Developing a mechanistic understanding of the ecological impact of climate change: neglected woodland insects

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Submitted for the degree of PhD

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September 2019

Abstract

Woodland insects are fundamental for ecosystem function. They comprise a diversity of species and are expected to be highly sensitive to climate change. Despite this, little is known about their population trends and responses to climatic change. Understanding community response and the mechanisms driving climate change impacts can increase the predictive capacity for insects and the wider woodland community. It could also facilitate the design of mitigative action. This thesis combines long-term data for a variety of insects and a controlled phenological mismatch experiment to address some of these knowledge gaps.

Declines in volant woodland insects, from 2009-2018, were detected for total insects, Hymenoptera and Homoptera, but not Diptera. Associations between weather and abundance were found for all focal taxa. Abundance typically decreased with mild wet winters and increased with warm summers with some divergence between taxa. Projections of milder winters, and uncertainty regarding summer weather suggests these declines may continue.

In a tri-trophic study on sycamore, aphids, and parasitoids, temperature drove phenology across all taxa. The precise time-window of temperature influence varied between species. Warmer winters delayed aphid emergence but not the interacting species, providing a potential mechanism for trophic mismatch. Limited demographic effects of mismatch or weather were detected, indicating resilience to climate change in these aphids. Phenological asynchrony can lead to a shift in the quality of host-food plants. In an experiment, *Orthosia cerasi* larvae fed on mature oak leaves showed reduced growth rates and smaller pupae compared to those fed younger leaves. This may impact populations through increased exposure to natural enemies and smaller pupae can indicate reduced fecundity.

This thesis contributes to knowledge of insect population trends and the potential role of climate in driving these declines. There is a need for further monitoring of woodland insects and research testing mechanisms proposed to drive insect responses to climate change. Such work should consider individual species and community-level response.

Acknowledgments

I am extremely grateful to my primary supervisor Karl, for guidance, support, and encouragement throughout this thesis. Thanks also to my secondary supervisor Tom, particularly for the initial R help and the guidance with the aphid chapter. Thanks also to Phil Warren and Ally Phillimore for an engaging viva and useful comments built into the thesis.

Thanks to Simon Leather for providing such a detailed and interesting data set on aphids, and to all the volunteers that helped to collect that data. Thanks also to Marc Botham for letting me take up some of your evenings to help me collect moths, without which my experiment would never have happened, thanks also for answering my endless questions about small quakers.

Thanks to everyone who I have shared an office with over the past four years. A special mention to Simon for being the fountain of R knowledge and to Leah for your friendship, chats about dogs and generally just making the office a brighter place.

Thanks to everyone who helped me with the collection of data in the Rivelin, particularly Tom Cavanagh for your dedication and enthusiasm.

A special mention to Bella, for working with me to figure out what to do with the Rivelin Valley data set and making it an enjoyable experience.

Thanks to my parents, for your unwavering support in whatever I want to do in life and my amazing Grandma for always having time to talk, and never letting me leave your house without the much-needed mountain of chocolate. Thanks to all of the friends who have helped and stuck with me along this journey. In particular, Curly for helping with fieldwork and making home life fun. Tash and the kids for being that escape from all things PhD that was often sorely needed, Vikki for your support even when you hate moths. Especially thank you to Claire, for being that one person that always understood and knowing exactly what to say to keep me going.

Also thank-you to new friends and colleagues at Reaseheath College for being amazing support during the end of my PhD and cheering me on for the viva.

The biggest thank you must go to my fiancé Jordan, without whom I would have quit and given up a long time ago. There are too many things to mention but thank you for sharing your knowledge, your help with all the fieldwork and feeding the caterpillars, cheering me on and still loving me even after you find caterpillars in my hair.

Finally, thank you to Flint the dog, for being the best fieldwork company and never failing to make me feel better.

Declarations

I declare that this thesis is a presentation of original work and I am the sole author. This work has not previously been presented for an award at this, or any other, University. All sources are acknowledged as references.

This thesis involved collaborations with various researchers: below I present the contributions of other researchers to each of my chapters. The work produced in this thesis was supported by the University of Sheffield Studentship.

In Chapter 2 I conducted the primary analyses and acted as lead author for this chapter, Karl Evans set up the long-term study and contributed to analyses decisions and writing edits.

Chapter 3 was submitted for publication in May 2019, accepted in January 2020 as Senior *et al.* (2020) in Global Change Biology. The chapter provided here is the initial submission and has undergone substantial changes for publication. Data for this chapter was collected by Simon Leather, I led on the paper conception and carried out all statistical analyses for initial submission with guidance from Karl Evans and statistical help from Tom Oliver. Luke Evans helped with additional analysis for the published version.

Chapter 4 is in preparation for submission. I led on the experimental concept and design with input from Karl Evans and Marc Botham. I led on the writing with input from both Karl and Marc.

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Chapter 1. Introduction

1.1.a Ecological impacts of climate change

Anthropogenic climate change is ranked as one of the most important threats to biodiversity (Sala *et al.* 2000). The past 100 years have observed almost a 1°C rise in average global temperature, with predictions suggesting a further increase to a global range of 2.0–4.9°C by 2100 (Raftery *et al.* 2017) (For UK based predictions see section 1.2). Current temperatures and those predicted to occur are within the range that organisms have experienced during previous climatic cycles. However, the rate of temperature change and the predicted future levels of CO_2 over the next 100 years are unprecedented (MacDonald 2010). These changes are already having a quantifiable ecological impact, with substantial shifts recorded in the distribution, phenology and population dynamics of organisms across a broad range of taxa worldwide (Walther *et al.* 2002, Parmesan 2006). Recently, the United Nations Framework Convention on Climate change Paris Agreement has pledged to limit warming to below 2°C, but ideally limiting the increase to 1.5°C (Rogelji *et al.* 2016). Predictions indicate that limiting increases to 1.5°C will impact ecosystems substantially less than a temperature increase of 2°C. For example, the number of plant and vertebrate species with a range loss of more than 50% is halved for the lower increase scenario and this reduction is even higher (66%) for insects (Warren *et al.* 2018). There is also an increasing consensus that extreme weather events are likely to become more frequent (Jentsch & Beierkuhnlein 2008; Harris 2018). The unpredictability of extreme conditions may be a greater challenge for many organisms than gradual shifts in mean conditions (Godfray 1994). Assessing and predicting the biological impacts of climate change is extremely important. Anticipation of change allows for proactive management for conservation and maintenance of ecosystem services (Root *et al.* 2003). There are, however, fundamental knowledge gaps surrounding the underlying biological mechanisms through which climate change is impacting biodiversity (Andrew *et al.* 2013). Understanding the mechanisms of biological impacts of climate change improves the capacity to predict and mitigate these impacts (Helmuth *et al.* 2005; Andrew *et al.* 2013).

1.1b. The importance of insects

Global climate change is affecting a variety of organisms which includes a strong impact on insect populations (Bale *et al.* 2002, Deutsch *et al.* 2008). Insects constitute the vast majority of terrestrial species richness and biomass (Favila and Halffter 1997). They are found in all habitats and support a considerable proportion of ecological functions and ecosystem services (Prather *et al.* 2013; Dangles & Casas 2019). Important functions include valuable prey items and ecosystem engineering (Weisser & Siemann 2013); pollination (Klein *et al.* 2006; Ollerton *et al.* 2011); nutrient cycling (Seastedt & Crossley 1984) and biological control of agroecosystem pests (Howarth 1991). The worth of insect services is estimated to be at least $57 billion in the US alone (Losey & Vaughn 2006). Many insect species are also important as detrimental agricultural pests, disease vectors and invasive species (Worner & Gevrey 2006).

Due to their central roles in many ecosystems, insects can also be important bioindicators for quantifying the effects of environmental change (McGeoch 1998; Thomas 2005). Recent research indicating large insect declines worldwide (Leather 2018; Forister *et al.* 2019) has significantly raised concerns about what is driving their declines, and what this indicates for wider ecosystems. Insects are ectothermic (their body temperature regulation depends on an external source) and are highly dependent on environmental cues for behaviours. Their distributions encompass the ranges of many other taxonomic groups (Favila & Halffter 1997). Insects are small in size and thus occupy more specific microhabitats and can be more thermally sensitive than other taxa. Insects are therefore highly sensitive to local conditions, they have a quick generation times and many have high mobility which aids them to move in response to environmental change (Wolda 1988). Changes in insect populations can, therefore, be indicative of other changes in the environment (Gerlach *et al.* 2013). Insect data sets can be generated relatively easily compared to other taxa. There are, however, several limitations with current insect research, particularly as they are under-represented relative to their diversity (Kharouba *et al.* 2018). Long-term monitoring data is limited and there are taxonomic and spatial biases, European insects, for example, are often over-represented (Cardoso & Leather 2019). Furthermore, even within these areas, there is a lack of good quality data for insects that aren't pests or butterflies (Andrew *et al.* 2013).

1.1c. Insect sensitivity to climate change

As effective bioindicators, insect population changes have the potential to provide a wider understanding of the ecological impacts of climate change (Erhardt and Thomas 1991; Hassall 2015). Moreover, insects are thought to be highly sensitive to changes in climate as their basic physiological functions, such as movement, development and reproduction, are strongly influenced by environmental temperature (Bale *et al.* 2002). Insect activity levels are also strongly governed by other climatic variables such as humidity and precipitation. They have complex and seasonal life stages making them highly sensitive to local conditions and thus local changes in climate. As insect populations often have a more rapid response to adverse environmental change than longer-lived organisms (Erhardt and Thomas 1991). They are thus likely to provide a rapid indication of climate change impacts on other taxa with which insects interact, such as vertebrates occupying higher trophic levels that depend on insects as food sources.

Temperature affects development time and fecundity and therefore the appearance and dynamics of insect populations are heavily influenced by ambient temperature (Kingsolver 1989). Ectothermic organisms, including insects, find optimum conditions for development within a certain range of temperature which varies between species (Netherer & Schopf 2010). Populations of a given species are established where the climatic requirements necessary for achieving adaptive seasonality are met (Régnière 2012). Many insects also rely on plants for food, shelter and oviposition, levels of precipitation and humidity directly impact the amount of vegetation and the structure and composition of plant communities, which thus in turn impact insect habitats. Changes in climatic conditions are therefore likely to determine insect habitat suitability.

Insects have distinct life-stages that vary in traits such as size, morphology and physiology. These life-stages often require different seasonal environments, including differing habitats and microclimates. The different stages of an insect life cycle are likely to have differing thermal sensitivities, physiological sensitivities and responses (Kingsolver *et al.* 2011). Insects are therefore more sensitive to climate change than species with less distinct life-stages as each life-stage is likely to have to deal with a different, and potentially opposing, shifts away from optimal climatic conditions. Furthermore, the life-stage that has the most influential impact on population dynamics can vary depending on climatic conditions (Dempster 1983; Kingsolver 1989; Crozier 2003).

Many temperate insects also undergo diapause, which requires specific environmental cues for induction and termination. Insects which overwinter often require a certain amount of temperature reduction to induce diapause or increase frost resistance (Bale & Hayward 2010). These species are likely to be negatively sensitive to increases in winter temperature (Bale *et al.* 2002; Forrest 2016). Changes in temperature and moisture, including humidity and precipitation, have been found to impact the duration and termination of diapause (Ingrisch 1986; Tauber *et al.* 1998; Bradshaw and Holzapfel 2010; Lehmann *et al.* 2017).

This reliance upon environmental conditions during overwintering leaves diapausing insects increasingly vulnerable to climate changes which disrupt the timing of these cues.

Organisms with a low tolerance for warming, such as those nearing their thermal limit in tropical habitats, may be at higher risk from climate change (Desutsch *et al.* 2008). In comparison, it was thought that insects in temperate habitats may, benefit from increased temperatures as these zones are typically several degrees below optimum for development (Bale *et al.* 2002). Recent research has challenged this and, by incorporating additional factors into their models, such as insect warming tolerance and temperature-dependent development, indicate that both tropical and temperate species are similarly sensitive to climate change (Johansson *et al.* 2019). The relative vulnerability of a species to changes in climate will be associated with many factors including dispersal ability, reproductive rates, diet and habitat requirements as well as physiological tolerences (Pacifici 2015). Determining the relative importance of these creates a number of challenges. There is also a considerable lack of knowledge regarding the relative sensitivities of various insects. For many species, the set of climatic parameters and their interaction with biotic factors, necessary for development is insufficiently defined (Ayres & Lombardero 2000; Netherer & Schopf 2010). It is therefore difficult to adequately assess their likely sensitivities to climate change without further research.

1.1d. Knowledge gaps

The generation of further data regarding the impact of climate change on insects would be highly beneficial for both preserving the ecosystem services that insects provide and also as a tool for understanding the ecological implications for the wider ecosystem. For insects there is an overall lack of quantitative data (Troudet *et al.* 2017). However, there has been substantive research assessing the potential insect responses to anthropogenic climate change. This has generated evidence showing the general patterns of change in insects such as range shifts and changes in phenology (e.g. Parmesan 1999; Hickling 2005; Visser & Holleman 2001). A review of the climate literature assessing insect populations by Andrew *et al.* (2013) shows that there is a general tendency for research to focus on these population changes with relatively fewer publications focusing on the biological mechanisms underlying these changes. This review is now six years old but their findings are still largely relevant to current research. Andrew *et al.* (2013) also show that the literature exhibits a strong focus on pest species, insects of conservation concern and Lepidoptera (Figure 1.1),

(specifically butterflies with a recent increase in the number of moth studies, e.g. Coulthard *et al.* 2019; Bell *et al.* 2019)

Thomas *et al.* (2005) argued that trends in butterflies are good representatives of environmental change in all except the saproxylic insect groups. However other studies have indicated that butterflies may not be good representatives of other taxa (Ricketts *et al.* 2002). Poor correlations, for example, were found between species richness of butterfly and dragonfly in the UK at a large spatial scale (Prendergast & Eversham 1997). Butterflies may differ strongly from other taxa as most UK butterflies are thermophiles and they may have different habitat requirements (Ricketts *et al.* 2002). These differences are likely to be significant enough, at least in some circumstances, to result in widely different responses to climate change between taxa. Despite the strong data sets and recordability of butterflies, further research is needed to corroborate the use of butterflies as indicators of wider insect, and ecosystem, climate change impacts (Fox *et al.* 2013).

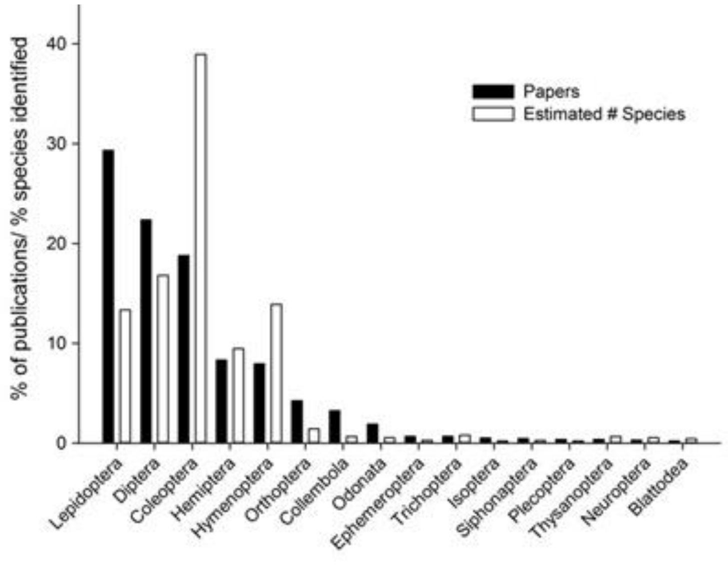

Figure 1.1. The proportion of published papers (n = 1703), of the top 18 studied insect orders, regarding climate change relative to the relative proportion of species in each order of all insects identified (n = 898 730 species) (Andrew *et al.* 2013).

1.2. UK Climate change trends

Concurrent with other parts of the world, the climate is also undergoing substantial changes in the UK. Central England Temperature (CET) has risen about one degree Celsius since the 1970s (Figure 1.2.) (Jenkins 2010). Mean annual temperature increases have been greater in winter (1.1°C) than in summer (0.2°C). Temperature in the UK has also risen at a more rapid rate than that of the global average land-surface and global mean temperature (Jenkins 2007). All regions of the UK have experienced an increase in the contribution to winter rainfall from heavy precipitation events and summer rainfall has shown a decrease in all regions apart from North-East England and North Scotland.

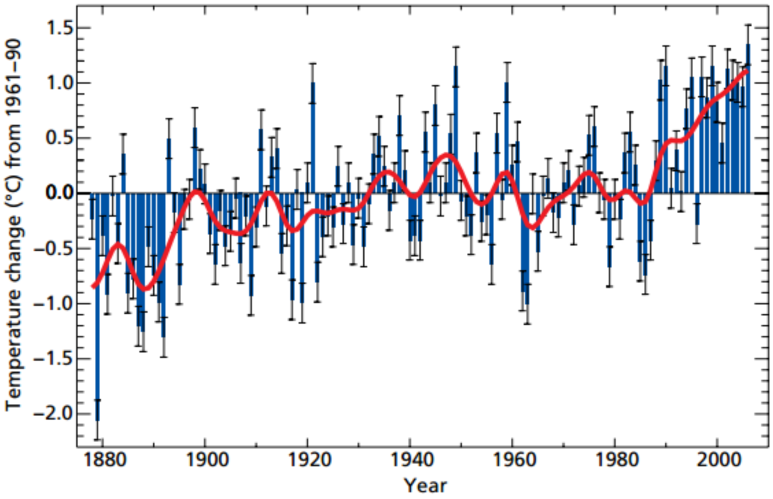

Figure 1.2. Changes in CET annual values (blue bars) from 1877 to 2006 relative to the average over the 1961-90 baseline period (about 9.5 ºC) in the UK. Error bars enclose the 95% confidence range. The red line emphasises decadal variations. (Jenkins 2010).

Many of these observed trends are attributed or directly linked to global man-made emissions of greenhouse gases. Most research agrees that the emissions are going to have a continuing impact on global climate and there are several projected scenarios for future climatic change within the UK. UK Climate Impact Programme (UKCIP) have indicated that the average UK temperature could rise by between 0.3 to 2.6 ^{o}C in low future emission scenarios and between 1.9 to 6.3 ^{o}C in high future emission scenarios, projected for 2080-2099 from the 1981-2000 baseline (Lowe *et al* 2018). Currently, targets to maintaining warming to less than 1.5° are not being met (Tollefson *et al.* 2018), with emissions continuing to rise it may be expected that the higher UK temperature increase is more likely. Projections indicate regional variation, with a north to south warming gradient and higher temperature increases predicted for the South overall. High summer temperatures will increase in their frequency potentially reducing soil moisture. Very cold weather in winter will decrease (Jenkins 2010) and the magnitude of winter warming may be higher in Scotland (Lowe *et al.* 2018).

Changes in precipitation levels are more unpredictable. The mean annual precipitation levels are expected to change very little, however, between years there is expected to be high levels of variability in precipitation (Lowe *et al.* 2018) and the relative precipitation of each season is expected to change. Winter precipitation is expected to increase with a reduction in snow and many areas experiencing long periods without snowfall. (Hulme 2002; Riley 2003). Summer precipitation projections are much more variable. Predictions indicate that there is likely to be reduced cloud cover (Hulme 2002) and, at the extreme, summers could become up to 50% drier or 10% wetter, with central predictions indicating that summers will become 20-30% drier. It is also important to note that an increase in extreme precipitation events is predicted and therefore, although summers may become drier on average, there is also a strong likelihood of more intense, heavier rainfall events (Jenkins 2010; Lowe *et al* 2018).

1.3. Climate change impacts on insects

1.3a. Abundance and range shifts in the UK.

Research addressing climate change impacts on insects often focuses upon species relative abundances and distributions. The majority of insect species are likely to shift their ranges toward higher latitudes and elevation, rather than adapt within current ranges to warmer temperatures (Thomas 2010). Range margin shifts, changes in distribution areas and changes in abundance have all been found to show positive associations with climate warming (Figure 1.3) (Parmesan *et al.* 1999; Roy *et al.* 2001; Warren *et al.* 2001). There are many insect species which have a northern range boundary in the UK. A warming climate results in more thermally suitable habitats at the cool edges of the species current distribution both across latitude and elevation (Walther *et al* 2002). Therefore, there is high potential for increased abundances and greater distributions of UK insect species (Although see section 1.3b for a discussion on current range expansions). A positive association has also been demonstrated between abundance and occupancy (Gaston *et al.* 2000), such as British butterfly species in which those that have expanded their population ranges have also increased in abundance (Figure 1.4) (Pollard and Moss 1995; Warren *et al.* 2001).

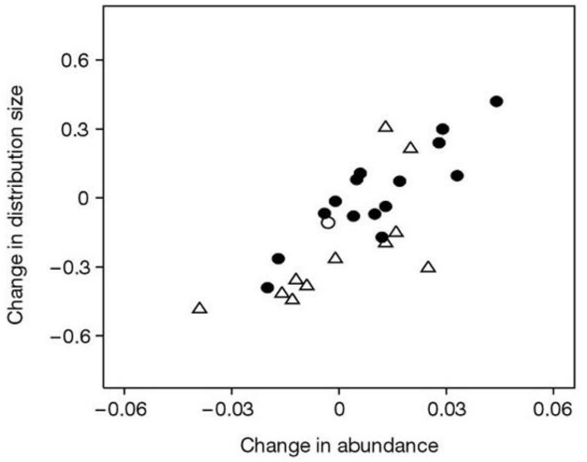

Figure 1.3. (**Left**) The range changes of the comma butterfly (*Polygonia c-album*) black circles show Comma records for 1970–82 and 1995–99. Green circles indicate apparent extinction (recorded 1970–82; not 1995–99); pink circles indicate colonization (no record 1970–82; record 1995–99) (Source: Warren *et al.* 2001).

Figure 1.4. (**Right**) The relationship between change in population abundance between 1976-2000 and the change in distribution size (the proportion of occupied sites) of UK butterfly species between 1970–82 and 1995–99. Open triangle for sedentary specialists, filled circles = mobile wider-countryside species open circle = mobile specialist (Source: Warren *et al.* 2001).

Empirical evidence has indicated a shift in northern range margins in UK insect populations. Many British butterfly species have expanded northward (Warren *et al.* 2001) and more recent research has shown that this trend is mirrored in many other insect groups (Thomas & Gillingham 2015). The brown argus (*Aricia agestis*) for example has shown a rapid increase in its northern range margin (Pateman *et al.* 2012). Southerly distributed British Odonata species increased in range size and expanded northwards at their range margins (Hickling *et al.* 2005). Insects are also shifting their range on an elevational scale, as conditions at higher elevations will become more suitable for organisms with continued climatic warming (Hodkinson 2005; Hardy 2010).

Most British insects are expected to expand their ranges in response to climate change. However, northerly distributed species, or those with a southern range boundary within the UK, will have little capacity to expand northwards (Robinet & Roques 2010). Warming southern ranges of insects may reduce thermally suitable habitats (Franco *et al.* 2006; Wilson *et al.* 2007; Maes *et al.* 2010) and is likely to result in range contractions and population declines (Hill *et al.* 2002). Contractions have been demonstrated far less frequently than range expansions. This may be a result of the methods of data collection, as a species must be lost within a region to be categorised as extinct, but the detection of one population in a new area is considered a range expansion (Menéndez 2006). Furthermore, species with their southern range in the UK are generally poorly studied (Hickling *et al.* 2006). Some research has investigated the declines of cold-adapted Lepidoptera (Chen *et al.* 2011; Dieker *et al.* 2011; Fox *et al.* 2014). Morecroft *et al.* (2009) found declines in moths at upland and northern sites and significant decreasing trends were shown in 94% of northern restricted UK Moths, compared to a variability in population trend for southern restricted moths (24% of species declined significantly, while 27% increased significantly) (Fox *et al.* 2014). Two, of the four northern restricted UK Odonata species, also showed declines in range size and northward shifts (Hickling *et al.* 2005). With regards to elevational range shifts, butterflies with montane distributions, for example, have become extinct at low elevation sites and colonized sites at higher elevations (Hill *et al.* 2002).

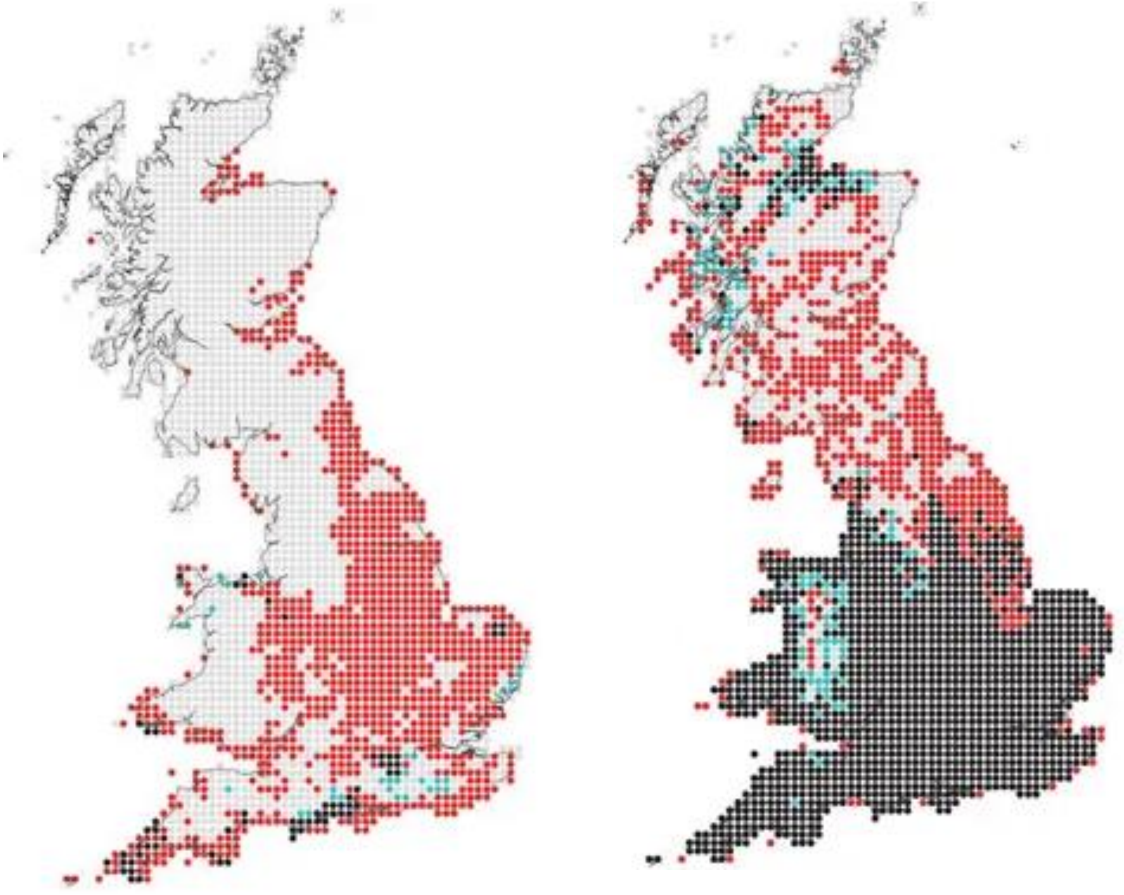

Figure 1.5. Indication of where range shifts are lagging behind climate change for UK butterfly species silver-studded blue, (*Plebejus argus*) (**left**) and speckled wood, (*Pararge aegeria*) (**right**). Black circles = suitable climate, species present. Grey circles = unsuitable climate, species absent (show where observed 1995–99 and simulated distributions agree). Red circles = predicted suitable climate, species not recorded. Blue circles = species recorded, climate deemed unsuitable (Warren *et al.* 2001).

1.3b. Variation in the rates of range shifts and their causes

Species response rates to climate change are highly divergent (Mair *et al.* 2012). There have been variable trends measured between species, many of which do not follow the predicted rate or pattern of change (Figure 1.5). Some species range expansions have exceeded the rate of warming whilst others have experienced range contractions where expansions were expected (Warren *et al.* 2001; Chen *et al.* 2011; Fox *et al.* 2014). British butterfly species are expected to expand their ranges in response to a warming climate, but many have experienced declines in distribution and range size due to declines in habitat availability and quality (Warren et al 2001; Oliver *et al.* 2012). The magnitude of range shift also varies interspecifically with shifts ranging from 35 to 240 km poleward (Parmesan *et al.* 1999). Some warm-adapted moth species have also experienced population declines in the south of the UK (Fox *et al.* 2014), these declines may therefore not be attributed to climate or this may be in response to changes other than temperature, such as changes in precipitation. Furthermore, contrasting to findings of Warren *et al.* (2001); Mair *et al.* (2009) found no evidence that butterfly species which had expanded their range northwards had also increased their population abundance.

Species, therefore may not be responding at the same rate as the climate is changing and are not tracking climate change as expected. Warming rates have differed over time (Solomon *et al.* 2007), and the rate of species response may be expected to mirror this variation, for instance, occur more quickly during periods of warming. Mair *et al.* (2012) investigated differences of range expansion in UK butterflies during two separate periods of warming (first period considered warming between 1970–1982 and 1995–1999, second period considered warming between 1995–1999 and 2005–2009). Their research revealed greater range expansion during the second period, despite having lower levels of warming. This indicated that range shifts were not occurring in direct relation to a period of warmer temperatures. The authors suggested that the butterflies may still be expanding from the first warming period during the second. Insect range expansion may, therefore, be lagging behind the rate of climate change. Menendez *et al.* (2006) also found that butterfly richness changes as a result of range expansions had only achieved a small proportion of what would be predicted under the level of warming (Menendez *et al.* 2006). Their results indicated that the level of climate warming that has already taken place is likely to continue to impact species range shifts and community composition for decades to come, even without any further changes in climate (Menendez *et al.* 2006). A translocation experiment also strengthened evidence of a lag in response to climate change by introducing two butterfly species, marbled white (*Melanargia galathea*) and small skipper (*Thymelicus sylvestris*) (small skipper) to an area which was beyond their current range boundary, but determined to be climatically suitable (Willis *et al.* 2009). Both species successfully colonised and expanded their range over a six-year period.

In addition to a delayed response to warming, habitat loss and fragmentation is also likely to be affecting a species ability to respond to climate change (Warren *et al.* 2001). Habitat degradation will have direct impacts on insect populations but is also likely to act synergistically with climate change (Fox *et al.* 2014). The spatial and temporal availability of habitat is crucial for the persistence of populations even within areas of suitable climate. Although suitable habitat may become thermally available as a result of climate warming, new habitats may be fragmented and too isolated to be colonised (Hill 1999). Research on both butterflies and moths in the UK has indicated that there are both synergistic and opposing effects of climate change and habitat loss (Warren *et al.* 2001; Fox *et al.* 2014).

Life history characteristics and other species traits are may also affect the colonisation of new habitats under a warming climate. Research has investigated traits including dispersal potential, generation time; offspring number; diet breadth and mating system. Beckman *et al.* (2015) found a positive relationship between oviposition behaviour, habitat specialism and geographical distribution and range shifts in British Orthoptera. Insect colour traits may also be related to how a species responds to climate change. Zeuss *et al.* (2014) found that dark-coloured insect species were favoured in cooler climates and light-coloured species benefited from a warming climate and in Sweden, moth species with more variable colour patterns were associated with more rapid range expansion (Forsman *et al.* 2016). Lurgi *et al.* (2012) further suggested that diet specialism and to some extent, body size are good predictors of how species within the same community will adapt to changing conditions. However, Angert *et al.* (2011) investigated traits considering many taxa and found, that although some traits were indicative of range shifts, they were limited in a predictive capacity. Furthermore, the results found by Beckman *et al.* (2015) were no longer significant when two strongly responding species were omitted.

Across the current literature, there is limited predictive and explanatory power from analyses of how traits are linked to rates of range shifts. Although a number of studies find significant associations, the variation explained is generally low, and the traits that are identified for a given taxonomic group often vary between studies (Beckman *et al.* 2015). It may be likely that characteristics of species beyond those commonly examined explain additional variation, such as physiology, trophic relationships or trait interactions (Beckmann *et al.* 2015). However, it has been suggested it is the extrinsic factors such as habitat fragmentation that will be the larger driver of range shift potential (Hill *et al.* 1999; Honnay *et al.* 2002; Ibanez *et al.* 2006; Heikkinen *et al.* 2010). The taxa which have been studied in relation to species traits in the UK have been relatively small.

1.4. Mechanisms driving change in insect populations

1.4.a Direct Impacts

1.4.ai Climate dependent activity levels

Insect flight and other active behaviours activities are influenced directly by environmental conditions such as ambient weather conditions (Netherer & Schopf 2010; Berthe *et al.* 2015). The time available for flight can strongly influence reproductive success (Kingsolver 1983; Springer & Boggs 1986). An increase in ambient temperature may facilitate greater daily flight activity (Figure 1.6) by increasing the occurrence of minimum thresholds required for flight (Battisti *et al.* 2006) and result in greater mate location and reproduction (Ishiguri & Shirai 2004). The purple edged copper, *Lycaena hippothoe*, showed mate-searching behaviour more frequently and in a wider area under warmer, more favourable conditions (Fischer & Fiedler 2001). An increase in temperature may also increase other mating activity levels such as in the brown planthopper, *Nilaparvata lugens*, which was found to increase acoustic mate-locating behaviour at higher temperatures (Long *et al.* 2012). Although relatively understudied, particularly for non-pest insects, the propensity for a warming climate to increase mating behaviours may be likely to contribute to an increase in a species abundance.

A warming temperature may increase the total distance which an insect can travel (Ishiguri & Shirai 2004). This allows for greater dispersal opportunity and thus is a likely mechanism driving range expansion. This has been shown for the pine processionary moth, *Thaumetopoea pityocampa*, which exhibited a rapid range shift during an unusually warm summer that created an increase in the number of dispersing females (Battisi *et al.* 2006). The decision to disperse can be affected directly by other climatic factors such as wind-speed, precipitation and humidity. Warming may also increase animal physiological demands for nutrients and energy and thereby motivate increased movement throughout their habitats and potentially further afield (Schmitz & Barton 2014).

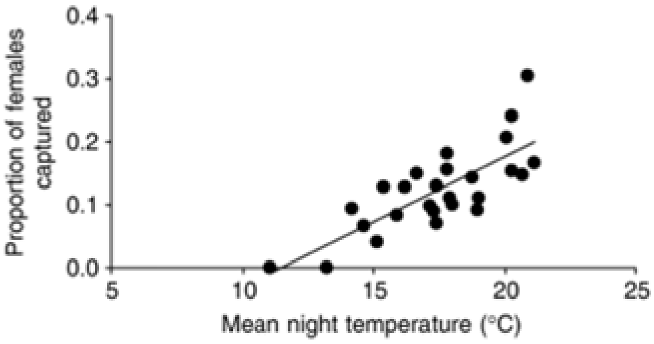

Figure 1.6. The relationship between mean night temperature and the level of flight activity of female pine processionary moths in an outdoor rearing cage (measured as a proportion of the number of females caught on a sticky trap compare to the total number of females) (Battisti *et al.* 2006)

1.4a ii Growth and Development

The development and growth of insects relies heavily on external conditions, especially temperature. A change in climatic conditions is therefore likely to impact the rate and success of insect growth and development. Generally, the temperature-body size rule indicates that increased temperatures should directly decrease the number of day degrees required for development and lead to a reduced total body size (Atkinson 1996). Insects undergo several key stages of growth and development and each life-stage requires certain environmental conditions to be met.

Eggs cannot thermoregulate as they lack mobility and functional organs, therefore embryos must rely on cellular mechanisms to survive thermal stress (Feder 1997). Development and survival of eggs, therefore, depend strongly on local temperature (Potter *et al.* 2009; Woods 2010). The temperature in which an egg is kept may only impact the embryonic stages such as survival, hatching size and time taken to hatch. It may also, however, have longer-term effects on larval and adult stages (Potter *et al.* 2010). Minor increases of daily temperatures during the egg stage of the Carolina sphynx moth (*Meduca sexta*), for example, lead to smaller larvae with slower growth rates. In some insects, however, the larvae stage is less resilient to temperature changes than the egg stage (e.g. Diptera: Chironomidae (Schütz & Füreder 2019)).

The development of juvenile insects, larvae and nymphs, has been shown to differ with a change in temperature. The rate at which an additional instar was achieved during nymphal development for British grasshoppers, for example, was found to increase with temperature (Willott & Hassall 1998). Body size and time to pupation decline with increasing temperatures up to an optimal threshold (Atkinson 1996; Davidowitz & Nijhout 2004) but the rate of growth increase varies between species. A more rapid larval growth and development due to higher temperatures may lead to early reproduction. Consequently, there is potential for subsequent generations to develop within the same season, rather than overwintering in a larval stage (Altermatt 2010). This may contribute to population growth and also an increased rate of evolutionary processes and adaptation to a changing environment. Adult body mass, however, is strongly correlated with production of eggs (Diamond and Kingsolver 2010) a smaller body size due to warming may, therefore, lead to reduced fecundity. Furthermore, the potential for additional generations can lead to a developmental or ecological trap, by which additional generations are unable to complete their life cycles before winter, thus suffering high mortality. This has been proposed as a major driver of decline in the wall butterfly *Lasiommata megera* in warmer parts of its European range (Dyck *et al.* 2014).

Endopterygote insects are those which undergo a pupal stage. Research considering the thermal sensitivity of pupae are more limited than for other life-stages (Fittinghoff & Riddiford 1990; Kingsolver *et al.* 2007). Some studies have shown that a change in climatic variables impacts pupal survival (Radchuk *et al.* 2013). The Carolina sphynx moth pupae experienced reduced survival, for example, at temperatures of 15^{o}C or 35^{o}C (Kingsolver *et al.* 2010). Rates of development also increased rapidly as temperatures warmed from 20^{o}C to 30^{o}C but declined above 30^{o}C. Pupal temperature may impact adult morphology, for example, the speckled wood butterfly, *Pararge aegeria*, developed smaller head sizes under increased temperature during pupation (Stevens 2004). Although other aspects of body size were unaffected, smaller heads could lead to impacted eye size (Rutowski 2000), proboscis (May 1992) and potentially flight ability by shifting the centre of gravity (Srygley & Dudley 1993). A more recent study on a global pest, the Diamondback moth (*Plutella xylostella*) found that exposing pupae to warmer temperatures typically exacerbated negative effects experienced by larvae also exposed to high temperatures (Zhang *et al.* 2015). The combination of high temperature during these two life-stages reduced almost all aspects of adult performance, including male longevity, female oviposition and overall fecundity (Zhang *et al.* 2015). There is relatively little investigation regarding the consequences of increased pupation temperatures. However, there is some evidence to suggest climate-driven changes to pupation temperature could hold significant consequences for insect development (Stevens 2004; Kingsolver *et al.* 2011; Zhang *et al.* 2015) which may impact population dynamics and additional research could uncover further effects of altered pupation conditions.

1.4a iii Over-winter success

Insects are able to survive cold winter temperatures through freeze-tolerant and freeze avoiding strategies (Salt 1966; Bale & Hayward 2010). With few exceptions (see Hart & Bale 1997) most UK insects adopt a freeze avoiding strategy and undergo a period of diapause, during winter (Denlinger 2002). Diapause enables insects to survive seasonally recurring environmental stress and to synchronise growth, development and reproduction with favourable annual conditions (Denlinger, 2002). There is little direct research on overwintering success and predictions on these effects have been based predominantly on the existing knowledge of thermal tolerance under controlled or natural conditions and a small number of manipulation experiments (Coulson *et al.* 2000; Konestabo *et al.* 2007). There are, however, several important ways in which a changing winter climate may impact insect populations.

Insect species may receive some benefits from warming winter temperatures, as insect mortality usually decreases with an increase in temperature (Bale & Hayward 2010). Crozier (2004), for example, found that warmer winter temperatures increased the overwintering survival of the skipper butterfly (*Atalopedes campestris*) at its northern range margin. Winter temperatures were directly influencing the persistence of this species at its northern range edge, and Crozier (2004) indicated that winter warming was a prerequisite for driving range expansion at these cool range edges.

Photoperiod is the primary cue for diapause initiation (Leather *et al.* 1993). Climate change will have no bearing on day length, but the effectiveness of day length as an indicator of seasonal conditions and temperature may be reduced (Bale & Hayward 2010). Higher temperatures which coincides with photoperiodic cues for the induction of diapause may reduce the occurrence of diapause or shorten the duration. Diapause can be averted if a certain threshold temperature is exceeded. In the UK, for example, the blue bottle fly (*Calliphora vicinia*) will not enter diapause under short-day conditions if it is warmer than 15°C (Vaz Nunes & Saunders, 1989; Saunders & Hayward, 1998). If a species is able to survive winter outside of diapause, a capacity to avert this overwintering strategy may provide a selective advantage (Tougou *et al.* 2009).

For many temperate species, the decoupling of photoperiod and temperature cues as a result of climatic warming may have detrimental impacts. Higher temperatures, which lead to late entry of diapause, increases the risk of an insect encountering cold stress prior to the establishment of cold-tolerance mechanisms (Bradshaw *et al.* 2004; Rinehart *et al.* 2007). Climate change is also unlikely to consistently impact throughout the winter season, aversion of diapause may occur if early winter temperatures are mild but more severe conditions later in winter could dramatically increase insect mortality.

Emerging from diapause and winter dormancy is also likely to be altered by climate change. Diapause is often terminated much earlier than the occurrence of favourable conditions. Insects will, however, then remain in a post-diapause quiescence (Hodek 1999) which usually maintains many of the stress-tolerance mechanisms of diapause (Hayward *et al.* 2005). During post-diapause, however, insects are ready to emerge and develop once they experience favourable conditions. The initiation of development is often concurrent with the termination of many stress-tolerating mechanisms (Hayward *et al.* 2005). Consequently, short warm spells after the termination of diapause could result in a premature resumption of development, exposing insects to later cold spells.

Low temperatures during winter reduce the energetic costs of diapause which allows the retention of nutrient reserves required for post-diapause processes (Hahn & Denlinger, 2007). Post-diapause energy reserves in larvae are required to support pupation, metamorphosis, construction of adult tissues, as well as feeding (Leather *et al.* 1993). Changes in climatic conditions during winter, such as warming temperatures, may disrupt the metabolic balance of diapause and result in impacts upon survival and fecundity. Warming winters may also have a delaying effect on emergence from diapause. Many insects require exposure to a level of chilling before termination of diapause (Hodek 2002; Lehmann *et al.* 2017). A lack of chilling due to warming winters has been shown in a small number of species to delay spring emergence (Bosch & Kemp 2003; Chuche & Thiéry 2009; Stålhandske *et al.* 2015). Most research has shown that early spring emergence is being increasingly recorded for many insect species (Roy & Sparks 2000; Gordo & Sanz 2006; Hassall *et al.* 2007; van Asch *et al.* 2007) but there are few studies exploring the delaying effects of warmer winters and the comparative physiological consequences upon survival and fitness of early or late-emerging insects.

Diapause can occur in any life-stage, egg, larva, pupa or adult, but the life-stage is consistent and specific within the same species. It has been suggested overwintering stage may have a substantial impact on a species vulnerability to climate change (Fox *et al.* 2013). Significant relationships between moth declines and overwintering life-stage have been found in both the UK and in the Netherlands (Conrad *et al.* 2004; Groenendijk & Ellis 2011). Moths which overwintered as eggs, showed the largest overall declines and those which overwinter as larvae or pupae were also exhibiting population reductions. Only those which overwinter as adults showed increasing population trends. Warmer winters, which have become more frequent due to climate change, are thought to be driving the relationship between overwintering-stage and population declines (Conrad *et al.* 2004). However little research has explored the underlying mechanisms of this relationship and the biological impacts of climate change upon these stages during diapause.

1.4.b. Indirect impacts

1.4. bi Host-Plant interactions

Many insects rely on a relationship with a host plant and a response to climate change, therefore, is likely to be strongly impacted through climate-mediated changes in plant growth and abundance. Plants may experience increased growth rate and lead to greater population abundances in insects. Climate change is likely to have an impact on the physical structure of host-plant vegetation. For example, simulated increases in summer rainfall lead to an increase in vegetative cover and a subsequent increase in the abundance of Auchenorrhyncha (Masters *et al.* 1998). Climate change is also expanding host-plant ranges, which may facilitate increased distribution and abundance of their associated insects (Bale *et al.* 2002).

However, insects are likely to respond more rapidly to climate change than their plant hosts. Obligate specialists, for example, might not track changing temperatures if they are dependent upon a poorly dispersing species (Gilman *et al.* 2010). The ability to switch hosts or utilize novel hosts may provide a means for more rapid range expansion. Research considering the pine processionary moth found that relative growth rate and mortality were not affected when the caterpillars were fed upon a secondary and novel host. This would allow for potential expansion out of its current range into areas lacking their primary host plant (Stastny *et al.* 2006). In the UK rapid expansion of the brown argus butterfly (*Aricia agestis*), at 2.3 times faster than the rate of climate warming, has been attributed to more widespread use of secondary plant hosts (Thomas *et al.* 2001). The brown argus was typically considered relatively specialised to using rockrose (*Helianthemum nummularium*). This host was typically utilised by the butterfly on south-facing slopes, where the plant grows in short turf and provides a warm micro-climate. Climate warming has increased the thermal suitability of other sites allowing for the successful use of Geraniaceae plant species, which are highly widespread (Pateman *et al.* 2012). For this species, increased temperature has facilitated a shift in species interactions and driven rapid population increase and range expansion.

1.4. bii Quality of food and resources

Elevated temperature and CO_2, typically alter the phytochemistry of leaves by increasing carbohydrates and decreasing nitrogen content (DeLucia *et al.* 2012). This is likely to have significant consequences on insect performance by altering foliar nutrient quality and plant defences (Jamieson *et al* 2015). Insect responses include prolonged development, increased food consumption and reduced growth (Roth & Lindroth 1995). These responses vary markedly between species and between the same species on different host plants. Increased food consumption may sufficiently compensate for reductions in nutritional quality, which has been shown for the gypsy moth feeding on paper birch (*Betula papyrifera*) exposed to high CO_2 (Roth & Lindroth 1995). However, increased consumption of aspen (*Populus tremuhid*), in the same study, resulted in greater exposure to plant defence compounds which lead to reduced food conversion efficiencies and ultimately a reduction in growth rate. The nutritional quality of host plants can also impact insect fecundity (Traw *et al.* 1996; Awmack & Leather 2002). Egg size and quality, the provision of resources to eggs, and the choice of oviposition locations may all be influenced by plant quality (Awmack & Leather 2002). Therefore, alterations in nutritional quality has the potential to impact population dynamics and viability.

1.4b iii Host-Plant Phenological Synchrony

The nutritional quality of available food may depend upon the timing of key insect life-stages. Generally, there is an annual pattern in temperate insect species as there is clear seasonality of favourable environmental conditions. Climate change may be shifting these activities as such that they may occur outside of these favourable conditions resulting in fitness consequences in terms of reduced survival or fecundity (van Asch & Visser 2007; Visser & Gienapp 2019). Successful growth and survival in herbivorous insects is often reliant on a closely synchronised relationship with host plant phenology (Bale *et al.* 2002). Insects exhibit phenotypic plasticity to respond to the annual variability of plant phenology.

Climate change is, however, altering the environment from that in which the plant-insect relationship has evolved (van Asch & Visser 2007). Both the type and strength of response to specific environmental changes and timing of environmental cues can vary widely between interacting species. Subsequently, there is a strong chance that insect-host plant asynchrony may occur. There have been several recorded shifts in insect spring phenology and the subsequent temporal mismatch with host plants. It is assumed that temporal mismatch is a result of species-specific responses to changes in climate (Renner & Zonner 2018) however the mechanisms by which these specific responses arise are largely unknown. There is also limited wider understanding of the subsequent biological impacts on insect physiology and the ultimate shift in population dynamics.

In response to asynchrony with interacting species, directional selection is likely to occur in the phenology of insects. However, the response to selection may not be strong enough to restore synchrony at a sufficient rate (Singer and Parmesan 2010). Climate change may disrupt the overlap between plant flowering phenology and that of associated pollinators (Memmot *et al.* 2007) reducing the availability of pollen and nectar resources for pollinating insects. This may be particularly prevalent in species with limited diet breadths (Memmot *et al.* 2007) and could lead to increase mortality rates. There is also, however, possibilities for novel pollinator-flower interactions to arise and buffer these effects (Burkle *et al.* 2013).

Phytophagous insects may also suffer survival and fitness consequences as a result of early or late emergence. In phytophagous insects, the winter moth (*Operophtera brumata*) eggs, for example, which hatch prior to the oak bud burst may starve or suffer growth and development consequences from delayed feeding. Those which hatch after the oak bud burst will commence their feeding on older leaves (Buse *et al.* 1996). Older leaves are nutritionally less suitable for many insect larvae, as they can be harder to digest and contain more tannins. Buse *et al.* (1998) found that in the winter moth, this lead to smaller females with a reduced egg load (Buse *et al.* 1998). More recent research has found similar trends in the western tent caterpillar (*Malacosoma californicum pluviale*) finding that a phenological mismatch increased development times due to a prolonged first instar (Kharouba *et al.* 2015). These observed trends are limited to a small number of species, typically Lepidoptera. Few other taxa have been studied although Sycamore aphids (*Drepanosiphum platanoides*) have also been shown to suffer reduced growth and fecundity in response to late-hatching relative to their host (Dixon 1976). Current predictions about wider Lepidoptera and other phytophagous insects are based on a small number of taxa which may not represent general response to phenological mismatch.

1.4b iv Insects in higher trophic levels

Phytophagous insects in the second trophic level have received the majority of attention when assessing impacts of climate on interactions between species (Visser & Holleman 2001). Conversely, the impacts on higher trophic levels are poorly understood (Chen *et al.* 2019). In insects, this includes predatory insects (Boullis *et al.* 2015), parasitoids (Castex *et al.* 2018) and hyperparasitoids (Chen *et al.* 2019). Within insects, as well as between insects and plants, there is also likely to be interspecific variation in the response to changes in climate (Hance *et al.* 2007).

Predation and parasitism rates may be reliant on a synchronous relationship with their prey or host. For parasitoids, this is especially important as each species is often highly specialised on a small number of host species, as well as upon specific life stages (i.e. eggs, larvae or pupae) (Godfray 1994). Parasitoids are therefore highly susceptible to shifts in host availability. Asynchronous shifts in emergence may lead to parasitoid species emerging prior to host emergence or when the host abundance is still low (Jeffs & Lewis 2013). Conversely, primary consumers may emerge much earlier than their predators and parasitoids allowing for a larger build-up of potential prey/hosts. The hosts may thus be exposed to high levels of parasitism, leading to local extinctions of the host and subsequently, also of the specialised parasitoids (Godfray 1994; Jeffs & Lewis 2013; Chidawanyika *et al.* 2019).

Warm temperatures may accelerate host growth and thus reducing the temporal window of accessibility to predators and of parasitoids to their species host stage (Jeffs & Lewis 2013). Effects of synchrony between herbivore and host plant will have knock-on effects for natural enemies by potentially increasing or decreasing abundance (Thomson *et al.* 2010). The interactions between bottom-up and top-down effects on each trophic level are not well understood. Further research is needed to understand both how climate-driven shifts in prey/hosts will impact those in higher trophic levels and how those will subsequently impact their host populations.

1.4b v Community shifts

Shifts in phenology, habitat use and range, as a consequence of climatic change, are likely to alter species interactions and community dynamics in complex ways. Increased consumption of plants by insect herbivores, for example, has been shown as a response to climate change. This could have consequences by altering the floral structures of the host plant (Kolb 2008) and thus reducing resources for associated pollinator species (Fabina *et al.* 2010). Phenological shifts in insects will also impact on insectivores. The timing of breeding in insectivores such as birds, mammals and bats is often timed to coincide with peak insect abundance (Vafidis *et al.* 2009). Asynchronous shifts between peak insect abundance and breeding in these taxa can lead to fitness and demographic consequences in insectivore populations (Miller-Rushing *et al.* 2010).

Increased competition may occur as a result of climate change. If two species compete exploitatively, the stronger competitor is the one which can persist at the lowest resource level, but competitive dominance can be subject to changes in abiotic conditions (Gilman *et al.* 2010). Davis *et al.* (1998) demonstrated this in three Drosophila species under a simulated 'habitat' controlled environment. Each species of Drosophila was differentially sensitive to temperature and as such the level of temperature impacted upon the outcome of competition. In pairwise interactions, *Drosophila subobscuira* eliminated *D. inelanogaster* or *D. sitnulans* at low temperatures but at high temperatures, this species was outcompeted.

Shifts in range may result in novel interactions between species which were geographically separated (Walther 2010). Interactions between new species can significantly influence their respective fitness due to a lack of coevolutionary history (Reznick & Ghalambor 2001). As already discussed, the use of new plant hosts may be beneficial for herbivorous insects and allow for rapid range expansion. Interactions may also occur in the form of new prey species or new predators or competitors (Gilman *et al.* 2010). Empirical research is needed to explore how novel interactions impact insect communities. Theoretical explorations, however, indicate, for example, that novel predators could be more effective than those currently present. Novel predators may have higher searching activity, they may encounter and detect resident prey with greater probability especially if prey are ineffective at avoiding the new predator (Saul & Jeschke 2015). Prey may also be unable to recognise a novel species as a predator (Jeschke *et al.* 2014). Conversely, species could gain advantages from changes in community interactions if they are able to expand more quickly than their natural enemies or competitors. Species which are weaker competitors can be superior dispersers

(Tilman 1994) and the range expansion of enemies are often predicted to lag behind that of their prey (Moorcroft *et al.* 2006). There is limited evidence for the impacts of species interaction shifts as a result of climate-induced range expansions (Gilman *et al.* 2010). Further research is needed to understand how climate change will influence the wider community level, particularly as most studies consider the thermal constraints on range definition or interactions between just two species.

1.4b v. Disease

Climate change is expected to affect the distribution and occurrence of disease (Harvell *et al.* 2002). Consequently, insects are likely to experience new relationships with their parasites and pathogens, including increased prevalence of disease and encountering novel pathogens (Le Conte & Navajas 2008). In temperate insects, the spread of viral, protozoan, and nematode parasites may benefit from increasing temperatures which increase the host's breeding season (Harvell *et al.* 2002). For example, a parasite of the monarch butterfly is more prevalent in populations that breed year-round in warm regions compared to those which live in more seasonal environments (Altizer *et al.* 2000). Conditions that enhance pathogen winter survival or extend host breeding periods should increase the abundance of many viral and protozoan insect parasites. Pathogens may also benefit from indirect impacts of climate change. As mentioned previously climate change can both change the nutritional value of leaves (Buse *et al.* 1998) and result in insects feeding on mature, less palatable, leaves through phenological mismatch (Stamp & Bowers 1990). Reduced nutrition can affect pathogen resistance and lead to a higher incidence of disease (Lee *et al.* 2006; Miller *et al.* 2018).

Disease incidence may also decrease with a warming climate. Entomopathogenic fungi of insects, for instance, are generally more successful and cause greater mortality under cool, humid conditions. Outbreaks of an insect pathogen (*Entomophthora muscae*) in muscoid flies, for example, are usually associated with periods of cool temperatures and high rainfall (Watson *et al.* 1993). Hot and dry conditions are thought to limit fungal growth. Climate warming may limit some insect fungal diseases and release insects from pathogen pressure (Harvell *et al* 2002). There is very little empirical evidence associated with climate change and disease prevalence in insect populations. Understanding how disease prevalence will change and influence population dynamics will require further investigation of the influence and interaction of temperature and moisture changes upon disease.

1.4c. Direct vs indirect impacts

Section 1.4 has considered a variety of the potential direct and indirect impacts of climate change on insects, the relative importance of these respective impacts, however, are not fully understood. Climate change will influence insect population dynamics directly, through impacts upon physiology and survival, and indirectly, though impacts upon biotic interactions including host-plant, competition, and predation. Shifts in population dynamics may be driven more strongly by indirect, biotic interactions compared to direct intrinsic factors. Recent review papers which consider a wide variety of taxa indicate that altered species interactions appear to be the bigger driver of climate-induced changes in population dynamics compare to the abiotic, or direct mechanisms (Cahill *et al.* 2012; Ockendon *et al.* 2014; Ogilvie *et al.* 2017). Many studies implicate biotic interactions as an important proximate cause, particularly climate-induced decline in food availability. However, Ockendon *et al.* (2014) also indicated that primary consumers, which includes many insect species, were more likely to be influenced by direct impacts.

Comparisons between abiotic and biotic impact on insects are difficult to make as there is limited research exploring these mechanisms in insects and invertebrates in general (Ockendon *et al.* 2014). Furthermore separating the impacts of direct effects from indirect ones can be particularly difficult as there is likely to be strong interaction between them. For example, increased temperature may induce phenological asynchrony, which slows development of larvae that emerged before leaf emergence, however, the levels of warming may then accelerate larval development once leaves are available (Kharouba *et al.* 2015). An expansion upon the research regarding the mechanisms driving population change as a result of climate change would enable a greater unravelling of the relationship between direct and indirect impacts upon insects. It will also allow for a better evaluation of which kinds of impacts are the greater drivers of change.

1.5. Conclusions and knowledge gaps

In the UK, climate has experienced significant warming and this is set to continue increasing for the remainder of the century. Impacts of this climate change are idiosyncratic. Species responses vary dramatically, as such it is difficult to uncover general patterns of change and different mechanisms may be more important in some species compared to others. Furthermore, there are likely to be both species which benefit and those which suffer declines. Warming impacts on growth, development, and survival have a strong potential to directly impact insect populations. For many temperate species, temperature increases will allow for faster growth, which may increase annual voltinism and boost population numbers and thus species dispersal capabilities. Equally important is the impacts of warming on overwintering survival as the very nature of overwintering diapause requires low temperature. Research has begun to indicate that there may be a highly significant influence of temperature of different life-stages, particularly overwintering life-stage and vulnerability to warming winters. However further exploration is needed to uncover the biological reasons that could be driving this observation.

Changes in species interactions will strongly influence insect population dynamics, particularly those which impact temporal relationships. Phenological shifts between insects and their food source is likely to hold substantial physiological consequences which influence population viability. The wider insect community may also experience knock-on effects. The literature documents observed mismatches in phenology, but there are few studies which explore the subsequent physiological, population-level and higher trophic-level impacts.

The potential climate-driven mechanisms of change in insect population dynamics are highly varied and complex. Pest insects, butterflies, moths and some other insect taxa have had recorded responses to these climatic changes in the form of range and distributional shifts and changes in abundance. Research is beginning to explore the potential mechanisms driving these ecological impacts, but there remains a significant lack in the understanding of how climate change is altering insect population dynamics and there is a strong call for studies considering species other than butterflies and pests.

1.6 Research objectives

The overall aim of this thesis was to uncover woodland insect response to climate change by investigating how overall woodland insect populations change at a local scale and exploring the mechanisms through which populations may shift by looking broadly at the response of natural insect populations and more specifically exploring direct biological impacts on individual insects. In chapter two, I take advantage of a data set generated through localised, repeated sampling across the flying insect community to explore how woodland insect populations trends are changing and how this may be linked with seasonal weather, here I aim to assess insect groups which are typically neglected in climate research, such as non-pollinator Hymenoptera and Diptera, both of which are important components for woodland habitats. In chapter three I take a more mechanistic approach, looking at the specific effects of weather across three trophic levels on specific species. This chapter also takes advantage of a long-term localised study but aims to provide a rare assessment which takes into consideration more than two trophic levels. It focuses on an aphid-sycamore-parasitoid system and assesses the impact of temperature and precipitation on the timing of spring emergence between these interacting species. It also aims to assess the relative effects of direct weather and phenological mismatch (indirect effects) on population dynamics. In chapter four, I aim to directly quantify the effects of a phenological mismatch on caterpillar growth and development and add to the very small amount of studies which have quantified expected consequences of a shift in the timing of species interactions as well as monitoring them through overwintering to eclosion to assess more long term affects. In the final chapter, I synthesise the potential mechanisms through which climate change may contribute shifts in woodland insect populations, provide an indication of how populations may change under the current predicted shifts in climate and discuss how the wider ecosystem may change in response.

Chapter 2. The influence of seasonal weather changes on temperate woodland insects and evidence of population declines.

2.1 Abstract

Woodland ecosystems response to climate change is not well understood. Focal species studies are not guaranteed to provide a good indicator of other species responses and are thus limited in their capacity to inform wider community or ecosystem response. Woodland insects form an integral component of temperate woodlands and support a diversity of taxa in higher trophic levels, shifts in their communities are therefore likely to have wider implications for woodlands as a whole. We use a ten-year data series on a woodland flying insect community to assess population trends for overall abundance, the specific orders Diptera, Hymenoptera, and sub-order non-aphid Homoptera and assess the relative associations with seasonal shifts in temperature and precipitation. We also compare the importance of changes in mean conditions and occurrence of extreme weather events. Significant declines were detected for Hymenoptera and Homoptera, but not for the most abundant order, Diptera. Despite this, significant declines were detected for overall abundance. Seasonal weather was associated with overall abundance with specific responses detected at the order level. Generally, insects respond to warmer and wetter winters with population declines and hotter, drier summers with population increases. Diptera response in contrast, showed population increases in cooler, wetter summers, Hymenoptera response to warmer winters was population increase. Notably, abundance changes were more frequently associated with extreme events. Although this may be due to high correlation with mean changes, for precipitation the magnitude of effect was much higher than changes in mean conditions. These findings demonstrate that declines may be associated with climatic change within woodlands. Our study site is exposed to similar threats as other temperate woodland (i.e. fragmentation and edge effects) and although additional research is needed to determine whether these relationships hold at a wider geographical scale, they are highly indicative that climate will impact insect abundances and subsequently the wider woodland community.

2.2 Introduction

Ecological responses to climate change have been well documented across natural systems (Parmesan 2006; Boggs 2016; Rozenzweig *et al.* 2008; Pecl *et al.* 2017). These effects include population shifts (both increases and declines), local extinctions and colonisations and global extinctions (McCarty 2001). Such changes have been demonstrated across a wide variety of taxa, such as birds (Stephens *et al.* 2016); frogs (Pounds *et al.* 2006) and insects, including butterflies (Thomas *et al.* 2005) and bees (Ogilvie *et al.* 2017). Understanding how populations respond to climatic change is important as population size and trends are used to assess the conservation status of species and determine priorities for conservation action (Gregory *et al.* 2005; Thomas *et al.* 2011). Understanding how species populations respond to climate change can also help with understanding and predicting shifts at the wider ecological level, including impacts on species that interact with the focal species (Forister *et al.* 2019).

For many species, the climatic drivers of shifts in their abundance have been well documented, but typically research has focused on charismatic fauna which are easy to study and have long term monitoring programmes (e.g. Roy *et al.* 2001; Oliver *et al.* 2015a; Thackeray *et al.* 2016). Insects, in particular, are thought to exhibit strong responses to climate change due to their ectothermic nature and short generation times, allowing them to rapidly respond to environmental change (Bale *et al.* 2002). Changes in seasonal temperature are the most commonly cited drivers of shifts in insect response to climate change (Bale *et al.* 2002). Precipitation is much less well understood, although is also likely to drive shifts in insect population abundance. In addition to changes in average conditions, climate change is also predicted to increase the occurrence of extreme weather events (Piessens 2009; Trenberth 2012). The unpredictability of extreme conditions may be a greater challenge for many organisms than gradual shifts in mean conditions (Godfray 1994). Changes are unlikely to be uniform across seasons and each insect life stage typically has different climatic requirements (Kingsolver *et al.* 2011), changes in winter, for example, will affect insect overwintering diapause (Bale & Hayward 2010), whereas shifts in spring weather will impact emergence and insect growth (Bale *et al.* 2002; Renner & Zonner 2018).

For insects, the climate impact literature exhibits a strong focus on Lepidoptera (predominantly butterfly species (Andrew *et al.* 2013), with more recent inclusion of moths (Martay *et al* 2016; Maurer *et al.* 2018; Coultard 2019)), pest species and specific species of conservation concern (Andrew *et al* 2013; Boggs 2016). Although debated (see Thomas

2005) it is thought that widely studied Lepidoptera, particularly butterflies, response to climate change is not representative of responses in other insect groups (Prendergast & Eversham 1997; Ricketts *et al.* 2002). It is essential to understand how climate impacts insect populations other than butterflies and moths, particularly in light of recent research uncovering alarming declines in insects worldwide (Leather 2018; Hallman 2017; Lister & Garcia 2018; Homburg 2019; Hallman *et al.* 2019). Some of these studies have understandable logistical constraints due to the lack of regular repeated sampling over long time periods. Hallman *et al.* 2017, for example, studied 63 nature reserves in Germany across 27 years, but a substantial proportion of these sites were only sampled once during this period. Similarly, the analysis of Lister & Garcia (2018) includes a comparison of insect biomass sampled over a very small area in Brazil in 1967 with repeated sampling in 2011 and 2012. Apparent trends could thus be unduly influenced by any unusual events that influenced population size in 1967. These issues have been minimised in more recent work, e.g. Hallman *et al.* (2019) who reported declines using data from repeated sampling at two sites over a twenty-year period for Lepidoptera (macro-moths), Coleoptera and Trichoptera. As a collective set of studies, these papers do highlight widespread declines in typically underappreciated and understudied insect groups that are of great importance due to their high contribution to biodiversity and key roles within ecosystems.

In contrast to general monitoring studies, those that attempt to assess climate change impacts tend to do so for individual species (e.g. Roy *et al.* 2000; Warren *et al.* 2001). Species are expected to show individualistic responses to climate change (Walther 2002; Thackeray *et al.* 2016) and research of this nature is vital for understanding precise mechanistic drivers of insect responses to climate. However, conducting research that unpicks species-specific responses to climate change, for even a fraction of insect species in a community, is extremely resource-intensive, and unlikely to be achieved anytime soon. Single species studies are thus rather limited in their capacity to inform our understanding of impacts on community or ecosystem-level responses as there is no guarantee that the focal species provides a good indicator of other species' responses. This thus makes it difficult, for example, to assess the consequences of climate change impacts on insects for higher trophic levels, e.g. avian insectivore responses to changes in insect abundance (Forrister *et al.* 2019). There is thus merit in understanding the climate change impacts on the abundance of broad insect groups as well as individual species.

Woodland insect communities in the UK are one group of insects for which the impacts of climate are poorly understood, with a lack of high-quality data on woodland insect populations trends. Woodland habitats have the most diverse invertebrate fauna of any habitat in Britain (Collins 2012; Neumann *et al.* 2015) as well as supporting a wide range of species in higher trophic levels (Shortall *et al.* 2009). Temperate woodland habitats are highly seasonal, and woodland insects often require different seasonal requirements for each life stage (Powell & Logan 2005) meaning that they are likely to be highly sensitive to the impacts of climate change across different seasons. Despite this, and the relative importance of woodland insects, very little is known about the magnitude and mechanisms of their response to climate change.

Woodland habitat quality has been significantly impacted through environmental change and management in the UK over the past few decades (Hopkins & Kirby 2007). Woodlands suffer from loss, fragmentation and degradation, unsympathetic forestry practices or lack of appropriate management, as well as the occurrence of new pests and diseases (Davies *et al.* 2017). Insect populations are thought to be highly sensitive to changes in woodland habitats (Thaxter *et al.* 2010). Changes in management practice, for example, have led to a loss of early successional and understory vegetation, increased shadiness and deadwood but reduced open space, which can impact invertebrate species and is thought to have contributed to the decline of six woodland butterfly species across the UK (Asher *et al.* 2011). A further contribution to loss of understorey and shifts in the biological community come from grazing by an increasing deer population (Fuller *et al.* 2001). Woodlands have also been influenced by other changes across the countryside, particularly agricultural changes, as farmland surrounds most UK woodlands (Dolman *et al.* 2007). Agricultural impacts can include exposure to fertiliser and pesticide drift and ammonia from livestock (Gove *et al.* 2007). Loss of woodland biodiversity has been described for a number of species, including some specific insect species, plants and birds (Bailey 2007). The factors driving declines in organisms in higher trophic levels, particularly birds, are not fully understood (Fuller *et al.* 2005). A large proportion of woodland birds feed on insects and other invertebrates (Leech & Crick 2007) and insect populations are thought to be highly linked with climate. It is therefore essential to understand how large groups of insects and insect communities are responding to climate change as this may enable us to further explain changes in woodland communities, such as the declines of insectivorous birds and other reliant taxa in higher trophic levels, such as bats.

In order to develop a greater understanding of the ecological impacts of climate change on woodland insect assemblages, a wide range of insect species and groups need to be sampled. Long-term insect monitoring programmes in the UK often sample nationwide. The Rothamsted of suction traps, for example, samples across England and Scotland (Shortall *et al.* 2009) however each trap samples across a large area (~80km) and thus changes cannot be associated with a particular site or habitat. The butterfly monitoring scheme, on the other hand, samples across very small sites so can be used to describe habitat-specific trends but is limited to one taxa. Thus, current sampling efforts typically make it particularly difficult to understand how woodland insects are responding to climate change. Although local sampling cannot generalise to regional patterns, standardisation and intensification of local sampling is easier. A highly standardised data set is essential in order to uncover the effects of local patterns (Shortall *et al.* 2009). These can then be further investigated in spatially replicated data. Hence, uncovering local ecological effects of shifts in weather patterns in a woodland habitat, over several years with high-quality data is an important step toward making more broad-scale predictions of how climate may affect woodland insects on a more long-term or regional scale.

We utilise a localised, ten-year study of the flying insect community in a woodland system. Our study focuses on overall woodland insect abundance and specific insect orders Diptera, Hymenoptera and sub-order Homoptera (non-aphid). These insect orders are highly abundant in woodlands (Fraser 2007; Williams 1993) and make up an important component of many avian diets, especially Diptera (Razeng *et al.* 2015; Nyffeler *et al.* 2018). Populations of these insects within these groups, along with many others, have shown recent changes including range shifts and changes in abundance. Diptera, for example, showed significant long-term declines in the Rothamsted suction trap samples in part of the UK (Shortall *et al.* 2009) whilst many aphid species appear to have a positive population trend (Martay *et al.* 2016). Fewer studies have considered Homoptera other than aphids, such as leafhoppers and population trends for Hymenoptera are also less well understood. Declines have been detected in some Hymenoptera but there is a strong bias towards assessing pollinator declines (Potts *et al.* 2010; Kerr *et al.* 2015), ignoring the effects on the more abundant Hymenopteran parasitoids (Fraser *et al.* 2007).

Our study has two core objectives: i) to determine population trends in woodland insects and within specific insect orders; ii) to determine the effects of seasonal changes in weather for spring, winter, autumn and summer on these insect groups, and for each season assess the effects of shifts in average conditions but also to compare this to extreme events and understand the relative importance of these changes in weather. This is important not only for insect conservation and climate mitigation but also for understanding and mitigating climate change impacts on wider ecosystem function, including availability of invertebrate food for breeding birds and other trophic interactions such as those between phytophagous insects and host plant and insects and their associated parasitoids.

2.3 Methods

Insect sampling occurred in the Rivelin Valley, Sheffield (Lat 53°23′N, Long 1°34′W) annually from 2009. Eight woodland areas were selected along the length and breadth of the valley. All sites contain a diverse range of broad-leaved tree species and tree ages although the precise composition, woodland age, aspect and altitude vary across the sites (Figure 2.1). Woodland at the western end of the valley is part of the Eastern Moors SSSI. The valley also contains open pasture and is bordered by crop fields to the north, the eastern edge is close (c. 0.5 km) to areas of suburban housing, and the western edge is flanked by heather moorland. Woodland in the area is subject to minimal management, which is mainly restricted to path clearance and improvement, although some Rhododendron and pine removal also occurs. Roe deer population size has increased from a low base during the course of the study but deer populations remain small and there is no evidence that deer browsing has changed the vegetation structure in the woodland.

Sampling was conducted approximately every 14 days from spring to late July or early August, i.e. covering the main breeding period for woodland passerines. Sampling started in mid-April in 2009 and 2010 and in early March in all other years. During each sampling date, insects were sampled using yellow sticky traps (24.5 cm x 10 cm). A total of five traps were placed at each site (40 traps in total) - trap locations were selected to ensure that at each location other traps were not visible and within a site were between 15 and 150 m apart (typically approximately 50m apart). Traps were placed in the same location on each sampling date, but when necessary elevated slightly to maintain visibility following vegetation growth later in the season. On each sampling day, traps were placed at each site following sunrise and collected prior to sunset. As sampling was conducted as early as March the timing of trap placement became progressively earlier from spring to summer, with times ranging from ~7:00 am in March to as ~5:30 am around summer solstice. Similarly, traps were collected in by ~6:00 pm in March and as late as 9:30 pm in mid-summer. Trap setting and collection was aimed to be completed within two hours although this varied up to ~three and a half hours dependent upon the number of people collecting traps. Collected traps were sealed in plastic (PVC) wrap and labelled with site, date and trap number. Samples were then transferred into a freezer for storage. All specimens were identified to order level, with some finer taxonomic resolution to suborder, with Homoptera separated into aphids and other Homoptera (except for 2009 for which Homoptera were not sub-divided). Insects on sticky traps are difficult to identify to high taxonomic resolution due to the method of capture (insects become squashed and damaged on sticky traps), but effects should be detectable at order level (Timms *et al.* 2012) to provide good indication of general response to weather.

2.3a Weather data

Daily meteorological weather for mean temperature, total precipitation, wind gust speeds, and sunshine hours were obtained from Weston Park Weather Station (Weston Park Weather Station, Museums Sheffield 2012), located approximately 5 km east of the study site. Temperature data recorded across the Rivelin Valley using ibuttons is strongly correlated with the Weston park weather station temperature data, and there is minimal divergence in precipitation recorded at the weather station and in the valley (Gullet *et al.* 2014).

2.3b Population abundance calculations

This study was interested in capturing the effects of seasonal weather effects on the abundance of insect orders. Our general approach to estimating an index of annual population size of each order was to model mean abundance per site as a function of date and weather conditions during sampling and then extract the area under the curve. This approach is similar to that used to estimate butterfly population sizes in the UK Butterfly Monitoring Scheme (Rothery & Roy 2001; Dennis *et al.* 2013). Weather variables were included in order to account for the daily weather which influences insect activity levels (Bale *et al.* 2002) and thus the number of insects sampled in one day. We use generalized additive models (GAM) (R Package mgcv, Wood 2019) in R version 3.6.0 (R Core Team 2019) to model the abundance of each order over the season for each sampling site within each year. Within a GAM part of the linear predictor contains one or more smoothing functions of predictor variables (Wood 2006). This method is, therefore, more flexible than fitting simple non-linear generalized models, as it allows the curve to fluctuate more than the quadratic or cubic equations. This is likely to be particularly advantageous when modelling data from multiple insect species as there are likely to be multiple peaks in abundance caused by different taxa having peaks in different parts of the year, and potentially the same species may have multiple generations within a year.

We develop our GAMs using the full range of sampling events available for each year (these varied in timings slightly; see Supplementary Material Table S1). For each sampling date within a year a mean abundance per sticky trap was calculated for each site for i) all orders; ii) Hymenoptera and iii) Diptera and iv) Homoptera. A GAM with Poisson distribution and a log link function was used to model mean abundance at each site (modelled as a random factor). Other predictor variables were: i) daily mean temperature (calculated as the mean temperature during the sampling period on a given sampling date); ii) daily sun hours (calculated as the total time the sun was shining on that date, this data was not available for the precise sampling period but, as sampling was conducted within a few hours of sunrise and sunset it is likely to be highly correlated with sun hours during sampling) ii) mean wind gust (calculated as the mean highest wind gust recorded during sampling period on the sampling date) and iv) duration sampled for (the total time (hours) traps were out at each site on the sampling date). For 2009 hourly weather data were unavailable, in this case, daily weather variables were used. We used a model comparison approach, building models with all possible combinations of these four variables including a model without any weather variables (site only). We used Akaike Information Criteria corrected for small sample sizes (AICc) values to distinguish between competing models, and all models that were within 2 AICc of the model with the lowest AICc value were used to estimate abundance using a model averaging approach based on model weights.

Population size on the data scale was estimated for the period between 1st April and 30th June. This period was chosen as it covers the avian breeding season and thus represents availability of insects as a food source for higher trophic levels, whilst also capturing the seasonal increase and decline in insect abundance. Data were available for this entire period for all years except for 2009, 2010 and 2013 when sampling commenced after 1st April, although sampling in these years captures the vast majority of the period for which insect population size is predicted (2009 71%; 2010 96%, 2013, 88%). A population estimate was generated at set points of every 14 days for our sampling period and our estimated population index is generated by summing up these predicted abundances.

2.3c Population trends

To assess the abundance trends for each focal group, we used linear mixed-effects models using the lme4 package (Bates et al. 2015) in R version 3.6.0 (R Core Team 2019).

Abundance for total insects, i.e. Diptera, Hymenoptera and Homoptera, and the abundances of each of these orders were modelled as a function of year as a fixed factor and site and year were included as random effects. The abundance of total insects, Hymenoptera and Homoptera were natural log-transformed to improve the spread of the data. Preliminary analysis indicated that modelling simple non-linear population trends did not substantially improve model fit and we thus only report the results from linear models.

2.3d Effects of weather on abundance

To investigate how annual abundance of total insects across all orders, Diptera, Hymenoptera and Homoptera is influenced by inter-annual variation in weather at certain times of year, we defined four seasons that capture weather conditions during different life cycle stages and the period for which we estimate population size. i) April–June (Spring: - and the period for which population size is estimated), ii) Jan-March (Winter, prior to the population size estimate), iii) October-December (the Autumn prior to the population size estimate) iii) July-September (the Summer prior to the population size estimate). Insects, particularly in temperate woodland habitats, have highly seasonal life cycles. Each life stage (i.e. egg, larvae, pupae and adult, or egg, nymphal instars, adult) will experience, and also require different environmental conditions. Spring weather, for example, is important for emergence and initial growth and development and thus contributing to population recruitment and influencing abundance (Robinet & Roques 2010). Temperate insects often undergo a dormant period called diapause during winter, the initiation, duration, and termination of which is determined by environmental cues (Bale & Hayward 2010), changes in winter weather may affect this dormancy. For example, diapause termination may occur in a period of low resource availability in warmer weather (Scriber *et al.* 2012), or increase the rate by which winter stores are depleted (Williams *et al.* 2015) impacting survival rates and thus population size. Modelling by season also allows us to compare the effects of changes in mean conditions and extreme weather for each season, as well as compare the effects of temperature and precipitation. It also allows us to test for these effects with a small number of predictor variables within each model, e.g. four predictors rather than 12 if we modelled mean weather conditions in each month. This is important given the limited numbers of years for which we have population size estimates. We modelled the abundance of each order as a response to weather variables in each of these periods, considering the effects of mean conditions and the occurrence of extreme events. All models are linear effects models conducted using the lme4 package (Bates *et al.* 2015) in R version 3.6.0 (R

Core Team 2019). Year and site were included as random factors to account for repeated measurements.

Weather conditions were calculated for each season (i.e. Spring, Winter, Autumn, Summer). These included mean conditions: i) mean daily temperature and ii) total precipitation. Two metrics of extreme weather were calculated. We first identified which days had extreme weather as those with the 5% most extreme high or low values for each season using data from all years in which the study was conducted. We then calculated i) the total number of extreme high days (temperature and rainfall) and low days (temperature and rainfall) and ii) the highest number of consecutive days with extreme high and low values for each weather variable.

For each abundance metric we constructed ten sets of models, each of which contained four predictor variables (one per season), i.e. the first model contained mean temperature in spring, summer, autumn and winter, the second model contained the total number of days with high temperatures in spring, summer, autumn and winter etc. Due to the limited number of sampling years, and thus limited power to detected statistically significant effects we also discuss marginally significant results, defined as $0.05 < P < 0.10$.

Figure 2.1. Map of Rivelin Valley Study Site. Sticky traps were placed across eight sites notated with red circles on the map.

2.4 Results

2.4a Abundance trends

Logged abundance showed significant decline with year in: overall insects, (estimate±95% confidence interval: -0.0831±0.078), p= 0.041), an overall decline of 15%, (Figure 2.2a); Hymenoptera (-0.104±0.10, p=0.042), an overall decline of 42%, (Figure 2.2b) and Homoptera (-0.203±0.142 , p =0.011) an overall decline of 83% (Figure 2.2c). There was no decline with year for Diptera (not logged) (-6.672±22.85, p = 0.536 Figure 2.2d.)

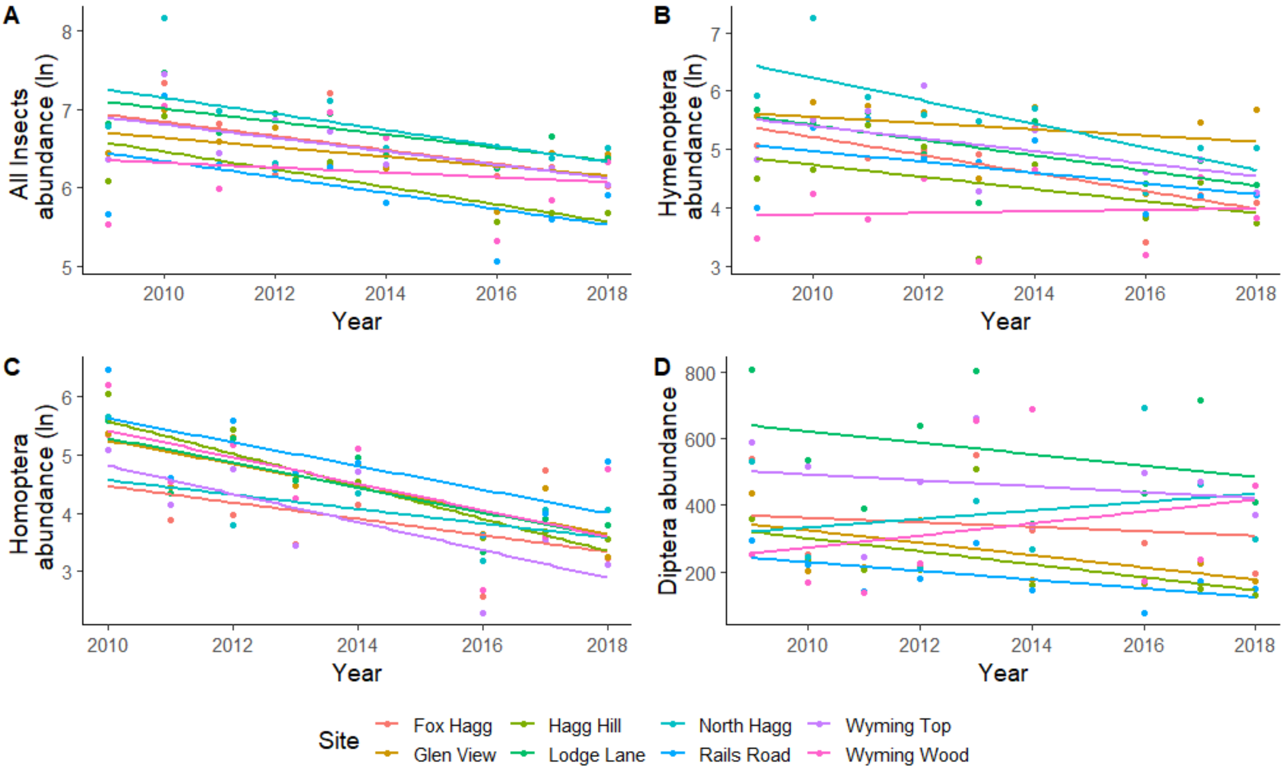

Figure 2.2. Changes in the abundance across the study period separated by site for a) All insect abundance; B Hymenoptera; C Homoptera and D Diptera.

2.4b Mean weather conditions

Logged total insect abundance was negatively associated with mean winter temperature, a 1°C increase in mean winter temperature, equating to an untransformed abundance decrease of 17% (Figure 2.3d). There were marginal negative effects of mean temperature in spring (1°C increase results in 22% decline, Figure 2.3a), autumn (1°C increase = 13% decline, Figure 2.3c) and marginal positive effects of temperature in the previous summer (1°C increase = 51% increase, Figure 2.3b) (Table 2.1). Logged Homoptera abundance was positively associated with mean summer temperatures (1°C increase = 174% increase, Figure 2.3e) (Table 2.1). Other changes in mean temperature across the four seasons were not associated with changes in insect abundance in any of our focal taxa.

Changes in total precipitation in winter were found to be negatively associated with logged total insect abundance (mean increase in 1mm rainfall equates to 0.4% decline, Figure 2.3f), and total precipitation in summer was positively associated with Diptera (untransformed) abundance (1mm increase = 0.7% increase, Figure 2.3i) and marginally associated with total spring rainfall (1mm increase = 0.2% increase Figure 2.3h). Total precipitation was not associated with logged Homoptera or Hymenoptera abundance in any season (Table 2.1).

Table. 2.1 Insect abundance Logn (All insects, Hymenoptera, Homoptera) and Diptera) as a function of weather variables mean temperature and total rainfall for each season. Models are mixed-effects models with year and site identity included as random effects in all models. Slopes are reported with SE. Bold indicates significance, grey indicates marginal significance (0.05<*P*<0.10.)

Weather	R^2 GLMM$_{(m)}$	R^2 GLMM$_{(c)}$	Summer	Autumn	Winter	Spring
All Insects						
Temp	0.29	0.809	0.415±0.282 + P=0.055	-0.140±0.205 P=0.077	-0.185±0.222 - **P=0.038**	-0.252±0.345 P=0.060
Rain	0.248	0.816	-0.0009±0.004 P=0.954	0.003±0.003 P=0.127	-0.004±0.003 **P=0.046**	-0.002±0.002 - P=0.051
Hymenoptera						
Temp	0.137	0.7855	0.519±0.440 P=0.115	-0.194±0.164 P=0.115	0.078±0.176 P=0.529	0.175±0.274 P=0.368
Rain	0.044	0.806	-1.74x10^{-3}±7.51x10^{-3} P=0.514	-6.891x10^{-5}±9.91x10^{-3} P=0.983	-3.634x10^{-3}±8.789x10^{-3} P=0.257	-9.574x10^{-4}±3.297 P=0.589
Homoptera						
Temp	0.198	0.866	1.010±0.710 **P=0.04475**	-0.169±0.270 P=0.328	-0.169±0.286 P=0.355	-0.414±0.442 P=0.768
Rain	0.71	0.887	-0.001±0.012 P=0.892	0.003±0.009 P=0.628	-0.006±0.008 P=0.259	-0.0013±0.007 P=0.768
Diptera						
Temp	0.0961	0.6911	63.93±88.25 P=0.312	-16.35±32.740 P=0.479	-30.61±35.45 P=0.233	-63.50±54.960 P=0.122
Rain	0.1769	0.6635	1.020±0.414 **P=0.006**	0.465±0.502 P=0.207	-0.318±0.485 P=0.361	0.386±0.276 P=0.071

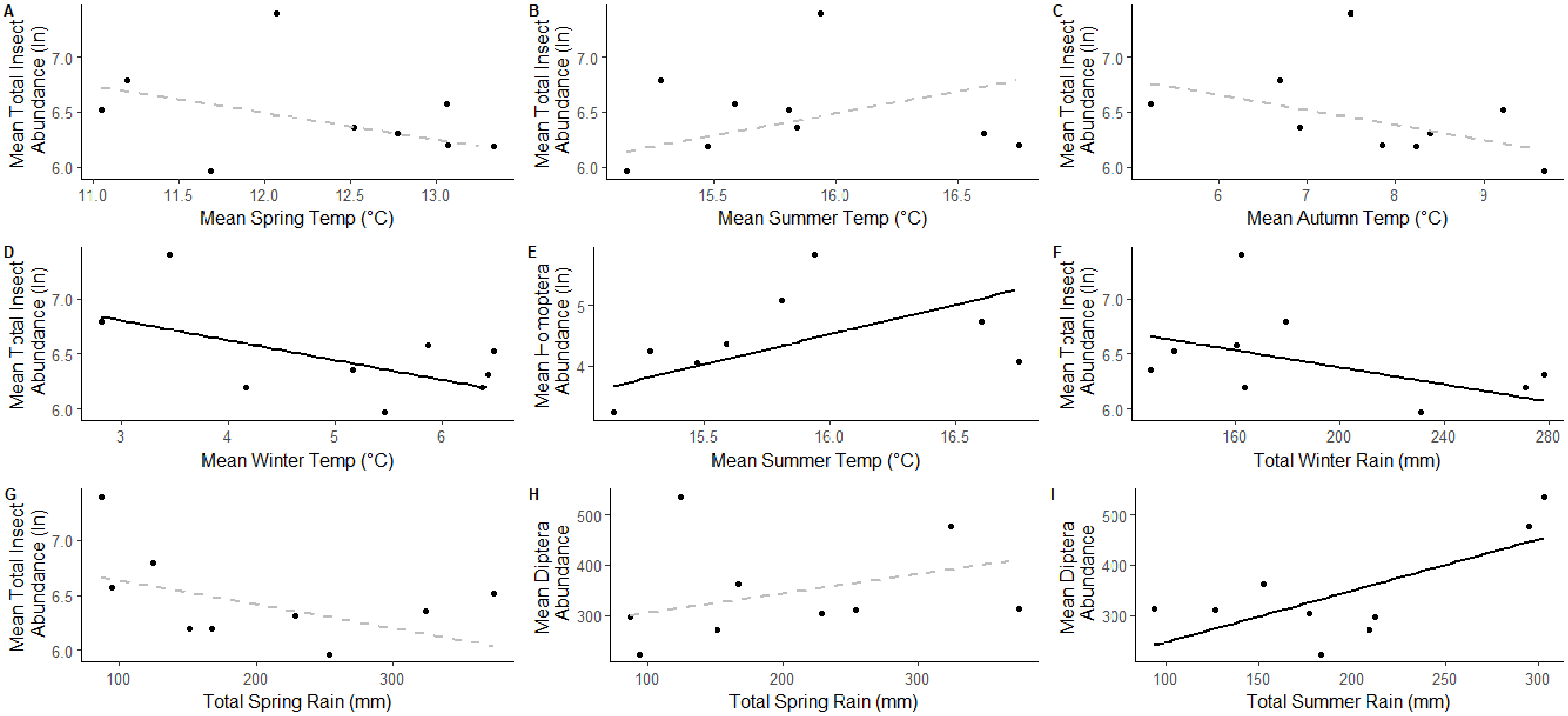

Figure 2.3 The relationship between mean temperature or total rainfall within seasons which were associated with insect abundance, **a-e** Mean temperature impacts, **f-i** total rainfall impacts. a) Spring temperature and overall insect abundance; b) Summer temperature and overall insect abundance; c) Autumn temperature and overall insect abundance; d) Winter temperature and overall insect abundance; e) Summer temperature and Homoptera abundance; f)Total winter rain and overall insect abundance; g) Total spring rain and overall insect abundance; h) Total spring rain and Diptera abundance; i) Total summer rain and Diptera abundance. Black symbols are observed values. The line is the model-averaged predicted fit from models presented in Table 1; a solid line indicates a p-value of <0.05, and a dashed line indicates 0.05<*P*<0.10.

2.4c Extreme weather conditions.

Total number of days with extreme weather (temperature or precipitation) were calculated for each season in each year. Correlation coefficients between extreme variables and mean weather conditions varied from 0.09 to 97.43 with 43% of the extreme variables being higher than 70% correlated with mean conditions (Table 2.2)

Table 2.2 Pearson correlation coefficients calculated for mean weather conditions and two extreme weather measures i) total number of extreme days in a season (days in the top 95% of temperature/rain and bottom 5%) and ii) the highest number of consecutive extreme days in a season.

Mean Conditions Variable	**Extreme Conditions**	**Pearson Correlation Coefficient**
Mean Spring Temp	TotalHighTempDays – Spring	**0.302**
Mean Spring Temp	Total Low Temp Days – Spring	**-0.817**
Mean Summer Temp	Total High Temp Days – Summer	**0.8059**
Mean Summer Temp	Total Low Temp Days – Summer	**-0.448**
Mean Autumn Temp	Total High Temp Days -Autumn	**0.091**
Mean Autumn Temp	Total Low Temp Days -Autumn	**-0.802**
Mean Winter Temp	Total High Temp Days -Winter	**0.684**
Mean Winter Temp	Total Low Temp Days -Winter	**-0.818**
Mean Spring Rain	Total High Rain Days -Spring	**0.974**
Mean Spring Rain	Total Low Rain Days -Spring	**-0.853**
Mean Summer Rain	Total High Rain Days – Summer	**0.840**
Mean Summer Rain	Total Low Rain Days – Summer	**-0.512**
Mean Autumn Rain	Total High Rain Days -Autumn	**0.857**
Mean Autumn Rain	Total Low Rain Days -Autumn	**-0.667**
Mean Winter Rain	Total High Rain Days -Winter	**0.842**
Mean Winter Rain	Total Low Rain Days -Winter	**-0.765**
Mean Conditions	**Extreme Conditions**	**Pearson Correlation**
Mean Spring Temp	Consecutive High Temp Days - Spring	**0.412**
Mean Spring Temp	Consecutive Low Temp Days – Spring	**-0.643**
Mean Summer Temp	Consecutive High Temp Days – Summer	**0.718**
Mean Summer Temp	Consecutive Low Temp Days – Summer	**-0.253**
Mean Autumn Temp	Consecutive High Temp Days – Autumn	**0.376**
Mean Autumn Temp	Consecutive Low Temp Days – Autumn	**-0.752**
Mean Winter Temp	Consecutive High Temp Days – Winter	**0.478**
Mean Winter Temp	Consecutive Low Temp Days – Winter	**-0.844**
Mean Spring Rain	Consecutive High Rain Days -Spring	**0.862**
Mean Spring Rain	Consecutive Low Rain Days – Spring	**-0.667**
Mean Summer Rain	Consecutive High Rain Days – Summer	**0.590**
Mean Summer Rain	Consecutive Low Rain Days - Summer	**-0.247**
Mean Autumn Rain	Consecutive High Rain Days – Autumn	**0.227**
Mean Autumn Rain	Consecutive Low Rain Days – Autumn	**-0.477**
Mean Winter Rain	Consecutive High Rain Days – Winter	**0.639**
Mean Winter Rain	Consecutive Low Rain Days – Winter	**-0.562**

2.4d Total extreme days

All insects

The frequency of days with extreme high temperatures (hot days) was not important for overall logged insect abundance in any season. Overall insect abundance was positively associated with the frequency of days with extreme low temperatures (cold days) in autumn (an increase of one additional day of low temperature equated to a 3% increase of unlogged abundance) and winter (one addition cold day = 6% increase) (Table 2.3). Overall insect abundance was negatively associated with an increase in the frequency of wet days in winter (one additional wet day = 8% decrease) and autumn (one additional wet day = 3% decrease).

Hymenoptera

The frequency of days with extreme high temperatures in winter were marginally associated with higher logged Hymenoptera abundances (one additional hot day = 28% increase). Hymenoptera showed no association with the frequency of extreme cold weather or extreme rainfall in any season (Table 2.3).

Diptera

The frequency of cold days in autumn (1 additional cold day = 2% increase) and summer (1 additional cold day = 3% increase) were positively associated with Diptera abundance but the frequency of cold days in autumn was negatively associated with Diptera abundance (1 additional cold day = 2% decrease). The frequency of high rainfall days in summer was associated with an increase in Diptera abundance (1 additional wet day = 8% increase) and marginally for spring (1 additional wet day = 4% increase). The frequency of high-temperature days and low rain days were not associated with Diptera abundance in any season (Table 2.3).

Homoptera

Logged Homoptera abundance was not associated with the frequency of high temperature, high rainfall or low rainfall days in any season. An increase in the frequency of cold days marginally increased Homoptera abundance (1 additional cold day = 12% increase) (Table 2.3).

Table 2.3. Insect abundance Logn (All insects, Hymenoptera, Homoptera) and Diptera) as a function of extreme weather variables calculated as the frequency of extreme days of low and high temperature and precipitation for each season. Models are mixed-effects models with year and site identity included as random effects in all models. Slopes are reported with ± SE.

Total number of extreme days	R^2 GLMM$_{(m)}$	R^2 GLMM$_{(c)}$	Summer	Autumn	Winter	Spring
All Insects						
High Temp	0.0915	0.843	-0.076±0.079 P=0.954	-0.061±0.073 P=0.238	0.014±0.046 P=0.661	0.01±0.045 P=0.774
Low Temp	0.306	0.806	-0.016±0.028 P=0.407	0.028±0.018 **P=0.045**	0.064±0.033 **P=0.046**	0.014±0.411 P=0.635
High Rainfall	0.222	0.821	0.012±0.071 P=0.407	0.007±0.067 P=0.872	-0.082±0.05 **P=0.038**	0.054±0.023 P=0.115
Low Rainfall	0.373	0.795	-0.047±0.046 P=0.162	-0.063±0.041 **P=0.045**	-0.006±0.026 P=0.733	0.009±0.033 P=0.680
Hymenoptera						
High Temp	*0.17*	*0.773*	0.00007±0.075 P=0.999	-0.056±0.069 P=0.257	0.063±0.043 P=0.061	0.014±0.047 P=0.670
Low Temp	0.155	0.782	-0.049±0.043 P=0.126	0.028±0.028 P=0.174	0.021±0.052 P=0.564	-0.046±0.064 P=0.317
High Rainfall	0.145	0.801	-0.044±0.114 P=0.580	-0.0569±0.108 P=0.456	-0.0997±0.042 P=0.104	-0.034±0.069 P=0.518
Low Rainfall	0.112	0.814	-0.011±0.074 P=0.823	-0.023±0.065 P=0.603	-0.0076±0.042 P=0.792	0.002±0.052 P=0.947
Homoptera						
High Temp	0.123	0.878	-0.011±0.155 P=0.908	-0.062±0.139 P=0.482	0.046±0.094 P=0.441	0.053±0.096 P=0.383
Low Temp	0.113	0.864	-0.058±0.07 P=0.209	0.0117±0.005 P=0.714	0.120±0.099 P=0.077	-0.083±0.139 P=0.351
High Rainfall	0.23	0.861	0.148±0.226 P=0.3069	-0.138±0.173 P=0.223	-0.103±0.122 P=0.200	0.007±0.123 P=0.931
Low Rainfall	0.087	0.884	-0.08±0.115 P=0.281	-0.08±0.093 P=0.191	-0.033±0.06 P=0.392	-0.025±0.079 P=0.619
Diptera						
High Temp	0.071	0.679	10.712±17.679 P=0.806	8.936±16.203 P=0.435	-11.333±10.25 P=0.136	-1.903±5.68 P=0.806
Low Temp	0.159	0.647	13.614±6.689 **P=0.015**	-8.280±4.396 **P=0.022**	14.841±8.102 **P=0.0251**	-8.610±9.893 P=0.233
High Rainfall	0.134	0.656	27.803±15.413 **P=0.027**	6.41±14.613 P=0.5352	0.185±11.02 P=0.981	12.763±10.095 P=0.097
Low Rainfall	0.076	0.677	-2.17±13.423 P=0.815	-2.818±11.786 P=0.730	3.807±7.663 P=0.479	0.71±9.455 P=0.914

2.4 e Length of the duration of extreme events

All insects

Logged overall insect abundance was positively associated with the duration of the longest dry (low rainfall) period during summer (an increase in the duration of the longest dry period by one additional day equated to an untransformed increase in overall insect abundance of 17%) and spring (dry period duration increase by 1 day = 8% increase) (Table 2.4).

Hymenoptera

The duration of the longest period of extreme warm weather in summer was marginally associated with logged Hymenoptera increase (warm period duration increase by 1 day = 23% increase). The duration of the longest period of extreme warm weather in winter was marginally associated with Hymenoptera abundance (warm period duration increase by 1 day = 28% increase). The duration of the longest dry period in summer was positively associated with Hymenoptera abundance (dry period duration increase by 1 day =21% increase) and the duration of the longest wet period in summer lead to Hymenoptera decline (duration increase by 1 day = 36% decline). The duration of the longest wet period in winter also had a negative effect on Hymenoptera abundance (duration increase by 1 day = 39% decline) (Table 2.4).

Diptera

Diptera abundance was positively associated with the duration of the longest extreme wet period in both spring (duration increase by 1 day = 15% increase) and summer (duration increase by 1 day = 18% increase). The duration of the longest dry period in autumn also increased Diptera population (duration increase by 1 day = 12% increase) (Table 2.4).

Homoptera

Logged Homoptera abundance was positively associated with the duration of the longest dry period during spring (duration increase by 1 day = 13% increase) and summer (duration increase by 1 day = 41% increase) (Table 2.4).

Table 2.4. Insect abundance Logn (All insects, Hymenoptera, Homoptera) and Diptera as a function of extreme weather variables calculated as the highest number of consecutive extreme days of low and high temperature and precipitation for each season. Models are mixed-effects models with year and site identity included as random effects in all models. Slopes are reported with ± SE.

Consecutive Weather	R^2 GLMM$_{(m)}$	R^2 GLMM$_{(c)}$	Summer	Autumn	Winter	Spring
All Insects						
High Temp	0.112	0.84	-0.020±0.158 P=0.857	-0.118±0.119 P=0.169	0.112±0.073 P=0.268	2.367x10^{-5}±0.163 P=0.100
Low Temp	0.29	0.809	0.003±0.067 P=0.954	0.053±0.045 P=0.117	0.114±0.099 P=0.122	0.010±0.083 P=0.857
High Rainfall	0.222	0.821	0.287±0.237 P=0.103	0.003±0.324 P=0.991	-0.197±0.219 P=0.212	-0.183±0.311 P=0.401
Low Rainfall	0.373	0.795	0.179±0.061 **P=0.0017**	0.069±0.069 P=0.174	-0.024±0.052 P=0.500	0.080±0.033 **P=0.00599**
Hymenoptera						
High Temp	0.201	0.771	0.208±0.143 P=0.064	0.026±0.108 P=0.728	0.249±0.129 **P=0.0192**	-0.015±0.147 P=0.882
Low Temp	0.139	0.785	0.014±0.104 P=0.842	0.033±0.07 P=0.505	0.044±0.155 P=0.6833	-0.122±0.129 P=0.193
High Rainfall	0.172	0.778	-0.366±0.289 P=0.094	0.092±0.395 P=0.738	-0.497±0.268 **P=0.023**	-0.400±0.379 P=0.153
Low Rainfall	0.203	0.771	0.196±0.099 **P=0.017**	0.092±0.114 P=0.265	0.054±0.084 P=0.3711	0.057±0.054 P=0.159
Homoptera						
High Temp	0.184	0.868	0.165±0.371 P=0.480	0.047±0.27 P=0.762	0.321±0.312 P=0.125	-0.009±0.321 P=0.963
Low Temp	0.165	0.871	0.028±0.183 P=0.805	-0.006±0.131 P=0.937	0.259±0.283 P=0.165	-0.162±0.253 P=0.316
High Rainfall	0.14	0.876	0.050±0.565 P=0.886	-0.158±0.837 P=0.762	-0.591±0.553 P=0.112	0.284±0.97 P=0.6022
Low Rainfall	0.517	0.814	0.345±0.128 **P=0.002**	0.027±0.359 P=0.905	-0.038±0.087 P=0.498	0.123±0.083 **P=0.041**
Diptera						
High Temp	0.097	0.67	29.787±33.909 P=0.226	-23.021±25.25 P=0.211	-27.483±30.18 P=0.211	-2.208±33.90 P=0.927
Low Temp	0.1159	0.663	17.550±18.731 P=0.200	-13.66±12.79 P=0.150	26.554±27.988 P=0.195	-0.991±23.317 P=0.951
High Rainfall	0.1343	0.656	111.81±53.1 **P=0.013**	-50.48±72.369 P=0.331	-28.57±49.16 P=0.331	89.99±69.53 **P=0.089**
Low Rainfall	0.076	0.677	16.306±25.014 P=0.359	35.721±28.853 **P=0.100**	-8.814±21.287 P=0.555	-6.538±13.672 P=0.497

2.5 Discussion

2.5a Population trends

There is currently increasing concern that insect populations are experiencing large declines across much of the globe (Hallmann *et al.* 2017; Hallman *et al.* 2019). Here we add further evidence for insect declines over the last decade (2009-2018) and extend the evidence base to temperate deciduous woodland. Rates of decline are particularly marked for Homoptera, but notably, we find no evidence that the most abundant order, Diptera, has declined during this period. Despite this, there is still a significant decline in overall insect abundance. Variation in declines between insect taxa were also evident by Hallman *et al.* (2019) and Lister & Garcia (2018) but there is a lack of studies which assess our focal taxa (Diptera, Homoptera and Hymenoptera) in temperate climates. Whilst we lack the ability to report declines for individual species our analyses at the community level for broad taxonomic groups highlight declines which are likely to influence the functional role of insect communities (Forister *et al.* 2019). Significant declines of a phytophagous group, for example, may reduce herbivory levels and reductions in Hymenoptera (predominantly parasitoids) could reduce top-down pressures on some insect groups. Declines in all insects, however, may have adverse impacts for taxa at higher trophic levels that utilise insects as a key food source (Forister *et al.* 2019).

2.5b Non-climatic drivers of population declines

Numerous factors are likely to be contributing to worldwide insect declines (Simmons *et al.* 2019). Our focal study site has experienced limited changes to the vegetation or its management during the course of the study (see methods) and the declines that we observed are unlikely to be a straightforward response to habitat change. Whilst our focal woodland sites are well connected to each other, and other woodland in the Rivelin valley, the woodland as a whole is isolated from other blocks of deciduous woodland. Such fragmentation can be a major driver of biodiversity loss, including in insects (Valladeres *et al.* 2006). Whilst the magnitude of fragmentation has not changed in the Rivelin Valley for a number of decades “extinction debt” (Tilman *et al.* 1994) arising from fragmentation can occur over a substantial time period for some taxa, e.g. 25-40 years (Krauss *et al.* 2010) and 100 years (Vellend *et al.* 2006). Most research on extinction debt focuses on plants and birds, with few studies assessing species with much shorter generation times, such as insects, whose population size is expected to respond more quickly to environmental change (Kuussaari *et al.* 2009). Whilst this has been shown to be the case for bees in grasslands (Bommarco *et al.* 2014), hoverflies (Diptera: Syrphidae) exhibit evidence of a temporal lag in response to habitat fragmentation that lasted decades (Bommarco *et al.* 2014; Herrault *et al.* 2016). We thus cannot rule out the possibility that extinction debt has contributed to the declines in insect population size that we observe.

Fragmentation also exposes populations to edge effects, and these may be particularly likely to arise in our study system due to the narrow width of woodland in much of the valley (Sites broadest widths ranged from 45m-500m, mean±SD: 241.3±167.6) resulting in a substantial proportion of the habitat being potentially subjected to edge effects. Insects at woodland edges are impacted by changes in microhabitat (Ouin *et al.* 2015) and shifts in species interactions all of which can contribute to population changes, often declines (Valladeres *et al.* 2006). Agricultural land to the north of our study site has little natural habitats such as off-crop strips and is thus unlikely to support high levels of biodiversity. It is also probable that artificial pesticides and fertilisers are used on this land. Pesticides are widely cited as causing declines in a number of insects (Goulson *et al.* 2015). The eastern moorland may also impact on woodland insect abundance, particularly as much of this habitat is managed through burning. Burning can generate particulate pollution (Allen 1964) as well as affect insect diversity in heather moorland (McFerran *et al.* 1995) and the prevailing westerly winds are also likely to carry pollution into the valley. Urbanisation can contribute to biodiversity declines through habitat loss and degradation as well as through pollution (Hardy 1999; New 2015), including light (Owens *et al.* 2020) and air pollution (Bignal *et al.* 2007). Road pollution, for example, has been shown to affect tree defoliation close to (within 100m) of a busy road (Bignal *et al.* 2007) and increased road traffic has also been associated with higher insect mortality (Martin *et al.* 2018). The Rivelin valley may be serving as an insect source which is being drained by the surrounding habitats acting as population sinks or ecological traps (Hallman *et al.* 2017).

2.5c Climatic drivers of population declines

Whilst site-based factors may contribute to the declines in Hymenoptera and Homoptera our core objective was to assess how insect population size was associated with inter-annual variation in weather as a means of assessing the potential for long term climatic changes to drive insect population trends. Our analyses find evidence that both mean climatic conditions and extreme events can influence the size of insect populations in our study system.

2.5ci Effects of mean climatic conditions

Warmer spring temperatures were associated, albeit with marginal statistical significance, with reduced total insect abundance. Such patterns were not detectable in analyses of our three focal taxonomic groups but our findings clearly contrast with other studies which suggest warmer springs boost population numbers in aphids (Harrington *et al.* 2007) and other insects (Ju *et al.* 2017) with this often being attributed to the capacity for more generations to complete development cycles in warmer conditions. Declining trends associated with warming in spring, however, may be driven by shifts in species interactions which are often cited as being more important than the direct impacts of weather (Ockendon *et al.* 2014; Ogilvie *et al.* 2017). The disruptions of trophic interactions by asynchronous responses to weather, for example, can be more pronounced in warmer springs (Visser *et al.* 1998; Burgess *et al.* 2018). Insects may be increasingly mistimed with the availability of their key food source (e.g. phytophagous insects and rapidly developing young leaves or parasitoids and their hosts), this can have potential impacts on insect survival, growth (Despland 2018) and fecundity (van Asch & Visser 2007). Few studies, however, have documented a population-level impact of these phenological mismatches for insect species.

Warmer summer mean temperatures, measured in the previous year to our focal sampling period, increased Homoptera abundance and marginally increased overall insect abundance. This contrast with the influence of spring warming may arise for two reasons. First, the negative impacts of trophic interactions are likely to be exclusively a consequence of warming in spring, rather than summer, as seasonal events have already occurred once summer starts (defined here as July-September). Second, summer warming can beneficially impact insect growth and development (Bale *et al.* 2002) and may increase the number of generations within a year and thus population size (Altermatt 2010). It has been shown in one Homoptera species that warmer temperatures during spring and summer can lead to increased recruitment of early instars, possibly as a result of adults laying more eggs or a higher number of eggs hatching in the warmer temperatures (Miles *et al.* 1997) which may boost population numbers. There is limited understanding as to whether this pattern may occur in other Homoptera as well as other insect taxa. Warmer temperatures also mean that weather conditions are more frequently suitable for insect activity, including flight, increasing the ability for insects to locate resources (Netherer & Schopf 2010) this may reduce direct mortality from starvation but also allow for improved winter body conditions, potentially increasing diapause survival rates.

Warmer winters significantly reduced overall insect abundance. The effects of winter weather have recently received more attention in climate change research but are still poorly understood relative to spring or summer (Williams *et al.* 2015). Many temperate insects undergo a period of dormancy, diapause, during winter (Bale & Hayward 2010). Although more well studied in plants there is increasing evidence that insects have a chilling requirement for the termination of diapause (Stalhandske *et al.* 2015; Renner & Zonner 2018)) which may not be met in warmer winters. This is also important in maintaining spring emergence synchrony with other trophic levels (Fuentealba *et al.*2017). Warmer winters may also increase energetic requirements in insects, leading to the more rapid loss of winter energy stores (Williams *et al.* 2012) which may cause direct mortality, or cause early emergence in spring with an increased frequency of inclement weather and limited resource availability.

Similarly, warmer autumns were also found to decrease insect abundance. Our Autumn period covers September-December which likely encompasses the initiation and part of the diapause phase. In addition to similar effects of warming winter of diapause maintenance and duration, warmer autumns may delay the onset of diapause. Whilst a longer active period can boost populations by allowing additional generations (Altermatt 2010), this can also lead to developmental traps, by which a new generation occurs instead of entering diapause and this can result in high mortality of that generation (Van Dyck *et al.* 2015) and therefore lead to potentially lower abundance in the following spring.

2.5cii Precipitation

The effects of changes in precipitation are not well understood for most insects. We find increased spring rain marginally drives declines in overall insect abundance. During periods of precipitation, insect flight activity is typically reduced, (although some taxa, such a thrips, may not be impacted (Jones *et al.* 2018)). Rainfall can reduce reproductive output, (e.g. in butterflies (Pardikes *et al.* 2015)) or limit resource location. Parasitism rates, for example, have been shown to decline during periods of high precipitation variability, possibly as a result of an inability to find their hosts in a more variable environment (Stireman *et al.* 2005), although we find no order specific effect of rainfall for Hymenoptera. Diptera, however, showed a marginal positive response to total spring rainfall, and a significant increase with higher summer rainfall in the previous year. This opposing effect upon Diptera may be due to their specific life strategies. Their larvae occupy multiple different habitats such as soil and standing water (Martay & Pierce-Higgins 2018). Dipteran larvae can be particularly susceptible to desiccation (Gibbons 1987; Briones *et al.* 1997) and thus increased rainfall may increase habitat availability and reduce this direct mortality.

In winter an increase in winter precipitation also led to overall insect declines. During winter, many insects undergo a dormant period which can often be underground or within plants (Leather *et al.* 1995). Increased rain may wash out or waterlog habitats leading to drowning. Combined with warmer temperature, pathogens may be more likely to persist in wet conditions (Burton & Turner 1970) but little research has explored implications of warmer and wetter winters on pathogen attack of insects during diapause.

2.5ci Effects of extreme climatic conditions

2.5cii Extreme temperature events

Extreme events may be more of a challenge to species as they are unpredictable and occur rapidly (Godfray *et al.* 1994; Parmesan *et al.* 1999). Extreme temperature events are likely to have different impacts depending upon the season (Hance *et al.* 2007; Mech *et al.* 2018). In spring, extreme temperatures were not associated with abundance of any of our focal taxa which suggests that in spring, mean shifts may be of more importance. In summer, mean increases of temperature had no effect on Hymenoptera, but we find an increased frequency of unusually hot weather is marginally beneficial to Hymenoptera populations. In our samples, Hymenoptera consisted largely of parasitoid wasps, which by definition are highly reliant on their host populations (Fraser 2007) Bursts of hot weather may increase the reproduction rate of host species such as aphids (although aphid abundance has also been negatively impacted by extreme heat (Sentis *et al.* 2012)) as well as accelerating their development, and thus the parasitoid offspring development (Moiroux *et al.* 2015) which may promote additional generations. This pattern was not evident in other taxa, Diptera, however, showed abundance increases with the frequency of extreme cool summer days. This mirrors the influence of total summer rainfall, as increased rainfall is also likely to be associated with cooler weather. The magnitude of effect is much higher, however than an increase in total rainfall. Cooler summer weather may similarly reduce the likelihood of larval desiccation by reducing evaporation from larval habitats. In a crop-field which assessed 8 Dipteran families, only one (Mycetophilidae, Fungus gnat) showed positive association with cold dry weather but was also positively influenced by hot dry weather (Ewald *et al.* 2015). Little is known about the effects of cooler summer temperatures on woodland insects in general, and further research is needed to determine what mechanisms are driving these positive effects in Diptera.

In winter, extreme cold events were beneficial for overall insect and Homoptera abundance. This reflects the negative associations of warmer mean temperatures and strengthens the evidence that a chilling requirement may be required for some insects (Stalhandske *et al.* 2015). It is possible that, as extremes are based on the range of temperatures for our specific study only, that these extreme cold days represent pre-warming winter temperatures, as these have increased under climate change (Lowe *et al.* 2018). It is worth noting that, the correlations between mean winter temperature and the frequency and duration of extreme cold period were high. Effects of extreme winter effects here, therefore, may be artefacts of changes in mean conditions. Moreover, where overall insects responded to both mean temperature and extreme low temperatures, mean temperature changes had a higher magnitude of effect. For example, an increase in 1°C in winter increased overall insects by 16% but an additional extreme cold day only increase populations by 6%. This could indicate that even if there are frequent cold snaps, an overall warmer winter would still negatively influence woodland insects.

Hymenoptera had a divergent response to winter extreme events relative to overall insects. Extreme warm winter events, both the occurrence of warm days and the duration of the warm events were associated with increases in Hymenoptera abundance. These extreme events are unlikely to be related to shifts in mean temperature, which was not found to drive Hymenoptera abundance and was only marginally correlated with these extreme measures. In mild winters, parasitoids (which make up a large proportion of our Hymenopteran samples) may shorten or avert diapause (Tougeron *et al.* 2017), there may be an increase in the number of active hosts (Tougeron *et al.* 2019) allowing parasitoids to persist throughout winter and a build-up of abundance. Alternatively, warming winters may accelerate diapause, this may lead to earlier spring emergence and thus the ability to attack hosts earlier, leading to increased potential for more generations. Both of these potential mechanisms, however, are reliant on the specificity of the parasitoids and availability of hosts (Andrade *et al.* 2016) and research exploring impacts on woodland parasitoid activity in winter, both on diapause occurrence and spring emergence, may enable a greater understanding of how winter temperatures drive their populations.

2.5ciii Extreme rainfall events

Many associations with extreme precipitation events followed a similar pattern to mean changes. For example, in spring, where increased rainfall had a negative impact on overall insect abundance prolonged periods of dry weather in spring also increased abundance.

Similar effects were found for dry periods in summer. Correlations between these extreme rainfall events and total rain were marginal or low, strengthening the indication that prolonged dry periods in spring and summer are important drivers of insect populations.

Heavy rainfall events in spring and summer, were, however more strongly correlated with the frequency of total rain days so the similar population increase in Diptera, to extreme and total rainfall, in these seasons may be an artefact of the impacts of overall rainfall across the season. The duration of the longest period of wet weather in summer, however, was only marginally correlated with total rain. This is concurrent with other studies which both larval and adult Diptera have been shown to increase with higher summer rainfall (Staley *et al.* 2007; Wise & Lensing 2019).

In winter an increase in the frequency of wet weather days drove overall insect declines. This extreme weather variable was highly correlated with overall winter rain. Despite this high collinearity, Hymenoptera showed no response to total rain in winter but did decline with extreme wet weather. Parasitoids adopt a variety of overwintering strategies which can often be as an immature stage within its host (Stamp 1982; Foerster 2006). Periods of extreme wet weather which cause mortality in hosts will therefore directly impact parasitoid populations, particularly as the overwintering larvae have no capacity to move in response to rainfall. We found no decline with extreme wet weather in a potential host taxa, non-aphid Homoptera, but other host groups (such as Lepidoptera and aphids) were not tested. Further research assessing the impacts of rain on host-parasitoid interactions may uncover a potentially important mechanism of decline in parasitoid populations.

In a study of cereal field insects, more taxa were significantly associated with mean changes than extreme events (Ewald *et al.* 2015). Whilst in some cases, the effects of extreme temperature or precipitation are difficult to discern from mean conditions, extreme events were sometimes important where mean conditions weren’t. This was particularly evident for extreme dry events in summer. The comparison of average conditions and extreme conditions impacts on insects are rare. Although they are typically well correlated to mean events, this is not always the case. We provide evidence that those extreme events which aren’t correlated with mean conditions can have significant associations with insect abundance, indicating that including them will be important for future analyses of insect response to climate change.

2.6 Conclusion

Total insect abundance and that of some, but not all, key taxonomic groups have declined. These declines have occurred in a block of isolated woodland that shares many similarities with much of the broadleaved woodland in the UK, but notably has not experienced any substantial changes in habitat or its management during the period of observed declines. Whilst it is possible that extinction debt and continuing edge effects from surrounding habitats have contributed to the declines these seem unlikely to be the only causal factors. Indeed, we find strong evidence that inter-annual variation in weather conditions is associated with variation in population size. Although difficult to distinguish completely effects of mean temperature and extreme events (due to correlations between the two and limited sample size, i.e. number of years) these models find evidence that the importance of extreme events versus average shifts in weather varies between taxa. Under predicted climate change in the UK, milder and wetter winters are expected (Lowe *et al* 2018), and our findings indicate that this will lead to an overall reduction in insects, but perhaps an increase in Hymenoptera. Summer weather is expected to become hotter and drier (Lowe *et al.* 2018), which may boost insect numbers, but drive declines in Diptera. Increased extreme wet events in both spring and summer, however, which are also projected, may boost Diptera populations. A significant impact on insect abundance can alter the provision of ecosystem processes such as population control by parasitoids and herbivory by phytophagous insects. It also has a high potential to alter the food available for higher trophic levels. Woodland community shifts may, therefore, be highly likely under altered climatic conditions.

Acknowledgements

We would like to thank all those which helped with the field collection of Rivelin Valley data and lab sorting of the samples. Thanks also to the Science Faculty at the University of Sheffield for their PhD studentship.

Chapter 3. Phenological responses in a sycamore-aphid-parasitoid system and consequences for aphid population dynamics: a 20-year case study

3.1 Abstract

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

3.2 Introduction

Climate change can influence species populations through direct and indirect mechanisms (Cahill *et al.* 2013; Ockendon *et al.* 2014). Changes in temperature and precipitation can directly alter individual growth rates, survival, and reproduction in a manner that affects population growth rate (Walther *et al.* 2002). Indirect effects occur through climate-induced alterations in resource availability and changes in species interactions (Tylianakis *et al.* 2008). Increasingly, evidence suggests that these shifts in species interactions are the principal factor driving demographic responses to climate change in multiple taxa including plants, insects, fish, birds, and mammals (Cahill *et al.* 2013; Ockenden *et al.* 2014; Ogilvie *et al.* 2017).

Insects are particularly sensitive to direct impacts of climate change as they are ectothermic and their physiologies, and resultant fitness, are strongly influenced by their surrounding microclimate (Bale *et al.* 2002). Warmer temperatures during spring and summer may enhance growth and reproductive rates (Deutsch *et al.* 2008) but also increase the possibility of heat stress (Kingolver *et al.* 2013) leading to increased mortality. Heat stress in temperate insect populations occupying closed habitats, such as woodland, are likely to be limited though as these insects typically experience conditions that are within their thermal tolerances (Deutch *et al.* 2008; Diamond *et al.* 2012; Sunday *et al.* 2014).

The direct effects of changes in precipitation and winter temperatures on insects are less well understood (Bale & Hayward 2010; but see Thackeray *et al.* 2016). In temperate regions, including the UK, there is much uncertainty regarding future changes in precipitation during spring and summer, i.e. when insects are active, with potential for droughts, increased rainfall and more intense rainfall events (Lowe *et al.* 2018). Droughts can increase insect mortality through desiccation (Torode *et al.* 2016). Heavy rainfall can increase mortality of terrestrial insects through drowning (Rosenzweig *et al.* Chivian 2001), and phytophagous insects may also be vulnerable to increased mortality if intense rainfall dislodges them from their host plants (Alford 2000).

Winter temperature in the UK is predicted to increase by 2-3°C by 2099 (Lowe *et al.* 2018). Warmer winter conditions can lead to insects failing to maintain nutritional reserves during the dormant diapause period, leading to increased mortality (Xiao *et al.* 2017), or reduced reproductive potential following diapause termination (Irwin & Lee Jr 2000). Warmer winters may also contribute to a higher incidence of pathogens in overwintering insects (Ferguson *et al.* 2017). Temperatures experienced during diapause interact with the duration of diapause to determine the timing of emergence in a non-linear manner, with both low and high temperatures potentially delaying diapause termination (Lehmann *et al.* 2017 Gotthard 2017). Some insects do, however, require a certain amount or duration of chilling in order to respond to warming spring temperatures that ultimately terminate diapause (Bosch & Kemp 2003; Chuche & Thiéry 2009, Stålhandske *et al.* 2015). Warmer conditions experienced during diapause could thus reduce both diapause incidence and duration exposing insects to unfavourable conditions that further increase mortality (Bale & Hayward 2010; Tougeron *et al.* 2017).

Indirect impacts are also likely to be a key determinant of insect response to climate change and frequently arise due to changes in the timing of key events including diapause termination and eclosion (Boggs & Inouye 2012; Høye *et al.* 2013; Kudo & Ida 2013). Earlier emergence and associated increased duration of the period suitable for insect activity could enable multivoltine insects to complete more generations per year, thus increasing population growth rates (Forrest 2016). Phenological shifts could also disrupt interspecific interactions if interacting species exhibit differential responses to climate change (Yang & Rudolph 2010). Changes in insect emergence date relative to host plant leaf burst may affect the abundance and quality of plant material available to phytophagous insects (Dixon 1976; Singer & Parmesan 2010). Similarly, changes in the relative timings of insect emergence and the phenology of their natural enemies could alter the duration and intensity of top-down pressures (Godfray *et al.* 1994; Hicks *et al.* 2007; Van Nouhuys & Lei 2004).

Variation in phenological responses between interacting species may arise frequently (Thackeray *et al.* 2016) and will occur when species respond to different cues or respond at different rates to the same cue. The phenological cues to which insects respond are not sufficiently understood, with current research focusing on the effects of spring temperature and less research addressing the effects of precipitation or winter temperature (Forrest 2016). There is increasing evidence from laboratory studies, however, that warmer winters can both advance (Tougeron *et al.* 2017) and delay (Stalhandske *et al.* 2015) insect activity periods, but the effect on population dynamics of wild populations is very rarely explored. Winter conditions are also often not considered in studies of insects' phenological responses (Thackeray *et al.* 2016).

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

Rushing et al. 2010). Such mismatches have been observed to reduce food availability and consequently breeding success and population size in birds (Both et al. 2006; Saino et al. 2011) and mammals (Plard et al. 2014). Empirical analyses of insect population responses to trophic mismatch have, however, received less attention, although there are some studies related to i) pests, e.g. mismatch with natural enemies which leads to reduced parasitism rates (Evans et al. 2013), ii) butterflies, e.g. larvae mismatch with host plants leading to local extinctions (McLaughlin et al. 2002) and iii) pollinators, e.g. mismatch of bee emergence with temporal distribution of floral resources (Ogilvie et al. 2017).

Impacts may be particularly prevalent in phytophagous insects, as 70% of these are specialist feeders (Price *et al.* 2011) and could also be influenced by the effects of temperature and precipitation on the abundance and nutritional quality of their host-plants (Cornelissen 2011; Thuiller *et al.* 2005). Phytophagous insects are also typically under pressure from natural enemies such as parasitoids. Climate change can influence the magnitude of these top-down pressures, in part due to phenological shifts that increase or decrease temporal refuge (Evans *et al.* 2013; Hicks *et al.* 2007; Tougeron *et al.* 2017).

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

3.3 Methods

3.3a Fieldwork

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

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

During each visit, 40 leaf buds or emerged leaves were selected haphazardly from those within reach, on which we recorded the number of *D. platanoidis* and *P. testudinaceus* aphids. Emergence phenology for *D. platanoidis* and *P. testudinaceus* was calculated as the date in which aphid abundance reached 10% of the total cumulative annual abundance recorded on the focal tree. This provides a population-level indicator of aphid emergence, which is more reliable than first emergence dates (Miller-Rushing & Primack. 2008; Tryjanowski & Sparks 2001). In some years *D. platanoidis* or *P. testudinaceus* were not recorded by the end of June on a small number of trees (*D. platanoidis* was absent from between 0 and 16 trees per year; *P. testudinaceus* absent from between 0 and 17 trees; Table S1). These trees thus lacked a spring population of the focal aphid species and were removed from the dataset for that year.

We also recorded the number of parasitized aphids, which were identified by their colour (Stary, 1970). As mummies were left *in situ* and not collected to hatch the parasitoid their specific identity is unknown, but all are Hymenoptera in the family Braconidae. Phenology of parasitoid attack occurrence was calculated as the date in which the number of aphids parasitized reached 10% of the total cumulative number of parasitised aphids. In some years, parasitized aphids were not found on some trees (between 1 and 37 trees per year; Table S3.1) which were thus not considered when analysing the phenology of parasitoid attack. Data on the number of aphids and aphid mummies were not collected in a small number of weeks (4.2% of potential observation were missing; Table S3.2). For these dates, we estimated the mean of the recorded values in weeks immediately either side of the missing data point prior to calculating phenological metrics. Daily meteorological records of maximum and minimum temperatures and total precipitation were obtained from a weather station located at the study site.

3.3b Statistical Analyses

3.3bi Effects of weather on sycamore, aphid and parasitoid phenology

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

We used Akaike Information Criteria corrected for small sample sizes (AICc) values to distinguish between competing models, which were constructed as linear mixed-effects models (LMERs) with Gaussian error structure, using the lme4 package (Bates *et al.* 2015) in R version 1.0.136 (R Core Team 2016). Year and individual tree ID were included as random factors to account for repeated measurements. Analyses were conducted in two stages; first, we fitted separate models for each set of weather variables (i.e. spring-summer temperature, spring-summer precipitation, see below) in order to assess the relative strength of association between phenology and these distinct types of weather variables, whilst also enabling us to identify the most influential time window for each type of weather variable. The second stage then combined the most influential time window for each weather variable into a multiple regression model that included predictors from the complete set of weather variables. This two-stage approach is required to restrict the number of predictor combinations to a manageable amount and follows standard practice (Drake & Martin 2018; van de Pol *et al.* 2016). In the first stage, we fitted separate models of phenology as a function of **i) temperature windows -** all weekly combinations of temperature which were relevant to the spring phenological period of each taxa respectively. For all taxa, weekly combinations of temperature began on Jan 1st and proceeded to April 29th for the sycamore tree (154 models), June 17th for *D. platanoidis* (300 models), June 10th for *P. testudinaceus* (276 models) and July 8th for parasitoids (378 models) and **ii) precipitation windows-** using all combinations of weekly precipitation. These models were constructed for each of our four phenological response variables, i.e.: sycamore budburst, *D. platanoidis* emergence, *P. testudinaceus* emergence and parasitoid attack and all contained tree identity and year as random factors. We compared the AICc of each of these models to that of a model without weather variables, i.e. which only contained year and tree identity as random factors. We considered all models within two AICc points (i.e. ΔAICc ≤ 2) of the best fitting model (that with the lowest AICc) to have similar goodness of fit to the data (provided that AICc is lower than the null model). For all trophic levels, this first stage modelling identified two distinct effects of temperatures between Jan-July, with periods earlier in the year in which higher temperatures had positive (delaying) effects on phenology and periods later in the year where temperature had negative (advancing) effects on phenology. A similar pattern occurred with regard to precipitation windows (see results). This first stage of modelling thus generated four sets of predictor variables for all study taxa that were carried over to the second stage of modelling, i.e. an advancing temperature window, a delaying temperature window, an advancing precipitation window, and a delaying precipitation window. Second stage modelling of each phenological event included these four predictor variables and mean winter temperature. The second stage of modelling used an information-theoretic approach to model selection using all possible combinations of our five weather predictors when modelling each phenological response. All models included year and individual tree number as random effects to account for repeated measures. We then conducted model averaging over all models within two AIC points of the best fitting model (and that had AICc values smaller than a null model that lacked weather predictors) for the given response variable.

3.3bi Population models

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

We conducted preliminary analyses to assess the nature of density dependence affecting these population growth rates. For each aphid species we modelled aphid population growth rate as a function of i) intra-specific density dependence – the population size of the same aphid species in the previous year, ii) inter-specific density dependence – the population size of the other aphid species in the previous years' population, and iii) inter and intraspecific density dependence – the combined population size of both aphid species in the previous year. The AICc values of these models were compared to that of a model which only contained random effects. For each aphid species, the model that only contained intra-specific density dependence had much lower AICc values than all other models, including the null model (Table S3.3), and so this form of density dependence was included in all subsequent population growth models.

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

We fitted population growth rate as a function of weather variables using LMERs that always included year and individual tree identity as random factors. We constructed separate models of aphid population growth rate as a function of i) temperature - all sequential monthly combinations of mean temperature (78 models), ii) precipitation - using all combinations of monthly precipitation as defined for temperature (78 models). We compared the AICc corrected for small sample sizes to that of a model with no weather variables, i.e. contained intraspecific density dependence as the only fixed factor and year and tree identity as random factors. We identified all models within two AICc points of the best fitting model (that with the lowest AICc). This stage thus helps us to compare the relative strength of direct weather effects on aphid population growth rates and we selected the temperature and precipitation windows with the lowest AICc values for use in the second stage of modelling.

In the second stage, we modelled aphid population growth rate as a function of density dependence, temperature and precipitation (best fitting variables selected from the first modelling stage), and included an estimate of the degree of temporal mismatch with budburst and parasitoid attack occurrence (year and tree number were also included as random effects). This allowed us to assess the relative importance of direct weather effects versus indirect effects of phenological mismatch with host plants or parasitoids. Phenological mismatches were calculated as the difference in number of days between aphid emergence and host tree leaf burst and the difference in number of days between aphid emergence and parasitoid attack occurrence. In this second stage, we constructed all possible models given our set of predictor variables (and included density dependence and random effects in all models) and then conducted model averaging over all models within two AIC points of the best model and with a lower AICc than the null model. In all our LMER models, the amount of variance explained by the fixed effects only and the combined fixed and random effects were calculated as the marginal R^2 ($R^2_{(m)}$) and conditional R^2 ($R^2_{(c)}$) respectively, as described by Nakagawa and Schielzeth (2012).

3.4 Results

3.4a Phenology

3.4ai Variation in phenology

Mean sycamore budburst date varied across the 20 year period by 17 days (April 6th – April 23rd, Figure 3.1) with a coefficient of variation (CV) of 4.79. *Drepanosiphum platanoidis* emergence varied by 76 days (March 28th – June 12th, Figure 3.1), with a CV of 17.30 and *Periphylus testudinaceus* emergence varied by 38 days (April 26th – June 3rd, Figure 3.1), with a CV of 7.42. Annual variation in the date of parasitoid attack occurrence varied by 61 days (May 8th-July 8th, Figure 3.1), CV 9.65.

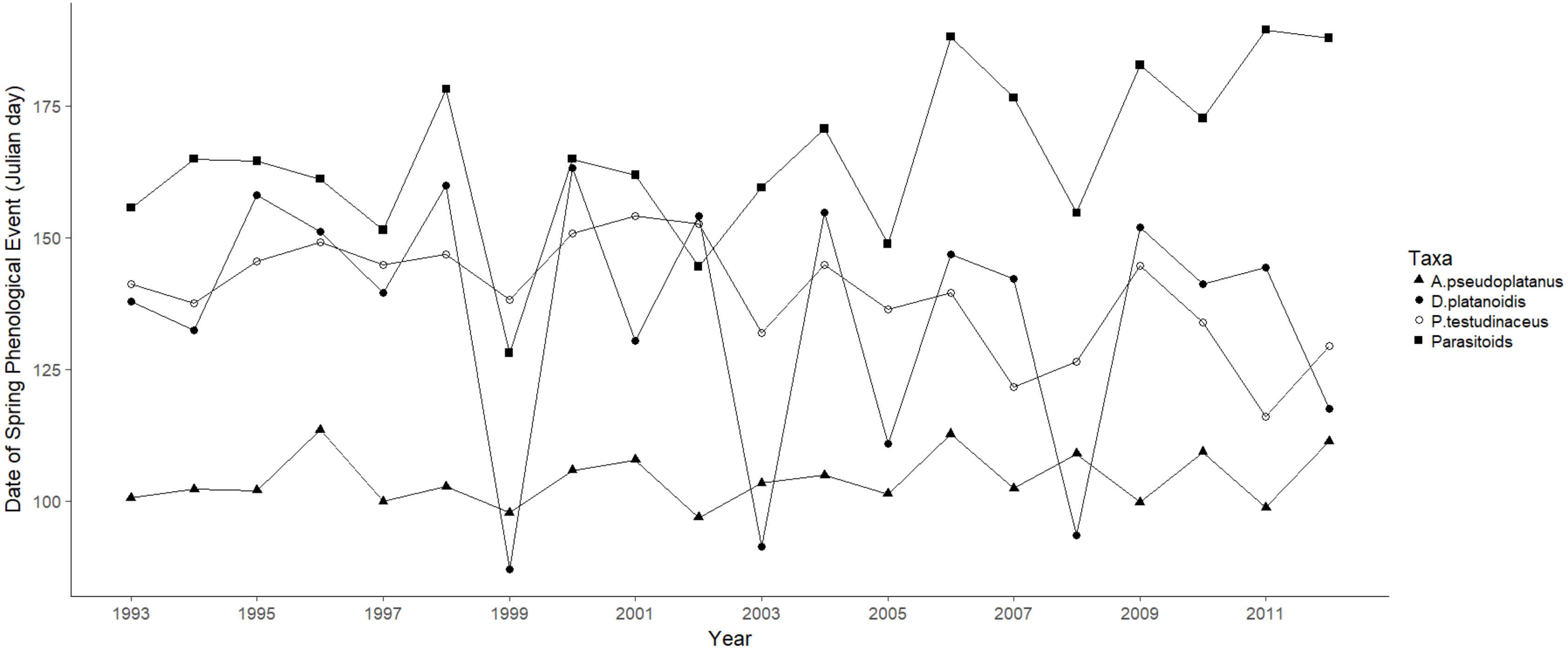

Figure 3.1. Changes in timing of spring phenological events within the plant-aphid-parasitoid tri-trophic system. Events are: i) sycamore bud-burst, ii) *Drepanosiphum platanoidis* emergence) iii) *Periphylus testudinaceus* emergence and iv) parasitoid attack (Braconidae; Hymenoptera).

3.4aii *Acer pseudoplatanus*

First stage modelling identified effects of temperature in weeks 11-16 (with an advancing effect on phenology), precipitation (in weeks 7-17; delaying effect) and precipitation (in weeks 1-9; advancing effect) (Table S3.4.a-S3.4d). Stage two modelling, however, demonstrated that only the advancing effect of temperature during weeks 11 to 16 had model-averaged (across eight models with ΔAICc < 2) parameter estimates whose 95% confidence intervals excluded zero, and the effect sizes of all other weather variables are estimated to be small (Table 1, Figure 3.2). A mean temperature increase of 1°C during weeks 11 to 16 (mid-March – early April) across the 20-year period advanced budburst by ~4.8 days (Figure 3.3a).

3.4a iii *Drepanosiphum platanoidis*

First stage modelling identified effects of temperature in weeks 21-22 (advancing effect on phenology), and weeks 6-7 (delaying effect) and precipitation in weeks 17-23 (advancing effect), and weeks 5-8 (delaying effect) on *D. platanoidis* emergence (Table S3.5a-S3.5d). Stage two modelling demonstrated that the delaying effect of temperature during weeks 6 to 7 was the only predictor for which non-zero effects could be excluded, with models suggesting that a 1°C increase in mean temperatures during weeks 6 and 7 (February) delayed emergence by 4.2 days (Figure 3.3b). Whilst non-zero effects for the advancing effect of temperature in weeks 21-22 (Late May – early June) could not be excluded (95% confidence intervals -14.0 to 1.8) the effect size is estimated to be larger than the delaying effect of temperatures earlier in the year, with a 1°C increase in mean temperatures during this period advancing the date of emergence by 6.1 days (Table 1, Figure 3.2).

3.4b iv *Periphylus testudinaceus*

First stage modelling identified effects of temperature (in weeks 6-7; delaying effect on phenology, and in weeks 13-17 advancing effect on phenology), precipitation (in weeks 4-7, delaying effect, and in weeks 19, advancing effect) on *P. testudinaceus* emergence (Table S3.6a-S3.6d). Stage 2 modelling found that all predictor variables had model-averaged 95% CI's that overlapped zero, but, the CIs of two variables almost excluded zero (Table 1, Figure 3.2), these were: i) temperatures during late March- April (week 13-17) (95% confidence intervals -9.0 to 0.2) for which a 1°C rise advanced emergence by 6.1 days (Figure 3.3c) and ii) temperatures during February (week 6-7) (95% confidence intervals -0.1 to 4.0) for which a 1°C rise delayed spring emergence by 2.0 days.

3.4b v Parasitoid attack

First stage modelling identified effects of temperature (in weeks 4-5; advancing effect on phenology and in weeks 15-26; delaying effects on phenology), precipitation in weeks 2-8 (advancing effect), and weeks 6-26 (delaying effect) (Table S3.7a-S3.7d). Stage two modelling demonstrated that advancing temperature in weeks 4 to 5 was the only predictor for which none zero effects could be excluded (i.e. 95% confidence intervals of parameter estimates did not overlap zero; Table 1, Figure 3.2). Across the 20-year period a mean increase in temperature of 1°C during January advanced parasitoid attack occurrence by approximately 5.3 days (Figure 3.3d). There was marginal evidence, i.e. non-zero effects could not be excluded (95% confidence intervals -2.5 to 15.8) that warmer temperatures during weeks 15-26 (April-June) delayed the date of parasitoid attack with an increase in temperature of 1°C shifting attack dates by 6.7 days.

Table 3.1. Phenological events (Sycamore budburst, *D. platanoidis* emergence, *P. testudinaceus* emergence and parasitoid attack) as a function of weather variables identified for each group with a moving window approach (Table S4a-S7d). Models are mixed-effects models with year and tree identity included as random effects in all models. For each species only models within 2 AICc points of the best model are presented alongside the results of model averaging these models (except for Parasitoid attack for which no models were within 2 AICc points of the model with the lowest AICc). ΔAICc is given relative to the model with the lowest AICc. Slopes are reported with ± 1SE. Random effects only models: i) Sycamore tree AICc = 6804.89 ii) *D. platanoidis* AICc =8759.1; *P. testudinaceus* AICc = 8334.6; Parasitoid attack AICc = 7100.3.

AICc	**Δ AICc**	**R^2 GLMM$_{(m)}$**	**R^2 GLMM$_{(c)}$**	**Temp delaying**	**Temp advancing**	**Precipitation advancing**	**Precipitation delaying**	**Winter temperature**
Sycamore bud-burst					***Week 11-16***	***Week 1-9***	***Week 7-17***	
6779.7	0	0.154	0.715		-4.75±0.88	-0.62±0.88	-0.10±1.33	
6779.7	0.1	0.154	0.714		-4.97±0.82		-0.40±1.2	
6780	0.4	0.153	0.713		-4.82±0.67			
6780	0.4	0.153	0.714		-4.72±0.69	-0.64±0.81		
6780.7	1.1	0.154	0.716		-4.77±0.98	-0.62±0.91	-0.12±1.53	0.03±0.66
6780.8	1.1	0.153	0.715		-4.75±0.88		-0.42±1.44	0.02±0.65
6781.4	1.7	0.153	0.714		-4.09±0.70			-0.07±0.56
6781.3	1.7	0.154	0.715		-4.72±0.71	-0.64±0.85		0.11±0.57
Model Averaging					*-4.82±0.81*	*-0.32±0.69*	*-0.14±1.03*	*0.00007±0.37*
D. platanoidis				***Week 6-7***	***Week 21-22***	***Week 17-23***	***Week 5-8***	
8743.1	0	0.2	0.6	4.77±2.36	-6.08±4.02	-0.12±1.03		-2.86±4.45
8743.7	0.6	0.2	0.61	4.77±2.36	-6.09±4.02		0.06±0.75	-2.85±4.44
8743.8	0.7	0.2	0.61	4.76±2.37	-6.10±4.03	-0.09±0.78	0.14±1.07	-2.84±4.44
Model Averaging				*4.76±2.36*	*-6.09±4.03*	*-0.09±0.88*	*-0.04±0.59*	*-2.85±4.44*
P. testudinaceus				***Week 6-7***	***Week 13-17***	***Week 19***	***Week 4-17***	
8314.8	0	0.133	0.285	1.88±1.07	-4.18±2.39	-1.33±1.41	4.41±3.50	-0.48±1.85
8315.9	1.1	0.134	0.278	1.80±0.99	-4.22±2.31	-1.37±1.36	4.17±3.27	
8316.2	1.8	0.13	0.281	2.20±1.01	-5.23±2.11		4.38±3.49	-0.66±1.83
Model Averaging				*1.94±1.05*	*-4.44±2.35*	*-1.03±1.35*	*4.33±3.44*	*-0.39±1.58*
Parasitoid attack				***Week 15-26***	***Week 4-5***	***Week 2-18***	***Week_6-26***	
7074.6	0	0.141	0.364	6.68±4.66	-5.30±1.71	6.15±7.57	7.17±8.64	-1.37±3.58

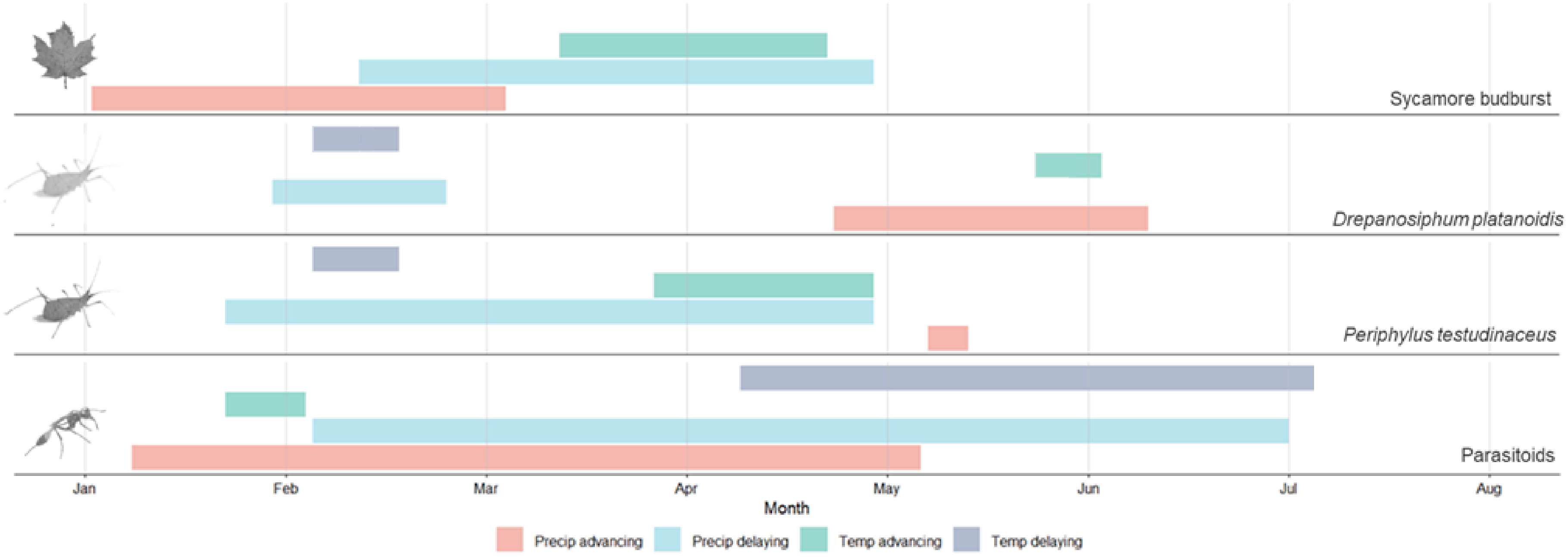

Figure 3.2. The sliding time windows of the weather variables identified as best predicting the phenology of sycamore budburst and the emergence of *D. platanoidis*, *P. testudinaceus* and parasitoid attack. The effects of different variables and their duration are shown with coloured bars. Models as described in Table 1 and Methods. Aphid emergence and parasitoid attack measured as the 10% cumulative abundance of aphids and parasitised aphids respectively.

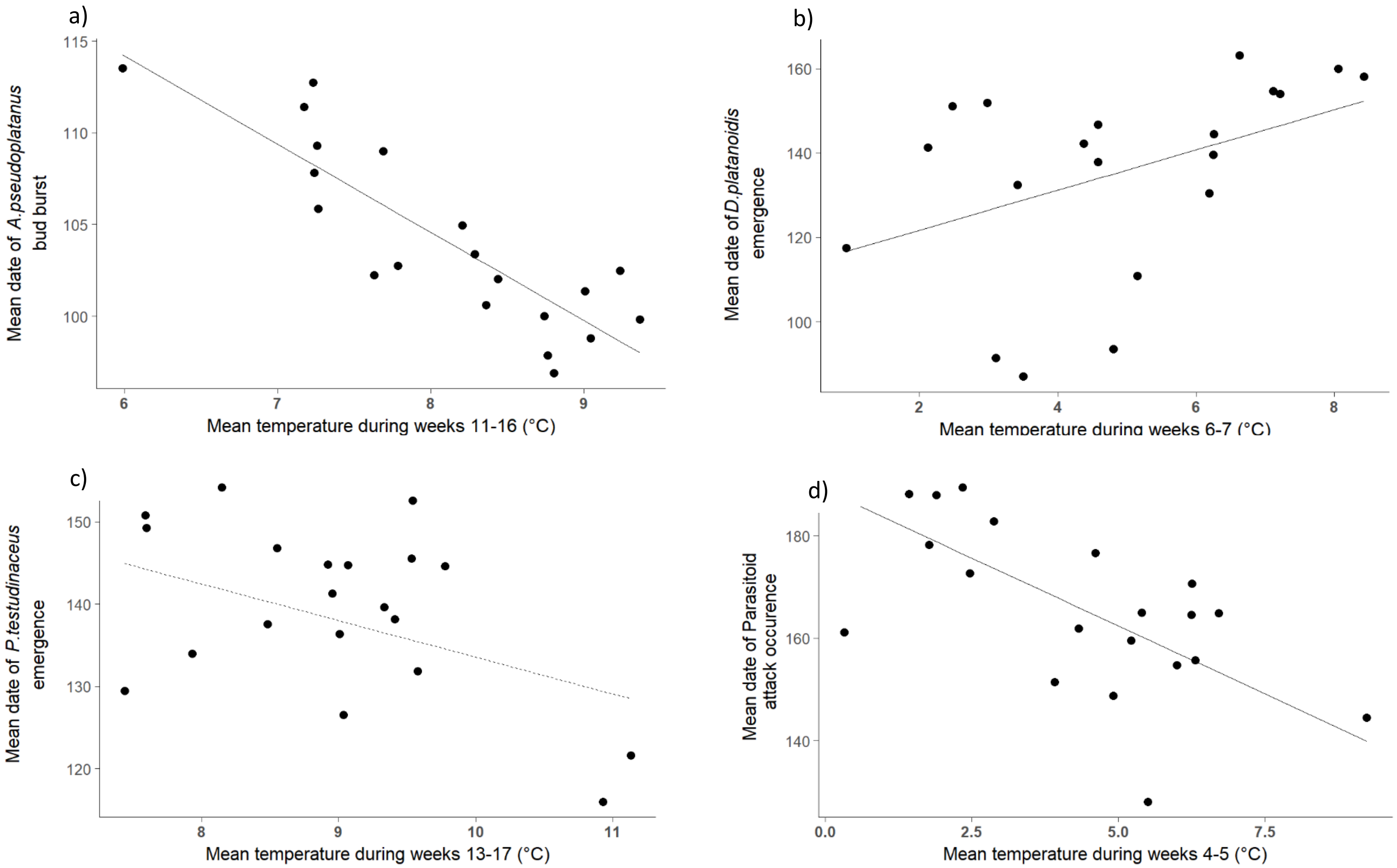

Figure 3.3. The relationship between temperature during key temporal windows and spring phenological events across three trophic levels: a) sycamore bud-burst, b) *D. platanoidis* emergence, c) *P. testudinaceus* emergence and d) the timing of attack by Hymenoptera parasitoids. For each phenological event plots illustrate the relationship with the weather variable that is most closely associated with phenology in mixed effect models that include tree and year as random effects and include the specific time windows identified in stage 1 modelling for each climatic variable. Black symbols are observed values. The line is the model-averaged predicted fit from models presented in Table 1; a solid line indicates that the 95% confidence intervals exclude zero, and a dashed line indicates that confidence intervals overlap zero. All dates are Julian dates (i.e. days since Jan 1st, and weeks since week 1 (1st -7th January).

3.4c Population growth rate analyses

Modelling of *D. platanoidis* and *P. testudinaceus* population growth rates as a function of density dependence found that negative intraspecific density dependence was the strongest form of density dependence with metrics that captured inter-specific density dependence having a weaker fit to the data (Table S3.3).

A moving window approach was used to select the time period during which monthly temperature and precipitation had the most influential effect on *D. platanoidis* and *P. testudinaceus* population growth rates whilst taking intra-specific density dependence into account. For both sets of weather variables, models that used alternative time windows and were within two AICc points of the best fitting model contained time windows that were very similar to the time window of the best fitting model (Tables S3.8a-3.9b).

3.4ci *Drepanosiphum platanoidis*

D. platanoidis population growth rate was modelled as a function of the weather variables selected in stage one modelling (temperature during March-July, precipitation during March-September) and the magnitude of mismatch with the other trophic levels, i.e. sycamore bud burst and parasitoid attack. This mismatch was substantial and highly variable between years - *D. platanoidis* emerged up to 48 days earlier and 117 days later than sycamore bud burst (mean ± SE: 30.64 ± 1.05 days later), and up to 168 days earlier and 49 days later than parasitoid attack occurrence (mean ± SE: 28.45 ± 1.33 earlier). Note, emergence can occur after parasitoid attack occurrence in years when parasitoid attack occurred before the date when aphid numbers had reached 10% of their total annual abundance. Two models were identified in this stage as having a similar goodness of fit to the best model (i.e. with ΔAICc < 2 relative to the model with the lowest AICc value). Mismatch with parasitoid attack and monthly mean precipitation from March to September were both retained in at least one of these models (Table 2). Model averaging and consideration of the 95% confidence intervals of parameter estimates indicate that density dependence effects and mismatch with parasitoid attack occurrence (Figure 3a) were the only predictors for which zero effects could be excluded (Table 2).

3.4c ii *Periphylus testudinaceus*

P. testudinaceus population growth rate was modelled as a function of the weather variables selected in stage one (temperature during February-September, precipitation during November), density dependence and the magnitude of mismatch with the other trophic levels, i.e. sycamore bud burst and parasitoid attack. *P. testudinaceus* emerged up to 38 days earlier and 110 days later than sycamore bud burst (mean ± SE: 35.45 ± 0.72), and up to 195 days earlier and 49 days later than parasitoid attack occurrence (mean ± SE -25.98 ± 1.37). Four models had AICc values within two points of the model with the lowest AICc value (Table 3.2). Mismatch with parasitoid attack occurrence, monthly mean precipitation from March to September and monthly mean temperature from February to September were all retained in at least one of these models. Model averaging and consideration of the 95% confidence intervals of parameter estimates indicate that intra-specific density-dependence effects and mismatch with parasitoid attack (Figure 3.3b) were the only predictors for which zero effects could be excluded (Table 3.2).

Table 3.2. *D. platanoidis* and *P. testudinaceus* population growth as a function of mismatch between tree and parasitoid attack and weather variables previously identified with a moving window approach (Table S8a-S9b). Models are mixed-effects models with year and tree identity included as random effects in all models. For each species, only models within 2 AICc points of the best model are presented alongside the results of model averaging these models. ΔAICc is given relative to the model with the lowest AICc. Slopes are reported with ±1SE. Random effects only models i) *D. platanoidis* AICc = 701.2, ii) *P. testudinaceus* AICc = 1250.8**.**

AICc	**ΔAICc**	**R^2 GLMM (m)**	**R^2 GLMM (c)**	**Density dependence**	**Parasitoid attack mismatch**	**Temperature**	**Precipitation**
D. platanoidis							***Mar-Sep***
697.7	-1.80	0.329	0.915	-0.68± 0.04	0.0019± 0.00046		-0.65±0.47
697.9	-1.65	0.318	0.917	-0.68± 0.04	0.0019±0.00046		
Model averaging				***-0.68±0.035***	***0.0019± 0.00046***		***-0.34±0.47***
P. testudinaceus						***Feb-Sep***	***Aug-Oct***
1230.4	0	0.433	0.858	-0.84±0.03	0.0042± 0.001		
1230.6	0.2	0.479	0.861	-0.84±0.03	0.0041± 0.001		0.42±0.25
1232.0	1.7	0.473	0.866	-0.84±0.03	0.0042± 0.001	0.29±0.25	
1232.2	1.8	0.519	0.870	-0.84±0.03	0.0041±0.001	0.290±0.239	0.43±0.25
Model averaging				***-0.84±0.034***	***0.0041±0.0001***	***0.088±0.191***	***0.20±0.27***

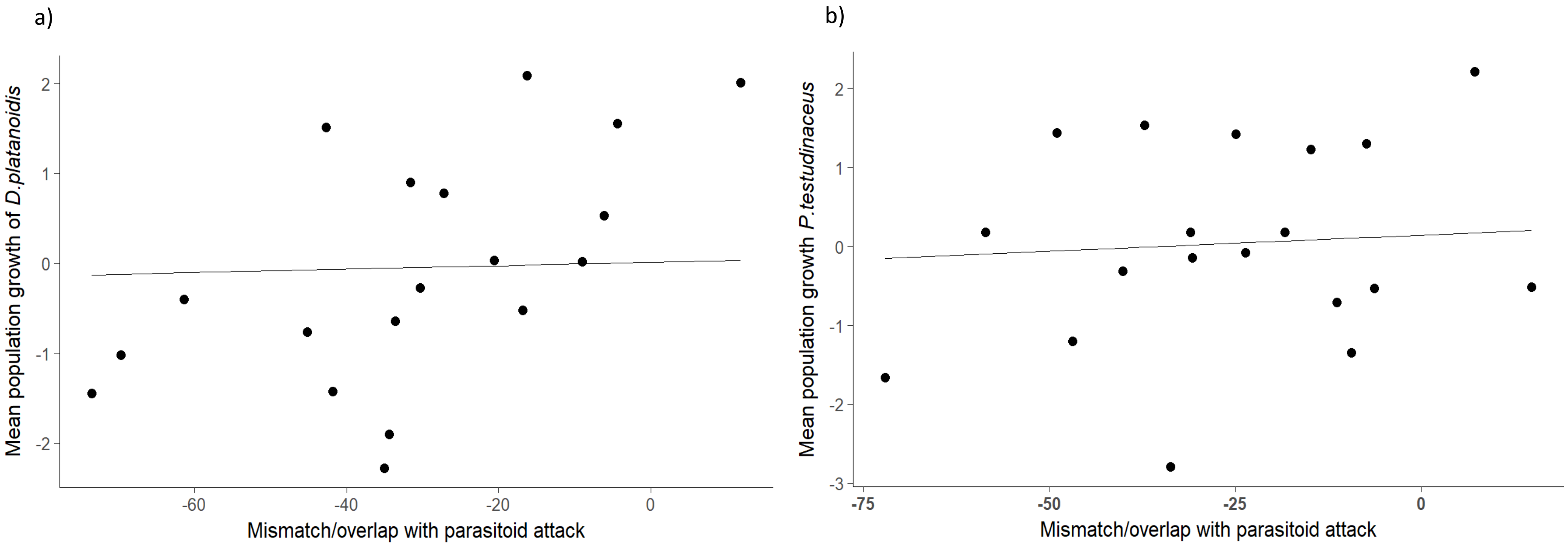

Figure 3.3 The relationship between mean population growth rate for a) *D. platanoidis* or b) *P. testudinaceus*, versus the magnitude of mismatch (in days) between aphid emergence and the timing of parasitoid attack – negative values indicate that aphids emerge earlier than parasitoids attack. Black symbols are observed values. The line is the model-averaged predicted fit from models that include the mismatch between aphid emergence and parasitoid attach as well as including tree and year as random effects and specific weather windows identified in stage one modelling and a density dependence variable as fixed effects (see Table 2).

3.5 Discussion

This study provides a rare assessment of temperature and precipitation variables, selected from across the annual cycle, associated with the phenology of closely interacting plants and insects in a tri-trophic sycamore-aphid-parasitoid system. We quantify how indirect effects arising from altered phenology of interacting species, and the direct effects of inter-annual variation in weather are associated with population growth rates of our two focal aphid species and the extent to which these effects are buffered by density dependence.

3.5a Effects of weather on phenology

3.5 ai Primary producer – Sycamore

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

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

3.5aii Primary consumers – D. platanoidis and P. testudinaceus.

Warming temperatures can drive earlier spring phenology in aphids, including *D. platanoidis* (Bell *et al.* 2015; Dixon 1976; Zhou *et al.* 1995). Here, we found that higher mean temperatures during late-May to early-June (*D. platanoidis*) and late-March to April (*P. testudinaceus*) were associated with earlier aphid emergence, although surprisingly, for both species non-zero effects could not be excluded, raising questions about the importance of this variable in driving phenology. Mean winter temperatures did not influence aphid phenology, however, our moving window approach found that an increase of mean temperatures by 1°C during February was clearly associated with later spring emergence of *D. platanoidis*. The aphid *P. testudinaceus* showed a similar pattern (albeit with 95% confidence intervals overlapping zero). On balance, our results provide reasonable indications that early-year warming can delay aphid phenology. Previous studies assessing impacts of spring temperature on aphid phenology and that of other insects rarely take such effects into account, and we would encourage future studies to do so. During the study period, the level of temperature variation experienced during the most important time windows for advancing phenology was lower when compared to the variation experienced during the most important windows for delaying phenology (Supplementary Figure S1). This contrast in magnitude of exposure may explain why we observe stronger support (with regard to excluding non-zero effects) for the effects of temperatures that delay phenology rather than the more effects of warmer temperatures later in the year that advance phenology.

The effects of warming winters and the importance of chilling effects are not well understood for natural insect populations. Experimental research on a limited number of insect species, including butterflies (Stålhandske *et al.* 2017) bees (Bosch & Kemp 2003) and leafhoppers (Chuche & Thiery 2009) have demonstrated delays in spring phenology when these insects experience warmer diapausing conditions. For many temperate insects, a sufficient level of chilling is critical for the termination of diapause (Hodek 1999). The degree of chilling experienced also affects the developmental sensitivity to increasing spring temperatures where warming requirements for eclosion can be affected by the magnitude of chilling. A few recent field studies have begun to demonstrate this delaying effect of warmer temperatures in natural populations, but these are generally limited to the effects on a small number of Lepidoptera (Stalhandske *et al.* 2017) and Hymenoptera species (Forrest & Thompson 2011) (see also Thackeray *et al.* 2016). Our results provide evidence for an effect of warmer temperatures delaying phenology in an additional order, suggesting that such impacts could be widespread in temperate insects. We also illustrate its importance within a specific time window as *D. platanoidis* was delayed by warming temperatures in February (with tentative evidence for a similar effect in *P. testudinaceus*). This suggests that chilling levels for these insects could be most critical towards the end of winter.

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

3.5aiii Natural enemies – Parasitoid attack

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

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

3.5a iv Divergent responses across species and potential for trophic mismatch

Mean sycamore budburst date varied across the 20 year period by 16 days (day 87-113), which is much less than variation at higher trophic levels. *D. platanoidis* emergence varied by 76 days (day 87-163) and *P. testudinaceus* emergence varied by 38 days (day 116-154). Parasitoid attack occurrence varied by 61 days (day 156-189). This supports previous work which shows primary consumers are more likely to exhibit, on average, greater phenological changes than primary producers (Thackeray *et al.* 2010; Thackeray *et al.* 2016), although disagrees with work which suggests secondary consumers would also show smaller phenological shifts than primary consumers (Thackeray *et al.* 2016).

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

3.5b Population-level effects

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

Insect populations can be strongly regulated by parasitoids (Hawkins *et al.* 1997; Schmidt *et al.* 2003). Despite this, there is a paucity of research assessing the effects of climate change-driven shifts in the timing of parasitoid attack on their host's population growth rates interactions and consequences for population dynamics. Most of the work that has been conducted concerns hosts that are arable crop pests, for example, warmer spring temperatures advances cereal leaf beetle (*Oulema melanopusm*) phenology more than the phenology of its parasitoids *Tetrastichus julis* resulting in reduced parasitism (Evans *et al.* 2013). In our study system, we find no evidence that earlier emergence relative to the timing of the parasitoid attack generates population growth rate benefits in either of our focal aphid species. It is plausible that this pattern arises in part because phenological advances are insufficient to completely avoid parasitoid attack, and that this simply occurs later during the aphid growth period. It is striking though that we find evidence that in models which take confounding factors into account, such as direct effects of weather, in years in which aphids emerging early, relative to parasitoid attack occurrence, population growth rates are reduced. Early emergence of aphids could generate higher aphid population densities at the time of parasitoid emergence which can facilitate host detection by parasitoids and increase attack rates (Walde & Murdoch 1988; Gunton & Pöyry 2016). Thus, aphids which emerge on trees much earlier than the occurrence of parasitoid attack may initially benefit from high population growth rates in a temporal refuge, but once parasitoids emerge the aphids could then suffer from high attack rates. Parasitoid-host relationships are, however, complex and varied. More detailed behavioural research on specific parasitoid species in this community is required to ascertain whether density-dependent attack rates explain the lower population growth when aphids emerge earlier than their parasitoids. It is also likely that density-dependent buffering partially protects aphid population growth rates from adverse impacts of parasitoid attack.

We find negligible evidence that population growth rates of *D. platanoidis* and *P. testudinaceus* are associated with direct impacts of weather. A recent meta-analysis of population growth in multiple UK taxa found that weather variables were driving population changes in a number of aphid species (Martay *et al.* 2016). Interestingly, however, this study included *D. platanoidis* and *P. testudinaceus* and found that whilst these aphids had positive population trends, monthly mean weather variables had negligible impacts on population growth rates. This is perhaps expected given that most temperate insect species, especially those in closed (rather than open) habitats experience temperatures that are well within their thermal limits (Deutch *et al.* 2008; Diamond *et al.* 2012; Sunday 2014). Therefore, although we find that both spring temperatures and summer temperatures vary by approximately 3.5°C degrees, this is not likely to cause extreme thermal stress which would limit fecundity and growth. Other studies do, however, suggest that warmer conditions enable many temperate insect species to increase the number of generations within an annual cycle (Yamamura & Kiritani, 1998). This mechanism may not apply to our focal aphid species as there is limited variation in the duration of the period during which either species was detected – with individuals being found in March and November even in the coolest years (See table S10).

Furthermore, density dependence effects are quite strong which may buffer indirect and direct effects of weather. Density dependence and species interactions both play roles in determining the magnitude of population change in response to climate change (Harrington *et al.* 2007; Woiwod & Sparks 1999). Negative density dependence, as exhibited by both aphid species, is important for population regulation (Nowicki *et al.* 2009). The effects of density dependence, however, may weaken under climate change (Ouyang *et al.* 2014). Climatic shifts over the threshold experienced in this study period could exacerbate these weak mismatch effects and have a more demonstrable effect on aphid population growth. Aphid populations appear to be more resilient than other groups to negative direct and indirect effects of climatic shifts (Harrington *et al.* 2007; Thackeray *et al.* 2010).

3.6 Conclusion

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

Acknowledgements

Thanks to the University of Sheffield for providing PhD Studentship funding and many thanks to the many students who helped with the data collection as part of their summer projects and the British Ecological Society for funding them.

Chapter 4. Phenological mismatch with oak *Quercus* leaf emergence increases the duration of caterpillar larval stages, lowers pupae mass, and increases the risk of wing abnormalities in a declining woodland moth *Orthosia cerasi*

4.1 Abstract

Consequences of climate change-driven shifts in the relative timing of spring activities of interacting species are poorly understood, especially for insects. We use a mismatch simulation experiment on a widespread moth *Orthosia cerasi*, whose UK population declines are associated with warming temperatures. We simulate a synchronised hatch treatment in which *O. cerasi* larvae are fed young oak *Quercus robur* leaves and a late hatch treatment in which larvae are fed older leaves that simulate a phenological mismatch arising from hatching after leaf emergence. We assess impacts on growth time, pupal size and overwintering duration and survival. Larvae in the phenological mismatch treatment had a longer larval period and smaller and lighter pupae. Larval diet did not carry over to influence emergence dates as earlier pupation of synchronised larvae was balanced out by an equivalent increase in the duration of the pupal stage. Increased time spent as caterpillars could increase predation rates from avian predators, whilst reducing the rate of seasonal decline in food availability for bird species that specialise on caterpillars. Reduced pupal size and weight are indicators of lower fecundity. Notably, and whilst sample sizes were small, we find that adults emerging from the mismatch treatment exhibited greater rates of abnormal vestigial wing development, which is likely to further reduce fitness. Phenological mismatch may thus contribute to the population declines observed in many woodland moth species due to increased mortality at larval stages, and adverse effects of early-life conditions that reduce the reproductive success of emerging adults.

4.2. Introduction

One of the key ecological consequences of climate change is the impact on the phenology of a species and associated trophic interactions (Dewar & Watt 1992, Masters *et al.* 1998, Visser *et al.* 1998, Bale *et al.* 2002, Parmesan 2006, van Asch and Visser 2007, Musolin 2007, Altermatt 2010, IPCC 2013, Hoye *et al.* 2014). This is particularly important in seasonal environments, such as temperate woodlands, as the precise timings of growth, reproduction, the transition from one life-stage to another and diapause are essential for survival and reproductive success of an individual. In insects, temperature is well known for driving phenological traits such as egg-hatching, pupation or adult emergence (Uvarov 1931, Howe 1967, Hallman & Denlinger 1998).

The mechanisms underpinning shifts in population size and distribution in response to climate change are not sufficiently understood (Bale *et al.* 2002; Andrew *et al.* 2013). It is widely considered, however, that changes in biotic interactions are typically more important than the direct effects of weather (Ockenden *et al* 2014; Ogilvie *et al.* 2017). Phenological shifts are an important cause of changes in biotic interactions (Visser & Both 2005; Renner & Zohner 2018). Different species, especially those occupying different trophic levels, tend to exhibit divergent changes in the timing of key life-cycle events (Both *et al.* 2009; Thackeray *et al.* 2016). This can lead to phenological mismatch, i.e. asynchronous timing of key life events between interacting species. These shifts can influence individual fitness as, in seasonal environments, the precise timing of phenological events (such as growth, reproduction, and transition between developmental stages and diapause of invertebrates) is essential to optimise survival and reproductive success (Chuine 2010). Asynchronous shifts have been observed in a range of interactions (Kharouba *et al.* 2018). The subsequent population-level impacts, however, are not well understood. In some species, phenological mismatch has been linked to population declines, e.g. caribou *Rangifer tarandus* (Post & Forchhammer 2008) and pied flycatcher *Ficedula hypoleuca* (Both *et al.* 2009). Yet, in other populations phenological mismatch does not appear to drive population declines (e.g. great tit Reed *et al.* 2013). Therefore, even in well studied vertebrate groups, it remains unclear how important trophic mismatch is in driving population changes. Even less is known regarding invertebrates although limited research has indicated local impacts on butterflies, e.g. *Euphydryas editha bayensis* species (McLaughlin *et al.* 2002) and impacts of temporal mismatch with floral-resources on bumblebee abundance (Ogilve *et al.* 2017). A better understanding of whether trophic mismatches induce growth and development impacts may help to quantify whether population-level impacts are likely.

The timing of spring emergence in many phytophagous insects is synchronised with early leaf development of their host plant. As the leaves of deciduous trees age, for example, their nitrogen and water content decreases (Feeny 1968; 1970), whilst leaf toughness and the concentration of defensive chemicals, such as tannins, increases (Tikkanen and Julkunen-Tiitto 2003; Coley *et al.* 1996). Palatability and nutritional quality thus decline as leaves age. Phenological shifts in spring leaf development and insect emergence may not respond to climate change at the same rate generating an increased likelihood of a desynchronisation of these phenological events (Thackeray *et al.* 2016).

Shifts in phenology may lead to phytophagous insects emerging earlier or later relative to the emergence of the leaves of their host plants, i.e. bud-burst. Hatching or emerging prior to the availability of a sufficient food source increases the likelihood of starvation. Five days of starvation during spring, for example, can cause a mortality rate of over 50% in winter moth caterpillars *Operophtera brumata* (Wint 1983; Tikkanen & Julkunen-Tiitto 2003). Phytophagous insects that emerge late relative to bud development could conversely be adversely affected by seasonal declines in leaf nutritional quality. Tests of this hypothesis are relatively rare and confined to a few well-studied species, notably the winter moth. In this species, studies suggest that feeding on older leaves, and thus with higher tannin concentrations, will result in smaller females with reduced egg loads (Buse *et al.* 1998). Feeding on mature leaves may also lead to a reduction in survival (Despland 2018), growth rate (Barbehenn *et al.* 2017), pupation weight, and fecundity in insect herbivores (van Asch & Visser 2007).

Assessing subsequent overwintering survival and emergence is even less well understood, although studies have shown that host plant nutrition can affect overwintering preparedness and survival (e.g. *Helicoverpa armigera* Liu *et al.* 2007; Liu *et al.* 2010). Smaller pupae are less likely to have sufficient reserves, and thus caterpillars which emerge late and feed on mature leaves may be forced to terminate diapause early (thus advancing their emergence date) or have reduced over-winter survival rates (Hann & Denlinger 2007). These effects of over-winter survival may partly arise as larvae with lower quality diets may have increased susceptibility to pathogens as the pupal stage (Martemyanov *et al.* 2015).

We also test whether lower quality diets arising from trophic mismatches could increase developmental abnormalities in adult moths, as such impacts have been observed when rearing Lepidoptera on artificial diets of low quality (Odell 1966; Kayser 2012). As far as we are aware this is a novel and previously untested hypothesis. We use an experimental simulation of a phenological mismatch to determine if *Orthosia cerasi* (Common quaker) larval and subsequent pupae performance is significantly affected by reduced synchrony between the timing of caterpillar emergence and bud-burst. Like many moths, this species is declining in the UK, and population trends are statistically associated with climatic variation including warming temperatures (Martay *et al.* 2016). The mechanisms driving these declines in *O. cerasi,* and other moth species, however, are very poorly understood (Fox 2013). The indirect effects from shifts in species interactions, such as phenological mismatch with their host plant may be a contributing factor. Moths in the genus *Orthosia* are widespread and often abundant (Waring and Townsend 2009). They are therefore likely to contribute significantly to the overall caterpillar biomass in woodland habitats in the UK and elsewhere in temperate Europe during spring months, and thus provide an important food resource for woodland birds. *Orthosia* species typically lay eggs in late March-April that hatch in early spring, with emerging caterpillars feeding on early developing buds and leaves of a number of deciduous tree species. Our experimental design enables us to establish phenological mismatch arising from late caterpillar emergence relative to bud-burst and assess the growth of these caterpillars relative to ones that hatch more synchronously with bud-burst. We measure caterpillar growth by quantifying the time taken to reach pupation, pupal size and weight (which are indicators of pupae quality and subsequent fecundity of emergent adults; Buse & Good 1996; van Asch & Visser 2007; Kharouba *et al.* 2015), emergence rates from pupation and the occurrence of wing abnormalities of emergent adults.

4.3Materials and methods

4.3a Egg collection

Orthosia cerasi (Common Quaker Moth) is widespread throughout the British Isles and Europe. They are generalist species which feed on multiple broad-leaved trees but are reported to exhibit the fastest growth rates on oak *Quercus* species (Royama 1970). In 2018 female moths were collected during *O. cerasi*'s peak flight season (early March) with 125W MV Robinson Moth Traps light traps from two oak-dominant woodlands in Oxfordshire approximately 20km apart, England (Little Wittenham Woods SU57409277; Bagley Woods SP51030236). Female moths were identified according to antennae morphology (females typically have more slender and single-stranded antennae compared to those of males which are broader and feathery), abdomen shape (narrower, with a sharper point and curving upwards in males). Female *Orthosia* moths caught in light traps have typically already mated and thus were placed into individual pots in outdoor ambient conditions and provided with an artificial substrate for egg-laying (tissue paper) from which the eggs could easily be collected. Adults were kept for 7 days after which all females had laid eggs. Eggs were obtained from 11 individual females and were kept at ~5°C to delay hatching (below the 7°C development threshold for other *Orthosia* species; Mols *et al.* 1998). Once hatching was observed individual larvae were randomly selected and assigned to each of the early and late-hatching treatment. The experiment ran from early May to early July in Sheffield, central England.

4.3b Experimental procedure

Newly hatched larvae were selected from each batch and separated into identical small plastic containers with a muslin lid to generate airflow, gaseous diffusion, and limit any moisture build-up. 9-13 caterpillars were selected randomly from each egg batch and assigned to an early treatment or late treatment. All caterpillars were fed young leaves for 7 days, so whilst the effects of feeding on mature leaves may be underestimated, this reduced early larval mortality and ensured that sufficient sample sizes were available for the experiment. Caterpillars were then assigned to a late-hatching or synchronised hatching treatment, which were run concurrently. The experiment thus mimics a natural situation in which most caterpillars can disperse to other trees to find young leaves (due to intra-specific variation in budburst at the local scale) but later hatching caterpillars are increasingly likely to be restricted to feeding on older leaves. Leaves were supplied ad-libitum and refreshed every two days (occasionally every third day in cooler weather conditions). During the course of the experiment, larvae were separated into pots of fewer individuals to reduce population densities and any associated competition. Records of population density were kept in order to allow us to take this into consideration during analyses (Figure S4.1). Caterpillars allocated to each treatment were similar in size prior to the start of the treatment (Figure S4.2).

Larval containers were housed in a garden greenhouse in a random block design. The greenhouse was divided into 8 areas and containers containing early and late treatment caterpillars were split across these blocks to control for any small spatial variation in environmental conditions. Summer (June-August) temperatures were approximately 2°C higher than the 1981-2010 long-term average (Met Office 2018), thus the greenhouse was protected from high temperatures by creating additional openings for airflow and using a white sheet to reflect light from the roof. During periodic heatwave events, caterpillars were also moved to a cooler, completely shaded, outdoor brick building to minimise any heat stress events. All caterpillars in both treatments experienced the same climatic conditions.

4.3c Leaf selection

Pedunculate oak *Quercus robus* leaves were obtained from natural oak populations in the Rivelin Valley, Sheffield, and saplings held at the Arthur Willis Environment Centre, University of Sheffield. Leaves were selected haphazardly but avoiding those with more than negligible amounts of prior insect attack or disease. Larvae in the synchronised treatment were consistently provided with young newly expanded leaves (bud burst stages 6 and 7, i.e. newly expanded, soft and light green; Figure S4.1). Larvae assigned to the late egg hatch treatment were fed on mature leaves, i.e. beyond bud burst stage 7 that were darker green and tougher in texture than the newly expanded leaves (Figure S4.3).

4.3d Measuring response variables

Caterpillars were monitored weekly until they ceased feeding and reached the final instar stage when caterpillars were provided with a layer of top-soil to burrow into and pupate (Waring & Townsend 2009). Larvae were then checked daily or every two days to determine pupation date. This was recorded as the first date that a caterpillar was observed to have burrowed into the soil and could no longer be detected at the surface. Time taken for pupation was measured as the number of days between the start of the experiment and pupation date. Pupated caterpillars were left undisturbed for between 7 and 14 days after the pupation date and then weighed. Pupal mass was recorded using a digital balance (to 0.001 g). Three readings were taken and the average mass was used when these readings were not identical.

Pupae size was measured using image analysis with ImageJ (Schneider *et al.* 2012). Each pupae was photographed using a DSLR camera from a standard height and angle with a millimetre-scale included in the image. Shadows were minimised by placing pupae on a lightbox and using flash. Images were taken of the back and front of each pupae to account for shape variation and possible effects of small shadows. Within ImageJ, images were converted to 8bit and the threshold was adjusted to produce a white background with a black pupae. Pupal length and width were calculated as the mean from the two available images and subsequently used to calculate pupal area (mm^2) thus providing a measure of pupal size in addition to pupal weight.

4.3e Overwintering survival and developmental abnormalities

After weighing, pupae were returned to original positions in larval containers (usually one, occasionally two or three per pot) and provided with equal measures of topsoil. Containers from each treatment were then allocated a random position in a small shed, with a large window allowing in natural light, from August 2018. Consequently, all pupae experienced the same climatic conditions during winter. From 1st February 2019 containers were monitored weekly for adult moth emergence. Following the first observed emergence containers were subsequently monitored every three days and any moth emergence was recorded. Recording of emergence date continued until March 28th at which point three subsequent checks had been made with no new emergences. All containers contained ample space to enable wing expansion and drying to develop normal wings. The sex of all emerged moths was recorded by assessing antennae and the abdomen for the presence of claspers (present in males). All moths were checked for developmental abnormalities, the only ones that were detected were the production of small wings that were non-functional for normal flight behaviour (Figure S4).

4.3f Statistical analyses

All analyses were conducted using the lme4 package (Bates *et al.* 2015) in R version 1.0.136 (R Core Team 2016) unless stated otherwise. Mixed-effects models, with Gaussian error structure, were used to analyse the effects of treatment on time taken to pupation (days); pupal weight and pupal size (mm^2). Each model included treatment type (synchronised or late egg hatch relative to budburst) and population density (recorded as the mean number of caterpillars that the focal caterpillar shared a pot with) as fixed factors. Experimental block (1-8) and egg batch (B1-B11) were included in all models as random factors. Final sample sizes were Sychnronised treatment n=40, late hatching treatment n=29 (this was smaller than the initial number of caterpillars due to some mortality and some caterpillars escaping).

A binary logistic regression model was used to analyse the effects of treatment on pupal survival rates, i.e. emergence success (emerged vs not emerged). The model included treatment type (synchronised or late egg hatch relative to budburst), population density (recorded as the mean number of caterpillars that the focal caterpillar shared a pot with) and pupal weight (in a small number of pots there was more than one pupae and as it was not possible to determine which specific pupae had emerged, pupal weights for these pots were taken as a mean across all pupae in that pot) as fixed factors. Experimental block (1-8) and egg batch (B1-B11) were initially included in the models as random factors, but as block explained zero variance it was removed from this model to prevent singularity issues. Final sample sizes were: synchronised treatment n=39 (1 pupae was accidentally damaged so removed from the experiment), late hatching treatment n = 29.

A mixed-effects model, with Gaussian error structure, was used to analyse the time taken to emerge (calculated as the total number of days from pupation to eclosion). This model included treatment type, population density, sex and pupal weight as fixed factors; block and egg batch were initially included as random factors, but as block explained zero variance it was removed from this model to prevent singularity issues. Final sample sizes were: synchronised treatment n=23, late hatching treatment n = 16.

A Fisher’s exact test was used to test if the occurrence of wing abnormalities differed between adults that emerged from the synchronised (n = 23) and late hatch (n = 16) treatments.

4.4 Results

Results

Time to pupation, and pupal size and weight

Treatment significantly affected time to pupation (P< 5.471x10-7 n = 60; Fig. 1a). Model parameter estimates indicate that synchronised larvae that were fed on younger leaves pupated approximately 8 days earlier than caterpillars in the late hatching treatment that were fed on older leaves (parameter estimate ± 95% confidence interval: 8.220 ± 2.836). Population density was not associated with time to pupation (-0.457±1.444, P = 0.588).

Treatment significantly affected pupal size ($P = 2.106\text{x}10^{-6}$, n= 69; Fig. 1b) and weight ($P = 3.921\text{x}10^{-6}$, n = 69; Fig 1c). Models estimated that synchronised larvae fed on younger leaves were approximately 7mm^2 larger (parameter estimate ± 95% confidence interval: -6.683 ± 2.508) and 0.003g heavier (parameter estimate ± 95% confidence interval: -0.031 ± 0.0006) than late hatching lavae fed on older oak leaves. Population density was not associated with pupal size (parameter estimate ± 95% confidence interval: -0.041 ± 1.262 P = 0.912) or weight (parameter estimate ± 95% confidence interval: 0.001 ± 0.003, P = 0.698).

Overwintering impacts - Pupal survival and time to emergence

55% of the late hatching treatment pupae emerged and 59% of the synchronised pupae emerged. Survival to eclosion was not associated with treatment(estimate ± 95% confidence interval = 0.140 ± 1.257, *P* = 0.827 n = 69;), . pupal weight (6.947 ± 19.130, *P* = 0.469) or population density (-0.110 ± 0.478, *P* = 0.647).

Treatment had a significant effect on time taken for spring emergence (*P* = 0.00436, n =39, Fig. 2). Pupae from synchronised larvae fed on younger leaves remained as pupae for nearly 9 days longer than the late hatching treatment larvae fed on mature leaves (parameter estimate ± 95% confidence interval: -8.897 ± 5.792). Male moths that emerged took approximately 8 days less to do so than females (-8.226 ± 5.212, *P* = 0.006) with males emerging 7 days earlier than females. Time taken for spring emergence was not significantly affected by pupal weight (-3.046 ± 83.213 *P* = 0.468) or population density (1.141 ± 2.174, *P* = 0.320).

Wing abnormalities

The occurrence of small and non-functional wings was significantly higher (*P* = 0.033, n = 39) when moths emerged from the late-hatch treatment (5 cases, 31%) than those that received the synchronised hatch treatment (1 case, 4%).

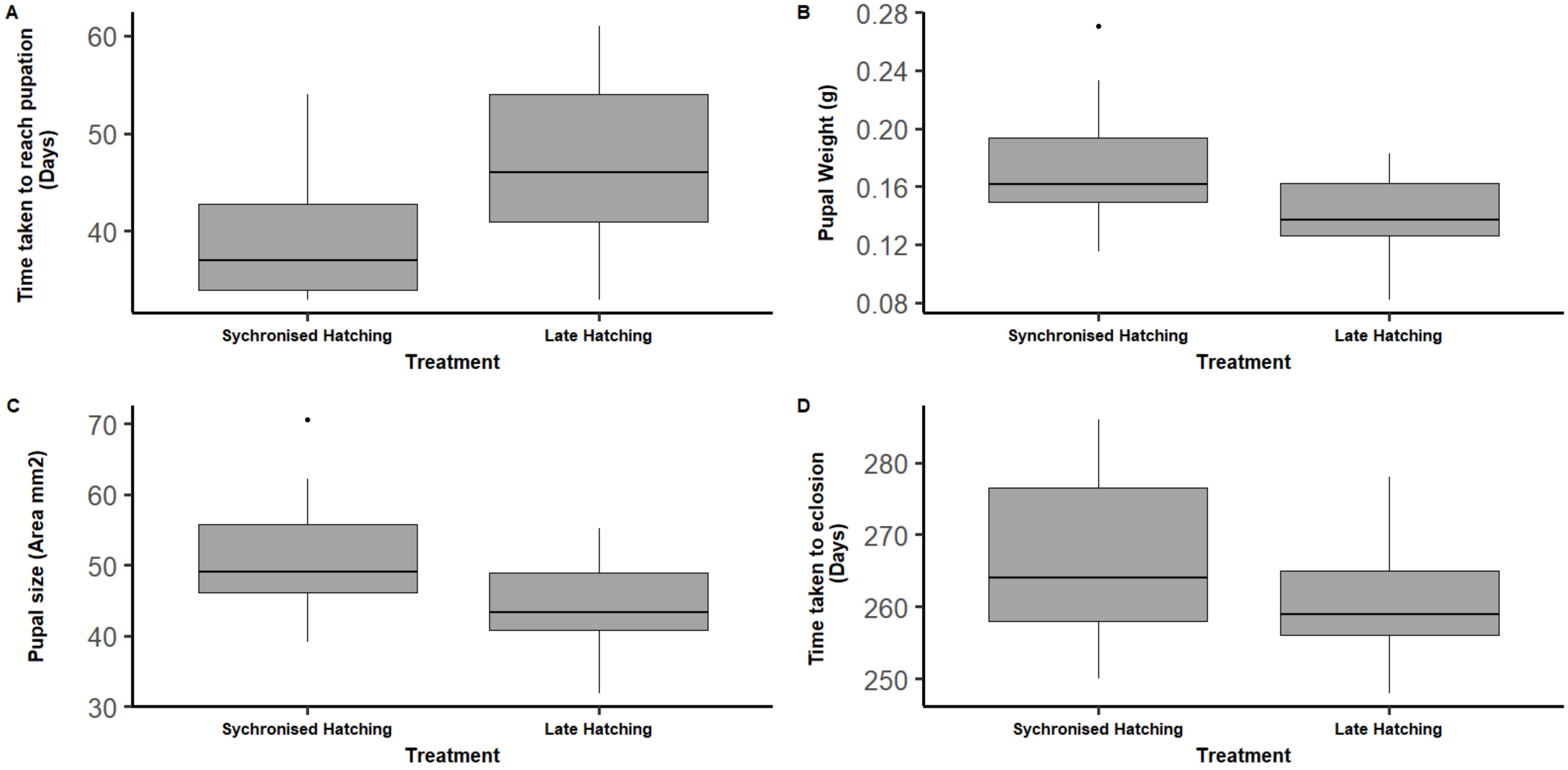

Figure 4.1. The effects of synchronised hatching simulation (young oak leaves) and late hatching simulation (old oak leaves) on *O. cerasi* larvae a) total time taken to reach pupation; b) pupal weight c) pupal size and d) time taken to eclosion. Figures are box-plots in which the solid black line represents the median, grey horizontal lines represent the upper and lower interquartile ranges, grey vertical lines represent the range of the data and black dots represent outliers.

4.5 Discussion

Moth populations and those of many other insect species are declining across the UK and elsewhere in Europe (Biesmeijer *et al.* 2006; Fox *et al.* 2011; Fox 2013; Leather 2018). Numerous factors probably contribute to these declines, but a statistically significant signal of climate change, including warmer temperatures, has been detected in the population declines of many UK moth species, including *O. cerasi* (Fox *et al.* 2014; Martay *et al.* 2016). Our work provides experimental evidence for causal pathways through which climate change-induced mismatches between larval hatching and host tree leaf emergence may drive population declines in *O. cerasi*, and other woodland moth species whose larvae exploit broadleaved trees. These pathways include increased exposure to larval predators that are likely to reduce survival rates and production of smaller and lighter pupae which are key indicators of an emergent adult's future fecundity (Honek 1993). Notably, we find support for our novel hypothesis that, whilst sample sizes are small, trophic mismatch generates a 7-fold increase in the risk of producing small vestigial wings that reduce adult mobility and thus probably their survival and reproductive rate. Whilst synchronised larvae pupated 8 days earlier than later hatching larvae their pupal stage was extended by a similar number of days. This meant that both late and synchronised treatments emerged at similar times in spring, indicating that environmental cues, such as temperature and photoperiod, were more important for emergence time than larval conditions. Consequently, larval mismatch does not influence adult emergence date creating a mechanism through which early life conditions do not carry over to influence subsequent egg-laying dates although fecundity of these adults is likely to be reduced.

The adverse effects that we document are likely to be underestimated as newly emerged caterpillars in the late hatch treatment were initially fed young leaves to minimise early mortality losses and ensure sufficient sample sizes in the later stages of the experiment. They also arise despite providing ad libitum food and thus any compensatory feeding (as documented by Buse *et al.* 1999; Cornelissen 2011) that arose in response to the lower nutritional quality of older leaves (Coley *et al.* 1996; Tikkanen & Julkunen-Tiitto 2003) was insufficient to mitigate the adverse effects of lower quality diets on larval growth and development. Our results suggest that increased asynchrony between emergence of caterpillars and the leaves of their larval host plant which arise from warner springs (Buse *et al.* 2002) is likely to have important demographic consequences for woodland moth populations and the tri-trophic plant-moth-insectivorous bird system in which they are embedded.

O. cerasi larvae that fed on mature oak leaves spent on average an extra 8 days as larvae than those fed on younger leaves. Woodland moth larvae experience significant predation pressure from a wide range of passerine birds with predation risk estimated as at least 5% day^{-1} in wooded temperate European habitats (Rowland *et al.* 2008; Gunnarson *et al.* 2018). The increased developmental time of caterpillars feeding on mature leaves as a consequence of climate change-induced mismatch with the timing of host plant bud-burst is thus likely to significantly increase larval mortality rates that may reduce moth population growth rates. On the other hand, numerous insectivorous woodland bird species specialise on feeding Lepidopteran larvae to their young (Perrins 1991; Smith *et al.* 2011; Seress *et al.* 2018). Seasonal declines in the availability of this preferred food source can lead to reduced avian fecundity (Reed *et al.* 2013), which in at least some species (e.g. pied flycatcher, *Ficedula hypoleuca*, Both *et al.* 2006) can generate population declines due to mismatches in the timing of avian reproduction and peak caterpillar availability. The prolonged availability of caterpillars to avian insectivores in years with warmer springs that induce mismatch may thus currently be reducing the magnitude of these mismatches.

O. cerasi larvae fed mature oak leaves were significantly smaller and lighter than those fed on younger recently emerged leaves. Sufficient reserves to meet metabolic needs during and after diapause must be attained pre-diapause (Hann & Denlinger 2007) or pre-pupation in the case of moths which overwinter as pupae such as *O. cerasi*. Smaller pupae are less likely to have sufficient reserves, and thus caterpillars which emerge late and feed on mature leaves may have reduced ability to survive winter (Gotthard *et al.* 1999; Liu *et al.* 2007). This is not, however, always the case (Zvereva 2002), and we found that pupal winter survival was not affected by treatment or pupal size with similar proportions of moths successfully emerging from each treatment. Termination of diapause may, however, be affected by body size and nutritional reserve levels (Hann & Denlinger 2007). Research regarding this area typically focuses on insects which have facultative, and not obligatory, diapause where smaller individuals may avert diapause, or have reduced diapause length (Hann & Denlinger 2007; Pieloor 2001). Few studies address the impact of pupal size on diapause initiation and termination in obligate diapausing species such as *O. cerasi*. We find, however, that those feeding on mature leaves in the late synchronised treatment had a significantly reduced eclosion time, spending 9 days less as a pupae compared to those fed on young leaves.

Notably, this compensates for the 8-day extension in time to pupation resulting in moths from both treatments emerging at very similar times of the year. The reduced period spent as a pupae may be due to insufficient reserves forcing earlier emergence (Hahn & Denlinger 2007) but as pupae from both treatments emerged at similar times, it seems more likely that environmental cues, such as photoperiod and temperature, are associated with eclosion in this species (Hodek 2002; Lehmann *et al.* 2017). Consequently, this means that larvae that feed primarily on older leaves do not experience adverse carry-over effects that delay the date of their emergence as adults. Phenological impacts in one year may, therefore, be mediated by environmental cues, and maintain the synchrony of adult eclosion during the mating period, which is likely to be important for maintaining population numbers (Salis *et al.* 2017). Pupal weight and size are good predictors of fecundity in many Lepidoptera (e.g. Honek 1993; Calvo & Molina 2005; Loewy *et al.* 2013; Régnière & Nealis 2016), including within other *Orthosia* species (Hesjedal 1983). Female moths arising from the smaller and lighter pupae induced by the late-hatching treatment are thus likely to have lower fecundity, especially as variation in larval diet can influence fecundity even when pupal body size is not affected (Danthanarayana 1975).

The substantially higher incidence of wing abnormalities in moths exposed to a simulated mismatch is likely to further reduce reproductive success of individuals that experienced mismatch as larvae as such abnormalities restrict adult moths' abilities to find mates and reproduce (Arbogast 1981). Insect wing abnormalities can arise from multiple factors including genetics (Swarup & Verheyen, 2012), pathogenic infection (Pierzynowska et al. 2019), and the biochemistry of larval diets (Łukasiewicz 2012). Notably, tannins (that occur in higher concentrations in older leaves) have been associated with increased incidence of Lepidopteran wing abnormalities (Turunen 1976; Barbahenn & Martin 1994; Pierzynowska et al. 2019).

We find that simulated trophic mismatch in which *O. cerasi* larvae feed on mature oak leaves are impacted in numerous ways that is likely to negatively impact demographic traits. Larval predation rates are likely to be increased by extension of the caterpillar stage, and whilst pupae survival rates are unaffected reproductive success of emerging adults is likely to be reduced due to reduced flight ability due to increased risk of wing abnormalities, and the lower pupal size and mass is likely to reduce female fecundity. Warmer spring temperatures have been associated with population declines in many moth species, including *O. cerasi*, and our research uncovers several mechanisms through which trophic mismatches arising from warmer springs could drive these population declines.

Acknowledgements

We would like to thank the Science Faculty at the University of Sheffield for their PhD studentship.

Chapter 5. General Discussion

5.1 Insect declines

Insects are ubiquitous across most terrestrial habitats and form an integral part of these ecosystems. Concurrent with other biodiversity trends, insects are experiencing losses as a result of environmental change (Forister *et al.* 2019). A recent and much-needed increase in the number of assessments of insect populations has uncovered wide-spread, alarming evidence of insect decline worldwide. Insect biomass has declined by ~75% between 1976 to 2012 in the Puerto Rican rainforest (Lister & Garcia, 2018). Insect biomass in Germany has undergone a 75% declines in protected areas (Hallman *et al.* 2017) with a 61% decline for macro-moths and 42% for ground beetles (Hallman *et al.* 2019). In the United Kingdom, 52% of butterfly species have declined in abundance over ten years in monitored areas (Fox *et al.* 2015) and 176 moth species declined by 20% between 1975 and 2014 in Scotland (Dennis *et al.* 2019). Caution has been made about interpreting the overall magnitude suggested in some studies (Simmons *et al.* 2019). There is clearly, however, an overall trend of a global insect crisis.

Despite the increased focus on insect populations, little research has assessed insect populations in broadleaved, temperate woodlands. Those which have addressed woodland insects are focused on a few species, typically lepidoptera (e.g. Martay *et al.* 2016) and overall woodland communities are therefore not well understood.. It has been suggested that around 50% of Europe’s 150,000-200,000 insect species are dependent upon woodland habitat (Warren & Key 1991) but there is little standardised monitoring of these taxa. Woodland insects provide integral ecosystem functions, including pollination (Motten 1986); population regulation and maintenance of species diversity (e.g. parasitic Hymenoptera (LaSalle & Gauld 1991; Fraser *et al.* 2007); decomposition (e.g. of leaf litter Bernaschini *et al.* 2016) as well as well as supporting populations of species that occupy higher trophic levels (e.g. insectivorous birds and bats (Leech & Crick 2007; Fuentes-Montemayor *et al.* 2013)).

Climate has been linked with insect declines (Thomas *et al.* 2006; Martay *et al.* 2016; Lister & Garcia 2018) and woodland insects are expected to be sensitive to climate change, especially given the highly seasonal nature of woodland habitats (Both *et al.* 2009). Despite this, and their integral roles in woodlands, insufficient research has explored the magnitude of climate change impacts on these insects or the mechanisms through which these impacts arise. Evidence of climate-driven insect abundance change is often limited to butterflies (Andrew *et al.* 2013) and species of economic concern (Rosenzweig *et al.* 2001; Deutsch *et al.* 2018) and are species-specific. Species-specific research is important but generally lacking for woodland insects, it is also difficult to extrapolate from these to understand the wider community or ecosystem response. Therefore, it is important to assess the climate change impacts on the abundance of broad insect groups as well as individual species in order to generate a much-needed idea of woodland insect population trends and how these link with climate.

In chapter two, I utilise a ten-year study of woodland insects in the Rivelin Valley, which benefits from repeated samples in the same location for a focal sampling period each year. I uncovered evidence of overall insect declines over the study period by 15%, as well as specific order declines of 88% in Homoptera and 42% in Hymenoptera, although no decline was detected for Diptera. I also found a significant influence of weather changes influencing insect populations which I will discuss in section 5.2. This research provides a rare assessment of a temperate woodland insect community. Although a relatively short time period and potentially, therefore, spurious results, highlighting these declines is important to identify and continue to monitor for conservation efforts, particularly as changes in the abundance of woodland insects is likely to have significant consequences for higher trophic levels.

Localised sampling in the Rivelin Valley makes temporal replication easier and provides robust data for assessing these population trends. Woodland in the UK and indeed other temperate areas have undergone substantial change over the past few decades (Hopkins & Kirby 2007). Most UK woodland is heavily fragmented (Bailey 2007) and typically set within agricultural landscape (Dolman *et al.* 2007) or in close proximity to urban towns and cities (Beckett 1998). Woodlands are therefore typically surrounded by areas with low levels of natural habitat reducing their connectivity (Bailey 2007). The Rivelin Valley is no exception and is subject to many of these environmental factors. Whilst it is shares characteristics of many other woodlands in the UK it is perhaps of higher environmental quality than typical woodlands. The site supports, for example, small populations of woodland bird species that have become locally extinct in many woodlands across the UK (wood warbler, willow tit and lesser spotted woodpecker). Furthermore, the environmental management has not changed and it has not experienced major increases in deer browsing intensity, that have removed understory and probably reduced insect populations in many woodlands (Stewart *et al.* 2001). It is thus possible that the declines I document are actually smaller than those that have occurred but are undocumented, in other woodlands. Regardless of the representativeness of the Rivelin valley, there is a clear need for wide-spread monitoring of woodland insects across the UK.

Systematic monitoring of insects is a complex undertaking as ideally identical protocols and repeated sampling is needed. Repeated, systematic sampling can require large resources, expenses and manpower. Whilst Rothamsted suction traps provide a robust method for monitoring insect populations their location and sampling radius (Macaulay 1988) renders them unsuitable for monitoring insect populations in specific habitats. One way of monitoring biodiversity for relatively low costs is to use citizen science, which can allow for ecological research at unprecedented scales (Dickinson *et al.* 2012). For UK insects, citizen science has been used for ladybirds (coccinellid beetles), butterflies (Dennis *et al.* 2013) and bumblebees (Lye *et al.* 2012; Birkin *et al.* 2015) and some of these have been used to assess population changes (e.g. Dennis *et al.* 2017). Citizen science could be an effective way to monitor woodland insect populations. The Rivelin Valley monitoring uses sticky traps, for example, which are relatively inexpensive, readily available at garden centres and easy to deploy and store (Heinz *et al.* 1992). Volunteers could be asked to set out a small number of sticky traps in their local woodland for a short period of time. Repeated samples may be more difficult to obtain but volunteers for other citizen science projects often engage repeatedly (e.g. the UK moth trapping network (Wilson *et al.* 2018)). A further potential issue of engaging volunteers with sticky trap sampling is public perception of killing insects, which can often be misunderstood and seen as negatively impacting the environment, especially charismatic insects such as bees (Sumner *et al.* 2018). A small amount of education may be needed, and the large amount of recent media highlighting insect declines may encourage engagement. Alternatively, engaging students in university courses which are typically repeated yearly could be another way to generate sticky trap samples. Another novel and straightforward way to sample invertebrates could be to measure insects collected on car windscreens. This method was adopted by the RSPB in 2004 (Leather 2016) where they asked members of the public to count the number of squashed insects on their licence plates after a journey. This sampling was only conducted for a single year, but the RSPB has other successful yearly monitoring schemes, such as the big bird watch (RSPB 2019) and the implementation of insect monitoring on a similar level, for example for people who regularly drive on routes through woodland habitats, could be an effective way to generate data for this habitat. Although the fragmented nature of woodland may make this approach more suitable for general monitoring of insects rather than habitat-specific monitoring.

The priority objectives for such sampling should be to assess overall abundance rather than phenological shifts as the frequency of sampling that would be required for phenological monitoring is likely to severely limit participation rates. Declines and associations with climate were detectable for insects in the Rivelin Valley at overall abundance level. Along with biomass, this is a common measure used to assess declines (Hallman *et al.* 2017; Lister & Garcia 2018). Abundance data are valuable on their own and an easy measure to obtain as it requires no biological knowledge, this also limits expenses and make things easier to standardise (Cardoso & Leather 2019). Furthermore, insect samples on a small section of the trap (e.g. 20%) have been shown to correlate well with overall counts, making it more time-effective (Heinz *et al.* 2002). Technologies can also be used to speed up the process, such as taking photographs of the samples and using software such as ImageJ, which can be automated to generate a crude measure of total insects. These are just some suggestions of how to tackle the data deficit on woodland insect population trends, but monitoring strategies such as these are vital in order to understand if and why woodland insects are declining and how climate is driving these changes. A greater understanding of this will aid biodiversity conservation and predictive capacity under further climatic shifts.

5.2 Climate change mechanisms

When considering data from the Rivelin Valley in chapter two I provide some of the only evidence that climatic change, both shifts in mean conditions and the occurrence of extreme events, can significantly influence woodland insect populations. Much of the climate literature on insects, in general, focuses on range and abundance shifts (Andrew *et al.* 2013), but it is also important to understand the mechanisms driving these shifts. Mechanisms can be considered as i) direct – abiotic factors which affect a species directly or ii) indirect – biotic factors in which the effect of climate is mediated via effects on other species (Ockendon *et al.* 2014). Evidence suggests that impacts on species interactions are more important than direct effects of weather (Cahill *et al.* 2013l Ockendon *et al.* 2014) however it is also worth noting that in primary consumers, which many temperate woodland insects are, the importance of direct effects is often larger than is the case for species at higher trophic levels (Ockendon *et al.* 2014).

5. 2a Direct effects of weather

Insects may be more sensitive to direct weather effects, particularly temperature, due to their endothermic nature (Bale *et al.* 2002). The relationships between weather and insect populations in Chapter 2, although not a specific mechanistic exploration, may indicate some direct impacts of weather on overall insects, but also impacts at order level. In Chapter 3, I also explore the effects of temperature and precipitation on population changes, but here I focus on two specific aphid species and, interestingly, find no evidence of temperature or precipitation change on population growth in either species.

Increased mortality is likely to be a direct effect of weather, this may be from mean shifts in temperature and precipitation but also from the occurrence of extreme events (Rosenzweig *et al.* 2001; Chen *et al.* 2019b). Conditions that exceed the hot or cold thresholds of a species will directly lead to mortality through physiological impacts. In temperate habitats, it has been suggested that insects are operating well within their thermal tolerances (Addo-Bediako 2000; Deutsch *et al.* 2008). Although more recent evidence suggests that both tropical and temperate species are similarly sensitive to climate change (Johansson *et al.* 2019) direct physiological impacts of hot or cold temperatures are less likely to occur in temperate habitats.

Direct temperature increases in spring and summer periods can, however, increase flight activity (Lutz *et al.* 2018) and growth rates (Netherer & Schopf 2010). Increased growth rates can reduce the life-cycle time and potentially allow for additional generations within a year, increasing overall abundance (Altermatt 2010). Increased flight activity can improve reproductive potential by affecting the time for mate searching (Ishiguri & Shirai 2004). The Rivelin valley insect population showed marginal responses to temperature in spring and summer. In summer, total insect abundance, Hymenoptera and Homoptera (excluding aphids), all showed abundance increases associated with warmer temperatures which could be linked with direct mechanisms of warming. The 20-year aphid data in Chapter 3 however, showed no such relationship, and models which accounted for interaction changes, showed only these biotic factors having importance for population change. Additional support for this may be apparent from the negative relationship with warming temperatures in spring for overall insect abundance in the Rivelin Valley system.

In comparison to the direct effects of temperature, little is known about how precipitation will directly impact insect population. Precipitation extreme events such as heavy rainfall may drive insect mortality through drowning, which is an issue particularly for small insects such as newly hatched larvae and early instars (Beirne *et al.* 1970). I find in Chapter 2, effects of precipitation in all seasons, with a variation of response between different orders. Positive effects of precipitation may be expected via indirect mechanisms for insects, for example by increasing the amount of vegetation for phytophagous insects in spring and summer (Masters *et al.* 1998). In the Rivelin Valley, insect population size was negatively associated with spring precipitation, indicating that precipitation may be more important as a direct driver of population change. This is further supported by the detailed look at weather drivers on insect phenology in Chapter 3, as precipitation was not found to be associated with the spring emergence of aphids or parasitoids. Similarly, Thackeray *et al. (*2016) also found limited significant associations between phenology and precipitation for a wide variety of taxa, including insects. Precipitation is therefore perhaps not like to affect interactions.

Conversely, Diptera responses to precipitation varied from that of overall insects, and wetter weather in both spring and summer appeared to boost their populations. Diptera have many different life-history strategies, but their larval forms often inhabit substrates such as soils (Frouz 1999) animal dung (Schweiger *et al.* 2007), and freshwater (Delettre 2000) and their eggs and larvae can be sensitive to desiccation (Briones *et al.* 1997). Wet weather may, therefore, promote the availability of these habitats. Documentation of precipitation effects on insects is rare, especially outside of an agricultural context, and mechanistic explorations are especially limited. Precipitation is expected to increase in variability in the UK, and whilst overall drier summers are expected, the frequency of extreme wet events are also expected to increase (Lowe *et al.* 2018). Research which assesses the mechanisms through which woodland insects respond to precipitation, such as through simulation rainfall experiments (Chen *et al.* 2019b) may help to determine how important these changes in precipitation could be, relative to temperature changes.

In the UK, the frequency of mild, wet winters is projected to increase under climate change (Lowe *et al.* 2018). For some insects, warming winter has been shown to promote survival and facilitate abundance increase (Robinet & Roques 2010) and range expansions (Crozier 2004). In the Rivelin Valley, however, warming winters and increased winter precipitation both decreased overall insect abundance, indicating that woodland insects may suffer under future climate change. Warming can delay entry into diapause (Tougeron *et al.* 2019) it can also increase the depletion rate of winter energy stores causing mortality directly (Williams *et al.* 2012) or forcing termination of dormancy during periods of low-resource availability

(Scriber *et al.* 2012). Warmer winters can also impact on the chilling requirements that insects may require to resume development post-diapause, this could potentially disrupt their phenology, the detrimental effects of which I will discuss in section 5.2b. Not all insects have this response, however, as Hymenoptera showed a positive association with winter temperatures. In milder winters it may be that remaining active in winter, assuming there are plentiful resources, is a beneficial strategy for Hymenoptera and in some warmer temperate regions, Hymenopteran parasitoids are losing their winter diapause (Tougeron *et al.* 2017). There is limited evidence that this is driving increased abundance. This does, however, provide argument for assessing impacts at order, or lower, taxonomic level as these divergent responses, particularly in key drivers of biodiversity such as parasitoids (Fraser 2007) may significantly influence overall community response to climate change.

5.2 b Indirect effects – changes in species interactions

One of the key impacts of climate on organisms is expected to be shifts in interactions, in particular, where interacting species change the timing of repeated key life stages leading to asynchrony between their populations (Renner & Zonner 2018). It is commonly cited that interacting species rarely respond to climate shifts in precisely the same way, and this has been observed in a number of interactions (e.g. Kharouba *et al.* 2015; Robinson *et al.* 2017). Such mismatches could arise from inter-specific variation in the identity of phenological cues or divergent rates of response to a shared cue, but the precise factors driving mismatches have rarely been quantified. By assessing a tri-trophic system of sycamore host, two aphid species and their associated parasitoids, I have uncovered substantial variation in the nature of the weather variables that influence phenology. Phenology, particularly in temperate insects and plants, is largely driven by temperature (Visser 2008; Cohen *et al.* 2018). Using the aphid data set I have shown that the precise effects of temperature impact each aspect of this study system at different times of year. Many studies which assess temperature effect on phenology use a broad window such as season (Roy & Sparks 2000) or month (Menzel *et al.* 2006), but I find that the most important period of temperature can vary in length from 1-12 weeks and therefore having very broad time-window may mean effects or their magnitude are missed.

I also find that temperature warming in different periods can have opposing effects on insect phenology depending upon which time of year it occurs. Typically, research suggests that spring warming advances insect phenology (Harrington *et al.* 2007; Brooks *et al.* 2017) which is concurrent with effects found in *P. testudinaceus* and *D. platanoidis* (see Chapter 3). Warming in winter, however, is considered less frequently, and here I show that winter warming (February) also delayed emergence in both aphid species. In a limited number of experimental studies, winter warming has been shown to delay spring emergence in insects due to the requirement of a chilling period in order to prompt diapause termination (Chuche & Thiery 2009; Stalhandske *et al.* 2015). I add to a small number of recent studies (e.g. Stalhandske *et al.* 2017) which have evidenced this delaying effect in natural populations and contribute a novel observation that interacting species (host plant and associated parasitoids) are not responding to this effect. Specifically, parasitoids attack was found to advance, rather than delay with warming temperatures in January. In this study system, winter warming is therefore likely to be a major driver of disruption to trophic interactions, and thus I highlight the importance of assessing winter effects on a wider number of taxa. Uncovering whether interacting species are having divergent responses to warming or responding in different periods should be a major consideration for further research. It is possible, that general patterns may occur between similar species, as for the two aphid species and winter in Chapter 3 but little other research assesses species in this way. If similar mechanisms are driving phenology in other insects, there is a high probability that warming, particularly aseasonal warming, will drive mismatch between interacting species.

Phenological mismatch may have demographic consequences by impacting upon species fitness and survival (Miller-Rushing 2010). These impacts, for herbivorous insects, are expected to occur as a result of host-plant quality, which changes as leaves age and develop more anti-herbivory defences (Feeny 1970). Empirical evidence for these effects, however, are limited to a small number of insects, typically Lepidoptera, such as the winter moth (Buse *et al.* 1998; Salis *et al.* 2017), with some examples for other pest species such as the forest tent caterpillar (Abarca & Lill 2014). Evidence was present for asynchrony between leaf burst and aphid emergence in Chapter 3 but this was not found to be associated with population growth, which was surprising considering that *D. platanoidis* weight and fecundity can be reduced when feeding on mature sycamore leaves (Dixon 1976).

In Chapter 4, I also add to the small number of studies which assess the impact of phenological mismatch through simulation. I find that, for a wide-spread woodland moth (*Orthosia cerasi*), feeding on mature oak leaves can significantly increase the growing period as well as reduce overall pupal size and weight. Population-level impacts may arise from this due to increased exposure to predation or parasitism from a longer growth period and smaller pupae is also linked with lower fecundity (Buse *et al.* 1998). Furthermore, adult *O. cerasi* emerging from the late-treatment exhibited greater rates of abnormal wing development which may hinder mate-searching ability. Impacts on individuals however, as exampled by *D. platanoidis* and in studies of other taxa, such as birds (Reed *et al.* 2013) do not always transfer to demographic shifts. A long-term data set which considers *O. cerasi* and the relationship between population trends and the magnitude of mismatch would aid in understanding whether impacts on the individual translate into population changes. Martay *et al.* (2016) assessed both *D. platanoidis* and *O. cerasi* for population changes related to climate, finding only effects of climate, and declining populations in *O. cerasi.* Moths and aphids have key differences, particularly as aphids produce multiple generations within a year (Harrington *et al.* 2007) and many temperate moths have only one or two (Bell *et al.* 2019). Aphids may have a greater capacity to generate numbers in a year with phenological mismatch compared to moths. Expanding phenological simulation experiments to a much wider variety of insects across taxa is very important as presently much is based on the assumptions that patterns will follow a small number of species and there is limited knowledge as to whether individual response translates to population shifts.

5.3 Further work to understand driving mechanisms

5.3a Warmer temperatures and insect life stages

Insect growth and survival can be strongly dependent on temperature (Kingsolver 2000). This can vary between species (Gilbert & Raworth 1996) and life-stages (Radchuck *et al* 2013). I assessed in Chapter 4 how phenological asynchrony affects growth and fecundity, but this can also be affected by temperature (Bowdon *et al.* 2015; Horne *et al.* 2017). Heat stress, for example, can influence maturation and reproductive success, and this has been shown in the diamond-back moth, to be more severe when heat stress occurs in later-stage larvae close to the adult stage (Zhang *et al.* 2015). Assessing the effects of temperature on growth is particularly important for predicting climate response, and considering more than one life stage will provide a much clearer understanding of this. This has been found to be particularly important for assessing thermal sensitivities, as whilst many assessments consider adult insects, larval stages are often soft-bodied and therefore could be more vulnerable to climatic changes (Levy *et al.* 2015). Dipteran larval stages, for example, are considered to be sensitive to desiccation; in Chapter 2 I uncover evidence that Diptera are increasing in cooler and wetter weather. Assessing the different life stages of Diptera would help uncover whether sensitivity at the larval stage is driving this relationship.

5.3b Voltinsim

Increased voltinism as a consequence of both an extended growing season, but also an increase in growth rates, is commonly suggested as a consequence of climate change. Although this has been shown in some butterfly species, which are usually uni or bivoltine in temperate climates (Altermatt 2010), increased voltinsm in other species, such as those which may have multiple generations in a year remains largely unknown. Assessing total life-cycle time under different temperature regimes in a small number, of diverse, woodland insects could help to determine whether additional generations can be achieved in warmer temperatures. This would be particularly useful to further explore the relative importance of direct effects on woodland insect populations, in comparison to those mediated by species interaction shifts.

5.3c Disease

Diseases are expected to alter occurrence and distribution under climate change (Harvell *et al.* 2002) but this is poorly understood for insects. Pathogens may be expected to prevail in milder, wetter winters in temperate climates (Williams *et al.* 2015). As insects in Chapter 2 were declining in warmer winters it is possible that this is a potential mechanism driving declines. To explore this, experiments that simulate overwintering in different climates and measure the rate of pathogen occurrence relative to temperature and precipitation would be valuable. This could be done, for example, by exploiting natural variation in climate at local or wider scale and naturally overwintering insects, pupae may be a particularly useful model for this, in different locations. This could be better than controlled experiments as, although would increase the number of confounding variables, it would allow the occurrence of natural pathogens,.

Phenological shifts leading to feeding on less nutritional leaves may also lead to shifts in immunity levels, affecting the relative susceptibility to different pathogens (Martemyanov *et al.* 2015). I find, although in a small sample size, an increase in the occurrence of small vestigial wings, which can be linked with pathogens and reduced leaf quality (Łukasiewicz 2012; Pierzynowska *et al.* 2019). During initial development (i.e. within 20 days) the nutritional quality of host plants has been suggested as the main impact of asynchrony on insect antiviral immunity (Martemyanov *et al.* 2015). Late emerging gypsy moth (*Lymantria dispar*) larvae, for example, show higher susceptibility to baculoviruses (Martemyanov *et al.* 2015). It is suggested that this is related to uptake of different chemicals when feeding on older leaves, which can decrease the midgut bacterial community (Martemyanov *et al.* 2016), but more research is needed to understand the underlying mechanisms.

5.3d Fecundity

In Chapter 4, I indicate that the significant reduction in pupal size on moths which were fed mature oak leaves is likely to indicate reduced fecundity. Adult body size is frequently associated with fecundity in insects, including for moths (Honek 1993), but this relationship can be complex (Leather 1988) and I was unable to directly measure this such as by counting the number of eggs a female has in her ovarioles. Larval diet can impact fecundity when body size isn't affected (Danthanarayana 1975), and thus a more robust measure of fecundity is needed in order to more accurately assess whether fecundity impacts are a potential mechanism of population shift under climate change. Fecundity could be measured through the number or mass of eggs produced by an adult. Size of individual eggs, as well as overall mass, may be important to assess carry-over effects from trophic mismatch, as smaller eggs may produce smaller offspring (Capinera & Barbosa 1977). Smaller offspring may suffer increased mortality (Beirne *et al.* 1970), but also may require longer growth or lead to reduced total size, even if phenological mismatch doesn't occur in the subsequent year. Recent research has also indicated that host-plant compounds from the larval diet may subsequently affect egg quality even when body size isn't impacted (Thiery *et al.* 2018). As with much of climate research, studies in this area are limited to Lepidoptera, and whilst more is needed to understand the mechanisms at play in this order it is widely unknown whether other insects exhibit similar fecundity impacts from mismatch. Multigenerational studies, which assess the long term impacts of phenological mismatch would give a greater understanding of whether asynchrony will act as a driver of declines.

5.3e Understanding insect community responses to climate change.

A major goal in the field of climate impacts on woodland impacts should be assessing community-level responses. In this thesis I have detected community-level effects by separating out different taxonomic groups at order and sub-order level. To assess the mechanisms driving these responses, it would be useful to determine the relative importance of direct and indirect impacts of climate. For example, using the Rivelin Valley data set, it would be possible to determine whether general patterns of phenological shift are detectable at the order level. This could be done by assessing whether there is a relationship between changes in weather at different times during the year, following a sliding window model as used in Chapter 3, and the phenological dates for each order measured as the time that they first start appearing in samples each year.

It is important to consider that the variation in biological characteristics within a specific order, can be significantly different. Homoptera, for example, are all phytophagous (Wiesenborn 2011), but Diptera express a multitude of diets including phytophagy and detrition (Woodcock *et al.* 2003). This could, in part, explain the lack of evident decline in Diptera in our populations, and it is probable given the evidence for insect declines, that Diptera composition has changed and some species have experienced declines. Community composition changes are equally likely to have subsequent ecological impacts as overall declines (Oliver *et al.* 2015b), particularly if there has been a specific loss of a functional guild. Functional and species traits have been shown, in some cases, to predict species response to climate and other environmental change (Diamond *et al.* 2011; Vegvari *et al.* 2015). It would be interesting to assess woodland insects to determine whether similar traits, such as diets, life-history or overwintering strategies predict response to climate change. Moreover, it may also be more effective to test for population shifts and their relationship with climate at a functional group level, instead of order. A complete functional categorisation, however, requires species-level identification of some groups, which is extremely resource-intensive and often not feasible for some sampling methods (including sticky traps). A more crude approach could be taken, such as sub-order identification, or selecting out-groups which may be more easily recognisable (e.g. pollinators: bees and hoverflies, or nematoceran flies (very common on sticky traps). Functional groups may also allow for more meaningful assessments of asynchrony, e.g. comparing pollinators to the general flowering phenology across an ecosystem.

5.4 The wider ecological impact

Despite some caveats to the inference of insect responses to climate change, from order-level analyses, this research can still be used to provide important information about the wider ecosystem in which they inhabit.

5.4a Herbivory rate

Many woodland insects are herbivorous, this includes the non-aphid Homoptera in Chapter 2. Here I find that warmer summers could increase Homoptera abundance which may lead to higher levels of herbivory on woodland trees. In a dynamic tri-trophic system such as that in Chapter 3, asynchrony between species will have subsequent impacts on all interacting components, including the host sycamore trees. Sycamore trees in this study were responding exclusively to spring warming and are thus likely to burst earlier and similar patterns have been observed in other temperate trees (Chen *et al.* 2019). The complex response of aphids to contrasting effects of temperature makes it difficult to predict how aphid phenology will track these shifts. The relative timing of activity in plants and their insect herbivores can influence the susceptibility to herbivory damage (Chen *et al.* 2001). Plants may be expected to benefit from asynchrony due to reduced herbivore pressure. Late emerging insects, such as simulated for *O.cerasi* in Chapter 4, can exhibit a longer growing period, and they may need to increase their consumption to compensate for the reduced nutritional quality (Chen *et al.* 2019b). Late bud burst relative to insect emergence can also lead to increased herbivory (Heimonen *et al.* 2017) which is likely due to the highly nutritious newly emerging leaves. Trees which emerge relatively early or late compared to others in the area may also provide nutritious leaves when resources are scarce (i.e. absent leaves on other trees or mature leaves on other trees) leading to higher consumption levels (Heimonen *et al.* 2017). Therefore, whilst mismatch with aphids or other herbivorous insects, has the potential to alter herbivory levels it is difficult to predict whether effects will be adverse or beneficial. This is also likely to be affected by interactions between the direction and magnitude of the asynchrony and the entire herbivore community present on the trees. A greater understanding of altered herbivory may be attained through similar long-term studies which also assess leaf damage from aphids or caterpillars or controlled experiments which simulate mismatch and assess leaf herbivory levels at different ages of leaf.

5.4b Parasitoid attack

As discussed in section 5.2a, Chapter 2 shows some of the potential direct effects of climate on insects occupying higher trophic levels such as parasitoids. Parasitoids by nature are highly reliant on their host populations (Hassell 2000). The effects upon parasitoids and insects in higher trophic levels depends upon the relative specialism upon their host or prey (Godfray *et al.* 1994; Evans *et al.* 2012: Romo *et al.* 2013). This means that indirect effects of climate are likely to be especially important. Annual fluctuations in the temporal matching between host and parasitoid populations can significantly impact the persistence of this relationship (Godfray *et al.* 1994). Whilst there are few empirical studies which address the effects of mismatch on higher trophic levels, modelling has suggested that if parasitoids emerge earlier than their hosts, then host populations can be significantly reduced due to the number of foraging insects present when they do emerge (Godfray *et al.* 1994). Host population growth may thus be limited reducing the host population in subsequent years resulting in parasitoid population crashes to very low levels.

5.4c Food availability for higher trophic levels

Woodland insects support a high diversity of higher trophic levels, including birds, rodents and bats (Hooks *et al.* 2003). Insect phenology and population-level shifts are likely to have wider implications for those insectivorous taxa. Declines in the availability of insects can lead to reduced fecundity in birds (Reed *et al.* 2013) and survival in bats (Blakely *et al.* 2016) both of which can lead to population declines. Insect population increases, either from direct changes in weather such as those for the Rivelin Valley insects or from phenological synchrony impacts such as those potentially identified in Chapters 3 and 4, may benefit woodland biodiversity by promoting increased survival in reliant taxa. Furthermore, as evidenced by the Orthosia mismatch experiment, feeding on mature leaves as a result of late emergence leads to a prolonged growing season, increasing the time window of food availability. For insectivorous birds in particular, which may rely on Lepidopteran caterpillars (Perrins 1991; Smith *et al.* 2011; Seress *et al.* 2018) this prolonged availability may be of particular importance as climate has shifted their breeding season, leading to potential mismatch with peak caterpillar availability. The magnitude of this mismatch may be lessened if the growing period of caterpillars is extended. Although many birds target caterpillars specifically, other insects can supplement their diets (Hooks *et al.* 2003; Barbaro & Battisti 2011). Climate change has driven asynchrony between caterpillar peaks and bird peak demand (Reed *et al.* 2013). As weather variables have impacted the taxa in this study differently, it would be useful to explore how overall insect abundance compares to that of caterpillars as, if this differs, there may be buffering capacity in years where caterpillar populations are low or vice versa. Determining trends between insect abundance and overall bird populations is an important area of research, as concurrent shifts in populations may indicate mechanisms of decline in birds and provide evidence that targeting insects in conservation as a priority.

5.5 Conclusions

There is a taxonomic bias across conservation research towards charismatic fauna (Mammides 2019), with a lack of data on insects overall despite their substantial contribution to biodiversity. This thesis provides evidence that insects have declined in a UK woodland. UK woodlands have undergone dramatic changes over the past century. Like many others, the Rivelin Study Site which I used to assess volant insect communities, suffers from fragmentation and edge effects. Notably, these changes are historic and the habitat has undergone little change or management during the period of sampling. Thus, declines in other fragmented woodland in the UK, that have undergone recent changes, may be more pronounced. Moreover, I provide evidence that changes in seasonal weather can be associated with insect population shifts, with important observations that the projected increase in mild-wet winters and heavy rainfall events in summers under climate change, will likely contribute to further insect declines.

Climate is likely to alter species interactions. This may lead to a reduction of the availability or the quality of available food for insects. The impacts of this may vary widely between different insect orders or even between species but the understanding of these effects are limited predominantly to Lepidoptera. Altered nutrition for a moth species, in this study, had impacts on growth rates, overall pupation size and the frequency of wing deformities. These could be linked with fecundity but the body-size fecundity relationship needs to be confirmed for *O.cerasi.* This thesis also demonstrates that phenological shifts can be driven by species-specific influences of weather, and often within a precise time window. Specifically, changes in winter were especially important for the sycamore-aphid-parasitoid system. Similar studies on other insects are needed to determine whether these mechanisms occur in other interacting species.

There is a clear need for further monitoring of insect populations and research testing mechanisms proposed to drive insect population responses to the direct and indirect effects of climate change. Specifically, this work indicates that winter may be of particular importance in driving population and interaction changes, and yet changes in winter conditions have received much less attention than those in spring. Further work needs to consider both impacts on individual species and responses at the community level. This will allow a greater understanding of how climate will affect temperate woodland biodiversity, both for insect species and the wide array of taxa they influence and support.

6.Supplementary material

Table S2.1 Rivelin Valley Sticky Trap Sampling periods for each year

Year	Start Date	End Date	Mean time between samples (days)	No of samples
2009	18-Apr	22-Jun	9.285714	7
2010	04-Apr	27-Jul	12.33333	10
2011	02-Mar	03-Aug	14	12
2012	01-Mar	08-Aug	20	9
2013	06-Apr	25-Jun	13.33333	7
2014	04-Mar	28-Jul	16.22222	10
2016	29-2	06-Aug	14.64286	12
2017	28-Feb	31-Jul	15.3	11
2018	05-Mar	25-Jul	14.3	11

Table S2.2 Overall insect abundance, models selected from all possible combinations of the number of sun hours (S) , mean temperature during the sampling period (T) , mean gust during sampling period (W) and time sampled for in hours (H). All models included year and site as random effects.

Year	Model	AIC	delta AIC	model weight		Year	Model	AIC	delta AIC	model weight
2009	j	964.16	0.00	1.000		2014	h	1365.68	0.00	0.173
2010	c	3417.31	0.00	0.173		2014	c	1366.05	0.37	0.144
2010	j	3417.32	0.01	0.171		2014	n	1366.06	0.38	0.144
2010	h	3417.36	0.05	0.169		2014	j	1366.36	0.67	0.124
2010	n	3417.36	0.05	0.168		2014	k	1366.61	0.92	0.109
2010	k	3418.75	1.44	0.084		2014	f	1366.66	0.98	0.106
2010	f	3418.84	1.53	0.080		2014	o	1366.72	1.04	0.103
2010	m	3418.90	1.59	0.078		2014	m	1366.86	1.17	0.096
2010	o	3418.93	1.62	0.077		2016	j	1689.46	0.00	0.137
2011	h	1924.49	0.00	0.130		2016	n	1689.47	0.01	0.136
2011	f	1924.53	0.04	0.127		2016	c	1689.48	0.02	0.135
2011	c	1924.54	0.05	0.127		2016	h	1689.61	0.15	0.126
2011	n	1924.56	0.07	0.125		2016	m	1689.74	0.28	0.119
2011	k	1924.58	0.08	0.124		2016	f	1689.76	0.30	0.118
2011	j	1924.60	0.11	0.123		2016	o	1689.80	0.34	0.115
2011	m	1924.61	0.12	0.122		2016	k	1689.81	0.35	0.115
2011	o	1924.61	0.12	0.122		2017	k	1423.39	0.00	0.128
2012	h	1114.57	0.00	0.133		2017	o	1423.42	0.03	0.126
2012	f	1114.57	0.00	0.133		2017	c	1423.43	0.03	0.126
2012	c	1114.70	0.14	0.124		2017	h	1423.43	0.04	0.125

2012	n	1114.71	0.14	0.124		2017	f	1423.44	0.05	0.124
2012	m	1114.75	0.18	0.122		2017	n	1423.44	0.05	0.124
2012	k	1114.75	0.18	0.121		2017	j	1423.46	0.06	0.124
2012	o	1114.76	0.19	0.121		2017	m	1423.46	0.07	0.123
2012	j	1114.76	0.19	0.121		2018	n	1607.05	0.00	0.155
2013	m	1036.64	0.00	1.000		2018	o	1607.38	0.33	0.132
						2018	h	1607.41	0.36	0.129
						2018	k	1607.52	0.47	0.123
						2018	c	1607.60	0.55	0.118
						2018	j	1607.65	0.60	0.115
						2018	m	1607.67	0.62	0.114
						2018	f	1607.67	0.62	0.114

Table S2.3 Homoptera abundance, models selected from all possible combinations of the number of sun hours (S) , mean temperature during the sampling period (T) , mean gust during sampling period (W) and time sampled for in hours (H). All models included year and site as random effects.

Year	Model	AIC	delta AIC	model weight		Year	Model	AIC	delta AIC	model weight
2010	S,H	816.11	0.00	0.165		2014	T	478.17	0.00	0.248
2010	S,H,W	816.37	0.26	0.145		2014	T,W	478.88	0.71	0.174
2010	H	816.62	0.51	0.128		2014	S,T	479.56	1.39	0.124
2010	H,W	816.69	0.58	0.123		2014	W	480.10	1.93	0.094
2010	T,H	816.87	0.76	0.113		2016	none	295.99	0.00	0.219
2010	T,H,W	816.89	0.78	0.111		2016	W	296.22	0.24	0.194
2010	S,T,H	816.92	0.81	0.110		2016	T	296.42	0.43	0.177
2010	S,T,H,W	817.01	0.89	0.105		2016	T,W	297.12	1.13	0.124
2011	T	739.89	0.00	0.133		2016	S	297.18	1.20	0.120
2011	S	739.90	0.02	0.132		2016	S,T	297.87	1.89	0.085
2011	none	740.25	0.36	0.112		2016	S+W	297.98	1.99	0.081
2011	S,T	740.26	0.38	0.110		2017	S,T	750.22	0.00	0.212
2011	S+W	740.60	0.71	0.093		2017	l	750.99	0.78	0.143
2011	T,W	740.60	0.71	0.093		2017	none	751.60	1.38	0.106
2011	W	740.84	0.95	0.083		2017	T	751.67	1.46	0.102
2011	l	740.86	0.98	0.082		2017	S,T,H	751.71	1.49	0.100
2011	T,H	741.44	1.55	0.061		2017	S	751.84	1.62	0.094
2011	S,T,H	741.84	1.96	0.050		2017	W	752.03	1.82	0.085
2011	S,H	741.88	1.99	0.049		2017	T,W	752.17	1.96	0.080
2012	T,H	493.53	0.00	0.266		2017	S+W	752.21	2.00	0.078
2012	T,H,W	494.82	1.30	0.139		2018	none	379.56	0.00	0.162
2012	S,T,H	494.98	1.46	0.129		2018	T	379.62	0.06	0.158
2012	S,H,W	495.03	1.51	0.125		2018	S	379.87	0.31	0.139
2012	S,T,H,W	495.06	1.54	0.124		2018	W	379.87	0.31	0.139
2012	S,H	495.25	1.73	0.112		2018	S+W	380.02	0.45	0.129
2012	H,W	495.40	1.88	0.104		2018	T,W	380.23	0.67	0.116
2013	W	442.13	0.00	0.213		2018	S,T	380.71	1.15	0.092
2013	H,W	442.80	0.67	0.152		2018	l	381.42	1.85	0.064
2013	S+W	443.08	0.95	0.132						
2013	none	443.23	1.10	0.123						
2013	S	443.42	1.29	0.111						
2013	T,W	443.49	1.36	0.108						
2013	S,H,W	444.03	1.90	0.082						
2013	T	444.11	1.98	0.079						

Table S2.4 Diptera abundance, models selected from all possible combinations of the number of sun hours (S) , mean temperature during the sampling period (T) , mean gust during sampling period (W) and time sampled for in hours (H). All models included year and site as random effects. Homoptera

Year	Model	AIC	delta AIC	model weight		Year	Model	AIC	delta AIC	model weight
2009	H	848.67	0.00	0.191		2014	H	912.85	0.00	0.153
2009	H,W	849.40	0.74	0.132		2014	S,T,H,W	913.03	0.17	0.141
2009	S,H,W	849.55	0.88	0.123		2014	H,W	913.04	0.19	0.139
2009	S,H	849.59	0.92	0.120		2014	S,H	913.39	0.54	0.117
2009	T,H	849.59	0.92	0.120		2014	S,T,H	913.40	0.54	0.117
2009	S,T,H	849.85	1.19	0.106		2014	T,H	913.43	0.58	0.115
2009	T,H,W	849.87	1.20	0.105		2014	T,H,W	913.51	0.66	0.110
2009	S,T,H,W	849.90	1.24	0.103		2014	S,H,W	913.57	0.71	0.107
2010	T	1034.17	0.00	0.241		2016	H,W	1082.00	0.00	0.168
2010	S	1035.06	0.89	0.154		2016	H	1082.01	0.00	0.167
2010	none	1035.19	1.02	0.145		2016	T,H,W	1082.40	0.39	0.138
2010	T,W	1035.30	1.13	0.137		2016	T,H	1082.46	0.46	0.133
2010	S+W	1035.55	1.39	0.120		2016	S,H	1082.95	0.95	0.104
2010	W	1035.67	1.50	0.114		2016	S,H,W	1082.98	0.97	0.103
2010	S,T	1036.16	2.00	0.089		2016	S,T,H	1083.16	1.16	0.094
2011	H	821.43	0.00	0.118		2016	S,T,H,W	1083.20	1.20	0.092
2011	S,H	821.44	0.01	0.118		2017	H	1068.19	0.00	0.133
2011	T,H	821.50	0.07	0.114		2017	H,W	1068.30	0.10	0.126
2011	S,T,H	821.66	0.23	0.105		2017	T,H	1068.31	0.11	0.125
2011	H,W	821.67	0.24	0.105		2017	S,H	1068.31	0.12	0.125
2011	T,H,W	821.69	0.26	0.104		2017	S,T,H	1068.31	0.12	0.125
2011	S,H,W	821.71	0.28	0.103		2017	T,H,W	1068.35	0.16	0.123
2011	S,T,H,W	821.81	0.38	0.098		2017	S,H,W	1068.36	0.17	0.122
2011	S	823.38	1.95	0.045		2017	S,T,H,W	1068.37	0.17	0.122
2011	none	823.38	1.95	0.045		2018	S+W	1162.13	0.00	0.150
2011	T	823.41	1.98	0.044		2018	T	1162.34	0.22	0.135
2012	H,W	947.80	0.00	0.180		2018	none	1162.41	0.28	0.130
2012	T,H,W	948.14	0.34	0.151		2018	l	1162.45	0.32	0.128
2012	S,H,W	948.27	0.47	0.142		2018	T,W	1162.52	0.39	0.123
2012	S,T,H,W	948.65	0.84	0.118		2018	W	1162.60	0.48	0.118
2012	S,T,H	948.68	0.87	0.116		2018	S	1162.74	0.62	0.110
2012	H	949.01	1.20	0.098		2018	S,T	1162.82	0.69	0.106
2012	S,H	949.02	1.22	0.098						
2012	T,H	949.04	1.23	0.097						
2013	S,H,W	803.72	0.00	0.172						
2013	S+W	804.22	0.50	0.134						
2013	S	804.93	1.21	0.094						
2013	l	805.28	1.56	0.079						
2013	W	805.31	1.58	0.078						

2013	S,T,H,W	805.31	1.58	0.078						
2013	S,T	805.37	1.65	0.076						
2013	T,W	805.42	1.70	0.074						
2013	none	805.43	1.70	0.073						
2013	T	805.48	1.75	0.072						
2013	S,H	805.51	1.78	0.071						

Table S2.5 Hymenoptera abundance, models selected from all possible combinations of the number of sun hours (S) , mean temperature during the sampling period (T) , mean gust during sampling period (W) and time sampled for in hours (H). All models included year and site as random effects.

Year	Model	AIC	delta AIC	model weight		Year	Model	AIC	delta AIC	model weight
2009	none	681.53	0.00	0.136		2014	W	614.06	0.00	0.099
2009	S	681.63	0.10	0.129		2014	T,W	614.17	0.11	0.093
2009	W	681.63	0.11	0.129		2014	none	614.22	0.16	0.091
2009	S+W	681.69	0.16	0.125		2014	S+W	614.23	0.16	0.091
2009	T	681.71	0.18	0.124		2014	S	614.38	0.31	0.084
2009	S,T	681.77	0.24	0.120		2014	T	614.49	0.42	0.080
2009	T,W	681.77	0.25	0.120		2014	l	614.53	0.46	0.078
2009	l	681.81	0.28	0.118		2014	S,T	614.80	0.74	0.068
2010	T,H	1619.32	0.00	0.180		2014	H,W	615.40	1.34	0.051
2010	H	1619.38	0.05	0.175		2014	T,H,W	615.52	1.46	0.048
2010	T,H,W	1619.38	0.06	0.175		2014	H	615.55	1.49	0.047
2010	H,W	1619.40	0.07	0.173		2014	S,H,W	615.57	1.50	0.047
2010	S,T,H	1620.96	1.64	0.079		2014	S,H	615.71	1.65	0.043
2010	S,T,H,W	1621.04	1.72	0.076		2014	T,H	615.82	1.75	0.041
2010	S,H	1621.18	1.86	0.071		2014	S,T,H,W	615.87	1.80	0.040
2010	S,H,W	1621.21	1.89	0.070		2016	W	523.82	0.00	0.126
2011	H	725.09	0.00	0.162		2016	S+W	523.90	0.08	0.121
2011	H,W	725.11	0.02	0.160		2016	T,W	523.97	0.15	0.117
2011	S,H	725.14	0.06	0.157		2016	l	524.11	0.29	0.109
2011	S,H,W	725.16	0.07	0.156		2016	none	524.87	1.06	0.074
2011	T,H	725.48	0.40	0.133		2016	S	525.00	1.18	0.070
2011	S,T,H	725.56	0.47	0.128		2016	T	525.01	1.19	0.070
2011	T,H,W	725.99	0.90	0.103		2016	H,W	525.03	1.21	0.069
2012	T,H	669.96	0.00	0.144		2016	S,H,W	525.14	1.32	0.065
2012	T,H,W	670.40	0.44	0.115		2016	S,T	525.14	1.32	0.065
2012	S,T,H	670.41	0.45	0.115		2016	T,H,W	525.34	1.52	0.059
2012	S,T,H,W	670.46	0.49	0.112		2016	S,T,H,W	525.52	1.70	0.054
2012	S,H,W	670.57	0.60	0.106		2017	l	726.81	0.00	0.102
2012	S,H	670.99	1.03	0.086		2017	S,T	727.20	0.39	0.084
2012	H	671.12	1.15	0.081		2017	S,T,H,W	727.24	0.43	0.082
2012	H,W	671.20	1.24	0.077		2017	T,W	727.38	0.57	0.076
2012	T	671.85	1.88	0.056		2017	S,T,H	727.63	0.82	0.067
2012	S,T	671.96	2.00	0.053		2017	S+W	727.81	1.00	0.062
2012	l	671.96	2.00	0.053		2017	T,H,W	727.82	1.01	0.061
2013	T,W	744.12	0.00	0.089		2017	T	727.83	1.02	0.061
2013	l	744.13	0.01	0.089		2017	S	727.96	1.16	0.057
2013	T	744.15	0.02	0.088		2017	none	727.97	1.16	0.057
2013	S,T	744.15	0.03	0.088		2017	W	727.98	1.17	0.056
2013	W	744.15	0.03	0.087		2017	S,H,W	728.25	1.44	0.049

2013	none	744.16	0.04	0.087		2017	T,H	728.26	1.45	0.049
2013	S+W	744.17	0.04	0.087		2017	S,H	728.40	1.59	0.046
2013	S	744.17	0.05	0.087		2017	H	728.41	1.60	0.046
2013	T,H,W	745.83	1.71	0.038		2017	H,W	728.43	1.62	0.045
2013	T,H	745.85	1.73	0.037		2018	T,H,W	768.51	0.00	0.184
2013	S,T,H	745.85	1.73	0.037		2018	S,H,W	768.90	0.38	0.152
2013	H,W	745.86	1.74	0.037		2018	S,H	768.92	0.41	0.150
2013	H	745.87	1.75	0.037		2018	H	768.92	0.41	0.150
2013	S,H,W	745.87	1.75	0.037		2018	H,W	768.98	0.47	0.145
2013	S,H	745.88	1.76	0.037		2018	S,T,H,W	769.16	0.65	0.133
						2018	S,T,H	770.00	1.49	0.087
						2018	T,H	969.41	200.90	0.000

Table S3.1. Total number of trees removed from the data set for respective analyses in each year due to the lack of presence of: *D. platanoidis* or *P. testudinaceus* (by the end of June); and parasitised aphids (at any time during the year)

	Removed trees (/52)		
Year	**D.platanoidis**	**P.testudinaceus**	**Parasitised aphids**
1993	8	1	2
1994	1	3	16
1995	0	1	3
1996	0	4	2
1997	0	0	8
1998	1	0	17
1999	2	2	16
2000	0	0	12
2001	14	4	38
2002	0	0	6
2003	1	12	41
2004	1	0	6
2005	7	17	37
2006	0	0	16
2007	16	12	26
2008	2	0	12
2009	0	0	7
2010	1	1	6
2011	3	10	2
2012	5	4	1
Total removed (/1040)	62	71	274
Total Percentage Removed	5.96%	6.83%	26.35%

Table S3.2. Total number of missing weeks in each year for which values were calculated for i) Sycamore leaf burst stage; ii*) D.platanoidis* abundance; iii) *P.testudinaceus* abundance and iv) Parasitised aphid abundance by taking the mean of the recoded values in the week immediately either side of the missing data point.

Year	**Start Day**	**End Day**	**Total Collection Period (Weeks)**	**Missing Weeks**	**Percentage of weeks missing**
1993	85	330	35	4	11.43%
1994	69	342	39	3	7.69%
1995	54	334	40	0	0.00%
1996	66	353	41	2	4.88%
1997	65	332	38	5	13.11%
1998	71	348	40	2	5.05%
1999	56	315	37	2	5.41%
2000	41	334	42	2	4.78%
2001	60	347	41	3	7.32%
2002	59	332	39	1	2.56%
2003	37	331	42	2	4.76%
2004	36	336	43	2	4.67%
2005	41	342	43	3	6.98%
2006	75	348	39	1	2.56%
2007	60	333	39	0	0.00%
2008	52	331	40	0	0.00%
2009	71	330	37	0	0.00%
2010	70	336	38	0	0.00%
2011	69	335	38	0	0.00%
2012	68	326	37	1	2.71%
Total			787	33	4.19%

Table S3.3. The relative strength of density dependence effects on population growth on *D.platanoidis* and *P.testudinaceus.* Population growth modelled as a function of i) intra-specific density dependence – the size of the same aphid species in the previous year, ii) inter-specific density dependence – the size of the other aphid species in the previous years' population, and iii) inter and intra specific density dependence – the combined population size of both aphid species in the previous year. ∆AICc given relative to model containing tree and year only. The model containing only inta-specific density gave the strongest reduction in AICc for both species.

	∆AICc Relative to random effects only		
Species	Intra specific	Inter Specific	Intra and inter specific
D.platanoidis	-308.867	6.818	6.942
P.testudinaceus	-398.61	4.533	-152.528

Phenology moving window models

Sycamore tree phenology

Table S3.4a. Sycamore bud burst phenology as a function of temperatures advancing budburst, weather variables selected as those with a negative coefficient from moving window approach which considered all consecutive weekly windows between Jan 1st and April 29th. Models are mixed effects models with year and tree identity included in all models. Slopes reported with ± 1SE, ΔAICc given relative best fitting model. Random effects only model AICc = 6804.856. Wk = Week.

***Denotes best model where used in stage two modelling.**

Time window (Week 1 = Jan 1st)	n	AICc	ΔAICc	Slope±1SE	R^2	
					R^2GLMM$_{(m)}$	R2GLMM$_{(c)}$
wk11towk16 *	**1036**	**6780**	**0**	**-4.821±0.668**	**0.153**	***0.713***
wk11towk17	1036	6780.8	0.8	-5.047±0.722	0.151	*0.713*
wk11towk15	1036	6782.8	2.8	-3.935±0.597	0.146	*0.713*
wk10towk16	1036	6782.9	2.9	-4.925±0.764	0.144	*0.713*
wk10towk17	1036	6783.8	3.8	-5.036±0.814	0.14	*0.713*
wk10towk15	1036	6783.9	3.9	-4.253±0.681	0.141	*0.713*
wk11towk14	1036	6784.3	4.3	-3.316±0.529	0.142	*0.713*
wk4towk17	1036	6785.5	5.5	-4.097±0.700	0.135	*0.713*
wk4towk16	1036	6785.7	5.7	-3.948±0.678	0.134	*0.713*
wk5towk17	1036	6786.1	6.1	-4.073±0.714	0.132	*0.713*
wk5towk16	1036	6786.4	6.4	-3.906±0.690	0.132	*0.714*
wk9towk17	1036	6786.6	6.6	-4.603±0.834	0.13	*0.714*
wk9towk16	1036	6786.7	6.7	-4.413±0.798	0.13	*0.714*
wk10towk14	1036	6786.9	6.9	-3.549±0.635	0.131	*0.714*
wk6towk17	1036	6787	7	-4.287±0.785	0.128	*0.714*
wk3towk16	1036	6787	7	-3.900±0.708	0.129	*0.714*
wk3towk17	1036	6787.2	7.2	-3.990±0.732	0.128	*0.714*
wk4towk15	1036	6787.2	7.2	-3.540±0.644	0.129	*0.714*
wk3towk15	1036	6787.4	7.4	-3.635±0.667	0.128	*0.714*
wk6towk16	1036	6787.8	7.8	-4.045±0.764	0.125	*0.714*
wk5towk15	1036	6787.9	7.9	-3.473±0.651	0.126	*0.714*
wk9towk15	1036	6788.2	8.2	-3.784±0.725	0.124	*0.714*
wk3towk14	1036	6789	9	-3.292±0.646	0.122	*0.714*
wk4towk14	1036	6789.1	9.1	-3.162±0.621	0.121	*0.714*
wk8towk17	1036	6789.3	9.3	-4.033±0.822	0.118	*0.714*
wk6towk15	1036	6789.3	9.3	-3.550±0.714	0.119	*0.714*
wk5towk14	1036	6789.5	9.5	-3.102±0.622	0.119	*0.714*
wk7towk17	1036	6789.9	9.9	-4.091±0.861	0.114	*0.714*
wk12towk17	1036	6790	10	-4.557±0.973	0.113	*0.714*

wk2towk16	1036	6790.2	10.2	-3.770±0.798	0.114	*0.714*
wk8towk16	1036	6790.2	10.2	-3.747±0.792	0.114	*0.714*
wk2towk15	1036	6790.2	10.2	-3.577±0.753	0.114	*0.714*
wk12towk16	1036	6790.3	10.3	-4.292±0.924	0.112	*0.714*
wk2towk17	1036	6790.4	10.4	-3.822±0.819	0.112	*0.714*
wk9towk14	1036	6790.7	10.7	-3.169±0.675	0.113	*0.714*
wk12towk15	1036	6790.7	10.7	-3.570±0.772	0.112	*0.714*
wk7towk16	1036	6790.8	10.8	-3.806±0.835	0.11	*0.714*
wk6towk14	1036	6790.9	10.9	-3.147±0.678	0.112	*0.714*
wk8towk15	1036	6791.3	11.3	-3.264±0.722	0.11	*0.714*
wk3towk13	1036	6791.3	11.3	-3.217±0.710	0.109	*0.714*
wk2towk14	1036	6791.6	11.6	-3.242±0.727	0.108	*0.714*
wk4towk13	1036	6791.7	11.7	-3.050±0.684	0.108	*0.714*
wk7towk15	1036	6791.9	11.9	-3.341±0.768	0.105	*0.715*
wk3towk12	1036	6792	12	-2.960±0.673	0.106	*0.714*
wk5towk13	1036	6792.4	12.4	-2.973±0.690	0.104	*0.714*
wk4towk12	1036	6792.5	12.5	-2.778±0.644	0.104	*0.714*
wk8towk14	1036	6792.5	12.5	-2.874±0.669	0.104	*0.715*
wk11towk13	1036	6792.6	12.6	-3.023±0.715	0.103	*0.715*
wk7towk14	1036	6792.8	12.8	-3.011±0.720	0.101	*0.715*
wk12towk14	1036	6793	13	-2.748±0.659	0.101	*0.715*
wk5towk12	1036	6793.1	13.1	-2.683±0.644	0.101	*0.715*
wk11towk12	1036	6793.4	13.4	-2.329±0.558	0.101	*0.715*
wk1towk16	1036	6793.5	13.5	-3.526±0.898	0.094	*0.715*
wk1towk17	1036	6793.6	13.6	-3.571±0.915	0.094	*0.715*
wk1towk15	1036	6793.7	13.7	-3.340±0.852	0.094	*0.715*
wk2towk13	1036	6793.8	13.8	-3.113±0.795	0.094	*0.715*
wk6towk13	1036	6794.3	14.3	-2.934±0.765	0.092	*0.715*
wk6towk12	1036	6794.5	14.5	-2.718±0.711	0.092	*0.715*
wk2towk12	1036	6794.6	14.6	-2.852±0.757	0.09	*0.715*
wk3towk11	1036	6794.7	14.7	-2.483±0.652	0.091	*0.715*
wk4towk9	1036	6794.7	14.7	-2.326±0.607	0.092	*0.715*
wk11towk11	1036	6794.8	14.8	-1.620±0.405	0.097	*0.715*
wk1towk14	1036	6794.9	14.9	-3.002±0.818	0.088	*0.715*
wk14towk14	1036	6794.9	14.9	-1.427±0.354	0.097	*0.715*
wk3towk9	1036	6795	15	-2.436±0.650	0.09	*0.715*
wk4towk11	1036	6795	15	-2.330±0.618	0.091	*0.715*
wk5towk11	1036	6795.8	15.8	-2.187±0.610	0.085	*0.715*
wk13towk15	1036	6796.1	16.1	-2.507±0.727	0.082	*0.715*
wk10towk13	1036	6796.3	16.3	-2.741±0.818	0.079	*0.715*
wk4towk8	1036	6796.3	16.3	-2.009±0.573	0.083	*0.715*

wk3towk10	1036	6796.3	16.3	-2.373±0.694	0.08	*0.715*
wk3towk8	1036	6796.3	16.3	-2.154±0.623	0.081	*0.715*
wk5towk9	1036	6796.4	16.4	-2.053±0.592	0.082	*0.715*
wk13towk14	1036	6796.4	16.4	-1.983±0.571	0.082	*0.715*
wk4towk10	1036	6796.6	16.6	-2.218±0.656	0.079	*0.715*
wk2towk11	1036	6796.8	16.8	-2.375±0.726	0.076	*0.715*
wk10towk12	1036	6796.9	16.9	-2.292±0.700	0.076	*0.715*
wk1towk13	1036	6797	17	-2.782±0.882	0.073	*0.715*
wk7towk13	1036	6797.1	17.1	-2.563±0.809	0.073	*0.715*
wk13towk17	1036	6797.1	17.1	-2.930±0.948	0.071	*0.715*
wk14towk15	1036	6797.3	17.3	-1.855±0.565	0.077	*0.715*
wk7towk12	1036	6797.3	17.3	-2.349±0.747	0.072	*0.715*
wk13towk16	1036	6797.5	17.5	-2.673±0.885	0.069	*0.716*
wk1towk12	1036	6797.5	17.5	-2.555±0.841	0.069	*0.716*
wk8towk13	1036	6797.6	17.6	-2.293±0.747	0.07	*0.716*
wk6towk11	1036	6797.8	17.8	-2.048±0.660	0.071	*0.716*
wk5towk10	1036	6797.8	17.8	-2.010±0.647	0.071	*0.715*
wk2towk9	1036	6797.8	17.8	-2.239±0.737	0.069	*0.716*
wk9towk13	1036	6797.8	17.8	-2.349±0.783	0.068	*0.716*
wk8towk12	1036	6798	18	-2.043±0.674	0.069	*0.716*
wk9towk12	1036	6798.3	18.3	-2.052±0.694	0.067	*0.716*
wk2towk10	1036	6798.4	18.4	-2.210±0.770	0.064	*0.716*
wk5towk8	1036	6798.4	18.4	-1.639±0.540	0.069	*0.716*
wk3towk7	1036	6798.5	18.5	-1.780±0.600	0.067	*0.716*
wk3towk6	1036	6798.7	18.7	-1.574±0.526	0.068	*0.716*
wk14towk17	1036	6798.8	18.8	-2.277±0.828	0.06	*0.716*
wk4towk7	1036	6798.9	18.9	-1.575±0.537	0.066	*0.716*
wk1towk11	1036	6799.2	19.2	-2.124±0.799	0.057	*0.716*
wk4towk6	1036	6799.3	19.3	-1.306±0.445	0.066	*0.716*
wk6towk9	1036	6799.3	19.3	-1.781±0.647	0.061	*0.716*
wk2towk8	1036	6799.3	19.3	-1.903±0.704	0.059	*0.716*
wk14towk16	1036	6799.5	19.5	-1.928±0.734	0.056	*0.716*
wk4towk5	1036	6799.9	19.9	-1.226±0.438	0.062	*0.716*
wk3towk5	1036	6800.1	20.1	-1.401±0.532	0.057	*0.716*
wk6towk10	1036	6800.2	20.2	-1.747±0.703	0.052	*0.716*
wk7towk11	1036	6800.4	20.4	-1.634±0.662	0.052	*0.716*
wk1towk9	1036	6800.4	20.4	-1.900±0.813	0.047	*0.716*
wk10towk11	1036	6800.6	20.6	-1.427±0.576	0.052	*0.716*
wk1towk10	1036	6800.7	20.7	-1.895±0.837	0.045	*0.716*
wk6towk8	1036	6800.7	20.7	-1.438±0.591	0.05	*0.716*
wk8towk11	1036	6801	21	-1.376±0.578	0.049	*0.716*

wk2towk6	1036	6801	21	-1.463±0.626	0.047	*0.716*
wk2towk7	1036	6801	21	-1.540±0.675	0.046	*0.716*
wk5towk6	1036	6801.1	21.1	-0.961±0.374	0.054	*0.716*
wk5towk7	1036	6801.1	21.1	-1.166±0.479	0.05	*0.716*
wk9towk11	1036	6801.4	21.4	-1.311±0.580	0.045	*0.716*
wk1towk8	1036	6801.6	21.6	-1.578±0.773	0.038	*0.717*
wk5towk5	1036	6801.6	21.6	-0.827±0.331	0.052	*0.716*
wk12towk13	1036	6802	22	-1.594±0.853	0.033	*0.717*
wk7towk9	1036	6802.6	22.6	-1.176±0.628	0.033	*0.717*
wk2towk5	1036	6802.7	22.7	-1.168±0.631	0.033	*0.717*
wk7towk10	1036	6802.8	22.8	-1.219±0.692	0.03	*0.717*
wk8towk8	1036	6802.9	22.9	-0.923±0.472	0.036	*0.717*
wk17to17	1036	6803	23	-1.336±0.859	0.024	*0.717*
wk3towk4	1036	6803	23	-1.067±0.594	0.031	*0.717*
wk1towk7	1036	6803	23	-1.216±0.732	0.027	*0.717*
wk1towk6	1036	6803.2	23.2	-1.131±0.691	0.026	*0.717*
wk4towk4	1036	6803.3	23.3	-0.873±0.471	0.033	*0.717*
wk6towk7	1036	6803.3	23.3	-0.930±0.518	0.031	*0.717*
wk6towk6	1036	6803.3	23.3	-0.727±0.365	0.037	*0.717*
wk7towk8	1036	6803.4	23.4	-1.000±0.600	0.027	*0.717*
wk12towk12	1036	6803.4	23.4	-0.985±0.601	0.026	*0.717*
wk8towk9	1036	6803.5	23.5	-0.853±0.489	0.029	*0.717*
wk8towk10	1036	6803.5	23.5	-0.949±0.584	0.026	*0.717*
wk15to17	1036	6804.2	24.2	-0.929±0.883	0.012	*0.717*
wk1towk5	1036	6804.6	24.6	-0.748±0.666	0.013	*0.717*
wk9towk10	1036	6804.8	24.8	-0.673±0.567	0.015	*0.717*
wk2towk4	1036	6804.9	24.9	-0.648±0.658	0.01	*0.717*
wk13towk13	1036	6804.9	24.9	-0.641±0.686	0.009	*0.717*
wk16to17	1036	6804.9	24.9	-0.621±0.759	0.007	*0.718*
wk15to15	1036	6805	25	-0.612±0.674	0.009	*0.717*
wk15to16	1036	6805.2	25.2	-0.500±0.742	0.005	*0.718*
wk9towk9	1036	6805.2	25.2	-0.528±0.426	0.016	*0.717*
wk7towk7	1036	6805.5	25.5	-0.462±0.565	0.007	*0.718*
wk1towk4	1036	6805.8	25.8	-0.248±0.656	0.002	*0.718*
wk3towk3	1036	6805.8	25.8	-0.416±0.467	0.009	*0.717*
wk10towk10	1036	6805.8	25.8	-0.374±0.552	0.005	*0.718*
wk16to16	1036	6806.2	26.2	-0.148±0.553	0.001	*0.718*
wk1towk3	1036	6806.4	26.4	-0.122±0.505	0.001	*0.718*
wk2towk3	1036	6806.4	26.4	-0.122±0.505	0.001	*0.718*
wk1towk2	1036	6806.4	26.4	0.255±0.420	0.004	*0.718*
wk1towk1	1036	6806.6	26.6	0.253±0.354	0.006	*0.718*

wk2towk2	1036	6806.8	26.8	0.135±0.392	0.001	*0.718*

Table 3.4b. Sycamore bud burst phenology as a function of temperatures delaying budburst, weather variables selected as those with a positive coefficient from moving window approach which considered all consecutive weekly windows between Jan 1st and April 29th. Models are mixed effects models with year and tree identity included in all models. Slopes reported with ± 1SE, ΔAICc given relative to random effects only model AICc = 6804.856. Wk = Week.

***Denotes best model where used in stage two modelling.**

Time window (Week 1 = Jan 1st)	n	AICc	ΔAICc	Slope±1SE	R^2	
					R^2GLMM$_{(m)}$	R2GLMM$_{(c)}$
wk1towk3*	**1036**	**6806.4**	**0**	**0.090±0.516**	**0.00034**	**0.717**
wk1towk2	1036	6806.4	0	0.255±0.420	0.00408	0.718
wk1towk1	1036	6806.6	0.2	0.253±0.354	0.00561	0.718
wk2towk2	1036	6806.8	0.4	0.135±0.392	0.00133	0.718

Table 3.4c. Sycamore bud burst phenology as a function of precipitation advancing budburst, weather variables selected as those with a negative coefficient from moving window approach which considered all consecutive weekly windows between Jan 1st and April 29th. Models are mixed effects models with year and tree identity included in all models. Slopes reported with ± 1SE, ΔAICc given relative to random effects only model. Random effects only model AICc = 6804.856. Wk = Week.

***Denotes best model where used in stage two modelling.**

Time window (Week 1 = Jan 1st)	n	AICc	ΔAICc	Slope±1SE	R^2GLMM$_{(m)}$	R2GLMM$_{(c)}$
Wk1toWk9 *	**1036**	**6802.9**	**0**	**-1.714±1.494**	**0.014**	**0.717**
Wk1toWk6	1036	6803	0.1	-1.541±1.145	0.019	0.717
Wk2toWk4	1036	6803	0.1	-1.356±0.898	0.023	0.717
Wk1toWk4	1036	6803	0.1	-1.463±1.060	0.02	0.717
Wk3toWk3	1036	6803.1	0.2	-1.024±0.585	0.03	0.717
Wk3toWk4	1036	6803.2	0.3	-1.070±0.629	0.028	0.717
Wk1toWk5	1036	6803.2	0.3	-1.434±1.111	0.017	0.717
Wk1toWk7	1036	6803.2	0.3	-1.487±1.378	0.012	0.717
Wk1toWk8	1036	6803.2	0.3	-1.494±1.508	0.011	0.717
Wk2toWk6	1036	6803.3	0.4	-1.332±0.990	0.019	0.717
Wk2toWk9	1036	6803.3	0.4	-1.421±1.312	0.012	0.717
Wk2toWk5	1036	6803.4	0.5	-1.260±0.951	0.018	0.717
Wk1toWk10	1036	6803.5	0.6	-1.255±1.619	0.007	0.718
Wk3toWk5	1036	6803.6	0.7	-1.067±0.738	0.021	0.717
Wk2toWk7	1036	6803.6	0.7	-1.247±1.198	0.012	0.717
Wk2toWk8	1036	6803.7	0.8	-1.204±1.301	0.009	0.717

Wk1toWk11	1036	6803.7	0.8	-1.022±1.607	0.004	0.718
Wk3toWk9	1036	6803.7	0.8	-1.176±1.101	0.012	0.717
Wk2toWk10	1036	6803.7	0.8	-1.088±1.469	0.006	0.718
Wk3toWk6	1036	6803.8	0.9	-1.040±0.770	0.019	0.717
Wk1toWk14	1036	6803.8	0.9	-0.036±1.885	0	0.718
Wk1toWk12	1036	6803.8	0.9	-0.729±1.673	0.002	0.718
Wk2toWk11	1036	6803.9	1	-0.888±1.471	0.004	0.718
Wk1toWk13	1036	6803.9	1	-0.249±1.757	0	0.718
Wk2toWk12	1036	6804	1.1	-0.629±1.548	0.002	0.718
Wk3toWk8	1036	6804	1.1	-0.995±1.074	0.009	0.717
Wk3toWk7	1036	6804	1.1	-0.996±0.960	0.012	0.717
Wk9toWk9	1036	6804.1	1.2	-0.950±0.779	0.015	0.717
Wk2toWk13	1036	6804.1	1.2	-0.182±1.634	0	0.718
Wk3toWk14	1036	6804.1	1.2	-0.022±1.640	0	0.718
Wk3toWk10	1036	6804.1	1.2	-0.904±1.237	0.006	0.718
Wk3toWk11	1036	6804.2	1.3	-0.760±1.262	0.004	0.718
Wk3toWk12	1036	6804.3	1.4	-0.564±1.354	0.002	0.718
Wk3toWk13	1036	6804.3	1.4	-0.197±1.468	0	0.718
Wk4toWk9	1036	6804.4	1.5	-0.776±1.087	0.006	0.718
Wk1toWk3	1036	6804.4	1.5	-0.808±0.946	0.008	0.718
Wk2toWk3	1036	6804.4	1.5	-0.820±0.809	0.011	0.717
Wk5toWk9	1036	6804.5	1.6	-0.516±1.216	0.002	0.718
Wk4toWk10	1036	6804.5	1.6	-0.453±1.245	0.001	0.718
Wk4toWk12	1036	6804.5	1.6	-0.095±1.327	0	0.718
Wk4toWk11	1036	6804.5	1.6	-0.324±1.250	0.001	0.718
Wk5toWk8	1036	6804.7	1.8	-0.104±1.223	0	0.718
Wk5toWk7	1036	6804.7	1.8	-0.199±1.164	0	0.718
Wk4toWk8	1036	6804.7	1.8	-0.519±1.036	0.003	0.718
Wk5toWk6	1036	6804.8	1.9	-0.639±0.853	0.006	0.718
Wk6toWk9	1036	6804.8	1.9	-0.331±1.083	0.001	0.718
Wk4toWk7	1036	6804.9	2	-0.534±0.907	0.004	0.718
Wk4toWk6	1036	6804.9	2	-0.633±0.690	0.009	0.717
Wk8toWk9	1036	6805	2.1	-0.490±0.865	0.004	0.718
Wk4toWk5	1036	6805.2	2.3	-0.562±0.630	0.009	0.717
Wk7toWk9	1036	6805.2	2.3	-0.008±0.933	0	0.718
Wk5toWk5	1036	6805.3	2.4	-0.376±0.784	0.003	0.718
Wk4toWk4	1036	6805.5	2.6	-0.475±0.462	0.011	0.717
Wk1toWk2	1036	6805.6	2.7	-0.013±0.766	0	0.718
Wk6toWk6	1036	6805.6	2.7	-0.403±0.599	0.005	0.718
Wk1toWk1	1036	6806.3	3.4	-0.066±0.531	0	0.718

Table 3.4d. Sycamore bud burst phenology as a function of precipitation delaying budburst, weather variables selected as those with a positive coefficient from moving window approach which considered all consecutive weekly windows between Jan 1st and April 29th. Models are mixed effects models with year and tree identity included in all models. Slopes reported with ± 1SE, ΔAICc given relative to random effects only model AICc = 6804.856. Wk = Week.

***Denotes best model where used in stage two modelling.**

Time window (Week 1 = Jan 1st)	n	AICc	ΔAICc	Slope±1SE	R^2GLMM$_{(m)}$	R2GLMM$_{(c)}$
Wk7toWk17 *	**1036**	**6799.9**	**0**	**3.685±1.802**	**0.038**	**0.717**
Wk7toWk16	1036	6800.7	0.8	3.229±1.791	0.031	0.717
Wk6toWk17	1036	6800.9	1	3.302±1.945	0.028	0.717
Wk8toWk17	1036	6801	1.1	2.977±1.693	0.03	0.717
Wk10toWk17	1036	6801.3	1.4	2.301±1.232	0.033	0.717
Wk7toWk15	1036	6801.4	1.5	2.771±1.728	0.025	0.717
Wk10toWk16	1036	6801.5	1.6	2.238±1.247	0.031	0.717
Wk8toWk16	1036	6801.6	1.7	2.682±1.710	0.025	0.717
Wk6toWk16	1036	6801.6	1.7	2.865±1.946	0.022	0.717
Wk5toWk17	1036	6801.7	1.8	2.789±1.967	0.02	0.717
Wk9toWk17	1036	6801.7	1.8	2.361±1.460	0.026	0.717
Wk10toWk15	1036	6801.9	2	2.046±1.200	0.028	0.717
Wk10toWk13	1036	6802	2.1	1.899±1.100	0.029	0.717
Wk7toWk14	1036	6802	2.1	2.358±1.643	0.021	0.717
Wk8toWk15	1036	6802	2.1	2.383±1.684	0.02	0.717
Wk10toWk14	1036	6802	2.1	1.931±1.152	0.028	0.717
Wk12toWk17	1036	6802.1	2.2	1.858±1.098	0.028	0.717
Wk9toWk16	1036	6802.1	2.2	2.188±1.483	0.022	0.717
Wk12toWk13	1036	6802.2	2.3	1.657±0.938	0.03	0.717
Wk5toWk16	1036	6802.2	2.3	2.385±1.970	0.015	0.717
Wk6toWk15	1036	6802.2	2.3	2.329±1.856	0.016	0.717
Wk10toWk10	1036	6802.4	2.5	1.467±0.834	0.03	0.717
Wk9toWk15	1036	6802.5	2.6	1.985±1.463	0.019	0.717
Wk8toWk14	1036	6802.5	2.6	2.057±1.625	0.017	0.717
Wk11toWk17	1036	6802.5	2.6	1.724±1.131	0.023	0.717
Wk7toWk13	1036	6802.6	2.7	1.953±1.529	0.017	0.717
Wk13toWk13	1036	6802.7	2.8	1.295±0.735	0.03	0.717
Wk12toWk16	1036	6802.7	2.8	1.591±1.053	0.023	0.717
Wk5toWk15	1036	6802.8	2.9	1.902±1.878	0.011	0.717
Wk6toWk14	1036	6802.8	2.9	1.872±1.750	0.012	0.717

Wk13toWk17	1036	6802.8	2.9	1.509±0.991	0.023	0.717
Wk9toWk14	1036	6802.8	2.9	1.764±1.418	0.016	0.717
Wk8toWk13	1036	6802.8	2.9	1.784±1.560	0.014	0.717
Wk11toWk16	1036	6802.9	3	1.551±1.116	0.02	0.717
Wk9toWk13	1036	6803	3.1	1.655±1.396	0.015	0.717
Wk4toWk17	1036	6803.1	3.2	1.583±1.835	0.008	0.718
Wk12toWk12	1036	6803.1	3.2	1.434±1.057	0.019	0.717
Wk12toWk15	1036	6803.1	3.2	1.373±0.980	0.02	0.717
Wk12toWk14	1036	6803.2	3.3	1.331±0.934	0.021	0.717
Wk2toWk17	1036	6803.2	3.3	1.168±2.157	0.003	0.718
Wk5toWk14	1036	6803.2	3.3	1.456±1.752	0.007	0.718
Wk10toWk12	1036	6803.2	3.3	1.378±1.064	0.017	0.717
Wk1toWk17	1036	6803.3	3.4	1.037±2.164	0.003	0.718
Wk6toWk13	1036	6803.3	3.4	1.403±1.589	0.008	0.717
Wk11toWk15	1036	6803.4	3.5	1.321±1.047	0.017	0.717
Wk4toWk16	1036	6803.4	3.5	1.244±1.829	0.005	0.718
Wk3toWk17	1036	6803.4	3.5	0.998±1.981	0.003	0.718
Wk2toWk16	1036	6803.5	3.6	0.692±2.097	0.001	0.718
Wk1toWk16	1036	6803.5	3.6	0.599±2.125	0.001	0.718
Wk7toWk12	1036	6803.5	3.6	1.283±1.493	0.008	0.718
Wk15to17	1036	6803.5	3.6	1.199±0.923	0.017	0.717
Wk13toWk16	1036	6803.5	3.6	1.195±0.916	0.018	0.717
Wk3toWk16	1036	6803.6	3.7	0.588±1.948	0.001	0.718
Wk5toWk13	1036	6803.6	3.7	1.081±1.610	0.005	0.718
Wk1toWk15	1036	6803.7	3.8	0.237±1.987	0	0.718
Wk11toWk14	1036	6803.7	3.8	1.146±0.973	0.015	0.717
Wk2toWk15	1036	6803.7	3.8	0.302±1.931	0	0.718
Wk4toWk15	1036	6803.7	3.8	0.857±1.701	0.003	0.718
Wk8toWk12	1036	6803.8	3.9	0.993±1.535	0.005	0.718
Wk11toWk13	1036	6803.8	3.9	1.097±0.922	0.015	0.717
Wk3toWk15	1036	6803.9	4	0.236±1.798	0	0.718
Wk2toWk14	1036	6803.9	4	0.022±1.785	0	0.718
Wk13toWk15	1036	6803.9	4	1.013±0.839	0.015	0.717
Wk9toWk12	1036	6804	4.1	0.923±1.379	0.005	0.718
Wk6toWk12	1036	6804	4.1	0.727±1.504	0.003	0.718
Wk14toWk17	1036	6804	4.1	0.999±0.885	0.013	0.717
Wk4toWk14	1036	6804	4.1	0.557±1.572	0.001	0.718
Wk7toWk11	1036	6804	4.1	0.835±1.378	0.004	0.718
Wk10toWk11	1036	6804.1	4.2	0.958±0.910	0.012	0.717
Wk5toWk12	1036	6804.1	4.2	0.469±1.520	0.001	0.718
Wk13toWk14	1036	6804.1	4.2	0.911±0.756	0.015	0.717
Wk7toWk7	1036	6804.2	4.3	0.922±0.827	0.013	0.717

Wk15to16	1036	6804.2	4.3	0.899±0.867	0.011	0.717
Wk8toWk11	1036	6804.3	4.4	0.452±1.418	0.001	0.718
Wk4toWk13	1036	6804.3	4.4	0.318±1.428	0.001	0.718
Wk6toWk11	1036	6804.3	4.4	0.346±1.399	0.001	0.718
Wk5toWk11	1036	6804.3	4.4	0.134±1.437	0	0.718
Wk5toWk10	1036	6804.4	4.5	0.024±1.398	0	0.718
Wk7toWk10	1036	6804.5	4.6	0.610±1.164	0.003	0.718
Wk9toWk11	1036	6804.5	4.6	0.386±1.255	0.001	0.718
Wk6toWk10	1036	6804.6	4.7	0.219±1.269	0	0.718
Wk8toWk10	1036	6804.6	4.7	0.255±1.218	0	0.718
Wk9toWk10	1036	6804.6	4.7	0.257±1.205	0.001	0.718
Wk15to15	1036	6804.7	4.8	0.699±0.802	0.008	0.718
Wk14toWk16	1036	6804.8	4.9	0.685±0.790	0.008	0.718
Wk6toWk8	1036	6804.9	5	0.123±1.067	0	0.718
Wk11toWk12	1036	6805	5.1	0.547±0.832	0.005	0.718
Wk7toWk8	1036	6805	5.1	0.511±0.839	0.004	0.718
Wk6toWk7	1036	6805.1	5.2	0.078±0.976	0	0.718
Wk14toWk15	1036	6805.2	5.3	0.529±0.726	0.006	0.718
Wk16to16	1036	6805.4	5.5	0.493±0.627	0.007	0.718
Wk8toWk8	1036	6805.6	5.7	0.092±0.751	0	0.718
Wk14toWk14	1036	6805.9	6	0.292±0.563	0.003	0.718
Wk11toWk11	1036	6806	6.1	0.135±0.597	0.001	0.718
Wk2toWk2	1036	6806.2	6.3	0.062±0.575	0	0.718

Drepanosiphum platanoidis – Sycamore aphid

Table S3.5a. *D.platanoidis* emergence phenology as a function of temperature advancing emergence, weather variables selected as those with a negative coefficient from moving window approach which considered all consecutive weekly windows between Jan 1st and June 17th Models are mixed effects models with year and tree identity included in all models. Slopes reported with ± 1SE, ΔAICc given relative to best fitting model. Random effects only model AICc = 8759.12. Wk = Week.

***Denotes best model where used in stage two modelling.**

Time window (Week 1 = Jan 1st)	n	AICc	ΔAICc	Slope±1SE	R^2GLMM$_{(m)}$	R2GLMM$_{(c)}$
wk21to22*	**979**	**8751.2**	**0**	**-9.088±3.648**	**0.138**	**0.586**
wk21to23	979	8753.2	2	-9.373±5.746	0.069	0.592
wk4towk4	979	8753.6	2.4	-4.516±2.156	0.104	0.597
wk3towk4	979	8754.3	3.1	-4.852±2.760	0.076	0.585
wk22to23	979	8754.4	3.2	-6.385±4.867	0.047	0.593
wk12to24	979	8754.6	3.4	-6.234±6.640	0.022	0.586
wk13to24	979	8754.8	3.6	-5.722±6.048	0.023	0.588
wk9to23	979	8754.8	3.6	-5.382±6.789	0.018	0.594

wk12to23	979	8754.9	3.7	-4.888±7.517	0.012	0.594
wk11to23	979	8754.9	3.7	-4.908±6.998	0.014	0.594
wk6to24	979	8755	3.8	-4.942±6.092	0.017	0.589
wk10to23	979	8755.1	3.9	-4.231±6.978	0.011	0.594
wk7to24	979	8755.1	3.9	-4.884±5.900	0.017	0.585
wk17to23	979	8755.1	3.9	-4.776±6.107	0.017	0.594
wk11to24	979	8755.1	3.9	-4.531±6.407	0.013	0.588
wk20to23	979	8755.1	3.9	-4.450±6.399	0.014	0.594
we9to24	979	8755.1	3.9	-4.438±6.340	0.013	0.588
wk13to23	979	8755.2	4	-4.007±6.675	0.01	0.594
wk9towk22	979	8755.2	4	-4.425±6.111	0.015	0.59
wk8to23	979	8755.2	4	-4.193±6.432	0.012	0.594
wk10to24	979	8755.2	4	-4.118±6.451	0.011	0.589
wk14to24	979	8755.2	4	-4.590±5.637	0.016	0.586
wk8to24	979	8755.2	4	-4.398±5.868	0.014	0.585
wk12towk22	979	8755.2	4	-3.779±6.581	0.009	0.59
wk9towk16	979	8755.2	4	-4.147±6.126	0.013	0.595
wk2to24	979	8755.2	4	-4.152±6.039	0.013	0.592
wk15to24	979	8755.2	4	-4.177±5.927	0.012	0.588
wk11towk22	979	8755.3	4.1	-3.929±6.217	0.011	0.59
wk9towk18	979	8755.3	4.1	-4.161±5.953	0.014	0.593
wk1to24	979	8755.3	4.1	-3.958±6.134	0.012	0.593
wk9towk17	979	8755.3	4.1	-3.691±6.379	0.009	0.593
wk9towk14	979	8755.3	4.1	-4.549±4.637	0.028	0.596
wk18to23	979	8755.3	4.1	-4.276±5.585	0.017	0.594
wk15to23	979	8755.3	4.1	-3.057±6.783	0.006	0.594
wk16to23	979	8755.3	4.1	-3.719±6.265	0.01	0.594
wk3to24	979	8755.3	4.1	-3.911±5.893	0.012	0.591
wk10towk22	979	8755.3	4.1	-3.395±6.282	0.008	0.591
wk5to24	979	8755.3	4.1	-3.739±5.949	0.011	0.591
wk14to23	979	8755.4	4.2	-3.100±6.408	0.007	0.594
wk16to24	979	8755.4	4.2	-3.788±5.766	0.011	0.59
wk20to22	979	8755.4	4.2	-4.267±4.759	0.021	0.584
wk9towk15	979	8755.4	4.2	-4.004±5.350	0.016	0.594
wk9towk19	979	8755.4	4.2	-3.604±5.809	0.011	0.593
wk1towk4	979	8755.4	4.2	-3.881±2.976	0.045	0.593
wk8towk22	979	8755.4	4.2	-3.433±5.831	0.01	0.591
wk10towk17	979	8755.4	4.2	-1.693±6.760	0.002	0.594
wk11towk17	979	8755.4	4.2	-2.300±6.516	0.003	0.594

wk10towk16	979	8755.4	4.2	-2.241±6.550	0.003	0.595
wk21to21	979	8755.5	4.3	-4.103±3.700	0.033	0.596
wk11towk16	979	8755.5	4.3	-2.879±6.196	0.006	0.595
wk4to24	979	8755.5	4.3	-3.129±5.982	0.008	0.592
wk17to22	979	8755.5	4.3	-3.920±5.042	0.017	0.588
wk11towk18	979	8755.5	4.3	-3.198±5.908	0.008	0.593
wk12towk17	979	8755.5	4.3	-0.921±6.796	0.001	0.594
wk10towk18	979	8755.5	4.3	-2.737±6.179	0.006	0.594
wk13towk22	979	8755.5	4.3	-3.136±5.851	0.008	0.59
wk7to23	979	8755.5	4.3	-1.747±6.543	0.002	0.595
wk12towk18	979	8755.5	4.3	-2.540±6.146	0.005	0.593
wk1to23	979	8755.5	4.3	-2.472±6.144	0.005	0.595
wk12towk16	979	8755.5	4.3	-1.611±6.463	0.002	0.595
wk11towk14	979	8755.5	4.3	-3.967±4.343	0.024	0.597
wk11towk19	979	8755.6	4.4	-2.799±5.836	0.007	0.593
wk12towk19	979	8755.6	4.4	-2.258±6.130	0.004	0.594
wk15to22	979	8755.6	4.4	-2.455±5.998	0.004	0.591
wk8towk18	979	8755.6	4.4	-3.035±5.645	0.008	0.594
wk16to22	979	8755.6	4.4	-3.143±5.464	0.009	0.589
wk10towk19	979	8755.6	4.4	-2.333±5.981	0.004	0.594
wk6to23	979	8755.6	4.4	-0.243±6.462	0	0.595
wk8towk17	979	8755.6	4.4	-2.424±5.896	0.005	0.594
wk9towk21	979	8755.6	4.4	-2.194±5.911	0.004	0.592
wk10towk14	979	8755.6	4.4	-3.513±4.883	0.015	0.596
wk3to23	979	8755.6	4.4	-1.815±6.029	0.003	0.595
wk10towk15	979	8755.7	4.5	-2.457±5.700	0.006	0.595
wk8towk16	979	8755.7	4.5	-2.643±5.578	0.006	0.595
wk12towk21	979	8755.7	4.5	-0.523±6.232	0	0.594
wk8towk19	979	8755.7	4.5	-2.677±5.529	0.007	0.594
wk18to18	979	8755.7	4.5	-3.342±2.477	0.041	0.598
wk2to23	979	8755.7	4.5	-1.153±6.115	0.001	0.595
wk4to23	979	8755.7	4.5	-1.150±6.096	0.001	0.595
wk17to24	979	8755.7	4.5	-1.964±5.798	0.003	0.592
wk1towk22	979	8755.7	4.5	-1.981±5.796	0.003	0.593

wk14towk22	979	8755.7	4.5	-2.344±5.591	0.005	0.591
wk9towk20	979	8755.7	4.5	-2.338±5.621	0.005	0.594
wk7towk22	979	8755.7	4.5	-1.241±5.987	0.001	0.594
wk17to18	979	8755.7	4.5	-3.594±4.152	0.02	0.592
wk11towk21	979	8755.7	4.5	-1.246±5.938	0.001	0.593
wk10towk21	979	8755.7	4.5	-0.911±6.006	0.001	0.593
wk11towk15	979	8755.7	4.5	-2.894±5.170	0.009	0.595
wk9towk13	979	8755.7	4.5	-3.457±4.423	0.018	0.592
wk12towk14	979	8755.7	4.5	-3.525±4.219	0.019	0.598
wk11towk13	979	8755.7	4.5	-3.254±4.640	0.014	0.591
wk1towk18	979	8755.8	4.6	-1.566±5.748	0.002	0.594
wk19to23	979	8755.8	4.6	-2.555±5.294	0.007	0.595
wk1towk5	979	8755.8	4.6	-3.512±3.107	0.034	0.598
wk1towk17	979	8755.8	4.6	-1.029±5.854	0.001	0.594
wk18to22	979	8755.8	4.6	-3.348±4.390	0.016	0.588
wk12towk20	979	8755.8	4.6	-0.821±5.887	0.001	0.595
wk8towk21	979	8755.8	4.6	-1.590±5.652	0.002	0.593
wk1towk16	979	8755.8	4.6	-1.189±5.773	0.001	0.595
wk7towk18	979	8755.8	4.6	-0.333±5.864	0	0.595
wk11towk20	979	8755.8	4.6	-1.480±5.642	0.002	0.594
wk3towk22	979	8755.8	4.6	-1.335±5.653	0.002	0.594
wk10towk20	979	8755.8	4.6	-1.128±5.705	0.001	0.595
wk2towk22	979	8755.8	4.6	-0.732±5.768	0	0.594
wk12towk15	979	8755.8	4.6	-2.039±5.379	0.004	0.595
wk8towk14	979	8755.8	4.6	-3.186±4.438	0.015	0.596
wk3towk5	979	8755.8	4.6	-3.335±2.782	0.037	0.598
wk8towk15	979	8755.8	4.6	-2.615±4.948	0.008	0.595
wk4towk22	979	8755.8	4.6	-0.698±5.669	0	0.594
wk1towk19	979	8755.8	4.6	-1.376±5.515	0.002	0.594
wk8towk20	979	8755.9	4.7	-1.728±5.393	0.003	0.594
wk7towk19	979	8755.9	4.7	-0.306±5.682	0	0.595
wk1towk21	979	8755.9	4.7	-0.765±5.593	0.001	0.594
wk2towk18	979	8755.9	4.7	-0.050±5.640	0	0.595
wk1towk15	979	8755.9	4.7	-1.297±5.469	0.002	0.595
wk13towk18	979	8755.9	4.7	-1.923±5.224	0.004	0.594
wk3towk17	979	8755.9	4.7	-0.104±5.617	0	0.595

wk3towk18	979	8755.9	4.7	-0.740±5.501	0.001	0.595
wk13towk17	979	8755.9	4.7	-0.416±5.503	0	0.594
wk3towk16	979	8755.9	4.7	-0.234±5.483	0	0.595
wk1towk20	979	8755.9	4.7	-0.864±5.405	0.001	0.595
wk13towk21	979	8755.9	4.7	-0.304±5.432	0	0.594
wk2towk19	979	8755.9	4.7	-0.058±5.444	0	0.595
wk3towk21	979	8755.9	4.7	-0.091±5.439	0	0.595
we18to24	979	8756	4.8	-1.609±5.090	0.002	0.59
wk1towk14	979	8756	4.8	-1.675±5.096	0.003	0.595
wk13towk19	979	8756	4.8	-1.620±5.104	0.003	0.594
wk3towk19	979	8756	4.8	-0.672±5.340	0	0.595
wk10towk13	979	8756	4.8	-2.059±4.850	0.005	0.593
wk1towk13	979	8756	4.8	-1.083±5.163	0.001	0.594
wk21to24	979	8756	4.8	-2.181±4.674	0.004	0.582
wk13towk14	979	8756	4.8	-3.157±3.269	0.025	0.599
wk3towk20	979	8756	4.8	-0.207±5.229	0	0.595
wk13towk16	979	8756	4.8	-0.940±5.130	0.001	0.595
wk17to17	979	8756.1	4.9	-3.011±3.611	0.013	0.597
wk3towk15	979	8756.1	4.9	-0.375±5.126	0	0.595
wk20to24	979	8756.1	4.9	-1.239±4.921	0.001	0.588
wk9towk12	979	8756.1	4.9	-2.761±3.937	0.014	0.594
wk13towk20	979	8756.1	4.9	-0.544±5.035	0	0.595
wk8towk13	979	8756.1	4.9	-2.324±4.303	0.009	0.593
wk2towk14	979	8756.1	4.9	-0.142±4.984	0	0.595
wk1towk12	979	8756.1	4.9	-0.729±4.875	0.001	0.595
wk3towk3	979	8756.2	5	-2.672±2.025	0.037	0.597
wk3towk13	979	8756.2	5	-0.123±4.881	0	0.595
wk19to24	979	8756.2	5	-0.475±4.811	0	0.592
wk3towk14	979	8756.2	5	-0.824±4.766	0.001	0.595
wk7towk14	979	8756.2	5	-0.538±4.771	0	0.595
wk15to19	979	8756.2	5	-0.300±4.766	0	0.595
wk13towk13	979	8756.2	5	-2.805±3.247	0.022	0.596
wk1towk1	979	8756.2	5	-2.365±1.605	0.057	0.593
wk12towk13	979	8756.2	5	-1.801±4.308	0.005	0.592
wk14towk18	979	8756.2	5	-0.743±4.661	0.001	0.594
wk14towk19	979	8756.2	5	-0.693±4.646	0.001	0.594

wk13towk15	979	8756.2	5	-1.493±4.413	0.003	0.595
wk15to18	979	8756.3	5.1	-0.244±4.634	0	0.595
wk19to22	979	8756.3	5.1	-2.070±4.018	0.007	0.59
wk4towk14	979	8756.3	5.1	-0.032±4.585	0	0.595
wk22to24	979	8756.3	5.1	-1.696±4.155	0.004	0.586
wk16to18	979	8756.3	5.1	-1.282±4.280	0.002	0.593
wk9towk9	979	8756.3	5.1	-2.520±1.993	0.041	0.597
wk1towk11	979	8756.3	5.1	-0.594±4.446	0.001	0.595
wk1towk10	979	8756.3	5.1	-0.191±4.477	0	0.595
wk2towk4	979	8756.4	5.2	-2.565±3.133	0.019	0.593
wk17to19	979	8756.4	5.2	-1.998±3.814	0.008	0.594
wk1towk9	979	8756.4	5.2	-0.253±4.369	0	0.595
wk17to21	979	8756.4	5.2	-0.196±4.351	0	0.594
wk8towk12	979	8756.4	5.2	-1.794±3.889	0.006	0.594
wk16to19	979	8756.4	5.2	-1.031±4.194	0.002	0.594
wk10towk12	979	8756.4	5.2	-1.079±4.163	0.002	0.594
wk1towk6	979	8756.4	5.2	-2.213±3.431	0.012	0.597
wk11towk12	979	8756.4	5.2	-1.903±3.667	0.008	0.594
wk2towk5	979	8756.5	5.3	-2.255±3.134	0.014	0.597
wk11towk11	979	8756.6	5.4	-2.367±2.487	0.024	0.598
wk9towk11	979	8756.6	5.4	-2.132±3.064	0.014	0.594
wk4towk5	979	8756.7	5.5	-2.262±2.269	0.025	0.599
wk17to20	979	8756.7	5.5	-0.478±3.678	0.001	0.595
wk1towk3	979	8756.8	5.6	-2.028±2.389	0.02	0.596
wk8towk11	979	8756.9	5.7	-1.373±3.117	0.006	0.594
wk9towk10	979	8756.9	5.7	-1.764±2.755	0.012	0.595
wk2towk6	979	8756.9	5.7	-0.588±3.328	0.001	0.595
wk18to19	979	8756.9	5.7	-1.476±2.907	0.008	0.594
wk3towk6	979	8756.9	5.7	-1.309±2.999	0.006	0.596
wk10towk11	979	8757	5.8	-0.723±3.141	0.002	0.594
wk12towk12	979	8757	5.8	-1.305±2.900	0.005	0.597
wk23to24	979	8757	5.8	-0.096±3.143	0	0.594
wk8towk10	979	8757	5.8	-1.010±2.945	0.003	0.595
wk18to20	979	8757.1	5.9	-0.247±3.002	0	0.595
wk14towk14	979	8757.2	6	-1.669±1.988	0.016	0.598
wk15to15	979	8757.3	6.1	-0.295±2.800	0	0.593
wk8towk9	979	8757.3	6.1	-1.224±2.485	0.007	0.594
wk4towk6	979	8757.5	6.3	-0.274±2.528	0	0.595

wk10towk10	979	8757.5	6.3	-0.417±2.484	0.001	0.595
wk2towk3	979	8757.6	6.4	-0.580±2.360	0.002	0.595
wk16to16	979	8757.7	6.5	-0.685±2.181	0.002	0.595
wk1towk2	979	8757.7	6.5	-0.969±1.993	0.007	0.595
wk19to19	979	8758	6.8	-0.732±1.819	0.004	0.596
we20to20	979	8758.1	6.9	-0.104±1.814	0	0.591
wk5towk5	979	8758.5	7.3	-0.555±1.390	0.003	0.595

Table **S3.5b**. *D.platanoidis* emergence phenology as a function of temperature delaying emergence, weather variables selected as those with a positive coefficient from moving window approach which considered all consecutive weekly windows between Jan 1st and June 17th Models are mixed effects models with year and tree identity included in all models. Slopes reported with ± 1SE, ΔAICc given relative to best fitting model. Random effects only model AICc = 8759.12. Wk = Week.

***Denotes best model where used in stage two modelling.**

Time window (Week 1 = Jan 1st)	n	AICc	ΔAICc	Slope±1SE	R^2GLMM$_{(m)}$	R2GLMM$_{(c)}$
wk6towk7*	**979**	**8752.1**	**0**	**5.417±2.219**	**0.126**	**0.594**
wk6towk8	979	8753	0.9	5.875±2.815	0.101	0.597
wk7towk8	979	8754	1.9	5.074±2.769	0.081	0.597
wk5towk8	979	8754.3	2.2	4.862±2.859	0.073	0.598
wk5towk7	979	8754.6	2.5	4.171±2.383	0.077	0.598
wk7towk7	979	8754.8	2.7	3.982±2.006	0.072	0.548
wk6towk9	979	8755.4	3.3	4.154±3.486	0.039	0.598
wk5towk9	979	8755.5	3.4	3.909±3.462	0.035	0.598
wk6towk17	979	8755.6	3.5	2.572±6.011	0.005	0.595
wk6towk10	979	8755.6	3.5	3.786±3.747	0.029	0.596
wk5towk17	979	8755.7	3.6	2.643±5.611	0.006	0.595
wk6towk16	979	8755.7	3.6	2.386±5.748	0.005	0.595
wk5to23	979	8755.7	3.6	0.193±6.145	0	0.595
wk7towk17	979	8755.7	3.6	0.752±6.099	0	0.595
wk5towk10	979	8755.7	3.6	3.651±3.686	0.028	0.596
wk5towk16	979	8755.7	3.6	2.520±5.407	0.006	0.595
wk6towk18	979	8755.7	3.6	1.336±5.838	0.002	0.595
wk6towk22	979	8755.8	3.7	0.149±5.948	0	0.595
wk6towk21	979	8755.8	3.7	1.697±5.678	0.003	0.596
wk7towk16	979	8755.8	3.7	0.523±5.792	0	0.595
wk7towk21	979	8755.8	3.7	0.493±5.758	0	0.595
wk2towk17	979	8755.8	3.7	0.645±5.741	0	0.595
wk5towk21	979	8755.8	3.7	1.856±5.425	0.003	0.596
wk5towk18	979	8755.8	3.7	1.610±5.508	0.002	0.595
wk5towk22	979	8755.8	3.7	0.544±5.706	0	0.595

wk6towk19	979	8755.8	3.7	1.125±5.611	0.001	0.595
wk4towk17	979	8755.9	3.8	0.833±5.621	0.001	0.595
wk2towk16	979	8755.9	3.8	0.536±5.642	0	0.595
wk6towk20	979	8755.9	3.8	1.485±5.397	0.002	0.595
wk6towk15	979	8755.9	3.8	1.914±5.180	0.004	0.595
wk2towk21	979	8755.9	3.8	0.472±5.538	0	0.595
wk6towk12	979	8755.9	3.8	2.896±4.469	0.013	0.596
wk5towk19	979	8755.9	3.8	1.390±5.338	0.002	0.595
wk4towk18	979	8755.9	3.8	0.057±5.522	0	0.595
wk6towk13	979	8755.9	3.8	2.446±4.823	0.008	0.596
wk7towk20	979	8755.9	3.8	0.306±5.495	0	0.595
wk4towk16	979	8755.9	3.8	0.704±5.438	0.001	0.595
wk4towk21	979	8755.9	3.8	0.591±5.441	0	0.595
wk5towk20	979	8755.9	3.8	1.662±5.167	0.003	0.595
wk15to21	979	8755.9	3.8	1.099±5.330	0.001	0.595
wk5towk15	979	8756	3.9	2.100±4.917	0.005	0.595
wk4towk8	979	8756	3.9	3.234±3.387	0.026	0.598
wk5towk13	979	8756	3.9	2.555±4.591	0.009	0.596
wk4towk19	979	8756	3.9	0.033±5.356	0	0.595
wk2towk15	979	8756	3.9	0.357±5.338	0	0.595
wk2towk20	979	8756	3.9	0.342±5.330	0	0.595
wk5towk12	979	8756	3.9	2.808±4.207	0.013	0.596
wk4towk20	979	8756	3.9	0.449±5.215	0	0.595
wk7towk15	979	8756	3.9	0.219±5.199	0	0.595
wk14towk21	979	8756.1	4	0.460±5.118	0	0.595
wk2towk13	979	8756.1	4	0.650±5.091	0	0.595
wk2towk8	979	8756.1	4	2.729±3.874	0.014	0.596
wk4towk15	979	8756.1	4	0.481±4.976	0	0.595
wk6towk14	979	8756.2	4.1	1.141±4.740	0.002	0.595
wk2towk12	979	8756.2	4.1	0.954±4.771	0.001	0.595
wk15to20	979	8756.2	4.1	0.723±4.782	0.001	0.595
wk6towk11	979	8756.2	4.1	2.577±3.813	0.013	0.596
wk5towk11	979	8756.2	4.1	2.615±3.720	0.014	0.596
wk7towk13	979	8756.2	4.1	0.601±4.758	0	0.595
wk16to21	979	8756.2	4.1	0.394±4.770	0	0.594
wk5towk14	979	8756.2	4.1	1.440±4.526	0.003	0.595
wk4towk13	979	8756.2	4.1	0.789±4.664	0.001	0.595
wk14towk17	979	8756.2	4.1	1.024±4.604	0.001	0.595
wk15to17	979	8756.2	4.1	1.928±4.239	0.005	0.596
wk14towk20	979	8756.2	4.1	0.195±4.678	0	0.595
wk2towk10	979	8756.2	4.1	1.576±4.373	0.004	0.595
wk2towk9	979	8756.3	4.2	1.632±4.250	0.004	0.596

wk3towk12	979	8756.3	4.2	0.221±4.567	0	0.595
wk7towk12	979	8756.3	4.2	1.095±4.388	0.002	0.595
wk4towk7	979	8756.3	4.2	2.652±3.013	0.022	0.597
wk20to21	979	8756.3	4.2	2.462±3.479	0.01	0.597
wk4towk12	979	8756.3	4.2	1.094±4.320	0.002	0.595
wk2towk11	979	8756.4	4.3	0.936±4.322	0.001	0.595
wk3towk8	979	8756.4	4.3	2.158±3.725	0.01	0.597
wk4towk10	979	8756.4	4.3	1.819±3.932	0.006	0.596
wk4towk9	979	8756.4	4.3	1.979±3.808	0.008	0.596
wk2towk7	979	8756.4	4.3	2.155±3.588	0.011	0.595
wk3towk10	979	8756.4	4.3	0.863±4.196	0.001	0.595
wk3towk9	979	8756.5	4.4	0.898±4.060	0.001	0.595
wk14towk16	979	8756.5	4.4	0.735±4.079	0.001	0.595
wk3towk11	979	8756.5	4.4	0.283±4.127	0	0.595
wk16to20	979	8756.5	4.4	0.073±4.131	0	0.595
wk1towk8	979	8756.5	4.4	0.825±4.031	0.001	0.595
wk7towk10	979	8756.5	4.4	1.888±3.515	0.008	0.595
wk4towk11	979	8756.5	4.4	1.084±3.888	0.002	0.595
wk7towk9	979	8756.6	4.5	2.042±3.206	0.011	0.596
wk15to16	979	8756.6	4.5	1.498±3.526	0.005	0.594
wk3towk7	979	8756.6	4.5	1.600±3.432	0.006	0.596
wk16to17	979	8756.7	4.6	1.187±3.554	0.003	0.596
wk7towk11	979	8756.7	4.6	0.982±3.615	0.002	0.595
wk23to23	979	8756.7	4.6	2.135±2.686	0.018	0.594
wk1towk7	979	8756.7	4.6	0.263±3.716	0	0.595
wk18to21	979	8756.7	4.6	0.046±3.715	0	0.594
wk14towk15	979	8756.9	4.8	0.536±3.331	0.001	0.595
wk19to21	979	8756.9	4.8	1.171±3.132	0.004	0.596
wk5towk6	979	8757.2	5.1	1.625±2.026	0.019	0.594
wk24to24	979	8757.4	5.3	0.229±2.642	0	0.593
wk8towk8	979	8757.6	5.5	0.082±2.395	0	0.594
wk19to20	979	8757.6	5.5	0.647±2.272	0.002	0.594
wk2towk2	979	8757.7	5.6	1.122±1.831	0.011	0.593
wk6towk6	979	8758.7	6.6	0.107±1.349	0	0.587
wk22to22	979	8758.9	6.8	0.004±1.194	0	0.584

Table S3.5c. *D.platanoidis* emergence phenology as a function of precipitation advancing emergence, weather variables selected as those with a negative coefficient from moving window approach which considered all consecutive weekly windows between Jan 1st and June 17th Models are mixed effects models with year and tree identity included in all models. Slopes reported with ± 1SE, ΔAICc given relative to best fitting model. Random effects only model AICc 8759.12. Wk = Week.

Time window (Week 1 = Jan 1st)	n	AICc	ΔAICc	Slope±1SE	R^2GLMM$_{(m)}$	R2GLMM$_{(c)}$
Wk17to23*	**979**	**8753.6**	**0**	**-9.727±7.382**	**0.047**	**0.593**
Wk17to24	979	8754	0.4	-8.164±6.939	0.038	0.596
Wk20to24	979	8754.2	0.6	-7.642±6.361	0.037	0.602
Wk16to23	979	8754.3	0.7	-7.433±7.069	0.031	0.594
Wk18to23	979	8754.4	0.8	-7.073±6.985	0.028	0.593
we18to24	979	8754.5	0.9	-6.800±6.831	0.027	0.596
Wk17to20	979	8754.5	0.9	-6.619±5.910	0.033	0.593
Wk19to24	979	8754.5	0.9	-6.621±6.645	0.026	0.6
Wk8to23	979	8754.5	0.9	-0.910±10.877	0	0.595
Wk15to23	979	8754.6	1	-6.349±7.612	0.02	0.594
Wk9to23	979	8754.6	1	-4.321±9.734	0.006	0.595
Wk10to23	979	8754.6	1	-5.148±8.828	0.01	0.594
Wk23to23	979	8754.7	1.1	-4.187±2.468	0.073	0.591
Wk12to23	979	8754.7	1.1	-4.429±8.650	0.008	0.595
Wk16to24	979	8754.7	1.1	-5.788±6.805	0.02	0.592
Wk20to23	979	8754.7	1.1	-5.885±6.329	0.025	0.594
Wk17to21	979	8754.8	1.2	-5.747±6.738	0.021	0.594
Wk11to23	979	8754.8	1.2	-4.425±8.496	0.008	0.595
Wk17to22	979	8754.8	1.2	-5.334±7.546	0.014	0.594
Wk13to23	979	8754.8	1.2	-4.711±8.076	0.01	0.595
we9to24	979	8754.8	1.2	-1.902±9.268	0.001	0.593
Wk9toWk21	979	8754.9	1.3	-0.964±9.281	0	0.595
Wk16to20	979	8754.9	1.3	-5.453±6.153	0.022	0.594
Wk9toWk20	979	8754.9	1.3	-1.673±9.027	0.001	0.595
Wk16to21	979	8754.9	1.3	-5.019±7.047	0.015	0.594
Wk15to24	979	8754.9	1.3	-4.713±7.232	0.012	0.593
Wk9toWk22	979	8754.9	1.3	-0.485±8.986	0	0.595
Wk19to23	979	8754.9	1.3	-5.051±6.670	0.016	0.594
Wk10to24	979	8755	1.4	-2.329±8.363	0.002	0.592
Wk9toWk19	979	8755	1.4	-0.781±8.607	0	0.595
Wk10toWk21	979	8755.1	1.5	-2.119±8.203	0.002	0.595
Wk10toWk20	979	8755.1	1.5	-2.772±7.969	0.003	0.595
Wk14to23	979	8755.1	1.5	-3.679±7.451	0.007	0.595
Wk15to20	979	8755.1	1.5	-4.229±6.922	0.011	0.594
Wk12to24	979	8755.1	1.5	-1.770±8.170	0.001	0.593
Wk10toWk22	979	8755.1	1.5	-1.634±8.200	0.001	0.595

Wk15to21	979	8755.1	1.5	-3.384±7.482	0.006	0.595
Wk13to24	979	8755.1	1.5	-2.656±7.699	0.003	0.593
Wk16to22	979	8755.1	1.5	-3.802±7.041	0.009	0.595
Wk1toWk3	979	8755.1	1.5	-4.840±4.415	0.034	0.594
Wk11to24	979	8755.1	1.5	-1.171±8.008	0.001	0.593
Wk12toWk21	979	8755.1	1.5	-1.085±8.011	0.001	0.595
Wk12toWk20	979	8755.2	1.6	-1.841±7.833	0.002	0.595
Wk11toWk21	979	8755.2	1.6	-1.416±7.825	0.001	0.595
Wk18to20	979	8755.2	1.6	-4.534±5.793	0.017	0.594
Wk12toWk22	979	8755.2	1.6	-0.609±7.892	0	0.595
Wk11toWk22	979	8755.2	1.6	-0.989±7.849	0	0.595
Wk11toWk20	979	8755.2	1.6	-2.053±7.596	0.002	0.595
Wk15to22	979	8755.2	1.6	-2.444±7.377	0.003	0.595
Wk13toWk20	979	8755.2	1.6	-2.397±7.392	0.003	0.595
Wk10toWk19	979	8755.2	1.6	-1.974±7.527	0.002	0.595
Wk13toWk21	979	8755.2	1.6	-1.605±7.614	0.001	0.595
Wk17to19	979	8755.2	1.6	-4.657±4.789	0.026	0.593
Wk9toWk18	979	8755.3	1.7	-0.733±7.607	0	0.595
Wk13toWk22	979	8755.3	1.7	-1.024±7.391	0.001	0.595
Wk14to24	979	8755.3	1.7	-2.015±7.140	0.002	0.593
Wk14toWk21	979	8755.4	1.8	-0.785±7.154	0	0.595
Wk12toWk19	979	8755.4	1.8	-0.871±7.069	0	0.595
Wk11toWk19	979	8755.4	1.8	-1.227±7.008	0.001	0.595
Wk18to22	979	8755.4	1.8	-2.098±6.733	0.003	0.595
Wk22to23	979	8755.4	1.8	-4.187±3.846	0.033	0.593
Wk21to24	979	8755.4	1.8	-3.849±5.332	0.015	0.596
Wk14toWk20	979	8755.5	1.9	-1.465±6.772	0.001	0.595
Wk14toWk22	979	8755.5	1.9	-0.323±6.884	0	0.595
Wk9toWk13	979	8755.5	1.9	-0.215±6.857	0	0.595
Wk18to21	979	8755.5	1.9	-2.765±6.125	0.006	0.595
Wk10toWk18	979	8755.5	1.9	-1.712±6.551	0.002	0.595
Wk13toWk19	979	8755.5	1.9	-1.331±6.513	0.001	0.595

Wk15to19	979	8755.6	2	-2.729±5.888	0.006	0.595
Wk16to19	979	8755.6	2	-3.542±4.959	0.014	0.594
Wk21to23	979	8755.6	2	-3.554±4.904	0.015	0.594
Wk10toWk17	979	8755.6	2	-0.431±6.368	0	0.595
Wk23to24	979	8755.7	2.1	-3.557±2.943	0.039	0.599
Wk2toWk3	979	8755.7	2.1	-3.652±3.836	0.025	0.594
Wk11toWk18	979	8755.7	2.1	-1.039±5.940	0.001	0.595
Wk17to18	979	8755.7	2.1	-3.591±3.386	0.03	0.593
Wk10toWk13	979	8755.7	2.1	-2.004±5.600	0.003	0.594
Wk12toWk18	979	8755.8	2.2	-0.752±5.919	0	0.595
Wk1toWk4	979	8755.8	2.2	-2.460±5.236	0.007	0.595
Wk14toWk19	979	8755.8	2.2	-0.522±5.797	0	0.595
Wk22to24	979	8755.8	2.2	-3.311±4.208	0.018	0.593
Wk17to17	979	8755.8	2.2	-3.416±3.184	0.03	0.592
Wk1toWk5	979	8755.9	2.3	-0.993±5.485	0.001	0.595
Wk13toWk18	979	8755.9	2.3	-1.105±5.366	0.001	0.595
Wk19to20	979	8755.9	2.3	-1.613±5.188	0.003	0.595
Wk10toWk12	979	8756	2.4	-1.181±5.255	0.001	0.595
Wk3toWk3	979	8756	2.4	-3.169±2.896	0.034	0.594
Wk15to18	979	8756	2.4	-2.255±4.721	0.006	0.594
Wk19to21	979	8756	2.4	-0.176±5.293	0	0.595
Wk18to19	979	8756.1	2.5	-2.443±4.280	0.009	0.594
Wk16to18	979	8756.1	2.5	-2.816±3.789	0.015	0.594
we20to20.y	979	8756.1	2.5	-2.336±4.205	0.009	0.594
Wk10toWk11	979	8756.1	2.5	-2.044±4.411	0.006	0.594
Wk10toWk10	979	8756.2	2.6	-2.233±4.235	0.008	0.594
Wk12toWk13	979	8756.2	2.6	-0.535±4.806	0	0.595
Wk14toWk18	979	8756.2	2.6	-0.462±4.718	0	0.595
Wk15to17	979	8756.3	2.7	-0.881±4.558	0.001	0.595
Wk11toWk13	979	8756.3	2.7	-0.899±4.527	0.001	0.595
Wk2toWk4	979	8756.3	2.7	-0.872±4.500	0.001	0.595
Wk1toWk2	979	8756.4	2.8	-2.254±3.582	0.012	0.594
Wk20to21	979	8756.4	2.8	-0.277±4.332	0	0.595
Wk16to17	979	8756.4	2.8	-2.016±3.646	0.009	0.594

Wk13toWk13	979	8756.5	2.9	-1.785±3.741	0.006	0.594
Wk11toWk12	979	8756.6	3	-0.042±3.983	0	0.595
Wk18to18	979	8756.7	3.1	-2.141±2.756	0.017	0.594
Wk3toWk4	979	8757	3.4	-0.055±3.201	0	0.595
Wk1toWk1	979	8757.2	3.6	-1.422±2.488	0.01	0.594
Wk11toWk11	979	8757.2	3.6	-0.681±2.825	0.002	0.595
Wk2toWk2	979	8757.2	3.6	-0.874±2.711	0.003	0.595
Wk24to24	979	8757.5	3.9	-0.240±2.512	0	0.595

Table S3.5d. *D.platanoidis* emergence phenology as a function of precipitation delaying emergence, weather variables selected as those with a negative coefficient from moving window approach which considered all consecutive weekly windows between Jan 1st and June 17th Models are mixed effects models with year and tree identity included in all models. Slopes reported with ± 1SE, ΔAICc given relative to best fitting model. Random effects only model AICc = 8759.12. Wk = Week.

***Denotes best model where used in stage two modelling.**

Time window (Week 1 = Jan 1st)	n	AICc	ΔAICc	Slope±1SE	$R^2GLMM_{(m)}$	R2GLMM$_{(c)}$
Wk5toWk8*	**979**	**8751.1**	**0**	**11.772±5.077**	**0.122**	**0.589**
Wk6toWk8	979	8751.3	0.2	10.332±4.420	0.122	0.588
Wk5toWk9	979	8751.8	0.7	10.933±5.171	0.104	0.589
Wk6toWk9	979	8752.2	1.1	9.548±4.616	0.099	0.589
Wk5toWk16	979	8752.4	1.3	14.630±9.054	0.063	0.59
Wk5toWk15	979	8752.4	1.3	14.048±8.514	0.064	0.589
Wk6toWk16	979	8752.4	1.3	14.502±9.124	0.061	0.59
Wk6toWk15	979	8752.4	1.3	13.940±8.549	0.062	0.589
Wk8toWk8	979	8752.4	1.3	6.989±3.148	0.114	0.589
Wk5toWk10	979	8752.5	1.4	11.048±6.080	0.078	0.589
Wk4toWk16	979	8752.6	1.5	13.071±8.201	0.061	0.59
Wk7toWk8	979	8752.8	1.7	7.418±3.607	0.1	0.59
Wk4toWk9	979	8752.8	1.7	8.967±4.763	0.087	0.591
Wk4toWk15	979	8752.8	1.7	12.009±7.591	0.059	0.589
Wk4toWk8	979	8752.9	1.8	8.517±4.505	0.088	0.591
Wk6toWk14	979	8752.9	1.8	12.079±8.052	0.053	0.59
Wk5toWk14	979	8752.9	1.8	11.989±7.960	0.055	0.59
Wk6toWk10	979	8753	1.9	9.564±5.567	0.07	0.589
Wk4toWk10	979	8753.1	2	9.267±5.489	0.071	0.591
Wk7toWk15	979	8753.1	2	11.599±8.297	0.049	0.591
Wk7toWk16	979	8753.2	2.1	11.744±8.778	0.047	0.592

Wk7toWk9	979	8753.2	2.1	7.490±4.043	0.082	0.59
Wk5toWk7	979	8753.3	2.2	8.623±5.118	0.07	0.591
Wk3toWk16	979	8753.3	2.2	11.335±8.844	0.042	0.592
Wk4toWk14	979	8753.3	2.2	10.250±7.062	0.051	0.59
Wk5toWk17	979	8753.3	2.2	11.505±9.430	0.037	0.592
Wk2toWk16	979	8753.4	2.3	11.480±9.571	0.037	0.592
Wk5toWk12	979	8753.4	2.3	9.811±6.828	0.05	0.59
Wk6toWk17	979	8753.4	2.3	11.155±9.553	0.034	0.592
Wk5toWk11	979	8753.5	2.4	9.450±6.425	0.053	0.591
Wk4toWk17	979	8753.5	2.4	10.632±8.496	0.039	0.591
Wk6toWk12	979	8753.5	2.4	9.674±6.788	0.048	0.59
Wk3toWk15	979	8753.5	2.4	10.255±8.160	0.04	0.592
Wk7toWk14	979	8753.5	2.4	10.069±7.854	0.042	0.592
Wk6toWk11	979	8753.6	2.5	9.084±6.273	0.051	0.59
Wk2toWk15	979	8753.6	2.5	10.273±8.811	0.035	0.592
Wk4toWk19	979	8753.6	2.5	10.350±9.764	0.028	0.592
Wk5toWk19	979	8753.6	2.5	10.326±10.679	0.024	0.593
Wk8toWk9	979	8753.7	2.6	6.689±3.816	0.075	0.59
Wk7toWk10	979	8753.7	2.6	7.936±5.222	0.056	0.59
Wk6toWk19	979	8753.7	2.6	9.665±10.848	0.021	0.593
Wk4toWk22	979	8753.7	2.6	9.743±10.286	0.024	0.593
Wk4toWk21	979	8753.8	2.7	9.717±10.184	0.024	0.593
Wk6toWk7	979	8753.8	2.7	7.071±4.306	0.067	0.591
Wk5toWk21	979	8753.8	2.7	9.456±11.067	0.019	0.593
Wk1toWk16	979	8753.8	2.7	9.613±9.817	0.025	0.593
Wk5toWk13	979	8753.8	2.7	9.149±7.405	0.038	0.591
Wk7toWk12	979	8753.8	2.7	8.884±6.895	0.041	0.591
Wk2toWk17	979	8753.8	2.7	9.418±10.044	0.023	0.593
Wk5toWk18	979	8753.8	2.7	9.351±9.868	0.023	0.593
Wk2toWk19	979	8753.8	2.7	8.802±11.491	0.016	0.594
Wk4to24	979	8753.8	2.7	8.993±11.201	0.017	0.598
Wk6toWk21	979	8753.9	2.8	8.814±11.282	0.016	0.594
Wk4toWk18	979	8753.9	2.8	9.219±8.967	0.027	0.592
Wk5toWk22	979	8753.9	2.8	8.909±10.809	0.018	0.594
Wk3toWk17	979	8753.9	2.8	9.156±9.186	0.026	0.593
Wk5toWk20	979	8753.9	2.8	8.822±10.828	0.017	0.593
Wk2to24	979	8753.9	2.8	7.884±12.462	0.011	0.598
Wk6toWk13	979	8753.9	2.8	8.800±7.392	0.035	0.591
Wk6toWk18	979	8753.9	2.8	8.918±10.094	0.02	0.593
Wk4toWk20	979	8753.9	2.8	8.963±9.838	0.021	0.593
Wk4toWk12	979	8753.9	2.8	8.119±5.979	0.046	0.591

Wk2toWk21	979	8753.9	2.8	8.057±11.776	0.013	0.594
Wk3toWk19	979	8753.9	2.8	8.680±10.539	0.018	0.593
Wk7toWk11	979	8753.9	2.8	8.215±6.295	0.042	0.591
Wk2toWk22	979	8753.9	2.8	7.915±11.652	0.013	0.594
Wk8toWk15	979	8753.9	2.8	8.794±8.136	0.031	0.593
Wk5to24	979	8753.9	2.8	7.883±11.756	0.012	0.598
Wk1toWk15	979	8753.9	2.8	8.816±9.167	0.024	0.593
Wk4toWk11	979	8754	2.9	7.785±5.634	0.048	0.591
Wk6toWk20	979	8754	2.9	8.136±11.044	0.014	0.594
Wk3toWk22	979	8754	2.9	8.138±10.972	0.015	0.594
Wk7toWk17	979	8754	2.9	8.704±9.236	0.024	0.593
Wk6toWk22	979	8754	2.9	8.152±10.892	0.015	0.594
Wk3toWk21	979	8754	2.9	8.120±10.940	0.015	0.594
Wk2toWk14	979	8754	2.9	8.503±8.201	0.028	0.593
Wk2toWk20	979	8754	2.9	7.341±11.495	0.011	0.594
Wk3toWk14	979	8754	2.9	8.374±7.504	0.032	0.592
Wk2toWk18	979	8754	2.9	7.823±10.588	0.015	0.594
Wk8toWk16	979	8754	2.9	8.395±8.390	0.027	0.593
Wk4to23	979	8754.1	3	7.105±11.382	0.011	0.594
Wk4toWk13	979	8754.1	3	7.908±6.503	0.037	0.592
Wk2toWk9	979	8754.1	3	7.721±6.135	0.043	0.593
Wk1toWk19	979	8754.1	3	6.615±11.480	0.009	0.594
Wk3to24	979	8754.1	3	6.122±11.914	0.007	0.596
Wk2to23	979	8754.1	3	4.446±12.713	0.003	0.595
Wk5to23	979	8754.1	3	5.671±12.075	0.006	0.594
Wk3toWk18	979	8754.1	3	7.749±9.712	0.017	0.593
Wk8toWk10	979	8754.1	3	7.347±5.503	0.044	0.591
Wk3toWk20	979	8754.1	3	7.246±10.510	0.012	0.594
Wk1toWk17	979	8754.1	3	7.479±10.148	0.014	0.594
Wk1toWk21	979	8754.1	3	6.007±11.709	0.007	0.594
Wk6to24	979	8754.1	3	6.001±11.696	0.007	0.597
Wk7toWk7	979	8754.1	3	6.049±3.786	0.065	0.591
Wk1toWk22	979	8754.2	3.1	5.982±11.574	0.007	0.594
Wk1to24	979	8754.2	3.1	4.742±12.328	0.004	0.596
Wk6to23	979	8754.2	3.1	4.482±12.174	0.004	0.595
Wk7toWk19	979	8754.2	3.1	6.880±10.399	0.012	0.594
Wk3to23	979	8754.2	3.1	4.923±11.932	0.005	0.595
Wk7toWk21	979	8754.2	3.1	6.313±10.932	0.009	0.594
Wk2toWk10	979	8754.2	3.1	7.659±6.817	0.034	0.593
Wk1toWk9	979	8754.2	3.1	7.637±7.094	0.032	0.593
Wk1toWk14	979	8754.2	3.1	7.524±8.737	0.02	0.593

Wk1to23	979	8754.2	3.1	2.570±12.532	0.001	0.595
Wk1toWk20	979	8754.2	3.1	5.287±11.383	0.006	0.594
Wk8toWk14	979	8754.2	3.1	7.597±7.818	0.025	0.593
Wk1toWk18	979	8754.3	3.2	5.995±10.704	0.008	0.594
Wk7toWk20	979	8754.3	3.2	5.745±10.811	0.008	0.594
Wk2toWk8	979	8754.3	3.2	7.230±6.059	0.039	0.593
Wk7toWk13	979	8754.3	3.2	7.339±7.352	0.026	0.593
Wk7toWk22	979	8754.3	3.2	5.742±10.375	0.009	0.594
Wk3toWk9	979	8754.3	3.2	6.690±5.128	0.046	0.593
Wk7toWk18	979	8754.4	3.3	6.308±9.633	0.012	0.594
Wk7to24	979	8754.4	3.3	4.088±11.167	0.004	0.597
Wk8toWk12	979	8754.4	3.3	7.093±7.155	0.025	0.593
Wk7to23	979	8754.4	3.3	1.979±11.669	0.001	0.595
Wk1toWk10	979	8754.4	3.3	7.029±7.604	0.023	0.593
Wk1toWk8	979	8754.4	3.3	7.046±7.129	0.027	0.594
Wk2toWk12	979	8754.5	3.4	6.791±7.179	0.024	0.593
Wk3toWk10	979	8754.5	3.4	6.623±5.725	0.036	0.593
Wk3toWk8	979	8754.5	3.4	6.282±4.981	0.043	0.593
Wk8toWk11	979	8754.5	3.4	6.534±6.551	0.026	0.593
Wk8toWk21	979	8754.6	3.5	3.162±10.387	0.003	0.595
Wk2toWk13	979	8754.6	3.5	6.251±7.589	0.018	0.594
Wk2toWk11	979	8754.6	3.5	6.421±6.860	0.024	0.594
Wk1toWk12	979	8754.6	3.5	6.090±7.823	0.016	0.594
Wk8toWk20	979	8754.6	3.5	2.498±10.253	0.002	0.595
Wk8toWk19	979	8754.6	3.5	3.529±9.800	0.004	0.595
Wk4toWk7	979	8754.6	3.5	5.611±4.124	0.048	0.592
Wk8to24	979	8754.6	3.5	1.414±10.345	0.001	0.595
Wk8toWk17	979	8754.6	3.5	5.255±8.576	0.01	0.594
Wk8toWk22	979	8754.6	3.5	3.074±9.883	0.003	0.595
Wk3toWk12	979	8754.7	3.6	6.203±6.264	0.026	0.593
Wk1toWk13	979	8754.7	3.6	5.476±8.216	0.012	0.594
Wk1toWk11	979	8754.7	3.6	5.776±7.564	0.016	0.594
Wk3toWk13	979	8754.7	3.6	6.020±6.798	0.021	0.593
Wk8toWk13	979	8754.8	3.7	5.169±7.545	0.012	0.594
Wk3toWk11	979	8754.8	3.7	5.732±5.875	0.026	0.593
Wk8toWk18	979	8754.8	3.7	3.052±8.837	0.003	0.595
Wk9toWk16	979	8755.1	4	3.189±7.387	0.005	0.594
Wk9toWk15	979	8755.1	4	3.351±7.223	0.006	0.594
Wk1toWk7	979	8755.3	4.2	3.218±6.679	0.007	0.595
Wk2toWk7	979	8755.3	4.2	4.104±5.751	0.015	0.594
Wk9toWk17	979	8755.3	4.2	0.886±7.386	0	0.595

Wk9toWk14	979	8755.3	4.2	2.223±6.971	0.003	0.595
Wk5toWk6	979	8755.5	4.4	4.058±3.984	0.028	0.593
Wk9toWk12	979	8755.5	4.4	1.125±6.600	0.001	0.595
Wk10toWk16	979	8755.6	4.5	1.357±6.394	0.001	0.595
Wk3toWk7	979	8755.6	4.5	3.674±4.589	0.018	0.594
Wk10toWk15	979	8755.7	4.6	1.331±6.111	0.001	0.595
Wk9toWk10	979	8755.8	4.7	1.767±5.692	0.003	0.595
Wk9toWk11	979	8755.8	4.7	0.277±5.954	0	0.595
Wk12toWk16	979	8755.8	4.7	2.454±5.253	0.006	0.595
Wk10toWk14	979	8755.8	4.7	0.288±5.859	0	0.595
Wk11toWk16	979	8755.8	4.7	1.822±5.538	0.003	0.595
Wk19to22	979	8755.8	4.7	0.349±5.728	0	0.595
Wk12toWk12	979	8755.8	4.7	2.198±5.225	0.005	0.594
Wk1toWk6	979	8755.8	4.7	0.692±5.676	0	0.595
Wk9toWk9	979	8755.8	4.7	3.391±3.747	0.022	0.594
Wk11toWk17	979	8755.9	4.8	0.173±5.685	0	0.595
Wk12toWk17	979	8755.9	4.8	0.639±5.590	0	0.595
Wk12toWk15	979	8755.9	4.8	2.505±4.844	0.007	0.594
Wk11toWk15	979	8755.9	4.8	1.793±5.149	0.003	0.595
Wk2toWk6	979	8756	4.9	1.708±4.891	0.004	0.595
Wk20to22	979	8756	4.9	0.287±5.196	0	0.595
Wk4toWk6	979	8756	4.9	3.076±3.261	0.024	0.593
Wk12toWk14	979	8756.1	5	1.806±4.640	0.004	0.595
Wk13toWk17	979	8756.1	5	0.213±4.977	0	0.595
Wk13toWk16	979	8756.1	5	1.846±4.510	0.005	0.595
Wk14toWk15	979	8756.2	5.1	2.835±3.419	0.019	0.594
Wk11toWk14	979	8756.2	5.1	0.939±4.773	0.001	0.595
Wk15to15	979	8756.2	5.1	2.568±3.824	0.013	0.594
Wk5toWk5	979	8756.2	5.1	2.640±3.678	0.015	0.594
Wk2toWk5	979	8756.2	5.1	0.337±4.708	0	0.595
Wk14toWk16	979	8756.3	5.2	2.352±3.771	0.011	0.594
Wk13toWk15	979	8756.3	5.2	1.936±4.101	0.006	0.595
Wk15to16	979	8756.3	5.2	1.691±4.202	0.005	0.595
Wk14toWk17	979	8756.4	5.3	0.791±4.324	0.001	0.595
Wk4toWk5	979	8756.4	5.3	2.473±2.989	0.019	0.594
Wk3toWk6	979	8756.4	5.3	1.725±3.799	0.006	0.595
Wk6toWk6	979	8756.5	5.4	2.412±2.809	0.021	0.594
Wk13toWk14	979	8756.6	5.5	1.173±3.706	0.003	0.595
Wk21to22	979	8756.6	5.5	1.116±3.706	0.003	0.595
Wk3toWk5	979	8756.7	5.6	0.810±3.680	0.001	0.595
Wk14toWk14	979	8756.7	5.6	2.130±2.636	0.019	0.594

Wk19to19	979	8756.7	5.6	0.144±3.661	0	0.595
Wk21to21	979	8757	5.9	0.958±3.080	0.003	0.595
Wk4toWk4	979	8757.1	6	1.736±2.210	0.017	0.594
Wk16to16	979	8757.1	6	0.169±3.014	0	0.595
Wk22to22	979	8757.6	6.5	0.343±2.364	0.001	0.595

Periphylus testudinaceus phenology

Table S3.6a. *P.testudinaceus* emergence phenology as a function of temperature advancing emergence, weather variables selected as those with a negative coefficient from moving window approach which considered all consecutive weekly windows between Jan 1st and June 10th Models are mixed effects models with year and tree identity included in all models. Slopes reported with ± 1SE, ΔAICc given relative to best fitting model. Random effects only model AICc = 8334.614. Wk = Week.

***Denotes best model where used in stage two modelling.**

Time window (Week 1 = Jan 1st)	n	AICc	ΔAICc	Slope±1SE	R^2GLMM$_{(m)}$	R2GLMM$_{(c)}$
wk13towk17*	**968**	**8327.9**	**0**	**-5.144±2.119**	**0.058**	**0.27**
wk13towk18	968	8328.6	0.7	-4.661±2.045	0.053	0.271
wk15to18	968	8328.6	0.7	-4.218±1.797	0.055	0.27
Wk19to19	968	8328.7	0.8	-3.419±1.396	0.056	0.267
wk16to18	968	8329	1.1	-3.819±1.681	0.053	0.27
wk17to17	968	8329.1	1.2	-3.772±1.682	0.052	0.271
wk15to17	968	8329.1	1.2	-3.750±1.677	0.05	0.27
wk13towk16	968	8329.4	1.5	-4.184±2.034	0.046	0.272
wk12towk17	968	8329.6	1.7	-5.015±2.773	0.037	0.273
wk12towk18	968	8329.9	2	-4.469±2.523	0.035	0.273
wk14towk18	968	8330	2.1	-3.626±1.884	0.041	0.272
wk17to18	968	8330	2.1	-3.343±1.694	0.042	0.272
wk13towk19	968	8330.1	2.2	-3.800±2.078	0.038	0.273
wk14towk17	968	8330.1	2.2	-3.545±1.875	0.039	0.272
wk16to17	968	8330.1	2.2	-2.954±1.451	0.044	0.271
wk11towk17	968	8330.2	2.3	-4.428±2.698	0.031	0.273
wk15to19	968	8330.2	2.3	-3.560±1.933	0.038	0.272

wk11towk18	968	8330.5	2.6	-3.967±2.462	0.03	0.273
wk12towk19	968	8330.7	2.8	-3.880±2.563	0.027	0.274
wk13to23	968	8330.9	3	-3.858±2.820	0.023	0.274
wk12towk16	968	8331	3.1	-3.689±2.713	0.022	0.274
wk15to16	968	8331	3.1	-2.558±1.443	0.035	0.273
wk9towk17	968	8331.1	3.2	-3.578±2.715	0.021	0.275
wk11towk19	968	8331.1	3.2	-3.429±2.466	0.023	0.274
wk15to23	968	8331.1	3.2	-3.639±2.872	0.02	0.275
wk13towk22	968	8331.1	3.2	-3.460±2.548	0.023	0.275
wk9towk18	968	8331.1	3.2	-3.445±2.536	0.023	0.275
wk14towk19	968	8331.1	3.2	-2.990±1.932	0.028	0.274
wk15to22	968	8331.1	3.2	-3.471±2.636	0.021	0.275
wk10towk17	968	8331.2	3.3	-3.471±2.878	0.018	0.275
wk12to23	968	8331.2	3.3	-3.560±3.234	0.015	0.275
wk13towk21	968	8331.3	3.4	-3.185±2.339	0.023	0.274
wk11towk16	968	8331.3	3.4	-3.330±2.624	0.02	0.275
wk10towk18	968	8331.3	3.4	-3.325±2.630	0.02	0.275
wk16to19	968	8331.3	3.4	-2.722±1.742	0.029	0.274
wk15to21	968	8331.4	3.5	-3.016±2.329	0.02	0.274
wk12towk22	968	8331.5	3.6	-3.174±2.926	0.015	0.275
wk14to23	968	8331.5	3.6	-3.113±2.736	0.016	0.275
wk11to23	968	8331.5	3.6	-3.149±3.026	0.014	0.275
wk8towk18	968	8331.5	3.6	-2.989±2.407	0.019	0.275
wk9towk19	968	8331.6	3.7	-2.967±2.495	0.018	0.275
wk8towk17	968	8331.6	3.7	-2.967±2.515	0.017	0.275
wk12towk21	968	8331.6	3.7	-2.988±2.737	0.015	0.275
wk14towk16	968	8331.6	3.7	-2.496±1.696	0.026	0.274
wk13towk15	968	8331.6	3.7	-2.577±1.848	0.024	0.274
wk14towk22	968	8331.7	3.8	-2.810±2.466	0.016	0.275
wk11towk22	968	8331.7	3.8	-2.8362.761	0.014	0.275
wk10towk19	968	8331.7	3.8	-2.797±2.568	0.015	0.275
wk9to23	968	8331.8	3.9	-2.759±2.963	0.011	0.275

wk9towk16	968	8331.8	3.9	-2.727±2.646	0.014	0.275
wk13towk20	968	8331.8	3.9	-2.605±2.129	0.019	0.275
wk11towk21	968	8331.8	3.9	-2.697±2.603	0.014	0.275
wk16to23	968	8331.8	3.9	-2.696±2.704	0.013	0.275
wk8towk19	968	8331.8	3.9	-2.623±2.374	0.016	0.275
wk14towk21	968	8331.9	4	-2.554±2.242	0.016	0.275
wk10to23	968	8331.9	4	-2.474±3.041	0.009	0.276
wk16to22	968	8331.9	4	-2.549±2.454	0.014	0.275
wk8to23	968	8332	4.1	-2.485±2.798	0.01	0.276
wk9towk22	968	8332	4.1	-2.493±2.723	0.011	0.276
wk10towk16	968	8332	4.1	-2.453±2.828	0.01	0.276
wk13towk13	968	8332	4.1	-2.034±1.376	0.027	0.275
wk12towk20	968	8332	4.1	-2.414±2.528	0.012	0.276
wk9towk21	968	8332	4.1	-2.402±2.600	0.011	0.276
wk3towk3	968	8332	4.1	-1.596±0.915	0.036	0.274
wk10towk22	968	8332.1	4.2	-2.261±2.802	0.009	0.276
wk7towk18	968	8332.1	4.2	-2.317±2.523	0.011	0.276
wk8towk22	968	8332.1	4.2	-2.248±2.579	0.01	0.276
wk15to20	968	8332.2	4.3	-2.253±2.035	0.015	0.275
wk11towk20	968	8332.2	4.3	-2.242±2.429	0.011	0.276
wk8towk16	968	8332.2	4.3	-2.235±2.407	0.011	0.276
wk7towk17	968	8332.2	4.3	-2.162±2.636	0.009	0.276
wk10towk21	968	8332.2	4.3	-2.142±2.651	0.009	0.276
wk8towk21	968	8332.2	4.3	-2.183±2.475	0.01	0.276
wk16to21	968	8332.3	4.4	-2.146±2.121	0.013	0.275
wk7to23	968	8332.3	4.4	-1.858±2.846	0.006	0.276
wk7towk19	968	8332.3	4.4	-2.010±2.456	0.009	0.276
wk9towk20	968	8332.3	4.4	-2.009±2.439	0.009	0.276
wk16to16	968	8332.4	4.5	-1.647±1.085	0.027	0.274
wk14towk20	968	8332.4	4.5	-1.989±2.003	0.013	0.275
wk17to23	968	8332.4	4.5	-1.649±2.698	0.005	0.276
wk7towk22	968	8332.5	4.6	-1.699±2.640	0.006	0.276

wk8towk20	968	8332.5	4.6	-1.860±2.337	0.008	0.276
wk10towk20	968	8332.5	4.6	-1.734±2.478	0.006	0.276
wk7towk21	968	8332.5	4.6	-1.628±2.532	0.005	0.276
wk15to15	968	8332.5	4.6	-1.752±1.373	0.02	0.274
wk21to23	968	8332.5	4.6	-1.440±2.683	0.004	0.276
wk17to19	968	8332.6	4.7	-1.832±1.636	0.016	0.275
wk6to23	968	8332.6	4.7	-0.997±2.827	0.002	0.276
wk7towk16	968	8332.6	4.7	-1.461±2.521	0.005	0.276
wk1to23	968	8332.6	4.7	-1.212±2.694	0.003	0.276
wk6towk18	968	8332.7	4.8	-1.320±2.553	0.004	0.276
wk2to23	968	8332.7	4.8	-1.052±2.676	0.002	0.276
wk12towk15	968	8332.7	4.8	-1.457±2.348	0.005	0.276
wk6towk17	968	8332.7	4.8	-1.012±2.645	0.002	0.276
wk2towk18	968	8332.7	4.8	-1.294±2.463	0.004	0.276
wk11towk15	968	8332.7	4.8	-1.496±2.264	0.006	0.276
wk17to22	968	8332.7	4.8	-1.425±2.322	0.005	0.276
wk9towk15	968	8332.7	4.8	-1.383±2.362	0.005	0.276
wk7towk20	968	8332.8	4.9	-1.341±2.394	0.004	0.276
wk6towk22	968	8332.8	4.9	-0.918±2.636	0.002	0.276
wk3to23	968	8332.8	4.9	-0.835±2.646	0.001	0.276
wk2towk17	968	8332.8	4.9	-1.076±2.513	0.002	0.276
wk2towk22	968	8332.8	4.9	-1.001±2.549	0.002	0.276
wk6towk19	968	8332.8	4.9	-1.133±2.457	0.003	0.276
wk5to23	968	8332.8	4.9	-0.321±2.696	0	0.276
wk4to23	968	8332.8	4.9	-0.309±2.677	0	0.276
wk2towk19	968	8332.9	5	-1.139±2.380	0.003	0.276
wk6towk21	968	8332.9	5	-0.855±2.518	0.002	0.276
wk10towk15	968	8332.9	5	-0.865±2.508	0.002	0.276
wk3towk18	968	8332.9	5	-1.049±2.411	0.003	0.276
wk3towk22	968	8332.9	5	-0.788±2.509	0.001	0.276
wk2towk21	968	8332.9	5	-0.939±2.443	0.002	0.276
wk2towk4	968	8332.9	5	-1.550±1.353	0.017	0.275

wk3towk17	968	8332.9	5	-0.809±2.466	0.001	0.276
wk8towk15	968	8332.9	5	-1.241±2.169	0.004	0.276
wk2towk16	968	8332.9	5	-0.676±2.472	0.001	0.276
wk6towk16	968	8332.9	5	-0.395±2.533	0	0.276
wk5towk22	968	8333	5.1	-0.299±2.533	0	0.276
wk18to23	968	8333	5.1	-0.525±2.488	0.001	0.276
wk3towk19	968	8333	5.1	-0.931±2.342	0.002	0.276
wk4towk22	968	8333	5.1	-0.288±2.519	0	0.276
wk3towk21	968	8333	5.1	-0.737±2.406	0.001	0.276
wk3towk4	968	8333	5.1	-1.478±1.291	0.017	0.275
wk16to20	968	8333	5.1	-1.452±1.782	0.009	0.276
wk5towk17	968	8333	5.1	-0.157±2.481	0	0.276
wk5towk18	968	8333	5.1	-0.508±2.425	0.001	0.276
wk4towk17	968	8333	5.1	-0.155±2.474	0	0.276
wk4towk18	968	8333	5.1	-0.484±2.428	0.001	0.276
wk2towk20	968	8333	5.1	-0.755±2.335	0.001	0.276
wk6towk20	968	8333	5.1	-0.616±2.371	0.001	0.276
wk3towk16	968	8333	5.1	-0.389±2.406	0	0.276
wk1towk15	968	8333	5.1	-0.387±2.406	0	0.276
wk21to21	968	8333	5.1	-1.432±1.649	0.01	0.275
wk4towk21	968	8333.1	5.2	-0.251±2.412	0	0.276
wk5towk21	968	8333.1	5.2	-0.258±2.411	0	0.276
wk4towk19	968	8333.1	5.2	-0.427±2.355	0	0.276
wk5towk19	968	8333.1	5.2	-0.445±2.350	0	0.276
wk3towk20	968	8333.1	5.2	-0.558±2.295	0.001	0.276
wk17to21	968	8333.1	5.2	-1.164±1.972	0.005	0.276
wk7towk15	968	8333.1	5.2	-0.588±2.278	0.001	0.276
wk2towk15	968	8333.1	5.2	-0.161±2.344	0	0.276
wk13towk14	968	8333.1	5.2	-1.397±1.495	0.011	0.276
wk2towk3	968	8333.1	5.2	-1.294±1.005	0.021	0.275
wk1towk4	968	8333.2	5.3	-1.379±1.326	0.014	0.275
wk4towk20	968	8333.2	5.3	-0.084±2.292	0	0.276

wk5towk20	968	8333.2	5.3	-0.080±2.275	0	0.276
wk22to23	968	8333.2	5.3	-0.212±2.237	0	0.276
wk1towk14	968	8333.2	5.3	-0.053±2.243	0	0.276
wk18to18	968	8333.2	5.3	-1.324±1.191	0.016	0.275
wk21to22	968	8333.3	5.4	-1.037±1.857	0.004	0.276
wk9towk14	968	8333.3	5.4	-0.618±2.083	0.001	0.276
wk11towk13	968	8333.3	5.4	-0.497±2.094	0.001	0.276
wk7towk14	968	8333.3	5.4	-0.089±2.096	0	0.276
wk8towk14	968	8333.3	5.4	-0.680±1.969	0.002	0.276
wk18to22	968	8333.4	5.5	-0.421±2.033	0.001	0.276
wk14towk15	968	8333.4	5.5	-1.193±1.456	0.009	0.276
wk9towk13	968	8333.4	5.5	-0.488±1.986	0.001	0.276
wk11towk14	968	8333.4	5.5	-0.550±1.956	0.001	0.276
wk8towk13	968	8333.4	5.5	-0.601±1.907	0.001	0.276
wk12towk14	968	8333.5	5.6	-0.223±1.919	0	0.276
wk1towk9	968	8333.5	5.6	-0.075±1.925	0	0.276
wk1towk3	968	8333.5	5.6	-1.126±1.039	0.015	0.275
wk17to20	968	8333.7	5.8	-0.628±1.608	0.002	0.276
wk18to21	968	8333.7	5.8	-0.307±1.703	0	0.276
wk8towk12	968	8333.7	5.8	-0.016±1.718	0	0.276
wk1towk5	968	8333.9	6	-0.641±1.421	0.003	0.276
wk2towk5	968	8334	6.1	-0.499±1.424	0.002	0.276
wk18to19	968	8334	6.1	-0.726±1.276	0.004	0.276
wk8towk11	968	8334.1	6.2	-0.492±1.372	0.002	0.276
wk7towk9	968	8334.1	6.2	-0.133±1.425	0	0.276
wk9towk11	968	8334.1	6.2	-0.415±1.361	0.001	0.276
wk22to22	968	8334.1	6.2	-0.169±1.410	0	0.276
wk8towk9	968	8334.2	6.3	-0.757±1.084	0.006	0.276
wk8towk10	968	8334.2	6.3	-0.364±1.296	0.001	0.276
wk3towk5	968	8334.3	6.4	-0.147±1.297	0	0.276
wk9towk9	968	8334.3	6.4	-0.751±0.905	0.009	0.275
wk11towk11	968	8334.3	6.4	-0.520±1.148	0.003	0.276

wk9towk10	968	8334.4	6.5	-0.208±1.223	0	0.276
wk8towk8	968	8334.5	6.6	-0.432±1.075	0.002	0.276
wk4towk4	968	8334.7	6.8	-0.026±1.067	0	0.276
wk14towk14	968	8334.7	6.8	-0.240±1.011	0.001	0.276
wk1towk2	968	8334.7	6.8	-0.507±0.872	0.005	0.276
wk2towk2	968	8334.9	7	-0.477±0.809	0.005	0.276
wk19to19	968	8335.2	7.3	-0.001±0.847	0	0.276
wk1towk1	968	8335.2	7.3	-0.328±0.741	0.003	0.276

Table S3.6b. *P.testudinaceus* emergence phenology as a function of temperature delaying emergence, weather variables selected as those with a positive coefficient from moving window approach which considered all consecutive weekly windows between Jan 1st and June 10th Models are mixed effects models with year and tree identity included in all models. Slopes reported with ± 1SE, ΔAICc given relative to best fitting model. Random effects only model AICc = 8334.614. Wk = Week.

***Denotes best model where used in stage two modelling.**

Time window (Week 1 = Jan 1st)	n	AICc	ΔAICc	Slope±1SE	R^2GLMM$_{(m)}$	R2GLMM$_{(c)}$
wk6towk7*	**968**	**8332**	**0**	**1.799±1.086**	**0.033**	**0.274**
wk5towk7	968	8332	0	1.763±1.066	0.033	0.274
wk4towk7	968	8332.3	0.3	1.838±1.282	0.026	0.275
wk12towk12	968	8332.3	0.3	1.825±1.272	0.023	0.273
wk5towk8	968	8332.5	0.5	1.734±1.313	0.022	0.275
wk4towk8	968	8332.7	0.7	1.728±1.485	0.018	0.275
wk20to23	968	8332.7	0.7	0.747±2.842	0.001	0.276
wk5towk12	968	8332.7	0.7	1.753±1.824	0.012	0.276
wk7towk7	968	8332.8	0.8	1.510±1.139	0.022	0.274
wk4towk12	968	8332.8	0.8	1.603±1.865	0.01	0.276
wk6towk12	968	8332.9	0.9	1.471±1.953	0.008	0.276
wk5towk10	968	8332.9	0.9	1.560±1.621	0.012	0.275
wk5towk13	968	8332.9	0.9	1.407±2.011	0.007	0.276
wk6towk8	968	8332.9	0.9	1.513±1.367	0.016	0.275

wk4towk13	968	8333	1	1.281±2.035	0.005	0.276
wk4towk10	968	8333	1	1.454±1.705	0.01	0.276
wk10towk12	968	8333	1	1.376±1.805	0.008	0.276
wk5towk16	968	8333.1	1.1	0.339±2.385	0	0.276
wk4towk16	968	8333.1	1.1	0.304±2.387	0	0.276
wk20to22	968	8333.1	1.1	0.642±2.282	0.001	0.276
wk19to23	968	8333.1	1.1	0.401±2.337	0	0.276
wk6towk13	968	8333.1	1.1	0.946±2.127	0.003	0.276
wk5towk6	968	8333.1	1.1	1.220±0.858	0.026	0.275
wk5towk9	968	8333.1	1.1	1.397±1.550	0.011	0.276
wk5towk15	968	8333.1	1.1	0.837±2.159	0.002	0.276
wk5towk14	968	8333.1	1.1	1.115±1.973	0.004	0.276
wk4towk15	968	8333.1	1.1	0.771±2.178	0.002	0.276
wk4towk9	968	8333.2	1.2	1.321±1.667	0.009	0.276
wk6towk15	968	8333.2	1.2	0.295±2.280	0	0.276
wk4towk14	968	8333.2	1.2	1.026±1.997	0.004	0.276
wk1towk13	968	8333.2	1.2	0.034±2.279	0	0.276
wk2towk13	968	8333.2	1.2	0.284±2.243	0	0.276
wk3towk15	968	8333.2	1.2	0.119±2.252	0	0.276
wk3towk12	968	8333.2	1.2	0.951±1.998	0.003	0.276
wk3towk13	968	8333.2	1.2	0.587±2.150	0.001	0.276
wk2towk12	968	8333.2	1.2	0.656±2.093	0.001	0.276
wk6towk14	968	8333.2	1.2	0.686±2.077	0.002	0.276
wk2towk14	968	8333.3	1.3	0.163±2.186	0	0.276
wk10towk13	968	8333.3	1.3	0.312±2.161	0	0.276
wk1towk12	968	8333.3	1.3	0.401±2.144	0	0.276
wk10towk14	968	8333.3	1.3	0.032±2.180	0	0.276

wk5towk11	968	8333.3	1.3	1.175±1.633	0.007	0.276
wk3towk14	968	8333.3	1.3	0.423±2.090	0.001	0.276
wk6towk10	968	8333.3	1.3	1.140±1.668	0.006	0.276
wk4towk6	968	8333.3	1.3	1.239±1.083	0.017	0.275
wk6towk6	968	8333.3	1.3	1.108±0.794	0.024	0.274
wk4towk11	968	8333.3	1.3	1.091±1.694	0.006	0.276
wk7towk13	968	8333.3	1.3	0.044±2.095	0	0.276
wk7towk12	968	8333.4	1.4	0.640±1.923	0.002	0.276
wk20to21	968	8333.4	1.4	0.774±1.838	0.002	0.276
wk3towk10	968	8333.4	1.4	0.740±1.841	0.002	0.276
wk3towk7	968	8333.5	1.5	1.097±1.496	0.007	0.276
wk1towk10	968	8333.5	1.5	0.164±1.967	0	0.276
wk2towk10	968	8333.5	1.5	0.419±1.925	0.001	0.276
wk1towk11	968	8333.5	1.5	0.012±1.956	0	0.276
wk3towk8	968	8333.5	1.5	0.929±1.651	0.004	0.276
wk12towk13	968	8333.5	1.5	0.097±1.938	0	0.276
wk2towk11	968	8333.5	1.5	0.226±1.901	0	0.276
wk2towk9	968	8333.6	1.6	0.181±1.879	0	0.276
wk3towk11	968	8333.6	1.6	0.492±1.813	0.001	0.276
wk6towk11	968	8333.6	1.6	0.768±1.686	0.003	0.276
wk3towk9	968	8333.6	1.6	0.519±1.793	0.001	0.276
wk6towk9	968	8333.6	1.6	0.889±1.587	0.004	0.276
wk19to22	968	8333.6	1.6	0.312±1.842	0	0.276
wk11towk12	968	8333.6	1.6	0.821±1.614	0.003	0.276
wk2towk8	968	8333.6	1.6	0.553±1.725	0.001	0.276
wk1towk8	968	8333.6	1.6	0.277±1.777	0	0.276

wk9towk12	968	8333.7	1.7	0.264±1.753	0	0.276
wk2towk7	968	8333.7	1.7	0.700±1.581	0.003	0.276
wk1towk7	968	8333.8	1.8	0.407±.628	0.001	0.276
we20to20	968	8333.8	1.8	0.982±0.985	0.013	0.276
wk7towk11	968	8333.9	1.9	0.010±1.591	0	0.276
wk7towk10	968	8333.9	1.9	0.248±1.555	0	0.276
wk1towk6	968	8334	2	0.005±1.536	0	0.276
wk5towk5	968	8334	2	0.884±0.769	0.017	0.275
wk2towk6	968	8334	2	0.266±1.480	0	0.276
wk10towk10	968	8334	2	0.817±1.145	0.007	0.276
wk7towk8	968	8334	2	0.616±1.330	0.003	0.276
wk19to21	968	8334	2	0.316±1.447	0.001	0.276
wk3towk6	968	8334.1	2.1	0.588±1.327	0.003	0.276
wk4towk5	968	8334.1	2.1	0.810±1.071	0.008	0.276
wk10towk11	968	8334.2	2.2	0.206±1.382	0	0.276
wk18to20	968	8334.3	2.3	0.048±1.318	0	0.276
wk23to23	968	8334.5	2.5	0.000±1.199	0	0.276
wk19to20	968	8334.6	2.6	0.480±0.995	0.003	0.276

Table S3.6c. *P.testudinaceus* emergence phenology as a function of precipitation advancing emergence, weather variables selected as those with a negative coefficient from moving window approach which considered all consecutive weekly windows between Jan 1st and June 10th Models are mixed effects models with year and tree identity included in all models. Slopes reported with ± 1SE, ΔAICc given relative to best fitting model. Random effects only model AICc = 8334.614. Wk = Week.

Time window (Week 1 = Jan 1st)	n	AICc	ΔAICc	Slope±1SE	R^{2}GLMM$_{(m)}$	R2GLMM$_{(c)}$
Wk19to19*	**968**	**8328.7**	**0**	**-3.419±1.396**	**0.056**	**0.267**
Wk2toWk3	968	8328.9	**0.2**	-3.545±1.508	0.059	0.272
Wk1toWk3*	968	8329.6	**0.9**	-3.714±1.800	0.047	0.273
Wk18to19	968	8330.7	**2**	-3.060±1.753	0.035	0.273
Wk3toWk3	968	8331.1	**2.4**	-2.227±1.203	0.04	0.274
Wk18to20	968	8331.5	**2.8**	-2.999±2.489	0.018	0.274
Wk19to20	968	8331.9	**3.2**	-2.508±2.209	0.016	0.274
Wk18to21	968	8332.2	**3.5**	-2.207±2.654	0.009	0.276

Wk18to22	968	8332.1	**3.4**	-2.147±2.923	0.007	0.276
Wk17to22	968	8332.3	**3.6**	-0.764±3.354	0.001	0.276
Wk1toWk2	968	8332.4	**3.7**	-1.876±1.526	0.02	0.275
Wk17to21	968	8332.6	**3.9**	-0.716±3.012	0.001	0.276
Wk9toWk10	968	8332.6	**3.9**	-1.459±2.485	0.004	0.276
Wk2toWk2	968	8332.7	**4**	-1.551±1.135	0.024	0.275
Wk19to21	968	8332.7	**4**	-1.483±2.298	0.006	0.276
Wk19to22	968	8332.7	**4**	-1.325±2.498	0.004	0.276
Wk17to20	968	8332.7	**4**	-0.953±2.673	0.002	0.276
Wk8toWk10	968	8332.8	**4.1**	-1.108±2.521	0.003	0.276
Wk17to19	968	8332.9	**4.2**	-1.377±2.131	0.006	0.276
Wk7toWk10	968	8332.9	**4.2**	-1.005±2.425	0.002	0.276
Wk10toWk10	968	8333	**4.3**	-1.414±1.844	0.008	0.276
Wk1toWk4	968	8333	**4.3**	-0.905±2.303	0.002	0.276
Wk16to19	968	8333.2	**4.5**	-0.345±2.205	0	0.276
Wk2toWk4	968	8333.4	**4.7**	-0.365±1.975	0	0.276
Wk7toWk9	968	8333.5	**4.8**	-0.344±1.935	0	0.276
Wk7toWk7	968	8333.6	**4.9**	-0.504±1.772	0.001	0.276
Wk7toWk8	968	8333.7	**5**	-0.331±1.758	0	0.276
Wk8toWk9	968	8333.6	**4.9**	-0.189±1.812	0	0.276
Wk9toWk9	968	8333.8	**5.1**	-0.174±1.681	0	0.276
Wk13toWk13	968	8333.8	**5.1**	-0.056±1.652	0	0.276
Wk8toWk8	968	8333.9	**5.2**	-0.131±1.559	0	0.276
Wk18to18	968	8334.2	**5.5**	-0.580±1.222	0.003	0.276
Wk1toWk1	968	8334.4	**5.7**	-0.481±1.096	0.003	0.276
Wk22to22	968	8334.7	**6**	-0.014±1.038	0	0.276

Table S3.6d. *P.testudinaceus* emergence phenology as a function of precipitation delaying emergence, weather variables selected as those with a positive coefficient from moving window approach which considered all consecutive weekly windows between Jan 1st and , June 10th Models are mixed effects models with year and tree identity included in all models. Slopes reported with ± 1SE, ΔAICc given relative to best fitting model. Random effects only model AICc = 8334.614. Wk = Week.

Time window (Week 1 = Jan 1st)	n	AICc	ΔAICc	Slope±1SE	R^2GLMM$_{(m)}$	R2GLMM$_{(c)}$
Wk4toWk17*	**968**	**8325.7**	**0**	**9.031±3.253**	**0.073**	**0.27**
Wk4toWk16	968	8326.3	0.6	8.597±3.268	0.068	0.27
Wk4toWk18	968	8326.6	0.9	8.731±3.490	0.063	0.271
Wk5toWk17	968	8327	1.3	8.942±3.756	0.058	0.271

Wk4toWk15	968	8327.4	1.7	7.328±3.107	0.057	0.271
Wk3toWk17	968	8327.7	2	8.090±3.676	0.052	0.272
Wk5toWk16	968	8327.7	2	8.227±3.785	0.05	0.272
Wk6toWk17	968	8327.8	2.1	8.269±3.889	0.049	0.272
Wk5toWk18	968	8328	2.3	8.281±3.988	0.047	0.272
Wk4toWk19	968	8328.1	2.4	8.139±3.980	0.046	0.272
Wk4toWk21	968	8328.1	2.4	8.361±4.138	0.045	0.272
Wk4toWk20	968	8328.2	2.5	8.068±3.987	0.045	0.272
Wk3toWk18	968	8328.3	2.6	7.871±3.922	0.045	0.272
Wk3toWk16	968	8328.4	2.7	7.361±3.665	0.045	0.272
Wk4toWk22	968	8328.4	2.7	8.068±4.220	0.041	0.272
Wk5toWk15	968	8328.6	2.9	7.095±3.644	0.042	0.272
Wk6toWk16	968	8328.7	3	7.378±3.908	0.04	0.272
Wk6toWk18	968	8328.7	3	7.663±4.152	0.039	0.273
Wk2toWk17	968	8328.7	3	7.631±4.142	0.039	0.273
Wk4toWk14	968	8328.9	3.2	5.903±2.964	0.044	0.272
Wk8toWk17	968	8329	3.3	6.493±3.483	0.04	0.273
Wk7toWk17	968	8329.1	3.4	6.790±3.833	0.036	0.273
Wk2toWk18	968	8329.1	3.4	7.341±4.391	0.033	0.274
Wk3toWk21	968	8329.2	3.5	7.351±4.558	0.031	0.273
Wk4toWk5	968	8329.3	3.6	2.787±1.163	0.061	0.272
Wk5toWk20	968	8329.3	3.6	7.217±4.532	0.03	0.273
Wk5toWk21	968	8329.3	3.6	7.318±4.647	0.029	0.274
Wk3toWk15	968	8329.3	3.6	6.077±3.449	0.036	0.273
Wk3toWk19	968	8329.3	3.6	7.029±4.412	0.03	0.274
Wk3toWk20	968	8329.4	3.7	6.965±4.376	0.03	0.274
Wk5toWk19	968	8329.4	3.7	7.045±4.514	0.029	0.274
Wk1toWk17	968	8329.4	3.7	6.726±4.234	0.03	0.274
Wk2toWk16	968	8329.4	3.7	6.583±4.082	0.031	0.274
Wk3toWk22	968	8329.5	3.8	7.015±4.604	0.027	0.274
Wk11toWk17	968	8329.5	3.8	4.452±2.266	0.043	0.273
Wk6toWk15	968	8329.5	3.8	6.193±3.746	0.032	0.273
Wk9toWk17	968	8329.6	3.9	5.307±2.993	0.037	0.274
Wk8toWk16	968	8329.6	3.9	5.851±3.525	0.033	0.274
Wk4toWk6	968	8329.7	4	2.888±1.296	0.055	0.273
Wk1toWk18	968	8329.7	4	6.505±4.486	0.025	0.274
Wk5toWk22	968	8329.7	4	6.564±4.582	0.025	0.274
Wk4toWk7	968	8329.8	4.1	3.499±1.710	0.048	0.273
Wk7toWk18	968	8329.8	4.1	6.024±4.038	0.027	0.274
Wk8toWk18	968	8329.9	4.2	5.656±3.659	0.029	0.274
Wk2toWk21	968	8329.9	4.2	6.566±5.006	0.021	0.274

Wk11toWk16	968	8329.9	4.2	4.153±2.234	0.04	0.273
Wk7toWk16	968	8329.9	4.2	5.746±3.807	0.027	0.274
Wk6toWk21	968	8329.9	4.2	6.408±4.806	0.022	0.274
Wk6toWk20	968	8329.9	4.2	6.306±4.692	0.022	0.274
Wk5toWk14	968	8329.9	4.2	5.431±3.478	0.029	0.274
Wk2toWk20	968	8329.9	4.2	6.375±4.879	0.021	0.274
Wk4toWk4	968	8329.9	4.2	2.041±0.860	0.06	0.273
Wk10toWk17	968	8330	4.3	4.495±2.588	0.035	0.274
Wk9toWk16	968	8330	4.3	4.950±3.043	0.032	0.274
Wk2toWk19	968	8330	4.3	6.267±4.911	0.02	0.274
Wk1toWk16	968	8330	4.3	5.850±4.204	0.023	0.274
Wk6toWk19	968	8330.1	4.4	6.001±4.658	0.02	0.274
Wk2toWk22	968	8330.1	4.4	6.108±4.981	0.018	0.274
Wk8toWk15	968	8330.1	4.4	5.219±3.474	0.027	0.274
Wk4toWk12	968	8330.2	4.5	4.275±2.562	0.033	0.274
Wk2toWk15	968	8330.2	4.5	5.258±3.816	0.023	0.274
Wk4toWk13	968	8330.2	4.5	4.448±2.775	0.031	0.274
Wk10toWk16	968	8330.3	4.6	4.274±2.624	0.032	0.274
Wk6toWk22	968	8330.3	4.6	5.593±4.676	0.018	0.275
Wk4toWk8	968	8330.3	4.6	3.583±1.991	0.038	0.274
Wk11toWk15	968	8330.3	4.6	3.690±2.095	0.036	0.274
Wk1toWk21	968	8330.3	4.6	5.609±5.009	0.016	0.275
Wk5toWk6	968	8330.3	4.6	3.128±1.638	0.043	0.274
Wk9toWk15	968	8330.4	4.7	4.541±3.004	0.028	0.274
Wk9toWk18	968	8330.4	4.7	4.640±3.157	0.026	0.274
Wk12toWk17	968	8330.4	4.7	3.848±2.283	0.034	0.274
Wk1toWk20	968	8330.4	4.7	5.377±4.866	0.015	0.275
Wk3toWk14	968	8330.4	4.7	4.600±3.227	0.025	0.274
Wk1toWk19	968	8330.4	4.7	5.306±4.932	0.014	0.275
Wk11toWk18	968	8330.5	4.8	3.935±2.441	0.031	0.274
Wk1toWk22	968	8330.5	4.8	5.220±4.973	0.014	0.275
Wk7toWk15	968	8330.5	4.8	4.765±3.667	0.021	0.274
Wk8toWk20	968	8330.6	4.9	4.924±4.357	0.016	0.275
Wk4toWk11	968	8330.6	4.9	3.836±2.436	0.03	0.274
Wk8toWk21	968	8330.6	4.9	4.905±4.424	0.016	0.275
Wk1toWk15	968	8330.6	4.9	4.745±3.973	0.018	0.275
Wk7toWk20	968	8330.6	4.9	4.887±4.643	0.014	0.275
Wk7toWk21	968	8330.6	4.9	4.891±4.705	0.014	0.275
Wk6toWk14	968	8330.6	4.9	4.573±3.590	0.02	0.274
Wk10toWk15	968	8330.7	5	3.828±2.529	0.028	0.274
Wk10toWk18	968	8330.8	5.1	3.892±2.732	0.025	0.275

Wk5toWk5	968	8330.8	5.1	2.740±1.504	0.039	0.274
Wk11toWk20	968	8330.8	5.1	4.090±3.199	0.02	0.275
Wk8toWk19	968	8330.9	5.2	4.335±4.195	0.014	0.275
Wk15to17	968	8330.9	5.2	3.101±1.866	0.033	0.274
Wk14toWk17	968	8330.9	5.2	2.996±1.764	0.034	0.274
Wk7toWk19	968	8330.9	5.2	4.323±4.507	0.012	0.275
Wk5toWk7	968	8330.9	5.2	3.460±2.272	0.029	0.274
Wk9toWk21	968	8330.9	5.2	4.265±3.950	0.015	0.275
Wk11toWk21	968	8330.9	5.2	4.083±3.301	0.019	0.275
Wk9toWk20	968	8330.9	5.2	4.198±3.841	0.015	0.275
Wk7toWk22	968	8331	5.3	4.109±4.492	0.011	0.275
Wk8toWk22	968	8331	5.3	4.131±4.241	0.012	0.275
Wk4toWk9	968	8331	5.3	3.281±2.150	0.029	0.274
Wk13toWk17	968	8331.1	5.4	3.150±2.056	0.029	0.274
Wk12toWk16	968	8331.1	5.4	3.248±2.190	0.027	0.275
Wk8toWk14	968	8331.1	5.4	3.846±3.401	0.016	0.275
Wk2toWk14	968	8331.1	5.4	3.879±3.591	0.015	0.275
Wk5toWk12	968	8331.1	5.4	3.715±3.039	0.019	0.275
Wk5toWk13	968	8331.1	5.4	3.751±3.266	0.017	0.275
Wk11toWk22	968	8331.1	5.4	3.750±3.332	0.016	0.275
Wk9toWk22	968	8331.2	5.5	3.698±3.848	0.012	0.276
Wk10toWk21	968	8331.2	5.5	3.686±3.501	0.014	0.275
Wk9toWk19	968	8331.2	5.5	3.692±3.678	0.013	0.275
Wk12toWk18	968	8331.2	5.5	3.331±2.480	0.022	0.275
Wk10toWk20	968	8331.2	5.5	3.654±3.402	0.015	0.275
Wk1toWk14	968	8331.2	5.5	3.585±3.821	0.011	0.275
Wk9toWk14	968	8331.2	5.5	3.490±2.954	0.018	0.275
Wk11toWk14	968	8331.2	5.5	2.953±1.978	0.027	0.274
Wk11toWk19	968	8331.2	5.5	3.482±2.968	0.018	0.275
Wk15to15	968	8331.3	5.6	2.602±1.586	0.033	0.274
Wk4toWk10	968	8331.3	5.6	3.230±2.477	0.021	0.275
Wk11toWk12	968	8331.3	5.6	2.603±1.635	0.031	0.274
Wk10toWk22	968	8331.4	5.7	3.383±3.514	0.012	0.276
Wk12toWk20	968	8331.4	5.7	3.283±3.356	0.012	0.276
Wk7toWk14	968	8331.4	5.7	3.266±3.518	0.011	0.275
Wk12toWk21	968	8331.4	5.7	3.252±3.434	0.012	0.276
Wk3toWk13	968	8331.5	5.8	3.171±2.953	0.015	0.275
Wk10toWk19	968	8331.5	5.8	3.183±3.224	0.013	0.276
Wk10toWk14	968	8331.5	5.8	3.021±2.470	0.019	0.275
Wk5toWk11	968	8331.5	5.8	3.102±2.893	0.015	0.275
Wk15to16	968	8331.5	5.8	2.582±1.750	0.027	0.275

Wk12toWk15	968	8331.5	5.8	2.769±2.040	0.023	0.275
Wk3toWk12	968	8331.6	5.9	3.010±2.731	0.016	0.275
Wk12toWk12	968	8331.6	5.9	2.824±2.205	0.021	0.275
Wk12toWk22	968	8331.6	5.9	2.854±3.399	0.009	0.276
Wk5toWk8	968	8331.7	6	2.779±2.451	0.017	0.275
Wk14toWk15	968	8331.7	6	2.224±1.436	0.03	0.275
Wk14toWk16	968	8331.7	6	2.338±1.579	0.027	0.275
Wk6toWk13	968	8331.7	6	2.731±3.307	0.009	0.275
Wk13toWk18	968	8331.7	6	2.705±2.272	0.018	0.275
Wk6toWk12	968	8331.8	6.1	2.746±3.075	0.01	0.275
Wk13toWk21	968	8331.8	6.1	2.607±3.290	0.008	0.276
Wk2toWk13	968	8331.8	6.1	2.559±3.338	0.008	0.276
Wk13toWk20	968	8331.8	6.1	2.594±3.197	0.009	0.276
Wk14toWk18	968	8331.8	6.1	2.523±1.985	0.02	0.275
Wk1toWk13	968	8331.8	6.1	2.329±3.608	0.006	0.276
Wk14toWk21	968	8331.8	6.1	2.611±3.081	0.01	0.276
Wk2toWk12	968	8331.8	6.1	2.548±3.171	0.008	0.276
Wk13toWk16	968	8331.9	6.2	2.459±1.903	0.021	0.275
Wk12toWk19	968	8331.9	6.2	2.569±3.045	0.009	0.276
Wk9toWk12	968	8331.9	6.2	2.611±2.831	0.011	0.275
Wk1toWk12	968	8331.9	6.2	2.330±3.448	0.006	0.276
Wk8toWk12	968	8331.9	6.2	2.476±3.171	0.008	0.276
Wk14toWk20	968	8331.9	6.2	2.507±2.918	0.01	0.276
Wk3toWk11	968	8331.9	6.2	2.525±2.577	0.013	0.275
Wk8toWk13	968	8332	6.3	2.193±3.313	0.006	0.276
Wk13toWk22	968	8332	6.3	2.195±3.205	0.006	0.276
Wk9toWk13	968	8332.1	6.4	2.213±2.962	0.007	0.276
Wk1toWk11	968	8332.1	6.4	1.824±3.348	0.004	0.276
Wk14toWk22	968	8332.1	6.4	2.135±2.980	0.007	0.276
Wk10toWk12	968	8332.1	6.4	2.316±2.242	0.014	0.275
Wk2toWk11	968	8332.1	6.4	2.051±3.045	0.006	0.276
Wk11toWk11	968	8332.1	6.4	1.808±1.165	0.029	0.274
Wk11toWk13	968	8332.2	6.5	2.221±1.918	0.017	0.275
Wk15to21	968	8332.2	6.5	1.735±3.278	0.004	0.276
Wk7toWk13	968	8332.2	6.5	1.586±3.293	0.003	0.276
Wk6toWk11	968	8332.2	6.5	1.994±2.871	0.006	0.276
Wk7toWk12	968	8332.2	6.5	1.719±3.137	0.004	0.276
Wk3toWk8	968	8332.2	6.5	2.196±2.220	0.013	0.275
Wk3toWk7	968	8332.2	6.5	2.173±1.983	0.016	0.275
Wk5toWk9	968	8332.2	6.5	2.139±2.484	0.01	0.275
Wk15to22	968	8332.3	6.6	1.452±3.231	0.003	0.276

Wk13toWk19	968	8332.3	6.6	1.874±2.828	0.006	0.276
Wk12toWk14	968	8332.3	6.6	2.111±1.983	0.015	0.275
Wk13toWk15	968	8332.3	6.6	2.058±1.745	0.018	0.275
Wk15to18	968	8332.3	6.6	2.107±2.027	0.014	0.275
Wk1toWk8	968	8332.3	6.6	1.355±3.199	0.002	0.276
Wk5toWk10	968	8332.3	6.6	1.772±2.873	0.005	0.276
Wk1toWk10	968	8332.3	6.6	0.683±3.415	0.001	0.276
Wk15to20	968	8332.3	6.6	1.535±3.049	0.003	0.276
Wk1toWk9	968	8332.4	6.7	1.133±3.203	0.002	0.276
Wk10toWk13	968	8332.4	6.7	1.949±2.421	0.009	0.276
Wk3toWk9	968	8332.4	6.7	1.958±2.308	0.01	0.276
Wk3toWk6	968	8332.4	6.7	1.930±1.613	0.019	0.275
Wk8toWk11	968	8332.4	6.7	1.436±2.935	0.003	0.276
Wk1toWk7	968	8332.4	6.7	1.372±2.934	0.003	0.276
Wk3toWk10	968	8332.4	6.7	1.756±2.571	0.006	0.276
Wk2toWk10	968	8332.4	6.7	1.045±3.086	0.002	0.276
Wk2toWk8	968	8332.5	6.8	1.575±2.737	0.004	0.276
Wk14toWk19	968	8332.5	6.8	1.751±2.512	0.007	0.276
Wk16to17	968	8332.5	6.8	1.847±1.555	0.018	0.275
Wk9toWk11	968	8332.5	6.8	1.620±2.585	0.005	0.276
Wk2toWk9	968	8332.5	6.8	1.364±2.790	0.003	0.276
Wk16to21	968	8332.5	6.8	0.347±3.135	0	0.276
Wk2toWk7	968	8332.5	6.8	1.636±2.530	0.006	0.276
Wk16to22	968	8332.5	6.8	0.276±3.115	0	0.276
Wk7toWk11	968	8332.6	6.9	0.833±2.885	0.001	0.276
Wk17to17	968	8332.7	7	1.692±1.386	0.018	0.275
Wk1toWk6	968	8332.7	7	1.307±2.474	0.004	0.276
Wk2toWk6	968	8332.8	7.1	1.538±2.123	0.007	0.276
Wk15to19	968	8332.8	7.1	0.836±2.592	0.001	0.276
Wk6toWk7	968	8332.8	7.1	1.548±1.992	0.008	0.276
Wk16to20	968	8332.8	7.1	0.115±2.759	0	0.276
Wk3toWk5	968	8332.9	7.2	1.598±1.572	0.014	0.276
Wk6toWk10	968	8332.9	7.2	0.329±2.636	0	0.276
Wk10toWk11	968	8332.9	7.2	1.463±1.915	0.008	0.276
Wk6toWk8	968	8333	7.3	1.146±2.198	0.004	0.276
Wk6toWk6	968	8333	7.3	1.443±1.209	0.019	0.275
Wk1toWk5	968	8333	7.3	0.404±2.409	0	0.276
Wk12toWk13	968	8333	7.3	1.139±2.093	0.004	0.276
Wk20to22	968	8333	7.3	0.837±2.273	0.002	0.276
Wk14toWk14	968	8333	7.3	1.390±1.131	0.02	0.276
Wk6toWk9	968	8333.1	7.4	0.812±2.246	0.002	0.276

we20to20.y	968	8333.1	7.4	1.245±1.839	0.006	0.276
Wk13toWk14	968	8333.2	7.5	1.307±1.601	0.009	0.276
Wk2toWk5	968	8333.2	7.5	0.794±2.058	0.002	0.276
Wk20to21	968	8333.3	7.6	0.895±1.889	0.003	0.276
Wk16to18	968	8333.4	7.7	0.984±1.673	0.005	0.276
Wk16to16	968	8333.6	7.9	1.057±1.299	0.009	0.276
Wk3toWk4	968	8333.8	8.1	0.799±1.392	0.005	0.276
Wk21to22	968	8333.8	8.1	0.164±1.630	0	0.276
Wk17to18	968	8333.9	8.2	0.506±1.528	0.001	0.276
Wk21to21	968	8334.2	8.5	0.250±1.353	0	0.276

Parasitoid attack phenology

Table S3.7a. Parasitoid attack occurrence phenology as a function of temperature advancing emergence, weather variables selected as those with a negative coefficient from moving window approach which considered all consecutive weekly windows between Jan 1st and July 8th Models are mixed effects models with year and tree identity included in all models. Slopes reported with ± 1SE, ΔAICc given relative to best fitting model. Random effects only model AICc = 7100.307. Wk = Week.

***Denotes best model where used in stage two modelling.**

Time window (Week 1 = Jan 1st)	n	AICc	ΔAICc	Slope±1SE	$R^2GLMM_{(m)}$	R2GLMM$_{(c)}$
wk4towk5*	**765**	**7091.7**	**0**	**-4.231±1.350**	**0.115**	**0.348**
wk3towk5	765	7092.7	1	-4.664±1.679	0.094	0.345
wk5towk5	765	7093.3	1.6	-2.928±1.019	0.101	0.347
wk3towk6	765	7093.3	1.6	-4.566±1.754	0.092	0.35
wk4towk6	765	7093.6	1.9	-3.849±1.474	0.092	0.35
wk11towk12	765	7094.3	2.6	-5.007±2.249	0.061	0.341
wk3towk12	765	7094.6	2.9	-5.670±2.802	0.059	0.346
wk4towk12	765	7094.9	3.2	-5.194±2.669	0.056	0.347
wk3towk7	765	7095	3.3	-4.356±2.102	0.066	0.349
wk3towk13	765	7095.3	3.6	-5.412±3.074	0.047	0.346
wk3towk14	765	7095.3	3.6	-5.283±2.982	0.049	0.347
wk4towk7	765	7095.3	3.6	-3.838±1.881	0.064	0.349
wk3towk9	765	7095.3	3.6	-4.725±2.541	0.051	0.345
wk1towk12	765	7095.4	3.7	-5.273±3.077	0.043	0.345
wk3towk15	765	7095.4	3.7	-5.400±3.237	0.044	0.347
wk2towk12	765	7095.5	3.8	-5.117±3.013	0.043	0.345
wk4towk14	765	7095.6	3.9	-4.913±2.880	0.046	0.348
wk4towk9	765	7095.6	3.9	-4.372±2.404	0.05	0.346
wk2towk6	765	7095.6	3.9	-3.960±2.090	0.054	0.347
wk4towk13	765	7095.6	3.9	-4.957±2.954	0.044	0.347
wk5towk6	765	7095.6	3.9	-2.716±1.242	0.07	0.349

wk3towk8	765	7095.6	3.9	-4.273±2.362	0.051	0.347
wk4towk15	765	7095.7	4	-5.066±3.154	0.042	0.347
wk3towk11	765	7095.7	4	-4.504±2.597	0.045	0.345
wk1towk14	765	7095.7	4	-5.106±3.254	0.038	0.345
wk5towk12	765	7095.8	4.1	-4.531±2.684	0.044	0.346
wk1towk15	765	7095.8	4.1	-5.245±3.513	0.034	0.345
wk1towk6	765	7095.8	4.1	-3.939±2.189	0.048	0.346
wk3towk17	765	7095.8	4.1	-5.289±3.616	0.033	0.346
wk3towk16	765	7095.8	4.1	-5.191±3.515	0.035	0.346
wk1towk13	765	7095.9	4.2	-5.012±3.323	0.035	0.345
wk3towk18	765	7095.9	4.2	-5.183±3.546	0.033	0.346
wk3towk10	765	7095.9	4.2	-4.406±2.660	0.042	0.345
wk2towk14	765	7095.9	4.2	-4.864±3.180	0.037	0.346
wk4towk17	765	7095.9	4.2	-5.181±3.622	0.033	0.346
wk4towk18	765	7095.9	4.2	-5.113±3.557	0.033	0.346
wk4towk8	765	7095.9	4.2	-3.870±2.193	0.05	0.348
wk2towk13	765	7096	4.3	-4.854±3.277	0.034	0.345
wk4towk16	765	7096	4.3	-5.007±3.493	0.033	0.347
wk2towk15	765	7096	4.3	-4.945±3.433	0.033	0.346
wk4towk11	765	7096	4.3	-4.101±2.462	0.043	0.346
wk10towk12	765	7096	4.3	-4.274±2.659	0.039	0.346
wk4towk4	765	7096	4.3	-2.946±1.504	0.053	0.344
wk2towk5	765	7096.1	4.4	-3.588±2.046	0.044	0.344
wk3to23	765	7096.1	4.4	-5.053±3.924	0.027	0.346
wk1towk18	765	7096.1	4.4	-4.945±3.753	0.027	0.345
wk3to24	765	7096.1	4.4	-5.037±3.954	0.026	0.346
wk1towk16	765	7096.1	4.4	-4.934±3.753	0.027	0.345
wk1towk17	765	7096.1	4.4	-4.964±3.819	0.026	0.345
wk4to23	765	7096.2	4.5	-5.006±3.964	0.027	0.346
wk3to25	765	7096.2	4.5	-5.016±4.007	0.026	0.346
wk3to26	765	7096.2	4.5	-5.109±4.269	0.024	0.346
wk4to24	765	7096.2	4.5	-4.999±3.998	0.026	0.346
wk4to25	765	7096.2	4.5	-4.980±4.053	0.025	0.346
wk4to26	765	7096.2	4.5	-5.053±4.325	0.023	0.347
wk4towk10	765	7096.2	4.5	-3.978±2.516	0.039	0.346
wk5towk14	765	7096.2	4.5	-4.286±2.903	0.036	0.347
wk3to27	765	7096.3	4.6	-4.970±4.402	0.022	0.347
wk3towk22	765	7096.3	4.6	-4.735±3.722	0.027	0.346
wk2towk18	765	7096.3	4.6	-4.657±3.683	0.025	0.345
wk1towk11	765	7096.3	4.6	-4.166±2.861	0.032	0.345
wk2towk17	765	7096.3	4.6	-4.667±3.752	0.024	0.345

wk4to27	765	7096.3	4.6	-4.869±4.450	0.021	0.347
wk3towk4	765	7096.3	4.6	-3.317±1.929	0.041	0.343
wk2towk16	765	7096.3	4.6	-4.611±3.675	0.025	0.345
wk5towk13	765	7096.3	4.6	-4.229±2.988	0.032	0.346
wk4towk22	765	7096.3	4.6	-4.630±3.733	0.026	0.347
wk5towk15	765	7096.3	4.6	-4.353±3.188	0.031	0.347
wk3towk19	765	7096.3	4.6	-4.511±3.476	0.027	0.346
wk1to24	765	7096.3	4.6	-4.737±4.075	0.022	0.345
wk1to23	765	7096.3	4.6	-4.717±4.041	0.022	0.345
wk1towk9	765	7096.3	4.6	-4.092±2.818	0.032	0.345
wk1to26	765	7096.4	4.7	-4.761±4.362	0.019	0.346
wk1to25	765	7096.4	4.7	-4.673±4.101	0.021	0.345
wk4towk19	765	7096.4	4.7	-4.425±3.487	0.027	0.346
wk1to27	765	7096.4	4.7	-4.686±4.514	0.018	0.346
wk11towk14	765	7096.4	4.7	-4.068±2.891	0.031	0.346
wk2towk9	765	7096.4	4.7	-3.960±2.753	0.032	0.345
wk2towk11	765	7096.4	4.7	-3.982±2.786	0.032	0.345
wk2to24	765	7096.4	4.7	-4.552±4.051	0.021	0.346
wk2to26	765	7096.4	4.7	-4.598±4.360	0.019	0.346
wk2to23	765	7096.4	4.7	-4.529±4.016	0.021	0.346
wk5towk18	765	7096.5	4.8	-4.392±3.609	0.024	0.346
wk2to25	765	7096.5	4.8	-4.527±4.093	0.02	0.346
wk12towk12	765	7096.5	4.8	-3.266±1.967	0.031	0.339
wk5towk17	765	7096.5	4.8	-4.400±3.693	0.023	0.346
wk1towk22	765	7096.5	4.8	-4.447±3.852	0.022	0.346
wk2to27	765	7096.5	4.8	-4.504±4.511	0.017	0.346
wk3towk20	765	7096.5	4.8	-4.236±3.407	0.026	0.346
wk3towk21	765	7096.5	4.8	-4.266±3.588	0.024	0.346
wk5to23	765	7096.5	4.8	-4.365±4.038	0.02	0.346
wk5to26	765	7096.5	4.8	-4.390±4.413	0.017	0.346
wk5to24	765	7096.5	4.8	-4.360±4.062	0.019	0.346
wk5to25	765	7096.6	4.9	-4.339±4.110	0.019	0.346
wk5towk16	765	7096.6	4.9	-4.205±3.551	0.023	0.346
wk1towk19	765	7096.6	4.9	-4.226±3.629	0.022	0.345
wk2towk22	765	7096.6	4.9	-4.275±3.826	0.021	0.346
wk10towk14	765	7096.6	4.9	-4.071±3.237	0.026	0.347
wk4towk20	765	7096.6	4.9	-4.116±3.402	0.025	0.346
wk9towk12	765	7096.6	4.9	-3.675±2.580	0.03	0.345
wk1towk10	765	7096.6	4.9	-3.871±2.903	0.028	0.345
wk4towk21	765	7096.6	4.9	-4.147±3.594	0.023	0.346
wk5to27	765	7096.6	4.9	-4.197±4.546	0.015	0.347

wk1towk5	765	7096.6	4.9	-3.267±2.078	0.036	0.344
wk2towk7	765	7096.6	4.9	-3.463±2.317	0.036	0.346
wk1towk7	765	7096.6	4.9	-3.501±2.385	0.034	0.346
wk2towk19	765	7096.7	5	-4.014±3.582	0.021	0.346
wk1towk20	765	7096.7	5	-3.999±3.554	0.021	0.346
wk5towk22	765	7096.7	5	-4.032±3.796	0.019	0.346
wk2towk10	765	7096.7	5	-3.729±2.848	0.027	0.345
wk1towk21	765	7096.7	5	-3.996±3.718	0.019	0.346
wk9towk14	765	7096.7	5	-3.806±3.108	0.024	0.346
wk1towk8	765	7096.8	5.1	-3.550±2.621	0.029	0.345

Table S3.7b. Parasitoid attack occurrence phenology as a function of temperature delaying emergence, weather variables selected as those with a positive coefficient from moving window approach which considered all consecutive weekly windows between Jan 1st and July 8th Models are mixed effects models with year and tree identity included in all models. Slopes reported with ± 1SE, ΔAICc given relative to best fitting model. Random effects only model AICc = 7100.307. Wk = Week.

***Denotes best model where used in stage two modelling.**

Time window (Week 1 = Jan 1st)	n	AICc	ΔAICc	Slope±1SE	R^2GLMM$_{(m)}$	R2GLMM$_{(c)}$
wk15to27*	**765**	**7097.3**	**0**	**0.140±5.029**	**0**	**0.346**
wk21to27	765	7097.4	0.1	0.158±4.743	0	0.346
wk13towk13	765	7097.6	0.3	2.545±2.175	0.022	0.345
wk15to16	765	7097.7	0.4	2.430±2.362	0.015	0.345
wk23to27	765	7097.7	0.4	0.866±3.954	0.001	0.346
wk13towk16	765	7097.7	0.4	1.894v3.465	0.005	0.346
wk23to26	765	7097.7	0.4	0.148±4.039	0	0.346
wk13towk17	765	7097.7	0.4	1.278±3.766	0.002	0.346
wk15to21	765	7097.9	0.6	0.470±3.768	0	0.346
wk13towk21	765	7097.9	0.6	0.045±3.795	0	0.346
wk13towk21	765	7097.9	0.6	0.045±3.795	0	0.346
wk15to17	765	7097.9	0.6	1.885±2.915	0.006	0.345

wk24to26	765	7098	0.7	0.283±3.515	0	0.346
wk13towk19	765	7098	0.7	0.111±3.496	0	0.346
wk13towk19	765	7098	0.7	0.111±3.496	0	0.346
wk15to19	765	7098.1	0.8	0.569±3.263	0	0.346
wk24to27	765	7098.1	0.8	0.788±3.190	0.001	0.346
wk15to20	765	7098.2	0.9	0.040±3.256	0	0.346
wk15to20	765	7098.2	0.9	0.040±3.256	0	0.346
wk15to18	765	7098.2	0.9	0.448±3.196	0	0.346
wk16to16	765	7098.3	1	1.810±1.750	0.015	0.344
wk21to21	765	7098.3	1	1.415±2.580	0.005	0.346
wk13towk15	765	7098.3	1	0.189±3.005	0	0.346
wk25to27	765	7098.4	1.1	1.183±2.654	0.003	0.346
wk25to26	765	7098.4	1.1	0.966±2.726	0.002	0.345
wk16to19	765	7098.4	1.1	0.002±2.878	0	0.346
wk16to19	765	7098.4	1.1	0.002±2.878	0	0.346
wk16to17	765	7098.4	1.1	1.216±2.498	0.003	0.346
wk14towk16	765	7098.5	1.2	0.315±2.774	0	0.346
wk26to26	765	7098.5	1.2	1.589±2.025	0.009	0.345
wk15to15	765	7098.6	1.3	1.322±2.207	0.005	0.346
wk26to27	765	7098.7	1.4	1.315±2.046	0.006	0.345
wk7towk10	765	7098.8	1.5	0.021±2.420	0	0.346
wk7towk10	765	7098.8	1.5	0.021±2.420	0	0.346
wk7towk8	765	7098.8	1.5	0.944±2.073	0.003	0.346
wk7towk7	765	7098.9	1.6	1.168±1.845	0.006	0.346
wk19to21	765	7098.9	1.6	0.095±2.246	0	0.346
wk19to21	765	7098.9	1.6	0.095±2.246	0	0.346
wk7towk9	765	7098.9	1.6	0.071±2.220	0	0.346

wk7towk9	765	7098.9	1.6	0.071±2.220	0	0.346
wk27to27	765	7099.3	2	0.718±1.721	0.003	0.346
wk8towk8	765	7099.5	2.2	0.278±1.677	0	0.346
wk2towk3	765	7099.5	2.2	0.111±1.640	0	0.346
wk2towk2	765	7099.6	2.3	0.868±1.257	0.007	0.346
wk1towk2	765	7099.9	2.6	0.119±1.367	0	0.346
wk19to19	765	7100	2.7	0.159±1.316	0	0.346

Table S3.7c. Parasitoid attack occurrence phenology as a function of precipitation advancing emergence, weather variables selected as those with a negative coefficient from moving window approach which considered all consecutive weekly windows between Jan 1st and July 8th Models are mixed effects models with year and tree identity included in all models. Slopes reported with ± 1SE, ΔAICc given relative to best fitting model. Random effects only model AICc = 7100.307. Wk = Week.

Time window (Week 1 = Jan 1st)	n	AICc	ΔAICc	Slope±1SE	$R^2GLMM_{(m)}$	R2GLMM$_{(c)}$
Wk2toWk18*	**765**	**7096.5**	**0**	**-0.060±7.443**	**0**	**0.346**
Wk2toWk17	765	7096.6	0.1	-1.410±7.122	0	0.346
Wk2toWk16	765	7096.6	0.1	-0.929±6.874	0	0.346
Wk1toWk17	765	7096.6	0.1	-0.394±7.145	0	0.346
Wk3toWk17	765	7096.8	0.3	-0.556±6.545	0	0.346
Wk2toWk15	765	7096.8	0.3	-0.925±6.308	0	0.346
Wk3toWk16	765	7096.8	0.3	-0.133±6.396	0	0.346
Wk1toWk15	765	7096.8	0.3	-0.035±6.507	0	0.346
Wk8toWk17	765	7096.9	0.4	-0.637±5.995	0	0.346
Wk4toWk17	765	7096.9	0.4	-0.429±6.165	0	0.346
Wk1toWk14	765	7096.9	0.4	-0.230±6.160	0	0.346
Wk8toWk16	765	7097	0.5	-0.110±5.957	0	0.346
Wk4toWk16	765	7096.9	0.4	-0.024±6.090	0	0.346
Wk2toWk14	765	7097	0.5	-1.034±5.811	0	0.346
Wk11to23	765	7097	0.5	-0.401±5.849	0	0.346
Wk8toWk15	765	7097	0.5	-0.247±5.814	0	0.346
Wk3toWk15	765	7097	0.5	-0.203±5.889	0	0.346
Wk1toWk13	765	7097	0.5	-0.202±5.733	0	0.346
Wk2toWk13	765	7097.2	0.7	-0.923±5.308	0	0.346
Wk8toWk14	765	7097.1	0.6	-0.576±5.547	0	0.346
Wk11toWk22	765	7097.2	0.7	-0.405±5.375	0	0.346
Wk1toWk12	765	7097.1	0.6	-0.177±5.477	0	0.346

Wk4toWk15	765	7097.1	0.6	-0.103±5.630	0	0.346
Wk2toWk12	765	7097.3	0.8	-0.886±5.042	0	0.346
Wk9toWk17	765	7097.2	0.7	-0.809±5.107	0	0.346
Wk8toWk13	765	7097.2	0.7	-0.586±5.279	0	0.346
Wk9toWk16	765	7097.2	0.7	-0.427±5.128	0	0.346
Wk3toWk14	765	7097.2	0.7	-0.354±5.353	0	0.346
Wk4toWk14	765	7097.2	0.7	-0.271±5.173	0	0.346
Wk1toWk11	765	7097.2	0.7	-0.120±5.282	0	0.346
Wk20to23	765	7097.3	0.8	-2.205±4.380	0.004	0.346
Wk9toWk13	765	7097.3	0.8	-1.037±4.762	0.001	0.345
Wk9toWk14	765	7097.3	0.8	-0.912±4.845	0	0.346
Wk2toWk11	765	7097.4	0.9	-0.831±4.805	0	0.346
Wk8toWk12	765	7097.3	0.8	-0.598±5.059	0	0.346
Wk9toWk15	765	7097.3	0.8	-0.581±5.035	0	0.346
Wk1toWk9	765	7097.3	0.8	-0.024±5.005	0	0.346
Wk9toWk12	765	7097.4	0.9	-1.150±4.578	0.001	0.345
Wk8toWk11	765	7097.5	1	-0.496±4.609	0	0.346
Wk3toWk13	765	7097.4	0.9	-0.298±4.776	0	0.346
Wk4toWk13	765	7097.4	0.9	-0.233±4.674	0	0.346
Wk2toWk5	765	7097.5	1	-2.587±3.145	0.011	0.346
Wk2toWk9	765	7097.5	1	-0.762±4.356	0.001	0.346
Wk10toWk17	765	7097.6	1.1	-0.297±4.402	0	0.346
Wk3toWk12	765	7097.5	1	-0.262±4.415	0	0.346
Wk1toWk5	765	7097.6	1.1	-1.961±3.725	0.004	0.346
Wk9toWk11	765	7097.6	1.1	-1.099±4.100	0.001	0.345
Wk2toWk8	765	7097.6	1.1	-0.432±4.291	0	0.346
Wk4toWk12	765	7097.6	1.1	-0.202±4.326	0	0.346
Wk10toWk15	765	7097.6	1.1	-0.012±4.240	0	0.346
Wk21to23	765	7097.7	1.2	-2.082±3.363	0.006	0.345
Wk20to22	765	7097.7	1.2	-1.958±3.505	0.005	0.345
Wk11toWk17	765	7097.7	1.2	-1.379±3.916	0.002	0.345
Wk11toWk16	765	7097.7	1.2	-1.167±3.824	0.001	0.346
Wk2toWk7	765	7097.7	1.2	-0.703±3.979	0.001	0.346
Wk11toWk18	765	7097.7	1.2	-0.419±4.089	0	0.346
Wk10toWk14	765	7097.7	1.2	-0.252±4.069	0	0.346
Wk3toWk11	765	7097.7	1.2	-0.210±4.127	0	0.346
Wk4toWk11	765	7097.7	1.2	-0.153±4.071	0	0.346
Wk11toWk12	765	7097.8	1.3	-2.188±2.730	0.007	0.342
Wk2toWk4	765	7097.8	1.3	-2.176±3.022	0.009	0.346
Wk11toWk13	765	7097.8	1.3	-1.915±3.127	0.004	0.344
Wk11toWk15	765	7097.8	1.3	-1.297±3.562	0.002	0.345

Wk1toWk4	765	7097.8	1.3	-1.240±3.590	0.002	0.346
Wk1toWk6	765	7097.8	1.3	-0.832±3.887	0.001	0.346
Wk10toWk13	765	7097.8	1.3	-0.274±3.916	0	0.346
Wk12toWk17	765	7097.8	1.3	-0.206±.840	0	0.346
Wk11toWk14	765	7097.9	1.4	-1.591±3.291	0.003	0.345
Wk2toWk6	765	7097.9	1.4	-1.438±3.331	0.003	0.346
Wk12toWk12	765	7097.9	1.4	-0.312±3.652	0	0.346
Wk10toWk12	765	7097.9	1.4	-0.279±3.667	0	0.346
Wk3toWk9	765	7097.9	1.4	-0.137±3.654	0	0.346
Wk11toWk11	765	7098	1.5	-2.101±1.901	0.014	0.34
Wk5toWk5	765	7098	1.5	-2.020±2.494	0.011	0.346
Wk4toWk9	765	7098	1.5	-0.074±3.557	0	0.346
Wk22to23	765	7098.1	1.6	-1.797±2.676	0.007	0.345
Wk21to22	765	7098.2	1.7	-1.791±2.499	0.008	0.345
Wk12toWk13	765	7098.1	1.6	-0.181±3.325	0	0.346
Wk13toWk17	765	7098.1	1.6	-0.140±3.403	0	0.346
Wk15to17	765	7098.3	1.8	-0.149±3.110	0	0.346
Wk12toWk14	765	7098.2	1.7	-0.128±3.200	0	0.346
Wk26to27	765	7098.2	1.7	-0.117±3.247	0	0.346
Wk3toWk7	765	7098.2	1.7	-0.036±3.192	0	0.346
Wk3toWk5	765	7098.3	1.8	-1.596±2.484	0.007	0.346
Wk10toWk11	765	7098.3	1.8	-0.183±3.075	0	0.346
Wk9toWk9	765	7098.4	1.9	-1.061±2.594	0.003	0.346
Wk2toWk3	765	7098.4	1.9	-1.029±2.673	0.002	0.346
Wk8toWk9	765	7098.4	1.9	-0.216±2.814	0	0.346
Wk14toWk17	765	7098.4	1.9	-0.111±2.951	0	0.346
Wk4toWk5	765	7098.5	2	-1.571±2.052	0.009	0.345
Wk3toWk6	765	7098.5	2	-0.669±2.605	0.001	0.346
Wk13toWk13	765	7098.6	2.1	-0.062±2.583	0	0.346
Wk3toWk4	765	7098.7	2.2	-1.060±2.167	0.004	0.346
Wk16to17	765	7098.7	2.2	-0.371±2.502	0	0.346
Wk13toWk14	765	7098.7	2.2	-0.045±2.537	0	0.346
Wk17to17	765	7098.8	2.3	-0.754±2.245	0.002	0.346
Wk4toWk6	765	7098.8	2.3	-0.623±2.286	0.001	0.346
Wk22to22	765	7098.9	2.4	-1.319±1.583	0.01	0.344
Wk26to26	765	7098.9	2.4	-0.147±2.203	0	0.346
Wk21to21	765	7099	2.5	-0.223±2.103	0	0.346
Wk2toWk2	765	7099.1	2.6	-0.855±1.843	0.004	0.346
Wk3toWk3	765	7099.1	2.6	-0.154±2.039	0	0.346
Wk4toWk4	765	7099.3	2.8	-0.973±1.525	0.006	0.345
Wk14toWk14	765	7099.3	2.8	-0.016±1.825	0	0.346

Table S3.7d. Parasitoid attack occurrence phenology as a function of precipitation delaying emergence, weather variables selected as those with a positive coefficient from moving window approach which considered all consecutive weekly windows between Jan 1st and July 8th Models are mixed effects models with year and tree identity included in all models. Slopes reported with ± 1SE, ΔAICc given relative to best fitting model. Random effects only model AICc = 7100.307. Wk = Week.

***Denotes best model where used in stage two modelling**

Time window (Week 1 = Jan 1st)	n	AICc	ΔAICc	Slope±1SE	$R^2GLMM_{(m)}$	R2GLMM(c)
Wk6to26*	**765**	**7095.2**	**0**	**8.505±8.871**	**0.013**	**0.345**
Wk6to27	765	7095.3	0.1	8.120±8.876	0.012	0.345
Wk6to25	765	7095.3	0.1	8.290±8.479	0.013	0.345
Wk5to26	765	7095.4	0.2	7.337±9.186	0.009	0.345
Wk5to25	765	7095.5	0.3	6.961±8.669	0.009	0.345
Wk5to27	765	7095.5	0.3	7.064±9.209	0.008	0.345
Wk2to27	765	7095.6	0.4	4.738±10.228	0.003	0.346
Wk2to26	765	7095.6	0.4	4.857±10.185	0.003	0.346
Wk7to27	765	7095.6	0.4	6.618±8.643	0.009	0.346
Wk7to26	765	7095.6	0.4	6.766±8.537	0.009	0.346
Wk3to27	765	7095.7	0.5	5.102±9.428	0.004	0.346
Wk1to27	765	7095.7	0.5	5.238±9.713	0.004	0.345
Wk3to26	765	7095.7	0.5	5.261±9.402	0.004	0.345
Wk1to26	765	7095.7	0.5	5.295±9.606	0.004	0.345
Wk6toWk20	765	7095.7	0.5	6.380±7.643	0.008	0.344
Wk7to25	765	7095.7	0.5	6.590±8.138	0.01	0.346
Wk6to24	765	7095.7	0.5	6.594±8.027	0.009	0.345
Wk24to25	765	7095.8	0.6	4.291±2.530	0.045	0.348
Wk2to25	765	7095.8	0.6	4.477±9.459	0.003	0.346
Wk3to25	765	7095.8	0.6	4.918±8.804	0.004	0.345

Wk1to25	765	7095.8	0.6	5.045±9.100	0.004	0.345
Wk4to27	765	7095.8	0.6	5.054±9.071	0.004	0.345
Wk4to26	765	7095.8	0.6	5.223±9.046	0.004	0.345
Wk18to20	765	7095.8	0.6	5.435±3.809	0.031	0.345
Wk6toWk21	765	7095.8	0.6	6.012±7.816	0.007	0.344
Wk6toWk19	765	7095.8	0.6	6.317±7.559	0.008	0.344
Wk4to25	765	7095.9	0.7	4.839±8.428	0.004	0.345
Wk5to24	765	7095.9	0.7	5.367±8.193	0.006	0.345
Wk2to24	765	7096	0.8	2.975±8.843	0.001	0.346
Wk1to24	765	7096	0.8	3.661±8.582	0.002	0.346
Wk6to23	765	7096	0.8	4.077±8.365	0.003	0.346
Wk8to27	765	7096	0.8	4.853±8.164	0.006	0.346
Wk8to26	765	7096	0.8	4.904±8.017	0.006	0.346
Wk7to24	765	7096	0.8	5.079±7.692	0.006	0.346
Wk3to24	765	7096.1	0.9	3.507±8.267	0.002	0.346
Wk10toWk10	765	7096.1	0.9	4.280±2.742	0.032	0.343
Wk5toWk21	765	7096.1	0.9	4.346±7.741	0.004	0.345
Wk7toWk21	765	7096.1	0.9	4.463±7.529	0.005	0.346
Wk5toWk19	765	7096.1	0.9	4.529±7.524	0.004	0.345
Wk5toWk20	765	7096.1	0.9	4.622±7.573	0.005	0.345
Wk8to25	765	7096.1	0.9	4.760±7.603	0.006	0.346
Wk7toWk20	765	7096.1	0.9	4.905±7.444	0.006	0.345
Wk2to23	765	7096.2	1	0.103±8.796	0	0.346
Wk1to23	765	7096.2	1	1.113±8.656	0	0.346
Wk1toWk21	765	7096.2	1	2.639±8.145	0.001	0.346
Wk5to23	765	7096.2	1	2.663±8.343	0.001	0.346
Wk1toWk19	765	7096.2	1	2.704±8.018	0.001	0.346
Wk4to24	765	7096.2	1	3.465±7.895	0.002	0.346

Wk6toWk22	765	7096.2	1	3.494±7.588	0.003	0.346
we9to27	765	7096.2	1	3.939±7.451	0.005	0.346
Wk7toWk19	765	7096.2	1	4.569±7.192	0.005	0.345
we18to25	765	7096.2	1	5.090±4.861	0.018	0.347
Wk2toWk22	765	7096.3	0	0.043±8.145	0	0.346
Wk3to23	765	7096.3	1.1	0.904±8.263	0	0.346
Wk1toWk22	765	7096.3	1.1	0.960±8.053	0	0.346
Wk2toWk19	765	7096.3	1.1	1.758±8.089	0.001	0.346
Wk2toWk21	765	7096.3	1.1	1.766±8.242	0.001	0.346
Wk2toWk20	765	7096.3	1.1	1.947±8.050	0.001	0.346
Wk3toWk21	765	7096.3	1.1	2.385±7.666	0.001	0.346
Wk7to23	765	7096.3	1.1	2.531±7.991	0.002	0.346
Wk1toWk20	765	7096.3	1.1	2.784±7.922	0.001	0.345
Wk8to24	765	7096.3	1.1	3.449±7.142	0.004	0.346
we9to26	765	7096.3	1.1	3.901±7.236	0.005	0.346
Wk6toWk18	765	7096.3	1.1	3.905±7.103	0.004	0.345
Wk10to27	765	7096.3	1.1	3.977±6.883	0.006	0.346
Wk12to26	765	7096.3	1.1	4.353±6.488	0.008	0.347
Wk12to27	765	7096.3	1.1	4.424±6.741	0.008	0.347
we18to26	765	7096.3	1.1	4.814±5.087	0.015	0.346
Wk3toWk22	765	7096.4	1.2	0.775±7.690	0	0.346
Wk4to23	765	7096.4	1.2	0.994±7.944	0	0.346
Wk5toWk22	765	7096.4	1.2	2.264±7.574	0.001	0.346
Wk3toWk19	765	7096.4	1.2	2.385±7.426	0.001	0.346
Wk3toWk20	765	7096.4	1.2	2.478±7.363	0.001	0.346
Wk8toWk21	765	7096.4	1.2	2.872±7.129	0.002	0.346

Wk8toWk20	765	7096.4	1.2	3.226±7.046	0.003	0.346
we9to25	765	7096.4	1.2	3.788±6.848	0.005	0.346
Wk10to26	765	7096.4	1.2	3.908±6.646	0.006	0.346
Wk18to19	765	7096.4	1.2	3.973±2.783	0.033	0.347
Wk13to26	765	7096.4	1.2	4.096±6.033	0.008	0.347
Wk13to27	765	7096.4	1.2	4.169±6.287	0.008	0.347
Wk12to25	765	7096.4	1.2	4.171±6.071	0.008	0.347
Wk4toWk22	765	7096.5	1.3	0.837±7.287	0	0.346
Wk1toWk18	765	7096.5	1.3	0.915±7.483	0	0.346
Wk8to23	765	7096.5	1.3	1.024±7.444	0	0.346
Wk7toWk22	765	7096.5	1.3	2.113±7.172	0.001	0.346
Wk6toWk17	765	7096.5	1.3	2.246±6.887	0.001	0.345
Wk4toWk21	765	7096.5	1.3	2.340±7.216	0.001	0.346
Wk4toWk19	765	7096.5	1.3	2.352±6.977	0.001	0.345
Wk5toWk18	765	7096.5	1.3	2.373±6.988	0.001	0.346
Wk4toWk20	765	7096.5	1.3	2.462±6.972	0.001	0.345
Wk11to27	765	7096.5	1.3	2.718±6.829	0.003	0.346
Wk8toWk19	765	7096.5	1.3	2.866±6.746	0.003	0.346
Wk6toWk16	765	7096.5	1.3	2.982±6.745	0.002	0.345
Wk10to25	765	7096.5	1.3	3.720±6.225	0.006	0.346
Wk13to25	765	7096.5	1.3	3.975±5.666	0.009	0.347
Wk17to25	765	7096.5	1.3	4.291±5.011	0.013	0.347
Wk19to25	765	7096.5	1.3	4.408±4.959	0.013	0.346
we18to27	765	7096.5	1.3	4.440±5.157	0.012	0.346
Wk1toWk16	765	7096.6	1.4	0.055±6.977	0	0.346
Wk7toWk18	765	7096.6	1.4	2.353±6.710	0.002	0.346

Wk11to26	765	7096.6	1.4	2.655±6.574	0.003	0.346
we9to24	765	7096.6	1.4	2.683±6.414	0.003	0.346
Wk6toWk15	765	7096.6	1.4	2.779±6.346	0.002	0.345
Wk14to27	765	7096.6	1.4	3.674±5.689	0.007	0.347
Wk15to27	765	7096.6	1.4	3.807±5.564	0.008	0.347
Wk17to27	765	7096.6	1.4	3.891±5.344	0.009	0.347
Wk15to26	765	7096.6	1.4	3.939±5.443	0.009	0.347
Wk15to25	765	7096.6	1.4	4.031±5.211	0.011	0.347
Wk24to27	765	7096.6	1.4	4.117±3.686	0.02	0.346
Wk17to26	765	7096.6	1.4	4.158±5.268	0.011	0.347
Wk18to21	765	7096.6	1.4	4.234±4.085	0.016	0.346
we18to24	765	7096.6	1.4	4.243±4.659	0.014	0.347
Wk9to23	765	7096.7	1.5	0.579±6.693	0	0.346
Wk3toWk18	765	7096.7	1.5	0.675±6.846	0	0.346
Wk7toWk17	765	7096.7	1.5	0.777±6.557	0	0.346
Wk8toWk22	765	7096.7	1.5	0.860±6.793	0	0.346
Wk5toWk17	765	7096.7	1.5	0.900±6.821	0	0.346
Wk5toWk16	765	7096.7	1.5	1.509±6.717	0.001	0.346
Wk9toWk21	765	7096.7	1.5	2.139±6.361	0.002	0.346
Wk9toWk20	765	7096.7	1.5	2.375±6.207	0.002	0.346
Wk11to25	765	7096.7	1.5	2.506±6.088	0.003	0.346
Wk16to27	765	7096.7	1.5	3.505±5.255	0.008	0.347
Wk14to25	765	7096.7	1.5	3.623±5.183	0.009	0.347
Wk16to26	765	7096.7	1.5	3.644±5.135	0.009	0.347
Wk14to26	765	7096.7	1.5	3.658±5.479	0.008	0.347
Wk16to25	765	7096.7	1.5	3.732±4.895	0.011	0.347

Wk24to26	765	7096.7	1.5	3.855±3.073	0.025	0.346
Wk19to26	765	7096.7	1.5	3.862±5.052	0.009	0.346
Wk6toWk10	765	7096.7	1.5	3.989±3.996	0.015	0.346
Wk4toWk18	765	7096.8	1.6	0.732±6.408	0	0.346
Wk5toWk15	765	7096.8	1.6	1.354±6.339	0.001	0.346
Wk7toWk16	765	7096.8	1.6	1.409±6.360	0.001	0.346
Wk9toWk19	765	7096.8	1.6	2.067±5.909	0.002	0.346
Wk6toWk14	765	7096.8	1.6	2.390±5.908	0.002	0.345
Wk10to24	765	7096.8	1.6	2.721±5.822	0.003	0.346
Wk12to24	765	7096.8	1.6	3.052±5.640	0.005	0.346
Wk15to21	765	7096.8	1.6	3.404±5.044	0.008	0.347
Wk19to27	765	7096.8	1.6	3.523±5.116	0.007	0.346
Wk15to20	765	7096.8	1.6	3.623±4.669	0.011	0.347
Wk6toWk7	765	7096.8	1.6	3.701±3.042	0.021	0.344
Wk9toWk22	765	7096.9	1.7	0.482±6.158	0	0.346
Wk8toWk18	765	7096.9	1.7	0.841±6.108	0	0.346
Wk10to23	765	7096.9	1.7	0.927±6.088	0	0.346
Wk12to23	765	7096.9	1.7	1.138±5.926	0.001	0.346
Wk7toWk15	765	7096.9	1.7	1.289±6.042	0.001	0.346
Wk10toWk21	765	7096.9	1.7	2.227±5.619	0.002	0.346
Wk10toWk20	765	7096.9	1.7	2.456±5.479	0.003	0.346
Wk20to27	765	7096.9	1.7	2.587±5.476	0.004	0.346
Wk12toWk21	765	7096.9	1.7	2.627±5.437	0.004	0.346
Wk20to26	765	7096.9	1.7	2.846±5.397	0.005	0.346
Wk13to24	765	7096.9	1.7	2.950±5.275	0.005	0.346
Wk12toWk20	765	7096.9	1.7	2.974±5.323	0.005	0.346

Wk13toWk20	765	7096.9	1.7	3.037±5.003	0.006	0.346
Wk15to24	765	7096.9	1.7	3.146±4.934	0.007	0.347
Wk20to25	765	7096.9	1.7	3.159±5.137	0.006	0.346
Wk19to24	765	7096.9	1.7	3.274±4.646	0.008	0.346
Wk16to21	765	7096.9	1.7	3.293±4.783	0.009	0.347
Wk17to24	765	7096.9	1.7	3.439±4.800	0.009	0.347
Wk17to21	765	7096.9	1.7	3.541±4.597	0.01	0.347
Wk17to20	765	7096.9	1.7	3.725±4.061	0.015	0.347
Wk19to20	765	7096.9	1.7	3.729±3.456	0.015	0.344
Wk10toWk22	765	7097	1.8	0.812±5.620	0	0.346
Wk7toWk14	765	7097	1.8	0.984±5.666	0	0.346
Wk5toWk14	765	7097	1.8	1.018±5.847	0	0.346
Wk11to24	765	7097	1.8	1.572±5.644	0.001	0.346
Wk6toWk13	765	7097	1.8	2.171±5.289	0.002	0.346
Wk13toWk21	765	7097	1.8	2.693±5.151	0.005	0.346
Wk14to24	765	7097	1.8	2.762±4.869	0.006	0.347
Wk16to24	765	7097	1.8	2.958±4.674	0.007	0.347
Wk19to19	765	7097	1.8	3.145±2.398	0.021	0.342
Wk16to20	765	7097	1.8	3.241±4.191	0.011	0.347
Wk11toWk21	765	7097.1	1.9	0.885±5.373	0	0.346
Wk5toWk13	765	7097.1	1.9	0.952±5.321	0	0.346
Wk12toWk22	765	7097.1	1.9	0.981±5.377	0.001	0.346
Wk13to23	765	7097.1	1.9	1.148±5.533	0.001	0.346
Wk15to23	765	7097.1	1.9	1.309±5.255	0.001	0.346
Wk1toWk10	765	7097.1	1.9	1.402±5.321	0.001	0.346
Wk10toWk19	765	7097.1	1.9	2.162±5.163	0.003	0.346
Wk6toWk12	765	7097.1	1.9	2.177±4.915	0.003	0.346
Wk12toWk19	765	7097.1	1.9	2.457±4.799	0.004	0.346
Wk14toWk21	765	7097.1	1.9	2.688±4.823	0.005	0.346
Wk14toWk20	765	7097.1	1.9	2.915±4.559	0.007	0.346

Wk5toWk10	765	7097.1	1.9	2.966±4.461	0.007	0.346
Wk6toWk8	765	7097.1	1.9	3.324±3.357	0.015	0.346
Wk9toWk18	765	7097.2	2	0.401±5.240	0	0.346
Wk7toWk13	765	7097.2	2	0.966±5.203	0	0.346
Wk11toWk20	765	7097.2	2	1.065±5.238	0.001	0.346
Wk14to23	765	7097.2	2	1.092±5.088	0.001	0.346
Wk17to23	765	7097.2	2	1.269±5.237	0.001	0.346
Wk15to22	765	7097.2	2	1.294±5.019	0.001	0.346
Wk17to22	765	7097.2	2	1.385±5.192	0.001	0.346
Wk18to23	765	7097.2	2	1.886±4.880	0.002	0.346
Wk21to27	765	7097.2	2	1.955±4.772	0.003	0.346
Wk6toWk11	765	7097.2	2	2.238±4.525	0.003	0.346
Wk13toWk19	765	7097.2	2	2.434±4.403	0.005	0.346
Wk15to19	765	7097.2	2	2.829±3.959	0.009	0.347
Wk7toWk10	765	7097.2	2	2.938±3.723	0.01	0.346
Wk1toWk8	765	7097.3	2.1	0.464±5.012	0	0.346
Wk11toWk19	765	7097.3	2.1	0.777±4.821	0	0.346
Wk5toWk12	765	7097.3	2.1	0.959±4.959	0.001	0.346
Wk13toWk22	765	7097.3	2.1	1.002±5.026	0.001	0.346
Wk7toWk12	765	7097.3	2.1	1.059±4.949	0.001	0.346
Wk16to23	765	7097.3	2.1	1.077±4.932	0.001	0.346
Wk16to22	765	7097.3	2.1	1.119±4.811	0.001	0.346
Wk20to24	765	7097.3	2.1	1.635±4.580	0.002	0.346
Wk18to22	765	7097.3	2.1	1.941±4.595	0.003	0.346
Wk21to26	765	7097.3	2.1	2.066±4.569	0.003	0.346
Wk21to25	765	7097.3	2.1	2.238±4.225	0.005	0.346

Wk24to24	765	7097.3	2.1	2.449±1.608	0.037	0.347
Wk9toWk10	765	7097.3	2.1	2.628±3.851	0.007	0.346
Wk23to25	765	7097.3	2.1	2.905±2.637	0.022	0.347
Wk23to26	765	7097.3	2.1	2.937±3.130	0.016	0.347
Wk23to27	765	7097.3	2.1	2.984±3.532	0.013	0.347
Wk2toWk10	765	7097.4	2.2	0.468±4.811	0	0.346
Wk14toWk22	765	7097.4	2.2	0.985±4.675	0.001	0.346
Wk5toWk11	765	7097.4	2.2	1.040±4.660	0.001	0.346
Wk7toWk11	765	7097.4	2.2	1.147±4.504	0.001	0.346
Wk8toWk10	765	7097.4	2.2	2.307±3.900	0.005	0.346
Wk7toWk7	765	7097.4	2.2	2.848±2.678	0.017	0.346
Wk17to19	765	7097.4	2.2	2.858±3.256	0.014	0.347
Wk10toWk16	765	7097.5	2.3	0.074±4.422	0	0.346
Wk1toWk7	765	7097.5	2.3	0.140±4.614	0	0.346
Wk19to23	765	7097.5	2.3	0.205±4.626	0	0.346
Wk10toWk18	765	7097.5	2.3	0.685±4.514	0	0.346
Wk22to27	765	7097.5	2.3	1.785±4.051	0.003	0.346
Wk5toWk8	765	7097.5	2.3	2.056±3.917	0.005	0.346
Wk14toWk19	765	7097.5	2.3	2.257±3.903	0.006	0.346
Wk19to21	765	7097.5	2.3	2.333±3.573	0.006	0.346
Wk25to25	765	7097.5	2.3	2.663±2.825	0.012	0.344
Wk5toWk7	765	7097.6	2.4	2.027±3.743	0.004	0.346
Wk16to19	765	7097.6	2.4	2.333±3.358	0.009	0.347
Wk12toWk18	765	7097.7	2.5	0.799±4.047	0.001	0.346
Wk3toWk10	765	7097.7	2.5	0.880±4.043	0.001	0.346
Wk4toWk10	765	7097.7	2.5	1.088±4.032	0.001	0.346

Wk5toWk9	765	7097.7	2.5	1.154±3.926	0.001	0.346
Wk25to27	765	7097.7	2.5	1.407±3.768	0.002	0.346
Wk22to26	765	7097.7	2.5	1.773±3.705	0.004	0.346
Wk22to25	765	7097.7	2.5	1.996±3.425	0.006	0.346
Wk6toWk9	765	7097.7	2.5	2.100±3.468	0.006	0.346
Wk19to22	765	7097.8	2.6	0.123±3.916	0	0.346
Wk21to24	765	7097.8	2.6	1.017±3.671	0.001	0.346
Wk12toWk16	765	7097.9	2.7	0.171±3.621	0	0.346
Wk13toWk18	765	7097.9	2.7	0.814±3.658	0.001	0.346
Wk3toWk8	765	7098	2.8	0.176±3.543	0	0.346
Wk12toWk15	765	7098.1	2.9	0.097±3.347	0	0.346
Wk4toWk8	765	7098.1	2.9	0.275±3.373	0	0.346
Wk14toWk18	765	7098.1	2.9	0.769±3.204	0.001	0.346
Wk15to18	765	7098.1	2.9	0.983±3.217	0.002	0.346
Wk25to26	765	7098.1	2.9	1.336±3.035	0.003	0.346
Wk7toWk8	765	7098.1	2.9	1.778±2.703	0.007	0.346
Wk1toWk3	765	7098.2	3	0.086±3.115	0	0.346
Wk7toWk9	765	7098.2	3	0.965±2.999	0.002	0.346
Wk4toWk7	765	7098.3	3.1	0.043±2.973	0	0.346
Wk13toWk16	765	7098.3	3.1	0.212±3.092	0	0.346
we20to20	765	7098.3	3.1	0.741±2.918	0.001	0.346
Wk22to24	765	7098.3	3.1	0.996±2.908	0.002	0.346
Wk23to24	765	7098.3	3.1	1.837±2.026	0.015	0.347
Wk13toWk15	765	7098.4	3.2	0.154±2.816	0	0.346
Wk20to21	765	7098.4	3.2	0.158±2.952	0	0.346
Wk15to16	765	7098.4	3.2	0.424±2.874	0	0.346

Wk5toWk6	765	7098.5	3.3	0.207±2.805	0	0.346
Wk15to15	765	7098.5	3.3	0.503±2.638	0.001	0.346
Wk16to18	765	7098.5	3.3	0.693±2.602	0.001	0.346
Wk14toWk16	765	7098.6	3.4	0.220±2.595	0	0.346
Wk18to18	765	7098.6	3.4	1.529±1.865	0.012	0.347
Wk1toWk2	765	7098.7	3.5	0.193±2.466	0	0.346
Wk8toWk8	765	7098.7	3.5	0.598±2.423	0.001	0.346
Wk17to18	765	7098.7	3.5	0.772±2.360	0.002	0.346
Wk6toWk6	765	7098.7	3.5	1.404±1.931	0.008	0.346
Wk14toWk15	765	7098.8	3.6	0.190±2.372	0	0.346
Wk16to16	765	7099.1	3.9	0.128±2.049	0	0.346
Wk1toWk1	765	7099.1	3.9	0.922±1.706	0.004	0.346
Wk23to23	765	7099.3	4.1	0.052±1.805	0	0.346

Population moving window models

Table S3.8a. *D.platanoidis* growth rates as a function of temperature, weather variables selected are all possible monthly combinations of temperature from November in the previous year to October in the focal year. Models are mixed effects models with density dependence, year and tree identity included in all models. Slopes reported with ± 1SE, ΔAICc given relative to best fitting model. Random effects only model AICc = 1038.438

***Denotes best model where used in stage two modelling**

Time window (Months)	n	AICc	ΔAICc	Slope±1SE	$R^2GLMM_{(m)}$	R2GLMM$_{(c)}$
Mar-Jul*	**954**	**1040.1**	**0.0**	**-0.735±3.828**	**0.309**	**0.911**
Mar-Jun	954	1040.2	0.1	-0.735±3.16	0.312	0.911
Mar-May	954	1040.2	0.1	-0.735±2.347	0.325	0.912
May-Jun	954	1040.3	0.2	-0.736±3.418	0.293	0.908
Dec-Jul	954	1040.4	0.2	-0.735±2.457	0.311	0.911
May	954	1040.4	0.2	-0.737±1.974	0.313	0.907

Dec-Oct	954	1040.4	0.3	-0.735±3.096	0.305	0.911
Mar-Apr	954	1040.5	0.4	-0.735±4.165	0.302	0.912
Dec-Jun	954	1040.5	0.4	-0.735±1.999	0.313	0.911
Mar-Aug	954	1040.5	0.4	-0.735±3.946	0.306	0.912
Nov-Oct	954	1040.5	0.4	-0.735±3.214	0.301	0.912
Nov-Jul	954	1040.6	0.4	-0.735±2.604	0.304	0.911
Dec-Aug	954	1040.6	0.4	-0.735±2.709	0.309	0.911
Dec-May	954	1040.6	0.5	-0.735±1.564	0.319	0.911
Apr-Jul	954	1040.6	0.5	-0.735±4.037	0.3	0.911
Dec-Sep	954	1040.6	0.5	-0.735±2.942	0.303	0.911
Jan-Jul	954	1040.6	0.5	-0.735±2.894	0.304	0.912
Apr-Jun	954	1040.6	0.5	-0.735±3.441	0.3	0.911
Jan-Oct	954	1040.7	0.5	-0.734±3.482	0.301	0.912
Mar-Sep	954	1040.7	0.5	-0.734±4.093	0.3	0.912
May-Jul	954	1040.7	0.6	-0.735±3.838	0.297	0.91
Nov-Aug	954	1040.7	0.6	-0.735±2.821	0.303	0.912
Nov-Sep	954	1040.7	0.6	-0.735±3.064	0.3	0.912
Nov-June	954	1040.7	0.6	-0.735±2.161	0.305	0.911
Dec-Jan	954	1040.7	0.6	-0.735±0.633	0.349	0.912
Jan-Aug	954	1040.8	0.6	-0.734±3.148	0.303	0.912
Nov-May	954	1040.8	0.7	-0.735±1.756	0.308	0.912
Apr-Oct	954	1040.8	0.7	-0.734±4.191	0.3	0.912
Jan-Sep	954	1040.8	0.7	-0.734±3.35	0.3	0.912
Apr-Aug	954	1040.8	0.7	-0.734±4.177	0.301	0.912
Feb-Oct	954	1040.9	0.8	-0.734±3.726	0.301	0.913
Dec-Apr	954	1040.9	0.8	-0.735±1.357	0.318	0.912

Feb-Jul	954	1040.9	0.8	-0.734±3.287	0.301	0.913
Jan-Jun	954	1040.9	0.8	-0.735±2.279	0.305	0.912
Apr-May	954	1040.9	0.8	-0.735±2.38	0.31	0.912
Apr-Sep	954	1040.9	0.8	-0.734±4.265	0.299	0.913
May-Oct	954	1040.9	0.8	-0.734±4.043	0.298	0.912
Mar-Apr	954	1041.0	0.9	-0.734±2.085	0.32	0.914
Dec-Mar	954	1041.0	0.9	-0.735±1.025	0.32	0.912
Feb-Sep	954	1041.0	0.9	-0.734±3.619	0.301	0.913
Feb-Aug	954	1041.0	0.9	-0.734±3.435	0.302	0.913
May-Aug	954	1041.0	0.9	-0.734±3.945	0.3	0.912
Nov-Apr	954	1041.1	0.9	-0.734±1.568	0.308	0.913
May-Sep	954	1041.1	1.0	-0.734±4.093	0.297	0.912
Jan-May	954	1041.1	1.0	-0.734±1.726	0.309	0.912
Dec	954	1041.1	1.0	-0.735±0.549	0.346	0.912
Feb-Jun	954	1041.1	1.0	-0.734±2.586	0.302	0.913
Mar	954	1041.3	1.1	-0.734±1.232	0.333	0.914
Jun-Oct	954	1041.3	1.1	-0.734±4.014	0.304	0.914
Nov-Mar	954	1041.3	1.1	-0.734±1.252	0.308	0.912
Jun-Sep	954	1041.4	1.3	-0.733±4.086	0.308	0.914
Aug-Oct	954	1041.4	1.3	-0.734±3.555	0.305	0.914
Jan-Apr	954	1041.4	1.3	-0.734±1.479	0.308	0.913
Jul-Oct	954	1041.4	1.3	-0.734±3.654	0.305	0.914
Feb-May	954	1041.5	1.3	-0.734±1.903	0.304	0.913
Jun	954	1041.5	1.3	-0.734±3.726	0.307	0.914
Dec-Feb	954	1041.5	1.4	-0.735±0.825	0.312	0.912
Nov-Jan	954	1041.5	1.4	-0.734±0.924	0.316	0.912

Jan	954	1041.5	1.4	-0.735±0.617	0.334	0.913
Aug-Sep	954	1041.6	1.4	-0.733±3.667	0.314	0.915
Jan-Mar	954	1041.6	1.4	-0.734±1.124	0.308	0.913
Jul-Sep	954	1041.6	1.5	-0.733±3.758	0.308	0.914
Jun-Aug	954	1041.6	1.5	-0.734±3.771	0.306	0.914
Feb-Apr	954	1041.6	1.5	-0.733±1.593	0.309	0.914
Jun-Jul	954	1041.7	1.5	-0.734±3.569	0.305	0.914
Nov-Feb	954	1041.7	1.6	-0.734±1.066	0.304	0.913
Sep-Oct	954	1041.8	1.6	-0.734±2.633	0.304	0.914
Sep	954	1042.0	1.9	-0.733±2.679	0.317	0.915
Oct	954	1042.0	1.9	-0.734±1.814	0.315	0.914
Jul-Aug	954	1042.0	1.9	-0.734±3.167	0.307	0.914
Apr	954	1042.0	1.9	-0.733±1.721	0.308	0.914
Feb-Mar	954	1042.0	1.9	-0.733±1.117	0.308	0.914
Nov	954	1042.1	2.0	-0.733±1.064	0.332	0.916
Feb	954	1042.1	2.0	-0.733±0.706	0.34	0.916
Jan-Feb	954	1042.1	2.0	-0.734±0.845	0.304	0.914
Nov-Dec	954	1042.2	2.1	-0.734±0.919	0.307	0.913
Aug	954	1042.4	2.2	-0.733±2.704	0.308	0.914
Jul	954	1042.4	2.3	-0.734±2.572	0.307	0.914

Table S3.8b. *D.platanoidis* growth rates as a function of precipitation, weather variables selected are all possible monthly combinations of Precipitation from November in the previous year to October in the focal year. Models are mixed effects models with density dependence, year and tree identity included in all models. Slopes reported with ± 1SE, ΔAICc given relative to best fitting model. Random effects only model AICc = 1038.438

***Denotes best model where used in stage two modelling**

Time window (Months)	n	AICc	ΔAICc	Slope±1SE	$R^2GLMM_{(m)}$	$R2GLMM_{(c)}$
Mar-Jul*	**954**	**1040.1**	**0**	**-0.735±3.828**	**0.309**	**0.911**

Mar-Jun	954	1040.2	0.1	-0.735±3.16	0.312	0.911
Mar-May	954	1040.2	0.1	-0.735±2.347	0.325	0.912
May-Jun	954	1040.3	0.2	-0.736±3.418	0.293	0.908
Dec-Jul	954	1040.4	0.2	-0.735±2.457	0.311	0.911
May	954	1040.4	0.2	-0.737±1.974	0.313	0.907
Dec-Oct	954	1040.4	0.3	-0.735±3.096	0.305	0.911
Mar-Apr	954	1040.5	0.4	-0.735±4.165	0.302	0.912
Dec-Jun	954	1040.5	0.4	-0.735±1.999	0.313	0.911
Mar-Aug	954	1040.5	0.4	-0.735±3.946	0.306	0.912
Nov-Oct	954	1040.5	0.4	-0.735±3.214	0.301	0.912
Nov-Jul	954	1040.6	0.4	-0.735±2.604	0.304	0.911
Dec-Aug	954	1040.6	0.4	-0.735±2.709	0.309	0.911
Dec-May	954	1040.6	0.5	-0.735±1.564	0.319	0.911
Apr-Jul	954	1040.6	0.5	-0.735±4.037	0.3	0.911
Dec-Sep	954	1040.6	0.5	-0.735±2.942	0.303	0.911
Jan-Jul	954	1040.6	0.5	-0.735±2.894	0.304	0.912
Apr-Jun	954	1040.6	0.5	-0.735±3.441	0.3	0.911
Jan-Oct	954	1040.7	0.5	-0.734±3.482	0.301	0.912
Mar-Sep	954	1040.7	0.5	-0.734±4.093	0.3	0.912
May-Jul	954	1040.7	0.6	-0.735±3.838	0.297	0.91
Nov-Aug	954	1040.7	0.6	-0.735±2.821	0.303	0.912
Nov-Sep	954	1040.7	0.6	-0.735±3.064	0.3	0.912
Nov-June	954	1040.7	0.6	-0.735±2.161	0.305	0.911
Dec-Jan	954	1040.7	0.6	-0.735±0.633	0.349	0.912
Jan-Aug	954	1040.8	0.6	-0.734±3.148	0.303	0.912
Nov-May	954	1040.8	0.7	-0.735±1.756	0.308	0.912
Apr-Oct	954	1040.8	0.7	-0.734±4.191	0.3	0.912
Jan-Sep	954	1040.81	0.7	-0.734±3.35	0.3	0.912
Apr-Aug	954	1040.8	0.7	-0.734±4.177	0.301	0.912
Feb-Oct	954	1040.9	0.8	-0.734±3.726	0.301	0.913
Dec-Apr	954	1040.9	0.8	-0.735±1.357	0.318	0.912
Feb-Jul	954	1040.9	0.8	-0.734±3.287	0.301	0.913
Jan-Jun	954	1040.9	0.8	-0.735±2.279	0.305	0.912
Apr-May	954	1040.9	0.8	-0.735±2.38	0.31	0.912
Apr-Sep	954	1040.9	0.8	-0.734±4.265	0.299	0.913
May-Oct	954	1040.9	0.8	-0.734±4.043	0.298	0.912
Mar-Apr	954	1041.0	0.9	-0.734±2.085	0.32	0.914
Dec-Mar	954	1041.0	0.9	-0.735±1.025	0.32	0.912
Feb-Sep	954	1041.0	0.9	-0.734±3.619	0.301	0.913
Feb-Aug	954	1041.0	0.9	-0.734±3.435	0.302	0.913
May-Aug	954	1041.0	0.9	-0.734±3.945	0.3	0.912

Nov-Apr	954	1041.1	0.9	-0.734±1.568	0.308	0.913
May-Sep	954	1041.1	1.0	-0.734±4.093	0.297	0.912
Jan-May	954	1041.1	1.0	-0.734±1.726	0.309	0.912
Dec	954	1041.1	1.0	-0.735±0.549	0.346	0.912
Feb-Jun	954	1041.1	1.0	-0.734±2.586	0.302	0.913
Mar	954	1041.3	1.1	-0.734±1.232	0.333	0.914
Jun-Oct	954	1041.3	1.1	-0.734±4.014	0.304	0.914
Nov-Mar	954	1041.3	1.1	-0.734±1.252	0.308	0.912
Jun-Sep	954	1041.4	1.3	-0.733±4.086	0.308	0.914
Aug-Oct	954	1041.4	1.3	-0.734±3.555	0.305	0.914
Jan-Apr	954	1041.4	1.3	-0.734±1.479	0.308	0.913
Jul-Oct	954	1041.4	1.3	-0.734±3.654	0.305	0.914
Feb-May	954	1041.5	1.3	-0.734±1.903	0.304	0.913
Jun	954	1041.5	1.3	-0.734±3.726	0.307	0.914
Dec-Feb	954	1041.5	1.4	-0.735±0.825	0.312	0.912
Nov-Jan	954	1041.5	1.4	-0.734±0.924	0.316	0.912
Jan	954	1041.5	1.4	-0.735±0.617	0.334	0.913
Aug-Sep	954	1041.6	1.4	-0.733±3.667	0.314	0.915
Jan-Mar	954	1041.6	1.4	-0.734±1.124	0.308	0.913
Jul-Sep	954	1041.6	1.5	-0.733±3.758	0.308	0.914
Jun-Aug	954	1041.6	1.5	-0.734±3.771	0.306	0.914
Feb-Apr	954	1041.6	1.5	-0.733±1.593	0.309	0.914
Jun-Jul	954	1041.7	1.5	-0.734±3.569	0.305	0.914
Nov-Feb	954	1041.7	1.6	-0.734±1.066	0.304	0.913
Sep-Oct	954	1041.8	1.6	-0.734±2.633	0.304	0.914
Sep	954	1042.0	1.9	-0.733±2.679	0.317	0.915
Oct	954	1042.0	1.9	-0.734±1.814	0.315	0.914
Jul-Aug	954	1042.0	1.9	-0.734±3.167	0.307	0.914
Apr	954	1042.0	1.9	-0.733±1.721	0.308	0.914
Feb-Mar	954	1042.0	1.9	-0.733±1.117	0.308	0.914
Nov	954	1042.1	2.0	-0.733±1.064	0.332	0.916
Feb	954	1042.1	2.0	-0.733±0.706	0.34	0.916
Jan-Feb	954	1042.1	2.0	-0.734±0.845	0.304	0.914
Nov-Dec	954	1042.2	2.0	-0.734±0.919	0.307	0.913
Aug	954	1042.4	2.2	-0.733±2.704	0.308	0.914
Jul	954	1042.4	2.3	-0.734±2.572	0.307	0.914

Table S3.9a. *P.testudinaceus* growth rates as a function of temperature, weather variables selected are all possible monthly combinations of temperature from November in the previous year to October in the focal year. Models are mixed effects models with density dependence, year and tree identity included in all models. Slopes reported with ± 1SE, ΔAICc given relative to best fitting model. Random effects only model AICc = 1250.8.

***Denotes best model where used in stage two modelling**

Time window (Months)	n	AICc	ΔAICc	Slope±1SE	R^{2}GLMM$_{(m)}$	R2GLMM$_{(c)}$
Feb-Sep*	**945**	**1808.5**	**0**	**-0.853±3.311**	**0.431**	**0.856**
Feb-Oct	945	1808.5	0.0	-0.853±3.425	0.428	0.856
Feb-Jul	945	1808.6	0.1	-0.854±3.031	0.423	0.855
Mar-Apr	945	1808.8	0.3	-0.853±3.906	0.418	0.855
Mar-Sep	945	1808.8	0.3	-0.853±3.822	0.42	0.856
Feb-Aug	945	1808.8	0.4	-0.853±3.177	0.422	0.856
May-Sep	945	1808.9	0.4	-0.853±3.783	0.428	0.857
Feb-Mar	945	1808.9	0.4	-0.854±1.006	0.443	0.857
Sep	945	1808.9	0.5	-0.853±2.414	0.444	0.857
May-Oct	945	1809.0	0.5	-0.853±3.764	0.422	0.856
Aug-Sep	945	1809.0	0.5	-0.853±3.358	0.438	0.858
Apr-Sep	945	1809.0	0.6	-0.853±3.977	0.415	0.855
Mar-Jul	945	1809.0	0.6	-0.854±3.657	0.408	0.854
Apr-Oct	945	1809.0	0.6	-0.853±3.925	0.413	0.855
Jun-Sep	945	1809.1	0.6	-0.853±3.764	0.425	0.856
Feb-Jun	945	1809.1	0.6	-0.854±2.400	0.416	0.855
Jan-Oct	945	1809.1	0.6	-0.853±3.283	0.413	0.855
Jun-Oct	945	1809.1	0.7	-0.853±3.719	0.42	0.856
Mar-Aug	945	1809.1	0.7	-0.853±3.738	0.41	0.855
Jul-Sep	945	1809.1	0.7	-0.853±3.451	0.432	0.857
Jan-Sep	945	1809.2	0.7	-0.853±3.150	0.413	0.856
Aug-Oct	945	1809.2	0.8	-0.853±3.292	0.422	0.856
May-Jul	945	1809.3	0.8	-0.853±3.631	0.415	0.855
Jul-Oct	945	1809.3	0.8	-0.853±3.384	0.422	0.856
Feb	945	1809.3	0.8	-0.854±0.642	0.446	0.856
Apr-Jul	945	1809.3	0.9	-0.854±3.836	0.403	0.854
Apr-Aug	945	1809.3	0.9	-0.853±3.945	0.406	0.855
Nov-Oct	945	1809.4	0.9	-0.853±3.064	0.403	0.854
Mar-Jun	945	1809.4	0.9	-0.854±3.044	0.403	0.854
May-Aug	945	1809.4	0.9	-0.853±3.707	0.416	0.856
Jan-Aug	945	1809.4	1.0	-0.853±2.985	0.407	0.855
Jan-Jul	945	1809.4	1.0	-0.853±2.757	0.405	0.855
Feb-May	945	1809.4	1.0	-0.854±1.770	0.416	0.855
Dec-Oct	945	1809.5	1.0	-0.853±2.969	0.404	0.855
Nov-Sep	945	1809.5	1.0	-0.853±2.915	0.403	0.854
Feb-Apr	945	1809.5	1.0	-0.854±1.474	0.414	0.854

May-Jun	945	1809.5	1.0	-0.853±3.292	0.409	0.855
Dec-Sep	945	1809.5	1.1	-0.853±2.815	0.404	0.855
Apr-Jun	945	1809.6	1.1	-0.853±3.293	0.399	0.854
Nov-Jul	945	1809.6	1.1	-0.853±2.499	0.399	0.854
Nov-Aug	945	1809.6	1.2	-0.853±2.696	0.4	0.854
Sep-Oct	945	1809.7	1.2	-0.853±2.442	0.416	0.855
Jan	945	1809.7	1.2	-0.855±0.578	0.421	0.851
Mar-May	945	1809.7	1.3	-0.853±2.282	0.402	0.854
Dec-Aug	945	1809.7	1.3	-0.853±2.609	0.401	0.854
Dec-Jul	945	1809.7	1.3	-0.853±2.382	0.4	0.854
Nov-June	945	1809.7	1.3	-0.853±2.073	0.399	0.854
Jan-Jun	945	1809.7	1.3	-0.853±2.175	0.402	0.854
Jun-Aug	945	1809.8	1.3	-0.853±3.526	0.41	0.855
Nov-Jan	945	1809.8	1.3	-0.854±0.867	0.42	0.854
Jun	945	1809.8	1.3	-0.854±3.498	0.401	0.854
Mar-Apr	945	1809.8	1.3	-0.853±1.987	0.399	0.854
Nov-Apr	945	1809.8	1.4	-0.853±1.492	0.401	0.854
Jun-Jul	945	1809.8	1.4	-0.853±3.335	0.408	0.854
Dec-Jan	945	1809.9	1.4	-0.854±0.612	0.421	0.853
Nov-May	945	1809.9	1.4	-0.853±1.687	0.399	0.854
Dec-Jun	945	1809.9	1.5	-0.853±1.940	0.399	0.854
Jan-May	945	1810.0	1.6	-0.853±1.652	0.401	0.854
Dec-Apr	945	1810.0	1.6	-0.853±1.308	0.4	0.854
Jan-Apr	945	1810.1	1.6	-0.853±1.404	0.4	0.854
Mar	945	1810.1	1.6	-0.853±1.176	0.414	0.855
Apr-May	945	1810.1	1.6	-0.853±2.293	0.399	0.854
Dec-May	945	1810.1	1.6	-0.853±1.522	0.399	0.854
Nov-Mar	945	1810.1	1.7	-0.853±1.196	0.399	0.854
Jul-Aug	945	1810.2	1.7	-0.853±2.965	0.411	0.856
Apr	945	1810.2	1.8	-0.853±1.612	0.411	0.856
Jan-Mar	945	1810.2	1.8	-0.853±1.068	0.404	0.855
Nov-Feb	945	1810.3	1.8	-0.854±1.009	0.401	0.854
May	945	1810.4	1.9	-0.853±1.951	0.41	0.855
Dec-Mar	945	1810.4	1.9	-0.853±0.995	0.399	0.854
Dec-Feb	945	1810.5	2.1	-0.854±0.793	0.4	0.853
Nov-Dec	945	1810.6	2.1	-0.853±0.865	0.41	0.855
Jul	945	1810.6	2.2	-0.853±2.407	0.409	0.855
Jan-Feb	945	1810.7	2.2	-0.853±0.800	0.399	0.854
Aug	945	1810.7	2.3	-0.853±2.544	0.406	0.855
Oct	945	1810.7	2.3	-0.853±1.724	0.4	0.854
Dec	945	1810.9	2.4	-0.854±0.540	0.414	0.854

Nov	945	1811.0	2.5	-0.853±1.016	0.402	0.854

Table S3.9b. *P.testudinaceus* growth rates as a function of precipitation, weather variables selected are all possible monthly combinations of precipitation from November in the previous year to October in the focal year. Models are mixed effects models with density dependence, year and tree identity included in all models. Slopes reported with ± 1SE, ΔAICc given relative to best fitting model. Random effects only model AICc = 1250.8.

***Denotes best model where used in stage two modelling**

Time window (Months)	n	AICc	ΔAICc	Slope±1SE	R^2GLMM$_{(m)}$	R2GLMM$_{(c)}$
Aug-Oct	945	1806.7	0	-0.853±0.575	0.477	0.86
Jul-Oct	945	1807.2	0.5	-0.853±0.762	0.445	0.857
Feb-Oct	945	1807.4	0.7	-0.853±0.872	0.432	0.857
Jan-Oct	945	1807.6	0.9	-0.853±1.008	0.417	0.855
Nov-Jul	945	1807.7	1	-0.852±0.931	0.433	0.859
May-Oct	945	1807.7	1	-0.853±0.822	0.432	0.857
Feb-Sep	945	1807.7	1	-0.853±0.951	0.415	0.855
Nov-Sep	945	1807.8	1.1	-0.853±1.158	0.409	0.856
Feb-Aug	945	1807.8	1.1	-0.853±0.884	0.414	0.855
Feb-May	945	1807.9	1.2	-0.853±0.646	0.428	0.856
Jan-Sep	945	1807.9	1.2	-0.853±1.071	0.402	0.854
Nov-Aug	945	1807.9	1.2	-0.853±1.101	0.412	0.856
Jan-Aug	945	1807.9	1.2	-0.853±1.037	0.402	0.854
Dec-Sep	945	1807.9	1.2	-0.853±1.131	0.4	0.854
Dec-Aug	945	1808	1.3	-0.853±1.118	0.4	0.854
Nov-Jun	945	1808	1.3	-0.853±0.947	0.423	0.858
Dec-Oct	945	1808	1.3	-0.854±1.057	0.402	0.854
Dec-Jul	945	1808	1.3	-0.853±0.918	0.414	0.856
Aug-Sep	945	1808	1.3	-0.853±0.550	0.442	0.857
May	945	1808	1.3	-0.853±0.448	0.45	0.859
Dec-Jan	945	1808	1.3	-0.851±0.569	0.472	0.864
Feb-Jun	945	1808	1.3	-0.853±0.829	0.412	0.855
Nov-Oct	945	1808.1	1.4	-0.853±1.118	0.398	0.854
Dec-Jun	945	1808.2	1.5	-0.853±0.947	0.406	0.855

Nov-Jan	945	1808.2	1.5	-0.851±0.568	0.477	0.865
Jan-Jun	945	1808.2	1.5	-0.853±0.925	0.399	0.854
Mar-Oct	945	1808.2	1.5	-0.853±0.779	0.417	0.856
Apr-Oct	945	1808.2	1.5	-0.853±0.731	0.426	0.858
Oct	945	1808.3	1.6	-0.853±0.431	0.465	0.859
Jun-Oct	945	1808.3	1.6	-0.853±0.805	0.417	0.856
Feb	945	1808.3	1.6	-0.856±0.415	0.423	0.85
Jan-Jul	945	1808.3	1.6	-0.853±0.867	0.401	0.854
Jul-Sep	945	1808.3	1.6	-0.853±0.801	0.408	0.854
May-Sep	945	1808.4	1.7	-0.853±0.819	0.406	0.855
Mar-Sep	945	1808.4	1.7	-0.853±0.825	0.403	0.855
Jan-May	945	1808.5	1.8	-0.854±0.752	0.403	0.854
Feb-Jul	945	1808.5	1.8	-0.853±0.776	0.4	0.854
Apr-Sep	945	1808.5	1.8	-0.853±0.768	0.408	0.856
Mar-Aug	945	1808.6	1.9	-0.853±0.761	0.402	0.854
Aug	945	1808.6	1.9	-0.854±0.383	0.449	0.857
Feb-Apr	945	1808.6	1.9	-0.853±0.607	0.41	0.854
Nov-Apr	945	1808.6	1.9	-0.852±0.732	0.425	0.858
Nov-May	945	1808.7	2	-0.853±0.803	0.41	0.856
Jun-Jul	945	1808.7	2	-0.854±0.414	0.426	0.855
Mar-Jul	945	1808.7	2	-0.854±0.627	0.399	0.853
Jun-Sep	945	1808.7	2	-0.853±0.749	0.399	0.854
Apr-Aug	945	1808.8	2.1	-0.853±0.689	0.407	0.855
Dec-May	945	1808.8	2.1	-0.853±0.766	0.399	0.854
Dec-Apr	945	1808.9	2.2	-0.853±0.706	0.408	0.855
May-Aug	945	1808.9	2.2	-0.853±0.652	0.404	0.855
Nov-Mar	945	1808.9	2.2	-0.852±0.646	0.433	0.86
Jan-Apr	945	1808.9	2.2	-0.853±0.692	0.399	0.854
Mar-Jun	945	1808.9	2.2	-0.853±0.617	0.398	0.854
Feb-Mar	945	1809	2.3	-0.854±0.503	0.397	0.851
Sep-Oct	945	1809.1	2.4	-0.853±0.481	0.432	0.857
May-Jul	945	1809.1	2.4	-0.854±0.542	0.402	0.853

Nov-Dec	945	1809.1	2.4	-0.851±0.499	0.462	0.864
Dec-Mar	945	1809.1	2.4	-0.853±0.640	0.417	0.857
Nov-Feb	945	1809.1	2.4	-0.852±0.635	0.432	0.86
Apr-Jul	945	1809.2	2.5	-0.854±0.557	0.397	0.853
Mar-May	945	1809.2	2.5	-0.853±0.516	0.408	0.855
Jan	945	1809.2	2.5	-0.853±0.472	0.437	0.859
May-Jun	945	1809.2	2.5	-0.853±0.552	0.399	0.854
Jul-Aug	945	1809.3	2.6	-0.853±0.543	0.404	0.854
Dec	945	1809.3	2.6	-0.852±0.464	0.451	0.861
Dec-Feb	945	1809.3	2.6	-0.853±0.640	0.413	0.857
Jul	945	1809.4	2.7	-0.853±0.375	0.425	0.856
Jan-March	945	1809.4	2.7	-0.853±0.573	0.399	0.854
Jun-Aug	945	1809.4	2.7	-0.853±0.552	0.399	0.854
Apr-May	945	1809.4	2.7	-0.853±0.433	0.424	0.858
Apr-Jun	945	1809.4	2.7	-0.853±0.516	0.401	0.854
Jan-Feb	945	1809.6	2.9	-0.854±0.561	0.396	0.853
Mar	945	1809.6	2.9	-0.853±0.395	0.41	0.856
Jun	945	1809.7	3	-0.854±0.350	0.41	0.853
Mar-Apr	945	1809.7	3	-0.854±0.436	0.398	0.854
Nov	945	1810.1	3.4	-0.852±0.427	0.442	0.861
Sep	945	1810.4	3.7	-0.853±0.385	0.4	0.854
Apr	945	1810.7	4	-0.853±0.332	0.402	0.855

Table. S3.10

Table showing the length of the aphid season for *D.platanoidis* and *P.testudinaceus*. Calculated as first week where aphids were present to first week where there had been two consequtive weeks without any aphids, or final date where records were collected if during November or December.

Year	D.platanoidis		P.testudinaceus	
	Start	Finish	Start	Finish
1993	26/03/1993	11/11/1993	02/04/1993	28/11/1993
1994	10/03/1994	01/12/1994	31/03/1994	08/12/1994
1995	16/03/1995	30/11/1995	06/04/1995	30/11/1995
1996	02/04/1996	26/11/1996	17/04/1996	26/11/1996
1997	13/03/1997	28/11/1997	03/04/1997	20/11/1997
1998	19/03/1998	14/12/1998	02/04/1998	14/12/1998
1999	11/03/1999	25/11/1999	01/04/1999	11/11/1999
2000	16/03/2000	29/11/2000	16/03/2000	29/11/2000
2001	29/03/2001	13/12/2001	12/04/2001	06/12/2001
2002	28/02/2002	28/11/2002	21/03/2002	21/11/2002
2003	13/03/2003	27/11/2003	03/04/2003	27/11/2003
2004	11/03/2004	01/12/2004	01/04/2004	24/11/2004
2005	17/03/2005	08/12/2005	31/03/2005	08/12/2005
2006	30/03/2006	14/12/2006	30/03/2006	07/12/2006
2007	01/03/2007	29/11/2007	08/03/2007	29/11/2007
2008	21/02/2008	26/11/2008	12/03/2008	12/11/2008
2009	02/04/2009	26/11/2009	02/04/2009	26/11/2009
2010	25/03/2010	02/12/2010	18/03/2010	02/12/2010
2011	10/03/2011	01/12/2011	10/03/2011	01/12/2011
2012	08/03/2012	21/11/2012	22/03/2012	21/11/2012

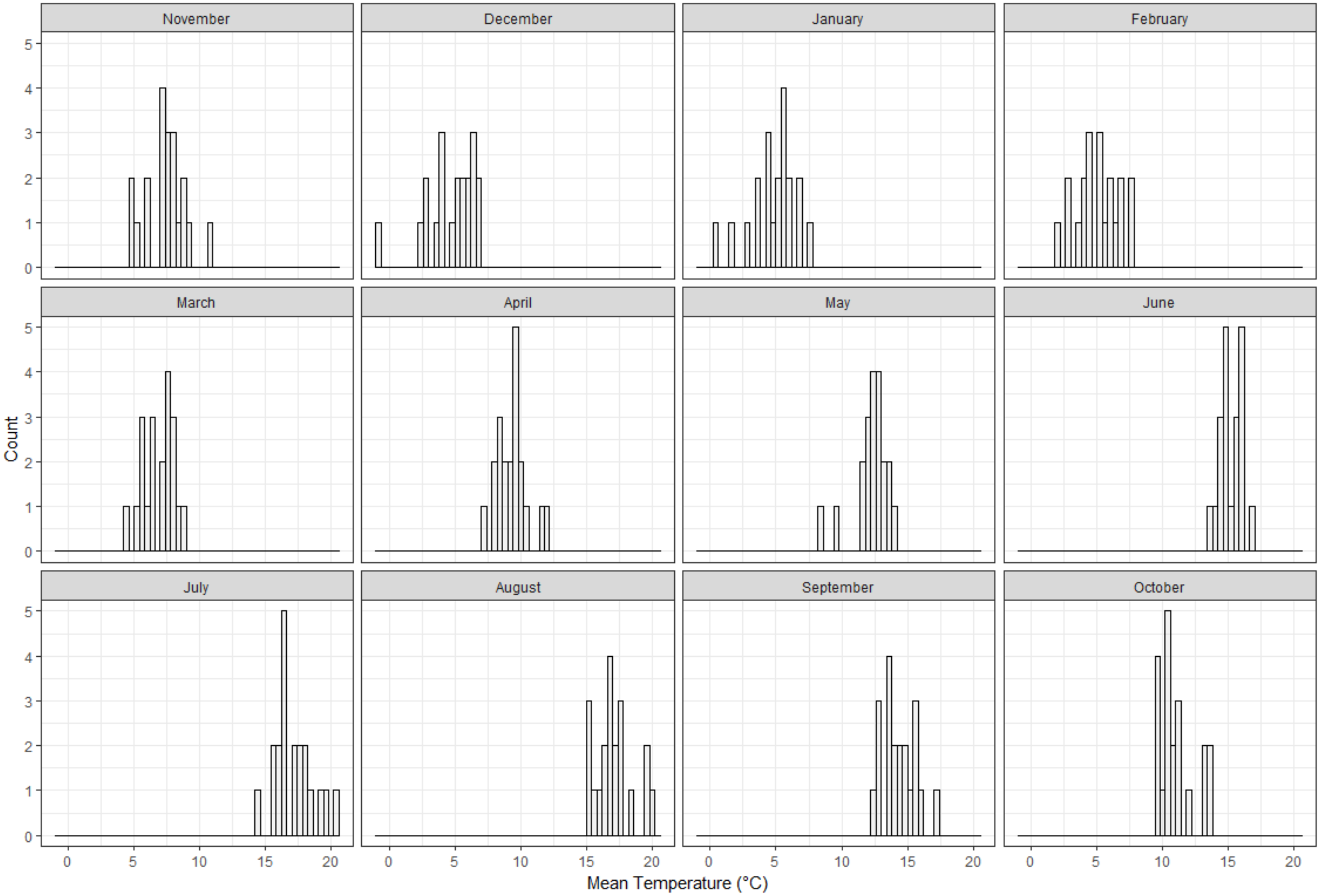

Figure S3.1. Variation in mean temperatrure in each month °C across the 20 year study period (1993-2012)

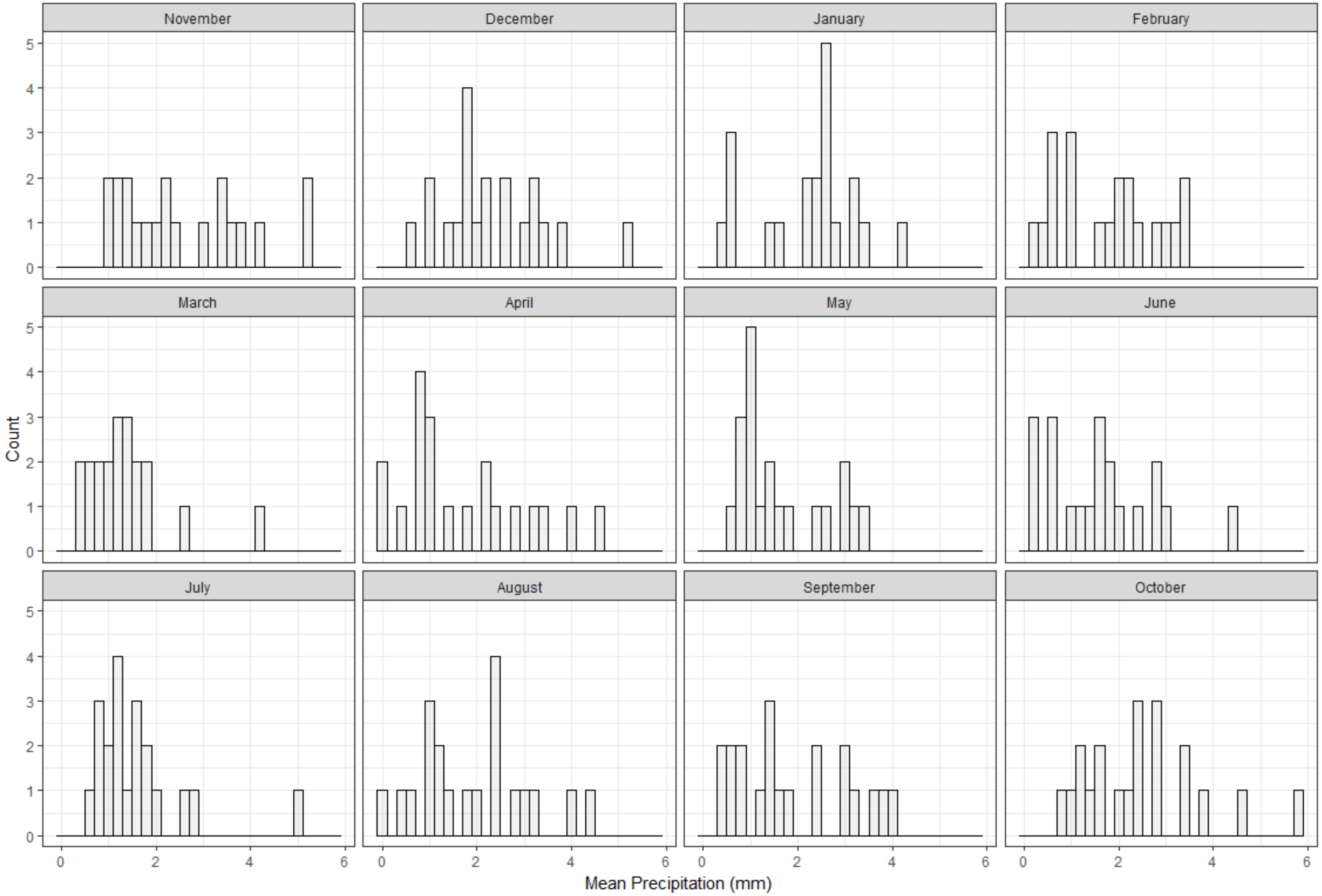

Figure S3.2. Variation in mean Precipitation in each month °C across the 20 year study period (1993-2012)

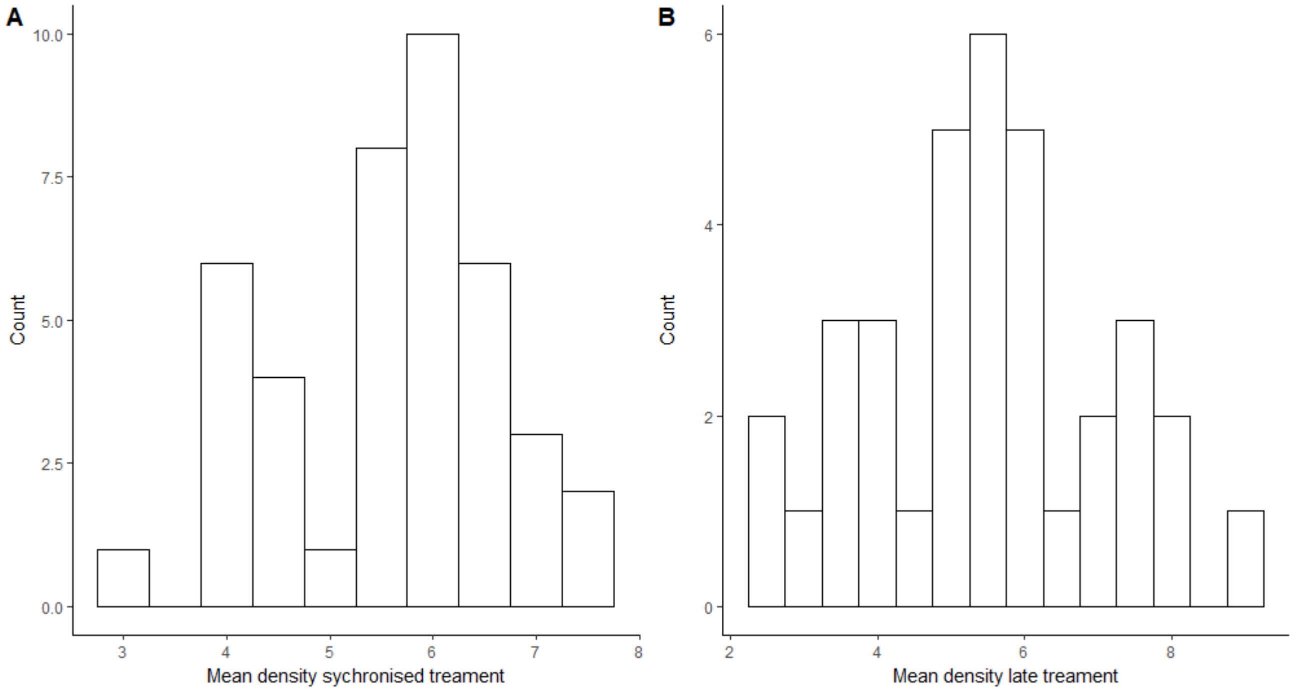

Figure S4.1. Histogram showing spread of mean density values of synchronised hatch treatment and late hatch treatment. Mean density calculated as mean number of caterpillars an individual shared a container with, recorded weekly to take into consideration mortality, escaped individuals and deliberate splitting into smaller densities.

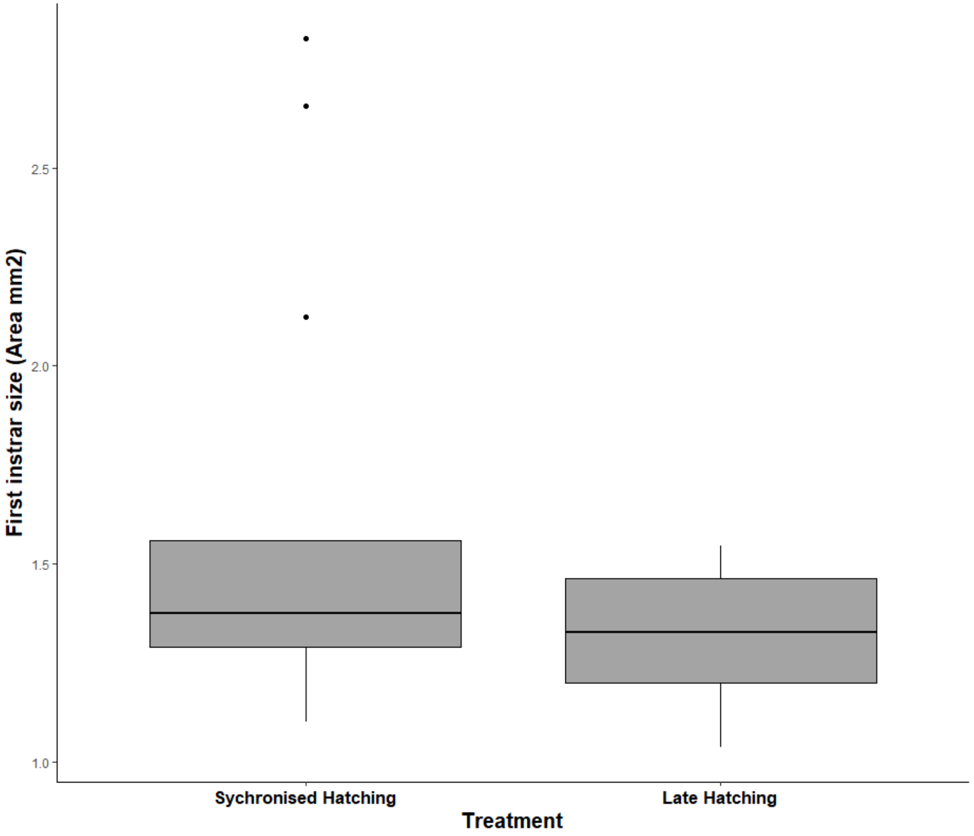

Figure S4.2. The initial larval size of *O. cerasi* in each treatment, prior to treatment application. Figures is a box-plot in which the solid black line represents the median, grey horizontal lines represent the upper and lower interquartile ranges, grey vertical lines represent the range of the data and black dots represent outliers. Wilcox test shows no significant difference between treatment., Z= -0.605, P=0.545.

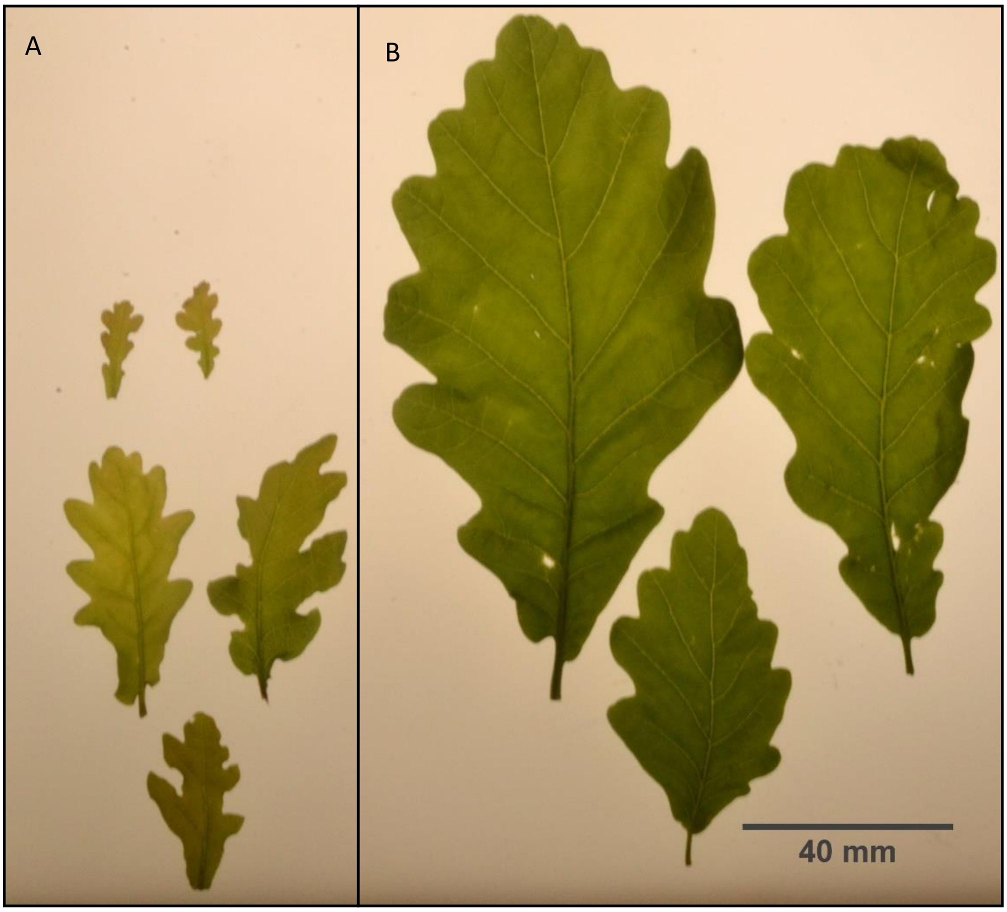

Figure S4.3. Image depicting leaf type. A) Young, rapidly developing leaves light in colour and soft in texture (stage 6 and 7). B) Mature, fully developed leaves tougher in texture (> stage7).

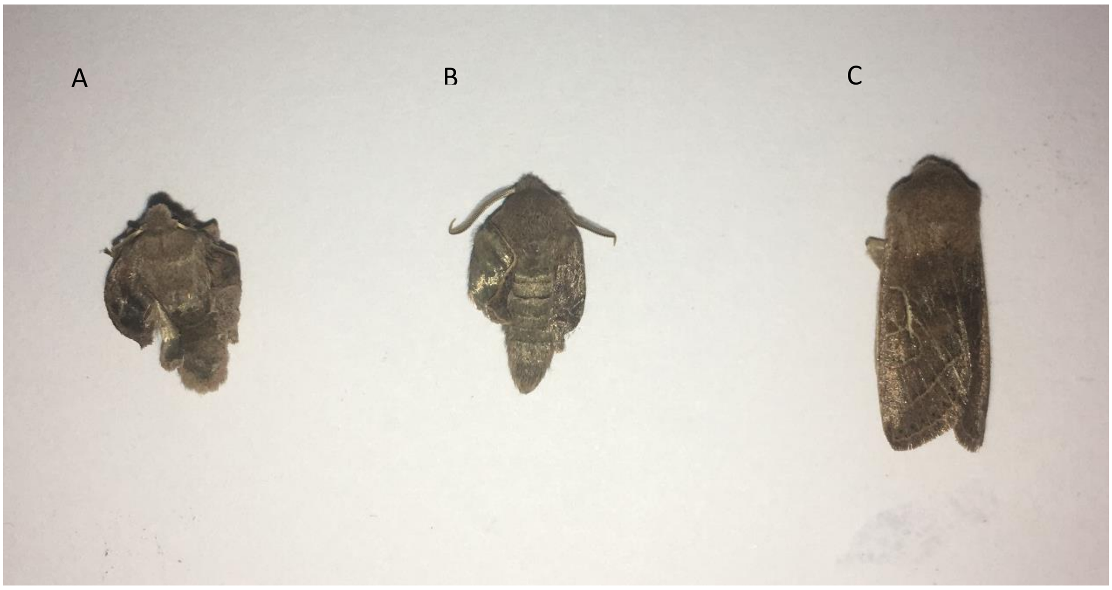

Figure S4. Image depicting wing abnormalities. a) and b) *O.cerasi* small wings that were non-functional for normal flight behaviour, c) *O.cerasi* with normally developed, fully functional wings.

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