Pears, pests and natural enemies: modelling tri-trophic interactions in a changing climate

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Declaration of original authorship

I confirm that this is my own work and the use of all material from other sources has been properly and fully acknowledged.

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Abstract

Pears are an important crop to the UK and global fruit industry, with 17.9 thousand tonnes of pears produced in the UK and over 26.3 million tonnes produced globally in 2022. Pests pose a threat to the industry, most notably pear psyllid. *Cacopsylla pyri* is the dominant species within the UK, causing an estimated £5 million in damage and control per year. These phloem feeding pests damage orchards; nymphs produce honeydew, a sugary secretion that encourages the growth of black sooty mould on fruits and leaves, whilst adults are vectors of 'pear decline' (*Candidatus* Phytoplasma pyri); which can reduce shoot and fruit growth and cause tree death. Due to insecticide withdrawal and increased pesticide resistance, many growers rely on integrated pest management (IPM) for managing pear psylla. In addition, future impacts on this agroecosystem should be considered. UK Climate Projections (UKCP18) predict hotter, drier summers and warmer, wetter winters, which could have considerable impacts on pear flowering phenology, pear psyllid and natural enemy emergence and trophic interactions.

The aim of this thesis was to highlight current methods used within pear psyllid management and potential changes that could occur under future climate scenarios, with emphasis on phenological shifts and trophic mismatches. Analysis of current management methods revealed the use of biorational compounds such as kaolin and the release of biological control agents was reasonably common within UK orchards. However, there were concerns whether biological control agents would continue to be effective in controlling psyllid populations, with respect to climate change. Findings indicated that all three trophic levels (pear, pest and natural enemies) are shifting with respect to climate change. Peak abundance date of first-generation *C. pyri* nymphs has become 14 days earlier compared to historical time periods, whilst pear flowering time has become 11 days earlier.

However, natural enemies *A. nemoralis* and *F. auricularia*, are likely to remain suitable biocontrol agents under future temperature scenarios; anthocorid functional responses did not significantly differ under current temperature regimes compared to temperatures predicted for 2080 (RCP4.5 and RCP8.5 scenarios). Whilst earwigs consumed significantly more *C. pyri* nymphs under the RCP8.5 scenario (43.7 nymphs) compared to the current temperature scenario (36.0 nymphs) and showed synchrony with pear psyllid populations in phenological models. The importance of long-term monitoring data should be noted, this thesis recommends the collection of UK wide pear psyllid and natural enemy abundance data to assess phenological shifts.

Thesis Publications

Chapters (1 – 5) in this PhD thesis are based on the publications or publications under review below:

Chapter 1 (Paper 1):

Reeves, L. A., Garratt, M. P., Fountain, M. T., & Senapathi, D. (2024) A whole ecosystem approach to pear psyllid (*Cacopsylla pyri*) management in a changing climate. J Pest Sci (2024). https://doi.org/10.1007/s10340-024-01772-3

Chapter 2 (Paper 2)

Reeves, L. A., Garratt, M. P., Fountain, M. T., & Senapathi, D. (2022) Climate induced phenological shifts in pears–a crop of economic importance in the UK. Agric Ecosyst Environ 338: 108109. https://doi.org/10.1016/j.agee.2022.108109

Chapter 3 (Paper 3)

Reeves, L. A., Garratt, M. P., Fountain, M. T., & Senapathi, D. (2023) Functional and Behavioural Responses of the Natural Enemy *Anthocoris nemoralis* to *Cacopsylla pyri*, at Different Temperatures. J Insect Behav 36, 222–238. https://doi.org/10.1007/s10905-023-09836-5

Chapter 4 (Paper 4)

Reeves, L. A., Garratt, M. P., Fountain, M. T., & Senapathi, D. (2024) Intraguild predation or spatial separation? The efficacy of using two natural enemy species for the biological control of pear psyllid (*Cacopsylla pyri*). J Insect Behav (under review).

Chapter 5 (Paper 5)

Reeves, L. A., Garratt, M. P., Fountain, M. T., & Senapathi, D. (2024) Exploring climate driven phenological mismatches in pears, pests and natural enemies – a multi-model approach. J Pest Sci (under review).

I declare that I designed all experiments and conducted all research for the scientific publications listed and was the primary author for these papers. My supervisors, and other co-authors, assisted in providing data or models for analyses and feedback for manuscripts and experimental design. Minor changes have been made to the references, so that all references are now in APA format.

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1 Literature review

This chapter is a version of the following paper, with minor changes to formatting and references to make the thesis more comprehensive:

Reeves, L. A., Garratt, M. P., Fountain, M. T., & Senapathi, D. (2024) A whole ecosystem approach to pear psyllid (*Cacopsylla pyri*) management in a changing climate. J Pest Sci (2024). https://doi.org/10.1007/s10340-024-01772-3

Author contributions: LR, DS, MG and MF conceived and designed the review. LR wrote the manuscript, created the figures and analysed the spray records and pest monitoring data. DS, MG and MF read and provided feedback on multiple drafts prior to submission.

1.1 Abstract

Whole ecosystem-based approaches are becoming increasingly common in pest management within agricultural systems. These strategies consider all trophic levels and abiotic processes within an ecosystem, including interactions between different factors. This review outlines a whole ecosystem approach to the integrated pest management (IPM) of pear psyllid (*Cacopsylla pyri* Linnaeus) within pear (*Pyrus communis* L.) orchards, focusing on potential disruptions as a result of climate change. Pear psyllid is estimated to cost the UK pear industry £5 million per annum and has a significant economic impact on pear production globally. Pesticide resistance is well documented in psyllids, leading many growers to rely on biological control using natural enemies during the summer months. In addition, three insecticides commonly used in pear psyllid control have recently been withdrawn from the UK and Europe, emphasizing the need for alternative control methods. There is growing concern that climate change could alter trophic interactions and phenological events within agroecosystems. For example, warmer temperatures could lead to earlier pear flowering and pest emergence, as well as faster insect development rates and altered activity levels. If climate change impacts pear psyllid differently to natural enemies, then trophic mismatches could occur, impacting pest populations. This review aims to evaluate current strategies used in *C. pyri* management; discuss trophic interactions within this agroecosystem and highlight potential changes in the top-down and bottom-up control of *C. pyri* as a result of climate change. This review provides a recommended approach to pear psyllid management, identifies evidence gaps and outlines areas of future research.

1.2 Introduction

Historically, agricultural pest management was an oversimplified process - an insecticide or biorational compound has been applied and a reduction in the pest population expected. The observed response is often far more complex - many pest species develop resistance to pesticides, requiring the frequent development of new compounds, in this evolutionary arms race (Chattopadhyay & Banerjee, 2020; Le Page, 2011). Secondary pest species can also become more problematic, filling vacant niches that insecticides had emptied (Ekström & Ekbom, 2011; Hill et al., 2017). Broad spectrum insecticides are a particular problem (insecticides that target characteristics that are common across multiple organisms), impacting non-target organisms such as natural enemies (El-Wakeil et al., 2013) and pollinators (Connolly, 2013; Kumar et al., 2018), altering the delivery of ecosystem services. Finally, weather variables can alter the persistence and mobility of insecticides (Edwards, 1975; Tiryaki & Temur, 2010), with light intensity, temperature and soil moisture impacting their breakdown within the environment. As these issues and challenges increased, in 1992 the United Nations Conference on Environment and Development stated that agrochemicals were the dominant form of pest control and that growers should transition to integrated pest management (IPM) (Ekström & Ekbom, 2011).

This review defines Integrated pest management as maintaining healthy crop growth whilst minimising disruption to agroecosystems, with focus on enhancing biological control (Moorthy & Kumar, 2004). IPM is a more sustainable approach to pest management that can use a combination of methods; including pest monitoring, biorational compounds, cultural control and biological control, whilst reducing the use of chemical control where possible. Since then, the whole ecosystem approach has become a common concept when managing agroecosystems. This review defines a whole ecosystem approach as considering multiple trophic levels, abiotic processes and interactions between different factors, when managing an ecosystem (Jian & Jayas, 2012; Jordan, 2013). A whole ecosystem approach can help maintain the integrity, structure and function of an ecosystem, as it considers the dynamic processes that occur within them. Pest monitoring and the application of thresholds are also important for ecosystem approaches and IPM (Shaw et al., 2021). An economic threshold is the population density at which it is more cost effective to control a pest, due to the economic losses from damage by leaving the crop untreated. For pear psylla, DuPont et al. (2023) quantified the economic threshold for pear psylla at 0.2–0.8 for third-generation nymphs per leaf, highlighting the importance of monitoring psyllid populations.

The ecosystem approach can be applied to pear orchards, helping enhance pest management and biological control, whilst minimising synthetic chemical input. Pears are an economically important crop within the UK contributing to 2.74% of total fruit production; with a planted area of 1,477 hectares and an economic value of £15.1 million in 2022 (Defra, 2023). This system has one main pest, the pear psyllid *Cacopsylla pyri*, thus there are fewer ecological interactions to consider. Situated within the superfamily Psylloidea, there are over 4,000 described species of psyllid worldwide (Mauck et al., 2024), of these there are 24 species known species of pear psyllid (Civolani et al., 2023). These phloem feeders have a significant impact on the pear industry, nymphs produce honeydew; a sugary secretion that encourages the growth of black sooty mould on pear fruit and leaves (Daniel et al., 2005) and adult *C. pyri* are a vector of the pathogen 'pear decline' (*Candidatus* Phytoplasma pyri); which reduces shoot and fruit growth and can lead to tree death (Carraro et al., 2001; Kucerová et al., 2007; Süle et al., 2007). In the past, pear growers have relied on synthetic insecticides to control *C. pyri* (Civolani et al., 2023), however over the last few decades, pear psyllid species have demonstrated resistance to multiple commonly available pesticides across the globe in particular in North America for *C. pyricola* (Harries & Burts, 1965) and Europe for *C. pyri* (Atger, 1979). In addition, three insecticides (thiacloprid, chlorpyrifos and spirodiclofen) commonly used for pear psyllid control have recently been withdrawn from UK use, with a fourth withdrawal planned for indoxacarb for 2024 (Hertfordshire, 2023; HSE, 2023), in addition, abamectin and spirotetramat are in the process of being phased out in Europe (Civolani et al., 2023). Therefore, integrated pest management (IPM) has become a priority for controlling pear psylla in pear orchards (Reeves et al., 2023; Shaw et al., 2021).

Cacopsylla pyri have a number of natural enemies in UK pear orchards as in other parts of the world (Civolani et al., 2023; Horton, 2024). The anthocorid *Anthocoris nemoralis* (Fabricius) is perhaps the most documented biological control agent of *C. pyri*, whilst the European earwig *Forficula auricularia* (Linnaeus), is another key predator in orchards over the summer. Other natural enemies include: ladybird adults and larvae (Coccinellidae) (Fountain et al., 2013; Prodanović et al., 2010), lacewing larvae (Neuroptera) (DuPont & John Strohm, 2020; DuPont et al., 2023), spiders (Araneae) (Petráková et al., 2016), other species of anthocorid including *A. nemorum* (Sigsgaard, 2010) and multiple *Orius* spp. (Vrancken et al., 2014). A few parasitoid species are also associated with pear psylla (Cross et al., 1999; Jerinić-Prodanović et al., 2019; Rieux et al., 1990), with *Trechnites insidiosus* (Crawford) commonly parasitizing nymphs in European pear orchards (Rieux et al., 1990; Sanchez & Ortín-Angulo, 2012; Tougeron et al., 2021). although only limited records exist in the UK. With multiple natural enemy species potentially contributing to biocontrol, it is vital to consider a whole ecosystem approach when managing pear psylla populations.

Weather variables are predicted to change significantly over the next 80 years with respect to climate change; UK Climate Projections (UKCP18) predict hotter, drier summers and warmer, wetter winters across the UK (Lowe et al., 2018a; Murphy et al., 2018). By 2070 summer temperatures could increase by as much as 5.1°C under the high emissions scenario, whilst becoming up to 45% drier (MetOffice, 2022), with more frequent and intense extreme weather events (MetOffice, 2019). All three trophic levels (pear trees, pear psyllids and natural enemies) are sensitive to abiotic factors within agroecosystems, thus changes in temperature, rainfall and extreme weather events could affect phenology, activity and behaviour, compromising biocontrol (Reeves et al., 2022). Climate change is likely to impact, development rates, generation times, oviposition, diapause, feeding and activity levels of insects (Karuppaiah & Sujayanad, 2012), including pear psyllids and their natural enemies.

Phenological shifts are also a real concern for agroecosystems (Reeves et al., 2022) and are likely to alter pest population dynamics (Becker et al., 2015; Thomson et al., 2010). Changes in climatic conditions can lead to shifts in the timing of phenological events, resulting in phenological mismatches; where shifts in other trophic levels do not match the corresponding shift for pest species (Damien & Tougeron, 2019). One example would be psyllid populations peaking earlier in the year due to earlier hatching time, but with this not coinciding with peak anthocorid or earwig emergence. In addition, climate change can lead to spatial shifts (Polce et al., 2014); altering the spatial distribution of pollinators, pests, pathogens and pear growing regions. An example of this is North America, where the pear growing region shifted from the eastern US to the western US during the mid-1900s. This geographic shift was largely due to difficulties in growing pear under the hot and humid summer conditions in eastern US, which increased the risk of infection from fireblight *Erwinia amylovora* (Davis & Tufts, 1941; Mitcham & Elkins, 2007).

Taking these different aspects into consideration, this review aims to 1) describe the life-history of pear psyllid, 2) outline current biological and agrochemical control strategies used against them and 3) identify potential phenological and trophic mismatches that could occur as a result of climate change and 4) propose an ecosystem-based approach to build resilience into pear production systems so sustainable pest control can be maintained.

1.3 Life history of *Cacopsylla pyri*

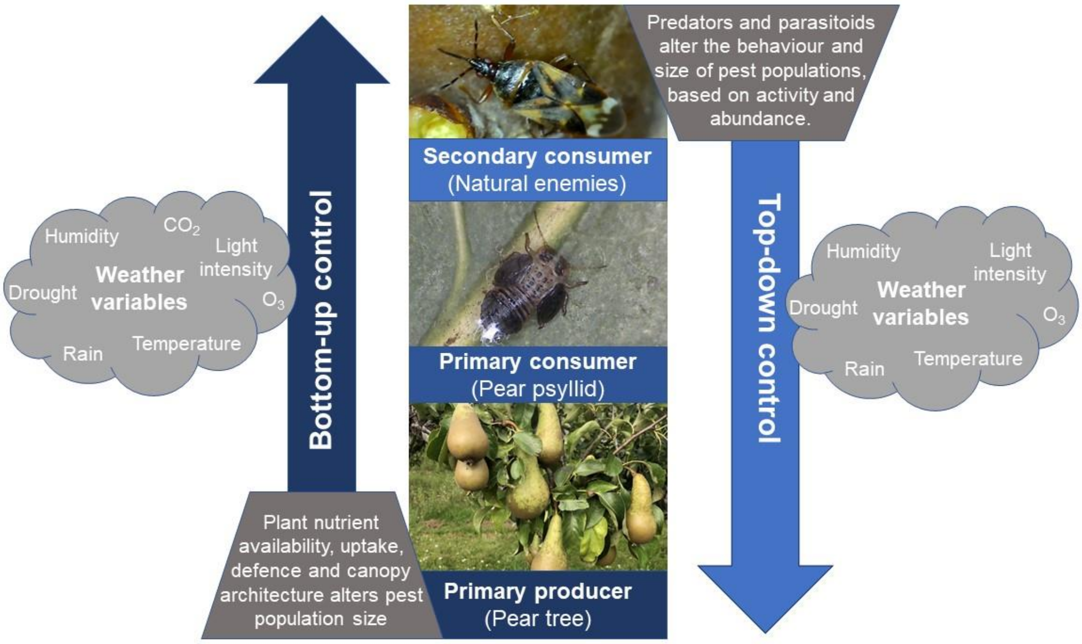

Figure. 1.1: Diagram outlining bottom-up and top-down control within a pear agroecosystem and the potential interaction with weather variables, with respect to climate change. With pear trees as the primary producer (*Pyrus communis*), pear psylla (*Cacopsylla pyri*) as the primary consumer and natural enemies (including *Anthocoris nemoralis*) as secondary consumers.

When taking a whole ecosystem approach to pest management, it is important to have a good understanding of the target pest's life history (Bird et al., 2009; Thomas, 1999), including knowledge of oviposition, emergence time, migration, habitat preference and feeding habit. This allows for informed bottom-up and top-down control as well as providing insights into when, where and how they should be applied, to optimise the pest management strategy (Figure 1.1). *Cacopsylla pyri* is currently the most frequently recorded pear psyllid species in the UK and is especially prevalent in Kent, whereas *Cacopsylla pyri*cola was previously more abundant during the 1970-1980s (Nagy et al., 2008). *Cacopsylla pyri* has two adult morphotypes (Bonnemaison & Missonnier, 1955; Nguyen, 1985), a larger dark-orange black winterform (2.6-2.9 mm) with smoky-coloured wings and a smaller light-brown summerform (2.1-2.7 mm), which first appears in early May and has transparent wings. During September winterform adults begin to appear, some of which disperse from the orchard, dispersal peaks in late-October or early-November, around the phenological stage of leaf fall (Civolani & Pasqualini, 2003). Adults overwinter in tree bark crevices (Næss, 2016), during which reproductive diapause occurs, with ovarian development happening slowly throughout the winter (Bonnemaison & Missonnier, 1955; Lyoussoufi et al., 1994; Nguyen, 1975; Schaub et al., 2005). By mid-late winter, female ovaries are fully developed (Schaub et al., 2005) and egg laying starts in late February to early March (Næss, 2016; Oz & Erler, 2021), when temperatures reach > 10 ˚C. For UK pear orchards mean average first oviposition date and other key phenological events are shown in Figure 1.2, based on 10 years of monitoring data.

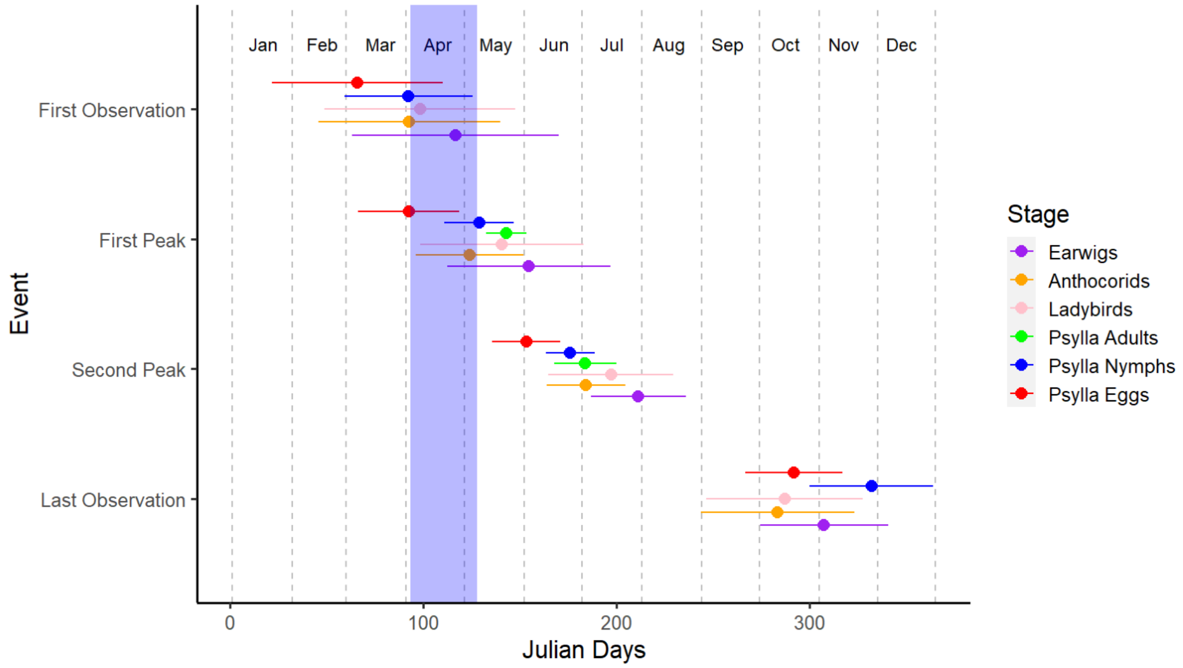

Figure 1.2: The timing of key life stages for *Cacopsylla pyri* (eggs, nymphs and adults) and its natural enemies (anthocorids, earwigs and ladybirds) in Julian days. Events include first observation in the orchard, average first peak abundance date, average second peak abundance date and last observation in the orchard. Data was collected from 17 different pear orchards in Kent, UK from 2012-2022, based on AHDB TF233 (Agriculture and Horticulture Development Board Tree Fruit) records. The dots represent the average time the event took place, lines represent standard deviation, the light blue rectangle is the mean average spread of flowering time for conference pear (*Pyrus communis* L.).

Cacopsylla pyri eggs begin to hatch in early spring (Sanchez & Ortín-Angulo, 2012), going from a creamy-yellow to orange when mature; the eyes are often visible prior to eclusion. Nymph emergence often coincides with bud opening and there are five nymphal stages, each ending in a moult (Civolani et al., 2023). Early stage nymphs (1-3) are light yellow coloured, whilst older stages (4-5, hardshell nymphs) are dark-brown and larger in size, with more developed wingpads (Le Goff et al., 2021). The first peak in the pear psyllid population is seen around April-May when summerforms emerge, this is followed by a second generation in early summer (Figure 1.2). The following generations overlap throughout the summer and autumn (Civolani et al., 2023), with a mean average of 3-5 generations per year (Süle et al., 2007), although generation number can be temperature dependant (Kapatos & Stratopoulou, 1999).

Pear psyllids use a stylet to feed on phloem sap (Civolani et al., 2011), this sap is comprised mostly of two sugars (sorbitol and sucrose), it also contains 17 free amino acids (Le Goff et al., 2019). In order to obtain essential amino acids, psyllids consume large amounts of phloem sap, egesting a large proportion of sugars as honeydew (Le Goff et al., 2019). Nymphs egest larger quantities of honeydew than adults (Civolani et al., 2023). Honeydew can be particularly problematic in pear orchards, encouraging the growth of black sooty mould, which reduces the photosynthetic ability of leaves and reduces economic value of fruits (Daniel et al., 2005). In addition, adults are a vector of pear decline phytoplasma (*Candidatus* Phytoplasma pyri) (Carraro et al., 2001; Süle et al., 2007); phloem sap is ingested by psyllids from an infected tree and transmitted to other pear trees via salivation into cells or tissues when feeding (Cruz et al., 2018; Sugio & Hogenhout, 2012). Pear decline can lead to reduced foliation, leaf drop and tree death, although susceptibility can depend on rootstock and cultivar (Avinent et al., 1997; Çağlayan et al., 2010; Carraro et al., 2001). Indeed, it is estimated that pear psyllid costs the UK pear industry £5 million per annum due to crop damage and control costs (AHDB, 2012).

1.4 Monitoring methods and abundance thresholds

Monitoring pear psylla is particularly important when considering the timing of control methods, as information on adult dispersal, spring oviposition and population densities and structure is required for management decisions (Horton, 1999), making it necessary to monitor pear orchards regularly throughout the year. DuPont et al. (2023) quantified the economic injury levels for pear psylla at 0.2–0.8 for third-generation nymphs per leaf, highlighting the importance of regular monitoring. Monitoring adults and eggs before budburst (late January onwards) is important, as this is when psylla are more active in orchards and begin oviposition and the application of kaolin is often necessary (Pasqualini et al., 2002). Adults can be monitored either using beat tray sampling or yellow sticky traps (Burts & Retan, 1973; Horton, 1999; Marcasan et al., 2022). Eggs can also be counted by inspecting the budwood using a hand lens or by taking a small sample and counting eggs under a light microscope (Horton, 1999). During spring and summer it is also important to sample *C. pyri* nymphs, as these produce large quantities of honeydew production leading to the growth of black sooty mould (DuPont et al., 2023; Nin et al., 2012). Furthermore, under warmer temperatures adults are more active and likely to fly away, so are more difficult to count via beat tray sampling (Horton, 1994).

1.5 Chemical control strategies and biorational compounds

Although, IPM focuses on minimising the use of agrochemicals, whilst conserving natural enemy populations (Wearing, 1988), the application of agrochemical sprays is sometimes necessary as a last resort (Deguine et al., 2021). IPM integrates the use of chemicals in an agroecosystem by: considering spray timing (Figure 1.3) and spraying when natural enemies are not yet present in orchards (Tang et al., 2010), selecting compounds that are specific to the target pest rather than broad spectrum insecticides (Zalucki et al., 2009), using biorational pesticides (pesticides made of natural products, with low environmental and mammalian risk) (Haddi et al., 2020) or biological control agents as alternatives when possible (Matthews, 1999) and rotating insecticide family usage, so that pests are less likely to develop resistance (Walker et al., 2001). In this section we will discuss the pesticides and biorational compounds commonly used in the control pear psylla (Table 1.1), providing an overview of how these control methods could be impacted by climate change.

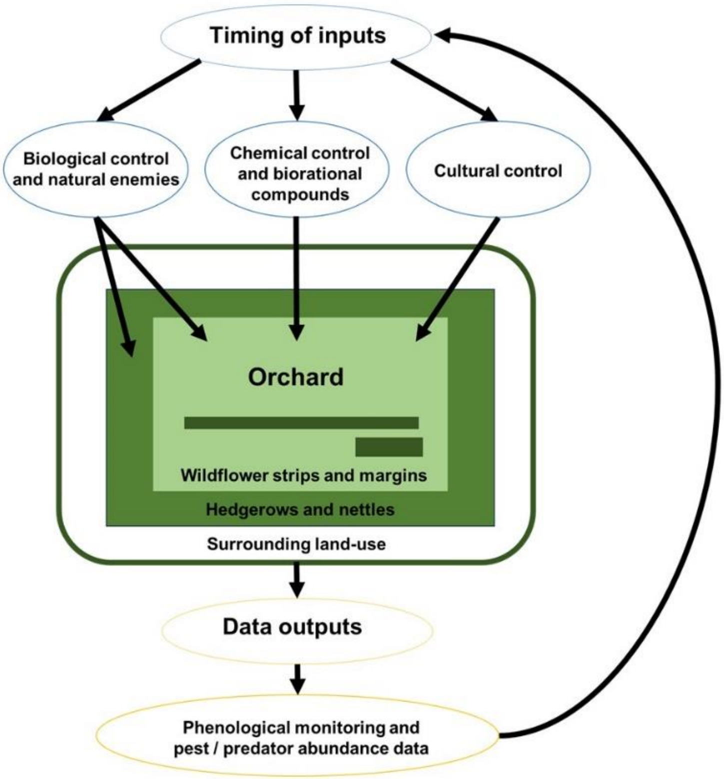

Figure 1.3: The inputs and outputs within a pear orchard that constitute pest management. Inputs include biological control, chemical sprays, biorational compounds (pesticides made of natural products, with low environmental and mammalian risk) and cultural control. Outputs are the data that growers, agronomists and researchers collect which go back into the system to optimise the timing of different control methods, maximising the control of the pest, whilst minimising damage to natural enemies, pollinators and other non-target organisms.

Table 1.1: Biorational compounds, agrochemical sprays and biocontrol agents used within UK orchards. Based on AHDB TF233 records from 20 orchards in Kent during 2016, 2017, 2018 and 2021. Including the name of the product used with its active ingredient in brackets, the average first application date for the product, the average number of applications pear year in an orchard, a brief description of how the product targets pear psyllid and the percentage of growers surveyed that use the compound or used the compound before its ban. Compounds still approved for use in the UK are in bold, based on the description in the Health and Safety Executive (HSE) (HSE, 2023) and the University of Hertfordshire Pesticide Properties DataBase (PPDB) (Hertfordshire, 2023).

Product name	**Average 1st application**	**Average no. applications**	**Growers using (%)**	**Activity**	**MAPP number**	**Approved/ Withdrawn**
Agricolle (Natural polysaccharides)	1st Jun	1	5.00	Immobilizes insect and clogs sphericles, causing rapid death through asphyxiation (broad spectrum).	NA	Approved
AnthoPAK 500 (*Anthocoris nemoralis* adults)	4th May	2.58	35.0	A natural enemy of pear psyllid that predates on its nymphs and eggs.	NA	Approved
Batavia (Spirotetramat)	9th Jun	1	20.0	Inhibits lipid biosynthesis in phloem sucking pests (broad spectrum).	18449	Approved until (31/07/2029)
Bittersaltz/ Epso Microtop/ Kieserite (Magnesium sulphate)	18th May	4.88	85.0	Primarily used as a fertilizer but can also help remove honeydew from leaves.	NA	Approved

Calcifert/ Lime (Calcium carbonate)	10th May	1	25.0	Primarily used as a fertilizer but can also help remove honeydew from leaves and strengthen leaf against feeding.	NA	Approved until (31/08/2024)
Calypso (Thiacloprid)	25th Mar	1.17	70.0	Disrupts the insect's nervous system by stimulating nicotinic acetylcholine receptors (broad spectrum).	11257	Withdrawn (31/03/2020)
Chlorpyrifos (Chlorpyrifos)	21st Mar	1	15.0	Impacts the insect's nervous system by inhibiting the breakdown of the neurotransmitter acetylcholine (broad spectrum)	13298	Withdrawn (01/04/2016)
Envidor (Spirodiclofen)	3rd Jul	1	65.0	Inhibits lipid biosynthesis in phloem sucking pests (broad spectrum)	17518	Withdrawn (31/01/2022)
Explicit/ Steward (Indoxacarb)	4th Jun	1.40	40.0	Blocks insect sodium ion channels, dysregulating neuron firing (broad spectrum).	18792	Withdrawal planned (31/10/2024)

Headland Magnesium (Magnesium)	29th May	1	15.0	Primarily used as a fertilizer but can also help remove honeydew from leaves.	NA	Approved
Headland Sulphur (Sulphur)	10th Apr	5	85.0	Primarily used as a scab and mildew treatment but can also help remove honeydew from leaves.	NA	Approved
Karamate (Mancozeb)	21st May	2.69	45.0	Primarily a fungicide but has also been shown to have insecticidal properties on pear psylla.	14632	Approved until (31/01/2024)
Mainman (Flonicamid)	10th May	1	5.0	Disrupts potassium ion channels, inhibiting the release of honeydew and saliva, leading to the cessation of feeding (specific to phloem feeders).	13123	Approved until (31/08/2026)
Soap (Sodium hydroxide)	9th Jun	1.67	15.0	Removes honeydew from leaves.	NA	Approved
Surround (Kaolin)	30th Mar	1	25.0	A mineral-based particle film, that forms a protective barrier, repelling pests and reducing	NA	Approved (31/08/2024)

				movement, feeding and oviposition.		
Wetcit (Alcohol Ethoxylate)	8th May	3	20.0	A wetting aid surfactant, that improves the spread and penetration of insecticides and other agrochemical sprays.	NA	Approved substance without pesticidal activity

To highlight which control methods were most common in the UK we compiled spray records from 20 different pear orchards. Orchards were selected as they were evenly distributed across Kent and were involved in AHDB TF233 project for this time period, all using the cultivar Conference pear (Pyrus communis cv. Conference), with the same rootstock and similar levels of pear psyllid abundance. Nine different agrochemical or biorational compounds were used in pear psyllid management, 5 involved in honeydew removal (including sulphur and magnesium sulphate for desiccation and soap to wash off honeydew), 1 surfactant used to enhance insecticide application and 1 biological control agent (Table 1.1). The most common insecticide used in *C. pyri* control between 2016-2019 was thiacloprid (product name Calypso, used in 70% of orchards), with recommendation of use before flowering. The active ingredient thiacloprid is a neonicotinoid insecticide which targets the nicotinic acetylcholine receptor and interrupts transmissions of synaptic signals, resulting in paralysis of insects (Bangels et al., 2010). Although effective in controlling the first generation of *C. pyri* (Bangels et al., 2009), the approval for UK usage was withdrawn in early 2020 (Bellis & Suchenia, 2022), due to toxicity to non-target organisms including multiple bee species (Claus et al., 2021; Orčić et al., 2022), natural enemies (Van de Veire & Tirry, 2003) and soil invertebrates (De Lima e Silva et al., 2017). In total, three insecticides (thiacloprid, chlorpyrifos and spirodiclofen) commonly used for pear psyllid control have been withdrawn for UK usage, with a fourth withdrawal planned for the active ingredient indoxacarb (Table 1.1). With the recent withdrawal of multiple insecticides used to target pear psylla, reliance on other insecticides and biorational compounds may become more common. Currently, spirotetramat (Batavia) is approved for use in UK orchards (HSE, 2023), it is a systemic insecticide that is translocated throughout the xylem and phloem, inhibiting lipid biosynthesis in sucking pest species (Brück et al., 2009; Nauen et al., 2008). Studies suggest that spirotetramat is particularly effective against psyllid nymphs (Civolani et al., 2015) and does not adversely impact European earwig (Shaw & Wallis, 2010) or *A. nemoralis* populations when applied in orchards (Pasqualini et al., 2012), although there is some concern about its impact on predatory mites (DuPont & John Strohm, 2020).

The use of the biorational compound Kaolin has become more frequent (DuPont et al., 2021; Pasqualini et al., 2002). This finely powdered clay can be sprayed onto plant surfaces, creating a non-toxic particle film (Erler & Cetin, 2007). The porous white barrier can deter adult psylla from colonising orchards, reduce oviposition and impair movement via the attachment of heavy particles to the bodies of psylla (Erler & Cetin, 2007; Saour et al., 2010). Pre-bloom application (February – April) of kaolin is recommended, when adult psylla are actively recolonising orchards, impact on natural enemies is minimal and spray coverage is optimal, without impacting photosynthesis as foliage is not yet present (DuPont et al., 2021). Oils are also effective biorational compounds used to suppress pear sucker during the pre-bloom stage (Civolani et al., 2023; Emami, 2023; Erler, 2004b), interfering with colonisation of orchards and egg deposition (Pasqualini et al., 2002). One study by Pasqualini et al. (2002) found that in early spring *C. pyri* egg numbers were 3.2 times lower on buds treated with mineral oil, compared to the untreated control. Whilst Erler (2004) found that cotton seed oil, fish-liver oil, neem oil and summer oil all promoted *C. pyri* oviposition deterrence, with fish-liver oil and summer oil exhibiting 100% deterrence in winterforms over the 3-week treatment period, however there is the issue of allergens in some oil types.

Reflective mulches have been demonstrated to suppress *C. pyricola* populations (Nottingham & Beers, 2020; Nottingham et al., 2022). These are ground covers that reflect solar light into the orchard canopy (Shimoda & Honda, 2013). Insects are particularly sensitive to UV light, ambient UV can promote flight behaviour (Nottingham & Beers, 2020), whilst direct UV can damage eggs and nymphs (Beard, 1972). Nottingham & Beers (2020) found significantly fewer first-generation (during May) pear psylla adults, eggs, and nymphs in reflective-mulch treatments compared to black-mulch and no mulch treatments. However, the second generation (June-July) of pear psylla was not supressed by reflective-mulch. This could be due to the fact multiple natural enemy groups (important for summer psyllid control) were also reduced in the reflective mulch treatment, as UV impacts multiple insect species. Therefore, using reflective mulch during the early-season may be more effective for pear psyllid control, as natural enemies are less abundant.

Pest monitoring and mating disruption through the use of pheromone lures, are deployed for multiple pest species in particular Lepidoptera (Ganai et al., 2017). To date the sex pheromone of the pear psyllid species *C. bidens* (Soroker et al., 2004) and *C. pyricola* has been identified, isolated and synthesised (Guédot et al., 2009a; Yuan et al., 2021). Furthermore, there is also evidence for increased levels of the same compound in cuticular extracts of adult *C. pyri* females (Ganassi et al., 2018b). Ganassi et al (2018) showed male *C. pyri* displayed a significant preference for odours from female conspecifics and female cuticular extracts in Y-tube olfactometer assays, suggesting that a similar female-produced pheromone is likely present in *C. pyri*. Visual and acoustic signals have the potential to enhance mating disruption (Jocson, 2023; Krysan & Horton, 1991). *Cacopsylla pyri* have a preference for green visual cues (525 to 537-nm) (Czarnobai De Jorge et al., 2023), which can be used in sticky traps for psylla monitoring and control. There is also potential to supplement these traps with pheromone lures (Guédot et al., 2009a; Yuan et al., 2021) to increase catch rate. Acoustic signals have an important role in psyllid mate choice (Liao et al., 2022; Percy et al., 2006), Eben et al. (2015) were first to describe the male and female acoustic signals for a pear psyllid (*C. pyri*). Jocson (2023) found that the playback of white noise and male psyllid song reduced offspring number compared to the control treatment, due to mating disruption. However, interactions between visual, acoustic and chemical signals involved in pear psyllid mate choice are under-researched.

1.6 Biological and cultural control strategies

Natural or biological control strategies encompass bottom-up or top-down control (Figure 1.1). Top-down control can be defined as a predator mediated process, when higher trophic levels influence levels below them, by altering prey behaviour or reducing pest populations through consumption of prey (Daugherty et al., 2007; Hayward et al., 2019). Top-down control is key to biological control methods used in IPM of pear sucker, either through conserving natural enemy populations, increasing recruitment of predators and parasitoids into orchards, or artificially releasing biocontrol agents (Daugherty et al., 2007). The anthocorid *A. nemoralis* is the dominant predator of *C. pyri* in the UK, with the average female estimated to consume approximately 5000 psyllid eggs in its lifetime (Yanik & Ugur, 2004). Adult anthocorids migrate into orchards April-May from surrounding hedgerows (Reeves et al., 2023). Eggs are laid and anthocorid populations peak mid-summer, allowing for the effective control of pear psyllid (Nagy et al., 2008; Scutareanu et al., 1999). However, natural anthocorid populations do not always establish quickly enough to keep *C. pyri* populations at an economically viable level (Civolani, 2012b; Sigsgaard et al., 2006b). Therefore, it has become common practice in some UK orchards to mass release *A. nemoralis* (Augmentative biological control) rather than relying on enhancing natural populations alone (Conservation biological control). This review found that 35% of the orchards surveyed used AnthoPAK 500 (Table 1.1), a product containing 500 adult *A. nemoralis* in a dispersing material (Bioplanet, 2023), available from multiple biological control companies. Sigsgaard et al (2006b), suggests between 1000–1500 adult *A. nemoralis* should be released per hectare at 5–6 points within a pear orchard. Furthermore, timing is critical for artificial releases of *A. nemoralis*, with evidence of successful releases during early-mid May (Sigsgaard et al., 2006a).

In addition to *A. nemoralis*, many other species of natural enemy are involved in pear psyllid management (DuPont et al., 2023; Nottingham et al., 2023), among them are spiders (Araneae) (Sanchez & Ortín-Angulo, 2012), European earwigs (*Forficula auricularia*) (Fountain et al., 2013) ladybird adults and larvae (Coccinellidae) which are generalist predators (Fountain et al., 2013; Prodanović et al., 2010), lacewing larvae (Neuroptera) (DuPont & John Strohm, 2020; DuPont et al., 2023) and the parasitoid *Trechnites insidiosus* (Sanchez & Ortín-Angulo, 2012). European earwigs are common in pear orchards; stage four earwig nymphs are arboreal, appearing in pear trees in late spring and peaking in June, whilst adult populations peak in mid-July (Gobin et al., 2008; Moerkens et al., 2011). Earwigs are effective predators of *C. pyri* (Gobin et al., 2008; Lenfant et al., 1994), and unlike *A. nemoralis* migrations their abundance in orchards is less dependent on *C. pyri* density. A study by Lenfant et al (1994) found that arboreal *F. auricularia* nymphs ate a daily maximum of 10mg of psyllid prey (1000 psylla eggs), highlighting their efficiency as biological control agents. Although, earwigs are omnivorous and sometimes consume plant material, damage to top-fruit is minimal (Solomon et al., 2000).

To date no biological control company rears *F. auricularia* for mass-release, thus the reliance on enhancing earwig populations and providing refugia is common in top-fruit orchards (Shaw et al., 2021). One such refuge is the Wignest; a wooden shelter baited with food, available from the bio-control company Russel IPM (Russel-IPM, 2023; Shaw et al., 2021). Artificial refuges can also be constructed using straws or corrugated cardboard in a bottle attached to a tree (Hansen et al., 2005; Solomon et al., 1999). Furthermore, dried cat-food is often placed in refuges as a prey supplement (Shaw et al., 2021). The benefits of using refuges in the tree canopy is that earwigs are housed arboreally and therefore more likely to forage on insects in the tree canopy when they emerge to feed at night.

Hedgerows (Nagy et al., 2008; Scutareanu et al., 1999), nettles (Shaw et al., 2021), cover crops (Horton et al., 2009) and wildflower strips (Balzan et al., 2014; Mateos-Fierro et al., 2021) can also enhance natural enemy populations, providing refuges for predators before they migrate into nearby orchard trees. Scutareanu et al (1999) found that the first peak of adult anthocorids in pear orchards was always later than the first peak in hedgerows, indicating that anthocorids use hedgerows as refugia before migrating into orchards when psyllid populations increase. Furthermore, hawthorn was the dominant source of *A. nemoralis* for migration to psylla infested trees. This is supported by Nagy et al (2008), who found high numbers of adults on hawthorn, goat willow and stinging nettle during mid-April to May.

Surrounding land-use also influences both pear psylla and their natural enemies (Miliczky & Horton, 2005; Rendon et al., 2021; Shaltiel & Coll, 2004); surrounding vegetation can act as a source or sink for pests and beneficials throughout the year, especially between growing seasons (Rendon et al., 2021). Impacts on pest populations can be dependent on land-use type (Karp et al., 2018), land-use diversity (Veres et al., 2013), size of surrounding land area and distance from orchard (Miliczky & Horton, 2005). Rendon et al (2021) found pear orchards surrounded by high cherry orchard cover had a negative correlation with predator abundance and higher pear psylla abundance, this could indicate that cherry is a less important source of pear psyllid predators, compared to more heterogenous landscapes.

Bottom-up control is important for IPM of pear psylla (Daugherty et al., 2007), this is a resource mediated process (Figure 1.1), where plant quality and chemical defences can influence pest populations, impacting prey abundance for predators (Han et al., 2022). Nutrient inputs have a significant impact on plant quality but can also influence pest populations (Daugherty et al., 2007; Kocourek et al., 2021); nitrogen is a limiting factor in the diets of pear psylla, as there are low levels of amino acids in phloem sap (Le Goff et al., 2019), thus the addition of nitrogen fertiliser can remove this limiting factor and increase the amount of nutritious new foliage for nymphs and adults to feed upon (Daugherty et al., 2007; McMullen & Jong, 1977). Daugherty et al (2007) found that pear trees given a high nitrogen fertiliser treatment had a significantly lower C:N ratio (higher N) in leaf samples and a significantly higher abundance of pear psylla (eggs, nymphs and adults) in mid-July, compared to low N treatments. Thus, controlling fertiliser inputs to provide just enough for fruit set (Civolani, 2012b; Daugherty et al., 2007; Nin et al., 2012), alongside an effective pruning method (Francke et al., 2022; Fuog, 1983), is important for IPM of pear psylla. Franke et al (2022), recommends removing watersprouts (soft vertical shoots) between late May - early June in a period of low rainfall, as an effective method of controlling psylla populations and reducing tree vigour.

Host resistance is another method of minimising damage from pear psylla populations (Nin et al., 2012; Shaltiel-Harpaz et al., 2014). Resistant phenotypes may exhibit antixenosis (pest deterrence) (Bell & Puterka, 2003; Nin et al., 2012), or antibiosis (when plants have a deleterious effect on a pest) (Peterson et al., 2017), reducing a pest's longevity, development rate or reproductive potential (Shaltiel-Harpaz et al., 2014). A resistant cultivar can be selected by monitoring pest oviposition rates, pest mortality, feeding and development rates and nymphal weight gain (Bell & Puterka, 2003; Berrada et al., 1995; Pasqualini et al., 2006). Based on the UK horticulture statistics, Conference pear (*Pyrus communis* cv. Conference) is the most common pear cultivar in the UK, accounting for 84.01% of total planted area of pears (Defra, 2023). However, cv. Conference alongside other common UK pear cultivars including Comice, Concorde and Williams Bon Chretien are susceptible to *C. pyri* (Berrada et al., 1995; Nin & Bellini, 2000). Hybridisation of susceptible species with resistant ones, can be successful in increasing host plant resistance (Harris, 1973; Nin et al., 2018). Multiple intraspecific pear hybrids demonstrate high resistance to *C. pyri* infestations (Robert & Raimbault, 2004). However, the fruit quality of hybrids are often a concern within breeding programs (Nin et al., 2012; Robert & Raimbault, 2004), highlighting the need to consider resistance, yield and fruit quality during cultivar selection. This challenge can be solved with the DNA marker (Montanari et al., 2015; Pasqualini et al., 2006).

A more recent approach to bottom-up control is through activating plant defence pathways using plant defence elicitors (PDEs) (Civolani et al., 2022; Orpet et al., 2021; Saour et al., 2010). One example is the Harpin 44-kDa protein, encoded by the hrpN gene from the bacterium *Erwinia amylovora*, which activates the salicylic acid, ethylene and jasmonic response pathways, stimulating plant growth and defence (Saour et al., 2010). A study by Saour et al. (2010) found numbers of *C. pyri* nymphs were significantly lower in the Harpin treatment compared to the untreated control and had a higher fruit load. However, other studies have only found partial or variable pear psyllid suppression using PDEs (Civolani et al., 2022; Cooper & Horton, 2017; Orpet et al., 2021), suggesting that PDEs should be used alongside other control methods. Weather dependence of control methods is also important in pear psyllid management (Civolani, 2012b). Rainfall is perhaps the most disruptive to chemical and biorational methods, with the ability to wash insecticides and particle films off foliage and plant material (Erler & Cetin, 2007) and disrupt pheromones or other chemical cues (Johnston et al., 2022). Whilst temperature may have more of an impact on biological control methods impacting feeding, development and oviposition of natural enemies. Potential disruptions to IPM with respect to weather variables are considered throughout this review.

1.7 Phenological shifts and mismatches within agroecosystems

Multiple studies suggest that temperature significantly influences budburst and flowering phenology (Amano et al., 2010; Auffret, 2021; Fitter & Fitter, 2002). Fitter & Fitter (2002), highlights that flowering time has advanced rapidly in the UK over the past few decades; with first flowering time averaging 4.5 days earlier compared with the previous forty years. Whilst Amano et al (2010) predicted first flowering to be an average of 5.0 days earlier for every 1˚C of warming, with February - April temperatures being most closely correlated to flowering phenology. This phenological advancement depending on temperature has been noted in several tree-fruit species including apples (Guédon & Legave, 2008), plums (Cosmulescu et al., 2010), cherry (Sparks et al., 2005) and pear (Chitu & Paltineanu, 2020). Many fruit trees go into a dormancy phase over the winter, a period of restricted growth that protects them from cold temperatures and frost damage (Campoy et al., 2011). A minimum amount of chilling time (a certain number of hours below a particular temperature), followed by forcing time (a certain number of hours above a particular temperature) is then required to stimulate vegetative growth and flowering (Guo et al., 2014). Chilling periods are often accumulated between October–December, whilst forcing times are accumulated from January–April (Drepper et al., 2020), although this can be location dependent.

Warmer forcing periods are likely to accelerate flowering due to faster heat accumulation (Ruiz et al., 2007), whilst warmer chilling periods can delay flowering due to insufficient chilling time (Guo et al., 2014). Reeves et al (2022) found that January–April temperatures had a significant effect on pear (*P. communis*) flowering time, with warmer temperatures associated with earlier flowering for 12 different pear cultivars and 4 phenological stages. Furthermore, this phenological advancement was predicted to continue, with full flowering becoming 18.5 days earlier under the highest emissions scenario (RCP 8.5) by 2080, providing chill requirements were met. Earlier budburst and flowering could have significant bottom-up impacts for this model system. Pear psylla nymphs often take shelter within rolled-leaves and flower buds, from natural enemies and adverse weather conditions (Reeves et al., 2022; Solomon et al., 1989), which could provide more protection for psyllids earlier in the year. In addition, adult females also increase oviposition rate when green foliage is present compared to dormant budwood (Horton, 1990b), thus if leaf flush is earlier, oviposition may also shift. With respect to spraying regimes, it is likely that pre-bloom sprays will need to shift, to account for earlier budburst, it is imperative that kaolin is applied pre-bloom to provide optimal spray coverage (Nottingham & Beers, 2020). For anthocorid releases, this is dependent on how pest populations respond to earlier flowering. If psyllid oviposition and nymph emergence peaks earlier, then release of biological control should also shift, especially if natural anthocorid migrations do not follow this. This emphasises the importance of psyllid monitoring for growers, to optimally time sprays and mass releases.

Phenological monitoring is important within an agricultural ecosystem, allowing growers to decide when to apply different biological, chemical and cultural control methods (Fig. 3). A phenological model for *C. pyri* has been developed for the first and second generation of pear psylla, this considers multiple variables including; termination of diapause, egg and nymph development, the pre-oviposition period and air temperature (Schaub et al., 2005). The model is now used in the SOPRA information system, for monitoring fruit pests in Switzerland, informing growers when to psylla are likely to emerge, when to monitor for them and the optimal time period to apply treatments (Samietz et al., 2007; Samietz et al., 2011). However, this model has not been applied to UK regions, only considers the pest and looks at air temperature rather than impacts of other weather variables. Thus, applying a pest forecasting system to UK pear orchards, which considers the phenology of pear, pear psylla and natural enemies with respect to weather variables would be optimal.

1.8 Development and voltinism

Pear psylla and their natural enemies are poikilotherms (Reeves et al., 2023), meaning their body temperature fluctuates with their environment (Régnière & Powell, 2013; Wojda, 2017). Thus, the rate of development of poikilotherms is dependent on ambient temperature, developmental rate can also influence other variables such as voltinism (generations per year), fecundity and mortality (Culos & Tyson, 2014). Insect development occurs between a critical thermal minima (CTmin) and a critical thermal maxima (CTmax) (Rebaudo & Rabhi, 2018). Above CTmin development rate increases slowly with temperature at first, then linearly before it reaches an optimum (Topt). Once Topt is reached there is a rapid decrease in development rate before the CTmax is reached. Temperature dependent development is evident in pear psylla (Kapatos & Stratopoulou, 1999), it is estimated that pear psylla have a CTmin of 10˚C for oviposition and egg development (Civolani, 2012) and a CTmax of 32.2 ˚C (McMullen & Jong, 1977). However, the CTmax is based on *C. pyricola*, as the CTmax of *C. pyri* has not been recorded (Kapatos & Stratopoulou, 1999; Schaub et al., 2005). Other Authors have reported minimum temperatures that allow egg and nymphal development as low as 2-4 ^{o}C for *C. pyri* (Beránková & Kocourek, 1994; Kapatos & Stratopoulou, 1999; Schaub et al., 2005) and changed with time of year due to temperature and changes in host quality (Civolani et al., 2023).

Studies predict that the number of generations per year is likely to increase in multivoltine insect species, due accelerated development resulting in the earlier completion of life cycles (Karuppaiah & Sujayanad, 2012; Tobin et al., 2008). For *C. pyri*, the number of generations per year does differ spatially, likely due to climatic differences; with 2 generations per year recorded in Norway (Næss, 2016), 3–4 generations in Switzerland (Daniel et al., 2005) and 5–6 generations in Greece (Stratopoulou & Kapatos, 1992b). Furthermore, nymphs in Sicily overwinter alongside adults, as winters are far milder (Nin et al., 2012). Voltinism of *C. pyricola* also shows a substantial latitudinal gradient, with earlier maturation of eggs postdiapause and additional generations depending on latitude (Civolani et al., 2023). Thus, with UK summer temperatures predicted to increase (MetOffice, 2022), elevated development rates could lead to an increased generation number. Differences in generational number have also been found for natural enemies of pear psylla; the multivoltine parasitoid *T. insidiosus*, completes 2-3 generations per year in France and Spain, whilst in Syria six generations have been reported, due to higher temperatures in this region (Tougeron et al., 2021)*. Anthocoris nemoralis* also varies in generation number, with two generations in the UK (Solomon & Fitzgerald, 1990), which can vary from 1-3 generations depending on location and host plant (Dempster, 1963; Saulich & Musolin, 2009).

Increased voltinism could have mixed effects for natural enemies depending on synchrony (Gaytán et al., 2022; Thomson et al., 2010), for parasitoids additional generations of hosts could provide a greater resource and increased time for population build-up (Horgan, 2020). Alternatively, if host stage is asynchronous to the parasitoid, then there may be fewer hosts available to oviposit in or less time to complete its lifecycle. Furthermore, there is concern whether univoltine parasitoids and predators will have the plasticity to become multivoltine (Tougeron et al., 2020). Although, there is evidence of multiple taxa shifting from univoltine to bivoltine lifecycles; for example the spruce bark beetle *Ips typographus* is usually univoltine in Norway, Sweden and Finland, however during warm summers the species becomes bivoltine (Lange et al., 2006). Similar shifts have been found for the lawn ground cricket, *Polionemobius mikado*, which is bivoltine in southern Japan and univoltine in the north, however this bivoltine lifecycle has slowly shifted northwards with respect to rising temperature (Matsuda et al., 2018).

1.9 Fecundity, mortality and diapause

From late September onwards winterform *C. pyri* adults begin to emerge (Bues et al., 1999). Winterform females are in reproductive diapause; where ovaries are still immature and experience a slow but constant development over the winter months (Lyoussoufi et al., 1994), whereas males have active sperm in the in the spermatheca (Civolani, 2012b; Hodkinson, 2009). However, there is discussion whether rising temperatures will reduce the length of diapause (Karuppaiah & Sujayanad, 2012; Kaur et al., 2023). For *C. pyri* diapause is induced by short photoperiods in late summer- early autumn and low temperatures (Hodkinson, 2009; Stratopoulou & Kapatos, 1995; Tougeron et al., 2021). Studies show that young nymphs (L1-L3) reared under short day length (LD 12:12) and low temperature (<15 ˚C) produce diapausal winterform adults (Hodkinson, 2009; Nguyen, 1972). For the duration and termination of diapause, temperature becomes a more important environmental cue as diapause progresses. Hodkinson (2009) states that diapause is termination for *C. pyri* when exposed to temperatures above 25 ˚C, irrespective of photoperiod. However, the minimum temperature for diapause termination is dependent on location and photoperiod. Thus, it is likely that climate change could impact the duration of *C. pyri* diapause, with milder winter temperatures resulting in advanced emergence of adults from shelters and earlier egg laying (Civolani, 2012b). Multiple natural enemies of *C. pyri* enter diapause overwinter, including anthocorids (adults diapause under short-day conditions (Saulich & Musolin, 2009), earwigs (enters a post-reproductive diapause under short photoperiods and low temperatures) (Goodacre, 1998) and the multivoltine parasitoid *T. insidiosus* (Tougeron et al., 2021) For *T. insidiosus,* larvae overwinter inside *C. pyri* mummies, however the photoperiodic or thermal cues required to induce this are unknown, highlighting an area of further research.

Mortality over winter is particularly high for *C. pyri* adults, likely due to adverse weather conditions, limited resources and active winter predators (Horton et al., 1992; Kapatos & Stratopoulou, 1996; Petráková et al., 2016). Kapatos & Stratopoulou (1996) found that on average only 23.2% of *C. pyri* females survived overwinter, until the beginning of the oviposition period. Furthermore, rainfall and temperature have been shown to significantly impact psyllid mortality over winter (Horton et al., 1992; McMullen & Jong, 1977), alongside habitat complexity (number of overwintering shelters) (Michalko et al., 2017) and predator abundance/activity (winter-active spiders such as *Anyphaena* and *Philodromus* can help to control psyllid populations) (Petráková et al., 2016), thus milder winters could reduce psyllid mortality. In addition, temperature has a significant impact on summerform mortality, McMullen & Jong (1977) found that mortality rates of *C. pyricola* eggs and nymphs was lowest at 21.1 ˚C, with a higher longevity of summerform adults at lower temperatures compared to elevated temperatures. Furthermore, longevity under elevated temperatures significantly differed depending on morphotype, with summerform adults surviving significantly longer than winterforms (for temperatures >30 ˚C). Higher temperatures also influenced fecundity in this study, with maximum fecundity at 21.1 ˚C (444.9 eggs during a female's lifetime), and significantly reduced oviposition rates at 35.0°C (2.8 eggs during a female's lifetime). Once again optimum fecundity temperature depended on morphotype and was significantly lower for winterform females (15.6 ˚C). However, studies are lacking for *C. pyri* on fecundity and mortality, unlike the wide range of temperature regimes McMullen & Jong (1977) use *for C. pyricola*. Thus, it is difficult to confirm whether there are any temperature specific differences between *C. pyri* and *C. pyricola*. Further exploration of how RH impacts mortality and development is required, as young nymphs and eggs are vulnerable to desiccation under high temperatures and low humidity (Wilde, 1964), suggesting these factors could interact synergistically.

1.10 Feeding rates and functional responses

Climate change is predicted to have mixed effects on the feeding rates of sap feeding insects (Evans & Borowicz, 2015; Kenneth & Jayashankar, 2020). Firstly, elevated CO_2 levels could increase the C:N ratio in crops due to the fertilisation effect (Gifford, 2004; González de Andrés, 2019); currently the rate of photosynthesis is limited as both CO_2 and O_2 compete for the active site of the rubisco enzyme used in photosynthesis. However, climate change may lead to higher levels of CO_2 saturating rubisco's active site; increasing amount of carbon fixation (McGrath & Lobell, 2013). Thus, as nitrogen is already a limiting factor in the diet pear psylla (Le Goff et al., 2019; Pfeiffer & Burts, 1984), the higher C:N ratio could result in increased compensatory feeding for phloem feeders to obtain essential amino acids (Ryan et al., 2010). Pfeiffer & Burts (1984) found that pear psylla had increased feeding rates and honeydew production on pear trees with lower nitrogen content, supporting this hypothesis. On the other hand, the upregulation of carbon-based chemical defence compounds may be enhanced under elevated CO_2 (Robinson et al., 2012; Ryan et al., 2010). A meta-analysis by Robinson et al (2012) found a significant increase in tannins and overall leaf toughness under elevated CO_2. However, increased leaf toughness may be more detrimental to folivores compared to phloem feeders, furthermore trichrome hairs which provide a physical barrier for phloem feeders were not found to increase in density under elevated CO_2, suggesting minimal impacts for sap-sucking insects with respect to plant defence.

Climate change may also alter transpiration rates of plants, depending on temperature, water stress, RH and CO_2 level (Kirschbaum, 2004; Mahato, 2014). Furthermore, many factors interact synergistically (Reynolds-Henne et al., 2010; Schulze et al., 1973). Schulze et al (1973) found higher temperatures increased stomatal conductance; however higher temperatures coupled with water stress significantly reduced stomatal conductance. Decreased transpiration rates can reduce plant vigour and accessibility to nutrients in the phloem for sap-sucking insects (Evans & Borowicz, 2015). However, intermittent drought stress may be beneficial for phloem feeders, due to the pulsed stress hypothesis; where periods of stress, followed by the recovery of turgor, result in stress-induced increases in plant nitrogen (Huberty & Denno, 2004). Therefore, it is important to consider interactions between weather variables, as well as their intensity and duration when predicting psyllid feeding rates with respect to climate change.

A functional response can be defined as the consumption rate of a predator depending on prey density (Holling, 1965; Real, 1977). It consists of attack rate; the rate at which a predator encounters a prey item and handling time; the time taken for a predator to consume the prey item (Juliano, 2020; Real, 1977). Functional responses are temperature dependent (Englund et al., 2011; Hassanzadeh-Avval et al., 2019); attack rates and handling times have been shown to vary with temperature in a hump-shaped manner (Uszko et al., 2017), and are often maximised at intermediate temperatures (Uiterwaal & DeLong, 2020). Reeves et al (2022) demonstrated that anthocorid *A. nemoralis*, did not significantly alter its attack rate or overall consumption rate of *C. pyri* nymphs depending on temperature, for current and predicted summer temperatures by 2080. However, this study concentrates on a small temperature range (18˚C - 23˚C) based on predicted UK average temperatures; for a larger temperature range significant differences may be evident. Hassanzadeh-Avval et al (2019) found significantly higher attack rates for *Anthocoris minki* Dohrn predating upon *Psyllopsis repens* Loginova at 30 °C compared to 15 °C, which may be relevant for maximum and minimum summer temperatures, however these intervals have not tested for *A. nemoralis*. Temperature also interacts with other weather variables, impacting functional response;

Yanik (2011) suggests that the combined effect of temperature and humidity had a significant impact on the consumption rate of *Ephestia kuehniella* Zeller eggs by *A. nemoralis*, whilst neither variable was significant alone.

1.11 Behaviour, activity and spatial distribution

Dispersal of *C. pyri* winterform adults from orchards begins in September, peaking late October to early November (Civolani & Pasqualini, 2003). The timing of this phenological event is dependent on temperature, humidity, precipitation and leaf fall (Horton et al., 1994). Civolani & Pasqualini (2003) showed early *C. pyri* dispersal was correlated with early leaf fall and temperature. Thus, if leaf fall shifts with respect to climate change, psyllid dispersal may follow suit. Additionally, Civolani & Pasqualini (2003) highlighted that *A. nemoralis* sought refuge when maximum temperature dropped below 10 °C, demonstrating sheltering behaviour. Similar findings were seen for Coccinellidae spp. but for a higher maximum temperature. Furthermore, Horton et al (1994) demonstrated for *C. pyricola* that warmer and drier autumns lead to earlier dispersal and increased psyllid flight activity compared to those that were cool and wet.

The spatial distribution of pear psylla within the tree canopy impacts their activity and varies throughout the year (Horton et al., 1994; Stratopoulou & Kapatos, 1992a). Stratopoulou & Kapatos (1992a) monitored the spatial distribution of *C. pyri* within pear trees (eggs and young nymphs), their findings indicated that during spring psylla density was higher in the upper canopy, especially south or west facing, however later in the year, numbers increased in the lower canopy. This could suggest that areas exposed to more sunlight were actively chosen as oviposition sites, to meet temperature requirements for development, however later in the year it may be more optimal to oviposit lower down in the canopy to reduce desiccation of eggs. Moreover, females displayed an oviposition preference for flowerbuds; 93.8% of eggs and nymphs were found in flowerbuds compared to leafbuds. This may be because it is more optimal for nymphs to develop inside flowers, as it provides more shelter from weather conditions and natural enemies (Reeves et al., 2022; Solomon et al., 1989). With respect to rising temperature, it is important to explore whether oviposition in the lower canopy increases during the summer, leading to spatial shifts in the psyllid population.

Spatial shifts in prey density under warming temperatures may lead to corresponding shifts for predators (Schmitz & Barton, 2014). For example, climatic warming could lead to higher temperatures in the upper part of a plant canopy, prey respond by moving down to the lower canopy. Predators and parasitoids may also shift spatially due to rising temperature or to follow the distribution of prey (Barton & Schmitz, 2009). For example, aphids often move downwards, occupying more shaded leaves in the lower canopy due to high summer temperatures (Dixon & Hopkins, 2010). Aphid parasitoids also been shown to follow the distribution of aphids; a field-study monitoring pecan aphids found that the parasitoid *Aphelinus perpallidus* (Gahan) was most abundant in the lower canopy, where the population of pecan aphids were highest during the summer (Slusher et al., 2022).

However, when multiple predators are present the interactions can become more complex, with respect to climatic warming prey (Barton & Schmitz, 2009; Schmitz & Barton, 2014). Predators that usually occupy separate spatial niches within the plant canopy may overlap, leading to interference competition (when one predatory species reduces prey capture for a second predator species) or intraguild predation (IGP, where different predators consume each other, in addition to their target prey) (Jonsson et al., 2017). Therefore, it is important to identify natural enemies of *C. pyri* that could resort to IGP if niches overlap, as well as predicting spatial shifts of pest populations within the plant canopy. *F. auricularia*, has a varied diet of insect, animal and plant material (Helsen et al., 1998), however they are nocturnal (Suckling et al., 2006), so are less likely to interact with other natural enemy species. IGP has been documented between ladybird and lacewings (Karami-jamour et al., 2018; Zarei et al., 2020), and between *A. nemoralis* and multiple coccinellid species (Batuecas et al., 2022), indicating an avenue for further research.

1.12 VOCs and trophic signalling

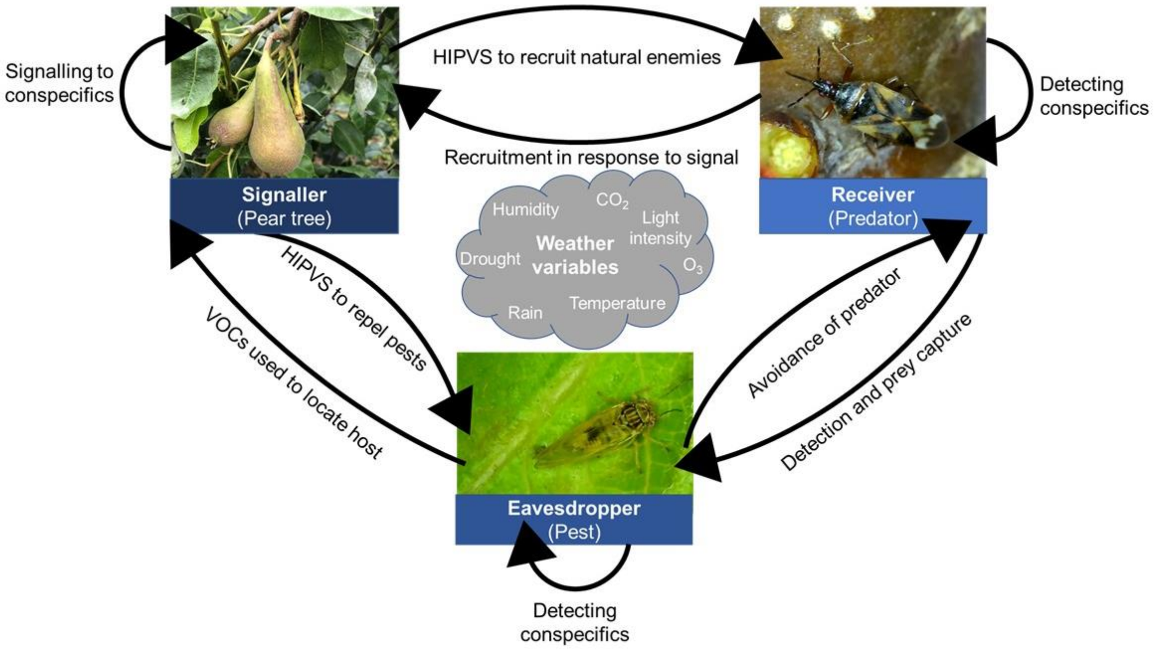

Figure 1.4: Signals and cues used within tri-trophic interactions between pears, pests and natural enemies, and the weather variables with the potential to alter or disrupt them. Cues and signals are used in a range of ways: HIPVs (herbivore-induced plant volatiles) can be used by plants to recruit predators and parasitoids and signal to conspecifics to upregulate genes for plant defence. However, plant VOCs (volatile organic compounds) can be eavesdropped upon by pests to detect hosts. Pheromones, acoustic and visual signals can be used to attract mates and detect conspecifics. Signals can also be eavesdropped upon by natural enemies in order to locate prey.

Pear psylla rely on a range of cues and signals reviewed in Civolani et al. (2023); including chemical cues for host choice and oviposition (Gallinger et al., 2023; Horton & Krysan, 1991), substrate-borne acoustic signals used in mate location (Eben et al., 2015; Jocson, 2023), tactile cues used when depositing eggs (Horton, 1990a) and visual cues used to locate host plants (Adams et al., 1983; Czarnobai De Jorge et al., 2023). Abiotic factors have the ability to disrupt or alter cues and signals; acting as environmental noise, so it is more difficult for the receiver to understand them (Lawson & Rands, 2019; Lawson et al., 2017). Rainfall, temperature, light intensity, wind, humidity, CO_2 and tropospheric ozone all have the ability to disrupt signals or create environmental noise (Lawson & Rands, 2019; Yuan et al., 2016). Signal disruption may be further exacerbated by climate change (Figure 1.4); via altered signal production, impacted transmission and changes in receiver perception (Becker et al., 2015; Yuan et al., 2009). Thus, it is vital to monitor how vulnerable pears, pear psyllid and their natural enemies are to signal disruption with respect to climate change.

One important set of infochemicals used in multitrophic communication are volatile organic compounds (Abbas et al., 2022; Yuan et al., 2009). In response to herbivory, plants often release herbivore-induced plant volatiles (HIPVs), which can recruit natural enemies (Allison & Daniel Hare, 2009; Valle et al., 2023), repel pests (Turlings & Ton, 2006) and can be used for plant-plant communication, resulting in increased upregulation of defence genes for receivers (Ninkovic et al., 2021). However, abiotic factors may influence VOCs; elevated temperature has been shown to alter the rate of transmission, emission and composition of VOCs (Helmig et al., 2007; Yuan et al., 2009). Isoprene is enhanced under climate warming and emission rates are positively correlated with temperature (Guenther et al., 1993; Loivamäki et al., 2008). A Free-Air Carbon dioxide Enrichment (FACE) experiment by Gallinger et al (2023), indicated that pear trees cultivated under elevated CO_2 differed in their release of VOC compounds compared to ambient controls. Despite altered VOC emission *C. pyri* females did not have a significant preference between trees grown in ambient or elevated CO_2, in olfactometer or binary choice oviposition assays. However, whether the detection of HIPVs by natural enemies were altered was not investigated. This suggests an avenue of further research, especially as HIPVs can result in attractive responses for both anthocorids (Drukker et al., 2000; Scutareanu et al., 1997) and lacewing larvae (Valle et al., 2023). Climate change may also impact insect pheromonal communication; temperature has been shown to increase volatility and diffusion rates of semiochemicals, impacting transmission rate (Boullis et al., 2016). The pear psyllid pheromone is a long chain cuticular hydrocarbon (13-Me C27) with a low volatility, so the pheromone is likely to act at close range or is contact based (Civolani et al., 2023). Therefore, the impact on transmission rate may be less important, although further research on the relationship between 13-Me C27 and temperature is required.

Acoustic signals used for mate location and courtship can be temperature dependent (Jocson, 2023; Larson et al., 2019; Yang et al., 2021). Different components of acoustic signals can be thermally sensitive, including the pulse frequency, duration and interval between pulses (Larson et al., 2019; Walker & Cade, 2003). An experiment by Jocson et al., (2023) demonstrated that song frequency of male pear psylla was temperature dependent, displaying a positive linear relationship with temperature (ranging from 180 to 1,900 Hz). However, no significant relationship was found between pulse interval, pulse length and number of pulses and temperature. Whether higher frequency calls were more attractive to female psyllids was not assessed, making it unclear if temperature is likely to disrupt mating. On the other hand rainfall is more pronounced in its disruption of acoustic communication, generating high-frequency vibrations of 3–4 kHz, acting as environmental noise for Homoptera (Tishechkin, 2013). Psyllids usually cease to produce signals entirely in the presence of wind and rainfall to reduce energy consumption, in the generation of disrupted signals (Liao et al., 2022; Tishechkin, 2013). Thus, alongside its ability to remove VOCs, increased rainfall can be disruptive to insect mating.

1.13 Discussion and future directions

Pear psylla (*Cacopsylla pyri*) are a still a key pest of UK pear orchards, causing damage especially through the production of honeydew by nymphs, resulting in the growth of black sooty mould on shoots, foliage and fruit (Civolani et al., 2023). With the diminishing number of approved pesticides to control *C. pyri* and the resistance to previously used agrochemicals (Civolani et al., 2023), it is clear that biorational compounds, biological control and cultural control methods are being adopted by UK pear growers, focusing on both top-down and bottom-up control. With application of the particle film kaolin and release of the biocontrol agent *A. nemoralis*, in several surveyed orchards (Table 1.1). It should be noted that multiple pesticides commonly used in pear psyllid management have been withdrawn over the past seven years (Hertfordshire, 2023; HSE, 2023), with a the withdrawal of a fourth compound (indoxacarb) currently planned for 2024. This review recommends applying a whole ecosystem approach to pear psyllid management, that utilizes regular pest monitoring, uses cultural and biological control methods and biorational compounds as alternatives to chemical sprays when possible and considers application timing depending on weather variables and phenological events.

The enhancement of natural enemies should be further encouraged for growers; *A. nemoralis* is a well-known natural enemy of *C. pyri*, currently mass released as a biocontrol agent in pear orchards (Sigsgaard et al., 2006a), however other methods are recommended to enhance wild natural enemies populations (Shaw et al., 2021), rather than relying solely on mass released biocontrol. Refugia are key to cultural control methods within pear orchards to increase natural enemy populations within the tree canopy (Solomon et al., 1999). This includes artificial refuges such as corrugated cardboard in a bottle (Hansen et al., 2005; Solomon et al., 1999) or wooden Wignests loaded with food attractant (Russel-IPM, 2023; Shaw et al., 2021) and natural refugia like native hedgerows (Nagy et al., 2008; Scutareanu et al., 1999), nettles (Shaw et al., 2021), cover crops (Horton et al., 2009) and wildflower strips or margins (Balzan et al., 2014; Mateos-Fierro et al., 2021). Furthermore, with the predicted surge in extreme weather events (MetOffice, 2019), shelter for natural enemies may become increasingly important.

Exploration of rearing of other natural enemies aside from *A. nemoralis* is recommended; although *A. nemoralis* is likely to be an effective predator under predicted UK temperatures (Reeves et al., 2023), studies indicate that diverse predator assemblages can be more effective at controlling pest populations (Tylianakis & Romo, 2010), providing there is niche separation. Earwigs have a lower dispersal distance, so need to be released at multiple points in an orchard (Moerkens et al., 2010), however they have good potential as biocontrol agents (Booth et al., 1992), thus rearing and mass release within pear orchards should be further explored, alongside factors that influence their abundance within and between orchards. *Trechnites insidiosus* is a parasitoid wasp of interest, specific to pear psylla, with the ability to oviposit in all 5 nymphal instars (with a preference for 3rd and 4th instars) (Le Goff et al., 2021; Tougeron et al., 2021). Tougeron et al (2021), proposes the release of *T. insidiosus* alongside other psyllid bicontrol agents during spring, although emphasises the need for further research into mass rearing to make the strategy cost-effective. However, there is a lack knowledge on the phenology of UK *T. insidiosus* populations, highlighting the need for parasitoid monitoring in UK orchards.

The use of a combination of methods as an alternative to chemical insecticides is recommended to suppress pear psylla below economic thresholds (Shaw et al., 2021). Thus, the use and further development of biorational compounds and cultural control methods are advocated alongside biological control. In addition to kaolin, there are several methods currently absent from surveyed orchards that have potential for psyllid control. Firstly, oils can be an effective oviposition deterrent and repellent for *C. pyri* adults during the pre-bloom stage (Civolani, 2012b; Emami, 2023; Erler, 2004b). Effective oils include mineral (Civolani, 2000), cotton seed, fish-liver, neem (Erler, 2004b) and peppermint oil (Li & Tian, 2020), although some oils contain allergens making them unsuitable for UK approval. Reflective plastic mulch is effective in psyllid population suppression (Nottingham & Beers, 2020; Nottingham et al., 2022), reflecting solar light into the tree canopy (Shimoda & Honda, 2013), promoting adult flight behaviour (Nottingham & Beers, 2020) and damaging psylla eggs and nymphs (Beard, 1972). However, there are concerns that elevated UV could impact natural enemies (Nottingham & Beers, 2020), highlighting a need for further field trials. Plant defences elicitors are a potential approach to bottom-up control via activating plant defence pathways (Civolani et al., 2022; Orpet et al., 2021; Saour et al., 2010), however studies have found variable pear psyllid suppression using PDEs (Civolani et al., 2022; Cooper & Horton, 2017; Orpet et al., 2021), suggesting that PDEs should be used alongside other control methods. Finally, the discovery of a sex pheromone, produced by *C. pyri* females is useful (Ganassi et al., 2018b), this could be valuable as a pheromone lure for monitoring, trapping or mating disruption (Guédot et al., 2009a). Acoustic signals also share this potential (Jocson, 2023), however further field trials are required to evaluate their proficiency in mating disruption.

Climate change is likely to alter multiple processes within this agroecosystem; pear flowering phenology has advanced significantly over the past sixty years in the UK with respect to rising air temperature (Reeves et al., 2022), whilst insect pests and their natural enemies are poikilothermic

(Régnière & Powell, 2013; Wojda, 2017), thus development rate (Rebaudo & Rabhi, 2018), voltinism (Karuppaiah & Sujayanad, 2012), functional response (Englund et al., 2011; Hassanzadeh-Avval et al., 2019), mortality, oviposition (Culos & Tyson, 2014) and even call frequency (Jocson, 2023) can be temperature dependent. Furthermore, climatic warming can lead to spatial shifts in prey density (Schmitz & Barton, 2014), predators can also shift their position within the plant canopy under higher temperatures, potentially resulting niche overlap, IGP and interference competition with other predator species (Barton & Schmitz, 2009). A large proportion climate change related studies focus solely on temperature, rather than other abiotic factors (Barton & Schmitz, 2009; Clusella-Trullas et al., 2011; Kollberg et al., 2015). However, other abiotic factors such as precipitation, humidity, CO_2 levels (Montoya & Raffaelli, 2010), ozone, nutrient availability (Agathokleous et al., 2020; Yuan et al., 2009) and frost days (Sunley et al., 2006) should also be considered, as they can significantly impact trophic interactions and ecosystem services, with the potential to interact additively, synergistically or antagonistically.

Phenological mismatches are a particular concern for agroecosystems, as not all species respond in similar ways to climate change (Damien & Tougeron, 2019; Renner & Zohner, 2018). Although phenological models have been created for pear psylla and natural enemies; they are often look at the organism in isolation rather than its interaction with other trophic levels (Moerkens et al., 2011; Schaub et al., 2005). These interactions could be particularly important, for example how pear budburst corresponds with pear psyllid oviposition or how anthocorid migration into pear orchards depends on psyllid population density, making it imperative to consider primary producers, pests and natural enemies when creating phenological models, as the shifting of one level could create mismatches for others. An App to record phenological monitoring data for multiple trophic levels (pear tree, pear psylla and natural enemies), would be beneficial for UK pear growers, allowing the input of data and guidance of when to apply certain control methods based on phenological stage and pest abundance. It would also provide data for researchers, allowing them to link key phenological events to weather variables and help model pear psyllid populations, for a year-on-year basis and under future climate scenarios.

1.14 Conclusion

This review proposes a whole-ecosystem based approach for pear psyllid management; that considers cultural, biological and chemical control methods, application timing, habitat management and abiotic processes that may disrupt pest management. There are a diverse range of methods currently used to control pear psylla. However, with the reduction in insecticides approved for UK use and the potential disruption to trophic interactions as a result of climate change, the timing of these control methods may need to shift or alternative methods may need to be applied. Climate change has the potential to alter both bottom-up and top-down processes within ecosystems. Abiotic factors such as temperature, humidity, rainfall, drought, light intensity, ozone and CO_2 could impact bottom-up control by affecting nutrient uptake, availability and plant defence, as well as top-down control impacting predator activity, IGP, interference competition and functional responses. Changes in phenology, feeding, oviposition and activity are all important factors that must be monitored in respect to climate change to inform effective and timely interventions. For monitoring tri-trophic interactions, signalling responses should be considered, including VOCs and pheromones for chemical signalling, tactile signals herbivores use for oviposition, acoustic and visual signals used to attract mates and gustatory cues to differentiate between hosts and non-hosts. The need for phenological data in monitoring trophic interactions is vital, few growers and agronomists regularly monitor their orchards and record this information. These data could be used to help make decisions on spray timing or natural enemy release, as well as inform phenological models that predict pest populations and natural enemy emergence based on weather variables. Thus, an easily accessible App and collective database is recommended for UK pest monitoring and control in pear orchards.

The aims for this thesis were to highlight the current control methods used within pear psyllid management and the potential challenges for this agroecosystem with respect to climate change. To monitor phenological shifts at each trophic level and potential mismatches between trophic levels within this system, under historical, current and future climate scenarios. This thesis also aimed to explore changes in behaviour and functional response, for natural enemies within this system under future temperature regimes.

2 Climate induced phenological shifts in pears – a crop of economic importance in the UK

This chapter is a version of the following paper, with minor corrections and changes to formatting and references to make the thesis more comprehensive:

Reeves, L. A., Garratt, M. P., Fountain, M. T., & Senapathi, D. (2022) Climate induced phenological shifts in pears–a crop of economic importance in the UK. Agric Ecosyst Environ 338: 108109. https://doi.org/10.1016/j.agee.2022.108109

Author contributions: LR, MG, MF and DS conceived and designed the study. LR carried out data collation, data analyses and drafted the manuscript with all authors providing feedback on multiple drafts prior to submission.

2.1 Abstract

Phenological advancements in flowering have been well documented in many food crop, ornamental, and native plant species, with respect to climate change. However, there is lack of information on how flowering times in crop species, especially fruit trees will react to future climate scenarios. This is important as changes in phenology could have implications for ecosystem services and function, biological interactions and agronomic outputs. Using 60 years of data from pear (*Pyrus communis* L.) orchards at two research organisations in Kent, UK this study explored temporal changes in flowering phenology, identified the weather variables driving this change, and predicted how flowering times may be altered by 2080 with respect to future emissions scenarios. We show pear flowering (1990-2020) in the last 30 years has advanced 11.44 days compared to historical data (1960-1989). Furthermore, we highlight this advancement is apparent in all twelve pear cultivars and the four phenological stages analysed, including Conference, the most common UK pear cultivar. Our results indicate that this advancement in flowering began after 1982; that air temperature and frost days significantly impact pear flowering; and this change in flowering phenology is likely to continue under future climate scenarios. Four Representative Concentration Pathways from the UK Climate Projections 2018 report were used to model the impact of future climate, including low, medium, medium-high and high emission scenarios. Under all scenarios a phenological advancement in flowering time was predicted by 2080 with the greatest advancement in flowering time observed under the high emission scenario. Earlier flowering and budburst could result in phenological

mismatches between plant and pollinators, alter agricultural spraying regimes, increase risk of frost exposure and exacerbate impacts of pest populations within an agroecosystem, thus it is vital to monitor advancements in flowering phenology.

2.2 Introduction

Global climate is predicted to change significantly over the next 80 years, with temperatures estimated to rise between 2.6-4.8 °C (Scott et al., 2016) and CO_2 levels predicted to increase above 900 ppm (Collins et al., 2013). The UK Climate Projections 2018 report (UKCP18) projects that all areas of the UK will be warmer by the end of 2100 (Met Office, 2019). The UK is likely to experience wetter winters and hotter drier summers (Murphy et al., 2018), with a higher frequency of extreme weather events such as flooding and heatwaves (Kennedy-Asser et al., 2020). Furthermore, climatic variability may increase within the UK alongside climate mean, with more variable interannual rainfall and temperature (Arnell, 2003).

Changes in weather variables could impact community structure (Kardol et al., 2011; Yang et al., 2011), biodiversity including species richness (Gitay et al., 2002; Iverson & Prasad, 2001), phenological events (Amano et al., 2010; Fitter & Fitter, 2002), and ecosystem services (Mooney et al., 2009; Scholes, 2016). One central phenological event for plants is flowering time; the timing of this event can alter the probability of successful pollination, impacting fruit set and yield (Fitter & Fitter, 2002; Rafferty & Ives, 2012). Alongside this, earlier flowering may increase the risk of exposure to spring frost, although spring frosts risk may be decreasing due to climatic warming (Cannell & Smith, 1986; Eccel et al., 2009). Finally earlier budburst and flowering may provide more shelter for pests earlier in the year, with denser plant canopies providing shelter from agrochemical sprays (Derksen et al., 2007), weather conditions (frost, wind, rainfall, and temperature extremes), and natural enemies (Norris, 2005). Furthermore, pests such as pear sucker (*Cacopsylla pyri*) nymphs are often found inside buds, flowers or rolled leaves (Solomon et al., 1989), which could provide more protection if available earlier in the year, altering pest populations within an agroecosystem.

There is evidence to suggest that flowering times of angiosperms are advancing (becoming earlier) globally and within the UK (Amano et al., 2010; Büntgen et al., 2022; Fitter & Fitter, 2002). Büntgen et al. (2022), compared flowering times of 406 plant species before and after 1986. The study found a shift in UK flowering times, with flowering becoming 26 days earlier for current (1987-2019) compared to historical time periods (1753–1986). Rapid advancements in flowering phenology may be occurring in crop species in addition to other angiosperms- research indicates that flowering phenology of fruit trees are advancing in Europe, with studies showing earlier flowering in apple, sweet cherry, pear, and plum (Cosmulescu et al., 2010; Sparks et al., 2005; Unterberger et al., 2018). This is cause for concern within the agricultural sector, as there are potential impacts on pollination, yield and ultimately food security (Craufurd & Wheeler, 2009).

Change point analyses, examining the point or points in time where a significant change has occurred (Taylor, 2000), have indicated that this advancement in flowering phenology began during the late 1980s (Drepper et al., 2020; Guédon & Legave, 2008; Kunz & Blanke, 2014). A phenological changepoint during the late 1980s may therefore correspond to the rapid temperature increase during this decade (Drepper et al., 2020; Hansen et al., 2006). Many studies focus on temperature as the driving factor influencing flowering phenology (Atkinson et al., 2004; Drepper et al., 2020; Fitter et al., 1995; Sparks et al., 2005); as a large proportion of fruit crops are influenced by chilling and forcing times including blackcurrant, pear, apple, sweet cherry, plum and peach (Atkinson et al., 2013; Atkinson et al., 2004). These crops go into a dormancy phase over winter, a period of restricted growth that protects them from cold temperatures and frost damage. Chilling periods for pear are often between October–December, whilst forcing times are from January-April (Drepper *et al*., 2020), although these time periods can vary depending on cultivar. Other weather variables also influence flowering phenology and budburst including frost days, rainfall, relative humidity, and solar radiation (Lesica & Kittelson, 2010; Mortensen, 1986; Nagy et al., 2013; Peñuelas et al., 2004; Westwood & Bjornstad, 1978).

Although, many studies have used temperature to explore phenology (Chitu & Paltineanu, 2020; Legave et al., 2015; Sparks et al., 2005), few have considered other factors or attempted to project based on future emission scenarios (Hoffmann & Rath, 2013; Mateescu et al., 2009). Furthermore, there is a gap within the scientific literature on how flowering phenology of crop species is advancing in the UK. Currently Sparks et al. (2005) is the main UK study concentrating on phenological advancement in agriculture; the study focuses on how flowering dates have become earlier over time and that flowering phenology is influenced by January-March temperatures in multiple crop species.

This study uses pear as a model system and the methods employed could be easily transferable to other crops. Pear is the fifth most produced fruit; with over 23 million tonnes grown per year globally and top producers based on weight include China, Europe and the U.S. (Silva et al., 2014). Pears are also an economically important crop within the UK, contributing to 4.0% of total fruit production; with a planted area of over 1500 hectares and an economic value of £22.8 million in 2019 (DEFRA, 2020), therefore an advancement in pear flowering time or reduction in yield would have significant economic implications.

This study aims to analyse whether pear flowering phenology is advancing over time within the UK, if this advancement differs depending on cultivar and which weather variables are driving this advancement. Furthermore, this study aims to predict how future Representative Concentration Pathways (RCP) emissions scenarios may impact flowering phenology in the future. We specifically tested three hypotheses 1) Pear flowering phenology is advancing over time in the UK and some cultivars are more sensitive than others, 2) Advancements in flowering due to climate change are driven by changes in weather variables including air temperature, frost days and rainfall, and 3) Flowering phenology will continue to advance in the future and be greatest under high emission scenarios.

2.3 Materials and Methods

Historical data on pear flowering times was collated from two sites in Kent, UK, comparing historical (1960-1989) and current (1990-2020) time periods and how flowering phenology changed depending on year. Flowering was also compared against several climate variables from local weather stations, to highlight which weather variables were most influential for phenological change. Finally, temperatures were predicted under four future Representative Concentration Pathways (RCPs), which are concentrations of released greenhouse gases that will result in radioactive forcing (the change in energy going in and out of the upper atmosphere) increasing by a specific amount by 2100 (Lowe et al., 2018b; Van Vuuren, Edmonds, et al., 2011) to explore how project how flowering would change by 2080.

2.3.1 Flowering data

Phenological data on pear flowering were collected for the following metrics (see Figure S1.1):

- first (first flower opens on a tree or flower's anthers are visible),
- ten percent (when 10% of flowers are open on the tree),
- full (when 50% of flowers have opened on the tree), and
- last (90% of petals have fallen)

These data were collected at two sites (Figure S1.2); from 1960-2020 at NIAB EMR (formerly East Malling Research, 51.2885° N, 0.4383° E) and 1960-2019 at the Brogdale Collection (51.3007° N, 0.8762° E). Records of 1991 flowering were missing for all cultivars at Brogdale (Table S1.1). Full and last flowering was recorded at both sites in the South-East of England, first flowering was only recorded in East Malling for 2 cultivars, whilst ten percent flowering was recorded at Brogdale for all cultivars. Both sites are valuable resources for pear production; Brogdale is part of the National Fruit Collection, with approximately 560 varieties of pear (Fernández-Fernández, 2010), whilst NIAB EMR is involved in developing best practice guides for the UK pear industry (Gregory, 2014). Phenological data was collated for twelve standard pear cultivars (cv.) including: Beurre Hardy LA (BH), Beurre Superfin (BS), Clapp's Favourite (CF), Conference (Con), Doyenne du Comice (DC), Durondeau LA (Du), Glou Morceau LA (GM), Louise Bonne of Jersey (LB), Nouveau Poiteau LA (NP), Packham's Triumph (PT), Precoce de Trevoux (PdT) and Williams' Bon-Chretien (WB).

2.3.2 Weather data

To analyse flowering phenology weather data (1959-2020) from the East Malling weather station (51.288° N, 0.448° E) in Kent were used for pear data from NIAM EMR. For Brogdale flowering phenology, Faversham (51.297° N, 0.878° E) weather data were used. The following weather data were collated from Met Office MIDAS data base (MetOffice, 2021): daily maximum and minimum temperature data and daily rainfall from East Malling. Daily maximum and minimum temperature data and daily rainfall from Faversham (Table S1.2). Mean temperatures were calculated from a mean average of maximum and minimum temperatures. Frost days were calculated by summing the number of days where the daily minimum temperature was below zero. Monthly mean, maximum and minimum temperatures, Frost days for each month (Oct-Dec and Jan-May) were calculated and total rainfall for each month were calculated, for use within the PCA analysis.

2.3.3 Future emissions scenarios

For historical temperature data, mean January to April temperatures were calculated from 1960-2020, using data from East Malling (51.288° N, 0.448° E) and Faversham (51.297° N, 0.878° E); Jan-Apr temperatures were chosen as these months were shown to be particularly important for influencing pear flowering in Drepper et al. (2020) and had lowest AIC (Akaike information criterion) during the model selection process. To calculate future temperature scenarios for 2080, data was extracted using the UK Climate Projections User Interface (UKCP, 2021a). A 2080 scenario was chosen as this year is commonly used in papers predicting future phenological events (Chung et al., 2011; Mateescu et al., 2009; Stöckle et al., 2010), thus the results of this paper can be easily compared to others. The predicted increase in mean air temperature at 1.5m for 2080 was calculated for January to April (baseline scenario 1981-2000) for a 25 km-by-25 km region in Kent, surrounding East Malling (562500.00, 162500.00), based on the mean average predicted increase from the UKCP18 model for 2080, using the 15 projections from the Met Office Hadley Centre climate model, for each of the four RCP scenarios (RCP2.6, RCP4.5, RCP6.0 and RCP8.5.). The predicted increase was added to the mean average 1981-2000 January-April air temperature (6.30˚C) from the East Malling weather station in Kent.

For historical frost day data, total frost days from January to April were calculated from 1960-2020, using data from East Malling (51.288° N, 0.448° E) and Faversham (51.297° N, 0.878° E). Frost days were calculated by totalling the number of days where the daily minimum temperature was below 0 ˚C. Jan-Apr temperatures were chosen as this model had lowest AIC during the model selection process. Future frost day scenarios were calculated for 2080 for RCP2.6 (low emissions) and RCP8.5 (high emissions) scenarios. Daily minimum temperature data for 2080 was extracted using the UK Climate Projections User Interface for a 60 km-by-60 km region in Kent. Frost days were calculated by summing the number of days where the minimum temperature was below 0 ˚C. RCP4.5 and RCP6.0 future frost day scenarios could not be calculated as minimum daily temperatures for these two scenarios were not available from the UK Climate Projections User Interface.

2.4 Data Analyses

2.4.1 Changes in flowering phenology over time

To test the hypothesis that flowering phenology has advanced over time (from 1960-2020), generalized additive models (GAM) were applied with model selection using AIC (Anderson & Burnham, 2002; Thomas et al., 2013; Zuur, 2012). GAMs with flowering time (in Julian days) as a dependent variable, year as a smoother and cultivar as a factor (with 12 levels) were selected. Site (Brogdale or East Malling) was removed from the model during the AIC selection process, this variable was not significant and did not improve model fit. The data were normally distributed and the residuals were also tested for normality and homogeneity. Separate models were plotted for first, ten percent, full and last flowering times, using the R package ‘mgcv’ (Wood & Wood, 2015) and ‘ggplot2’ (Wickham et al., 2016). The late 1980s was identified as the changepoint in flowering times in previous phenological studies (Drepper et al., 2020; Kunz & Blanke, 2014), so the two flowering time periods 1960-1989 (historical) and 1990-2020 (current) and the impact of cultivar were tested using a 2-way ANOVA.

2.4.2 Impact of weather variables

Weather variables were condensed into TempPC1, RainPC1 and FrostPC1, using principal component analyses (PCA) in R (Thomas et al., 2013), using the 'stats' package, version 4.2.0 (R, 2022). TempPCA used minimum, maximum and mean temperatures from May – Dec (previous year) and Jan – Apr (current year), RainPCA used total monthly rainfall from May – Dec (previous year) and Jan – Apr (current year) and FrostPCA total frost days from May and Oct – Dec (previous year) and Jan – Apr (current year), data from 1959 - 2020 were used. To test which weather variables were influencing flowering phenology linear mixed models (LMM) were applied; model selection using AIC was used as before. The PC1 from each weather variable (TempPC1, RainPC1, FrostPC1) was extracted from the PCA analyses and used within the LMM as fixed effects and cultivar as the random effect. LMMs with flowering time as a dependent variable, TempPC1 and FrostPC1 as fixed effects and cultivar as a random effect were selected for first, ten percent, full, and last flowering. Residuals were tested for normality and homogeneity. Separate models were plotted for first, ten percent, full and last flowering times, using the R package 'nlme' (Pinheiro et al., 2017).

2.4.3 Predicting the effect of future emissions scenarios

For future temperature scenarios LMMs with flowering time as a dependent variable, mean Jan-Apr temperature (˚C) as a fixed effect and cultivar as a random effect (with 12 levels), were chosen for first, ten percent, full and last flowering. January – April temperature ranges from the four RCP scenarios were used to predict flowering dates under the four future climate scenarios, alongside historical (1960-1989) and current (1990-2020) temperature scenarios, using the predict function using the 'stats' package version 4.2.0 (R, 2022). These RCP scenarios were RCP2.6 (low emissions scenario), RCP4.5 (medium emissions scenario), RCP6.0 (medium-high emissions scenario) and RCP8.5 (high emissions scenario).

For future frost day scenarios LMMs with flowering time as a dependent variable, total Jan-Apr frost days as a fixed effect and cultivar as a random effect (with 12 levels), were chosen for first, ten percent, full and last flowering. Total January – April frost days from RCP2.6 and RCP8.5 scenarios were used to predict flowering dates under future climate scenarios, alongside historical (1960-1989) and current (1990-2020) temperature scenarios, using the predict function using the 'stats' package version 4.2.0 (R, 2022). Only RCP2.6 and RCP8.5 gave daily temperature values, allowing us to predict future frost day scenarios.

The temperature ranges, frost days and standard deviations for each RCP scenario are specified in Table 2.4. AIC selection was used to choose the optimal model and residuals were tested for normality and homogeneity. Separate models were analysed and plotted for first, ten percent, full and last flowering times, using the R package 'nlme' (Pinheiro et al., 2017) and 'gglpot2' (Wickham et al., 2016).

2.5 Results

2.5.1 Flowering phenology for historical and current time periods

Full flowering time has advanced considerably over the past few decades; becoming 11.44 days (± 14.16, SD) earlier in 1990-2020 compared to the 1960-1989 time-period. Similar trends are also apparent for first (7.91 days earlier ± 14.43, SD), ten percent (9.82 days earlier ± 15.24, SD) and last (11.22 days earlier ± 13.13, SD) flowering times (Figure 2.1, Table S1.3-S1.6). Significant differences in flowering time between the two time periods were found within 2-way ANOVAs; with flowering being significantly earlier in 1990-2020 compared to 1960-1989, for all four phenological stages. For first flowering time there was a significant difference in flowering time depending on time period ($F_{(1)} = 41.18$, $p < 0.001$) and cultivar ($F_{(1)} = 19.94$, $p < 0.001$), however the interaction between time-period and cultivar was non-significant ($F_{(1,1)} = 0.343$, $p = 0.559$). For ten percent flowering, there was also a significant difference in flowering time depending on time period ($F_{(1)} = 144.33$, $p < 0.001$) and cultivar ($F_{(11)} = 4.676$, $p < 0.001$), however the interaction between time-period and cultivar was non-significant ($F_{(1,11)} = 0.349$, $p = 0.974$). For full flowering, there was a significant difference in flowering time depending on time period ($F_{(1)} = 320.9$, $p < 0.001$) and cultivar ($F_{(11)} = 7.297$, $p < 0.001$) but no significant difference depending between sites ($F_{(1)} = 1.23$, $p = 0.268$). The interaction between time-period and cultivar was also non-significant ($F_{(1,11)} = 0.794$, $p = 0.646$). For last flowering, there was a significant difference in flowering time depending on time period ($F_{(1)} = 366.5$, $p < 0.001$) and cultivar ($F_{(11)} = 9.460$, $p < 0.001$) but no significant difference depending on site ($F_{(1)} = 0.572$, $p = 0.450$). The interaction between time-period and cultivar was also non-significant ($F_{(1,11)} = 0.419$, $p = 0.948$). As there were no significant differences in flowering time between the two sites (Figure S1.3), data were combined for subsequent analyses.

All pear cultivars showed a much earlier average flowering for first, ten percent, full, and last flowering stages in 1990-2020 (current) compared to 1960-1989 (historical) (Figure 2.1).

2.5.2 Changes in flowering phenology depending on year

The models on first, ten percent, full, and last flowering phenology, year had a significant effect on flowering time (Table 2.1). Cultivar also had a significant effect on flowering phenology (p and F values stated in Table 2.1), with Louise Bonne of Jersey and Precoce de Trevoux showing earlier ten percent, full, and last flowering times than other cultivars, whilst Nouveau Poiteau LA had later flowering (Figure S1.4). However, all twelve cultivars responded similarly to year, with an advancement of 16.67 days per decade between 1983-1993 in full flowering time (Figure 2.2). Deviance explained by the models ranged from 25.3% - 38.3% (Table 2.1). Models for first, ten percent, full, and last flowering all seem to indicate an advancement in flowering time between 1982 and 1994/1995, indicated by the highlighted blue areas in Figure 2.2. Furthermore, there seems to be the start of a second advancement in flowering phenology from 2014 onwards.

2.5.3 Effect of temperature, frost, and rainfall

TempPC1 explained the largest amount of variation for first (24.5%), ten percent (30.3%), full (28.5%) and last flowering (28.5%). Whilst FrostPC1 explained the second largest amount of variation in the dataset for first (20.8%), ten percent (23.0%), full (22.1%) and last (22.1%) flowering. RainPC1 explained the least amount of variation in the dataset for first (16.0%), ten percent (16.2%), full (16.0%) and last (16.0%) flowering. Loadings for PC1 and PC2 for temperature, frost and rainfall for each month are shown in biplots (Figure S1.5-S1.8). More information on the biplots and PCAs can be found in appendix 1.

First, ten percent, full, and last flowering models were significant for both TempPC1 and FrostPC1 (Table 2.2), with marginal R^2 values that ranged from 41.80% - 44.43% and conditional R^2 values that ranged from 47.92% - 56.08% (Table 2.2). There was a strong negative relationship between TempPC1 and flowering time for all phenological stages (first, ten percent, full and last), with higher TempPC1 values (representing higher min, max and mean monthly temperatures) resulting in earlier flowering (Figure 2.3). A similar negative relationship occurred between FrostPC1 and flowering time; with higher FrostPC1 values (representing less frost during Dec-Apr) resulting in earlier flowering. Therefore, higher monthly temperatures and reduced frost days from December to April are likely to result in earlier flowering.

2.5.4 Effect of future emission scenarios

Even the lowest emissions scenario (RCP2.6) projecting future temperatures predicted a significant advancement in full flowering time by 2080; 5.11 days (± 2.58, SD) earlier compared to current values (1990-2020). Similar observations were seen in first (4.90 days ± 2.48, SD), ten percent (5.07 days ± 2.55, SD) and last (4.68 days ± 2.37, SD) flowering times. However, for the RCP8.5 scenario, this advancement in flowering time by 2080 was far greater, for first (17.76 days ± 8.69, SD), ten percent (18.25 days ± 5.29, SD), full (18.52 days ± 9.29, SD) and last (16.99 ± 8.53, SD) flowering compared to current values (1990-2020). Flowering times for first and ten percent flowering were quite similar (Table 2.4), suggesting there was little time difference from when the first and ten percent of flowers opened. There was a significant advancement in flowering time depending on January-April temperature for all flowering stages, with higher temperatures resulting in earlier flowering (Table 2.3). For first, ten percent, full and last flowering models (LMMs) there was a significant negative relationship between January - April temperatures and flowering times (Figure 2.4). With marginal R^2 values ranging from 58.35% - 66.64% and conditional R^2 values ranging from 70.27% - 73.72%. R^2 values explained a large proportion of the variance for all phenological stages.

There was also a significant advancement in flowering time, with respect to future frost day projections. Earlier flowering was predicted for all phenological stages and emissions scenarios by 2080 (Table 2.4). The lowest emission scenario (RCP2.6) predicted full flowering times to become 11.28 days (± 5.69, SD) earlier by 2080, whilst the highest emission scenario predicted a 14.77 day (± 7.42, SD) advancement in flowering time compared to current values (1990-2020). Similar advancements were seen for first, ten percent and last flowering times under both future frost day scenarios (Table 2.4). There was a significant advancement in flowering time depending on total January-April frost days for all flowering stages, with lower numbers of frost days resulting in earlier flowering (Table 2.3). For first, ten percent, full and last flowering models (LMMs) there was a significant positive relationship between total January - April frost days and flowering times (Figure 2.5). With marginal R^2 values ranging from 38.89% - 44.16% and conditional R^2 values ranging from 47.65% - 55.38%. R^2 values explained a reasonable proportion of the variance for all phenological stages, however January-April temperature explained a higher proportion.

2.6 Discussion

2.6.1 Advancements in flowering phenology over time

This study tested three hypotheses: 1) whether pear flowering phenology is advancing over time, 2) if advancements in flowering are driven by changes in weather variables frost and temperature and 3) if flowering phenology will continue to advance under future emission scenarios. The results demonstrated that pear (*Pyrus communis* L.) flowering phenology has advanced in several cultivars and phenological stages within UK orchards (Figure 2.2). In addition, these studies showed that both temperature and frost days impacted flowering time, although there may be a correlation between the two variables and that flowering time is predicted to advance under all future climate emissions scenarios by 2080, for both temperature and frost. Current full flowering times (1990-2020) have advanced by a mean average of 11.44 days (± 14.16, SD) compared to historical conditions (1960-1989), with similar results in all twelve tested pear cultivars and four flowering phenological stages analysed (Table S1.3-S1.6). There were also significant differences in flowering time depending on pear cultivar, for example Louise Bonne of Jersey and Precoce de Trevoux had earlier ten percent, full, and last flowering times compared to other cultivars, whilst Nouveau Poiteau LA indicated later flowering (Figure S1.4). However, all twelve pear cultivars responded similarly to year, temperature and frost days.

Results from this study indicate that advancement in pear flowering occurred after 1982, which although slightly earlier than some other changepoints (Drepper et al., 2020; Guédon & Legave, 2008; Kunz & Blanke, 2014), is within the range of other studies (Dose & Menzel, 2006; Menzel & Dose, 2005). For example, sweet cherry (*Prunus avium* L.), and lime (*Tilia platyphyllos* L.), changepoints were between 1980 and 1990 (Dose & Menzel, 2006), while multiple flowering records in Germany revealed a maximum change point probability in the mid-1980s for most of the species analysed (Menzel & Dose, 2005). Therefore, perhaps this rapid advancement in flowering time begins earlier than the late-1980s changepoint that Guédon and Legave (2008) use for their study on pear and apple flowering phenology.

2.6.2 Impacts of weather variables

The models that looked at effects of weather variables within our study, indicate that both temperature and frost may influence flowering phenology, while no significant effect of rainfall was detected. Much of the scientific literature focuses solely on how temperature impacts flowering time (Atkinson et al., 2004; Drepper et al., 2020; Fitter et al., 1995; Sparks et al., 2005). For example, Sparks et al (2005) indicated that for every 1˚C of warming for January-March temperatures, pear flowering was 7.2 days earlier, supporting the hypothesis that higher temperatures result in earlier flowering phenology. However, our study highlights that the impact of other variables like frost days need to be studied as well. Although there is a large amount of information in papers about frost damaging flower buds or resulting in floral abscission (Anderson & Seeley, 1993; Guo et al., 2019; Rodrigo, 2000), there is a lack of information on frost directly impact flowering time. This may be due to the fact it is difficult to isolate the impacts of frost from low temperatures, indicating the need for further research.

2.6.3 Future advancements in flowering phenology

Results indicate that flowering times are likely to continue to advance in the future, with respect to the four RCP scenarios. These findings are supported by other studies (Babálová et al., 2018; Chung et al., 2011; Mateescu et al., 2009; Schmidt et al., 2010), for example, an analysis on multiple fruit tree species in Romania (apricot, plum, pear and apple) predicted an intermediate emissions scenario (2˚C increase from 1961-2004 baseline), could advance pear full flowering times from 106 Julian days (current flowering times) to 96 Julian days by 2080 (10 days) (Mateescu et al., 2009), closely corresponding to our RCP4.5 scenario (Table 2.4). Mateescu et al., (2009) also used a 1˚C increase in air temperature from baseline scenario (1961-2004) where pear flowering advances by 5 days, comparable to the low emissions temperature scenario (RCP2.6) used in this study (5.11 day advancement).

There are a lack of European fruit tree studies that concentrate on phenological changes under high emissions scenarios (Funes et al., 2016; Mateescu et al., 2009). A European study on multiple deciduous tree species found leaf unfurling dates were predicted to advance 14-18 days by 2070-2100 in the RCP8.5 scenario, compared to the 1980-2012 baseline scenario, whilst in the RCP2.6 scenario flowering was predicted to advance by around 4 days (Zhao et al., 2021) although this study focussed on woodland tree species rather than fruit crops. The latter studies are similar to our scenarios.

It is important to highlight the potential issues with using the RCP8.5 scenario. Recent articles by Hausfather and Peters (2020a,b) described the RCP8.5 scenario as misleading because it does not account for potential reductions in coal usage and drop in renewable energy costs. This description has been highly contested by Schwalm et al. (2020) who speculated the RCP8.5 was the optimal scenario at tracking CO_2 emissions until 2050, and even by 2100 RCP8.5 was feasible. Therefore, the RCP8.5 scenario has been included in this paper but should be used with some discretion. In addition, the standard deviations for all RCPs scenarios should also be considered, these are larger for the RCP8.5 scenarios, suggesting a high coefficient of variation. Although a high coefficient of variation is expected due to the large sample size and number of years covered, there is still some uncertainty for scenarios with smaller time differences.

2.6.4 Potential impacts of earlier flowering in an agroecosystem

Earlier flowering times could have consequences for ecosystem function and services; impacting pollination, pest populations and crop yield. Firstly, earlier flowering and budburst could impact pesticide application (Paltineanu & Chitu, 2020). Kaolin a foliar spray used to control pear psyllid, is recommended for pre-bloom application (February-April), however, when budburst and flowering occurs poor spray coverage of particle films is likely (Nottingham & Orpet, 2020). Therefore, spraying regimes should shift to earlier in the year, which may not be optimal for controlling pest populations, depending on pest emergence. Recent surveys suggest that pear psyllid, *Cacopsylla pyri* (L.), most common pest in UK pear orchards, is estimated to cost the UK pear industry £5 million per annum due to crop damage and control costs (AHDB, 2012). Pear psylla also cause considerable economic damage across Europe (Lethmayer et al., 2011; Sanchez et al., 2021), North America (Bartlett, 1978), and Asia (Burckhardt, 1994). Psyllid nymphs produce honeydew; a sugary secretion that encourages the growth of black sooty mould, reducing the economic value of fruit and photosynthesis of leaves (Daniel et al., 2005; Montanari et al., 2015; Salvianti et al., 2008), adults are also a vector of pear decline phytoplasma; which can reduce growth and lead to tree death (Carraro et al., 2001; Kucerová et al., 2007; Süle et al., 2007), thus impacts on psyllid populations may have considerable impacts on global pear production. Earlier budburst and flowering could provide more shelter for pests earlier in the year; plant canopies may provide shelter from agrochemical sprays (Derksen et al., 2007), weather variables (frost, wind, rainfall and temperature extremes), and natural enemies (Norris, 2005). Furthermore, pear pests such as psyllid nymphs are often found sheltering inside buds, flowers or rolled leaves (Solomon *et al*., 1989), which could provide more protection if available earlier in the year.

Earlier flowering may also result in mismatches between pollinators, if flowering occurs earlier in the year but pollinator emergence does not. This could potentially reduce pollination and impact crop yield (Hegland et al., 2009; Memmott et al., 2007; Vanbergen & Initiative, 2013). Pollinators are vital in the role of pear production; a reduction in pollination services can significantly impact yield quality, quantity and variability (Belien et al., 2021; Fountain et al., 2019; Hünicken et al., 2021; Hünicken et al., 2020). Hünicken et al. (2021) found a 50% reduction in pear fruit set during pollinator exclusion experiments. Whilst another study found that higher quality pears were positively associated with proximity to mason bee (*Osmia* spp.) nesting boxes (Belien et al., 2021). An experiment highlighting the impact of plant-pollinator phenological mismatches looked at advancing flowering in apple (*Malus x domestica*), where flowering was 2 ½ weeks earlier (17th-19th of April) than control trees (Kőrösi et al., 2018). Findings suggested that the pollinator community visiting advanced trees differed from the control; with more wild bees, with lower abundances of honey bees and hoverflies. However, there are few plant-pollinator mismatch studies on pear which, as an earlier flowering crop than apple, could experience more pronounced plant-pollinator mismatches. A reduction in pollination due to phenological mismatches, could potentially impact pear yield and quality, highlighting the need for plant-pollinator shift experiments.

Finally, there is also the potential for increased frost damage; a shift to earlier flowering could increase the risk of exposure of pear flowers to spring frost. Spring frost can have a significant impact on fruit yield; one study on pear flowering found that early spring frosts damaged 64% of flowers in Conference pear, reducing yield by 2 kg per tree and resulting in an economic loss of €1200 ha^{-1}, compared to those that were protected from frost damage using gibberellin (Yarushnykov & Blanke, 2005). However, spring frost risk is also decreasing with respect to climate change (Atkinson et al., 2004; Eccel et al., 2009). Sunley et al. (2006) found that spring frost severity had decreased by 50.4% at East Malling compared to historical levels (1969 – 1979), thus despite earlier flowering, there may be less risk of damage.

2.7 Conclusions

Flowering phenology has advanced considerably since the early 1980s and this study indicates a continued advancement in the future. Earlier pear flowering times are likely for all phenological stages analysed in the study (first, ten percent, full and last flowering times) and for all RCP scenarios (RCP2.6, RCP4.5, RCP6.0 and RCP8.5). Models for flowering times based on January-April mean temperatures, explained a large proportion of the variance for all phenological stages, with total January-April frost days also explaining a considerable proportion, suggesting that these variables could be important to consider with respect to flowering. Our data suggests that air temperature, followed by frost days have the greatest influence flowering, with less influence from monthly average rainfall. Earlier flowering and budburst could alter pollination and yield, frost damage risk and potentially enhance pest populations, by influencing canopy microclimate; providing shelter from adverse weather conditions, agrochemical sprays and natural enemies earlier in the year. However, these impacts also depend on the shift in pest and natural enemy populations within the ecosystem; if psyllid nymphs emerge earlier in the year compared to budburst, or if natural enemies do not shift their emergence or migration times, there is the potential for trophic mismatches. Thus, it is vital to consider the responses of all three trophic levels; the primary producer (pear tree), the primary consumer (pear psyllid) and secondary consumer (natural enemy) when predicting responses to climate change. The methods used within this study could be easily applied to other crops, making broader predictions about the impact of climate change on multiple fruit tree and crop species, highlighting the need for long-term phenological data within agriculture.

2.8 Figures and Tables

Table 2.1: Results of models for flowering times of first, ten percent, full and last pear (*Pyrus communis* L.) flowering depending on year and cultivar, for 12 varieties of pear (2 varieties for first flowering). With flowering time (in Julian days) as a dependent variable, year as a smoother and cultivar as a factor. Reporting P-values, F-values, R2 values and an estimate of the intercept, significant P-values are in bold.

Response variable	Fixed effects	Estimate	F-value	p-value
First flowering	R^2 (adj) = 22.7%, Deviance explained = 25.3%, e.d.f. value = 7.82			
	Year	101.96	6.86	**< 0.001**
	Cultivar		21.67	**< 0.001**
Ten-percent flowering	R^2 (adj) = 25.5%, Deviance explained = 27.7%, e.d.f. value = 8.11			
	Year	105.87	21.01	**< 0.001**
	Cultivar		4.88	**< 0.001**
Full flowering	R^2 (adj) = 22.7%, Deviance explained = 25.3%, e.d.f. value = 7.82			
	Year	110.71	43.89	**< 0.001**
	Cultivar		7.72	**< 0.001**
Last flowering	R^2 (adj) = 22.7%, Deviance explained = 25.3%, e.d.f. value = 7.82			
	Year	122.20	49.19	**< 0.001**
	Cultivar		9.80	**< 0.001**

Table 2.2: Results of models for flowering times of first, ten percent, full and last pear (*Pyrus communis* L.) flowering, depending on TempPC1 and FrostPC1, for 12 varieties of pear (2 varieties for first flowering). Reporting P-values, F-values, R2 values and an estimate of the intercept. With flowering time (in Julian days) as a dependent variable, TempPC1 and FrostPC1 as fixed effects and cultivar as a random effect selected. Significant P-values are in bold.

Response variable	Fixed effects	Estimate	F-value	p-value
First flowering	R^2 (marginal) = 44.12%, R^2 (conditional) = 56.08%, intercept = 104.74			
	TempPC1	-0.994	150.36	**< 0.001**
	FrostPC1	-4.341	107.87	**< 0.001**

Ten-percent flowering	R^2 (marginal) = 44.12%, R^2 (conditional) = 56.08%, intercept = 106.34			
	TempPC1	-0.543	312.32	**< 0.001**
	FrostPC1	-4.721	216.43	**< 0.001**
Full flowering	R^2 (marginal) = 44.12%, R^2 (conditional) = 56.08%, intercept = 110.24			
	TempPC1	-1.018	581.76	**< 0.001**
	FrostPC1	-3.958	239.66	**< 0.001**
Last flowering	R^2 (marginal) = 44.12%, R^2 (conditional) = 56.08%, intercept = 120.63			
	TempPC1	-1.170	609.39	**< 0.001**
	FrostPC1	-3.104	165.55	**< 0.001**

Table 2.3: Results of models for flowering times of first, ten percent, full and last pear (*Pyrus communis* L.) flowering, depending on January – April temperatures (T) and frost days (F), for 12 varieties of pear (2 varieties for first flowering). Reporting P-values, F-values, R2 values and an estimate of the intercept. With flowering time (in Julian days) as a dependent variable, January – April mean temperature/ frost days as fixed effects and cultivar as a random effect selected. Significant P-values are in bold.

Model	**F-value (Jan-Apr temp/frost)**	**P-value (Jan-Apr temp/frost)**	**Estimate (intercept)**	**R^2 (marginal)**	**R^2 (conditional)**	**d.f.**
First (T)	504.41	**< 0.001**	153.77	58.35%	70.27%	255
Ten percent (T)	1427.09	**< 0.001**	155.66	63.87%	70.54%	647
Full (T)	2314.61	**< 0.001**	160.35	66.64%	73.72%	903
Last (T)	2081.96	**< 0.001**	166.64	62.73%	72.44%	905
First (F)	1398.71	**< 0.001**	85.55	43.46%	55.38%	255
Ten percent (F)	13176.07	**< 0.001**	88.70	44.16%	50.57%	647
Full (F)	15644.49	**< 0.001**	92.60	43.49%	49.65%	903
Last (F)	15211.43	**< 0.001**	104.84	38.89%	47.65%	905

Table 2.4: Predicted first, ten percent, full and last pear (*Pyrus communis* L.) flowering times (Julian days ± SE) by 2080 depending on January - April temperatures (T) and frost days (F). Based on different time periods and emissions scenarios; these include 1960-1989 (before changepoint), 1990-2020 (after changepoint), RCP2.6 scenario, RCP4.5 scenario, RCP6.0 scenario and RCP8.5 scenario. With flowering time (in Julian days) as a dependent variable, Jan-Apr temperature/ frost days as fixed effects and cultivar as a random effect. Frost days not available for RCP 4.5 and 6.0.

Flowering	**1960-1989**	**1990-2020**	**RCP 2.6**	**RCP 4.5**	**RCP 6.0**	**RCP 8.5**
Jan-Apr temp (˚C)	5.55 ± 0.06	6.85 ± 0.06	7.47 ± 0.09	8.05 ± 0.09	8.16 ± 0.10	9.10 ± 0.11
First (T)	109.98 ± 2.80	99.73 ± 2.80	94.83 ± 2.82	90.26 ± 2.86	89.39 ± 2.87	81.97 ± 2.97
Ten percent (T)	110.65 ± 0.93	100.12 ± 0.94	95.09 ± 0.97	90.39 ± 1.01	89.49 ± 1.02	81.87 ± 1.13
Full (T)	114.69 ± 0.92	104.00 ± 0.93	98.89 ± 0.95	94.12 ± 0.98	93.22 ± 0.98	85.48 ± 1.05
Last (T)	124.71 ± 1.01	114.88 ± 1.02	110.20 ± 1.03	105.82 ± 1.06	104.99 ± 1.07	97.89 ± 1.13
Jan-Apr total frost days	31.93 ± 2.13	23.74 ± 1.51	6.73 ± 1.49	~	~	1.47 ± 0.43
First (F)	107.92 ± 2.81	102.19 ± 2.81	90.26 ± 2.95	~	~	86.58 ± 3.03
Ten percent (F)	110.05 ± 0.94	104.57 ± 0.93	93.20 ± 1.07	~	~	89.68± 1.15
Full (F)	113.77 ± 0.89	108.34 ± 0.88	97.06 ± 1.00	~	~	93.57 ± 1.06
Last (F)	123.78 ± 0.99	118.92 ± 0.98	108.83 ± 1.08	~	~	105.71 ± 1.13

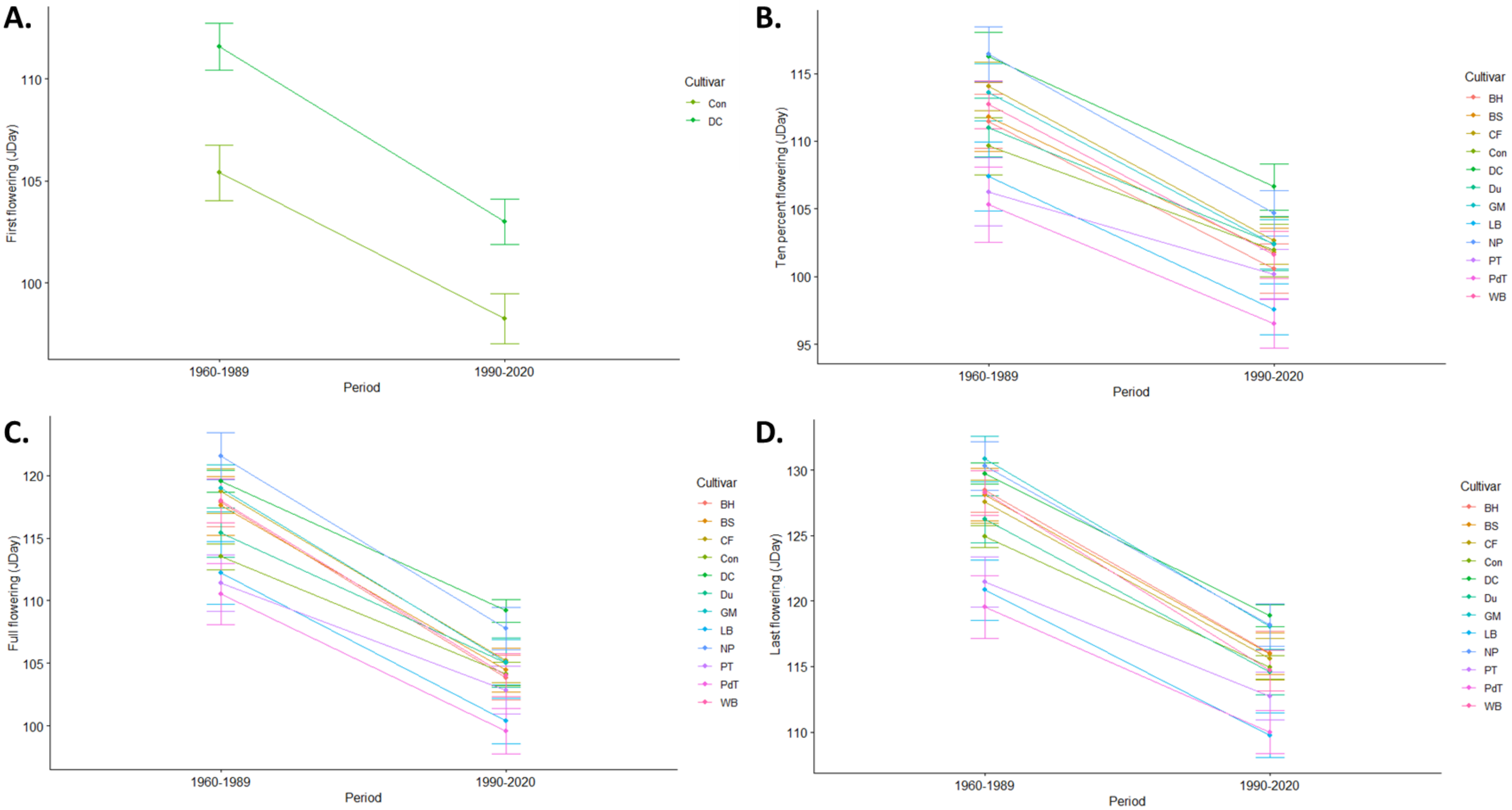

Figure 2.1: Flowering times (Julian Days) in pear (*Pyrus communis* L.) for first (**A.**), ten percent (**B.**), full (**C.**) and last (**D.**) flowering, comparing two different time periods 1960-1989 and 1990-2020. For first flowering two cultivars (Conference and Doyenne du Comice) were recorded, for ten percent, full and last flowering 12 cultivars were recorded. These included Beurre Hardy LA (BH), Beurre Superfin (BS), Clapp's Favourite (CF), Conference (Con), Doyenne du Comice (DC), Durondeau LA (Du), Glou Morceau LA (GM), Louise Bonne of Jersey (LB), Nouveau Poiteau LA (NP), Packham's Triumph (PT), Precoce de Trevoux (PdT) and Williams' Bon-Chretien (WB).

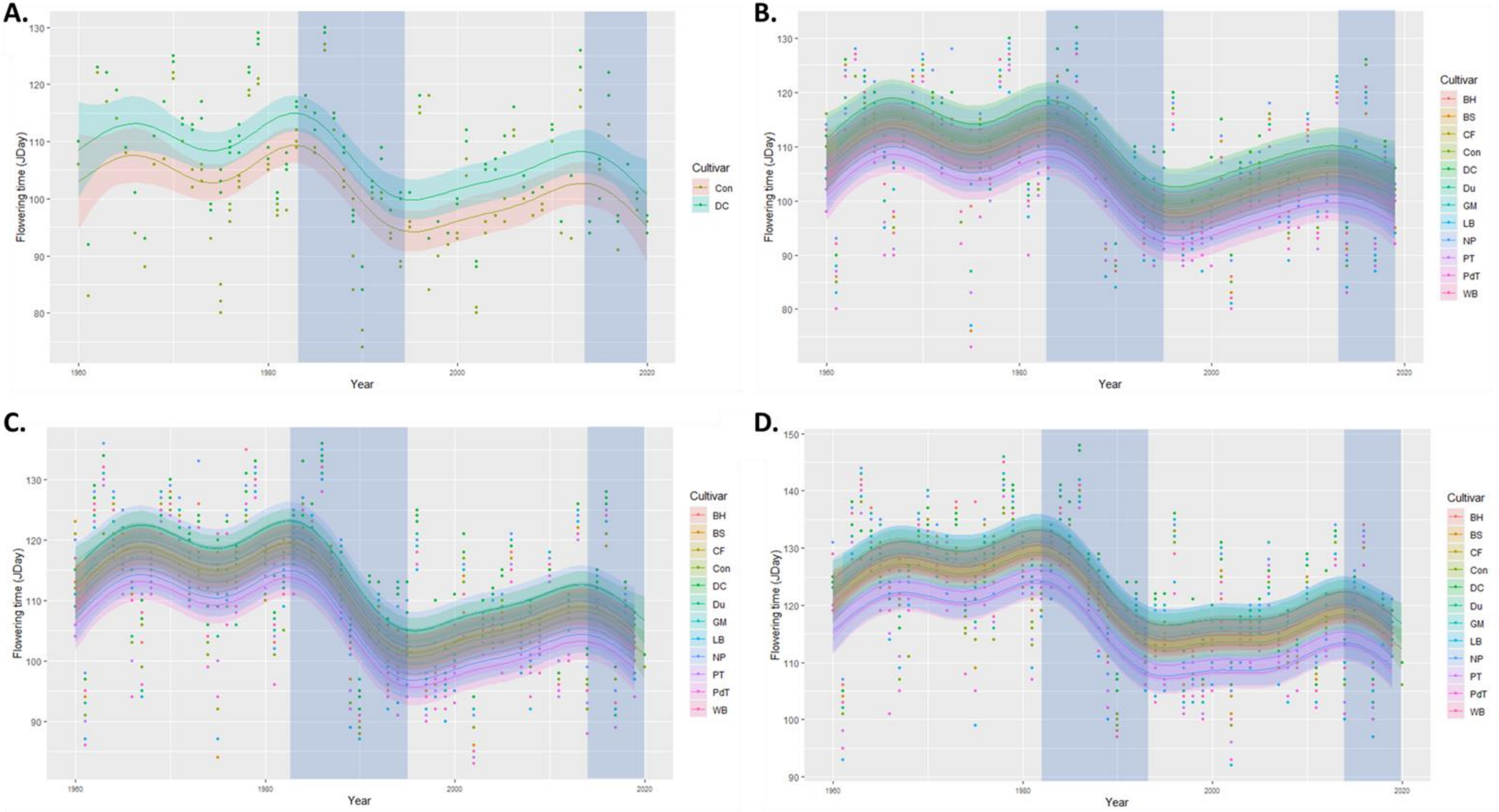

Figure 2.2: Flowering times for **A.** first, **B.** ten percent, **C.** full and **D.** last pear (*Pyrus communis* L.) flowering Observed values indicated as points with lines representing predicted values with 95% confidence intervals, for x varieties of pear denoted by different colours, blue shaded areas represent rapid advancements in flowering. For first flowering two cultivars (Conference and Doyenne du Comice) were recorded, for ten percent, full and last flowering 12 cultivars were recorded. Including: Beurre Hardy LA (BH), Beurre Superfin (BS), Clapp's Favourite (CF), Conference (Con), Doyenne du Comice (DC), Durondeau LA (Du), Glou Morceau LA (GM), Louise Bonne of Jersey (LB), Nouveau Poiteau LA (NP), Packham's Triumph (PT), Precoce de Trevoux (PdT) and Williams' Bon-Chretien (WB).

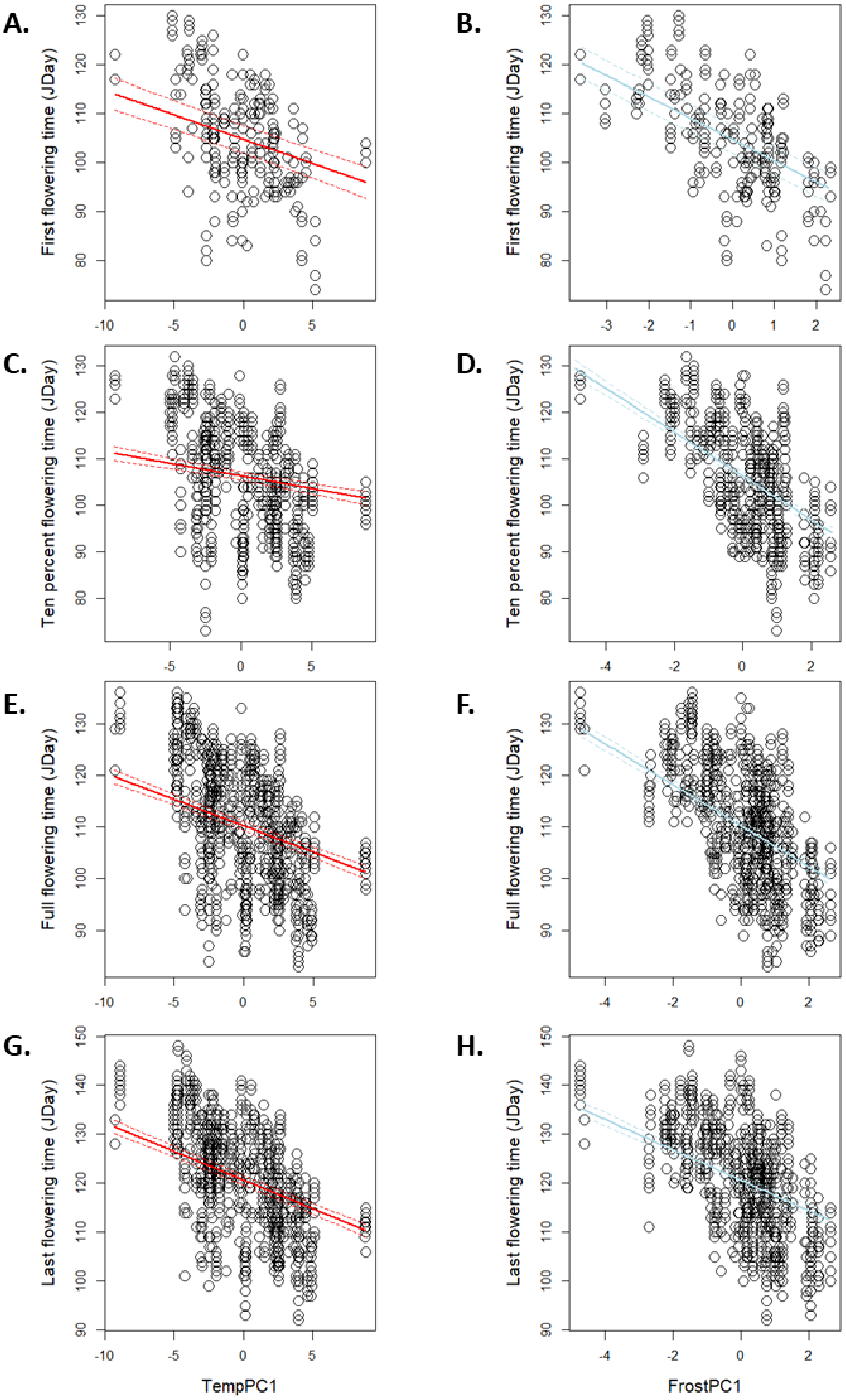

Figure 2.3: Flowering times for first (**A**, **B**), ten percent (**C**, **D**), full (**E**, **F**) and last (**G**, **H**) pear (*Pyrus communis* L.) flowering, based on temperature and frost. Lines represent Julian day values with 95% confidence intervals predicted from TempPC1 based on average FrostPC1 values (**A**, **C**, **E**, **G**) and FrostPC1 based on average TempPC1 values (**B**, **D**, **F**, **H**), points represent observed values. With flowering time as a dependent variable, TempPC1 and FrostPC1 as fixed variables and cultivar as a random factor. Year and RainPC1 were not used in the models, due to AIC selection.

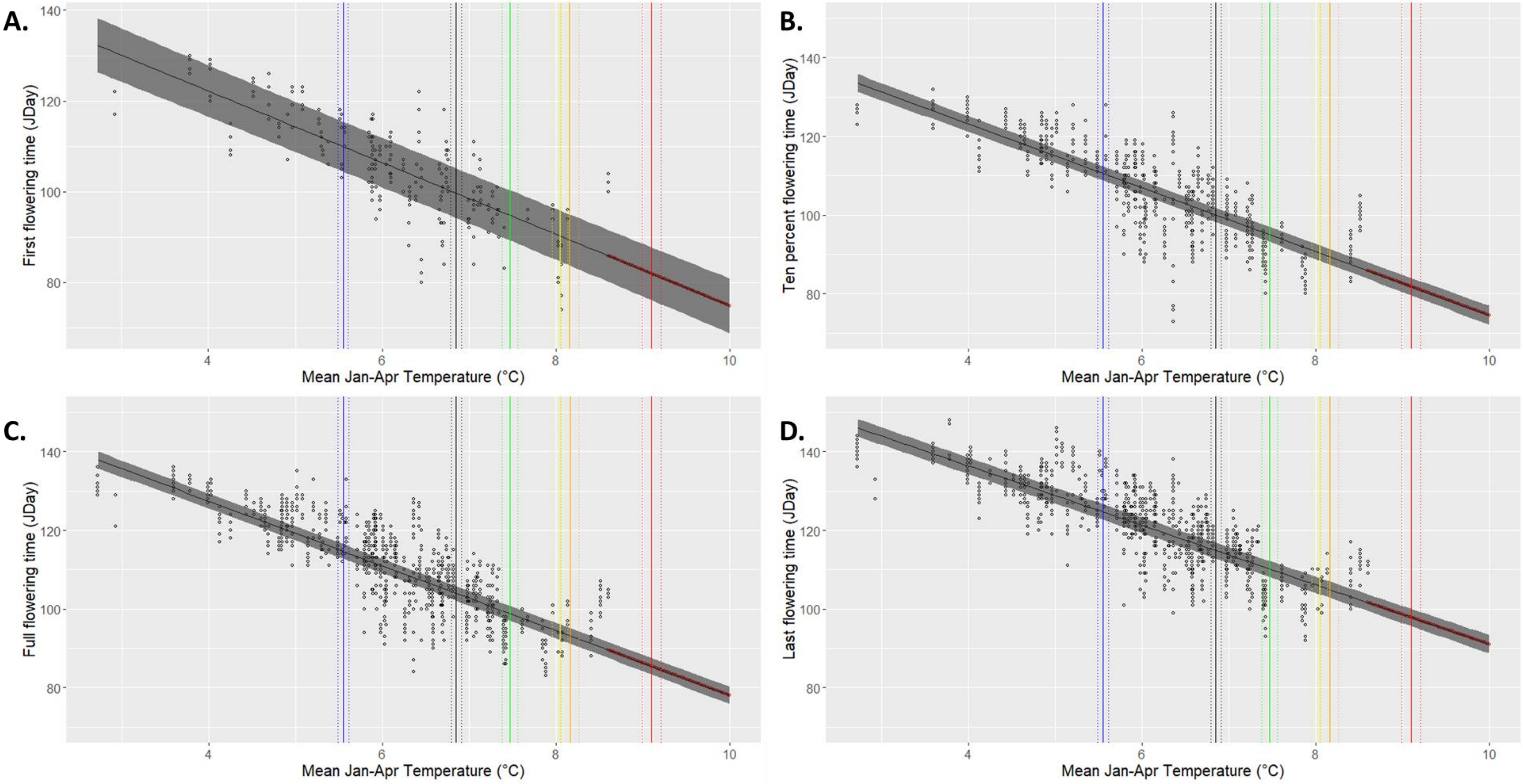

Figure 2.4: Flowering times for first (**A**), ten percent (**B**), full (**C**) and last (**D**) pear (*Pyrus communis* L.) flowering, based on January-April mean temperature. The diagonal line represents Julian day values with 95% confidence intervals predicted from January-April mean temperature, black circles represent observed values, red circles represent values beyond previously observed temperatures. With flowering time as a dependent variable, January-April mean temperature as a fixed variable and cultivar as a random factor. Coloured lines represent different time periods and emissions scenarios, with dotted lines as ± SE: blue (1960-1989), black (1990-2020), green (RCP2.6), yellow (RCP4.5), orange (RCP6.0) and red (RCP8.5). For first flowering two cultivars (Conference and Doyenne du Comice) were recorded, for ten percent, full and last flowering 12 cultivars were recorded.

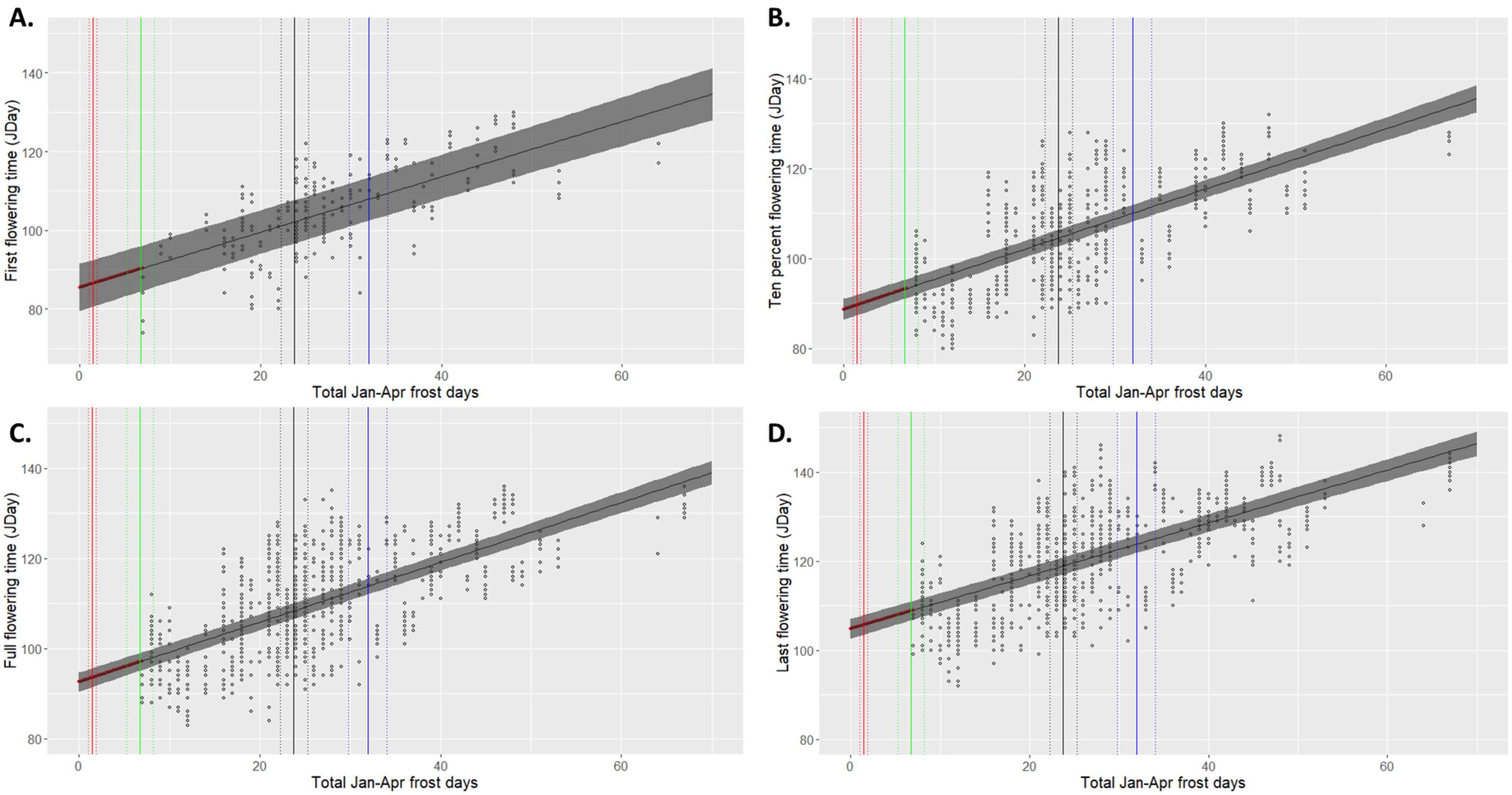

Figure 2.5: Flowering times for first (**A**), ten percent (**B**), full (**C**) and last (**D**) pear (*Pyrus communis* L.) flowering, based on January-April total frost days. The diagonal line represents Julian day values with 95% confidence intervals predicted from January-April total frost days, black circles represent observed values, red circles represent values beyond previously observed temperatures. With flowering time as a dependent variable, January-April total frost days as a fixed variable and cultivar as a random factor. Coloured lines represent different time periods and emissions scenarios, with dotted lines as ± SE: blue (1960-1989), black (1990-2020), green (RCP2.6) and red (RCP8.5), RCP4.5 and RCP6.0 scenarios were unavailable for calculating future frost days. For first flowering two cultivars (Conference and Doyenne du Comice) were recorded, for ten percent, full and last flowering 12 cultivars were recorded.

3 Functional and behavioural responses of the natural enemy *Anthocoris nemoralis* to *Cacopsylla pyri*, at different temperatures.

This chapter is a version of the following paper, with minor corrections and changes to formatting and references to make the thesis more comprehensive:

Reeves, L. A., Garratt, M. P., Fountain, M. T., & Senapathi, D. (2023) Functional and Behavioural Responses of the Natural Enemy *Anthocoris nemoralis* to *Cacopsylla pyri*, at Different Temperatures. J Insect Behav 36, 222–238. https://doi.org/10.1007/s10905-023-09836-5

Author contributions: LR, MG, MF and DS conceived and designed the study. LR carried out the lab work, data analyses and drafted the manuscript with all authors providing feedback on multiple drafts prior to submission.

3.1 Abstract

Anthocoris nemoralis is the dominant predator of pear sucker (*Cacopsylla pyri*) in the UK. *Anthocoris nemoralis* migrates into orchards in spring or is introduced as a biocontrol agent, reaching peak population levels in July-August, contributing to effective control of summer pear sucker populations. However, due to temperature dependent development and metabolism there are concerns that *C. pyri* populations or feeding rates may increase due to changing climatic conditions. Thus, how *A. nemoralis* responds to temperature, impacts its ability as a biocontrol agent. Functional response assays, monitoring attack rate and handling time of *A. nemoralis* and behavioural assays, using Ethovision tracking software were undertaken, to assess the impact of temperature on predation. Experiments were conducted at current and future July-August mean temperatures, predicted using RCP4.5 and RCP8.5 (medium and high, representative concentration pathway) emissions scenarios, using 2018 UK Climate Projections (UKCP18). All treatments demonstrated a Type II functional response, with female anthocorids demonstrating shorter handling times and higher attack rates than males. Males showed longer prey handling times at 18 °C compared to 23 °C and more time was spent active at lower temperatures for both sexes. Females did not show significant differences in attack rate or handling time in response to temperature. Overall prey consumption was also not significantly affected by temperature for either sex. This study suggests that anthocorids are likely to remain effective natural enemies under future predicted temperatures,

due to non-significant differences in prey consumption, providing that prey abundance and feeding rates remain constant.

3.2 Introduction

The anthocorid, *Anthocoris nemoralis* (Fabricius), is the main natural enemy of pear sucker (*Cacopsylla pyri* L.) in the UK and Europe (Nagy et al., 2008; Sigsgaard, 2010; Solomon et al., 2000). The estimated cost of pear sucker to the UK pear industry is £5 million per annum in damage and control costs (AHDB, 2012). These phloem feeding insects damage pear trees in three main ways: nymphs produce honeydew, a sugary secretion that encourages the growth of black sooty mould (Daniel et al., 2005; Montanari et al., 2015; Salvianti et al., 2008), adult *C. pyri* are a vector of pear decline disease (*Candidatus* Phytoplasma pyri); which reduces shoot and fruit growth in pear and can lead to tree death (Carraro et al., 2001; Kucerová et al., 2007; Süle et al., 2007) and high numbers of *C. pyri* can cause 'psylla shock'; toxic saliva is injected into pear leaves, resulting in defoliation and fruit drop (Erler, 2004a; Oz & Erler, 2021; Saour et al., 2010). With a high resistance to commonly available pesticides (Erler, 2004a; Sek Kocourek & Stará, 2006) many growers currently practice integrated pest management (IPM) of pear sucker, focusing on maximizing natural enemy populations, to control pear sucker (Shaw et al., 2021). Natural migrations of anthocorids can reduce pear sucker populations during the summer (Nagy et al., 2008). Adult *A. nemoralis* often overwinter in hedgerows or on unmanaged vegetation, migrating into orchards in April-May to lay eggs, when pear sucker populations are increasing (Nagy et al., 2008; Shaltiel & Coll, 2004). *Anthocoris nemoralis* populations usually peak during July-August, helping to control *C. pyri* numbers (Fields & Beirne, 1973; Scutareanu et al., 1999). However, anthocorids can also be released artificially into orchards as a biocontrol agent, to reduce pear sucker populations more rapidly (Beninato & Morella, 2000; Gajski & Pekár, 2021). Nymphs and adult *A. nemoralis* predate upon pear sucker eggs and nymphs (Sigsgaard, 2010) and have a pierce-sucking stylet to feed (Bulgarini et al., 2021). A single anthocorid is estimated to consume almost 5000 eggs during its lifetime (Yanik & Ugur, 2004), with no significant preference shown between eggs and nymphs based on biomass (Sigsgaard, 2010).

There is increasing concern that rising temperatures may impact pest populations (Barford, 2013; Sable & Rana, 2016; Zidon et al., 2016). Insects are poikilothermic, this means they have a body temperature that fluctuates with their environment (May, 1979; Sable & Rana, 2016; Wojda, 2017). Therefore, rising temperatures could impact pest development (Campolo et al., 2014; Ratte, 1984), fecundity (Boggs, 2016; Kindlmann et al., 2001), number of generations per year (Tobin et al., 2008), overwintering times (Ladányi & Horváth, 2010) and behaviour (Mellanby, 1939). Pear sucker have temperature dependent development (Kapatos & Stratopoulou, 1999; Schaub et al., 2005); faster development rates at warmer temperatures could lead to shorter generation times, potentially increasing pest populations. There is concern that warmer temperatures could alter the feeding behaviour, activity and fecundity of phloem feeders (Liu et al., 2021; McMullen & Jong, 1972). One explanation for increased feeding rate under high temperatures is due to altered metabolism (Yuan et al., 2009), as metabolic rate increases exponentially with temperature up to a certain threshold, increasing demand for energy and nutrients (Frances & McCauley, 2018; Schmitz & Barton, 2014). Furthermore, the scale of metabolic increase is largely dependent on body size, with smaller species having higher increases in metabolism than larger species (Frances & McCauley, 2018). Thus, as prey species are often smaller than their predators, their metabolism may increase at a faster rate with respect to warming, leading to an enhanced feeding rate. For example, *C. pyri* adults are less than 3 mm and nymphs in their 5th instar are 1.9 mm in length (Chireceanu, 1998), compared to *A. nemoralis* adults which have a body length of 3.5 – 4 mm (BPDB, 2022). Therefore, feeding rates of pear sucker prey may increase more than their anthocorid predators due to body size.

It is important, therefore, to establish whether the feeding rate of *A. nemoralis* increases with temperature, to understand if it will be an efficient natural enemy of *C. pyri* under future predicted temperature conditions. One of the most effective ways of monitoring predator-prey interactions is by fitting functional responses; a functional response can be defined as the change in the consumption rate for a predator depending on prey density, therefore whether it is density dependent (Holling, 1965; Real, 1977). The functional response of a predator is determined by different parameters including: attack rate ($\boldsymbol{a}$); rate of discovery of a prey item and handling time ($\boldsymbol{h}$); the time period when the predator consumes its prey (including killing, capturing, eating and sometimes digesting) (Juliano, 2020; Real, 1977). There are three main "Types" of functional responses, which all have different shapes and can be defined as follows: a Type I response shows a linear increase in consumption rate depending on prey density (up to a certain threshold), as the time needed to consume or process prey is negligible (DeLong, 2021; Jeschke et al., 2004; Real, 1977). A Type II functional response differs from a Type I functional response as it includes handling time ($\boldsymbol{h}$); a time period when the predator consumes its prey (including killing, capturing, eating and digesting), therefore to begin with consumption rate of prey increases as prey density increases, but eventually levels off and remains constant at high densities (Juliano, 2020; Real, 1977). Type III functional response resembles Type II at high prey densities; however at low densities the consumption rate of a predator increases slowly, due to learning time or prey switching, giving the response curve a sigmoidal shape (DeLong, 2021; Real, 1977).

In biological control, Type I functional responses are scarce as they are almost exclusive to filter feeders, as handling time is rarely negligible in other species (Jeschke et al., 2004; Real, 1977).

Having a Type II functional response is more optimal than a Type III for a biological control agent, as natural enemies are still able to detect and attack pests at low densities (Lopes et al., 2009). However, Type III responses allow a negative density-dependent response of the prey survival with prey population density, compared to type II which may help stabilize prey populations, making them less likely to fluctuate (Cuthbert et al., 2021). Functional responses are also influenced by multiple biotic and abiotic factors including; life-stage of predator or prey (Farhadi et al., 2010), sex of predator (Mohammad Saeed Emami et al., 2014), species of prey (Milonas et al., 2011), temperature (Englund et al., 2011) and arena size (Uiterwaal & DeLong, 2018). Although functional responses can be largely influenced by temperature (Englund et al., 2011), there are no studies to date on the natural enemy *A. nemoralis*, using the prey species *C. pyri*, at multiple temperature regimes. Although, other functional response experiments have occurred on other anthocorid species (Hassanzadeh-Avval et al., 2019; Kheradmand et al., 2017) and *A. nemoralis* (Mohammad Saeid Emami et al., 2014) at a single temperature (27 °C), allowing comparison.

Changes in behavioural responses are important when monitoring trophic interactions between predator and prey (Boege et al., 2019; Chen et al., 2015; Duffy et al., 2015). For example, changes in walking velocity or distance travelled by a natural enemy could alter the probably of encountering a prey item or host (Milton, 2004). Whilst changes in cleaning/grooming behaviour may increase risk of disease; as grooming is an important sanitary behaviour, involved in the removal of pathogens (Zhukovskaya et al., 2013).

This study aims to monitor the behaviour and functional response of the natural enemy, *A. nemoralis*, to determine whether it would be an efficient biological control agent under future UK predicted temperatures. Behavioural and functional responses were monitored at three temperature regimes (18 °C, 21 °C and 23 °C) selected based on current mean July-August temperatures and mean temperatures predicted for July-August by RCP 4.5 and RCP 8.5 emissions scenarios for 2080. Our study tested four hypotheses: 1) Anthocorids demonstrate a Type II functional response, 2) Handling time is shortened and attack rates are increased at higher temperatures, 3) Behaviours including movement, feeding and cleaning of anthocorids increase under elevated temperatures and 4) The sex of anthocorid impacts the functional response, with shorter handling times and higher attack rates for females, due to a larger body size.

3.3 Materials and Methods

3.3.1 Pear psyllid and anthocorid husbandry

Pear psyllid nymphs (L4-L5, the fourth or fifth nymph stage in a pear psyllid's life history) were collected from cv. Conference pear trees (*Pyrus communis*) at NIAB East Malling (51.2885° N, 0.4383° E). Nymphs were removed from trees daily, using a soft, fine tipped paintbrush, to minimize damage to insects. These nymphs were used for functional response experiments and behavioural assays. Adult *C. pyri* were collected using beat tray sampling. A pear tree branch was tapped with a foam-covered stick, with a white tray (260 mm by 460 mm) held underneath. Adult *C. pyri* were kept in ventilated Tupperware pots (diameter 94.7 mm, height 115 mm) containing 3 pear shoots (110 mm in length) in damp tissue. Individuals were kept in a controlled temperature (CT) cabinet at 21 °C. Semi-mature pear sucker eggs (yellow-white in colour) were collected from the Tupperware pots daily, these were used for the egg treatment within behavioural assays. *C. pyri* adults and nymphs were identified to species level using the Psyllid key from RLP Agroscience (Agroscience, 2022).

A batch of 500 *A. nemoralis* adults were ordered from the biocontrol company Koppert each week of the study. This product was called Anthobug and ordered from Koppert UK Ltd, Suffolk, CB9 8PJ. These were approximately 4-10 days after their final moult, when used in behavioural and functional response experiments. Anthocorids were kept in a ventilated plastic container, with the carrier material they arrived in and fed *C. pyri* eggs daily. Individuals were allowed to mate, with males and females kept in the same container in a CT cabinet at 21 °C. Five batches of anthocorids were used for behavioural response assays and seven batches for functional response experiments. Following a Kruskal Wallis test no significant difference was found between batches depending on velocity, distance travelled, number of *C. pyri* eggs or nymphs eaten or time spent exhibiting a behaviour, apart from cleaning, where there was a significant difference in the time spent cleaning between batch 3 and 5 (Table S2.1). Therefore, batch number was not included within models. Male and female anthocorids were identified using a light microscope based on differences in genitalia. If there was some uncertainty in the sex of the anthocorid, individuals were dissected after the experiment to find parameres, if male (Hassanzadeh-Avval et al., 2020), or copulatory tubes if female (Ke & Bu, 2007).

3.3.2 **Functional response experiments**

For functional response experiments, adult *A. nemoralis* were starved for approximately 24 hrs at either 18 °C, 21 °C or 23°C in controlled temperature (CT) cabinets. Then, a male or female individual was added to a triple-vented Petri dish (55 mm in diameter). The floor of the dish was covered with 1% set agar to provide moisture and support for leaf disks as used in the functional response experiments of Hassanzadeh-Avval et al. (2019). The leaf disks were 20 mm in diameter and were created using a cork borer from *P. communis* 'Conference' leaves. The Petri dish also contained *C. pyri* nymphs (4th - 5th instar), at one of five densities (5, 10, 15, 30 and 50 nymphs).

After the anthocorid was added, the Petri dish was sealed with plastic paraffin film to prevent *C. pyri* nymphs escaping (similar to Emami et al. (2014)) and returned to the same temperature treatment (from which they had been taken from) for 24 hrs. Nymphs were not replaced during the experiment. After 24 hrs the anthocorid and numbers of *C. pyri* nymphs were recorded as alive or dead. There were 10 replicates for *A. nemoralis* male and female tests at each temperature treatment, for the 5 prey densities, giving a total of 300 observations. Five control treatment replicates of *C. pyri* nymphs were set up for each temperature, to quantify natural mortality.

3.3.3 Behavioural assays

Similar to the functional response experiments, adult *A. nemoralis* were starved for 24 hrs, in one of the three temperature treatments (18 °C, 21 °C and 23 °C) in CT cabinets. After this the anthocorid was moved to a CT room with insect behaviour tracking software; Ethovision (Noldus et al., 2001, 2002). The anthocorid was then added to a triple-vented Petri dish (55 mm in diameter). The Petri dish contained a 5 mm piece of leaf with either, 2 *C. pyri* nymphs (4-5th instar), 15 semi-mature *C. pyri* eggs, or no prey (as a control). The numbers of eggs and nymphs were chosen as they were approximately equivalent to each other in weight. The leaf containing the food was placed in the center of the Petri dish (marked with a cross), the anthocorid was then placed in the 20 mm center circle (not on the leaf) and given 10 minutes to acclimatize. After this period the Ethovision camera was set to record for 20 minutes, then the anthocorid was removed and the number of nymphs/eggs consumed were counted.

Movement and behaviours of anthocorids were recorded using Ethovision XT tracking software (Noldus et al., 2001, 2002); the velocity, distance travelled, time spent in the center (20 mm diameter center circle) and edge (up to 10 mm from the edge) zones and time spent displaying certain behaviours were recorded. Recording occurred in a temperature-controlled room, using a

GigE vision camera acA1300-60gc. These measurements were tracked from the center-point of the anthocorid's body. The 6 recorded behaviours were, feeding (when the anthocorid was stationary and had its stylet in an egg or nymph), moving (when the anthocorid was walking or flying), moving leaf (when the anthocorid was moving the leaf around the arena), antennating (when the anthocorid was stationary and repeatedly touching a surface with its antennae), cleaning (when an anthocorid was grooming its legs or antennae) and stationary (when an anthocorid was completely still and not feeding). All behaviours were independent of each other, for example an anthocorid that was stationary could not also be cleaning. There were ten replicates each of the three food treatments, three temperature treatments and if the anthocorid was male or female, giving a total of 180 observations.

3.3.4 Temperature regimes and controlled temperature cabinets

The three temperature treatments (18, 21 or 23 °C) were determined based on the current mean July-August temperature (1990-2020) and mean July-August temperatures predicted in 2080, based on the RCP4.5 (medium emissions) and RCP8.5 (high emissions) scenarios. A 2080-time frame was chosen as this year is commonly used in studies predicting future trophic interactions (Aartsma et al., 2019; Duffy, 2014; South et al., 2018), thus the results of this paper can be compared to others. July-August temperatures were chosen as this is when anthocorids are most abundant in pear orchards (Fields & Beirne, 1973; Scutareanu et al., 1999). The current temperature was calculated using mean July-August temperatures (1990-2020) from East Malling weather station (51.288° N, 0.448° E) in Kent. To calculate future temperatures for 2080, data was extracted using the UK Climate Projections User Interface, based on UKCP18 projections (UKCP, 2021a). The predicted increase in mean air temperature at 1.5 m for 2080 was calculated for July to August (baseline scenario 1981-2000) for a 25 km x 25 km region in Kent, surrounding East Malling (562500.00, 162500.00), these temperatures were calculated for each of the RCP4.5 and RCP8.5 scenarios and added to the average 1981-2000 July-August temperature (17.41 °C). The predicted temperatures were rounded up to the nearest degree (Table S2.2), as many functional response experiments use temperatures to the nearest degree (Ding-Xu et al., 2007; Hassanpour et al., 2020; Hassanzadeh-Avval et al., 2019), allowing comparison.

The three controlled temperature (CT) cabinets (set at 18, 21 and 23 °C) had two containers half-filled with water to keep humidity constant (Table S2.2). On average humidity was 22.41 ± 6.95 for the 18 °C temperature regime, 25.92 ± 7.74 for the 21 °C temperature regime and 24.72 ± 5.29 for the 23 °C temperature regime, relative humidity did not significantly differ between temperature regimes. Temperature and humidity were monitored using EasyLog USB dataloggers (Table S2.2).

The daylight cycle within the cabinets was 16 hrs light, 8 hrs dark, based on average summer day length in the UK.

3.4 Data Analyses

3.4.1 Functional response experiments

The type of functional response for each of the treatments (sex and temperature) was selected and fitted using the R package FRAIR (Pritchard et al., 2017). This method involved three different steps: model selection, model fitting and model comparison. Firstly, polynomial logistic functions were fitted to the data to identify the 'Type' of functional response (Type I, Type II or Type III), as outlined by Juliano (2001). Within a logistic regression a Type II functional response can be identified by a negative first-order term (where prey consumption is negatively proportional to prey density), whereas a Type III functional response has a positive first-order term. The frair-test function within the 'FRAIR' package in R was used for model selection; classifying the type of functional response, based on the sign and significance of first-order and second-order terms within logistic regressions (Pritchard et al., 2017). For model fitting the frair-fit function was used. This function undertakes optimization by maximum likelihood estimation (MLE), giving information on the model fit, maximum likelihood estimators and a regression output.

Due to the fact resources were being depleted throughout the experiment (nymphs were not replaced when eaten), the Rogers Random predator equation was used (Rogers, 1972), as this equation is applicable to non-replacement experiments and is solved via the 'lambertW' function (Bolker, 2008; DeLong, 2021; Pritchard et al., 2017). For all Type II functional responses within this experiment the following equation was used:

$$\boldsymbol{N_a = N_0[1 - \exp\big(a(T_h N_a - T)\big)]} \qquad (1)$$

$\boldsymbol{N_a}$ is the number of prey (pear sucker nymphs) consumed by the predator (anthocorid), $\boldsymbol{N_0}$ is the number of prey initially offered to the predator, $\boldsymbol{a}$ is the attack rate, $\boldsymbol{T_h}$ is the handling time and $\boldsymbol{T}$ is the time in hours that the prey are exposed to the predator (24 hrs).

Finally, the functions frair-compare and frair-boot within the FRAIR package were used to compare differences between temperature treatments and sex of anthocorid. The frair-compare function used a difference test, with the null hypothesis that fitted parameters $\boldsymbol{D_a}$ (difference in attack rate) and $\boldsymbol{D_h}$ (difference in handling time) do not differ, depending on treatment (temperature and sex). The frair-boot function uses nonparametric bootstrapping, generating 95% confidence intervals (CI) for attack rate ($\boldsymbol{a}$) and handling time ($\boldsymbol{h}$), to see if CIs overlap between treatments. These bootstrap outputs for 95% CIs were plotted using the function drawpoly. The difference between number of prey eaten depending on density at the 3 different temperatures was tested using a Kruskal-Wallis test, as data were non-normally distributed.

3.4.2 Behavioural assays

For behavioural response assays, stacked bar charts were created using the ‘ggplot2’ package in R. Stacked barcharts displayed the percentage of time *A. nemoralis* spent demonstrating certain behaviours (feeding, moving, moving leaf, cleaning, stationary and antennating) over the 20-minute time period, for three different temperatures and three food treatments. Heatmaps were created to show the proportion of time *A. nemoralis* spent in the center zone (containing food/leaf), middle and edge of the arena. Heatmaps were created using Ethovision XT tracking software (Noldus et al., 2001). For statistical analysis a Kruskal-Wallis H test, followed by pairwise comparisons using a Wilcoxon rank sum test, as data were non-normally distributed, which was recognised using a Q-Q plot. These tests were used to compare differences in behaviour, time spent in zones, velocity and distance travelled, depending on treatment.

3.5 Results

3.5.1 Functional response experiments

For the control experiments, without an anthocorid present, there was a mean average of 0.43 dead nymphs per sample. This ranged from 0 deaths in the 5-nymph density, to 1.27 ± 1.62 deaths in the 50 nymph density. The number of dead nymphs in the control experiment was significantly lower compared to the corresponding treatments containing anthocorids ($\chi^2 = 174.01$, df = 5, $p < 0.001$), based on a Kruskal-Wallis test with pairwise comparisons using the Wilcoxon rank sum test. Therefore, it was likely that the anthocorids were causing nymph deaths rather than other factors. The number of nymphs eaten significantly differed depending on density; Kruskal Wallis: $\chi^2 = 126.97$, df = 4, $p < 0.001$. With an average of 3.82 ± 1.14 nymphs eaten over 24 hrs at the lowest density and an average of 10.02 ± 3.57 nymphs eaten at the highest density. However, the Wilcoxon rank sum test indicated that the number of nymphs eaten at the density 30 did not significantly differ from the density of 50 ($p = 0.285$), suggesting that the saturation point for prey consumption had been reached. This non-significant difference between 30 and 50 nymphs occurred for both male and female anthocorids. There was a significant difference in number of nymphs eaten depending on sex of anthocorid; Kruskal Wallis: $\chi^2 = 66.51$, df = 1, $p < 0.001$, with an average of 11.97 ± 3.41 nymphs eaten by females at the highest density and an average of 8.07 ± 2.45 eaten by males. However, the number of nymphs eaten depending on temperature did not significantly differ for females (Kruskal Wallis: $\chi^2 = 2.44$, df = 2, p = 0.296) or males (Kruskal Wallis: $\chi^2 = 1.70$, df = 2, p = 0.427), with an average of 9.85 ± 4.13 nymphs killed at 18 °C, 9.90 ± 2.99 nymphs at 21 °C and 10.30 ± 3.66 nymphs at 23 °C, for the highest prey densities.

During model selection a Type II functional response was chosen for both male and female anthocorids, for all three temperature regimes, due to the fact the first order term (density) from logistic regressions was negative and significant for all treatments (Table 3.1, Figure 3.1). Attack rates ($\boldsymbol{a}$) generated from the maximum likelihood optimisation output ranged from 0.049 (23M) to 0.156 (21F). Whilst handling time ($\boldsymbol{h}$) ranged from 3.27 (18M) to 1.65 (23F) (Table 3.2). The maximum number of nymphs that were attacked per day $(\boldsymbol{T}/\boldsymbol{T_h})$ was 14.54 (23F) and the minimum number was 7.34 (18M).

For model comparison there was a significant difference between male and female anthocorids for all temperature treatments (Table 3.3). The difference in attack rate $(\boldsymbol{D_a})$ and handling time $(\boldsymbol{D_h})$ was significant for the 23F~23M and 21F~21M comparisons, however for the 18F~18M comparison only $\boldsymbol{D_h}$was significant. For comparisons between temperatures, 23M had a significantly lower handling time than 18M (Table 3.4). However, there were no significant differences for any of the other temperatures. For the bootstrapping method, CIs for $\boldsymbol{a}$ and $\boldsymbol{h}$ overlapped for all different temperature treatments (Table S3.3). However, the CIs for $\boldsymbol{a}$ did not overlap between male and female anthocorids, at higher temperature treatments. On average the temperature recorded was 18.54 ˚C ± 0.72 in the 18 ˚C cabinet, 21.40 ˚C ± 0.59 in the 21 ˚C cabinet and 22.92 ˚C ± 0.34 in the 23 ˚C cabinet, which did not significantly differ from 18 ˚C, 21 ˚C and 23 ˚C respectively.

3.6 Behavioural assays

3.6.1 Velocity and distance travelled

There was a significant difference in the average velocity of *A. nemoralis* depending on food treatment (Kruskal Wallis: $\chi^2 = 61.10$, df = 2, p > 0.001), the average velocity was significantly lower for the nymph treatment (0.069 cm/s ± 0.14) compared to eggs (0.16 cm/s ± 0.14) and no food (0.22 cm/s ± 0.26). This was also similar for average distance travelled by *A. nemoralis* depending on food treatment (Kruskal Wallis: $\chi^2 = 61.53$, df = 2, p > 0.001), the average distance travelled was significantly lower for the nymph treatment (80.79 cm ± 164.9) compared to eggs (184.1 cm ± 163.1) and no food (308.0 cm ± 265.9). There was no significant difference in velocity (Kruskal Wallis: $\chi^2 = 0.066$, df = 1, p = 0.797) or distance travelled (Kruskal Wallis: $\chi^2 = 0.075$, df = 1, p = 0.784) depending on the sex of anthocorid, nor velocity (Kruskal Wallis: $\chi^2 = 3.44$, df = 2, p = 0.179) or distance travelled (Kruskal Wallis: $\chi^2 = 3.41$, df = 2, p = 0.181) depending on temperature.

3.6.2 Time spent in different zones

There was a significant difference in the time *A. nemoralis* spent in the center zone depending on food source (Kruskal Wallis: $\chi^2 = 58.04$, df = 2, p > 0.001), the average time spent was significantly higher for the nymph treatment (945.2 s ± 439.9) compared to eggs (488.9 s ± 476.8) and no food (159.0 s ± 303.4) (Figure 3.2, 3.4). There was also a significant difference in time spent in the edge zone depending on food source (Kruskal Wallis: $\chi^2 = 45.32$, df = 2, p > 0.001), the average time spent was significantly higher for the no-food treatment (452.1 s ± 327.1) compared to eggs (297.7 s ± 307.74) and nymphs (132.0 s ± 273.9). There was no significant difference between the amount of time spent in the center (Kruskal Wallis: $\chi^2 = 0.735$, df = 2, p = 0.391) or edge (Kruskal Wallis: $\chi^2 = 0.003$, df = 2, p = 0.956) zones depending on sex of the anthocorid. For the egg treatment, there was a significant difference in time spent in the center zone depending on temperature (Kruskal Wallis: $\chi^2 = 10.91$, df = 2, p =0.004), with significantly more time spent in the center zone (Fig. 2,3) in the 23 °C (753.5 s ± 478.8) treatment compared to 21 °C (422.4 s ± 442.5) and 18 °C (290.8 s ± 401.6). However, there was no significant difference for time spent in center zone depending on temperature for the nymphs (Kruskal Wallis: $\chi^2 = 1.09$, df = 2, p = 0.580) or no-food treatment (Kruskal Wallis: $\chi^2 = 1.58$, df = 2, p = 0.455).

3.6.3 Behaviours demonstrated and prey eaten

On average 3.90 ± 4.70 eggs were eaten by *A. nemoralis* in the 18 °C treatment, compared to 5.70 ± 5.80 eggs and 7.65 ± 5.49 for the 21 °C and 23 °C treatments. However, the number of eggs eaten did not significantly differ depending on temperature (Kruskal Wallis: $\chi^2 = 5.19$, df = 2, p = 0.075). Sex also did not significantly impact the number of eggs eaten (Kruskal Wallis: $\chi^2 = 0.498$, df = 2, p = 0.481). The average amount of time spent feeding in the egg treatment was 252.5 ± 361.6 s in the 18 °C treatment, compared to 342.9 ± 402.2 s and 543.0 ± 468.1s for the 21 °C and 23 °C treatments (Fig. 4), ranging from 0s to 1200s spent feeding. However, there was no significant difference in the amount of time spent feeding depending on temperature in the egg (Kruskal Wallis: $\chi^2 = 4.90$, df = 2, p = 0.086) or nymph (Kruskal Wallis: $\chi^2 = 1.46$, df = 2, p = 0.481) treatments. The amount of time spent feeding by *A. nemoralis* significantly differed depending on the food treatment (Kruskal Wallis: $\chi^2 = 39.14$, df = 1, p > 0.001), with an average of 379.5 ± 424.0s spent feeding in the egg treatment and 934.1 ± 438.6s spent feeding in the nymph treatment. There was no significant difference in time spent feeding depending on sex (Kruskal Wallis: $\chi^2 = 0.003$, df = 1, p = 0.955).

Anthocoris nemoralis spent significantly more time moving in the 18 °C treatment, compared to the 21 °C and 23 °C treatments, for no-food (Kruskal Wallis: $\chi^2 = 9.57$, df = 2, p = 0.008) and eggs (Kruskal Wallis: $\chi^2 = 9.62$, df = 2, p = 0.008) but not nymphs (Fig. 4). Anthocorids spent significantly more time cleaning at 18 °C and 21 °C compared to 23 °C the egg treatment (Kruskal Wallis: $\chi^2 = 7.38$, df = 2, p = 0.025). There was also a significant difference in the time spent antennating depending on temperature for the egg treatment (Kruskal Wallis: $\chi^2 = 10.95$, df = 2, p = 0.004), with more time spent antennating at 18 °C compared to 23 °C. For the no-food treatment, significantly more time was spent stationary (Kruskal Wallis: $\chi^2 = 11.39$, df = 2, p = 0.003) at 21 °C and 23 °C compared to 18 °C. However, there was no significant difference in the time spent on moving the leaf depending on temperature (Kruskal Wallis: $\chi^2 = 5.06$, df = 2, p 0.080), or time spent on any of the behaviours depending on sex.

3.7 Discussion

3.7.1 Functional response of A. nemoralis to C. pyri prey

For this study both male and female *A. nemoralis* exhibited Type II functional responses for all three temperature treatments tested, when feeding on hardshell (4th and 5th instar) *C. pyri* nymphs (Figure 3.1). Thus, confirming the first hypothesis. A Type II functional response demonstrates that at lower prey densities the consumption rate of prey increases as prey density increases, but eventually levels off and remains constant at high densities (Juliano, 2020; Real, 1977). This corresponds to multiple other studies, where a Type II functional response was reported for adult anthocorid species of feeding on psyllid nymphs; including *A. minki* predating on *Psyllopsis repens (Hassanzadeh-Avval et al., 2019)*, *A. nemoralis* on *C. pyricola* (Mohammad Saeed Emami et al., 2014), *A. minki pistaciae* on *Agonoscena pistaciae (Kheradmand et al., 2017)* and *Orius vicinus* on *Bactericera cockerelli (Tran et al., 2012)*. A Type II functional response may be more optimal than a Type III response (where consumption rates are lower than Type II responses at low prey densities) for anthocorids, as biological control agents are able to detect and attack prey more effectively at low densities (Lopes et al., 2009). Although, Type II functional responses can be destabilizing in comparison to Type III; high consumption rates of prey at low prey densities can lead to prey population destabilization (Cuthbert et al., 2021; Dick et al., 2014). However, Type III responses allow a negative density-dependent response of the prey survival with prey population density, stabilizing prey populations and making them less likely to fluctuate (Cuthbert et al., 2021).

3.7.2 Functional response and temperature

All three temperature treatments exhibited a Type II functional response. Although males within the 23 °C treatment had a shorter handling time than those at 18 °C, female handling time was not significantly impacted by temperatures tested in this study. Handling times may have decreased with temperature, due to reduced time required for digestion as a result of an increased metabolic rate (Robertson & Hammill, 2021; Sentis et al., 2013). Furthermore, male *A. nemoralis* have a smaller body size than females (Coblentz et al., 2022), thus may be more sensitive to changes in temperature, resulting in a higher increase in metabolic rate (Frances & McCauley, 2018). Other studies found decreases in handling time with temperature (Knutsen & Salvanes, 1999; Robertson & Hammill, 2021; Sentis et al., 2013), for example the spined soldier bug (*Podisus nigrispinus*) handling time for the prey species *Spodoptera exigua* decreased at higher temperatures (Clercq, 2001).

Attack rates have been indicated to increase with rising temperature in other studies, demonstrating a hump-shaped response, with highest attack rates at intermediate temperatures (Robertson & Hammill, 2021; Uiterwaal & DeLong, 2020). The non-significant difference in temperature dependent attack rates, may be due to the small intervals between testing at different temperatures, therefore larger intervals between treatments may be required to detect differences. Many other functional response experiments use temperatures with higher intervals between them; for example, Hassanzadeh-Avval et al (2019) used 15, 24 and 30 °C with the anthocorid *A. minki* and significant differences in attack rate were only seen between the 15 and 30 °C treatments. Whilst 20, 25 and 30 °C were temperature treatments used for functional responses of *Orius laevigatus* (Hassanpour et al., 2020), with a significantly higher attack rate of female anthocorids at 30 °C compared to 20 °C. Therefore, UK mean temperatures predicted for 2080, are unlikely to impact the feeding rates of anthocorids compared to current temperatures. However, *C. pyri* population growth and feeding rates have not been observed under these temperatures. Therefore, if pests respond differently compared to anthocorids, summer pear sucker populations could be difficult to control, highlighting an area of future research. In addition, maximum UK temperatures and future predicted temperatures for other pear growing regions have not been studied, thus future climate could still impact predator-pest dynamics at larger temperature intervals.

3.7.3 Functional response and sex of anthocorid

This study found that female anthocorids had a significantly higher attack rate and shorter handling time than males, supporting the fourth hypothesis, that sex of anthocorid influences functional response. This is similar to the findings of Emami et al. (2014a), where *A. nemoralis* females had higher attack rates, maximal consumption rates and shorter handling times for *C. pyricola* nymphs than males. Hassanzadeh-Avval et al. (2019) also found the maximal consumption rate for ash psyllid, *P. repens*, L4 nymphs (a similar sized prey type to *C. pyri*) was higher for females than males, for the anthocorid *A. minki*. Therefore, female *A. nemoralis* may be a more effective biological control agent of *C. pyri* nymphs than males, although sex ratios of *A. nemoralis* are both 1:1 in summer (in pear orchards) and overwintering populations (McMullen & Jong, 1967), so it is unlikely that this will have implications for pest control as numbers of females and males found in orchards are approximately equal.

The differences in attack rate and handling time depending on sex may be due to differences in body size as male *A. nemoralis* are smaller than females, with a lower body weight (Campbell, 1977). Body size has a significant effect on the feeding rate of a predator (Aljetlawi et al., 2004; Coblentz et al., 2022; DeLong, 2021; Robertson & Hammill, 2021); handling time may decrease as predator body size increases as it may be easier to handle and subdue large prey items (Hammill et al., 2015; Robertson & Hammill, 2021). Conversely, attack rate may increase with body size, as larger predators may cover more distance, increasing the chance of encountering prey (DeLong, 2021), although difference in distance travelled depending on sex was not apparent in the behavioural assays. There is also the possibly that females have higher nutritional requirements than males (Coblentz et al., 2022), in order to produce eggs, therefore need to consume more prey, as females were likely mated within this study. This emphasizes the need for further research, exploring whether differences in prey consumption between males and females is sex dependent or size dependent.

3.7.4 Changes in *A. nemoralis* activity and behaviour in response to temperature

Results from the behavioural assays found that anthocorids spent less time moving at higher temperatures (Fig. 4). When no prey or only eggs were available, anthocorids spent more time moving at 18 °C, compared to 21 °C and 23 °C. There was also less time spent antennating and cleaning at higher temperatures in the no-food or egg treatments. For no-food treatment, significantly more time was spent stationary at high temperatures compared to low. This suggests that *A. nemoralis* may spend more time active at current UK temperatures (18 °C) compared to future temperature regimes, as 23 °C resulted in the lowest activity levels.

However, despite less time spent active at higher temperatures, there was no difference in velocity or distance travelled overall, suggesting that the speed of the anthocorid when it was moving may be faster at higher temperatures. Hence, anthocorids can travel similar distances, suggesting they will be efficient predators at high temperatures tested here; as a high walking velocity is important for a biological control agent (Milton, 2004), allowing a predator to seek out prey items effectively, especially if prey is sparse. Our study also revealed a reduction in cleaning behaviour at the highest temperature treatment in the egg treatment. A reduction in cleaning behaviour may increase the risk of disease; grooming is an important sanitary behaviour, involved in reducing the risk of pathogenic infection, including parasites and fungal pathogens (De Roode & Lefèvre, 2012; Zhukovskaya et al., 2013). However, more research is required to see if reduced grooming in anthocorids increases disease risk, as increased disease risk could reduce the efficiency of a biological control agent.

3.7.5 Anthocorid feeding behaviour and prey preference

There was no significant difference in the time spent feeding at each of the three temperature treatments (for eggs and nymph treatments) or number of eggs eaten (Figure 3.4). This suggests that temperature did not significantly affect the rate of feeding for these temperature intervals. Time spent feeding was higher for nymphs compared to eggs, furthermore there was a far higher number of replicates where 0 eggs were eaten, compared to replicates where 0 nymphs were eaten, suggesting a preference for *C. pyri* (L4 – L5 nymphs) compared to eggs. Conversely, the study by Sigsgaard (2010), found no significant preference between *C. pyri* eggs or nymphs depending on biomass for *A. nemoralis*; however their study used L1-L3 nymphs rather than L4-L5, perhaps larger darker nymphs, are easier to find than eggs for *A. nemoralis*. In addition, there could be a difference in amount or type of volatiles given off by different stages of *C. pyri* nymphs and eggs, making nymphs easier to detect via olfactory cues. Although, there is evidence for volatile emission in pear sucker adults (Ganassi et al., 2018a), no studies have occurred for other stages of *C. pyri*, emphasizing the need for further research. Despite the differences in attack rate and handling time depending on sex of anthocorid, there was no difference in time spent feeding, number of eggs eaten or any other variables monitored in our behavioural assays, possibly due to the short, 20-minute, duration of our assays with few prey items, whereas the functional response experiments occurred over 24 hrs at larger prey densities. Therefore, perhaps assays over a longer time period are required to observe sex specific differences.

3.8 Conclusions

The anthocorid, *A. nemoralis,* is likely to be an effective predator of *C. pyri* nymphs under future predicted temperatures, although this depends on how pear psyllids respond under future temperature scenarios. Attack rates and overall prey consumption by anthocorids did not significantly differ depending on temperature, although males did show significantly shorter handling times at 23 °C compared to 18 °C. However, it is important to note that only UK average summer temperatures (current and predicted) were monitored under laboratory conditions, therefore looking at functional responses for a larger temperature range may be necessary for other pear growing regions. Despite the likelihood that anthocorid feeding rates will be similar for current and future UK summer temperatures, there is still the possibility that pear sucker feeding and growth rates could change. The body size of pear sucker nymphs and adults are smaller than anthocorids, making them more sensitive to changes in temperature, which could lead to increased feeding and growth rates. Therefore, if there is a mismatch between pear sucker and anthocorid population growth or feeding rates, it may be more difficult to control summer pest populations. This highlights the importance of monitoring multiple trophic levels within an agricultural ecosystem (primary producer, pest and natural enemy), to observe interactions and potential mismatches between them. This study suggests that future research should focus on these trophic interactions using mesocosm studies, field or glasshouse experiments.

3.9 Figures and Tables

Table 3.1: Evidence for Type II or Type III functional responses using the frair-test function, for different temperature treatments (18°C, 21 °C and 23°C) and male or female *Anthocoris nemoralis*. This method uses forward selection based on the sign and significance of first (density) and second-order terms within logistic regressions. A significant negative estimate of density provides evidence for Type II response.

Temperature (°C)	Sex	Estimate (density)	SE	Z value	P value	Evidence for Type II response
18	M	-0.038	0.0045	-8.28	**<0.001**	Yes
21	M	-0.039	0.0045	-8.82	**<0.001**	Yes
23	M	-0.037	0.0044	-8.38	**<0.001**	Yes
18	F	-0.048	0.0042	-11.39	**<0.001**	Yes
21	F	-0.059	0.0044	-13.43	**<0.001**	Yes
23	F	-0.056	0.0043	-13.01	**<0.001**	Yes

Table 3.2: Maximum likelihood estimates (MLE) of attack rate (a) and handling time (h) and their standard errors (SE), for male and female *Anthocoris nemoralis* at three different temperature treatments (18 °C, 21 °C and 23 °C). Logistic regressions use a Rogers Type II response, as prey is not replaced during the experiment.

Temp (°C)	Sex	Coeff	Estimate	SE	Z value	P value	Response	Log L
18	M	a	0.069	0.020	3.51	**<0.001**	Rogers Type II	200.28
		h	3.27	0.361	9.06	**<0.001**		
21	M	a	0.069	0.018	3.77	**<0.001**	Rogers Type II	190.74
		h	2.95	0.325	9.08	**<0.001**		
23	M	a	0.049	0.010	5.12	**<0.001**	Rogers Type II	205.57
		h	2.33	0.266	8.78	**<0.001**		
18	F	a	0.108	0.019	5.82	**<0.001**	Rogers Type II	199.85
		h	1.85	0.146	12.64	**<0.001**		
21	F	a	0.156	0.025	6.26	**<0.001**	Rogers Type II	191.61
		h	1.78	0.116	15.41	**<0.001**		
23	F	a	0.135	0.021	6.50	**<0.001**	Rogers Type II	218.78
		h	1.65	0.114	14.43	**<0.001**		

Table 3.3: Comparisons of male and female *Anthocoris nemoralis* at three different temperature treatments (18 °C, 21 °C and 23 °C). Using the difference method, with difference in attack rate (D_a) and difference in handling time (D_h), p values in bold show a significant difference.

Comparison	Coefficients	Estimate	SE	Z value	P value	Response
18F~18M	D_a	0.039	0.027	1.43	0.152	Rogers Type II
	D_h	-1.43	0.390	-3.66	**0.0003**	
21F~21M	D_a	0.087	0.031	2.83	**0.0047**	Rogers Type II
	D_h	-1.17	0.345	-3.40	**0.0007**	
23F~23M	D_a	0.086	0.023	3.76	**0.0002**	Rogers Type II
	D_h	-0.68	0.289	-2.37	**0.0179**	

Table 3.4: Comparisons of three different temperature treatments (18 °C, 21 °C and 23 °C), for male and female *Anthocoris nemoralis*. Using the difference method, with difference in attack rate (D_a) and difference in handling time (D_h), p values in bold show a significant difference.

Temperature	Coefficients	Estimate	SE	Z value	P value	Response
18M~21M	D_a	0.0003	0.027	0.013	0.990	Rogers Type II
	D_h	0.317	0.487	0.652	0.515	
18M~23M	D_a	0.020	0.022	0.907	0.365	Rogers Type II
	D_h	0.946	0.449	2.11	**0.035**	
21M~23M	D_a	0.020	0.021	0.957	0.339	Rogers Type II
	D_h	0.631	0.420	1.50	0.133	
18F~21F	D_a	-0.048	0.031	-1.54	0.124	Rogers Type II
	D_h	0.066	0.186	0.353	0.724	
18F~23F	D_a	-0.028	0.028	-0.987	0.324	Rogers Type II
	D_h	0.203	0.185	1.10	0.273	
21F~23F	D_a	0.020	0.032	0.619	0.536	Rogers Type II
	D_h	0.138	0.162	0.847	0.397	

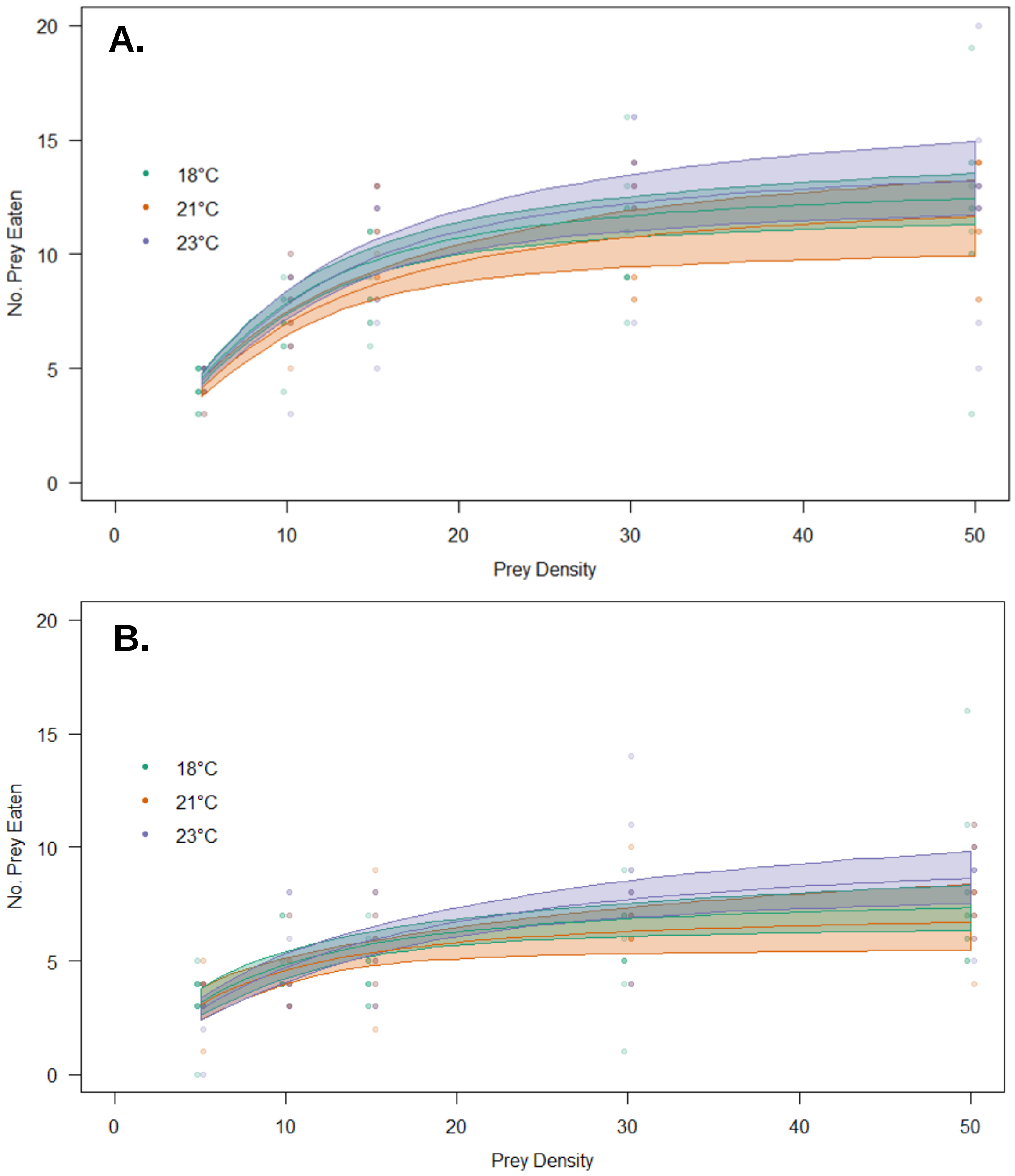

Figure 3.1: The number of prey eaten (*Cacopsylla pyri* nymphs) by the predator *Anthocoris nemoralis*, depending on prey density. For both **A.** female and **B.** male *Anthocoris nemoralis*, at three different temperature regimes (18 °C, 21 °C and 23 °C). Type II functional response curves based on bootstrapped model fits for 95% confidence intervals.

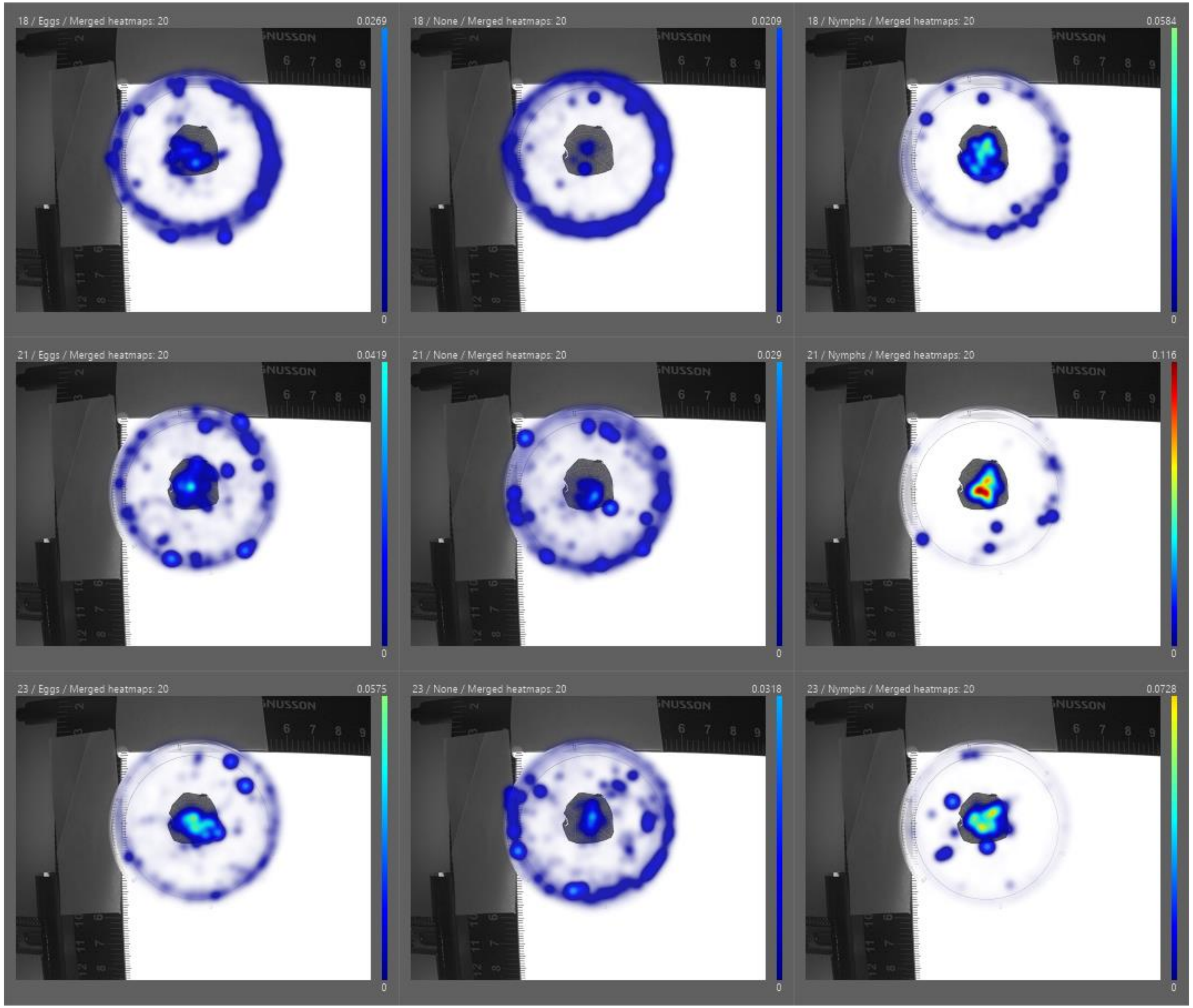

Figure 3.2: The proportion of time spent by the anthocorid predator *Anthocoris nemoralis* in different areas within the arena (55mm in diameter), depending on temperature treatment (**A- C.**18 °C, **D-F.** 21 °C and **G-I.** 23 °C) and food type (**A, D, G.** eggs, **B, E, H.** no-food and **C,F,I.** nymphs) for *Cacopsylla pyri* prey. The center zone is marked out by the grey circle (20mm in diameter).

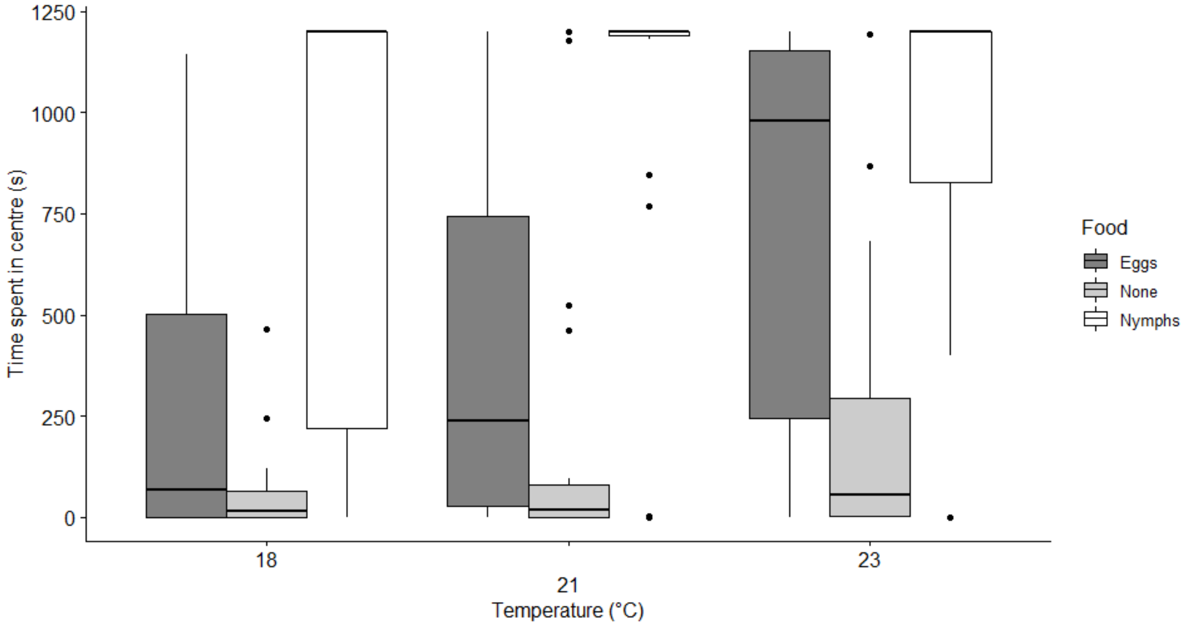

Figure 3.3: The amount of time (s) spent in the center of the arena (20 mm in diameter) containing the food source or leaf, for the 20-minute (1200s) time period, depending on temperature treatment (18 °C, 21 °C and 23 °C) and food type (eggs, no-food and nymphs) for the anthocorid predator *Anthocoris nemoralis* for *Cacopsylla pyri* prey.

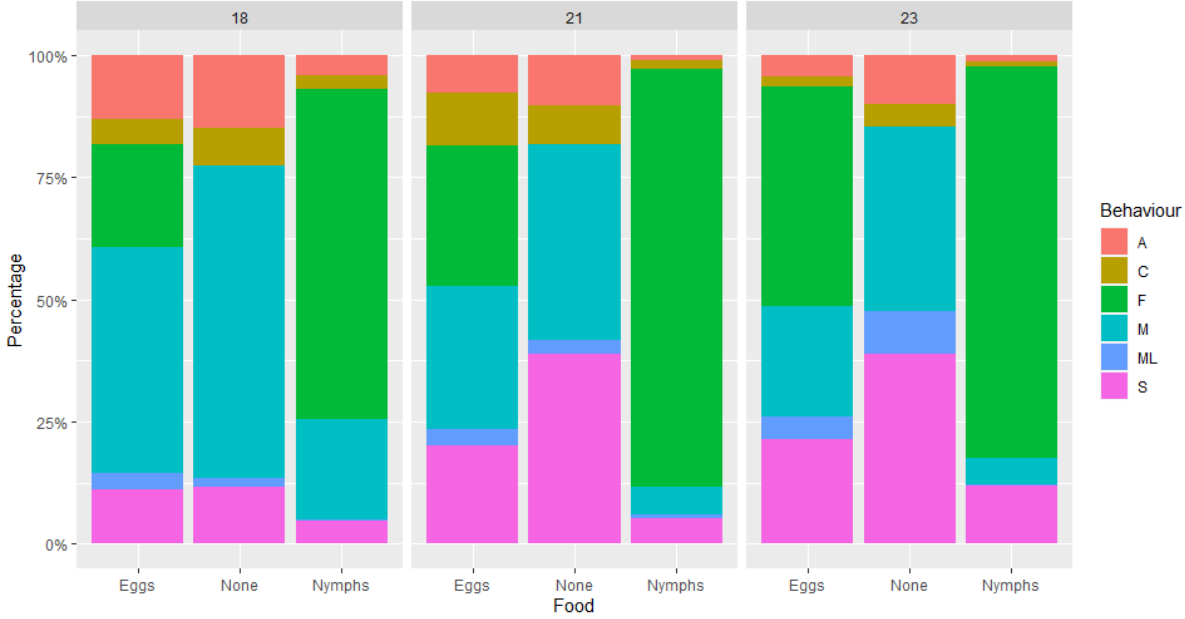

Figure 3.4: The percentage of time spent demonstrating six different behaviour types (F- feeding, M- moving, ML- moving leaf, C- cleaning, S- stationary and A- antennating), depending on temperature treatment (18 °C, 21 °C and 23 °C) and food type (eggs, no-food and nymphs) for *Anthocoris nemoralis* for *Cacopsylla pyri* prey.

4 Intraguild predation or spatial separation? The efficacy of using two natural enemy species for the biological control of pear psyllid (*Cacopsylla pyri*).

This chapter is a version of the following paper, with minor corrections and changes to formatting and references to make the thesis more comprehensive:

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Author contributions: LR, MG, MF and DS conceived and designed the study. LR carried out the lab work, data analyses and drafted the manuscript with all authors providing feedback on multiple drafts prior to submission.

4.1 Abstract

Pear psyllid (*Cacopsylla pyri*) is a persistent pest to the pear industry; with an estimated cost of £5 million per annum in the UK alone. Multiple insecticides used to control this pest have recently been withdrawn from UK use, necessitating the use of alternative control strategies. Many pear growers practice integrated pest management (IPM) of pear psyllid, focusing on maximising natural enemy populations, whilst minimising the use of agrochemical sprays. The anthocorid *Anthocoris nemoralis* and the European earwig *Forficula auricularia* are particularly effective at controlling pear psyllid populations during the summer months. Despite the effectiveness of both natural enemies, there is a lack of understanding on whether both species should be promoted together or separately, due to the risk of intraguild predation (IGP) or interference competition. Furthermore, abiotic factors including temperature may influence behaviour, altering activity level and niche overlap. Although IGP and interference competition have been documented between multiple species of natural enemies neither have been studied between these two specific predators. Using microcosm experiments, olfactometer assays and survival analyses this study demonstrated whether *A. nemoralis* and *F. auricularia* can be used in synchrony to control pear psyllid. Results indicated that IGP is present; *F. auricularia* will consume *A. nemoralis* when predators are not spatially separate and in absence of psyllid prey. There was no evidence for interference competition, although both predators consumed more prey at higher temperatures. This confirms that pear growers can encourage both predators for the control of pear psyllid without losing predation efficacy.

4.2 Introduction

Pear psyllid (*Cacopsylla pyri*), is the dominant pest of UK pears, with an estimated cost of £5 million per annum (AHDB, 2012). These phloem feeding pests are resistant to a number of commonly available pesticides (Erler, 2004a; Sek Kocourek & Stará, 2006); furthermore multiple insecticides used in psyllid control have been withdrawn for UK usage in the past decade (Hertfordshire, 2023; HSE, 2023). Therefore, integrated pest management (IPM) has become more widespread for controlling psyllid in pear orchards (DuPont & John Strohm, 2020; Nottingham et al., 2022), focusing on keeping pest populations below economic threshold, whilst minimising chemical input and disruption to agroecosystems (Moorthy & Kumar, 2004). Biological control is a common technique used in pear psyllid IPM (Civolani, 2012a; DuPont & John Strohm, 2020). Biocontrol can be augmentative; where a predator or parasitoid is usually commercially reared and mass released in order to manage pest populations (Collier & Van Steenwyk, 2004; Van Lenteren, 2012). The anthocorid *Anthocoris nemoralis* is a key biocontrol agent reared and available for mass release (Bioplanet, 2023; Koppert, 2023), helping to control *C. pyri* populations when wild populations are slow to build up in orchards. By contrast conservation biocontrol promotes the preservation and enhancement of wild populations of natural enemies (Naranjo, 2001). The enhancement of natural enemies such as the European earwig (*Forficula auricularia*), has been recommended to improve pest control in orchards (Belien et al., 2012b; Fountain et al., 2013; Hanel et al., 2023; Solomon et al., 2000), with Wignests (wooden shelters for earwigs) commercially available to growers within the UK, which encourage earwigs to forage in the tree canopy where pear psyllids are present (Shaw et al., 2021).

Increased predator diversity has been shown to enhance prey suppression in several agroecosystem studies (Snyder et al., 2008; Snyder et al., 2006; Tylianakis & Romo, 2010), especially if predators show spatial or temporal niche separation or respond differently to abiotic factors (Snyder et al., 2008); as the pest population can be controlled throughout the year, with other predator guilds continuing to control pests when some species are less abundant. However, high natural enemy diversity is not always beneficial (Snyder & Wise, 2001); if species occupy similar niches then interference competition (when one predatory species reduces prey capture for a second predator species) (Stiling & Cornelissen, 2005) or intraguild predation (IGP, where different predators consume each other, in addition to their target prey) is more likely (Jonsson et al., 2017). Furthermore, abiotic factors such as temperature can increase the likelihood of IGP or interference competition due to increased niche overlap (Barton & Schmitz, 2009; Schmitz & Barton, 2014)

With summer temperatures predicted to increase by as much as 5.1°C under the high emissions scenario by 2070 (MetOffice, 2022), climate change is likely to impact insect behaviour, activity and prey consumption (Karuppaiah & Sujayanad, 2012). Prey consumption may increase under higher temperatures due to an elevated metabolism (Yuan et al., 2009); increasing demand for energy and nutrients (Frances & McCauley, 2018; Schmitz & Barton, 2014), this could also increase the risk of IGP if alternative prey sources aren't available. Climate change can also alter predator behaviour; Barton & Schmitz (2009) investigated the niche overlap of two predatory spiders *Phidippus rimator,* and *Pisaurina mira* and their grasshopper prey (*Melanoplus femurrubrum*). Under ambient temperatures spiders filled spatially separate niches but under elevated temperatures (+3 ˚C) *P. mira*, moved downwards in the plant canopy. Whereas *P. rimator* did not shift spatially, leading to niche overlap and IGP. *Phidippus rimator* was consumed by *P. mira* in all elevated temperature replicates. This led to a higher grasshopper density and reduced biomass of herbs in the +3 ˚C treatment compared to the control. Thus, it is important to consider how predator interactions may change with respect to climatic warming, helping us to predict whether current biological control agents will still be effective predators under future temperature scenarios.

In pear orchards both *A. nemoralis* and *F. auricularia* are key biological control agents; *F. auricularia* has a maximal consumption rate of approximately 10 mg of psyllid eggs or nymphs per day (Lenfant et al., 1994), whilst an average *A. nemoralis* female has a maximum consumption rate of 14.5 nymphs per day (Reeves et al., 2023) or 5000 *C. pyri* eggs in its lifetime (Yanik & Ugur, 2004). However, a key question is whether both *A. nemoralis* and *F. auricularia* can be used in combination within an agroecosystem, or if IGP or interference competition will reduce their efficacy as natural enemies. This will allow growers to decide whether to release *A. nemoralis* and enhance *F. auricularia* populations, or if only one species should be encouraged, to optimise pest management.

Both *A. nemoralis* and *F. auricularia* show temporal overlap; adult anthocorids migrate into orchards in April-May from surrounding hedgerows (Nagy et al., 2008; Reeves et al., 2023), eggs are laid and anthocorid populations peak mid-summer (Nagy et al., 2008; Scutareanu et al., 1999). European earwigs start to appear in pear trees in May; third and fourth earwig instars are arboreal and show population peaks in June, whilst adults peak in mid-July (Gobin et al. 2008; Moerkens et al. 2009; Moerkens et al. 2011). Thus, there is the potential for niche overlap in late spring and throughout the summer when effective pear psyllid control is most importance.

IGP is likely to be unidirectional (only one predator consumes the other) rather than bidirectional between these two species, as larger natural enemies often predate on those with smaller body sizes (Yano, 2006). Adult earwigs (length 13–14 mm) and all arboreal nymph stages (9–11 mm) are significantly larger than adult *A. nemoralis* (3.5–4 mm) (Capinera, 2008; Reeves et al., 2023). *Forficula auricularia*, has a varied diet of insect, animal and plant material (Helsen et al., 1998), thus there is potential for earwigs to consume other natural enemies. Weak IGP has been documented between *F. auricularia* and young ladybird larvae (*H. axyridis*) when pest density was low (Dib et al., 2020), and between *A. nemoralis* and several coccinellid species (Batuecas et al., 2022). IGP has yet to be studied between *F. auricularia* and *A. nemoralis*. However, earwigs are nocturnal foragers (Kölliker, 2007; Suckling et al., 2006), demonstrating diurnal sheltering behaviour when other natural enemies are active (Lame, 1974), so it may be less likely that earwigs and anthocorids interact directly, due to differences in activity period.

Natural enemies often rely on "infochemicals"; chemical compounds which carry information and can be used to help locate prey (Hatano et al., 2008; Vet & Dicke, 1992). These chemical signals can be HIPVs (herbivore-induced plant volatiles) emitted from herbivorized plants (Allison & Daniel Hare, 2009; Valle et al., 2023) or kairomones emitted by pests themselves, on which natural enemies eavesdrop (Ayelo et al., 2021). Infochemicals may also play a role in IGP and interference competition; they may allow predators to actively avoid areas with heterospecific predators or be attracted to them if alternative prey sources are scarce (Gnanvossou et al., 2003; Tapia et al., 2010). Moreover, temperature can alter signal composition, transmission and perception (Becker et al., 2015; Yuan et al., 2009), as the volatility and diffusion rates of VOCs (Volatile organic compounds) are temperature dependent (Niinemets et al., 2004; Yuan et al., 2009). Earwigs are dependent on olfactory cues and signals; *F. auricularia* relies on chemical signals in offspring care (Mas, 2011) and also release an aggregation pheromone (Hehar et al., 2008; Walker et al., 1993). Whilst the earwig species *Doru luteipes* Scudder, responds to HIPVs released by herbivorized maize plants (Naranjo-Guevara et al., 2017). However, the use of infochemicals in the location of psyllid prey by *F. auricularia* has not been investigated.

Combining microcosm experiments, olfactometry assays and survival analyses, this study aims to assess whether *F. auricularia* and *A. nemoralis* in combination could deliver better control of pear psyllid, or if IGP or interference competition is likely to disrupt biological control, all experiments took place at two temperature regimes based on current summer temperatures and those predicted under the high emissions scenario (RCP8.5) for 2080. Our study tested four hypotheses: (1) *F. auricularia* demonstrates unidirectional IGP for *A. nemoralis* when alternative prey is absent, (2) *F. auricularia* and *A. nemoralis* show similar rates of psyllid consumption in the same microcosm, compared to total prey consumption of *F. auricularia* and *A. nemoralis* in separate microcosms (additive), demonstrating the absence of interference competition, (3) the likelihood of IGP is dependent on sex and stage of *F. auricularia,* and (4) *F. auricularia* shows a positive olfactory response to *C. pyri* prey but not to *A. nemoralis,* highlighting a preference for psyllid prey.

4.3 Materials and methods

4.3.1 Pear psyllid, earwig and anthocorid husbandry

Pear psyllid hardshell nymphs (L4-L5, the fourth or fifth nymph stage in a pear psyllid's life history) were collected from cv. Conference pear trees (*Pyrus communis*) at NIAB East Malling (51.2885° N, 0.4383° E). Nymphs were removed from trees daily, using a soft, fine tipped paintbrush, to minimise damage. Prior to nymph collection the orchard was sampled for psyllid adults for several weeks via beat tray sampling of 30 trees; to check whether the majority of pear psyllids were *C. pyri*. Adult psyllids were identified, based on genitalia using a light microscope. A large proportion of individuals were *C. pyri* (95.92%) but *C. pyricola* were also present but in small numbers. Hence, the majority of the nymphs used within experiments were likely *C. pyri*, but it is difficult to distinguish between the two species at juvenile stage. For beat tray sampling a pear tree branch was tapped with a foam-covered stick, with a white tray (260 mm by 460 mm) held underneath, adults were then collected into a plastic test tube. Adult *C. pyri* were kept in ventilated Tupperware pots (diameter 105 mm, height 75 mm) containing pear shoots (70 mm in length) in water tubes (40 mm height, 15 mm diameter) to keep moist. Individuals were kept in a controlled temperature (CT) cabinet at 12.1°C during dark and 22.0°C during light conditions. Semi-mature pear psyllid eggs (yellow-white in colour) were collected from the Tupperware pots daily, these were used for feeding anthocorids. Earwigs were fed dry cat food and mealworms; water was available in a small plastic dish. *Cacopsylla pyri* adults and nymphs were identified to species level using the Psyllid key from RLP Agroscience (Agroscience, 2022).

A batch of 500 *A. nemoralis* adults were ordered from the biocontrol company Koppert each week (Anthobug) of the study. These were approximately 4-10 days after their final moult, when used in all experiments. Anthocorids were kept in a ventilated plastic container, with the carrier material they arrived in and fed *C. pyri* eggs daily. These were kept in a CT cabinet at 12.1°C during dark and 22.0°C during light conditions. Five batches of anthocorids were used for survival analyses and microcosm experiments, 4 were used for olfactometer assays. Female anthocorids were identified using a light microscope based on differences in genitalia. Third and fourth instar *F. auricularia* nymphs and adults were collected from NIAB East Malling at the beginning of each week from orchard Wignests (Russel-IPM, 2023) and using beat trays. Third and fourth instar nymphs and adults were chosen as these are the arboreal stages (Moerkens et al., 2009), thus are more important for *C. pyri* predation in pear orchards. Earwigs were housed in Tupperware containers (diameter 105 mm, height 75 mm) at 12.1°C during dark and 22.0°C during light conditions in CT cabinets, which also contained a pear shoot in a water tube to keep moist, a small water dish and a wooden wignest (59 mm, length 48 mm width, 14 mm height) for shelter.

4.3.2 Microcosm experiments

Microcosms consisted of a ventilated Tupperware pot (diameter 105 mm, height 75 mm), containing a pear shoot with four leaves collected from cv. Conference pear trees (*Pyrus communis*), kept moist in a plant holder (20 mm diameter, 57 mm height), with a small stick attached so that natural enemies could crawl to the top of the holder, a wignest for earwigs to shelter in (59 mm, length 48 mm width, 14 mm height) and a small dish of distilled water (20 mm diameter, 10 mm height) (Figure 4.1). Plant holders were cylindrical plastic tubes filled with distilled water, supplied by NOLITOY. For the purposes of recording whether there was spatial overlap between earwigs and anthocorids, the microcosm was divided into four different zones: top (T), middle (M), bottom (B) and wignest shelter (S).

Adult anthocorid females and earwigs were starved for 24 h at one of the two temperature regimes, current (12.1°C during dark and 22.0°C during light conditions) or RCP8.5 (15.9°C during dark and 26.4°C during light conditions) in a microcosm, within a controlled temperature cabinet. There were seven treatments: 1. earwig, anthocorid and *C. pyri* nymphs, 2. earwig and *C. pyri* nymphs, 3. anthocorid and *C. pyri* nymphs, 4. earwig, anthocorid no prey, 5. earwig no prey, 6. anthocorid no prey and 7. control with no predators, each treatment only contained one individual of the species to avoid the impacts of intraspecific competition. After 24 h, 100 L4-5 stage *C. pyri* nymphs and anthocorids were added to the required treatments. The prey density was above the combined natural enemies' saturation points for maximal prey intake, so prey consumption could be compared between treatments. Microcosms were monitored after 2 h dark and 2 h light for two minutes to check the position of the earwig or anthocorid (top, middle, bottom or shelter) and the behaviour demonstrated (Antennating, Cleaning, Feeding, Interacting, Moving and Stationary). A red-light torch was used during behavioural observations to minimise disturbance. After 24 h natural enemies were removed and whether they were alive was recorded. The number of live *C. pyri* nymphs was also recorded. Each treatment was replicated ten times.

4.3.3 Survival analyses

For survival analyses, *F. auricularia* and adult *A. nemoralis* were starved for approximately 24 h at either Current (12.1°C during dark and 22.0°C during light conditions) or RCP8.5 (15.9°C during dark and 26.4°C during light conditions) temperature regimes in controlled temperature (CT) cabinets, in separate triple vented Petri dishes (55 mm in diameter) containing a leaf disk of *P. communis*

‘Conference’ (20 mm in diameter) and moist kitchen towel. The Petri dish was sealed with plastic paraffin film to prevent insects escaping and returned to the CT cabinet. After 24h the earwig was added to the Petri dish containing the anthocorid and resealed, each treatment only contained one individual of each predator species to avoid the impacts of intraspecific competition. There were five different treatments (stage 3 nymph, stage 4 nymph, adult female, adult male *F. auricularia* and a control where no earwig was added). The Petri dish was checked after 6 h, 12 h and then at 12 h intervals, to see if anthocorid and earwig were still alive or had been consumed, over a period of 10 days. The Petri dish was sprayed with distilled water every 24 h, to keep the leaf disc moist. There was a total of 10 replicates for each treatment and temperature, giving a total of 100 observations.

4.3.4 Olfactometer assays

For olfactometer assays, female earwigs were starved for 24h in CT cabinets at Current and RCP 8.5 temperature treatments. Glass chambers at the end of each arm contained either *C. pyri* nymphs and adult *A. nemoralis*, *C. pyri* nymphs and nothing and adult *A. nemoralis* and nothing, as control treatments. Experimental set-up of the glass Y-tube olfactometer (main arm, 15 cm long; side arms: 10 cm long; 0.9 cm internal diameter) is as shown in Figure 4.2. Air was pumped through for 10 mins prior to releasing the earwig, using a Dymax 8 vacuum pump, average air flow was 1.6 L/min. Each arm had an activated carbon filter to remove other odours and VOCs from the air. The earwig was then added to the base of the olfactometer, whilst air was still being circulated. This was videoed in darkness with a red-light torch over the equipment, in the CT cabinet to minimise disturbance. After 10 minutes video footage was viewed and the time taken for the earwig to reach the end of one of the arms was recorded, as well as the choice made (Left or Right arm). Any individuals that did not make a choice after 10 minutes were disregarded; 2 individuals were disregarded during the experiment. After each replicate, the equipment was washed using 70% ethanol and distilled water, then dried. The position of prey on the left or right arm was randomized and prey changed between experiments. There were 20 replicates for each treatment and temperature giving a total of 120 observations.

4.3.5 Temperature regimes

The two temperature treatments were determined based on the current average minimum and maximum June-August temperature (1990-2020) and the average minimum and maximum June-August temperatures predicted in 2080, based on the RCP8.5 (high emissions) scenario (Table S3.1). A 2080 timeframe was chosen as this year is commonly used in studies predicting future trophic interactions (Aartsma et al., 2019; Duffy, 2014; South et al., 2018), thus the results of this paper can be compared to others. June-August temperatures were chosen as this is when anthocorids and earwigs are most abundant in pear orchards (Fields & Beirne, 1973; Scutareanu et al., 1999). The current temperature was calculated using the average minimum and maximum June-August temperatures (1990-2020) from East Malling weather station (51.288° N, 0.448° E) in Kent. To calculate future temperatures for 2080, data was extracted using the UK Climate Projections User Interface, based on UKCP18 projections (UKCP, 2021a). The predicted increase for minimum and maximum air temperature at 1.5 m for 2080 was calculated for June to August (baseline scenario 1981-2000) for a 25 km x 25 km region in Kent, surrounding East Malling, this temperature was calculated for the RCP8.5 scenario and added to the average minimum and maximum 1981-2000 June-August temperature.

The first CT cabinet was set at 12.1°C during dark and 22.0°C during light conditions (Current temperature treatment) and the second was set at 15.9°C during dark and 26.4°C during light conditions (RCP8.5 temperature treatment). The CT cabinets had two containers half-filled with water to keep humidity constant. Temperature and humidity were monitored using OM EL USB 2 dataloggers (OMEGA, 2023). The daylight cycle within the cabinets was 8hrs dark followed by 16hrs light, based on average summer day length in the UK.

4.4 Data analyses

4.4.1 Intraguild predation and prey consumption

To compare prey consumption between natural enemy treatments the total prey eaten for single earwigs and anthocorids in the same batch were added together (additive), then compared to the corresponding treatment containing both earwigs and anthocorids (combination) in the same batch. To account for natural mortality in each treatment, average mortality from the control treatment (for each temperature) was subtracted from all other treatments. Any microcosms where a predator had died during the experiment were removed from the analysis. As data was normally distributed a Two-way ANOVA was carried out to test if there was a significant difference in prey mortality depending on treatment, temperature and interaction between temperature and treatment. For pairwise comparisons between treatments a Tukey HSD test was done, all statistical analysis were done using base R version 4.3.0 (R, 2023), plots were generated using the package ‘ggplot2’ (Wickham et al., 2016).

4.4.2 Behavioural observations, activity and position within the microcosm

For behavioural observations, stacked bar charts were created using the ‘ggplot2’ package in R. These show the percentage of time *A. nemoralis* and *F. auricularia* spent exhibiting certain behaviours (feeding, moving, interacting, cleaning, stationary and antennating) over the 2-minute time period, for both light and dark observations. Stacked bar charts also show time spent at different heights within the microcosm (top, middle, bottom or shelter). For statistical analysis a Linear discriminant analysis occurred (LDA) to define the positional and behavioural profiles of earwigs and anthocorids during the night and day. Discriminant function analyses are commonly used in behavioural studies to demonstrate whether species show different behavioural profiles or niches, or whether there is overlap between groups (Kramer et al., 2009; Martha & Jones, 2002). In an LDA the probability of individuals belonging to the different groups is calculated; individuals are then assigned to groups with the highest probability score. The LDA was performed using the “MASS” package (Ripley et al., 2013) and biplots were created using the “ggord” package (Beck, 2017). The predictor variables for the analysis were the behaviours ‘Antennating, Cleaning, Feeding, Moving and Stationary’ and positions in the microcosm ‘Shelter, Bottom, Middle and Top’, with time of day and predator species as dependent variables. The interacting behaviour was excluded due to the low frequency of observations. The data was split and 80% of it was used for training the model and 20% was used to test the model, the preProcess() function was used to centre and scale the data, in order to standardize it. The lda() function was used to perform the analysis, producing coefficients of linear discriminants. The predict() function was used to predict classes for observations within the training dataset, so that model accuracy could be calculated. Activity of each predator was calculated by adding the total time spent (s) ‘Antennating, Cleaning, Feeding, Interacting, Moving and Stationary’. As variables were normally distributed, a multi-way ANOVA was carried out to observe if there was a significant difference in predator activity depending on treatment, temperature and time of day (after 2 h dark or after 2 h light), or an interaction between the variables. For pairwise comparisons between treatments a Tukey HSD test was done.

4.4.3 Olfactometry assays and survival analysis

Differences in choice number by *F. auricularia* between 1) the control odour source and *A. nemoralis*, control odour source and 2) *C. pyri* nymphs and 3) *A. nemoralis* and *C. pyri* nymphs were tested using a two-sided binomial exact test with H0 = 0.5, using the binom.test() function (R, 2023), as this analysis is commonly used on binary count data from two-arm olfactometers (Meza et al., 2020; Roberts et al., 2023). Differences in choice number depending on temperature was analysed using a χ2 goodness of fit test. Differences in time taken to make a decision depending on temperature and odour source were analysed using a Two-way ANOVA, as data were normally distributed.

Survival analyses were performed using the “survival” and “surviminer” packages (Kassambara et al., 2017; Therneau & Lumley, 2013). This method of analysis is common in insect survival studies (Boff et al., 2021; Hüftlein et al., 2023; Pal et al., 2022). By means of the survfit() function a survival analysis was conducted, using the Kaplan-Meier estimate of survival probability at a given time (hrs), depending on temperature (current or RCP8.5) and stage of earwig (stage 3, stage 4, adult female, adult male or control). Significant between-group differences were tested using a log-rank test, using the survdiff() function to highlight whether there was a significant difference in survival time depending on temperature or stage of earwig. For pairwise comparisons the function pairwise_survdiff() was used, with the Benjamini–Hochberg correction to account for multiple testing. For plotting survival curves the function ggsurvplot() from the “surviminer” package was used.

4.5 Results

4.5.1 Prey consumption and Interference competition

The number of nymphs consumed significantly differed depending on treatment ($F_{(4,79)}$ = 71.61, p <0.001), a Tukey HSD test demonstrated that earwigs consumed significantly more *C. pyri* nymphs than anthocorids (p <0.001), that earwigs and anthocorids combined consumed more a than single Earwig (p < 0.001) or Anthocorid (p < 0.001, Figure 4.3). However, the number of *C. pyri* nymphs consumed in the combined treatment (earwig and anthocorids in the same microcosm) did not significantly differ from earwig + anthocorid in separate microcosms (additive), p = 0.171, suggesting that interference competition is unlikely at high prey density. The interaction between temperature and treatment was non-significant ($F_{(4,79)}$ = 0.581, p = 0.677). For natural mortality without predators present there was an average of 3.20 ± 0.84 (SD) dead *C. pyri* nymphs per sample at Current temperatures and 5.40 ± 2.61 (SD) at RCP8.5 temperatures. These averages were subtracted from all treatments to account for natural mortality. One anthocorid died during the course of this experiment, therefore these data were removed from the analysis. Significant differences between treatments and temperatures were found using a Two-way ANOVA; results indicated that there was a significant difference in prey consumption depending on temperature ($F_{(1,79)}$ = 5.12, p = 0.0264), with an average of 43.70 ± 13.15 (SD) nymphs consumed by earwigs at the higher temperature

(RCP8.5) compared to the lower temperature (Current) with an average of 36.0 ± 11.67 (SD) nymphs consumed (Figure 4.3). Higher numbers of nymphs were also consumed by anthocorids at the high temperature (14.4 ± 9.33, SD) compared to the lower temperature treatment (10.2 ± 3.37, SD).

4.5.2 Intraguild predation and survival analysis

After 8.5 days all anthocorids were dead at all temperatures and treatments. For treatments containing earwigs, 45.0% of the anthocorids were eaten, no earwigs were consumed or injured by anthocorids during this timeframe. The survival rate of anthocorids differed depending on treatment and temperature ($\chi2 = 25.06$, d.f.= 5, $p < 0.001$), in all treatments anthocorids in combination with earwigs had a significantly lower survival rate than those alone ($p = 0.0448$, Table 4.1) and anthocorid survival rate significantly differed depending on temperature ($p = 0.001$), with higher temperatures leading to lower average survival rates, however this was dependent on stage (Table 4.1, Figure 4.4). Pairwise comparison tests with the BH correction applied found that Current and RCP8.5 control treatments significantly differed from all other treatments containing both anthocorids and earwigs. Mortality rates of anthocorids did not significantly differ depending on sex of earwig at Current ($p = 0.952$) or RCP8.5 ($p = 0.909$) temperature treatments, based on pairwise comparison tests.

4.5.3 Activity, behaviour and position within the microcosm

Predator activity significantly differed depending on the interaction between treatment and time of day (Two-way ANOVA: $F_{(3,144)} = 29.97$, $p < 0.001$, Figure 4.5); a Tukey HSD test demonstrated that earwigs were significantly more active at night compared to during the day ($p<0.001$), conversely anthocorids were significantly more active during the day compared to at night ($p = 0.030$). However, no significant differences were found between time spent active for earwigs alone or in combination during the night ($p = 1.000$) or for anthocorids alone or in combination during the day ($p = 0.955$), indicating that the presence of another predator is unlikely to interfere with their activity level. Furthermore, temperature (Two-way ANOVA: $F_{(1,144)} = 2.417$, $p = 0.122$) or the interaction between treatment and temperature (Two-way ANOVA: $F_{(1,144)} = 2.417$, $p = 0.152$) did not significantly impact time spent active.

The time spent stationary significantly differed depending on predator and time of day (Figure 4.6, Kruskal Wallis: $\chi2 = 52.70$, $p < 0.001$); earwigs spent more time stationary during the day than at night (Pairwise Wilcox: $p< 0.001$), and more time stationary than anthocorids during the day ($p< 0.001$). However, time spent stationary did not significantly differ depending on temperature (Kruskal Wallis: $\chi2 = 1.45$, $p = 0.229$) or whether the predator was alone or in combination (Kruskal

Wallis: $\chi2 = 0.872$, $p = 0.350$). Interactions between predators were very uncommon with only 2 brief interactions observed between earwigs and anthocorids across the entire experiment. Feeding behaviour also differed depending on treatment (Figure 4.6, Kruskal Wallis: $\chi2 = 20.33$, $p < 0.001$), earwigs spent significantly more time feeding at night compared to daytime (Pairwise Wilcox: $p< 0.001$). Time spent feeding did not significantly differ depending on temperature (Kruskal Wallis: $\chi2 = 0.0030$, $p = 0.956$), or a significant difference in feeding depending on whether the predator was alone or in combination (Kruskal Wallis: $\chi2 = 3.94$, $p = 0.051$). Time spent antennating also differed depending on treatment (Figure 4.6, Kruskal Wallis: $\chi2 = 66.64$, $p < 0.001$), earwigs spent significantly more time antennating at night compared to daytime (Pairwise Wilcox: $p = 0.038$), whereas anthocorids spent more time antennating in the day than at night. Time spent antennating did not significantly differ depending on temperature (Kruskal Wallis: $\chi2 = 0.268$, $p = 0.605$), or a significant difference in antennating depending on whether the predator was alone or in combination (Kruskal Wallis: $\chi2 = 0.0004$, $p = 0.985$). Findings were similar for no food treatments (Fig S1), except no feeding behaviour was demonstrated by anthocorids or earwigs. Once again temperature and whether the predator was alone or in combination did not significantly affect time spent demonstrating these behaviours.

The time spent in the shelter within the microcosm differed significantly depending on predator and time of day (Figure 4.7, Kruskal Wallis: $\chi2 = 129.58$, $p < 0.001$), earwigs spent significantly more time in the shelter than anthocorids during the night and day (Pairwise Wilcox: $p< 0.001$). Earwigs spent the most time in the shelter during the day (Pairwise Wilcox: $p< 0.001$) compared to night-time. The temperature regime (Kruskal Wallis: $\chi2 = 0.107$, $p = 0.743$) and whether the predators were alone or in combination (Kruskal Wallis: $\chi2 = 0.0441$, $p = 0.834$) did not significantly impact the time spent within the shelter. Time spent in different locations for anthocorids was far more variable, on average anthocorids spent the majority of time at the bottom of the microcosm during the night and day (Figure 4.7), this was significantly higher than earwigs (Kruskal Wallis: $\chi2 = 55.55$, $p < 0.001$). Time spent at the bottom did not significantly differ depending on temperature (Kruskal Wallis: $\chi2 = 1.05$, $p = 0.306$), time of day (Kruskal Wallis: $\chi2 = 55.55$, $p = 1.00$) or whether the predator was alone or in combination (Kruskal Wallis: $\chi2 = 0.136$, $p = 0.712$). Both predators spent a very low proportion of time in the middle of the microcosm, earwigs spent significantly more time in the middle during the night compared to the day (Kruskal Wallis: $\chi2 = 10.31$, $p = 0.0067$). However, all other variables were non-significant. Time spent at the top of the microcosm significantly differed depending on predator and time of day (Figure 4.7, Kruskal Wallis: $\chi2 = 13.39$, $p = 0.004$), earwigs spent significantly more time at the top during the night than the day (Pairwise Wilcox: $p = 0.019$). Once again, temperature and predator combination did not significantly impact behaviour. Findings were similar for no food treatments (Fig S2), earwigs spent a large proportion of time in the shelter whilst anthocorids spent most time in the bottom of the microcosm. Temperature and whether the predator was alone or in combination with another predator did not significantly affect time spent in a position.

For the behavioural analysis a linear discriminant analysis was undertaken; groups were significantly different from each other based on the behavioural and positional predictor variables (Wilk's lambda = 0.0665, F = 24.52, df = 3,156, $p < 0.001$). With respect to model accuracy 78.13% of the observations within the test dataset were assigned to the correct group when using the predict function. However, despite the high model accuracy the 95% confidence intervals overlapped between groups (Figure 4.8); there was overlap between earwigs at night and earwigs during the day, as well as anthocorids at night and anthocorids during the day. However, confidence levels for earwigs and anthocorid groups did not show any overlap with each other, suggesting a distinct spatial and behavioural niche for each species. The first linear discriminant (LD1) explained a large proportion (91.60%) of all between-class variance, whilst the second and third linear discriminants explained a much lower proportion of variance (Table 4.2). The predictor variables with the highest linear discriminant scores for LD1 were strong positive scores for stationary, and feeding behaviour (Table 4.2).

4.5.4 Olfactometer assays

For olfactometer assays there was a significant preference by earwigs for arms containing *C. pyri* nymphs compared to the control treatment (Binomial exact test: p = 0.038, N = 40, Fig S3), 67.5% of the choices were for *C. pyri*. However, the preference for arms containing *C. pyri* nymphs compared to *A. nemoralis* was not quite significant (Binomial exact test: p = 0.081, N = 40), the preference between arms containing *A. nemoralis* compared to the control treatment was non-significant (Binomial exact test: p = 0.430, N = 40). There was no significant preference for left or right arms of the olfactometer (Binomial exact test: p = 0.235, N = 120). There was no significant difference in arm choice depending on temperature for *A. nemoralis* and control ($\chi 2$ = 0.1023, d.f.= 1, p = 0.749), *A. nemoralis* and *C. pyri* ($\chi 2$ = 0.440, d.f.= 1, p = 0.507) and *C. pyri* and control ($\chi 2$ = 0.114, d.f.= 1, p = 0.736). Temperature did not have a significant effect on time taken to choose an arm (Two-way ANOVA: $F_{(1,114)} = 0.182$, p = 0.671), neither did the odour source within the arm (Two-way ANOVA: $F_{(2,114)} = 0.546$, p = 0.581), or the interaction between temperature and odour source (Two-way ANOVA: $F_{(2,114)} = 1.561$, p = 0.214). On average, it took earwigs approximately 26.14 seconds ± 47.07 (SD) to make a decision at the low temperature treatment and 22.81 seconds ± 38.06 (SD) at the high temperature treatment.

4.6 Discussion

We found unidirectional intraguild predation (IGP) between earwigs and anthocorids, as *A. nemoralis* was eaten by *F. auricularia* during survival analyses. IGP was exhibited by adult male and female *F. auricularia* and stage 3 and 4 juveniles. This was anticipated as larger generalist natural enemies usually predate on those with smaller body sizes (Yano, 2006), and all earwig stages used were larger than adult *A. nemoralis*. However, it is probable that IGP is only likely to occur if both predators are in close proximity, when alternative food sources are unavailable. This is evident in behavioural analyses, as there were few interactions observed between *A. nemoralis* and *F. auricularia*, within microcosms. Both predators occupy different behavioural niches with little positional overlap, as highlighted in the LDA analysis. Earwigs were more active at night and spent most of the day stationary in the Wignest shelter, whilst anthocorids were far more active during the day spending a large proportion of time at the bottom of the microcosm. This is supported by the scientific literature that earwigs are nocturnal (Kölliker, 2007; Suckling et al., 2006), spending their free-foraging phase active during the night, whilst during the day they are inactive, hidden within shelters (Lame, 1974). However, it is important to note that these were laboratory-based experiments containing a single individual of each species and only one prey density (100 nymphs) within the microcosm. Thus, the interactions between predator and prey species are likely to be far more complex in field experiments, with the potential for intraspecific competition, increased search times, increased habitat complexity, and variable prey density.

Niche separation may explain the reason for IGP within the petri dish but lack of predator-predator interaction within the microcosm. Niche separation is when species have a distinct niche due to using the environment differently from others, this may be temporal, spatial or behavioural so that coexistence can occur (Hurlbert, 1978; Lear et al., 2021; Schirmer et al., 2020). Thus, in a simplified arena (Petri dish) *F. auricularia* may exhibit IGP due to niche overlap, however when predators occupy different levels within more complex plant canopy niche separation occurs. This supports the experiment by Barton & Schmitz (2009) where two spider species were spatially segregated within the vegetation canopy, however as *P. mira*, shifted downwards in the plant canopy in response to temperature resulting in spatial overlap IGP occurred. However, unlike Barton & Schmitz (2009), there is no evidence for spatial shifts with respect to temperature in our study.

Anthocorids and earwigs did respond differently under the two temperature regimes; both predator species consumed significantly more *C. pyri* prey under the RCP8.5 scenario compared to the current temperature scenario. One explanation for differences in feeding rate is due to altered metabolism (Yuan et al., 2009); metabolic rate increases exponentially with temperature up to a certain threshold, increasing demand for both energy and nutrients (Frances & McCauley, 2018; Schmitz &

Barton, 2014). Furthermore, other studies on *F. auricularia* (Quach, 2019) and *Anthocoris* spp. (Simonsen et al., 2009; Yanik & Unlu, 2011), also found that temperature significantly impacts prey consumption and functional response. In our study prey consumption of earwigs was higher than anthocorids, at the current temperature regime compared to anthocorids. The number of nymphs consumed by anthocorids are supported by Reeves et al., (2023) who found that on average *A. nemoralis* consumed 9.90 ± 2.99 *C. pyri* nymphs at 21 °C in functional response experiments in 24 h. However, it is more difficult to find studies confirming prey consumption by *F. auricularia*, as few involve *C. pyri* prey. Experiments by Quach (2019) found *F. auricularia* had a maximum prey consumption rate of 46.0 rosy apple aphid *Dysaphis plantaginea* per day, in similar temperatures to our regimes during the night. As *D. plantaginea* is of similar size to *C. pyri* this supports our findings. There was little evidence for interference competition between predators, as additive and combination treatments showed no significant difference in the number of *C. pyri* nymphs eaten, furthermore few behavioural interactions were observed between the two predators within the microcosm. A study on *F. auricularia* and *Episyrphus balteatus* predators consuming rosy apple aphid nymphs *D. plantaginea*, also found no evidence for interference competition; microcosms containing stage three *F. auricularia* and *E. balteatus* had an additive effect on *D. plantaginea* consumption rather than a negative one (Yanik & Unlu, 2011) . Furthermore, no evidence for IGP was observed between predators within these microcosms; as both *F. auricularia* and *E. balteatus* are nocturnal predators, it is likely due to spatial or behavioural niche separation rather than temporal.

Forficula auricularia did not show a significant positive response to anthocorids olfactometry assays. This suggests that earwigs do not show a preference for *A. nemoralis* based on their volatile kairomones. Earwigs do rely on olfactory cues and signals for prey location and detection of conspecifics (Naranjo-Guevara et al., 2017; Walker et al., 1993). *Forficula auricularia* relies on chemical signals in offspring care (Mas, 2011) and also releases an aggregation pheromone (Hehar et al., 2008; Walker et al., 1993). Whilst the earwig species *Doru luteipes* Scudder, has been shown to respond to HIPVs released by herbivorised maize plants (Naranjo-Guevara et al., 2017). Therefore, the fact that *F. auricularia* does have a preference for *C. pyri* nymphs over a control treatment but shows no preference for *A. nemoralis*, may suggest it does not actively seek out anthocorids as prey. For *C. pyri* nymphs, earwigs may potentially be responding to kairomones on the insect or in its honeydew. Adult pear psyllid females have been shown to produce higher levels of a pheromone (13-Me C27) (Guédot et al., 2009b; Yuan et al., 2021), which attracts *C. pyri* males (Ganassi et al., 2018b). However, there is currently little research on infochemicals produced by *C. pyri* nymphs or how predators respond to them.

Predators and parasitoids could also be attracted to VOCs within nymphal honeydew. A study on *Vespula vulgaris* wasps found that they responded to kairomones from sooty scale insect honeydew (*Ultracoelostoma*) (Brown et al., 2015). Wasps showed positive responses to baited traps containing 8 different compounds found within *Ultracoelostoma* honeydew compared to controls. Anthocorids show significant responses to HIPVs produced from psyllid infested trees (Drukker et al., 1995). Honeydew has the potential to act as a attractant and a defence mechanism for pear psyllids; natural enemies can be attracted to honeydew due to the VOCs emitted, however predators can be slowed down due to honeydew's viscosity, so they take longer to find prey items (Ge et al., 2020; Tougeron et al., 2021). Furthermore, the parasitoid *Trechnites insidiosus*, has been found to oviposit in honeydew drops, in the absence of pear psyllid hosts (Tougeron et al., 2021); this could reduce parasitoid search time for other psyllid nymphs. Thus, other natural enemies may be attracted to infested foliage or nymphal honeydew containing similar compounds, highlighting an area of further research.

These results have a significant implication on biological control in pear orchards, as both *F. auricularia* and *A. nemoralis* can be used in synchrony without concerns about reduced efficiency due to IGP or interference competition. Relying on more than one predator may be more efficient due to efficacy backup (Lawson et al., 2017); if one predator species is less prevalent then there are others that can act as a back-up for effective biological control, reducing variability of biological control (Snyder et al., 2008). This is supported by Stiling & Cornelissena (2005), in a meta-analysis comparing single species and multi-species releases of biological control agents. Results indicated that releasing multiple biocontrol agents was 27.2% more effective in decreasing pest abundance than single species releases. Natural enemy populations can be enhanced in a variety of ways, including the use of natural refugia; these can provide shelter and resources before migration into nearby orchard trees (Nagy et al., 2008; Scutareanu et al., 1999). Nagy et al. (2008), found high numbers of adult *A. nemoralis* on hawthorn, goat willow and stinging nettle surrounding orchards during spring. Artificial refuges can also be especially beneficial for earwig populations (Solomon et al., 1999), this includes corrugated cardboard in a bottle (Hansen et al., 2005; Solomon et al., 1999) or commercially available wooden Wignests (Russel-IPM, 2023; Shaw et al., 2021).

Anthocorids are also commercially available for mass release (Bioplanet, 2023; Koppert, 2023; Sigsgaard et al., 2006a), when wild populations are slow to build up in orchards. Sigsgaard et al. (2006), suggest between 1000–1500 adult *A. nemoralis* should be released hectare at 5–6 points within a pear orchard during the spring. *F. auricularia* is currently not available commercially for mass release, however Hanel et al. (2023) recommends sourcing earwigs from stone fruit crops (where they are a notable pest) and mass releasing them into pear orchards as a biocontrol agent.

The study found that mass release of 500 earwigs annually, significantly decrease pear psyllid populations. It should also be noted that earwigs are particularly sensitive to pesticide usage and soil tillage (Le Navenant et al., 2021; Moerkens et al., 2012), therefore avoiding tilling soil to >5 cm depth during the underground nesting period and not applying certain insecticides during the earwig's arboreal phase is advised (Orpet et al., 2019).

The response of both natural enemy species to temperature is also notable within our study. The fact that earwigs and anthocorids ate a significantly higher number of *C. pyri* nymphs, without changing other behaviours or position within the mesocosm under the high temperature regime, suggests they will still be effective pear psyllid predators under future climate scenarios. However, experiments were undertaken in a small microcosm, so there is unlikely to be significant differences in temperature depending on height. In a tree canopy this is very different; the microclimate can vary significantly depending on position within the canopy with differences in humidity, temperature and exposure to solar radiation (Pangga et al., 2011, 2013). Thus, if studies were undertaken in a plant canopy with height dependent temperature differences, there may be more distinct changes in predator position. Moreover, we did not look at pear psyllid position; the spatial distribution of pear psyllid varies within the canopy throughout the year (Horton, 1994; Stratopoulou & Kapatos, 1992a). Stratopoulou & Kapatos (1992a) monitored the spatial distribution of *C. pyri* (eggs and nymphs); during the spring psyllid density was higher in the upper canopy, however later in the year, numbers increased in the lower canopy. This could suggest areas exposed to more sunlight were actively chosen to meet temperature requirements for development earlier in the year, however later in the year it may be more optimal to oviposit lower down in the canopy to reduce desiccation of eggs. Therefore, predators may move to match the spatial distribution of their prey source, highlighting the need to observe predator behaviour in situ, alongside their prey.

4.7 Conclusion

To conclude, *F. auricularia* and *A. nemoralis* are likely to be suitable in combination for pear psyllid management, both are effective predators of *C. pyri* nymphs, with no evidence of interference competition and little IGP when a habitat is spatially complex. Furthermore, *F. auricularia* does not show a preference for *A. nemoralis* based on olfaction. However, there was a significant preference for psyllid prey in olfactometry assays, highlighting an area of further research. Temperature had a significant impact on prey consumption for both earwigs and anthocorids, with higher prey consumption at the RCP8.5 temperature regime compared to current climatic temperatures. Behaviour, position and activity were not significantly influenced by temperature treatment, although results were based on 2-minute observations, perhaps observations using EthoVision tracking software over longer time periods would be a more viable approach to analyse this behaviour. It is also worth noting that these studies were laboratory based, in small microcosms and petri dishes. Interactions in field-based studies are likely to be far more complex with the potential for intraspecific competition and increased search-times, especially at low prey density. We recommend that future field studies compare single and combined predator treatments in psyllid infested orchards, alongside DNA analysis of *F. auricularia* gut contents to determine whether IGP or interference competition is prevalent at a larger spatial scale.

4.8 Figures and Tables

Table 4.1: Average and median survival times (hrs) for anthocorids *A. nemoralis* depending on temperature and stage of earwig *F. auricularia* (control with no earwig present, stage 3, stage 4 juvenile, adult male and adult female). Standard error (SE) and upper and lower 95% confidence intervals are also provided.

Stage	**Temperature**	**Mean survival**	**SE**	**Median survival**	**LCL**	**UCL**
Control	**Current**	122.4	16.78	114	72	168
	RCP8.5	88.8	8.69	96	72	108
Stage 3	**Current**	99.6	9.90	108	72	120
	RCP8.5	54.0	9.33	48	24	84
Stage 4	**Current**	83.4	11.01	90	72	108
	RCP8.5	54.0	7.45	48	48	72
Adult F	**Current**	57.6	12.76	66	12	96
	RCP8.5	45.6	9.98	36	24	72
Adult M	**Current**	58.8	11.06	54	24	84
	RCP8.5	44.4	9.57	48	12	60

Table 4.2: Results from the linear discriminant analysis, displaying the first 3 linear discriminants, based on five behavioural variables and four positional variables measured for anthocorid (*A. nemoralis*) and earwig (*F. auricularia*) predators. Proportion of trace represents the proportion of between-class variance explained by discriminant functions, whilst the coefficients of linear discriminants is the linear combination of predictor variables used within the LDA decision rule.

Linear discriminant	**LD1**	**LD2**	**LD3**
Proportion of trace	0.916	0.0753	0.0087
Coefficients of linear discriminants			
Antennating	2.83	-16.35	-11.49
Cleaning	2.70	-18.54	-13.99

Feeding	7.17	-45.51	-33.03
Moving	6.30	-39.67	-28.81
Stationary	10.60	-68.29	-48.23
Shelter	2.96	-0.360	-0.450
Bottom	-0.240	0.0707	0.0358
Middle	-0.0863	-0.103	0.158
Top	-0.203	0.0736	-0.0821

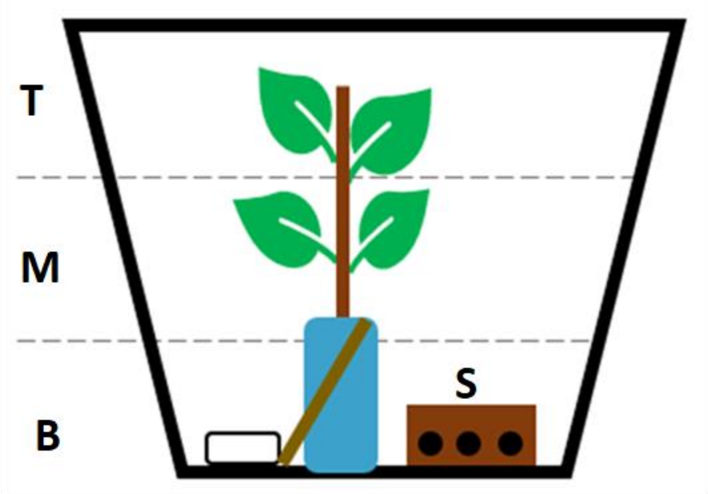


Figure 4.1: A ventilated microcosm (diameter 105 mm, height 75 mm) containing a wignest (brown box) and a pear tree shoot with four leaves collected from cv. Conference pear trees (*Pyrus communis*), kept moist in a plant holder (blue tube), with a small stick attached so that natural enemies can crawl to the top of the holder. The white dish contained distilled water. Four different areas were labelled within the microcosm; top (T), middle (M), bottom (B) and wignest shelter (S).

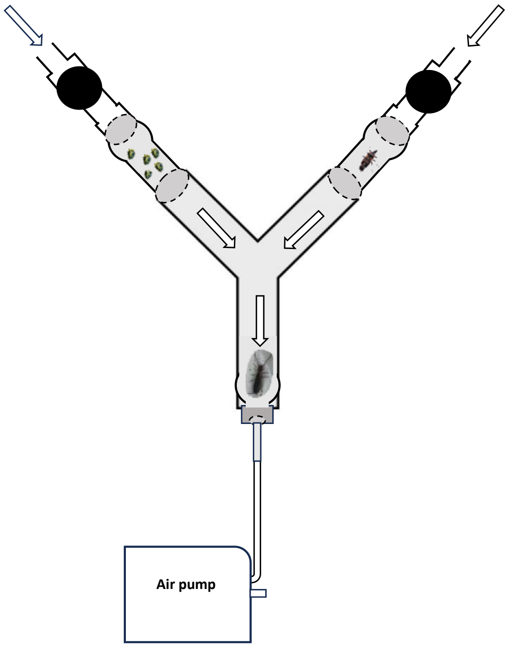


Figure 4.2: Experimental set-up for the Y-tube olfactometer assays, earwigs were placed at the start of the tube and given a binary choice between two prey types (*C. pyri* nymphs and adult *A. nemoralis*, *C. pyri* nymphs and nothing and adult *A. nemoralis* and nothing). Arrows represent the direction of air flow, black dots are activated carbon filters and dashed circles are mesh to stop prey escaping.

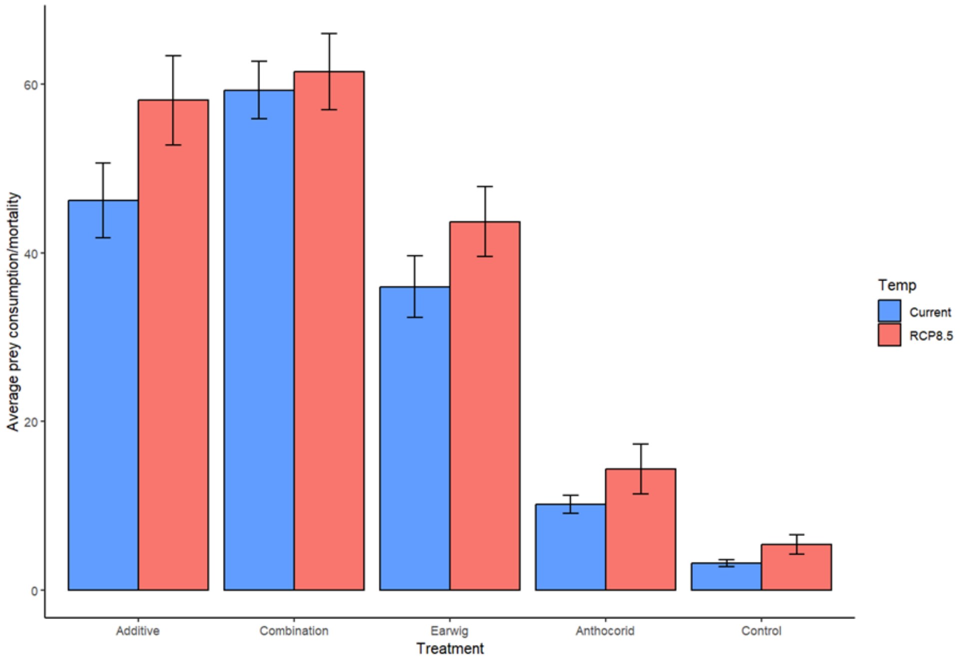


Figure 4.3: The mean (±SE) number of *C. pyri* nymphs consumed by natural enemies in Earwig, Anthocorid and Combination (an earwig and anthocorid in the same microcosm) treatments, as well as the average prey consumption of earwig + anthocorid in separate microcosms (Additive) and a control treatment representing average natural mortality. Error bars represent the ± SE for each treatment. The control treatment for each temperature was subtracted from each of the predator treatments to account for natural mortality, n = 80.

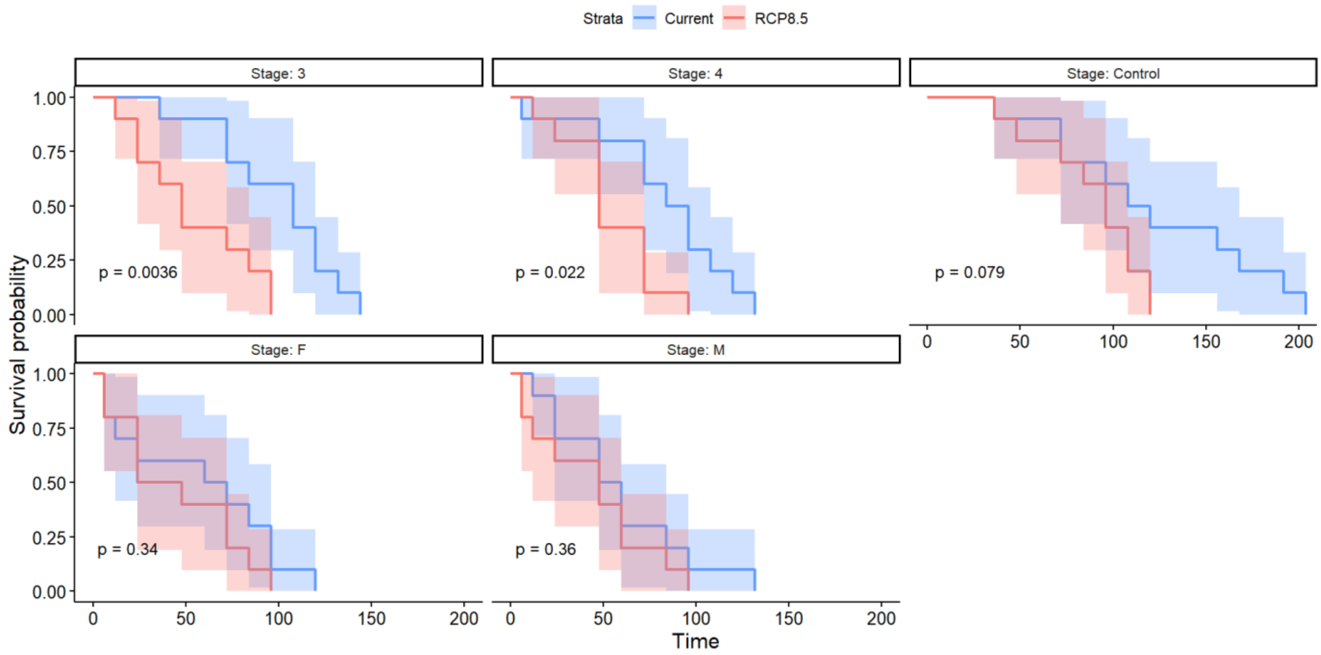


Figure 4.4: Probability of survival over time (hrs) depending on temperature (Current or RCP8.5) and stage of earwig *F. auricularia* (stage 3, stage 4, adult female, adult male and control with no earwig). Red (RCP8.5) and blue lines (Current) represent the mean proportion of surviving anthocorids *A. nemoralis*, with shaded areas representing the confidence intervals.

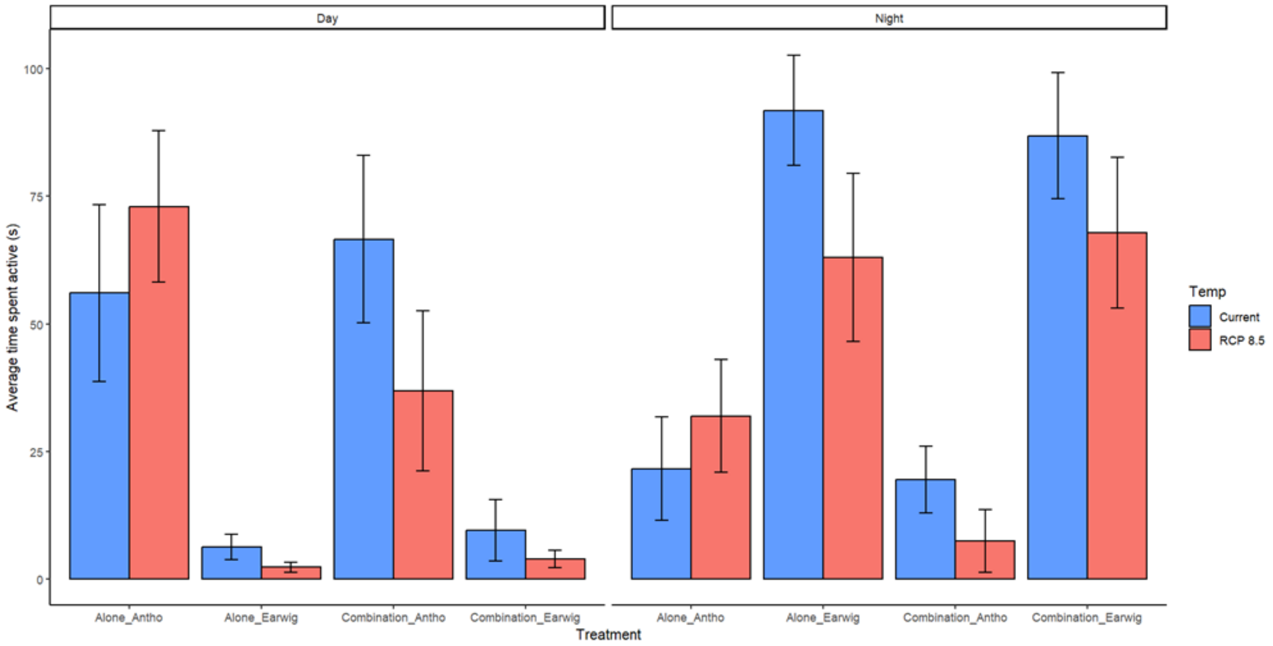


Figure 4.5: The mean activity levels (total time spent feeding, cleaning, interacting, moving and antennating in seconds) of anthocorid (*A. nermoralis*) and earwig (*F. auricularia*) predators in combination (both earwig and anthocorid in the same microcosm) and alone (a microcosm containing only one predator), for predators provided with *C. pyri* nymphs (food treatment), n= 80. Error bars represent the ± SE for each treatment.

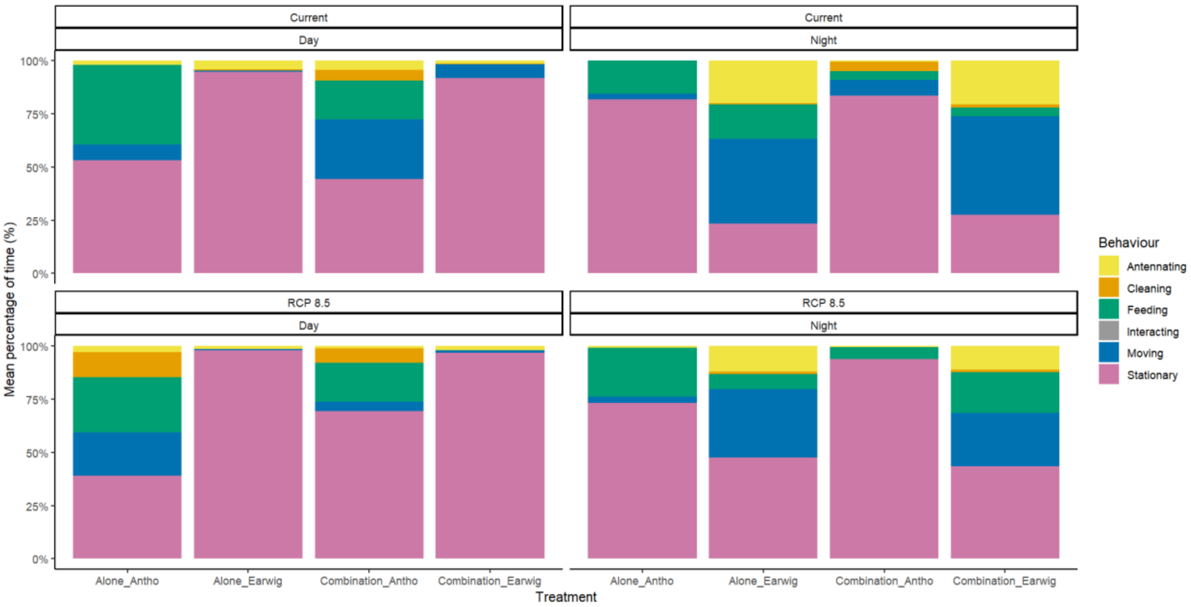


Figure 4.6: Mean percentage of time spent feeding, cleaning, interacting, moving and antennating for anthocorid (*A. nermoralis*) and earwig (*F. auricularia*) predators in combination (both earwig and anthocorid in the same microcosm) and alone (a microcosm containing only one predator), depending on temperature, for predators provided with *C. pyri* nymphs (food treatment), n = 80.

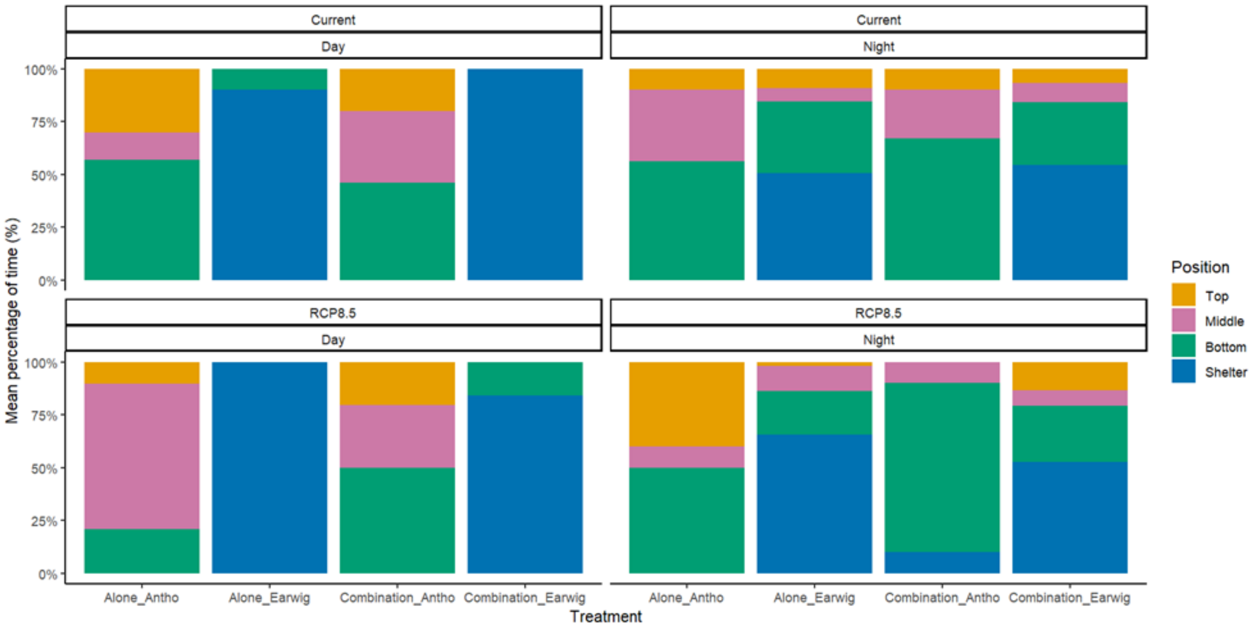


Figure 4.7: Mean percentage of time spent in different locations within the microcosm (top, middle, bottom and shelter) for anthocorid (*A. nermoralis*) and earwig (*F. auricularia*) predators in combination (both earwig and anthocorid in the same microcosm) and alone (a microcosm containing only one predator), depending on temperature, for predators provided with *C. pyri* nymphs (food treatment).

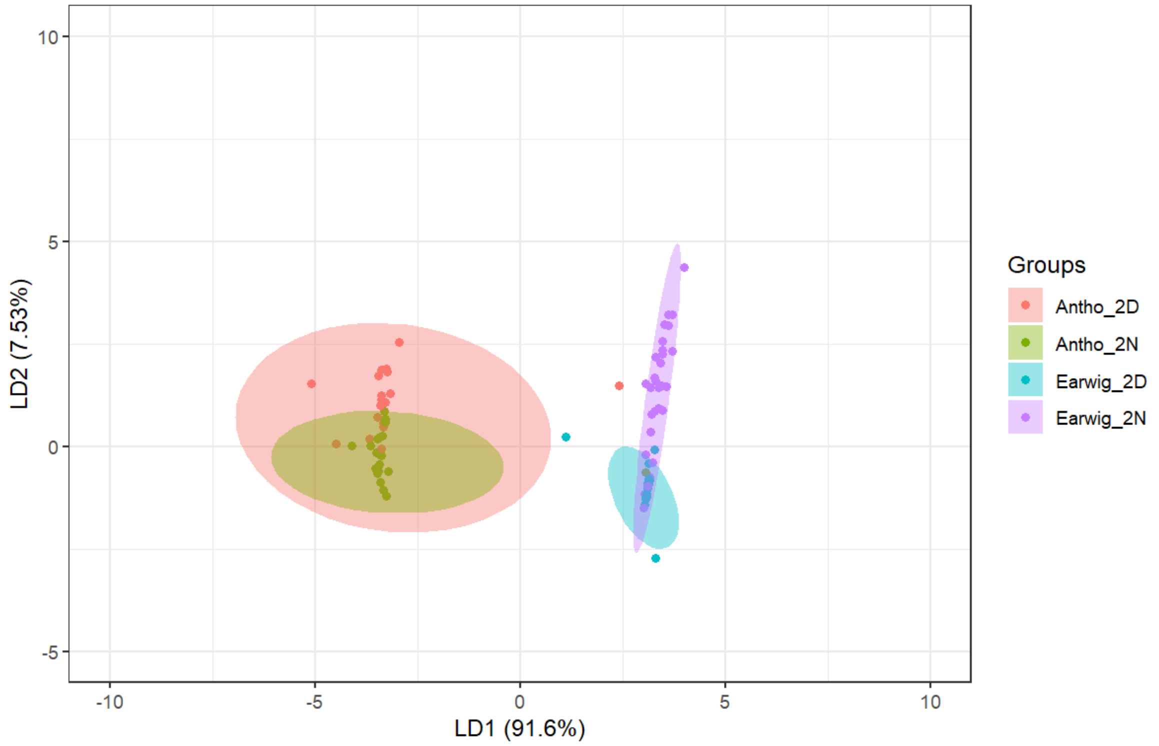


Figure 4.8: A linear discriminant analysis based on position and behaviour of predators; for anthocorids (*A. nemoralis*) during the day (Antho_2D), anthocorids at night (Antho_2N), earwigs (*F. auricularia*) during the day (Earwig_2D) and earwigs at night (Earwig_2N). Axes represent the first (LD1) and second (LD2) linear discriminants, percentages show the proportion of between-class variance that is explained by the discriminant functions. Ellipses represent 95% confidence levels.

5 Chapter 5: Exploring climate driven phenological mismatches in pears, pests and natural enemies – a multi-model approach.

This chapter is a version of the following paper, with minor corrections and changes to formatting and references to make the thesis more comprehensive:

Reeves, L. A., Belien T., Garratt, M. T., Senapathi, D., M. P., Fountain, (2024) Exploring climate driven phenological mismatches in pears, pests and natural enemies – a multi-model approach. J Pest Sci (under review).

Author contributions: LR, MG, MF and DS conceived and designed the study. TB provided R code for the pear psyllid phenology model and earwig degree day model. LR carried out data analyses and drafted the manuscript with all authors providing feedback on multiple drafts prior to submission.

5.1 Abstract

Pear psyllid (*Cacopsylla pyri*) is the dominant pest of UK pear orchards, with an estimated cost of £5 million per annum. Insecticide withdrawal has led many growers to depend more on natural enemies for pest management including earwigs. However, there is concern how phenological events may shift with future climate change, which may result in phenological mismatches between pear psylla emergence, natural enemy abundance and pear flowering time. This study evaluates three models for predicting timing of phenological events within UK orchards, these models include the *C. pyri* phenology model, the earwig degree day model and the Phenflex model (to predict flowering time). Phenological events predicted by models included: first, full and last flowering time for *Pyrus communis*; peak psyllid abundance date for first generation (G1) *C. pyri* nymphs and second-generation (G2) eggs, nymphs and adults; and peak abundance date for stage 4 *Forficula auricularia* and adults. Findings indicated that the timing of several phenological events were advancing for all trophic levels, becoming significantly earlier over the past few decades. Furthermore, predictions indicated that timings events would continue to advance under the RCP8.5 scenario. However, not all phenological events advanced at the same rate; the date of peak *C. pyri* G1 nymph abundance advanced at a faster rate than full flowering time, which could potentially result in a phenological mismatch by 2071 between the two trophic levels. On the other hand, *C. pyri* and the natural enemy *F. auricularia*, showed phenological synchrony, with peak abundance date advancing at a similar rate under the RCP8.5 scenario, which could be beneficial for biological control. This study aimed to determine shifts in timing of phenological events for three trophic levels

within an agroecosystem, under current and future climate scenarios, and predict phenological mismatches or synchronies between trophic levels.

5.2 Introduction

There are over 4,000 described species of psyllid globally (Mauck et al., 2024) and 24 known species of psyllid identified from pear (*Pyrus* spp.) (Civolani et al., 2023). The dominant pear psyllid species in the UK is currently *Cacopsylla pyri* (Nagy et al., 2008; Reeves et al., 2024). These phloem feeders can cause significant damage to orchards: nymphs produce honeydew; a sugary secretion that encourages the growth of black sooty mould on pear fruit and leaves (Daniel et al., 2005), adults are a vector of the pathogen ‘pear decline’ (*Candidatus* Phytoplasma pyri); which can reduce shoot and fruit growth and can lead to tree death (Carraro et al., 2001; Kucerová et al., 2007; Süle et al., 2007). The pear industry is of economic importance with 17.9 thousand tonnes of pears produced in the UK (Defra, 2023) and over 26.3 million tonnes produced globally in 2022 (FAOSTAT, 2022), thus changes to the phenology or control of *C. pyri* could have a significant economic impact.

Researchers have demonstrated that pear psyllids display resistance to a range of commonly available pesticides (Erler, 2004a; Harries & Burts, 1965; Sek Kocourek & Stará, 2006), furthermore three insecticides often used in pear psyllid management have recently been withdrawn from UK use (Reeves et al., 2024). Thus, integrated pest management (IPM) has become a priority for managing pear psylla (Reeves et al., 2023; Shaw et al., 2021); aiming at maintaining healthy crop growth whilst minimising disruption to agroecosystems, with focus on enhancing biological control (Moorthy & Kumar, 2004). There are a wide range of pear psyllid natural enemies (Civolani et al., 2023; Horton, 2024). The anthocorid *Anthocoris nemoralis* (Fabricius) is a well-documented biological control agent of *C. pyri* (Nagy et al., 2008; Sigsgaard, 2010). *Anthocoris nemoralis* populations usually peak during July-August, helping to control *C. pyri* populations (Fields & Beirne, 1973; Scutareanu et al., 1999). It has become common practice for growers to mass release *A. nemoralis* into pear orchards, if natural populations are slow to build-up (Reeves et al., 2024). In addition, the European earwig *Forficula auricularia* (Linnaeus) is a key natural enemy of pear psylla; stage four earwig nymphs are arboreal, appearing in pear trees in late spring, with numbers peaking in June, whilst adult populations peak in mid-July (Gobin et al., 2008; Moerkens et al., 2011). Arboreal *F. auricularia* nymphs can consume up to 1000 psylla eggs a day, highlighting their importance as biological control agents (Lenfant et al., 1994). Although *F. auricularia* is not commonly reared for mass release, enhancing earwig populations by providing refugia is recommended in top-fruit orchards (Shaw et al., 2021). Other natural enemies of *C. pyri* include; ladybird adults and larvae (Coccinellidae) (Fountain et al., 2013; Prodanović et al., 2010), lacewing larvae (Neuroptera) (DuPont & John Strohm, 2020; DuPont et al., 2023), spiders (Araneae) (Petrakova et al., 2016) other anthocorid species (Sigsgaard, 2010; Vrancken et al., 2014) and a few parasitoid species (Prodanović et al., 2010; Tougeron et al., 2021).

Cacopsylla pyri overwinter as adults in tree bark crevices (Næss, 2016), during which reproductive diapause occurs (Lyoussoufi et al., 1994; Schaub et al., 2005). By mid-late winter, ovaries are fully developed (Schaub et al. 2005) and egg laying starts in late February (Næss, 2016; Oz & Erler, 2021). Pear psyllid eggs hatch in early spring, often coinciding with bud opening, there are five nymphal stages, each ending in a moult (Civolani et al., 2023). The first peak in the pear psyllid population is often seen around April–May, followed by a second-generation in early summer (Reeves et al., 2024). Subsequent generations overlap throughout the summer and early autumn (Civolani et al., 2023), with an average of 3–5 generations per year (Süle et al., 2007), although this can be temperature dependant (Kapatos & Stratopoulou, 1999) and will likely affect the impact it has as a pest.

Climate is predicted to change significantly over the next 80 years globally and UK Climate Projections (UKCP18) predict hotter, drier summers and warmer, wetter winters (Lowe et al., 2018a; Murphy et al., 2018). This will likely affect psyllid development and its interactions with natural enemies. By 2070, summer temperatures could increase as much as 5.1 °C under the RCP8.5 high emissions scenario, whilst becoming up to 45% drier (MetOffice, 2022). Representative Concentration Pathways (RCPs) are the concentrations of greenhouse gases that will result in total radiative forcing increasing by a certain threshold by 2100, compared to pre-industrial levels. Total radiative forcing is the difference between incoming and outgoing radiation within the atmosphere (MetOffice, 2018). These scenarios are often used to model how future climate will change with respect to different emissions scenarios; with RCP2.6 (low emissions scenarios) representing a significant reduction in greenhouse gas emissions (Van Vuuren, Stehfest, et al., 2011) and RCP8.5 (high emissions scenario) is a ‘business-as-usual’ scenario where greenhouse gas emissions increase unchecked (MetOffice, 2018).

There is growing concern that climate change could alter trophic interactions and phenological events within agroecosystems (Harrington et al., 1999; Reeves et al., 2024; Renner & Zohner, 2018; Wyver et al., 2023). Phenological mismatches are a particular concern for agricultural ecosystems; where shifts in other trophic levels do not match the corresponding shift for pest species (Damien & Tougeron, 2019). Phenological synchrony is important within this agroecosystem; whether peak natural enemy abundance corresponds to peak pear psyllid abundance is central to pest management (Reeves et al., 2024). Pear psyllid nymphs are reliant on their emergence corresponding to budburst, as flower buds provide shelter for nymphs from adverse weather conditions, agrochemical sprays and natural enemies earlier in the year (Derksen et al., 2007; Reeves et al., 2022). All three trophic levels (pear trees, pear psyllid and their natural enemies) are likely to be influenced by climate change. Pear flowering phenology is heavily influenced by chilling time (the amount of time spent below a certain temperature) and forcing time (the time spent above a certain temperature post-chilling) (Cesaraccio et al., 2004; Drepper et al., 2020). Thus, if higher temperatures are experienced during the forcing period but chilling requirements are still met, earlier flowering is likely. In addition, pear psyllids have temperature dependent development (McMullen & Jong, 1977; Schaub et al., 2005); the *C. pyri* phenology model by Schaub et al. (2005), indicates that development rates of pear psyllid nymphs and eggs are linearly dependent on temperature, up to a certain threshold. Higher temperatures are likely to advance pest emergence and could potentially impact voltinism (number of generations per year) (Karuppaiah & Sujayanad, 2012). Development rates of *Forficula auricularia* have a non-linear response to temperature, in the form of a sigmoidal curve (Moerkens et al., 2011). Therefore, comparing if pear psyllids and their natural enemies respond to temperature at the same rate is important to understand potential phenological mismatches and future pest control scenarios.

The aim of this study was to: 1) Combine the psyllid phenology model developed by Schaub et al., (2005), the Earwig phenological day degree model Moerkens et al., (2011) and the Phenoflex flowering time model Luedeling (2023), applying the models to UK data to assess if they are relevant for UK predictions 2) Predict how all three trophic levels (pear, pest and natural enemy) could respond under future temperature scenarios and 3) Observe whether all three trophic levels are advancing at the same rate or if phenological mismatches are likely. This study provides a multi trophic approach that can be easily applied to other agroecosystems, highlighting its importance within the scientific literature.

5.3 Materials and methods:

5.3.1 Long term pear sucker and natural enemy monitoring data

Long term pear psyllid and natural enemy data was collected by agronomists from 18 different sites in Kent, UK between 2011-2021. Pear psyllid abundance was calculated by sampling 30 trees across each orchard using beat tray sampling and collecting leaf material, every week from mid-March to August each year. Adult pear psyllid and natural enemy species: earwigs, ladybirds and anthocorids (nymphs and adults), were monitored using beat tray sampling, a white plastic tray (390 mm by 235 mm) was held underneath a randomly selected tree branch on each tree and total numbers were recorded. For monitoring pear sucker nymphs and eggs, six rosette and six young shoot leaves were randomly selected, these were examined using a hand lens, to count the total number of *C. pyri* nymphs and eggs. When leaves were not present, a bud with 6cm of the branch underneath was examined. Samples were collected from cv. Conference pear (*Pyrus communis*) orchards.

5.3.2 Pear flowering data

Historical data on pear flowering times was collated from 1960-2021 at NIAB (formerly East Malling Research, 51.2885° N, 0.4383° E) in Kent, UK (Reeves et al., 2022).
Phenological data on pear flowering were collected for the following metrics:

- First (first flower opens on a tree or flower's anthers are visible),
- Full (when 50% of flowers have opened on the tree), and
- Last (90% petal fall)

Phenological data was analysed for cv. Conference pear trees (*P. communis*), as this cultivar was present in all orchards used for pear sucker monitoring and based on the UK horticulture statistics, Conference pear (*P. communis* cv. Conference) is the most common pear cultivar in the UK, accounting for 84.01% of total planted area of pears (Defra, 2023). This data was used to calibrate and validate the Phenoflex model.

5.3.3 Temperature data and future scenarios

Hourly air temperature data was extracted from weather stations across Kent from the CEDA data archive (CEDA, 2023). The closest weather station was matched to each orchard for pear psyllid and natural enemy monitoring data and data was extracted from 2011-2021. This also occurred for weather data used to calibrate and validate the Phenoflex model, data was extracted from the East Malling weather station from 1959-2021. For temperature records that were unavailable, if gaps were short (less than 3 days) then hourly temperatures were generated using the interpolate_gaps function in chillR (Luedeling, 2023), which averages temperature before and after the gap. For longer time periods hourly temperatures were used from the next closest weather station in Kent. If hourly temperatures were unavailable, then hourly temperatures were generated from daily maximum and minimum mean temperatures using the stack_hourly_temps function in the chillR package (Luedeling, 2023).
For predicting temperature data for Kent; maximum and minimum daily air temperature (°C) above 1.5 m was generated from the UKCP18 (UK Climate Projections) for a 60 km by 60 km grid cell surrounding Kent (UKCP, 2021b). Data was generated for both RCP2.6 and RCP8.5 emissions scenarios from 1960-2099, based on the full 15-member Hadley Centre's Perturbed Physics

ensemble (PPE-15). Once again hourly temperatures were generated from daily maximum and minimum mean temperatures using the stack_hourly_temps function in the chillR package (Luedeling, 2023). The RCP2.6 and RCP8.5 scenarios were chosen as Schwalm et al. (2020) speculates that the business as usual (RCP8.5) scenario is the optimal scenario at tracking CO_2 emissions until 2050, and even by 2100 RCP8.5 is still feasible, whilst the RCP2.6 scenario contrasts most strongly with this, allowing predictions for a scenario where emissions are strongly reduced. Furthermore, the UKCP18 provides daily data for both scenarios, in order to run phenological models under future climate scenarios.

5.4 Data Analyses

5.4.1 Flowering phenology

The chillR package was used to predict current and future flowering phenology for first, full and last flowering times for cv. Conference pear (Luedeling, 2023), using the Phenoflex model (Luedeling, 2024; Luedeling et al., 2021). This model looks at chilling (the minimum period of exposure to cold temperatures required for a tree to blossom) and forcing/heating (the minimum period of exposure to warmer temperature required for a tree to blossom) periods in order to predict fruit tree blossom date. The Phenolflex model uses the Dynamic model to calculate chill requirements (Fishman et al., 1987a, 1987b) and the Growing Degree Hours (GDH) model for forcing/heating requirements (Anderson et al., 1985), and requires hourly air temperature for these calculations. For model calibration and validation, the data was divided into two subsets, with approximately 75% of the data in the model calibration subset (46 years) and approximately 25% of the data in the model validation subset (16 years), as demonstrated in Wyver et al. (2024). A generalised simulated annealing (GenSA) algorithm was then used to optimise the parameters within the Phenoflex model and minimise the residual sum of squares (RSS) (Tsallis & Stariolo, 1996; Xiang et al., 2013). Up to 1,000 iterations of this algorithm were run, stopping when there was no additional improvement in model fit after 250 consecutive iterations, as demonstrated in Wyver et al. (2024). Initial parameters were based on those established in other PhenoFlex studies (Fernandez et al., 2022; Wyver et al., 2024b). To evaluate the model performance, the Root Mean Square Error (RMSE) and Ratio of Performance to InterQuartile distance (RPIQ) were both calculated. The parameter optimisation process was run multiple times, with staring parameters changed to that of the previous optimisation. This process was stopped after there was no improvement found to RMSE or RPIQ. Standard errors of optimum parameters were calculated using bootstrapping, using 10 iterations, as described in multiple phenology studies (Fernandez et al., 2022; Luedeling et al., 2021; Wyver et al., 2024b).

5.4.2 Pear psyllid phenology

Pear psyllid phenology was predicted using the model by Schaub et al, (2005) and R code generated for this model by Belien et al. (2017). This model relies on a time distributed delay and uses hourly temperatures with a microclimate correction to predict egg, nymph and adult percentage abundance for the first two generations of pear psyllid, with a start date of 01 Jan. The termination of diapause in psyllid females was based on a Weibull distribution and was dependent on the time spent above the thermal threshold (3.5 °C) (Schaub et al., 2005). For females where diapause had been terminated, oviposition began, summerform females had a preoviposition period of 10 days. Oviposition was age specific and the cumulative oviposition density was 1. Both egg and nymph developmental rates and adult ageing was linearly dependent on temperature based on slopes and thresholds stated within Schaub et al. (2005). A microclimate correction was also used, as demonstrated in Schaub et al. (2005). For model calibration, predicted and observed peak egg, nymph and adult pear psyllid abundance (1st and 2nd generation) were compared using a Kruskal Wallis test. If differences between observed and predicted were significant then abundances were shifted based on average peak difference. Future temperatures predicted under RCP2.6 and RCP8.5 scenarios were then used to predict psyllid percentage abundance from 1960-2080 based on calibrated models.

5.4.3 Earwig phenology

Earwig phenology was predicted using the degree day model developed by Moerkens et al. (2011), which was developed into a management tool to predict peak dates of *F. auricularia* abundance (Belien et al., 2012a; Belien et al., 2013). The degree day model predicts the first and peak appearance dates of *F. auricularia* life stages and variation in development time of earwig life stages in trees (Moerkens et al., 2011), with a start date of 01 Jan. Degree days were summed between the minimum and maximum developmental temperature threshold, until the minimum number of day degrees was reached for hatching or moulting at each life stage. For this model day degrees between T_0 and T_{max} were calculated using a sine wave method. Variation in development time was modelled using a using a two-parameter Weibull function, due to environmental and individual variation in moulting and hatching within the population. A daytime microclimate correction is not present within this model as *F. auricularia* are nocturnal foragers (Kölliker, 2007; Suckling et al., 2006), often found sheltering in dark crevices during the daytime (Lame, 1974), thus are not generally impacted by tree microclimate during the day (Moerkens et al., 2011).

For model calibration, predicted and observed peak stage 4 nymph abundance dates and peak adult abundance dates, for single brood populations were compared using a Kruskal Wallis test. Only these two stages were compared, as these are both arboreal stages that agronomists were likely to observe in orchard trees and hence predate pear psylla (Gobin et al., 2008; Moerkens et al., 2011). If differences between observed and predicted were significant then abundances were shifted based on average peak difference, based on Kruskal Wallis tests between predicted and observed values. Observed data spanned from 2011-2021. Future temperatures predicted under RCP2.6 and RCP8.5 scenarios were then used to predict earwig percentage abundance from 1960-2080 based on calibrated models.

5.4.4 Future climate scenarios and phenological mismatches

This study tested for shifts in timing of phenological events, including: flowering time (first, full and last), pear psyllid phenology (peak egg and nymph and adult abundance) and earwig phenology (peak stage 4 and adult emergence) depending on year (1960-2080). First, years were split into 3 different categories Historical (1960-1982), Current (1983-2021) and Future (2022-2080, for RCP2.6 and RCP8.5 emissions scenarios). Timing of phenological events were then predicted using maximum and minimum temperatures generated from UKCP18 (UK Climate Projections) for a 60 km by 60 km grid cell surrounding Kent (UKCP, 2021b), using the three models. The change in timing of phenological event depending on year was tested using Generalised Additive Models (GAMs), however if the GAM had an edf < 2 and did not show a non-linear relationship then a GLM was fitted instead, as used in Wyver et al. (2023). To identify phenological mismatches the slopes of two phenological events were compared based on GAMs or GLMs generated. Phenological comparisons included: 1) first *C. pyri* nymph emergence and first flowering time, 2) peak first-generation (G1) *C. pyri* nymph abundance and full flowering time, 3) peak second generation (G2) *C.pyri* nymph abundance and 4th instar *F. auricularia* peak abundance. These phenological mismatches were chosen as they are all relevant interactions between trophic levels within the pear agroecosystem. For example, G1 *C. pyri* nymphs shelter in flower buds, whilst 4th instar *F. auricularia* nymphs are a key predator of *C. pyri* nymphs during the summer, thus these trophic levels are likely to interact with each other at phenological stages chosen for the models. The phenological mismatches between each of these events were also calculated; this was calculated by subtracting the date (Julian days) of one phenological event from another, as demonstrated in Wyver et al. (2023). A GAM or GLM of the phenological mismatch depending on year was then plotted.

5.5 Results

5.5.1 Flowering phenology calibration and validation

From parameters optimised by the GenSA algorithm, the average chilling requirement was 35.97 ± 0.18 chill units for first flowering time, 47.69 ± 1.48 for full flowering and 41.56 ± 0.27 for last flowering. Whilst the average forcing/heating requirement was 237.67 ± 0.56 heat units for first flowering, 287.11 ± 4.57 for full flowering and 227.88 ± 0.58 for last flowering, other model parameters can be found in Table 5.1. Model quality was assessed by RMSE and RPIQ for calibration and validation datasets (Figure 5.1). For the calibration dataset the RMSE was 4.67 days for first flowering, 4.46 days for full flowering and 5.33 days for last flowering, with an RPIQ of 3.43 days (first), 2.75 days (full) and 2.44 days (last). For the validation dataset the RSME was 7.45 days (first), 3.04 days (full) and 4.29 days (last), whilst the RPIQ was 1.21 (first), 5.26 days (full) and 3.96 days (last). On average the observed flowering time was 12th Apr ± 10.91 (first), 18th Apr ± 10.39 (full) and 30th Apr ± 9.75 (last), whilst the predicted flowering time was 12th Apr ± 11.96 (first), 19th Apr ± 11.72 (full) and 29th Apr ± 10.44 (last, Table 5.2). Kruskal Wallis tests showed non-significant differences between predicted and observed values for first ($\chi^2 = 0.0150$, df = 1, p = 0.903), full ($\chi^2 = 0.0637$, df = 1, p = 0.801) and last ($\chi^2 = 0.0529$, df = 1, p = 0.818) flowering phenology. Chill tended to accumulate between October and January, whilst heat accumulation was between January and April, before the yc and zc thresholds were reached (Figure 5.2). For temperature response curves optimal chill accumulation was between 1 °C and 7.5 °C (Figure S1), with no chill accumulation occurring above 11 °C, whilst optimal heat accumulation was between 26 °C and 28 °C, with no heat accumulation occurring above 37 °C.

5.5.2 Pear psyllid model validation

The peak abundance of G1 psylla nymphs was predicted to be far earlier than those observed within orchards (Table 5.2, Figure 5.3A); on average predicted peak date was 14.36 ± 17.86 (SD) days earlier than observed values in orchards. A Kruskal Wallis test showed a significant difference between observed and expected values ($\chi^2 = 33.84$, df = 1, $p < 0.001$), however the difference between individual orchards was non-significant ($\chi^2 = 15.70$, df = 17, p = 0.546). The model was therefore adjusted for G1 egg and nymph abundances, shifting them both 14.36 days later. The peak abundance of psylla eggs was not compared, as multiple orchards started monitoring after the abundance of eggs had peaked, thus we shifted the egg abundance by the same as the G1 nymph abundance.

The peak abundance of summerform adults was much closer for predicted and observed values (Table 5.2, Figure 5.3B). On average predicted peak date was 2.34 ± 9.74 (SD) days later than observed values in orchards but this was not significant (Kruskal Wallis: χ^2 = 1.903, df = 1, p = 0.168). The difference between individual orchards was also non-significant (Kruskal Wallis: χ^2 = 13.75, df = 17, p = 0.685). The peak abundance of generation 2 eggs was also closer for predicted and observed values (Table 5.2, Figure 5.3C). On average predicted peak date was 0.63 ± 17.11 (SD) days earlier than observed values in orchards which was not significant (Kruskal Wallis: χ^2 = 0.121, df = 1, p = 0.728), the difference between individual orchards was also non-significant (Kruskal Wallis: χ^2 = 14.64, df = 17, p = 0.745). Finally, the peak abundance of generation 2 nymphs was close for predicted and observed values (Table 5.2, Figure 5.3D). On average predicted peak date was 0.42 ± 12.74 (SD) days later than observed values in orchards (Kruskal Wallis: χ^2 = 0.924, df = 1, p = 0.336), the difference between orchards was also non-significant (χ^2 = 20.86, df = 17, p = 0.233). Thus, we did not shift the summerform adult, G2 egg or G2 nymph values within the model.

5.5.3 Earwig model validation

The predicted and observed dates of peak *F. auricularia* stage 4 nymph abundance did not significantly differ from each other (Kruskal Wallis: χ^2 = 1.15, df = 1, p = 0.284, Table 5.2, Figure 5.3E). On average the predicted date for peak 4th instar emergence was the 21 Jun ± 7.39 (SD) whilst the observed date was the 18 Jun ± 17.09 (SD). This was also true for peak adult emergence (Table 5.2, Figure 5.3F); predicted and observed values did not differ significantly from each other (Kruskal Wallis: χ^2 = 2.06, df = 1, p = 0.151). On average the predicted date for peak adult emergence was 17 Aug ± 7.33 (SD), whilst the average observed value was 15 Aug ± 16.43 (SD). Observed peak dates did not significantly differ from each other depending on orchard, for both 4th instar (Kruskal Wallis: χ^2 = 15.87, df = 17, p = 0.666) and adult *F. auricularia* (Kruskal Wallis: χ^2 = 8.67, df = 17, p = 0.926). Only 4th instar and adult peaks were examined, as these are arboreal stages likely to be present within orchard trees (Gobin et al., 2008; Moerkens et al., 2011). Due to the non-significant differences between predicted and observed values, the model was not shifted for either stage of *F. auricularia*.

5.5.4 Climate predictions and phenological shifts

All flowering stages (first, full and last) were predicted to show significant advancement in flowering time depending on year, becoming significantly earlier over the current time period (1983-2021, Table 5.3). However, this advancement was not significant for the historical time period (1960-1982), suggesting the advancement began in the 1980s. Based on the Phenoflex model average first flowering time was predicted to advance from the 04 May ± 4.66 SD (1960-1983) to 19 Apr ± 4.63 SD (2011-2021), becoming 15 days earlier. Whilst full flowering time shifted from 13 May ± 3.99 SD (1960-1983) to 29 Apr ± 4.05 SD (2011-2021), a 14-day advancement. This phenological shift was predicted to continue under future emissions scenarios, a GLM predicted earlier first flowering time depending on year (2022-2080, Table 5.4), at a rate of -0.177 days per year under the RCP8.5 (high) emissions scenario. On average first flowering date was predicted to be 07 Apr ± 2.69 SD between 2060-2080, under RCP8.5. However, this phenological shift was not significant for the RCP2.6 (low) emissions scenario (Table 5.4). For full flowering time, flowering phenology advanced significantly under both RCP2.6 and RCP8.5 emissions scenarios, at a rate of -0.053 days and -0.197 days per year, with an average full flowering date predicted as 20 Apr ± 2.21 SD (RCP2.6) and 16 Apr ± 2.31 SD (RCP8.5).

Cacopsylla pyri phenology peak G1 nymph abundance was predicted to significantly change depending on year, under the current time period (1983-2021). Once again, the change depending on year was not significant for the historical time period (1960-1982). On average peak G1 nymph abundance date was 25 May ± 8.37 SD (1960-1982) and 11 May ± 14.52 (2011-2021). This phenological shift was predicted to continue under future emissions scenarios, a GLM predicted earlier G1 peak *C. pyri* nymph abundance depending on year (2022-2080, Table 5.3), at a rate of -0.413 days per year under the RCP8.5 (high) emissions scenario. On average G1 peak nymph abundance date was predicted to be 16 Apr ± 11.37 SD between 2060-2080, under RCP8.5. However, this phenological shift was not significant for the RCP2.6 (low) emissions scenario (Table 5.3, Figure 5.4). For first G1 peak *C. pyri* nymph emergence, phenology did not significantly change depending on year for historic, current or RCP2.6 emissions scenarios. Only under the RCP8.5 scenario did emergence times become significantly earlier (Figure S4.2), at a rate of -0.125 days per year. For G2 *C. pyri* nymphs, peak abundance also differed significantly depending on year under the current time period, shifting at rate of -0.403 days per year (Figure 5.6). On average peak abundance date was 11 Jul ± 4.47 SD for the historical time period (1960-1982) and 26 Jun ± 11.10 SD for 2011-2021. Peak abundance for G2 nymphs was predicted to continue to shift under the RCP8.5 emissions scenario (2022-2080) at a rate of -0.315 days per year, however this shift was non-significant for the RCP2.6 scenario (Table 5.3).

Forficula auricularia stage 4 nymph peak abundance date was predicted to change significantly depending on year, under the current time period (1983-2021), at a rate of -0.375 days per year (Table 5.3). On average peak *F. auricularia* nymph abundance date was 08 Jul ± 4.59 SD (1960-1982) and 22 Jun ± 10.11 SD (2011-2021). Peak abundance for *F. auricularia* nymphs was predicted to continue to shift under the RCP8.5 emissions scenario (2022-2080) at a rate of -0.288 days per year, however this shift was non-significant for the RCP2.6 scenario (Table 5.3). This was also similar for the peak abundance date of *F. auricularia* adults, under the current time period peak abundance date advanced significantly, at a rate of -0.508 days per year (Table 5.3). Peak abundance date shifted from an average of 06 Sep ± 8.97 (1960-1982) to 12 Aug ± 10.56 (2011-2021). Peak abundance for *F. auricularia* adults was predicted to continue to shift under the RCP8.5 emissions scenario (2022-2080) at a rate of -0.224 days per year, however this shift was non-significant for the RCP2.6 scenario (Table 5.3).

5.5.5 Phenological differences and mismatches

The phenological difference between full flowering time and G1 peak *C. pyri* nymph abundance date, was not significant depending on year for historical, current or RCP2.6 scenarios (Table 5.5). However, the phenological difference did significantly change at a rate of 0.216 days per year under the RCP8.5 scenario. Shifting from an average difference of -11.74 ± 13.01 SD days (2011-2021), to an average difference of 0.349 ± 12.40 SD days between the two trophic levels. The average advancement in phenology for *C.pyri* G1 peak nymph abundance is predicted to shift at a faster rate (-0.413) compared to full flowering time (-0.197) under RCP8.5. This could potentially lead to a phenological mismatch, where peak nymph abundance occurs before full flowering time after 2071 (Figure 5.4). For all other phenological events (first flowering and G1 *C. pyri* first nymph emergence, G2 *C. pyri* peak egg emergence and *F. auricularia* peak stage 4 nymph abundance and G2 *C. pyri* peak nymph emergence and *F. auricularia* peak stage 4 nymph abundance), no significant relationship was found between the phenological difference and year, for all other pairs of trophic levels (Table 5.5). The rate of change for G2 *C. pyri* peak nymph emergence and *F. auricularia* peak stage 4 nymph abundance dates was very similar (Figure 5.6), under current (-0.403 and -0.375) and RCP8.5 (-0.315 and -0.288) scenarios. Furthermore, there was a large amount of overlap between *C. pyri* and *F. auricularia* nymph abundance peaks for all scenarios (Figure 5.8), highlighting their phenological synchrony.

5.6 Discussion

5.6.1 Phenological shifts over time

The three aims of this study were to: 1) Combine the psyllid phenology model developed by Schaub et al. (2005), the earwig phenological day degree model Moerkens et al. (2011) and the PhenoFlex flowering time model Luedeling (2023), applying the models to UK data to assess if they are relevant for UK predictions, 2) Predict how all three trophic levels (host plant, pest and natural enemy) could respond under future temperature scenarios and, 3) Observe whether the three trophic levels are advancing at the same rate or if phenological mismatches are likely to occur in the future. Our analyses suggest that the timing of at least one phenological event has changed for each trophic level. Firstly, flowering time for first, full and last phenological stages has become earlier in the year as a result of climate change. This is supported by multiple studies, suggesting that temperature significantly influences budburst and flowering phenology (Amano et al., 2010; Auffret, 2021; Fitter & Fitter, 2002). Pear trees are heavily influenced by temperature; entering endodormancy during late autumn where growth is inhibited (Atkinson et al., 2013; Atkinson et al., 2004; Drepper et al., 2020), until the chill requirement (hours below a certain temperature) is met. Once the chilling requirement has been reached, ecodormancy begins, where growing degree hours are accumulated, thus elevated temperatures can lead to earlier flowering times (Drepper et al., 2020; Fadón et al., 2023). Studies have documented phenological advancements in pear flowering time depending on year and temperature (Drepper et al., 2020; Reeves et al., 2022; Sparks et al., 2005); Sparks et al. (2005) found that average first flowering time of pear had shifted to 15 Apr compared to 23 Apr for the historical time period, advancing at a rate of -0.306 days per year.

The timing of *C. pyri* phenological events have shifted over time. Generation 1 and G2 *C. pyri* peak nymph abundance, G2 peak egg abundance and peak summerform adult abundance, have all advanced significantly by approximately 14-15 days (current compared to historical time periods). Pear psylla are poikilothermic, (Kapatos & Stratopoulou, 1999; McMullen & Jong, 1977) and so elevated temperatures can have a significant impact on their metabolism, especially in increasing the rate of enzymatically catalysed reactions (Neven, 2000). McMullen & Jong (1977) found that the development rate of *C. pyricola* eggs and nymphs was significantly slower at lower temperatures; on average taking 61.8 days to complete development at 10 °C, compared to 27.0 days at 27 °C, development rate reached a critical thermal maximum at 32.2 °C, as psyllid mortality was 100%. Earwigs are also poikilothermic (Moerkens et al., 2011) and development is highly temperature dependant (Belien et al., 2012a; Helsen et al., 1998; Moerkens et al., 2011). Similar to *C. pyri*, *F. auricularia* peak abundance dates have advanced; with stage 4 nymphs becoming 16 days earlier and adults becoming 25 days earlier (current compared to historical predictions).

5.6.2 Phenological synchrony and mismatches

Based on the analyses from this study, G1 and G2 peak *C. pyri* nymph emergence date, first, full and last flowering times and *F. auricularia* stage 4 nymph and adult peak emergence date, were all predicted to advance between 2022 and 2080, under the RCP8.5 emissions scenario. Phenological shifts have been predicted for multiple pest species under future temperature scenarios (Ju et al., 2017; Lee et al., 2016; Stoeckli et al., 2012). One study by Stoeckli et al. (2012) looked at peak larval emergence for G1 and G2 of the Lepidoptera orchard pest, codling moth (*Cydia pomonella*) under current and predicted future climate scenarios (2045–2074). Findings indicated a significant two-week phenological advancement, for multiple phenological events including adult flight date, oviposition and larval emergence, supporting our predictions in phenological shifts. In addition, there was a significant increase in risk of a third generation of *C. pomonella*, as Switzerland currently only experiences two generations. This increase in voltinism is pertinent, as the number of generations of *C. pyri* per year is also climate dependent (Kapatos & Stratopoulou, 1999; Reeves et al., 2024); with an average of 3-5 generations per year in the UK (Reeves et al., 2024). However, in warmer climates such as Greece *C. pyri* produce 5-6 generations (Stratopoulou & Kapatos, 1992b), whilst in cooler climates such as Norway produce 2 generations (Næss, 2016). Therefore, a psyllid phenology model that considers the number of generations per year, rather than just the first two generations would be ideal, to allow researchers to identify whether population peaks of *C. pyri* match those of natural enemies later in the season and the abundance of adults overwintering into the following year.

There are concerns that not all trophic levels within agroecosystems are advancing at the same rate, which can result in trophic mismatches and increased challenges for pest management (Harrington et al., 1999; Reeves et al., 2024; Renner & Zohner, 2018; Wyver et al., 2023). One significant phenological difference within our study was between full flowering time and G1 *C. pyri* peak nymph abundance date; on average full flowering time was significantly earlier than peak G1 *C. pyri* nymph abundance for current and historical scenarios. Under the RCP8.5 scenario peak flowering time and nymph emergence began to overlap and by 2071 peak nymph emergence date becomes earlier than full flowering time. Availability of open flower buds may be important to *C. pyri*; nymphs often shelter inside them (Solomon et al., 1989), providing protection from harsh weather conditions, agrochemical sprays and natural enemies (Reeves et al., 2022, 2024). This may be especially beneficial for younger softshell nymphs earlier in the season, (L1-L3) as they are smaller and more vulnerable to harsh weather conditions. Thus, phenological synchrony between *C. pyri* nymphs and full flowering time would be sub-optimal for pear growers. Instead, nymph emergence that peaks before the appearance of budburst, foliage and flowering may be more manageable when applying crop protection products. This is relevant for the application of kaolin, a non-toxic clay particle film that can be sprayed onto plant surfaces, creating a barrier that can deter oviposition and reduced movement of *C. pyri* (Erler & Cetin, 2007; Saour et al., 2010). However, coverage of this spray is improved pre-bloom (February to early April) when there is less foliage, furthermore photosynthesis is not impacted (DuPont et al., 2021; Nottingham & Beers, 2020). Thus, it may allow growers to apply a second spray of kaolin or shift current spraying regimes, so that trees can be sprayed when nymphs are at their peak but before flowering occurs. Currently the average kaolin application in the 18 orchards assessed was around 30 March, which is still within the pre-bloom stage under the future RCP8.5 emissions scenario.

No significant differences between any other key trophic interactions were detected. This may be beneficial for pear growers, as the interaction between G2 *C. pyri* nymphs and earwigs remained unchanged. In historical and current scenarios, the phenological difference between peak G2 *C. pyri* nymph abundance and peak stage 4 earwig abundance dates was small; on average there was a 4-day difference between the two peaks under the current time period, suggesting phenological synchrony. This phenological difference did not significantly change under future climate scenarios; under the RCP 8.5 scenario the average difference was 2 days. However, there is still the question of how other natural enemies will react to rising temperatures, especially the key biological control agent *A. nemoralis*. Anthocorids show temperature dependent development (Bonte et al., 2012; Martínez-García et al., 2018; Yanik & Unlu, 2011); a study by Yanik & Unlu, (2011) found that *Anthocoris minki* nymphs took 18.6 days to develop under 20 °C and 11.8 days under 30 °C. However, degree day models are yet to be developed for *A. nemoralis*. Based on the 18 orchards assessed, on average *A. nemoralis* were released on 04 May and adult populations peaked 04 July. Therefore, whether this biological control agent needs to be released earlier in the year depends on its development under higher tempertures, and requires future research.

5.6.3 Model evaluation

Observed and predicted results did not significantly differ from each other for the PhenoFlex model, *C. pyri* phenology model and *F. auricularia* degree day model, with the exception of G1 *C. pyri* peak nymph abundance date, which was on average 14 days later than predicted. There may be a number of reasons for the difference between the predicted and observed G1 peak nymph dates; firstly the pear psyllid phenology model was originally optimised based on data from Switzerland (Schaub et al., 2005), so there may be differences compared to UK climate, it also only considers temperature. The accuracy of the weather station itself could also explain the difference, as most orchards were a few miles away from their corresponding weather stations, thus temperatures experienced in orchards may not be exact. Moreover, the pear psyllid model is sensitive to (small) systematic errors in temperature; for example, a change of 1- 2 °C produced simulations that were 5 or 10 days earlier in Schaub et al. (2005), this could be more apparent in March-May when temperatures are often more variable. Therefore, this study recommends the collection of temperature data within orchards alongside phenological monitoring data.

It should be highlighted that the data from this study was based on grower and agronomist monitoring data, assessed every week, so perhaps more regular sampling is required, as phenological peaks can be easily missed. Furthermore, pear psyllid nymphs are more visible when shoot growth has started after flowering; before flowering nymphs often hide in the buds or bud scales and L1-L3 nymphs are much smaller (Chang, 1977). This may make it more difficult for growers to observe smaller instars earlier in the season, especially as the method used a hand-lens. To help mitigate this bias of 'hidden nymphs' the 'wash down' method can be used; washing-down foliage and budwood using water containing 1% detergent, then straining through filter paper to concentrate the nymphs and using a binocular dissecting microscope for more accurate counts (Jenser et al., 2010). This could be used to evaluate bias, however it may be more labour intensive and require specialist equipment, making it less suitable for growers. Finally, the heterogeneity of the landscape could explain the later observed G1 nymph peak; adult psyllids often disperse over the winter away from the host plant, however the proportion of an orchard's population that overwinters in the orchard rather than dispersing is not known and appears to vary between years and regions (Horton, 1999). One theory is that areas with large pear monocultures see much lower rates of dispersal, thus may have earlier peaks for egg laying and G1 nymph abundance. However, the orchards used within our study were surrounded by a much more heterogenous landscape compared to those used in Schaub et al. (2005), therefore more time is required for re-entry into the orchard, resulting in later peaks. This study also recommends the evaluation of the model for other regions within the UK, as data was only from 18 orchards in Kent.

For the earwig degree day model a previous study found significant differences between observed and predicted emergence dates, for all life stages within apple orchards in Spain (Lordan et al., 2015); on average peak abundance date was predicted as 29 Apr for stage 4 *F. auricularia* nymphs but observed date was 13 May. Thus, this model may be sub-optimal for Mediterranean orchards. However, for UK orchards, observed and predicted dates for *F. auricularia* stage 4 nymphs and adults did not differ significantly. Therefore, the use of this model within UK pear orchards may be effective at predicting emergence dates, however the prediction of egg hatching and stage 1 to stage 3 peak abundance dates still need to be evaluated for UK orchards. Another limitation within the study is the temperature data used within the *F. auricularia* degree day model. Moerkens et al. (2011) recommends the use of soil temperature (5-10 cm below the soil surface) to predict earwig development and emergence for earlier egg and nymph stages (egg, L1 and L2), however hourly soil temperature was not available between 2011-2021 for the majority of weather stations in Kent or for UKCP18 temperature predictions. This is especially important for double-brood populations due to a higher proportion of time spent within the soil throughout the year (due to two broods in the soil a year), therefore when looking at double-brood populations and earlier nymph stages, collection of hourly soil temperature is vital.

It should also be noted that the earwig degree day model and *C. pyri* phenology model, are independent of each other. However, it is likely that models would interact, as *F. auricularia*, can significantly reduce pear psyllid populations, although earwigs are unlikely to migrate into orchards based on psyllid density (Lenfant et al., 1994). Thus, a time distributed delay model that also considers predator-prey interactions, such as those seen in the stagePop package in R may be beneficial to growers, as well as the introduction of phenological models for other important natural enemy species such as *A. nemoralis*, as this may alter decisions on agrochemical sprays or the further release of biological control agents.

5.7 Conclusion

To conclude the PhenoFlex model, *C. pyri* phenology model and *F. auricularia* degree day model were reasonably accurate in predicting key phenological events in UK pear orchards. Observed and predicted results did not significantly differ from each other, with the exception of G1 *C. pyri* peak nymph abundance date, which was on average 14 days later than predicted. Therefore, this part of the psyllid phenology model may need to be adapted, or more detailed monitoring data collected. All phenological events were predicted to advance under the RCP8.5 emissions scenario but only pear flowering time (full and last) was predicted to significantly advance under the RCP2.6 scenario. However, there was only a significant change in phenological difference between *C. pyri* peak G1 nymph abundance and full flowering time, as nymph abundance date was advancing at a faster rate. The phenological synchrony between stage 4 earwig nymphs and *C. pyri* G2 nymphs was evident in all scenarios, due to a minimal phenological difference that did not significantly change over time. However, the pear psyllid phenology model only included the first two generations, so we could not assess changes in voltinism, breeding period or overlap between natural enemies later in the year. In addition, a degree day model has not been developed for *A. nemoralis*, which is a key biological control agent for *C. pyri*. This study is highly relevant within the field of integrated pest management; linking models of crops, pests and natural enemies to better predict trophic interactions and optimise timing of management methods with respect to peak abundance dates. The PhenoFlex model can be easily optimised to multiple tree fruit crops, whilst phenological degree day models can be adapted to other pest and natural enemy development times. Thus, we recommend the long term collection of phenological monitoring data for multiple agroecosystems, to help validate and develop a range of phenological models for key crop, pest and natural enemy species, within the UK and globally.

5.8 Figures and Tables

Table 5.1: Parameters used within the Phenoflex model, including the initial start values and upper and lower bounds used for calibration. As well as the optimal parameters for each flowering stage (first, full and last) for cv. Conference pear trees (*Pyrus communis*) after bootstrapping.

Parameters	**Description**	**Initial value (lower, upper)**	**Optimal parameters for flowering stage**		
			First	**Full**	**Last**
y_c	Chill requirement (defines the end of the chilling period)	40 (20, 80)	35.97 ± 0.18	47.69 ± 1.48	41.56 ± 0.27
z_c	Heat requirement (defines the end of the forcing period)	190 (100, 500)	237.67 ± 0.56	287.11 ± 4.57	227.88 ± 0.58
s_1	Slope parameter, defining the transition between chilling and forcing periods	0.5 (0.1, 1.0)	0.989 ± 0.231	0.211 ± 0.233	0.29 ± 0.18
T_u (°C)	Optimal temperature for the GDH model	25 (0, 30)	28.04 ± 0.00	26.73 ± 0.320	28.53 ± 0.00
E_0 (K)	Activation energy required to form the precursor to the dormancy-breaking factor (PDBF) within the Dynamic model	3372.8 (3000.0, 4000.0)	3373.12 ± 0.00	3324.80 ± 0.00	3371.86 ± 0.00
E_1 (K)	Activation energy required to destroy the precursor to the dormancy-breaking factor (PDBF) within the Dynamic model	9900.3 (9000.0, 10000.0)	9898.92 ± 0.32	9853.98 ± 0.439	9901.74 ± 0.33
A_0 (h^{-1})	Amplitude for compound formation of PDBF within the Dynamic model	6319.5 (6000.0, 7000.0)	6090.75 ± 20.41	6218.27 ± 66.87	6008.99 ± 0.036
A_1 (h^{-1})	Amplitude for compound destruction of PDBF within the Dynamic model	5.939917e13 (5e13, 6e13)	5.939915e13 ± 6.12 e07	5.939902e13 ± 9.56 e07	5.939898e13 ± 1.34 e08

T_f (°C)	Transition temperature of the sigmoidal function within the Dynamic model	4 (0, 10)	4.56 ± 0.58	0.0589 ± 2.11	0.507 ± 1.08
T_c (°C)	Upper temperature threshold for the GDH model	36 (0, 40)	38.58 ± 1.88	27.24 ± 3.50	32.55 ± 4.05
T_b (°C)	Base temperature for the GDH model	4 (0, 10)	0.691 ± 0.022	1.21 ± 0.00	2.72 ± 0.02
s (K^{-1})	Sigmoidal function slope within the Dynamic model producing Chill Portions	1.60 (0.05, 50.00)	1.79 ± 2.56	22.00 ± 15.12	8.92 ± 11.26

Table 5.2: Average predicted and observed (data collected from orchards) peak abundance dates and difference between predicted and observed values, for cv. Conference pear (*Pyrus communis*) flowering time (first, full and last), peak abundance of *Cacopsylla pyri* eggs, nymphs and adults and peak abundance of *Forficula auricularia* arboreal nymphs and adults. P values in bold show significant differences between predicted and observed values based on Kruskal Wallis tests.

Phenological stage	Species	Predicted peak date	Observed peak date	Difference (days)	P value
First flowering	*Pyrus communis*	12 Apr ± 1.24	12 Apr ± 1.52	0.57 ± 0.71	0.903
Full flowering	*Pyrus communis*	19 Apr ± 1.32	18 Apr ± 1.49	0.57 ± 0.63	0.801
Last flowering	*Pyrus communis*	29 Apr ± 1.23	30 Apr ± 1.33	-0.62 ± 0.64	0.818
G1 nymphs	*Cacopsylla pyri*	24 Apr ± 1.13	09 May ± 1.95	-14.36 ± 1.94	**< 0.001**
Summerform adults	*Cacopsylla pyri*	25 May ± 0.80	23 May ± 1.13	2.34 ± 1.06	0.168
G2 eggs	*Cacopsylla pyri*	02 Jun ± 0.83	02 Jun ± 1.88	- 0.63 ± 1.84	0.728
G2 nymphs	*Cacopsylla pyri*	25 Jun ± 0.77	25 Jun ± 1.38	0.42 ± 1.38	0.336
4th instar nymphs	*Forficula auricularia*	21 Jun ± 0.85	18 Jun ± 1.96	2.54 ± 2.12	0.284
Adults	*Forficula auricularia*	17 Aug ± 0.92	15 Aug ± 2.05	2.68 ± 1.81	0.151

Table 5.3: Model parameters for each phenological event and scenario, based on the relationship between event date (Julian days) and year. GLMs were fitted if the edf of the GAM was <2, p-values in bold show a significant relationship.

Stage	Scenario	Model Type	Gradient	SE	Edf	Intercept	F statistic	R^2 adjusted	p-value
First flowering *Pyrus communis*	Historical	GLM	-0.254	0.140	1.00	624.62	3.32	9.53	0.0828
	Current	GAM	~	0.621	2.81	113.90	15.61	58.50	**<0.001**
	RCP2.6	GLM	-0.0443	0.0226	1.00	193.20	3.87	4.71	0.0540
	RCP8.5	GLM	-0.177	0.0206	1.00	464.22	74.42	55.87	**<0.001**
Full flowering *Pyrus communis*	Historical	GLM	-0.1998	0.123	1.00	526.77	2.62	11.09	0.120
	Current	GAM	~	0.542	2.82	123.56	16.71	63.23	**<0.001**
	RCP2.6	GLM	-0.0528	0.0197	1.00	220.17	7.18	9.63	**0.00961**
	RCP8.5	GLM	-0.197	0.0181	1.00	514.20	119.20	67.09	**<0.001**
Last flowering *Pyrus communis*	Historical	GLM	-0.161	0.101	1.00	459.39	2.54	6.55	0.126
	Current	GAM	~	0.487	5.36	134.78	10.48	63.20	**0.0004**
	RCP2.6	GLM	-0.0657	0.0174	1.00	257.50	14.27	18.61	**<0.001**
	RCP8.5	GLM	-0.222	0.0160	1.00	575.45	191.77	76.68	**<0.001**
G1 *Cacopsylla pyri* first nymph emergence	Historical	GLM	-0.152	0.500	1.00	339.37	0.0925	-4.30	0.764
	Current	GLM	-0.328	0.212	1.00	696.86	2.40	3.55	0.130
	RCP2.6	GAM	~	1.36	4.30	35.41	1.12	5.43	0.408
	RCP8.5	GLM	-0.125	0.0524	1.45	287.87	5.71	7.52	**0.0202**
G1 *Cacopsylla pyri* nymph peak abundance	Historical	GLM	-0.0524	0.269	1.00	248.65	0.0379	-4.57	0.848
	Current	GAM	~	2.10	2.92	138.00	2.43	17.64	**0.0138**
	RCP2.6	GLM	0.0710	0.109	1.00	-22.44	0.422	-1.01	0.519
	RCP8.5	GLM	-0.413	0.0908	1.00	961.42	20.70	25.36	**<0.001**
G1 *Cacopsylla pyri* summerform adults peak abundance	Historical	GLM	0.0464	0.197	1.00	70.46	0.0558	4.48	0.816
	Current	GAM	~	1.61	2.67	154.41	3.26	20.50	**0.0263**
	RCP2.6	GLM	0.0499	0.0787	1.00	39.22	0.402	1.04	0.528
	RCP8.5	GLM	-0.362	0.0754	1.00	875.78	23.12	28.85	**<0.001**
G2 *Cacopsylla pyri* egg peak abundance	Historical	GLM	0.0652	0.190	1.00	41.02	0.118	-4.17	0.734
	Current	GLM	-0.428	0.140	1.00	1018.14	9.28	17.90	**0.004**
	RCP2.6	GLM	0.0421	0.0750	1.00	62.69	0.315	-1.20	0.577
	RCP8.5	GLM	-0.353	0.0727	1.00	865.54	23.62	28.06	**<0.001**

G2 *Cacopsylla pyri* nymph peak abundance	Historical	GLM	-0.00988	0.144	1.00	211.56	0.00472	4.74	0.946
	Current	GLM	-0.403	0.130	1.00	990.79	9.67	18.57	**0.004**
	RCP2.6	GLM	0.0140	0.0669	1.00	142.72	0.0437	1.68	0.835
	RCP8.5	GLM	-0.315	0.0627	1.00	810.54	25.29	29.52	**<0.001**
Forficula auricularia stage 4 peak nymph abundance	Historical	GLM	-0.0148	0.148	1.00	218.08	0.0101	-0.0471	0.921
	Current	GLM	-0.375	0.120	1.00	930.24	9.75	18.72	**0.003**
	RCP2.6	GLM	-0.00625	0.0611	1.00	181.11	0.0105	-1.74	0.919
	RCP8.5	GLM	-0.288	0.0629	1.00	752.88	20.99	25.63	**<0.001**
Forficula auricularia peak adult abundance	Historical	GLM	-0.132	0.287	1.00	510.20	0.212	3.71	0.650
	Current	GLM	-0.508	0.138	1.00	1251.01	13.61	24.92	**0.001**
	RCP2.6	GLM	-0.025	0.0595	1.00	268.90	0.177	1.44	0.676
	RCP8.5	GLM	-0.224	0.0608	1.57	672.54	13.57	19.23	**0.001**

Table 5.4: Average predicted dates ± standard error for phenological events depending on scenario (historic, current, RCP2.6 and RCP8.5). Events include cv. Conference pear (*Pyrus communis*) flowering time (first, full and last), peak abundance of *C. pyri* eggs, nymphs and adults and first emergence of *Cacopsylla pyri* nymphs and peak abundance of *Forficula auricularia* arboreal nymphs and adults.

Phenological stage	Species	Historical (1960-1983)	Current (2011-2021)	RCP 2.6 (2060-2080)	RCP 8.5 (2060-2080)
First flowering	*Pyrus communis*	04 May ± 0.97	19 Apr ± 1.39	11 Apr ± 0.54	07 Apr ± 0.59
Full flowering	*Pyrus communis*	13 May ± 0.85	29 Apr ± 1.22	20 Apr ± 0.48	16 Apr ± 0.50
Last flowering	*Pyrus communis*	23 May ± 0.69	10 May ± 1.09	01 May ± 0.50	25 Apr ± 0.48
G1 nymphs (First emergence)	*Cacopsylla pyri*	08 Feb ± 3.13	07 Feb ± 3.89	07 Feb ± 2.65	28 Jan ± 0.83
G1 nymphs (Peak emergence)	*Cacopsylla pyri*	25 May ± 1.75	11 May 4.38	06 May ± 3.15	16 Apr ± 2.48
Summerform adults	*Cacopsylla pyri*	11 Jun ± 1.28	27 May ± 3.40	23 May ± 2.37	05 May ± 1.94
G2 eggs	*Cacopsylla pyri*	19 Jun ± 1.23	04 Jun ± 3.39	31 May ± 2.28	14 May ± 1.91
G2 nymphs	*Cacopsylla pyri*	11 Jul ± 0.93	26 Jun ± 3.35	21Jun ± 2.03	08 Jun ± 1.43
4th instar nymphs	*Forficula auricularia*	08 Jul ± 0.96	22 Jun ± 3.05	18 Jun ± 1.90	06 Jun ± 1.38
Adults	*Forficula auricularia*	06 Sep ± 1.79	12 Aug ± 3.19	06 Aug ± 1.92	28 Jul ± 1.82

Table 5.5: Model parameters for the difference between two phenological events, depending on scenario, based on the relationship between phenological difference (Julian days) and year. GLMs were fitted if the edf of the GAM was <2, p-values in bold show a significant relationship.

Difference	Scenario	Model Type	Gradient	SE	Edf	Intercept	F statistic	R^2 adjusted	p-value
First flowering and First *Cacopsylla pyri* nymph emergence	Historical	GLM	-0.102	0.577	1.00	285.24	0.0312	-4.61	0.862
	Current	GLM	-0.0625	0.194	1.00	198.45	0.104	-2.42	0.749
	RCP2.6	GAM	~	1.35	4.39	66.84	1.35	7.30	0.296
	RCP8.5	GLM	-0.0519	0.0566	1.58	176.35	0.841	-0.275	0.363
Full flowering and Peak *Cacopsylla pyri* G1 nymph emergence	Historical	GLM	-0.147	0.294	1.00	278.12	0.251	-3.52	0.621
	Current	GLM	0.138	0.169	1.00	-291.45	0.674	-0.866	0.417
	RCP2.6	GLM	-0.123	0.107	1.00	242.61	1.35	0.605	0.250
	RCP8.5	GLM	0.216	0.0937	1.00	-447.22	5.31	6.92	**0.0248**
Peak G2 *Cacopsylla pyri* egg abundance and Peak *Forficula auricularia* stage 4 nymph abundance	Historical	GLM	0.0800	0.145	1.00	-177.06	0.305	-3.26	0.587
	Current	GAM	-	0.832	3.06	-18.28	1.03	7.69	0.344
	RCP2.6	GLM	0.0483	0.0389	1.00	-118.42	1.54	2.64	0.219
	RCP8.5	GLM	-0.0652	0.0365	1.00	112.66	3.20	3.65	0.0790
Peak G2 *Cacopsylla pyri* nymph emergence and Peak *Forficula auricularia* stage 4 nymph abundance	Historical	GLM	0.00494	0.0823	1.64	-6.52	0.00361	-4.74	0.953
	Current	GAM	~	0.600	3.03	4.615	0.543	2.87	0.626
	RCP2.6	GLM	0.0202	0.0261	1.00	-38.39	0.603	-0.690	0.441
	RCP8.5	GLM	-0.0270	0.0202	1.00	57.65	1.79	1.34	0.186

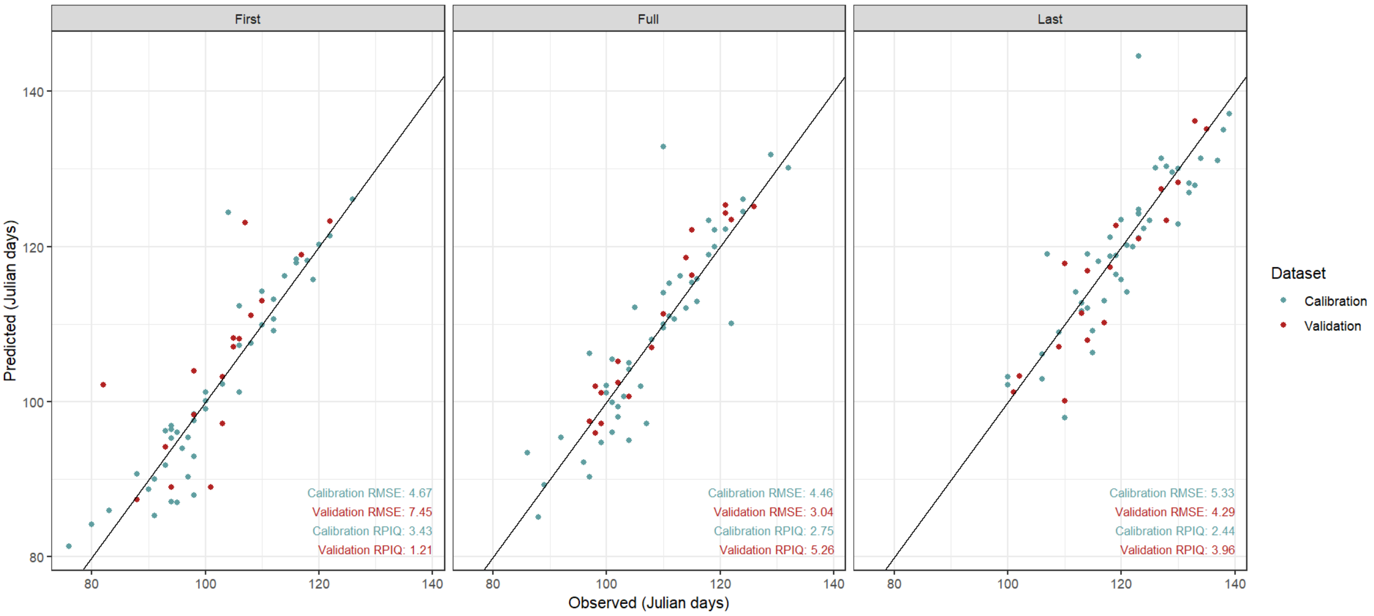


Figure 5.1: Observed and predicted flowering dates (Julian days) from calibration and validation datasets, generated from the Phenoflex model, for first, full and last flowering stages for cv. Conference pear trees (*Pyrus communis*). With the Root Mean Square Error (RMSE) and Ratio of Performance to InterQuartile distance (RPIQ) for predicted and observed values.

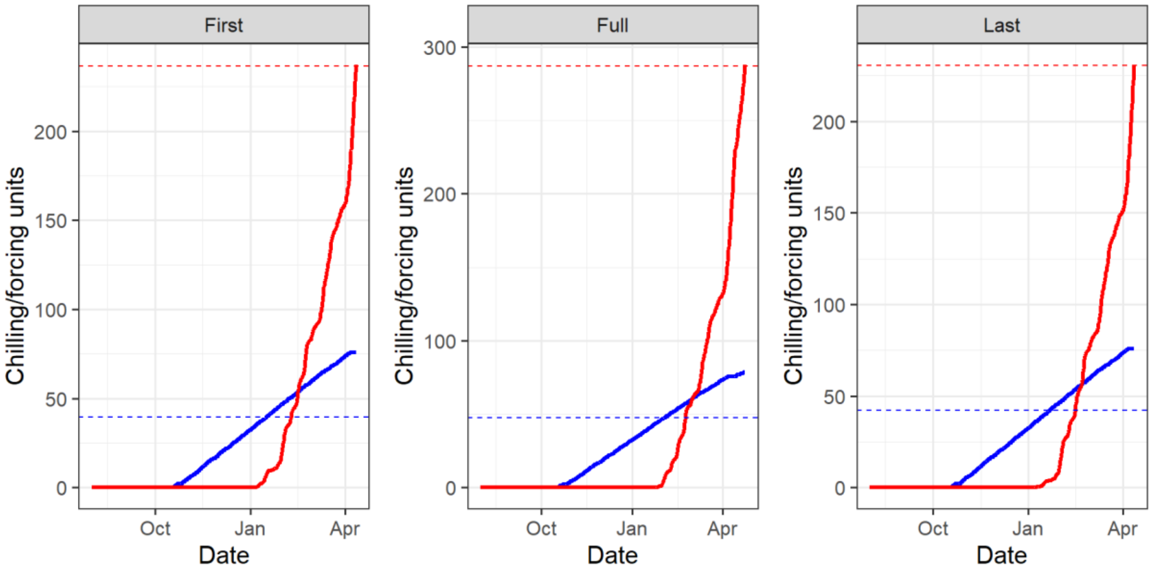


Figure 5.2: Chill and heat accumulation curves for cv. Conference pear trees (*Pyrus communis*), for first, full and last flowering phenology, during 2021. The blue solid line represents chill accumulation and the red solid line represents heat accumulation. The blue dashed line represents yc (the threshold for end of chill accumulation) and the red dashed line represents zc (the threshold for end of heat accumulation).

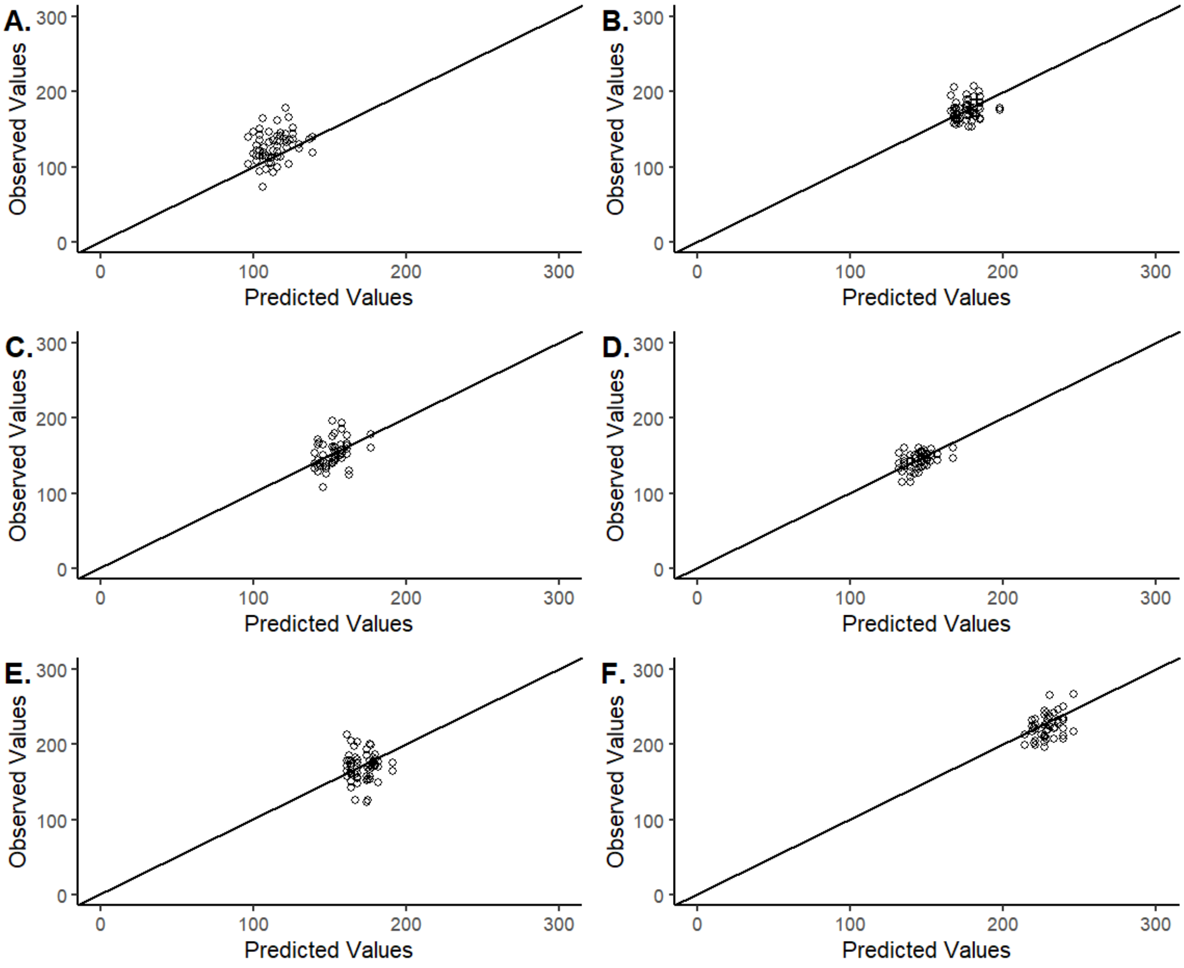


Figure 5.3: The observed and predicted values (Julian days) for *Cacopsylla pyri* and *Forficula auricularia* phenological events, generated from the psyllid phenology model, for A. peak *Cacopsylla pyri* G1 peak nymph abundance, B. peak *Cacopsylla pyri* G2 peak nymph abundance, C. peak *Cacopsylla pyri* G2 peak egg abundance, D. peak *Cacopsylla pyri* peak summerform adult abundance, E. peak *Forficula auricularia* stage 4 nymph abundance and F. peak *Forficula auricularia* adult abundance.

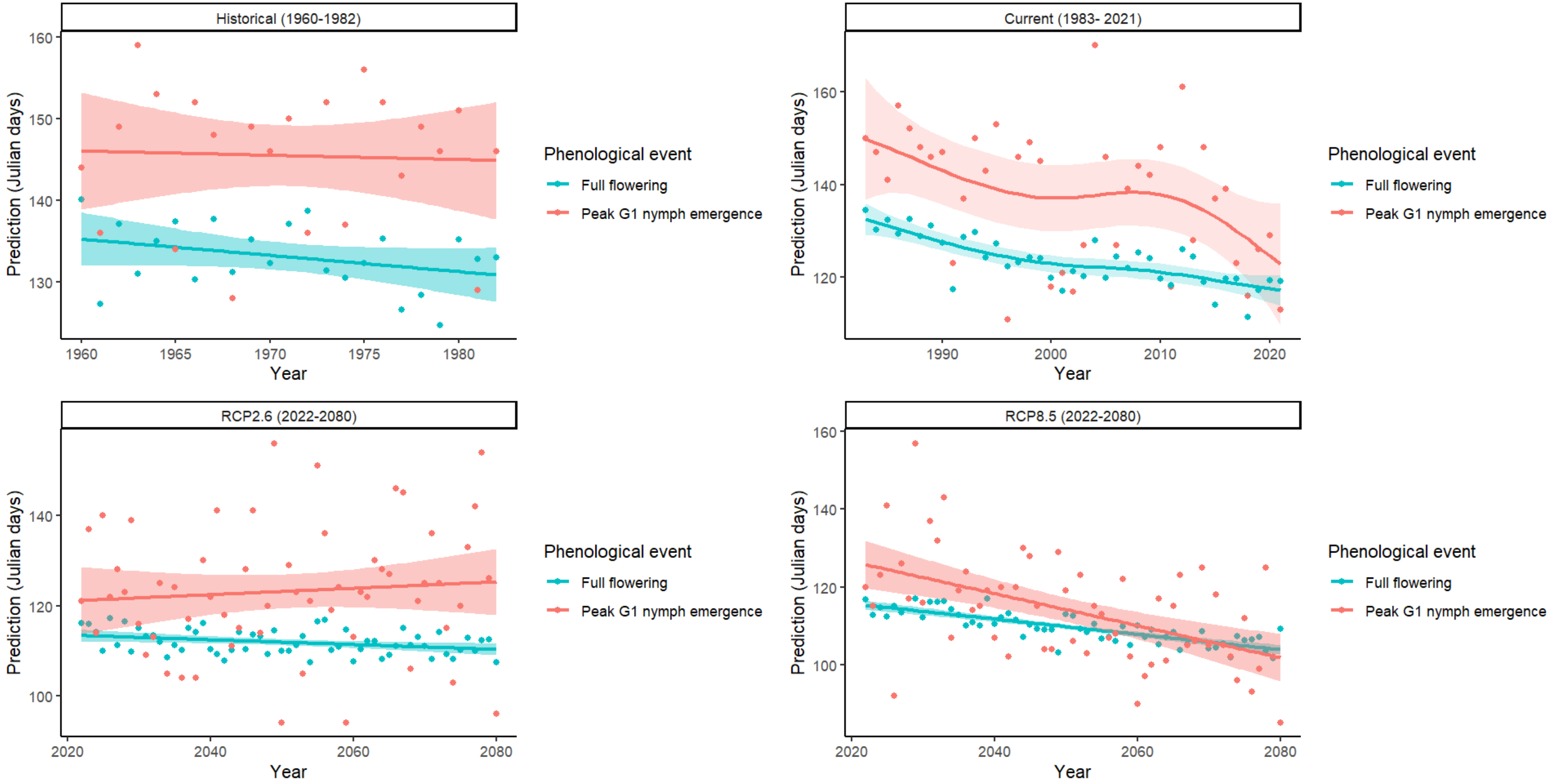


Figure 5.4: The phenological shift in full flowering time (Julian days) for cv. Conference pear trees (*Pyrus communis*) and *Cacopsylla pyri* G1 peak nymph abundance date, depending on year (1960-2080) and RCP scenario (RCP2.6 and RCP8.5).

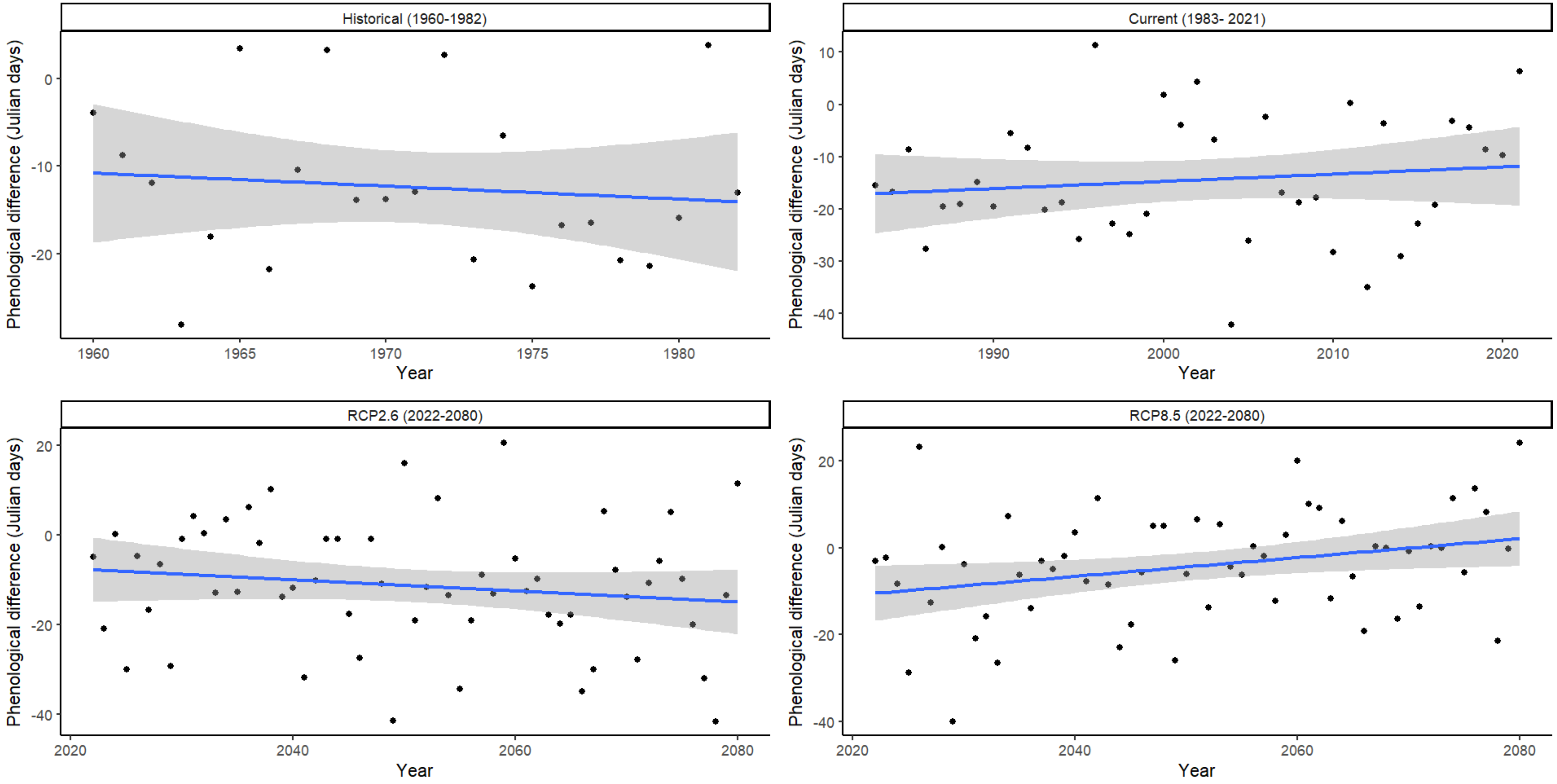


Figure 5.5: The phenological difference between full flowering time (Julian days) for cv. Conference pear trees (*Pyrus communis*) and *Cacopsylla pyri* G1 peak nymph abundance date, depending on year (1960-2080) and RCP scenario (RCP2.6 and RCP8.5).

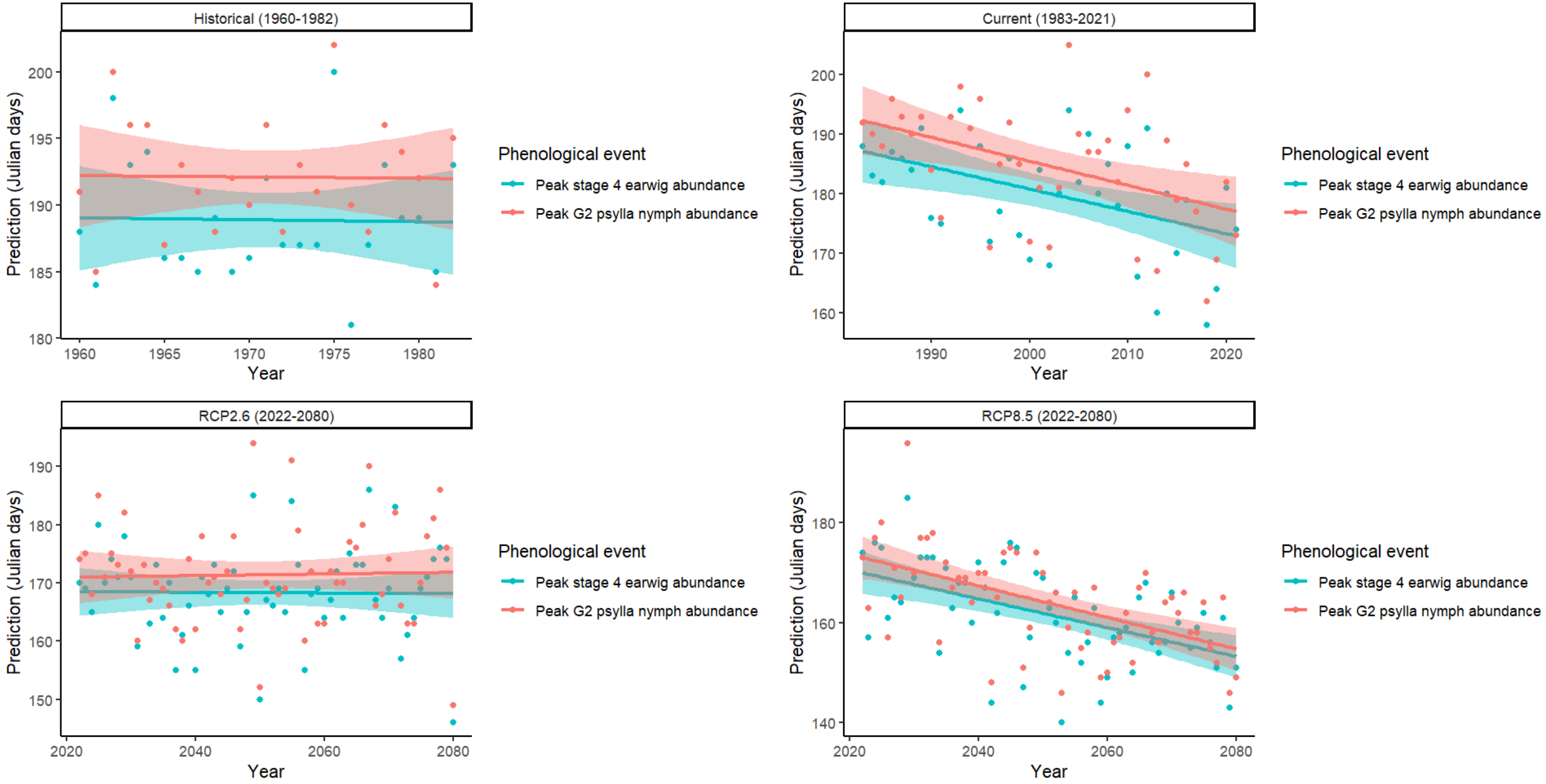


Figure 5.6: The phenological shift in *Cacopsylla pyri* G2 peak nymph abundance date (Julian days) and *Forficula auricularia* stage 4 peak nymph abundance date, depending on year (1960-2080) and RCP scenario (RCP2.6 and RCP8.5).

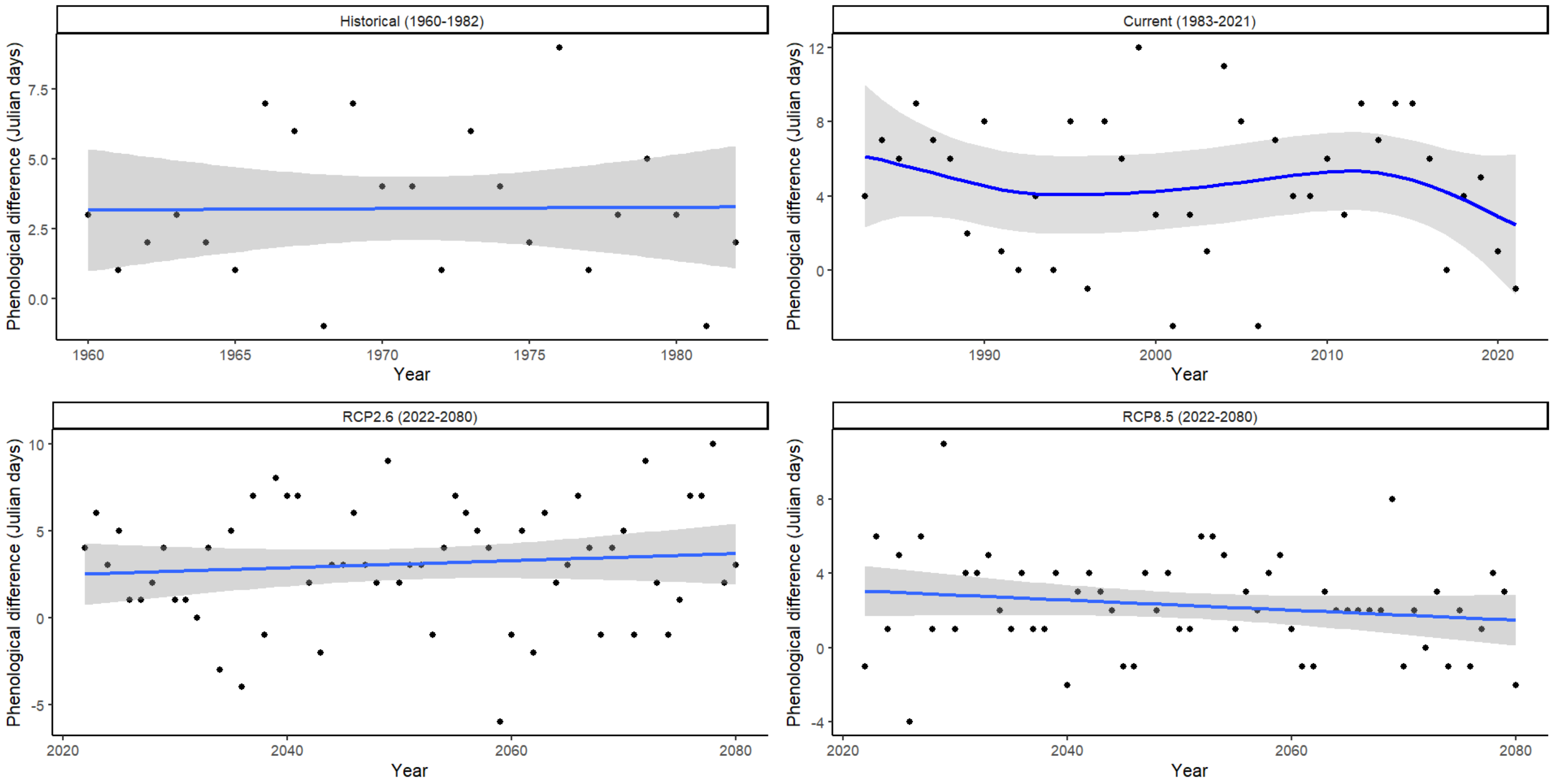


Figure 5.7: The phenological difference between *Cacopsylla pyri* G2 peak nymph abundance date (Julian days) and *Forficula auricularia* stage 4 peak nymph abundance, depending on year (1960-2080) and RCP scenario (RCP2.6 and RCP8.5).

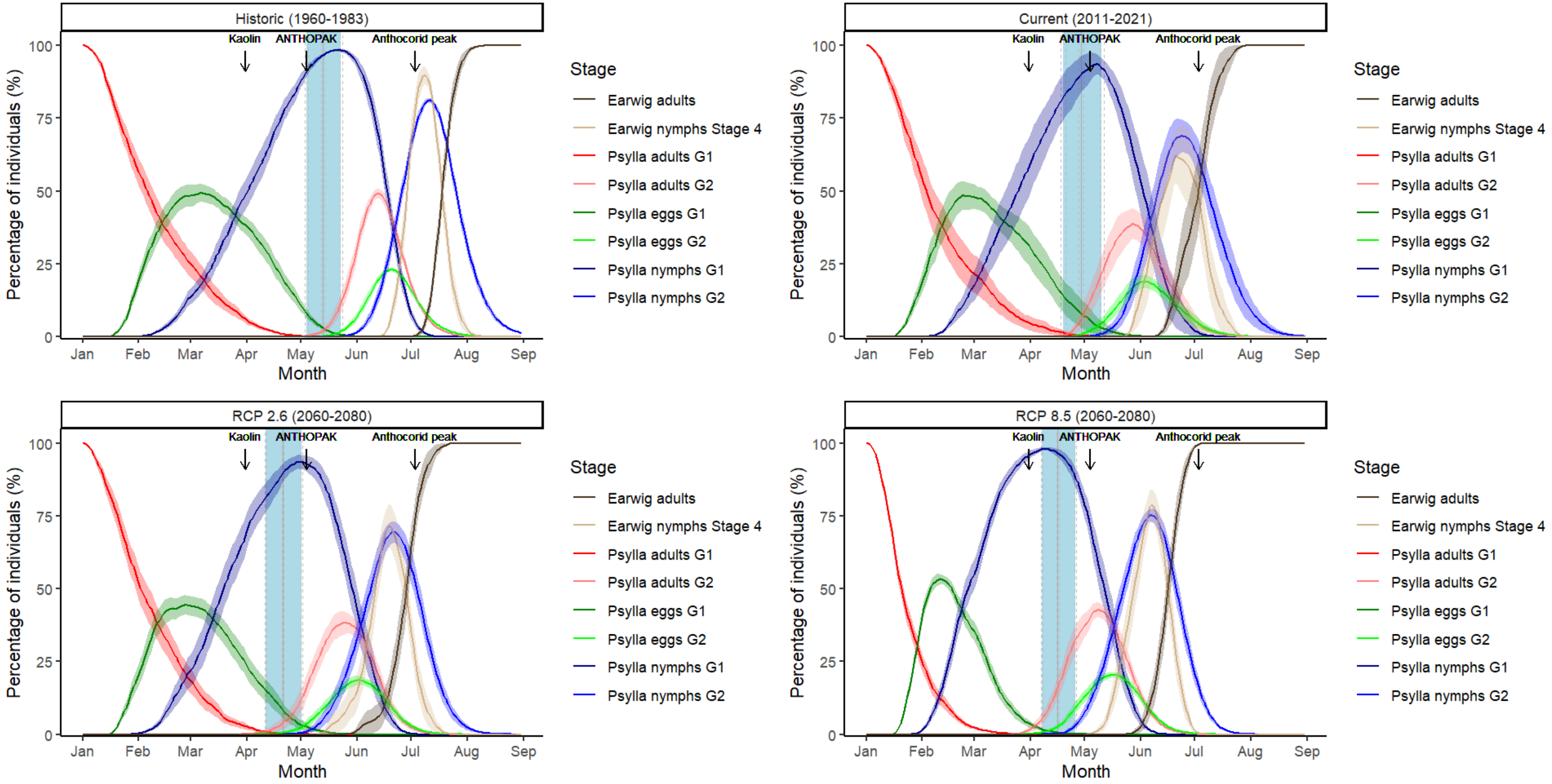


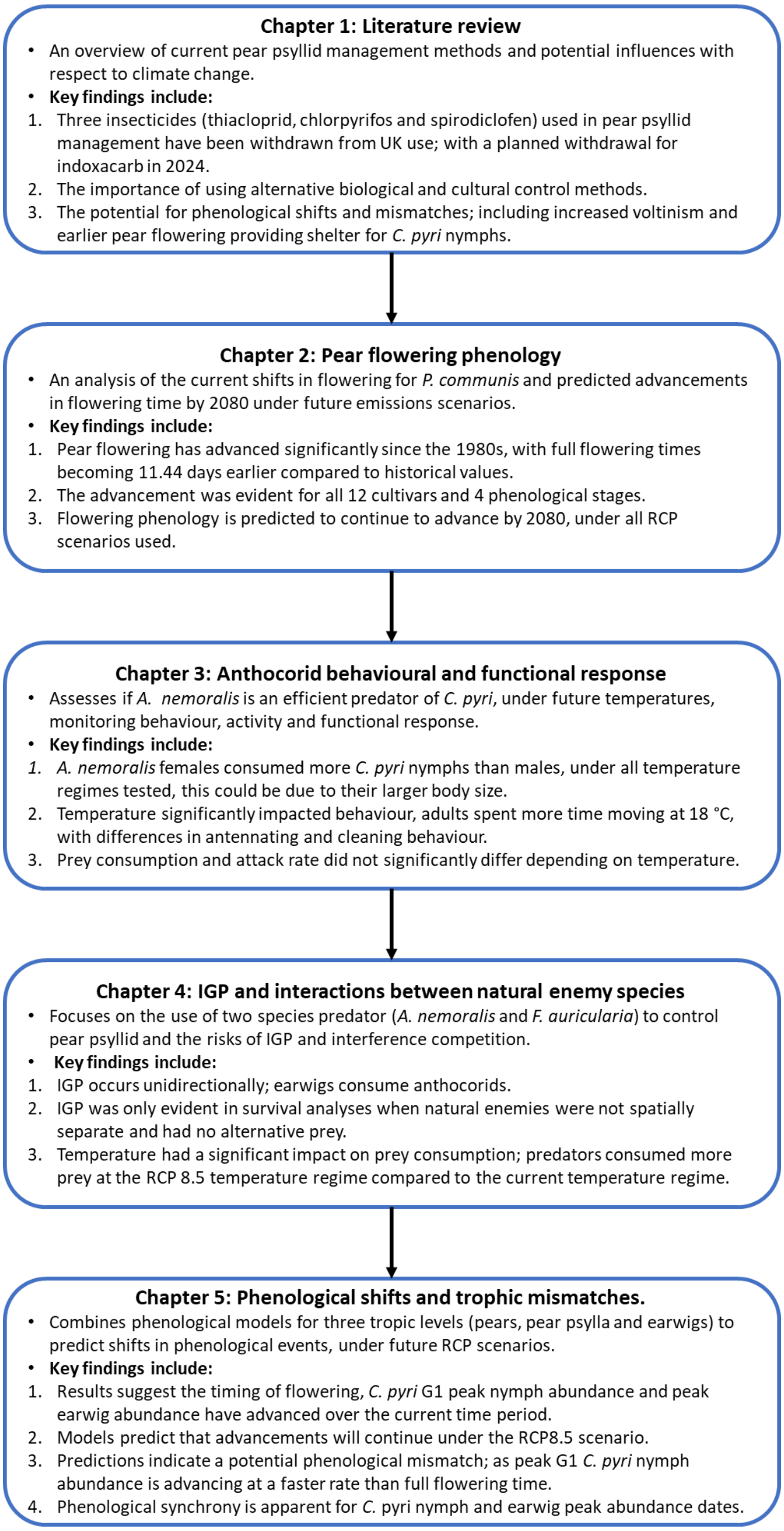
Figure 5.8: The average percentage abundance of *Cacopsylla pyri*: G1 adults (red), G1 eggs (green), G1 nymphs (blue), G2 adults (orange), G2 eggs (purple), G2 nymphs (pink) and *Forficula auricularia* stage 4 nymphs (light brown) and adults (dark brown) depending on month, for each scenario. The light blue rectangle represents the flowering spread of *Pyrus communis* (from first flowering to last flowering), solid grey line the average full flowering time and dotted grey lines the standard errors. Black arrows represent key times for spray application or biological control including average Kaolin application time, average ANTHOPAK application (artificial mass release of anthocorid adults) and average anthocorid peak within orchards.

6 General discussion

6.1 Overview

This thesis aimed to apply a whole ecosystem approach to pear psyllid management (Figure 6.1), considering multiple trophic levels and their interactions (Figure 6.2), current chemical, biological and cultural control methods used within this system, weather variables and how climate change could alter future management methods. This research is relevant to pear growers, to inform the application timings of management methods and how these could shift with respect to climatic warming. Pear psylla are a widely-studied pest, with a range of information on their life history (Horton, 1999), signalling behaviour (Ganassi et al., 2018a; Jocson et al., 2023), diet (Le Goff et al., 2019), natural enemies (Civolani et al., 2023; Horton, 2024) and control methods (Civolani et al., 2023; Reeves et al., 2024). However, pear psyllid management within the context of climate change is under researched; warming temperatures are likely to lead to phenological shifts and even mismatches between trophic levels (Reeves et al., 2022, 2024) leading to potential future challenges for sustainable control of this pest. Therefore, this thesis aimed to address this gap within the scientific literature, focusing on plants, pests and natural enemies and their interactions in a changing climate. Furthermore, data analyses, behavioural assays, functional response experiments and phenological models used within this thesis, are highly applicable to other agroecosystems featuring trophic interactions. This general discussion will summarise the key findings of each thesis chapter, explain how these findings are useful in the context of orchard management, discuss the possible limitations of experimental design and monitoring data and outline areas of future research for pear psyllid monitoring and IPM.

6.2 Chapter findings



Chapter 1: Literature review

- An overview of current pear psyllid management methods and potential influences with respect to climate change.
- **Key findings include:**

1. Three insecticides (thiacloprid, chlorpyrifos and spirodiclofen) used in pear psyllid management have been withdrawn from UK use; with a planned withdrawal for indoxacarb in 2024.
2. The importance of using alternative biological and cultural control methods.
3. The potential for phenological shifts and mismatches; including increased voltinism and earlier pear flowering providing shelter for *C. pyri* nymphs.

Chapter 2: Pear flowering phenology

- An analysis of the current shifts in flowering for *P. communis* and predicted advancements in flowering time by 2080 under future emissions scenarios.
- **Key findings include:**

1. Pear flowering has advanced significantly since the 1980s, with full flowering times becoming 11.44 days earlier compared to historical values.
2. The advancement was evident for all 12 cultivars and 4 phenological stages.
3. Flowering phenology is predicted to continue to advance by 2080, under all RCP scenarios used.

Chapter 3: Anthocorid behavioural and functional response

- Assesses if *A. nemoralis* is an efficient predator of *C. pyri*, under future temperatures, monitoring behaviour, activity and functional response.
- **Key findings include:**

1. *A. nemoralis* females consumed more *C. pyri* nymphs than males, under all temperature regimes tested, this could be due to their larger body size.
2. Temperature significantly impacted behaviour, adults spent more time moving at 18 °C, with differences in antennating and cleaning behaviour.
3. Prey consumption and attack rate did not significantly differ depending on temperature.

Chapter 4: IGP and interactions between natural enemy species

- Focuses on the use of two species predator (*A. nemoralis* and *F. auricularia*) to control pear psyllid and the risks of IGP and interference competition.
- **Key findings include:**

1. IGP occurs unidirectionally; earwigs consume anthocorids.
2. IGP was only evident in survival analyses when natural enemies were not spatially separate and had no alternative prey.
3. Temperature had a significant impact on prey consumption; predators consumed more prey at the RCP 8.5 temperature regime compared to the current temperature regime.

Chapter 5: Phenological shifts and trophic mismatches.

- Combines phenological models for three tropic levels (pears, pear psylla and earwigs) to predict shifts in phenological events, under future RCP scenarios.
- **Key findings include:**

1. Results suggest the timing of flowering, *C. pyri* G1 peak nymph abundance and peak earwig abundance have advanced over the current time period.
2. Models predict that advancements will continue under the RCP8.5 scenario.
3. Predictions indicate a potential phenological mismatch; as peak G1 *C. pyri* nymph abundance is advancing at a faster rate than full flowering time.
4. Phenological synchrony is apparent for *C.* pyri nymph and earwig peak abundance dates.

Figure 6.1: Summary of each chapter within the thesis, alongside key findings. The thesis begins with a broadscale review of pear psyllid management and potential changes and risks to the agroecosystem with respect to climate change. Before addressing each trophic level: from primary producer (chapter 2) to primary consumer (chapter 3), as well as the potential interactions and mismatches within (chapter 4) and between (chapter 5) trophic levels. Chapter 5 compiles all three trophic levels explored within this thesis to give an overview of potential phenological shifts with respect to climate change.

Chapter 1 gives a general overview of pear psyllid management methods and how these are likely to be influenced by climate change. The chapter draws attention to the fact that three insecticides (thiacloprid, chlorpyrifos and spirodiclofen), commonly used for pear psyllid control have been withdrawn from UK use, with a fourth withdrawal planned for the active ingredient indoxacarb in 2024 (Hertfordshire, 2023; HSE, 2023). This stresses the importance of biological control, cultural control and use of biorational products for pear psylla control. In addition, the chapter looks at management methods within 20 UK orchards, highlighting the use of the biological control agent *Anthocoris nemoralis* in 35% of orchards and the biorational compound kaolin in 25% of orchards, which are both effective tools in pear psyllid management (Beninato & Morella, 2000; DuPont et al., 2021; Pasqualini et al., 2002). The review addresses the potential phenological mismatches that could occur within this agroecosystem, filling a gap in the scientific literature. In particular the chapter notes that earlier pear flowering could provide shelter for *C. pyri* nymphs from adverse weather conditions, agrochemical sprays and natural enemies earlier in the year (Reeves et al., 2022, 2024). Changes in voltinism and diapause, were also potential concerns for pear psyllid management; as number of generations per year vary depending on climate (Civolani et al., 2023), thus warmer temperatures could lead to more generations per year and prolonged oviposition periods and greater crop damage.

Chapter 2 demonstrates that pear flowering phenology has advanced significantly since the 1980s, with full flowering times becoming 11.44 days (± 14.16, SD) earlier compared to historical data. This advancement was apparent in all 12 of the cultivars and the flowering stages analysed. Furthermore, flowering times are predicted to advance by 2080 under all RCP scenarios, with full flowering time becoming 18.5 days earlier under RCP8.5. This predicated advancement in pear flowering time is supported by multiple phenological studies (Drepper et al., 2020; Guédon & Legave, 2008; Sparks et al., 2005). Sparks et al. (2005) indicated that for every 1°C of warming for January-March temperatures, pear flowering was 7.2 days earlier, which is similar to values found in our models. The chapter also draws attention to potential impacts of earlier flowering in an agroecosystem; including altering the timing of application for agrochemical sprays (Paltineanu & Chitu, 2020), likelihood of spring frost damage to blossoms (Sunley et al., 2006), the chance of plant-pollinator phenological mismatches (Kőrösi et al., 2018) and the potential for flower buds to provide shelter for nymphs earlier in the year (Reeves et al., 2024; Solomon et al., 1989).

Chapter 3 focuses on a natural enemy activity, behaviour and functional responses under different temperature scenarios, determining whether the anthocorid *A. nemoralis* is still an efficient predator of *C. pyri*, under predicted UK temperature regimes. This natural enemy is often mass released by pear growers within the UK (Reeves et al., 2024), thus it is necessary to consider the efficacy of this biocontrol agent under future temperature scenarios. Important discoveries from this chapter are that *A. nemoralis* females consumed more *C. pyri* nymphs than males, under all temperature regimes tested. Higher temperatures had a significant impact on anthocorid behaviour, *A. nemoralis* adults spent significantly more time moving in the 18 °C treatment, compared to the 21 and 23 °C treatments, with significant differences also found for antennating and cleaning behaviours. However, despite this prey consumption and attack rate did not significantly differ between temperature regimes tested. This could suggest that *A. nemoralis* adults are still likely to be effective predators of *C. pyri*, depending on how C. pyri populations respond to elevated temperatures. Although it should be noted that these experiments occurred in small Petri dishes, thus it is recommended to assess anthocorid functional response at a larger spatial scale.

Chapter 4 focuses on the use of two natural enemy species (*A. nemoralis* and *F. auricularia*) to control pear psyllid, as increased predator diversity has been shown to enhance prey suppression in several agroecosystem studies (Snyder et al., 2008; Snyder et al., 2006; Tylianakis & Romo, 2010). However, there is a risk of intraguild predation (IGP) and interference competition, especially if both natural enemy species occupy a similar niche (Stiling & Cornelissen, 2005). Furthermore, this risk may be enhanced by temperature due to increased niche overlap (Barton & Schmitz, 2009), for example higher temperatures may lead to one predator species moving further down within the plant canopy, increasing spatial overlap. Key findings from this chapter suggest that IGP occurs unidirectionally between the two natural enemy species; earwigs consume anthocorids. However, IGP was only evident in survival analyses when natural enemies were not spatially separate and had no alternative prey. Furthermore, there was no evidence for interference competition or IGP in the microcosm experiments where natural enemies showed spatial separation, suggesting that pear growers can encourage both predators for the control of pear psyllid without losing predation efficacy. Temperature did have a significant impact on prey consumption; predators consumed more prey at the RCP 8.5 temperature regime compared to the current temperature regime. Although there was no evidence for the risk of IGP or interference competition increasing with temperature.

Chapter 5 explores phenological shifts for all three trophic levels (pears, pear psylla and natural enemies) under future RCP scenarios for 2080. This combined the pear psyllid phenology model by Schaub et al. (2005), the earwig phenology model by Moerkens et al. (2011) and the PhenoFlex flowering model by Luedeling et al. (2021), to identify potential phenological mismatches. Results suggest that the phenology of all three trophic levels (full flowering time, first peak nymph abundance and peak earwig abundance) will advance by 2080. However not all three trophic levels are likely to advance at the same rate, predictions indicate that G1 *C. pyri* peak nymph abundance is advancing at a faster rate than full flowering phenology. Phenological synchrony between flowering time and nymph emergence is advantageous for pear psylla, as flower buds provide nymphs a shelter in which to hide (Reeves et al., 2022, 2024; Solomon et al., 1989). If peak nymph abundance date precedes flowering period, this may be optimal for growers; as it is easier to apply future agrochemical sprays and biorational compounds such as kaolin; giving a better coverage rate in the absence of foliage and targeting the population peak.

6.3 A pear agroecosystem under future climate scenarios

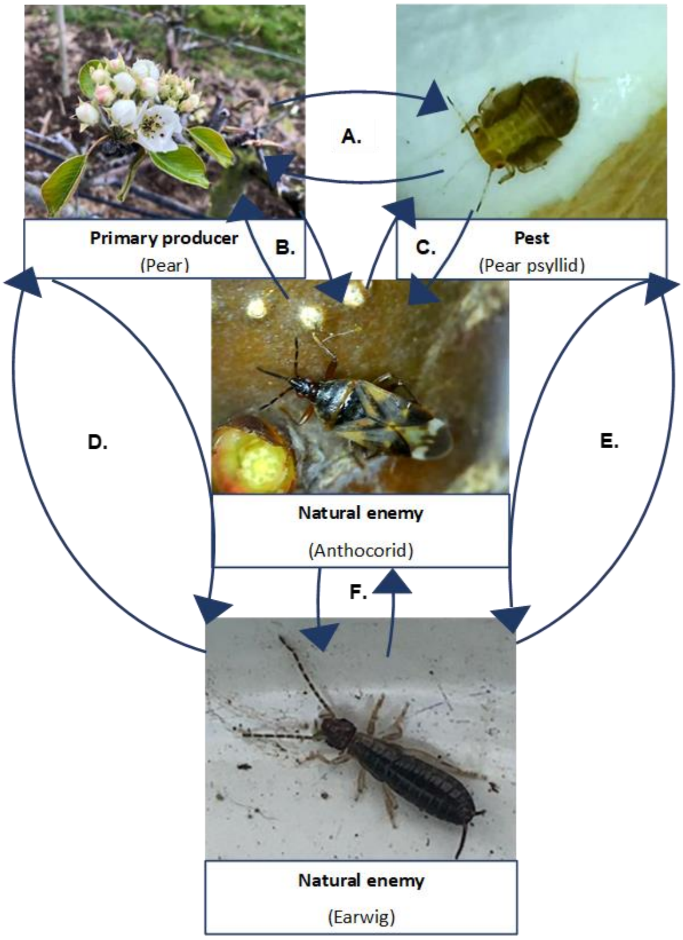


Figure 6.2: Potential interactions between primary producer (pear trees *Pyrus communis*), primary consumer and pest (pear psyllid *Cacopsylla pyri*) and secondary consumers or natural enemies: anthocorids (*Anthocoris nemoralis*) and earwigs (*Forficula auricularia*), many of which can be enhanced or altered by temperature. **A.** Interactions between primary producer a pest may include the use of flower buds and foliage for shelter, phloem feeding by pests, the use of cues to locate pear trees and enhanced chemical and physical defences in response to herbivory. **B, D.** Natural enemies' responses to plant signals may include increased migration into trees due to herbivore induced plant volatiles (HIPVs). **C, E.** Natural enemies' responses to pests may include increased migration into orchards in response to their chemical cues and prey switching to the most abundant food source, whilst prey may change their position in the orchard canopy to avoid predators. **F.** Potential interactions between natural enemies include intraguild predation and interference competition, due to lack of spatial separation or food source, or changes in behaviour to avoid other predator species.

The pear agroecosystem could face multiple challenges in the context of climate change. Most notably is the shift in flowering time; linear mixed models (Chapter 2) predict an 18.5-day advancement in full flowering time for *P. communis* by 2080, under the most extreme RCP8.5 scenario, with similar shifts observed for other phenological stages (first, 10% flowering and last), shifts were also observed for less intense RCP2.6, RCP4.5 and RCP6.0 emissions scenarios. This is also supported by the PhenoFlex model (Chapter 5), which considers both chilling and forcing times, based on hourly temperature data, which may be a more accurate. The model predicted a significant advancement for *P. communis* cv. Conference under the RCP8.5 emission scenario. Any advancement in flowering time may be a risk for pear growers; as earlier flowering could increase the risk of exposure to spring frost, resulting in an increased risk of injury (Augspurger, 2013; Eccel et al., 2009; Unterberger et al., 2018). In addition, there is the potential for plant-pollinator mismatches due to earlier flowering, which can significantly reduce fruit set and crop yield (Gérard et al., 2020; Kudo & Ida, 2013). Wyver et al. (2023), found a variable mismatch between UK peak pollinator flight and peak flowering dates over time, after the mid-1980s apple flowering phenology advanced more rapidly, but pollinator phenology remained stable. Thus, there is a similar concern for pears, which as an earlier flowering top fruit, may be more prone to mismatches. Lastly, advances in flowering time could provide more shelter for *C. pyri* nymphs in flower buds, protecting them from agrochemical sprays, harsh weather conditions and natural enemies (Reeves et al., 2022, 2024). Thus, phenological synchrony between flowering time and peak nymph abundance may be optimal for *C. pyri*. G1 *C. pyri* peak nymph abundance and flowering time, show overlap under the RCP8.5 emissions scenario, which may be beneficial for psyllid nymphs. However, after 2071 *C. pyri* nymph emergence is predicted to precede full flowering, which could be more beneficial for growers.

In addition to earlier flowering times, the phenology of pests and natural enemies should also be considered; *C. pyri* (G1 nymph and G2 egg, nymph and adult) and *F. auricularia* abundance date (stage 4 nymph and adult) was predicted to advance under the RCP8.5 scenario (Chapter 5). However, both stage 4 *F. auricularia* nymphs and G2 psyllid nymphs showed phenological synchrony, as both shifted at a similar rate under current and RCP8.5 scenarios, therefore a phenological mismatch is unlikely. Phenological synchrony is important between pests and natural enemies (Damien & Tougeron, 2019; Evans et al., 2013). However, the resistance and resilience of an agroecosystem to mismatches can be dependent on multiple factors: whether the natural enemy is a generalist or a specialist, the number of alternative predator or parasitoid species present, spatial heterogeneity and phenotypic plasticity of the predator or pest, allowing adaptation to climatic changes (Abarca & Spahn, 2021; Damien & Tougeron, 2019). Alongside the predicted phenological synchrony between *F. auricularia* and pear psyllid nymphs, earwigs are generalist predators (Dib et al., 2011), often switching between different prey species within orchards when others are unavailable (Quach, 2019); thus they may be less vulnerable to phenological mismatches with respect to prey availability. On the other hand, parasitoids may be more vulnerable to phenological mismatches; as they require phenological synchrony in order to oviposit within a specific host species, during a susceptible stage of their lifecycle (Abarca & Spahn, 2021; Damien & Tougeron, 2019; Wetherington et al., 2017). This is evident in an experiment by Wetherington et al. (2017); which monitored rates of parasitism of the emerald ash borer (*Agrilus planipennis*) by the egg parasitoid (*Oobius agrili*) at different temperatures, findings indicated that moderate temperature increases altered parasitoid emergence times, decreasing parasitism and survival rates. *Trechnites insidiosus* is an important parasitoid wasp, that is specific to pear psylla (Le Goff et al., 2021; Tougeron et al., 2021), thus could be more vulnerable to phenological mismatches. Although one advantage is that *T. insidiosus* has the ability to oviposit in all 5 nymphal instars (Le Goff et al., 2021; Tougeron et al., 2021), this gives a greater time window for phenological synchrony, as long as *C. pyri* nymphs are present, highlighting the importance of developing a phenological model for *T. insidiosus*, as well as further research into its use as a commercial biocontrol agent.

It is important to consider how behaviour and interactions of natural enemy species may change under future climate scenarios. In Chapter 4, anthocorid functional response did not significantly differ with temperature for females, whilst for males the handling time was significantly shorter at elevated temperatures. Moreover, there was no difference in velocity or distance travelled overall depending on temperature, suggesting that *A. nemoralis* travels similar distances. A high walking velocity is important for a biological control agent, allowing a predator to seek out prey items effectively, especially if prey is sparse (Milton, 2004). Therefore, this response to elevated temperature suggests *A. nemoralis* will still be an effective natural enemy under future climate scenarios. However, *A. nemoralis* did spend significantly less time grooming under the RCP8.5 temperature regime. A reduction in cleaning behaviour may increase the risk of disease; grooming is an important sanitary behaviour, involved in reducing the risk of pathogenic infection, including parasites and fungal pathogens (De Roode & Lefèvre, 2012; Zhukovskaya et al., 2013). The response of *F. auricularia* to elevated temperatures suggest it will continue to be an effective predator; consuming an average of 43.7 *C. pyri* nymphs over 24hrs, under the RCP8.5 temperature regime compared to 36.0 under current temperatures, whilst showing no significant differences in all other behaviours observed.

6.4 Risk mitigation in the context of orchard management

These potential implications lead to the question of how growers can mitigate risks through orchard management. Firstly, the risk of spring frost due to earlier flowering; evidence suggests spring frost severity and frequency is declining in the UK and that this trend is predicted to continue under future climate scenarios (Atkinson et al., 2004, Sunley et al., 2006), thus this risk may be significantly reduced in the future. However as pear is an early flowering crop, it may be more at risk, furthermore, a single event of sub-zero temperatures can damage and often kill flower buds during the bloom phase (Eccel et al., 2009). The use of foliar applications of plant hormones, such as gibberellins, is effective method of frost protection (Drepper, 2022; Yarushnykov & Blanke, 2005). Yarushnykov & Blanke (2005) found that applying both GA_3 and GA_{4+7} at full bloom significantly increased initial and final fruit set. Furthermore, growers cultivating *P. communis* cv. Conference often use gibberellic acid to enhance fruit set (Drepper, 2022), thus the risk of frost damage is minimised as a byproduct during flowering. Although a plethora of interventions have been trialled to reduce spring frost damage; some successful techniques include sprinkler systems, wind machines and heat cannons, although these typically have a high installation and operational cost (Drepper, 2022; Vanhoutte & Remy, 2021).

The sustainable use of agrochemical and biorational products to address current and emerging challenges should also be considered within this agroecosystem. Firstly, the use of kaolin clay; a non-toxic particle film (Erler & Cetin, 2007; Nottingham & Orpet, 2021) that can deter adult psylla from colonising orchards, reduce oviposition and impair movement of nymphs via the attachment of heavy particles (Erler & Cetin, 2007; Saour et al., 2010). Nottingham & Orpet (2021) currently recommend the use of kaolin as a pre-bloom spray between February and April. In the orchards surveyed in this study the average timing of kaolin application was 30 March. The application of at least one prebloom kaolin spray is standard in many conventional orchards (Nottingham et al., 2022). Under future climate scenarios it may be optimal to have one spray when adults are becoming active, to deter them from recolonising orchards, and another spray when G1 nymphs peak; to reduce nymph mobility and increase mortality. For future kaolin application, sprays should be applied pre-bloom, as coverage can be less optimal when flowers or foliage is present (DuPont et al., 2021).

Due to withdrawl of several compounds frequently used within pear psyllid management (Hertfordshire, 2023; HSE, 2023), the need to adopt alternative management methods is apparent. Alternative management methods are discussed in Chapter 1 of the thesis, however there are benefits and limitations that need to be considered for each method. One of these alternatives is the use of oils in the pre-bloom stage, as an oviposition deterrent and repellent for *C. pyri* adults (Civolani, 2012b; Emami, 2023; Erler, 2004b). Effective oils include mineral (Civolani, 2000), cotton seed, fish-liver, neem (Erler, 2004b) and peppermint oil (Li & Tian, 2020), although some oils contain allergens making them unsuitable for UK approval. The use of reflective plastic mulch can also effectively suppress pear psyllids (Nottingham & Beers, 2020; Nottingham et al., 2022), reflecting solar light into the tree canopy (Shimoda & Honda, 2013), promoting adult flight behaviour (Nottingham & Beers, 2020) and damaging psylla eggs and nymphs (Beard, 1972). However, there are concerns that elevated UV could impact natural enemies (Nottingham & Beers, 2020).

Host resistance should be considered for future pear cultivars; Host resistance is another method of minimising damage from pear psylla populations (Nin et al., 2012; Shaltiel-Harpaz et al., 2014). Hybridisation of susceptible species with resistant ones, can be successful in increasing host plant resistance (Harris, 1973; Nin et al., 2018). Multiple intraspecific pear hybrids demonstrate high resistance to *C. pyri* infestations (Robert & Raimbault, 2004); for example the genotype NY 10355 (*Pyrus ussuriensis × P. communis*) is particularly resistant to pear psylla infestations (Harris, 1973; Nin et al., 2018; Robert et al., 1999). However, the fruit quality of hybrids are often a concern within breeding programs (Nin et al., 2012; Robert & Raimbault, 2004), highlighting the need to consider resistance, yield and fruit quality during cultivar selection.

In addition, the use of augmentative (commercial mass release) or conservation (enhancing wild populations) biological control plays an important role in the future of pear psyllid IPM (Reeves et al., 2024). The use of multiple natural enemy species is a key consideration for growers; as increased predator diversity can enhance prey suppression within the agroecosystem (Snyder et al., 2008; Snyder et al., 2006; Tylianakis & Romo, 2010). Chapter 5 suggests that the use of both anthocorids and earwigs, is feasible due to the lack of interference competition and intraguild predation when psyllid prey is present. Furthermore, it is likely that *F. auricularia* does not actively seek out anthocorids as prey, highlighted within olfactometry assays. Thus, it would be beneficial to actively encourage both earwigs and anthocorids in orchards, as they occupy different diurnal niches and are complementary to pear psyllid control. The use of artificial refuges can be beneficial for earwig populations (Solomon et al., 1999), for example Wignests provide shelter for earwig nymphs and adults (Russel-IPM, 2023; Shaw et al., 2021). Additionally natural refugia like native hedgerows (Nagy et al., 2008; Scutareanu et al., 1999), nettles (Shaw et al., 2021), cover crops (Horton et al., 2009) and wildflower strips or margins (Balzan et al., 2014; Mateos-Fierro et al., 2021), can be beneficial for *A. nemoralis* and other natural enemy species.

Alongside these two predatory species, parasitoids have potential as part of *C. pyri* management. *Trechnites insidiosus* is a parasitoid wasp of interest, specific to pear psylla, with the ability to oviposit in all 5 nymphal instars (Le Goff et al., 2021; Tougeron et al., 2021). Tougeron et al. (2021), proposes the release of *T. insidiosus* alongside other psyllid biocontrol agents during spring, although further research is required into its mass rearing. With respect to phenological shifts it is vital that there is synchrony between the pest and natural enemy, *T. insidiosus* prefers stage 3-4 *C. pyri* instars, although it will oviposit in all nymphal stages. Thus, a mass release when stage 3 *C. pyri* are at their peak may be optimal. Phenological synchrony is also important for anthocorids; in the study orchards, on average, *A. nemoralis* was released on 04 May and adult summerform populations peaked 04 July. However, further research is required to determine how anthocorid development is impacted by temperature, and if phenological synchrony is predicted between anthocorids and *C. pyri* under future climate scenarios.

6.5 Appendix 1: Supplementary material from Chapter 2

This appendix contains supplementary material on flowering stages, location of orchards, phenological records, additional information from PCAs and data analyses.

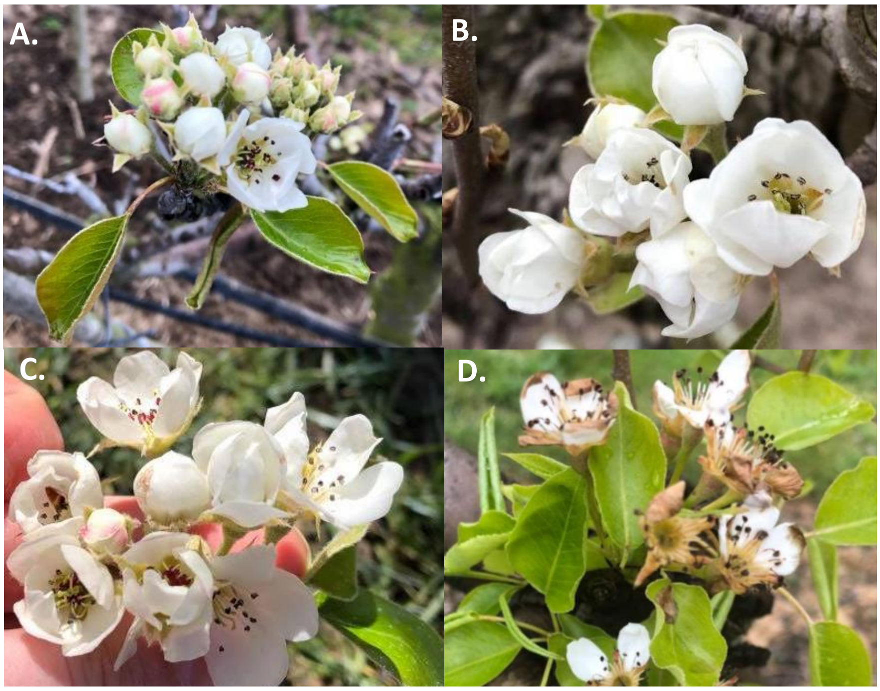


Figure S1.1: Phenological stages of pear flowering: **A.** first flowering- first flower opens on a tree or flower's anthers are visible, **B.** 10% flowering- when 10% of flowers are open on the tree **C.** full flowering- when over 50% of flowers have opened on the tree, **D.** last flowering- 90% petal fall. Full and last flowering data was collected from Brogdale and East Malling, first flowering was recorded at East Malling, 10% flowering recorded at Brogdale.

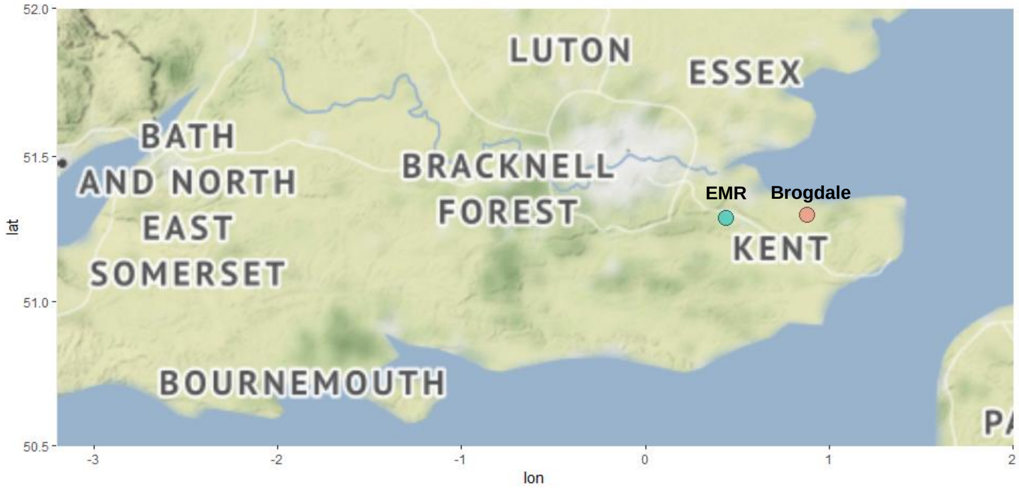


Figure S1.2: A map of South East England featuring the two fieldsites where phenological data was collected; East Malling NIAB EMR (51.2885° N, 0.4383° E) and Brogdale Collections (51.3007° N, 0.8762° E). The map was sourced from google using the get_map function and plotted with ggmap and ggplot2 packages in R.

Table S1.1: Flowering data recorded depending on site, cultivar, year and phenological stage, missing years are also noted.

Site	**Cultivars recorded**	**Years recorded**	**Phenological stages recorded**	**Missing years**
Brogdale	Beurre Hardy LA, Beurre Superfin Clapp's Favourite Conference Doyenne du Comice Durondeau LA Glou Morceau LA Louise Bonne of Jersey Nouveau Poiteau LA Packham's Triumph Precoce de Trevoux Williams' Bon-Chretien	1960-2019 (1991 missing for all cultivars.)	Ten percent flowering Full flowering Last flowering	1974, 1976 (BH) 1973, 1974, 1977, 1980, 1990 (BS) 1973, 1974, (CF) 1973, 1974, 2001-2004 (Du) 1960, 1973, 1974 (GM) 1973, 1974, 1977, 1980, 1990 (LB) 1974, 1975, 1984-1987, 1990, 1992 (NP) 1974, 1978, 1983-1987, 1990, 1992 (PT) 1973, 1977, 1980, 1982, 1990 (PdT)
East Malling	Conference Doyenne du Comice	1960-2020 (No missing years for any cultivars)	First flowering Full flowering Last flowering	No years missing

Table S1.2: Weather data collated depending on site and year, missing years and replacements are also noted.

Site	Station used	Weather data collated	Year	Weather data calculated	Missing years and replacements
Brogdale	Faversham (51.297° N, 0.878° E)	daily maximum and minimum temperature daily rainfall	1959-2019	Mean monthly temperature Total monthly rainfall Total monthly frost days	March 1990-April 1998 temperature data replaced by Charing station (51.197° N, 0.782° E). 1959-1960 missing rainfall data replaced by Whitstable (51.358° N, 1.032° E).
East Malling	East Malling (51.288° N, 0.448° E)	daily maximum and minimum temperature daily rainfall	1959-2020	Mean monthly temperature Total monthly rainfall Total monthly frost days	July 1998 to November 1999 temperatures replaced by Goudhurst weather station (51.077° N, 0.46° E).

Table S1.3: Average first flowering dates ± SE (standard error) in Julian days depending on time period (1960-1989 compared to 1990-2020) and cultivar.

Cultivar	Average first flowering date (1960-1989) ± SE	Average first flowering date (1990-2020) ± SE	Difference (days) ± SE
Conference	105.40 ± 1.37	98.26 ± 1.23	-7.14 ± 1.84
Doyenne du Comice	111.59 ± 1.15	103.00 ± 1.13	-8.59 ± 1.61
Average of all Cultivars	108.52 ± 0.93	100.61 ± 0.86	-7.91 ± 1.27

Table S1.4: Average ten percent flowering dates ± SE (standard error) in Julian days depending on time period (1960-1989 compared to 1990-2019) and cultivar.

Cultivar	Average 10% flowering date (1960-1989) ± SE	Average 10% flowering date (1990-2019) ± SE	Difference (days) ± SE
Beurre Hardy (LA)	111.46 ± 2.01	100.58 ±1.8	-10.88 ± 2.70
Beurre Superfin	111.81 ± 2.56	101.78 ± 1.78	-10.03 ± 3.11
Clapp's Favourite	114.04 ± 1.80	102.66 ± 1.75	-11.38 ± 2.51

Conference	109.63 ± 2.11	101.93 ± 1.93	-7.70 ± 2.86
Doyenne du Comice	116.27 ± 1.79	106.62 ± 1.72	-9.65 ± 2.48
Durondeau (LA)	111.00 ± 2.16	102.44 ± 2.00	-8.56 ± 2.94
Glou Morceau (LA)	114.93 ± 2.42	102.38 ± 1.84	-12.55 ± 3.04
Louise Bonne of Jersey	107.38 ± 2.54	97.57 ± 1.86	-9.81 ± 3.15
Nouveau Poiteau (LA)	116.42 ± 2.04	104.67 ± 1.67	-11.75 ± 2.64
Packham's Triumph	106.26 ± 2.51	100.15 ± 1.87	-6.11 ± 3.13
Precoce de Trevoux	105.31 ± 2.79	96.54 ± 1.82	-8.77 ± 3.33
Williams' Bon-Chretien	112.70 ± 1.76	101.59 ± 1.73	-11.11 ± 2.47
Average of all Cultivars	111.40 ± 0.65	101.58 ± 0.53	-9.82 ± 0.84

Table S1.5: Average full flowering dates ± SE (standard error) in Julian days depending on time period (1960-1989 compared to 1990-2020) and cultivar.

Cultivar	**Average full flowering date (1960-1989) ± SE**	**Average full flowering date (1990-2020) ± SE**	**Difference (days) ± SE**
Beurre Hardy (LA)	117.82 ± 1.90	103.86 ± 1.78	-13.96 ± 2.61
Beurre Superfin	117.57 ± 2.36	104.46 ± 1.75	-13.11 ± 2.94
Clapp's Favourite	118.76 ± 1.80	105.21 ± 1.72	-13.55 ± 2.49
Conference	113.51 ± 1.02	104.16 ± 0.93	-9.35 ± 1.38
Doyenne du Comice	119.55 ± 0.87	109.20 ± 0.91	-10.35 ± 1.26
Durondeau (LA)	115.43 ± 1.96	105.04 ± 1.97	-10.39 ± 2.78
Glou Morceau (LA)	118.96 ± 1.89	105.07 ± 1.81	-13.89 ± 2.62
Louise Bonne of Jersey	112.23 ± 2.49	100.39 ± 1.82	-11.84 ± 3.08
Nouveau Poiteau (LA)	121.54 ± 1.88	107.78 ± 1.70	-13.76 ± 2.54
Packham's Triumph	111.39 ± 2.26	102.85 ± 1.89	-8.54 ± 2.95
Precoce de Trevoux	110.54 ± 2.44	99.57 ± 1.80	-10.97 ± 3.03
Williams' Bon-Chretien	117.97 ± 1.75	104.03 ± 1.72	-13.93 ± 2.45
Average of all Cultivars	116.38 ± 0.49	104.94 ± 0.44	-11.44 ± 0.66

Table S1.6: Average last flowering dates ± SE (standard error) in Julian days depending on time period (1960-1989 compared to 1990-2020) and cultivar.

Cultivar	**Average last flowering date (1960-1989) ± SE**	**Average last flowering date (1990-2020) ± SE**	**Difference (days) ± SE**
Beurre Hardy (LA)	128.46 ± 1.69	116.03 ± 1.65	-12.43 ± 2.36
Beurre Superfin	128.12 ± 2.01	115.96 ± 1.58	-12.15 ± 2.56
Clapp's Favourite	127.58 ± 1.65	115.59 ± 1.58	-11.99 ± 2.29
Conference	124.92 ± 0.86	114.92 ± 0.90	-9.99 ± 1.25
Doyenne du Comice	129.72 ± 0.80	118.90 ± 0.84	-10.82 ± 1.16
Durondeau (LA)	126.25 ± 1.80	114.60 ± 1.73	-11.65 ± 2.50
Glou Morceau (LA)	130.85 ± 1.73	118.07 ± 1.74	-12.78 ± 2.45
Louise Bonne of Jersey	120.85 ± 2.29	109.75 ± 1.69	-11.10 ± 2.85
Nouveau Poiteau (LA)	130.29 ± 1.86	118.19 ± 1.62	-12.11 ± 2.46
Packham's Triumph	121.43 ± 1.92	112.74 ± 1.83	-8.69 ± 2.65
Precoce de Trevoux	119.54 ± 2.38	110.00 ± 1.64	-9.54 ± 2.89
Williams' Bon-Chretien	128.27 ± 1.70	114.69 ± 1.58	-13.58 ± 2.32
Average of all Cultivars	126.71 ± 0.45	115.49 ± 0.42	-11.22 ± 0.61

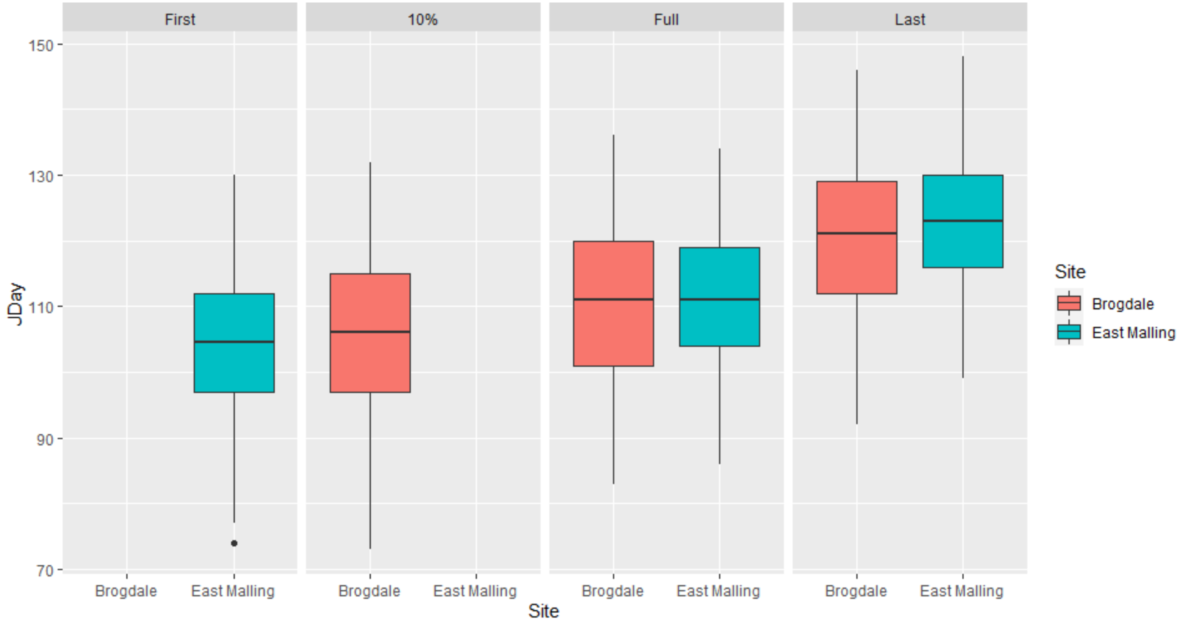


Figure S1.3: A Boxplot of first, 10%, full and last flowering times (in Julian days) depending on Site: East Malling NIAB EMR (51.2885° N, 0.4383° E) and Brogdale Collections (51.3007° N, 0.8762° E), data collected from

Brogdale (1960-2019) and East Malling (1960-2020). First flowering data was only collected from East Malling whilst 10% flowering was only collected from Brogdale.

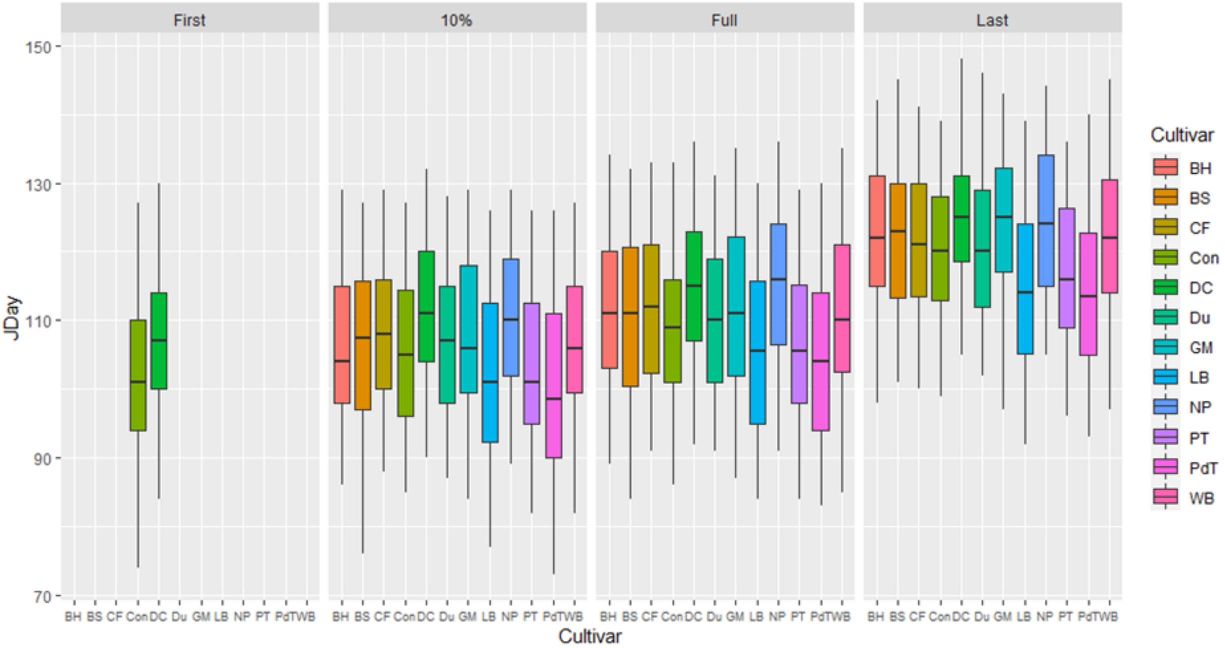


Figure S1.4: A Boxplot of first, 10%, full and last flowering times (in Julian days) depending on Cultivar: Beurre Hardy LA (BH), Beurre Superfin (BS), Clapp's Favourite (CF), Conference (Con), Doyenne du Comice (DC), Durondeau LA (Du), Glou Morceau LA (GM), Louise Bonne of Jersey (LB), Nouveau Poiteau LA (NP), Packham's Triumph (PT), Precoce de Trevoux (PdT) and Williams' Bon-Chretien (WB) data collected from Brogdale (1960-2019) and East Malling (1960-2020).

6.5.1 Effect of temperature, frost, and rainfall- PCA Analysis

Temperature PC1 explained 24.5% of the variation in the dataset for first flowering, 30.28% for ten percent flowering, 28.49% for full flowering and 28.49% for last flowering. The first 11 principal components (PCs) explained over 90% of the variation for all four flowering times. Loadings for TempPC1 and TempPC2 on maximum, minimum and mean daily temperatures for each month are shown for flowering times (Figure S1.5-S1.8). The direction and length of the vectors (arrows) in the biplot show the variance explained by each monthly temperature (max, min and mean). PC1 had positive loadings for all monthly temperature variables, with colder years being associated with negative values. Conversely, PC2 had loadings that were dependent on season; for ten percent, full, and last flowering negative values were associated with December to March temperatures. Positive values were associated with June to November temperatures (maximum, minimum and mean), with colder winters and warmer summers/autumns associated with positive values.

For the PCA analysis on rainfall PC1 explained 15.99% of the variation in the dataset for first flowering, 16.21% for ten percent flowering, 15.95% for full flowering and 15.92% for last flowering. The first 10 principal components (PCs) explained over 90% of the variation for all four different flowering times. Loadings for RainPC1 and RainPC2 on total rainfall for each month for flowering times are in Figure S1.5-S1.8. The direction and length of the vectors (arrows) in the biplot show the variance explained by each month. PC1 had positive loadings for September-March and negative values for June-August, with wetter years with drier summers being associated with positive values for first flowering, this was the same for ten percent, full and last flowering (although August was a positive value). For PC2 all loadings were negative apart from September for first flowering, therefore wetter years with a drier September were associated with more negative loadings, the same was seen for ten percent, full and last flowering (except May was also negative).

Frost explained 20.84% of the variation in the dataset for first flowering, 22.95% for ten percent flowering, 22.07% for full flowering and 22.10% for last flowering. The first 7 principal components (PCs) explained over 90% of the variation for all four different flowering times. Loadings for FrostPC1 and FrostPC2 on total frost days for each month for flowering times are in Figure S1.5-S1.8. The direction and length of the vectors (arrows) in the biplot show the variance explained by each month. PC1 had negative loadings for December-April and positive loadings for October-November for first flowering, with frostier years (higher total frost days) with milder autumns being associated with negative values, this was the same for ten percent, full and last flowering (except ten percent flowering where October was negative).

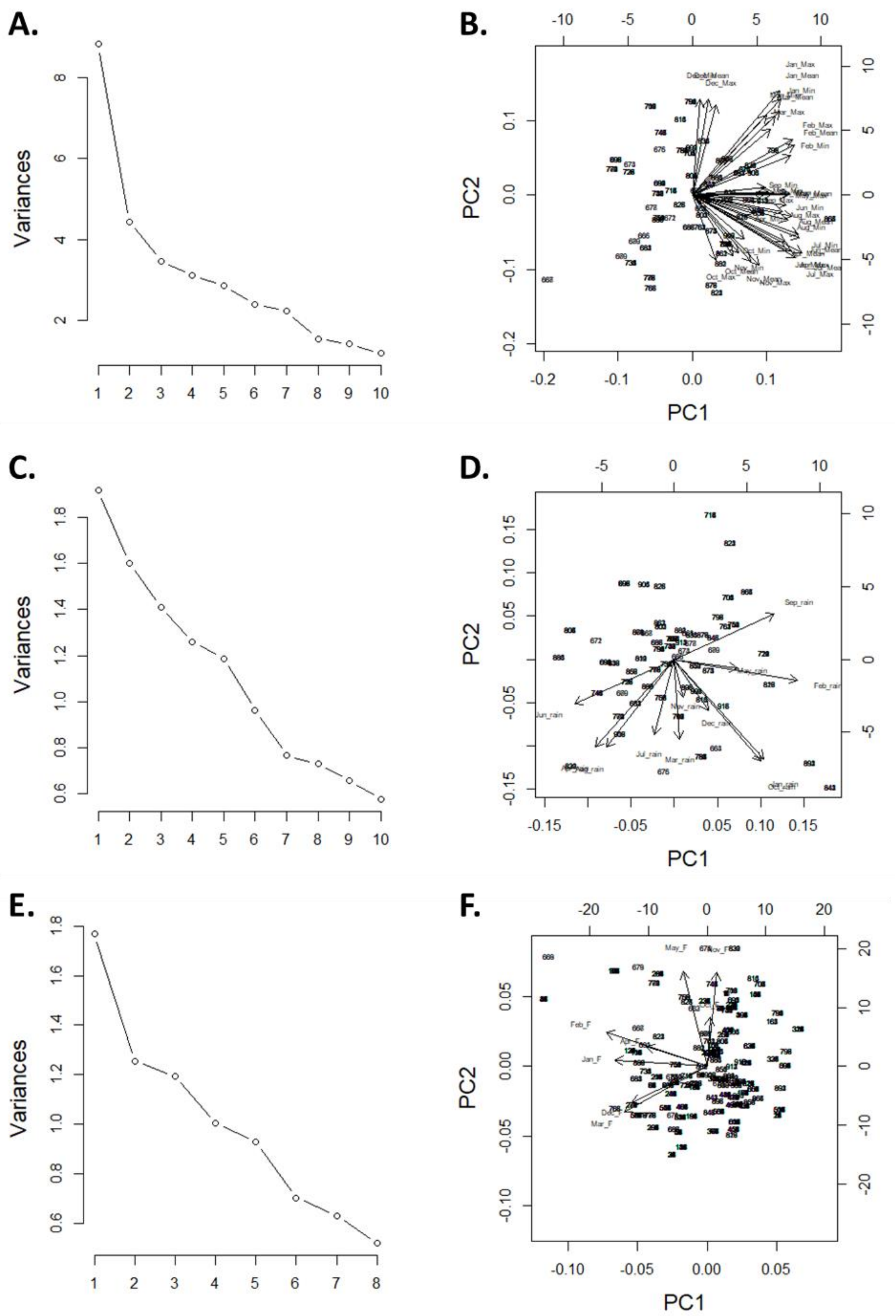


Figure S1.5: (**A**, **C**, **E**) Scree plots for temperature (**A**), rainfall (**C**) and frost (**E**), looking at the variance captured depending on principal component, for full flowering time. (**B**, **D**, **F**) Biplots for temperature (**B**), rainfall (**D**) and frost (**F**), looking at the loadings from PC1 and PC2 from the PCA analysis, for first flowering time. Red arrows represent vectors for each month, data from 1959-2020.

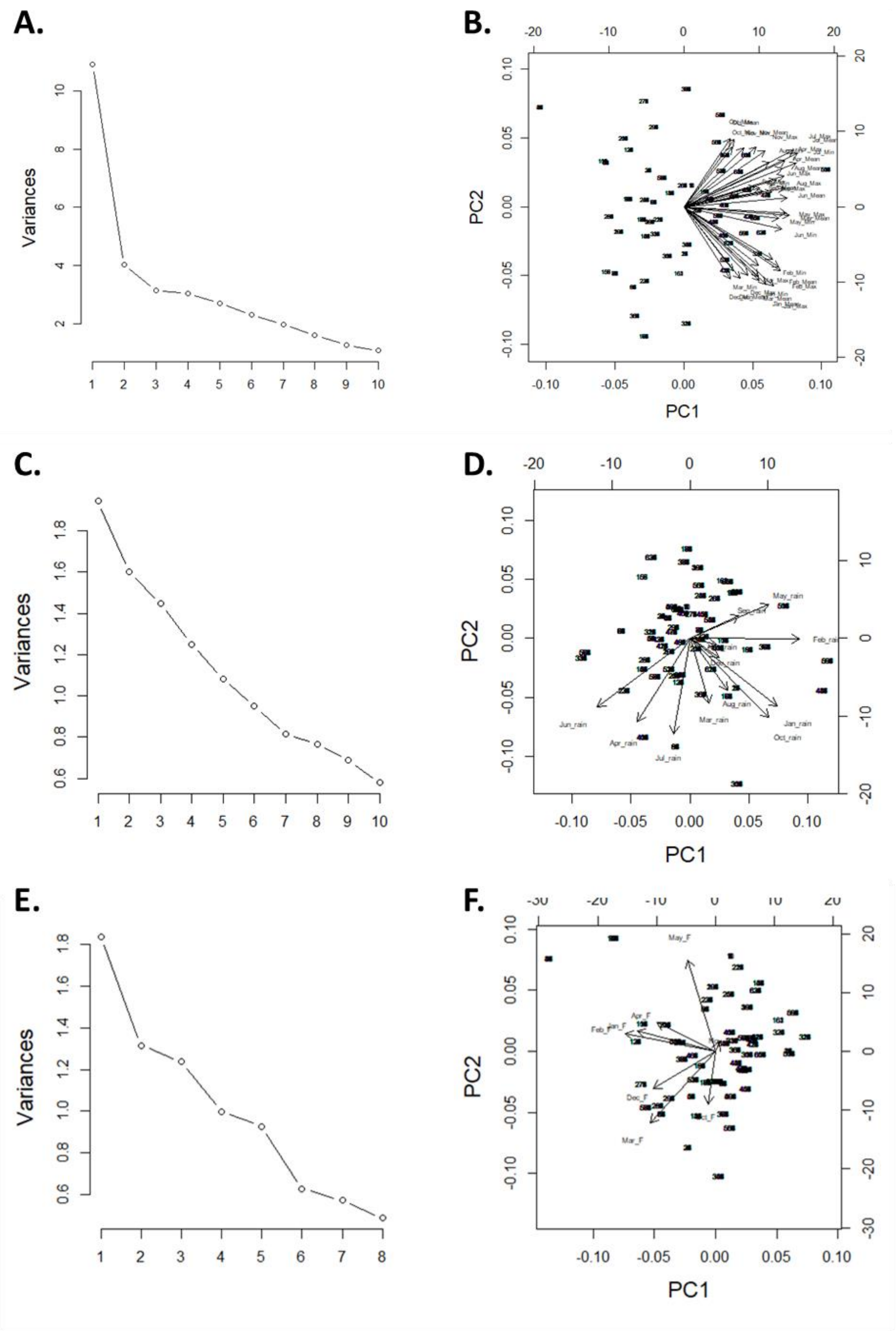


Figure S1.6: (**A**, **C**, **E**) Scree plots for temperature (**A**), rainfall (**C**) and frost (**E**), looking at the variance captured depending on principal component, for full flowering time. (**B**, **D**, **F**) Biplots for temperature (**B**), rainfall (**D**) and frost (**F**), looking at the loadings from PC1 and PC2 from the PCA analysis, for ten percent flowering time. Red arrows represent vectors for each month, data from 1959-2020.

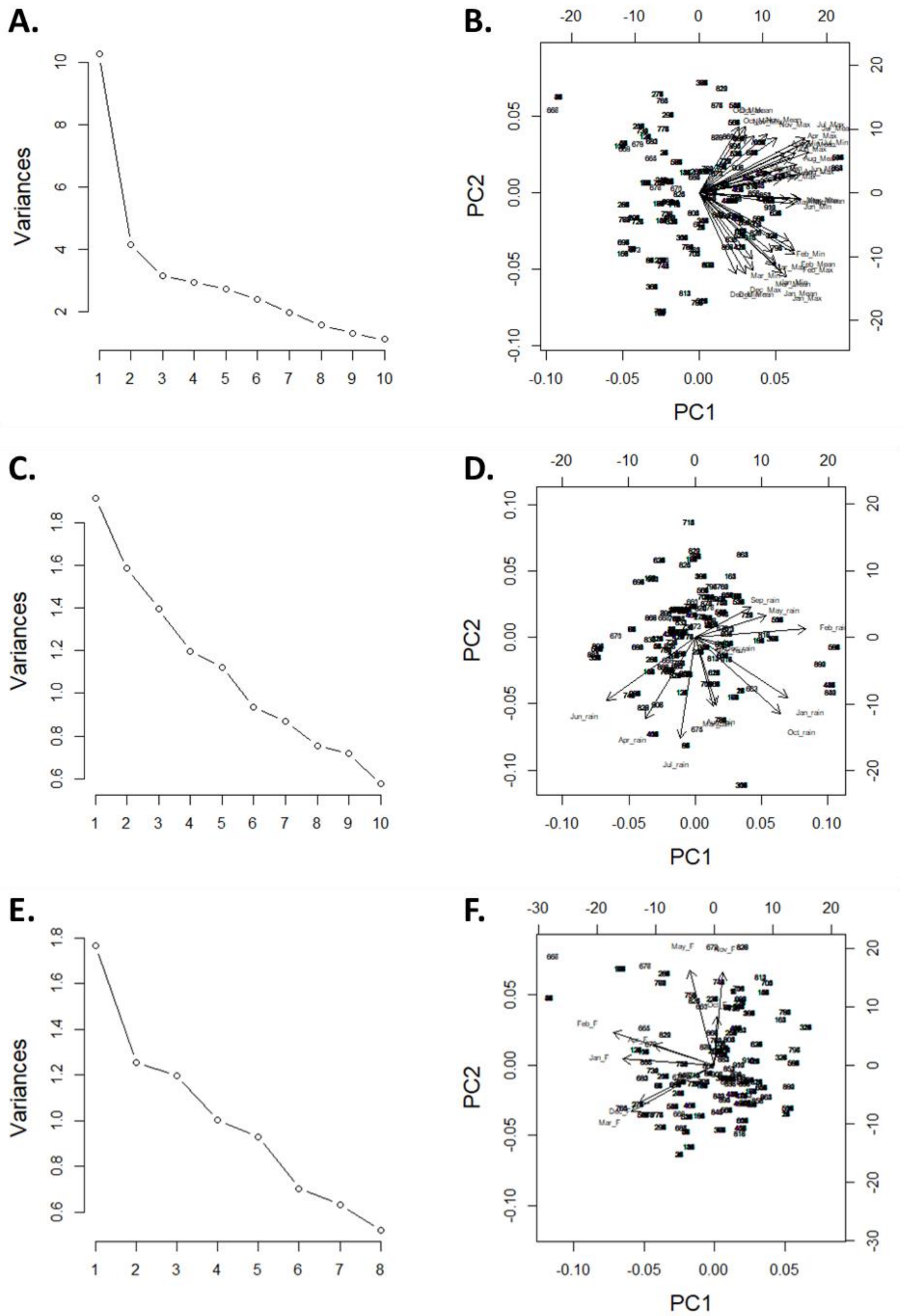


Figure S1.7: (**A**, **C**, **E**) Scree plots for temperature (**A**), rainfall (**C**) and frost (**E**), looking at the variance captured depending on principal component, for full flowering time. (**B**, **D**, **F**) Biplots for temperature (**B**), rainfall (**D**) and frost (**F**), looking at the loadings from PC1 and PC2 from the PCA analysis, for full flowering time. Red arrows represent vectors for each month, data from 1959-2020.

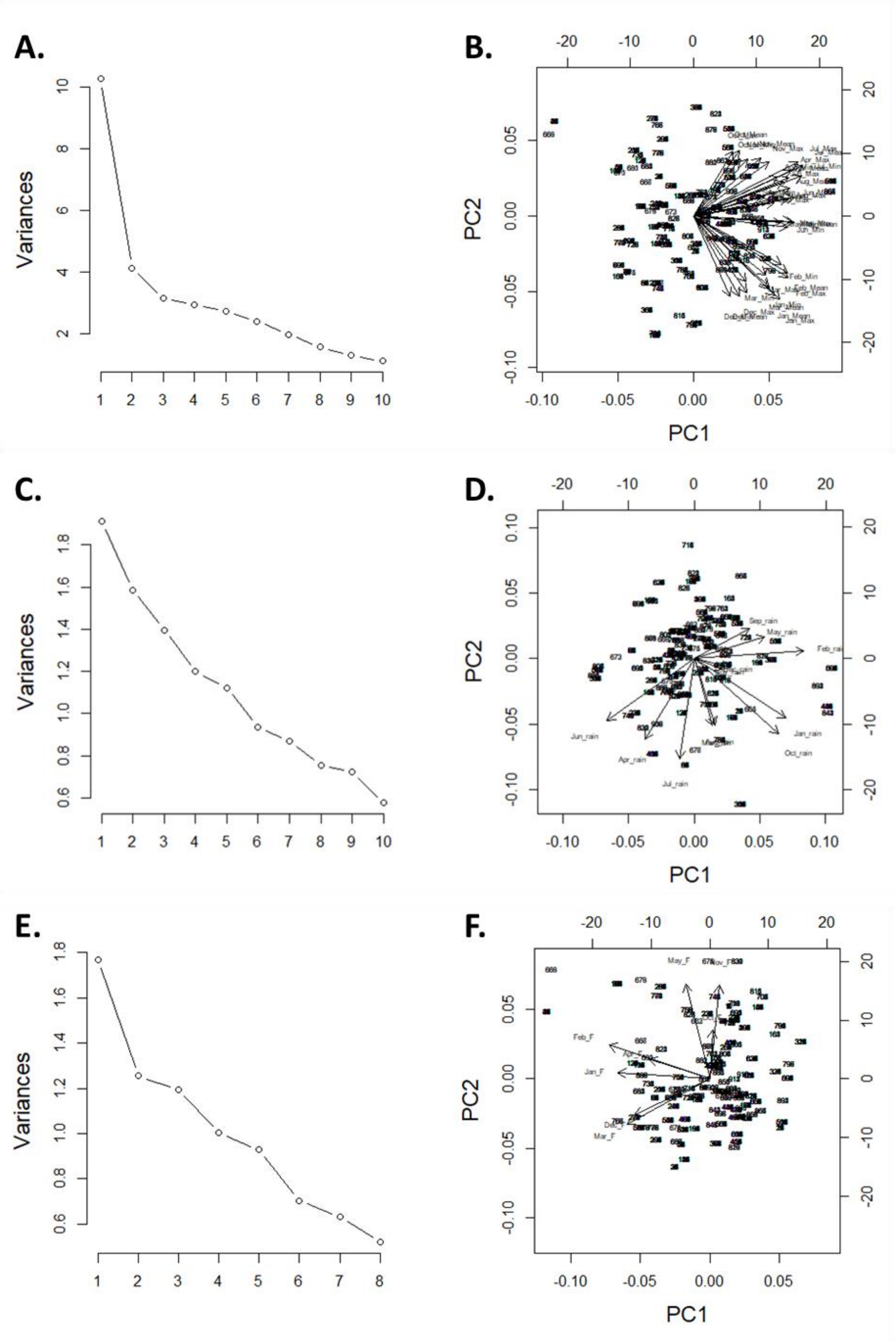


Figure S1.8: (**A**, **C**, **E**) Scree plots for temperature (**A**), rainfall (**C**) and frost (**E**), looking at the variance captured depending on principal component, for full flowering time. (**B**, **D**, **F**) Biplots for temperature (**B**), rainfall (**D**) and frost (**F**), looking at the loadings from PC1 and PC2 from the PCA analysis, for last flowering time. Red arrows represent vectors for each month, data from 1959-2020.

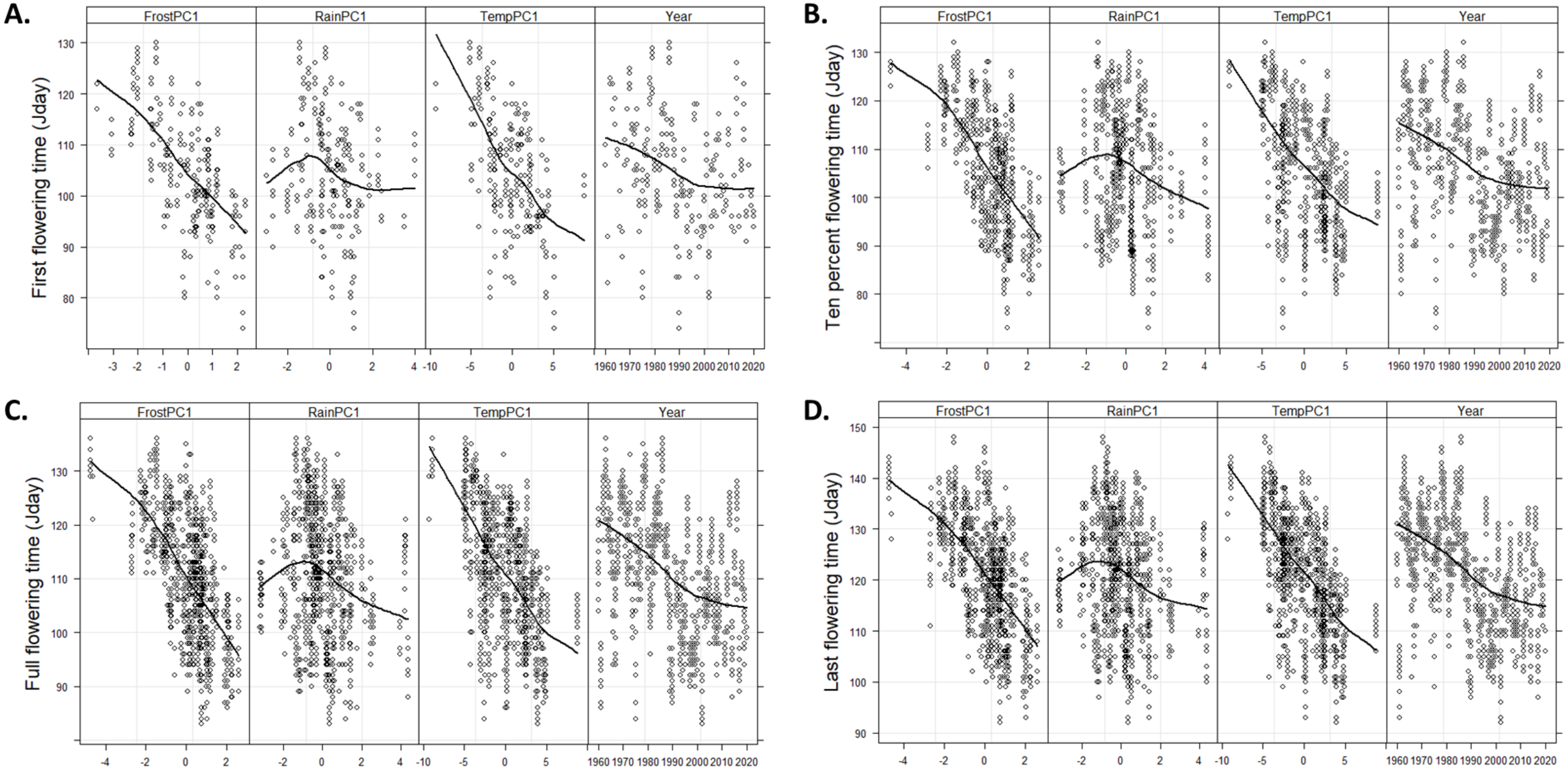


Figure S1.9: Xyplots with loess smoothers, plotting FrostPC1, RainPC1, TempPC1 (from the PCA) and year depending on first (**A**), ten percent (**B**), full (**C**) and last (**D**) flowering times, using the function my MyXyplot from highstat library version 13 in R.

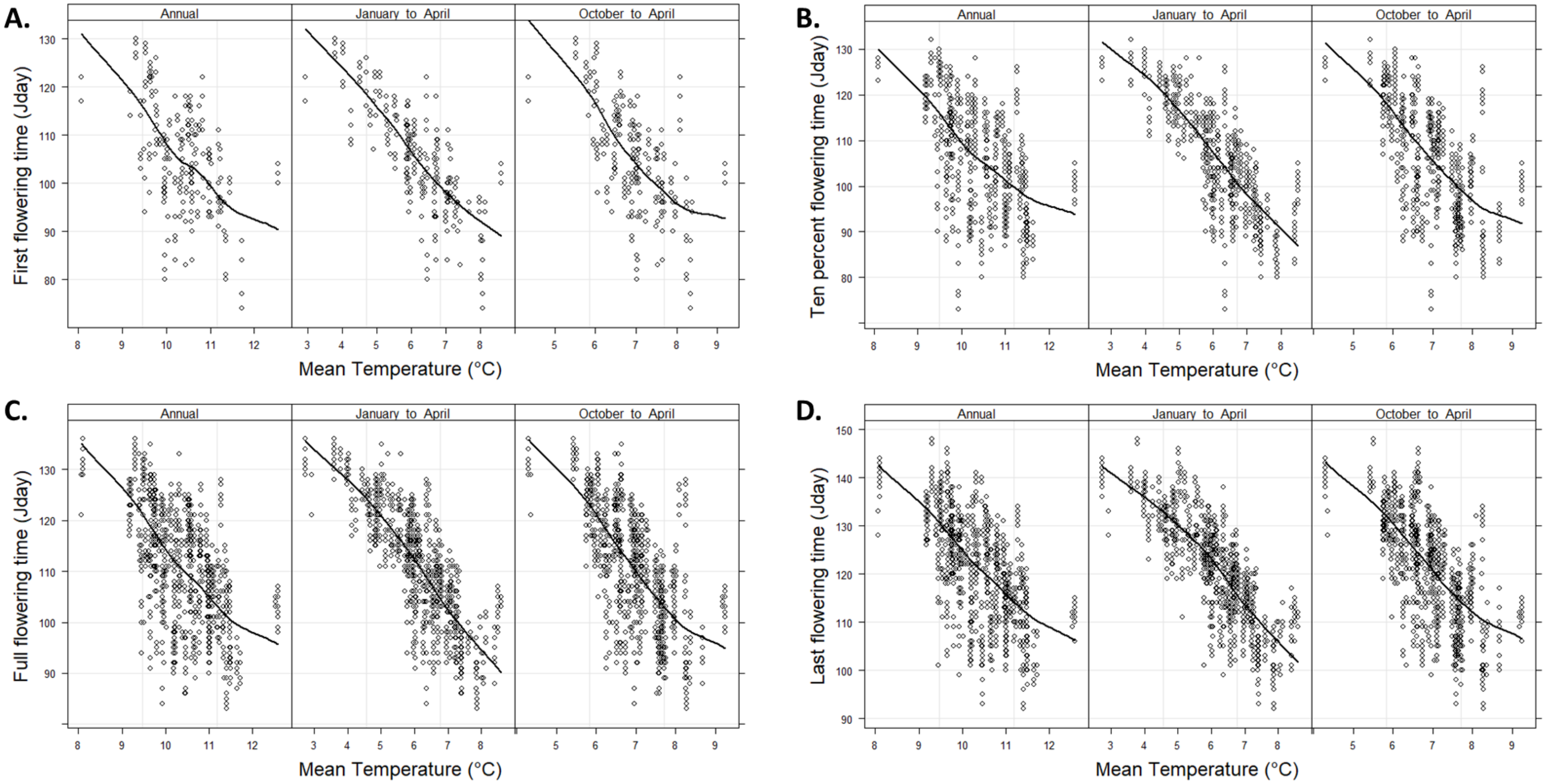


Figure S1.10: Xyplots with loess smoothers, plotting mean annual, Jan-Apr and Oct-Apr temperature (˚C) depending on first (**A**), ten percent (**B**), full (**C**) and last (**D**) flowering times, using the function my MyXyplot from highstat library version 13 in R.

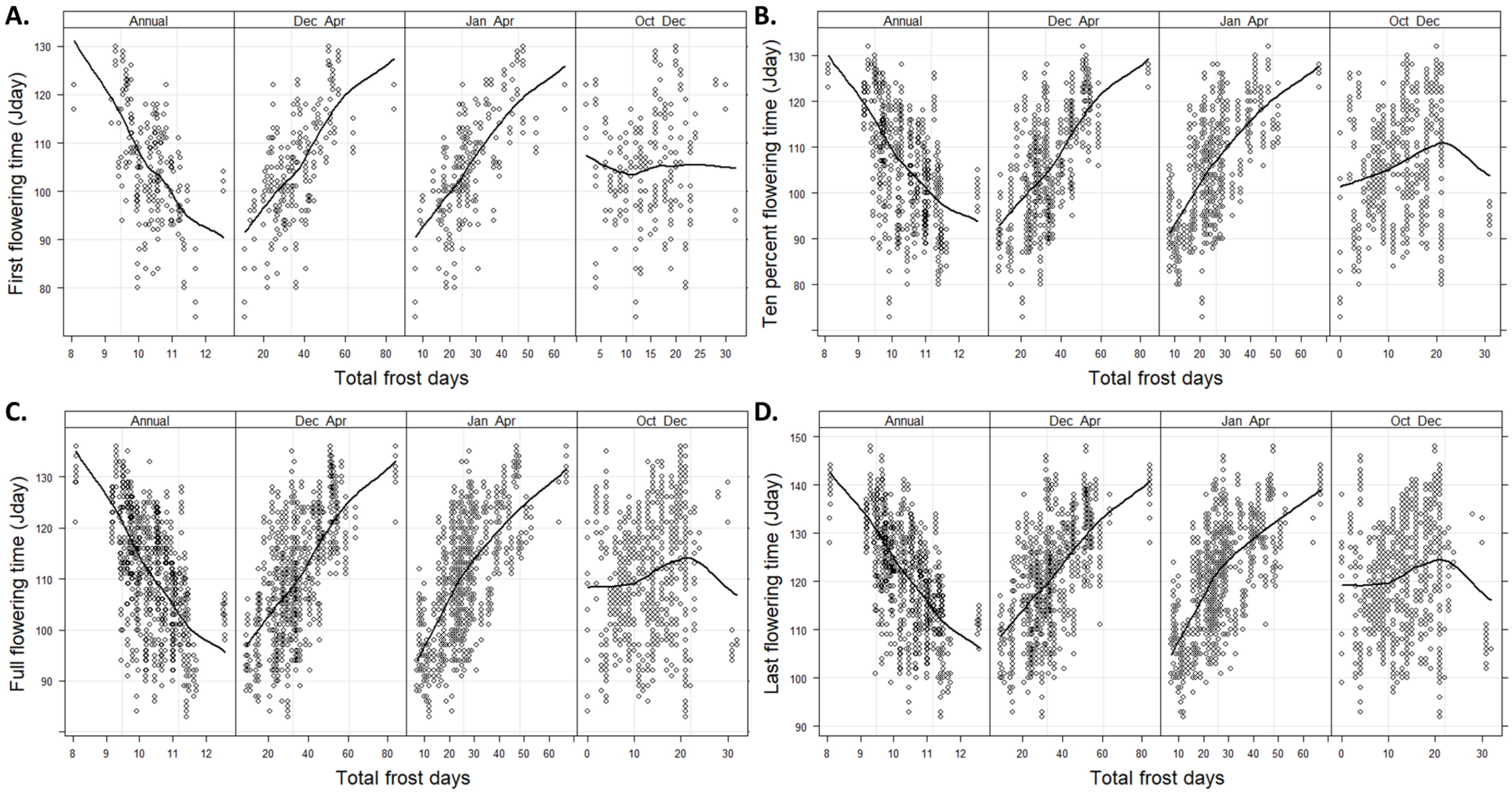


Figure S1.11: Xyplots with loess smoothers, plotting total annual, Dec-Apr, Jan-Apr and Oct-Dec frost days depending on first (**A**), ten percent (**B**), full (**C**) and last (**D**) flowering times, using the function my MyXyplot from highstat library version 13 in R.

6.6 Monitoring, thresholds and data recording

One key message for growers and agronomists is the importance of monitoring pests and beneficials, this can help optimise the timing and quantity of agrochemical sprays, biorational compounds and biological control (Mărcășan et al., 2022; Prasad & Prabhakar, 2012) and highlight when pest populations are above or likely to exceed economic thresholds (Arnaudov et al., 2012; Cross & Berrie, 2003; DuPont et al., 2023). An economic threshold is the population density at which it is more cost effective to control a pest, due to the economic losses from damage by leaving the crop untreated. For example, DuPont et al. (2023) quantified the economic injury levels for pear psylla at 0.2–0.8 for third-generation nymphs per leaf, whilst Westigard et al. (1979) quantified thresholds as below 0.2 eggs and nymphs per leaf for spring and summer psyllid populations. This highlights the importance of regular monitoring to make sure the pest population is controlled before reaching these thresholds. The monitoring method used for pear psyllid in this thesis was adapted from Cross & Berrie (2003); 30 trees were assessed in a W distribution across the orchard. Nymphs and eggs were assessed by looking at rosette and young shoot leaves under a light microscope or hand lens, or budwood if budburst had not occurred. Whilst psyllid adults and natural enemies were monitored using beat tray sampling; for more information refer to the methodology in Chapter 5. This method is a simple yet standardised approach that this thesis recommends for growers and agronomists and requires minimal equipment. Orchards should be monitored every 2 weeks before budburst until leaf fall, with weekly monitoring in the warmer summer months.

Monitoring data can also be used to optimise parameters within phenological models (Prasad & Prabhakar, 2012), allowing predictions for pest emergence and peak abundance (Belien et al., 2017; Schaub et al., 2005), helping to optimise timing of management practices. One model that was used within this thesis was the phenological model of *C. pyri* by Schaub et al. (2005), with R code created by Belien et al. (2017). UK monitoring data used in this thesis to validate model predictions for peak psyllid abundances and explore synchrony between timing of peaks and different management methods. Due to the accuracy of model predictions, this thesis recommends the use of the Schaub et al. (2005) model for predicting *C. pyri* populations within UK orchards, although the G1 predicted nymph emergence date should be shifted 14 days earlier, for calibration. Furthermore, the development or adoption of a pear psyllid pest forecasting system for growers and agronomists within the UK is highly recommended. This is readily available for much of Europe due to the Swiss forecasting tool SOPRA (Razavi et al., 2012; Samietz et al., 2007) and the decision support tool available from pcfruit (Belien et al., 2017). If the extent of either tool could be extended to the UK, this would be beneficial for growers to decide when to monitor or apply certain management methods.

6.7 Potential limitations and areas of future research

The limitations of this thesis should also be discussed, as this will allow readers to use their discretion when considering management methods for this agroecosystem and highlight gaps within this field of study. Firstly, there were limitations for the long-term and short-term monitoring data used within Chapters 1,2 and 5; the flowering data although temporally diverse (considering 12 pear varieties from 1960-2021) only considered 2 sites within Kent. Thus, predicted advancements in flowering time do not represent all regions within the UK. Although hourly temperature data is available for different UK regions, phenological data would be required to validate the model. The citizen science initiative Fruitwatch has collected phenological data for multiple tree fruit species including pear, throughout the UK since 2022 (Wyver, 2024; Wyver et al., 2024a). Therefore, if this is continued, then data collected could be used to validate phenological models predicting future shifts in pear flowering time.

The short-term monitoring data, observing weekly pear psyllid and natural enemy abundance was for 18 orchards in Kent and only from March-August 2011-2021. This emphasizes the need for long-term UK wide pest monitoring data, that is collected regularly throughout the year, to detect shifts in phenology and changes in abundance. Perhaps creating a citizen science or agronomist monitoring app ‘Pestwatch’ would be beneficial; monitoring fruit trees for their dominant pests and natural enemies. Although, this would be more labour intensive and require more training and regular sampling, it would be essential for validating phenological models, such as the pear psyllid phenology model (Schaub et al., 2005) and the earwig degree day model (Moerkens et al., 2011) and help to optimise management methods throughout the UK. Furthermore, growers and agronomists may be more incentivised if the monitoring scheme is included within paid environmental land management (ELM) schemes; this is highlighted by Wyver (2024) who recommends for phenological monitoring of crop flowering to be included within future ELM schemes, thus this could easily be extended to corresponding fruit tree pests.

In addition, there were some limitations to the phenological models used; start date or biofix date for the single brood *F. auricularia* model and the *C. pyri* phenology model used in Chapter 5 were both 01 January. As diapause can be temperature dependent for pear psylla (Horton et al., 1998) and soil temperatures can impact *F. auricularia* development over winter (Goodacre, 1998), perhaps models should incorporate winter temperatures, indicating the need for further research into an earlier biofix date. In addition, the *C. pyri* phenology model only generates an output for the first 2 generations of pear psyllid (Schaub et al., 2005), given the concerns for extended egg laying periods for *C. pyri*, overwintering nymphs and increased voltinism (Reeves et al., 2024), the model should be extended to predict psyllid phenology throughout the year. Finally, the potential to link phenological models should be discussed, as predators influence pest populations and may migrate into orchards with higher prey densities, responding to HIPVs released from infested trees (Drukker et al., 1995; Scutareanu et al., 1997), Thus, a time distributed delay model that also considers predator-prey interactions, such as those seen in the stagePop package in R (Kettle & Nutter, 2015) may be optimal. Therefore, research extending or linking current phenological models and developing phenological models for key natural enemies (including *A. nemoralis* and *T. insidiosus*), should be prioritised within the field of IPM.

The laboratory-based nature of the natural enemy studies within this thesis should considered; the microcosms used the IGP and interference were small scale, over short recording periods, so significant differences in temperature were not detected between the top and the bottom of the microcosm. Height-dependent temperature differences are often evident within a plant canopy, and pest and natural enemy species may shift their distribution because of this (Barton & Schmitz, 2009; Schmitz & Barton, 2014; Slusher et al., 2022). For example, aphids often move downwards, to a more shaded part of the canopy due to high summer temperatures (Dixon & Hopkins, 2010). Aphid parasitoids have also been shown to follow the distribution of aphids (Slusher et al., 2022). Thus, a behavioural study monitoring movement of pest and natural enemy within an orchard canopy, may capture spatial shifts more effectively than a mesocosm study alone. In addition, a field trial assessing efficacy of using both *A. nemoralis* and *F. auricularia* within pear psyllid management is also recommended, to assess the impacts of IGP and interference competition on a larger scale.

Finally, although this thesis conducted experiments on the feeding rate of natural enemy species, experiments did not occur for pear psylla. As climate change is predicted to increase feeding rates in some phloem feeders (Robinson et al., 2012; Ryan, 2012), this could lead to the secretion of more honeydew as a waste product (Blanchard et al., 2019; Blanchard et al., 2022; Sun et al., 2009), which could increase the growth of black sooty mould. Thus, research into pear psyllid feeding rate, honeydew production and composition under different temperatures should be prioritised. This could be achieved by using methods similar to Blanchard et al. (2022) for honeydew collection and Le Goff et al. (2019) for honeydew composition analysis, using a Dionex ICS-5000 Chromatography system.

7 Conclusion

To conclude this thesis emphasises the future challenges a pear-based agroecosystem could face with respect to climate change. Phenological shifts are predicted for all three trophic levels (pear flowering time, pear psyllid nymph abundance and earwig abundance date) under the high emissions scenario (RCP8.5), however the phenological synchrony between G1 *C. pyri* and full flowering time could be less beneficial to growers, as it could provide shelter for nymphs from agrochemical sprays and harsh weather conditions. Conversely, the phenology synchrony predicted between *F. auricularia* and *C. pyri* nymphs under the RCP8.5 scenario is likely to be beneficial, as there is overlap between predator and prey. This thesis also indicates how temperature is likely to change predator behaviour and interactions; under temperature regimes predicted from the RCP8.5 scenario, earwigs ate significantly more *C. pyri* nymphs. Frequency of interactions between anthocorids and earwigs did not significantly change and neither did the risk of IGP and interference competition, which may be advantageous for growers. However, these were lab-based studies in small microcosms; highlighting the importance of field-based trials as an area of future research. In a broader context this thesis recommends the collection of long-term monitoring data for multiple crop species, their dominant pest species and key natural enemies, for a UK wide database. This would help highlight phenological shifts and evaluate degree day models, in order to predict pest emergence and optimise timing of management methods, including the release of biological control agents. In addition, the collection of weather data alongside monitoring data is also required for evaluation of phenological models; especially soil temperature, due to the lack of weather stations recording this variable in Kent. This can easily be resolved by supplying orchards with data loggers and incentivising data collection via paid ELM schemes, this would include training for growers and agronomists, in order to obtain standardised data across UK growing regions.

8 Appendices

8.1 Appendix 2: Supplementary material from Chapter 3

This appendix contains supplementary material on data analyses from chapter 3 including Kruskal-Wallis tests, temperature scenarios and confidence intervals.

Table S2.1: Kruskal-Wallis tests of the significance in difference in behaviour (feeding, moving, moving leaf, cleaning, stationary and antennating), time spent in zone, number of eggs eaten, velocity and distance travelled for *A. nemoralis* depending on batch number.

Observation/behaviour	**df**	**χ^2**	**P value**
Feeding	4	5.96	0.201
Cleaning	4	10.39	**0.0342**
Antennating	4	8.48	0.0755
Moving	4	9.39	0.0522
Moving leaf	4	6.48	0.166
Velocity	4	4.33	0.362
Distance travelled	4	4.49	0.343
Time spent in Centre zone	4	5.62	0.229

Table S2.2: The July-August mean temperature predicted for the RCP 4.5 and RCP 8.5 emissions scenarios in 2080 (±SD), as well as the current July-August mean temperature (1990-2020). Also shown are the scenarios rounded to the nearest degree and the temperature/ relative humidity recorded in each of the controlled temperature cabinets during the study.

Scenario	**Temp Scenario (˚C)**	**Temp rounded (˚C)**	**Temp recorded (˚C)**	**Humidity recorded (RH)**
Current	17.78 ± 2.53	18	18.54 ± 0.72	22.41 ± 6.95
RCP 4.5	20.57 ± 2.39	21	21.40 ± 0.59	25.92 ± 7.74
RCP 8.5	22.55 ± 3.05	23	22.92 ± 0.34	24.72 ± 5.29

Table S2.3: 95% confidence intervals (CIs), provided nonparametric bootstrapping. CIs provided for three different temperature treatments (18°C, 21 °C and 23 °C), for male and female *A. nemoralis*.

Temp (°C)	**Sex**	**Coeff**	**CI (lower)**	**CI (upper)**
18	**M**	$\boldsymbol{a}$	0.033	0.152
		$\boldsymbol{h}$	2.17	4.01
21	**M**	$\boldsymbol{a}$	0.041	0.120
		$\boldsymbol{h}$	2.40	3.64
23	**M**	$\boldsymbol{a}$	0.034	0.077
		$\boldsymbol{h}$	1.86	2.82
18	**F**	$\boldsymbol{a}$	0.078	0.157
		$\boldsymbol{h}$	1.53	2.20
21	**F**	$\boldsymbol{a}$	0.113	0.216
		$\boldsymbol{h}$	1.60	2.03
23	**F**	$\boldsymbol{a}$	0.093	0.197
		$\boldsymbol{h}$	1.39	1.92

8.2 Appendix 3: Supplementary material from Chapter 4

This appendix contains supplementary material on data analyses from chapter 4 including temperature scenarios, behaviours demonstrated and olfactometer assays.

Table S3.1: Historical, current and predicted summer temperature senarios for East Malling from East Malling weather station (51.288° N, 0.448° E) in Kent. To calculate future temperatures for 2080, data was extracted using the UK Climate Projections User Interface, based on UKCP18 projections. Scenarios in bold are the ones used for our temperature regimes.

	Mean Jun-Aug temp	Mean July-Aug temp	Min Jun-Aug temp	Min July-Aug temp	Max Jun-Aug temp	Max Jul-Aug temp
Historical (1960-1989)	15.9	16.5	11.1	11.7	20.8	21.4
Current (1990-2020)	17.0	17.8	**12.1**	12.8	**22.0**	22.8
RCP 2.6 (2080)	18.8	19.7	13.5	14.2	23.6	24.6

RCP 4.5 (2080)	19.6	20.6	14.6	15.3	24.6	25.4
RCP 6.0 (2080)	19.9	21.1	14.7	15.3	24.9	25.8
RCP 8.5 (2080)	21.6	22.6	**15.9**	16.9	**26.4**	27.0

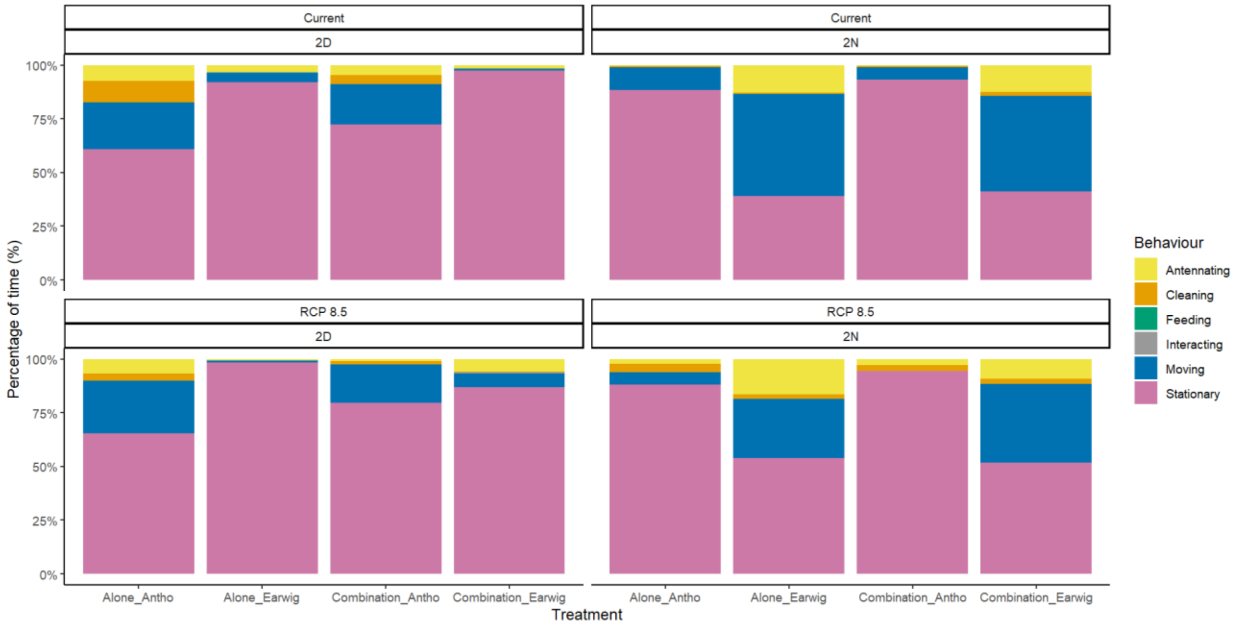


Figure S3.1: Percentage of time spent feeding, cleaning, interacting, moving and antennating for anthocorid (*A. nermoralis*) and earwig (*F. auricularia*) predators in combination (both earwig and anthocorid in the same mesocosm) and alone (a mesocosm containing only one predator), depending on temperature, for predators provided with *C. pyri* nymphs (no-food treatment).

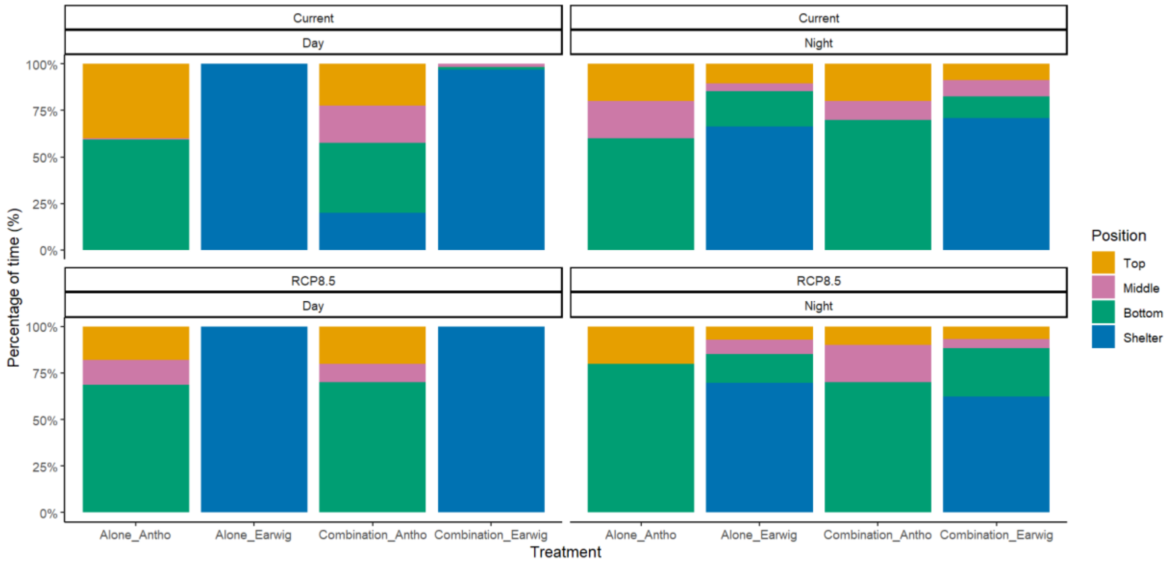


Figure S3.2: Percentage of time spent in different positions shelter, bottom, middle and top for anthocorid (*A. nermoralis*) and earwig (*F. auricularia*) predators in combination (both earwig and anthocorid in the same mesocosm) and alone (a mesocosm containing only one predator), depending on temperature, for predators provided with *C. pyri* nymphs (no-food treatment).

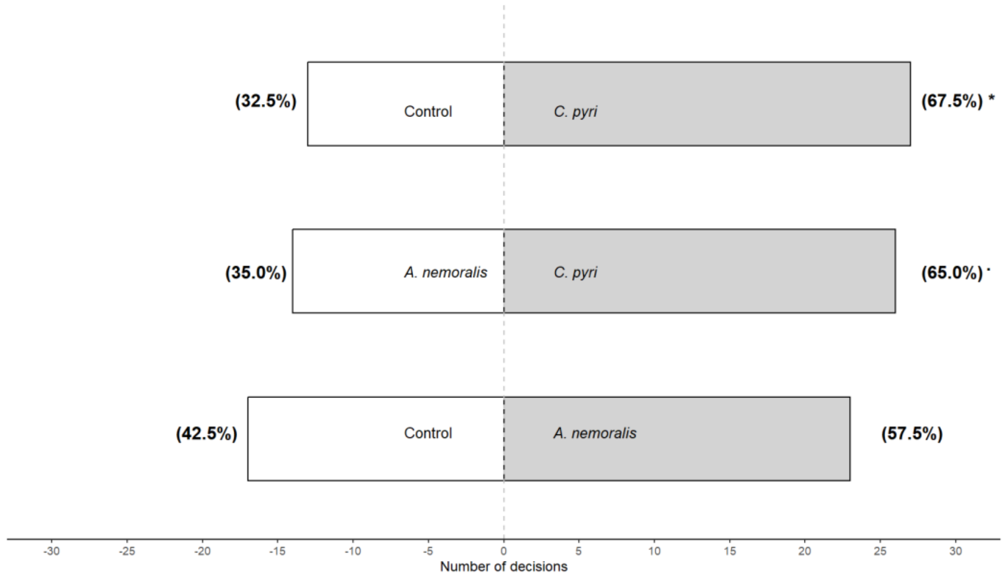


Figure S3.3: Number of decisions made by the European earwig *F. auricularia*, in olfactometer assays depending on the odour source within each arm. Choices were between 1) *C. pyri* nymphs and a control, 2) *C. pyri* nymphs and an adult *A. nermoralis* and 3) an adult *A. nermoralis* and a control. Percentages are given for each of the odour sources and significant results are marked with an asterisk, based on binomial exact tests.

8.3 Appendix 4: Supplementary material from Chapter 5

This appendix contains supplementary material on data analyses from chapter 5 including temperature response curves and GLMs of timing of phenological events and differences.

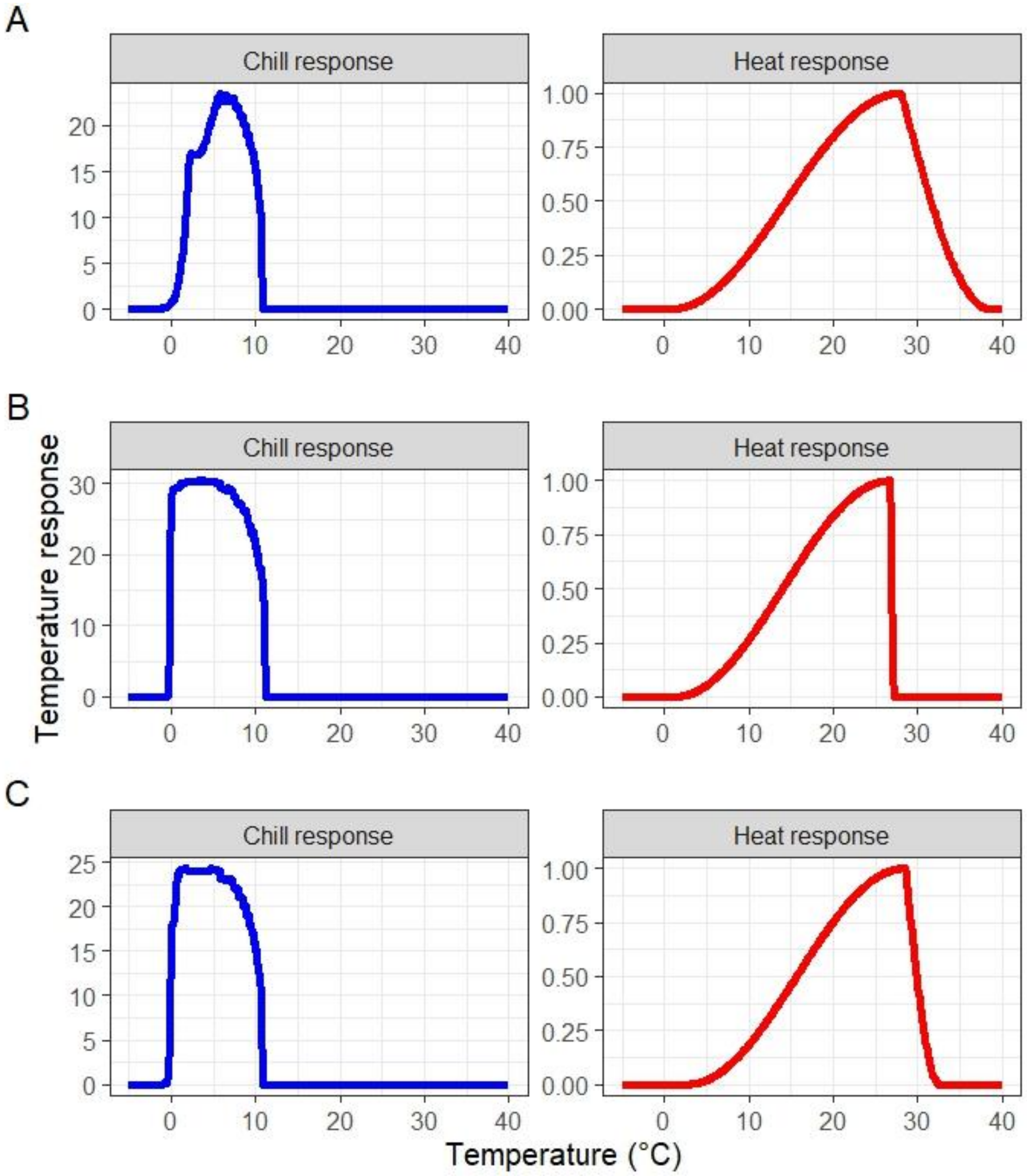


Figure S4.1: Chill and heat response curves for cv. Conference pear trees (*P. communis*), for first (A), full (B) and last (C) flowering phenology, the blue line shows absolute arbitrary units for chill effectiveness after 1,200 hours at a constant temperature between -5 ° C and 40 ° C and the red line shows heat efficiency for constant temperature between -5 °C and 30 ° C.

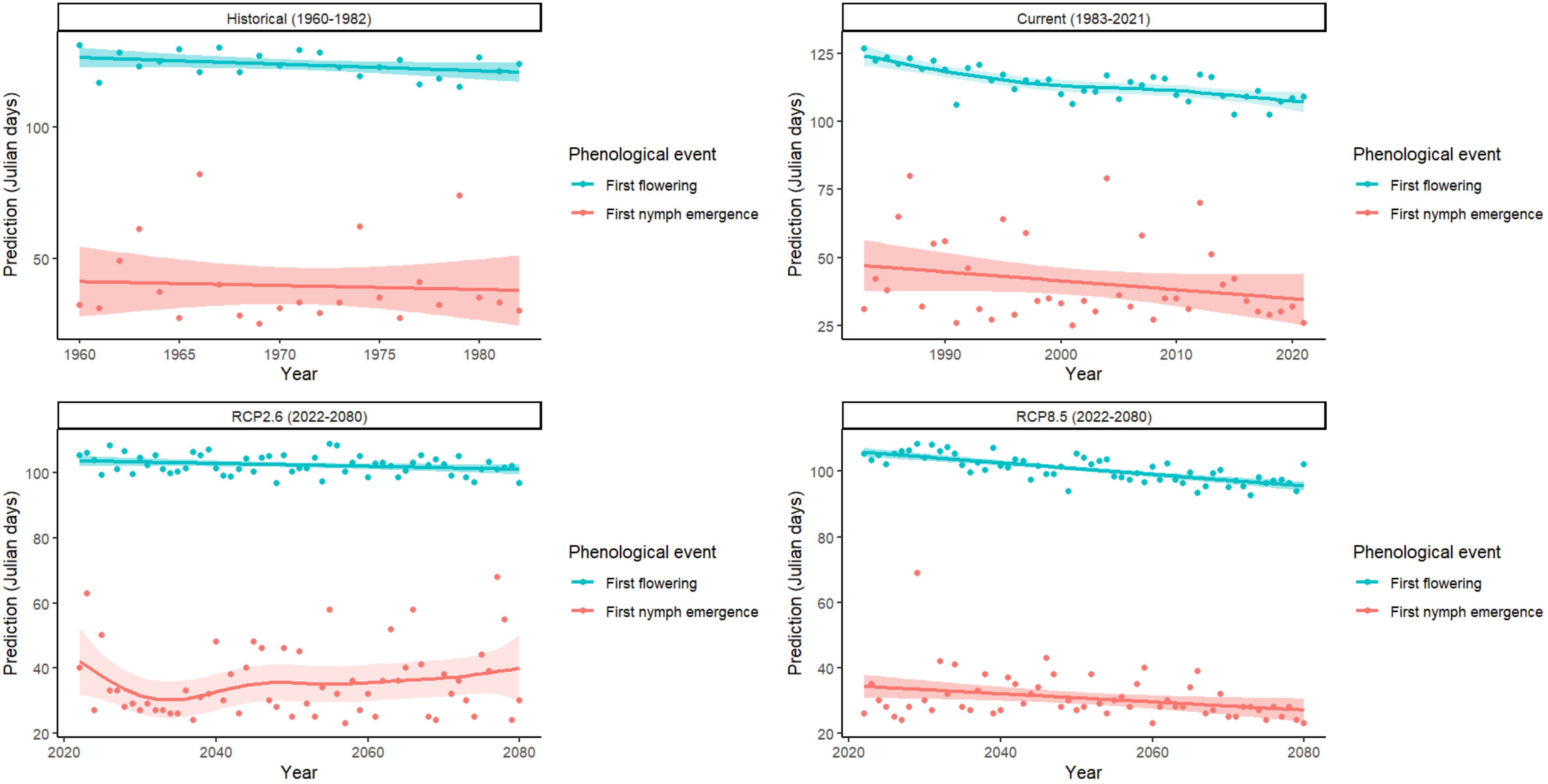


Figure S4.2: The phenological shift in first flowering time for cv. Conference pear trees (*P. communis*) and first *C. pyri* G1 nymph emergence, depending on year (1960-2080) and RCP scenario (RCP2.6 and RCP8.5).

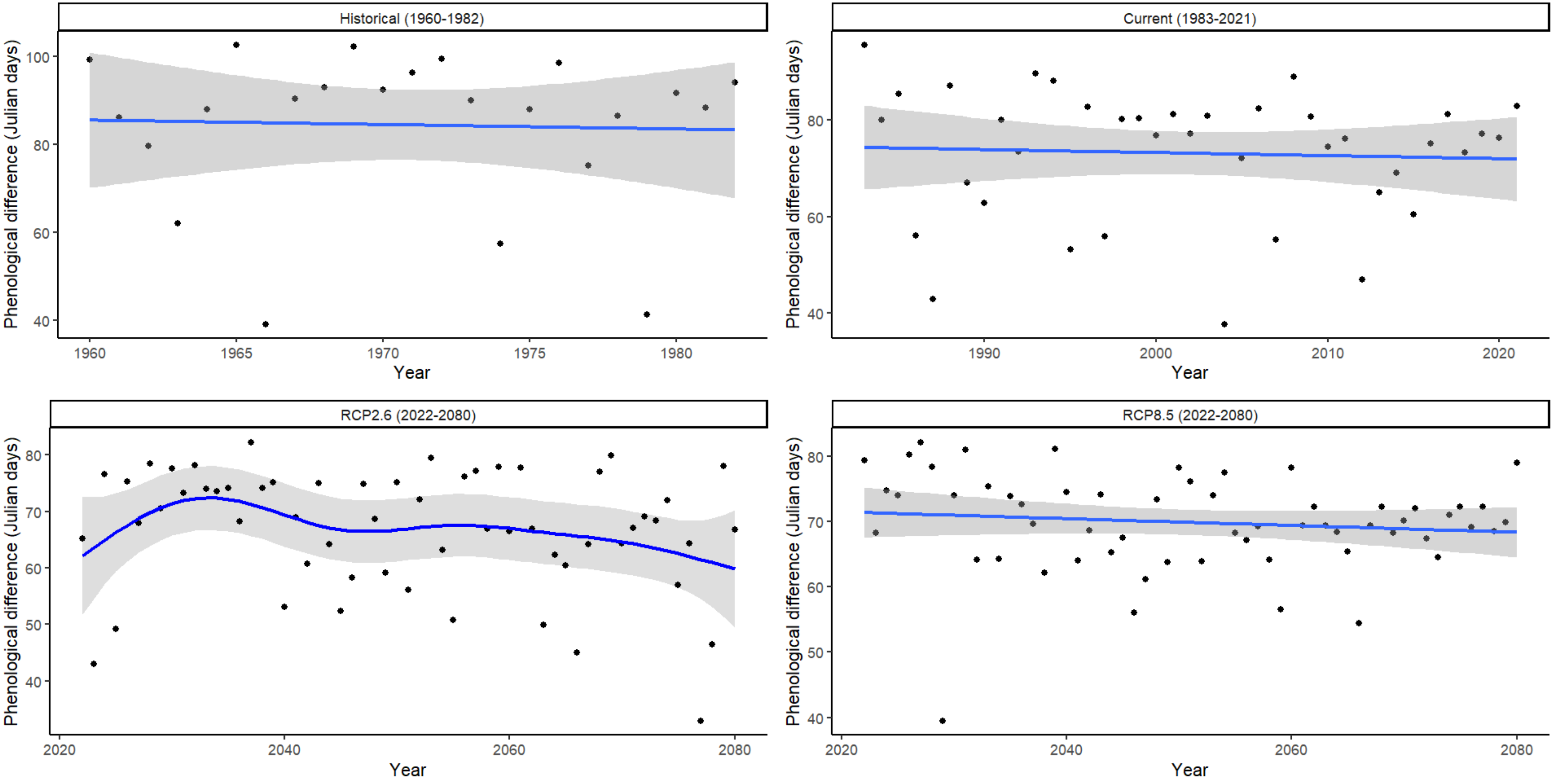


Figure S4.3: The phenological difference between first flowering time for cv. Conference pear trees (*P. communis*) and first *C. pyri* G1 nymph emergence, depending on year (1960-2080) and RCP scenario (RCP2.6 and RCP8.5).

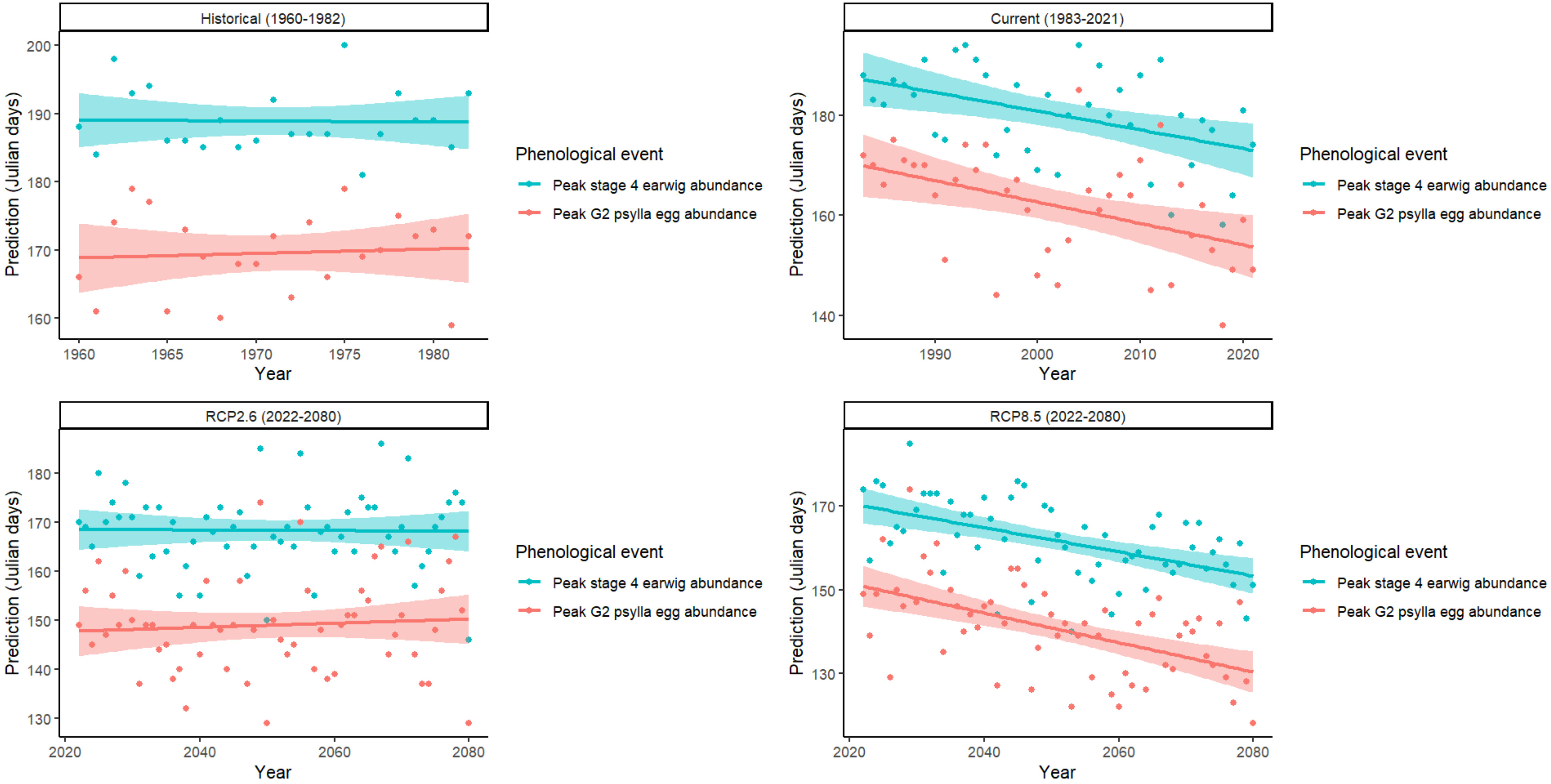


Figure S4.4: The phenological shift in *C. pyri* G2 peak egg emergence, depending on year (1960-2080) and RCP scenario (RCP2.6 and RCP8.5).and *F. auricularia* stage 4 peak nymph abundance.

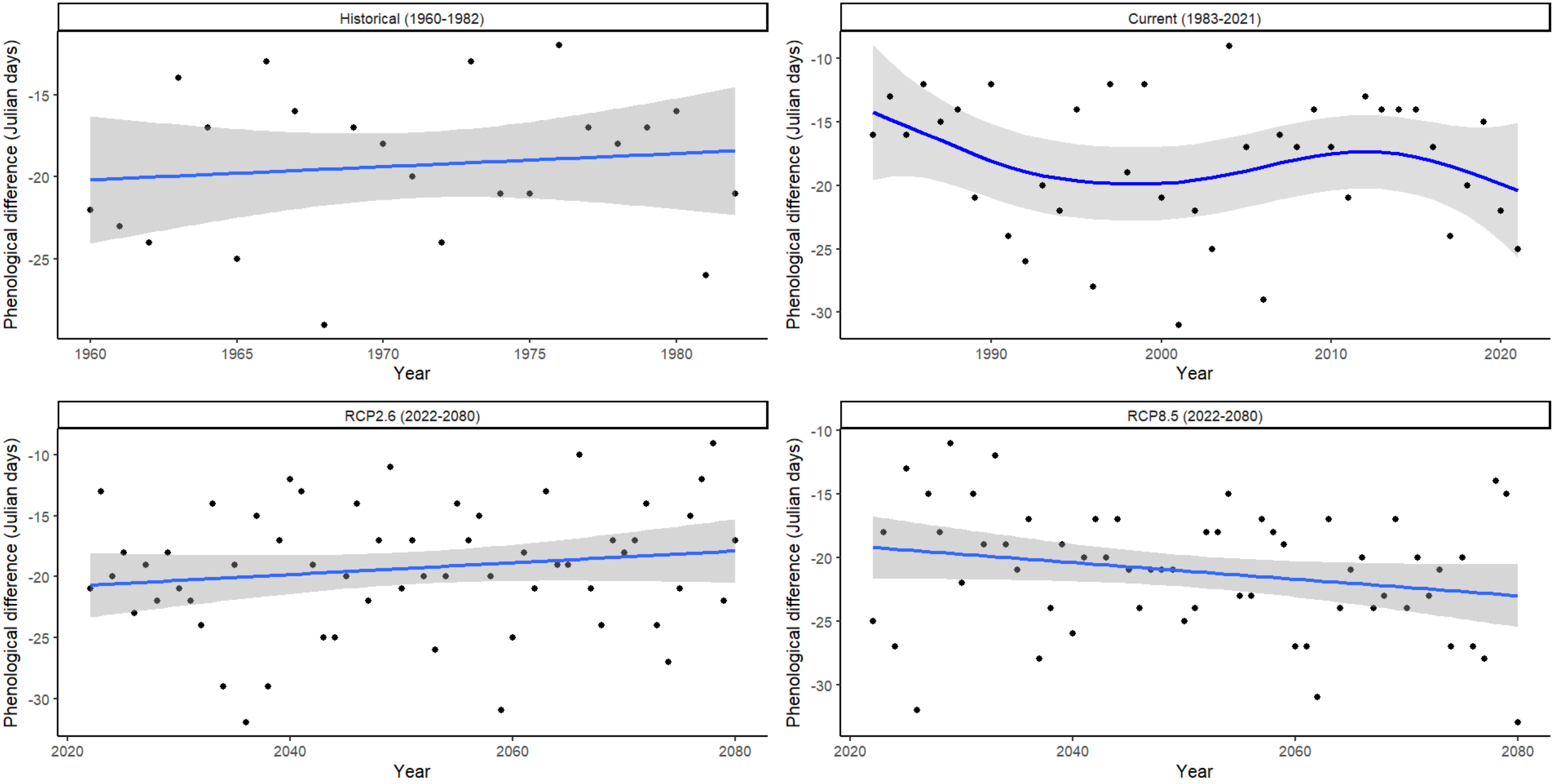


Figure S4.5: The phenological difference between *C. pyri* G2 peak egg emergence, depending on year (1960-2080) and RCP scenario (RCP2.6 and RCP8.5).and *F. auricularia* stage 4 peak nymph abundance.

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