The forgotten season: the impact of autumn phenology on a specialist insect herbivore community on oak

ADAM EKHOLM,[1] AYCO J.M. TACK,[2] KJELL BOLMGREN[3] and TOMAS ROSLIN[1]   [1]Department of Ecology, Swedish University of Agricultural Sciences, Uppsala, Sweden, [2]Department of Ecology, Environment and Plant Sciences, Stockholm University, Stockholm, Sweden and [3]Unit for Field-based Forest Research, Swedish University of Agricultural Sciences, Lammhult, Sweden

Abstract. 1. Variation in spring phenology – like tree budburst – affects the structure of insect communities, but impacts of autumn phenology have been neglected. Many plant species have recently delayed their autumn phenology, and the timing of leaf senescence may be important for herbivorous insects.

2. This study explored how an insect herbivore community associated with *Quercus robur* is influenced by variation in autumn phenology. For this, schools were asked to record, across the range of oak in Sweden, the autumn phenology of oaks and to conduct a survey of the insect community.

3. To tease apart the relative impacts of climate from that of tree phenology, regional tree phenology was first modelled as a function of regional climate, and the tree-specific deviation from this relationship was then used as the metric of relative tree-specific phenology.

4. At the regional scale, a warmer climate postponed oak leaf senescence. This was also reflected in the insect herbivore community: six out of 15 taxa occurred at a higher incidence and five out of 18 taxa were more abundant, in locations with a warmer climate. Similarly, taxonomic richness and herbivory were higher in warmer locations.

5. Trees with a relatively late autumn phenology had higher abundances of leaf miners (*Phyllonorycter* spp.). This caused lower community diversity and evenness on trees with later autumn phenology.

6. The findings of the present study illustrate that both regional climate-driven patterns and local variation in oak autumn phenology contribute to shaping the insect herbivore community. Community patterns may thus shift with a changing climate.

Key words. Citizen science, climate change, community ecology, phenology, spatial ecology, temporal ecology.

Introduction

Climate change has advanced, and is predicted to further advance, phenology in a wide array of temperate organisms (Menzel *et al.*, 2006; Parmesan, 2007; Thackeray *et al.*, 2016). The rate of advance is expected to be unequally distributed among taxa and trophic levels (Thackeray *et al.*, 2016). Much research has thus addressed whether currently synchronised species interactions will stay synchronised in a warmer climate. Importantly, most of this research has been aimed at springtime

phenology (Visser *et al.*, 2012; Kudo & Ida, 2013; Schwartzberg *et al.*, 2014; Stålhandske *et al.*, 2016; Uelmen *et al.*, 2016). By contrast, effects of autumn phenology have been largely neglected, with only one-half to one-third as many papers dealing with autumn as with spring phenology (Gallinat *et al.*, 2015). Despite this, climate change is clearly affecting autumn phenology too: numerous tree species have delayed their autumn phenology (Menzel *et al.*, 2001; Kolarova *et al.*, 2014), with autumn leaf colouring of, for example, *Quercus robur* being delayed by 22 days between 1976 and 2010 (Kolarova *et al.*, 2014).

Trees show high intraspecific variation in spring and autumn phenology (Crawley & Akhteruzzaman, 1988; Vitasse *et al.*, 2009; Cole & Sheldon, 2017). Such differences show a

Correspondence: Adam Ekholm, Department of Ecology, Swedish University of Agricultural Sciences, Box 7044, SE-750 07 Uppsala, Sweden. E-mail: adam.ekholm@slu.se

substantial genetic component (Faticov *et al.*, 2019), and persist over time (Crawley & Akhteruzzaman, 1988). The timing of budburst has proved to be important in determining the herbivore damage on host plants, but also in affecting the occurrence and abundance of herbivorous insects (Crawley & Akhteruzzaman, 1988; Mopper & Simberloff, 1995; Sinclair *et al.*, 2015; Heimonen *et al.*, 2017). Similar effects could emerge in autumn, as intraspecific variation in autumn leaf coloration is well established (Crawley & Akhteruzzaman, 1988). In autumn leaves, the yellow colour is a result of nutrients being withdrawn from the senescing leaf, and as plant cells die the leaf is turning brown (Matile, 2000). From the perspective of herbivorous insects with a late seasonal ocurrence, a leaf with late autumn phenology will provide the herbivore with resources for a longer time, compared with a leaf with early autumn phenology (Connor *et al.*, 1994; Mopper & Simberloff, 1995). This implies that the decision regarding which tree to oviposit on could be of great importance for offspring survival, with added effects of the surounding landscape (Gripenberg & Roslin, 2005; Gripenberg *et al.*, 2007, 2008).

Not all species are likely to be equally affected by variation in the phenology of their host tree. For example, free-feeding insects and leaf miners mostly rely on the background level of nutrients available in the leaf. By contrast, gall producers manipulate their host plant to allocate nutrients and photoassimilate before autumn colour initiation, when the gall is developing (Stone *et al.*, 2002). Although some leaf miners are also known to affect leaf physiology and delay autumn leaf senescence (Engelbrecht *et al.*, 1969; Kaiser *et al.*, 2010), gallers as a guild can be expected to be less vulnerable to host plant autumn phenology than are other guilds such as free feeders and leaf miners.

Apart from climatically and genotypically determined variation in host tree phenology, temperature as such has an important role in determining the geographic distribution of insects. The performance and distribution of many species are limited by temperature, and it is reasonable to expect that areas with colder temperature generally hold fewer species (Parmesan *et al.*, 1999; Luoto *et al.*, 2006). Thus, one may expect lower species richness and lower abundances of insect species towards the northern distribution limit of a host tree species (Hardwick *et al.*, 2016).

In this study, we explored the influence of climate and oak autumn phenology on the community structure of gall wasps, leaf miners and free-feeding insects associated with *Q. robur* sensu lato. To this end, we designed a nationwide citizen science project, where we asked students to record the autumn phenology of individual oak trees and to conduct a survey of the insect herbivore community present on these trees. This allowed us to examine how regional variation in temperature and local variation in oak tree autumn phenology shape the plant-feeding insect community on oak. More specifically, we asked: (i) how does regional variation in climate affect oak autumn phenology and the distribution, local abundance and community structure of plant-feeding insects on oak; and (ii) how does local variation in oak tree autumn phenology shape the incidence and abundance of plant-feeding insects, and how is this reflected in the structure of the insect herbivore community?

Materials and methods

Study system

Among European trees, oaks in the family Fagaceae are known to host a particularly rich insect community, encompassing a wealth of taxa and guilds (Southwood, 1961; Southwood *et al.*, 2004, 2005). Sweden harbours two highly related oak species, the sessile oak *Quercus petraea* and the pedunculate oak *Q. robur*. Both species reach their northern limit in Sweden, where *Q. petraea* is mainly restricted to the coastal parts in southern Sweden and *Q. robur* is more common and found throughout the nemoral and boreonemoral vegetation zones (Stenberg & Mossberg, 2003). The two species frequently hybridise and their species limits are both genetically and morphologically ill-defined (Aas, 1993; Muir *et al.*, 2000); hence, we will treat them as the compound taxon *Q. robur* sensu lato. Notably, oak budburst can differ by up to 1 month among individuals within a population, with roughly equally large variation in leaf senescence (Crawley & Akhteruzzaman, 1988).

Of the oak-associated insect community, leaf miners, gall wasps and their associated parasitoids have received particular attention (Tack *et al.*, 2009, 2011; Kaartinen & Roslin, 2012), with most of these species being highly specific to oak (Coulianos & Holmåsen, 1991; Svensson, 1993). The galling and leaf-mining species are easy to find and collect in the field due to their sedentary life stage, and most species form characteristic leaf mines and galls which makes identification easy (Hering, 1957; Heath, 1983; Heath & Emmet, 1985; Redfern & Shirley, 2002).

Citizen science project

To assess how variation in oak phenology and temperature is reflected in the overall insect herbivore community structure, we aimed for a nationwide survey of oaks and oak-associated insects. For this purpose, we took advantage of a pre-existing citizen science project called 'Höstförsöket', organised by the Swedish National Phenology Network. Höstförsöket maintains a well-established network of collaborating schools across Sweden, involving students from pre-school to upper secondary school. Within this network, students have been reporting autumn phenological observations from different tree species since 2013. In the autumn of 2016, we added a sub-project, where we asked students to collect data on the phenology of individual oak trees and the oak-associated insect herbivore community (https://bit.ly/2HTJm0D). With the help of students, we were able to record oak phenology and survey insect communities across the full range of oak distribution in Sweden [latitude range, 55–60°N; annual mean temperature range in 2016, 5–9 °C (www.smhi.se); the range of annual accumulation of growing degree days, with 5 °C as the lower threshold (GDD5), 1402–1895 °C; Fig. 1].

Experimental design

For an oak tree to be included in the project, it had to be at least 5 m high, have a stem so thick that your fingers did not touch
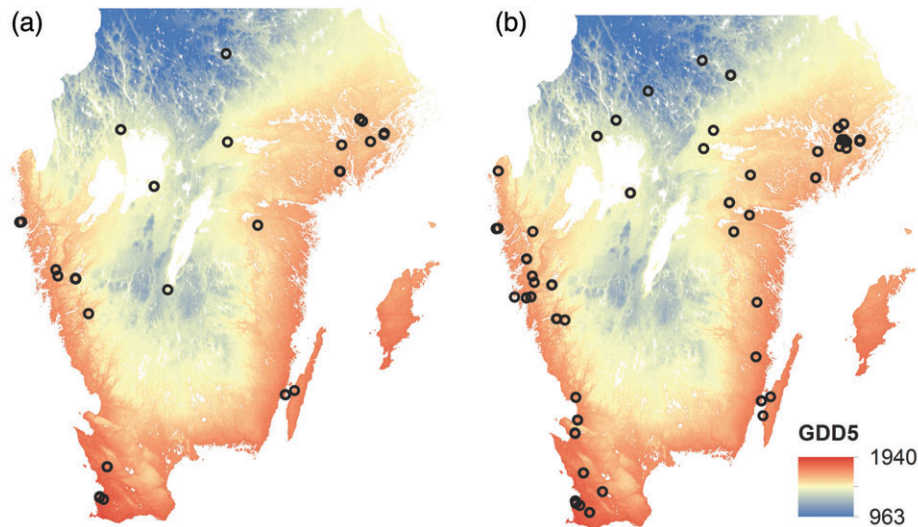
Fig. 1. Geographic location of the oak trees included in the study, with each tree represented by a circle. (a) Trees for which the autumn phenology was surveyed (*n* = 70); (b) trees where the insect herbivore community was surveyed (*n* = 127). The background colour of the maps represents the annual accumulation of growing degree days, with 5 °C as the lower threshold (GDD5). [Colour figure can be viewed at wileyonlinelibrary.com].

if you embraced the stem (minimum circumference *c*. 35 cm) and show no signs of disease or summer drought (with the latter criterion used to control for the simplest effects of tree quality due to other factors). Coordinates were obtained for most of the oaks included in the study. For oaks without coordinates, we estimated new coordinates by randomly placing the oak tree within an area of 400 × 400 m, with the main building of the school in the centre. In total, students surveyed autumn phenology on 70 oak trees (16 without coordinates; Fig. 1a; Table S1) and surveyed the insect herbivore community on 127 oak trees (41 without coordinates; Fig. 1b; Table S1). From these, 58 oak trees were surveyed for both autumn phenology and the insect herbivore community.

To investigate spatial and temporal patterns in oak phenology, students recorded the autumn phenology on oak trees by weekly collecting *c*. 20 haphazardly selected leaves, photographing them and submitting the photographs to the project web page (https://bit.ly/2qRkv6e). Leaves were then scored by a single researcher into two categories: presence of > or < 50% of green colour on a leaf. During autumn (late August to early November), each tree was visited between two and eight occasions.

To relate oak phenology to the insect herbivore community, students collected two insect samples: (i) a sample where as many leaf mines and galls as possible were collected for at least 20 min (referred to as sample 1); and (ii) a standardised sample of *c*. 250 haphazardly collected leaves (referred to as sample 2). To facilitate the identification of insects, we created an illustrated guide to common and easily identified insects associated with oak (https://bit.ly/2qQlGTw; Table S2). Sample 2 was scheduled to coincide with the time point when one-third of oak leaves were exhibiting autumn colours. This time point was estimated from an extensive dataset consisting of multi-year observations of autumn phenology (Arnell, 1923, 1927; Arnell & Arnell, 1930). After the sampling event, students placed the two samples in separate plastic bags and mailed them to the University of

Helsinki for species identification. Here, all the identification was done by three people jointly trained in recognising the species-specific morphological structure of galls and leaf mines (Hering, 1957; Heath, 1983; Heath & Emmet, 1985; Redfern & Shirley, 2002).

The first and second samples allowed us to estimate species richness for each tree, while sample 2 allowed us to determine the incidence and tree-level abundance of leaf miners and galls, species diversity, species evenness and herbivory (i.e. the proportion of leaves with damage from leaf miners, gallers or free-feeding herbivores). When measuring species abundances, diversity (Shannon–Wiener index) and species evenness (Pielou's evenness), we used the species-specific number of occupied leaves per tree rather than the exact number of individuals per tree [as the number of individuals on a single leaf can be very high for species like *Trioza remota* (Hemiptera: Triozidae) and *Neuroterus quercusbaccarum* (Hymenoptera: Cynipidae)]. Species incidence was estimated as the presence or absence of a species on an oak. For species richness we counted the total number of species found in samples 1 and 2 (with slight variation in the realised number of leaves examined in sample 2).

To investigate the effect of temperature on oak phenology and the insect herbivore community, we assessed the growing degree days (GDD) for each oak tree. The GDD measure is based on the specific temperature interval in which insect development can occur. The annual accumulation of degree days has proved to be a good indicator of spring phenology among insects (Cayton *et al.*, 2015). In northern Europe, a minimum threshold of 5 °C (from now on referred to as GDD5) for insect development is commonly used, whereas no upper threshold is usually needed in a temperate climate (Luoto *et al.*, 2006; Pöyry *et al.*, 2009; Hodgson *et al.*, 2011). In the context of trees, accumulated cold degree days will sometimes serve as the primary trigger of autumn phenology (Archetti *et al.*, 2013; Fu *et al.*, 2017; Yingying *et al.*, 2018), but importantly different metrics of growing

and cold degree days are typically highly correlated ($r > 0.9$; T. Roslin, unpublished). How the GDD5 metric behaves and what it reflects can be illustrated by a simple example. For a warm year, daily mean temperatures will quickly exceed the threshold value (+5 °C in our case) in spring, resulting in the start of temperature accumulation. Summer and autumn temperatures will continue to accumulate the temperature sum, until the daily mean temperature drops below the threshold value. At the end of the year, a high value of accumulated degree days will then represent a location with warm spring, summer and autumn temperatures. Because warm summers and autumns can postpone leaf senescence (Estrella & Menzel, 2006; Menzel *et al.*, 2008), the use of cumulative GDD will offer a good proxy of climatic influences on autumn phenology. We extracted GDD5 from a high-resolution microclimatic map over Sweden with 50×50-m grid cells (Meineri & Hylander, 2016, 2017).

Statistical methods

To investigate the contribution of climate and oak tree autumn phenology on the insect herbivore community structure, we used a two-step approach:

To characterise the relative phenology of trees (i.e. whether an individual tree has an early or late autumn phenology compared with trees growing under similar temperature conditions), we first modelled the overall phenology of oak trees across Sweden as a function of GDD5, Julian date and their interaction, with tree identity as a random factor. We then derived an estimate of the relative tree-specific phenology from the random intercept term of the resultant model. This value provided us with a continuous value of tree-specific autumn phenology as related to the average phenology of trees growing under similar temperature conditions – i.e. a metric of whether a specific oak tree was characterised by an early or late phenology, in comparison to other oak trees growing under the same temperature conditions. For clarity, we will henceforth refer to it as 'relative tree-specific phenology'.

In the second step of the modelling, we examined the effects of temperature and relative tree-specific phenology on the local insect herbivore community. For this, we modelled our response variables (species incidence, abundance, species richness, diversity, evenness, and herbivory) as a function of temperature (GDD5) and relative tree-specific phenology. These two values, relative tree-specific phenology and temperature, are not correlated with each other ($r = 0.015$, $n = 58$; $P = 0.91$) – i.e. they are orthogonal, as they should be if the effect of GDD5 on tree-level phenology has been successfully accounted for in the previous step of the modelling. What is left in our estimate of relative tree-specific phenology is the part of phenology not directly attributable to temperature. All of the analyses below were performed in R (R Core Team, 2017). In further detail, the respective modelling steps were implemented as follows.

Oak autumn phenology. To assess the relationship between temperature and oak autumn phenology, we modelled oak autumn phenology as a function of the continuous fixed effects temperature (GDD5), Julian date and their interaction, assuming a binomial distribution and a logit link. To account for repeated observations from the same tree, we included tree identity as a random effect. We fitted the model using a penalised quasi-likelihood method with the function 'glmmPQL' in the package MASS (Venables & Ripley, 2002). We assumed that the weekly observations of autumn colours were temporally autocorrelated, with subsequent observations being more similar to each other than observations in general. Therefore, we added a temporal correlation structure (corCAR1) from package NLME to the model, assuming that values were correlated with the previous observation but not beyond (Pinheiro *et al.*, 2017). Significance of the fixed effects was assessed using a Wald *t*-test (Bolker *et al.*, 2009). From this model, we extracted an estimate of tree phenology in the form of the tree-specific estimate of the random intercept term. This estimate offers a descriptor of the phenology of each tree, i.e. the deviation between the phenology of the focal oak tree and the mean phenology of trees growing under similar temperature conditions. Hence, this value allowed us to quantify the effect of phenology – and to distinguish between the effects of temperature and phenology in our analysis. As stated earlier, we refer to this random intercept term as 'relative tree-specific phenology'.

The effect of temperature and relative tree-specific autumn phenology on species-specific distribution, local abundance and insect herbivore community structure. We next modelled species incidence, abundance, species richness, diversity, evenness, and herbivory as a function of temperature (GDD5) and relative tree-specific phenology. Diversity was calculated using the VEGAN package (Oksanen *et al.*, 2017), and evenness was calculated following Pielou (1966). Given the difference in the number of replicates for each predictor (cf. Tables 1 and 2), we fitted several separate regression models. As species densities may also be affected by temperature, we included GDD5 as a covariate when modelling relative tree-specific phenology. This covariate will capture the effect of temperature on the insect herbivore community, beyond the effect mediated by relative host tree phenology.

Species incidence, species abundance, species richness, and herbivory were modelled with generalised linear mixed models, using a penalised quasi-likelihood method with the function glmmPQL in the package MASS (Venables & Ripley, 2002; Dormann *et al.*, 2007). Species diversity and evenness were modelled using generalised least-squares with the function gls in the package MASS (Venables & Ripley, 2002). To assess the significance of individual terms we again used a Wald *t*-test (Bolker *et al.*, 2009). Species incidence and abundance were modelled by a hurdle approach – first modelling incidence across the full set of data, then focusing on abundances for occupied trees only. Due to slight variation in the realised number of leaves examined per tree, we included the number of leaves as a covariate when modelling incidence. To account for spatial autocorrelation among oaks, we included a negative exponential correlation structure in all models using the function corExp from the NLME package (Pinheiro *et al.*, 2017). Thus, we assumed an exponential decay in similarity with a linear

Table 1. The effect of the annual accumulation of growing degree days, with 5 °C as the lower threshold (GDD5) on the incidence and abundance of leaf miners and gall wasps associated with *Quercus robur* in Sweden.

Functional group	Species	Number of trees present	Incidence			Abundance		
			t	d.f.	P	t	d.f.	P
Leaf miner	*Acrocercops brongniardellus*	20	−1.09	124	0.28	0.94	18	0.36
Leaf miner	*Bucculatrix ulmella*	69	2.71	124	0.01*	0.43	67	0.67
Leaf miner	*Caloptilia alchimiella*	51	3.68	124	< 0.01*	0.97	49	0.34
Leaf miner	*Coleophora* spp.	30	1.81	124	0.07	0.21	28	0.83
Leaf miner	*Ectoedemia albifasciella*	47	3.66	124	< 0.01*	2.84	45	0.01*
Leaf miner	*Phyllonorycter* spp.	126	_[a]	_[a]	_[a]	2.66	124	0.01*
Leaf miner	*Stigmella* spp.	119	_[a]	_[a]	_[a]	4.17	117	< 0.01*
Leaf miner	*Tischeria ekebladella*	63	0.51	124	0.61	1.82	61	0.07
Leaf miner	*Tischeria dodonaea*	12	1.07	124	0.29	2.41	10	0.04*
Leaf miner	*Profenusa pygmaea*	52	2.93	124	< 0.01*	−1.52	50	0.14
Leaf miner	*Orchestes quercus*	27	2.66	124	0.01*	1.54	25	0.14
Gall wasp	*Cynips divisa*	10	0.35	124	0.73	0.68	8	0.52
Gall wasp	*Cynips longiventris*	29	0.26	124	0.79	0.06	27	0.95
Gall wasp	*Neuroterus anthracinus*	121	_[a]	_[a]	_[a]	2.62	119	0.01*
Gall wasp	*Neuroterus quercusbaccarum*	89	1.46	124	0.15	0.55	87	0.58
Other	*Macrodiplosis dryobia*	27	0.48	124	0.63	−1.28	25	0.21
Other	*Macrodiplosis volvens*	25	2.35	124	0.02*	−0.40	23	0.70
Other	*Trioza remota*	113	−1.02	124	0.31	−1.62	111	0.11

[a]Species absent from fewer than 10 trees were excluded from incidence analyses (given the limited information content).
Shown are *t*-values, degrees of freedom (d.f.) and *P*-values from species-specific generalised linear mixed-effects models described in the text. Significant *P*-values are denoted with an asterisk.

Table 2. The effect of relative tree-specific phenology on the incidence and abundance of leaf miners and gall wasps associated with *Quercus robur* in Sweden.

Functional group	Species	Number of trees present	Incidence			Abundance		
			t	d.f.	P	t	d.f.	P
Leaf miner	*Bucculatrix ulmella*	27	1.60	54	0.12	0.90	24	0.38
Leaf miner	*Caloptilia alchimiella*	24	−1.21	54	0.23	−0.39	21	0.70
Leaf miner	*Ectoedemia albifasciella*	20	0.95	54	0.35	0.73	17	0.48
Leaf miner	*Phyllonorycter* spp.	57	_[a]	_[a]	_[a]	−2.75	54	0.01*
Leaf miner	*Stigmella* spp.	52	_[a]	_[a]	_[a]	0.12	49	0.90
Leaf miner	*Tischeria ekebladella*	31	−1.12	54	0.27	0.71	28	0.48
Leaf miner	*Tischeria dodonaea*	10	0.61	54	0.54	−2.06	7	0.08
Leaf miner	*Profenusa pygmaea*	26	0.75	54	0.46	0.01	23	0.99
Leaf miner	*Orchestes quercus*	14	−0.81	54	0.42	0.28	11	0.78
Gall wasp	*Cynips longiventris*	15	2.07	54	0.04*	−2.23	12	0.05*
Gall wasp	*Neuroterus anthracinus*	56	_[a]	_[a]	_[a]	0.14	53	0.89
Gall wasp	*Neuroterus quercusbaccarum*	2	1.18	54	0.24	0.11	39	0.91
Other	*Macrodiplosis dryobia*	14	−0.46	54	0.65	0.21	11	0.84
Other	*Macrodiplosis volvens*	10	0.20	54	0.84	0.17	7	0.87
Other	*Trioza remota*	54	_[a]	_[a]	_[a]	−1.21	51	0.23

[a]Species absent from fewer than 10 trees were excluded from incidence analyses, due to their limited information content.
Shown are *t*-values, degrees of freedom (d.f.) and *P*-values from species-specific generalised linear mixed-effects models. Significant *P*-values are denoted with an asterisk.

decrease in distance between sites, using the spatial location of the tree as coordinates. For species abundances and herbivory, we assumed a binomial distribution and a logit link, whereas for species richness we assumed a Poisson distribution and a log link. For species incidence we assumed a binary distribution and a logit link, and only included species that were present on or absent from at least 10 trees (as data on excessively rare or common species will essentially be devoid of information). Similarly, we only analysed species abundances for species that occupied at least 10 trees.
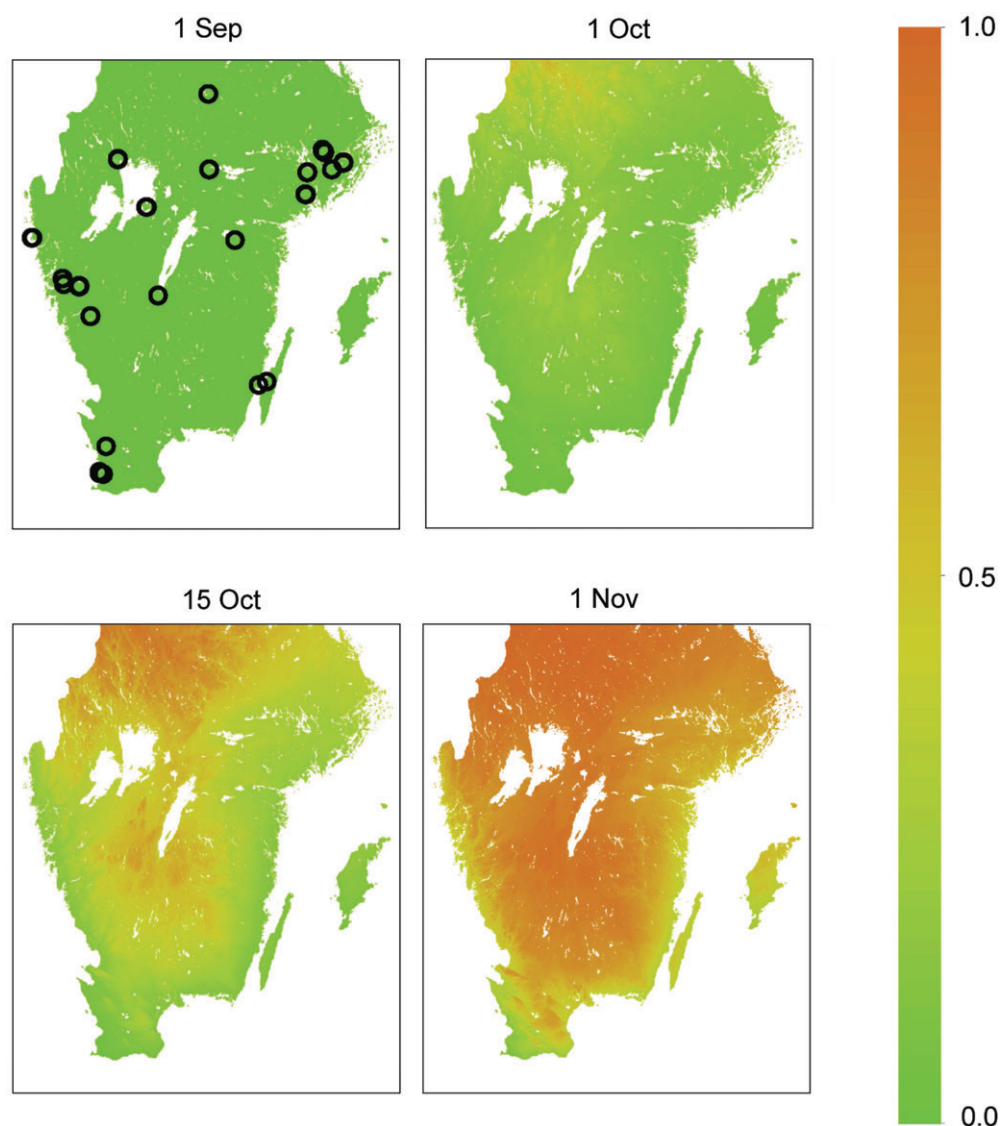
Fig. 2. The impact of date and GDD5 (annual accumulation of growing degree days, with 5 °C as the lower threshold) on the autumn phenology of *Quercus robur* in Sweden. Panels (a)–(d) show leaf senescence (probability of a leaf being < 50% green) at four time points in autumn. The circles in (a) represent original data points (see Fig. 1a), with interpolation based on the model presented in the text. [Colour figure can be viewed at wileyonlinelibrary.com].

Data availability

All data needed to replicate the analyses are available at the Dryad Digital Repository (provisional doi: 10.5061/dryad.n9f35h2).

Results

Oak autumn phenology

Leaf senescence increased through time (Julian date: $t_{270} = 15.14$, $P < 0.01$) and occurred earlier in colder areas (GGD5; $t_{68} = -2.74$, $P = 0.01$). Moreover, the impact of

temperature on autumn phenology became more pronounced over time ($t_{270} = -2.17$, $P = 0.03$) (Fig. 2).

The effect of temperature on species-specific distribution, local abundance, and insect herbivore community structure

For six out of 15 insect taxa, incidence within the oak range showed a positive relationship with GDD5 (Table 1). For species abundance where present, five out of 18 species showed a positive relationship with GDD5 (Table 1). Of the community level metrics, GDD5 had a positive effect on species richness ($t_{125} = 4.33$, $P < 0.01$; Fig. 3d). However, species diversity was not affected by GDD5 ($t_{127} = 1.47$, $P = 0.14$), and neither
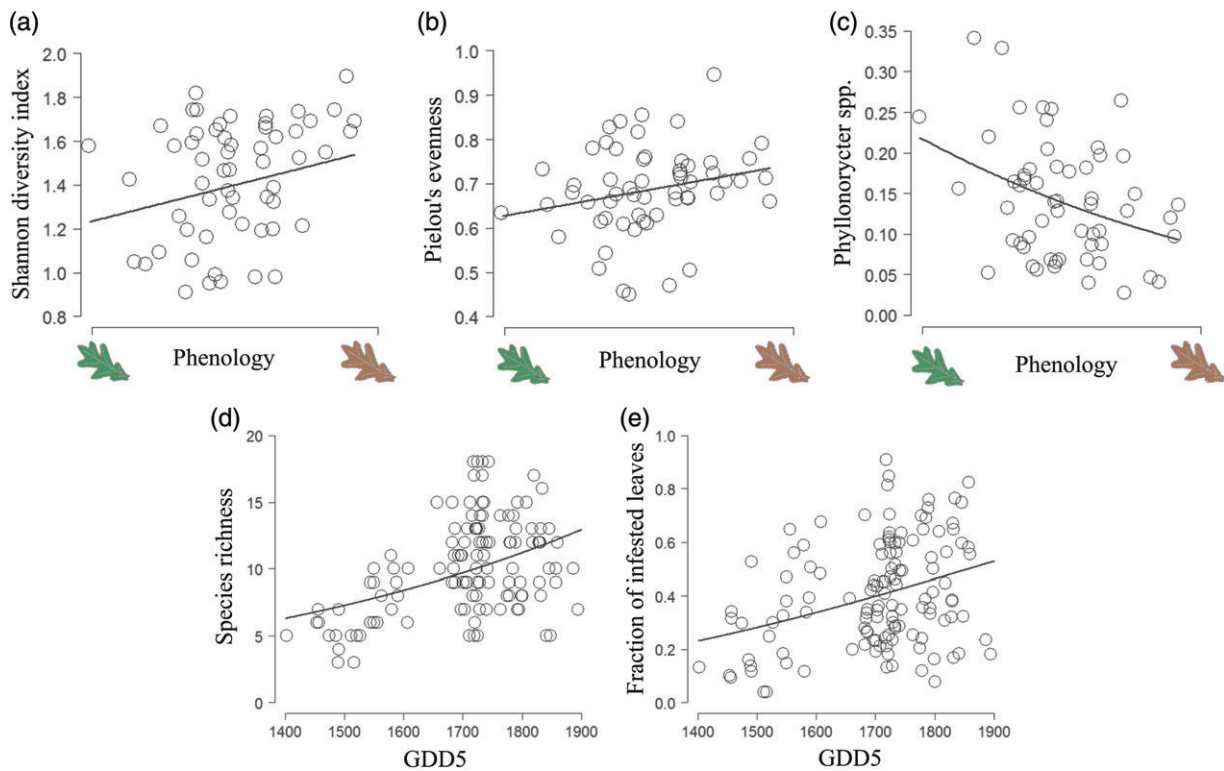
Fig. 3. The impact of relative tree-specific phenology and GDD5 (annual accumulation of growing degree days, with 5 °C as the lower threshold) on the oak insect herbivore community. (a–c) Deviation between the phenology of the focal oak tree and the mean phenology of trees growing under similar temperature conditions on species diversity (a), species evenness (b) and abundance (c) of *Phyllonorycter* spp. (d, e) Impact of GDD5 on species richness (d) and the fraction of leaves infested by leaf-mining, free-feeding or galling herbivores (i.e. herbivory) (e). Shown are raw data with model-estimated trend. [Colour figure can be viewed at wileyonlinelibrary.com].

was species evenness ($t_{127} = -1.20$, $P = 0.23$). Finally, we found that GDD5 showed a positive relationship with herbivory ($t_{125} = 3.92$, $P < 0.01$; Fig. 2e).

The effect of relative tree-specific autumn phenology on species-specific distribution, local abundance, and insect herbivore community structure

The gall wasp *Cynips longiventris* (Hymenoptera: Cynipidae) had a higher incidence on trees with relatively early phenology, whereas no effect was detected for the remaining 14 species (Table 2). We found higher numbers of the leaf miner *Phyllonorycter* spp. (Lepidoptera: Gracillariidae) and *C. longiventris* on trees of relatively late phenology (Fig. 3c), whereas no effect of phenology on species abundance was detected across the remaining 13 species (Table 2). Of the community-level metrics, we found higher species diversity on trees of relatively early phenology ($t_{58} = 2.72$, $P = 0.01$; Fig. 3a). Similarly, species evenness was higher on trees of relatively early phenology ($t_{58} = 1.88$, $P = 0.07$; Fig. 3b), whereas species richness did not vary significantly with host tree phenology ($t_{55} = 0.31$., $P = 0.75$). Finally, we found no effect of host tree phenology on herbivory ($t_{55} = -0.17$, $P = 0.86$).

Discussion

To our knowledge, this is the first study to relate insect herbivore community structure to the autumn phenology of host trees. Overall, we found that leaves stayed greener for a longer time in locations with a warmer climate, with substantial variation among individual trees. Across Sweden, six out of 15 species proved more common, and five out of 18 species were more abundant, at locations with a warmer climate. Similarly, herbivory and species richness were higher at warmer sites. Against this backdrop, we found higher species diversity and species evenness on oak trees with relatively early autumn phenology. At the level of herbivorous insect species, the specific phenology of a host tree had the clearest effect on the abundance of the leaf miner *Phyllonorycter* spp., which was more abundant on trees of relatively late phenology.

Oak tree autumn phenology

We found oak autumn phenology to covary with climate at a large spatial scale. Several studies have demonstrated the importance of temperature-related factors as triggers of autumn phenology (Estrella & Menzel, 2006; Archetti *et al.*, 2013; Fu *et al.*, 2017; Yingying *et al.*, 2018). Some studies have proved temperature as such to be especially important

in comparison to other factors regulating autumn phenology. Yingying *et al.* (2018) found that cold autumns (accumulation of cold degree days) had a stronger effect on autumn phenology compared with other climate/weather variables. Similarly, Fu *et al.* (2017) found that the autumn phenology of *Fagus sylvatica* (Fagaceae) was mainly controlled by temperature, when not limited by nutrients or water. In addition, studies have detected a delay in the autumn phenology of several tree species in recent years (Menzel *et al.*, 2008; Kolarova *et al.*, 2014), suggesting a general effect of climate warming.

Clearly, the current pattern observed across 520 km may also reflect variation in the genetic make-up of the oak population, including patterns of local adaptation. Yet, genetic variation in the Swedish oak population has been thoroughly reshuffled by geological history. During the Pleistocene, oaks were restricted to three refugia in southern Europe: Iberia, Italy, and the Balkans (Brewer *et al.*, 2002; Petit *et al.*, 2002a). At the end of the latest glacial period, oak populations from these refugia gradually expanded northwards and occupied different parts of Europe (Petit *et al.*, 2002a,b). In Sweden, the genetic material is dominated by haplotypes originating from Iberia and Italy, and there are no clear patterns in the geographic structure of these haplotypes (Jensen *et al.*, 2002; Petit *et al.*, 2002b).

Therefore, based on the existing literature and our results, it seems likely that the autumn phenology of *Q. robur* is based on well-mixed genetic variation across the overall population, with an added ingredient of phenotypic plasticity. With ongoing climate change, oaks across Sweden are then likely to delay their autumn phenology. Such a delay will most likely leave an imprint on the insect herbivore community.

Large-scale patterns in the insect herbivore community

In our study, species showed variable responses to temperature: species were either unaffected by temperature (e.g. *Acrocercops brongniardellus*, *Coleophora* spp., *Cynips longiventris*) or became more common or abundant (e.g. *Stigmella* spp., *Phyllonorycter* spp., *Neuroterus anthracinus*) towards warmer areas. Similarly, both species richness and herbivory were higher in warmer areas. Previous studies have identified the length of the growing season as an important environmental driver of species distribution (Parmesan *et al.*, 1999; Luoto *et al.*, 2006). As the length of the growing season is expected to increase with climate change, oak-associated species may become more abundant in places where they are now rare, and overall herbivory may also increase. Yet species-specific changes may be conditional on species-specific traits, including traits related to temperature, such as the lower thermal threshold of each species. For instance, low winter temperatures can sometimes cause high mortality for hibernating species (Battisti *et al.*, 2005; Jepsen *et al.*, 2008), but also affect a species' ability to feed (Battisti *et al.*, 2005; Jepsen *et al.*, 2008). Apart from temperature, other traits, such as mobility, host plant and habitat preferences, could mediate range expansions (Pöyry *et al.*, 2009).

The impact of oak tree autumn phenology on the insect herbivore community

Previous studies have demonstrated an important role of host tree spring phenology in shaping the insect community. Such variation has been shown to be important for both spring generations of leaf miners and gall wasps, but also for autumn generations of gall wasps (Crawley & Akhteruzzaman, 1988; Mopper & Simberloff, 1995; Sinclair *et al.*, 2015). Yet, because autumn phenology has not been separately addressed, imprints of spring phenology could, to an unknown extent, reflect covariance in the spring versus autumn phenology of individual oaks.

In the current study, we found an effect of relative autumn phenology on incidence for one (*C. longiventris*) out of 11 species, and an effect of abundance for two (*C. longiventris*, *Phyllonorycter* spp.) out of 15 taxa. In terms of emergent community properties, we found that species diversity and species evenness were higher for trees with relatively early autumn phenology. This association was most likely to be explained by the most abundant species in the dataset (*Phyllonorycter* spp.), which dominated the community on 62 out of 127 oak trees. *Phyllonorycter* spp. was more abundant on trees with a relatively late autumn phenology, thus affecting patterns in species diversity and community evenness. The mechanisms behind the higher abundance of *Phyllonorycter* spp. on trees with relatively late autumn phenology are so far unknown, but circumstantial evidence may shed some light: in relation to the other leaf miners included in this study, *Phyllonorycter* spp. larvae can stay active up to a month longer in the autumn (Svensson, 1993). Female *Phyllonorycter* spp. should therefore benefit from ovipositing on a food resource that will maintain high quality throughout the autumn. In the leaf miner *Cameraria hamadryadella* (Lepidoptera: Gracillariidae), years with relatively early leaf fall caused a dip in larval survival, and following a year with late autumn phenology, the abundance of *C. hamadryadella* could increase 10-fold compared with the abundance of the previous autumn population (Connor *et al.*, 1994). Similarly, Mopper and Simberloff (1995) showed that early leaf abscission was a major source of late-instar mortality in the leaf miner *Stilbosis quadricustatella* (Lepidoptera: Cosmopterigidae). In addition, previous studies have demonstrated a hump-shaped relationship of both herbivory and leaf miner abundance with leaf life span – where fully deciduous and evergreen trees tend to be less infested (Pearse & Karban, 2013; Zhang *et al.*, 2017). This implies that, for some herbivores, the decision of which tree to oviposit on – a tree with early versus late autumn phenology – could be of great importance for offspring survival.

As an important distinction between the inference of Connor *et al.* (1994) and the current study, we note that Connor *et al.* (1994) were explicitly concerned with how year-to-year variation affects the abundance of *C. hamadryadella*. In our study, we focus on spatial variation in autumn phenology, and explicitly assume that differences in phenology observed during a single year offer an indication of long-term differences in relative phenology – as supported by persistent changes among oak trees and genotypes within oak stands (Faticov *et al.*, 2019; Crawley & Akhteruzzaman, 1988). Thus, the effects

examined by Connor *et al.* (1994) reflect phenotypic plasticity alone (as being related to temporal variation within the same oak individuals), whereas in the setting of our study, changes in oak phenology with climate change are likely to reflect both phenotypic plasticity and evolutionary change within the oak population.

As hypothesised *a priori*, we found little effect of relative tree-specific phenology on the gall wasps included in the study. It is likely that gall wasps are able to manipulate host plant allocation of resources to the gall early in the autumn, when the host plant is still of high quality. Furthermore, of our focal taxa, both *N. quercusbaccarum* and *Neuroterus anthracinus* are known to drop to the ground before the leaf falls of the tree, and should therefore not be as strongly affected by autumn phenology as are other gall wasps (Coulianos & Holmåsen, 1991). Overall, the occurrence and abundance of the gall wasp species presented in this study might be more affected by spring phenology than by autumn phenology. In previous studies, both Crawley and Akhteruzzaman (1988) and Sinclair *et al.* (2015) found that the autumn generation of *N. quercusbaccarum* preferred oak trees with late spring phenology, whereas no relationship was found for the autumn generation of *N. anthracinu*s (Sinclair *et al.*, 2015). One species, *C. longiventris*, did show a positive response to later leaf senescence. This is a species that drops to the ground attached to the leaf blade, and which may thus potentially benefit from a continued nutrient supply in the autumn (Coulianos & Holmåsen, 1991). Overall, differential effects of host phenology on gallers and leaf miners, and potential differences in spring versus autumn effects, bode for interesting changes in community structure with progressing climate change.

Overall herbivory in a warming climate

We found that warmer locations experienced higher herbivory (a higher fraction of herbivore-infested leaves). This is in line with large-scale latitudinal patterns in the northern hemisphere (Zhang *et al.*, 2016) and warming experiments (Liu *et al.*, 2011; Birkemoe *et al.*, 2016; but see Lemoine *et al.*, 2014). Interestingly, an increase in the herbivory as a response to higher mean temperature is also supported by the higher folivory rates observed during warmer geological periods (Currano *et al.*, 2008; Wilf, 2008).

Regional patterns in temperature did not reflect patterns of relative tree-specific phenology: across Sweden, warmer sites had both later autumn phenology and higher total herbivory, whereas no effect of relative tree-specific phenology on tree-level herbivory could be discerned. Thus, the observed increase in herbivory at warmer locations could be a result of higher herbivore abundance and species richness rather than an effect mediated by large-scale variation in phenology *per se*.

Conclusions

In the context of climate change, it is essential to assess how direct and indirect effects of changes in the abiotic environment influence individual species and local communities. In this study, we reveal an impact of temperature on a key host tree and its associated insect herbivore community. We show that temperature affects both the autumn phenology in *Q. robur* and the distribution, species richness, and herbivory among its associated insects. Importantly, we also demonstrate an imprint of relative host tree autumn phenology on the local community structure. Overall, we tentatively suggest that species will expand their geographic distribution and increase in abundance as a response to a warmer climate, and that this range expansion together with increased consumption rates will result in higher herbivory. Finally, as most studies to date have focused on the impact of spring phenology on local insect communities, we hope that our contribution will stimulate more studies spanning both spring and autumn phenology, thus resolving the relative impact of the two.

Author contributions

All authors contributed to designing and implementing the citizen science project. AE analysed the data with support from TR and AT. AE wrote a first version of the manuscript and all authors contributed to further revision.

Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. A list of all 139 trees included in the study with information about their location, and what surveys were done on each tree. The insect survey refers to trees where the insect community was sampled, whereas the phenology survey refers to trees where oak leaves were photographed during the autumn to assess oak autumn phenology.

Table S2. A list of the 33 insect taxa encountered in the study.

Table S3. A list of Swedish schools participating in the citizen science project. Each school sampled one or several oak insect herbivore communities and recorded oak phenology on one or several trees (with the exception of nine of the schools listed, for which the data were unfortunately lost).

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