlling for their genetic background.

In Europe, *Q. robur* supports one of the most species-rich insect communities of any tree species (Southwood 1961, Southwood et al. 2004). A subset of this community comprising leaf-mining and gall-inducing species has been particularly well studied (e.g., Tack et al. 2010, Kaartinen and Roslin 2011, Sinclair et al. 2015, Ekholm et al. 2019) and is easy to sample due to their sedentary larval life stage. Galls induced on oaks by gall wasps (Hymenoptera; Cynipidae, tribe Cynipini) can be inhabited by a rich community of insects consisting of the gall inducer itself, inquilines (which can also be gall wasps of the tribes Ceroptresini and Synergini (Ronquist et al. 2015)) and chalcid parasitoids (Askew 1961, Askew et al. 2013). With few exceptions (Abe et al. 2011), cynipid inquilines cannot induce galls de novo, but instead induce the development of nutritive tissues on which they feed in galls initiated by other cynipids (Askew 1961, Stone et al. 2002). Most oak feeding gall wasps are bivoltine, with a sexual generation in spring and an asexual generation in autumn (Stone et al. 2002).

Among the rich community of galls found on *Q. robur*, we found particularly high densities of two gall types in this study: the asexual (autumn) generations of *Andricus quercustozae* and of *Cynips quercusfolii* (Hymenoptera: Cynipidae). These two taxa produce large galls on the buds and on the underside of leaves, respectively (Melika et al. 2000). Both species can be inhabited by a large number of inquilines and parasitoids (Askew et al. 2013), which makes them suitable for rearing experiments. In addition, all individuals within a gall share the same

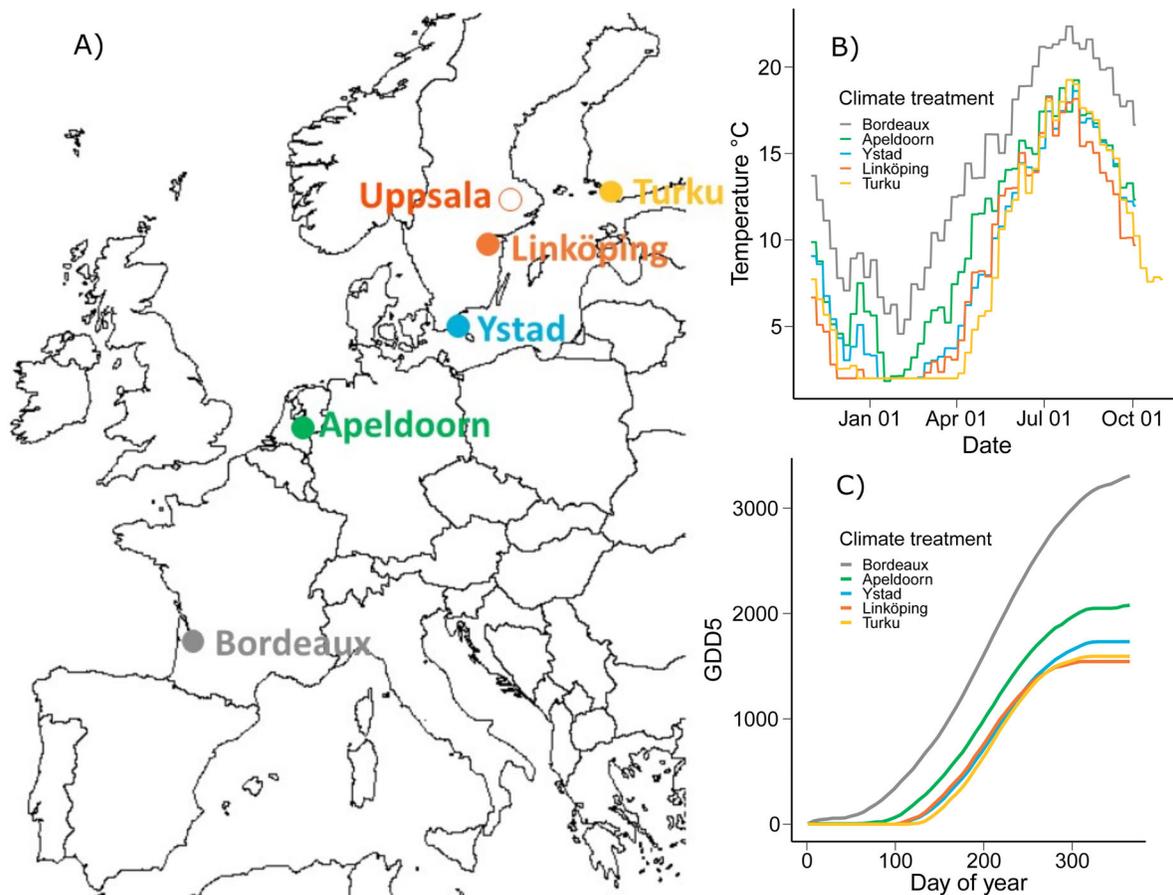


Fig. 1. (A) The five locations (filled circles) from which insects and acorns were sampled. The open circle represents an additional location where only acorns were sampled. The text next to the circles represents the city closest to the sampling location. Maps have been extracted from the package ggmap (Kahle and Wickham 2013). (B) The mean temperature in each climate treatment during the experiment period (minimum temperature in climate treatments was $\sim 0^{\circ}\text{C}$) and (C) the accumulation of GDD5 (growth degree-days above a threshold of 5°C) in the five climate treatments over a whole year, based on data recorded between years 2011 and 2015 from a meteorological station close to the respective sampling location. For the intended vs. the realized temperature in each climate treatment, see Appendix S1: Fig. S3.

environment and are part of a community of interacting insects. Of the parasitoid species attacking either one or both of *C. quercusfolii* and *A. quercustozae*, we reared particularly high and analyzable densities of *Torymus auratus* (Hymenoptera: Torymidae), *Torymus geranii* (Hymenoptera: Torymidae), and *Eurytoma brunniiventris* (Hymenoptera: Eurytomidae). Of these, *T. auratus* is bivoltine and attacks inquilines, gall inducers, and other parasitoids (Askew 1961), while *E. brunniiventris* is abundant throughout the season and attacks gall wasps and inquilines but

can also feed on gall tissue (Askew 1965). Apart from the species associated with gall wasps, we also reared high densities of the leaf miner *Tischeria ekebladella* (Lepidoptera: Tischeriidae). *Tischeria ekebladella* is a well-studied species that occurs across Europe (Gripenberg et al. 2007, 2008), is specialized in *Quercus* spp. (but can sometimes also attack *Castanea* spp.), and is easy to sample due to its sedentary larval development. The larva forms a mine on the upper side of the leaf (Bengtsson et al. 2008). *Tischeria ekebladella* is univoltine in northern Europe, but has

been reported to have two or three generations at other locations (Hering 1957, Bengtsson et al. 2008, Yefremova et al. 2013).

Experimental design

Community sampling along a climate gradient.—To represent local communities of different climatic origins, we sampled acorns as well as insects from the oak leaf miner and gall wasp community described above at five locations along a latitudinal gradient (Turku, Finland, 60.19° N, 21.62° E; Linköping, Sweden, 58.42° N, 15.57° E; Ystad, Sweden, 55.39° N, 14.20° E; Apeldoorn, the Netherlands, 52.18° N, 6.00° E; and Bordeaux, France, 44.57° N, −1.03° E; Fig. 1). Acorns were sampled at the same locations where we sampled insects, and at one additional sampling site (Uppsala 59.82° N, 17.64° E; Fig. 1). The collection sites differ substantially in their climate, with the two southern locations (Bordeaux and Apeldoorn) experiencing a substantially warmer climate than the three northern locations (Ystad, Linköping, and Turku; Fig. 1).

In order to sample acorns and insects at the same development stage across locations, we followed the progress of autumn, starting with the most northern location and finishing at the most southern location (site-specific sampling dates: Turku: 15–17th of September, Linköping: 27–28th of September, Ystad: 30th September–1st of October, Apeldoorn: 10–12th of October, Bordeaux: 11–13th of October, and Uppsala: 28th of October). At each site, one or two persons (AE and MF) targeted all oak branches accessible from the ground, sampling oak leaves infested with leaf miners or gallers for a total time of c. 48 h. Acorns were sampled from several trees at each site, and no record was taken on the number of oaks sampled per site. After samples had been collected from all locations, we sorted acorns into cassettes containing 20 small slots of c. 50 mL each, by first filling each slot with soil (same soil for all acorns) and then planting an acorn in each slot at a depth of 2–3 cm (for photograph, see Appendix S1; Fig. S1). Leaf mines and leaf galls of *C. quercusfolii* were sorted into open tubes (50 mL) protected by a mesh net at both ends, allowing air to circulate through the tube (see Appendix S1: Fig. S2). The number of individual galls and mines differed slightly between tubes. The large galls of *A. quercustozae* were placed

into mesh bags. The sorting of acorns and insects was done between 19th and 28th of October.

Common garden overwintering of samples at multiple temperatures.—The common garden experiment (initiated 1st of November) involved placing insects and acorns from each sampling location into five different climate treatments in climate chambers (Termaks KB8400L, Termaks KB8400FL, Termaks, Bergen, and Norway). Each climate treatment matched the local day and night temperature in one of the five sampling locations. The temperature profile was based on recordings from 2011 to 2015 at a weather station close to the sampling location (Fig. 1). Data were obtained from national meteorological institutes.

As the number of sampled individuals of each species varied among sites, we first placed species into the climate treatment representing their native climate. Then, depending on the number of individuals collected, we divided the rest of the individuals into either one or several climate chambers (Appendix S2: Tables S1 and S2). Due to low sample size and to maximize ability to detect an effect of temperature, we divided acorns and *A. quercustozae* galls from Bordeaux between two climate treatments with a large temperature difference (Bordeaux and Turku).

All galls of *C. quercusfolii* originated from Ystad and were exposed to all climate treatments. Since *C. quercusfolii* overwinters as an adult and emerges between December and February (Coulianos and Holmåsén 1991), any detailed record of its phenology would assume recording throughout the winter. In our case, we started to record emergence dates only later in the year and then found several already-emerged and dead individuals of *C. quercusfolii*. Therefore, we focus our analyses of this species on the synchrony between its inquilines and parasitoids, both of which emerge somewhat later, and for which our recording scheme captured the full phenological distribution.

For each meteorological station, we first averaged the day (12:01–00:00) and night temperatures (00:01–12:00) for each day of the year between 2011 and 2015 and then averaged the day and night temperature for each week of the year. The temperature in each climate treatment was then changed on a weekly basis, to mimic the advance of the season as recorded by the temperature profile obtained from the meteorological

stations. To validate our treatments, we recorded the realized climate regime in each climate treatment using temperature loggers (Signatrol SL54TH, Signatrol, Tewkesbury, and England; Appendix S1: Fig. S3) and to exclude chamber effects, we repeatedly shifted climatic treatments and randomly moved the samples between climate chambers during the experiment. Given that the inhabitants of galls develop within opaque woody tissues, and inhabitants of mines typically develop shielded from light under other fallen leaves, we did not manipulate the light regime, but simply set each climate treatment to an identical and constant photoperiod (12-h light:12-h dark). For more details regarding the rearing procedures, see Appendix S1 in supplementary materials.

Phenology.—As our measurements of phenology, we recorded the timing of insect emergence and of three development stages of germinating acorns: root development, shoot development, and leaf development. As each slot in the cassette had an open bottom end, we were able to observe root growth as the roots penetrated the open end of the cassette. Root development was defined as the first visual observation of a root that has grown past the bottom end of the cassette, shoot development as the first visual observation of a shoot rising above the soil, and leaf development as the emergence of the first leaf. Details regarding the analysis and results of root and shoot development are presented in Appendix S2 in the supplementary materials, while results on leaf development (of relevance to herbivores) are presented in the main paper. In this study, we assume leaf development of acorns to be representative of oak phenology, although seedlings can have an earlier phenology than adult trees (Vitasse 2013).

We used two complementary metrics of phenology: the date of the phenological observation (ordinal days, where day one is the 1st of January) and the accumulation of growing degree-days required for the phenological observation. We calculated degree-days, starting from the 1st of January, based on the equation $\sum [(T_{\max} + T_{\min})/2 - T_{\text{base}}]$ where T_{\max} is the maximum daily temperature, T_{\min} is the minimum daily temperature, and T_{base} is the minimum temperature for development to begin. If $(T_{\max} + T_{\min})/2 < T_{\text{base}}$, then the degree-day was set to 0. While T_{base} can differ

between species (Valtonen et al. 2011), we decided to use a value of 5°C as widely adopted in studies of deciduous trees (Sykes et al. 1996, Zohner et al. 2018) and of the distribution, voltinism, and phenology among northern European insect species (Luoto et al. 2006, Pöyry et al. 2009, 2011, Hodgson et al. 2011). Most importantly, values of growing degree-days are highly correlated across realistic values of T_{base} , for which reason the results are robust to the choice of the exact value of T_{base} —a fact demonstrated in further detail by Delgado et al. (2020). The accumulation of growing degree-days with 5°C as a threshold (from now on referred to as GDD5) is shown for the different common garden climate treatments in Appendix S1: Fig. S4.

To describe timing not only as a function of the heating-days accumulated, but also of the absolute day when an event occurred, we used the alternative metric of ordinal days. While less related to the developmental physiology of ectotherm organism, it provides an intuitive way of measuring species phenology, and—most importantly—provides a direct metric of whether different phenological events will coincide in time or by how many days they are separated.

As GDD5 may be seen as a more mechanistic metric of phenology (sensu “heating needed to trigger the response”) and ordinal day as a complementary phenotypic trait (sensu “observed phenology for when the event was expressed”), we present the results of analyses of both metrics. For brevity, tables and figures for analyses of ordinal day are reported in the Supplementary Online Material.

Statistical analyses

All analyses described below were performed in R version 3.6.1 (R Core Team 2017), using generalized least square models in *gls* (Pinheiro et al. 2018), with significance tested with a marginal ANOVA (Pinheiro et al. 2018). After running each model, we tested for homogeneity of variance using Levene’s test or Fligner-Killeen test. If the assumption of homogeneity was violated, or if a separate variance function reduced the AIC value of the model (Zuur et al. 2009), we fitted a separate variance function to one or several of the explanatory variables (*varPower* for continuous effects and *varIdent* for factors) from the *nlme* package (Pinheiro et al. 2018). To each model, we

applied model simplification so that interactions with a P -value >0.10 were dropped from the final model. As we were interested in how phenology changed along a temperature gradient, we analyzed the effect of treatment as a continuous effect, where each climate treatment was given a value corresponding to the annual accumulation of GDD5 of the climate it was representing. For an overview of all models used in this study, see Appendix S2: Table S3. In all plots, model least squares means were extracted using the package *emmeans* (Lenth 2018) and plotted with the package *ggplot2* (Wickham 2016).

The effect of population origin and local climate on the synchrony across trophic levels.—We examined whether temperature had an effect on the phenological synchrony between *Q. robur* and *T. ekebladella*, and between gall wasps, inquiline, and their associated parasitoids. In doing so, we also wanted to test whether populations of *Q. robur* and *T. ekebladella* differed in their response to temperature. Thus, we modeled the natural logarithm of the temperature sum (GDD5) and ordinal days required for the event to occur, respectively, as separate linear functions of the climate treatment (i.e., the climatic regime of the climate chamber), species (*Q. robur* or *T. ekebladella* in one analysis, and gall wasp host, parasitoid, or inquiline in the second), population of origin (in the analysis of *Q. robur* and *T. ekebladella*), and all interactions (see Appendix S2: Table S3, model 1 for *Q. robur* and *T. ekebladella*, models 2 and 3 for the gall wasp-centered communities). The temperature sum and ordinal days were log-transformed in all analyses, except when analyzing species associated with the gall *A. quercustozae*. In analyzing the synchrony in ordinal days between *Q. robur* and *T. ekebladella*, we also included a squared term of climate treatment (a continuous variate), to better fit the observed shape of the response. Testing of the species \times climate treatment interaction and of the three-way population \times species \times climate treatment interaction allow assessment of the extent to which the responses of species (2-way interactions) and populations within species (3-way interaction) are different. Significant 2- or 3-way interactions indicate the potential for a temperature-mediated phenological mismatch between species. The analysis of the interaction between *Q. robur* vs. *T. ekebladella* built on data

for only five sites (since there were no samples of *T. ekebladella* from Uppsala).

To find out whether the phenological distribution (i.e., within-population variation) in the species' responses to GDD5 differed among populations, we calculated the standard deviation of insect emergence period and acorn leaf development period for each population in each climate treatment. We then modeled the population-specific standard deviation as a function of population or species and climate treatment (see Appendix S2: Table S3, models 4 and 5 for *Q. robur*/*T. ekebladella*, and model 6 for the gall wasp communities).

RESULTS

The effect of population origin and local climate on the synchrony between a plant and an insect herbivore

In each climatic treatment, and regardless of their origin, acorns developed leaves before *T. ekebladella* emerged. Both species required a higher temperature sum to emerge in warmer climate treatments (GDD5: Fig. 2, Table 1; ordinal days: Appendix S2: Fig. S1, Table S4). We also detected a population-specific response to temperature, and this response differed between the two species (significant population \times species interaction; GDD5: Fig. 2; Table 1; ordinal days: Appendix S2: Fig. S1, Table S4). Contrary to our a priori expectation, the phenological synchrony between *T. ekebladella* emergence and acorn leaf development did not change along the temperature gradient in terms of GDD5 required to trigger the event (no significant three-way or species \times climate treatment interaction (Fig. 2; Table 1)). However, for ordinal days, we found a change in synchrony where *T. ekebladella* emergence and acorn leaf development occurred further apart in warmer climate treatments (significant species \times climate treatment interaction; Appendix S2: Fig. S1, Table S4).

Oak leaf development showed no difference in phenological distribution between populations or along the climatic gradient (Fig. 3A; Table 2; Appendix S2: Fig. S2A, Table S5). In contrast, the phenological distribution of *T. ekebladella* differed among populations and was wider at warmer temperatures (Fig. 3B; Table 2; Appendix S2: Fig. S2B, Table S5).

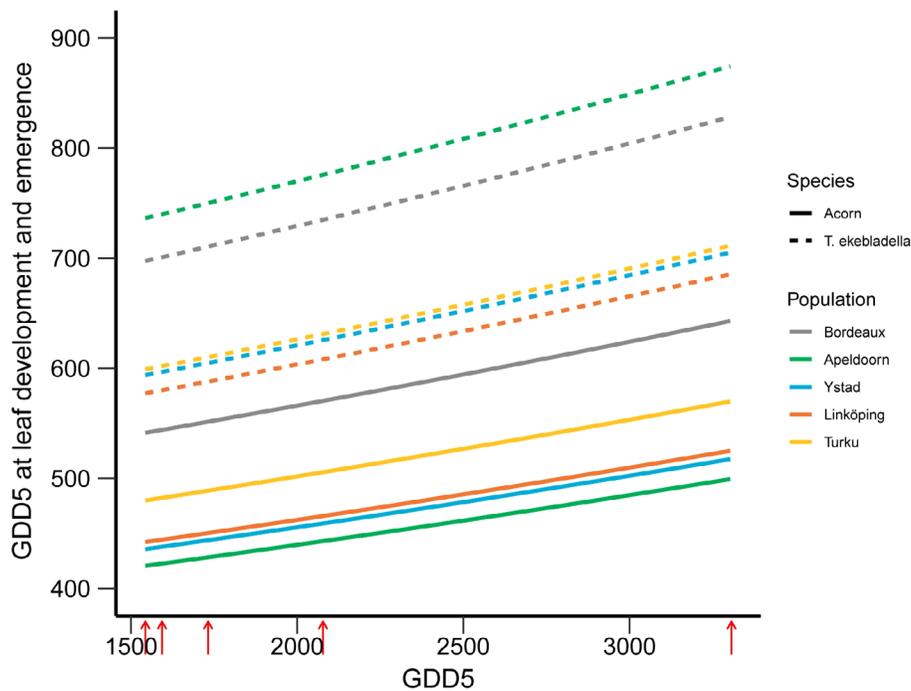


Fig. 2. Model fitted values of the accumulated GDD5 (growth degree-days above a threshold of 5°C) required for *T. ekebladella* emergence and acorn leaf development for samples from five geographically separated populations under five different climate regimes. The x -axis corresponds to the annual accumulation of GDD5, and the thermal regimes corresponding to each site are shown with an arrow on the x -axis (from left: Linköping, Turku, Ystad, Apeldoorn, Bordeaux). Dotted lines are values for *T. ekebladella*, and full lines are for acorns. For visual clarity, this figure shows fitted means only, whereas raw data (together with model predictions) are visualized in Appendix S4: Fig. S1.

The effect of temperature on the phenological synchrony between gall wasps and associated inquilines and parasitoids

In asexual galls of *C. quercusfolii*, *T. auratus* required more accumulated warming (GDD5) to emerge in warmer climate treatments, while the accumulated warming required to emerge was similar among climate treatments for *T. geranii* and inquilines (Fig. 4A, Table 1). In terms of ordinal days, *T. auratus* emerged at approximately the same day in all climate treatments, while *T. geranii* and inquilines emerged earlier in warmer treatments (Appendix S2: Fig. S3A, Table S4). From galls of *A. quercustozae*, the host (*A. quercustozae*) emerged in closer synchrony with its inquilines and with the parasitoid *E. brunniventris* in the warmer than colder climate treatment (significant species \times climate treatment interactions; Fig. 4C; Table 1; Appendix S2: Fig. S3C, Table S4).

Interestingly, the phenology of inquilines associated with *A. quercustozae* was separated into two emergence periods in both climates (Fig. 4C; Appendix S2: Fig. S3C). Thus, the identity of a subset of individuals showing each emergence phenology was checked post hoc by DNA barcoding (for methods and details, see Appendix S3). This analysis revealed that the two emergence patterns represented two different inquiline taxa—both morphologically allied to the polyphyletic Linnaean species *Synergus umbraculus*. One group of specimens corresponds to molecular operational taxon (MOTU) *Synergus* species 7 in Acs et al. (2010), while the second represents a new and closely related *Synergus* MOTU. Members of the new MOTU emerged earlier than *Synergus* sp. 7 in both climatic treatments, although both taxa showed concordant shifts in phenology between climates (Appendix S3: Fig. S1).

Table 1. The effect of species, climate treatment, and population origin on the sum of GDD5 (growth degree-days above a threshold of 5°C) required for insects to emerge and acorns to produce leaves.

Response/Source	df	F	P
Species (S)			
Acorn, <i>T. ekebladella</i>	319, 1	17.06	<0.01
<i>C. quercusfolii</i>	149, 2	11.44	<0.01
<i>A. quercustozae</i>	778, 2	1143.61	<0.01
Population (P)			
Acorn, <i>T. ekebladella</i>	319, 4	3.72	0.01
<i>C. quercusfolii</i>	–	–	–
<i>A. quercustozae</i>	–	–	–
Climate treatment (C)			
Acorn, <i>T. ekebladella</i>	319, 1	48.55	<0.01
<i>C. quercusfolii</i>	149, 1	20.78	<0.01
<i>A. quercustozae</i>	778, 1	1482.65	<0.01
P × C			
Acorn, <i>T. ekebladella</i>	314, 4	1.7	0.15
<i>C. quercusfolii</i>	–	–	–
<i>A. quercustozae</i>	–	–	–
P × S			
Acorn, <i>T. ekebladella</i>	319, 4	4.97	<0.01
<i>C. quercusfolii</i>	–	–	–
<i>A. quercustozae</i>	–	–	–
C × S			
Acorn, <i>T. ekebladella</i>	314, 1	1.99	0.16
<i>C. quercusfolii</i>	149, 2	5.69	<0.01
<i>A. quercustozae</i>	778, 2	384.18	<0.01
P × C × S			
Acorn, <i>T. ekebladella</i>	310, 4	1.25	0.29
<i>C. quercusfolii</i>	–	–	–
<i>A. quercustozae</i>	–	–	–

Notes: Three separate linear models have been fitted to data on (1) acorn leaf development and *T. ekebladella* emergence, (2) emergence of inquilines and parasitoids associated with galls of *C. quercusfolii*, and (3) emergence of gall wasps, inquilines, and parasitoids associated with galls of *A. quercustozae*. Shown are *F* values from a marginal ANOVA, with column df providing the denominator and numerator degrees of freedom as separated by a comma. Significant *P* values ($P < 0.05$) are shown in bold.

The phenological distribution of the two parasitoid species *T. auratus* and *T. geranii*, but not the inquilines, was wider in warmer climate treatments when analyzing accumulated temperature (near significant species × climate treatment interaction; Fig. 4B; Table 2), while for ordinal days, all species had a wider phenological distribution in the warmer treatments (Appendix S2: Fig. S3B). For species associated with the gall *A. quercustozae*, we detected no visually apparent effect of climate treatment on the phenological distribution of both degree-

days and ordinal days (Fig. 4D; Appendix S2: Fig. S3D).

DISCUSSION

Warmer temperatures might advance phenology asymmetrically in different trophic levels and taxa (Schwartzberg et al. 2014, Thackeray et al. 2016, Uelmen et al. 2016, Kharouba et al. 2018), with knock-on shifts in interaction strength among temporally co-occurring species (Liu et al. 2011). Importantly, if local populations differ in their temperature responses, such changes in phenological synchrony are likely to vary in space. In this study, we exposed interacting partners from local populations to five alternative thermal climate regimes. While both plant and herbivore populations differed in phenology, we found no evidence of any detectable shift in phenological synchrony between leaf development of a host plant and emergence of a leaf-mining herbivore under different climates. In contrast, we found the phenological synchrony between an herbivorous inquiline and one of its parasitoids (*T. auratus*) to shift in warmer climates. Overall, climate had an effect on the temporal distribution of phenological events: At higher temperatures, this distribution widened for both an herbivore and two parasitoids, while no detectable effect was found for the host plant. Overall, these results suggest that some interactions could be vulnerable to changes in local temperature, with potential consequences for the geographic distribution of species interactions.

Temperature affects the phenological synchrony between trophic levels

With accumulation of temperature, we detected no change in the temporal overlap between oaks and *T. ekebladella* across climate treatments, while we detected a slight change for ordinal days. A previous meta-analysis has reported a range of outcomes, with time series data indicating an increase, a decrease, or no change in phenological synchrony between interacting species (Kharouba et al. 2018). Studies have also shown that in plant–herbivore interactions, either plants (Schwartzberg et al. 2014, Uelmen et al. 2016) or insects (Dewar and Watt 1992) can shift their phenology more than the other in response to changes in temperature.

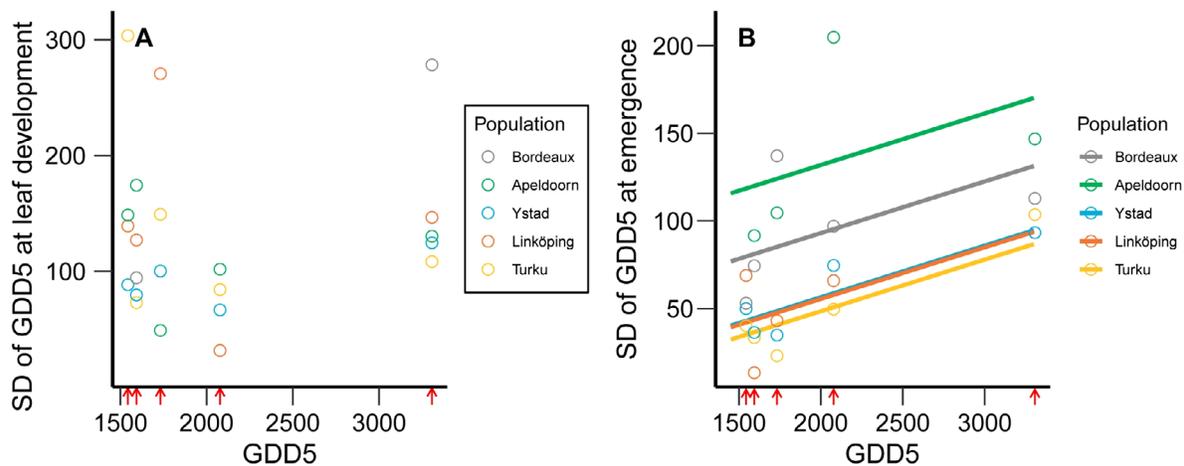


Fig. 3. The phenological distribution in GDD5 (growth degree-days above a threshold of 5°C) of (A) leaf development and (B) *T. ekebladella* emergence in five populations (see legend) exposed to five climate treatments (x-axis). The x-axis corresponds to the annual accumulation of GDD5, and the climate treatments corresponding to each site are shown with an arrow on the x-axis (from left: Linköping, Turku, Ystad, Apeldoorn, Bordeaux). The phenological distribution of insect emergence and leaf development is defined as the population-specific standard deviation of the accumulated GDD5 required for insects to emerge or leaves to develop. Hollow circles indicate the phenological distribution for a population in a climate treatment. Where significant, fitted values are shown as solid lines.

Table 2. The effect of species origin or species identity and climate treatment on the phenological distribution in (1) populations of acorns, (2) populations of *T. ekebladella*, and (3) species associated with the gall of *Cynips quercusfolii*, from a linear model.

Response/Source	df	F	P
Population (P)/Species (S)			
Leaf development	16, 4	0.65	0.63
<i>T. ekebladella</i>	17, 4	6.80	<0.01
<i>C. quercusfolii</i>	9, 2	0.83	0.47
Climate treatment (C)			
Leaf development	16, 1	0.09	0.77
<i>T. ekebladella</i>	17, 1	9.45	0.01
<i>C. quercusfolii</i>	9, 1	1.25	0.29
P/S × C			
Leaf development	12, 4	0.95	0.47
<i>T. ekebladella</i>	13, 4	0.16	0.96
<i>C. quercusfolii</i>	9, 2	3.64	0.07

Notes: The phenological distribution of insect emergence and leaf development is defined as the population or species-specific standard deviation of the accumulated GDD5 (growth degree-days above a threshold of 5°C) required for insects to emerge or leaves to develop. Shown are *F* values from a marginal ANOVA, with column df providing the denominator and numerator degrees of freedom as separated by a comma. Significant *P* values ($P < 0.05$) are shown in bold.

Based on our data, we suggest that the phenological synchrony between oaks and *T. ekebladella* will be relatively robust to changes in temperature. Whether or not the timing of leaf-out in small oak seedlings is identical to that of larger trees is perhaps debatable. Yet, the important point is whether insect emergence and host phenology overall are likely to respond to the same cues in the same way. For assessing this, acorn phenology is as good as any other host foliage trait. We found that while both insect emergence, acorn germination, and leaf-out occurred during short, well-defined time periods (Appendix S4), we found no detectable difference in the timing between these two trophic layers across different combinations of populations and climatic regimes. This suggests that the phenological responses assayed for the insects and the plant respond to the same cues (accumulation of temperature sums and absolute dates) in much the same way. From the perspective of herbivory, the fate of seedling foliage does seem representative of that of larger trees. Galmán et al. (2019) compared insect herbivory between saplings (<1 m tall) and adult, reproducing trees in eight species

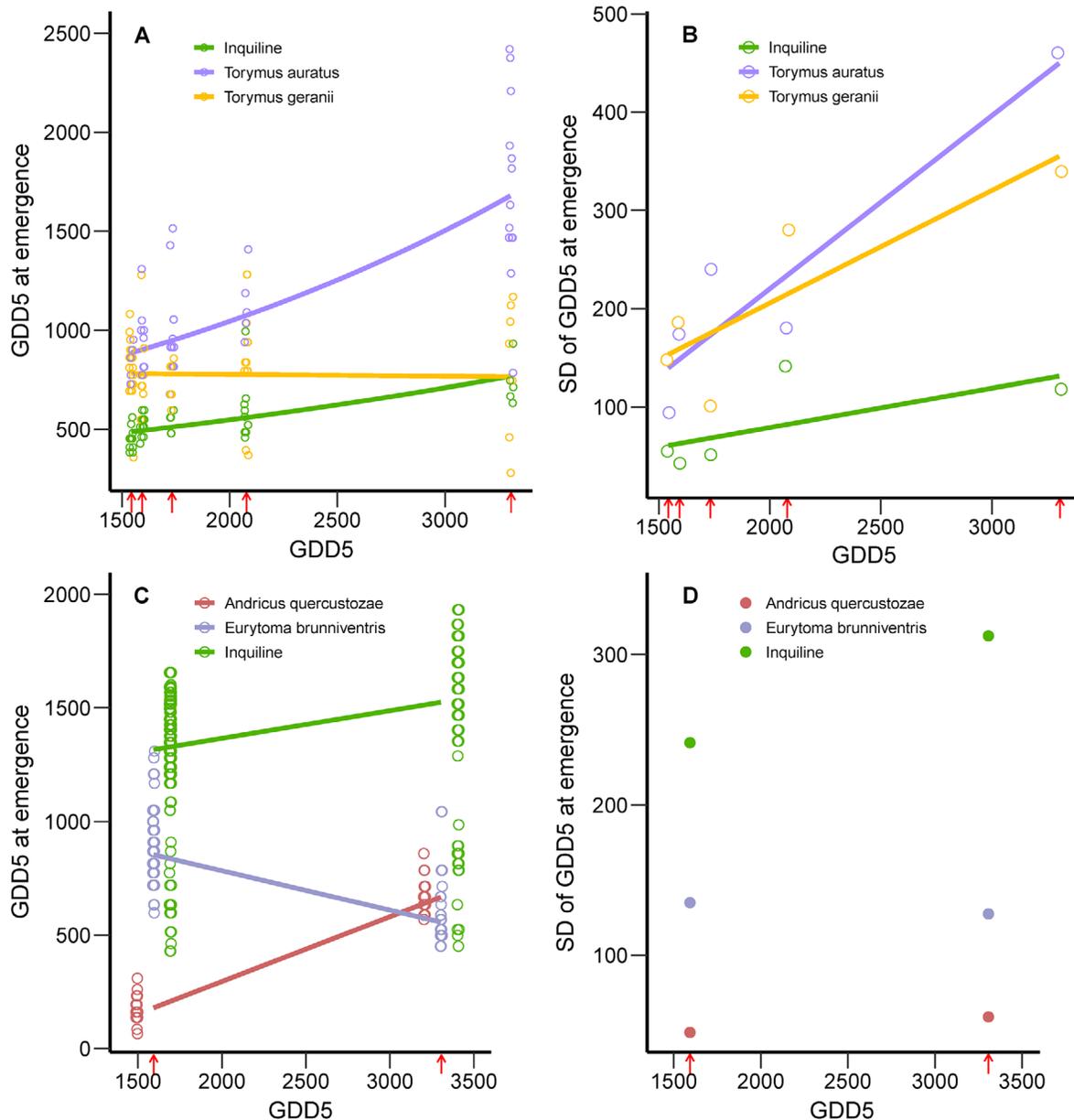


Fig. 4. GDD5 (growth degree-days above a threshold of 5°C) required for insects to emerge, and the phenological distribution in different climate treatments. Shown in (A,B) are results for inquilines and the parasitoids *T. auratus* and *T. geranii* associated with galls of *C. quercusfolii*. Shown in (C,D) are results for the gall wasp *A. quercustozae*, inquilines, and the parasitoid *E. brunniventris*. The x-axis corresponds to the annual accumulation of GDD5, and the thermal regimes corresponding to each site are shown with an arrow on the x-axis (figure A, B from left: Linköping, Turku, Ystad, Apeldoorn, Bordeaux; figure C, D from left: Turku, Bordeaux). The phenological distribution is defined as the species-specific standard deviation of the accumulated GDD5 required for insects to emerge. In the graphs, raw data are indicated by hollow and filled circles (jittered), while model fitted values are displayed as lines.

of *Quercus* and found no difference in herbivory. Thus, overall, a focus on seedlings seems well justified from an ecological perspective, and as the only possible solution from a logistical perspective.

In contrast to the lack of detectable change in synchrony observed for oaks vs. herbivores, we found that variation in temperature changed the phenological synchrony in emergence dates in two out of three herbivore–parasitoid interactions. The emergence of the parasitoid *T. auratus* showed a different response to temperature than did *T. geranii* and inquilines. The observed pattern suggests that *T. auratus* does not necessarily respond to temperature as such and that the phenology of this parasitoid could be triggered by a different cue. A lack of phenological response to temperature in parasitoids has also been documented by Klapwijk et al. (2010).

We found the phenological distribution of a herbivore (*T. ekebladella*) and two parasitoids (*T. auratus* and *T. geranii*) to be extended at warmer temperatures. A similar pattern has been observed in the orange tip butterfly *Anthocharis cardamines* (Lepidoptera), where fewer chilling days during winter-diapause resulted in both longer and more variable post-winter development time (Stålhandske et al. 2015). As our warmest and coldest climate treatments came with a distinct difference in the number of chilling days, we suggest that similar mechanisms were triggered here. A change in the width of the phenological distribution will presumably also influence the interaction strength among synchronized species (Linden 2018). For instance, if a local population of a species attains a wider phenological distribution, then this will weaken its interactions with temporally overlapping species, since fewer individuals co-occur with the interacting species. However, a wider phenological distribution might also buffer local populations of interacting species against the decoupling effects of divergence in mean phenology. Such consequences could also allow new or strengthened interactions with species that previously did not co-occur in time. In terms of the leaf development period, we detected no impact of temperature, although such effects have been suggested to occur in several plant species (Zohner et al. 2018). Whether this lack of effect was due to the very young age of oak seedlings

studied, to a lack of resolution in our scoring regime, or to something else, we cannot know. However, the pattern observed suggests that temperature has no major influence on the phenological distribution of oak leaf development and that this pattern is consistent across all populations. It will be interesting to carry out similar studies incorporating data for budburst and leaf development in mature trees of *Q. robur*, for example, using available geographically distributed provenance trials for this oak (Sinclair et al. 2015).

In summary, the observed shift in temporal overlap and phenological distribution suggests that a change in local temperature could alter the interaction network, at least in terms of herbivore–parasitoid interactions. If different trophic levels become temporally decoupled from each other, then species might start interacting more with species with which they overlap in time (Toftegaard et al. 2019). However, we leave it for future studies to establish exactly how shifts in synchrony are reflected in the property of food webs.

Ordinal days and growth degree-days as a response

Regardless of whether we used ordinal days or degree-days as response, a majority of the analyses produced qualitatively similar results—with one major exception: Focusing on timing in units of ordinal day, we detected a change in synchrony between leaf development and *T. ekebladella* phenology, whereas there was no corresponding change in units of degree-days (Fig. 2; Table 1; Appendix S2: Fig. S1). In our experiment, this discrepancy most likely results from differences in the climate between the timing of leaf development and insect emergence. Hence, the phenology of both species is driven by degree-days and the warmest climate treatment (that of Bordeaux) had the mildest winter climate, where several days only slightly exceeded the development threshold of 5°C. This resulted in a slow accumulation of degree-days. In contrast, the other climate treatments reached the degree-day threshold closer to summer, when the climate was warm. Thus, we believe that this resulted in a faster accumulation of degree-days and thereby also a shorter temporal distance between leaf development and insect emergence.

For both oaks and the leaf miner *T. ekebladella*, we observed that more degree-days were required to emerge under warmer temperatures. Such a pattern could be a result of a non-linear accumulation of temperature, where development ceases to increase linearly above a certain threshold temperature, but it could also be due to the fact that a low number of chilling days in winter can delay phenology in both plants and insects (Heide 2003, Fu et al. 2015, Roberts et al. 2015, Stålhandske et al. 2017). More chilling days in winter generally speed up spring development of insects and plants (Hanninen and Tanino 2011, Stålhandske et al. 2015). However, it has also been shown that high temperatures in autumn can increase the number of chilling days required to break buds in spring (Heide 2003). All in all, our results seem to be in line with several other studies that insects subjected to higher winter temperatures generally require more heat to emerge in spring.

Evolutionary patterns among populations

We detected an effect of population origin on spring phenology in both oaks and *T. ekebladella*. Local adaptation in phenology has previously been shown to occur in both plants and insects (Olson et al. 2013, Vitasse et al. 2013, Posledovich et al. 2014, Stålhandske et al. 2014, Delgado et al. 2020). We found that populations from more southern locations generally required more degree-days to emerge or develop leaves than did individuals from northern populations. Hence, southern populations—which tend to live at warmer locations—were not as responsive to temperature as northern populations, which is in line with the notion of countergradient variation (Conover and Schultz 1995, Delgado et al. 2020). In our case, this suggests that the developmental rate of species is more rapid in populations at colder locations. This could be related to the fact that northern populations in the Northern Hemisphere generally experience longer winters and shorter summers than populations from southern latitudes. If species are limited by the length of the season, then it can be advantageous for northern populations to be more responsive to temperature, as this will allow them to become active earlier and utilize the whole season.

For *T. ekebladella*, countergradient variation was detectable when comparing the northern

populations (Turku, Linköping, Ystad) to each of the southern populations (Apeldoorn, Bordeaux). Previous work has also shown countergradient variation in flowering phenology of *Cerastium fontanum* (Valdes et al. 2019), while cogradient variation (faster development in populations at warmer locations) has been found in Swedish populations of the orange tip butterfly *A. cardamines* (Stålhandske et al. 2014). In our study, some signs of countergradient variation were also apparent among oak populations, as acorns from Bordeaux generally required more degree-days to produce shoots and leaves compared with the other populations (although this pattern was highly influenced by an outlier (Appendix S4: Fig. S1)). A similar pattern, that populations originating from lower latitudes require a higher temperature to develop leaves, has also been detected in *Populus balsamifera* (Olson et al. 2013). However, there is also a genetic component to oak spring phenology (Tack et al. 2010), and oaks from Bordeaux represent the result of postglacial range expansion from a single southern refugium, while the other populations have been colonized by three refugial lineages (Petit et al. 2002). Therefore, genetic differences may combine with countergradient variation in explaining why oaks from Bordeaux differ in their temperature response in comparison with the other populations in this study.

In line with the hypothesis of evolutionary adaptation to local climate and countergradient variation, we find that populations differ in their response to temperature and that northern populations generally develop at a faster rate. As we lack any direct evidence on whether and to what extent the patterns are actually adaptive in nature (i.e., associated with fitness benefits), we stress that our results point to a clear hypothesis amenable to testing by, for example, extensive translocation experiments: that over time local organisms should be better attuned to the local temperature regime than individuals from elsewhere, as indicated by higher fitness.

CONCLUSION

How communities respond to a temperature-induced shift in phenology will depend on the set of component species involved, and how local populations of these species differ in their

phenological responses to climatic variation. Our findings suggest that temperature can modify the interaction network within a community, by altering the phenology and the phenological distribution of interacting species. Still, the magnitude of change can differ among interacting species. For both acorns and *T. ekebladella*, all populations responded equally to a shift in temperature, which implies that this interaction shows a similar response across a large geographical scale. We encourage future studies to assess how shifts in phenology are reflected in the structure of the community. Despite the fact that studies of full communities often are resource demanding, they give us essential insights into how communities will respond to a warmer climate.

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DATA AVAILABILITY

All data are available from Dryad: <https://doi.org/10.5061/dryad.t1g1jw2z>.

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3785/full>