The full phenological distribution and the match/mismatch hypothesis

Kirsty Macphie

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Authorship Declaration

I composed this thesis with guidance from my primary supervisor, Ally Phillimore. The data used within the thesis has been collected over nine years by a team of five to six people each year, with particularly large input from Jack Shutt. I have contributed to data collection for six years, three of which were as the data collection component of my PhD. I had guidance from my primary and secondary supervisors, Ally Phillimore and Jarrod Hadfield, for all the statistical analyses within this thesis.

Whilst most of the work within this thesis is my own, I detail any additional contributions of others below:

Chapter 2: This chapter was prepared as a manuscript for the Journal of Animal Ecology and received comments from co-authors: Jelmer Samplonius, James Pearce-Higgins, Jarrod Hadfield and Ally Phillimore. It is available on EcoEvoRxiv (DOI: 10.32942/osf.io/cfmvy).

Chapter 3: This chapter was prepared as a manuscript for Ecology Letters and received comments from co-authors: Jelmer Samplonius, Joel Pick, Jarrod Hadfield and Ally Phillimore. Joel Pick also supported me in coding the main statistical model and Wolfgang Veichtbauer advised on appropriate meta-analysis composition using an R package he designed, “metafor”. It is under review at Ecology Letters and is available on EcoEvoRxiv (DOI: 10.32942/osf.io/fh3xv).

Chapter 4: For this chapter I had particularly strong support from Ally Phillimore and Jarrod Hadfield in designing the study and coding the model.

This work has not been submitted for any other degree or professional qualification.

Kirsty Macphie

Thesis Abstract

Shifts in the timing of key life history events are some of the most documented biological responses to climate warming. Synchronous timing between a consumer and ephemeral resource can be important for consumer fitness, with asynchrony between the two parties often having a negative effect, as outlined by the match-mismatch hypothesis (MMH). Differences in the thermal sensitivity of phenology among species occupying different trophic levels leave consumers at risk of asynchrony within time-sensitive trophic interactions under climate warming. There is abundant evidence that secondary consumers shift their phenology by less than their resources, resulting in them lagging behind the resource as temperatures increase. As such, phenology and the MMH have become prominent in research regarding the impacts of climate warming on biological systems.

The phenology of individuals within a population is often summarised using the mean. However, interactions are not just sensitive to the mean of each trophic level, but instead the synchrony among individuals. The range of timings among individuals forms the phenological distribution, described by the maximum number of individuals (height), the range of dates over which the event will occur (duration), and the relative shape (width). Differences in the height, duration and width of the phenological distribution of an ephemeral resource are likely to have implications for the MMH, affecting the prevalence of food available to the consumer at any point in time, and also at different levels of asynchrony to the mean timing of the resource. For example, with a wider resource distribution, the difference in food available to synchronous consumers versus asynchronous consumers will be less than when there is a narrower resource distribution. As such, if the fitness of consumers is affected by variation in the phenological distribution of food availability, differences in the distribution of a resource could affect consumer mean population fitness and the strength of selection on timing. Given the possible implications that shifts in these aspects of the full phenological distribution have for trophic interactions, it is surprising that it has been the focus of minimal research to date.

In this thesis, I utilise data on the spring peak in arboreal caterpillars within deciduous woodland systems and the breeding phenology and breeding success of blue tits (*Cyanistes caeruleus*). I explore variations in the phenological distribution of caterpillars and the implications for the phenological fitness function of blue tits, an insectivorous bird that relies on caterpillars to feed young. Data have been collected across 44 sites spanning an elevation range of 10-433m and 2° latitude through Scotland over nine years. The sites vary both in woodland tree composition and in temperature. In Chapter 1, I introduce phenology, the MMH, the full phenological distribution and the deciduous woodland study system. Chapters 2 and 3 then focus on habitat and temperature as drivers of the phenological distribution of caterpillars. In Chapter 4, I examine the consequences of the full phenological distribution of caterpillars for blue tit fitness relative to breeding phenology, and in Chapter 5 I discuss the broader implications of my work, limitations and future directions and opportunities.

In Chapter 2 I examine variation in the phenological distribution of caterpillars in relation to woodland tree composition using data on the abundance and mass of caterpillars on ten different tree taxa throughout spring, and information about the local tree taxa composition more specifically. I find that there is substantial variation in the abundance of caterpillars supported by different deciduous tree taxa and that the prevalence of oak trees in the local woodland has an additional effect, increasing the abundance of caterpillars found throughout the site. I also found that there is substantial variation in the height of the caterpillar peak hosted by different tree taxa, and some minimal variation in the timing of the peak and the duration. There was no significant difference in the ultimate mass of caterpillars among taxa meaning that the differences in the peak in biomass among tree taxa largely mirrored patterns seen for the peak in abundance. These results show that woodland tree composition contributes to variation in the phenological distribution of caterpillars between locations, suggesting that studying the MMH in a range of woodland types may be of benefit to accurately predict the consequences of climate warming at the meta-population level.

In Chapter 3, I identified the time periods within spring during which average temperature best predicted the timing, height and width of the phenological distribution of caterpillar abundance. I found mean timing to be better predicted by temperatures earlier in spring with height predicted by temperatures that were slightly later, whilst there was substantial uncertainty in the period over which average temperature best predicted width. In this chapter I develop a novel method to phenology research, testing for thermal sensitivity in the mean timing, height and width of the phenological distribution of caterpillars from raw data of abundance over time. I found that the height of the phenological distribution increases substantially with an increase in temperature and that the shape becomes more steeply peaked, falling over a similar duration of time. These results suggest climate warming is having a substantial impact on the phenological distribution of a key resource in temperate woodlands and provides additional insights into the impacts of climate change past shifts in mean timing alone.

In Chapter 4 I present an extension to the MMH in which the full phenological distribution of caterpillars affects the full phenological fitness function of blue tits. I achieve this by extending the statistical method from Chapter 3 and use site and year specific estimates of the mean timing, height and width of the caterpillar peak to predict the equivalent metrics in the blue tit fledging success fitness function. This framework has the potential to allow tests of how the timing of the caterpillar peak affects the optimal breeding timing for blue tits, whether the maximum height of the caterpillar peak affects the maximum fitness of blue tits, and whether the width of the caterpillar peak affects the width of the phenological fitness function which may have implications for the strength of selection. However, having identified no optimum hatch date for blue tits within the fledging success data, the data do not conform with the structure of the framework described. As an alternative, I examined the effect of the mean timing, height and width of the caterpillar phenological distribution among site by year combinations on a straight-line fitness function for the birds, allowing the intercept and slope of fledging success over time to vary with each caterpillar parameter. I found no effect of the mean timing, height or width of the caterpillar peak on the blue tit phenological fitness function which shows no evidence of the MMH affecting these populations. Alternatively, I suggest parental quality may have a stronger effect than environmental factors on fledging success. As the effect of the MMH has varied among fitness traits in other passerine species this does not rule out any effect of the

phenological distribution extension of the MMH, but presents an opportunity for further work on this topic. Nevertheless, the conceptual framework put forwards holds an interesting progression for how we perceive the dynamics within these ephemeral trophic interactions.

In this thesis, I have introduced approaches that allow more nuanced insights into the impacts of climate change on phenology and the consequences of phenology for fitness. The phenological distribution of caterpillars varies with woodland tree composition, contributing to spatial heterogeneity in a key resource and guild of herbivores. The increase in height and narrowing shape of the phenological distribution with an increase in temperature shows that reducing the caterpillar peak to mean timing misses important information about how the resource is responding to a warming climate. By extending the conceptual framework of the MMH we gain insight into how the resource distribution can influence the strength of selection and population persistence, highlighting the value of considering the full phenological distribution in phenology and MMH research. The theory and statistical methods employed in this thesis are transferable to a vast range of species and interactions. To accurately interpret and predict the impacts of climate warming in biomes driven by the strong seasonality of events, it may be essential to move on from focusing on mean timing and begin to incorporate the full phenological distribution.

Lay Summary

The timing of seasonal biological events such as reproduction, flowering and migration can be important for the survival and reproduction of animals and plants. One habitat in which timing appears to be very important is deciduous woodlands. For example, some birds that breed in deciduous woodlands rely on caterpillars as an important food to feed their nestlings. However, caterpillars are only present in the woodland for four-six weeks because they feed on young deciduous leaves as the leaves grow, and once the leaves have matured, they are no longer a viable food source. Caterpillars tend to increase in biomass through late spring coming to a maximum at a mid-point in the time they are present, before decreasing again through early summer; this short-lived biomass of caterpillars is known as the caterpillar peak. The abundance of caterpillars can be used as a proxy for biomass. It can be important for birds that rely on this spring peak in caterpillars to breed at a time which means their nestlings are most demanding of food when caterpillars are most abundant, known as the caterpillar peak date. Birds can either be synchronous with the caterpillar peak resource, or asynchronous, i.e. too early or too late. As less food is available to asynchronous birds this often reduces the success of their breeding attempt, which may mean they fledge fewer offspring or that the offspring that fledge are in a worse condition and less able to survive.

The timing of spring events such as bird breeding and the caterpillar peak date in temperate deciduous woodlands are often sensitive to spring temperatures, with warmer conditions causing the event to shift earlier within the year. However, the caterpillar peak date is generally advancing by more than the timing of breeding for birds that rely on it. Under climate warming, this increases the chance of birds being asynchronous with the caterpillars and increases the chance of unsuccessful breeding attempts which may be detrimental to the bird populations. These ideas about the importance of timing are known as the match/mismatch hypothesis and have attracted particular research interest in recent decades due to the importance of understanding the impacts of climate change on species populations and how they interact. However,

previous research has generally only considered the peak timing of the food group, such as caterpillars, and not how the abundance of caterpillars on each day throughout the spring could change. The caterpillar peak date represents the date when caterpillars are at their maximum abundance, but the maximum abundance reached may vary between locations or years. The rate of change in abundance over time, described by the width of the peak, and the duration of time over which the caterpillars are available could also vary. The peak date, maximum abundance, width and duration describe the full caterpillar peak over time. The negative consequences of asynchrony are thought to occur because there is less food available to the birds when they breed further away from the caterpillar peak date, yet differences in the maximum, width and duration of the full caterpillar peak will also affect the abundance of caterpillars available at any point in time. Therefore, I hypothesise that the full caterpillar peak will affect the breeding success of birds relative the timing at which they breed.

In this thesis, I explore this topic using data on caterpillar abundance and blue tit breeding timing and success collected at 44 sites across Scotland over nine years. I first explore drivers of variation in the caterpillar peak, looking at the effect of woodland tree composition and temperature. Having established that the caterpillar peak varies by more than just the peak date, I then look at how the full caterpillar peak affects the breeding success of blue tits relative to the timing at which they breed.

I first analyse how the caterpillar peak date, maximum abundance, width and duration differ between difference tree taxa (distinct groupings of species such as oaks, willows, and birches) and whether the prevalence of different tree taxa in the local woodland has any additional effect on the abundance of caterpillars (Chapter 2). I found that there are substantial differences in the maximum abundance reached on different tree taxa, with the most pronounced effects in oak hosting more caterpillars and alder hosting fewer. The prevalence of oak trees within the local woodland also has an additional positive effect on the number of caterpillars found on any tree at that site. These results show that the different compositions of tree taxa in different woodlands will affect the caterpillar peak at that location, which could be useful information for forestry, as caterpillars are herbivores which can damage the trees. Understanding how tree composition affects the caterpillar peak could also be of use for the conservation of species that comprise the group of caterpillars feeding on deciduous trees, with further potential benefits for birds that feed on the caterpillars as well.

Next, I analysed the effect of temperature on the caterpillar peak date, maximum abundance, width and duration (Chapter 3). I found that as temperature increases the peak date becomes earlier, the maximum abundance increases and the width decreases. As the width decreases, the rate of change in abundance over time before and after the peak date increases, which when paired with the increase in maximum abundance results in the full caterpillar peak lasting for a similar duration as temperature changes. These results show that temperature can affect more than just the peak date of an event and that the changes in the full peak can show changes in a population that may be important for how they interact with other levels of the food chain. For example, as temperature increases the increase in the maximum abundance of caterpillars is likely to increase the level of herbivory on trees.

Lastly, I look at how the peak date, maximum abundance and width of the full caterpillar peak within a location in a particular year affects the number of offspring to fledge from a nest depending on the time at which they breed (Chapter 4). Fledging success is expected to be highest when the birds breed synchronously with the caterpillar peak, reducing to either side. However, I found no evidence of fledging success reaching a maximum. Instead, fledging success was predicted to be higher at earlier dates in the year. My results in this chapter were contrary to my expectations based on the match/mismatch hypothesis, and I discuss the possible reasons for the results found. Nevertheless, the novel approach I developed presents a more complete test of the match/mismatch hypothesis than has previously been explored and has great potential for use in future work.

The topics addressed within this thesis show that the full caterpillar peak can be affected by the local woodland tree composition and by temperature, not just the peak date alone. The novel approach to testing the effect of the full caterpillar peak on bird breeding success relative to timing increases the detail in which we can understand how species interact within the food chain and presents extensive opportunities for future work. Given the changes in the caterpillar peak with temperature, it is possible that including the full caterpillar peak in analyses of bird breeding success will be necessary to accurately estimate how birds will be affected by climate warming and the methods and approaches used in this thesis have broad applicability to different study species and food chains.

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Landowners and managers of Phenoweb field sites:

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Berthapark Farm
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Table of Contents

Chapter 1 - General Introduction

Climate change and phenology

Under anthropogenic climate warming temperature is increasing at a far greater rate than expected under the historic baseline. The mean global surface temperature between 2001-2020 was 0.99°C higher than in 1850-1900, and under all climate scenarios considered it is set to continue increasing until at least the middle of the century (IPCC, 2021). These global trends are consistent with UK records where between 2011-2020 it was on average 1.1°C warmer than 1961-1990 (Kendon *et al.*, 2021). Whilst all seasons have warmed, for the UK the increase is higher in winter and spring with the most recent decade's seasons averaging 1.1 and 1.2°C higher than those between 1961-1990 (Kendon *et al.*, 2021).

Phenology describes the timing of seasonal biological events. In plants and animals, environmental temperature is one of the most studied factors known to drive phenological shifts (Forrest and Miller-Rushing, 2010) which describe the change in the timing of an event. Whilst other environmental conditions are of importance, at mid and high latitudes, temperature is one of the primary drivers of phenology (Wolkovich, Cook and Davies, 2014; Cohen, Lajeunesse and Rohr, 2018). Phenological traits capture the interests of both naturalists and laymen through noticeable seasonal shifts in the natural environment. Phenology has become an important sector of research for understanding the effects of climate change on biological systems. The widespread recognition of seasonal events, paired with their sensitivity to climate, has resulted in phenological shifts under anthropogenic climate warming being well documented in a broad range of species across multiple trophic levels and ecosystems; examples of taxa include plants, plankton, Lepidoptera, amphibians, mammals and birds (Parmesan, 2006, 2007; Thackeray *et al.*, 2010; Roslin *et al.*, 2021). Evidence suggests there are particularly prominent distinctions in the thermal sensitivity of phenology among trophic levels (Roslin *et al.*, 2021), with producers (autotrophs) and primary consumers (consumers of autotrophs) in particular shifting on average at a faster rate than secondary consumers (consumers of primary consumers), both in response to temperature and over time as the climate has warmed (Thackeray *et al.*, 2010, 2016).

Phenology determines the abiotic conditions experienced during key life history events and can impact interactions with other trophic levels and competing species; as a result, it can have a strong impact on fitness (Perrins, 1970; Walther *et al.*, 2002; Parmesan and Yohe, 2003; Root *et al.*, 2003; Cohen, Lajeunesse and Rohr, 2018). Timing can be particularly important in regions with strong seasonality; for example, in temperate regions where there are four distinct seasons, the reproduction and growth of most species are confined to a particular period each year when conditions are most suitable.

The match/mismatch hypothesis

When the consumer within a trophic interaction is highly reliant on an ephemeral resource, synchronous timing between the maximum prevalence of resource and the period of highest resource demand can be important for maximising consumer fitness, as insufficient food will be available when the consumer is mistimed. This concept was first proposed by Cushing whilst studying fish spawning and plankton productivity in the 1960-70s, thereafter known as the match/mismatch hypothesis (MMH) (Cushing, 1990). The seasonality of abiotic conditions means that at some latitudes many species rely on ephemeral resources during important life history events (e.g. reproduction). For example, caribou in the Arctic benefit from matching the timing of migration to their summer range with the onset of the plant growing season prior to calving (Post and Forchhammer, 2007), in temperate Northern Europe the adult stage of the parasitoid wasp species *Cotesia melitaearum* requires synchronous timing with the larval stage of their host species, Melitaea cinxia, to successfully reproduce (Van Nouhuys and Lei, 2004) and in East Asia rhinoceros auklets benefit from breeding when Japanese anchovy are abundant (Watanuki *et al.*, 2009). As these time-sensitive trophic interactions are widespread throughout nature, there appear to be numerous systems in which the MMH might operate and negative consequences of asynchrony for consumer fitness have now been observed in a range of taxa; though it has only tested in a small subset of species that are likely to be susceptible (Samplonius *et al.*, 2020).

There has been a lot of focus on the MMH in the context of climate change as spring warming may uncouple historically synchronous events (Visser and Both, 2005; Renner and Zohner, 2018). Differences in the thermal phenological sensitivity of interacting species will affect their relative timing and, assuming the historic interactions were near synchronous, the resulting alterations to synchrony are predicted to have negative consequences for consumer fitness under the MMH. For example, in the Netherlands, great tit breeding phenology was less responsive to temperature than the arboreal caterpillar peak which lead to lower reproductive success when asynchrony was greater (Visser, Holleman and Gienapp, 2006), and in western North America, phenology of the parasitoid wasp *Tetrastichus julis* was unresponsive to temperature, whilst its host, the cereal leaf beetle, *Oulema melanopus*, advances its phenology, reducing parasitism at warmer temperatures (Evans *et al.*, 2013). There is variation in the phenological shifts both within and between trophic levels (Roslin *et al.*, 2021), but generally speaking, primary consumers have been found to advance at a higher rate in response to temperature than secondary consumers (Thackeray *et al.*, 2016). Secondary consumers that become more asynchronous are predicted to be more susceptible to the negative fitness consequences of trophic asynchrony, though within a broader array of species interactions which were not limited to those spanning trophic levels, just 43% were found to be becoming more asynchronous, with 57% becoming more synchronous (Kharouba *et al.*, 2018). Whilst these food chains are most often viewed from a bottom-up perspective (in which the resource affects the consumer), top-down effects (where the consumer affects the resource) are also feasible through alterations in predation/herbivory pressure, though there has been little work on this to date. There may also be cascading effects through trophic levels, for example, reduced parasitism of the cereal leaf beetle, *Oulema melanopus*, is liable to increase herbivory of the agricultural plants they feed on, reducing the effectiveness of the parasitoids as a biological control (Evans *et al.*, 2013).

The full phenological distribution

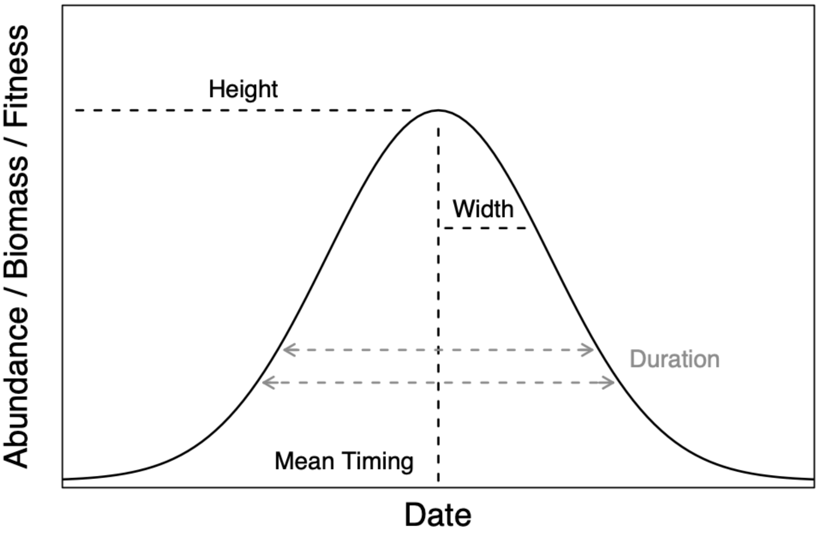

Figure 1.1: The full phenological distribution of an ephemeral life history event is primarily governed by three parameters (black dashed lines): mean timing, the most common timing within the population/guild or the optimum timing for a fitness trait; height, the maximum response (e.g. abundance, biomass or fitness) value reached, and width, the variation in phenology around the mean which determines the curvature. Duration (grey dashed arrows) describes the number of days where the response falls above a given threshold and is influenced by the height, width and chosen threshold level, as illustrated by the two lines.

The timing of an event will usually vary among individuals within a population and the temporal distribution of the range of timings among individuals in a population reflects the phenological behaviour of the entire population (Miller-Rushing *et al.*, 2010), defined in this thesis as the phenological distribution (Fig. 1.1). Summarising this distribution for analysis requires the choice of a representative metric. In past phenological literature, and some ongoing citizen science schemes, population phenology was frequently studied using the first observation of an event within a year (Sparks and Carey, 1995; Both, Bijlsma and Visser, 2005), likely due to the ease of measuring it in the field and aligning well with people’s natural history interests. However, most scientific study of phenology has shifted to summarising population phenology by the mean timing, as it was identified to be a more accurate phenological estimate compared to first observations which are heavily influenced by sample/population size (Miller-Rushing *et al.*, 2008; Moussus, Julliard and Jiguet, 2010). However, whilst the mean timing represents the central, most common timing among individuals, the phenological distribution also reaches a height which describes either how many individuals, or what proportion of individuals, exhibit the mean timing, a width which describes the relative shape of the spread of timing among individuals and a duration of time over which the event occurs (Fig. 1.1), though these aspects of the phenological distribution are less frequently considered.

Describing population-level phenology by mean timing alone represents the average timing well (Moussus, Julliard and Jiguet, 2010), but disregards all information about the height, width and duration of the distribution which are likely to be important for how that population interacts both intra- and interspecifically. Since the MMH was first proposed, the interactions have been depicted as two Gaussian distributions, shifting from side to side to illustrate changes in the mean timings and the level of synchrony between a resource and consumer (Cushing, 1990; Reed, Jenouvrier and Visser, 2013; Visser and Gienapp, 2019), and synchrony is almost always quantified as the difference between the mean timing of the resource and either individual phenology or population mean timing for the consumer (Charmantier *et al.*, 2008; Watanuki *et al.*, 2009; Bartomeus *et al.*, 2013; Reed *et al.*, 2013). An extension to the MMH proposes that the abundance of a resource is also important for fitness, in addition to synchronous timing (Cushing, 1982; Durant *et al.*, 2005, 2007). Differences in the maximum height, width, or duration of a phenological distribution will affect the volume of resource available to the consumer at any fixed degree of asynchrony and determine the relative difference in resource between individuals with differing phenology. The full phenological distribution may also be important from a top-down perspective, where differences in the height and width of the phenological distribution of a consumer will affect the rates of herbivory/predation over time, suggesting mean timing alone is also likely to provide an incomplete representation of herbivory or predation risk.

Phenology and fitness

Where climate change leads to a change in the optimum for a phenotypic trait value, the ability of a population to track that change through plasticity and adaptive genetic change is fundamental to population persistence (Chevin, Lande and Mace, 2010; Gienapp *et al.*, 2013). Phenology has been studied as a fitness trait for which temperature may directly set the optimum timing, but temperature will also indirectly affect the optimum via the timing of the resource (Visser, te Marvelde and Lof, 2012; Gienapp *et al.*, 2013; Vedder, Bouwhuis and Sheldon, 2013). The ability of a population to plastically (b) track the slope of the optimum (B), i.e. where |B-b| is small, has important implications for the ability of the population to persist under faster rates of environmental change (Chevin, Lande and Mace, 2010; Chevin, Visser and Tufto, 2015).

In the context of the MMH, the timing of the resource may determine the optimum timing of the consumer (Reed *et al.*, 2013; Vedder, Bouwhuis and Sheldon, 2013), but whether the effect is direct or indirect, the optimum timing is sensitive to temperature. Therefore, in the absence of adaptive genetic change, the difference between the temperature sensitivity of selection on optimum timing and phenotypic plasticity of phenology will determine the change in lag from the baseline between the population mean timing and the optimum (Charmantier *et al.*, 2008; Chevin, Lande and Mace, 2010; Vedder, Bouwhuis and Sheldon, 2013). However, the temperature sensitivity of selection and plasticity are focused on the mean timing of the phenological distribution, yet the height and width of the phenological distribution of the consumer timing trait and fitness function contribute to individual fitness relative to timing and the strength of directional and stabilising selection on timing (Chevin, Lande and Mace, 2010; Chevin, Visser and Tufto, 2015; de Villemereuil *et al.*, 2020). Therefore, temperature sensitivity in a population-level phenological trait and the full phenological fitness function may affect individual fitness and demographic trends, with the potential to influence the resilience of the population to climate warming (Miller-Rushing *et al.*, 2010; Samplonius *et al.*, 2020), though there is little evidence of demographic consequences in the literature (Reed *et al.*, 2013; McLean *et al.*, 2016). The effect of trophic asynchrony on individual fitness has been studied in 47 taxa, with 72% showing a negative effect of asynchrony, whilst demographic consequences, such as population size or growth rates, have received less attention with just 10 taxa having been studied: five showing a negative effect and five neutral (Samplonius *et al.*, 2020).

Woodland study system

The tri-trophic food chain of deciduous trees – caterpillars – cavity nesting passerines in temperate forests during spring has become the most prominent study system in MMH research (Samplonius *et al.*, 2020; Cole, Regan and Sheldon, 2021; Visser *et al.*, 2021). This chain includes ephemeral resources at two trophic levels (Thomas *et al.*, 2001; Visser, Holleman and Gienapp, 2006; Charmantier *et al.*, 2008; Both *et al.*, 2009; Samplonius *et al.*, 2016; Shutt *et al.*, 2019), driven by the distinct changes in climatic conditions moving from winter to spring. Deciduous leaves are required by arboreal caterpillars to grow to pupation (Feeny, 1970; van Asch and Visser, 2007; Forkner *et al.*, 2008) but the leaves remain immature and palatable for a short period of time, as they develop toughness and accumulate secondary defence metabolites which make mature leaves a sub-optimal resource (Feeny, 1968). Many breeding bird species then rely on the arboreal caterpillars as a resource for feeding their offspring (Betts, 1955; Bańbura *et al.*, 1994; Sanz, 1998; Wilkin, King and Sheldon, 2009), though this resource is only abundant in the environment for roughly four to six weeks while the leaves remain young (Holliday, 1985; Visser, Holleman and Gienapp, 2006). Consequently, for bird species relying predominantly on the peak in caterpillar abundance to successfully fledge offspring, the optimal time for breeding is expected to fall when the highest demand of the nestlings matches the highest volume of caterpillars (Thomas *et al.*, 2001; Visser and Both, 2005). Therefore in this system, phenological synchrony across the trophic levels is important for fitness in both the caterpillars and the birds (Visser, Holleman and Gienapp, 2006; van Asch and Visser, 2007; Simmonds *et al.*, 2017).

Much research on the MMH has focused on hole-nesting insectivorous passerines due to their susceptibility to trophic asynchrony, competition among species for nest sites and the ephemeral caterpillar resource, and the ability to monitor them through nest box schemes which enables reliable and high-resolution phenological data collection (Culina *et al.*, 2021). Great tits - *Parus major*, blue tits - *Cyanistes caeruleus* and pied flycatchers - *Ficedula hypoleuca* are the most frequently studied species due to their high amenability to nestbox studies in northwestern Europe, where this topic has gained particular interest (Buse *et al.*, 1999; Visser, Holleman and Gienapp, 2006; Porlier *et al.*, 2012; Burgess *et al.*, 2018; Samplonius *et al.*, 2018). All three are advancing the timing of their reproduction in response to warmer temperatures with great tits advancing their timing on average by 2.8 – 4.1 days $^{o}C^{-1}$ (Visser, Holleman and Gienapp, 2006; Charmantier *et al.*, 2008; Burgess *et al.*, 2018; Samplonius *et al.*, 2018; Bailey *et al.*, 2022), blue tits by 2.5 – 4 days $^{o}C^{-1}$ (Porlier *et al.*, 2012; Burgess *et al.*, 2018; Samplonius *et al.*, 2018; Bailey *et al.*, 2022) and pied flycatchers by 1.5 – 2 days $^{o}C^{-1}$ (Burgess *et al.*, 2018; Samplonius *et al.*, 2018). Intra-specific variation in phenological temperature sensitivity among great tit and blue tit populations is high and differs between habitat types and across spatial gradients (Bailey *et al.*, 2022), in addition, there is also potential for other non-temperature-related trends to be contributing to phenological shifts in a similar direction to climate (Mclean *et al.*, 2022).

Temperature-mediated advances in the mean timing of caterpillar abundance/biomass have also received considerable attention, with the peak in guild (and winter moth, *Operophtera brumata*) biomass found to advance on average by 4.0 – 6.0 days $^{o}C^{-1}$ (Visser, Holleman and Gienapp, 2006; Charmantier *et al.*, 2008; Burgess *et al.*, 2018). The caterpillar guild is defined in this thesis as the larvae of a range of insect species that spend their larval stage on deciduous trees: mainly lepidopteran species but also some Hymenoptera, Diptera and Coleoptera (Shutt, Burgess and Phillimore, 2019). Whilst the uncertainty in estimates of the tit species and caterpillar guild thermal sensitivities may overlap, the point estimates suggest a shallower slope for the birds, with the migratory pied flycatchers deviating from the caterpillar timing most substantially and often having chicks in the nest considerably later than the span of the caterpillar peak (Burgess *et al.*, 2018; Samplonius *et al.*, 2018).

Asynchrony between the period of highest resource demand of nestlings and the timing of the caterpillar peak availability is often detrimental to nestling condition, with varied effects on breeding success, recruitment and demography among species (Both *et al.*, 2006; Visser, Holleman and Gienapp, 2006; García-Navas and Sanz, 2011; Reed *et al.*, 2013; Reed, Jenouvrier and Visser, 2013; Visser *et al.*, 2015; Pakanen *et al.*, 2016; Samplonius *et al.*, 2016; Simmonds *et al.*, 2017). There is evidence that asynchrony impacts negatively on the nestling condition of great tits (Visser, Holleman and Gienapp, 2006), blue tits (Thomas *et al.*, 2001; García-Navas and Sanz, 2011; Vatka, Rytkönen and Orell, 2014) and pied flycatchers (Samplonius *et al.*, 2016). Findings of impacts of asynchrony in relation to fledging success are more variable; whilst there is evidence of negative effects in great tits (Visser, Holleman and Gienapp, 2006; Reed, Jenouvrier and Visser, 2013; Vatka, Rytkönen and Orell, 2014; Simmonds *et al.*, 2017) and blue tits (Dias and Blondel, 1996; Vatka, Rytkönen and Orell, 2014), this was not the case for pied flycatchers (Visser *et al.*, 2015). From a demographic perspective, asynchrony has been suggested as a cause of population decline in pied flycatchers (Both *et al.*, 2006), though it had no effect on their recruitment (Visser *et al.*, 2015) but there is some evidence of a reduction in recruitment to the population in great tits (Reed, Jenouvrier and Visser, 2013; Pakanen *et al.*, 2016). Relative timing between the caterpillar peak and breeding attempts is clearly of importance to some insectivorous birds within this biome, however it is possible that other effects of climate change on the MMH are missed through most research considering only the mean phenology of the caterpillar guild and not the height or width.

Drivers of variation in the phenological distribution of arboreal caterpillars

The peak in abundance/biomass of arboreal caterpillars throughout spring and early summer in each year forms an important central component of the widely studied tri-trophic woodland system (Gibb, 1950; Southwood *et al.*, 2004). The phenological distribution of caterpillars has clear bottom-up importance for breeding consumer species under the MMH (Buse *et al.*, 1999; Visser, Holleman and Gienapp, 2006; Reed, Jenouvrier and Visser, 2013), but also describes a substantial component of the herbivore guild feeding on deciduous leaves at their most vulnerable, with possible effects on tree growth, survival and forest productivity (Kulman, 1971; Whittaker and Warrington, 1985; Whitham *et al.*, 1991; Marquis and Whelan, 1994). However, despite the potential for the full phenological distribution of caterpillars to have a major impact on trophic interactions, and to be influenced by woodland tree composition and temperature, these relationships have received relatively little attention.

Woodland tree taxonomic composition, hereafter referred to as woodland tree composition, at various spatial scales, is likely a source of variation in the phenological distribution of the arboreal caterpillar guild. There is a vast range of mechanisms through which caterpillar abundance, survival and growth could differ among tree taxa; for example, the nutritional content of leaves can vary among species (Schultz, Nothnagle and Baldwin, 1982; Yanar *et al.*, 2017) affecting survival and growth, females of some species will preferentially lay eggs on particular hosts affecting abundance (Thompson and Pellmyr, 1991; Kakimoto, Fujisaki and Miyatake, 2003) and larvae can disperse among trees (van Asch and Visser, 2007; Forkner *et al.*, 2008) in search of palatable young leaves which may further affect abundance if they show a preference for particular tree taxa. As tree taxa differ in leafing phenology (Murray, Cannell and Smith, 1989; Roberts *et al.*, 2015), the mean timing of the caterpillar phenological distribution may vary among taxa to match the resource, either at the individual tree level (Hinks *et al.*, 2015) or at a larger spatial scale through local adaptation to the phenology of a dominant tree taxa (Tikkanen, Carr and Roininen, 1999). However, the high variation in phenology both between and within tree taxa (Crawley and Akhteruzzaman, 1988; Cole and Sheldon, 2017) may make taxon-specific timing less likely (Tikkanen, Carr and Roininen, 1999). The species composition of the caterpillar guild is also likely to vary between tree taxa or among pockets of woodland with differing dominant taxa (Kennedy and Southwood, 1984), and the relevance of each of the fore-mentioned mechanisms may also differ among species comprising the caterpillar guild.

Determining differences in the phenological distribution of caterpillars associated with the taxonomic composition of trees (Burger *et al.*, 2012) is likely to have implications for caterpillar consumers and the trees on which they feed. If the caterpillar phenological distribution influences the fitness function of the breeding birds that rely on it, the spatial heterogeneity in the caterpillar resource is likely to affect spatial variation in breeding success, contributing to a stabilising spatial portfolio effect of meta-population fitness (Schindler, Armstrong and Reed, 2015). Differences in the phenological distribution of caterpillars associated with woodland tree composition could also have implications for tree health and growth via impacts on herbivory rates (Kulman, 1971; Whittaker and Warrington, 1985; Whitham *et al.*, 1991; Marquis and Whelan, 1994). Implications for tree health and growth may be important in forestry if certain woodland tree compositions may be detrimental to productivity. Impacts on tree health and growth would also need to be considered in line with the benefits for the caterpillar guild for reforesting or rewilding projects to permit healthy, growing trees but also consider conservation of the caterpillar guild and the importance of caterpillars as a resource for many insectivorous birds.

Previous work on differences in caterpillar abundance and biomass among tree taxa has often focused on the differences between deciduous and coniferous woodland rather than among deciduous taxa (van Balen, 1973; Mägi *et al.*, 2009; Veen *et al.*, 2010; Burger *et al.*, 2012). In general, oak trees (*Quercus* spp.) are suggested to host narrow caterpillar peaks, reaching greater maximum abundances than taxa such as birch (*Betula* spp.), alder (*Alnus incana*) and coniferous trees (van Balen, 1973; Visser, Holleman and Gienapp, 2006; Mägi *et al.*, 2009; Veen *et al.*, 2010; Burger *et al.*, 2012; Phillimore *et al.*, 2016; Shutt, Burgess and Phillimore, 2019). However, birch trees have also been found to host more caterpillars than multiple other deciduous taxa, and willow trees (*Salix* spp.) were found to host as many as oak (Shutt, Burgess and Phillimore, 2019). Other taxa, such as lime *Tilia cordata*, hornbeam *Carpinus betulus* and maple *Acer platanoides*, may exceed oak in hosting the greatest herbivore populations as suggested by levels of defoliation in Białowieża Forest, Poland (Wesołowski and Rowiński, 2006). Whilst the above studies have begun to investigate the effects of woodland composition on the timing and height of the caterpillar peak, all focus on few tree species, compare mixed-species woodlands or have relatively low power to detect differences in the full phenological distribution.

A European bias toward studying the MMH and caterpillar biomass in oak dominated woodlands (Varley, Gradwell and Hassell, 1974; Visser, Holleman and Gienapp, 2006; Hinks *et al.*, 2015; Burgess *et al.*, 2018) has presented limited opportunities for considering the impact of woodland tree composition on the phenological distribution of caterpillars. Whilst species of oak are important across much mature woodland in Europe, oak-woodland does not represent the average contemporary woodland habitat, making up just 16% of broadleaf woodlands in the UK (Stagg and Ward, 2019), and many lepidopteran and passerine species are relatively generalist and found in a variety of woodland habitats (Allan, 1979; Perrins, 1979; Hagemeijer and Blair, 1997; Skinner, 2009). Studying the MMH across a representative range of habitats will be important for understanding metapopulation level consequences of climate warming; for example, there are distinct trends in the thermal sensitivity of breeding phenology among great tit and blue tit populations in different habitats, which may be associated with differences in the phenological distribution of caterpillars as an important resource during breeding (Bailey *et al.*, 2022).

Spring temperatures have the potential to impact each of the parameters that govern the full phenological distribution, yet the only parameter for which the thermal sensitivity is well established is the mean timing, which is known to advance with an increase in temperature (Visser, Holleman and Gienapp, 2006; Charmantier *et al.*, 2008; Burgess *et al.*, 2018). There is also reason to believe that the height and width of the phenological distribution may also respond to temperature (Fig. 1.2); for example, thermal sensitivity in the variance in hatch date among individuals, rate of larval development (Stamp, 1990; Buse *et al.*, 1999), feeding activity, mortality risk (Battisti *et al.*, 2005) and starvation tolerance (Abarca and Lill, 2015) of caterpillars could alter the maximum abundance or biomass of caterpillars reached, the rate of change in abundance or biomass throughout spring and the duration over which the guild is prominent within the environment. If the species comprising the caterpillar guild differ in their thermal sensitivities this could generate changes to the turnover (differences in guild species composition), within a year, where the relative differences in the phenological distribution among species changes, or in the species composition of the caterpillar guild over time or space.

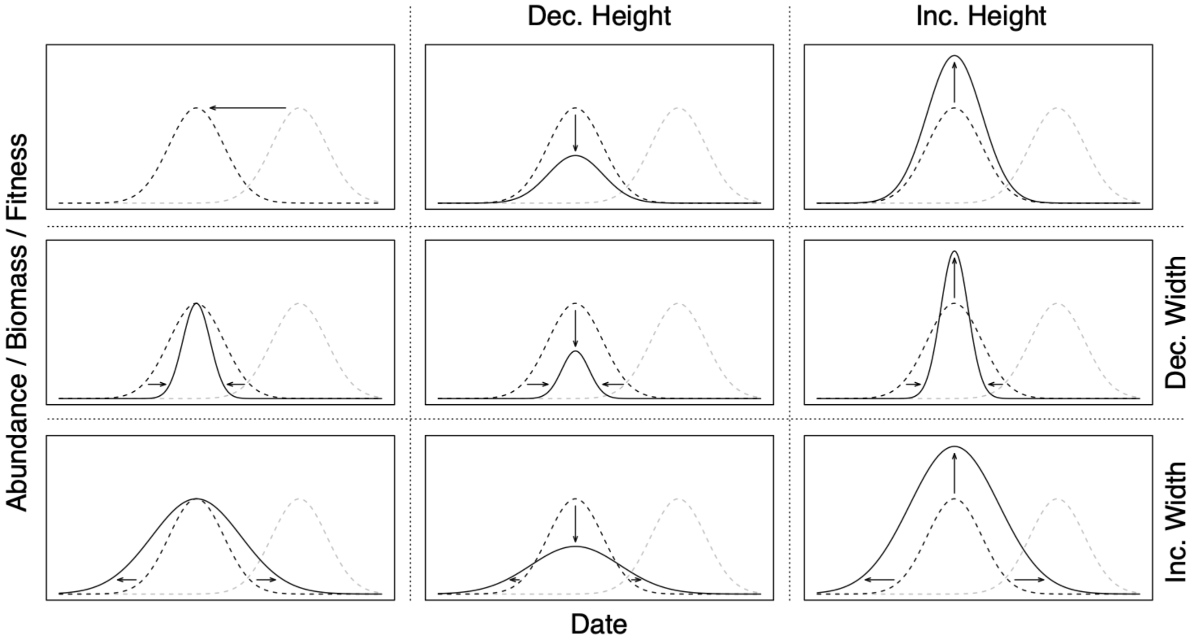

Figure 1.2: The full phenological distribution of an ephemeral event is described by a mean timing (position on the x-axis), height (maximum level of the response variable) and width (variation in timing around the mean). The top left plot shows a negative shift in the mean timing of an event, falling earlier in time moving from the grey to black dashed peaks, the metric most frequently studied in phenology research. In the remaining eight plots, the solid black line and arrows show a change to the height and/or width of the phenological distribution, in addition to a consistent shift in mean timing. The second and third columns show a decrease (dec.) or increase (inc.) in height, and the second and third rows show a decrease or increase in width. These plots illustrate how alterations to the height and width of the phenological distribution have consequences for the response variable (abundance, biomass, fitness) on a specific date, despite a consistent shift in mean timing among the plots.

Temperature-driven alterations to the phenological distribution of caterpillars could have important implications for bottom-up interactions with breeding birds and top-down interactions with the trees on which they feed, yet this topic has gone largely unexplored. Some attention has been given to the height and duration of the peak, suggesting that the duration decreases with temperature (Visser, Holleman and Gienapp, 2006; Smith *et al.*, 2011) and the height does not correlate with temperature (Nadolski *et al.*, 2021); yet no study has addressed the thermal sensitivity of the full phenological distribution of caterpillars in one framework (Fig. 1.2). Given the warming climate (IPCC, 2021), thermal sensitivity in the full phenological distribution of caterpillars could have important consequences for how we predict the outcome of interactions within the tri-trophic chain, in addition to possibly adding detail to our understanding of spatial variation in phenology and the MMH.

The match/mismatch hypothesis with phenological distributions

As aforementioned, the MMH is most frequently studied by comparing the thermal sensitivity of the mean timing for interacting species or guilds and testing how asynchrony affects fitness. Asynchrony is typically either defined as the difference between the mean timing of the peak consumer demand and the mean timing of the resource, or the difference between each individual consumer's peak demand and the mean timing of the resource. This approach assumes that the resource availability will be consistent at any specific level of asynchrony among sites or years, or that any variation in resource availability will have minimal effect on fitness. Given the above discussion that both biotic and abiotic conditions may drive variation in the phenological distribution of arboreal caterpillars, a key resource for insectivorous birds while breeding in deciduous woodlands, we can then also examine the implications that changes in the phenological distribution mean timing, height and width may have within the MMH.

Changes to the height and width of the phenological distribution of a resource will result in a different abundance of resource being available to consumers at a given level of asynchrony; for example, if the caterpillar peak reaches a higher maximum abundance and lasts for a longer duration of time, then more food will be available to the consumer at the same level of asynchrony compared to when the caterpillar peak is lower and shorter. If the relative abundance of resource available to those that are synchronous compared to those that are asynchronous changes through an alteration to the caterpillar peak width, this is also likely to change the relative consequences of being asynchronous within the population - altering how the MMH manifests among individuals exposed to differing resource distributions. This illustrates why the full phenological distribution of the resource may be relevant in comparing measures of asynchrony from multiple sites or years, and how habitat- or temperature-driven variation in the caterpillar peak would be of high importance with ongoing climate warming and spatial heterogeneity in woodland composition. Previous work has compared the performance of using a measure of relative timing versus a measure of overlap between the temporal distributions (characterised differently to the phenological distributions discussed in this thesis) of arboreal caterpillars and great tits (Ramakers, Gienapp and Visser, 2019), finding that the simpler relative timing metric served as a better predictor of recruitment probability and the strength of selection on egg laying than the temporal overlap. Whilst Ramakers *et al*. (2019) found relative timing to be a better predictor, the way in which temporal variation in the caterpillar resource was brought into the prediction of great tit breeding success is distinct from the phenological distribution orientated framework discussed here. The temporal overlap variable used by Ramakers *et al*. involved more calculation and estimation of resource requirement versus availability in the environment, compared to the exploration of comparable distribution parameters described in this thesis. Whilst resource requirement and availability are more biologically relevant and the uncertainty in the estimates of overlap were explored as part of Ramakers *et al*. study, the uncertainty in relative timing and overlap were not incorporated into the main analyses, and in using multiple steps of manipulation and prediction from raw data prior to analysis, the likelihood of inaccuracies accumulating will be increased compared to that of a more direct approach.

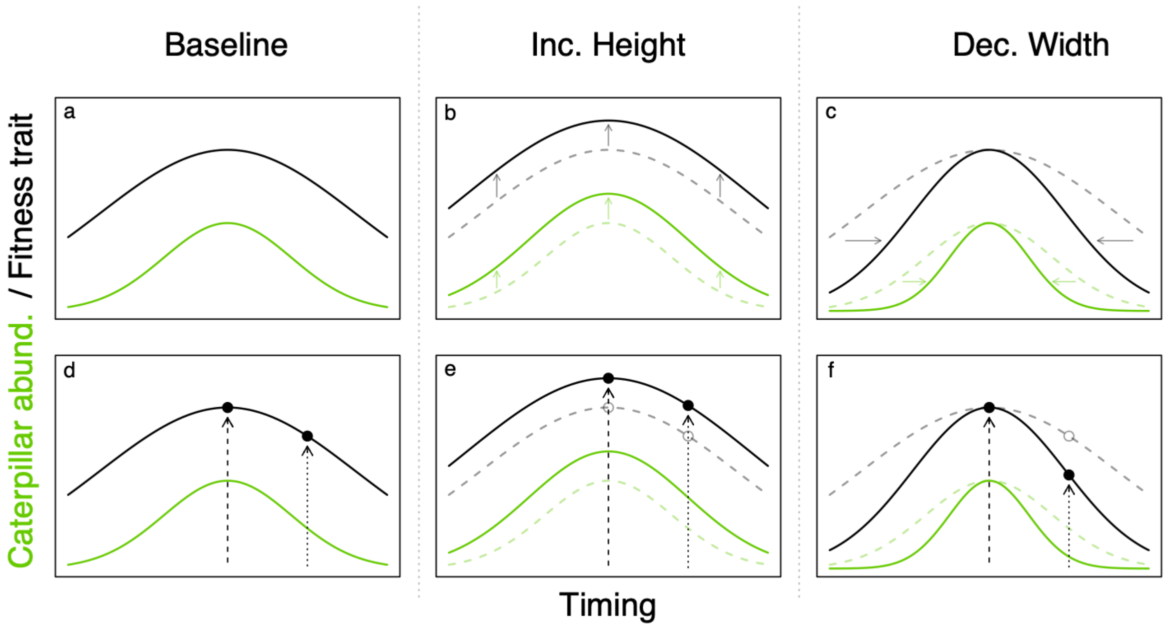

Figure 1.3: The match/mismatch hypothesis (MMH) in the context of full phenological distributions: plots show the phenological distribution of caterpillar abundance (green) and the phenological fitness function of breeding birds (black). Plot a) represents a baseline of how a phenologically sensitive fitness trait (e.g. fledging success) is predicted to vary in line with the phenological distribution of caterpillars under the MMH, in which fitness is maximised when the peak demand for resource is synchronous with the mean timing of the caterpillar distribution. b-c) illustrate how an increase in height (b) and decrease in width (c) of the caterpillar phenological distribution are predicted to have similar effects on the phenological fitness function of the birds, changing fitness relative to timing. d-f) show the predicted fitness (black point) of a synchronous bird, with a dashed arrow, and an asynchronous bird, with a dotted arrow. The dashed phenological distribution lines (b-c, e-f) show the baseline caterpillar and fitness distributions with empty points for the predicted fitness without considering differences in the height and width of the phenological distribution.

If the height or width of the phenological distribution of caterpillars impacts fitness relative to breeding phenology, then each parameter defining the full phenological distribution of caterpillars would be predicted to correlate positively with the equivalent parameter for the phenological fitness function of bird breeding success (Fig. 1.3). For example, there is evidence that asynchrony with the caterpillar peak reduces the number of chicks fledged in great tits (Visser, Holleman and Gienapp, 2006; Reed, Jenouvrier and Visser, 2013; Simmonds *et al.*, 2017) because fewer caterpillars are present as asynchrony increases (Fig. 1.3a,d), therefore fledging success is used as the fitness trait in the following examples. If the phenological distribution of caterpillars was to increase in height, then more food would be available to breeding birds throughout the season, and this would be predicted to increase the number of offspring fledged in a similar manner (Fig. 1.3b,e). With an increase in height, all nests would be expected to fledge more offspring than they would at the same level of asynchrony when breeding in an environment with the original lower caterpillar peak (Fig. 1.3e). If the phenological distribution of caterpillars was to become narrower in width, then there would be a greater difference in the volume of food available to nests that are synchronous and asynchronous, predicted to reduce the number of offspring fledged from more asynchronous nests and increase the magnitude of the negative effect of being mistimed (Fig. 1.3c,f), increasing the strength of directional selection on timing (Darwin, 1859). The narrower peak would also mean less food was available to the asynchronous birds than would have been when breeding with the wider caterpillar peak (Fig. 1.3f), again predicted to reduce the fledging success of mistimed birds compared to when breeding in an environment with a wider peak.

The extended conceptual framework of the MMH, in which the full phenological distribution of a resource is predicted to affect the full phenological fitness function of a consumer, is novel to MMH research, yet there is some evidence to suggest the extension proposed may hold in the interaction between breeding birds and the caterpillar resource. Despite stronger support for use of relative timing rather than overlap with the caterpillar peak for predicting recruitment in great tits (Ramakers, Gienapp and Visser, 2019), other work has shown higher biomasses of caterpillars both pre- and post-fledging to increase recruitment to the population in great tits and willow tits (*Poecile montanus*) (Pakanen *et al.*, 2016), caterpillar peak height had more of an effect on the seasonal decline in the number of chicks fledged than synchrony with the peak timing in pied flycatchers, though it did not affect recruitment (Visser *et al.*, 2015), and evidence suggests annual variation in nestling condition and fledging success of blue tits is due to differences in the height of the caterpillar peak (García-Navas and Sanz, 2011; Vatka, Rytkönen and Orell, 2014).

If the phenological distribution of caterpillars affects the phenological fitness function of birds, then reducing the resource to guild or species mean timing is likely to miss some key implications of the MMH for populations. A change in the height or width of the fitness function may reflect a shift in the mean population fitness with possible consequences for population growth, though evidence in great tits suggests negative impacts on individual fitness do not necessarily lead to demographic effects (Reed *et al.*, 2013; Reed, Jenouvrier and Visser, 2013). The width of the fitness function in combination with the width of the phenological distribution of the consumer population defines the strength of stabilising selection, and when paired with the lag between the optimum timing and mean population timing, it also defines the strength of directional selection (de Villemereuil *et al.*, 2020). As the strength of stabilising selection and the lag between population timing and the optimum are all important for the rate of environmental change through which a population can persist (Chevin, Lande and Mace, 2010), assessing the effects of the resource phenological distribution on the consumer fitness function may increase the accuracy of our estimates of population responses to climate warming.

Study system: Phenoweb transect

The Phenoweb transect monitors 44 deciduous woodland sites, spread over 220km from Edinburgh (central east Scotland; 55°980 N, 3°400 W) to Dornoch (north-east Scotland; 57°890 N, 4°080 W) (Fig. 1.4a). The sites have been monitored since 2014, providing an average temperature range among years of 1.58°C (from mean daily temperatures among sites from mid-Feb to mid-June each year, Fig. 1.4b); and include an elevation range of 10-433m above sea level, producing an average spatial temperature range of 2.85°C (from mean daily temperatures among years from mid-Feb to mid-June for each site, Fig. 1.4b). The tree composition also varies, including oak, beech, alder, birch, sycamore and willow-dominated sites, as well as more mixed deciduous woodlands (Fig. 1.4c). A modal average of eight nest boxes (entrance 26mm) have been installed at each site to target breeding blue tits, see Box 1.1 for species information. The caterpillar guild abundance and biomass has been monitored on a range of trees representing the local habitat at each site throughout spring each year.

Box 1.1: Blue tit species information

Blue tits, *Cyanistes caeruleus*, show a preference for broad-leaved deciduous woodland habitats where they feed mainly on insects in summer, and insects and seeds in winter (Perrins, 1979). They naturally nest in tree cavities, but also use artificial nest boxes or other anthropogenic cavities (Perrins, 1979). British blue tits rarely have second broods, with second nesting attempts generally the result of a predated first nest; true second broods are more common in continental European populations (Perrins, 1979). Clutch size is highly variable but usually between 7-13 eggs (Perrins, 1979). In the UK, they are largely resident birds, with roughly 20% found to move more than 10 miles, though continental individuals will travel further (Perrins, 1979; Cramp and Perrins, 1993). The average juvenile survival rate is 0.38 in the first year, with annual adult survival rate higher, at 0.53 (Siriwardena, Baillie and Wilson, 1998). Among the Phenoweb populations, on average 42% of the breeding adults are first-year birds, with 1.3% of the offspring recruiting to breed within the project nest boxes.

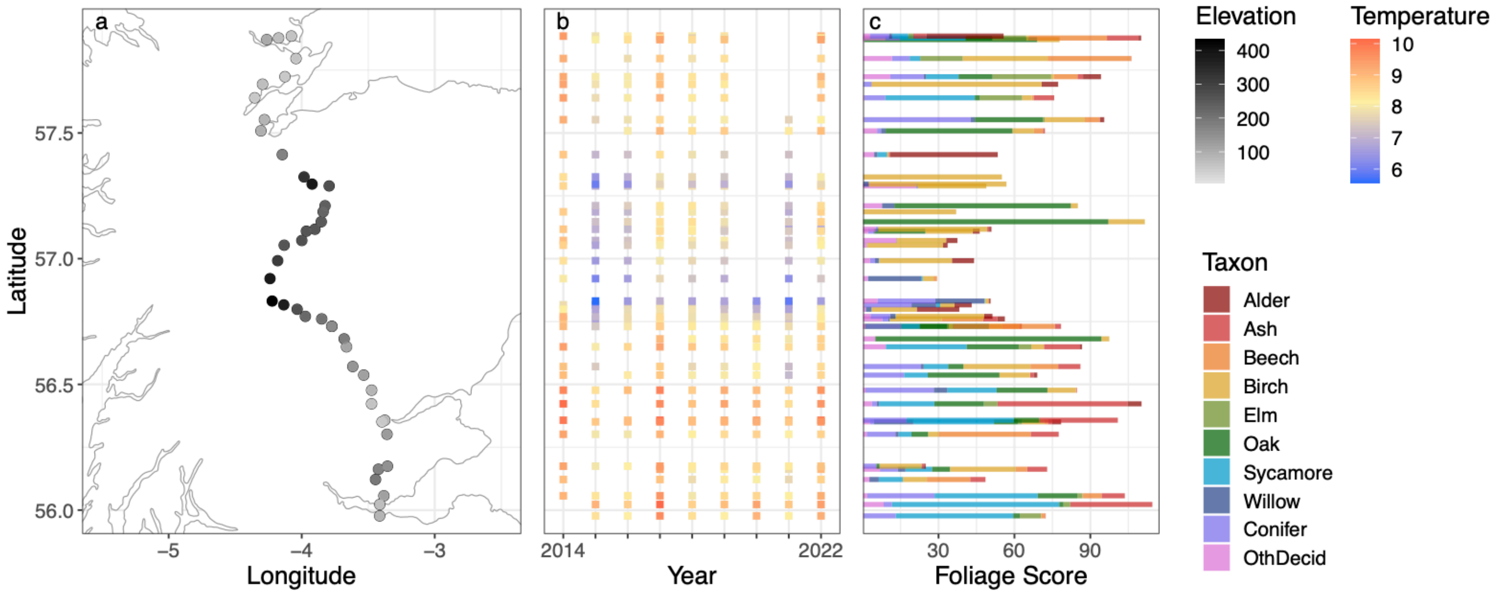

Figure 1.4: Summary of site location, temperature and tree composition along the Phenoweb transect through Scotland: a) a map of the site locations with point shade representing the elevation, b) the average temperature at each site (by latitude) in each year from mid February to late June, gaps indicate years in which sites were not monitored, and c) the average woodland tree composition throughout each site (by latitude), using a metric representing the amount of foliage of each taxon (see Chapter 3), with particular focus on the 10 most common deciduous taxa among sites, with other deciduous taxa (OthDecid) and conifers grouped.

Data from the Phenoweb transect makes it possible to study both spatial and temporal variation in the phenological distributions of arboreal caterpillar abundance and biomass, and blue tit breeding phenology and fitness. Long-term multi-population study of phenology and fitness in the tri-trophic deciduous woodland food chain makes it possible to explore differences in phenology and the MMH associated with woodland tree composition, spatial gradients and temporal trends among years. When considering the thermal sensitivity of phenology, if temperature has a causal effect on phenology then the effect is expected to be similar in space and time (Dunne *et al.*, 2004; Phillimore *et al.*, 2010); however, the effect may differ in space and time if different processes are operating, such as local adaptation in space, or if a variable correlated with temperature also drives phenology (Tansey, Hadfield and Phillimore, 2017). This topic is often overlooked when using spatial or spatio-temporal temperature as a predictor of temporal trends, and the Phenoweb transect provides a novel opportunity to compare thermal sensitivity in space versus time (Phillimore *et al.*, 2010; Roberts *et al.*, 2015; Tansey, Hadfield and Phillimore, 2017).

Thesis outlines and aims

In this thesis, I study drivers of variation in the full phenological distribution of arboreal caterpillars in spring, and how aspects of this distribution in turn affect the phenological fitness function of blue tits. In Chapter 2 I examine how the timing, height and width of the peak in caterpillar guild abundance and biomass varies among tree taxa, and whether the local woodland composition has any further effect on abundance. Differences in the phenological distribution of caterpillars among tree taxa and woodland tree compositions provide insight into the spatial heterogeneity in the caterpillar peak; important for understanding variation in herbivory pressure on trees and the volume of food available to a range of birds while they breed. In Chapter 3 I analyse the thermal sensitivity of the mean timing, height and width of the peak in caterpillar guild abundance, assessing whether the increasing temperatures under climate warming will affect more than just the mean timing of the caterpillar phenological distribution (Fig. 1.2). Thermal sensitivity in the mean timing, height and width of the phenological distribution of caterpillars not only affects the level of phenological synchrony within the tri-trophic food chain, as is more frequently studied, but will also alter the intensity and duration of herbivory on trees and the spread and total abundance of food available to the breeding birds. In Chapter 4 I propose an extension to the standard framework of the MMH in which the full phenological distribution of a resource (caterpillar abundance) is predicted to affect the full phenological fitness function of a consumer (hatch date and fledging success of blue tits) (Fig. 1.3). As a combination of the mean timing, height and width of a resource phenological distribution determines the food available on any specific date, I predict that each parameter governing the resource distribution will affect the equivalent parameter of the consumer fitness function. The extended framework provides a more complete test of the match/mismatch hypothesis allowing a more accurate estimate of population fitness and the strength of selection on timing.

Based on the present understanding of larval insect ecology and life history, there is reason to believe that host plants and temperature will influence the phenological distribution of the arboreal caterpillar guild, and that in turn, this variation in the caterpillar resource among sites and years may drive variation in attributes of the phenological fitness function of blue tits. I aim to address these questions and hypotheses using an outstanding data set with 44425 records of caterpillar abundance, 38387 records of biomass and 1138 records of blue tit breeding phenology and fledging success; collected across 44 deciduous woodland sites over nine years (Fig. 1.4). I aim to advance the level of detail in which we study trophic interactions, as understanding sources of spatial and temporal variation in phenology and the MMH will improve our ability to estimate the effects of global change on species and how they interact. Reducing population or guild phenology to mean timing in MMH research may overlook among-individual variation in (a)synchrony that explains additional variation in fitness and the consequences of trophic asynchrony. Understanding sources of variation in the full phenological distribution may improve our ability to accurately forecast population persistence in the face of ongoing climate warming.

Chapter 2 - Host tree and guild-level differences in the timing and abundance of spring caterpillars

Abstract

Climate warming is causing many spring biological events to advance in timing and where the phenology of a resource and consumer advance at different rates this can result in trophic asynchrony. While the temperate study system of deciduous tree – caterpillar – insectivorous passerine has been widely studied, little work has examined whether the phenological distribution of caterpillars differs among tree taxa and habitats. If differences among tree taxa exist, they have the potential to underpin spatial variation in the match-mismatch hypothesis in this food web. My first hypothesis was that both the host tree taxon and the local tree guild composition would affect caterpillar abundance. My second hypothesis was that the phenological distribution of caterpillar abundance and the trend in the mass of individuals over time would differ among host tree taxa, with caterpillar guild biomass the product of these two metrics. We collected data on caterpillar abundance and mass throughout spring for seven years at 44 sites with varied woodland compositions. I estimated the effects of tree taxa on the caterpillar abundance and decomposed these effects into those of the tree taxon the caterpillars lived on (host-level) and those of the taxa in the local tree guild the caterpillars lived in (guild-level). Second, I analysed differences in the phenological distribution of spring caterpillars among host tree taxa, focusing on caterpillar abundance, mass and biomass. I found substantial variation in the caterpillar abundance supported among host tree taxa, in addition to evidence that an increase in the density of oak foliage within a woodland can increase the abundance of caterpillars found at the guild-level. Some aspects of the phenological distribution of caterpillars differed at the host-level, in particular, the height of the peak was highest on oak and lowest on alder. I show minimal, but significant, variation in timing and duration among hosts, whereas we did not find much evidence for variation in the shape of the phenological distribution or mass gain of caterpillars. I show that the abundance and phenological distribution of caterpillars differs between deciduous trees and that oak is distinct from most other common taxa. Woodland tree composition is likely to influence differences in caterpillar abundance and biomass between locations; contributing to spatial heterogeneity in an important component of the woodland ecosystem and an ephemeral resource relied upon by many consumer species.

Introduction

Climate warming is driving species across multiple taxa and trophic levels to advance the timing of seasonal events (Parmesan, 2006; Thackeray *et al.*, 2016; Cohen, Lajeunesse and Rohr, 2018). The shifts in timing vary between species and trophic levels, with secondary consumers generally responding at a slower rate than producers and primary consumers (Thackeray *et al.*, 2010, 2016). When a consumer is reliant upon an ephemeral resource with which it has become asynchronous this can be detrimental to fitness, referred to as the match-mismatch hypothesis (MMH) (Cushing, 1990; Visser and Both, 2005; Durant *et al.*, 2007; Samplonius *et al.*, 2020).

The temperate terrestrial tri-trophic food chain of deciduous tree – caterpillars – cavity nesting insectivorous passerine is perhaps the system in which asynchrony has been studied most (Thomas *et al.*, 2001; Visser, Holleman and Gienapp, 2006; Charmantier *et al.*, 2008; Both *et al.*, 2009; Samplonius *et al.*, 2016; Shutt *et al.*, 2019). This system includes ephemeral resources at two trophic levels making it highly susceptible to the MMH; young palatable leaves which the caterpillars require to grow to pupation (Feeny, 1970; van Asch and Visser, 2007; Forkner *et al.*, 2008), and the caterpillars are a key food source for many breeding birds (Betts, 1955; Bańbura *et al.*, 1994; Sanz, 1998; Wilkin, King and Sheldon, 2009; García-Navas and Sanz, 2011; Samplonius *et al.*, 2016). The temporally peaked distribution of caterpillar abundance/biomass is central to this woodland system (Gibb, 1950; Southwood *et al.*, 2004), with potential implications for breeding consumer species (Buse *et al.*, 1999; Visser, Holleman and Gienapp, 2006; Reed, Jenouvrier and Visser, 2013) and herbivory damage to deciduous trees, possibly influencing tree growth, survival and forest productivity (Kulman, 1971; Whittaker and Warrington, 1985; Whitham *et al.*, 1991; Marquis and Whelan, 1994).

Three main components describe the phenological distribution of the spring caterpillar peak; peak date (mean timing), height (maximum abundance/biomass) and width (shape/duration) (Shutt, Burgess, & Phillimore, 2019). If components of the phenological distribution differ among individual host trees, species, the tree guild within an area and more broadly between woodlands, this has the potential to result in a stabilising spatial portfolio effect (Schindler, Armstrong and Reed, 2015) and buffer consumer metapopulations from the MMH, as some caterpillar consumer (e.g. birds) and resource (i.e. trees) populations are synchronous while others are mistimed. Extensions of the MMH recognise that if the availability of the resource is important for consumer fitness then the height and width of the resource peak may matter in addition to its timing (Durant *et al.*, 2005; Miller-Rushing *et al.*, 2010).

The majority of studies within the woodland tri-trophic study system are focused on oak-dominated (*Quercus* spp.) woodlands or mainly collect data about caterpillar abundance or biomass in relation to oak trees (Varley, Gradwell and Hassell, 1974; Visser, Holleman and Gienapp, 2006; Hinks *et al.*, 2015; Burgess *et al.*, 2018). Oak trees and woodlands are thought to be preferred by some breeding passerines, such as tits (Perrins, 1979), and are described as a good resource for the development of caterpillars, at least for the winter moth, *Operophtera brumata*, although statistical comparison among host tree taxa has been low powered (Feeny, 1970; Wint, 1983). Oak-dominated woodland, however, is not representative of the habitat present across all deciduous woodlands in these temperate environments. For instance, in Great Britain, although oak trees are the second most common broadleaf tree taxon, they make up just 16% of the area covered by broadleaf woodlands (Stagg and Ward, 2019), and many lepidopteran and passerine species in this system will feed, forage and nest in a variety of woodland habitats (Allan, 1979; Perrins, 1979; Hagemeijer and Blair, 1997; Skinner, 2009). The extent to which inferences about the caterpillar phenological distribution made in relation to oak can be generalised to other habitats is largely unknown (Shutt, Burgess, *et al.*, 2019). Therefore, it is important to consider how the phenological distribution of caterpillars varies among woodlands with different habitat compositions when aiming to understand the potential for trophic asynchrony and the portfolio effect across heterogeneous temperate deciduous woodlands (Burger *et al.*, 2012).

Tree composition of woodland habitats may be an important determinant of spatial variation in the phenological distribution of the caterpillar peak, however, relatively few studies have explored this topic. Most relevant work has focused on differences between deciduous, mixed and coniferous woodlands (van Balen, 1973; Mägi *et al.*, 2009; Veen *et al.*, 2010; Burger *et al.*, 2012), with minimal focus on the differences among deciduous woodland compositions and specific tree taxa. Mägi et al. (2009) suggested that the phenological distribution of caterpillars in mixed birch (*Betula pendula*) and alder (*Alnus incana*) woodland in 2004 was more similar to that of coniferous woodlands than oak; characterised as having a low and wide peak, compared to the high but narrow peak in oak woodlands (van Balen, 1973; Visser, Holleman and Gienapp, 2006; Veen *et al.*, 2010). Birch (*Betula* spp.) and coniferous mixed woodlands were also found to host lower abundances of caterpillars (Burger *et al.*, 2012). However, in a spatially replicated study of caterpillars on individual trees in Scotland, birch trees were found to host more caterpillars than many other deciduous species (Shutt, Burgess, & Phillimore, 2019). The same study also found that the height of the caterpillar peak differs among four deciduous tree taxa, with the peak on oak trees reaching much greater maximum abundances and some evidence of increased peak heights on willow (*Salix* spp.) trees as well (Shutt, Burgess and Phillimore, 2019). Oak may not support the greatest abundance of all deciduous trees however; as in Białowieża Forest, Poland, hornbeams (*Carpinus betulus*) , maples (*Acer platanoides*) and limes (*Tilia cordata*) were found to receive more herbivory damage than oak (*Q. robur*) (Wesołowski and Rowiński, 2006).

There are a number of ways that woodland tree composition may influence the height of the peak in caterpillar abundance and biomass. Tree species differ in leaf nutritional quality (Schultz, Nothnagle and Baldwin, 1982; Yanar *et al.*, 2017), which can affect abundance through Lepidopteran fecundity (Awmack and Leather, 2002) and survival (Wint, 1983; Yanar *et al.*, 2017), and mass through effects on growth (Loader and Damman, 1991). Preferential laying by females on specific hosts (Thompson and Pellmyr, 1991; Kakimoto, Fujisaki and Miyatake, 2003), or dispersal by larvae (van Asch and Visser, 2007; Forkner *et al.*, 2008) may also amplify differences in abundance among tree taxa, impacting biomass as the product of the abundance and mass of caterpillars in the guild. Studies of spring caterpillars report differences in abundance and biomass between deciduous tree species, with oak and willow having the highest peaks (Veen *et al.*, 2010; Shutt, Burgess and Phillimore, 2019), however, both studies had quite low power to detect among species differences, and the sensitivity of biomass to changes in mass versus abundance is yet to be explored. Differences in abundance among host tree species may also have knock-on effects at the tree guild-level. Indiscriminate egg laying and the dispersal of larvae could result in the taxonomic tree composition of a woodland influencing the abundance of caterpillars recorded on any tree throughout the area, in addition to the general differences among host tree species.

The width or duration of the peak may also vary through multiple mechanisms. For example, the diversity of the Lepidopteran guild differs between tree species (Kennedy and Southwood, 1984), which may impact the peak width if Lepidopteran species differ in their hatching phenology or growth rate. In addition, differences in nutritional quality or the phenology of the nutrition provided by different tree taxa (Schultz, Nothnagle and Baldwin, 1982; Loader and Damman, 1991; Kakimoto, Fujisaki and Miyatake, 2003) could generate among-tree variation in the time caterpillars take to reach pupation, influencing peak duration in addition to the aforementioned impact on height. Finally, the timing of peak abundance or biomass may vary among tree species as a result of differences in their leafing phenology (Murray, Cannell and Smith, 1989; Roberts *et al.*, 2015). Such phenological differences among trees could select for adaptation of a caterpillar species' phenology or sort for caterpillar species that differ in their timing. However, the large variation in tree phenology within tree species (Murray, Cannell and Smith, 1989; Cole and Sheldon, 2017), and even within individual trees, will reduce the strength of selection to coincide with the phenology of a particular tree species. Shutt, Burgess, *et al*., (2019) explored among-tree species variation in peak timing in Scotland using three years of data with 6089 records of caterpillar presence/absence (575 caterpillars). They found no difference in peak timing between oak, willow, birch and sycamore (*Acer pseudoplatanus*), though credible intervals were broad, implying low power to detect a difference of a few days.

In this chapter, I use 31215 caterpillar samples collected over 7 years from 44 deciduous Scottish woodland sites, that vary in their tree composition, to analyse tree and habitat-driven variation in the phenological distribution of caterpillar abundance and biomass throughout spring. First, I explore the hypothesis that atemporal caterpillar abundance varies among host tree taxa and that there are additional effects of local woodland density and tree guild composition (Hypothesis 1). Second, I hypothesise that the phenological (temporal) distribution of caterpillars through spring differs among host tree taxa as measured by i) abundance (Hypothesis 2) ii) mass (Hypothesis 3) and their product iii) biomass (Hypothesis 4). Throughout I primarily compare each taxon to the average trend among taxa, but also to oak specifically as the focus of much previous literature. Together this programme examines the capacity of woodland composition to provide spatial heterogeneity in herbivory pressure to trees, MMH buffering for secondary consumers and tests the extent to which oak-dominated study systems are representative of other deciduous woodlands.

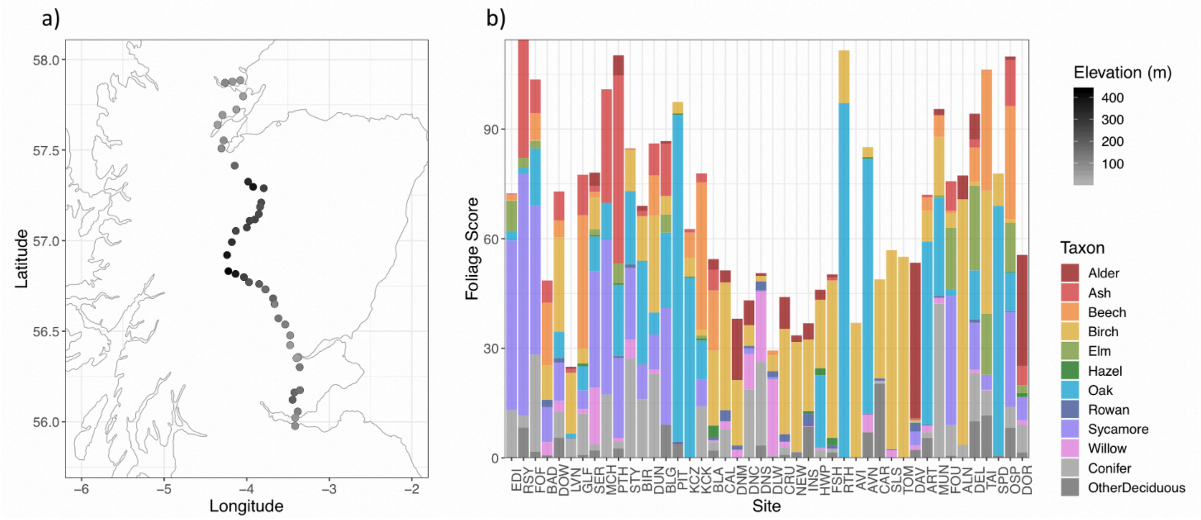

Figure 2.1: a) Map of site locations in Scotland, the darkness of the points indicates the site elevation and b) shows the woodland habitat composition at each site displayed as a foliage score which accounts for tree size, 1 unit of foliage score = 1 small tree (circumference at chest height 0.4-0.99m) and 39 units = 1 large tree (circumference >2.50m), sites are ordered by increasing latitude from left to right.

Materials and Methods

Study System

This study was carried out using 44 woodland sites along a 220 km transect between Edinburgh (55°980 N, 3°400 W) and Dornoch (57°890 N, 4°080 W) (Fig. 2.1a). This includes the 40 sites monitored between 2014-16 in Shutt, Bolton, Cabello, Burgess, & Phillimore (2018) with an additional four sites monitored from 2017 onwards. During spring 2020 the field season was restricted to the 22 most southern sites due to the Covid-19 pandemic. Woodland habitat composition has been surveyed at a 15m radius around each nest box installed at sites (n = 334 since 2017), including all trees with a trunk circumference of ≥40cm at chest height or a 'stand' with ≥6 branches within 20cm of each other at the base (mainly hazel *Corylus avellana* and willow *Salix* spp.). Trees were identified to the genus level with the exception of some conifers. Trees were recorded by size catergories based on circumference at chest height: small = 0.4-0.99m, medium = 1.0-2.49m and large ≥ 2.5m. Stands with six to 21 trunks were classed as 0.5 small trees, and with more than 21 trunks as one small tree.

Foliage scores were calculated, as in Shutt *et al*. (2018), to describe the prevalence of each tree taxon around each nest box, weighting for the categorical sizes of the trees. The minimum cross-sectional trunk area for each size category was calculated (e.g. $\pi[40/(2\pi)]^2$ for small trees, $\pi[250/(2\pi)]^2$ for large trees) and each was divided by the value for small trees. Therefore, one small tree was worth 1.0 unit, one medium tree was worth 6.25 units, one large tree was worth 39.06 units and the foliage scores represent the equivalent number of small trees after accounting for size. For each tree taxon, these values were multiplied by the number of trees recorded for each size and summed. The average score for each tree taxon was calculated among the next boxes at each site to give a mean foliage score for each tree taxon at each site (Fig. 2.1b).

Caterpillar Sampling

Caterpillar sampling followed the branch beating methodology described in (Shutt, Burgess and Phillimore, 2019). A selection of trees at each site, representative of the site's woodland composition, were monitored for leafing phenology (Shutt *et al.*, 2019) and those that had a branch of minimum length 1m and between 0.5-1.5m above the ground were also beaten. The tree taxa sampled include alder (*Alnus glutinosa*), ash (*Fraxinus excelsior*), beech (*Fagus sylvatica*), birch (*Betula* spp.), elm (*Ulmus glabra*), hazel (*Corylus avellana*), oak (*Quercus* spp.), rowan (*Sorbus aucuparia*), sycamore (*Acer pseudoplatanus*) and willow (*Salix* spp.). A branch, meeting the height and length criteria, was marked and beaten every four days. The trees sampled at each site were divided into two groups and each group was beaten alternately at two days intervals. The branch was held consistent between years unless damaged, broken or dead. The average number of trees sampled at each site was 3, 6, 6, 14, 14, 15 and 14 for 2014-20 respectively, with a total of 31215 beating samples recorded across the 7 years. Sampling began each year when 45% of the monitored trees across all sites had reached the 'first leaf' stage and continued until the end of the blue tit breeding season (Shutt, Burgess, *et al*., 2019), except for in 2020 when sampling began when we were able to begin fieldwork. Sampling periods extended between ordinal dates 120-166, 125-175, 130-173, 123-167, 129-172, 117-168 and 130-170 for 2014-20 respectively.

Branch beating was carried out using a clear plastic rubble sack measuring 76cm x 51cm. The bag was fully extended over the branch's foliage and closed with one hand at the maximum length, keeping the open end facing upwards. The bag was then beaten 30 times at a consistent impact and rate (roughly two per second) to dislodge any free-living invertebrates on the branch. After careful removal from the branch, all caterpillars (larvae of Lepidoptera (>90%), Hymenoptera, Diptera and Coleoptera; Shutt, Burgess, *et al.*, 2019) with an estimated diameter of ≥1mm were counted and collected. We chose this threshold due to an assumption that the smallest caterpillars would be of minimal value to avian consumers, and as they are hard to see and collect, excluding them increases the consistency between samples and recorders. From 2017 onwards, the biomass of each sample was recorded to 0.01g using a Myweigh Triton T3R-500 Digital Scale. We found that some samples were of insufficient mass (< 0.02g) to show a read on the balance and were recorded as such.

Statistical analysis

All analyses used Bayesian generalized linear mixed models (GLMM) in the MCMCglmm package (Hadfield, 2010) in R version 3.5.3 (R Core Team, 2019) and I present full models (Tables A.1-5). Poisson GLMMs were used for all models looking at variation in caterpillar abundance and posterior predictive checks were used to confirm that the data were not zero-inflated as compared with model expectation. Gaussian GLMMs were used to model caterpillar mass. Fixed effects were considered significant if the 95% credible intervals (CIs) do not overlap zero. Random effects were considered significant if the lower credible interval for their variance was removed from 0. I used the mean of the posterior distribution when estimating parameters from the fixed effects, the median when random effects were included and the mode for reporting the random term variances. Estimates on the data scale that marginalise over random effects are the exponentiated link-scale mean rather than the mean expectation on the data scale. All models were run with sufficient iterations to ensure an effective sample size of >1000 for each focal parameter and convergence was assessed by visual inspection of the trace plots. Parameter-expanded priors were used for all models (V=1, nu=1 [2 or 3 for terms with random regression], alpha.mu=0, alpha.V=10000), the prior induces a scaled $F_{1,1}$ prior on the variance, and an inverse gamma distribution with shape=scale=0.002 was used for the residual variance. Default flat priors were used for the fixed effects.

Some structural random terms were included in all models (Table 2.1). These were site, year (as a factor), site by year (site*year) and day by site by year (day*site*year) to allow for spatiotemporal differences in caterpillar abundance and mass. I also included the unique tree ID and recorder of each beating sample as random terms.

Table 2.1: Model compositions. Date refers to ordinal date which was mean-centred and sd-scaled (mean = 146.77, SD =14.04), year was included as a factor and woodland composition refers to multi-membership component explained in the text. Int = intercept, abund = abundance, VCV = variances and covariances.

Model	Abundance decomposition (Table S1)	Habitat abundance (Table S2)	Abundance phenology model (Table S3)	Mass phenology model (Table S4)
Motivation	Decomposition of variance in abundance	Differences in the abundance of caterpillars among tree taxa and effect of woodland density and composition (Hypothesis 1)	Differences in phenological distribution of caterpillar abundance among tree taxa (Hypothesis 2 and 4)	Differences in phenological distribution of caterpillar mass among tree taxa (Hypothesis 3 and 4)
Response	Caterpillar abundance	Caterpillar abundance	Caterpillar abundance	log(Mean mass per caterpillar)
Fixed effects	Date Date^2	Total foliage score	Date Date^2	Date Date^2
Random terms	Site Tree taxa Tree ID Site*year Day*site*year Year Year-day Recorder	Tree taxa Woodland-composition Site Year Site*year Day*site*year Tree ID Recorder	Int, Date and Date^2 VCV across Tree taxa Int, Date and Date^2 VCV across Site Int, Date and Date^2 VCV across Year Site*year Day*site*year Tree ID Recorder	Int and Date VCV across Tree taxa Int and Date VCV across Site Year Site*year Sqrt(1/abund) VCV across units Day*site*year TreeID Recorder
Family	Poisson	Poisson	Poisson	Censored-Gaussian
Iterations (thin)	2500000 (500)	4500000 (800)	1050000 (100)	5500000 (500)
Burnin	50000	500000	50000	500000
Sample Size	4900	5000	10000	10000

Abundance

Variance decomposition of caterpillar abundance

I decomposed the variance in caterpillar abundance throughout spring to gauge the relative contributions of spatial and temporal factors to the total variance observed in our data (abundance decomposition model, Table 2.1). The response variable was the number of caterpillars recorded in each beating sample with date and date^2 included in the fixed effects to account for the peaked temporal distribution. Date refers to ordinal date and was mean-centred and sd-scaled in all models (prior to scaling: mean = 146.77 [27th May, 26th in leap years], SD = 14.04). The variance explained by date (x) and date^2 (y) was calculated by matrix multiplication between the parameter estimates and covariance matrix of the two variables using the quadratic equation:

Equation 2.1: $$[\beta_x \quad \beta_y] * \begin{bmatrix} \sigma_x^2 & \sigma_{x,y} \\ \sigma_{x,y} & \sigma_y^2 \end{bmatrix} * [\beta_x \quad \beta_y]^T$$

The random terms included each day in each year (day*year) and the host tree taxon (tree taxa) in addition to the structural terms listed above. I calculated the mean percentage of variance on the log scale that is attributable to the date and date^2 fixed effects and each random term across the posterior distribution.

Habitat variation in caterpillar abundance

I assessed differences in the abundance of caterpillars supported by different tree taxa (host-level), the effect of local foliage density and whether the foliage score of each tree taxon (guild-level) contributing to local woodland composition, from the habitat surveys, has any additional effect (habitat abundance model, Table 2.1). To calculate the site guild-level foliage scores for non-focal tree taxa, I combined all of the coniferous tree taxa into a ‘conifer’ group and all deciduous tree taxa that are less common and not sampled at the host-level were grouped as ‘other deciduous’. The *i*th observation of caterpillar abundance on host species *j* at site *k* was modelled as:

Equation 2.2: $$y_{ijk} = b_0 + u_j^{(h)} + \sum_s (b_1 + u_s^{(g)})(f_{sk} - \bar{f})$$

Here b_0 is the intercept, $u_j^{(h)}$ is the effect of host species *j*, f_{sk} is the foliage score for each guild taxon *s* at site *k*. $\bar{f}$ is the average foliage score of all taxon site combinations such that the composition foliage scores for each tree taxon (guild-level) at each site are globally mean centred across all taxa and sites, $(f_{sk} - \bar{f})$. b_1 is the average effect of foliage score on *y* (irrespective of guild composition) and $u_s^{(g)}$ is the deviation from this average for species s in the tree guild. $u_j^{(h)}$ and $u_s^{(g)}$ are random effects with estimated variance.

I assessed the difference in abundance supported by different tree taxa using the posterior distributions of the host-level tree taxon random effects. At the guild-level, as several tree taxa were associated with each observation, the woodland composition component used a multi-membership approach with a random regression term (Equation A.1 shows Equation 2.2 rearranged as it was modelled), whereby the random effect for each tree taxon corresponded to deviations from the fixed effect slope for total foliage score at a site ($\sum_s (f_{sk} - \bar{f})$). The multiple membership modelling approach differs from random regression as multiple variables are associated with each response data point, in comparison to subsets of data associated with each variable, as in random regression. The guild-level taxon-specific slopes intersect at the average amount of any tree taxon present at any site, and random effects were drawn from a distribution with a single variance estimated by the model. This allowed me to test for an effect of the amount of foliage of each tree taxon at a site, regardless of which host tree taxa the sample was collected from.

Phenological Distributions

Caterpillar abundance

To quantify differences in the phenological distribution of caterpillar abundance throughout spring on different tree taxa I allowed each taxon to have a distinct temporal trend in abundance over the course of the spring (abundance phenology model, Table 2.1). The fixed effects included date and date^2, allowing for a peaked trend over time. The focal random terms were the tree taxa random intercepts and slopes for date and date^2. In addition to the structural random terms, I also included date and date^2 random slopes for site and year to account for spatiotemporal differences in the peak timing and shape. To facilitate the interpretation of the model I used the intercept, date and date^2 coefficients for each tree taxon to generate posterior distributions for the mean timing (peak date) of the peak in abundance, the maximum abundance reached (height), and the width of the distribution (peak width) calculated at half the height of the peak. In addition, I also calculated the relative width of the peak among tree taxa (peak duration), calculated at a consistent abundance of 0.01 caterpillars, roughly half the height of the taxon peak reaching the lowest maximum abundance. I primarily present peak width, describing the shape of the distribution, and also discuss peak duration (which includes an effect of peak height) due to its relevance to the phenological synchrony of consumers.

I assessed the adequacy of the quadratic function in describing the shape of the phenological distribution of caterpillar abundance by also modelling the peak including a cubic date term; allowing an asymmetrical trend over time (Table A.5). Details of the analysis can be found in Appendix A.

Caterpillar Mass

To obtain the mean mass per caterpillar in a sample I divided the mass for each sample by the number of caterpillars weighed. Due to restrictions in measuring small masses in the field, we have uncertainty in the accuracy of measurements ≤0.02g. All samples meeting this criterion were interval censored to a lower bound of 0.001g, the minimum mass viable for a caterpillar sampled in line with the methodology (J. C. Weir, unpublished data), and an upper bound of 0.02g divided by the number of caterpillars. The mass measurements were log-transformed and modelled as interval-censored Gaussian.

The mass model included date and date^2 in the fixed effects, allowing a curved trend if appropriate (mass phenology model, Table 2.1). The focal random terms were the tree taxa random intercepts and date slope. In addition to the structural random terms, I included a date random slope for sites, allowing for spatial variation. Year was solely included as a random intercept to improve model convergence as there were just 4 years of mass data. The residual variance for each observation was modelled as inversely proportional to the number of caterpillars sampled (*n*) since $VAR\left(\frac{\Sigma_j^n m_j}{n}\right) = \frac{VAR(m)}{n}$ and the resulting variance parameter should be equal to the variance in mass of individual caterpillars. To assess differences in the ultimate mass of a caterpillar on different tree taxa during our sampling period, the posterior distributions of the fixed effects and tree taxa random intercepts and slopes were used to calculate the predicted mass at day 168 (16th June). The date on which the predictions are calculated may slightly affect the differences among host taxa, so I chose the latest date on which a caterpillar has been sampled from all tree taxa.

Caterpillar biomass

I combined the model outputs for the phenological distribution of caterpillar abundance and mass to calculate the distribution of biomass. As abundance and mass were both estimated on the log scale, equations describing the change in caterpillar abundance and mass over time, for each tree taxon and the fixed effect mean trend, can be summed across each iteration of the posterior distribution to convert to a temporal prediction of biomass. Ideally this would be analysed using a bivariate model to allow for covariance between abundance and mass across random terms, however due to the interval censoring required for the mass data this could not be implemented. The coefficients for biomass have been used to calculate the same peak metrics as discussed for the abundance results, with peak duration estimated at a biomass of 0.35mg.

All results comparing caterpillar abundance, mass or biomass among host tree taxa are presented primarily as deviations from the fixed effect prediction, which represents an average tree taxon, and also as deviations from the prediction for oak, described fully in Appendix A.

Results

Within our dataset, 11% of branch beating yielded at least one caterpillar. Where a caterpillar was present, in 68% of cases there was just 1 and in 16% there were 2, with a maximum abundance of 107, recorded during an outbreak at one of our sites during 2019.

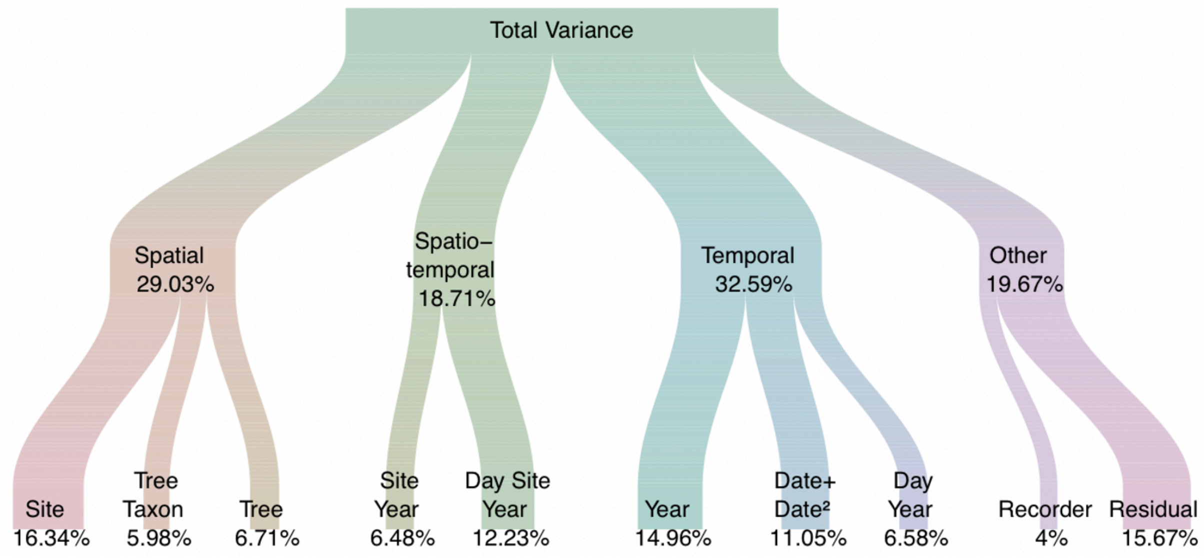

Figure 2.2: Riverplot depicting the percentage variance composition of caterpillar abundance estimated from terms in a Poisson GLMM (Table A.1). All variables were included as random terms except for Date+Date^2 which were continuous variables included as fixed effects accounting for the peaked shape of the phenological distribution.

Abundance

Caterpillar abundance variance decomposition

The posterior distributions of variance for all terms included in the abundance decomposition model (Table 2.1, A.1), including the calculated variance explained by the fixed effects, were removed from zero, indicating that each variable contributes to the variance in caterpillar abundance observed. The environmental components (all excluding the ‘Other’ category) explained 80.33% (CIs: 73.76 - 86.78%) of the variance, with temporal and spatial components explaining similar amounts of 32.59% (CIs: 20.21 - 49.42%) and 29.03% (CIs: 18.02 - 41.10%) respectively (Fig. 2.2). The tree taxon sampled explained 5.98% (CIs: 1.24 - 14.08%) of the variance (Fig. 2.2).

Habitat variations in caterpillar abundance

I found substantial variance in the abundance of caterpillars sampled among host tree taxa in the habitat abundance model (Table A.2). Alder and ash support significantly fewer caterpillars than average and birch, oak and willow support more (Fig. 2.3a). Alder hosts 0.64 (CIs: 0.41 - 0.95) times as many caterpillars as an average taxon, ash hosts 0.52 (CIs: 0.32 - 0.81), birch hosts 1.43 (CIs: 1.01 - 2.03), oak hosts 1.53 (CIs: 1.09 - 2.22) and willow hosts 1.65 (CIs: 1.10 - 2.46). We found that alder, ash, beech, elm, rowan and sycamore all support significantly fewer caterpillars than oak (Fig. A.1).

The posterior for the variance in the slope predictions for the guild-level tree taxon foliage scores was not removed from zero (Table A.2), suggesting there is no community effect on caterpillar abundance that varies among guild tree taxa. However, when I looked at the guild-level tree taxon random effects I found that an increase in the amount of oak at a site was predicted to significantly increase the abundance of caterpillars found on the branches of any tree at a site (Fig. 2.3b, Fig. 2.3c). Exponentiating the coefficient shows that a branch will have 1.02 (CIs: 1.002 - 1.03) times as many caterpillars on it for every additional unit of oak foliage (equivalent to one small oak tree). Within the woodland compositions across our sites, branches of any tree taxon within mature oak-dominated woodlands can reach 5.19 (CIs: 1.73 – 17.45) times the caterpillar abundance of a woodland without oak, purely attributed to the local habitat composition (Fig. 2.3c). I found no relationship between the guild-level total foliage score and the number of caterpillars recorded (Table A.2).

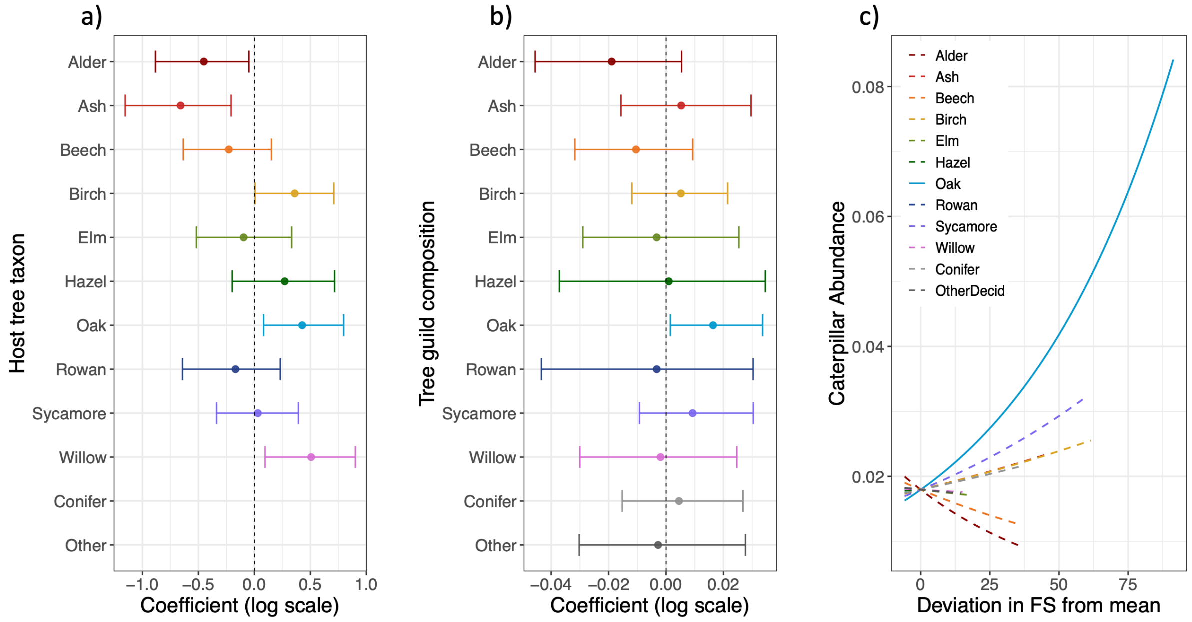

Figure 2.3: a-b) Posterior median and 95% credible intervals for random effects in a Poisson GLMM (Table A.2). Predicted coefficients for a) the log difference in abundance of caterpillars sampled from each host tree taxon (conifers and other deciduous trees were not sampled) and b) the log change in caterpillar abundance on an average branch with an increase in the amount of foliage of the tree taxon within the local tree guild composition (globally mean centred foliage scores). c) Slope predictions from a Poisson GLMM (Table A.2) analyzing the change in caterpillar abundance with change in the amount of foliage of each tree taxon present in the tree guild at each site (globally mean centred). The intercept falls at the mean foliage score (FS) of any taxon at any site and mean total FS across all sites. Dashed lines indicate a non-significant difference in slope from zero and the solid line indicates a significant result. All lines represent the range of foliage scores of each taxon present across all sites.

Phenological distributions

Caterpillar abundance

Annual peaks in the temporal distribution of caterpillar abundance in our data are clear (Fig. A.2) and supported by the significant negative quadratic date term from the abundance phenology model (-0.84, CIs: -1.18 - -0.52, Table A.3). I found substantial variance in the tree taxon intercepts and date slope effects of the abundance phenology model (Table 2.1), but not the date^2 effects (Table A.3). The fixed effects indicated the phenological distribution of abundance on an average tree taxon, in an average site and year, and predicted a mean peak date of 154.03 (CIs: 146.96 - 161.31), 3rd June, peak height of 0.06 (CIs: 0.02 - 0.14) caterpillars per branch, peak width of 25.91 days (CIs: 21.14 – 31.47 days) and duration of 40.43 days (CIs: 26.08 – 54.79 days), calculated at a threshold of 0.01 caterpillars per branch. In calculating peak width and duration a small proportion (< 1%) of the posterior samples yielded NAs due to some iterations either not predicting a negative quadratic term or predicting a peak height beneath the threshold for peak duration. These iterations were excluded which will make the mean and CIs underestimates. The low peak height value was likely due to the large variance among sites and years and 89% of the beating samples recording zero caterpillars.

Investigating tree taxon-specific peaks showed differences in the phenological distributions of caterpillar abundance (Fig. 2.4a). The peak timing on sycamore was significantly earlier than for the average taxon (-2.81 days, CIs: -6.33 - -0.29, Fig. 2.4b). The height of the peak in caterpillar abundance was significantly different to an average taxon for three taxa [alder; 0.58 (CIs: 0.35 - 0.93), oak; 1.87 (CIs: 1.25 - 2.87) and willow; 1.61 (CIs: 1.02 - 2.61) times the average peak height] (Fig. 2.4c). As a proportional change, CI removal from one was the threshold for significance.

The peak width, representing the relative shape of the peak, did not significantly differ between any taxon (Fig. 2.4d). This suggests that the shape of the peak in caterpillar abundance was relatively consistent among tree taxa. Due to the relatively consistent shape but variable peak height, the peak duration showed more variation among taxa with the peak on willow lasting for a significantly longer duration than the average trend by 8.17 days (CIs: 0.33 - 19.01 days) (Fig. A.3). The peak on oak was found to be significantly later than rowan and sycamore, higher than all tree taxa tested except hazel and willow and lasting for a longer duration than peaks on alder, ash, beech, rowan and sycamore (Fig. A.4).

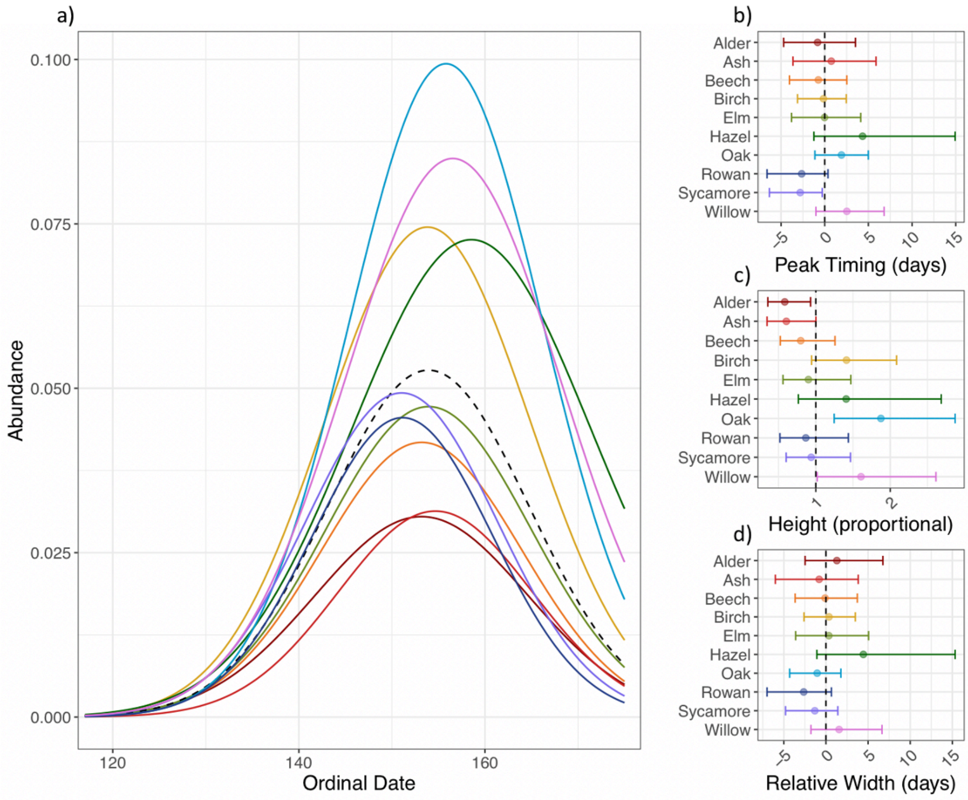

Figure 2.4: Model predictions for the phenological distribution of caterpillar abundance throughout spring on branches of different tree taxa (Table A.3). a) shows the model predictions for the change in caterpillar abundance over time (ordinal date) for each tree taxon, the black dashed line depicts the curve prediction from the fixed effects. Plots b-d) show the difference between each tree taxon and the fixed effect prediction (indicated by a black dashed line at zero or one) for the b) timing of the peak in abundance, c) proportional height of the peak (maximum abundance) and d) width of the peak at half of the height. The median and 95% credible intervals were calculated using the posterior distributions for the fixed effects and tree taxa random effects and interactions.

In the peak asymmetry model (Table A.5), we found that although the cubic term was significant (Table A.6), the resulting asymmetry in the peak estimate was low (Fig. A.8) and therefore the use of a quadratic function adequately described the shape of the peak.

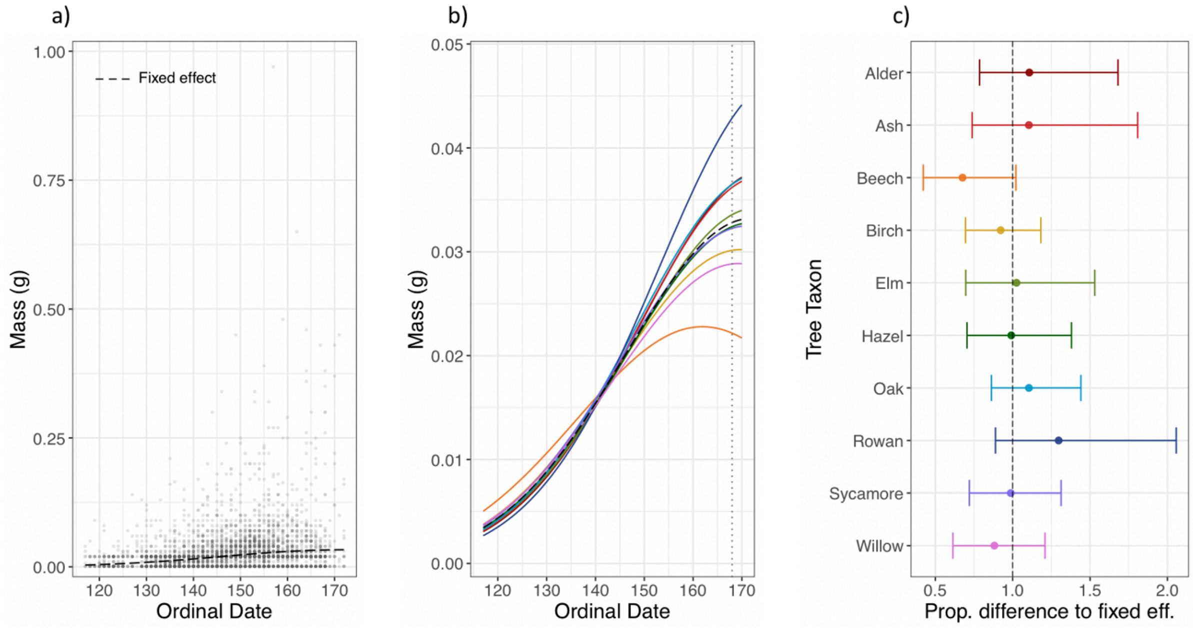

Figure 2.5: Slope predictions from a model analyzing the change in caterpillar mass throughout spring (Table A.4). a) The black dashed line indicates the change in mass over time from the fixed effects. The points show the mass data, with transparency indicating the frequency of the point. The two bolder lines of points highlight the two levels of interval censored samples making up 4.9% of all samples. b) shows the model predictions for the change in mass over time for caterpillars on each tree taxon with the black dashed line showing the fixed effect trend from plot a). The grey dotted vertical line indicates day 168 (16th June), the latest date with caterpillar mass data for all tree taxa. c) shows the posterior median and 95% credible intervals for the proportional difference in day 168 mass between each tree taxon and the fixed effect prediction.

Caterpillar mass

Most caterpillars throughout spring weighed less than 0.1g, although caterpillars of up to 0.96g (n=1) have been recorded (Fig. 2.5a). There was a significant and pronounced trend for mass to increase over the course of the spring and for the rate of increase to decline (Fig. 2.5b, Table A.4). There was no significant variance among tree taxa in the intercept or date slope, however there was slightly more variance estimated in the slope estimates than intercept which is why the predicted trends intersect at a central date (Fig. 2.5b, Table A.4). The day 168 mass of caterpillars (in mid-June) predicted from the fixed effects, representing an average tree taxon, was 0.033g (CIs: 0.023 - 0.047g). Whilst the curves and day 168 masses do not differ significantly between any tree taxon and the fixed effect trend (Fig. 2.5b-c), I found the ultimate mass of caterpillars was significantly less for those sampled from beech compared to oak (Fig. A.5).

Caterpillar biomass

The combined fixed effects from the abundance and mass phenology models (Tables 2.1, A.3, A.4) predicted a peak date for the distribution of biomass on an average taxon of 156.84 (CIs: 150.94 - 163.39), 5th June; two days later than the peak in abundance not accounting for mass. The maximal biomass peak height was predicted to be 1.5mg (CIs: 0.6 - 3.7mg) per branch. The peak width was 23.80 days (CIs: 20.00 - 28.13), suggesting a more strongly peaked shape than the distribution of abundance, and the peak duration was 30.90 days (CIs: 16.68 - 45.45) at a threshold of 0.35mg of caterpillars per branch. Similarly to the abundance peaks, some iterations (<2% in general, but 5-7% for alder, ash and beech peak duration) produced NAs in the calculations of peak width and duration so the median and CIs are underestimates.

The most noticeable differences between the phenological distributions of caterpillar abundance and biomass were the increased relative height of the caterpillar peak on oak compared to other taxa and decreased relative height on beech, becoming more similar to the peaks on alder and ash (Fig. 2.4a, 2.6a). Unlike in abundance, the biomass peak on sycamore was not significantly earlier than an average taxon (Fig. 2.6b).

The height of the peak in caterpillar biomass remained significantly different to an average taxon on oak trees, reaching 2.10 (CIs: 1.33 - 3.37) times the mean maximum mass (Fig. 2.6c) and whilst the biomass peak height on alder remained lower than the average (0.61, CIs: 0.36 – 1.11), the CIs include one.

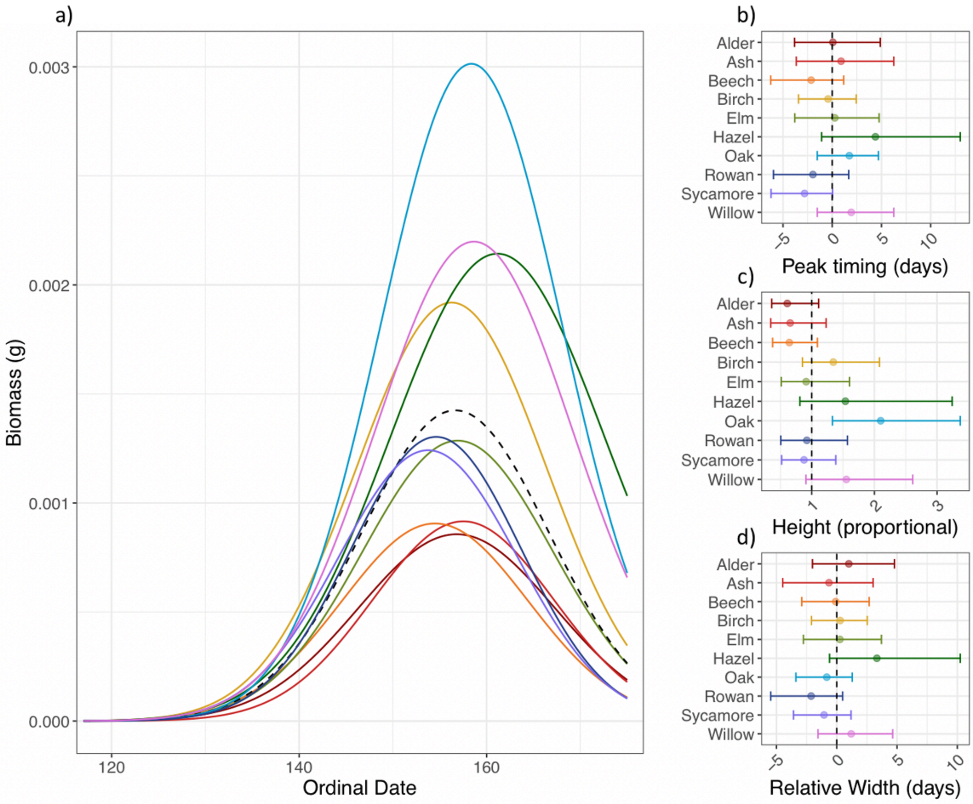

Figure 2.6: Predictions for the phenological distribution of caterpillar biomass throughout spring on branches of different tree taxa (based on models in Tables A.3, A.4). a) shows the model predictions for the change in caterpillar biomass over time (ordinal date) for each tree taxon, the black dashed line depicts the curve prediction from the fixed effects. Plots b-d) show the difference between each tree taxon and the fixed effect prediction (indicated by a black dashed line at zero or one) for the b) timing of the peak in biomass, c) proportional height of the peak (maximum biomass) and d) width of the peak at half of the height. The median and 95% credible intervals were calculated using the posterior distributions for the fixed effects and tree taxa random effects and interactions.

The biomass peak width, representing the relative shape of the peak, continued not to differ significantly between any taxon (Fig. 2.6d). Consequently, the peak duration at a consistent height again showed more variation, yet did not significantly differ between any taxon and the average trend (Fig. A.6) because there was no distinct variation in the phenological distribution of mass. The biomass peak timing, height and duration on oak differed from other taxa similarly to the peaks in abundance, with the addition of the peak on beech now also falling significantly earlier than on oak (Fig. A.7).

Discussion

In this chapter, I show that the prevalence of oak within the woodland tree guild increases the number of caterpillars hosted by any tree, regardless of taxon (Fig. 2.3c), whilst more generally the tree guild composition does not affect caterpillar abundance. I found that several aspects of the phenological distributions of abundance and biomass are sensitive to tree taxon (Fig. 2.4, 2.6). The major difference was in the peak height and I found that caterpillars are most abundant on oak and willow, with alder and ash especially poor (Fig. 2.3a, 2.4c, 2.6c), adding higher resolution and a broader tree guild perspective to results from previous studies (Mägi *et al.*, 2009; Veen *et al.*, 2010; Shutt, Burgess and Phillimore, 2019). I show the mean timing of the phenological distribution of caterpillar abundance falls earlier on sycamore trees than on an average taxon (Fig. 2.4b), however generally the timing differences between host tree taxa were quite slight, in agreement with Shutt *et al*. (2019). Whilst the shape of the peak is generally consistent (Fig 2.4d, 2.6d), I show the peak in abundance lasts for a significantly longer period on willow than average (Fig. A.3). I suggest among taxa differences in biomass are more attributable to variation in abundance than mass, as I found no evidence for caterpillar mass gain differing among tree taxa (Fig. 2.5), although caterpillars on beech reach a significantly lower mass than those on oak (Fig. A.5).

The impact of oak foliage density, increasing caterpillar abundance throughout the local tree guild (Fig. 2.3c), suggests that oak-dominated woodlands may be unique in spring caterpillar prevalence when compared to other woodland compositions. The increased caterpillar abundance throughout an area with an increase in oak in the tree guild is likely driven by the strong positive host-level effect of oak trees. There are two main mechanisms through which the high productivity of caterpillars on oak could influence the abundance on non-oak species: oak-raised females indiscriminately laying eggs on other tree taxa and caterpillar dispersal throughout the season. The same process may not occur for other highly productive tree taxa, such as willow, due to differences in the morphology of the trees. Tree structure could influence the likelihood of dispersal throughout an area for both the caterpillars and adults, particularly for species with wingless females such as *Operophtera* spp., which made up 56% of previously identified samples in this system (Shutt, Burgess and Phillimore, 2019).

The host-level effect of oak on caterpillar abundance could be driven by a range of factors. Whether caterpillars on oak trees have increased survival rates or more successful pupation remains unknown, however increased fecundity is unlikely to have a wide-spread impact (Honěk, 1993) as caterpillars from oak show no significant increase in mass compared to those on an average tree. Fecundity may, however, influence the differences in abundance between oak and specific taxa, such as beech, as the divergence in mass is more substantial. However, this difference could also be driven by differing lepidopteran guild compositions. The increased abundance on oak also appears not to be driven by the general density of foliage, as the site foliage density effect was close to zero and non-significant (Table A.1). These findings imply that the common practice of monitoring caterpillar prevalence purely on oak (Visser, Holleman and Gienapp, 2006; Hinks *et al.*, 2015; Burgess *et al.*, 2018) may miss spatial-heterogeneity in caterpillar abundance both between locations and within larger sites. However, the increased caterpillar abundance on oak could make these habitats the most important to consumers; acting as a source that contributes to the repopulation of areas with lower consumer breeding success, as the prevalence of oak within an area has been shown to increase fledging success (Shutt *et al.*, 2018).

The results presented in this chapter strongly support previous work that finds the phenological distribution of caterpillar abundance on oak trees reaches a high abundance but is present for a relatively brief portion of the year (van Balen, 1973; Varley, Gradwell and Hassell, 1974; Visser, Holleman and Gienapp, 2006; Veen *et al.*, 2010). The very high abundance and biomass of caterpillars observed in oak woodlands appear not to be representative of other woodland types that are more common across the UK (Stagg and Ward, 2019), despite its use as a baseline for comparison when the distribution in other woodland compositions has been studied (Mägi *et al.*, 2009). On the contrary, the results of my analyses suggest the phenological distribution of caterpillars on elm, rowan and sycamore are most representative of an average deciduous tree, particularly concerning peak height as there are fewer distinctive differences in timing and duration. Generally speaking, oak, hazel, willow and to some extent birch deviate towards hosting larger caterpillar abundances than average, whilst alder, ash and to some extent beech deviate in hosting smaller abundances. These differences in the phenological distribution of spring caterpillar abundance provide evidence for biotic drivers of divergent caterpillar prevalence among tree taxa.

A range of mechanisms could influence these differences in caterpillar abundance among host tree taxa. Caterpillar guild species richness differs between tree taxa, with willow, oak and birch hosting the greatest range of species (Shutt, Burgess and Phillimore, 2019). If the carrying capacity of each tree is not reached, the variation in caterpillar richness is likely to impact the guild-level abundance among host tree taxa. Differences in the accumulation of secondary defence metabolites among taxa, which are detrimental to caterpillar development (Feeny, 1968), could also influence abundance through impacts on fecundity (Awmack and Leather, 2002) and survival (Wint, 1983; Yanar *et al.*, 2017), though explicit examination of different defence levels among deciduous tree species is currently lacking in the literature.

I show that the phenological distribution of the mass of the sampled caterpillar guild increases rapidly in early spring before asymptoting (Fig. 2.5). The decrease in the mass curve prediction for beech towards the end of the sampling period could either be a true decrease or a constraint of the quadratic term. I found minimal difference in caterpillar growth rate and the mass of caterpillars at the end of spring when comparing each taxon to an average tree; although caterpillars from beech weighed significantly less than those sampled from oak (Fig. A.5). These results are consistent with rearing experiments using winter moth (*O. brumata*) that found more successful growth and mass at pupation from feeding on oak compared to hazel and beech (Feeny, 1970; Wint, 1983). From my finding that oak hosts a higher abundance paired with these experimental findings, it is perhaps surprising that the caterpillars sampled do not reach a higher mass or asymptote earlier than on other trees. My measure of mass will have captured various processes including individual growth, and the appearance and disappearance of species from the guild through both varied phenologies among caterpillar species and beta diversity between locations.

When I combined the minimal among tree difference in caterpillar mass with abundance estimates I did see some effect on the phenological distribution of biomass, primarily through adjustments to peak height (Fig. 2.4, 2.6). The greatest difference in peak dimensions between the distributions of abundance and biomass among tree taxa was the increase in oak peak height, and decrease in beech, relative to the other trees (Fig. 2.6, A.7). As most studies use frass fall or half-fall to quantify the peak in biomass (Visser *et al.*, 1998; Charmantier *et al.*, 2008; Smith *et al.*, 2011; Hinks *et al.*, 2015), the contribution of abundance and mass phenology to the biomass peak timing is unexplored. With just a two-day difference in peak phenology between abundance and mass, my results suggest that the trend in abundance is more prominent than mass in dictating the timing of the biomass peak. Therefore, factors impacting caterpillar abundance differentially between locations are likely to have a greater impact on spatial variation in caterpillar phenology than those impacting mass.

The taxonomic tree composition within a woodland seems likely to influence MMH buffering through the variation it drives in dimensions of the site-level caterpillar phenological distribution. The results of this chapter suggest the habitat-driven buffering potential may be stronger than previously suggested (Bell *et al.*, 2019; Shutt, Burgess and Phillimore, 2019), as I have identified further differences in the caterpillar peak among tree taxa, particularly in peak height but also some deviations in timing and duration. The differences in peak height between tree taxa could impact the consequences of asynchrony between different areas within a similar region or more broadly between woodlands and geographical locations as the tree composition present is likely to influence the maximum caterpillar density reached, potentially altering the negative consequences of trophic asynchrony for the consumer. The peak on willow lasts for eight days longer than average, providing a food source for an additional third of the time many consumers spend in the nest. The peak duration on alder, ash, beech, rowan and sycamore were all shorter than on oak (Fig. A.4), implying that the peak may vary substantially in duration between an oak-dominated woodland

and one with mixed composition. There is also potential for within-site peak duration to be influenced by tree composition through deviations in peak phenology, as the peak falls three days earlier on sycamore than on average tree taxa (Fig. 2.4) and three-five days earlier on beech, rowan and sycamore than on oak (Fig. A.4).

Habitat composition can be manipulated by foresters and land managers and here I examine the implications of our findings in this context. First, in general, increased defoliation negatively impacts tree health and productivity (Kulman, 1971; Whittaker and Warrington, 1985; Whitham *et al.*, 1991; Marquis and Whelan, 1994). Winter moth, the most common species in our study system (Shutt, Burgess and Phillimore, 2019), exhibits cyclic population dynamics with outbreaks causing severe defoliation (Tenow, 1972; Hogstad, 1997), also observed at one of our sites during spring 2019. Defoliation may be minimised if there is a lower density of oak, thereby preventing the additive effect it has on the abundance of caterpillars overall. However, with the exception of oak, caterpillar abundance appeared to be insensitive to the amount of other tree taxa present. My capacity to tease apart trends in caterpillar abundance driven by woodland habitat composition will have been limited by the categorical structure of the tree guild data used and the lack of certainty in how trunk size correlates with tree foliage volume or whether the relationship differs among taxa. The second implication relates to the conservation of consumer populations for whom more caterpillars are expected to be beneficial, though the importance of resource abundance versus resource timing relative to breeding is relatively underexplored (but see Naef-Daenzer and Keller, 1999; Ramakers, Gienapp and Visser, 2019). The high density of prey in oak woodlands is thought to be a driver of preference for this habitat by some breeding passerines (Perrins, 1979). Alterations to the site-level peak height through the addition of oak trees may be most beneficial to consumers, however increased willow could also serve to increase the peak height and duration whilst avoiding the effect of oak throughout the tree-guild which may inflate the likelihood of detrimental outbreaks. As the divergence I found in peak timing occurred mainly in sycamore, a taxon that hosted an average peak height in general, and both reached lower heights and lasted for a shorter duration than the peak on oak, it is most likely that variable peak phenology among host-taxa will not influence site-level peak duration and buffering of the MMH. In addition, this work reveals substantial site effects on the phenological distribution of caterpillar abundance (Table A.3), and some site effects on mass (Table A.4), which implies that factors in addition to woodland composition play an important role (Fig. 2.2).

I have shown new detailed insights into habitat-driven variation in caterpillar abundance and the phenological distribution of caterpillar abundance and biomass among tree taxa. My results highlight the spatiotemporal differences in spring caterpillar phenology between different woodland compositions. I show that the phenological distribution of spring caterpillars in oak-dominated study systems are not representative of the distributions present across the broader range of deciduous woodland compositions also at risk of temperature-mediated consequences of the MMH. These findings have applications in woodland management and reforesting for the conservation of woodland lepidopteran and insectivore communities.

Chapter 3 - Warmer springs lead to earlier and higher peaks of arboreal caterpillars

Abstract

Advances in spring phenology are among the clearest biological responses to climate warming. Quantifying the effect of climate on phenology is key to predicting impacts on species interactions. In the ephemeral temperate deciduous forest food webs, at the vanguard of research on temperature's effect on trophic interactions, most work has focused on the average timing of phenological events. In comparison, the effects of temperature on the abundance of individuals and their seasonal spread is understudied but has the potential for profound impacts on trophic interactions. Here I develop and apply a new method to show that for the guild of forest caterpillars, warmer spring conditions advance the timing of the phenological distribution of abundance by -4.96 days $^{\circ}C^{-1}$ and increase its height by 34% $^{\circ}C^{-1}$, with no significant change in its duration. An increase in the maximum density of arboreal caterpillars with rising temperatures has implications for understanding climate impacts on forest food chains, both in terms of herbivory pressure and the resources available to secondary consumers. These results also highlight that reducing phenological distributions to the mean timing risks discarding vital information about the biotic impacts of climate warming. The method I have developed is novel to phenology research, allowing the thermal sensitivity in the full phenological distribution to be modelled from raw data, providing a flexible method with broad applicability within global change research.

Introduction

Anthropogenic climate warming is having profound impacts on ecological systems, with phenological shifts one of the most reported biotic responses (Walther *et al.*, 2002; Parmesan and Yohe, 2003). Temperature is a key driver of phenology for extra-tropical taxa, though there is heterogeneity in thermal sensitivity among species and trophic levels (Thackeray *et al.*, 2016; Cohen, Lajeunesse and Rohr, 2018; Roslin *et al.*, 2021). Many species interactions depend on synchrony between ephemeral life history events and, as the thermal sensitivity of interacting species or guilds may differ, warming temperatures have the potential to disrupt interactions, including those between consumers and their resources (Thackeray *et al.*, 2016; Kharouba *et al.*, 2018; Samplonius *et al.*, 2020).

Phenology is most frequently quantified as the mean or first timing of an event (Fig. 3.1a) among individuals in a population (Thomas *et al.*, 2001; Charmantier *et al.*, 2008; Both *et al.*, 2009; Reed, Jenouvrier and Visser, 2013; Thackeray *et al.*, 2016; Burgess *et al.*, 2018; Roslin *et al.*, 2021) and the thermal sensitivity of mean (or first) timing has been examined for many species and guilds (Thackeray *et al.*, 2016; Cohen, Lajeunesse and Rohr, 2018; Roslin *et al.*, 2021). In comparison, very few phenology-focused studies have addressed how temperature affects the abundance of individuals exhibiting the mean timing (height), how the timing within a population or guild is spread around the mean (width), or the length of time over which the frequency of a phenological event falls above a given threshold (duration) (Dennis *et al.*, 2016; Ramakers, Gienapp and Visser, 2019; Shutt, Burgess and Phillimore, 2019; Hällfors *et al.*, 2020) (Fig. 3.1a), all of which may impact on interactions with other species. Removed from a phenological context, there is evidence across a range of taxa that temperature affects temporal trends in abundance (Bowler *et al.*, 2017) and spatial and temporal trends in the duration of life history events (Vitasse *et al.*, 2009; Møller *et al.*, 2010; Ahmad *et al.*, 2021), although responses vary among species and events.

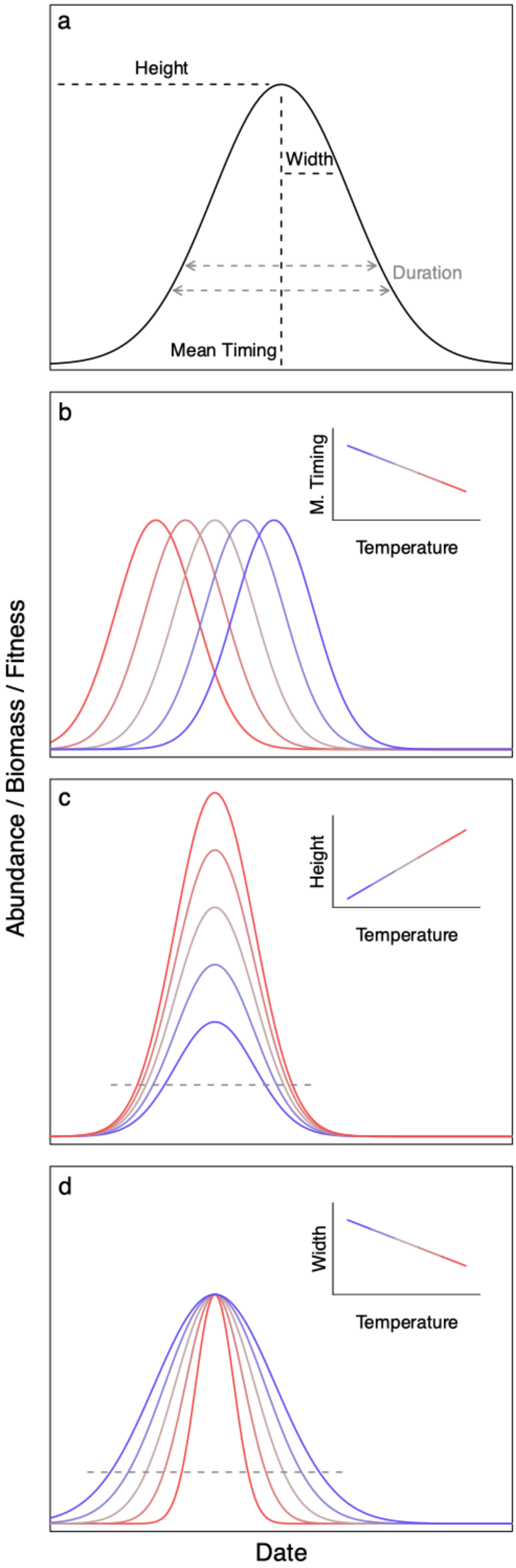

Figure 3.1: Using the Gaussian function to describe the peaked phenological distribution of an ephemeral life history event. a) a Gaussian function showing the three parameters that govern the phenological distribution (black) and a derived statistic of biological importance (grey): mean timing is the most common timing within the population/guild, height describes the maximum response (e.g. abundance, biomass or fitness) value reached, width corresponds to the standard deviation of the function and therefore it’s curvature, and duration describes the number of days where the response falls above a given threshold. The chosen threshold level will influence the duration, as illustrated by the two lines. b-d) Show examples of how a slope in thermal sensitivity for each parameter could influence the phenological distribution while the other parameters are held constant. The grey dashed lines in c) and d) show that a change in the height or width parameter both influence the duration at a given value and therefore duration is not defined by width alone as would be for a Gaussian distribution.

The match/mismatch hypothesis (MMH) posits that in seasonal trophic interactions phenological synchrony between a peak in consumer demand and an ephemeral resource benefits the fitness of the consumer (Cushing, 1969). Where the thermal sensitivity of phenology differs between trophic levels (Thackeray *et al.*, 2016), this will alter the synchrony between a consumer and its resource (Kharouba *et al.*, 2018). The MMH is most often studied through the comparison of consumer phenology to the resource population/guild mean timing. However, the height and width (Fig. 3.1a,c,d) of the resource distribution determines the duration of time for which the resource is above a given threshold, the amount of food available given a particular amount of phenological asynchrony and how the relative amount of food available differs among synchronous and asynchronous consumers. Therefore, temperature-mediated shifts in the height and width of phenological distributions are also expected to have important implications for trophic interactions.

In phenology and MMH research, the temperate forest system of deciduous trees, caterpillars and cavity nesting passerines in spring has become a classic system for studying the seasonality of the tri-trophic interactions (Thomas *et al.*, 2001; Charmantier *et al.*, 2008; Both *et al.*, 2009; Cole, Regan and Sheldon, 2021). Within this system, the phenological distribution of caterpillars may have both top-down and bottom-up effects through interactions with both the leafing trees and breeding birds respectively. The phenological distribution of the caterpillar guild of primary consumers – comprised of many species (Shutt, Burgess and Phillimore, 2019) – is usually summarised by the mean timing, which has been found to advance by approximately 4-6 days $^{\circ}C^{-1}$ (Visser, Holleman and Gienapp, 2006; Charmantier *et al.*, 2008; Burgess *et al.*, 2018); largely tracking the shift in timing of deciduous tree leafing, but a little steeper than the advance of insectivorous passerine breeding (Both *et al.*, 2009; Burgess *et al.*, 2018; Cole, Regan and Sheldon, 2021). Effects of spring temperature on the height or width of the caterpillar phenological distribution have been largely overlooked. The exceptions are a study that reported no correlation between spring temperature and the height of the caterpillar biomass distribution over 16 years in Poland (Nadolski *et al.*, 2021) and studies that found the width of the biomass distribution to be narrower under warmer spring conditions across nine years in the

Netherlands (Visser, Holleman and Gienapp, 2006) and across 19 sites in the UK (Smith *et al.*, 2011). However, all previous studies are low-powered (n ≤ 20) and relied on a two-step analytical approach whereby phenological parameters were estimated for each site-year combination and then estimates were treated as data in a subsequent model. This two-step approach will underestimate the true error in slopes, in comparison to estimating all parameters of interest from the raw data within a single model. One reason for the scarcity of phenological research beyond mean timing is that the field has lacked a statistical framework for examining the thermal sensitivity of all three parameters that govern the phenological distribution.

Spring temperatures could affect the phenological distribution of the arboreal caterpillar guild abundance throughout spring via various intraspecific and interspecific effects. Warmer temperatures have been shown to drive earlier emergence for species that overwinter as eggs or larvae (Visser, Holleman and Gienapp, 2006; Charmantier *et al.*, 2008), shifting the mean timing of the guild phenology. Temperature could affect the width of the phenological distribution by changing intraspecific variation in larval emergence, though no effect was found in previous work on *Malacosoma disstrial* (Uelmen *et al.*, 2016), and the period over which each individual feeds before pupation through altering the rate of development (Stamp, 1990; Buse *et al.*, 1999), which is predicted to narrow the width and reduce the duration, consistent with the findings of previous work (Visser, Holleman and Gienapp, 2006; Smith *et al.*, 2011). Multiple mechanisms could drive a relationship between temperature and the height of the phenological distribution. Where low temperature presents a challenge, an increase in temperature may increase pre- and post-emergence survival and post-emergence growth (Battisti *et al.*, 2005), such that increasing temperatures could increase the guild abundance and distribution height. However, colder temperatures can increase the starvation tolerance of caterpillars (Abarca and Lill, 2015), meaning the phenological synchrony between caterpillars and their host may alter the effect of temperature on the distribution height.

Here I use data on temperature and caterpillar abundance throughout spring, collected at 44 sites across 8 years (Fig. 3.2), yielding 293 site-by-year combinations, to analyse the effect of temperature on the phenological distribution of 8,196 arboreal caterpillars sampled from 37,674 branch beatings. I develop and apply a novel statistical method, using the Gaussian function, to estimate the thermal sensitivity of the three parameters that govern the phenology of abundance: mean timing, height and width (i.e. standard deviation) (Fig. 3.1). I also examine whether estimated thermal sensitivities over space and time are consistent with a causal effect.

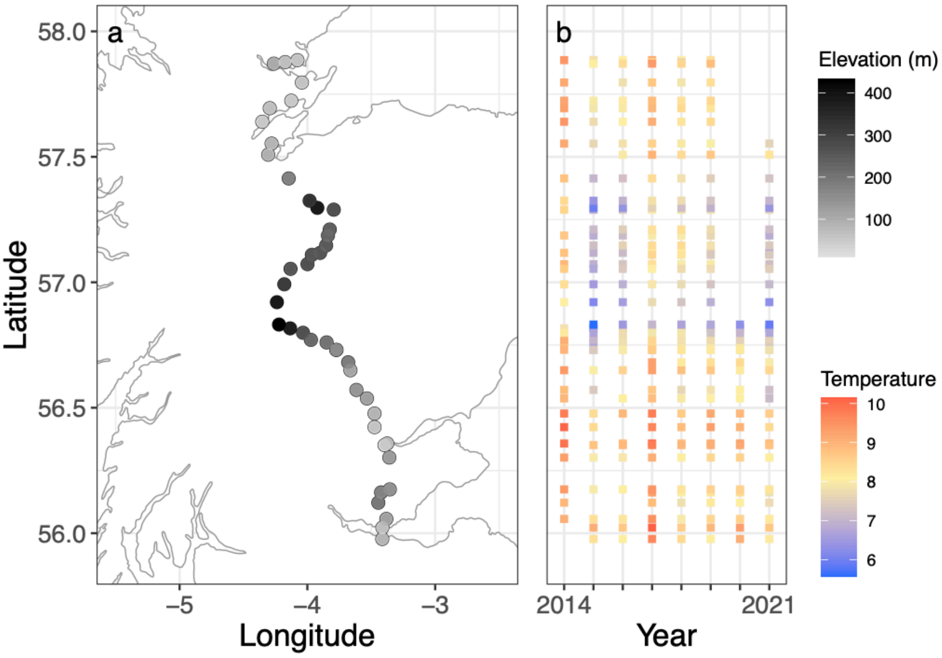

Figure 3.2: a) Map of site locations in Scotland with elevation above sea level indicated by a scale of grey to black, and b) shows the mean annual temperatures from mid-February to late June for each site in each year by latitude. Gaps in the temperature data reveal years when sites were not monitored.

Materials and Methods

Study System

Data were collected between 2014 and 2021 at 44 deciduous woodland sites along a 220km transect from Edinburgh (55°980 N, 3°400 W) to Dornoch (57°890 N, 4°080 W) in Scotland (Shutt *et al.*, 2018) (Fig. 3.2a). The sites vary in temperature and extend across two degrees of latitude and a 440m elevation range (Fig. 3.2b). Two iButton temperature loggers, recording hourly temperature, were installed in mid-February at different locations at each site, on the north side of a tree and in a shaded area to avoid direct sunlight. The latest installation among years was ordinal date 58 (27th February) and recording continued until the end of the season with the earliest retrieval date among years being day 161 (9/10th June). As one site had no temperature data for 2017, we used temperature data for the nearest site in 2017, correcting for the annual average difference in temperatures between the two sites.

Caterpillar sampling used a branch beating method, recording the abundance of caterpillars on each branch monitored on different dates throughout spring (Chapter 2 and Shutt, Burgess and Phillimore, 2019). At each site, tree leafing phenology was monitored on a selection of trees and each year caterpillar sampling began once 45% of the trees had their first leaf across all sites. The branch beating continued until the end of the field season in mid/late June (2021 sampled from ordinal dates 133 to 157; see Chapter 2 for 2014-20 details). An average of 14 trees (range: 10-17) were sampled at each site in each year from 2017-21, prior to that, 5 trees per site (range: 3-7) were sampled from 2014-16. One branch on each tree was marked for sampling and the species of trees at each site varied to represent the local habitat. Each site was visited every two days with half of the focal trees sampled on alternating visits, leaving four days between each branch beating to allow for recolonisation. The same branches were sampled across and within years unless damaged or dead.

Approximating the caterpillar peak using a Gaussian function

I modelled the number of caterpillars recorded on each branch as Poisson distributed with an expectation that follows a Gaussian function of scaled (mean = 147.9, sd = 14.1) ordinal date (x; Eq. 3.1) using the RStan package (Stan Development Team, 2020). The Gaussian function (Eq. 3.1) is well suited to describing the phenological distribution of caterpillar abundance over time as it consists of three parameters that describe the mean timing (μ), height ($\mathrm{A_{max}}$) and width (σ) (Fig. 3.1a):

Eq. 3.1: $$A(x) = A_{max}exp\left(-\frac{(x-\mu)^2}{2\sigma^2}\right)$$

Eq. 3.1 can be rearranged into Eq. 3.2 allowing the height and width parameters to be modelled on the log scale:

Eq. 3.2: $$A(x) = exp\left(logA_{max} - \frac{(x-\mu)^2}{2exp(log\sigma)^2}\right)$$

For my main analysis (spatiotemporal temperature model) I modelled $logA_{max}$, $log\sigma$ and μ (the phenological parameters) using a Generalised non-linear mixed model with fixed effects including an intercept and a temperature slope for each phenological parameter, allowing a change in each parameter with temperature (Fig. 3.1b-d). The temperature variables were mean-centred for the analysis and differed between the phenological parameters, each comprising the mean site by year daily temperatures from periods identified using a sliding window approach; see section below. Site, year and site by year interaction effects were fitted as random for each phenological parameter, and the covariance between the phenological parameters for each of these terms was calculated from a single correlation matrix, assuming the same correlation structure among random terms, with term-specific variances. Each day at each site in each year, unique tree identity, recorder of the sample and each observation were also fitted as random terms for $logA_{max}$ to account for other important sources of variance in caterpillar abundance (Chapter 2), the latter term dealing with any over-dispersion with respect to the Poisson. The data and Stan model code can be found in the following GitHub repository: https://github.com/KHMacphie/CaterPeakTemp.

Where suitably replicated spatiotemporal data have been collected, as in this study, it presents an opportunity to estimate separate regressions of biotic responses on temperature in both space and time. Where the effect of temperature is similar in space and time, this increases my confidence that the effect is causal and the processes involved in space and time are similar (Dunne *et al.*, 2004; Phillimore *et al.*, 2010). To test for any difference in the thermal sensitivity of the caterpillar phenological distribution in space and time, I included two fixed effect temperature slopes for each phenological parameter (space vs time temperature model): one using the site mean temperatures and another for the annual deviations from the mean of each site; employing within-site centering (Van De Pol and Wright, 2009). Within the timescale of the study, a difference in slopes could arise where different processes are operating in space and time, such as local adaptation or species turnover in space but not time, or if a third variable correlated with temperature also drives phenological processes (Tansey, Hadfield and Phillimore, 2017). As the among-site variance in my temperature estimates is quite high, I anticipate that site estimates of mean temperatures will be quite close to the true mean and slope estimates will be largely unbiased (Phillimore *et al.*, 2010; Westneat *et al.*, 2020). The site mean temperatures were obtained from a linear mixed-model using the lme4 package (Bates *et al.*, 2015) to estimate a mean site temperature which is not biased by the years in which each site has been monitored (Fig. 3.2b). Separate linear mixed models were used for the temperature associated with each Gaussian function parameter and included temperature as the response variable with site and year random intercepts. The mean site temperatures from the models were mean-centred for use in the model, summarised below. The random term structure was the same as in the spatiotemporal temperature model.

Derived parameters and mean expectations on the arithmetic scale

Duration: The width parameter is equivalent to a standard deviation, describing the curvature of the distribution, meaning that when the height is held constant a change in the width parameter defines a change in duration (Fig. 3.1d). When the height parameter changes with a constant width this also alters the duration (Fig. 3.1c), so by allowing slopes of change in both the height and the width parameters with temperature, changes in the width parameter do not uniquely define changes in duration, but this can be calculated posthoc. I define the duration of the distribution as the number of days that the expected abundance exceeds some threshold. The choice of abundance threshold is arbitrary without an informed reason, and the relative difference in duration between distributions will differ depending on the threshold at which it is calculated.

Area under the phenological distribution: The formula for the area under the Gaussian function (T) can be attained by rearranging the integral of the Gaussian function (Eq. 3.3) and Gaussian probability function (Eq. 3.4), for which the area is equal to one.

Eq. 3.3:
$$T = \int_{-\infty}^{\infty} A_{max} exp\left(-\frac{(x-\mu)^2}{2\sigma^2}\right) dx$$

Eq. 3.4:
$$1 = \int_{-\infty}^{\infty} \frac{1}{\sigma\sqrt{2\pi}} exp\left(-\frac{(x-\mu)^2}{2\sigma^2}\right) dx$$
$$\sigma\sqrt{2\pi} = \int_{-\infty}^{\infty} exp\left(-\frac{(x-\mu)^2}{2\sigma^2}\right) dx$$

Combining Eq. 3.3 and Eq. 3.4 shows the area under the distribution can be described by Eq. 3.5, which rearranges to Eq. 3.6 when the height and width parameters are estimated on the log scale.

Eq. 3.5:
$$T = A_{max}\sigma\sqrt{2\pi}$$

Eq. 3.6:
$$T = exp\left(logA_{max} + log\sigma + \log\left(\sqrt{2\pi}\right)\right)$$

This shows the area under the phenological distribution depends log-linearly on temperature with a slope equal to the sum of the log-scale slope estimates for the change in height and width. Slopes for the change in the area under the distribution with changing temperature were calculated for the spatiotemporal temperature model and both components of the space vs time temperature model (Table 3.1).

Mean expectation on the arithmetic scale: When a variable is normally distributed on the log scale, the mean on the arithmetic scale is equal to the sum of the log-scale mean and half of the log-scale distribution variance exponentiated. Within my models the height and width parameters are assumed to come from a log-normal distribution, meaning that the expectation on the arithmetic scale across sites by years must include half of the variance attributed to the random terms being marginalised. Details of the methods of estimation on the arithmetic scale for results shown in Fig. 3.3 and 3.4 can be found in Appendix B.

Determination of temperature variable using sliding windows

It is feasible that the period during which temperature is most influential for the mean timing, height and width of the phenological distribution may differ among the three phenological parameters; therefore, I began my analyses by identifying the periods during which temperature best predicted the thermal sensitivity of each peak parameter simultaneously using a sliding window approach. Using a similar model composition to the spatiotemporal temperature model, I estimated the mean timing, height and width of the caterpillar phenological distribution at each site in each year (site by year model). These were then used as the response variable in a frequentist multi-variate meta-analytic model, using the metafor package (Viechtbauer, 2010), under a sliding window framework, simultaneously testing the period during which temperature best predicts each distribution parameter. I also performed a post hoc sliding window analysis to explore potential spatial variation in the thermal windows identified. Details of the site by year model, the sliding window analysis and the posthoc spatial analysis can be found in Appendix B. The mean daily temperatures for each site by year combination during the identified windows were then used within the Gaussian function models described above.

All analyses used R version 4.0.2 (R Core Team, 2020), and models including the Gaussian function used the RStan package (Stan Development Team, 2020). Models were run using four chains with 2500 iterations after warmup with a thinning of 5; the spatiotemporal temperature model and space vs time model had a warm-up of 2000 and the site by year model had a warmup of 1500 iterations. Convergence was checked using the Rhat (all < 1.02) and through graphical inspection. Effective sample sizes were all over 600, and over 1100 for all focal coefficients. The space vs time temperature model had 3 divergent transitions after the warmup which was 0.15% of the 2000 iterations retained.

Results

Of the 37,674 branch beatings, 3,950 of the samples recorded one or more caterpillars totalling 8,196 individuals. Of the samples in which one or more caterpillars were present, 69% recorded one and 16% recorded 2, with a maximum abundance of 109.

In the sliding window analysis, I found mean timing was most sensitive to temperatures from early March to mid-April (ordinal dates 65-106, 5th March - 15th April in non-leap year, Fig. 3.3a), height was most sensitive to temperatures later in the spring (100-141, 9th April -20th May, Fig. 3.3a) and width to temperatures that spanned the spring (58-155, 27th February - 3rd June, Fig. 3.3a). I used the mean temperature during each of these windows as the temperature variable for the respective Gaussian parameter in all subsequent analyses.

Spring temperatures had a significant effect on all three phenological parameters, with the most profound effects being that the caterpillar phenological distribution is earlier and higher in warmer years (Fig. 3.3b-c, 3.4a). I found that mean timing shifted by -4.96 days $^{\circ}C^{-1}$ (95% credible intervals [CIs]: -6.21 - -3.64 days $^{\circ}C^{-1}$, Fig. 3.3b). The appearance of two groups with different intercepts within the site by year estimate points in Fig. 3.3b is caused by the year effects, discussed further in Appendix B. When looking at the expected change in distribution height independently of the other parameters (see Appendix B), the maximum abundance increased by 34% $^{\circ}C^{-1}$ (CIs: 5 - 61% $^{\circ}C^{-1}$, Fig. 3.3c), though I still find substantial variation in height among sites, years and site-years (Table B.3). When I account for the uncertainty in all three parameters to attain the mean expectations of abundance on each day in spring (see Appendix B), I found the distribution height increased by 28% (CIs: 1 - 52%) when temperature increased by one degree above the mean (Fig. 3.4a). The width parameter decreased by 9% $^{\circ}C^{-1}$ (CIs: 1 – 17% $^{\circ}C^{-1}$, Fig. 3.3d), indicating the shape of the distribution narrows as spring temperature increases.

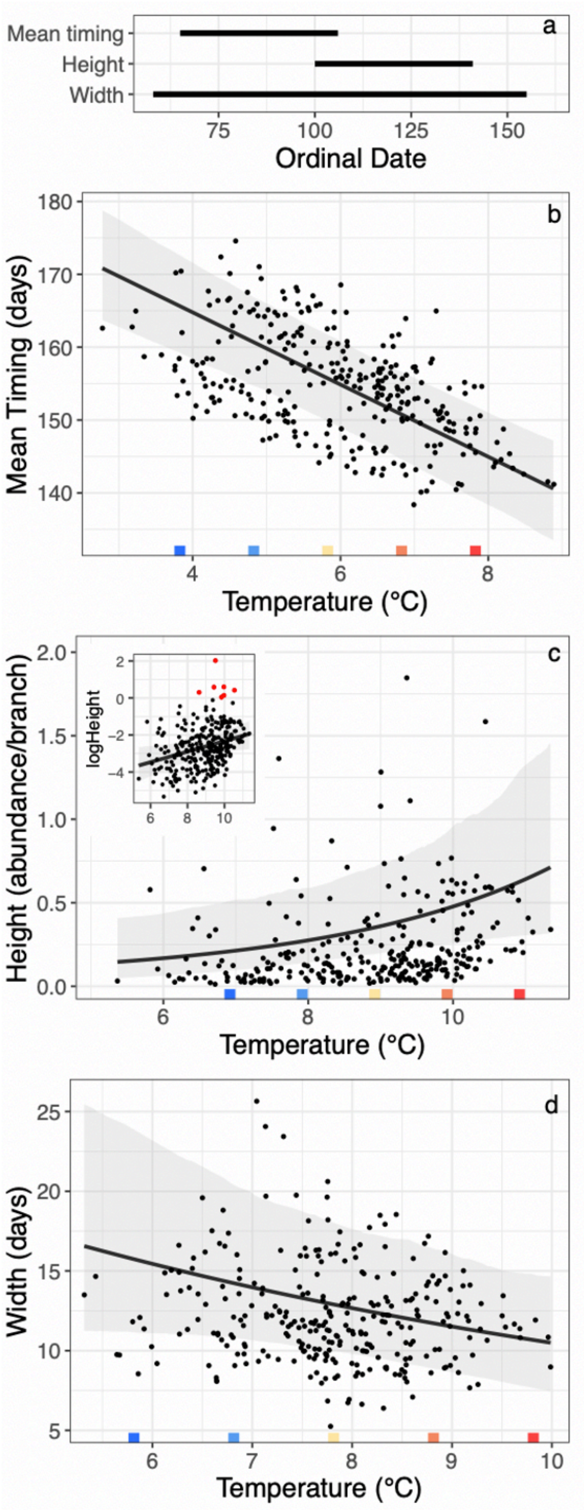

Figure 3.3: a) windows of time where spring temperature was identified as the best predictor of each parameter of the phenological distribution. b-d) show the model predictions (black points) for the mean timing, height and width of the caterpillar peak, as a function of temperature during the identified windows for each site by year combination. Mean estimate on the data scale (black line) and 95% credible intervals (grey band). c) The inset plot shows log scale estimates and red points indicate points excluded from the data scale plot. Coloured squares along the x-axis show the mean temperature in yellow with +/- 1 and 2 degrees in blues/reds which correspond to the plots in Figure 3.4.

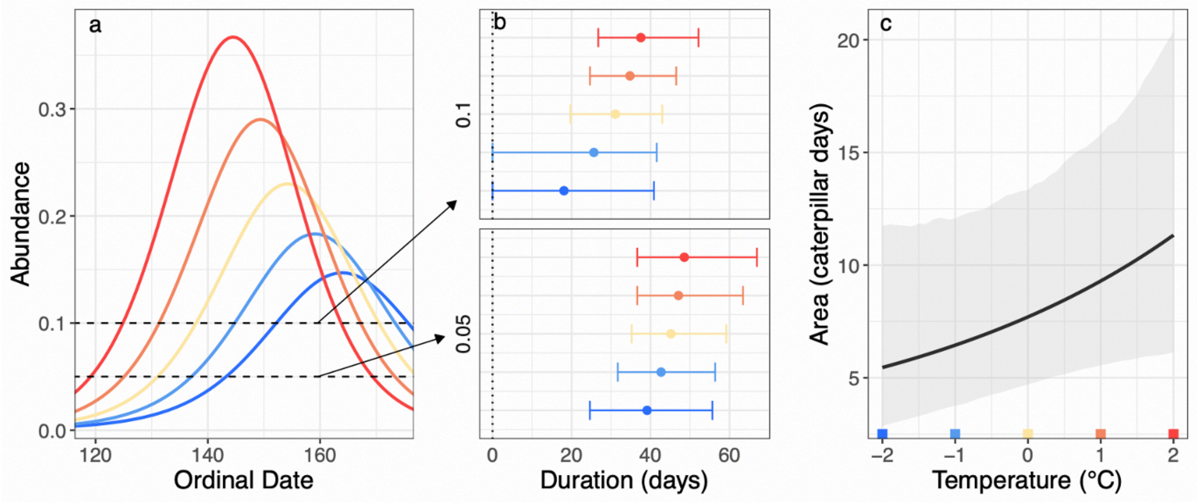

Figure 3.4: a) posterior mean expected abundance on the data scale of the full phenological distribution at different temperatures: the mean of each temperature window (mean timing = 5.85°C, height = 8.92°C, width = 7.81°C; yellow), +1°C (orange), +2°C (red), -1°C (light blue) and -2°C (dark blue); calculated from the posterior predictive distribution. b) shows the mean and 95% credible intervals (95% CIs) for the duration of the peak at an abundance of 0.1 and 0.05 caterpillars for distribution at each temperature calculated from the posterior distributions of the simulated expectations of abundance across dates; and c) shows the mean and 95% CIs for the area under the phenological distribution from -2 to 2°C around the mean (centred) temperature, calculated from the simulations under the model.

The duration of the distribution will be affected by both the height and width parameters and varies depending on the abundance threshold at which it is calculated (Fig. 3.1); I, therefore, chose to present duration at two thresholds. The purpose of quantifying duration was to assess any change in the period throughout which caterpillars are present, making lower abundance thresholds most informative; I chose 0.05 and 0.1 caterpillars per branch as in the absence of a biological motivation the choice of abundance was arbitrary and these allowed comparison across a 4°C range (blue to red lines in Fig. 3.4a) that is within the temperature variation I find across sites and years within this study. I found no significant effect of temperature on duration at either threshold across the 4°C range within the data (Fig. 3.4b; mean [CIs] difference between 2°C and -2°C at 0.1 = 19.45 days [-4.23 - 47.90]; at 0.05 = 9.42 days [-7.75 -

29.58]). Whilst the change in duration at the chosen abundance levels was not significant, the mean point estimates show a slight increase with temperature, particularly at the higher threshold. This illustrates that whilst the shape of the peak is narrowing through a reduction in the width parameter, the substantial increase in height maintains (or may even increase) the period of time where caterpillars are present above a particular abundance. I can also derive the thermal sensitivity of the area under the phenological distribution; and whilst the slope estimate of 1.21 times the area per ^{o}C suggests an increase in area with temperature, this effect was not significantly removed from one (CIs: 0.97 - 1.44, Fig. 3.4c).

I found that spatial and temporal slopes were generally in the same direction as the main spatiotemporal model (Table 3.1), except for the temporal width parameter slope. For the mean timing parameter, the estimates in space and time were not significantly different and both were in the same direction with CIs removed from zero. Whilst there was no significant difference in the mean timing slopes across space and time, the difference in the point estimates was consistent with a co-gradient, a steeper spatial slope. For the thermal sensitivity of the distribution height, the spatial and temporal estimates did not significantly differ and point estimates were in the same direction, possibly suggested a co-gradient pattern; however, neither effect was significant. The thermal sensitivity of the width parameter was significantly different in space versus time, with a significant negative spatial slope but no effect of temperature across years. The effect of temperature on the area under the phenological distribution is similar in the main model and over space and time, all showing positive but non-significant effects.

Table 3.1: Summary of results for the effect of temperature on the mean timing, height, width and area under the phenological distribution of spring arboreal caterpillars, showing posterior mean effect with 95% credible intervals (CI) in brackets beneath. Spatiotemporal slopes come from a model using temperatures for each site-year to estimate the thermal sensitivity of the parameters. The spatial and temporal slopes come from a model employing a within-site centring approach to separate the effects in space and time. The difference column indicates the difference between the spatial and temporal slope estimates calculated from the spatial slope minus the temporal. Slope estimates are exponentiated or unscaled where applicable and ‘prop.’ in the unit column implies proportional changes (i.e. exponentiated slopes). For the slope estimate columns: red text indicates a negative effect, blue text indicates a positive effect and coloured CI text indicates the effect was significant. For the mean timing parameter and the difference column CI removal from 0 suggests a significant effect, whereas for the three parameters in units of proportional change CI removal from 1 suggests significance.

Parameter	Unit	Spatiotemporal slope	Spatial slope	Temporal slope	Difference (S-T)
Mean Timing	days $°C^{-1}$	-4.96 (-6.21 - -3.64)	-5.77 (-7.39 - -4.18)	-3.39 (-5.49 - -1.46)	-2.37 (-4.77 - 0.17)
Height	prop. change $°C^{-1}$	1.34 (1.05 - 1.61)	1.66 (0.97 - 2.63)	1.17 (0.81 - 1.49)	0.49 (-0.31 - 1.55)
Width	prop. change $°C^{-1}$	0.91 (0.83 - 0.99)	0.85 (0.75 - 0.96)	1.05 (0.89 - 1.21)	-0.20 (-0.39 - -0.01)
Area	prop. change $°C^{-1}$	1.21 (0.97 - 1.44)	1.40 (0.90 - 2.12)	1.22 (0.89 - 1.53)	0.18 (-0.41 - 0.95)

Discussion

I found that spring temperatures affect the mean timing, height and width of the caterpillar phenological distribution. These results show that in addition to the distribution mean timing shifting by -4.96 days $°C^{-1}$, which is consistent with results from previous studies (Visser, Holleman and Gienapp, 2006; Charmantier *et al.*, 2008; Burgess *et al.*, 2018), the phenological distribution height increases by 34% $°C^{-1}$ and decreases in width by 9% °C^{-1} (Fig. 3.3b-d). Whilst the shape of the peak narrows through the decrease in width, when paired with the substantial increase in height I found no change in the duration of distribution with changing temperature (Fig. 3.4b). The results show important insight into thermal sensitivity in the full phenological distribution, a concept often overlooked in phenology and MMH research.

My finding that spring temperatures have a substantial impact on the maximum height of the caterpillar guild phenological distribution (an increase of 34% °C^{-1}) is likely to have cascading effects through interactions within the forest community. Even an increase in temperature of 1.5°C could yield more than a 50% increase in the maximum abundance of arboreal caterpillars. The resulting increase in herbivory pressure at the mean timing of the herbivorous caterpillar guild represents a potentially major indirect effect of temperature on the severity of tree defoliation (Kulman, 1971; Whittaker and Warrington, 1985; Whitham *et al.*, 1991; Marquis and Whelan, 1994). However, the impacts on tree defoliation and growth are likely to depend on how synchronous caterpillars are to the tree and the level of defences the leaves have acquired at the time of maximum herbivory (Schwartzberg *et al.*, 2014; Bellemin-Noël *et al.*, 2021). Should the increased maximum abundance translate to a greater prevalence of pest outbreaks and defoliation, further work into whether the change is driven by a few specific species or is consistent throughout the guild will be important for the design of effective and targeted pest management interventions. An increase in the height of the caterpillar phenological distribution is also liable to have profound consequences for secondary consumers, a theme to which I will return.

The positive effect of spring temperature on the height of the phenological abundance distribution that I observe departs substantially from the Nadolski *et al*. (2021) report of a lack of correlation between annual temperature variation and maximum caterpillar biomass in Poland (n=16). Whilst it is possible that this reflects true differences in response between regions or differential effects of temperature on caterpillar abundance and biomass, it is entirely possible that my slopes do not in fact differ from theirs; whilst Nadolski *et al*. do not report a slope or confidence interval, the interval is likely to be broad. The extent to which the increase in height with temperature is attributable to within-species shifts in abundance versus between-species thermal responses (turnover) will require further investigation at the species rather than guild level as, within the caterpillar guild, the average phenological distribution may vary among species, as could the thermal sensitivity of mean timing (Hällfors *et al.*, 2021), height and width.

The spatiotemporal estimate of a shift in the mean timing of -4.96 days$^{o}C^{-1}$ is broadly consistent with European estimates for the thermal sensitivity of the timing of leaf out in oak trees and other deciduous species (Vitasse *et al.*, 2010; Roberts *et al.*, 2015; Tansey, Hadfield and Phillimore, 2017). In contrast, the estimate of the temporal slope for mean caterpillar timing is slightly shallower than that of some dominant UK trees, e.g., *Quercus* sp leaf-out was found to have sensitivity to forcing temperatures of -8.81 +/- 0.52 days $^{o}C^{-1}$ (Roberts *et al.*, 2015). This means that increasing temperatures could alter the phenological (a)synchrony between caterpillars and deciduous trees, despite previous studies suggesting that caterpillars are maintaining synchrony with oak (Both *et al.*, 2009; Burgess *et al.*, 2018). An increase in tree-caterpillar asynchrony may impede the increase in the height of the caterpillar phenological distribution and prevent the most extreme detrimental effects for the trees (Schwartzberg *et al.*, 2014), whilst greater synchrony could exacerbate the increase in herbivory pressure (Schwartzberg *et al.*, 2014; Bellemin-Noël *et al.*, 2021); highlighting an important direction for future analyses.

Moving up the food chain to the insectivorous bird-caterpillar trophic interaction, a study of bird species in the UK and Netherlands showed an average advance in lay date of 3.24 days $^{o}C^{-1}$ (SE = 0.4) (Mclean *et al.*, 2022), which is shallower than my spatiotemporal estimate for the shift in caterpillar mean timing, albeit with overlapping confidence/credible intervals. However, whilst my caterpillar mean timing slopes over space and time did not differ significantly, my temporal estimate for the caterpillar mean timing is similar to temporal estimates for many UK birds (Mclean *et al.*, 2022), which may allow the average bird species to track the change in caterpillar phenology from year to year.

For forest birds that rely on caterpillars as a food resource to feed nestlings, the impact of temperature on the shape and height of the caterpillar peak could have stark consequences for how the MMH manifests. The increase in peak height means that under warmer spring conditions far more food is predicted to be available to consumers that remain synchronous with the caterpillars. However, the relative abundance of food available to synchronous versus asynchronous consumers changes with temperature, with the reduction in peak width driving a steeper decline in abundance to either side of the mean timing under warmer conditions. These changes to the phenological distribution of the resource could alter the dynamics of the MMH for consumers as the relative fitness consequences of asynchrony within the population could change with temperature, potentially increasing the strength of selection on breeding phenology. Whilst the strength of selection within the bird population may increase, as the duration remains constant and the maximum height increases, late birds at increased temperatures will have access to more resource than at cooler temperatures, suggesting a focus on asynchrony in mean timing alone may give an overly pessimistic view of the bird's ability to cope under a warming climate. Much of the previous work on the effects of the MMH on consumer fitness has focused on the strength of selection on phenology attributed to asynchrony between consumers and the mean resource timing (Charmantier *et al.*, 2008; Reed, Jenouvrier and Visser, 2013). Very few studies have examined the effects of the height or width of the resource distribution on fitness (Ramakers, Gienapp and Visser, 2019); this presents an important direction for future work to fully understand the impact of climate-mediated mismatch on fitness.

By allowing temperature during different windows to affect each distribution parameter in the sliding window I have gained new insights into the thermal sensitivity of the caterpillar phenological distribution. The window identified as most influential for mean timing falls before the onset of the main peak in abundance, most likely influencing hatching phenology rather than altering the mean timing through impact on developmental rate, and is similar to that identified as important in other European studies (Visser, Holleman and Gienapp, 2006; Porlier *et al.*, 2012; Simmonds *et al.*, 2020). The height of the distribution however is most sensitive to temperatures around the onset of the peak and in the weeks following, suggesting the thermal sensitivity in height is driven more by thermal effects on the larvae and potentially their host plants than the eggs. For width, my time window is broader than identified by Visser *et al.* (2006), though I note a high degree of uncertainty in the position of the window for this phenological parameter (Fig. B.1). The sliding window approach involves a very high level of multiple testing (13231 window combinations in my case) (van de Pol *et al.*, 2016), which inflates the type I errors. In the context of this study, I anticipate that this is most likely to affect the slope of temperature on the width parameter, which is the weakest of the correlations I identify.

By separating the effects of temperature in space and time I can assess my confidence in the causality of the trends found and begin to predict the processes underlying them. For the mean timing parameter, the similar estimates in space and time suggest temperature has a causal effect and is consistent with plasticity being responsible for much of the spatiotemporal variation in mean timing (Charmantier *et al.*, 2008; Phillimore *et al.*, 2010; Burgess *et al.*, 2018). The non-significant difference in the point estimates was consistent with a co-gradient pattern, which may suggest some local adaptation or differing species turnover within the guild. My estimates differ in magnitude from previous results from across eight localities in the UK, which reported a significant negative temporal slope in mean timing, but a shallow and non-significant negative slope in space (Burgess *et al.*, 2018). For the thermal sensitivity of the distribution height, the general direction of the estimates and lack of difference in space versus time suggests a causal effect of temperature, with a possible co-gradient pattern; yet neither effect was significant. While all point estimates are in the same direction, there is large uncertainty when this relationship is separated into spatial and temporal trends; therefore, I suggest analyses with increased power through greater temporal replication would be of value in future work. For the thermal sensitivity of the width, the lack of a trend in time but a significant negative effect in space was consistent with the findings of Smith *et al*. (2011). This suggests the effect of temperature on distribution width in my main model may not be causal, alternatively driven by spatially correlative variables or differences in guild species composition. The positive but non-significant effect of temperature on the area under the phenological distribution was similar in both space and time and the spatiotemporal model; I, therefore, cannot conclude that there is any effect of temperature on the area under the curve within this data set, though this presents an interesting avenue for future work.

I anticipate that this statistical approach offers great potential for modelling the effects of climate on many phenological distributions. My approach is similar to the Gaussian model functions described in de Villemereuil *et al*. (2020) and Dennis *et al*. (2016), with the major difference being that I include a linear effect of temperature on the three parameters that control the position, shape and height of the phenological distribution. My approach also has advantages over the use of a GLM/GLMM with a Poisson response and quadratic date term to estimate the effects of an environmental variable on mean timing (Chevin, Visser and Tufto, 2015; Edwards and Crone, 2021), which forces an undesirable non-linear relationship between the environmental variable and height (see Appendix B for further details).

Introducing a novel phenological method, I have shown that temperature has an effect not only on the mean timing of the phenological distribution of spring arboreal caterpillars but also on the height and width of the peak. I report an increase in the height accompanied by a decrease in the width, resulting in a similar duration of the distribution as temperature increases. The alterations to the shape of the phenological distribution of caterpillars not only identify shifts in dynamics within the caterpillar guild that are attributed to temperature, but it will also impact the herbivory pressure on deciduous trees and alter the food availability throughout spring for breeding birds with possible implications for the MMH. The methods I present have broad applicability to other research systems and questions within phenology and the MMH, and I encourage more work to study the full phenological distribution of biological events rather than focusing on mean timing. To predict the biotic impacts of ongoing climate warming, it will often be essential to take these additional components of change into account.

Chapter 4 - An extended conceptual framework for the match/mismatch hypothesis: incorporating the full phenological distribution

Abstract

The match/mismatch hypothesis (MMH) states that synchronous timing between an ephemeral resource and a consumer that it relies on will be important for consumer fitness, with asynchrony reducing the success of consumers. This topic has garnered particular interest in recent decades because the thermal sensitivity of timing can vary between trophic levels and secondary consumers are often responding with a shallower slope than their resource, increasing the risk of asynchrony under climate warming. Research on the MMH most often focuses on the mean timing within a population, particularly for the resource, however, the phenological distribution of an ephemeral event also reaches a maximum height and has a width which describes the spread over time. The change in fitness of a consumer over time forms a phenological fitness function which can be described by an optimum timing, maximum fitness and width. The optimum timing, where fitness is highest, is expected to be affected by the mean timing of the resource phenological distribution as that is when food is most abundant. However, the full phenological distribution of a resource determines the availability of food at any given point in time and therefore I propose an extension to the conceptual framework of the MMH in which the full phenological distribution of a resource is predicted to affect the full phenological fitness function of the consumer. I tested this hypothesis using data on the deciduous woodland arboreal caterpillar peak and blue tit, *Cyanistes caeruleus,* hatching phenology and fledging success. I found no effect of the caterpillar peak on blue tit fledging success and detected no optimum blue tit hatching timing within the data. I consider possible explanations for this lack of evidence for the MMH. Whilst the blue tit and caterpillar data do not conform to model expectations, the proposed extension to the MMH presented here provides a more complete framework for identifying the importance of ephemeral trophic interactions for fitness. Incorporating the full phenological distribution of a resource when studying drivers of change in consumer fitness has the potential to provide a more complete prediction of the indirect impacts of climate change on population fitness and the strength of selection, parameters that influence a population’s ability to persist in the warming climate.

Introduction

Trophic interactions that rely on synchronous timing are vulnerable to being phenologically uncoupled because of the warming climate. This is because at mid to high latitudes temperature is one of the main drivers of the phenology of many seasonal life history events (Forrest and Miller-Rushing, 2010; Wolkovich, Cook and Davies, 2014; Cohen, Lajeunesse and Rohr, 2018) and whilst thermal sensitivity in phenology is common, the rate of response or period to which timing is most sensitive is not always consistent among species. As a result, different species exhibit different phenological shifts in response to the same change in climate, with previous work suggesting phenological shifts differ among a broad range of taxa, ecosystems and between trophic levels (Parmesan, 2006, 2007; Thackeray *et al.*, 2010; Roslin *et al.*, 2021). There are particular differences in the thermal sensitivity of phenology between primary and secondary consumers, making interactions between these levels particularly susceptible to uncoupling as the climate warms (Thackeray *et al.*, 2016).

When the resource within a trophic interaction is ephemeral and forms a key component of the consumer's diet, synchronous timing with the resource can be important for consumer fitness, with negative consequences of being asynchronous, as outlined by the match/mismatch hypothesis (MMH) (Cushing, 1990). The standard application of the hypothesis describes a peaked phenological fitness function for the consumer, where fitness varies with some phenological trait in relation to the timing of the resource and is maximised (optimum timing) where the maximum resource requirement is synchronous with the maximum volume of resource that is available over time (Fig. 4.1). An extension of this hypothesis recognises that the abundance of the resource positively impacts consumer fitness in addition to the benefits of more synchronous timing (Durant *et al.*, 2005, 2007). These nuances were introduced by Cushing (1982) but infrequently considered in recent work around the MMH, though some exceptions include Miller-Rushing *et al.* (2010), Ramakers, Gienapp and Visser (2019), Nadolski *et al.* (2021) and Visser et al. (2015).

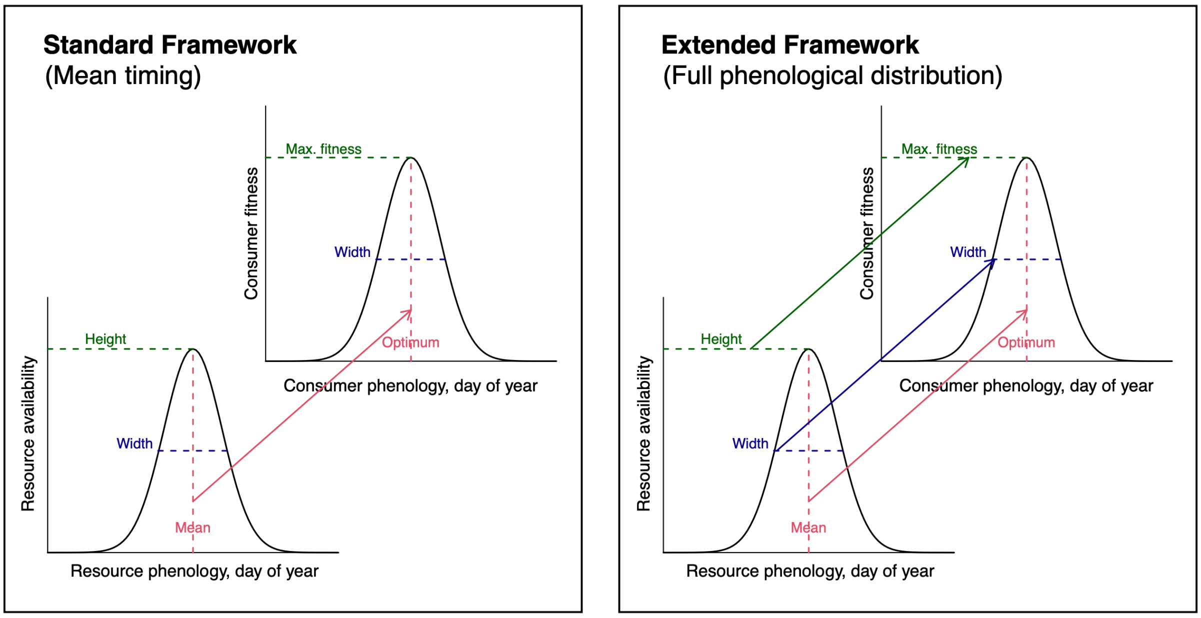

Figure 4.1: Schematic illustrating the standard framework of the match/mismatch hypothesis and the proposed extended framework. In the standard framework, the mean timing of the resource phenological distribution affects the optimum timing of the consumer phenological fitness function and the maximum fitness and width of the fitness function are assumed to remain consistent. In the extended framework, the mean timing of the resource affects the optimum timing for the consumer, the height of the resource distribution affects the maximum fitness of the consumer and the width of the resource distribution affects the width of the consumer fitness function.

There is interest in how climate change may impact fitness and whether it will give rise to directional selection on traits. From the shape of the phenological fitness function and the distribution of the phenological trait for a population, one can infer the difference between the optimum timing and the mean phenology of a population (lag), mean population fitness and the strength of directional and stabilising selection on the phenological trait (Latter, 1970; Lande, 1976; de Villemereuil *et al.*, 2020). The strength of directional selection increases with an increase in lag (Charmantier *et al.*, 2008; Reed, Jenouvrier and Visser, 2013), however, a cross-species (n=17) analysis of birds found no evidence that the strength of directional selection on phenology increasing with temperature (Radchuk *et al.*, 2019) though there is consistently negative directional selection on timing (Kingsolver *et al.*, 2012). Most work on phenology and fitness has focused on the strength of directional selection, with stabilising selection receiving less attention (but see Visser *et al.*, 2015; Ramakers, Gienapp and Visser, 2019; de Villemereuil *et al.*, 2020), however, selective pressure can be both stabilising and directional at the same time (de Villemereuil *et al.*, 2020), and both could be subject to change under a warming climate. Understanding how population fitness responds to climatic variables and accurately estimating the strength of direction and stabilising selection are critical to predicting a population's capacity to persist through climate warming (Chevin, Lande and Mace, 2010; Vedder, Bouwhuis and Sheldon, 2013).

Given the widespread interest in the MMH and its fitness consequences under climate change, relatively few studies have actually examined the fitness consequences of asynchrony (Samplonius *et al.*, 2020). Of those that do, the majority of MMH research focuses on synchrony between the resource population (or guild) mean timing and individual consumer phenology (or sometimes the consumer population mean timing) (e.g. Visser *et al.*, 1998; Charmantier *et al.*, 2008; Reed *et al.*, 2013). Most studies examining variations in fitness influenced by timing relative to the resource use the standard framework centred around relative timing (Fig. 4.1), in which the level of asynchrony determines where the population phenological trait falls within the phenological fitness function (Fig. 4.1, 4.2), which alters the strength of directional selection (Fig. 4.2) (Lande, 1976; de Villemereuil *et al.*, 2020). However, the peaked phenological distribution of a fitness function or resource availability (abundance or biomass) is described by more than mean timing alone, it can also vary in height, describing the maximum fitness or resource availability reached, and width, describing the spread of fitness or resource availability over time (Chapter 3). Very little work has explored whether the height and width of the resource phenological distribution affect the phenological fitness function. These additional parameters of the resource distribution, the height and width, could vary among years and locations and be sensitive to temperature (Chapter 3), and therefore a more complete test of the MMH, predicting that resource availability affects consumer fitness, would also involve these parameters. Variation in the height and width of the resource phenological distribution alters the volume of food available at any given point in time; if such change inflicted similar trends in the height and width of the phenological fitness function this could impact the population mean fitness and the strength of both directional and stabilising selection (Fig. 4.2).

In this study I propose an extension to the MMH framework and hypothesise that the full phenological distribution of a resource will influence the full phenological fitness function of the consumer (Fig. 4.1). As theory behind the phenological fitness function for the consumer under the MMH is based on changes in the availability of food given the relative timing to the resource, other sources of variation in food availability are also predicted to influence consumer fitness. The role of food abundance in the MMH has been discussed before (Cushing, 1982; Durant *et al.*, 2005, 2007) and an increase in resource height has been found to affect fledging success, recruitment, nestling condition and the seasonal decline in fitness (García-Navas and Sanz, 2011; Vatka, Rytkönen and Orell, 2014; Visser *et al.*, 2015; Pakanen *et al.*, 2016). However, to date, no study has framed a test of the MMH in the context of two full phenological distributions, one for resource availability and one for consumer fitness. The proposed phenological distribution extension of the MMH generates three predictions: **prediction 1**: that *the mean timing of the resource phenological distribution is positively correlated with the optimum timing of the consumer phenological fitness function*; **prediction 2** that *the height of the resource distribution is positively correlated with maximum fitness of the consumer fitness function* (though with a plateauing trend as the height increases above some threshold) and **prediction 3** that *the width of the resource distribution is positively correlated with the width of the consumer fitness function*. The standard framing of the MMH captures only the first of these predictions (Fig. 4.1).

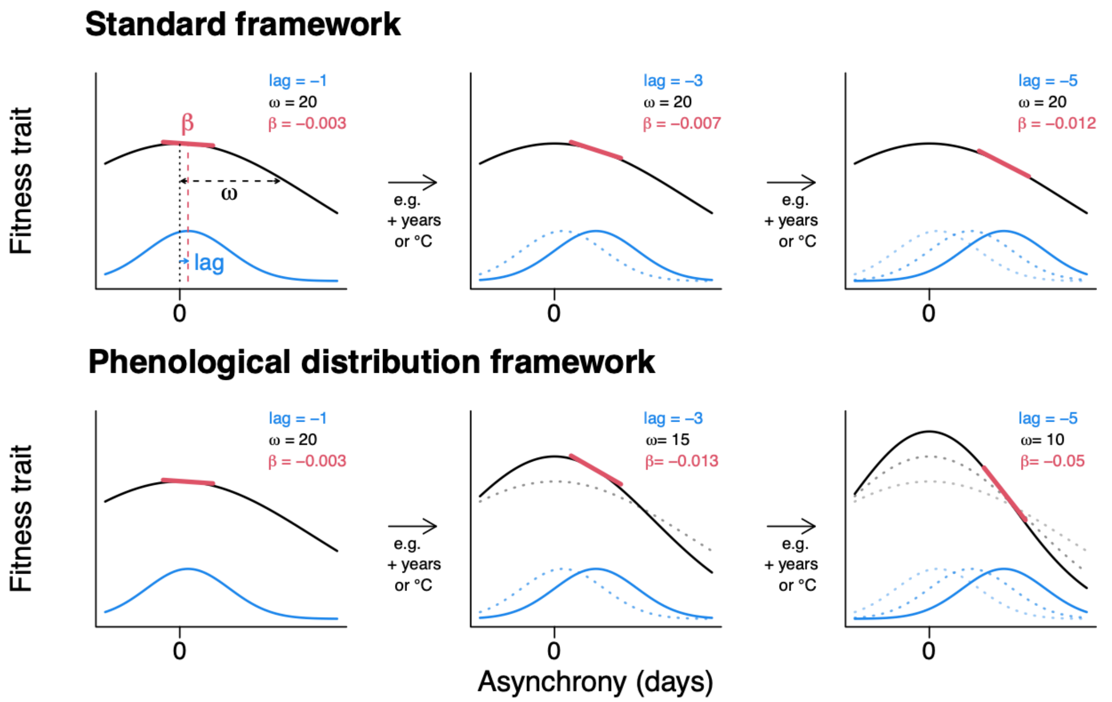

Figure 4.2: Schematic illustrating the estimation of selection under the standard conceptual framework of the MMH versus the phenological distribution framework proposed in this chapter. The black line shows fitness as a function of asynchrony to the resource; the blue line shows the population phenological trait with increasing asynchrony in plots from left to right, representing an increase in years or temperature (previous plots' lines as faded dots). The location of the trait distribution within the fitness function will determine population fitness. The blue arrow in the first plot indicates lag (the difference between the optimum timing of the fitness function and the mean timing of the phenological trait). The width (ω) of the fitness function (and the trait, which is held consistent in this example) influences the strength of stabilising selection, and both the width of the fitness function, trait and the lag influence the strength of directional selection (β). The red slope illustrates how lag influences directional selection. Under the standard framework only a change in lag can alter directional selection and stabilising selection is assumed to remain consistent. In the phenological distribution framework the same changes in lag can be accompanied by alteration to the height and width of the phenological fitness function, hypothesised to result from similar shifts in the resource phenological distribution. This allows directional and stabilising selection to be estimated from a more accurate fitness function, rather than assuming the function retains the same shape; these differences in selection would go undetected or misinterpreted under the standard framework.

Under the proposed phenological distribution extension of the MMH, spatiotemporal heterogeneity in resource availability, resulting from differences in the height and width of the resource distribution among years and locations (Chapters 2 and 3), is expected to influence the consumer fitness function in space and time. The widths of the resource distribution and consumer fitness function are expected to influence the strength of directional and stabilising selection on consumer timing (Fig. 4.2), with potential implications for the microevolution of phenological traits. If temperature impacts the height and width of the resource phenological distribution (Chapter 3), then the standard approach may wrongly estimate or interpret the effects of temperature on the strength of directional and stabilising selection (Fig. 4.2). As the strength of selection is important for a populations resilience to environmental change (Chevin, Lande and Mace, 2010), it is important to incorporate additional drivers of change to accurately predict a species response to the changing climate.

Here I explore the phenological distribution extension of the MMH in one of the best-studied systems within MMH research, the temperate deciduous woodland food chain. The spring arboreal caterpillar peak is an important resource for many breeding passerines in spring (Betts, 1955; Bańbura *et al.*, 1994; Sanz, 1998; Wilkin, King and Sheldon, 2009), with evidence that they form a large component of nestling diets and higher proportions in the diet increases nestling condition (Visser, Holleman and Gienapp, 2006; García-Navas and Sanz, 2011; Samplonius *et al.*, 2016). The mean timing of the caterpillar phenological distribution is generally advancing in response to temperature at a faster rate than the breeding passerines studied (Visser, Holleman and Gienapp, 2006; Charmantier *et al.*, 2008; Burgess *et al.*, 2018), making these species susceptible to the negative consequences of the MMH.

In this chapter, I study the effect of the phenological distribution of the caterpillar resource on the phenological fitness function of blue tits, *Cyanistes caeruleus,* using data collected over nine years across 44 sites. The phenological distribution extension to the conceptual framework of the MMH allows a more complete test of the MMH, with flexibility in the full phenological distribution being incorporated into the study of trophic interactions. By considering the phenological distribution extension of the MMH we can more accurately understand the dynamics between ephemeral resources and their consumers and improve estimates of the effects of trophic interactions on population fitness and the strength of selection timing.

Materials and Methods

Study System

Data were collected over nine years, from 2014 to 2022, at 44 deciduous woodland sites between Edinburgh (55°980 N, 3°400 W) and Dornoch (57°890 N, 4°080 W) along a 220km transect through Scotland. The sites include an elevational range of 10-433m above sea level and vary in woodland tree composition and temperature. From 2014-2016 between 30 and 37 sites were monitored, the majority of which had six nest boxes (26mm hole Schwegler 1B) installed to target breeding blue tits (Shutt *et al.*, 2018). In 2017 this was increased to 44 sites with eight nest boxes at most, though seven sites had six boxes and one had four. In 2020 monitoring was restricted to most southern 22 sites due to the Covid-19 pandemic, increasing to 37 sites in 2021, and back to 43 sites in 2022, with a single site not monitored due to a high frequency of nest predation in 2021. Each site was visited every second day from 1st April each year (except 2020 when monitoring began on 7th May), until late June.

Arboreal caterpillar abundance

The abundance of arboreal caterpillars present from late spring into early summer was monitored using a branch beating method, recording the abundance of caterpillars on each branch sampled on dates throughout spring, described fully in Chapter 2 and in Shutt, Burgess and Phillimore (2019). An average of 14 trees were sampled at each site in each year from 2017-22 (five trees per site prior to that). On each tree, one branch is marked and half of the trees at each site are sampled on alternating visits meaning every tree is beaten every four days, allowing for some caterpillar recolonisation, with samples taken from every site every two days. The branch sampled was held consistent throughout each season and across years unless broken or dead. The leafing phenology was recorded for a selection of trees at each site, and sampling began once 45% of trees across all sites had unfurled the first leaf, continuing until the end of the field season in mid/late June. Sampling information for 2014-21 can be found in Chapters 2 and 3, and sampling in 2022 ran from ordinal dates 119 to 170.

Blue tit breeding phenology and success

At each site, all nest boxes were checked every second day to monitor blue tit breeding phenology, recording the progression of clutch size and the onset of incubation. Once incubation had begun, the nest was undisturbed for 10 days after which checks on alternate days resumed to determine the hatch date within a two-day window of uncertainty (1.1% of nests [n=13] have a higher uncertainty due to missed checks: 10 had a three-day uncertainty window and three had up to seven days). The ordinal date on which hatched chicks were first observed in the nest was used as the hatch date, including the nests with higher uncertainty, with a total of 1138 nests included in the analyses. There were 265 nest records from 2017-19 removed due to involvement in a cross-fostering experiment.

Nestlings were fitted with a unique ring, under licence from the British Trust for Ornithology, six days after hatching was first observed (or when nestlings were predicted to be six days old for the 13 nests with a delayed hatch observation). The nests were checked again 12 days after the observed (or predicted) hatch date to record which individuals were still alive. From 18 days after the observed hatch date the nests were monitored every second day for fledging until all nestlings had left the nest. Once empty, the nests were searched for any unsuccessful individuals which were identified by their unique ring number, from this we could identify how many young had fledged.

To identify the female bird breeding at each nest box, adult birds were caught on the nest ≥10 days after hatching. There was one nest where 2 females were caught so this nest was given a unique female identity. The female identity is known for 85% of all nests and was treated as unique for the remaining 15%.

The phenological distribution extension of the MMH using the Gaussian function

Phenological fitness function: the Gaussian function is well suited to describing the phenological fitness function because it is governed by three parameters which define the optimum timing (θ), the maximum fitness (W_{max}) and the width of the distribution (ω), as described in de Villemereuil *et al.* (2020):

Eq. 4.1: $$W(x) = W_{max} exp\left(-\frac{(h-\theta)^2}{2\omega^2}\right)$$

Eq. 4.1 can be rearranged to model the maximum fitness and width on the log scale:

Eq. 4.2: $$W(x) = exp\left(logW_{max} - \frac{(h-\theta)^2}{2exp(log\omega)^2}\right)$$

I used the Eq. 4.2 arrangement of the Gaussian function in a non-linear model to analyse how the fledging success of a nest (W) changes with hatch date (h, centred to a midpoint of caterpillar and hatching data: day 146 [25th or 26th May]), and how the optimum timing, maximum fitness and width of the distribution are affected by the equivalent parameters describing the phenological distribution of the ephemeral caterpillar resource.

The caterpillar peak: caterpillar abundance (A) across ordinal date (x, also centred to day 146) was modelled using the same composition, estimating the mean timing (μ), maximum height ($logA_{max}$) and width ($log\sigma$) of the caterpillar peak (with height and width on the log scale):

Eq. 4.3: $$A(x) = exp\left(logA_{max} - \frac{(x-\mu)^2}{2exp(log\sigma)^2}\right)$$

Each phenological parameter included an intercept in addition to site, year and site by year interaction effects fitted as random, allowing the mean timing, log height and log width of the caterpillar peak to be calculated for each site in each year. A day by site by year interaction, the recorder of each sample, the unique tree identity and an observation-level residual were also included as random terms for $logA_{max}$ to account for other sources of variation in caterpillar abundance.

The caterpillar peak as a predictor of blue tit fitness: The predicted caterpillar phenological parameters for each site in each year were then used as predictors of the blue tit phenological fitness function (Eq. 4.2). These predictions resulted in four slopes: (i) the effect of μ on $\theta,$ which allowed the mean timing of the caterpillar peak to effect the optimum timing of the blue tit phenological fitness function, (ii) the effect of $logA_{max}$ on $logW_{max},$ which allowed the maximum height of the caterpillar peak to effect the maximum fledging success at the optimum time of breeding for blue tits, and the effect of (iii) $log\sigma$ on $log\omega$ and of (iv) $logA_{max}$ on $log\omega$, which allowed width of the caterpillar peak to effect the width of the blue tit fitness function at a consistent caterpillar peak height and the height of the caterpillar peak to effect the width of the blue tit fitness function at a consistent caterpillar peak width. The width of the fitness function has two slopes because the height and width parameters both influence the duration over which the caterpillar peak falls and these parameters negatively covary. Site, year and site by year interaction effects were fitted as random for each of the phenological fitness parameters, estimating the covariance between the parameters for each of these terms from a single correlation matrix, assuming the same correlation structure among random terms, with term-specific variances. The female identity for each nest was also included as a random term for $logW_{max}$, allowing the number of offspring fledged to also vary among females.

Zero-inflated hurdle model composition: all unmanipulated nests (not included in a cross-fostering experiment, which involved 265 nests) which had hatched were included in the analysis as breeding attempts. As any nests that were unsuccessful fledged zero offspring (n=150 of 1138) but the average number of offspring fledged per nest was 6.4 among those that were not abandoned, the data were zero-inflated with a bimodal distribution. To allow for this I used a hurdle model composition with i) a Bernoulli model (logit link function) estimating the probability of success (fledging at least one) and ii) a zero-truncated generalised-Poisson (TGP) model (log link function) estimating the number of offspring to fledge from a nest conditional on it being a successful breeding attempt. The generalised-Poisson distribution was used because the variance in the data was lower than the mean, meaning that the data are under-dispersed for a standard Poisson distribution. The generalised-Poisson distribution was parameterised by two values: one defining the mean of the distribution and the other defining the over- or under-dispersion with a standard Poisson distribution described by a value of 0; however, as the distribution was zero-truncated the mean parameter was no longer the true mean and was likely to be slightly overestimated within the model. The Bernoulli and TGP models were linked by three regression coefficients, one for each phenological fitness parameter. These coefficients used the Bernoulli random effects for the site, year and site by year terms to predict the equivalent generalised-Poisson effects, with the covariance matrix among phenological parameters for the TGP model estimating the residual deviations from the regression. The same regression coefficient was used for site, year and site by year terms for each parameter.

The full mismatch model: The model was coded in RStan (Stan Development Team, 2022) within one framework, estimating the caterpillar phenological distribution parameters from the raw abundance data with the estimates for each site in each year feeding into the Bernoulli and TGP of the blue tit phenological fitness function. This allowed any uncertainty in the caterpillar peak estimates to be incorporated into the model, reducing the bias in our estimates.

Undetectable optimum timing: Sampling under the model framework described above with our data showed poor mixing and failed convergence among different MCMC (Markov chain Monte Carlo) chains. Whilst theory (Lande, 1976; Price, Kirkpatrick and Arnold, 1988) and some previous studies of blue tits (García-Navas and Sanz, 2011; de Villemereuil *et al.*, 2020) suggest the phenological fitness function incorporates an optimum, making the Gaussian function an appropriate composition, our data does not appear to fit this expectation which has also been observed in other populations (Porlier *et al.*, 2012; Biquet *et al.*, 2022). I confirmed the lack of an optimum by applying two models to the bird fledging data alone. First, I used the Gaussian function model composition described above but removed the caterpillar predictors and, similarly to the model including the caterpillar predictors, this did not mix well or converge in a single area of parameter space. Second, retaining the equivalent hurdle model composition with Bernoulli and TGP components for modelling fledging success, I used a linear model alternative parameterisation which included hatch date and a quadratic hatch date term. A quadratic hatch date parameter equal to zero would indicate a straight-line trend and a negative parameter would fit a negative parabola, similar to the Gaussian function. The quadratic linear model estimated a quadratic parameter of 0.09 (95% credible intervals [CIs]: -0.08 - 0.37) for the Bernoulli model and -0.0004 (CIs: -0.0011 0.0003) for the TGP model, both of which are consistent with a straight-line trend. Within site by year combinations, 67 of 325 and 271 of 316 (some site by year combinations had no successful nests) had a negative quadratic parameter point estimates for the Bernoulli and TGP models respectively but no site by year had an upper CI removed from zero. Lastly, I fitted a linear model that allowed for a slope of change in fledging success with hatch date which was a better fit to our data than models trying to estimate an optimum and predicted a decrease in breeding success with increasing hatch date.

One possibility for not detecting an optimum is that our blue tit data only spans the descending trend of the Gaussian function (Fig. 4.3a), failing to capture the optimum among these populations. There are two main reasons why the optimum would not fall within our data: first, the relatively small sample size from each population in each year may not include enough examples of early breeders meaning I lack the statistical power to detect the optimum and second, the blue tit populations sampled from may not breed early enough to permit sampling of dates prior to the optimum, suggesting almost all individuals show some lag. Without a distinguishable turning point in the Gaussian function within the data, it is not possible for the model sampling to converge on a clear range of values among the parameters as a vast range of coefficients could predict various compositions of lines through the data.

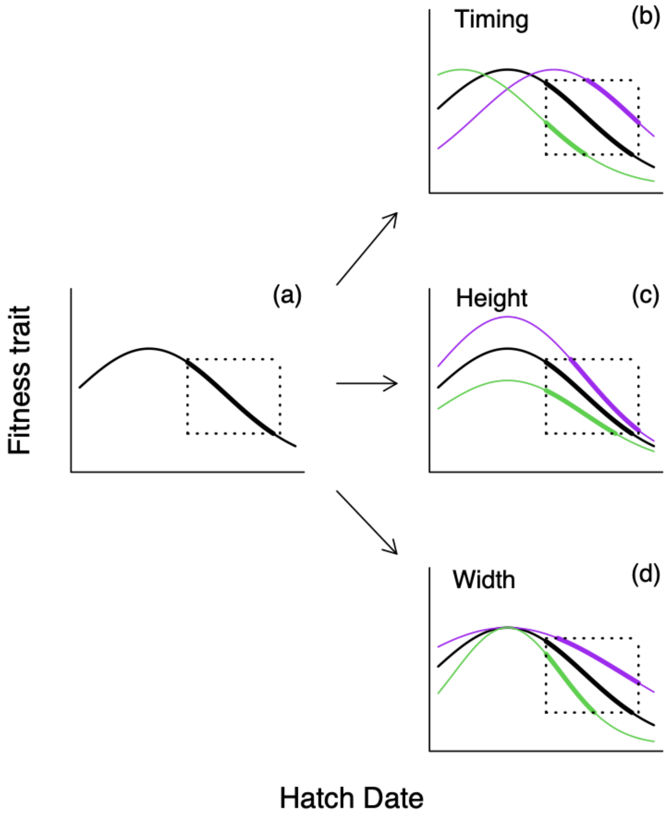

Figure 4.3: Schematic illustrating why our data may not find an optimum hatch date using the Gaussian function to model change in fledging success by hatch date, but instead fits a negative slope. The box in a) shows a range of dates that could be sampled without encountering the optimum, resulting in a decreasing trend rather than peaked. Under the proposed hypothesis in which the resource phenological distribution influences the consumer phenological fitness function alterations (purple line shows an increase, green line shows a decrease) to the b) timing, c) height and d) width of the fitness function could still be detected in the straight line through adjustments to the intercept and slope.

Alternative test of the phenological distribution extension of the MMH

Despite the lack of a detectable phenological optimum for blue tits, it is still possible to test the hypothesis that a resource phenological distribution influences the consumer phenological fitness function. If the decreasing trend in fledging success by hatch date depicts the descending slope of the Gaussian function (Fig. 4.3a) and the caterpillar peak timing, height and width influence the equivalent components of the Gaussian bird fitness function, then changes in the caterpillar phenological distribution would alter the intercept and slope of the descending line of the bird phenological fitness function (Fig. 4.3b-d). As illustrated in Fig. 4.3b-d, I predict the timing of the caterpillar peak will alter the intercept of the blue tit phenological fitness function, and the slope depending on the extent of the shift, and the height and width of the caterpillar peak to alter the intercept and slope of the blue tit phenological fitness function.

Alternative linear model composition: To test the effect of the caterpillar phenological distribution on the linear blue tit phenological fitness function the model followed a similar composition to the initial Gaussian function model. The caterpillar peak mean timing, height and width were estimated within the same framework as the previous model, feeding in as predictors of both the Bernoulli and TGP components for blue tits. Both blue tit models included an intercept, date (date = absolute ordinal day of year) slope, slopes for the effect of the caterpillar mean timing, height and width, and mean timing*date, height*date and width*date interactions. Site, year and sites by years were included as random intercepts and random regressions on the date slope, with covariance estimated from a single correlation matrix among random terms but different variances. The female at each nest was included as a random intercept. The two bird models remained linked via a regression of the random effects with a slope for the intercept terms and second for the random regressions. As the intercept and date slope were estimated at a caterpillar timing, height and width of zero, the coefficient estimates were centred on the mean of each caterpillar parameter post-hoc for interpretation within our range of data. All results shown are from this model and are presented as the posterior medians and 95% credible intervals.

Expectations on the arithmetic scale: Calculating expectations on the arithmetic scale from models using the logit or log link function requires incorporation of some variance from the terms being marginalised across to attain the true mean.

Eq. 4.4: $$\sigma^2 = \sigma_i^2 + \sigma_s^2 d^2 + \sigma_{i,s} 2d$$

To marginalise across all random terms within each bird model respectively, I summed the variance attributed to each random term, using Eq. 4.4 to calculate the variance (σ^2) attributed to any terms with both random intercepts (i) and slopes (s) across date (d). As the Bernoulli random effects (b) for sites, years and sites by years were used as predictors of the TGP equivalent effects (p), the variances and covariances needed for Eq. 4.4 for TGP terms were calculated from the regression coefficients (β_i and β_s) and variance-covariance matrices for each random term in both models:

Eq. 4.5:

$$\sigma_i^2 = \sigma_{i_p}^2 + \beta_i \sigma_{i_b}^2$$

$$\sigma_s^2 = \sigma_{s\_p}^2 + \beta_s \sigma_{s\_b}^2$$

$$\sigma_{is} = \sigma_{i\_p,s\_p} + \beta_i \beta_s \sigma_{i\_b,s\_b}$$

The variance is then combined with the link scale mean ($X\beta$) before transforming the estimate back to the arithmetic scale, this uses Eq. 4.6 for the logit link function (Bernoulli model) and Eq. 4.7 for the log link function (TGP model) (Diggle *et al.*, 2004; Hadfield, 2010).

Eq. 4.6:

$$E[y] = logit^{-1}\left(\frac{X\beta}{\sqrt{1 + \left(16\sqrt{3}/15\pi\right)^2 \sigma^2}}\right)$$

Eq. 4.7:

$$E[y] = \exp\left(X\beta + 0.5\sigma^2\right)$$

The posterior of the expectation for the probability of success and the number fledged was calculated across the range of hatch dates in our data and at a few combinations of caterpillar peak parameters. Firstly, the expectations across hatch date were calculated at the mean point estimates of caterpillar peak timing, height and width. Secondly the expectations were calculated at the upper and lower mean point estimates among site by year combinations for each peak parameter, whilst the other two were at their mean, to allow the effect of each peak parameter to be visualised. As the height and width parameters covary among site by year combinations, the upper-and lower-point estimates for height and width were from the range of site by year point estimates that fell close to zero for width and height, respectively.

Results

Of the 1138 breeding attempts included in the analysis 150 failed to fledge any young. The 988 successful nests fledged an average of 6.4 offspring (standard deviation = 2.5), with 285 nests having fledged 6-7 young. A maximum of 14 having fledged was observed once and 3 nests fledged 13. There were 20 nests that fledged just one offspring. The earliest hatch date recorded was ordinal date 123 (2nd or 3rd May) and the latest was 175 (23rd or 24th June).

There were significant negative slopes for the effect of hatch date on the probability of success and number of offspring fledged (Table 4.1, Fig. 4.4a-b). The probability of a successful nesting attempt at the start of the season (day 123) was 0.89 (CIs: 0.77 - 0.96) decreasing to 0.46 (CIs: 0.29 - 0.63) at the end of the season (day 175) (Fig. 4.4a). The number of offspring fledged is multiplied by 0.985 (CIs: 0.977 – 0.994) per day with a marginal expectation of 6.02 offspring fledged (CIs: 5.33 - 6.78) at mid-season (Fig. 4.4b); the expected number to fledged at the start of the season is 8.69 (CIs: 7.22 - 10.70) decreasing to 4.47 (CIs: 3.43 - 6.30) at the end.

I found no significant effect of any caterpillar peak parameter on the intercept or date slope for the probability of success or the number of offspring fledged (Table 4.1). The credible intervals around the expectations of the probability of success by hatch date show large uncertainty (Fig. 4.4c,e,g), particularly at later dates. In comparison, for the number fledged by hatch date the credible intervals are relatively narrow (Fig. 4.4d,f,h) reflecting higher certainty in the estimates.

Table 4.1: Model output (posterior median for fixed effects and posterior mode for variances/covariances, with 95% credible intervals) for a zero-inflated hurdle linear mixed model analysing the effect of individual-level blue tit hatch date (centred on ordinal date 146) and the site-level phenological distribution of caterpillars (timing, height and width) on the probability of successfully fledging offspring and the number of offspring fledged (conditional on it being a successful breeding attempt). The intercept and hatch date parameters are the estimates at the average timing, height and width of the caterpillar peak among site by year combinations. All values are presented on the link scale: logit for the probability of success and log for the number fledged.

Parameter	Median	2.5% CI	97.5% CI
a) Probability of Success: Fixed Effects			
Intercept	105.046	37.447	201.694
Blue Tit Hatch Date	-4.112	-9.622	-1.233
Caterpillar Timing	-0.406	-2.913	1.612
Caterpillar Width	23.996	-8.946	59.334
Caterpillar Height	-7.939	-29.297	3.174
Caterpillar Timing : Blue Tit Hatch Date	0.086	-0.194	0.481
Caterpillar Width : Blue Tit Hatch Date	-0.413	-11.392	9.209
Caterpillar Height : Blue Tit Hatch Date	-0.559	-3.217	1.425
b) No. fledged (cond. on success): Fixed Effects			
Intercept	1.759	1.622	1.869
Blue Tit Hatch Date	-0.015	-0.023	-0.006
Caterpillar Timing	0.001	-0.005	0.006
Caterpillar Width	-0.141	-0.411	0.087
Caterpillar Height	-0.011	-0.061	0.033
Caterpillar Timing : Blue Tit Hatch Date	0.000	-0.001	0.001
Caterpillar Width : Blue Tit Hatch Date	-0.002	-0.027	0.023
Caterpillar Height : Blue Tit Hatch Date	0.001	-0.004	0.006

Table 4.1 continued

Parameter	Mode	2.5% CI	97.5% CI
c) Probability of Success: Random Term Variances			
Site Intercept Var	13.200	1.615	2519.599
Site Slope Var	0.128	0.003	35.102
Site Intercept:Slope Cov	0.4047	-65.629	27.128
Year Intercept Var	199.542	28.339	8482.585
Year Slope Var	0.127	0.002	25.111
Year Intercept:Slope Cov	0.797	-74.934	47.863
SiteYear Intercept Var	41.197	2.268	7746.106
SiteYear Slope Var	0.868	0.017	157.063
SiteYear Intercept:Slope Cov	0.186	-121.912	136.326
Female ID	5897.716	1310.550	45091.04
d) No. fledged (cond. on success): Random Term Variances			
Site Intercept Var	0.023	0.015	0.050
Site Slope Var	0.000	0.000	0.000
Site Intercept:Slope Cov	0.000	-0.000	0.001
Year Intercept Var	0.009	0.005	0.061
Year Slope Var	0.000	0.000	0.001
Year Intercept:Slope Cov	0.000	-0.000	0.002
SiteYear Intercept Var	0.010	0.001	0.020
SiteYear Slope Var	0.000	0.000	0.000
SiteYear Intercept:Slope Cov	0.000	-0.000	0.001
Female ID	0.017	0.005	0.034

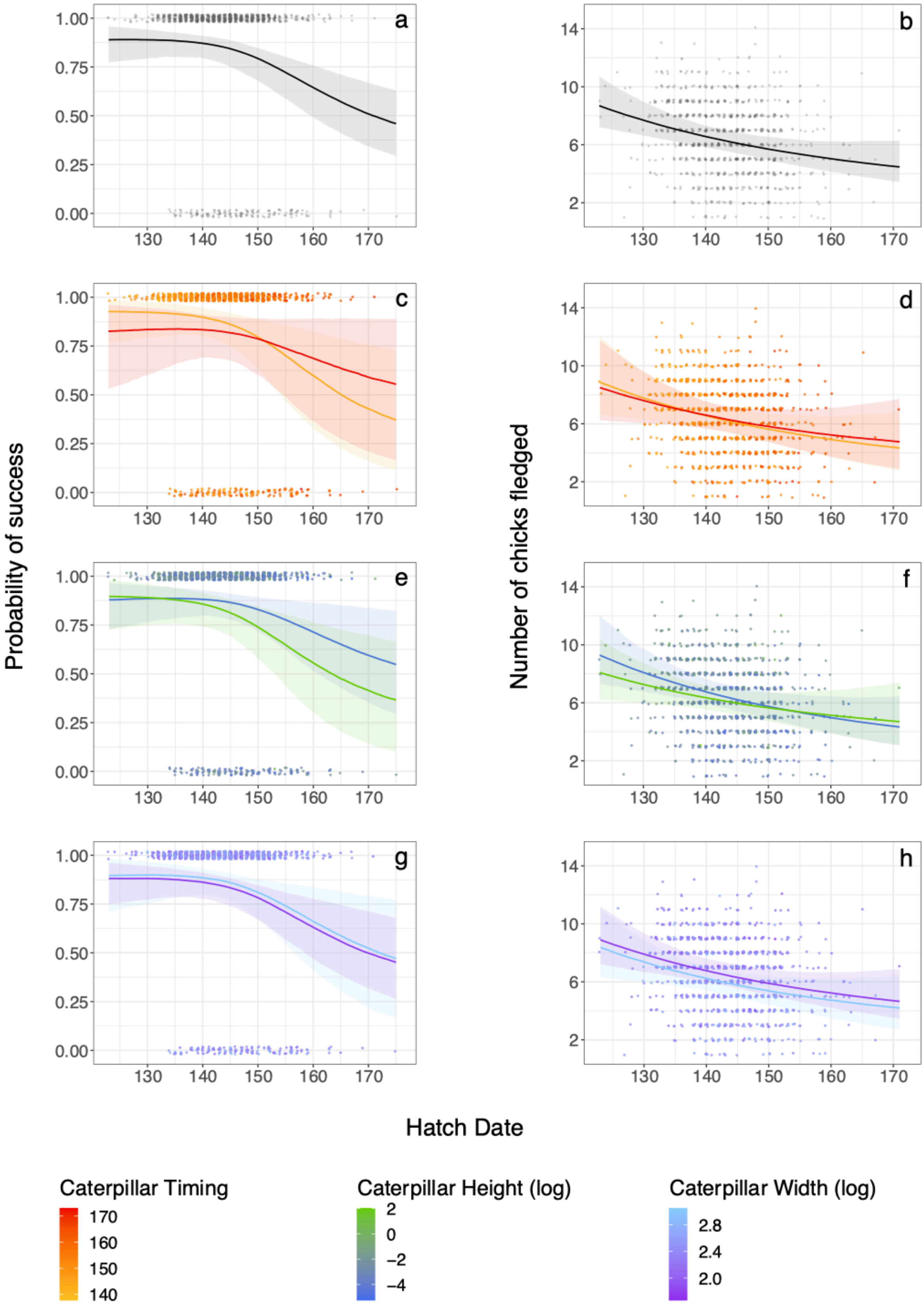
a
b
c
d
e
f
g
h
Probability of success
1.00
0.75
0.50
0.25
0.00
Number of chicks fledged
14
10
6
2
130
140
150
160
170
Hatch Date
Caterpillar Timing
170
160
150
140
Caterpillar Height (log)
2
0
−2
−4
Caterpillar Width (log)
2.8
2.4
2.0

Figure 4.4: Model expectations (posterior median and 95% credible intervals) for the effect of hatch date and the caterpillar phenological distribution on the probability of breeding success and number of offspring fledged in blue tits. Each plot shows the data plotted as points, in a-b) the darkness represents the frequency of the point, in the remaining plots the colour represents the timing (c-d), height (e-f) or width of the caterpillar peak (g-h) associated with each data point and line. Plots a-b show the predicted trend at the average value of each caterpillar parameter among site by year combinations. Plots c-h show the predicted trends by hatch date at the upper and lower caterpillar parameter whilst the others are held at their mean. The values were taken from the mean predictions for each parameter among site by year combinations. As the height and width parameters covary the upper and lower height and width values were taken from the site by year combinations in which the width or height estimates, respectively, fall close to zero to avoid extrapolation.

Discussion

In this chapter, I present an extension to the conceptual framework of the match/mismatch hypothesis in which the timing, height and width of the phenological distribution of a resource affect the optimum timing, maximum fitness and width of the consumer phenological fitness function (Fig. 4.1). Whilst research to date has mostly focused on the effects of relative timing within trophic interactions on consumer fitness (e.g. Charmantier *et al.*, 2008; Reed *et al.*, 2013), the full phenological distribution of a resource determines the volume of food available at any point in time, which will, in turn, covary with habitat composition and temperature (Chapters 2 and 3). Conceptualising the MMH as a complete test of how the phenology of resource availability affects consumer fitness as a function of timing allows more accurate estimation of the effects of trophic asynchrony on consumer fitness and the strength of both directional and stabilising selection; factors of great importance to species persistence under climate warming (Chevin, Lande and Mace, 2010). Within the blue tit populations studied I did not find evidence of an optimum hatch date or detect any impact of the caterpillar phenological distribution on the blue tit phenological fitness function. Instead, I found fledging success to be consistently higher with earlier hatch dates and both the probability of success and the number of offspring fledged (conditional on success) decrease linearly throughout the breeding season.

Non-detection of an optimum within the data is contrary to a general expectation based on theory (Lande, 1976; Price, Kirkpatrick and Arnold, 1988), evidence in support of an optimum across a range of species and traits (de Villemereuil *et al.*, 2020) and studies of blue tit fledging success and mass (García-Navas and Sanz, 2011; Vatka, Rytkönen and Orell, 2014; de Villemereuil *et al.*, 2020). However, the seasonal decrease in fitness trend is similar to the trend seen in a Mediterranean population (Porlier *et al.*, 2012; Biquet *et al.*, 2022) and evidence of directional but not stabilising selection found across a range of traits in great tits (Reed, Jenouvrier and Visser, 2013), yet other work has shown evidence of stabilising selection (Simmonds *et al.*, 2017; Ramakers, Gienapp and Visser, 2019). The relative importance of parental quality versus timing (and the MMH) as an explanation for directional, but not stabilising, selection for earlier breeding timing remains unclear (Verhulst and Nilsson, 2008) as higher quality parents often breed earlier (Verhulst, Van Balen and Tinbergen, 1995). Without exploring the relative contributions of quality and environment within these populations, for example, through the experimental manipulation of timing, I cannot conclude which mechanism dominates the observed trend. An alternative explanation for the non-detection of an optimum is that the populations are already lagging behind (Burger and Lynch, 1995; Radchuk *et al.*, 2019). However, the blue tit populations in this study do not appear to lag behind the caterpillars on average, as they have an average hatch date ten days earlier than the average caterpillar peak mean timing (hatch date=145, caterpillar peak=155), which suggests that if an optimum timing were to exist then the caterpillar peak may not be the sole determinant of it.

The absence of evidence for an effect of the phenological distribution of caterpillars on the blue tit phenological fitness function shows no evidence of trophic asynchrony impacting fledging success in these populations. Among blue tit populations, one previous study of breeding success over 13 years found a negative quadratic effect of asynchrony with the caterpillar resource peak on the number of offspring fledged, and a positive effect of the caterpillar peak height (Vatka, Rytkönen and Orell, 2014). Whereas another three year study found no effect of asynchrony on the number fledged, though there was an effect on both the proportion of the clutch size and number to hatch that fledged (Dias and Blondel, 1996). It is possible that the effects on fledging success are more pronounced in relation to the number of offspring that could have been fledged as a proportion of the clutch size, with the effects on the absolute number fledged more detectable with greater statistical power from long-term data. Whilst the effect on fledging success may be more detectable as a proportion of the clutch size, the absolute number fledged may be more relevant as a measure of fitness. If we consider other insectivore bird species, no effect of asynchrony was found on fledging success in pied flycatchers (Visser *et al.*, 2015), but studies in Hoge Veluwe (Netherlands) and Wytham Woods (UK) find an effect in great tits, though whether an optimum was detected or not differed among studies (Visser, Holleman and Gienapp, 2006; Reed, Jenouvrier and Visser, 2013; Simmonds *et al.*, 2017). These studies of fitness in relation to the MMH all consider asynchrony directly as the predictor variable, rather than using the caterpillar peak timing and bird phenology as ordinal dates as in this study.

It is possible that the MMH does not apply to the blue tit and caterpillar trophic interaction and resource availability does not affect fitness, though there are also a few alternative explanations for the observed results. First, as suggested in relation to the absence of an optimum, the lack of evidence of the MMH within these populations could arise if the importance of parental quality is driving the decreasing trend over time (Verhulst, Van Balen and Tinbergen, 1995; Verhulst and Nilsson, 2008), which may mask the MMH timing effect in an analysis of absolute rather than relative (ie. asynchrony) timing. Second, it is also possible that the effects of caterpillar peak on the blue tit fitness function are relatively trait specific. For example, whilst I found no effect on fledging success, the offspring that fledge may differ in condition as previously recorded in blue tits (García-Navas and Sanz, 2011; Vatka, Rytkönen and Orell, 2014), and this may influence recruitment to the population (Monrós *et al.*, 2002). The effects of asynchrony on various fitness traits have differed between studies and populations (Dias and Blondel, 1996; Visser, Holleman and Gienapp, 2006; García-Navas and

Sanz, 2011; Reed *et al.*, 2013; Reed, Jenouvrier and Visser, 2013; Vatka, Rytkönen and Orell, 2014; Visser *et al.*, 2015; Pakanen *et al.*, 2016; Samplonius *et al.*, 2016; Simmonds *et al.*, 2017), therefore the analysis of additional traits that are also susceptible to the impacts of resource limitation may be required to fully interpret the effects of the MMH in the populations studied here. A third explanation is largely statistical in that the spatiotemporal structure within the data may also have influenced the results found. In the original model composition that employed two Gaussian functions, the timing of the caterpillar peak was allowed to predict the timing of the blue tit optimum, and if this effect existed then deviations from the predicted timing would be in units interpretable as asynchrony. Whereas in the final model used, in which the Gaussian function parameters for the caterpillar peak are predictors for a linear model of blue tit fitness, there is no blue tit timing parameter to couple with the caterpillar timing, and all timings are on an absolute temporal scale, meaning there is no measure of asynchrony. This means that two birds may have the same absolute phenology, but one be an early bird at a late site and another be a late bird at an early site and the model would not distinguish these two different temporal contexts, except through the random terms. Therefore this conflating of spatial and temporal (including year to year) variation in timing may add noise to (and mask) the effects of asynchrony with the resource on the fitness intercept. Adjustments to the model, either through some form of mean centring within sites or changing the hatch date variable to estimated asynchrony with the caterpillar peak, may improve the model's ability to estimate the effects of interest within these interactions by refocusing the phenological variable to a relative scale among sites.

A further possibility that may obscure evidence for the MMH is the level of uncertainty in a few components of my analysis, which may limit the power to detect the effects. The credible intervals around the estimates of the number of offspring fledged by hatch date at high and low values of each caterpillar peak parameter are relatively narrow (Fig 4.4), which suggests the effects are being estimated well and I do not find any effect on this metric within the focal populations. However, the credible intervals around the trends estimated for the probability of success are much broader, particularly at later dates. This large uncertainty in the phenological fitness function at different levels of each caterpillar parameter indicates that I may not have the required power to be sure of an effect on this fitness metric. Just 13% of nests to hatch- within the data used- failed to fledge any offspring, with 62% of site by year combinations only containing successful nests; it is possible I would obtain more accurate and precise estimates of these effects with either an increase in the number of years monitored or data on more nests within each site in each year. Whilst my estimates of the average caterpillar phenological distribution and more general trends within it are reasonably precise, there is higher uncertainty in the estimates of the mean timing, height and width of the caterpillar peak at the site by year level. Though it is important to address the uncertainty in these estimates when using them as predictors of bird fitness within the model, this will also increase the uncertainty in the estimated effect sizes.

The extended conceptual framework for the MMH presented here provides a platform for future work in this field. By allowing flexibility in the full phenological distribution of each player within an ephemeral trophic interaction, it becomes possible to determine the importance of synchronous timing, implications for population fitness relative to timing and shifts in the strength of directional and stabilising selection with greatly increased accuracy, and all within one framework. The approach I present here has broad applicability across the wide range of systems predicted to be susceptible to the negative consequences of trophic asynchrony under the MMH; for example fish relying on plankton blooms (e.g. Jolley *et al.*, 2010), sea birds relying on ephemeral fish (e.g. Watanuki *et al*., 2009) and parasitoids requiring hosts (e.g. Senior *et al.*, 2020). The framework is best suited to consumer populations for which there is phenology and fitness data that at least in some years encompasses an optimum, allowing estimation of the effects between equivalent attributes of the distributions. Long-term studies may be the most suitable given the potential for consumer populations to be lagging behind the optimum in more recent years. This framework also requires good quality data on the change in resource over time, which may be the main restraint on the progression of this approach, as the resource is often recorded at a lower resolution than its consumer counterpart.

The phenological distribution extension of the MMH provides a route towards a better understanding of how and why the strength of selection may change in the future. Under the standard framework that focuses on mean timing, the increased mistiming under climate warming is expected to decrease population fitness and increase the strength of directional selection on phenology, with effect sizes estimated from the increase in lag (Fig. 4.2). However, if the height and width of the resource phenological distribution are affected by climate warming (Chapter 3) and the full phenological distribution of the resource influences the consumer phenological fitness function, though no evidence was found in this work, then these assumptions may wrongly estimate or interpret the effects on population fitness and the strength of selection (Fig. 4.2). As the strength of selection affects a populations resilience to environmental change (Chevin, Lande and Mace, 2010) it may be important to incorporate these additional drivers of change to ensure accurate predictions of a species response and persistence though climate warming.

Further extensions to the framework presented provide the opportunity to directly test the effects of environmental conditions on the MMH. For example, by including slopes to test the effects of temperature on the resource and/or consumer distributions it would be possible to estimate the thermal sensitivity of the optimum (B) as in Chevin *et al*. (2010), as well as effects of spring temperatures on directional and stabilising selection and absolute fitness, none of which has been estimated before as far as I am aware. These parameters have implications for populations' ability to persist in a changing environment (Chevin, Lande and Mace, 2010). The equations presented by Chevin *et al*. (2010) do not consider that stabilising selection may vary with climate and it is a topic that has received relatively little attention (but see Visser *et al.*, 2015; Ramakers, Gienapp and Visser, 2019; de Villemereuil *et al.*, 2020). Temperature could affect the consumer fitness function width either directly or indirectly through the caterpillars. If the width is affected by temperature, the phenological distribution extension of the MMH including temperature would be able to detect thermal sensitivity in the strength of stabilising selection associated with the fitness function (a change in the phenological trait distribution width would also have an effect).

I have presented an extension to the conceptual framework of the MMH in which the phenological distribution of the resource is predicted to affect the phenological fitness function of a consumer. The hypothesis was tested in the deciduous woodland food chain between blue tit fledging success and the arboreal caterpillar peak, however, no effect of the resource was found and there was no optimum timing within the blue tit population. Fledging success was chiefly affected by a negative trend with hatch date. Therefore, I found no evidence that asynchrony with the phenological distribution of caterpillars negatively affects fledging success in line with the MMH in these blue tit populations, though there is a range of alternative explanations for the lack of evidence that need to be followed up. The framework proposed provides the opportunity for a more comprehensive test of the MMH, including tests of the importance of timing, determinants of population fitness and estimation of the strength of directional and stabilising selection on timing.

Chapter 5 - General Discussion

Summary and synthesis of key results

Summary of main results

The majority of work on the match/mismatch hypothesis (MMH) to date has focused on how the timing of a consumer relative to the mean of a resource population or guild affects consumer fitness, overlooking that fitness may also be affected by the height and width of the resource phenological distribution. The full phenological distribution of a resource may vary in space and time, which could have important implications for understanding the fitness consequences of the MMH if the height and width of the resource distribution affect consumer fitness. Differences in the full phenological distribution of a resource will affect the absolute and relative availability of food over time, which I hypothesise will affect the full phenological fitness function of the consumer. In this thesis, using data collected across 44 sites over 9 years in the well-established deciduous woodland tri-trophic study system of deciduous tree – caterpillars – insectivorous passerine, I start by exploring the potential sources of spatial and temporal differences in the full phenological distribution of caterpillars. First by examining differences in the caterpillar phenological distribution among deciduous tree taxa and woodland tree compositions (Chapter 2) and then by estimating the thermal sensitivity of the mean timing, height and width (Chapter 3). In Chapter 2, I found substantial variation in the maximum caterpillar abundance and biomass (height) reached among host tree taxa, with an additional positive effect of the prevalence of oak trees in the surrounding woodland on caterpillar abundance. In Chapter 3, I also found substantial effects of temperature on the caterpillar phenological distribution, which not only drives an advance in the mean timing of caterpillars but also increases the maximum height reached and reduces the variance of the distribution (width), with the duration over which it lasts remaining relatively consistent. These effects of woodland tree composition and temperature on the caterpillar phenological distribution show some evidence of spatiotemporal differences in the ephemeral resource, with the potential to affect trophic interactions in space and time.

Having established variation in the caterpillar phenological distribution, in Chapter 4 I proposed an extension to the classic – mean timing focused – conceptual framework of the MMH to test the prediction that the full phenological distribution of a resource affects the full phenological fitness function of a consumer. I applied this framework to the relationship between blue tit breeding phenology and fledging success in relation to the phenological distribution of caterpillars. However, contrary to my predictions based on the MMH, I found no effect of the caterpillar phenological distribution, including the mean timing, on the fledging success of blue tits and found no evidence for an optimum hatching timing for blue tits within the range of data. I speculate that this may be linked to the effects of parental quality masking the environmental components (Verhulst, Van Balen and Tinbergen, 1995; Verhulst and Nilsson, 2008), the possibility that the populations are consistently lagging behind the optimum (Burger and Lynch, 1995; Radchuk *et al.*, 2019) or the potential for effects of absolute timing estimated over space to obscure effects estimated over time.

Spatiotemporal variation in the phenological distribution of caterpillars

The effects of host tree taxon and woodland tree composition on the phenological distribution of associated caterpillars identified in Chapter 2, are likely to drive substantial spatial heterogeneity in the caterpillar peak among woodlands that vary in their composition. The prevalence of a key primary consumer resource, such as caterpillars, will influence the quality of habitat for secondary consumers, such as insectivorous birds, which suggests that woodland tree composition has the potential to drive variation in habitat quality between distinct fragments of woodland with differing taxonomic tree compositions, as well as areas within a woodland that differ in the tree taxa present. Small-scale spatial differences in woodland tree composition may even contribute to differences in quality between neighbouring breeding territories of birds. Previous work has shown evidence that great tit breeding phenology can be sensitive to fine-scale spatial variation in the phenology of oak tree leafing and the mean timing of caterpillars' (Hinks *et al.*, 2015), indicating that very localised conditions can influence these trophic interactions. The additional effect of oak prevalence on the abundance of caterpillars throughout the local area (Chapter 2) will also drive spatial heterogeneity in caterpillar prevalence, though the scale at which the effect is most pronounced and the mechanism by which it occurs remain to be uncovered which presents an interesting direction for further work. Oak species are known to be a key component of climax deciduous woodland habitats in much of the UK, associated with a vast array of species throughout the entire biotic community (Southwood, Moran and Kennedy, 1982; Mitchell *et al.*, 2019), yet at present, it represents a relatively small proportion of national woodland cover (Stagg and Ward, 2019). Increasing the prevalence of oak trees throughout deciduous woodlands may benefit the conservation of species comprising the caterpillar guild through increasing their abundance; however, analysis of the turnover in caterpillar guild species composition among woodlands with differing taxonomic tree compositions and in association with the local prevalence of oak trees would be required to determine the relative benefits among caterpillar species; a topic I will return to.

The thermal sensitivity of the phenological distribution of caterpillars that I identify in Chapter 3 has implications for spatiotemporal heterogeneity in the caterpillar peak under climate change. Spatial gradients that correlate with temperature, such as elevation and latitude, and more locally specific factors such as aspect and air movement will all contribute to local temperature, affecting the caterpillar phenological distribution in a particular location. Annual fluctuations in temperature, and long-term trends over time, will also affect the phenological distribution of caterpillars at a location in a particular year. The spatiotemporal heterogeneity in the phenological distribution of caterpillars driven by temperature will contribute to spatial differences in herbivory pressure on trees and cause annual fluctuations.

A combination of the woodland tree composition and temperature at a location within each year will impact the phenological distribution of caterpillars (Chapter 2 and 3). There was a limited effect of tree taxon on the mean timing of caterpillars (Chapter 2), contrasting to a substantial effect of temperature (Chapter 3) which suggests spatial variation in caterpillar mean timing will be driven more by thermal responses, which will also drive variation between years. The thermal sensitivity of caterpillar mean timing was similar in space and time (Chapter 3) which is consistent with temperature having a causal effect on timing, as expected from previous experimental work on timing in caterpillars (Buse and Good, 1996; van Asch *et al.*, 2013). The height of the phenological distribution is affected by both woodland tree composition and temperature, meaning both components could contribute to the maximum abundance reached at any site, and this is also likely to vary between years due to annual fluctuations in temperature. There was large uncertainty in the width and duration of the caterpillar peak among tree taxa meaning I am unable to conclude that it differs substantially between taxa, however increasing temperature decreases the width of the peak, which when paired with the increased height resulted in the duration remaining relatively similar. Therefore, based on the factors considered here (woodland tree composition and temperature), the duration of the caterpillar peak is likely to be relatively similar across locations and years.

Potential spatiotemporal and interspecific variation in the MMH

Having established that the phenological distribution of caterpillars is liable to vary in space and time gives reason to predict that the consequences of the MMH may vary in both space, due to woodland tree composition and temperature, and time, due to temperature. The MMH was proposed on the basis that the availability of an ephemeral resource varies over time and that the timing of consumer demand relative to resource availability should affect the fitness of the consumer (Cushing, 1990). Given that the full phenological distribution affects resource availability over time, I predict that the full phenological distribution of the resource will impact consumer fitness, and therefore variation in the resource in space and time will contribute to spatiotemporal variation in consumer fitness. Whilst I have not found evidence in support of the full phenological distribution extension of the MMH in the analysis of fledging success (Chapter 4), this does not necessarily represent an absence of effects consistent with the extended MMH. The impacts of asynchrony on consumer fitness have differed depending on the trait considered, and for fledging success, there has been no consistent result across blue tit populations (Dias and Blondel, 1996; Vatka, Rytkönen and Orell, 2014). These findings, combined with my own, raise the prospect that this trait may not be the most sensitive to the MMH.

Viewed more broadly, the phenological distribution extension to the MMH represents an advance in how we examine the dynamics of these trophic interactions, allowing a more complete assessment of the implications of population- or guild-level timing on the consumer fitness function. If evidence in support of the hypothesis is found, it will demonstrate the importance of timing relative to a resource for consumer populations and has the potential to provide valuable additional insights into spatiotemporal heterogeneity in population fitness, the consequences of asynchrony and the strength of directional and stabilising selection on timing. Given the effect of woodland tree composition and temperature on the caterpillar phenological distribution (Chapter 2 and 3), both of which vary in space, it is likely to be important to study the MMH across a representative range of habitats and temperatures of a consumer species distribution range to accurately predict the consequences of climate warming at the meta-population level (Culina *et al.*, 2021; Bailey *et al.*, 2022).

Whilst I did not find effects consistent with the MMH, there is some value in examining how such a framework could be applied to examine the temperature sensitivity of consumer fitness in other systems. If I had found evidence in support of the phenological distribution extension of the MMH, then the thermal sensitivity in the caterpillar phenological distribution (Chapter 3) would predict long-term shifts in fitness and selection driven by climate warming. The combined effects of temperature and woodland tree composition would generate spatial heterogeneity in the caterpillar phenological distribution (Chapters 2 and 3), which would lead to variation in fitness among consumer populations within each year and give rise to variation in the strength of selection on timing among populations. In time, an increase in caterpillar maximum height with increasing temperatures (Chapter 3) would be predicted to increase fitness for populations or individuals that are relatively synchronous with the caterpillar mean timing. The decrease in width with increasing temperature (Chapter 3) would increase the strength of selection on timing; with increasing directional selection if the mean timing of the phenological distribution of bird breeding phenology lagged behind (preceded) the fitness function optimum and increasing stabilising selection if the phenological distribution of bird breeding phenology overlapped the fitness function optimum, the two are not mutually exclusive (de Villemereuil *et al.*, 2020). Whilst the increased strength of selection on timing could lead to rapid evolution of timing for populations or species with sufficient additive genetic variation, it may reduce the fitness of populations or species that lack the ability to track the required adaptive change.

Among species that rely on caterpillars to fledge offspring, as temperature increases, species with later breeding phenology may be at more of a competitive disadvantage compared to those that are more synchronous. The decrease in width of the caterpillar phenological distribution with increasing height means the increase in caterpillar availability is more pronounced close to the mean timing (Chapter 3). This change in the shape of the resource phenological distribution changes the relative availability of caterpillars with increasing asynchrony, increasing the difference in resource levels available among species relying on it at different times. For example, pied flycatchers advance their breeding phenology less than great tits (Samplonius *et al.*, 2018) which may increase the relative difference in caterpillar resource available to each species as temperature increases, possibly giving great tits more of a competitive advantage.

Limitations

Design trade-offs

Designing a study across many sites and years inevitably involves accepting trade-offs. In the case of this study in Scotland, the major compromise is the sample size recorded at each site. This is particularly true for the number of nest boxes, as with just 8 boxes and ~60% occupancy among sites this results in an average of 4-5 breeding attempts being recorded at each site in each year. The increased branch beating effort since 2017 has vastly improved the precision of estimates of the caterpillar phenological distribution. The large number of sites and repetition each year allows the inclusion of varied woodland tree compositions, an increased range of temperatures within each year and provides good statistical power when looking at general trends marginalising over site by year combinations. However, the compromise on sample size per site results in substantial uncertainty within each site by year combination for phenological distribution parameters of both the blue tits and the caterpillars. This is particularly disadvantageous for the phenological distribution extension of the MMH analysis (Chapter 4) as the uncertainty in the parameters governing the site by year estimates of the caterpillar phenological distribution is being incorporated into the predictors of the blue tit phenological fitness function.

Caterpillar abundance, mass and biomass

The branch beating method used to sample caterpillars is extremely useful for recording a relatively large number of samples in the time available during fieldwork, though there are several drawbacks to the data this yields. As this approach relies on the caterpillars that are present being dislodged from the branches when beaten, it is likely to under-sample groups such as leaf rollers and leaf miners (Shutt, Burgess and Phillimore, 2019). Though if these taxa are more difficult to dislodge then it is possible they are less conspicuous and less likely to form a substantial part of the consumer diet, which is our primary focus in this study. A strength of the branch-beating method is that it can capture both the abundance and biomass of the caterpillar guild. However, with an average of 90% of samples recording zero caterpillars, it currently provides a more precise estimate of seasonal variation in abundance than biomass. This is unfortunate given that biomass is likely to be more relevant as a measure of resource availability to breeding birds. The biomass of each sample has been recorded since 2017, however, due to the limitations of weighing small samples in the field we have higher uncertainty in the biomass of any samples recorded as ≤0.02g which then requires interval censoring in analyses. Of the 3923 samples (2017-2022) for which we have a measure of biomass, 45% are treated as interval-censored. As the biomass data set increases each year this will become less of a constraint, however, at the present time the abundance data provides higher resolution information on the arboreal caterpillar peak and therefore has been the main caterpillar variable included in this thesis.

Caterpillar sampling biases

When relying on beating branches of trees close to the ground as a means of sampling caterpillar availability, I have assumed that the caterpillar guild present will be relatively homogeneous throughout the tree. The severity of the bias that is introduced by sampling only part of a tree will depend on how the abundance of caterpillars varies with tree height and how the effects of tree height vary among tree species and individuals. The branch beating method the field team employs records the density per branch rather than absolute abundance or biomass throughout the whole tree, which is a drawback with regards to estimating the absolute caterpillar prevalence as a resource to breeding birds at the tree or site level, rather than relative differences in density. Collecting the required data to identify the implications of these components of the branch beating method would be labour intensive and time consuming and therefore was not feasible within the time frame of my PhD, though it would be a valuable addition to future work when possible.

Spatial versus temporal effects of temperature and habitat

As there are spatial trends in the woodland tree composition (Shutt *et al.*, 2018) and temperature (Shutt *et al.*, 2019) among the sites used, some of the effects of woodland tree composition estimated in Chapter 2 may arise due to effects of temperature on tree composition that play out over much longer timescales, and some of the spatial effects of temperature estimated in Chapter 3 may reflect the effects of tree composition. This means that the temperature slopes estimated not only encompass spatial and temporal variation in temperature but may also capture some indirect effects of temperature over a longer period of time via temperature-driven spatial trends in woodland tree composition. To determine the direct effect of temporal temperature on the phenological distribution with more certainty, and independently of any effects of habitat, would require an increase in the variation of temperatures sampled through temporal fluctuations, thus requiring data collected over many more years. However, the approach taken was ecologically relevant to the analysis of the thermal sensitivity of the caterpillar peak across the spatial scale included.

Future directions and opportunities

The three data chapters presented in this thesis contribute a range of new insights into phenology and the MMH both within the deciduous food chain study system and from a broader conceptual perspective. The results discussed prompt various follow-up research questions, providing ample directions and opportunities for future work within the deciduous woodland study system and more broadly.

Further examination of the phenological distribution of caterpillars in space and time

More detailed knowledge of what drives the differences in the phenological distribution of caterpillars among tree taxa (Chapter 2) and whether any additional components of woodland tree composition affect the broader woodland-scale distribution of caterpillars would be of value for accurately estimating the relative contribution of woodland tree composition to spatial heterogeneity in caterpillar availability. For example, the diversity and density of species supported can vary with woodland age (Fuentes-Montemayor *et al.*, 2022), thus including woodland or tree age within the tree taxa comparison would provide further insight into how older established woodlands, modified established woodlands and newly generated woodlands would differ in their expected contributions to the local phenological distribution of arboreal caterpillars. Understanding sources of spatial heterogeneity in the phenological distribution of caterpillars is important for the conservation of species comprising the caterpillar guild, predicting herbivory levels within forestry areas and food availability for insectivorous birds relying on caterpillars to feed nestlings. It is likely to also be of value to these sectors mentioned to determine the mechanisms by which the prevalence of oak within a woodland affects the abundance of caterpillars throughout (Chapter 2), and at which scale or tree density the effect is most pronounced.

There are various ways in which the analysis presented in Chapter 3 to examine thermal sensitivity in the arboreal caterpillar peak could be extended. First, the analysis could consider the effects of temperature on the phenological distribution of biomass, which is likely of greater relevance to consumers and estimating herbivory impact. Second, analysing the effects of temporal temperature change, independently of spatial effects, with more power would allow me to go further in identifying whether the effect of temperature is causal and perhaps make some inferences about the processes that underpin spatial variation. As discussed in Chapter 3, spatial or spatiotemporal responses to temperature may not represent the temporal responses which are of most interest given the projected temporal change in temperature (Phillimore *et al.*, 2010; Roberts *et al.*, 2015). Whilst I attempted to separate the effects that variation in spatial and temporal temperature have on the parameters that govern the caterpillar phenological distribution, with just eight years of data the credible intervals were large and analysis of data including many more years would be required to estimate the effects over time with more certainty.

The work presented in this thesis has utilised caterpillar guild abundance and mass data without assessing the guild species composition. As a result, it remains unclear whether the differences in caterpillar abundance and biomass among tree taxa and temperature are associated with turnover in species composition and if so at what scale. Species composition could be tree taxon specific, more generally influenced by the site-wide tree composition and/or influenced by local temperature. Differences in the guild species composition between woodland compositions and how species turnover differs with temperature over space vs time are of interest for the conservation of insects with national reforesting and ongoing climate warming and may provide information about insect population declines associated with changes in temperature or woodland tree composition. Determining sources of turnover in caterpillar guild composition would also be of importance to consumer fitness should there be a preference for or fitness advantages of particular species, or broader levels of taxonomic groupings, in the diet (García-Navas and Sanz, 2011); a topic that presents further research opportunities itself.

Further examination of the phenological distribution extension of the MMH

The phenological distribution extension of the MMH that I present in Chapter 4 presents a wide range of opportunities for further work. First, there are alternative blue tit fitness and phenological variables that could be used to address a similar question of how the phenological distribution of a resource affects the phenological fitness function of a consumer. Second, there are additional components of interest that can also be addressed through the novel framework.

The model composition used to test the phenological distribution extension of the MMH could be modified so that the blue tit phenological variable is a measure of synchrony with the caterpillar mean timing rather than absolute hatch date. Using synchrony rather than hatch date should determine whether the spatial trends in timing among the blue tit populations were masking effects of timing relative to the caterpillars in results from Chapter 4. It would also be interesting to compare the effects of the resource phenological distribution on the consumer phenological fitness function across several blue tit fitness traits. A range of traits will contribute to the absolute fitness of an individual and therefore the combined impacts among traits will be necessary to accurately estimate individual fitness and the strength of selection on timing. For example, the mass of chicks at fledging (or close to, from a practical perspective) might represent an informative fitness variable as it may affect the likelihood of recruitment to the population (Monrós *et al.*, 2002). Alternatively, looking at recruitment directly would be of most value to the demographic consequences of the MMH (Reed, Jenouvrier and Visser, 2013; Samplonius *et al.*, 2020), however, due to the small size of the sites included in this study, recruitment rates are very low. It would also be interesting to explore the consequences of relative timing on parent condition and survival to the following year and relate this to provisioning effort and nestling diet as the effects of the MMH may also manifest in the parent (Thomas *et al.*, 2001; Te Marvelde *et al.*, 2011), affecting lifetime reproductive success and absolute fitness. My results suggest fledging success is not affected by the phenological distribution of caterpillars, however, the condition of offspring fledged and the likelihood of recruiting may be affected (Monrós *et al.*, 2002; García-Navas and Sanz, 2011; Vatka, Rytkönen and Orell, 2014;

Samplonius *et al.*, 2016) or the condition of the parents following the breeding season (Te Marvelde *et al.*, 2011), reducing their survival (Nur, 1984).

The framework in Chapter 4 could be further extended to examine how the effects of climate warming on the MMH may vary across woodlands of different compositions. Understanding how species interactions and population fitness may vary between woodlands under climate warming would be useful for determining whether particular woodland tree compositions may be most beneficial for the conservation of arboreal insects and insectivorous birds, and possibly mammals, particularly relevant with considerable reforesting efforts planned in coming decades. To further aid projections of species responses to the changing climate, comparison across multiple populations, spanning the geographic range of a species, would be of the greatest benefit to predict meta-population change, and networks such as SPI-Birds, which works to collate such data across projects (Culina *et al.*, 2021), will be invaluable in assisting the undertaking of such work.

The phenological distribution extension of the MMH could also be of value for looking at the interactions between competing consumer species within the deciduous woodland community. The way in which the phenological distribution of caterpillars affects the phenological fitness function of an insectivorous bird may differ among bird species. Considering how a more complete test of the MMH affects each competing consumer species fitness function may increase the detail in which we can understand these inter-specific interactions, possibly of particular importance with ongoing climate warming as the synchrony and overlap in timing between some breeding bird species are changing over time (Samplonius *et al.*, 2018; Hällfors *et al.*, 2020). For example, as previously discussed, great tits and pied flycatchers compete for nest locations but the migratory pied flycatchers have advanced their breeding phenology by less than the resident great tits and are likely to be subject to more negative consequences of the MMH (Samplonius *et al.*, 2018); incorporating the impacts of change in the resource phenological distribution within these interactions may help to accurately determine the competitive outcome of each species.

Including the phenological distribution in tests of parental quality versus environment

One explanation for the lack of a detectable optimum hatch date and the absence of any effect of the caterpillar phenological distribution on the blue tit fledging success phenological fitness function is a strong effect of parental quality. Revealing the impact of parental quality on fitness presents another direction for further work. Clutch swap experiments have been used to separate the effect of parental quality and chosen timing from the effects of environment and absolute timing (Verhulst, Van Balen and Tinbergen, 1995; Verhulst and Nilsson, 2008). A review of previous studies suggests both quality and environment are important, and quality limits an individuals' ability to breed earlier (Verhulst and Nilsson, 2008). However, as far as I am aware, the effect of quality on fitness has never been explored within the context of phenological mismatch, nor where timing influences the height and width of the resource distribution. One study has incorporated feeding rates into an analysis examining the effect of mistiming on nestling condition which included experimental manipulation of timing (Samplonius *et al.*, 2016). However, the experimental and control groups were combined for the analysis, therefore, failing to test the effect of feeding rates and quality on fitness relative to timing. The framework presented in Chapter 4, paired with a clutch swap experiment that was run for three years among blue tit nests boxes within each study site (2017-2019), presents a novel opportunity to advance our understanding of how parental quality and environment interact to affect breeding success.

Application of methods to examine the phenological distribution to other study systems

The concepts presented throughout this thesis present opportunities for further study not only in the deciduous woodland system but also within any research focused on the environmental sensitivity of an ephemeral trait or fitness variable. The approaches used in Chapters 2 and 3 allow estimation of the effects of categorical and continuous variables on the phenological distribution of ephemeral life history events. Examples of ephemeral events that may be suitably approximated by the phenological distribution include planktonic blooms, fish or amphibian spawning events, migration and reproduction metrics for mammals or birds, tree leafing and senescence, flowering, fruiting and the number of individuals newly parasitised. Examples of categorical variables that may be of interest include host plants, rock type, land use, food type and years in the short term. Examples of continuous variables that may be of interest include temperature, rainfall, the density of interspecific competitors, predators, parasites or pollinators, the volume of food available and years in the long term. The phenological distribution extension of the MMH, proposed in Chapter 4, is relevant throughout the range of ecosystems in which the MMH is suspected to have an effect e.g. fish relying on plankton blooms (e.g. Jolley *et al.*, 2010), sea birds feeding on ephemeral spikes in fish abundance (e.g. Watanuki et al., 2009) or parasitoids and their hosts (e.g. Senior *et al.*, 2020). The main restraint on the use of the phenological distribution and the phenological distribution extension of the MMH in other systems would be the assumption that the phenological events and fitness functions are symmetrically distributed, however, future extensions allowing asymmetry are possible.

Summary

In this thesis, I have extended the conceptual framework and statistical toolbox for understanding links between climate, phenology and the MMH. The majority of previous research has focused on the mean timing of the resource and how asynchrony to it impacts consumer fitness. Where some work has begun to explore the height or duration of the resource distribution and their effects on consumer fitness, no work has considered variation in the full phenological distribution within one framework. Using the arboreal caterpillar phenological distribution, I have shown that habitat and temperature can change the phenological distribution of a resource. I then present an extension to the classic conceptual framework of the MMH, which provides a complete test of how the phenological distribution of a resource affects the phenological fitness function of a consumer, testing the hypothesis on the phenological distribution of caterpillars and blue tit breeding phenology and fledging success. Whilst I found no effect of the phenological distribution extension of the MMH, I also found no effect of the classic mean timing focused test of the MMH. My results prompt a diversity of opportunities for future work and the approaches are applicable to many study systems outside of the deciduous woodland food chain. The complete phenological distribution framework of the MMH may be required to accurately interpret ephemeral trophic interactions. Given the importance of the phenological fitness function in estimating population fitness and the strength of selection, this complete framework for the MMH has the potential to greatly increase the precision with which we can estimate the evolution of seasonal timing and predict population persistence through climate warming.

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Appendix A - Supplementary information for Chapter 2

Multi-membership model methods

Rearranging Equation 2.2 gives the model composition for the focal parameters of the habitat abundance model (Table 2.1) including the random regression multi-membership component.

Equation A.1: $y_{ijk} = b_0 + u_j^{(h)} + b_1 \sum_s (f_{sk} - \bar{f}) + \sum_s u_s^{(g)} (f_{sk} - \bar{f})$

Supplementary results

I found that alder, ash, beech, elm, rowan and sycamore all support significantly fewer caterpillars than oak (Fig. A.1), hosting 0.42 (CIs: 0.29 - 0.58), 0.34 (CIs: 0.22 - 0.54), 0.52 (CIs: 0.39 - 0.69), 0.59 (CIs: 0.41 - 0.84), 0.55 (CIs: 0.39 - 0.78) and 0.67 (CIs: 0.53 - 0.84) times as many caterpillars respectively.

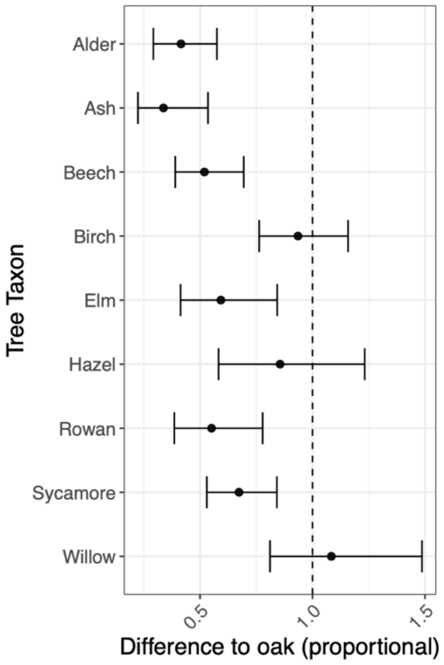


Figure A.1: Posterior median and 95% credible intervals of the model prediction for the proportional difference in caterpillar abundance between each tree taxon and oak. Calculated from tree taxa random effects in a Poisson GLMM (Table A.1). Black dashed line at 1.0 indicates no difference to oak/significance threshold.

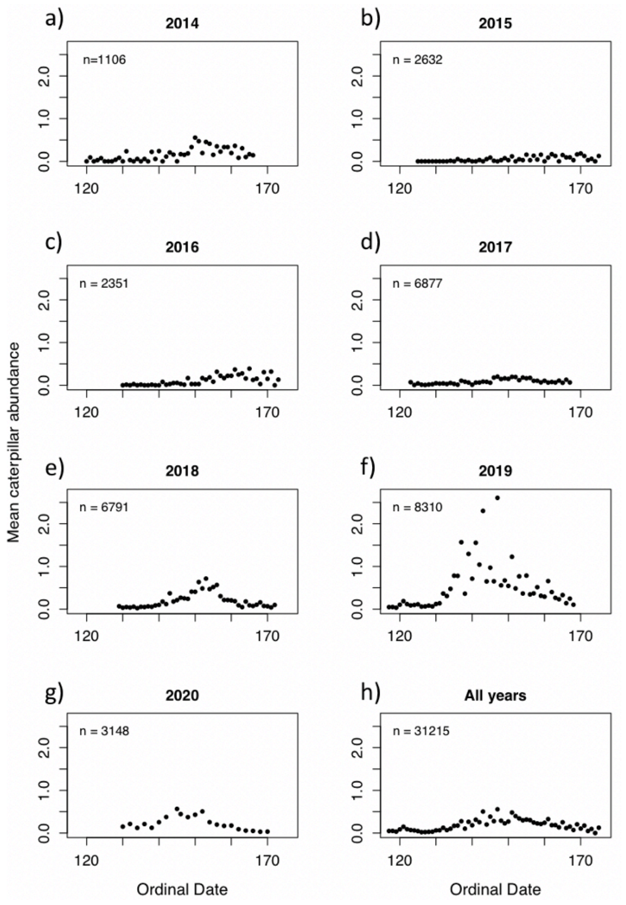
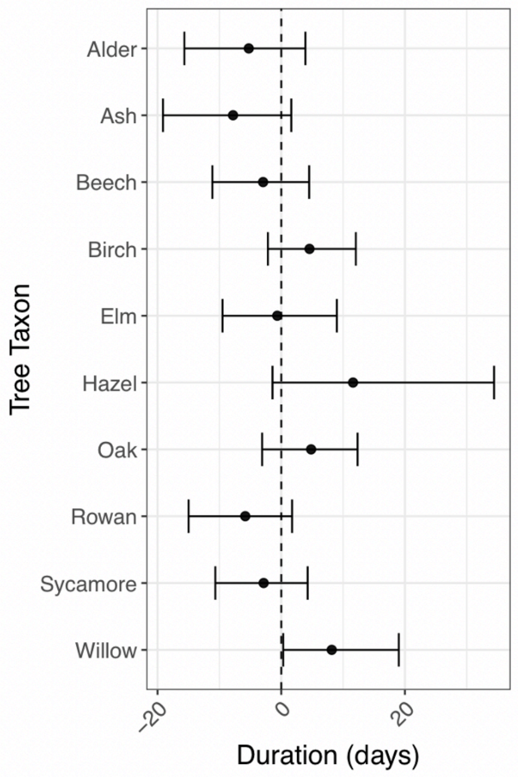


Figure A.2: Plots a-g show the mean abundance of caterpillars sampled on each day of each year and plot h shows the mean abundance on each day across all years, calculated from the mean at each site on each day, n indicates the total number of beating samples within each year or the total for all years.

Figure A.3: Posterior median and 95% credible intervals for model prediction of the difference in peak duration (at an abundance of 0.01 caterpillars) for each taxon compared to the fixed effect trend. Calculated from the posterior distributions for the fixed effects and tree taxa random effects and interactions in a Poisson GLMM (Table A.4).



When comparing the abundance peak metrics of each taxon to the peak on oak, I found a greater number of significant differences than compared to the average trend. The peak on rowan and sycamore trees was significantly earlier than on oak by -4.79 (CIs: -7.84 - -1.90) and -4.94 (CIs: -7.70 - -2.52) days respectively (Fig. A.4). The peak on alder, ash, beech, birch, elm, rowan and sycamore were all found to have a significantly lower height, reaching 0.31 (CIs: 0.20 - 0.47), 0.32 (CIs: 0.20 - 0.51), 0.43 (CIs: 0.30 - 0.59), 0.75 (CIs: 0.59 - 0.97), 0.48 (CIs: 0.32 - 0.72), 0.46 (CIs: 0.29 - 0.73) and 0.50 (CIs: 0.34 - 0.71) times the height of the peak on oak trees, respectively. The width of the peak at half the height did not differ significantly between any taxon and oak. The peaks on alder, ash, beech, rowan and sycamore last for a significantly shorter duration by -10.18 (CIs: -20.34 - -0.71), -12.91 (CIs: -22.40 - -2.82), -6.11 (CIs: -14.56 - -1.04), -11.12 (CIs: -18.39 - -4.38) and -8.02 (CIs: -14.15 - -2.98) days respectively (Fig. A.4).

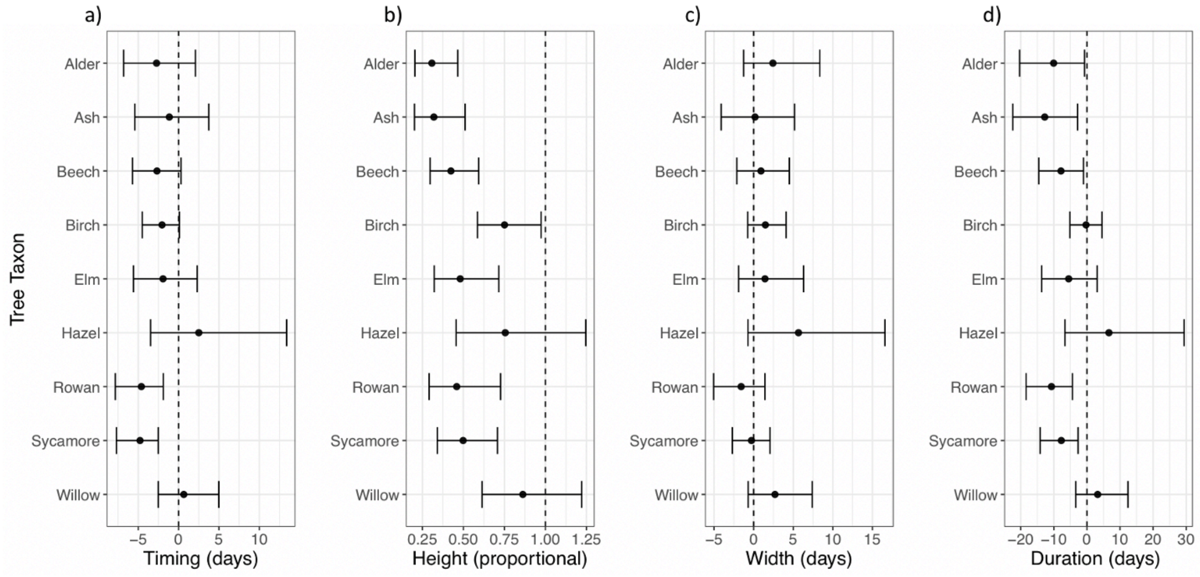


Figure A.4: Posterior median and 95% credible intervals for (Table A.4) predictions of the difference between each tree taxon and oak for different properties of the phenological distribution of caterpillar abundance in spring, calculated from the posterior distributions for the fixed effects and tree taxa random effects and interactions. Plots show a) the difference in the timing of the peak in abundance, b) the proportional difference in the height of the peak (maximum abundance), c) the difference in the peak width at half of the peak height and d) the difference in the duration of the peak (at a set abundance of 0.01 caterpillars).

When comparing the day 168 mass of caterpillars on each tree taxa to those from oak, I found caterpillars sampled from beech weighed significantly less at 0.60 (0.38 - 0.97) times the mass of those sampled from oak (Fig. A.5). Birch and willow also show non-significant trends towards a lower mass, reaching 0.83 (CIs: 0.65 - 1.03) and 0.79 (CIs: 0.55 – 1.08) times the mass respectively (Fig. A.5).

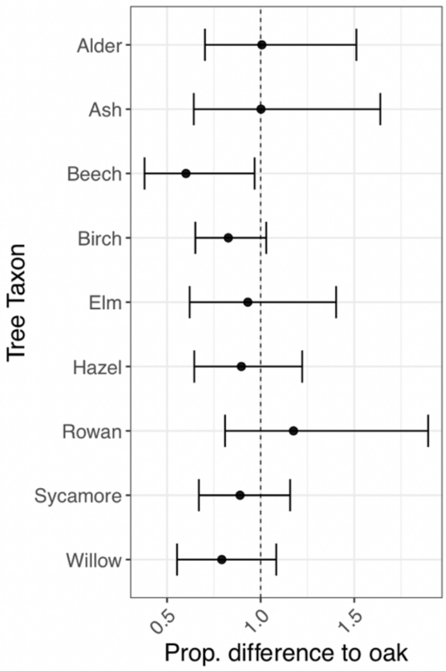
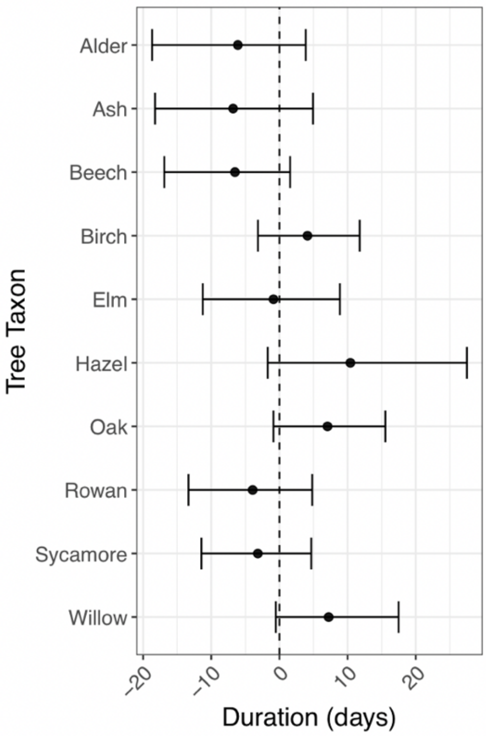


Figure A.5: Posterior median and 95% credible intervals for model predictions of the proportional difference in caterpillar mass between each tree taxon and caterpillars sampled from oak (Table A.5). Calculated for day 168 (16th June) for the average year and site, the latest date with caterpillar mass data for all tree taxa, using the posterior distributions for all fixed effect parameters and tree taxa random effects and interactions in a censored-gaussian GLMM.

Figure A.6: Posterior median and 95% credible intervals for model prediction of the difference in peak duration (at a biomass of 0.35mg of caterpillars) for each taxon compared to the fixed effect trend (Table A.4, A.5). Calculated from the posterior distributions for the fixed effects and tree taxa random effects and interactions in a bivariate censored-gaussian (mass) and Poisson (abundance) GLMM.



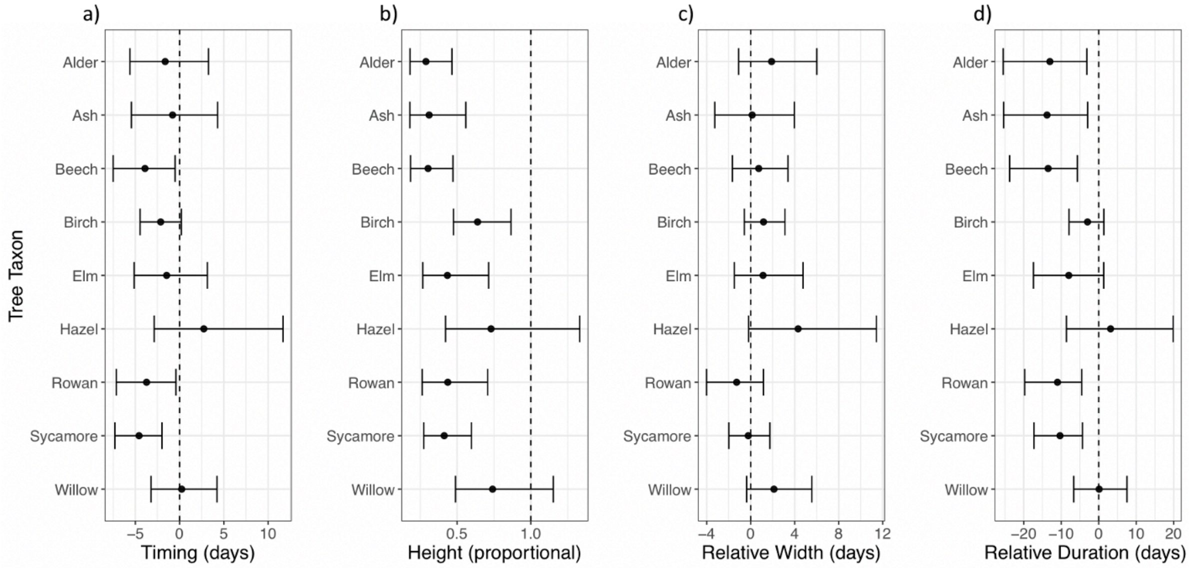


Figure A.7: Posterior median and 95% credible intervals for combined censored-gaussian (mass) and Poisson (abundance) GLMM (Table A.4, A.5) predictions of the difference between each tree taxon and oak for different properties of the phenological distribution of caterpillar biomass in spring, calculated from the posterior distributions for the fixed effects and tree taxa random effects and interactions. Plots show a) the difference in the timing of the peak in biomass, b) the proportional difference in the height of the peak (maximum biomass), c) the difference in the peak width at half of the peak height and d) the difference in the duration of the peak (at a set biomass of 0.35mg of caterpillars).

As with the distributions of caterpillar abundance among tree taxa, there were multiple differences between each taxon and oak in the biomass peak metrics (Fig. A.7). The peak on beech, rowan and sycamore trees were significantly earlier than on oak by -3.91 (CIs: -7.51 - -0.51), -3.73 (CIs: -7.15 - 0.42) and -4.58 (CIs: -7.31 - -1.99) days respectively (Fig. A.7), and the peak timing on birch trees also showed a strong trend towards falling -2.14 (CIs: -4.46 - 0.20) days earlier. The biomass peaks on alder, ash, beech, birch, elm, rowan and sycamore were found to have a significantly lower height, reaching 0.29 (CIs: 0.18 - 0.47), 0.31 (CIs: 0.18 - 0.56), 0.31 (CIs: 0.18 - 0.47), 0.64 (CIs: 0.48 - 0.87), 0.43 (CIs: 0.27 - 0.71), 0.44 (CIs: 0.26 - 0.71) and 0.41 (CIs: 0.27 – 0.60) times the height of the peak on oak trees, respectively. The width of the peak at half the height on birch, hazel and willow showed non-significant trends towards being broader than on oak by 1.67 (CIs: -0.58 - 3.11), 4.31 (CIs: -0.18 - 11.43) and 2.12 (CIs: -0.37 - 5.56) days respectively. The peak duration on alder, ash, beech, rowan and sycamore lasted for a significantly shorter duration by -13.01(CIs: -25.47 - -3.16), -13.78 (CIs: -25.36 - -2.69), -13.48 (CIs: -23.74 - -5.69), -11.00 (CIs: -19.73 - -4.53) and -10.32 (CIs: -17.27 - -4.32) days respectively, and peaks on birch and elm also show strong non-significant trends towards a shorter duration by -2.98 (CIs: -7.91 - 1.39) and -7.98 (CIs: -17.40 - 1.34) days (Fig. A.7).

Model output tables

Table A.1: Poisson GLMM for variance composition of caterpillar abundance. Date refers to ordinal date (scaled: mean = 146.7727, SD =14.04083).

	Coefficient/Variance (Mean/mode and CI)	Effective sample size
Fixed Terms		
Intercept	-3.319 (-4.111 - -2.533)	4900
Date (scaled)	0.48 (0.388 - 0.57)	4655
Date^2 (scaled)	-0.442 (-0.528 - -0.355)	4482
Random Terms		
Site	0.667 (0.36 - 1.075)	1844
Tree ID	0.273 (0.222 - 0.34)	4900
Tree Taxa	0.146 (0.048 - 0.608)	1657
Day Site Year	0.491 (0.424 - 0.598)	4148
Day	0.272 (0.195 - 0.364)	4539
Site Year	0.258 (0.184 - 0.359)	3392
Year	0.278 (0.077 - 1.885)	1111
Recorder	0.103 (0.048 - 0.33)	2814
Residual	0.641 (0.563 - 0.739)	3885

Table A.2: Poisson GLMM analysing differences in caterpillar abundance between the different tree taxa sampled, the effect of site foliage density and the effect of the amount of foliage of each tree taxon within the local woodland composition, included using multi-membership.

	Coefficient/Variance (Mean/mode and CI)	Effective sample size
Fixed Terms		
Intercept	-4.02 (-4.892 - -3.192)	4707
Total Foliage Score	0.001 (-0.019 - 0.018)	3842
Random Terms		
Sampled Tree Taxa	0.126 (0.038 - 0.594)	3146
Habitat Composition	0 (0 - 0.001)	1063
Site	0.388 (0.194 - 0.696)	3547
Year	0.288 (0.062 - 1.796)	816
Site Year	0.232 (0.158 - 0.336)	5000
Tree ID	0.269 (0.221 - 0.338)	5000
Day Site Year	1.032 (0.916 - 1.166)	5000
Recorder	0.166 (0.069 - 0.484)	3030
Residual	0.643 (0.57 - 0.746)	4589

Table A.3: Poisson GLMM for analysing variations among tree taxa in the phenological distribution of caterpillar abundance throughout spring. Date refers to ordinal date (scaled: mean = 146.7727, SD =14.04083).

	Coefficient/Variance (Mean/mode and CI)	Effective sample size
Fixed Terms		
Intercept	-3.164 (-4.191 - -2.225)	10000
Date (scaled)	0.864 (0.042 - 1.743)	8866
Date^2 (scaled)	-0.841 (-1.177 - -0.523)	7069
Random Terms		
TreeTaxa- Intercept var	0.154 (0.036 - 0.626)	1340
TreeTaxa- Intercept:Date slope covar	0.02 (-0.097 - 0.154)	8865
TreeTaxa- Intercept:Date^2 slope covar	0.002 (-0.102 - 0.081)	8750
TreeTaxa- Date slope var	0.046 (0.011 - 0.212)	3123
TreeTaxa- Date slope:Date^2 slope covar	0 (-0.04 - 0.068)	8719
TreeTaxa- Date^2 slope var	0.02 (0 - 0.129)	2586
Site- Intercept var	0.872 (0.553 - 1.548)	6973
Site- Intercept:Date slope covar	-0.104 (-0.337 - 0.056)	6315
Site- Intercept:Date^2 slope covar	-0.229 (-0.437 - -0.124)	5703
Site- Date slope var	0.243 (0.145 - 0.425)	3166
Site- Date slope:Date^2 slope covar	0.018 (-0.041 - 0.092)	6168
Site- Date^2 slope var	0.105 (0.057 - 0.186)	5096
Year- Intercept var	0.472 (0.159 - 3.22)	473
Year- Intercept:Date slope covar	-0.293 (-1.975 - 0.367)	7155
Year- Intercept:Date^2 slope covar	0.038 (-0.269 - 0.491)	5163
Year- Date slope var	0.501 (0.171 - 2.851)	578
Year- Date slope:Date^2 slope covar	-0.052 (-0.627 - 0.149)	5671
Year- Date^2 slope var	0.047 (0.005 - 0.339)	1302
Site Year	0.259 (0.197 - 0.37)	5472
Recorder	0.146 (0.064 - 0.355)	2616
Day Site Year	0.266 (0.204 - 0.333)	4355
Tree ID	0.263 (0.212 - 0.328)	6000
Residual	0.64 (0.555 - 0.727)	2203

Table A.4: Censored-gaussian GLMM for analysing variations among tree taxa in the phenological distribution of log caterpillar mass throughout spring. Date refers to ordinal date (scaled: mean = 146.7727, SD =14.04083).

	Coefficient/Variance (Mean/mode and CI)	Effective sample size
Fixed Terms		
Intercept	-3.884 (-4.131 - -3.651)	10446
Date scaled	0.533 (0.38 - 0.687)	3491
Date^2 scaled	-0.147 (-0.207 - -0.088)	1549
Random Terms		
TreeTaxa- Intercept var	0 (0 - 0.026)	2113
TreeTaxa- Intercept:Date slope covar	0 (-0.006 - 0.024)	3714
TreeTaxa- Date slope var	0.001 (0 - 0.086)	1011
Site- Intercept var	0.029 (0 - 0.078)	948
Site- Intercept:Date slope covar	-0.009 (-0.04 - 0.016)	2207
Site- Date slope var	0.044 (0.015 - 0.098)	1652
Year	0 (0 - 0.183)	1063
Site Year	0.02 (0 - 0.052)	824
Recorder	0.006 (0 - 0.04)	2522
Day Site Year	0.128 (0.087 - 0.184)	2677
Tree ID	0.041 (0.021 - 0.071)	2614
Weighting	0.97 (0.863 - 1.069)	1388
Residual	0.023 (0.002 - 0.055)	671

Asymmetry in the abundance peak

Methods

It is already established that there is a peaked phenological distribution of caterpillar abundance throughout spring in temperate deciduous woodlands (Gibb, 1950; van Balen, 1973; Southwood *et al.*, 2004; Shutt, Burgess and Phillimore, 2019), though the shape of peak has not been examined. I assessed the adequacy of the quadratic function in describing the shape of the phenological distribution of caterpillar abundance by also modelling the peak including a cubic date term; allowing an asymmetrical trend over time. The extent of asymmetry was quantified by comparing the percentage of the peak width predicted to fall before and after the vertex of the curve.

The peak asymmetry model included the caterpillar abundance per sample as the response variable with an intercept, date, $date^2$ and $date^3$ in the fixed effects, allowing an asymmetrical peak (Table A.5). Date refers to ordinal date and was scaled (prior to scaling: mean = 146.77, SD =14.04). The random terms allowed for each site*year to have a separate intercept, date, $date^2$ and $date^3$ slopes and for covariance among these terms. Separate site and year random intercepts and slopes were not included to aid model convergence. I do not anticipate this will pose an issue, as my primary interest was to identify the general phenological trend. I calculated the extent of asymmetry at each quartile of the peak height across the posterior distribution because the ratio of duration to the left and right of the peak is not necessarily constant.

Table A.5: Model composition for the peak asymmetry model. Date refers to ordinal date which was scaled (mean = 146.77, SD =14.04). Int = intercept and VCV = variances and covariances.

Model	Peak asymmetry (Table A.6)
Motivation	Evidence of asymmetry in peak shape
Response	Caterpillar abundance
Fixed effects	Date Date^2 Date^3
Random terms	Int, Date, Date^2 and Date^3 VCV across Site*year Day*Site*Year Tree ID Recorder
Family	Poisson
Iterations (thin)	2000000 (1000)
Burnin	50000
Sample Size	1950

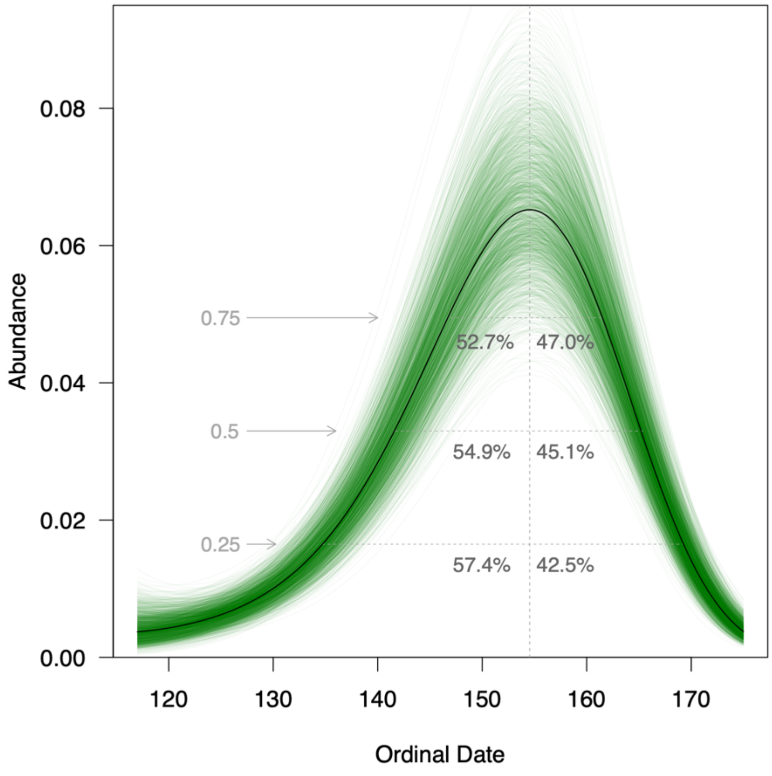


Figure A.8: Posterior distribution for Poisson GLMM allowing a cubic (asymmetrical) relationship between caterpillar abundance and ordinal date (Table A.3). Percentage of peak width falling before and after the peak date at 0.25, 0.5 and 0.75 of the peak height are shown in grey.

Results

Annual peaks in the temporal distribution of caterpillar abundance in our data are clear (Fig. A.2), and supported by the significant date^2 term (-0.632, CIs: -0.739 - -0.521, Table A.6) in the peak asymmetry model. The cubic parameter was significant and negative (-0.229, CIs: -0.315 - -0.156), indicating a negatively skewed peak (Table A.6), however, the resulting asymmetry in the curve is quite small (Fig. A.8). Each quartile shows 53-57% of the peak duration to the left and 43-47% to the right. On the basis of the quite minor asymmetry, I conclude that the inclusion of the quadratic date term, without cubic, is sufficient.

By including a date^3 by site*year random term, the variance in the cubic term among site by year combinations was estimated. The estimated variance of 0 (CIs: 0 - 0.032) indicates that the cubic term, and therefore asymmetry in the peak, does not vary among site by year combinations.

Table A.6: Poisson GLMM using a cubic function to analyse possible skew in the distribution of caterpillar abundance across ordinal date (scaled: mean = 146.7727, SD =14.04083).

	Coefficient/Variance (Mean/mode and CI)	Effective sample size
Fixed Terms		
Intercept	-3.002 (-3.263 - -2.695)	1721
Date (scaled)	0.911 (0.727 - 1.081)	1950
$Date^2$ (scaled)	-0.632 (-0.739 - -0.521)	1155
$Date^3$ (scaled)	-0.229 (-0.315 - -0.156)	1472
Random Terms		
SiteYear- Intercept var	1.652 (1.288 - 2.062)	1950
SiteYear- Intercept:Date slope covar	-0.337 (-0.607 - -0.118)	1828
SiteYear- Intercept:$Date^2$ slope covar	-0.446 (-0.585 - -0.305)	1950
SiteYear- Intercept:$Date^3$ slope covar	0.029 (-0.035 - 0.102)	1768
SiteYear- Date slope var	0.713 (0.534 - 1.074)	1684
SiteYear- Date slope:$Date^2$ slope covar	0.094 (-0.014 - 0.197)	1950
SiteYear- Date slope:$Date^3$ slope covar	-0.047 (-0.128 - 0.008)	1211
SiteYear- $Date^2$ slope var	0.193 (0.136 - 0.284)	1950
SiteYear- $Date^2$ slope:$Date^3$ slope covar	0 (-0.029 - 0.023)	1950
SiteYear- $Date^3$ slope var	0 (0 - 0.032)	1315
Recorder	0.154 (0.065 - 0.39)	1395
Site Day	0.221 (0.164 - 0.292)	1805
Tree ID	0.34 (0.269 - 0.406)	1950
Residual	0.629 (0.558 - 0.728)	1950

Appendix B - Supplementary information for Chapter 3

Mean expectation on the arithmetic scale

There are two forms of expectations on the arithmetic scale that I was interested in from the spatiotemporal temperature model: i) the average value of each phenological parameter at different temperatures, and ii) the average value of mean caterpillar abundance on each date throughout spring at different temperatures which depends on all phenological parameters. Both required marginalising random terms, but the method to do this differed.

(i) To estimate the height or width at different temperatures (Fig. 3.3c-d), half of the variance for each random term associated with each parameter was added to the estimate before exponentiating.

(ii) Since an analytical solution was not available, marginalisation was carried out by simulating from the posterior predictive distribution 10,000 times for each date:temperature combination and taking the average abundance. This allows visualisation of the changes to the full phenological distribution with changing temperature (Fig. 3.4a). The duration was calculated for each temperature as the dates on which the average abundance exceeded the threshold (Fig. 3.4b), and the area was calculated as the sum of the average abundance across dates (Fig. 3.4c). Due to the uncertainty in the mean timing of the distribution the maximum average abundances reached are lower than those predicted from i).

Sliding window analysis

Methods

I began the analyses by identifying the periods during which temperature best predicted the thermal sensitivity of the mean timing, height and width parameters of the caterpillar phenological distribution. As it is feasible that the most influential period could differ for each parameter, I used a sliding window approach which allowed such. Therefore, as the number of windows to consider was the product of the number of windows considered for each parameter, for efficiency I applied a frequentist meta-analytic approach (using the metafor package (Viechtbauer, 2010)) to the site by year estimates for the three parameters. This allowed me to compare sliding windows based on AIC.

To obtain estimates of the three phenological parameters for each site in each year I modelled the phenological distribution of at each site in each year using the same model composition as the spatiotemporal temperature model using RStan (Stan Development Team, 2020), but excluding the temperature fixed effects. From the model output the intercept and random intercepts for each site, year and site by year combination could be summed to obtain the estimate of each phenological parameter for each site in each year. The posterior mode (calculated using the MCMCglmm package (Hadfield, 2010) function) was used as the estimate of mean timing, height and width for each site by year combination for the response variable in metafor multivariate meta-analyses. The variance-covariance matrix of the posterior distributions for the three parameters in each site in each year was included as the sampling variance.

I modelled the effect of temperature on each distribution parameter under a sliding window framework, allowing each parameter to be predicted by different time windows of temperature. For mean timing the window start dates ranged from day 58 to day 100, shifting in 7 day increments. For the height and width the window start dates ranged from 58 to 128, shifting in 14 day increments. The incremental shifts in start date were slightly higher resolution and restricted to an earlier period of the year for the mean timing parameter due to stronger a priori predictions from previous studies (Visser, Holleman and Gienapp, 2006); whereas much less is known about the time windows that best predict the distribution height and width (see Visser *et al*. 2006) so I allowed larger increments to reduce the extent of multiple testing. All three parameters had windows ranging in duration from 28 to 98 days, increasing in duration in 14-day increments. This produced 30 window options for the mean timing variable and 21 for the height and width, resulting in 13231 models in total.

The metafor multivariate models included independent intercepts and temperature slopes for each of the response variables, as well as including year and each site in each year (site-year) as random terms for each response. As it is only possible to include two random terms that are independent for each response variable in the metafor package I selected year and site-year but not site. Random terms were estimated using an unstructured variance-covariance matrix. The models were fitted using maximum likelihood rather than restricted maximum likelihood to enable model comparison using AIC.

Results

Of the 13231 models run, 7 did not converge, the details of which can be found in Table B.1.

As seen in Fig. B.1, all models with AIC's within 2 of the best fitting model for the mean timing and height parameters included the windows that were also in the best fitting model, however, for the width parameter the windows used in models within 2 AICs of the best fitting were more varied, suggesting there is no particular time period between mid-Feb and late June during which temperature predicts the change in peak shape to a much greater extent. As the aim of this work was to identify the effect of spring temperatures on each metric of the caterpillar peak and not to identify the most influential time period of temperature throughout the year I proceeded using the windows of temperature identified in the best fitting model despite the lack of a clear optimal window for estimating the width parameter.

Table B.1: Window combinations for the models that did not converge in a sliding window analysis which allowed different temperature periods to predict the three parameters that describe the phenological distribution of caterpillar abundance. Shows the start date and duration of each window.

Mean Timing		Height		Width	
Start	Duration	Start	Duration	Start	Duration
93	28	72	70	100	28
93	28	72	84	100	28
93	28	58	98	100	28
100	56	72	70	128	28
100	56	72	70	114	42
100	56	72	84	128	28
100	56	58	98	128	28

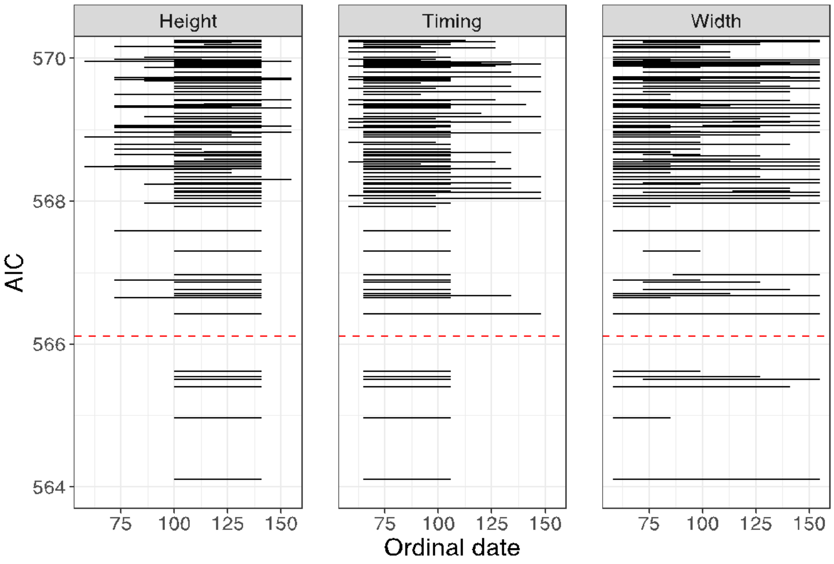


Figure B.1: Plot of the AICs from models using different windows of temperature (horizontal black lines) as predictors of the three parameters describing the phenological distribution of caterpillar abundance. All lines beneath the red dashed line are within two AICs of the model with the lowest AIC value. Cropped Y axis, only showing subset of models with lower AICs.

Temperature mean, standard deviation and range in the identified windows:

The mean temperature during the mean timing parameter window was 5.83°C, ranging from -3.05 to 3.06°C with a standard deviation (sd) of 1.22 after mean centring (spatial: -1.73 - 1.48°C; temporal: -2.13 - 1.57°C). The mean temperature during the width parameter window was 7.81°C, ranging from -2.50 to 2.17°C with a sd of 0.85 after mean centring (spatial: -1.58 - 1.16°C; temporal: -1.15 - 1.18°C). The mean temperature during the height parameter window was 8.92°C, ranging from -3.55 to 2.43°C with a sd of 1.20 after mean centring (spatial: -1.59 - 1.05°C; temporal: -2.40 - 2.01°C).

Table B.2: Comparison of the best windows identified for each pair of parameters (timing, height and width). Proportional overlap is the number of days that intersect divided by the summed number of days. Temperature correlations capture the correlation between the average temperatures obtained for pairs of parameters and is partitioned into spatiotemporal (using site-year mean temperatures), spatial (using site means) and temporal (using annual deviations from site means) estimates.

Parameter pairs	Prop. overlap	Spatiotemporal cor.	Spatial cor.	Temporal cor.
MeanTiming:Height	0.08	0.31	0.94	-0.06
MeanTiming:Width	0.3	0.78	0.98	0.58
Height:Width	0.3	0.79	0.99	0.71

Correlation among temperatures in identified windows:

The temperatures that contribute to each of the three best windows (one for timing, height and width) are overlapping (Figure 3.3a, Table B.2). Therefore, one would expect the effect of a change in temperature to lead to a somewhat correlated response. When I estimate the pairwise correlations in temperatures between windows, I find that in space the correlations are very high (Table B.2), whereas in time the correlation is weaker and there is no temporal correlation between the temperatures that predict timing and height. The stronger correlations between different windows in space (across sites) versus time (across years) are consistent with information about the position of the sliding windows stemming mainly from the temporal replication in the data (Shutt *et al.*, 2019).

Allowing the windows to differ in space

Due to the large spatial scale of the Phenoweb project, incorporating sites across both latitudinal and elevational gradients, I performed a posthoc test of the sliding window analysis to see whether different windows would be identified for different spatial subsets of sites. The 44 sites were split into four groups: Group 1= southern low elevation (10 sites), Group 2= southern mid elevation (9 sites), Group 3= high elevation (15 sites) and Group 4= northern low elevation (10 sites), these were allocated so that groups contained a reasonable number of sites, similar in both elevation and latitude (Figure B.2). Due to differences in the number of years in which each site has been sampled the number of site by year combinations within each group also varies: Group 1 n=74, Group 2 n=62, Group 3 n=101 and Group 4 n=56.

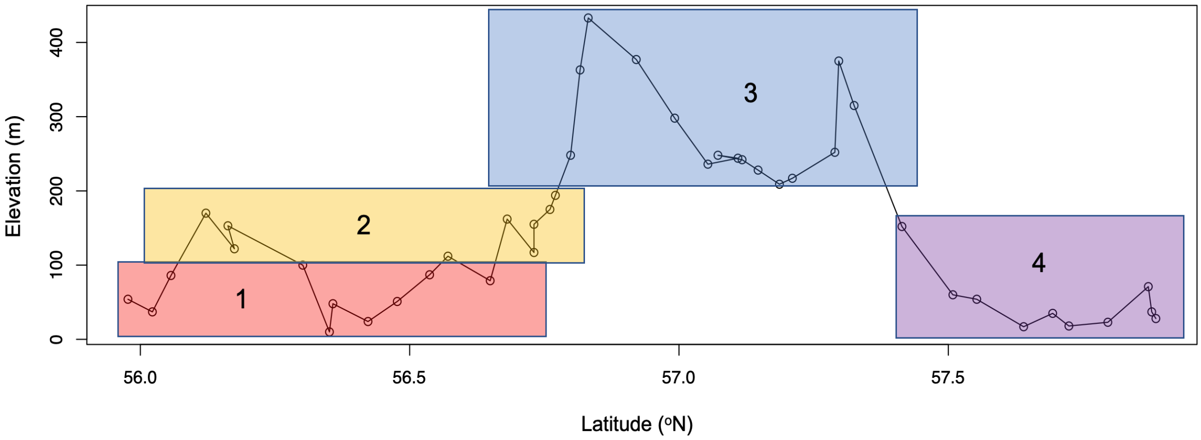


Figure B.2: The Phenoweb transect sites, plotted by latitude and elevation, with numbered and coloured boxes showing the grouping of sites with similar latitudes and elevations, then used for independent analyses.

The caterpillar peak phenological parameters for each site by year combination were split into four data sets using the site groupings outlined above. I then ran the same sliding window analyses as above, with the exception of estimating the window for the mean timing parameter separately from the height and width. Using a univariate model for mean timing and bivariate for height and width, made the posthoc analysis more timely, whilst still allowing for the strong covariance between the height and width parameters. The difference in structure does mean that the windows identified are not directly comparable with those of the main analysis, however, the purpose was to explore whether the windows differ between site groups, which this approach allows.

The results of the sliding window analysis for each phenological parameter and site group are shown in Fig. B.3a. The windows identified for timing were more clearly defined for Groups 1 and 2, with more falling within 2 AIC of the lowest for Group 3 and 4. All fall within a similar time period, however, the best fitting by AIC and additional windows identified by AICs for Groups 3 and 4 tend towards including later dates than the periods identified for Groups 1 and 2. This may suggest temperature at later dates influences the mean timing of the caterpillar peak more further north, however, the differences are non-distinct. The mean timing windows for all groups (start ranges from day 79 to 100, end ranges from day 120 to 128) are slightly later than was identified in the multivariate analysis of all sites (multivariate analysis timing window = day 65-106; Fig. B.3b). The difference may arise from estimating the three parameters within one model, accounting for the covariances between them, even though timing covaries with height and width far less than they do with each other.

There were multiple models within two AIC of the best fitting model for the height and width parameters in all site groups. For Groups 1, 2 and 3 this appears to be driven by uncertainty in the duration of temperature windows best predicting the phenological parameters, particularly for the width. The windows identified for Group 4 are more varied, likely suggesting no clear predictive period, possibly influenced by that being the group with the least data.

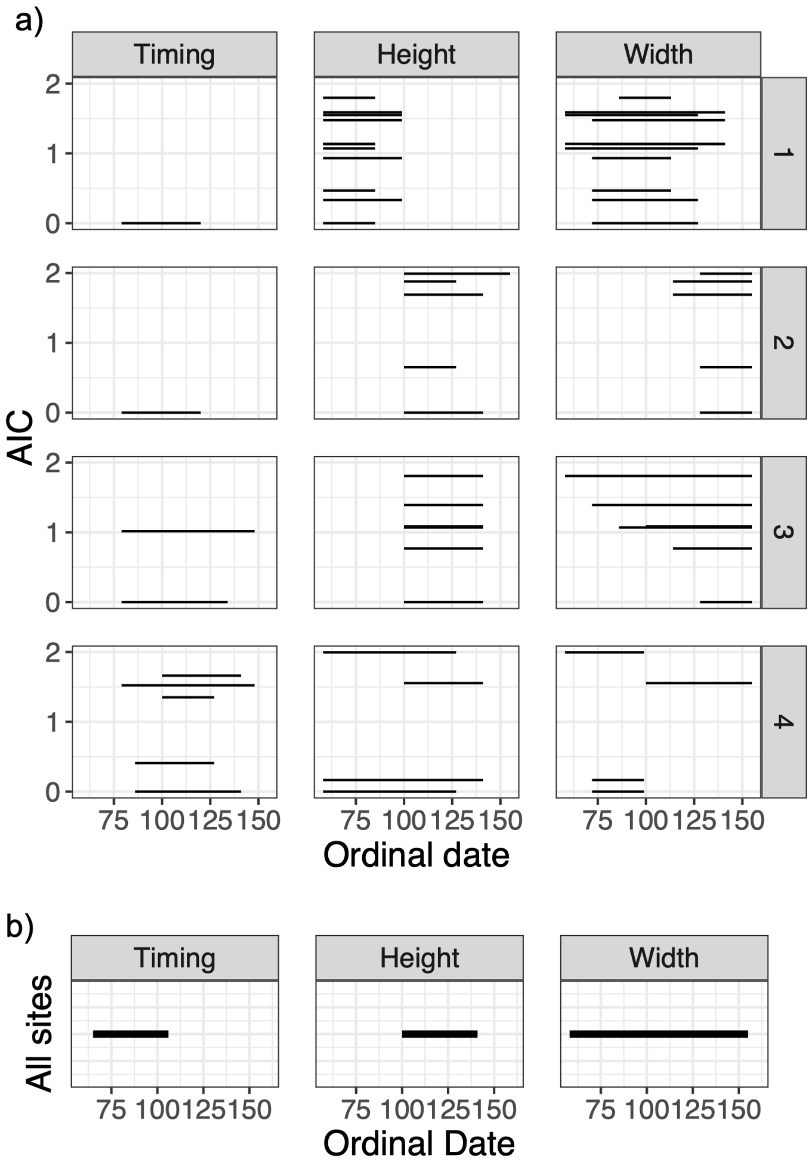


Figure B.3: a) shows a grid of the sliding window results for each phenological parameter by site groups. The lines within each plot show the time periods identified with AICs within 2 of the lowest AIC. AICs are shown as deviations from the lowest AIC among models run for each parameter/group sliding window (timing or height and width by site groups 1-4), meaning the bottom most line at AIC 0 for each plot was the best fit, but any others shown were not deemed substantially worse. b) shows the window identified for each phenological parameter from the main sliding window analysis which modelled all three parameters within one multivariate model and in which all site temperatures were taken from the same time periods.

For the height and width parameters, between Groups 1-3 there is a trend towards later periods of temperature being identified for the higher elevation/more northern sites (Groups 2 and 3), though with more uncertainty for the width parameter in Group 3. The lack of clarity in Group 4 prevents discussion of whether this trend is driven more by latitude or elevation.

The windows identified for the height parameter in the site group analyses suggest the window identified in the main multivariate analysis was likely influenced more by the higher elevation sites than lower, making up 163 of the 293 site by year combinations. The combination of earlier windows identified for the width parameter for Group 1 compared to 2 or 3 could suggest the lack of clarity and extreme breadth of the window identified for width in the main multivariate analysis was due to the difference in windows between elevations, however, the uncertainty in which window or duration is the best predictor among site groups also suggests there may not be a distinct period when temperature best predicts the width of the peak, similarly to the conclusion of the main sliding window analysis.

Grouped points in the timing by temperature plot

The appearance of two groups of points in the timing by temperature plot in Chapter 3 (Fig. 3.3b) is caused by the year effects for the timing parameter (Fig. B.4). With just 8 years in the random term, the effects will not necessarily smoothly outline a normal distribution (Fig. B.5), despite being estimated from a normal distribution with associated variance. This suggests the years sampled have included more distinctly earlier and later years, with few in between.

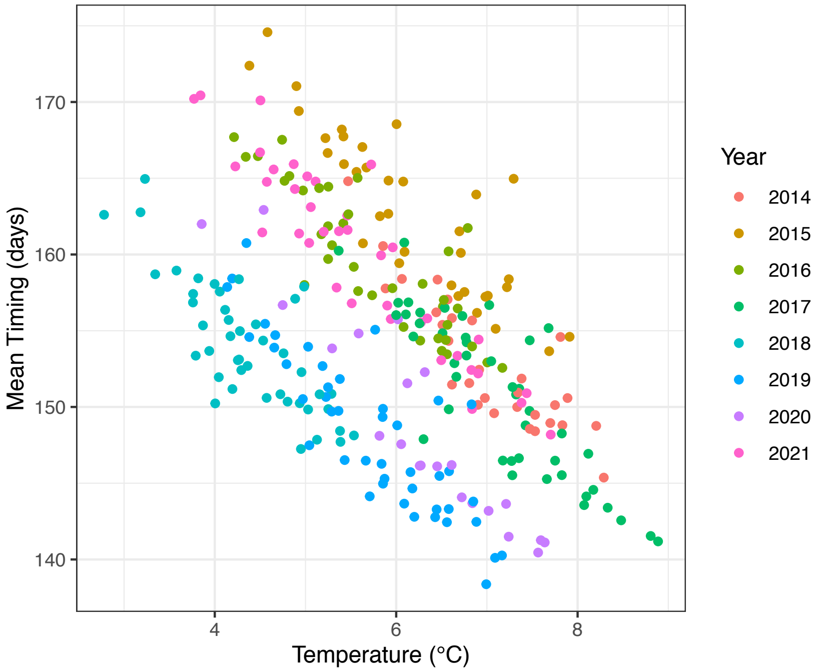


Figure B.4: Figure showing the year associated with each site by year estimate point from Fig. 3.3b in Chapter 3.

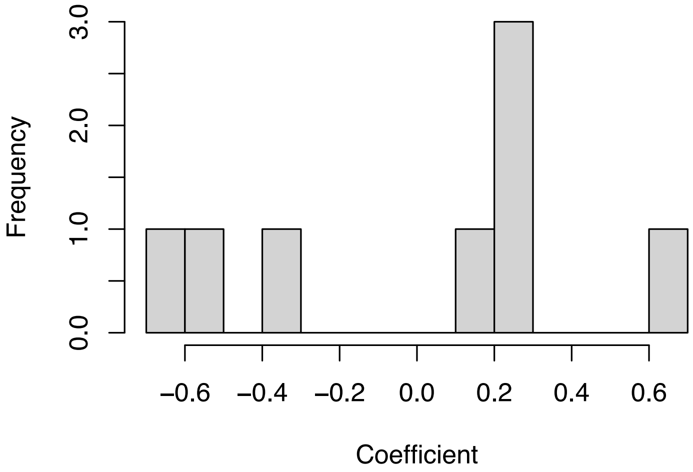


Figure B.5: Histogram of the posterior mean year effect coefficients for the timing parameter in the spatiotemporal temperature model from Chapter 3.

Site, year and site-year variance in models

The variance in timing, height and width that is distributed among site, year and site-year quantify are captured by random terms in the model, and all terms are significantly removed from 0 (Table B.3).

Table B.3: Posterior mode (95% credible intervals) for the variance attributed to the site, year and site-year (each site in each year) random terms for the timing, height and width parameters of the phenological distribution of caterpillars. Outlined for two models: the main spatiotemporal temperature model and the equivalent model that excludes the fixed effect temperature slopes for each parameter. As estimates are directly from the model the width and height terms are on the log-scale and the timing and width terms are scaled (original sd = 14.1)

	Random term	Spatiotemporal temperature model	Site by year model
Timing	Site	0.043 (0.025 - 0.096)	0.145 (0.085 - 0.254)
	Year	0.142 (0.089 - 1.033)	0.119 (0.06 - 0.782)
	Site-year	0.012 (0.006 - 0.031)	0.019 (0.01 - 0.042)
Height	Site	0.744 (0.516 - 1.333)	0.860 (0.559 - 1.415)
	Year	0.134 (0.028 - 1.267)	0.397 (0.216 - 3.123)
	Site-year	0.459 (0.369 - 0.636)	0.462 (0.354 - 0.611)
Width	Site	0.029 (0.011 - 0.066)	0.029 (0.014 - 0.076)
	Year	0.055 (0.021 - 0.508)	0.020 (0.01 - 0.258)
	Site-year	0.034 (0.018 - 0.065)	0.037 (0.016 - 0.066)

In the site by year model (i.e. a model without temperature predictors) I find substantial variation in timing among sites and years. When temperature is included in the model this leads to a substantial reduction in the among-site variance.

The variation in height is greatest among sites, but also substantial among years and site-years and this variance is substantially reduced among years when temperature is included in the model (though credible intervals are broad). An implication of the substantial site-year variance is that the height of the caterpillar guild abundance peak may be quite idiosyncratic in space and time and not solely predictable on the basis of temperature.

For the width parameter, the main difference seen was an increased variance among years when the temperature slope was included, supporting my finding from the space vs time model that temporal temperature variation does not affect the width of the phenological distribution.

Why use the Gaussian function rather than a Poisson GLMM?

The non-linear Gaussian function used by my study has more often been modelled as the re-parameterised linear form in a Poisson GLMM (Eq. B.1).

Eq. B.1: $y = \beta_0 + \beta_1 d + \beta_2 d^2$

Previous work has suggested that by extending Eq. B.1 to include an interaction between a temperature variable and the date parameter, d (Eq. B.2) it is possible to estimate the change in mean timing with temperature (Chevin, Visser and Tufto, 2015; Edwards and Crone, 2021).

Eq. B.2: $y = \beta_0 + \beta_1 d + \beta_2 d^2 + \beta_3 t + \beta_4 dt$

The maximum height (H) of the distribution is reached at the mean timing (M), which can be simplified to $A + Bt$ (Eq. B.3) where $A = -\frac{\beta_1}{2\beta_2}$ and B=$-\frac{\beta_4}{2\beta_2}$.

Eq. B.3:

$$M = -\frac{(\beta_1+\beta_4 t)}{2\beta_2}$$

$$= -\frac{\beta_1}{2\beta_2} - \frac{\beta_4}{2\beta_2}t$$

$$= A + Bt$$

When quantifying the height of the phenological distribution ($d = M$) in Eq. B.2, I found the composition of the model forces the height to be a quadratic function of temperature (Eq. B.4).

Eq. B.4:

$$H = \beta_0 + \beta_1(A+Bt) + \beta_2(A+Bt)^2 + \beta_3 t + \beta_4(A+Bt)t$$

$$= \beta_0 + \beta_1 A + \beta_1 Bt + \beta_2 A^2 + \beta_2 2ABt + \beta_2 B^2 t^2 + \beta_3 t + \beta_4 A + \beta_4 Bt^2$$

$$= \beta_0 + \beta_1 A + \beta_2 A^2 + \beta_4 A + (\beta_1 B + \beta_2 2AB + \beta_3)t + (\beta_2 B^2 + \beta_4 B)t^2$$

As my interest was modelling a change in the mean timing, height and width of the phenological distribution, this linear model composition has undesired properties. Therefore, I proceeded with the non-linear Gaussian function.