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Phenological responses in a sycamore-aphid-parasitoid system and consequences for aphid population dynamics: a 20-year case study

Climate change and species interactions.

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ABSTRACT

Species interactions have a spatio-temporal component driven by environmental cues, which if altered by climate change can drive shifts in community dynamics. There is insufficient understanding of the precise time-windows during which inter-annual variation in weather drives phenological shifts and the consequences for mismatches between interacting species and resultant population dynamics – particularly for insects. We use a 20-year study on a tri-trophic system: sycamore *Acer pseudoplatanus*, two associated aphid species *Drepanosiphum platanoidis* and *Periphyllus testudinaceus*, and their hymenopteran parasitoids. Using a sliding window approach, we assess climatic drivers of phenology in all three trophic levels. We quantify the magnitude of resultant trophic mismatches between aphids and their plant hosts and parasitoids, and then model the impacts of these mismatches, direct weather effects and density dependence on local-scale aphid population dynamics. Warmer temperatures in mid-March to late-April were associated with advanced sycamore budburst, parasitoid attack and (marginally) *D. platanoidis* emergence. The precise time-window during which spring weather advances phenology varies considerably across each species. Crucially, warmer temperatures in late winter delayed the emergence of both aphid species. Seasonal variation in warming rates thus generate marked shifts in the relative timing of spring events across trophic levels and mismatches in the phenology of interacting species. Despite this, we found no evidence that aphid population growth rates were adversely impacted by the magnitude of mismatch with their host plants or parasitoids, or direct impacts of temperature and precipitation. Strong density dependence effects occurred in both aphid species and probably buffered populations, through density dependent compensation, from adverse impacts of the marked inter-annual climatic variation that occurred during the study period. These findings explain the resilience of aphid populations to climate change and uncover a key mechanism, warmer winter temperatures delaying insect phenology, by which climate change drives asynchronous shifts between interacting species.

Key Words – emergence, pests, phytophagous insects, population size, Hymenopteran parasitoids, woodland

INTRODUCTION

Climate change can influence species populations through direct and indirect mechanisms (Cahill et al. 2013; Ockendon et al. 2014) although indirect mechanisms arising from climate-induced alterations in species interactions frequently appear to be the principal factors driving demographic responses to climate change (Cahill et al. 2013; Ockenden et al. 2014; Ogilvie et al. 2017). The ectothermic physiology of insects means that their fitness is strongly influenced by their surrounding microclimate (Bale et al. 2002). Warmer temperatures during spring and summer may thus directly enhance growth and reproductive rates (Deutsch et al. 2008) but also increase the possibility of heat stress (Kingolver, Diamond and Buckley 2013) leading to increased mortality. Heat stress in temperate insect populations occupying closed habitats, such as woodland, are likely to be limited though as these insects typically experience conditions that are within their thermal tolerances (Deutch et al. 2008; Diamond et al. 2012; Sunday *et al.* 2014).

The direct effects of changes in precipitation and winter temperatures on insect demography are less well understood than the direct impacts of temperature during spring and summer (Bale & Hayward 2010). Droughts can increase insect mortality through desiccation (Torode et al. 2016), whilst heavy rainfall can remove phytophagous insects from their host plants and increase mortality rates (Alford 2000; Rosenzweig, Iglesias, Yang, Epstien & Chivian 2001; Walker, Nault & Simonet 1984). This risk of mortality probably explains why rainy conditions reduce mating behaviour of aphids and other insects – which could thus slow down population growth rates in years of high precipitation (Pellegrino et al 2013). Whilst future changes in spring and summer precipitation in temperate regions, including the UK, are uncertain (with potential for droughts, increased rainfall and more intense rainfall events; Lowe et al. 2018) these changes could influence insect demography.

Winter temperature in the UK is predicted to increase by 2-3°C by 2099 (Lowe et al. 2018) which could influence insect demography through a number of mechanisms. Warmer winter conditions can reduce nutritional reserves during the dormant diapause period, leading to increased mortality (Xiao, Chen, Chen, Chen & Wu 2017), and reduced reproductive potential following diapause termination (Irwin & Lee Jr 2000). Warmer winter temperatures may also delay diapause termination (Lehmann, Van Der Bijl, Nylin, Wheat & Gotthard 2017). Some insects do, however, require a certain amount or duration of chilling in order to respond to warming spring temperatures that ultimately terminate diapause (Bosch & Kemp 2003; Chuche & Thiéry 2009, Stålhandske et al. 2015). Warmer conditions experienced during diapause could thus reduce both diapause incidence and duration exposing insects to unfavourable conditions that further increase mortality (Bale & Hayward 2010; Tougeron et al. 2017).

Indirect impacts are also likely to be a key determinant of insect response to climate change and frequently arise due to changes in the timing of key events including diapause termination and eclosion (Boggs & Inouye 2012; Høye, Post, Schmidt, Trojelsgaard & Forchammer 2013; Kudo & Ida 2013). Earlier emergence and associated increased duration of the period suitable for insect activity could enable multivoltine insects to complete more generations per year, thus increasing population growth rates (Forrest 2016). Phenological shifts could also disrupt interspecific interactions if interacting species exhibit differential responses to climate change (Yang & Rudolph 2010). Changes in insect emergence date relative to host plant leaf burst may affect the abundance and quality of plant material available to phytophagous insects (Dixon 1976; Singer & Parmesan 2010). Similarly, changes in the relative timings of insect emergence and the phenology of their natural enemies could alter the duration and intensity of top-down pressures (Godfray, Hassell & Holt 1994; Hicks, Aegerter, Leather & Watt 2007; Van Nouhuys & Lei 2004), although experimentally simulated earlier aphid emergence did not result in aphids escaping subsequent control from late arriving predators (Fuchs *et al.* 2017).

Variation in phenological responses between interacting species may arise frequently (Thackeray *et al.* 2016) and will occur when species respond to different cues or respond at different rates to the same cue. Spring temperature is clearly associated with advancing phenology in temperate regions, with ectotherms and herbivores exhibiting the strongest responses (Cohen et al. 2018). There is increasing evidence from laboratory studies, however, that warmer winters can both advance (Tougeron et al. 2017) and delay (Stalhandske, Lehmann, Pruisscher & Leimar 2015) insect activity periods and recent meta-analyses have demonstrated that while both seasonal advancing and delaying effects of temperature are common, they vary within taxa and between trophic levels (Thackeray et al. 2016).

Climate-induced changes in synchrony between the phenology of insects and that of their resources and natural enemies may have important demographic consequences (Miller-

Rushing, Hoye, Inouye & Post 2010). Such mismatches have been observed to reduce food availability and consequently breeding success and population size in birds (Both, Bouwhuis, Lessells & Visser 2006; Saino et al. 2011; Visser, Holleman & Gienapp 2006; but see Franks et al. 2018) and mammals (Plard et al. 2014). Empirical analyses of insect population responses to trophic mismatch have, however, received less attention, although there are some studies related to: i) pests, e.g. mismatch with natural enemies which leads to reduced parasitism rates (Evans, Carlile, Innes & Pitigala 2013), ii) Lepidoptera, e.g. larvae mismatch with host plants leading to local extinctions (McLaughlin, Hellman, Boggs & Ehrlich 2002), e.g. adverse demographic impacts of mismatch in timing of egg hatching in winter moth *Operophtera brumata* and host plant phenology driving rapid adaptive responses in egg hatching (van Asch, Salis, Holleman, van Lith & Visser 2013) and iii) pollinators, e.g. mismatch of bee emergence with temporal distribution of floral resources (Ogilvie *et al.* 2017).

Adverse impacts may be particularly prevalent in phytophagous insects, especially specialist ones, and could also be influenced by the effects of temperature and precipitation on the abundance and nutritional quality of their host-plants (Cornelissen 2011; Thuiller, Lavorel, Araujo, Sykes & Prentice 2005). Phytophagous insects are also typically under pressure from natural enemies such as parasitoids. Climate change can influence the magnitude of these top-down pressures, in part due to phenological shifts that increase or decrease temporal refuge (Evans et al. 2013; Hicks et al., 2007; Tougeron, Lann, Brodeur & van Baaren 2017).

Insect populations are thus highly vulnerable to direct and indirect effects of climate change on their phenology and resultant population dynamics. Given the major and diverse roles of insects in contributing to ecosystem function and ecosystem services (Losey & Vaughn 2006), and evidence for widespread collapses in insect populations (Hallman et al. 2017; Simmons et al. 2019) insufficient research has addressed these issues, especially with regards to wild populations, with the exception of crop pests and some Lepidoptera (Andrew et al. 2013). This is primarily due to the lack of long-term, spatially matched data on interacting species (Miller-Rushing et al. 2010; Renner & Zonner 2018). Here we use one such dataset, generated from a 20-year study of a tri-trophic plant-aphid-parasitoid system comprising: sycamore *Acer pseudoplatanus*, two aphids (*Drepanosiphum platanoidis* and *Periphylus testudinaceus*) and braconid parasitoid wasps (Braconidae, Hymenoptera). The focal aphid species differ in their selectivity of host plants with *D. platanoidis* being largely confined to sycamore (Douglas 1993), whilst *P. testudinaceus* select a wider range of tree species within the *Aceraceae* family (Wilkaniec & Sztukowska 2008). Our study has two core objectives: i) to use a sliding window approach to determine how temperature and precipitation determine the phenology of all three trophic levels; in doing so we provide a rare example of the antagonistic effects of pre-spring vs spring temperatures in determining the phenology of wild insect populations; ii) to tease apart the direct effects of weather on aphid population growth rates versus those of trophic mismatches with budburst and thus food availability (bottom-up control) and attack from parasitoids (top-down control). We also determine the capacity of density-dependent compensation to buffer aphid populations from adverse climate impacts. These objectives are important because developing a mechanistic understanding of how climate change drives divergent responses between our study species can provide a basis to understand common causes of divergent response across other interacting taxa. Determining the causes of phenological shifts also allows for greater predictive capacity when assessing the impacts of further changes in climate on biotic interactions as well as understanding the potential population consequences of asynchronous phenological shifts.

METHODS

Fieldwork

Data were obtained from 1993 to 2012 at Silwood Park, southern England (lat: 58.813742, long: 8.371582), which is a topographically homogenous 100 ha area of parkland and deciduous woodland. Three 300 m transects were located, 200m apart, within the deciduous woodland, along which a total of 52 healthy sycamore trees were haphazardly selected. Trees were selected to represent a range of sizes, from 3.5 cm to 300 cm diameter at breast height, (mean ± SD = 41.56 ± 56.25).

On each tree, leaf phenology was recorded weekly from the 1st March. In any given week, the phenological score of each tree was assigned as the dominant stage of budburst, assessed over the entire tree. Following Leather (1996) budburst was scored using six stages: 1- dormant; 2- bud partly swollen; 3- bud highly swollen; 4- budburst; 5- leaves exposed but still folded; and 6- leaves expanded. Sycamore leafing phenology was calculated as the closest Julian date at which 50% of the trees had achieved bud burst (stage 4).

During each visit, 40 leaf buds or emerged leaves were selected haphazardly from those within reach, on which we recorded the number of *D. platanoidis* and *P. testudinaceus* aphids. Emergence phenology for *D. platanoidis* and *P. testudinaceus* was calculated as the date in which aphid abundance reached 10% of the total cumulative annual abundance recorded on the focal tree. This meets our requirement for a population-level indicator of the start of aphid emergence, and thus the point from which aphids were available to be attacked, whilst avoiding first emergence dates as these are less reliable due to their sensitivity to outliers (Miller-Rushing & Primack. 2008; Tryjanowski & Sparks 2001).

In some years *D. platanoidis* or *P. testudinaceus* were not recorded by the end of June on a small number of trees (*D. platanoidis* was absent from between 0 and 16 trees per year; *P. testudinaceus* absent from between 0 and 17 trees; Table S1). These trees thus lacked a spring population of the focal aphid species and were removed from the dataset for that year.

We also recorded the number of parasitised aphids, which were identified by their colour (Stary 1970). As mummies were left *in situ* and not collected to hatch the parasitoid their specific identity is unknown, but all are Hymenoptera in the family Braconidae. Phenology of parasitoid attack occurrence was calculated as the date in which the number of aphids parasitised reached 10% of the total cumulative number of parasitised aphids. In some years, parasitised aphids were not found on some trees (between 1 and 37 trees per year; Table S1) which were thus not considered when analysing the phenology of parasitoid attack. This might be problematic if recording only covered part of the season (as the event may have occurred after recording ceased) but data were collected throughout the season and would thus have enabled the timing of parasitoid attack to be documented even if it occurred at the end of the season.

Data on the number of aphids and aphid mummies were not collected in a small number of weeks (4.2% of potential observation were missing; Table S2). For these dates, we estimated the mean of the recorded values in weeks immediately either side of the missing data point prior to calculating phenological metrics. Daily meteorological records of maximum and minimum temperatures and total precipitation were obtained from a weather station located at the study site.

Statistical Analyses

Effects of weather on sycamore, aphid and parasitoid phenology

We modelled the phenology of sycamore budburst, the emergence of the two aphid species and occurrence of aphid parasitism as a function of temperature and precipitation. The precise time periods over which weather influences phenology is uncertain and so following standard approaches (van de Pol & Bailey 2016) we used a model competition approach that allowed our data to inform the selection of the temporal window for each variable that generates the best fit to the data. We calculated mean temperature (°C) and mean precipitation (mm) for each of the 27 weeks from 1st January (day 1) to July 8th (day 189) giving 27 weekly periods. We then used these data to calculate mean temperature and mean precipitation during all possible consecutive weekly stages (e.g. mean temperature during week 1, i.e. 1st-7th January, weeks 1-2, 1-3, 1-4 etc., weeks 2-3, 2-4, 2-5 etc.) giving a total of 378 weekly combinations. We only used combinations whose time span did not include dates after the latest mean observation of each phenological measure when modelling that outcome (e.g. the latest observation of mean sycamore budburst was April 23rd and so we only used time windows that occurred before that date in models of sycamore phenology). The magnitude of winter chilling can influence both plant and insect phenology (Renner & Zohner 2018). The potential for such effects are taken into account by the inclusion of temperatures from January 1st in the sliding window approach and the use of an additional variable capturing mean winter temperature (1st November to 28th February) was included to adjust for any effects of overall winter coldness.

We used Aikaike Information Criteria corrected for small sample sizes (AICc) values to distinguish between competing models, which were constructed as linear mixed effects models (LMERs) with Gaussian error structure, using the ‘bobyqa’ optimizer in the lme4 package (Bates, Maechler, Bolker & Walker 2015) in R version 3.6.1 (R Core Team 2019). Year and individual tree ID were included as random factors to account for repeated measurements. Analyses were conducted in two stages; first, we fitted separate models for each set of weather variables (i.e. spring-summer temperature, spring-summer precipitation, see below) in order to assess the relative strength of association between phenology and these distinct types of weather variables, whilst also enabling us to identify the most influential time window for each type of weather variable. The second stage then combined the most influential time window for each weather variable into LMER models that included the best predictors from the complete set of weather variables (see explanation below). This two-stage approach is required to restrict the number of predictor combinations to a manageable amount and follows standard practice (van de Pol *et al.* 2016). In the first stage (Equation (1)), we fitted separate models of phenology each with a single fixed effect predictor variable based on **i) temperature windows** – all time periods which were relevant to the spring phenological period of each taxa. Sliding windows began on Jan 1st for all taxa and proceeded to April 29th for the sycamore tree (153 models), June 17th for *D. platanoidis* (300 models), June 10th for *P. testudinaceus* (276 models) and July 8th for parasitoids (378 models) or **ii) precipitation windows-** using the same range of durations of sliding windows as used for temperature. These models were constructed for each of our four phenological response variables, i.e.: sycamore budburst, *D. platanoidis* emergence, *P. testudinaceus* emergence and parasitoid attack and all contained tree identity and year as random factors.

$\text{Phenology}_{ijk} \sim N(\mu_{ijk},\sigma)$

1. $\mu_{ijk} = \text{Tree}_i + \text{Year}_j + \text{Temp.window}_j + \varepsilon$
2. $\mu_{ijk} = \text{Tree}_i + \text{Year}_j + \text{Precip.window}_j + \varepsilon$

$\text{Tree}_i \sim N(0, \sigma^2_{\text{tree}})$

$\text{Year}_j \sim N(0, \sigma^2_{\text{year}})$

$\varepsilon \sim N(0, \sigma^2)$

(Equ. 1)

Where Phenology_{ijk} is the *k*th observation of emergence time of tree *i* and year *j* with Tree_i and Year_j as random intercepts with mean 0 and variance σ^2, and ε as a normally distributed error term. The temperature and precipitation windows were fitted as fixed effects across two models.

We compared the AICc of each of these models to that of a model without weather variables, i.e. which only contained year and tree identity as random factors. We considered all models within two AICc points (i.e. $\Delta\text{AICc} \leq 2$) of the best fitting model (that with the lowest AICc) to have similar goodness of fit to the data (provided that AICc is lower than the null model). For all trophic levels, this first stage modelling identified two distinct effects of temperatures between Jan-July, with periods earlier in the year in which higher temperatures had positive (delaying) effects on phenology (as expected if insufficient winter chill delays termination of diapause) and periods later in the year where temperature had negative (advancing) effects on phenology. A similar pattern occurred with regard to precipitation windows (see results). This first stage of modelling thus generated four sets of predictor variables for all study taxa that were carried over to the second stage of modelling, i.e. an advancing temperature window, a delaying temperature window, an advancing precipitation window, and a delaying precipitation window. Second stage modelling of each phenological event included these four predictor variables and mean winter temperature (Equation (2)). The second stage of modelling also used an information theoretic approach to model selection, using all possible combinations of our five weather predictors when modelling each phenological response. All models included year and individual tree number as random effects to account for repeated measures.

$$\text{Phenology}_{ijk} \sim N(\mu_{ijk},\sigma)$$

$$\mu_{ijk} = \text{Tree}_i + \text{Year}_j + \text{Temp.window.adv}_j + \text{Precip.window.adv}_j + \text{Temp.window.delay}_j + \text{Precip.window.delay}_j + \text{mean.winter.temp}_j + \varepsilon$$

$$\text{Tree}_i \sim N(0, \sigma^2_{tree})$$

$$\text{Year}_j \sim N(0, \sigma^2_{year})$$

$$\varepsilon \sim N(0, \sigma^2)$$

(Equ. 2)

Where Phenology_{ijk}, error and random effects are as in equ. (1) and the fixed effects of advancing and delaying window are included along with mean winter temperature. We then conducted model averaging over all models within two AIC points of the best fitting model (and that had AICc values smaller than a null model that lacked weather predictors) for the given response variable.

Population models

For each aphid species, we modelled population growth rate as a function of the previous years' density (to account for density dependence), temperature and precipitation variables (to test for direct weather effects), and phenological mismatch/overlap with host and parasitoids (indirect weather effects) whilst including individual year as a random factors in all models (Equation 3). Tree identity was not included as a random effect as, for both species, intercepts were singular and models with the random effect removed had lower AICc values. Population growth rates for *D. platanoidis* and *P. testudinaceus* were calculated as inter-annual growth rates, i.e. $\mathbf{log}(N_t/N_{t-1})$**,** where N_t is the population size in year t.

We conducted a preliminary analysis to assess the nature of density dependence affecting these population growth rates. For each aphid species we modelled aphid population growth rate as a function of i) intra-specific density dependence – the population size of the same aphid species in the previous year, ii) inter-specific density dependence – the population size of the other aphid species in the previous years' population, and iii) inter and intra-specific density dependence – the combined population size of both aphid species in the previous year. The AICc values of these models were compared to that of a model which only contained random effects. For each aphid species, the model that only contained intra-specific density dependence had much lower AICc values than all other models, including the null model (Table S3), and so this form of density dependence was included in all subsequent population growth models.

Census error can result in spurious detection of density dependence. To guard against this we followed the recommendations of Freckleton et al. (2016) and, for both aphid species, we evaluated the relationship between inter-annual growth rate and log population size using a linear model. This relationship is expected to be strictly linear if density dependence is caused by census error. We found that the relationship was non-linear as models containing an additional quadratic term had lower AICc values, supporting an interpretation of genuine density dependence (Table S4).

The population growth models were constructed using a similar sliding window approach to the phenology models in order to identify the specific time window in which population growth was sensitive to weather. We calculated mean temperature and precipitation for each month (°C) starting from November in the previous year to October in the year of interest giving a full year of 12 months. We then used these data to calculate mean temperature or precipitation across all possible consecutive monthly periods, giving a total of 78 monthly combinations for each. We use wider individual time windows (months) than used for modelling phenology (weeks) as i) inter-annual population growth rates depend on population performance over the entire annual cycle rather than a narrower time period which thus requires finer subdivision, and ii) use of monthly or even longer time windows is a commonly used approach for assessing how population growth rates respond to weather variables with negligible evidence that use of finer temporal windows improves fit (e.g. Martay et al. 2016; Mills et al. 2017).

We fitted population growth rate as a function of weather variables using LMERs that always included year and individual tree identity as random factors (Equation (3)). We constructed separate models of aphid population growth rate as a function of i) temperature - all sequential monthly combinations of mean temperature (78 models), ii) precipitation - using all combinations of monthly precipitation as defined for temperature (78 models).

$\text{Pop.growth.rate}_{ijk} \sim N(\mu_{ijk},\sigma)$

1. $\mu_{jik} = \text{Tree}_i + \text{Year}_j + \text{Temp.window}_j + \text{Density}_{i(j-1)} + \varepsilon$
2. $\mu_{jik} = \text{Tree}_i + \text{Year}_j + \text{Precip.window}_j + \text{Density}_{i(j-1)} + \varepsilon$

$\text{Tree}_i = 0$

$\text{Year}_j \sim N(0, \sigma^2_{\text{year}})$

$\varepsilon \sim N(0, \sigma^2)$

(Equ 3)

Where $\text{Pop.growth.rate}_{ijk}$ is the *k*th observation of inter-annual growth rate, Density as the intra-specific density on tree *i* of the previous year (*j*-1), and ε as a normally distributed error term. The random effect structure differs from equ (1) and (2) due to the removal of tree identity as a random intercept (as its variance was zero and thus generating singularity in model fit). The fixed effects of temperature and precipitation windows were fitted in separate models.

We compared the AICc corrected for small sample sizes to that of a model with no weather variables, i.e. contained intraspecific density dependence as the only fixed factor and year and tree identity as random factors. We identified all models within two AICc points of the best fitting model (that with the lowest AICc). This stage thus helps us to compare the relative strength of direct weather effects on aphid population growth rates and we selected the temperature and precipitation windows with the lowest AICc values for use in the second stage of modelling.

In the second stage, we modelled aphid population growth rate as a function of density dependence, temperature and precipitation (best fitting variables selected from the first modelling stage), and included an estimate of the degree of temporal mismatch with budburst and parasitoid attack occurrence (year and tree number were also included as random effects) (Equation (4)). This allowed us to assess the relative importance of direct weather effects versus indirect effects of phenological mismatch with host plants or parasitoids. Phenological mismatches were calculated as the difference in the number of days between aphid emergence and host tree leaf burst and the difference in number of days between aphid emergence and parasitoid attack occurrence.

$$\text{Pop.growth.rate}_{ijk} \sim N(\mu_{ijk},\sigma)$$

$$\mu_{ijk} = \text{Tree}_i + \text{Year}_j + \text{Temp.window}_j + \text{Precip.window}_j + \text{Density}_{i(j-1)} + \text{Parasit.mis}_{ij} + \text{Tree.mis}_{ij} + \varepsilon$$

$$\text{Tree}_i = 0$$

$$\text{Year}_j \sim N(0, \sigma^2_{\text{year}})$$

$$\varepsilon \sim N(0, \sigma^2)$$

(Equ 4)

Where inter-annual growth rate, weather windows, intra-specific density dependence and random effects are as in equ (3), but with Parasit.mis_{ij} as the mismatch with the parasitoid on tree *i* of year *j* and Tree.mis_{ij} the mismatch with budburst. In this second stage we constructed all possible models given our set of predictor variables (and included density dependence and random effects in all models) and then conducted model averaging over all models within two AIC points of the best model and with a lower AICc than the null model. In all our LMER models, the amount of variance explained by the fixed effects only and the combined fixed and random effects were calculated as the marginal R^2 ($R^2_{(m)}$) and conditional R^2 ($R^2_{(c)}$) respectively, as described by Nakagawa & Schielzeth (2012).

Phenology and mismatch are correlated, and we thus conducted a post-hoc analysis to investigate the possibility that aphid phenology, rather than a mismatch with parasitoids, affected inter-annual growth rates. We compared AICc values of separate models fitted with either phenology or parasitoid mismatch along with the random intercepts, density dependence and weather windows. Mismatch had lower AICc than phenology for both species suggesting that mismatch better explained growth rates than phenology *per se*. If both variables are fitted in the same model then AICc multi-model selection for models with delta AICc ≤ 2 includes models with mismatch as a predictor but none with phenology. Further details are presented in the supplementary materials (Table S5)

RESULTS

Phenology

Variation in phenology

Mean sycamore budburst date varied across the 20 year period by 17 days (April 6th – April 23rd, Figure 1) with a coefficient of variation (CV) of 4.79. The insect components of this tri-trophic system exhibited much more plasticity in their phenology. *Drepanosiphum platanoidis* emergence (measured as 10% cumulative abundance) varied by 76 days (March

28th – June 12th, Figure 1), with a CV of 17.30 and *Periphylus testundinaceus* emergence varied by 38 days (April 26th – June 3rd, Figure 1), with a CV of 7.42. Annual variation in the date of parasitoid attack occurrence varied by 61 days (May 8th-July 8th, Figure 1), CV 9.65.

Acer pseudoplatanus

First stage modelling identified effects of temperature in weeks 11-16 (with an advancing effect on phenology), precipitation (in weeks 7-17; delaying effect) and precipitation (in weeks 1-9; advancing effect) (Table S6a-S6d). Stage two modelling, however, demonstrated that only the advancing effect of temperature during weeks 11 to 16 had model-averaged (across eight models with ΔAICc < 2) parameter estimates whose 95% confidence intervals excluded zero, and the effect sizes of all other weather variables are estimated to be small (Figure 2, Table 1). A mean temperature increase of 1°C during weeks 11 to 16 (mid-March – early April) across the 20-year period advanced budburst by ~4.8 days (Figure 3a).

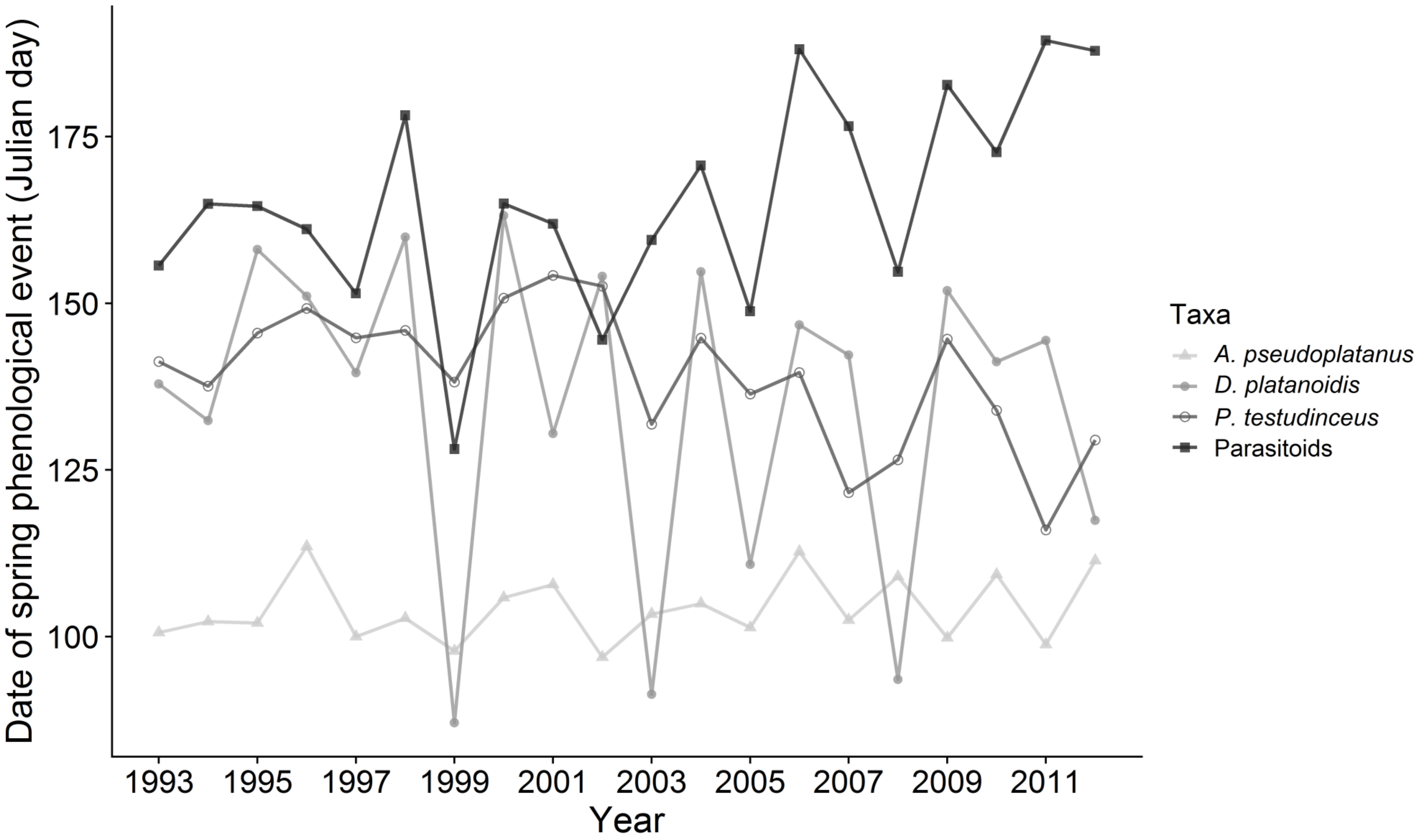
Date of spring phenological event (Julian day)
100
125
150
175
Year
1993
1995
1997
1999
2001
2003
2005
2007
2009
2011
Taxa
A. pseudoplatanus
D. platanoidis
P. testudinceus
Parasitoids

Figure 1. Changes in the timing of spring phenological events within the plant-aphid-parasitoid tri-trophic system. Events are: i) sycamore bud-burst, ii) *Drepanosiphum platanoidis* emergence iii) *Periphylus testudinaceus* emergence and iv) parasitoid attack (Braconidae; Hymenoptera). Aphid emergence and parasitoid attack measured as the 10% cumulative abundance of aphids and parasitised aphids respectively.

Drepanosiphum platanoidis

First stage modelling identified effects of temperature in week 22 (advancing effect on phenology), and week 7 (delaying effect) and precipitation in weeks 17-23 (advancing effect), and weeks 5-8 (delaying effect) on *D. platanoidis* emergence (Table S7a-S7d). Stage two modelling demonstrated that the delaying effect of temperature during week 7, and the advancing effect of temperature in week 22, were the only predictors for which none zero effects could be excluded (Figure 2). Models suggested that a 1°C increase in mean temperatures during weeks 7 (February) delayed emergence by 6.4 days (Figure 3b). For the advancing effect of temperature in week 22 (Late May – early June) (95% confidence intervals -0.99 to -9.38) the effect size is estimated to be similar to the delaying effect of temperatures earlier in the year, with a 1°C increase in mean temperatures during this period advancing the date of emergence by 5.12 days.

Periphyllus testudinaceus

First stage modelling identified effects of temperature (in weeks 6-7; delaying effect on phenology, and in weeks 13-17 advancing effect on phenology), precipitation (in weeks 4-17, delaying effect, and in week 19, advancing effect) on *P. testudinaceus* emergence (Table S8a-S8d). Stage 2 modelling found that all predictor variables had model-averaged 95% CI's that overlapped zero, but, the CIs of two variables almost excluded zero (Figure 2, Table 1), these were: i) temperatures during late March- April (week 13-17) (95% confidence intervals -9.0 to 0.2) for which a 1°C rise advanced emergence by 6.1 days (Figure 3c) and ii) temperatures during February (week 6-7) (95% confidence intervals -0.1 to 4.0) for which a 1°C rise delayed spring emergence by 2.0 days.

Parasitoid attack

First stage modelling identified effects of temperature (in weeks 4-5; advancing effect on phenology and in weeks 15-27; delaying effects on phenology), precipitation in weeks 2-18 (advancing effect), and weeks 6-26 (delaying effect) (Table S9a-S9d). Stage two modelling demonstrated that advancing temperature in weeks 4 to 5 was the only predictor for which none zero effects could be excluded (i.e. 95% confidence intervals of parameter estimates did not overlap zero; Table 1, Figure 2). Across the 20-year period a mean increase in temperature of 1°C during January advanced parasitoid attack occurrence by approximately 5.3 days (Figure 3d). There was marginal evidence, i.e. non-zero effects could not be excluded (95% confidence intervals -2.5 to 15.8) that warmer temperatures during weeks 15-27 (April-June) delayed the date of parasitoid attack with an increase in temperature of 1°C shifting attack dates by 6.7 days.

Table 1. Phenological events (Sycamore budburst, *D. platanoidis* emergence, *P. testudinaceus* emergence and parasitoid attack) as a function of weather variables identified for each group with a sliding window approach (Table S6a-S9d). Models are mixed-effects models with year and tree identity included as random effects in all models. For each species only models within 2 AICc points of the best model are presented alongside the results of model averaging these models (except for Parasitoid attack for which no models were within 2 AICc points of the model with the lowest AICc). ΔAICc is given relative to the model with the lowest AICc. Slopes are reported with ± 1SE. Marginal and conditional R^2 are denoted GLMM$_{(m)}$ and GLMM$_{(c)}$ respectively. Random effects only models: i) Sycamore tree AICc = 6804.89 ii) *D. platanoidis* AICc =8759.1; *P. testudinaceus* AICc = 8334.6; Parasitoid attack AICc = 7100.3.

AICc	**ΔAICc**	**R^2 GLMM$_{(m)}$**	**R^2 GLMM$_{(c)}$**	**Temp delaying**	**Temp advancing**	**Precipitation advancing**	**Precipitation delaying**	**Winter temperature**
Sycamore budburst					***Week 11-16***	***Week 1-9***	***Week 7-17***	
6779.7	0	0.154	0.715		-4.75±0.88	-0.62±0.88	-0.09±1.33	
6779.7	0.05	0.153	0.714		-4.97±0.82		-0.40±1.24	
6780	0.4	0.155	0.714		-4.72±0.69	-0.64±0.81		
6780	0.4	0.154	0.713		-4.82±0.67			
6780.7	1.1	0.154	0.716		-4.77±0.98	-0.62±0.91	-0.12±1.53	0.03±0.66
6780.8	1.1	0.153	0.715		-4.97±0.92		-0.42±1.44	0.02±0.65
6781.3	1.7	0.154	0.715		-4.72±0.72	-0.64±0.85		0.01±0.57
6781.4	1.7	0.153	0.714		-4.81±0.70			-0.07±0.56
Model Averaging					*-4.82±0.81*	*-0.32±0.69*	*-0.14±1.03*	*0.00077±0.37*
D. platanoidis				***Week 7***	***Week 22***	***Week 17-23***	***Week 5-8***	
8726.6	0	0.37	0.6	6.40±2.06	-5.18±2.14	-1.79±5.37	6.5 ± 3.82	-5.12±3.76
P. testudinaceus				***Week 6-7***	***Week 13-17***	***Week 19***	***Week 4-17***	
8314.8	0	0.133	0.285	1.88±1.07	-4.18±2.39	-1.33±1.41	4.41±3.50	-0.48±1.85

8315.9	1.1	0.133	0.285	1.80±0.99	-4.22±2.31	-1.37±1.36	4.17±3.27	
8316.2	1.8	0.130	0.281	2.20±1.01	-5.23±2.11		4.38±3.49	-0.66±1.83
Model Averaging				*1.94±1.05*	*-4.44±2.35*	*-1.03±1.35*	*4.33±3.43*	*-0.39±1.58*
Parasitoid attack				***Week 15-27***	***Week 4-5***	***Week 2-18***	***Week 6-26***	
7074.6	0	0.141	0.365	6.68±4.66	-5.30±1.71	6.15±7.57	7.17±8.4	-1.37±3.58

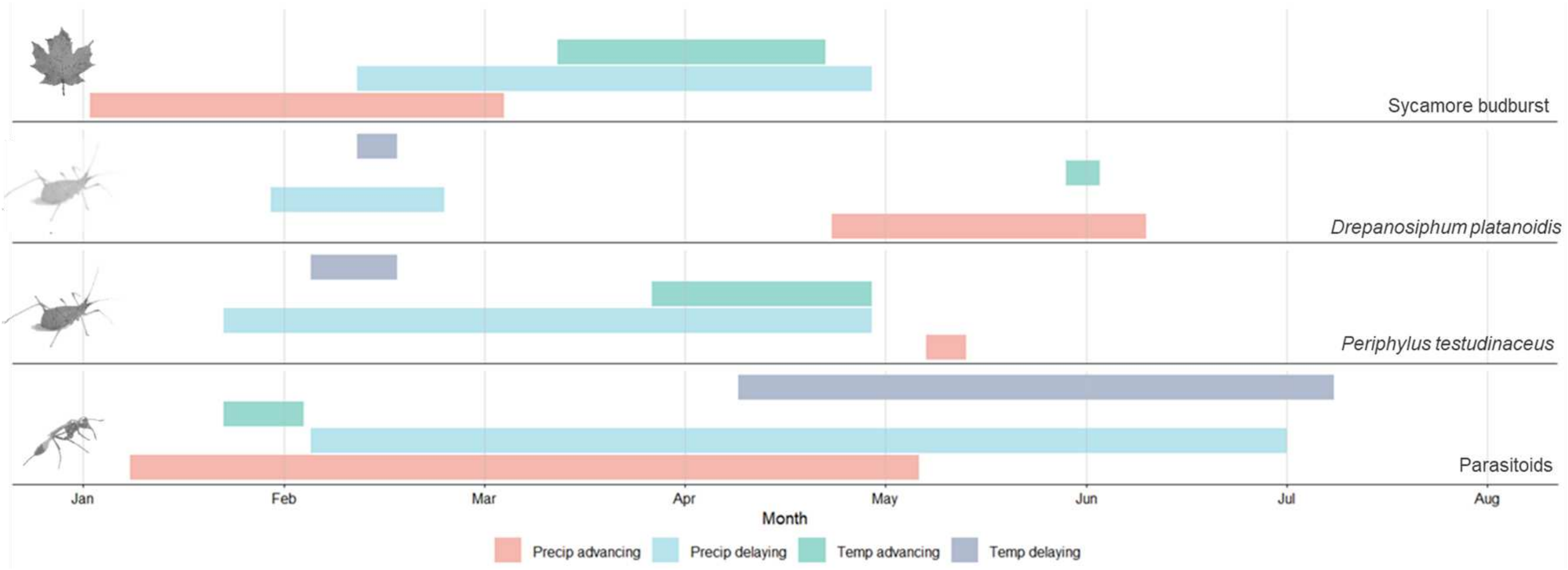

Figure 2. The sliding time windows of the weather variables identified as best predicting the phenology of sycamore budburst and the emergence of *D. platanoidis*, *P. testudinaceus* and parasitoid attack. The effects of different variables and their duration are shown with coloured bars. Models as described in Table 1 and Methods. Aphid emergence and parasitoid attack measured as the 10% cumulative abundance of aphids and parasitised aphids respectively.

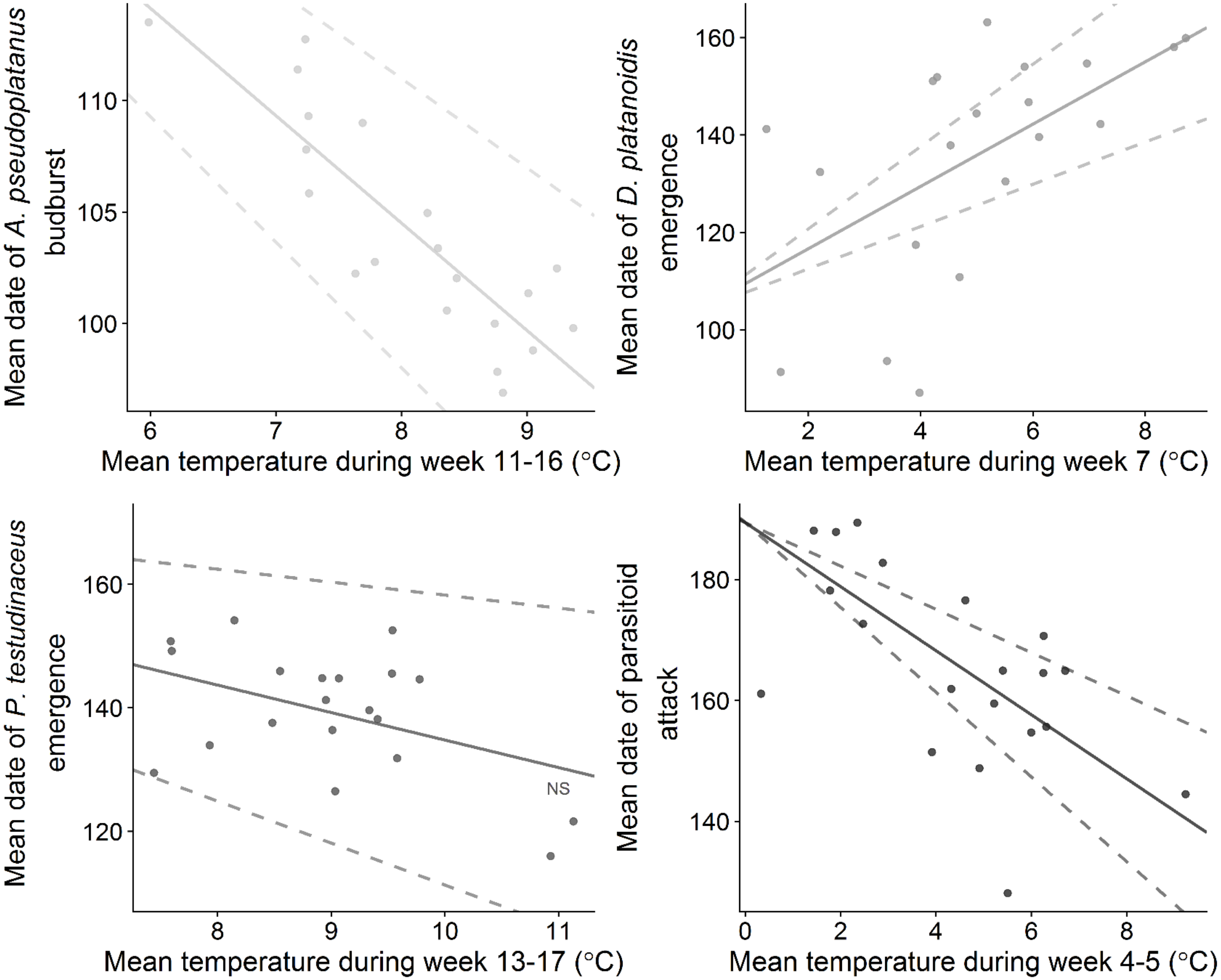
Mean date of *A. pseudoplatanus* budburst
110
105
100
6
7
8
9
Mean temperature during week 11-16 (°C)
Mean date of *D. platanoidis* emergence
160
140
120
100
2
4
6
8
Mean temperature during week 7 (°C)
Mean date of *P. testudinaceus* emergence
160
140
120
NS
8
9
10
11
Mean temperature during week 13-17 (°C)
Mean date of parasitoid attack
180
160
140
0
2
4
6
8
Mean temperature during week 4-5 (°C)

Figure 3. The relationship between temperature during key temporal windows and spring phenological events across three trophic levels: a) sycamore bud-burst, b) *D. platanoidis* emergence, c) *P. testudinaceus* emergence and d) the timing of attack by Hymenoptera parasitoids. For each phenological event, plots illustrate the relationship with the weather variable that is most closely associated with phenology in mixed effect models that include tree and year as random effects and include the specific time windows identified in stage 1 modelling for each climatic variable. Points are observed values. The solid line is the model-averaged predicted fit from models presented in Table 1 and the dashed lines the standard error; in c) the model fit is non-significant. All dates are Julian dates (i.e. days since Jan 1st, and weeks since week 1 (1st -7th January).

Population growth rate analyses

Modelling of *D. platanoidis* and *P. testudinaceus* population growth rates as a function of density dependence found that negative intraspecific density dependence was the strongest form of density dependence with metrics that captured inter-specific density dependence having a weaker fit to the data (Table S3).

A sliding window approach was used to select the time period during which monthly temperature and precipitation had the most influential effect on *D. platanoidis* and *P. testudinaceus* population growth rates whilst taking intra-specific density dependence into account. For both sets of weather variables, models that used alternative time windows and were within two AICc points of the best fitting model contained time windows that were very similar to the time window of the best fitting model (Supplementary Tables 10a-11b).

Drepanosiphum platanoidis

D. platanoidis population growth rate was modelled as a function of the weather variables selected in stage one modelling (temperature during March-July, precipitation during March-September) and the magnitude of mismatch with the other trophic levels, i.e. sycamore bud burst and parasitoid attack. This mismatch was substantial and highly variable between years - *D. platanoidis* emerged up to 48 days earlier and 117 days later than sycamore bud burst (mean ± SE: 30.64 ± 1.05 days later), and up to 168 days earlier and 49 days later than parasitoid attack occurrence (mean ± SE: 28.45 ± 1.33 earlier). Note, emergence can occur after parasitoid attack occurrence in years when parasitoid attack occurred before the date when aphid numbers had reached 10% of their total annual abundance. Three models were identified in this stage as having similar goodness of fit to the best model (i.e. with ΔAICc < 2 relative to the model with the lowest AICc value). Mismatch with parasitoid attack and monthly mean precipitation from March to September were both retained in at least one of these models (Table 2). Model averaging and consideration of the 95% confidence intervals of parameter estimates indicate that density dependence effects and mismatch with parasitoid attack occurrence (Figure 4a) were the only predictors for which zero effects could be excluded (Table 2).

Periphyllus testudinaceus

P. testudinaceus population growth rate was modelled as a function of the weather variables selected in stage one (temperature during February-September, precipitation during November), density dependence and the magnitude of mismatch with the other trophic levels, i.e. sycamore bud burst and parasitoid attack. *P. testudinaceus* emerged up to 38 days earlier and 110 days later than sycamore bud burst (mean ± SE: 35.45 ± 0.72), and up to 195 days earlier and 49 days later than parasitoid attack occurrence (mean ± SE -25.98 ± 1.37). Four models had AICc values within two points of the model with the lowest AICc value (Table 2). Mismatch with parasitoid attack occurrence, monthly mean precipitation from March to September and monthly mean temperature from February to September were all retained in at least one of these models. Model averaging and consideration of the 95% confidence intervals of parameter estimates indicate that intra-specific density dependence effects and mismatch with parasitoid attack (Figure 4b) were the only predictors for which zero effects could be excluded (Table 2).

Table 2. *D. platanoidis* and *P. testudinaceus* population growth as a function of mismatch between tree and parasitoid attack and weather variables previously identified with a sliding window approach (Table S10a-S11b). Models are mixed effects models with year and tree identity included as random effects in all models. For each species only models within 2 AICc points of the best model are presented alongside the results of model averaging these models. ΔAICc is given relative to the model with the lowest AICc. Slopes are reported with ±1SE. Random effects only models i) *D. platanoidis* AICc = 701.2, ii) *P. testudinaceus* AICc = 1250.8**.**

AICc	**ΔAICc**	**R^2 GLMM$_{(m)}$**	**R^2 GLMM$_{(c)}$**	**Density dependence**	**Parasitoid attack mismatch**	**Temperature**	**Precipitation**
D. platanoidis							***Mar-Sep***
742.4	0	0.099	0.892	-0.37± 0.03	0.002± 0.001		
744.1	0.65	0.106	0.895	-0.37± 0.03	0.002±0.001		-0.47±0.58
745.4	1.91	0.077	0.895	-0.35± 0.03			
Model averaging				***-0.36±0.03***	***0.002± 0.001***		***-0.47±0.58***
P. testudinaceus						***Feb-Sep***	***Aug-Oct***
1288.4	0	0.316	0.780	-0.55±0.03	0.005± 0.001		0.48±0.28
1288.4	0.05	0.241	0.772	-0.55±0.03	0.005± 0.001		
1289.6	1.26	0.382	0.796	-0.55±0.03	0.005± 0.001	0.34±0.27	0.48±0.28
1289.7	1.37	0.308	0.788	-0.55±0.03	0.005±0.001	0.34±0.29	
Model averaging				***-0.55±0.03***	***0.005±0.001***	***0.12±0.23***	***0.24±0.31***

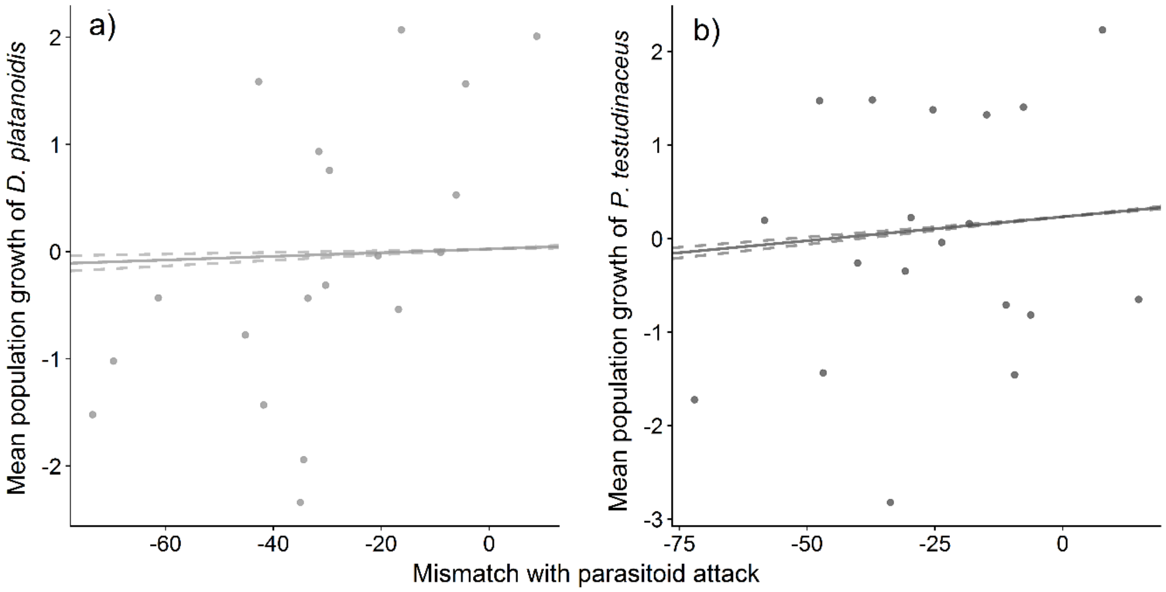

Figure 4. The relationship between mean population growth rate for a) *D. platanoidis,* or b) *P. testudinaceus*, versus the magnitude of mismatch (in days) between aphid emergence and the timing of parasitoid attack – negative values indicate that aphids emerge earlier than parasitoids attack. Points are observed values and highlight the high noise to signal ratio. The solid line is the model-averaged predicted fit from models that include the mismatch between aphid emergence and parasitoid attach as well as including year as a random effect and specific weather windows identified in stage one modelling and a density dependence variable as fixed effects, dashed lines show standard error (see Table 2).

DISCUSSION

This study provides a rare assessment of temperature and precipitation variables, selected from across the annual cycle, associated with the phenology of a tri-trophic plant-phytophagous insect (aphids)-parasitoid system and resultant aphid population dynamics.

Effects of weather on phenology

Primary producer – Sycamore

Sycamore bud burst advanced by approximately 4.8 days with a 1°C increase in temperature during March and April, which concurs with Vitasse et al. (2009) (5.4 days with a 1°C increase in March to May) and Tansey, Hadfield & Phillimore (2017) (5.1 days with a 1°C increase in early spring). There was negligible evidence that precipitation and temperature during winter influenced sycamore phenology. Studies have shown that precipitation influences spring phenology in some temperate plants, particularly grasses (Stewart & Dwyer, 1994; Yuan, Zhou, Wang, Han & Wang 2007), however, our results support there being little to no effect within temperate trees (Dose & Menzel, 2004; Morin, Roy, Sonie & Chuine 2010) – presumably because the much deeper rooting systems of trees enables them to access soil moisture even during dry springs.

Some temperate tree species require significant chilling to initiate bud burst (Hänninen 1995) and thus milder winters may delay spring phenology. There appears to be geographical variation in the response of sycamore trees to winter chilling, with spring bud burst of sycamore in Germany (Laube *et al.* 2014), but not the UK (Tsai, Young, Warren & Maltby 2016; Tansey et al. 2017), being influenced by exposure to winter chill. It is unclear if this is due to reduced exposure to winter chill (e.g. trees in our UK study were exposed to mean winter temperatures between 3.3°C and 7.5°C, whilst trees in the German study were exposed to much lower mean temperatures, of approximately -10°C) or regional intra-specific variation in the effects of winter chill. The observed range of winter and spring temperatures within our dataset, capture much of the plausible projections of future UK temperatures up to at least 2070 (Lowe et al. 2018) suggesting that sycamore bud burst will continue to advance over this time period and not be delayed by insufficient winter chilling that is predicted to influence vegetation phenology some UK species (Cook, Wolkovicj & Parmesan 2012).

Primary consumers – *D. platanoidis* and *P. testudinaceus*

As expected, warmer spring temperatures were associated with earlier aphid emergence (*D. platanoidis*, late-May to early-June; *P. testudinaceus,* late-March to April) although non-zero effects could not be excluded. More surprisingly, and whilst mean winter temperatures did not influence aphid phenology, an increase in February temperatures was associated with delayed aphid emergence in both aphid species (although non-zero effects could not be excluded for *P. testudinaceus*). Our inability to exclude non-zero effects may be a consequence of the twenty-year length of our time series with longer series more likely to find stronger effects (Cohen *et al.* 2018). During the study period, the level of temperature variation experienced during the most important time windows for advancing phenology was lower when compared to the variation experienced during the most important windows for delaying phenology (Supplementary Figure S1). This contrast in magnitude of exposure may explain why we observe stronger support (with regard to excluding non-zero effects) for the effects of temperatures that delay phenology. Delayed insect phenology arising from early-year warming may arise because winter chill requirements have not been met and thus diapause termination is delayed (Lehman et al. 2017; Tougeron et al. 2017). The effects of warming winters and the importance of chilling effects on insect phenology are not well understood for natural populations. Experimental research on a limited number of insect species, including butterflies (Stålhandske et al. 2017) bees (Bosch & Kemp 2003) and leafhoppers (Chuche & Thiery 2009) have demonstrated delays in spring phenology when these insects experience warmer diapausing conditions. For many temperate insects, a sufficient level of chilling is critical for the termination of diapause (Hodek 1999). The degree of chilling experienced also affects the developmental sensitivity to increasing spring temperatures where warming requirements for eclosion can be affected by the magnitude of chilling. A few recent field studies have begun to demonstrate this delaying effect of warmer temperatures in natural populations, but these are currently limited to the effects on a small number of Lepidoptera (Stalhandske, Gotthard & Leimar 2017) and Hymenoptera species (Forrest & Thompson 2011). Our results provide an indication for an effect of warmer temperatures delaying phenology in an additional order, suggesting that such impacts could be widespread in temperate insects. We also illustrate its importance within a specific time window as *D. platanoidis* was delayed by warming temperatures in February (with tentative evidence for a similar effect in *P. testudinaceus*). This suggests that chilling levels for these insects could be most critical towards the end of winter. Impacts of warmer winters on insect phenology are rarely documented and are assessed far less regularly than the advancing effects of spring temperature (Cohen et al. 2018) – we would encourage insect phenology studies to assess the impacts of temperature across the annual cycle and more research on underlying physiological mechanisms is required.

Insect phenology can respond to precipitation, with UK populations experiencing opposing delaying and advancing effects in different seasons (Thackeray *et al.* 2016). Our preliminary analyses found some evidence for such a pattern, e.g. for *P. testudinaceus* precipitation increases in week 1-3 advanced their emergence and increases between week 16-20 delayed emergence. These advancing and delaying effects of precipitation were retained in the best fitting models for both aphids but 95% confidence intervals for this effect overlapped zero suggesting that precipitation may not be a major driver of aphid phenology in our study system.

This concurs with the conclusions of a global analysis that precipitation is more likely to influence phenology at lower latitudes (Cohen *et al.* 2018).

Natural enemies – Parasitoid attack

The effects of climate on the phenology of higher trophic levels such as hymenopteran parasitoids are typically rarely studied. We find that the occurrence of Hymenopteran parasitoid attack of aphids is driven primarily by warmer temperatures during winter, advancing attack phenology. Across the 20-year period, a mean increase in January temperature advanced parasitoid attack, strengthening the evidence that insect phenology in this system is sensitive to temperatures during the winter period. The limited research conducted to date has contrasting conclusions with some studies finding no effect of temperature on parasitoid (Hymenoptera: Braconidae) development (Klapwijk, Grobler, Ward, Wheeler & Lewis 2010), whilst others report earlier emergence of adult parasitoids (Hymenoptera: Braconidae) under warmer conditions during April and May (Van Nouhuys & Lei. 2004). Some parasitoids can also avert overwintering (diapause) in milder conditions if sufficient resources are available (Andrade, Krespi, Bonnardot, van Baaren & Outreman 2016) and other species completely lose their winter diapause (Tougeron et al. 2017). Such patterns are likely to lead to larger parasitoid populations at the timing of aphid emergence which would increase the probability of earlier parasitoid attack on aphids.

Studies have shown that precipitation might be important for synchronising parasitoid (Hymenoptera: Pteromalidae) emergence with their hosts (Chavalle, Buhl, Censier & de Proft 2015). Few other studies have, however, addressed this and it is likely to be specific to species whose hosts are also driven by precipitation – which is compatible with the lack of strong precipitation effects on phenology in our system.

Divergent responses across species and potential for trophic mismatch

Mean sycamore budburst date varied across the 20 year period by 16 days (day 87-113). Variation was greater at higher trophic levels (*D. platanoidis* - 76 days (day 87-163); *P. testudinaceus* - 38 days (day 116-154); parasitoid attack - 61 days (day 156-189)). This concurs with meta-analyses that primary consumers are more likely to exhibit greater phenological changes than primary producers (Thackeray et al. 2010; Thackeray et al. 2016), although disagrees with work which suggests secondary consumers would also show smaller phenological shifts than primary consumers (Thackeray et al. 2016).

Across trophic levels there is substantial variation in the nature of the weather variables that influence phenology. Monitoring multiple species over 20 years has allowed us to show that changes in weather and, specifically, aseasonal warming effects may be particularly important due to the temporal variation in the phenological response to weather cues between the different trophic levels, in part due to primary and secondary insect consumers, but not plants, responding to winter temperatures. This creates considerable trophic level variation in the timing of phenological events which can lead to trophic mismatch. There was a wide variation in mismatch between both *D. platanoidis* and *P. testudinaceus* aphid emergence with the phenology of their host tree and parasitoid natural enemies. Emergence was up to 48 days earlier and 117 days later than budburst for individual trees and up to 195 days earlier and 49 days later than the occurrence of parasitoid attack. The mismatch between aphids and parasitoids, in particular, is likely explained as the effects of warming temperatures during January-February have a divergent response on their spring activity. Mild winters may, therefore, delay aphid emergence whilst driving an earlier occurrence of parasitoid attack which may dramatically alter the populations of either taxa (Van Nouhuys & Lei 2004; Evans *et al.* 2013).

Population level effects

Despite the often substantial mismatch between sycamore bud-burst date and timing of aphid emergence, we found no evidence that the magnitude of mismatch adversely affected the population growth rate of our focal aphid species. This contrasts with the typically well-supported theory that phytophagous insects are sensitive to trophic mismatch due to a rapid seasonal increase in chemicals that defend plant material from attack by insect herbivores (Feeny 1970; Tikkanen & Julkunen-Tiitto 2003). Whilst phloem, upon which aphids feed, is generally free of such toxins and feeding deterrents (Douglas 2006) there is still a seasonal increase in the carbon:nitrogen ratio of tree leaves, with older leaves having the lowest amino acid concentrations (Dixon 1963; Chuche, Desvignes, Bonnard & Thiéry 2015). This reduced protein availability probably contributes to the experimental finding that *D. platanoidis* fed on older leaves have lower body mass, increased time to maturation, and higher levels of mortality than individuals fed on younger leaves (Dixon 1976). It is clear, however, that in our study system any such reductions in food quality arising from trophic mismatches are not driving population growth rates. This may partly be due to strong buffering effects from density dependent compensation.

Insect populations can be strongly regulated by parasitoids (Hawkins, Cornell & Hochberg 1997; Schmidt et al. 2003). Despite this, there is a paucity of research assessing the effects of climate change driven shifts in the timing of parasitoid attack on their host's population growth rates. Most of the work that has been conducted concerns hosts that are arable crop pests, for example warmer spring temperatures advance cereal leaf beetle *Oulema melanopus* phenology more than the phenology of its parasitoids *Tetrastichus julis* resulting in reduced parasitism (Evans et al. 2013). In our study system, we find no evidence that earlier emergence relative to the timing of parasitoid attack generated greater population growth rates due to escape from natural enemies. Whilst we caution that our analyses were unable to take other forms of top-down control into account it is plausible that this pattern arises in part because phenological advances are insufficient to completely avoid parasitoid attack, and that this simply occurs later during the aphid growth period. Indeed, top-down control of the aphid *Rhopalosiphum padi* is effective even when aphid emergence is advanced by two weeks (Fuchs *et al.* 2017). It is striking though that we find evidence that in models which take confounding factors into account, such as direct effects of weather, in years in which aphids emerging early, relative to parasitoid attack occurrence, population growth rates are reduced. Early emergence of aphids could generate higher aphid population densities at the time of parasitoid emergence which can facilitate host detection by parasitoids and increase attack rates (Walde & Murdoch 1988; Gunton & Pöyry 2016). Thus, aphids which emerge on trees much earlier than the occurrence of parasitoid attack may initially benefit from high population growth rates in a temporal refuge, but once parasitoids emerge the aphids could then suffer from high attack rates. Parasitoid-host relationships are, however, complex and varied. More detailed behavioural research on specific parasitoid species in this community is required to ascertain whether density-dependent attack rates explain the lower population growth when the gap between aphid emergence and parasitoid emergence is larger.

We find negligible evidence that population growth rates of *D. platanoidis* and *P. testudinaceus* are associated with direct impacts of weather. A recent meta-analysis of population growth in multiple UK taxa found that weather variables were driving population changes in a number of aphid species (Martay et al. 2016). Interestingly, however, this study included *D. platanoidis* and *P. testudinaceus* and found that whilst these aphids had positive population trends, monthly mean weather variables had negligible impacts on population growth rates. This is perhaps expected given that most temperate insect species, especially those in closed (rather than open) habitats experience temperatures that are well within their thermal limits (Deutch et al. 2008; Diamond et al. 2012; Sunday 2014). Therefore, although we find that both spring temperatures and summer temperatures vary by approximately 3.5°C degrees, this is not likely to cause extreme thermal stress which would limit fecundity and growth. Other studies do, however, suggest that warmer conditions enable many temperate insect species to increase the number of generations within an annual cycle (Yamamura & Kiritani, 1998). This mechanism may not apply to our focal aphid species as there is limited variation in the duration of the period during which either species was detected – with individuals being found in March and November even in the coolest years (See Table S12).

We uncover substantial variation across trophic levels in the precise nature of weather variables that drive spring phenology in a tri-trophic sycamore-aphid-parasitoid system over a 20 year time period. Notably, we find that spring emergence of woodland aphid species are delayed by warmer conditions in late winter (February), while the attack by their parasitoids is advanced by warming during January. Furthermore, weather later in the year, i.e. warmer springs, have a smaller influence on these phenological events. The climatic conditions driving insect phenology in this system thus appear to differ markedly from those determining the base trophic level, as sycamore bud burst is earlier when spring is warmer but does not respond to winter temperature. Climate change projections of warmer winter and spring conditions are thus likely to substantially alter the timing of trophic interactions in this system. Our data capture substantial variation in the timing of such interactions. Contrary to the expectation that phytophagous insects will exhibit reduced population growth as a result of phenological mismatch, aphid population growth rates appear to currently be resilient to delayed emergence relative to sycamore bud burst. This is at least partly due to strong buffering effects of density dependence. Climate change can weaken the effects of density dependence (Ouyang et al. 2014) and thus climatic shifts over the threshold experienced in this study period could exacerbate these weak mismatch effects and have a more demonstrable effect on aphid population growth. Aphid population growth rates are highest when their emergence is most closely matched with the timing of parasitoid attack, this apparent paradox may arise because the resultant lower density of aphid populations hinder the detection of aphid hosts. Aphid and parasitoid phenology appear to be responding to temperatures during different winter phases, respectively February and January, and thus the impacts of future climate change on aphid populations will in part be determined by the precise nature of seasonal variation in warming patterns.

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Data availability statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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