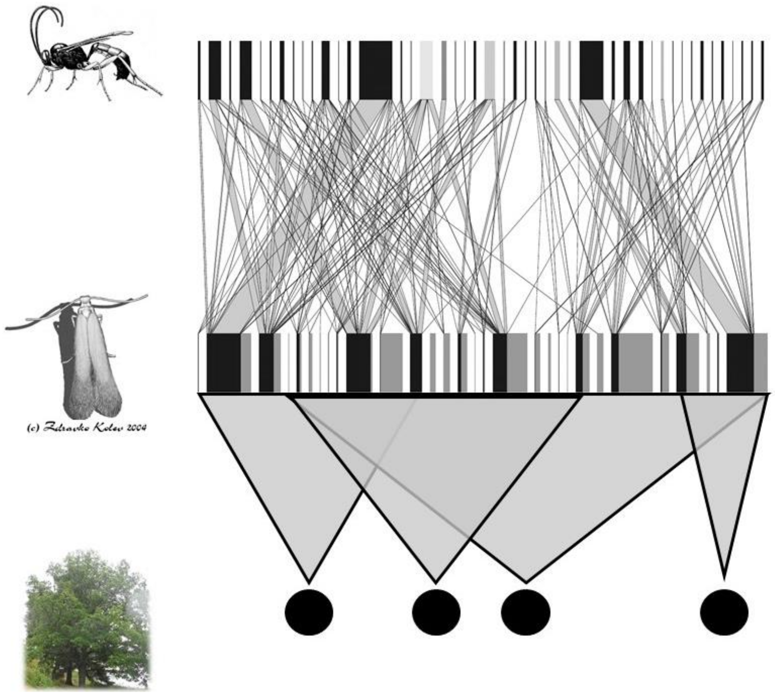
Sveriges lantbruksuniversitet
Swedish University of Agricultural Sciences
Department of Ecology

Temporal asynchrony due to climate change and its impact on host–herbivore–predator interactions

Adam Ekholm



Introductory Research Essay

Department of Ecology

SLU
Uppsala 2017

Abstract

Emission of greenhouse gases is causing a shift in the global climate. As a consequence, organisms have altered their spatial and temporal distribution. For species temporally synchronized by biotic interactions, a shift in temporal distribution might lead to reduced synchrony. This is especially pertinent in terms of phenological events, as for example a herbivore needs to match its activity with the flowering of its host plant. In this paper, I specifically focus on temporally synchronized biotic interactions in insect host-herbivore-predator communities. The main objective is to investigate four questions: i) How temperature and precipitation affect the development of species; ii) How temporal asynchrony affects single biotic interactions between plants – herbivores and herbivores – predators iii) How temporal asynchrony affects more extensive, multitrophic-level communities; and iv) How biotic interactions will change in the future. A majority of the studies covered in this paper suggests that individual species will increase their development rate if temperature is increased. Moreover, temperature seems to have a more pronounced impact on development rate than humidity condition does. The rate of development increase could vary among species, indicating that temporal asynchrony among currently interacting species could become more common in the future. A major related issue is then to determine if species will be able to locally adapt to the new prevailing conditions, whether they will go extinct or whether they will start interacting more with other species. If selective pressure is hard and genetic variation sufficient, then species may stay synchronized. Furthermore, it is important to assess how temperature will increase in the future. More fluctuating and extreme temperatures might alter species responses. To address these questions we need more studies examining: i) synchrony in herbivore–predator interactions and across several trophic levels; ii) the capacity of synchronized species to adapt to new conditions; and iii) species responses to fluctuating and extreme temperatures.

1. **Introduction**

The emission of greenhouse gases has already impacted the global climate. Global warming has resulted in temperature elevations, a rise of the global sea level and an acidification of the oceans (IPCC 2014). The warming experienced so far is minor relative to future scenarios, but an impact on wildlife is already apparent: species have rapidly evolved (Miller-Struttmann et al. 2015), the flowering season has shortened in the arctic (Schmidt et al 2016), plant phenology has shifted (Menzel et al. 2006) and both tree lines and plants have advanced in altitude (Grabherr et al. 1994; Harsch et al. 2009). If emissions of greenhouse gases continue, more difficulties can be expected in the future, such as extreme weather events, a further rise of the sea level and an increased frequency of flooding events (IPCC 2014). This could affect ecosystems (Sukumar et al. 1995; Wu et al. 2011) with outcomes such as habitat loss, increased amount of endangered species (Dirnbock et al. 2011; Thuiller et al. 2005) and alterations in biotic interactions (Zarnetske et al. 2012).

In response to a changing climate, the lifecycle of organisms attuned to their environment might shift in time (Menzel et al. 2006; Schmidt et al. 2016) or space (Grabherr et al. 1994). In this context, it is of particular interest to study how organisms synchronized with each other in terms of biotic interactions respond to temporal shifts caused by global warming. These synchronized biotic interactions are common in biological communities. For example, the timing of algal blooming is of great importance for survival of haddock larvae (*Melanogrammus aeglefinus)* (Platt et al. 2003); the timing of budburst in oak (*Quercus robur*) is of great importance to the survival of winter moth larvae (*Operophtera brumata*) (VanDongen et al. 1997) and the timing of peak ant activity is of key importance for dispersal of myrmechcochorous plant seeds (Guitian & Garrido 2006). This raises a particularly interesting question: in response to climate change, will synchronized biotic interactions stay in synchrony, or slide out of phase and become desynchronized (Fig.1A)?

Communities consisting of plants, herbivorous insects and their predators provides interesting opportunities to study synchronized biotic interactions (Fig.1A). In these communities, herbivore fitness and population dynamics depend on how well they match plant development (Forkner et al. 2008; Singer 1972; van Asch et al. 2007). For example, *O. brumata* development is timed with the budburst of *Q. robur* (VanDongen et al. 1997) and *Q.robur* is host to over 200 species of Lepidoptera. Furthermore, most of the insect biomass on oak in spring consists of Lepidoptera larvae (Southwood et al. 2004), indicating that spring phenology of *Q.robur* is important for lepidopteran performance.

Apart from plant-herbivore interactions, predators and parasitoids can regulate herbivore insects by top-down influences (Gomez & Zamora 1994) and indirectly enhance plant performance (Dyer et al. 2013). The potential of parasitoids to suppress herbivores has made them highly useful as biological control agents (Hawkins & Cornell 1994; Lee & Pemberton 2005; Neuenschwander 2001). Asynchrony in the herbivore-parasitoid interaction may result in a loss of this service. Conversely, a more closely synchronized interaction may result in low survival of herbivores, which in the next generation could result in parasitoid extinction due to insufficient host herbivores. These scenarios could be considered to be especially true for herbivores which have a few discrete generations per year and that are only susceptible to parasitoids during a short time window.

Besides single biotic interactions between two trophic levels, an organism is also subjected to direct or indirect interactions from other trophic levels. For example, predators and parasitoids can often enhance the performance of plants via suppression of herbivores (Gomez & Zamora 1994; Schmitz et al. 2000). To study how a species respond to alterations in biotic and abiotic variables, it is therefore important to assess the response of the whole community including the different trophic levels. Furthermore, the community often consists of a highly complex web of interactions (Fig.1B) and it is easy to imagine how alterations in one interaction could have cascading effects that alter the structure of the entire food web.

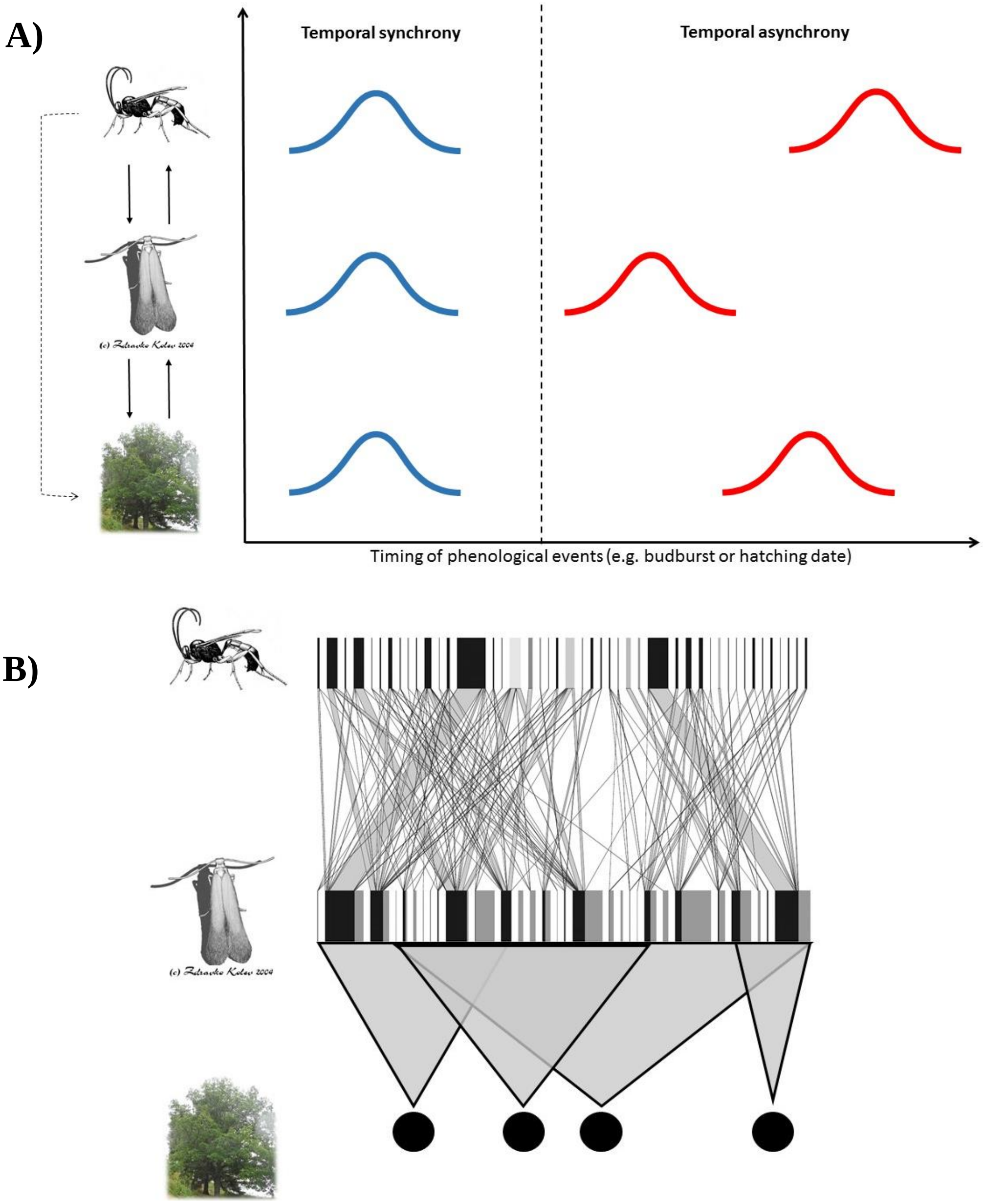


Fig. 1. A) Tritrophic food chain consisting of a plant, an herbivorous insect and its predator (a parasitoid). The food chain is characterized by direct (solid arrows) and indirect interactions (dashed arrow). The phenology of each trophic level is displayed in the graph for two different scenarios; where interactions between the three trophic levels are synchronized (blue normal distribution curves) and desynchronized (red normal distribution curves). B) Tritrophic food web consisting of plants, herbivore insects and their predators (parasitoids). Note that the food web is much more complex than the simplified food chain of (A), as it encompasses all of the interactions within the community.

Future climate change could alter the temporal activity period of species, which in the worst case would lead to asynchrony in biotic interactions. The asynchrony could impact local food web structure and lead to extinctions, trophic cascades and pest outbreaks. In this paper I aim to assess how global warming-induced alterations in temperature and precipitation affect plant-herbivore-predator communities. To explore these effects, I will divide this paper into three different parts and assess (Fig.2): i) How temperature and precipitation affect the development of species. I will do this by investigating budburst of plants, respectively development rate of insects and their emergence success. ii) How temporal asynchrony affects single biotic interactions between plants–herbivores and herbivores–predators. iii) How temporal asynchrony affects more extensive, multitrophic-level communities. iv) How biotic interactions will change in the future.

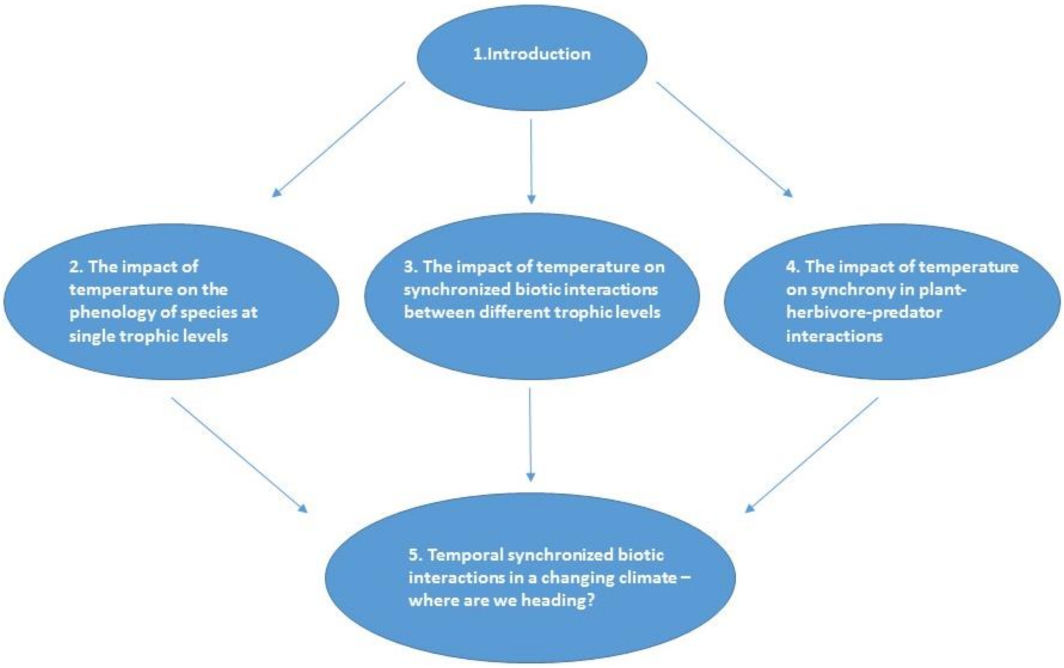


Fig.1. The essay is divided into five parts, where parts 2,3 and 4 deal with synchrony between single- and multiple trophic levels. In the fifth and final part, I summarize how biotic interactions may change in the future.

2. **The impact of temperature on the phenology of species at single trophic levels**

2.1 *Direct effects of temperature and precipitation on plants*

Future climatic scenarios predict a global increase in temperature and changes in precipitation (IPCC 2014), both important for insect and plant development. In plants, phenological events such as flowering, fruiting and leafing have started to occur earlier in the season (Menzel et al. 2006). However, the response of plants to global warming differs among species. For example, in a climate chamber experiment with tree saplings, Fu et al. (2013) found that leaf unfolding was more sensitive to temperature changes in *Q. robur* compared to birch (*Betula pendula*) or beech (*Fagus sylvatica*). Interestingly, in the warmest treatment, the authors observed that the increase in leaf unfolding sensitivity was drastically reduced in both *Q. robur* and *F. sylvatica*, but not in *B. pendula*. The effect on plants differs according to life history strategy. The phenology of early-flowering plants and annuals appears to be most affected by warming, while early-flowering insect pollinated species are more strongly affected than wind pollinated species (Fitter & Fitter 2002). Temperature rather than water availability appears to be the major determinant of phenological patterns (Morin et al.

2010; Studer et al. 2005), although precipitation could be of regional importance in currently arid areas (Studer et al. 2005).

2.2 *Direct effects of temperature and humidity on insect development*

Irrespective of plants, temperature also affects the development rate of insects. For example, development time of the lepidopteran *Polygonia c-album* has been found to be strongly dependent on temperature. For this species, an increase from 17 to 23 degrees almost halved the development time (Nylin 1992). This pattern has also been observed in other studies of Lepidoptera (e.g. Bryant et al. (1999)). de Pedro et al. (2016) found that high and low temperatures (15 and 30 degrees, respectively) significantly affected the development and survival rate of the parasitoid *Aganaspis daci*. Furthermore Arakawa and Namura (2002) reared three parasitoid species (*Trissolcus spp.*) at different temperatures. They found that only a few of the individuals exposed to 15 degrees emerged successfully. However warmer temperatures, up to 27.5 degrees, increased the development rate.

Development rate of insects can likewise be affected by humidity. At low humidity, Gross (1988) found fewer emerged adults of the parasitoid *Trichogramma pretiosum* per host egg. By contrast, Duale (2005) found a strong effect of temperature but no effect of humidity on the development of the parasitoid *Pediobius furvus*. Relative humidity within the range of 60-90% appears to be beneficial for insects (Gross 1988; Orr et al. 1985). Hagstrum and Milliken (1988) compiled literature published on different species of Coleoptera and suggested that temperature is more important than moisture for determining the rate of their development. However, moisture is not irrelevant and must also be taken in to account when determining the development rate.

Since development rates of species do not respond in a uniform way, it is likely that species might respond differently to global warming. Bale et al. (2002) argued that developmental response to higher temperatures is likely to increase faster for univoltine species than for species with a longer generation span. Moreover, an increase in temperature could affect the relative frequency of generations and produce an additional annual generation (Altermatt 2010; Pollard & Yates 1993; Poyry et al. 2011). As a result, this might alter the temporal distribution of species, which in turn could affect with which other species they interact.

2.3 *Effects of temperature on the overall phenology of different taxa and trophic levels*

A wealth of studies have explored the effects of temperature on the phenology of organisms (Crick et al. 1997; Forrest 2016; Meineke et al. 2014; Menzel et al. 2006; Parmesan 2007; Thackeray et al. 2016). The general trend is that phenological events advance in time as the climate gets warmer. However, the specific rate of advance varies among species. Thackeray et al. (2016) analyzed several long term data sets covering the phenology of a wide range of different taxa. They created three different climate sensitivity profiles (CSP) to which they matched the different phenological time series. The CSP most consistent with species phenology was characterized by two periods of climate sensitivity; one early season period (far away from the phenological event) and one late season period (close to the phenological event). Warming in early season caused a delay in the phenological event, while warming in late season hastened the phenological event. According to the study, early season warming had the greatest impact on mammals and freshwater phytoplankton. It has also been shown that early season temperature (or winter temperature) has an effect on insects.

For example, poor emergence success was observed for the butterfly *Anthocharis cardamines* if it was exposed to an insufficient number of chilling days. Subsequently, few chilling days increased variation in emergence dates, while a longer chilling period increased emergence synchrony (Stalhandske et al. 2015). In addition, Thackeray et al. (2016) demonstrated that among the species in their data set, the phenology of primary consumers advances more rapidly than that of primary producers and secondary consumers. This implies that synchrony between different trophic levels might be disrupted by changing temperatures.

3. **The impact of temperature on synchronized biotic interactions between different trophic levels**

3.1 *Synchrony in plant-herbivore interactions*

A wealth of plants and herbivores are synchronized through biotic interactions. For some herbivore species, host plants are only available as a food source during a short time window (Ivashov et al. 2002; Singer 1972). In the context of *Q. robur*, leaf texture and chemical composition vary over the vegetation season. The leaves become less nutritious and develops a tougher surface as the plant develops, making it less beneficial for larvae to feed on older leaves (Feeny 1970; Ivashov et al. 2002; Salminen et al. 2004). For a herbivore, this implies that it needs to be active within a critical time window, after the leaf has started to flush and before the leaf loses most of its nutrients or becomes too tough. An alteration in synchrony of these interactions could affect insect performance and is potentially of great importance (Mopper & Simberloff 1995; Tikkanen & Julkunen-Tiitto 2003). Forkner et al. (2008) found that spring-feeding Lepidoptera associated with *Quercus alba* and *Quercus velutina* were characterized by higher population variability than were summer-feeding species, implying that synchrony with budburst is of great importance for population dynamics.

In response to climate change, synchronous interactions between plant and herbivore (and also between the herbivore and parasitoid) could shift through three scenarios: synchrony is maintained, species become more synchronized or species become desynchronized (Fig.3). Maintaining synchrony will essentially maintain the *status quo*, with no implications for population dynamics. In contrast, an increase in synchrony could have a significant impact, since this is likely to increase the fitness of the consumer (Tikkanen & Julkunen-Tiitto 2003; van Asch et al. 2007). This could result in a pest outbreak with an increased herbivore population and heavily defoliated host plants. The final scenario is that species become desynchronized, which would result in the extinction of species specialized on each other. For polyphagous species, asynchrony with the main plant may result in a switch to other host plants (Liu et al. 2011; Uelmen et al. 2016). This in turn might reduce the fitness of the local population, in case the alternative host plants are of lower quality than the primary host (Tikkanen et al. 2000).

It is important to remember that even species synchronized with each other are not necessarily in perfect synchrony. In fact, they could be slightly desynchronized in the natural state. Singer (1972) found that 23 of 30 egg-masses laid by the butterfly *Euphydryas editha* hatched after the host plant had gone through senescence, resulting in no larvae from these clutches reaching the third instar. Furthermore van Asch and Visser (2007) found that eggs of the winter moth *O. brumata* have for several years been hatching before the budburst of its host plant. In response to climate change, such populations might be particularly sensitive to additional asynchrony.

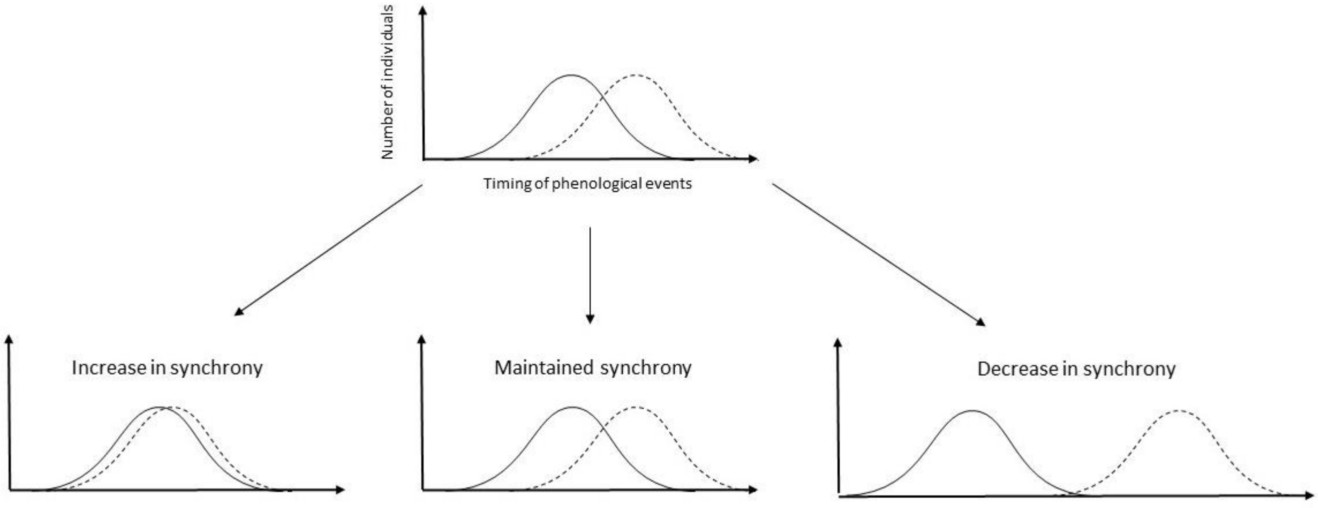


Fig. 3. Three scenarios for changes in phenological timing of a resource (bold line) and its consumer (dashed line) under climate change; species become more synchronized, synchrony is maintained, or species become desynchronized.

Different studies have yielded somewhat disparate results in terms of how climate change affects synchronized biotic interactions between plants and herbivores. Thackeray et al. (2016) suggested that under likely climatic scenarios, insects are in general more likely to advance their phenology than many other taxa. In a meta-analysis covering the northern hemisphere that included time series ranging over at least 10 years between the years 1951-2001, Parmesan (2007) showed that butterfly emergence had advanced three times faster than the first flowering of herbs. Accordingly, Visser and Holleman (2001) suggested that *O. brumata* is advancing faster than its host plant *Q. robur* in response to warmer climate. However, Buse and Good (1996) suggested that these species maintain synchrony in a warmer climate.

Contrary to these results, Schwartzberg et al. (2014) examined synchrony between the tent caterpillar *Malacosoma disstria* and its respective host plant under experimental warming. They found that both caterpillars and plants advanced in phenology under warming, but that plants advanced more than caterpillars. This experiment resulted in a more synchronized interaction between plant and caterpillar. In a similar study of the same species, Uelmen et al. (2016) found that plant phenology advanced more than caterpillar phenology but the interaction did not become more synchronized. In a study conducted by Liu et al. (2011), experimental warming delayed the emergence and increased the density of the herbivore *Melanchra pisi*, while its host plants advanced in phenology. However, these studies were only short-term experiments and provide no information on long-term effects within these study systems. Nevertheless it is a concern that the phenology of plants and herbivores might switch at different rates. This concern would be even greater if the same pattern were to be observed across other interactions, for example between herbivores and predators.

3.2 *Synchrony in herbivore – predator interactions*

In accordance with shifts observed in plant-herbivore interaction, it is likely that herbivore-predator interaction could become desynchronized as a response to warmer climate. For example, one study explored the larvae of the Glanville fritillary butterfly (*Melitaea cinxia*), which can accelerate their development in spring by locating sunny spots on cold days (i.e. basking behavior). In contrast, its parasitoid *Cotesia melitaearum* is in an immobile pupal stage during spring. This allows *M. cinxia* to find temporal refuge by speeding up its development in cold springs, reaching an instar not vulnerable to parasitism. In warm springs, basking behavior is less beneficial, leading to higher synchronization between the larvae and the parasitoid (Van Nouhuys & Lei 2004). With an increase in synchrony, *C. melitaearum* could diminish populations or even cause the local extinction of *M. cinxia* (Lei & Hanski 1997). Conversely, Van Nouhuys and Lei (2004) found *M. cinxia* populations to be little affected by the population size of *C. melitaearum*. In another study, Klapwijk et al. (2010) investigated the interaction between the parasitoid *Cotesia bignellii* and its host herbivore *Euphydryas aurinia*. Here, *C. bignellii* development time varied widely and was not affected by increased temperature. Although the development time of *E. aurinia* was affected by temperature, the two species still maintained synchrony. Another study from North America has investigated the synchrony between the pest beetle *Oulema melanopus* and its parasitoid *Tetrastichus julis*. In cool springs, the beetle population sustained a higher proportion of parasitism. But in warmer springs, larvae emerged later in relation to the parasitoid, resulting in asynchrony between host and parasite and thus a lower parasitism rate (Evans et al. 2013). In concordance with Van Nouhuys and Lei (2004), Evans et al (2013) thus suggest that differential impacts of environmental conditions on the host (which is sensitive to aboveground conditions) and the parasitoid (which is sensitive to soil conditions) might set the stage for asynchrony.

A modelling exercise by Godfray et al. (1994) suggested that constant temporal asynchrony between years acts as a stabilizing factor on herbivore-parasitoid interaction. However, large yearly fluctuations could destabilize the interaction and lead to extinction of one of the two species, especially when parasitoids that usually emerge late suddenly occur early in a particular year. For those interactions that will shift their relative timing in response to climate change, a key question is whether interacting species can find a new stable equilibrium. If not, it is likely that one of them will become extinct.

In urban areas, Meineke et al. (2014) observed a phenological mismatch between the herbivore scale insect *Parthenolecanium quercifex* and a part of its parasitoid community. *P. quercifex* was able to oviposit at an earlier date in warmer parts of the city, an ability not matched by the parasitoids. Furthermore, in warmer areas parasitized individuals produced twice as many eggs as unparasitized individuals. However, the parasitism rate did not differ between the warm and cold sites.

For birds, it is critical to match the timing of spring egg clutches with peak food availability (see Perrins (1991) for an example). Visser et al. (1998) compared egg-laying date of great tits *Parus major* and caterpillar peak date in a dataset ranging between the years 1973-1995. They found an advance in caterpillar peak date, but not in *P. major* egg laying date. This has led to asynchrony between the two species, which might result in lower numbers of surviving fledglings.

4. The impact of temperature on synchrony in plant-herbivore-predator interactions

Since organisms are members of larger communities, bipartite interactions between specific plants and herbivores, or between herbivores and their predators, are but a subset of all interactions in the community. Adding a third trophic level increases complexity, because the abundance of the consumer is not only affected by the availability of resources (bottom-up force) but also on the predation rate (top-down force). Both et al. (2009) investigated phenological changes in a community consisting of four trophic levels (trees, caterpillars, passerines, avian predator). In this context, all three predator-prey interactions became less synchronous over time. No such reduced synchrony was observed between the plant and the herbivore, but this has previously been shown to occur (VanDongen et al. 1997). The decrease in synchrony might result from constraints in adapting to the new phenology for the predator, but may also arise as an adaptation for the prey to escape from predation. In a closed experiment inside incubators, Dyer et al. (2013) studied the impact of increased temperature in a tritrophic food web. Interestingly, in this system parasitoids had a negative effect on the biomass of the host plant of their target herbivores. This was explained by a temporal decoupling of the herbivore-parasitoid interaction, resulting in herbivore pupation before the parasitoids were able to eclose. Furthermore, this led to a higher consumption rate among parasitized herbivores, but with no associated herbivore mortality. Higher consumption rate among parasitized herbivores coincide with other studies in plant-herbivore-parasitoid interactions, e.g. higher seed predation as observed by Xi et al. (2015), thus contradicting the belief that predators and parasitoids via indirect interactions facilitate plant performance (Gomez & Zamora 1994; Schmitz et al. 2000).

In a warming experiment, de Sassi and Tylianakis (2012) discovered that warming increased herbivore biomass significantly more than plant or parasitoid biomass. When nitrogen was added to the warming treatment, both plant and herbivore biomass had a similar and higher increase compared to parasitoid biomass. Their results suggest that herbivores will benefit most from a warmer and nitrogen-rich environment.

If parasitoids are not able to eclose before pupation, this could lead to poor recruitment of parasitoids in the next generation, resulting in local parasitoid extinction. In such a scenario, top down control by the parasitoid will be reduced, thus emphasizing the importance of studying the outcome in the plant-herbivore interaction.

5. **Temporal synchronized biotic interactions in a changing climate – where are we heading?**

This literature survey suggests that elevated temperatures reduce the development time of both plants and insects. Furthermore, it reveals that humidity is an important determinant of development rate – although not as important as temperature. The overall consequence of climate change is that the majority of taxa has become active earlier in the season. Regarding the synchrony among trophic levels, most studies show changes in synchrony in response to warmer temperatures, both between plants and herbivores and herbivores and predators. It is therefore of great importance to understand how species will react; will they locally adapt to the new prevailing conditions, go extinct, or start interacting more with other species and alter local community structure?

5.1 *Local adaptation and adaptive mismatch*

Under rapid climate change, phenotypic plasticity may not suffice for species to adjust to a new set of climatic conditions. According to Visser (2008), it is thus important to examine how quickly species are able to genetically adapt. Local adaptation to the new climate is essential because cues that accurately predict present conditions might be misleading in the future climate. Moreover, it has been argued that populations from warmer locations do not need to adapt to a warmer temperature. These populations will simply migrate to a colder climate when the local climate becomes warmer. This is not completely true, although temperature conditions are suitable migrating species will need to adapt to local conditions beyond merely temperature (see more in Visser (2008)).

So what determines whether species will be able to adapt to the new conditions and stay synchronized? If a species is characterized by a lot of genetic variation and subject to selection pressure, it is more likely to adapt to the new phenology of its host (van Asch et al. 2007). By using a quantitative genetic model and comparing it to a long term data set and by conducting experiments, van Asch et al. (2013) suggested that *O. brumata* has genetically adapted to match the phenology of its host plant *Q. robur*. Few studies have demonstrated this kind of rapid adaptation, but genetic change in response to climate change has been previously shown in the mosquito *Wyeomyia smithii* (Bradshaw & Holzapfel 2001).

Even though species are able to adapt to the new climate, the synchronized interaction might not stay intact. Hence, adaptive mismatches have been suggested to occur in a predator-prey community. Visser et al. (2012) reviewed several studies of shifts in synchrony between a bird and its food resource (one article referred to the host as not being a food resource). Most of the bird species were able to maintain interaction synchrony when their individual phenologies were shifted. Nevertheless, a few of the bird-prey interactions were not able to maintain synchrony. The authors suggested that the reason for this could either be that species respond differently to different cues, such as spring temperatures (cue hypothesis), or that other factors reduce the total fitness of the bird if it remains synchronized with the food source (constraint hypothesis). If the latter hypothesis is correct, then the interactions might have adapted to a temporal mismatch. In other words, other constraints reduce the fitness of species if they stay synchronized. An illustrative example of this is the timing of bird egg laying and peak density of insects. If the peak density of insects starts to occur earlier, then birds will have to lay their eggs earlier in spring. However, due to temperature or other constraints, an early clutch might reduce the survival rate of offspring. This could make it more beneficial to become somewhat desynchronized with the peak density of insects and continue to lay eggs at a later stage. Subsequently, the temporal overlap between the predator and prey will be decreased and the top down pressure on the herbivore relaxed, possibly resulting in higher numbers of herbivores.

Adaptive mismatches may also occur in the insect community. As an example thereof, Doi et al. (2008) showed that the butterfly *Pieris rapae* and some of its host plants among *Prunus spp.* responded to temperature cues occurring within different time periods. The timing of flower unfolding in *Prunus spp.* responded to temperature 30-40 days prior to this event, whereas the emergence of *P. rapae* responded to temperature only 15 days previously. Since temperatures at this location showed a significant increase only 30-40 days prior to flower unfolding but not 15 days prior to butterfly emergence, this led to reduced synchrony between the two species. Hence for the butterfly to maintain synchrony with its host plant, it will need to adapt to the new conditions and emerge during an earlier, and probably colder, part of the spring. This kind of heterogeneous increase in temperature during different parts of the spring could be accentuated in the future. For example, in Sweden climate change is expected to increase temperatures differently across seasons (Kjellström et al. 2014). If this is true at a smaller temporal scale, some periods in spring might increase more in temperature than other. If the spring phenology of species at different trophic levels respond to temperature within different time periods, then future climate change might induce an adaptive mismatch, resulting in shifts in synchrony between species.

5.2 *Alterations in community structure*

A worrying consequence of shifting phenologies is that species might change with whom they interact, or alter the strength of an interaction. Moreover, species previously isolated in time might now come into contact. This could have major consequences in food webs encompassing complex interactions. For example, Stålhandske et al. (2016) studied host plant preferences of the butterfly *Anthocharis cardamines* originating across several different geographical regions. Interestingly, female butterflies exhibited no consistent preference in terms of host plant species. What they did choose was the phenological stage (and height) of the host plant. Likewise, a warming experiment conducted by Liu et al. (2011) revealed a host switch by the herbivore *Melanchra pisi* to a host plant which it had rarely exploited before. This drastically reduced the reproductive capacity of the new host plant. Similar observations were made by Uelmen et al. (2016), who noticed that the phenology of *Malacosoma disstria* was not advancing at the same pace as that of its host plants. Furthermore the authors suggested that in the future this could lead to a host substitution, with the herbivore switching to later developing and synchronous plants.

5.3 *Extreme weather events and sub-additive effects*

In the future, more extreme and fluctuating temperatures could exert impacts on insect responses different from those caused by changes in average temperature. For example, species and sexes might differ in their tolerances to extreme low and high temperatures (Le Lann et al. 2011). This implies that extreme temperatures might benefit certain species more than others. Ma et al. (2015) found that extreme temperatures can affect community structure and benefit the relative abundance of certain aphid herbivores. Moreover, an increase in the severity and frequency of extreme temperatures negatively affected demographic measures such as lifespan of and survival in the aphids. A shorter lifespan might result in a reduction in the temporal overlap between interacting species, leading to a greater chance of asynchrony. Moreover, skews in sex ratio could be disadvantageous by reducing the chances of the more abundant sex to find mates.

Climate change will not only alter temperature, but also other variables such as CO_2 concentrations and precipitation regimes (IPCC 2014). To date, many studies have focused exclusively on responses to single variables, e.g. temperature (Liu et al. 2011; Schwartzberg et al. 2014; Uelmen et al. 2016). Thus focus should be increasingly directed towards the effect of several drivers in combination. For example, Romo and Tylianakis (2013) studied an herbivore-parasitoid interaction under three environmental regimes: elevated temperature, drought and the combination of both. Interestingly, they found that elevated temperature and drought separately increased parasitism rates in herbivores. However the combination of these drivers led to a sub-additive effect and parasitoids were not able to control herbivore population when the drivers were combined. Consequently, it can be concluded that the effect of climate change on species interactions might differ depending on how many drivers that are affected, and the interplay between them.

5.4 *Conclusions*

Several studies indicate that organisms will change their temporal activity in response to climate change. While the main driver of these shifts will be temperature, it is important to take all drivers of climate change into consideration – in particular since the combined effect of several drivers might differ from the additive effect of single drivers. For species communities bound by biotic interactions, it is hard to predict the outcome of climate change. But studies indicate that both different taxa and trophic levels might respond dissimilarly to increased temperature, thus setting the stage for temporal decoupling. However, more studies are needed that investigate synchrony in host - herbivore – predator interactions. With increasing temperatures, it becomes essential for organisms to genetically adapt to the new climate. If selective pressure is high and genetic variation sufficient, then species may stay synchronized. Nonetheless, future interactions might still be threatened by adaptive mismatches. Species that cannot adapt might drift apart, go extinct or shift towards interacting with new species, thereby resulting in a shift in local community structure. Finally, it is important to assess how both the mean and the variance in temperatures will increase in the future, since they may have different impacts on species and their interactions.

References

Altermatt, F. 2010. Climatic warming increases voltinism in European butterflies and moths. Proceedings of the Royal Society B-Biological Sciences **277**:1281-1287.

Arakawa, R., and Y. Namura. 2002. Effects of temperature on development of three Trissolcus spp. (Hymenoptera: Scelionidae), egg parasitoids of the brown marmorated stink bug, Halyomorpha halys (Hemiptera: Pentatomidae). Entomological Science **5**:215-218.

Bale, J. S., G. J. Masters, I. D. Hodkinson, C. Awmack, T. M. Bezemer, V. K. Brown, J. Butterfield, A. Buse, J. C. Coulson, J. Farrar, J. E. G. Good, R. Harrington, S. Hartley, T. H. Jones, R. L. Lindroth, M. C. Press, I. Symrnioudis, A. D. Watt, and J. B. Whittaker. 2002. Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. Global Change Biology **8**:1-16.

Both, C., M. van Asch, R. G. Bijlsma, A. B. van den Burg, and M. E. Visser. 2009. Climate change and unequal phenological changes across four trophic levels: constraints or adaptations? Journal of Animal Ecology **78**:73-83.

Bradshaw, W. E., and C. M. Holzapfel. 2001. Genetic shift in photoperiodic response correlated with global warming. Proceedings of the National Academy of Sciences of the United States of America **98**:14509-14511.

Bryant, S. R., J. S. Bale, and C. D. Thomas. 1999. Comparison of development and growth of nettle-feeding larvae of Nymphalidae (Lepidoptera) under constant and alternating temperature regimes. European Journal of Entomology **96**:143-148.

Buse, A., and J. E. G. Good. 1996. Synchronization of larval emergence in winter moth (Operophtera brumata L) and budburst in pedunculate oak (Quercus robur L) under simulated climate change. Ecological Entomology **21**:335-343.

Crick, H. Q. P., C. Dudley, D. E. Glue, and D. L. Thomson. 1997. UK birds are laying eggs earlier. Nature **388**:526-526.

de Pedro, L., F. Beitia, B. Sabater-Munoz, J. D. Asis, and J. Tormos. 2016. Effect of temperature on the developmental time, survival of immatures and adult longevity of Aganaspis daci (Hymenoptera: Figitidae), a natural enemy of Ceratitis capitata (Diptera: Tephritidae). Crop Protection **85**:17-22.

de Sassi, C., and J. M. Tylianakis. 2012. Climate Change Disproportionately Increases Herbivore over Plant or Parasitoid Biomass. Plos One **7**.

Dirnbock, T., F. Essl, and W. Rabitsch. 2011. Disproportional risk for habitat loss of high-altitude endemic species under climate change. Global Change Biology **17**:990-996.

Doi, H., O. Gordo, and I. Katano. 2008. Heterogeneous intra-annual climatic changes drive different phenological responses at two trophic levels. Climate Research **36**:181-190.

Duale, A. H. 2005. Effect of temperature and relative humidity on the biology of the stem borer parasitoid Pediobius furvus (Gahan) (Hymenoptera : Eulophidae) for the management of stem borers. Environmental Entomology **34**:1-5.

Dyer, L. A., L. A. Richards, S. A. Short, and C. D. Dodson. 2013. Effects of CO2 and Temperature on Tritrophic Interactions. Plos One **8**.

Evans, E. W., N. R. Carlile, M. B. Innes, and N. Pitigala. 2013. Warm springs reduce parasitism of the cereal leaf beetle through phenological mismatch. Journal of Applied Entomology **137**:383-391.

Feeny, P. 1970. Seasonal changes in oak leaf tannins and nutrients as a cause of spring feeding by winter moth caterpillars. Ecology **51**:565-581.

Fitter, A. H., and R. S. R. Fitter. 2002. Rapid changes in flowering time in British plants. Science **296**:1689-1691.

Forkner, R. E., R. J. Marquis, J. T. Lill, and J. Le Corff. 2008. Timing is everything? Phenological synchrony and population variability in leaf-chewing herbivores of Quercus. Ecological Entomology **33**:276-285.

Forrest, J. R. K. 2016. Complex responses of insect phenology to climate change. Current Opinion in Insect Science **17**:49-54.

Fu, Y. S. H., M. Campioli, G. Deckmyn, and I. A. Janssens. 2013. Sensitivity of leaf unfolding to experimental warming in three temperate tree species. Agricultural and Forest Meteorology **181**:125-132.

Godfray, H. C. J., M. P. Hassell, and R. D. Holt. 1994. the population-dynamic consequences of phenological asynchrony between parasitoids and their hosts. Journal of Animal Ecology **63**:1-10.

Gomez, J. M., and R. Zamora. 1994. top-down effects in a tritrophic system - parasitoids enhance plant fitness. Ecology **75**:1023-1030.

Grabherr, G., M. Gottfried, and H. Pauli. 1994. Climate effects on mountain plants. Nature **369**:448-448.

Gross, H. R. 1988. Effect of temperature, relative-humidity, and free-water on the number and normalcy of trichogramma-pretiosum riley (Hymenoptera, Trichogrammatidae) emerging from eggs of heliothis-zea (boddie) (Lepidoptera, Noctuidae). Environmental Entomology **17**:470-475.

Guitian, J., and J. L. Garrido. 2006. Is early flowering in myrmecochorous plants an adaptation for ant dispersal? Plant Species Biology **21**:165-171.

Hagstrum, D. W., and G. A. Milliken. 1988. Quantitative-analysis of temperature, moisture, and diet factors affecting insect development. Annals of the Entomological Society of America **81**:539-546.

Harsch, M. A., P. E. Hulme, M. S. McGlone, and R. P. Duncan. 2009. Are treelines advancing? A global meta-analysis of treeline response to climate warming. Ecology Letters **12**:1040-1049.

Hawkins, B. A., and H. V. Cornell. 1994. Maximum parasitism rates and successful biological-control. Science **266**:1886-1886.

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.)]. . Page 151, Geneva, Switzerland.

Ivashov, A. V., G. E. Boyko, and A. P. Simchuk. 2002. The role of host plant phenology in the development of the oak leafroller moth, Tortrix viridana L. (Lepidoptera : Tortricidae). Forest Ecology and Management **157**:7-14.

Kjellström, E., R. Abrahamsson, P. Boberg, E. Jernbäcker, and M. Karlberg. 2014. Update regarding the state of the climate from the climate sciences. Klimatologi. Page 65, Norrköping.

Klapwijk, M. J., B. C. Grobler, K. Ward, D. Wheeler, and O. T. Lewis. 2010. Influence of experimental warming and shading on host-parasitoid synchrony. Global Change Biology **16**:102-112.

Le Lann, C., O. Roux, N. Serain, J. J. M. Van Alphen, P. Vernon, and J. Van Baaren. 2011. Thermal tolerance of sympatric hymenopteran parasitoid species: does it match seasonal activity? Physiological Entomology **36**:21-28.

Lee, J. H., and R. W. Pemberton. 2005. Larval parasitoids of the apple ermine moth, Yponomeuta malinellus in Korea, Japan, and China. Biocontrol **50**:247-258.

Lei, G. C., and I. Hanski. 1997. Metapopulation structure of Cotesia melitaearum, a specialist parasitoid of the butterfly Melitaea cinxia. Oikos **78**:91-100.

Liu, Y. Z., P. B. Reich, G. Y. Li, and S. C. Sun. 2011. Shifting phenology and abundance under experimental warming alters trophic relationships and plant reproductive capacity. Ecology **92**:1201-1207.

Ma, G., V. H. W. Rudolf, and C. S. Ma. 2015. Extreme temperature events alter demographic rates, relative fitness, and community structure. Global Change Biology **21**:1794-1808.

Meineke, E. K., R. R. Dunn, and S. D. Frank. 2014. Early pest development and loss of biological control are associated with urban warming. Biology Letters **10**.

Menzel, A., T. H. Sparks, N. Estrella, E. Koch, A. Aasa, R. Ahas, K. Alm-Kubler, P. Bissolli, O. Braslavska, A. Briede, F. M. Chmielewski, Z. Crepinsek, Y. Curnel, A. Dahl, C. Defila, A. Donnelly, Y. Filella, K. Jatcza, F. Mage, A. Mestre, O. Nordli, J. Penuelas, P. Pirinen, V. Remisova, H. Scheifinger, M. Striz, A. Susnik, A. J. H. Van Vliet, F. E. Wielgolaski, S. Zach, and A. Zust. 2006. European phenological response to climate change matches the warming pattern. Global Change Biology **12**:1969-1976.

Miller-Struttmann, N. E., J. C. Geib, J. D. Franklin, P. G. Kevan, R. M. Holdo, D. Ebert-May, A. M. Lynn, J. A. Kettenbach, E. Hedrick, and C. Galen. 2015. Functional mismatch in a bumble bee pollination mutualism under climate change. Science **349**:1541-1544.

Mopper, S., and D. Simberloff. 1995. Differential herbivory in an oak population - the role of plant phenology and insect performance. Ecology **76**:1233-1241.

Morin, X., J. Roy, L. Sonie, and I. Chuine. 2010. Changes in leaf phenology of three European oak species in response to experimental climate change. New Phytologist **186**:900-910.

Neuenschwander, P. 2001. Biological control of the cassava mealybug in Africa: A review. Biological Control **21**:214-229.

Nylin, S. 1992. Seasonal plasticity in life-history traits - growth and development in polygonia-c-album (Lepidoptera, Nymphalidae). Biological Journal of the Linnean Society **47**:301-323.

Orr, D. B., D. J. Boethel, and W. A. Jones. 1985. Development and emergence of telenomus-chloropus and trissolcus-basalis (Hymenoptera, Scelionidae) at various temperatures and relative humidities. Annals of the Entomological Society of America **78**:615-619.

Parmesan, C. 2007. Influences of species, latitudes and methodologies on estimates of phenological response to global warming. Global Change Biology **13**:1860-1872.

Perrins, C. M. 1991. Tits and their caterpillar food-supply. Ibis **133**:49-54.

Platt, T., C. Fuentes-Yaco, and K. T. Frank. 2003. Spring algal bloom and larval fish survival. Nature **423**:398-399.

Pollard, E., and T. J. Yates 1993. Monitoring Butterflies for Ecology and Conservation. Chapman & Hall, London.

Poyry, J., R. Leinonen, G. Soderman, M. Nieminen, R. K. Heikkinen, and T. R. Carter. 2011. Climate-induced increase of moth multivoltinism in boreal regions. Global Ecology and Biogeography **20**:289-298.

Romo, C. M., and J. M. Tylianakis. 2013. Elevated Temperature and Drought Interact to Reduce Parasitoid Effectiveness in Suppressing Hosts. Plos One **8**.

Salminen, J. P., T. Roslin, M. Karonen, J. Sinkkonen, K. Pihlaja, and P. Pulkkinen. 2004. Seasonal variation in the content of hydrolyzable tannins, flavonoid glycosides, and proanthocyanidins in oak leaves. Journal of Chemical Ecology **30**:1693-1711.

Schmidt, N. M., J. B. Mosbacher, P. S. Nielsen, C. Rasmussen, T. T. Høye, and T. Roslin. 2016. An ecological function in crisis? The temporal overlap between plant flowering and pollinator function shrinks as the Arctic warms. Ecography **39**:001-003.

Schmitz, O. J., P. A. Hamback, and A. P. Beckerman. 2000. Trophic cascades in terrestrial systems: A review of the effects of carnivore removals on plants. American Naturalist **155**:141-153.

Schwartzberg, E. G., M. A. Jamieson, K. F. Raffa, P. B. Reich, R. A. Montgomery, and R. L. Lindroth. 2014. Simulated climate warming alters phenological synchrony between an outbreak insect herbivore and host trees. Oecologia **175**:1041-1049.

Simmons, A. M. 1993. Effects of constant and fluctuating temperatures and humidities on the survival of spodoptera-frugiperda pupae (Lepidoptera, Noctuidae). Florida Entomologist **76**:333-340.

Singer, M. C. 1972. Complex components of habitat suitability within a butterfly colony. Science **176**:75-&.

Singer, M. C., and C. Parmesan. 2010. Phenological asynchrony between herbivorous insects and their hosts: signal of climate change or pre-existing adaptive strategy? Philosophical Transactions of the Royal Society B-Biological Sciences **365**:3161-3176.

Southwood, T. R. E., G. R. W. Wint, C. E. J. Kennedy, and S. R. Greenwood. 2004. Seasonality, abundance, species richness and specificity of the phytophagous guild of insects on oak (Quercus) canopies. European Journal of Entomology **101**:43-50.

Stalhandske, S., P. Lehmann, P. Pruisscher, and O. Leimar. 2015. Effect of winter cold duration on spring phenology of the orange tip butterfly, Anthocharis cardamines. Ecology and Evolution **5**:5509-5520.

Studer, S., C. Appenzeller, and C. Defila. 2005. Inter-annual variability and decadal trends in alpine spring phenology: A multivariate analysis approach. Climatic Change **73**:395-414.

Stålhandske, S., M. Olofsson, K. Gotthard, J. Ehrlen, C. Wiklund, and O. Leimar. 2016. Phenological matching rather than genetic variation in host preference underlies geographical variation in host plants used by orange tip butterflies. Biological Journal of the Linnean Society **119**:1060-1067.

Sukumar, R., H. S. Suresh, and R. Ramesh. 1995. Climate change and its impact on tropical montane ecosystems in southern India. Journal of Biogeography **22**:533-536.

Thackeray, S. J., P. A. Henrys, D. Hemming, J. R. Bell, and M. S. Botham, Burthe, Sarah., Helaouet, Pierre., Johns, David G., Jones, Ian D., Leech, David I., Mackay, Eleanor B., Massimino, Dario, Atkinson, Sian, Bacon, Philip J., Brereton, Tom M., Carvalho, Laurence., Clutton-Brock, Tim H., Duck, Callan., Edwards, Martin., Elliott, J. Malcolm., Hall, Stephen J.G., Harrington, Richard., Pearce-Higgins, James W., Hoye, Toke T., Kruuk, Loeske E.B., Pemberton, Josephine M., Sparks, Tim H., Thompson, Paul M., White, Ian., Winfield, Ian J., Wanless, Sarah. 2016. Phenological sensitivity to climate across taxa and trophic levels. Nature **535**:241-245.

Thuiller, W., S. Lavorel, M. B. Araujo, M. T. Sykes, and I. C. Prentice. 2005. Climate change threats to plant diversity in Europe. Proceedings of the National Academy of Sciences of the United States of America **102**:8245-8250.

Tikkanen, O. P., and R. Julkunen-Tiitto. 2003. Phenological variation as protection against defoliating insects: the case of Quercus robur and Operophtera brumata. Oecologia **136**:244-251.

Tikkanen, O. P., P. Niemela, and J. Keranen. 2000. Growth and development of a generalist insect herbivore, Operophtera brumata, on original and alternative host plants. Oecologia **122**:529-536.

Uelmen, J. A., R. L. Lindroth, P. C. Tobin, P. B. Reich, E. G. Schwartzberg, and K. F. Raffa. 2016. Effects of winter temperatures, spring degree-day accumulation, and insect population source on phenological synchrony between forest tent caterpillar and host trees. Forest Ecology and Management **362**:241-250.

van Asch, M., L. Salis, L. J. M. Holleman, B. van Lith, and M. E. Visser. 2013. Evolutionary response of the egg hatching date of a herbivorous insect under climate change. Nature Climate Change **3**:244-248.

van Asch, M., P. H. Tienderen, L. J. M. Holleman, and M. E. Visser. 2007. Predicting adaptation of phenology in response to climate change, an insect herbivore example. Global Change Biology **13**:1596-1604.

van Asch, M., and M. E. Visser. 2007. Phenology of forest caterpillars and their host trees: The importance of synchrony. Pages 37-55. Annual Review of Entomology.

Van Nouhuys, S., and G. C. Lei. 2004. Parasitoid-host metapopulation dynamics: the causes and consequences of phenological asynchrony. Journal of Animal Ecology **73**:526-535.

VanDongen, S., T. Backeljau, E. Matthysen, and A. A. Dhondt. 1997. Synchronization of hatching date with budburst of individual host trees (Quercus robur) in the winter moth (Operophtera brumata) and its fitness consequences. Journal of Animal Ecology **66**:113-121.

Visser, M. E. 2008. Keeping up with a warming world; assessing the rate of adaptation to climate change. Proceedings of the Royal Society B-Biological Sciences **275**:649-659.

Visser, M. E., and L. J. M. Holleman. 2001. Warmer springs disrupt the synchrony of oak and winter moth phenology. Proceedings of the Royal Society B-Biological Sciences **268**:289-294.

Visser, M. E., L. te Marvelde, and M. E. Lof. 2012. Adaptive phenological mismatches of birds and their food in a warming world. Journal of Ornithology **153**:S75-S84.

Visser, M. E., A. J. van Noordwijk, J. M. Tinbergen, and C. M. Lessells. 1998. Warmer springs lead to mistimed reproduction in great tits (Parus major). Proceedings of the Royal Society B-Biological Sciences **265**:1867-1870.

Wu, Z. T., P. Dijkstra, G. W. Koch, J. Penuelas, and B. A. Hungate. 2011. Responses of terrestrial ecosystems to temperature and precipitation change: a meta-analysis of experimental manipulation. Global Change Biology **17**:927-942.

Xi, X. Q., N. Eisenhauer, and S. C. Sun. 2015. Parasitoid wasps indirectly suppress seed production by stimulating consumption rates of their seed-feeding hosts. Journal of Animal Ecology **84**:1103-1111.

Zarnetske, P. L., D. K. Skelly, and M. C. Urban. 2012. Biotic Multipliers of Climate Change. Science **336**:1516-1518.