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Seasonal interactions between oaks and insects

Evolutionary adaptations and predictions for climate
change

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change

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Abstract

Many species are expected to advance their phenology in response to global warming. As some interactions are dependent on the interacting species being synchronized in time, it is important to assess whether species shift their phenology in synchrony or not. Whether or not they do will dictate how communities and ecosystem functioning respond to climate change. Species-specific phenological responses could shift interaction strengths, with possible consequences for species fitness. In the context of a community of interacting species, phenological shifts can modify the interaction network and allow new interactions to occur and cause old interactions to disappear. In addition, if populations are locally adapted to temperature, then local communities might differ in their phenological response.

In this thesis, I aim to explore how temperature influence the phenology of different species and populations and how this is reflected in the structure of a community. To this aim, I focus on a tri-trophic community consisting of *Quercus robur*, its insect herbivores and associated parasitoids. I assess i) how temperature influence spring phenology of acorns and insects associated with *Q. robur* ii) how temperature influence the spring and autumn phenology of *Q. robur*, and whether oak genotypes differ in their response, and iii) how variation in *Q. robur* phenology is reflected in the structure of the insect community.

I detected that both species and populations differed in their response to temperature. I also found that overwintering temperatures influenced the timing of bud burst in *Q. robur*. In autumn, warm temperatures in spring advanced phenology, while leaf coloration was delayed for *Q. robur* growing at warmer locations. Interestingly, both the timing of spring and autumn phenology influenced the structure of the herbivore community, while *Q. robur* phenology had no detectable impact on the performance of herbivores in summer.

Overall, my findings suggest that temperature-induced changes in phenology can alter the temporal overlap between species, and that such changes affect the community structure. If the population-specific responses to temperature observed here extend widely across species, then local communities will differ in their response to temperature. With a changing climate, these patterns may result in changes in community structure for species active in spring and autumn, with different responses among local communities. This complicates current predictions regarding the biotic responses to ongoing climate change.

Keywords: Community ecology, Phenology, Temporal dynamics, Climate change, Citizen Science, Trophic interactions, Phenological mismatch.

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Årstidsbundna interaktioner mellan ekar och insekter

Sammanfattning

Den globala uppvärmningen gör att många arter kommer att förskjuta sin fenologi. Eftersom att en del interaktioner behöver vara synkroniserade i tid för att inträffa, så behöver växelverkande arter förskjuta sin fenologi i samma takt för att inte komma i otakt med varandra. Om arter kommer i otakt kan det få konsekvenser på fortplantningsframgången hos båda arter. Dessutom kan arter börja växelverka mer med andra arter, vilket kan leda till att nya interaktioner uppstår och att strukturen på artsamhället förändras. Därtill kan också arter vara lokalt anpassade till sin miljö, vilket betyder att populationer kan förskjuta sin fenologi i olika mån. Detta kan resultera i att lokala artsamhällen reagerar olika på temperaturförändringar.

I denna avhandling undersökte jag vilken inverkan temperatur har på olika arters och populationers fenologi, och hur detta avspeglar sig i strukturen på artsamhället. För att undersöka detta använder jag mig av ett artsamhälle bestående av tre trofiska nivåer: *Quercus robur*, dess växtätande insekter och associerade parasitoider. Sedan bedömde jag i) vilken inverkan övervintringstemperatur har på vårfenologi hos ekollon av *Q. robur* och dess insekter, ii) hur temperaturen påverkar vår- och höstfenologi hos olika genotyper av *Q. robur*, och iii) hur variation i ekfenologi påverkar insektsamhället.

Jag upptäckte att både arter och populationer reagerade olika på variation i temperatur. Övervintringstemperaturer hade en effekt på fenologi hos både *Q. robur* och dess insekter. Varmare temperaturer på våren tidigarelade höstfenologin hos *Q. robur*, medan ekar som växte på varmare lokaler hade en senare höstfenologi. Både vår- och höstfenologin hade en inverkan på artsamhället, medan ekätande insekter aktiva under sommaren var mindre påverkade av ekfenologi än de som var aktiva under våren och hösten.

Sammanfattningsvis tyder mina resultat på att växelverkande arter kan komma i otakt med varandra och att detta kan få betydande konsekvenser för artssamhället. Därtill kan även temperaturen modifiera fenologin olika mycket hos populationer, vilket kan göra att lokala artsamhällen reagerar olika på en förskjutning i fenologi. Detta innebär att de pågående klimatförändringarna kan ha speciellt stor inverkan på artsamhällen aktiva under vår och höst, och att effekterna kan skilja sig mellan lokala artsamhällen.

Nyckelord: Samhällsekologi, Fenologi, Temporal dynamik, Klimatförändringar, Medborgarforskning, Trofiska interaktioner, Fenologisk mismatch

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Dedication

To everyone that has supported me in producing this thesis

You miss 100 percent of the shots you never take.

Wayne Gretzky

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List of publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

- I **Ekholm, A***. Faticov, M. Tack, AJM. Berger, J. Stone, GN. Vesterinen, E. and Roslin, T. Community phenology of insects on oak – local differentiation along a climatic gradient (submitted).
- II **Ekholm, A***. Tack, AJM. Pulkkinen, P. and Roslin, T. (2020). Host plant phenology, insect outbreaks and herbivore communities – The importance of timing. *Journal of Animal Ecology* (89), 829-841.
- III **Ekholm, A***. Faticov, M. Tack, AJM. and Roslin, T. Herbivory in a changing climate – effects of specific leaf age do not extend into the summer season (manuscript).
- IV **Ekholm, A***. Tack, AJM. Bolmgren, K. and Roslin, T. (2019). The forgotten season: the impact of autumn phenology on a specialist insect herbivore community on oak. *Ecological Entomology* (44), 425-435.

Papers II and IV are reproduced with the permission of the publishers.

* Corresponding author

The contribution of Adam Ekholm to the papers included in this thesis was as follows:

- I Sampled insects, acorns and conducted the experiment with MF. Analysed the data, and lead the writing of the paper.
- II Conducted the experiment. Analysed the data and lead the writing of the paper.
- III Conducted the experiment with MF. Analysed the data and lead the writing of the paper.
- IV Designed and conducted the project together with co-authors. Analysed the data and lead the writing of the paper

1 Introduction

1.1 Are species losing track of their environment?

In temperate climates, it is important for species to stay in tune with their environment. By keeping track of environmental cues, such as temperature, species can become active when conditions are favourable in spring and decrease activity in autumn when conditions are less favourable. However, as environmental cues are expected to change with global warming, they might become less accurate in predicting favourable conditions. As a consequence, species could become less synchronized with their environment. This could for instance result in plants flowering before pollinators are active, or insect herbivores becoming active before leaf out in trees. To assess consequences of climate change on species interactions, we therefore need to understand how species shift their phenology¹ in response to new environmental conditions. In this thesis, I aim to explore how temperature influence the phenology of different species and populations and how this is reflected in the structure of a community.

1.2 What determines phenology?

To understand how species shift their phenology, it is necessary to identify the cues influencing phenology and how they are expected to shift in response to climate change. Studies have demonstrated that cues such as temperature, photoperiod and precipitation are important in determining the phenology of

1. Phenology is defined according to Lawrence (2011) as the “recording and study of periodic biological events, such as flowering, breeding and migration, in relation to climate and other environmental factors”. Phenological events occur frequently, especially in temperate habitats with pronounced seasons. Examples of phenological events are emergence of insects, leaf senescence in trees, calving period of ungulates and migration of birds.

organisms (e.g. Lindestad *et al.*, 2019; Cohen *et al.*, 2018; Flynn & Wolkovich, 2018; Salis *et al.*, 2018; Vitasse & Basler, 2013; Bradshaw & Holzapfel, 2007; Menzel *et al.*, 2006; Roy & Sparks, 2000). As temperature gradually increase and day length becomes longer in spring, these cues serve as good indicators signalling when conditions are suitable to become active after a cold winter. Similarly, shorter and colder days in autumn signals that organisms should prepare for winter. In areas with more stable temperature and photoperiod, such as the tropical and subtropical zones, other cues such as precipitation are more important in determining phenology (Cohen *et al.*, 2018). Since temperature is expected to increase in the near future and it has a large impact on species phenology, it is of particular interest to understand how this cue influences phenology.

1.2.1 Phenology and temperature

Warmer temperatures usually advance spring phenology in a wide range of organisms (Thackeray *et al.*, 2016), but can also delay autumn phenology (Zohner & Renner, 2019; Fu *et al.*, 2018). Several studies have already detected an effect of global warming on phenology (e.g. Kharouba *et al.*, 2018; Menzel *et al.*, 2006; Roy & Sparks, 2000). However, understanding to what extent different species might shift their phenology is more complex. For example, warm temperatures in spring usually advance phenology (i.e. “forcing”), while warm temperatures in winter can have the opposite effect and delay spring phenology. This is believed to occur because many species require a certain amount of cold days in winter, also called “chilling period”. If individuals are exposed to insufficient chilling days, they become less responsive to warm temperatures in spring (Flynn & Wolkovich, 2018; Stålhandske *et al.*, 2017; Laube *et al.*, 2014; Bosch & Kemp, 2003). In fact, leaf unfolding in trees has become less responsive to climate warming, a phenomenon which has been attributed to a reduced chilling period during warm winters (Fu *et al.*, 2015). However, it might also be related to a higher heat requirement for leaves to unfold earlier in season when the photoperiod is shorter (Fu *et al.*, 2019).

1.2.2 Phenological response among species

Species can differ in their response to temperature and shift their phenology at different rates (Cohen *et al.*, 2018; Kharouba *et al.*, 2018; Thackeray *et al.*, 2016). There are several reasons for this. First, species can differ in the cues they respond to, and how strongly they respond. For example, some species are highly responsive to forcing and chilling temperatures, while others are more sensitive

to chilling and photoperiod (Flynn & Wolkovich, 2018). Secondly, species can be sensitive to temperature during different parts of the year (Senior *et al.*, 2020; Tansey *et al.*, 2017). As global warming can increase temperature unevenly throughout the year (Renner & Zohner, 2018), this could result in different responses among species. Thirdly, certain characteristics of species traits such as body size and thermoregulation (ectotherm vs. endotherm) have been shown to influence phenology, where ectothermic species and species with low body mass are generally more sensitive to temperature (Cohen *et al.*, 2018). An unequal response to temperature could be problematic for species that need to overlap in time to interact, as it can shift the interaction strength and with whom a species interact. Therefore, assessing how interacting species will shift their phenology in relation to each other is essential in understanding how species interactions might change in the future.

1.3 Are species becoming mistimed?

1.3.1 Changes in mean phenology

A diversity of interactions across several taxa are vulnerable to becoming mistimed in their phenology (Box 1). A shift in temporal overlap between interacting species, a phenological mismatch (fig. 2B), could influence the performance of higher trophic levels, with possible consequences on fitness (Burgess *et al.*, 2018; Doiron *et al.*, 2015; Plard *et al.*, 2014; Both *et al.*, 2009; Post & Forchhammer, 2008; Edwards & Richardson, 2004; Tikkanen & Julkunen-Tiitto, 2003; Visser *et al.*, 1998). Among these interactions, plant – pollinator interactions provide an illustrative example of an interaction that could suffer from becoming phenologically mismatched: plants benefit from flowering when pollinators are active. If plants and pollinators respond differently to environmental cues, they could slide out of synchrony with each other and interact less frequently. As a consequence, pollinators might be left without nectar resources and plants without pollinators. Apart from becoming mismatched, species can also become more synchronised in their phenology, strengthening the interaction (Liu *et al.*, 2011). Nonetheless, understanding how phenological synchrony between species will change is difficult. In a meta-analysis covering phenological synchrony in 54 interactions, Kharouba *et al.* (2018) found that over recent decades species interactions have shown a multitude of responses, with some interactions increasing, others decreasing and some showing no detectable change in synchrony. Beyond changes in the mean phenology, temperature can also modify the phenological distribution (i.e.

within-population variation in phenology). This could impact the interaction strength among species, which is discussed below.

Box 1. Interactions vulnerable to a phenological mismatch.

Several types of interactions are vulnerable to becoming phenologically mistimed with their interaction partner, with potential knock-on effects on species' fitness. Below are three examples:

Larvae of the winter moth *Operophtera brumata* feeding of *Q. robur* needs to match bud burst of *Q. robur*. Timing is essential for the larvae. Emerging before buds have broken can lead to starvation, while feeding on old leaves results in a higher mortality, a lower weight, and less fecund individuals (fig. 1A; Tikkanen & Julkunen-Tiitto, 2003).

Warmer springs advance caterpillar phenology more than egg-laying date of the great tit *Parus major*. This can reduce prey availability for *P. major* at the time when great tits need to raise their young (fig. 1B; Visser *et al.*, 1998).

The roe deer *Capreolus capreolus* benefit from giving births to their young in synchrony with the emergence of nutritious vegetation in spring. The nutritious vegetation is needed, because a lot of energy is required for mammals to produce milk (Gunn & Skogland, 1997; Cluttonbrock *et al.*, 1989). In recent years, vegetation phenology has advanced, but the timing of birth in *C. capreolus* has not. Therefore, in years with a mismatch between vegetation phenology and birth date, fawn survival has decreased. This has resulted in a reduced population growth rate and fitness of females (fig. 1C; Plard *et al.*, 2014).

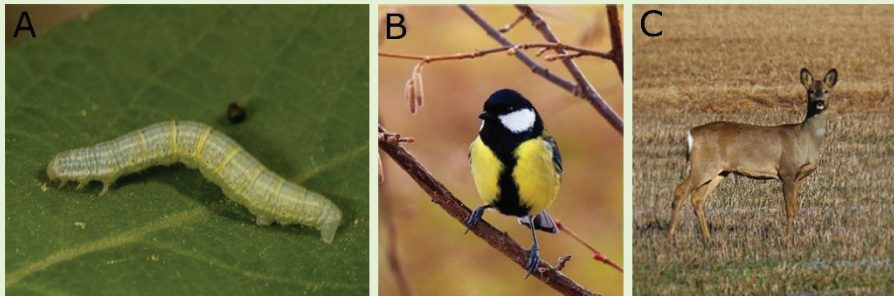


Figure 1. Three species that could slide out of synchrony with their respective resources in a warmer climate: A) The winter moth, B) Great tit and C) Roe deer. Photo: A) Kimmo Silvonen, B-C) Ola Borin

1.3.2 Changes in phenological distribution

A change in the distribution around mean phenology could also shift the temporal overlap between species (fig. 2; Linden, 2018). As an example, intraspecific variation in leaf unfolding can be higher in warmer climates (Zohner *et al.*, 2018). For herbivores specialized on feeding on an ephemeral resource such as young leaves, a higher variation in leaf unfolding among individual plants will make the resource available over a longer time span, but at a lower frequency. If the resource demand of the herbivore is low, then a wider distribution will likely buffer the species from a mismatch (fig. 2C). However, a high resource demand of the herbivore will likely be negative for the herbivore, as the resource is available at a lower frequency (fig. 2D). To understand how species interactions change with a shift in temperature, it is therefore important to understand changes in both the mean phenology and in the distribution around the mean.

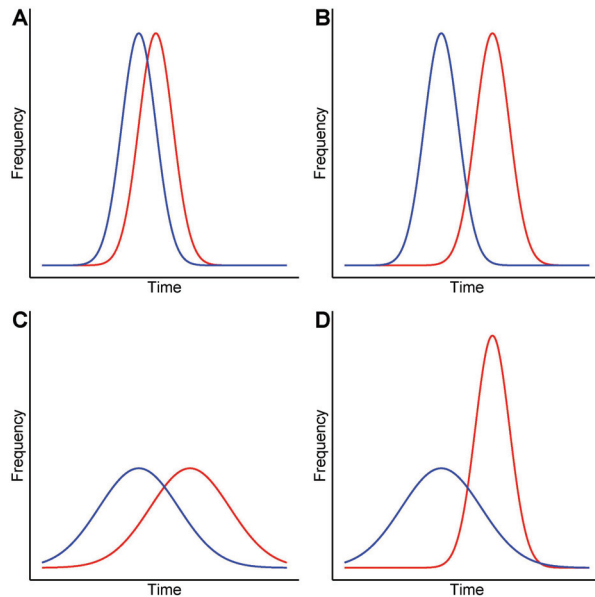


Figure 2. The phenological synchrony between a resource (blue line) and a consumer (red line) in ambient climate (A) and in three scenarios with elevated temperature (B, C, D). In the ambient climate (A), the consumer and the resource are in synchrony and can interact. In scenario B, species has become desynchronized, with only a small fraction of the populations overlapping and being able to interact. In C, the mean phenology has shifted as in scenario B, but the higher intraspecific variation in phenology buffer species from a mismatch. In scenario D, the mean phenology has shifted as in scenario B, but intraspecific variation in the phenological occurrence of the resource is larger than in the occurrence of the consumer. Here, species overlap in time, but high numbers of consumers results in a high demand on a resource occurring at a low frequency.

1.3.3 Phenological synchrony among genotypes

Apart from keeping up synchrony between two species, some consumer might depend on being synchronized with certain host genotypes. For instance, many insect herbivores benefit from feeding on fresh leaves in spring, because young leaves are nutritious and have a weak leaf surface (Falk *et al.*, 2018; Salminen *et al.*, 2004; Feeny, 1970). Plant genotypes can differ in their timing of leaf unfolding (Vitasse *et al.*, 2013), but also in other traits such as concentration of defensive compounds and nutrition (Falk *et al.*, 2018; Barbour *et al.*, 2015), making them more or less susceptible to herbivores. Therefore, a temperature-induced shift in synchrony between a given plant genotype and its herbivores could result in reduced synchrony in time, but an increased synchrony with alternative plant genotypes (yielding a genotype x environment interaction). As herbivore performance can differ among genotypes, the new interaction might then influence the performance of both the herbivore and the plant genotype. To date, few studies have investigated such an interactions between genotypes and shifts in the environment.

1.4 Are populations adapted to local environmental cues?

Species that occur across a broad range of climates are, per definition, exposed to different environmental conditions. To optimize the phenology in each climate, it is likely that species adapt to local environmental conditions. In fact, local populations, and/or different genotypes within a species, have been shown to differ in their phenological response to temperature (Valdes *et al.*, 2019; Stålhandske *et al.*, 2014; Vitasse *et al.*, 2013). If populations are locally adapted in their phenology, then interacting species will display different phenological responses to temperature, depending on their genetic makeup. Therefore, to fully understand how phenological synchrony between interacting species respond to temperature, it is necessary to assess how species interactions change across climatic gradients.

1.5 Could shifts in phenology alter community structure?

In a community context, shifts in phenological synchrony between interacting species could influence community structure (Korosi *et al.*, 2018). If two species slide out of synchrony, then the original interactions between them might be replaced by strengthened interactions with other community members, with which they now overlap in time. Hence, the phenological stage of the interacting

partner could be more important than the identity of the species in determining interactions (Toftegaard *et al.*, 2019; Posledovich *et al.*, 2018). Given the diverse phenological response of species to a shift in temperature (Kharouba *et al.*, 2018), it is likely that different types of communities differ in their phenological response to temperature. In the same vein, given that populations within species can vary in their phenological response, it is likely that local realizations of a given community will differ in their phenological response to temperature. However, few studies have examined how changes in phenological synchrony within a community is reflected in the community structure.

1.5.1 Phenological impacts on communities via population outbreaks

Phenological impacts may potentially be amplified in the context of outbreaking species, which could cascade and have an effect on the community. It is known that host plant phenology can influence abundance of both herbivores and their natural enemies (Korosi *et al.*, 2018; Sinclair *et al.*, 2015; Crawley & Akhteruzzaman, 1988), and that abundance of outbreaking species can influence community composition (Timms & Smith, 2011; Roslin & Roland, 2005). In fact, phenological synchrony between outbreak species and plants can be important in determining outbreak regimes. For instance, *Choristoneura fumiferana* is expected to become more synchronised with a secondary host in response to warmer temperatures, which might result in a range expansion that follows the distribution of the secondary host (Pureswaran *et al.*, 2019; Pureswaran *et al.*, 2015). Similarly, the observed northern expansion of the outbreak moth *Agriopsis aurantiaria* has been explained by a closer synchrony with its host plant (Jepsen *et al.*, 2011). In contrast, the moth *Zeiraphera diniana* has experienced outbreak cycles on average every 9th year in the past millennium. Since 1982 only two strong outbreaks have been observed (year 2017, 2018) and the reason for this is thought to be a loss in phenological synchrony between *Z. diniana* and its host plant (Büntgen *et al.*, 2020; Esper *et al.*, 2007). Hence, it seems likely that phenological synchrony can be important in determining outbreak regimes for some species and that outbreaks in turn can influence species composition. However, to my knowledge, no studies have so far addressed this question.

1.6 Could shifts in phenology influence ecosystems?

While little investigated (Beard *et al.*, 2019), shifts in phenological synchrony could impact ecosystems and the services they provide. For instance, the timing

of arrival of the migratory bird *Branta bernicla nigricans* to its breeding grounds has an impact on the uptake of greenhouse gas emission (Kelsey *et al.*, 2018). Also, pollination can be vulnerable to a change in synchrony, where a mismatch can lower the seed set rates of plants (Kudo & Cooper, 2019). If climate warming alters outbreak dynamics of insect pests, then this will likely have an effect on the growth of trees used in timber production (Esper *et al.*, 2007) and also influence soil decomposition rates (Sandén *et al.*, 2020). Hence, as changes in phenological synchrony are already ongoing (e.g. Doiron *et al.*, 2015; Plard *et al.*, 2014; Visser *et al.*, 1998), it is crucial to assess the consequences of these on the services that the ecosystem provide.

2 Aims

In my thesis, I examine how temperature influences the spring and autumn phenology of species in a tritrophic community consisting of *Quercus robur*, insect herbivores and their associated parasitoids. I then assess how a change in phenology is reflected in the structure of the insect community and the performance of its members. This is done in four projects:

In **paper I**, I investigate how overwintering temperatures influence the spring phenology of a tritrophic community sampled at five locations along a latitudinal gradient. Here, I specifically test for species- and population-specific responses to overwintering temperatures.

In **paper II**, I examine whether variation in the spring phenology of *Q. robur* interacts with plant genotype in shaping tree infestation by an outbreaking insect herbivore. I then examined how infestation levels and *Q. robur* genotype together shape the insect herbivore community.

In **paper III**, I investigate whether temperature and autumn phenology in the previous year influence bud burst of *Q. robur* in the next year, and whether phenology of *Q. robur* differ among genotypes. I then assess how variation in bud burst of *Q. robur* is reflected in the performance of herbivores active in the summer.

In **paper IV**, I assess how timing in autumn leaf coloration of *Q. robur* varies over southern Sweden. Drawing on a citizen science project, I also examine how local variation in *Q. robur* autumn phenology is reflected in the herbivore insect community.

3 Methods

3.1 Study system

In Europe, the pedunculate oak *Quercus robur* (Fagaceae) is a common tree occurring over a large part of the continent (Eaton *et al.*, 2016). The species is characterized by substantial individual-level variation in phenology: within a population, the timing of leaf unfolding and autumn leaf coloration can vary between 20 – 30 days among individuals (Delpierre *et al.*, 2017). In line with many other plants, spring phenology in *Q. robur* is determined by both winter (chilling) and spring (forcing) temperatures, with photoperiod playing an added role (Fu *et al.*, 2019). Similarly, temperature and photoperiod also influence autumn phenology (Delpierre *et al.*, 2009). In *Q. robur*, the properties of a leaf change rapidly after bud burst, where young leaves are characterized by high concentrations of defensive compounds, high nutritional value and a weak leaf surface (Salminen *et al.*, 2004; Feeny, 1970). Then, from early summer and onwards, the concentration of defensive compounds decrease along with nutrient content and the leaf surface becomes tougher (Salminen *et al.*, 2004; Feeny, 1970).

Q. robur is known to be associated with a high number of insect species (Southwood, 1961). Some of these are leaf mining and galling species as well as free-feeding lepidopteran larvae (Box 2). In terms of empirical work, there are many advantages with studying gall inducing and leaf mining species. Their sedentary life stage makes them easy to collect and they can be reared *ex situ*. By observing insects emerging from galls and mines, it possible to establish which species are associated with each other and to create association webs. As the individuals living in a mine or a gall all share the same environment, they can conveniently be used in temperature experiments.

Box 2. The study system: herbivores of *Quercus robur*

Q. robur is known to be associated with a high number of insect species (Southwood, 1961). Herbivory on this species is often high in spring, with a peak after bud burst (Shutt *et al.*, 2019; Southwood *et al.*, 2004). Among herbivores, leaf mining and galling species as well as free-feeding lepidopteran larvae are common consumers of *Q. robur* (fig. 3; Southwood *et al.*, 2004). Leaf mining species spend their larval stage within leaves, feeding on different leaf layers (Hering, 1951), and then exit the leaf once they become adults. Similarly, gall wasps (Hymenoptera; Cynipidae; tribe Cynipini) develop shielded from the outside in gall structures on plants. These structures are produced by the plant, but induced by the egg or the larvae of the gall wasp (Stone *et al.*, 2002). Gall wasps have two generations per year: a sexual (♀♂) generation which emerges from galls in spring and an agamic (♀♀) generation which emerges from galls in autumn. Galls can often be inhabited by inquilines (Hymenoptera; Cynipidae; tribe Synergini). Inquilines are usually not lethal to the gall inducer, except for a group of moth inquilines (Lepidoptera). Most inquilines are unable to induce galls themselves, and instead feed of the tissue in existing galls (Stone *et al.*, 2002). Gall wasps and leaf miners are known to fluctuate in numbers among years (Blanchet *et al.*, 2018). Leaf miners, gall wasps and inquilines can all be attacked by hymenopteran parasitoids. Apart from insects, the fungal pathogen powdery mildew *Erysiphe alphitoides* (Erysiphales: Erysiphaceae) is a common pathogen on oak. The mycelium of this species can easily be distinguished as a white surface on the upper side of oak leaves (Woodward *et al.*, 1929). *E. alphitoides* usually infests oak leaves early in spring with the release of sexual ascospores. If bud burst occurs prior to the release of ascospores, then it is possible for oaks to escape infestation of *E. alphitoides* (Dantec *et al.*, 2015).

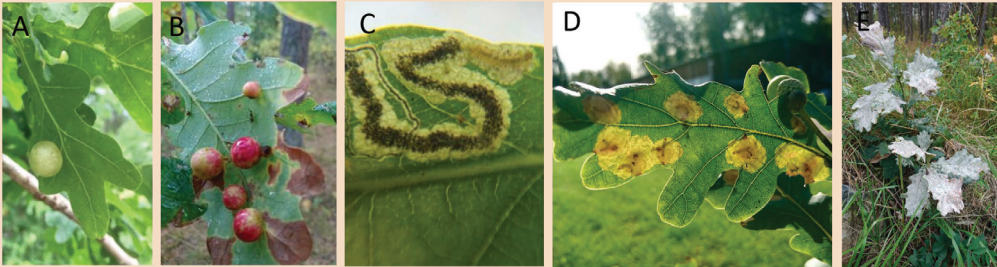


Figure 3. Photos of gall structures induced by two species of gall wasps (A: *Neuroterus quercusbaccarum* ♀♂ and B: *Cynips quercusfolii* ♀♀), two species of leaf miners and their characteristic mines (C: *Stigmella* spp. and D: *Tischeria ekebladella*) and one fungi pathogen (E: *Erysiphe alphitoides*). Photo: A-B, D-E) Adam Ekholm, C) Maria Faticov.

3.2 Spring phenology and insect communities (**Paper I, II, III**)

To assess how spring phenology responds to temperature among local populations of plants and insect species, and how these responses are reflected in the community structure, I designed three projects. First, I assessed how the spring phenology of local populations of *Q. robur* and insects respond to different overwintering temperatures (**Paper I**). Second, I assessed how both i) a shift in phenological synchrony between *Q. robur* and a spring-active herbivore and ii) *Q. robur* genotype is reflected in the structure of the insect herbivore community (**Paper II**). Finally, I tested whether observed effects of host plant phenology on insect herbivores in spring extend to herbivores active in summer, and if plant phenology differs among genotypes (**Paper III**).

3.2.1 Community phenology along a climatic gradient (**Paper I**)

To understand how different overwintering temperatures are reflected in the phenology of local communities consisting of *Q. robur*, insect herbivores and their associated parasitoids, we (AE and MF) sampled insects and acorns from five populations along a 2300 km latitudinal transect in Europe (fig. 4A). The sampling was timed to match the autumn phenology of *Q. robur* at the five locations, starting in northern Europe in September and ending in southern Europe in October. At each location, we sampled acorns and insects for a total of *c.* 48 hours from several individuals of *Q. robur*. Once samples had been collected, we initiated a common garden experiment in climate chambers (fig 4B; Kawecki & Ebert, 2004). Here, each population was exposed to both its original overwintering climate and to the climates of the other four sampling locations. As we only had access to a finite number of samples, we were unable to complete a fully-reciprocal design. Instead, we first exposed populations to their local climate and then, depending on the number of individuals collected, we divided the rest of the samples into one or all of the climate chambers. In the following spring, we then noted the day of emergence and estimated the amount GDD5 required to emerge (Box 3).

3.2.2 Host plant spring phenology and insect communities (**Paper II, III**)

To examine i) how leaf unfolding is influenced by temperature in the current and previous year (**Paper III**), ii) whether host plant phenology differs among genotypes (**Paper III**), and iii) how host plant phenology and genotype is reflected in both the structure of the insect herbivore community, the performance of herbivores active in summer and a plant pathogen (**Paper II**,

III), I established two warming experiments during two consecutive years (2017, 2018). In these experiments, we used a set of grafted *Q. robur* plants. These grafts originate from a population of oaks in south western Finland (60.19 °N, 21.64 °E). Between years 2011 – 2013, multiple shoots were collected from several mother trees and planted onto a random root stock in 50 litre pots. We refer to root stocks with shoots from the same mother tree as an “oak genotype”.

In 2017, we exposed the grafted oaks to two temperature treatments at a field site in Lövsta, Uppsala (59.84 °N, 17.81 °E). Oaks were exposed to elevated or ambient temperatures in mesh net cages (5 x 5 x 2.2 m) from May until October. Temperatures in the warm cages were elevated by *c.* 2 °C above ambient by using ceramic infrared heaters (Kimball, 2005), while the other cages acted as controls (see Faticov *et al.* (2020) for more information about the experimental setup in 2017). In 2018, we used the same set of oaks and exposed a subset of these to elevated temperatures in a greenhouse from late March to early May, while the remaining oaks were exposed to ambient temperature in the field. After the buds had started to develop in the greenhouse treatment, we transported oak trees from both treatments to our field site in Länna (59.87°N, 17.96°E). At the field site, we divided oaks into five blocks. Within each block, we included oaks from all spring treatment x genotype combinations (fig. 5A).

Box 3. Growing degree days

Since arthropods are ectothermal organisms, they are dependent on external energy. As a consequence, they are likely to respond to changes in the rate with which energy accumulates over time. Thus, the accumulation of degree days has been used as a thermal variable to explain species distributions, voltinism and phenology (Zohner *et al.*, 2018; Hodgson *et al.*, 2011; Pöyry *et al.*, 2011; Pöyry *et al.*, 2009; Luoto *et al.*, 2006; Sykes *et al.*, 1996). Degree days is calculated by taking a mean of the minimum and maximum temperature for each day, starting at the 1st of January. Then, a threshold temperature, below which development is assumed to not occur, is subtracted from the mean (for which reason degree days cannot assume a negative value). In northern Europe, a threshold of 5 °C is commonly used (e.g. Zohner *et al.*, 2018; Pöyry *et al.*, 2011; Pöyry *et al.*, 2009), which is referred to as GDD5 (accumulation of growing degree days with a threshold of 5 °C).

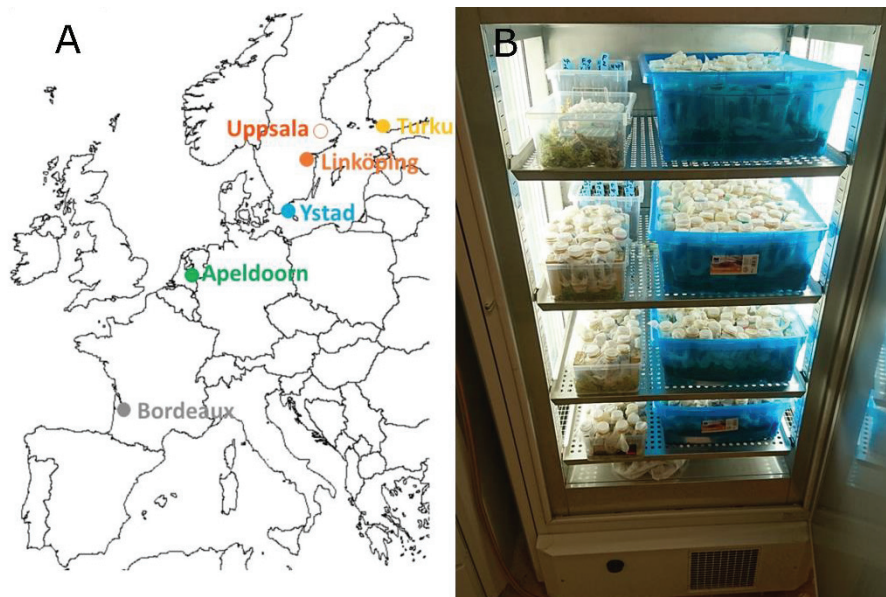


Figure 4. A) The five locations where acorns, leaf miners and gall wasps were sampled (filled circles). Acorns were sampled at an additional location (hollow circle). B) The climate chambers where insects and acorns overwintered. Photo: Adam Ekholm.

To examine if oak genotypes, autumn phenology in the previous year and temperature treatment in previous (2017) and current year (2018) influenced oak spring phenology, I scored leaf development on both the tree and shoot level in the spring of 2018. To further understand if oak phenology and genotype had an effect on the spring-active and outbreaking leaf miner *Acrocercops brongniardellus* (Lepidoptera; fig. 6B - D), I assessed the proportion of infested leaves and tree-incidence of the outbreak species on each oak tree. To detect signs of intraspecific competition in *A. brongniardellus*, I also measured pupal weight of *A. brongniardellus* on oaks with varying infestation levels. At five occasions during summer, we scored presence of other herbivores (14 June, 27 June, 19 July, 24 August and 28 September) and the aphid *Tuberculatus annulatus* (Hemiptera; 4 July, 23 July, 1 August, 17 August and 28 August) to assess whether infestation by *A. brongniardellus* influenced the herbivore community and aphid population dynamics. I also scored the presence of the oak pathogen *Erysiphe alphitoides* on five occasions (30 June, 16 July, 3 August, 27 August, 16 September), to examine whether oak phenology and genotype influenced *E. alphitoides* incidence. To understand whether host plant spring phenology and genotype influenced the performance of herbivores active in summer, I also performed two feeding experiments with lepidopteran larvae in early (*Orthosia gothica*) and late summer (*Polia nebulosa*). The experiment was

conducted in growth chambers (fig. 4B), where each larvae was fed with a leaf originating from one of the grafted oak trees. After 48 h, I measured the weight gain and ingested leaf mass of the herbivores. Then, at the end of the growing season, I examined if spring phenology had an impact on autumn phenology and tested if autumn phenology differed among plant genotypes by measuring the chlorophyll content and autumn leaf coloration on oaks at five dates (30 August, 12 September, 19 September, 1 October).

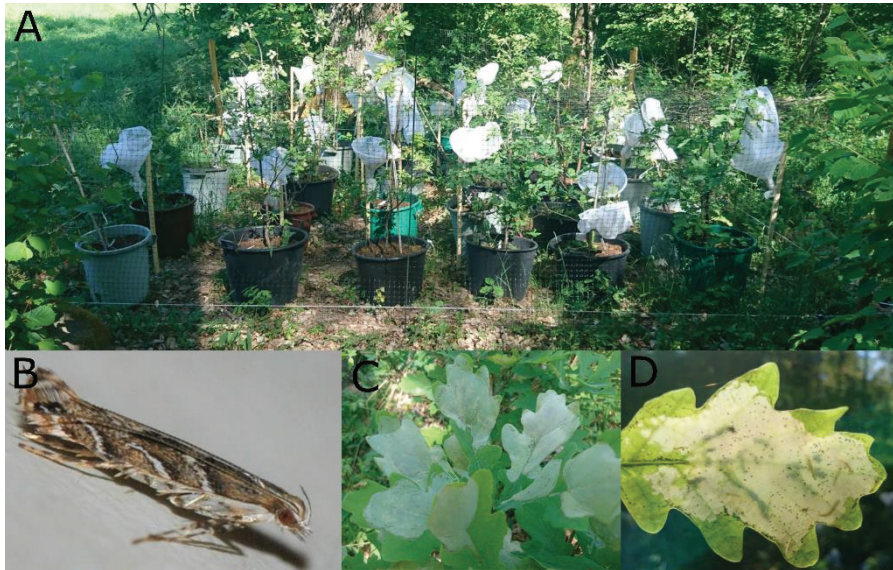


Figure 5. A) One out of five blocks from the experiment in Länna, Uppsala. B) An adult of the leaf mining moth *Acrocercops brongniardellus*. C) Leaves infested with *A. brongniardellus*; here the mined area of the leaf emerges as a white blotch. D) A mined leaf with larvae of *A. brongniardellus* visible within the leaf (see right-hand side of leaf). Photo: Adam Ekholm

3.3 Autumn phenology and insect communities (Paper IV)

Many phenological studies have focused on synchrony between species active in spring, whereas little attention has been directed towards species active in autumn (Gallinat *et al.*, 2015). In this study, I wanted to understand i) how oak autumn phenology and the insect community varies with temperature and ii) if the timing of host plant leaf coloration in autumn influences the insect community. To investigate this, I initiated a citizen science project involving pupils from 58 schools across southern Sweden. In 2016, participating schools received instructions of how to record oak autumn phenology and survey the insect community on oaks in their vicinity. Autumn phenology was surveyed by

photographing *c.* 20 haphazardly collected oak leaves every week in autumn. In total, we received data from 70 oaks with observations from at least two weeks in autumn that we used in our analysis (fig. 6a). For the insect community, we asked teachers and pupils to collect two samples. First, a sample where students collected as many leaf mining and gall inducing species as possible for at least 20 minutes. Then, we asked them to collect a second standardized sample of *c.* 250 haphazardly collected leaves. To estimate species richness of each oak, we counted the number of species found in sample 1 and 2. Focusing solely on sample 2, we then estimated herbivory, herbivore diversity, community evenness and species-specific abundances and incidences.

In total, we received insect samples from 127 oaks and of these 58 oaks included observations of both the autumn phenology and the insect community (fig. 6b). Then, to assess how temperature varied across the sampling locations, we extracted the annual accumulation of GDD5 from a micro-climatic map (Box 2; Meineri & Hylander, 2017; Meineri & Hylander, 2016). The temperature data, together with the survey on oak autumn phenology and the insect community allowed us to estimate i) how oak autumn phenology and insect communities vary with temperature, and ii) how autumn phenology influences the insect community structure.

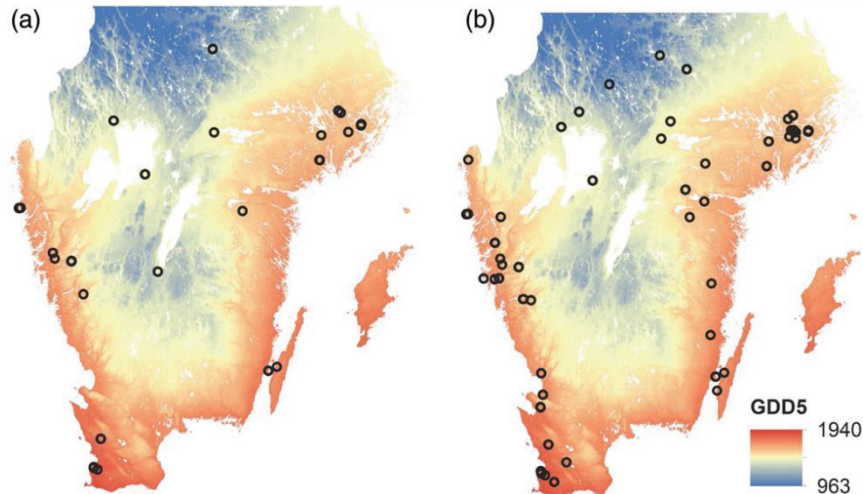


Figure 6. The location of the oak trees surveyed in the citizen science project. In total, autumn phenology was surveyed on 70 oaks (a), while the insect community was surveyed on 127 oak trees (b). The background color represents the annual accumulation of GDD5 across Sweden, where red colors indicates a higher sum of degree days and blue indicates a lower sum.

4 Results and Discussion

In this thesis, I show that both species and populations can differ in their phenological response to temperature, and that such differences can shift the phenological overlap between interacting species (**Paper I**). A consequence of shifting phenologies is demonstrated in **Paper II**, where a shift in synchrony between a plant and a spring-active herbivore alters the interaction strength, which then cascades into a modified herbivore community structure. In contrast to this pronounced effect detected for herbivores active in spring, I found no impact of shifts in oak phenology on herbivores active in summer (**Paper III**). In the autumn, herbivores were again influenced by the phenology of the host plant (**Paper IV**). Apart from the effects of plant phenology, I found that genetic variation within a population of plants had little effect on the herbivore community structure and the performance of herbivores (**Paper II, III**). Below, I will examine each finding in turn.

4.1 How does temperature influence the phenology of species and local populations?

4.1.1 Temperature in specific seasons influences plant spring and autumn phenology

Acorns exposed to warmer overwintering temperatures produced leaves earlier, but also required a higher accumulation of GDD5 to do so (**Paper I**). Temperature in the previous year had no effect on the timing of leaf unfolding in the following spring, while warm temperature in spring advanced both leaf unfolding and loss of chlorophyll content in autumn of the grafted oak trees (**Paper III**). In autumn, oaks growing at warmer locations stayed greener for a longer time (**Paper IV**). Together, these results suggest that temperature in

winter and spring are important in determining spring phenology, while warm temperatures in summer and autumn may delay autumn leaf coloration.

My results agree with previous studies which have demonstrated how both warm temperatures in spring advance leaf unfolding and how longer periods of cold temperatures in winter make plants more responsive to temperature (Zohner & Renner, 2019; Flynn & Wolkovich, 2018; Tansey *et al.*, 2017; Fu *et al.*, 2013). In addition, autumn phenology can be advanced by warm temperatures in spring (Zohner & Renner, 2019), while warm summer and autumn temperatures can have the opposite effect and delay autumn phenology (Zohner & Renner, 2019; Fu *et al.*, 2018). However less is known about how temperature in the previous year influence phenology in the next. It has been suggested that autumn phenology and temperature in the previous autumn can influence bud burst in the next (Fu *et al.*, 2014; Heide, 2003), but also that flowering phenology is affected by temperature in the previous year and sometimes even two years prior (Mulder *et al.*, 2017). Nonetheless, I detected no such ‘legacy’ effects in this thesis.

In terms of the phenological distribution, I detected no effect of temperature on the within-population variation in date of acorn leaf production in spring (**Paper I**). This result contrasts with that reported by Zohner *et al.* (2018), who found that leaf-out synchrony among individual plants decreased in warmer springs – a pattern which they attributed to individual variation in photoperiod sensitivity among plants. The lack of such effects in my thesis could be due to the low resolution in scoring plant phenology (once per week), to the fact that we used acorns instead of older plants, or to some other unknown factor.

Overall, my current results suggests that temperature has an important role in determining both spring and autumn phenology of *Q. robur*. Warm temperatures in winter makes *Q. robur* less responsive to temperature in spring, while warm temperatures in spring advance both spring and autumn phenology. In autumn, phenology is delayed for *Q. robur* growing at warmer locations.

4.1.2 Insect species differ in their phenological response to temperature

In **Paper I**, I found that *Tischeria ekebladella* required more GDD5 to emerge at warmer overwintering temperatures. For species associated with the galls of *Andricus quercustozae* and *Cynips quercusfolii*, the phenological response to temperature differed among species (fig. 7A, C). Interestingly, the parasitoid *Torymus auratus* did not respond to temperature (fig. 7A). The warmest overwintering climates (climate chambers that simulated the climate of the two most southern locations: Apeldoorn and Bordeaux; fig. 4A) had both a warmer winter and spring climate. As with plants, insects can also be more responsive

to warm temperatures in spring if they experience a long chilling period during winter (Stålhandske *et al.*, 2017; Bosch & Kemp, 2003). Therefore, the higher requirement of GDD5 for some species to emerge in warmer climates is probably the result of a shorter chilling period.

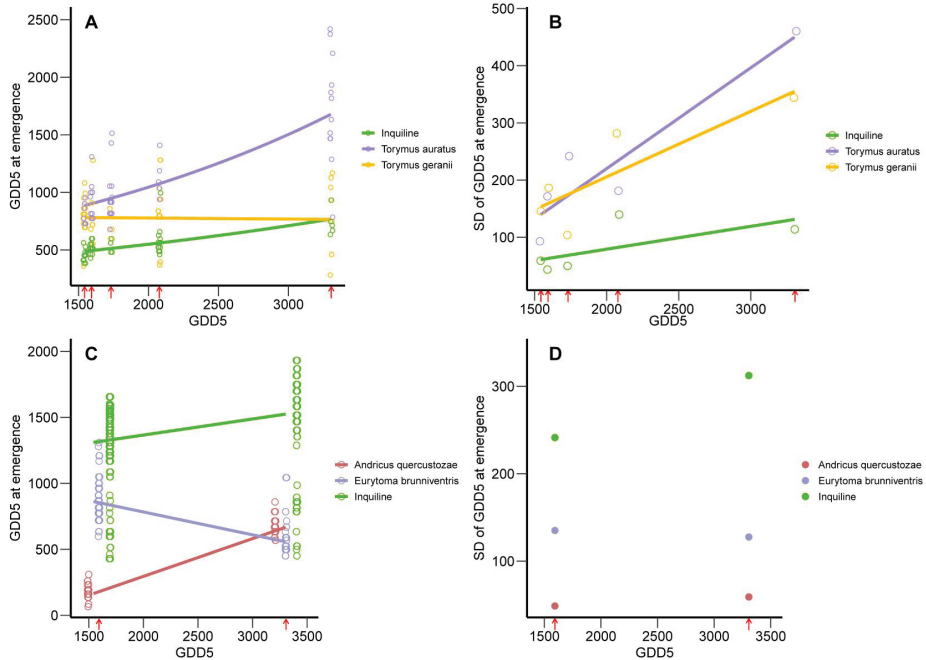


Figure 7. The amount of GDD5 required by insects to emerge (A, C) and the standard deviation of the mean emergence (B, D) for species associated with the gall *Cynips quercusfolii* (A, B) and *Andricus quercustozae* (C, D). The x-axis corresponds to the annual accumulation of GDD5 in each climatic treatment, where red arrows denote each treatment. From left to right, the red arrows on the x-axes in panels A, B correspond to the climate of the three Nordic locations of Linköping, Turku, Ystad, and the two southern locations of Apeldoorn and Bordeaux. For the x-axes in panels C, D, the left-hand arrow corresponds to the climate of Turku and the right-hand arrow corresponds to the climate of Bordeaux.

I also noted that several species (*T. geranii*, *T. auratus* and *T. ekebladella*) had a higher variation in the accumulation of GDD5 required to emerge (i.e. wider phenological distribution) in warmer climates (fig. 7B, *T. ekebladella* not shown here). These findings match previous reports from other species. A longer chilling period during winter resulted in a wider phenological distribution for the orange tip butterfly *Anthocharis cardamines* (Stålhandske *et al.*, 2015), which could also be the case in our study. In terms of species interactions, a shift in the phenological distribution could buffer species from becoming desynchronized. On the other hand, it will reduce the number of individuals to interact with at a

specific time point, which could influence the strength of species interaction (fig. 2).

When combined with the temperature response of *Q. robur*, my observations of insects suggest that some species are less responsive to warm temperatures in spring if they have been exposed to warm winter temperatures. However, not all insects showed this pattern. In addition, the fact that several insect species emerged over a larger range of GDD5 value under warmer overwintering conditions is a factor that could buffer some interactions from becoming decoupled in time.

4.1.3 Phenology differs among populations of oaks and insects

On a regional level, I detected that the timing of shoot and leaf development in acorns and the emergence of *T. ekebladella* differed among populations (**Paper I**). On a local level, I also found that spring and autumn phenology differed among oak genotypes that originated from the same population. In addition, the rank order of spring phenology did not detectably differ with spring-time climate among genotypes (i.e. there was no genotype x environment interaction; **Paper III**).

These findings match with several previous findings showing that both plant and insect populations can differ in terms of local phenology (Valdes *et al.*, 2019; Stålhandske *et al.*, 2014; Vitasse *et al.*, 2013). In this context, we found that populations of *T. ekebladella* from warmer locations (Bordeaux and Apeldoorn) and acorns from the warmest location (Bordeaux) required a higher accumulation of GDD5 to emerge (although the latter observation was highly influenced by an outlier). These observations are in line with countergradient variation (Conover & Schultz, 1995), a type of adaptation where the expression of a trait has the opposite direction of the environmental gradient. For instance, Valdes *et al.* (2019) studied the plant *Cerastium fontanum* growing on geothermal soils in Iceland and found that plants flowered earlier in warmer soils. When seeds from plants growing in different soil temperatures were grown in a common garden under the same conditions, seeds from the colder soils flowered earlier. In this case, the flowering time (the trait) was earlier for plants growing at colder locations (the opposite direction of the environmental gradient). Therefore, my results suggests that species are locally adapted in phenology, following a pattern of countergradient variation. As the vegetation season at high latitudes in the northern hemisphere is generally shorter than at lower latitudes, it can be beneficial to be more responsive to temperature at high latitudes if the length of the vegetation season limits the performance of the species.

4.2 What are the consequences of a shift in phenological synchrony on the insect community?

As shown above, species and populations can differ in their phenological response to temperature. The logical next question is then what implications this could have on the community structure. Below, I present and discuss the consequences of such changes on species interactions and how it is reflected in the insect community structure. In addition, I also present genotypic effects of the host plant on herbivores and assess if the genotypic effect depends on host plant phenology (testing for genotype x environment interaction).

4.2.1 A shift in phenological synchrony alters interaction strength

In spring, infestation rates of the outbreaking herbivore *A. brongniardellus* were higher on oaks with late spring phenology (fig. 8A; **Paper II**). The mechanism behind this is unknown, but could be related to the chemical and/or physical properties of the leaf. Young leaves contain high levels of secondary metabolites that decrease as the leaves becomes older, while old leaves are also less nutritious and have a tougher leaf surface (Falk *et al.*, 2018; Salminen *et al.*, 2004; Feeny, 1970). Specialized herbivores can sometimes overcome secondary metabolites (Roslin & Salminen, 2008), while herbivores feeding on older foliage can experience lower growth rates, body mass and survival (Fuentelba *et al.*, 2017; Tikkanen & Julkunen-Tiitto, 2003). Since *A. brongniardellus* is specialized on oak (Bengtsson & Johansson, 2011), it could be capable of dealing with the secondary metabolites and thereby be restricted to feed on young and nutritious leaves. Thus, *A. brongniardellus* could be a phenological specialist that is only able to infest its host during a certain time window, just after leaves have unfolded. In addition, the pupal weights of *A. brongniardellus* on heavily infested oaks were lower than pupae weight on oaks with lower infestation. This could be a result of more intraspecific competition or a stronger herbivore-induced response in oaks with higher infestation. As pupal weight can serve as a proxy for fecundity (Tammaru *et al.*, 1996; Honěk, 1993; Haukioja & Neuvonen, 1985), it is possible that high infestation levels can influence future outbreaks.

In summer, I found that two species of free-feeding lepidopteran herbivores, *O. gothica* and *P. nebulosa* (active in early and late summer, respectively) did not differ in either ingested leaf mass or weight gain when fed with leaves of different spring phenology (**Paper III**). As the chemical and physical properties of leaves are relatively stable during the summer compared to spring (Salminen *et al.*, 2004), it is likely that leaves of different age reflect a resource of similar quality in summer.

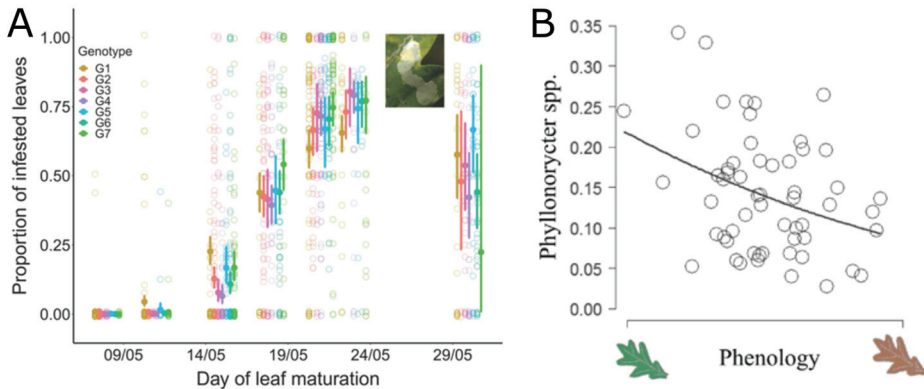


Figure 8. A) The relationship between proportion of infested leaves by *A. brongniardellus* (photo) and oak spring phenology. The x-axis corresponds to oak spring phenology, defined as the date (dd/mm) when “the first leaves are spread out over 90% of the crown”. Each color represents an oak genotype. Shown are model predictions with standard errors. Raw data is displayed as hollow circles in the background (jittered vertically). B) The proportion of infested leaves by leaf miners from the genus *Phyllonorycter* spp. on oaks with different autumn phenology. On the x-axis, the green leaf represents oaks with late autumn phenology, while the brown leaf represents oaks with early autumn phenology. Raw data is displayed as hollow circles in the background.

In autumn, I found that leaf miners from the genus *Phyllonorycter* spp. were more common on oaks with a late autumn phenology (fig. 8B; **Paper IV**). Many species from this genus produce two generations per year, and the second generation is usually active late in autumn (Svensson, 1993). For the second generation, oak trees with a late autumn phenology probably mirror a high quality resource, as they provide the moth with green and nutritious leaves late in autumn. Host plant autumn phenology has previously been shown to impact herbivores. Early leaf abscission or leaf fall can cause mortality in leaf miners (Mopper & Simberloff, 1995; Connor *et al.*, 1994), and the timing of leaf fall has been suggested to be the driver of herbivore outbreaks (Connor *et al.*, 1994).

In summary, host plant phenology has an impact on herbivores active in spring and autumn, while such effects seem to be absent on summer-active herbivores. This indicates that not all herbivores will be influenced by a shift in host plant synchrony, with effects probably being accentuated among species mostly active in spring and autumn.

4.2.2 Shifts in phenological synchrony can influence the community structure

Shifts in synchrony between plants and herbivores could cascade into a modified community structure: At outbreak densities, *A. brongniardellus* can infest up to 93 % of the oak leaves in spring and consume a majority of the leaf mass. In

Paper II, I found that heavily infested oaks had an impact on the herbivore community structure: highly infested oaks had a lower species richness and were less likely to be infested by four out of six surveyed herbivore species. In line with this, I found that the aphid *T. annulatus* had lower population growth and was found on a lower proportion of infested leaves on highly infested oaks. As *A. brongniardellus* is among the first herbivores to colonize oak leaves, they can consume a majority of the resource before herbivores active later in the season arrive. This could then shift the oviposition preference of late-arriving herbivores towards uninfested leaves (Gripenberg *et al.*, 2010). For aphids, damaged midribs in leaves caused by leaf miners can disrupt the flow of phloem and reduce leaf quality (Johnson *et al.*, 2002). The same mechanisms could also explain the negative effect of *A. brongniardellus* on aphids in our study. Interestingly, the two galling species (*Neuroterus* spp. and *Macrodiplosis dryobia*) did not show a negative trend with infestation levels of *A. brongniardellus*, which might be due to the fact that some galls are able to stimulate photosynthesis and allocate carbon from neighboring leaves (Bagatto *et al.*, 1996; Fay *et al.*, 1993).

In autumn, I detected an imprint of the timing in autumn leaf coloration on the insect community (**Paper IV**). Both species diversity and community evenness was higher on oaks with an early autumn phenology. This pattern was mainly attributed to a group of abundant leaf miners (*Phyllonorycter* spp.) that was more common on oaks with late autumn phenology (discussed above).

To conclude, the results in this thesis suggest that both spring and autumn phenology could have an impact on the insect community. If the synchrony between host plant and herbivores shift in a warmer climate, then this could lead to changes in the overall community structure.

4.2.3 Small impact of host plant genotype on the insect community

Even though host plant genotype has been shown to influence herbivore abundance, community composition and food-web complexity (Barbour *et al.*, 2016; Barbour *et al.*, 2015), I detected that host plant genotype had none or a small effect on the insect community. In **Paper II**, I found that species richness differed among oak genotypes and that the leaf miner *Tischeria ekebladella* was the only species out of six that was influenced by oak genotype. For aphids, incidence differed among plant genotypes but proportion of infested leaves and growth did not differ among plant genotypes. In **Paper III**, weight gain differed between oak genotypes but not ingested leaf mass for the early-summer herbivore *O. gothica*. In contrast, the late-summer herbivore *P. nebulosa* tended to differ in the amount of ingested leaf mass between genotypes, while no

difference was detected in weight gain. Previous studies within the same study system have shown that plant genotype and plant genetic diversity can influence herbivores abundance (Pohjanmies *et al.*, 2015; Tack & Roslin, 2011). However, compared to other factors, such as spatial location of the host plant, the effect of oak genotype is of minor importance in structuring the insect community (Tack *et al.*, 2010).

In terms of the interactive effect between host plant phenology and genotype, I found the influence of genotype on the herbivores *A. brongniardellus*, *O. gothica* and *P. nebulosa* and the pathogen *E. alphitoides* to be independent of plant phenology (**Paper II, III**). This suggests that changes in phenology do not alter the susceptibility of certain plant genotypes to plant attackers more than with other genotypes (i.e. no genotype x environment interaction). In other words, the interaction structure between plants and plant attackers is relatively unaffected by plant genotype, independent of the phenological stage of the host plant.

5 Conclusion and future directions

In my thesis, I demonstrate that both species and populations can differ in their phenological response to temperature, and that changes in phenological synchrony between interacting species can alter the structure of tritrophic-level, plant-based communities. The multitude of differential phenological responses to temperature observed among species suggest that individual communities may respond differently to climate change. What adds another layer of complexity is that populations can be adapted to local environmental cues, which opens up for further differentiation in responses among local communities. However, to what extent communities and local communities differ in their phenological response to temperature is poorly understood and requires more attention.

Among the many interactions occurring within a community, those involving abundant species with a high effect on the overall resource basis may come with disproportionate effects. How they are affected by shifts in climate and phenology is then a question of particular interest. My thesis shows that impacts on the outbreaking herbivore *A. bronniardellus* may influence the overall herbivore community of oaks in Sweden.

Importantly, not all interactions are equally vulnerable to a shift in synchrony. In the context of plant-herbivore interactions, synchrony had an effect on herbivores in spring and autumn while no effect was found during summer. This insight is helpful in identifying the interactions and/or communities most and least vulnerable to shifts in phenological synchrony.

In terms of genotypic effects, I found that the effect of host plant genotype on plant attackers was mostly absent or weak. Interestingly, the effect of plant genotype did not depend on host plant phenology. These results indicate that if plants and herbivores modify their phenological synchrony, then plant genotype will have a similar effect on herbivores (no genotype x environment interaction). This insight suggest that the effect of plant genotype may remain unchanged in the face of future temperature increase.

Overall, my findings highlight the challenges involved when trying predict changes in interactions among species in a changing climate. Species respond to multiple cues and these cues can interact with each other in complex ways. In my thesis, I specifically focused on the role of temperature. However, more studies are required to understand how interactions are influenced by temperature-induced shifts in phenological synchrony, and what the consequences of such shifts are on the community and ecosystem levels. As the next step in this field of research, I recommend future studies exploring the following avenues:

- i) *In situ* experiments which manipulate the phenology of several trophic levels and assess how this affects community composition.
- ii) Studies that examine how species active in autumn are influenced by a shift in synchrony and how this is reflected in the community composition.
- iii) Reciprocal transplant experiments that establish to what extent communities and local communities differ in their phenological response to temperature.
- iv) Studies assessing how temperature and other cues interact in determining species phenology.

While each of these experiments are fraught with several logistic challenges, they may together reveal the overall impact of phenology on communities. Deriving a general understanding of climate change influence communities remains an urgent priority, given the current rate and ubiquity of climate change (IPCC, 2014).

References

- Bagatto, G., Paquette, L.C. & Shorthouse, J.D. (1996). Influence of galls of *Phanacis taraxaci* on carbon partitioning within common dandelion, *Taraxacum officinale*. *Entomologia Experimentalis Et Applicata*, 79(1), pp. 111-117.
- Barbour, M.A., Fortuna, M.A., Bascompte, J., Nicholson, J.R., Julkunen-Tiitto, R., Jules, E.S. & Crutsinger, G.M. (2016). Genetic specificity of a plant-insect food web: Implications for linking genetic variation to network complexity. *Proceedings of the National Academy of Sciences of the United States of America*, 113(8), pp. 2128-2133.
- Barbour, M.A., Rodriguez-Cabal, M.A., Wu, E.T., Julkunen-Tiitto, R., Ritland, C.E., Miscampbell, A.E., Jules, E.S. & Crutsinger, G.M. (2015). Multiple plant traits shape the genetic basis of herbivore community assembly. *Functional Ecology*, 29(8), pp. 995-1006.
- Beard, K.H., Kelsey, K.C., Leffler, A.J. & Welker, J.M. (2019). The Missing Angle: Ecosystem Consequences of Phenological Mismatch. *Trends in Ecology & Evolution*, 34(10), pp. 885-888.
- Bengtsson, B.Å. & Johansson, R. (2011). *Nationalnyckeln till Sveriges flora och fauna. Fjärilar: Bronsmalar-rullvingemalar. Lepidoptera: Roeslerstammiidae-Lyonetiidae*. Ardatbanken, SLU, Uppsala.
- Blanchet, F.G., Roslin, T., Kimura, M.T., Huotari, T., Kaartinen, R., Gripenberg, S. & Tack, A.J.M. (2018). Related herbivore species show similar temporal dynamics. *Journal of Animal Ecology*, 87(3), pp. 801-812.
- Bosch, J. & Kemp, W.P. (2003). Effect of wintering duration and temperature on survival and emergence time in males of the orchard pollinator *Osmia lignaria* (Hymenoptera : Megachilidae). *Environmental Entomology*, 32(4), pp. 711-716.
- Both, C., van Asch, M., Bijlsma, R.G., van den Burg, A.B. & Visser, M.E. (2009). Climate change and unequal phenological changes across four trophic levels: constraints or adaptations? *Journal of Animal Ecology*, 78(1), pp. 73-83.
- Bradshaw, W.E. & Holzapfel, C.M. (2007). Evolution of animal photoperiodism. *Annual Review of Ecology Evolution and Systematics*, 38, pp. 1-25.
- Burgess, M.D., Smith, K.W., Evans, K.L., Leech, D., Pearce-Higgins, J.W., Branston, C.J., Briggs, K., Clark, J.R., du Feu, C.R., Lewthwaite, K., Nager, R.G., Sheldon, B., Smith, J.A., Whytock, R.C., Willis, S.G. & Phillimore, A.B. (2018). Tritrophic phenological match-mismatch in space and time. *Nature Ecology & Evolution*, 2(6), pp. 970-975.

- Büntgen, U., Liebhold, A., Nievergelt, D., Wermelinger, B., Roques, A., Reinig, F., Krusic, P.J., Piermattei, A., Egli, S., Cherubini, P. & Esper, J.J.O. (2020). Return of the moth: rethinking the effect of climate on insect outbreaks. *Oecologia*, 192(2), pp. 543-552.
- Cluttonbrock, T.H., Albon, S.D. & Guinness, F.E. (1989). Fitness Costs Of Gestation And Lactation In Wild Mammals. *Nature*, 337(6204), pp. 260-262.
- Cohen, J.M., Lajeunesse, M.J. & Rohr, J.R. (2018). A global synthesis of animal phenological responses to climate change. *Nature Climate Change*, 8(3), pp. 224-228.
- Connor, E.F., Adamsmanon, R.H., Carr, T.G. & Beck, M.W. (1994). The effects of host plant phenology on the demography and population dynamics of the leaf-mining moth, *Cameraria hamadryadella* (Lepidoptera: Gracillariidae). *Ecological Entomology*, 19(2), pp. 111-120.
- Conover, D.O. & Schultz, E.T. (1995). Phenotypic similarity and the evolutionary significance of countergradient variation. *Trends in Ecology & Evolution*, 10(6), pp. 248-252.
- Crawley, M.J. & Akhteruzzaman, M. (1988). Individual variation in the phenology of oak trees and its consequences for herbivorous insects. *Functional Ecology*, 2(3), pp. 409-415.
- Dantec, C.F., Ducasse, H., Capdevielle, X., Fabreguettes, O., Delzon, S. & Desprez-Loustau, M.L. (2015). Escape of spring frost and disease through phenological variations in oak populations along elevation gradients. *Journal of Ecology*, 103(4), pp. 1044-1056.
- Delpierre, N., Dufrene, E., Soudani, K., Ulrich, E., Cecchini, S., Boe, J. & Francois, C. (2009). Modelling interannual and spatial variability of leaf senescence for three deciduous tree species in France. *Agricultural and Forest Meteorology*, 149(6-7), pp. 938-948.
- Delpierre, N., Guillemot, J., Dufrene, E., Cecchini, S. & Nicolas, M. (2017). Tree phenological ranks repeat from year to year and correlate with growth in temperate deciduous forests. *Agricultural and Forest Meteorology*, 234, pp. 1-10.
- Doiron, M., Gauthier, G. & Levesque, E. (2015). Trophic mismatch and its effects on the growth of young in an Arctic herbivore. *Global Change Biology*, 21(12), pp. 4364-4376.
- Eaton, E., Caudullo, G., Oliveira, S. & de Rigo, D. (2016). *Quercus robur and Quercus petraea in Europe: distribution, habitat, usage and threats*. In: San-Miguel-Ayanz, J., de Rigo, D., Caudullo, G., Houston Durrant, T., Mauri, A. (Eds.), European Atlas of Forest Tree Species. Publ. Off. EU, Luxembourg, pp. e01c6df+.
- Edwards, M. & Richardson, A.J. (2004). Impact of climate change on marine pelagic phenology and trophic mismatch. *Nature*, 430(7002), pp. 881-884.
- Esper, J., Büntgen, U., Frank, D.C., Nievergelt, D. & Liebhold, A. (2007). 1200 years of regular outbreaks in alpine insects. *Proc. R. Soc. B*, 274(1610), pp. 671-679.
- Falk, M.A., Lindroth, R.L., Keefover-Ring, K. & Raffa, K.F. (2018). Genetic variation in aspen phytochemical patterns structures windows of opportunity for gypsy moth larvae. *Oecologia*, 187(2), pp. 471-482.
- Faticov, M., Ekholm, A., Roslin, T. & Tack, A.J.M. (2020). Climate and host genotype jointly shape tree phenology, disease levels and insect attacks. *Oikos*, 129(3), pp. 391-401.
- Fay, P.A., Hartnett, D.C. & Knapp, A.K. (1993). Increased photosynthesis and water potentials in silphium-integrifolium galled by cynipid wasps. *Oecologia*, 93(1), pp. 114-120.
- Feeny, P. (1970). Seasonal changes in oak leaf tannins and nutrients as a cause of spring feeding by winter moth caterpillars. *Ecology*, 51(4), pp. 565-581.

- Flynn, D.F.B. & Wolkovich, E.M. (2018). Temperature and photoperiod drive spring phenology across all species in a temperate forest community. *New Phytologist*, 219(4), pp. 1353-1362.
- Fu, Y.S.H., Campioli, M., Deckmyn, G. & Janssens, I.A. (2013). Sensitivity of leaf unfolding to experimental warming in three temperate tree species. *Agricultural and Forest Meteorology*, 181, pp. 125-132.
- Fu, Y.S.H., Campioli, M., Vitasse, Y., De Boeck, H.J., Van den Berge, J., AbdElgawad, H., Asard, H., Piao, S.L., Deckmyn, G. & Janssens, I.A. (2014). Variation in leaf flushing date influences autumnal senescence and next year's flushing date in two temperate tree species. *Proceedings of the National Academy of Sciences of the United States of America*, 111(20), pp. 7355-7360.
- Fu, Y.S.H., Piao, S., Delpierre, N., Hao, F., Hänninen, H., Liu, Y., Sun, W., Janssens, I.A. & Campioli, M. (2018). Larger temperature response of autumn leaf senescence than spring leaf-out phenology. *Global Change Biology*, 24, pp. 2159-2168.
- Fu, Y.S.H., Zhang, X., Piao, S.L., Hao, F.H., Geng, X.J., Vitasse, Y., Zohner, C., Penuelas, J. & Janssens, I.A. (2019). Daylength helps temperate deciduous trees to leaf-out at the optimal time. *Global Change Biology*, 25(7), pp. 2410-2418.
- Fu, Y.S.H., Zhao, H.F., Piao, S.L., Peaucelle, M., Peng, S.S., Zhou, G.Y., Ciais, P., Huang, M.T., Menzel, A., Uelas, J.P., Song, Y., Vitasse, Y., Zeng, Z.Z. & Janssens, I.A. (2015). Declining global warming effects on the phenology of spring leaf unfolding. *Nature*, 526(7571), pp. 104-107.
- Fuentealba, A., Pureswaran, D., Bause, E. & Despland, E. (2017). How does synchrony with host plant affect the performance of an outbreaking insect defoliator? *Oecologia*, 184(4), pp. 847-857.
- Gallinat, A.S., Primack, R.B. & Wagner, D.L. (2015). Autumn, the neglected season in climate change research. *Trends in Ecology & Evolution*, 30(3), pp. 169-176.
- Gripenberg, S., Mayhew, P.J., Parnell, M. & Roslin, T. (2010). A meta-analysis of preference-performance relationships in phytophagous insects. *Ecology Letters*, 13(3), pp. 383-393.
- Gunn, A. & Skogland, T. (1997). *Responses of caribou and reindeer to global warming*. In: (eds) Oechel, W. C., Callaghan, T., Gilmanov, T., Holten J. I., Maxwell B., Molau U., Sveinbjörnsson B. Global change and Arctic terrestrial ecosystems, pp. 189-200. Springer-Verlag, New York.
- Haukioja, E. & Neuvonen, S. (1985). The relationship between size and reproductive potential in male and female *Epirrita-autumnata* (lep, geometridae). *Ecological Entomology*, 10(3), pp. 267-270.
- Heide, O.M. (2003). High autumn temperature delays spring bud burst in boreal trees, counterbalancing the effect of climatic warming. *Tree Physiology*, 23(13), pp. 931-936.
- Hering, E.M. (1951). *Biology of the leaf miners*. Berlin: Uitgeverij Dr W. Junk, 's-Gravenhage.
- Hodgson, J.A., Thomas, C.D., Oliver, T.H., Anderson, B.J., Brereton, T.M. & Crone, E.E. (2011). Predicting insect phenology across space and time. *Global Change Biology*, 17(3), pp. 1289-1300.
- Honěk, A. (1993). Intraspecific variation in body size and fecundity in insects - a general relationship. *Oikos*, 66(3), pp. 483-492.

- IPCC (2014). *Climate Change 2014: Synthesis Report*. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Core Writing Team, R.K. Pachauri and L.A. Meyer (eds.)]. IPCC, Geneva, Switzerland, 151 pp.
- Jepsen, J.U., Kapari, L., Hagen, S.B., Schott, T., Vindstad, O.P.L., Nilssen, A.C. & Ims, R.A. (2011). Rapid northwards expansion of a forest insect pest attributed to spring phenology matching with sub-Arctic birch. *Global Change Biology*, 17(6), pp. 2071-2083.
- Johnson, S.N., Mayhew, P.J., Douglas, A.E. & Hartley, S.E. (2002). Insects as leaf engineers: can leaf-miners alter leaf structure for birch aphids? *Functional Ecology*, 16(5), pp. 575-584.
- Kawecki, T.J. & Ebert, D. (2004). Conceptual issues in local adaptation. *Ecology Letters*, 7(12), pp. 1225-1241.
- Kelsey, K.C., Leffler, A.J., Beard, K.H., Choi, R., Schmutz, J.A. & Welker, J.M. (2018). Phenological mismatch in coastal western Alaska may increase summer season greenhouse gas uptake. *Environmental Research Letters*, 13(4).
- Kharouba, H.M., Ehrlen, J., Gelman, A., Bolmgren, K., Allen, J.M., Travers, S.E. & Wolkovich, E.M. (2018). Global shifts in the phenological synchrony of species interactions over recent decades. *Proceedings of the National Academy of Sciences of the United States of America*, 115(20), pp. 5211-5216.
- Kimball, B.A. (2005). Theory and performance of an infrared heater for ecosystem warming. *Global Change Biology*, 11(11), pp. 2041-2056.
- Korosi, A., Marko, V., Kovacs-Hostyanszki, A., Somay, L., Varga, A., Elek, Z., Boreux, V., Klein, A.M., Foldesi, R. & Baldi, A. (2018). Climate-induced phenological shift of apple trees has diverse effects on pollinators, herbivores and natural enemies. *PeerJ*, 6, p. 21.
- Kudo, G. & Cooper, E.J. (2019). When spring ephemerals fail to meet pollinators: mechanism of phenological mismatch and its impact on plant reproduction. *Proceedings of the Royal Society B-Biological Sciences*, 286(1904).
- Laube, J., Sparks, T.H., Estrella, N., Høfler, J., Ankerst, D.P. & Menzel, A. (2014). Chilling outweighs photoperiod in preventing precocious spring development. *Global Change Biology*, 20(1), pp. 170-182.
- Lawrence, E. (2011). *Henderson's Dictionary of Biology*. 15. ed. Harlow: Pearson Education Limited
- Linden, A. (2018). Adaptive and nonadaptive changes in phenological synchrony. *Proceedings of the National Academy of Sciences of the United States of America*, 115(20), pp. 5057-5059.
- Lindestad, O., Wheat, C.W., Nylin, S. & Gotthard, K. (2019). Local adaptation of photoperiodic plasticity maintains life cycle variation within latitudes in a butterfly. *Ecology*, 100(1).
- Liu, Y.Z., Reich, P.B., Li, G.Y. & Sun, S.C. (2011). Shifting phenology and abundance under experimental warming alters trophic relationships and plant reproductive capacity. *Ecology*, 92(6), pp. 1201-1207.
- Luoto, M., Heikkinen, R.K., Pöyry, J. & Saarinen, K. (2006). Determinants of the biogeographical distribution of butterflies in boreal regions. *Journal of Biogeography*, 33(10), pp. 1764-1778.
- Meineri, E. & Hylander, K. (2016). Data from: Fine-grain, large-domain climate models based on climate station and comprehensive topographic information improve microrefugia detection. Dryad Digital Repository.

- Meineri, E. & Hylander, K. (2017). Fine-grain, large-domain climate models based on climate station and comprehensive topographic information improve microrefugia detection. *Ecography*, 40(8), pp. 1003-1013.
- Menzel, A., Sparks, T.H., Estrella, N., Koch, E., Aasa, A., Ahas, R., Alm-Kubler, K., Bissolli, P., Braslavska, O., Briede, A., Chmielewski, F.M., Crepinsek, Z., Curnel, Y., Dahl, A., Defila, C., Donnelly, A., Filella, Y., Jatcza, K., Mage, F., Mestre, A., Nordli, O., Penuelas, J., Pirinen, P., Remisova, V., Scheifinger, H., Striz, M., Susnik, A., Van Vliet, A.J.H., Wielgolaski, F.E., Zach, S. & Zust, A. (2006). European phenological response to climate change matches the warming pattern. *Global Change Biology*, 12(10), pp. 1969-1976.
- Mopper, S. & Simberloff, D. (1995). Differential herbivory in an oak population - the role of plant phenology and insect performance. *Ecology*, 76(4), pp. 1233-1241.
- Mulder, C.P.H., Iles, D.T. & Rockwell, R.F. (2017). Increased variance in temperature and lag effects alter phenological responses to rapid warming in a subarctic plant community. *Global Change Biology*, 23(2), pp. 801-814.
- Plard, F., Gaillard, J.M., Coulson, T., Hewison, A.J.M., Delorme, D., Warnant, C. & Bonenfant, C. (2014). Mismatch Between Birth Date and Vegetation Phenology Slows the Demography of Roe Deer. *Plos Biology*, 12(4).
- Pohjanmies, T., Tack, A.J.M., Pulkkinen, P., Elshibli, S., Vakkari, P. & Roslin, T. (2015). Genetic diversity and connectivity shape herbivore load within an oak population at its range limit. *Ecosphere*, 6(6), pp. 1-11.
- Posledovich, D., Toftegaard, T., Wiklund, C., Ehrlén, J. & Gotthard, K. (2018). Phenological synchrony between a butterfly and its host plants: Experimental test of effects of spring temperature, 87(1), pp. 150-161.
- Post, E. & Forchhammer, M.C. (2008). Climate change reduces reproductive success of an Arctic herbivore through trophic mismatch. *Philosophical Transactions of the Royal Society B-Biological Sciences*, 363(1501), pp. 2369-2375.
- Pureswaran, D.S., De Grandpre, L., Pare, D., Taylor, A., Barrette, M., Morin, H., Regniere, J. & Kneeshaw, D.D. (2015). Climate-induced changes in host tree-insect phenology may drive ecological state-shift in boreal forests. *Ecology*, 96(6), pp. 1480-1491.
- Pureswaran, D.S., Neau, M., Marchand, M., De Grandpre, L. & Kneeshaw, D. (2019). Phenological synchrony between eastern spruce budworm and its host trees increases with warmer temperatures in the boreal forest. *Ecology and Evolution*, 9(1), pp. 576-586.
- Pöyry, J., Leinonen, R., Soderman, G., Nieminen, M., Heikkinen, R.K. & Carter, T.R. (2011). Climate-induced increase of moth multivoltinism in boreal regions. *Global Ecology and Biogeography*, 20(2), pp. 289-298.
- Pöyry, J., Luoto, M., Heikkinen, R.K., Kuussaari, M. & Saarinen, K. (2009). Species traits explain recent range shifts of Finnish butterflies. *Global Change Biology*, 15(3), pp. 732-743.
- Renner, S.S. & Zohner, C.M. (2018). Climate Change and Phenological Mismatch in Trophic Interactions Among Plants, Insects, and Vertebrates. In: Futuyma, D.J. (ed. *Annual Review of Ecology, Evolution, and Systematics, Vol 49*). (Annual Review of Ecology Evolution and Systematics, 49), pp. 165-182.
- Roslin, T. & Roland, J. (2005). Competitive effects of the forest tent caterpillar on the galls and leaf-miners of trembling aspen. *Ecoscience*, 12(2), pp. 172-182.

- Roslin, T. & Salminen, J.P. (2008). Specialization pays off: contrasting effects of two types of tannins on oak specialist and generalist moth species. *Oikos*, 117(10), pp. 1560-1568.
- Roy, D.B. & Sparks, T.H. (2000). Phenology of British butterflies and climate change. *Global Change Biology*, 6(4), pp. 407-416.
- Salis, L., van den Hoorn, E., Beersma, D.G.M., Hut, R.A. & Visser, M.E. (2018). Photoperiodic cues regulate phenological carry-over effects in an herbivorous insect. *Functional Ecology*, 32(1), pp. 171-180.
- Salminen, J.P., Roslin, T., Karonen, M., Sinkkonen, J., Pihlaja, K. & Pulkkinen, P. (2004). Seasonal variation in the content of hydrolyzable tannins, flavonoid glycosides, and proanthocyanidins in oak leaves. *Journal of Chemical Ecology*, 30(9), pp. 1693-1711.
- Sandén, H., Mayer, M., Stark, S., Sandén, T., Nilsson, L.O., Jepsen, J.U., Wäli, P.R. & Rewald, B.J.E. (2020). Moth Outbreaks Reduce Decomposition in Subarctic Forest Soils, 23(1), pp. 151-163.
- Senior, V.L., Evans, L.C., Leather, S.R., Oliver, T.H. & Evans, K.L. (2020). Phenological responses in a sycamore-aphid-parasitoid system and consequences for aphid population dynamics: a 20-year case study. *Global Change Biology*, Accepted.
- Shutt, J.D., Burgess, M.D. & Phillimore, A.B. (2019). A Spatial Perspective on the Phenological Distribution of the Spring Woodland Caterpillar Peak. *American Naturalist*, 194(5), pp. E109-E121.
- Sinclair, F.H., Stone, G.N., Nicholls, J.A., Cavers, S., Gibbs, M., Butterill, P., Wagner, S., Ducouso, A., Gerber, S., Petit, R.J., Kremer, A. & Schonrogge, K. (2015). Impacts of local adaptation of forest trees on associations with herbivorous insects: implications for adaptive forest management. *Evolutionary Applications*, 8(10), pp. 972-987.
- Southwood, T.R.E. (1961). The Number of Species of Insect Associated with Various Trees. *Journal of Animal Ecology*, 30(1), pp. 1-8.
- Southwood, T.R.E., Wint, G.R.W., Kennedy, C.E.J. & Greenwood, S.R. (2004). Seasonality, abundance, species richness and specificity of the phytophagous guild of insects on oak (*Quercus*) canopies. *European Journal of Entomology*, 101(1), pp. 43-50.
- Stone, G.N., Schonrogge, K., Atkinson, R.J., Bellido, D. & Pujade-Villar, J. (2002). The population biology of oak gall wasps (Hymenoptera : Cynipidae). *Annual Review of Entomology*, 47, pp. 633-668.
- Stålhandske, S., Gotthard, K. & Leimar, O. (2017). Winter chilling speeds spring development of temperate butterflies. *Journal of Animal Ecology*, 86(4), pp. 718-729.
- Stålhandske, S., Gotthard, K., Posledovich, D. & Leimar, O. (2014). Variation in two phases of post-winter development of a butterfly. *Journal of Evolutionary Biology*, 27(12), pp. 2644-2653.
- Stålhandske, S., Lehmann, P., Pruißscher, P. & Leimar, O. (2015). Effect of winter cold duration on spring phenology of the orange tip butterfly, *Anthocharis cardamines*. *Ecology and Evolution*, 5(23), pp. 5509-5520.
- Svensson, I. (1993). Lepidoptera calender. Kristianstad (In Swedish). Self-published. In.
- Sykes, M.T., Prentice, I.C. & Cramer, W. (1996). A bioclimatic model for the potential distributions of north European tree species under present and future climates. *Journal of Biogeography*, 23(2), pp. 203-233.

- Tack, A.J.M., Ovaskainen, O., Pulkkinen, P. & Roslin, T. (2010). Spatial location dominates over host plant genotype in structuring an herbivore community. *Ecology*, 91(9), pp. 2660-2672.
- Tack, A.J.M. & Roslin, T. (2011). The relative importance of host-plant genetic diversity in structuring the associated herbivore community. *Ecology*, 92(8), pp. 1594-1604.
- Tammaru, T., Kaitaniemi, P. & Ruohomaki, K. (1996). Realized fecundity in *Epirrita autumnata* (Lepidoptera: Geometridae): Relation to body size and consequences to population dynamics. *Oikos*, 77(3), pp. 407-416.
- Tansey, C.J., Hadfield, J.D. & Phillimore, A.B. (2017). Estimating the ability of plants to plastically track temperature-mediated shifts in the spring phenological optimum. *Global Change Biology*, 23(8), pp. 3321-3334.
- Thackeray, S.J., Henrys, P.A., Hemming, D., Bell, J.R., Botham, M.S., Burthe, S., Helaouet, P., Johns, D.G., Jones, I.D., Leech, D.I., Mackay, E.B., Massimino, D., Atkinson, S., Bacon, P.J., Brereton, T.M., Carvalho, L., Clutton-Brock, T.H., Duck, C., Edwards, M., Elliott, J.M., Hall, S.J.G., Harrington, R., Pearce-Higgins, J.W., Hoye, T.T., Kruuk, L.E.B., Pemberton, J.M., Sparks, T.H., Thompson, P.M., White, I., Winfield, I.J. & Wanless, S. (2016). Phenological sensitivity to climate across taxa and trophic levels. *Nature*, 535(7611), pp. 241-245.
- Tikkanen, O.P. & Julkunen-Tiitto, R. (2003). Phenological variation as protection against defoliating insects: the case of *Quercus robur* and *Operophtera brumata*. *Oecologia*, 136(2), pp. 244-251.
- Timms, L.L. & Smith, S.M. (2011). Effects of gypsy moth establishment and dominance in native caterpillar communities of northern oak forests. *Canadian Entomologist*, 143(5), pp. 479-503.
- Toftegaard, T., Posledovich, D., Navarro-Cano, J.A., Wiklund, C., Gotthard, K. & Ehrlen, J. (2019). Butterfly-host plant synchrony determines patterns of host use across years and regions. *Oikos*, 128(4), pp. 493-502.
- Valdes, A., Marteinsdottir, B. & Ehrlen, J. (2019). A natural heating experiment: Phenotypic and genotypic responses of plant phenology to geothermal soil warming. *Global Change Biology*, 25(3), pp. 954-962.
- Visser, M.E., van Noordwijk, A.J., Tinbergen, J.M. & Lessells, C.M. (1998). Warmer springs lead to mistimed reproduction in great tits (*Parus major*). *Proceedings of the Royal Society B-Biological Sciences*, 265(1408), pp. 1867-1870.
- Vitasse, Y. & Basler, D. (2013). What role for photoperiod in the bud burst phenology of European beech. *European Journal of Forest Research*, 132(1), pp. 1-8.
- Vitasse, Y., Hoch, G., Randin, C.F., Lenz, A., Kollas, C., Scheepens, J.F. & Korner, C. (2013). Elevational adaptation and plasticity in seedling phenology of temperate deciduous tree species. *Oecologia*, 171(3), pp. 663-678.
- Woodward, R.C., Waldie, J.S.L. & Steven, H.M. (1929). Oak mildew and its control in forest nurseries. *Forestry*, 3, pp. 38-56.
- Zohner, C.M., Mo, L.D. & Renner, S.S. (2018). Global warming reduces leaf-out and flowering synchrony among individuals. *Elife*, 7.
- Zohner, C.M. & Renner, S.S. (2019). Ongoing seasonally uneven climate warming leads to earlier autumn growth cessation in deciduous trees. *Oecologia*, 189(2), pp. 549-561.

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Popular science summary

A warming climate may shift the time period when species are active. Some species are expected to shift their activity period more than others, which could impact the synchrony between species. For instance, if plant-feeding insects emerge in spring before their favourite tree species leaf out, they might start feeding on other trees which have already produced leaves. Such shifts could influence the overall structure of species communities. In addition, for species with a wide geographical distribution, populations may be adapted to the local climate and respond differently across its range to changing climates.

In this thesis, I investigated how temperature influences the activity period of different species and how a shift in activity is reflected in the structure of a particular insect community. By studying the pedunculated oak, its plant-feeding insects and predatory insects, I ask i) How does temperature influence the timing of insect activity, leaf out in spring, and autumn leaf coloration of oaks? Do individuals with different geographical origin vary in how temperature influences insect activity and leaf out in oaks? ii) How does the timing of leaf out and autumn leaf coloration influence the community of insect herbivores?

I found that both insect species and individuals of different geographical origin within a species responded differently to temperature. Oaks and insects exposed to warm winter temperatures generally required higher temperatures in spring to become active. In addition, warm temperatures during summer and autumn delayed autumn leaf coloration among oaks. Also, both the timing of leaf out and autumn leaf coloration of oaks had an impact on the herbivore community structure. Here, herbivores active in spring and autumn were mostly influenced, whereas herbivores active during the summer were less sensitive to climate change. For instance, oaks flushing early in the season were able to escape infestation by the outbreaking brown oak slender moth, and some species of *Phyllonorycter* moths preferred oaks that stayed green for a long time in autumn.

My results suggests that the synchrony between interacting species could change in a warmer climate, especially among species active in spring and autumn. As a consequence, species might start to interact more with species with which they did not

interact before. Such changes could impact species communities. Since individuals of different geographical origin varied in their response to temperature, communities in different regions are likely to differ in their responses. These differential responses complicate the exact prediction of how shifts in climate translate to shifts in community composition and structure.

Populärvetenskaplig sammanfattning

Ett varmare klimat gör att arter förskjuter den period när de är aktiva. Dock kan vissa arter förskjuta sin aktivitet mer än andra, vilket gör att arter kan komma i otakt med varandra. Tänk dig till exempel att en växtätande insekt vaknar till liv innan knopparna har spruckit på dess favoritträd. Då kan den börja äta av en annan trädart där knopparna spruckit istället, vilket kan få konsekvenser för artsamhällets struktur. Ännu mer komplicerat blir det ifall arter har stor geografisk spridning och är anpassade till det lokala klimatet. Då kan inte bara arter utan även individer av olika ursprung reagera olika på ett varmare klimat.

Syftet med denna avhandling var att undersöka när arter blir aktiva i ett varmare klimat, och hur detta avspeglas i artsamhället. Genom att studera eken, dess växtätande insekter och rovinsekter, utredde jag två frågor i) Hur påverkar temperaturen den tidpunkt då insekter blir aktiva på våren, samt knoppsprickning och höstlövsfärgning hos ek? Skiljer sig tidpunkten för dessa händelser mellan individer av samma art, fast med olika geografiskt ursprung? ii) Hur påverkar tidpunkten för knoppsprickning och höstlövsfärgning samhället av växtätande insekter?

Jag upptäckte att insekter reagerade olika på temperaturförändringar, och blev aktiva under olika tidpunkter på våren när temperaturen förändrades. Ifall vintern var varm krävdes mer värme på våren innan vare sig ekar och insekter blev aktiva. Dessutom resulterade en varm temperatur på sommaren och hösten i att eklöven var gröna längre in på hösten. Jag upptäckte också att individer av olika geografiskt ursprung reagerade olika när temperaturen förändrades. Både tidpunkten för knoppsprickning och höstlövsfärgning förändrade artsamhället av växtätande insekter. Mest påverkades de insekter som är aktiva under vår och höst, medan insekter aktiva under sommaren var relativt okänsliga för förändringarna. Till exempel så var ekar med tidig knoppsprickning inte alls attackerade av den annars så talrika snedstreckade ekstyltmalen. Även vissa guldmalar trivdes extra bra på ekar som hade gröna löv långt in på hösten.

Mina resultat tyder på att timingen mellan arter kan förändras i ett varmare klimat, speciellt mellan arter aktiva under vår och höst. Detta innebär att arter kan börja samskola mer med andra arter, vilket kan få konsekvenser för artsamhället. Eftersom individer av

olika geografiskt ursprung reagerar olika på förändringar i temperatur, kan effekterna på artsamhället skilja sig mellan olika platser. I förlängningen betyder detta att arter kommer att förskjuta sin aktivitet olika mycket i ett varmare klimat. Hur mycket det kommer att påverka olika artsamhällen är svårt att förutsäga.

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Global warming could cause interacting species to shift their phenology at different rates, changing interaction strength and altering community structure. This thesis explores how a tritrophic community of *Quercus robur* and associated organisms respond to temperature change. Shifts in climatic conditions are shown to affect phenological synchrony between trophic levels, thereby altering community structure. Differential change at the level of both species and populations thus emerges as a major challenge when predicting community-level consequences of phenological change..

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