Climate Change and the Phenology of Moths and their Hostplants in England and Wales

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The more one learns of this intricate interplay of soil, altitude, weather and the living tissue of plant and insect...the more the mystery deepends. Knowledge does not dispel mystery.

The Living Mountain - Nan Shephard

Abstract

The impact of Global Climatic Change (GCC) on the phenology of species has been well established. Consequential impacts of altered phenology on the interactions in an ecosystem has been hypothesised, with some evidence of species decline as a result. However, the drivers of phenological changes are less well understood, knowledge of which could be key to predicting the impacts of GCC on phenology of organisms in the future, and the potential impacts on ecosystem functioning. In this thesis, this contribution seeks to determine the drivers of moth phenology and their hostplants in England and Wales, whether their phenology varied in space, and whether their phenology was losing synchrony. To achieve this data was obtained from the National Moth Recording Scheme, Garden Moth Scheme, Woodland Trust Nature's Calendar, and Met Office. Linear Mixed Effects (LME) models were used to analyse phenological shifts for 149 moth species and 132 plant species, followed by an in-depth analysis of four moth species and five hostplants using Integrated Nested Laplace Approximations (INLA). Overall, the LME analyses found a significant difference in the phenology of moths and plants with different life history strategies, with a consistent impact of temperature on phenological shifts. The INLA analyses demonstrated spatial variation in moth phenological shifts, but there was no spatial variation in the hostplant phenology, and only *Spilosoma lutea* had a significant spatial relationship with its hostplant *Hedera helix*. These findings demonstrate that large scale phenological studies should consider how species with different life history traits may respond to GCC. Further, as *S. lutea* is a pupa overwintering polyphagous species, this highlighted that species with generalist diets may still be impacted by GCC and should not be discounted from studies on phenological asynchrony.

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same when it's your turn.

Declaration

All moth data were collected by recorders for the National Moth Recording Scheme and the Garden Moth Scheme. Plant data were collected by recorders for Woodland Trust and collated into Nature's Calendar. All weather data was collected by the Met Office.

Emily J. Hickinbotham did all other work.

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List of Acronyms

Places

UK - United Kingdom

Organisations

NMRS - National Moth Recording Scheme

GMS - Garden Moth Scheme

Phenological variables

FE - First Emergence

PE - Peak Emergence

ESD - Emergence SD

FF - First Flowering

SA - Seasonal (Aestival)

EA - Evergreen (Always)

EP - Evergreen (Partial)

Modelling

AIC - Akaike information criterion

DIC - deviance information criterion

INLA - integrated nested Laplace approximation

BYM - Besag York Mollie

CSR - A metric that represents the competitive (C) ability, stress (S) tolerance, and level of ruderalism (R) of plant species, developed by Grime et al. (1988).

Chapter 1

Introduction

1.1 Global Climatic Change

Global Climatic Change (GCC) is a well known and studied anthropogenic phenomenon that is resulting in changes to the environment (IPCC, 2023). Increases in extreme weather events such as heatwaves and heavy precipitation as well as species extinctions have occurred as a result of a warming environment (IPCC, 2023). These changes to the environment are projected to worsen with as yet no global assessment of adverse impacts on terrestrial, freshwater and ocean ecosystems (IPCC, 2023). In the UK recent decades have been warmer and wetter with more extreme temperatures, and an overall increase in temperature at a slightly higher rate than the global mean (Kendon et al., 2023). Due to its utility as a measure of the impacts of GCC on the natural world, the study of changes in the timing of species life cycles, also known as phenology, has increased in popularity in recent decades.

1.2 Phenology as a measure of GCC

The phenology of many species is influenced by environmental cues, such as daylength or temperature, that may aid organisms in tracking optimal timing of different life stages each year (Rathcke & Lacey, 1985; Visser & Gienapp, 2019). Thus, within the context of climate change the inherent relationship between phenology and the environment means it can be used as a measure of GCC and its impacts on the natural world. The study of phenology is not a new science, as those interested in nature have monitored phenological events for thousands of years (Boggs et al., 2003). There have been many approaches to using phenology as a

GCC indicator, with the majority of studies falling into either experimental (Anderson et al., 2023), modelling studies primarily using GCC projections (Gronchi et al., 2023), or analysis of existing data (Menzel & Dose, 2005; Menzel et al., 2020). Consistently, evidence has been found for phenological shifts, particularly for birds (e.g Mayor et al., 2017; Bell et al., 2019; Burgess et al., 2018), insects (e.g Bell et al., 2019; Hulle et al., 2010; Hällfors et al., 2021; Burgess et al., 2018) and plants (e.g. Tansey et al., 2017; Phillimore et al., 2012; Burgess et al., 2018) due to abundant data available for these groups. Indeed, the utility of citizen science data for phenological studies cannot be underestimated, as they are a useful source of long-term data (O'Neill et al., 2012).

1.3 Phenological shifts

The phenological shifts researchers have currently found fall into two important categories, advances and delays in a measured life event of a species (Thackeray et al., 2010). Advances in phenology, where a measured part of a species life history happens *earlier* in the year than previously measured, seem to be in the majority, for example: migration and egg laying in birds (Both & Visser, 2001; Both et al., 2006; Mayor et al., 2017; Dunn et al., 2011), emergence in insects (Musolin & Saulich, 2012; Bell et al., 2019; Hulle et al., 2010; Altermatt, 2010b, 2010a), flowering and leafing out in plants (de Manincor et al. (2023) ; Fitter & Fitter (2002); Büntgen et al. (2022)), blooming of phytoplankton (Gronchi et al., 2023; Hays et al., 2005), and foraging emergence in bats (Frick et al., 2012). However, delays have also consistently been found(Cook et al., 2012; Diamond et al., 2014), such as delayed emergence of butterflies in urban areas (Diamond et al., 2014), experimental drought leading to phenological delays in semiarid trees (Adams et al., 2015), and delayed autumn leaf senescence with experimental nitrogen addition in larch (Wang et al., 2022b). Furthermore, the *degree* to which species' phenology is shifting varies significantly, with some species shifting their timing by a few days and other species by weeks (Memmott et al., 2007). Although most research has been done on spring phenology, there is also evidence of changes to autumn phenology, as well as overall changes to the length of the growing season(Menzel & Fabian, 1999; Menzel et al., 2020). However, changes in phenology are not uniform across space due to variation in important environmental cues. There is the possibility that organisms will avoid shifting their phenology in response to GCC by tracking their ideal climate, for example by moving north or to higher altitudes where it is cooler. The alternative is to undergo phenological shifts in their location,

potentially resulting in population mismatch as populations in different locations experience different levels of GCC (Faltýnek Fric et al., 2020).

1.4 Lepidoptera and their hostplants

There are several organisms that suit the study of phenology, usually due to the availability of data and ease of monitoring. The focus of this thesis is the phenology of Lepidoptera and their hostplants. Lepidoptera are ideal study organisms for phenology, due to the widely available citizen science occurrence records, in-depth knowledge of their lifecycles and abundance of species to study (Wagner, 2020; Butterfly Conservation, 2022; Heikkinen et al., 2010; Hill et al., 2021). Further, being insects, they are more dependent on their environment due to their poikilothermic nature, and as such are more responsive to temperature changes (O'Neill et al., 2012).

1.5 Temperature sensitivity in insects

Sensitivity to temperature can be seen at all stages of an insect's life cycle. In particular, the growth rate of insects can be impacted, with higher temperatures potentially leading to faster development due to temperature-dependent chemical reactions, which can lead to a shift towards earlier phenology for many insects, such as first emergence (Tikkanen et al., 2006; Milonas & Savopoulou-Soultani, 2000; Xing et al., 2015; García-Barros, 2000). This appears to have varying impacts on body size, as historically body size is likely to be larger where there are higher mean annual temperatures (García-Barros, 2000; Davies, 2019), but increased temperatures due to GCC could shorten development time, leading to an overall smaller body size (Hill et al., 2021). Furthermore, besides altered body size itself potentially having impacts on fecundity (Honěk, 1993), changes in temperature can alter the ability of adult Lepidopteran females to lay as many eggs, as well as impacting egg size (Torres-Vila & Rodríguez-Molina, 2002; Pimentel et al., 2010). While the effect of temperature on body and egg size may be more prominent in early life stages, it is likely that phenology will be more responsive to temperatures in the later life stages, as there is more flexibility in the response of an adult to changes in the environment (Fenberg et al., 2016). The link between temperature and phenology has been consistently shown for Lepidoptera (Prior et al., 2009; Sparks et al., 2006; Lindestad et al., 2020; Keret et al., 2020). Generally, studies have found that increases

in temperature lead to advanced phenology for Lepidopteran species, with many estimates showing advances of several days per decade (Bonoan et al., 2021; Sparks et al., 2006; Teder, 2020; Altermatt, 2010b). However, this pattern varies considerably depending on the traits of the species analysed (See Section 1.6).

1.6 Life history strategies and response to GCC

The way in which a Lepidopteran species goes through its life cycle could influence the way it responds to GCC. Diet has a role to play, with the disparity in phenological response between specialist and generalist species being noted in several studies, with specialist species generally having larger phenological responses to GCC than generalists (Macgregor et al., 2019; Davies, 2019; Heikkinen et al., 2010; Altermatt, 2010b). This is important when considering impacts of body size, as larger individuals historically have been found to tend towards polyphagy (Loder et al., 1998). Further, host and habitat specialists generally have poorer dispersal abilities (Warren et al., 2001), which could be problematic given range shifts are likely to occur, and potentially necessary, for species' survival with ongoing GCC (Keret et al., 2020). The life stage at which species overwinter has the potential to impact phenology, and thus a species' response to GCC, with many studies finding species overwintering at a later life stage emerge earlier the next year (Keret et al., 2020; O'Neill et al., 2012; Altermatt, 2010b; Hällfors et al., 2021). As with diet, dispersal ability can also be impacted by overwintering stage, as Hällfors et al. (2021) found that species overwintering as pupae were less likely to alter their range.

The degree of a species' plasticity will likely be a crucial factor in their responsiveness to climate change. Species more generalist in nature, whether in diet or habitat preference, will have more options when responding to the conditions of the season or year, and thus may be at a large advantage with ongoing GCC (Van Asch et al., 2010; Végvári et al., 2015; Fenberg et al., 2016). Indeed, the effect of plasticity is starting to be seen with species' voltinism; Altermatt (2010a) found an increase in the number of generations for some species. Such changes may be advantageous as it could lead to population increases and as well as increasing the speed of microevolutionary processes (Altermatt, 2010a; Merckx et al., 2021). Species that have varied voltinism, where they have more generations in the south compared to the north, may be more likely to increase generation number in response to GCC (O'Neill et al., 2012). Alterations in flight period length have also been found, with similar increases

in population as a result (Bonoan et al., 2021), as well as the entire flight period shifting (O'Neill et al., 2012). However, this plasticity has limits, as the timing of a species life cycle is undoubtedly a result of millions of years of evolution leading to genetic a differences as species specialise in their ecological niche. Thus, there are genetic constraints on the ability of a species to adapt to climate change (Park & Post, 2022). Furthermore, it has the risk of becoming a developmental trap, where organisms capable of plastic responses may respond inappropriately to changes in environmental cues, for example by having an extra generation when there is not time for one before winter, or when the hostplant is not present (Van Dyck et al., 2015; Merckx et al., 2021). Thus, determining the impact of life history stategies on Lepidoptera species' phenological response is important for determining species most at risk from GCC and losing synchrony with their hostplants.

1.7 Hostplants

For most Lepidopteran species their lower trophic level is their hostplant, which they rely on as a food source as well as somewhere to spend their earlier life stages before they reach adulthood. Plant phenology has been studied for hundreds of years, with the Marsham record being particularly famous (Roberts et al., 2015). In seasonal habitats, both the onset of spring and end of the growing season have been the topic of study, as these indicate how species are responding to GCC at different points in the year. Warming experiments are a useful way to measure potential impacts of GCC in plant phenological research on the early growing season, which often results in early leaf-out and flowering phenology (Grossiord et al. (2022); de Manincor et al. (2023); Sherry et al. (2007); Chen et al. (2023)). Experimental results have been corroborated by analysis of long-term data, for example Büntgen et al. (2022) found that plants were flowing a month earlier in the UK. Although advancement of spring phenology has been commonly found, at the end of the growing season phenology tends to be delayed; Sherry et al. (2007) found that species that flower towards the end of the season had delayed flowering and fruiting phenology, which corroborates the finding that early-flowering species are more sensitive to temperature changes by Chen et al. (2023). Precipitation is also important for determining the timing of plant phenology as well as the type of phenological shift, as Adams et al. (2015) found a ~45% reduction in precipitation along with warming resulted in lower growth rates and later phenology for semiarid trees. This is in contrast to studies that predict a longer growing season as a result of warming based on existing data records (Menzel et al.,

2020). Another explanation for delays in plant phenology is lack of winter chilling, where some temperate deciduous plants require a cold period in winter to trigger spring phenology (Menzel & Dose, 2005; Roberts et al., 2015). These differing responses of plants to temperatures at different points in the season could lead to a change in the order of spring events (Roberts et al., 2015).

Moreover, the advancing spring phenology of some species may lead to vulnerability to late spring frosts, leading to damage of vulnerable plant organs such as young leaves (Vitasse et al., 2018). Late spring frosts, also known as "false springs", have historically determined temperate plant species range limits (Chamberlain et al., 2019), but the species at risk of false spring impacts have shifted with GCC, with early-leafout species being particularly threatened (Chamberlain et al., 2021). As environmental variables vary in space, Chamberlain et al. (2021) found that spring temperature, distance from the coast and North Atlantic Oscillation (NAO) had a consistent effect on species' exposure to false springs, however elevation was less consistent. Nevertheless, there was an overall decreased risk at higher elevations with increasing climate change which reflects more uniform budbursts found across elevational gradients with warming, with advancing phenologies at higher elevations heightening the frost damage risk (Chamberlain et al., 2021; Vitasse et al., 2018). Despite a more uniform budburst across elevational gradients due to warming, air temperature consistently decreases with increasing elevation, meaning that in higher elevations budburst will almost certainly be delayed when compared to lower elevations, especially if there is insufficient chilling due to warming (Wu et al., 2023). Yet, plants can be extremely plastic when it comes to responding to their environment, with a previous study by Tansey et al. (2017) finding that temperature-mediated phenological plasticity is adaptive for many species.

As opposed to spring phenology, for northern latitudes autumn senescence is generally found to be delaying due to GCC (Wang et al., 2022a), however this could potentially be due to deposition of atmospheric Nitrogen as well as temperature (Wang et al., 2022b). Conversely, warming-associated drought could lead to earlier onset of autumn senescence, with Wu et al. (2022) predicting the effect of drought could reverse the impacts of warming and lead to an overall earlier autumn by 2100. Further, Wang & Liu (2023) found that a larger variation in diurnal temperatures also lead to advanced autumn senescence.

Microclimates could become important as cooler areas such as north-facing slopes act as microrefugia, potentially buffering the effects of increased temperatures in localised areas (Maclean et al., 2015). Evidently, there is no consensus on the overall direction of phenological

shifts for autumn or the drivers of these shifts. This reflects the overall findings on plant phenology, where "overall" estimations of GCC impact are difficult when averaging over species with such different life histories and ecological drivers. Indeed, a recent study by Horbach et al. (2023) found that herbaceous plants had much more variable phenology than woody species with different drivers for leaf senescence on a species-specific basis. This is possibly due to the weaker association between herbaceous plant phenology and warming when compared to woody species (Geissler et al., 2023). The faster microevolution potential of herbaceous plants may mean they are more adaptable to GCC, as Franks et al. (2007) showed that an annual plant was able to pass on earlier flowering time as an evolutionary response to drought. This plasticity may mean that herbaceous plants could have an advantage over woody species which generally have longer generation times. Nevertheless, plant phenology is certainly changing in response to GCC, as evidenced by lack of trends during the recent warming hiatus from 1998-2012 (Wang et al., 2019). Evidently, plants are able to adapt to their environment, whether by tracking GCC and adapting their phenology (Tansey et al., 2017), or by being able to tolerate GCC (Grossman, 2023). The myriad of possible responses of plants to GCC means an understanding of the drivers of their phenological response is necessary for understanding the potential impacts on ecosystem functioning.

1.8 Match-mismatch hypothesis

The match-mismatch hypothesis, first proposed by Cushing (1973) in relation to recruitment in fish populations, proposes that "mismatches" occur when the consumer peak does not align with the prey peak. In the phenology context this is a potentially increasing problem because of GCC-induced phenological shifts. There is no certainty that phenological shifts will happen at the same rate, or even in the same direction, for species dependent on one another in an ecological network. If a species' phenology shifts at a stage in their lifecycle where they are dependent on their hostplant resources, this could lead to a mismatch in their phenology and species may miss the phenological window of their food resource. Thus, the importance of specialist vs. generalist diet again becomes important. A mismatch for a specialist species may have much higher consequences than for a generalist species that could conceivably feed on plants with different phenological windows. The presence of phenological asynchrony has already been found (Both & Marvelde, 2007; Burgess et al., 2018), but there are concerns that many studies do not currently match the criteria for confirmation of the

Cushing (1973) match-mismatch hypothesis (Kharouba & Wolkovich, 2023). Further, there is also the possibility that warming could lead to *re*-synchronisation where before asynchrony was a survival strategy of lower trophic levels, as with the herbivore-plant system investigated by Ren et al. (2020).

1.9 Inter and intra-specific variation in species phenology

While so far species have been discussed as a whole, individuals within a population or species can have divergent responses, resulting in differing phenological shifts between individuals. Further, these differences can happen at the population level when space is considered. Populations in more northern latitudes may experience a different degree of GCC, and thus respond accordingly. Due to northern latitudes and higher altitudes being colder, organisms may avoid the higher temperatures in southern locations and consequential phenological shifts by altering their distribution (Lenoir et al., 2020). Yet, changes in the spatial distribution of Lepidopteran species can again result in a mismatch with their hostplants, but in space rather than time. Although their hostplants may also track their ideal climate and alter their distribution, insects are inherently more mobile than their hostplants and will make this change more rapidly. Further, Lenoir et al. (2020) found that the presence of human activities impedes range expansion for terrestrial species which may enhance the differences in consumer and prey distribution due to dispersal abilities differing in human-altered environments. Thus, it is evident the role of the lower trophic level *must* be considered when modelling phenological *and* spatial shifts, as we cannot understand the impacts of these changes on a species without considering their interactions.

1.10 Data availability and advances

A common problem when addressing scientific research questions on the impacts of GCC on species is lack of adequate long-term data. By its very nature phenological research is the study of long term trends and appropriate data are often not available to answer many key questions in phenological research; hence, the recent use of citizen science data to investigate phenological questions (O'Neill et al., 2012; Dickinson et al., 2010). Amateur naturalists have been recording the natural world for hundreds of years, with more than 80 recording schemes and societies in the UK alone (Roy et al., 2014). Records of species presence can be used in

many ways, from range shifts to species richness and community composition (Dickinson et al., 2012). Such large-scale data that citizen science offers is a crucial resource for monitoring the response of the natural world to GCC, but there are many caveats that must be noted when using such data (Dickinson et al., 2012). Recorder bias is a significant problem, as there is undoubtedly a period of training as amateur naturalists learn to identify organisms, as well as a preference for particular locations and times of recording (O'Neill et al., 2012; Dickinson et al., 2012).

While some schemes have been deliberately set up with standardisation in mind, such as through volunteer training, many citizen science schemes are non-standardised in nature (Dickinson et al., 2012). Partial standardisation is possible, for example, the Garden Moth Scheme (GMS) in the UK accumulates data from volunteers using light traps in their back garden once a week from March to November, but the type of light trap, sampling night and weather conditions are not standardised (GMS, 2023). Other, larger, data on moths in the UK accumulated by the National Moth Recording Scheme (NMRS) use occurrence data of moth species that are then verified by Lepidopterists (Butterfly Conservation, 2022). Nature's Calender, part of the UK Phenology Network, records spring and autumn phenology for a range of UK species (www.naturescalendar.org.uk). Unlike the GMS and NMRS moth data which are occurrence records with the location and date the species was collected, the Nature's Calendar raw occurrence data is not available as it is pre-standardised before distribution to users into phenological variables for each species at each location each year. However, spatial biases in recording effort mean there are generally more records available in England and Wales than in Scotland. Additionally, the traits of both moths and plants are available in the UK. Work by Grime et al. (1988) determined the main traits of many plant species in the UK and developed the CSR metric, which records the competitive (C) ability, ability to tolerate stress (S) and level of ruderalism (R) of these species. Moth life history traits were recently documented and assimilated into a single database of traits on 968 species in the UK (Cook, 2022).

1.11 Knowledge gaps

There are a myriad of ways in which species can and have responded to GCC. It is the *drivers* of these divergent responses that are now important to ascertain, enabling better predictions for species' responses to GCC. The life history strategies of Lepidoptera and plants vary

considerably from species to species but could be crucial in how they alter their phenology with changes in the environment. The interactions between different species, such as Lepidopotera and their hostplants, will also likely change as a result, with potential impacts ecosystem functioning. However, in order to determine the drivers of Lepidoptera and plant phenology, as well as whether the interactions between them may be losing synchrony, long-term data is required. Further, an in-depth knowledge of the life history strategies of both the Lepidopteran species *and* their hostplants is needed. Fortunately, the UK fulfills both of these important requirements. The UK has a rich history of both entomology and botany, meaning the traits of these groups are well known. In addition to this, there are multiple citizen science recording schemes with long-term data to analyse.

1.12 Aims of thesis

The overall aim of this thesis is to determine the key drivers of the phenology of Lepidoptera (specifically moths) and plants in England and Wales, and to assess whether changes in the phenology of Lepidoptera and their hostplants have led to loss of synchrony (mismatch). This research also considers spatial variation in species' phenological response to climate change. Due to a lack of records in Scotland, the analyses were carried out for England and Wales only.

The objectives are to:

1. Assess the current literature on phenology and identify any knowledge gaps
2. Identify the drivers of moth phenology in England and Wales
3. Identify the drivers of plant phenology in England and Wales
4. Assess the extent to which moth and hostplant phenology is synchronised in England and Wales, and whether this varies spatially.

1.13 Thesis outline

Chapter 1

Introduction. Provides an introductory overview of the key topics of this thesis: Global Climatic Change (GCC), Phenology as a measure of GCC, Phenological Shifts, Lepidoptera and their hostplants, Temperature sensitivity in insects, Life history strategies and response to GCC, Hostplants, Match-mismatch hypothesis, Inter and intra-specific variation in species phenology, Data availability and advances.

Chapter 2

30 Years of Climate Related Phenological Research: Themes and Trends. Topic modelling is used to identify trends in the literature, how these have changed through time, and what gaps might be present in current knowledge. Previously submitted to Biological Reviews with reviewers comments now incorporated.

Objectives

1. Identify the most popular areas of phenological research over the last 30 years and assess how topic popularity has changed over time.

2. Assess which areas of phenological research are studied in isolation, and which are commonly linked, to identify key knowledge gaps in this field.

Chapter 3

Drivers of Moth Phenology in England and Wales. Data from the National Moth Recording Scheme and the Garden Moth Scheme are used to investigate drivers of moth phenology from 1970-2019 in England and Wales. Submitted to Journal of Insect Conservation Special Issue: Conserving Lepidoptera in a Changing World, under review.

Objectives

1. Identify whether there have been phenological changes for each species using three "emergence variables" that represent different parts of the season, over 50 years.
2. Assess the extent to which patterns in species phenological responses are dependent on their recorded life history traits.

Chapter 4

Drivers of Plant Phenology in England and Wales. Data from Nature's Calendar on common plant species in the UK and the modelling techniques from Chapter 3 are used to identify drivers of plant phenology.

Objectives

1. Identify whether plant life history traits and CSR metrics will have a large influence on their phenological response to climate change.
2. Identify whether the CSR metric will influence phenological response more than individual life history traits.
3. Assess the dependency of plant phenology on the phenology of the previous year.

Chapter 5

Spatial Variation in Moth and Plant Phenology and the Synchrony of their Phenologies. Data from Chapters 3 and 4 are utilised to determine whether the phenology of moths and their hostplants varies spatially. Then, the Peak Emergence of moths and First Flowering of their hostplants are compared to assess whether moths are losing synchrony with their hostplants.

Objectives

1. Determine whether spatial variation in environmental variables will influence the phenology of moths, resulting in spatial variation in phenology.

2. Assess whether oligophagous species will be more synchronised with their hostplant than polyphagous species.

3. Assess whether larva overwintering species will be more synchronised with their hostplants than pupa overwintering species.

Chapter 6

Discussion. Discusses the key findings of this thesis and how they might be utilised for further phenological research.

Chapter 2

30 years of Climate Related Phenological Research: Themes and Trends

2.1 Introduction

Phenology is the study of seasonal timing of life-cycle events for all living organisms on Earth (Rathcke & Lacey, 1985). Both biotic and abiotic cues fine-tune phenology to determine an 'optimal time window' each year, enabling species to synchronise with important seasonal events (Visser & Gienapp, 2019). However, temporal shifts in phenology have occurred as a result of anthropomorphic climate change (Memmott et al., 2007; Thackeray et al., 2010). There has been an overall advancement of phenological events such as spring phenology, but delays in autumn events have led to an overall lengthening of the growing season (Abu-Asab et al., 2001; Wolfe et al., 2005; Menzel & Fabian, 1999). Phenological changes have been documented for a selection of taxa in a variety of locations, making them a reliable indicator of the impact of climate change on ecosystems (Walkovszky, 1998; Penuelas et al., 2002; Thackeray et al., 2016). Understanding the potential impacts of shifts in species' phenology on biodiversity is important for progress towards the global research agenda and to inform the United Nations (UN) Sustainable Development Goals (SDGs), particularly SDGs 14 and 15 and the Convention of Biological Diversity's (CBD) Post-2020 targets (CBD, 2020). With changes in climate potentially leading to species extinctions as a result of phenological changes, it is timely to synthesise the themes and trends of climate related phenological research to date,

to determine future research direction to achieve these targets (Campbell et al., 2009).

The wealth of literature on the impacts of climate change on phenological processes has revealed concerning patterns in species' phenology. The differences in phenological changes between species and across trophic levels can lead to asynchrony, or 'mismatching', where species become temporally separated (Visser & Gienapp, 2019). These differences can be due to the direction of phenological changes; changes in temperature have generally been found to result in advanced phenology, while changes in precipitation may result in delays, and the strength of these environmental cues can determine whether the overall phenological change is an advance or delay (Thackeray et al., 2016; Ahas et al., 2002; Cleland et al., 2006). Similarly, the magnitude of phenological changes can be different, where the degree of plasticity in species' phenology determines whether it shifts by days or even weeks (Memmott et al., 2007). Earlier seasonal phenology has also impacted the way humans interact with the environment, with conservation consequences; for example, ground-nesting birds in Finland now nest an average of 8 days earlier than the sowing date of barley field, leaving their nests at risk of being destroyed by farming equipment(Santangeli et al., 2018).

The variation in phenological response is also strongly influenced by species' traits; for example, species that respond to environmental cues such as degree days are more likely to experience an advance in their phenology (McMaster & Wilhelm, 1997; Hughes, 2000; Penuelas et al., 2002). Consequently, the inherently higher sensitivity to temperature of ectotherms, or other organisms more reliant on temperature such as poikilothermic insects, mean that the impact of climate change on developmental rates, and thus phenology, of these organisms is expected to be stronger (Hughes, 2000; Thackeray et al., 2010; Damien & Tougeron, 2019). Ecological generalists utilise a range of environmental cues, making them better equipped to respond and adapt to changes in their environment (Koerner & Basler, 2010; Chmura et al., 2019). Furthermore, the time of year when species are active is important; flowering time is more variable in early-flowering plant species, and time of year results in plankton populations showing either large advances or delays in their phenology (Hays et al., 2005; Thackeray et al., 2016; Beaubien & Freeland, 2000). Reproductive strategies are also critical: with shorter generation time comes faster microevolution, and short-distance migrants are more responsive to temperatures, while long-distance migrants rely on photoperiod to predict the best time to arrive at breeding grounds (Thackeray et al., 2010, 2016; Bradley et al., 1999; Both & Visser, 2001; Crick et al., 1997).

The complexity of phenological changes, along with variability in species responses and

nonuniform environmental impact from climate change, make this a challenging subject to approach. Indeed, many of the factors expected to influence phenology described in the preceding paragraphs have recorded exceptions (see Chmura et al., 2019). Numerous techniques have been used to monitor and predict the influence of climate change on temporal shifts in phenology (Cleland et al., 2007). The four main avenues of research have either used long-term data (Sparks & Carey, 1995), remote sensing (Myneni et al., 1997; Schwartz, 1998), experimental design such as warming experiments (Arft et al., 1999), and statistical modelling (Chuine et al., 2000; Bascompte & Jordano, 2007; Morin et al., 2009). The range in use of methodology has also changed over time due to technological advances. This confers an additional need for better integration of knowledge on phenological changes, but the volume and range of literature makes synthesis difficult (Renner & Zohner, 2018).

Topic modelling enables rapid semi-qualitative synthesis of large diverse bodies of literature. We used topic modelling to explore broad trends, and identify research gaps in the field of phenological responses to climate change over the last 30 years (1989-2019). Our objectives are 1) to identify the most popular areas of phenological research over the last 30 years and assess how topic popularity has changed over time, and 2) assess which areas of phenological research are studied in isolation, and which are commonly linked, to identify key knowledge gaps in this field.

2.2 Methods

We use topic modelling *sensu* Westgate et al. (2015) utilising the code and approach of Mair et al. (2018). The *a priori* protocol, data and code are available at https://osf.io/ghnwp/.

2.2.1 *Literature search and screening*

The electronic databases Web of Science and Scopus were searched using the terms: "phenolog*" & ("global change" | "climate change" | "global warming"). Results were included if they were classed as reviews or articles and published in English. This gave an overall result of 12,991 articles (Web of Science = 7296, Scopus = 5695, see Figure 2.1).

The results of each database search were imported into EndNote. Duplicate articles were automatically removed using EndNote, after which articles were manually searched for any missed duplicates, leaving 8317 articles. Where possible, abstracts were found for articles

with no abstract listed. Articles without an abstract were removed. The articles were then screened for inclusion (Figure 2.1) using the following criteria: articles measured a phenological response or a possible response (whether hypothetical or experimental) to a change in climate or environment (including all variations e.g. wind/ light/ temperature/ moisture/ precipitation/ mineral content/ etc.) that is a direct measured response to or could be interpreted/extrapolated as a response to ongoing anthropogenic climate change. A second reviewer checked 20% of articles to ensure efficacy in the abstract screening protocol, which were randomly sampled using R (R Core Team, 2020). The agreement between the two reviewers was calculated using Cohen's kappa.

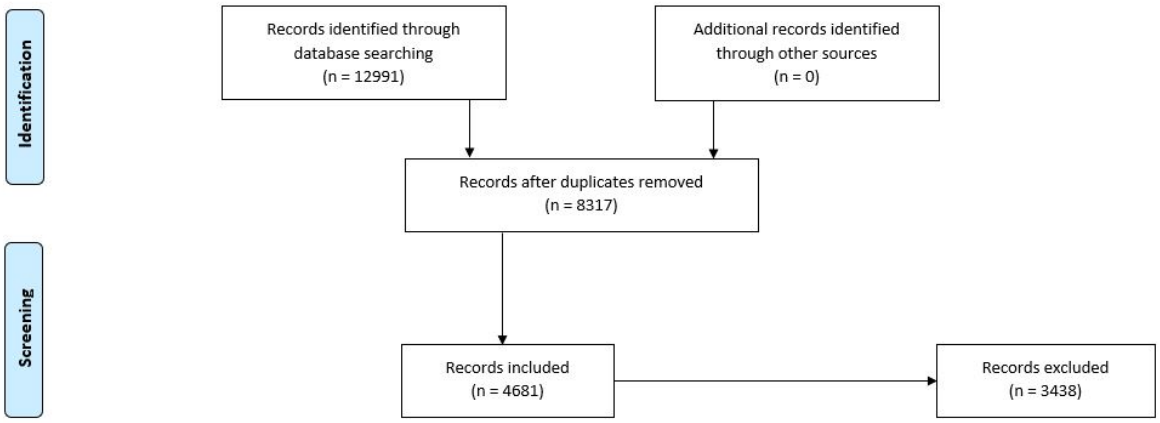


Figure 2.1: A modified PRISMA diagram of the sorting process of studies for the topic model. Every study included was sorted into a category. Only studies that were excluded that could be useful for modelling in the future, for example detailing changes in temperature or the phenology of a species, were sorted into relevant categories.

2.2.2 *Abstract cleaning*

Once screened, the articles that met the criteria were imported into R using the *revtools* package (Westgate, 2019). Some articles contained both English and French or Spanish abstracts. The non-English abstracts were removed during the screening process in EndNote. Using the package *tm* (Feinerer et al., 2008), abstracts were transformed into a corpus ('body of literature') and processed. Search terms, numbers written as words (Grun & Hornik, 2011), English stop-words in the *tm* package (Feinerer et al., 2008) and expanded as per Mair et al. (2018), and terms added for copyright reasons by publishers, were removed. Hyphens and forward slashes were changed to spaces and all other punctuation was also removed. The

words leftover were reduced to their common root by removing suffixes, and words that then appeared in five or fewer abstracts being removed completely (Griffiths & Steyvers, 2004; Lu et al., 2017).

2.2.3 *Topic modelling*

Topics ("a distribution over a fixed vocabulary of terms", (Blei & Lafferty, 2009)) were identified using the R package *topicmodels* (Grun & Hornik, 2011), by fitting a Latent Dirichlet Allocation (LDA) model with Gibbs sampling (Blei & Jordan, 2003). Block-cross validation models were used to indicate the number of topics with the least perplexity, where perplexity is the uncertainty in predicting a single word. Thus, the higher the perplexity, the more likely the model is performing no better than chance. The number of topics tested were 10, 20, 30, 40, 50, 60, 100, and 200 (sensu Mair et al., 2018). Perplexity decreased from 40 topics (Appendix A Figure A.1). Therefore, 40 topics represented a sufficient trade-off in perplexity versus representation of the corpus.

The weight, a measure of importance of each word underpinning a topic, declines with an increasing number of words. We used 20 words to describe each topic, as word weight began to decline at approximately 20 words and the top five words represented the highest weight (Appendix A Figure A.2, Appendix A Table A.1). These words were used to name topics and classify them into themes (Table. 2.1.) (Westgate et al., 2015; Mair et al., 2018). The five themes identified were: (1) 'Impact', topics that are a result of a change in climate or a phenological shift, (2) 'Plants', topics which are primarily associated with plants, (3) 'Climate', topics that refer to location, weather, and phenological events related to the environment, (4) 'Scientific approach', topics associated with the techniques used to assess phenology, and finally (5) 'Recipients', topics that refer to a taxonomic group, separate from plants, that are the receivers of an impact.

Table 2.1: The topic number, 5 highest weighted words, topic name and theme.

No.	Top 5 words	Topic name	Theme
1	Season, grow, length, end, start	Growing season	Climate
5	Event, increase, frost, extrem, risk	Disruptive events	Climate
6	Precipit, veget, studi, grassland, region	Rain determining SOS	Climate
10	Ecosystem, product, carbon, dynam, atmospher	Ecosystem function	Climate
11	Northern, north, latitude, region, rang	Geographical location	Climate
13	Spring, winter, warm, summer, temperatur	Warming impact on seasonality	Climate
17	Ice, lake, snow, cover, arctic	Ice and snow phenology	Climate
22	Annual, climat, year, variabl, rainfal	Latitude and climate	Climate
30	Water, soil, drought, increase, product	Water stress	Climate
33	Studi, area, differ, urban, result	Urban impacts	Climate
36	Site, elev, high, snowmelt, gradient	Elevation	Climate

Table 2.1: The topic number, 5 highest weighted words, topic name and theme.

No.	Top 5 words	Topic name	Theme
39	Temperature, degree, increase, air, mean	Temperature fluctuation	Climate
8	Factor, respons, climat, import, understand	Processes that drive phenology	Impact
14	Ecology, impact, research, system, includ	Ecological impact of changes	Impact
19	Effect, affect, interact, impact, direct	Outcomes	Impact
20	Trend, term, long, show, chang	Trends	Impact
24	Popul, resource, mismatch, declin, size	Consequences of mismatching	Impact
27	Chang, shift, respons, time, advanc	Temporal shifts	Impact
32	Speci, community, respons, among, distribut	Biogeography	Impact
35	Popul, adapt, trait, select, plastic	Environmental genetics	Impact
37	Variat, time, pattern, across, spatial	Spatial-temporal variation	Impact
38	Year, earli, late, period, may	Direction of shift	Impact

Table 2.1: The topic number, 5 highest weighted words, topic name and theme.

No.	Top 5 words	Topic name	Theme
40	Day, date, advance, signific, year	Timing	Impact
2	Leaf, Forest, Tree, Decidu, Temper	Plant leaf phenology	Plants
3	Growth, bud, tree, burst, differ	Plant life-history events	Plants
16	Chill, require, temperature, pollen, accumul	Plant chilling and heat requirements	Plants
18	Flower, plant, time, fruit, pollin	Plant-pollinator interactions	Plants
21	Develop, seed, stage, studi, delay	Agricultural phenology	Plants
34	Crop, yield, wheat, period, increas	Agronomy	Plants
7	Migrat, arriv, bird, time, migratori	Bird migration	Recipients
9	Time, sea, bloom, water, phytoplankton	Marine phenology	Recipients
15	Insect, develop, emerg, host, generat	Insect phenology	Recipients
28	Breed, nest, lay, time, egg	Bird reproduction	Recipients

Table 2.1: The topic number, 5 highest weighted words, topic name and theme.

No.	Top 5 words	Topic name	Theme
31	Reproduct, time, life, condit, histori	Reproductive plasticity	Recipients
4	Warm, plant, respons, treatment, experi	Plant experiments	Scientific approach
12	Data, observ, use, studi, record	Methodology	Scientific approach
23	Climat, future, scenario, region, project	Modelling future climate change	Scientific approach
25	Use, time, analyzi, analyz, method	Analysis	Scientific approach
26	Model, predict, use, simul, base	Predictive modelling	Scientific approach
29	Veget, green, land, ndvi, use	Remote sensing	Scientific approach

2.2.4 *Topic prevalence over time*

The weights for each topic per decade were calculated by summing the weight of the topic for each article each year within each decade (Westgate et al., 2020). The only article from 1989 was removed for this analysis, leaving three decades: 1990s, 2000s, 2010s.

2.2.5 *Topic co-occurrence within articles*

The co-occurrence of pairs of topics in abstracts was determined using the distribution of topic weights. The weights for each of the 40 topics within each abstract was $\log_{10}$ transformed. Euclidean distances were calculated on a scale from zero, where the pair of topics never co-occurred in the same abstract, to one where there the pair of topics always co-occurred (Westgate et al., 2015).

2.2.6 *Topic generality vs. specificity*

The distribution of topic weights within the corpus was used to determine topic generality. General topics represent a concept that applies to a wide range of articles in the corpus, whereas more specific topics apply to only a few. The topic with the highest weight for each article was selected, and the mean weight when selected vs. the mean weight when not selected was plotted (Westgate et al., 2015).

2.2.7 *Geographic bias*

The frequency of studies based in each country was determined by searching abstracts for every country name, with additional variations where countries may have multiple names (e.g. "UK", "Britain", "USA", "America"). The number of articles per country was then plotted on a world map.

2.2.8 *Topic popularity*

Topic popularity was assessed using both the total number of articles published on each topic, and the change in the number of articles published on each topic over the study period (Westgate et al., 2015). The package *lme4* (Bates et al., 2015) was used to fit a GLMM

specified with a Poisson distribution and log-link, with year and topic as explanatory variables and the number of articles per topic per year as the response variable. A popular topic was indicated by a positive random intercept, showing a higher-than-average number of articles published on that topic during the study period. A topic that increased in popularity was indicated by a positive slope showing an increase in articles published on that topic during the study period (Figure. 2.7.) (Westgate et al., 2015).

2.2.9 *Journal publication contribution*

Additionally, the publication contribution of journals in the corpus was assessed by quantifying the number of articles per journal. The distribution of articles among topics for the top five journals was then be compared.

2.3 Results

Of the 8317 articles screened, 4681 articles with 3884 words were included in the analysis. There was moderate agreement between the two reviewers (Cohen's Kappa = 0.52) (McHugh, 2012). The 20 highest weighted words for each of the 40 topics (Appendix A Table A.1) were used to name each topic and classify them into one of five overarching themes: 'Climate' (12/40), 'Impact' (11/40), 'Plants' (6/40), 'Scientific approach' (6/40), and 'Recipients' (5/40) (Table.2.1.). The theme 'Recipients' contained topics with some of the highest frequencies of articles (*Bird migration*, *Bird reproduction*, *Insect phenology*, and *Marine phenology*), where these topics had the highest weight in these articles (Figure. 2.2.).

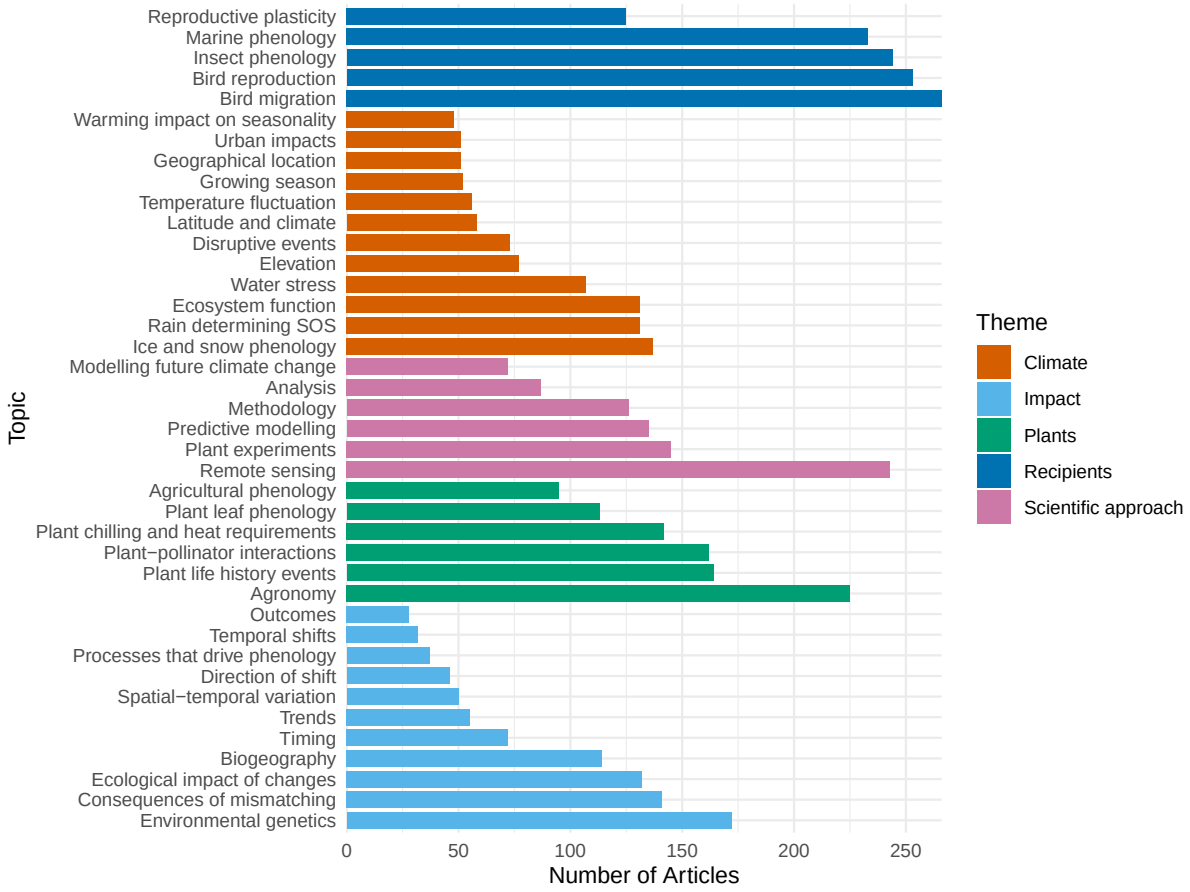


Figure 2.2: Frequency of topics across the number of articles in the corpus, given the topic weight for each article. Topics are grouped by themes based on their highest weighted words.

The topics *Remote sensing* in 'Scientific approach', *Agronomy* in 'Plants', and *Environmental genetics* in 'Impact' also had a high frequency of articles. Topics such as *Trends*, *Outcomes*, and *Timing* in 'Impact' are somewhat contextual, as they refer to the outcomes of phenological changes. Similarly, the topics *Analysis* and *Methodology*, and *Agricultural phenology* and *Agronomy*, were conceptually related (*Analysis* contained the word 'method') but were still identified as distinct topics by the model. For some topics, the taxa/region commonly used to study them were confounded with the topic subject, such as *Plant leaf phenology* (which included 'oak'), *Plant life history events* ('pine', 'boreal'), *Rain determining SOS* ('plateau', 'China'), *Geographical location* ('Europ', 'America'), *Plant-pollinator interactions* ('bee'), *Insect phenology* ('moth', 'butterfli'), *Bird reproduction* ('tit'), and *Water stress* ('Mediterranean') (Appendix A Table A.1). (See Appendix A Figure A.3 for similarity between topics and themes).

2.4 *Topic prevalence over time*

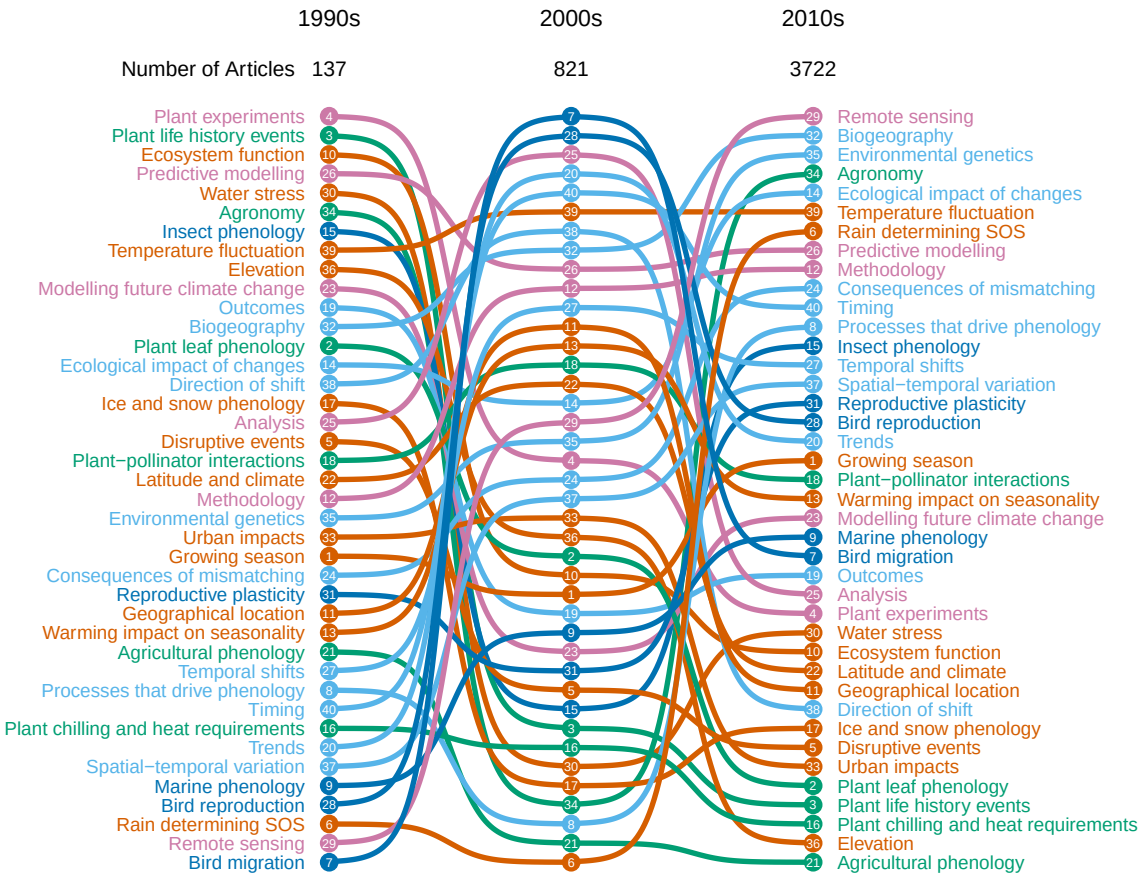


Figure 2.3: Decadal change in the prevalence of 40 topics. Numbers refer to topic number (Westgate et al., 2015).

The highest weighted topics (Figure. 2.3.) were not consistent across the three decades. The topic *Remote sensing* consistently increased in overall weight, rising from position 39 to 17, and then to position 1 in the 2010s. Other topics that consistently increased were *Biogeography* (position 12 to 2), *Methodology* (21 to 9), *Environmental genetics* (22 to 3), *Consequences of mismatching* (25 to 10), *Spatial-temporal variation* (35 to 15), and *Marine phenology* (36 to 23). The topic *Temperature fluctuation* only changed a few positions, from 8th to 6th, across decades.

For some topics, the change in popularity was not consistent. The lowest weighted topic in the 1990s, *Bird migration*, switched and became the highest weighted topic in the 2000s, before decreasing again to position 24 in the 2010s. Similar patterns can be seen for *Direction of shift* (15-7-32), *Analysis* (17-3-26), *Latitude and climate* (20-15-30), *Urban impacts* (23-22-35), *Geographical location* (27-12-31), *Warming impact on seasonality* (28-13-21), *Temporal shifts*

(30-11-14), *Timing* (32-5-11), *Trends* (34-4-18), and *Bird reproduction* (37-2-17). Although *Plant-pollinator interactions* was also similar (19-14-20), overall, it only dropped one position across decades.

Conversely, the topic *Rain determining SOS* initially decreased from position 38 to 40, before increasing to position 7. Again, other topics followed this trend: *Water stress* (5-35-28), *Agronomy* (6-37-3), *Insect phenology* (7-32-13), *Modelling future climate change* (10-29-22), *Outcomes* (11-27-25), *Ecological impact of changes* (14-16-5), *Ice and snow phenology* (16-36-33), *Growing season* (24-26-19), *Reproductive plasticity* (26-30-16), and *Processes that drive phenology* (31-38-12).

Despite an apparent increase in popularity in Figure. 2.7, the topic *Agricultural phenology* (21) decreased in overall weight, falling from position 29 to 40 across the decades. Other topics that decreased were *Plant life history events* (2 to 37), *Ecosystem function* (3 to 29), *Elevation* (9 to 39), *Plant leaf phenology* (13 to 36), *Disruptive events* (18 to 34), and *Plant chilling and heat requirements* (33 to 38). The plant-based topics are consistent with the topic *Plant experiments* decreasing from position 1 to 27, which commonly co-occurs with plant topics, especially *Agricultural phenology* (Figure. 2.4).

2.5 *Topic co-occurrence within articles*

Some of the frequently co-occurring topics were due to topic similarity, for example *Predictive modelling* and *Modelling future climate change*, and *Analysis* and *Methodology* (Figure. 2.4.). Within themes, only 'Climate' had frequently co-occurring topics, these were: *Rain determining SOS* and *Growing season*, *Elevation* and *Urban impacts*, and *Water stress* and *Ecosystem function*. Across themes, some important frequently co-occurring topics were *Reproductive plasticity* and *Consequences of mismatching*, and *Disruptive events* and *Modelling future climate change*. Topics that did not commonly co-occur were also identified in the analysis. The topic *Remote sensing* did not tend to co-occur with most 'Recipients' topics, and only rarely co-occurred with 'Scientific approach', 'Impact', 'Climate' and 'Plants' topics, with exceptions being *Spatial-temporal variation* and *Rain determining SOS*. The topics *Bird migration* and *Bird reproduction* did not frequently co-occur with *Plant-pollinator interactions*, despite *Bird reproduction* in particular having a strong association with *Consequences of mismatching*. The topic *Agronomy* also did not frequently co-occur with *Biogeography* or *Bird migration*.

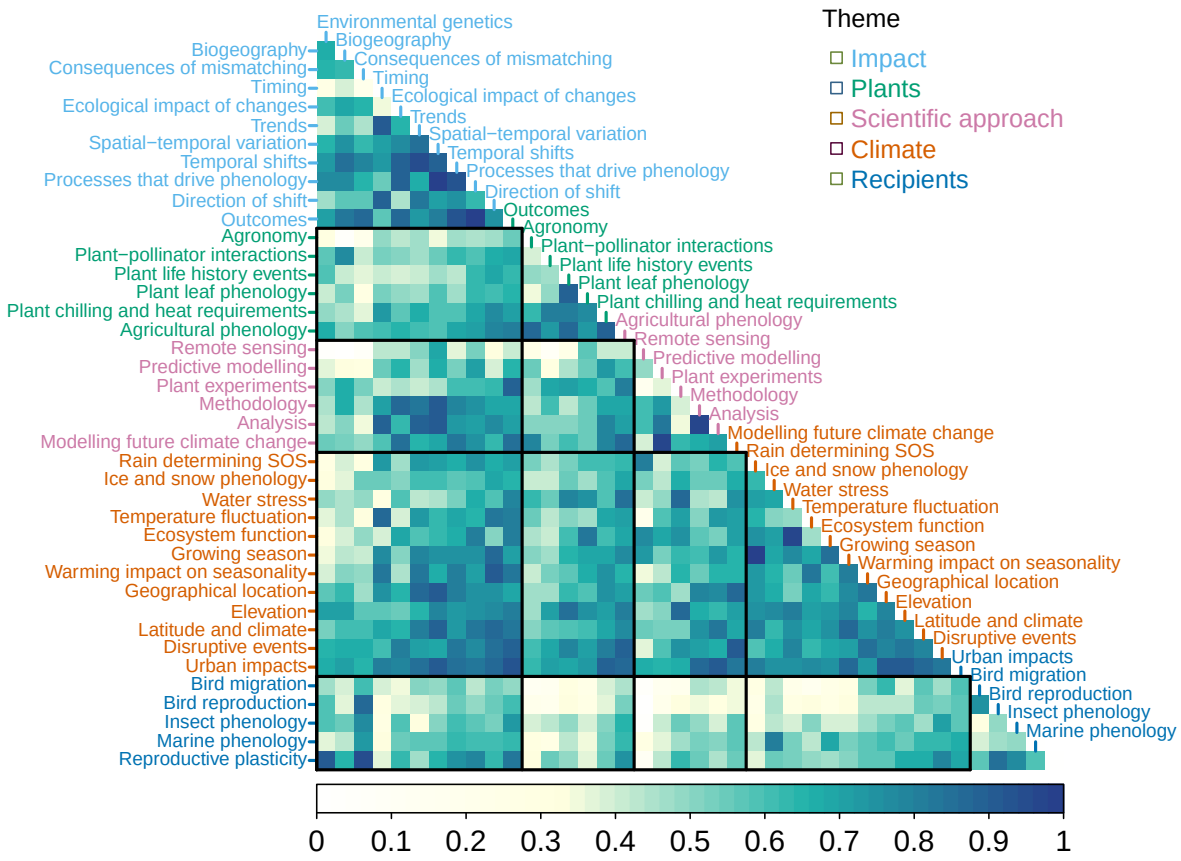


Figure 2.4: Co-occurrence matrix showing the relationships between topics (Westgate et al., 2015). Darker blues indicate a stronger relationship, 1 = topics co-occur within articles, 0 = topics do not co-occur within articles.

2.6 *Topic generality vs. specificity*

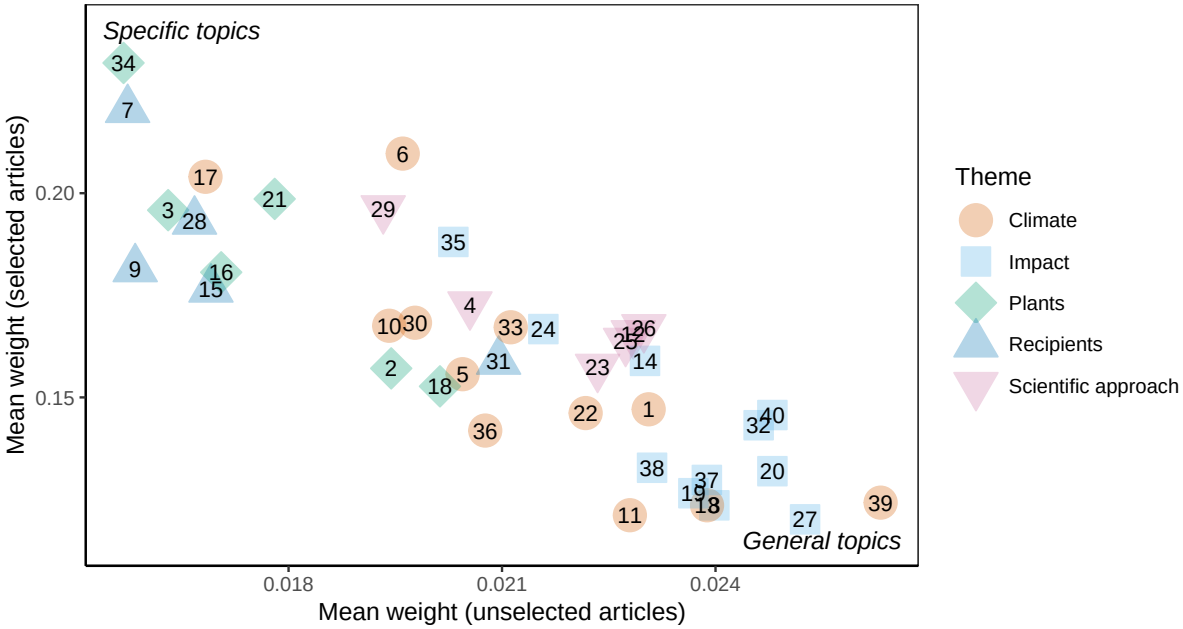


Figure 2.5: Topic generality, shown by the weight each topic has within articles where it is has the highest weight (selected) vs when it is not the topic with the highest weight (unselected).

Topic specificity is related to topic frequency, as a specific topic is more likely to have the highest weight within any given article. Topics in the themes 'Climate' and 'Scientific approach' tended to be more general overall, with only the topics *Remote sensing* (29) and *Plant experiments* (4) being more specific. The most specific topic was *Agronomy* (34), followed by *Bird migration* (7) (Figure 2.5). Specific topics were primarily in 'Recipients' and 'Plants', with only one 'Climate' topic, *Ice and snow phenology* (17), being highly specific, indicating this is usually studied in isolation. Of the 'Recipients' topics, only *Reproductive plasticity* (31) was general. General topics mostly consisted of those in the theme 'Impact', but the most general topic *Temperature fluctuation* (39) was in 'Climate'.

2.7 *Geographic bias*

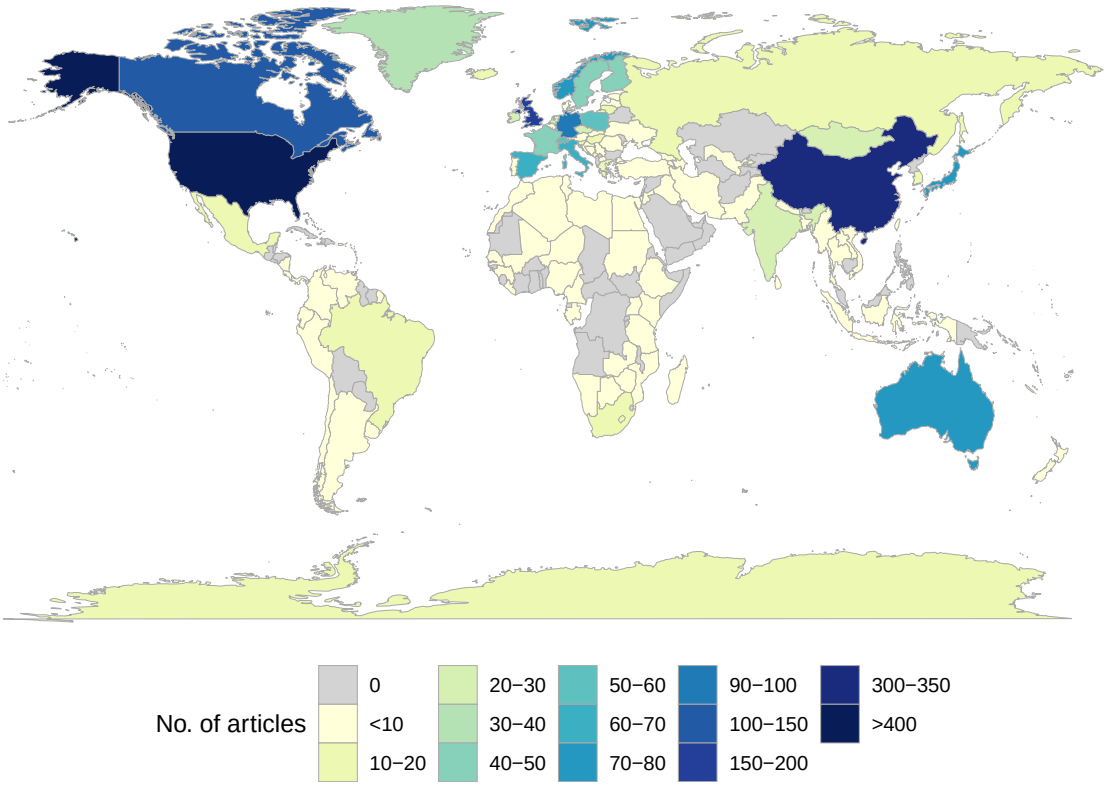


Figure 2.6: The geographic distribution of published articles included in the study, by frequency per country.

The map of article frequency per country revealed large geographic bias in the locations of phenological studies. Generally, there was a bias towards the Northern hemisphere, with a focus on particular countries such as the USA, UK and China. In the Southern hemisphere, only Australia appears to have a higher frequency of articles, with other countries in the global south commonly having fewer than 20 articles associated with them. There are also many areas with very little phenological information, particularly towards the tropics. While it is possible this is due phenological changes not being as clear or consistent as in higher latitudes, and thus not commonly being the subject of phenological research, it is also likely this is also due to research scarcity in these areas.

2.8 *Topic popularity*

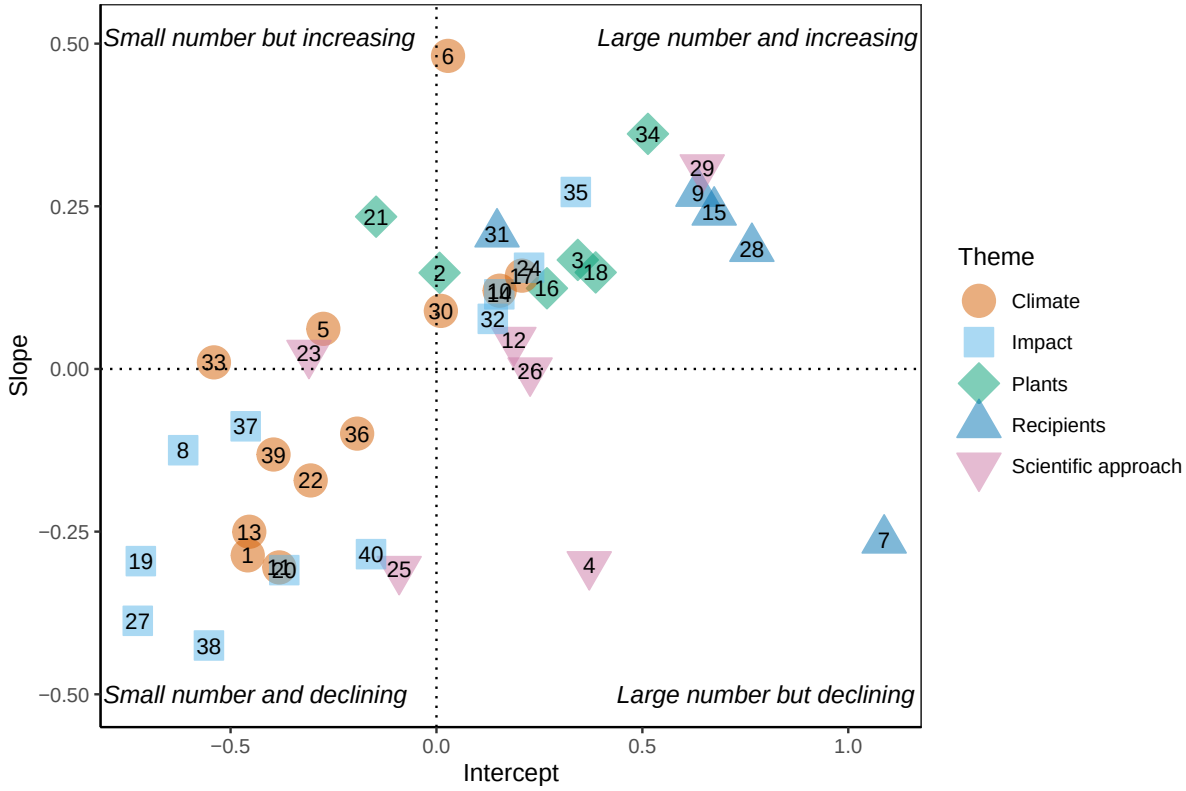


Figure 2.7: Topic Popularity, shown by the number of articles published across years.

Overall, topic popularity is not consistent over time as there was little clustering around a slope of zero (Figure. 2.7.). The topics *Bird migration* (7) and *Plant experiments* (4), which have been frequently published (Figure. 2.2.), were decreasing in popularity. The topic *Agricultural phenology* (21) appeared to increase in popularity. There were several "Hot" topics clustered together, where the topic has a high frequency of articles which is increasing, particularly *Rain determining SOS* (6) which had a relatively small intercept but the largest slope, as well as *Agronomy* (34), *Remote sensing* (29), *Environmental genetics* (35), and *Marine phenology* (9). The "Cold" topics Direction of shift (38), *Temporal shifts* (27), and *Outcomes* (19), were all in the theme Impacts.

2.9 *Journal publication contribution*

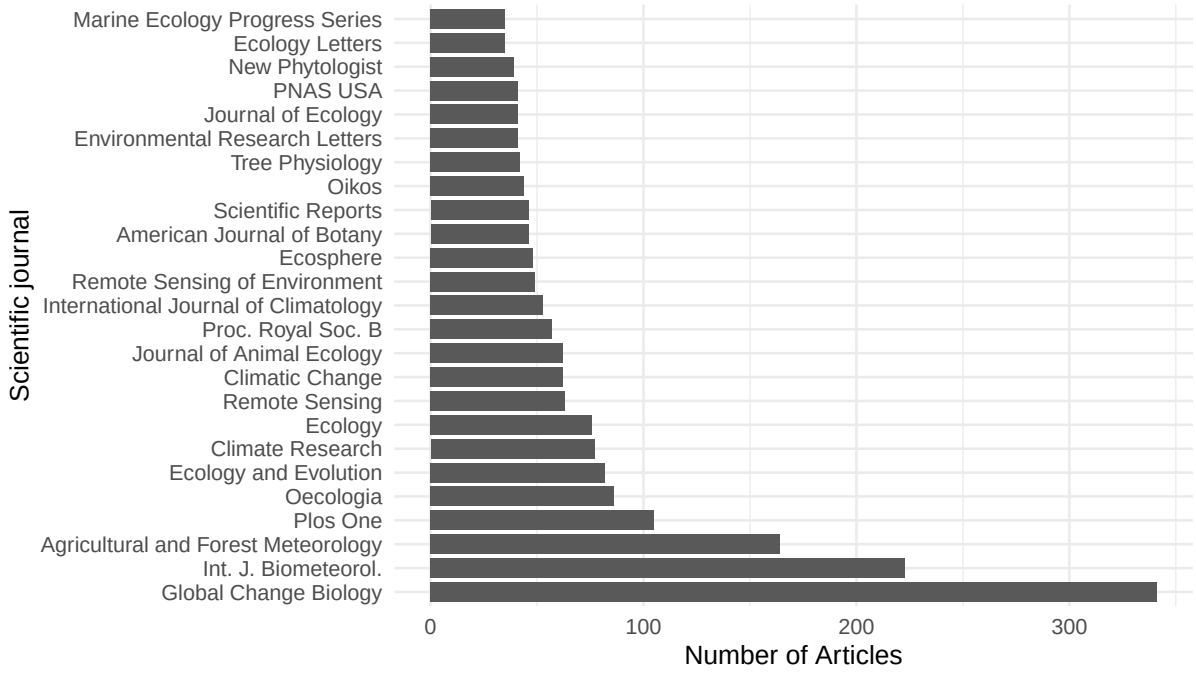


Figure 2.8: The 25 journals with the highest number of articles.

The corpus consisted of 729 journals, and the top 25 contributed 42% of all articles (Figure. 2.8.). Global Change Biology had the largest number of articles (341, Appendix A Figure A.4), primarily publishing on the topics *Marine phenology*, *Plant experiments*, and *Bird migration*, with 'Recipients' being the most published theme. The International Journal of Biometeorology (Appendix A Figure A.5) and the journal Agriculture and Forest Meteorology (Appendix A Figure A.6) mostly published within the theme 'Plants'. The most published topics for the International Journal of Biometeorology were *Plant chilling and heat requirements*, *Plant leaf phenology* and *Analysis*. For the journal Agriculture and Forest Meteorology, only one article was published within the theme 'Recipients', and the most published topics were *Agronomy*, *Predictive modelling* and *Plant chilling and heat requirements*. Both PLoS ONE (Appendix A Figure A.7) and Oecologia (Appendix A Figure A.8) published most within the theme 'Recipients'. The most published topics for PLoS ONE were *Bird reproduction*, *Bird migration* and *Marine phenology*, and for Oecologia were *Insect phenology* and *Bird reproduction*.

2.10 Discussion

We used topic modelling to quantify the scientific literature on phenology, in the context of climate change, over a 30-year period. Popular topics of research have changed dramatically, with a focus on plant phenology at a regional scale dominating in the 1990s, to the use of novel technologies to assess phenological change at larger spatial scales in the 2010s. Our results show a bias towards study locations, particularly China, Europe, and America (Topics 6 and 11, Appendix A Table A.1), as well as study organisms, particularly moths and tit (bird) species (Topics 15 and 28, Appendix A Table A.1). There is also incoherence in the research paradigm, resulting in little inter-connectivity between different methods of studying phenology, or the integration of new ideas. Topic modelling enables rapid synthesis of large diverse bodies of literature using machine learning algorithms. The approach can suffer from "order effects" and is vulnerable to inaccuracies arising from selective reporting and a mismatch between evidence and authors interpretation of evidence, but is useful in revealing broad patterns and changes in literature over time. Remote sensing has become the most popular method of monitoring since the 2010s, however, this has been applied in isolation to previous areas of phenological research (Figure. 2.3, Figure. 2.4.). Mismatching was also studied in isolation, which can lead to loss of knowledge of the greater impacts of climate change on ecosystems (*Consequences of mismatching*, Figure. 2.4.)

2.10.1 *Changes in topics over time*

As the complex relationship between species' phenology and environmental heterogeneity is further understood, the focus of research in this field has subsequently changed over the last 30 years (Chmura et al., 2019). In the 1990s popular topics focused on determining the impact of climate change on plants by conducting controlled experiments (position 1, Figure. 2.3.) and studies on phenology predominantly assessing phenological changes in a regional (study area) context with changing climate. Hence topics such as *Latitude and climate*, *Geographical location*, and *Elevation*, which commonly co-occurs with *Urban impacts*, were also popular in the 1990s. Studies utilised the more extreme seasonal temperature changes at higher latitudes or elevations, where there were expected changes in snowmelt date with additional warming.This hypothesises that phenological changes may be more severe for species nearer the poles, yet there has been no consensus on the direction of these shifts (Bradley et al., 1999; Chmura et al., 2019; Linhart & Grant, 1996; Inouye, 2008).

Following this was an increase in analyses of long-term data, as the possibility of using species' phenology as a bioindicator of climate change impacts became apparent (De Groot et al., 1995; Sparks & Carey, 1995). This is a potential explanation for the rise in popularity of bird focused topics in the 2000s (shown by topics *Bird migration* and *Bird reproduction* in Figure. 2.3.), as both their reproduction and migration are useful phenological indicators, and there are numerous long-term records of these events (De Groot et al., 1995). The variability in insect phenological research and continuing decline of plant research during the 2000s may be a result of this shift in focus to birds phenology with climate change.

Towards the end of the study period in the 2010s, studies have evolved from focusing on the climate influenced phenological change of one species, to how these changes impact pairwise interactions. (Figure. 2.3.). This ecosystem-view of phenology led to topics related to seasonality (*Warming impact on seasonality*, *Growing season*, and *Rain determining SOS*) increasing in popularity in the 2010s (Figure. 2.3.). Studies have thus evolved from simply quantifying phenological changes in different taxa, to understanding the variation in phenological responses and how this can impact on species interactions, along with their interactions with the landscape (Chmura et al., 2019; Visser & Gienapp, 2019). For example, loss of trophic interactions can happen as species track their ideal climate by migrating to higher latitudes or elevations to avoid temporal shifts, thus causing spatial mismatching between trophic levels (Chuine & Beaubien, 2001; Penuelas & Boada, 2003; Memmott et al., 2007; Thackeray et al., 2010). This is reflected in the shift in geographical topics from the immovable *Latitude and climate* and *Geographical location*, to the more organism-centric *Spatial-temporal variation* and *Biogeography*. Within the same spatial area, species that have ancestral associations, such as a predator-prey or plant-pollinator relationship, can become mismatched temporally due to asynchronous phenology (Memmott et al., 2007; Hegland et al., 2009; see Visser & Gienapp, 2019). Furthermore, secondary consumers (predators) seem to have lower climate sensitivity which could exacerbate mismatches as primary consumers and producers benefit from the lost interaction (Thackeray et al., 2010, 2016). This relatively new direction in phenological research led to the topic *Consequences of mismatching* rising 15 places from the 1990s to position 10 in the 2010s (Figure. 2.3.).

The topic *Reproductive plasticity*, which commonly co-occurs with *Consequences of mismatching*, also increased in popularity in the 2010s (Figure. 2.3.). While mismatching can be advantageous through lessening or removing an antagonistic interaction with a predator, it is possible that natural selection could spur resynchronisation for species in mutualistic

interactions due to impacts of mismatching on fitness (Vanschaik et al., 1993; Renner & Zohner, 2018; Damien & Tougeron, 2019; Visser & Gienapp, 2019). However, phenotypic selection on phenology may not be strong enough for resynchronisation to occur, especially for generalist species or those with long generation times (Kingsolver et al., 2001; Memmott et al., 2007). A resultant local genetic differentiation could mean loss of intra-species synchronisation across populations (Linhart & Grant, 1996). Thus, this increased focus on species-species interactions and the potential impacts of mismatching on fitness spurred the involvement of genetics, and the topic *Environmental genetics* increased in popularity from position 22 to 3 from the 1990s to the 2010s (Figure. 2.3.).

2.10.2 *Popularity of research topics*

Remote sensing increased in popularity, from position 39 in the 1990s to one in the 2010s. The popularity of remote sensing studies is likely in part due to an increase in all publishing on climate change related phenology, as well as the introduction of new technology, particularly the Moderate Resolution Imaging Spectroradiometer (MODIS), which made phenological remote sensing studies more accurate and easier to conduct (Kang et al., 2003). Four methodology types were highlighted topic model in the analysis: *Plant experiments*, *Modelling future climate change*, *Predictive modelling*, and *Remote sensing*. While *Plant experiments* and *Modelling future climate change* did co-occur with some frequency, likely because plant experiments were simulating climate change, there was little overlap with the other two methods (Figure. 2.4). This is partly to be expected, due to the restrictions imposed by the methodology of remote sensing (Kang et al., 2003).

Within the top 5 journals there was a split in focus, where some journals primarily published plant-related topics (Appendix A Figures A.5 and A.6), while others focused on fauna (Appendix A Figures A.4, A.7 and A.8). However, a drawback of this analysis is that topic popularity is intrinsically linked with topic specificity. As the organism being studied is more likely to become the highest-weighted topic in an article, the topics with the highest number of articles were all related to organisms (Bird migration, Bird reproduction, Insect phenology, Marine phenology, and Agronomy), except for remote sensing, which is also specific (Figure. 2.2). While Figure. 2.7. shows whether the number of articles with a topic as the highest weight has increased over time, it does not show this in proportion to the total number of articles published. For example, the increase in *Agricultural phenology* in Figure. 2.7 is likely due to an overall increase in the number of articles published on the subject (Figure. 2.3.);

the decline in Figure. 2.3 indicates that despite the increase in research into *Agricultural phenology*, it was still a small proportion of all research into phenology. This emphasises that limiting an article to one topic could be misleading. Additionally, the technique used to identify topics in topic modelling is semi-qualitative. While the analysis brings out the top 20 words associated with the prescribed number of topics, the topic names are decided by the researchers, which introduces bias and a descriptive quality to the model. Alongside this is positive publication bias, where studies that show phenological changes due to climate change are more likely to be published, which influences any summary we may make on the subject (Hughes, 2000; Thackeray et al., 2010).

2.10.3 *Research bias*

There is a lack of connectivity between some topics, particularly reflected by research on insect phenology. The topic *Insect phenology* commonly co-occurs with mismatching and bird topics, yet it rarely co-occurs with plant-based topics (Figure. 2.4.). This is surprising, considering the model identified a topic on the relationship between insects and plants, *Plant-pollinator interactions* which does commonly co-occur with plant-based topics, particularly agriculture. Evidently, there is a disparity in the way insect phenology is studied within phenological research in the context of climate change; it is either considered as the plant-pollinator or the predator-prey relationship, rarely both. Despite the transition to the population- and ecosystem-view of phenology, impacts are commonly considered in a pairwise manner. Loss of synchrony will undoubtedly have impacts on an entire ecosystem and consequently biodiversity, thus, species need to be considered together as part of a network, such as the oak-caterpillar-bird and sycamore-aphid-parasitoid systems in the UK (Burgess et al., 2018; Senior et al., 2020). In these mutualistic communities phenological timing can be crucial for the management and conservation of these ecosystem interactions (Morellato et al., 2016).

Further, new areas of research are not well integrated with the rest of phenological research, illustrated in Figure. 2.4. The topic *Consequences of mismatching* rarely co-occurs with most plant topics, the exception being *Agricultural phenology*. This indicates that while mismatching studies have increased in popularity (Figure. 2.7), they rarely consider the impacts of mismatching with the lowest trophic level, the primary producers. This is concerning, considering that primary producers tend to have stronger alterations to their phenology in response to environmental changes, likely in part due to their inability to move among microhabitats to track their ideal climate (Thackeray et al., 2010). The only 'Climate'

topics *Consequences of mismatching* tend to co-occur with are those that involve changes in temperature due to geography, and it strongly co-occurs with the 'Recipients' topics. This indicates that mismatching studies have focused on fauna and food production, and how geographical changes can impact their phenology and cause mismatching. However, the additional lack of co-occurrence with other methodologies in phenological research means that we are not fully utilising the tools at our disposal to detect this phenomenon. This supports the existing calls (see Renner & Zohner, 2018) for transdisciplinary work and integration of data.

In each article, the organism being studied is more likely to become the highest-weighted topic, due to high word frequency specific to that organism. Thus, the high frequency of the 'Recipients' topics (Figure. 2.2) and their top 20 words (Appendix A Table A.1), as well as the necessity for an entire theme dedicated to plants, indicate that the common study organisms for phenological studies are: agricultural crops, birds (particularly migratory), insects whose development is clearly impacted by temperature such as butterflies and moths, and phytoplankton in marine studies. This is exemplified by the topic *Bird reproduction*, which contained the word "tit", a common study organism (Appendix A Table A.1). However, there are clear problems with basing predictions of possible ecological impacts on the phenological changes of a few species. Underrepresentation of other taxonomic groups will hinder our ability to predict how phenological changes will impact ecosystems with further climate change.

In terms of geographical data disparities, there is also a bias towards study areas in the Northern hemisphere, as within the 20 highest-weighted words for the topics *Geographical locations* and *Rain determining SOS* were Europe, America, China, and "plateau", which refers to the Tibetan Plateau (Appendix A Table A.1). This is also evidenced by the number of articles per study location (Figure. 2.6), with all countries containing more than 100 articles in the northern hemisphere. In the global south, Australia is the only country that has more than 70 articles (Figure. 2.6). Increasing evidence of mismatching destabilising trophic interactions means these biases need to be addressed; despite the likelihood that phenological changes will occur more often in northern latitudes due to stronger warming, phenological changes are still expected to occur nearer the tropics (Parmesan, 2007). A lack of studies from the global South mean we are less likely to understand how phenological changes may impact ecosystems, as studies based on species in the northern hemisphere may not be applicable to species in the southern hemisphere. Study bias towards locations and species, and especially the lack of studies near the tropics (Figure. 2.6), prevents us from being able to predict how

trophic interactions may be impacted by phenological changes for vulnerable species as climate changes become more severe.

2.11 *Conclusion*

Over a 30-year period, the scientific literature on climate related phenological changes has expanded substantially. However, the connectivity between different spheres of research has not followed suit. Different methodologies and research foci have led to a fragmentation of phenological research, where the same topic is studied multiple times in isolation. There are common study organisms and areas that dominate the literature: Migratory birds, crops, insects, and phytoplankton are frequently the focus. While studies that investigate pairwise interactions are useful, these interactions are unlikely to represent an ecological network, and the impacts that phenological changes may have on them. The majority of phenological studies are conducted in the Northern hemisphere. To get a more comprehensive view of the global impacts of phenological changes, we need to first focus on research in the global south. Transdisciplinary research needs to become the norm, both to aid progress towards CBD targets and to improve our understanding of the ramifications of these responses to global climate change.

Chapter 3

Drivers of Moth Phenology in England and Wales

3.1 Introduction

Climate change is impacting many species, especially in relation to their phenology, or timing of their life cycles (Scheffers et al., 2016; Visser & Holleman, 2001; Van Asch et al., 2007; Cohen et al., 2018). Lepidoptera are ideal subjects for studying the impact of climate change on a large scale, due to their wide distribution, and well-understood life-history and taxonomy (Heikkinen et al., 2010; Hill et al., 2021). As poikilothermic insects, Lepidoptera are responsive to temperature (O'Neill et al., 2012), and being such a large group, they contain both pest species and those with a high conservation status (Sparks et al., 2006). Due to their short generation times, Lepidoptera can adapt quickly to the impacts of climate change, which along with their considerable phenotypic plasticity, means we are able to see trends over relatively short time scales (Hill et al., 2021; Välimäki et al., 2013). Further, being charismatic insects, extensive long-term citizen-science data exist in some countries that can be utilised to examine the large-scale impacts of climate change on phenology (O'Neill et al., 2012).

Much research has been done on the phenology of Lepidoptera. Key findings include advanced first emergences (Bonoan et al., 2021; Hällfors et al., 2021; Roy & Sparks, 2000), changes in mean flight date (Randle et al., 2019) and flight period length (O'Neill et al., 2012; Altermatt, 2010b; Valtonen et al., 2011), and increasing multivoltinism (Altermatt, 2010b; Välimäki et al., 2013; Teder, 2020), as well as cases of altered body size and fecundity (García-Barros, 2000; Honěk, 1993; Davidowitz & Nijhout, 2004), likely due to temperature altering growth rates.

Furthermore, changes in phenology could lead to changes in distribution, as both Macgregor et al. (2019) and Hällfors et al. (2021) found that species who shift their phenology may benefit from the ability to alter their distribution faster than species with a smaller phenological shift. These diverse responses make predicting the impacts of climate change on Lepidoptera difficult.

The timing of environmental cues can influence the timing of Lepidopteran phenology, as well as that of their larval hostplants. Higher temperatures can cause plants to leaf out earlier (Steltzer & Post, 2009; Sherry et al., 2007), and for Lepidoptera to end overwinter diapause earlier (Lindestad et al., 2020; Parmesan, 2007). For Lepidoptera species that are dietary specialists, they may lose synchrony with their host plants, leading to mismatched phenology with fitness consequences for the larva, and impacts on population viability (Visser & Holleman, 2001; Pelini et al., 2009; Van Asch et al., 2007; Navarro-Cano et al., 2015). Similarly, species that utilise other environmental cues, such as photoperiod, for diapause induction and termination face a further risk of mismatching if their hostplants are responding to temperature (Sims, 2007; Lindestad et al., 2020). A longer favourable season means that Lepidoptera species that have the capacity for multiple generations may take advantage of earlier emergence to build larger populations and/or have more generations (Keret et al., 2020; Macgregor et al., 2019; Michielini et al., 2021). Multivoltine species generally have more facultative diapause, for example by lowering the photoperiodic response threshold, but risk being caught out in a developmental trap if they are not ready to enter diapause when winter begins (Musolin & Saulich, 2012; Teder, 2020; Tauber et al., 1986; Van Dyck et al., 2015). The life stage at which species enter diapause appears important for their ability to respond to climatic changes. The later the life stage, the faster a species is able to reach adulthood after they exit diapause once the conditions are favourable, and thus the better their ability to respond to climatic changes (O'Neill et al., 2012; Végvári et al., 2015). Further, the life stage of diapause can influence the way they respond to climate change; Hällfors et al. (2021) found that while overwintering adults were more likely to advance their phenology, species that overwintered as pupa were more likely to undergo range shifts. While it is evident that life history traits play an important part in species' response to climate change, the relative importance of different traits in determining species' responses is still unclear. Many studies have sought to find traits that can predict species response to climate change, but this may not be possible due to the heterogeneous nature of both individual species' and the anthropogenic forces that may impact them (Tordoff et al., 2022; Wagner et al., 2021; Fox, 2013). Nevertheless, trait-based studies

such as Tordoff et al. (2022) have linked various life history traits to distribution trends of moths in the UK, so while predicting the response of data-deficient species based on their traits may be difficult, it is evident that traits do play a part in species' responses to environmental changes. Thus, although we now have knowledge of which traits impact species' distribution, the relationship between life history traits and phenological shifts is less clear.

The way in which a species' phenology is measured may impact the measured response, as species may respond differently to environmental changes at different parts of the season. As well as this, the type of data has to be considered when calculating phenological metrics, and data scarcity has led to an increase in the use of citizen science data for phenological studies (O'Neill et al., 2012; Dickinson et al., 2010; Bishop et al., 2013). Amateur naturalists have been recording the natural world for hundreds of years, with more than 80 recording schemes and societies in the UK alone (Roy et al., 2014). Recorder bias is a significant problem, as there is undoubtedly a period of training as amateur naturalists learn to identify organisms, as well as preference for particular locations and times of recording (O'Neill et al., 2012; Dickinson et al., 2012). However, the development of recording schemes to collect datasets with enough information to show long-term spatial and temporal changes is a difficult challenge that requires a large amount of effort on behalf of the volunteer recorders and organisers (Bishop et al., 2013). Such problems are an important consideration in studies that use citizen science data as these can impact results, but there are ways to standardise data to improve reliability of conclusions drawn (van Strien et al. (2008)).

In this article, we utilise long-term citizen science data from 1970 to 2019 on spatial distributions of 149 moth species in Great Britain to investigate drivers of the phenological response of these species to climate change. First, we analyse whether there have been phenological changes for each species using three "phenological variables" that represent different parts of the season, over 50 years (Objective 1). We postulate that the way in which species respond to environmental cues, and thus how their phenology responds to global climatic changes, is influenced by their life history traits. We therefore assess the extent to which patterns in species phenological responses are dependent on their recorded life history traits (Objective 2). To achieve these objectives, we used Linear Mixed Effects (LME) modelling to investigate how species differ in their response in space through the random effects of species and Watsonian Vice County. These models were used to investigate how phenology of moths was related to climatic variables and life history traits, as predictors and fixed effects.

3.2 Methods

3.2.1 *Data sources*

To analyse changes in moth phenology in Britain, data were sourced from two schemes: the National Moth Recording Scheme (NMRS) (Butterfly Conservation, 2022); and the Garden Moth Scheme (GMS) (GMS, 2023). The NMRS data comprise presence records of species occurrence from across Britain collected in a non-standardised way by citizen scientists and verified by experienced Lepidopterists (Fox et al., 2011). Spatial and temporal coverage of NMRS records is extensive but has increased dramatically over time (Fox et al., 2011; Randle et al., 2019). We used NMRS data from 1970 to 2019. Life history trait data for each moth species were obtained from (Cook, 2022), which is an up-to-date source of trait information for macro-moths in Britain and Ireland. The GMS data are more standardised than those from the NMRS. As part of the GMS, citizen scientists use light traps in their residential gardens to count widespread moth species once a week from March to November (Bates et al., 2013). However, the trap type, sampling night and weather conditions are not standardised across sites. The scheme started in the West Midlands region of England in 2003 but was expanded across the UK from 2007, with 347 gardens participating in 2019 (Passey, 2020). By obtaining data from both NMRS and GMS we aimed to increase the number of records each species and increase the accuracy of the phenological measures. The final list of 149 species used after standardisation and filtering from the NMRS and GMS data can be found in Appendix B. While we recognise that there is a inherent problem with citizen science, in that the data are likely to be noisy and error-prone, we propose the advantages far outweigh these negatives (van Strien et al. (2008); Dickinson et al. (2012)). Citizen science provides a large amount of data that allows us to investigate questions that would be otherwise impossible to answer, and with a larger number of records it is possible to detect much smaller patterns (van Strien et al. (2008)). Here, we use 3,687,320 records for 149 species from the combined NMRS and GMS data to generate temporally and spatially explicit phenological variables. However, it is worth noting that as these are all adult records and thus the data is not temporally structured in terms of development, hence the inclusion of life history traits. Temperature data were obtained from the UK's Meteorological Office (Met Office et al., 2018), and a Cumulative Mean Temperature (CMT) variable was calculated for every 365 day period over the 50 year study period. Thus, for each day of the year, there was an associated CMT value that represented the temperature for the previous year (e.g. a CMT value for 23rd March 2016

to 23rd March 2017, then for the 24th March 2016-2017 and so on). This CMT value was calculated for each 10km x 10km grid square (coarse easting and northing) where data was available, and then averaged for each Watsonian Vice County (VC) in England and Wales. The VC system was first developed for plant species distributions and has been used since its conception at the end of the 19th century, meaning comparisons between modern and historical records are easier and more accurate (Watson, 1883). The result was a single mean CMT value for each VC for each day of the whole of the study period. The process of cleaning these data for analysis is illustrated in Appendix B Figure B.1. Data were standardised in accordance with the methods of Hällfors et al. (2021).

3.2.2 *Modelling strategy*

We investigated the effects of life history traits and phenological variables hypothesised as being important in determining moth species phenology, utilising three "phenological variables" as measures of phenology at different parts of the season (see section 3.2.3 Phenological Variables). Due to our concern that voltinism may be changing (Teder, 2020), and the complications this would add for peak emergence, we only analysed univoltine moth species. Further, we calculated each emergence variable within each VC for each year, where there was enough data to do so. Moreover, by modelling at the VC level we remove zeros due to species absences, instead only concentrating on VCs where they are present. However, as a result of calculating at the VC level we had to remove all data from Scotland as there were too few records, and thus the analysis has been conduced for England and Wales only. Phenological measures can be biased due to recording effort and population changes, and this has to be considered when developing phenological measures from occurrence data (Bonoan et al. (2021); van Strien et al. (2008)). Thus, each species was filtered separately in each VC using the methods of van Strien et al. (2008), whereby we we only included species that had at least 30 records a year for at least 10 years in each VC. We further filtered the species to those with available trait data, resulting in 149 species included in the analyses. To determine which of the trait and phenological variables explained the most variation, and therefore were the most important, we developed a series of Linear Mixed Effects (LME) models with phenological variables, listed in Table 3.1, and species' traits as fixed effects, listed in Table 3.2. We included VC, Year, Species and Cumulative Mean Temperature (CMT) as random effects, with Year and CMT included as random slopes and VC and Species as intercepts. We then implemented a model selection process whereby the simplest model that

explained the most variation was obtained by using stepwise reduction. For each overwintering stage and each emergence variable combination we included all fixed effects hypothesised to be important in determining phenological shifts and then removed non-significant variables stepwise until we obtained the "best" model. We compared each model iteration using AIC and marginal R^2. Once we had the "best" model in terms of fixed effects, we tested the model with combinations of random effects in terms of AIC and conditional R^2, until we obtained the final "best" model for each overwintering stage/emergence variable combination. The random effects we tested were Year, VC, Species, and Family, as we wanted to test whether there was variation in species' response in each of these groups. We used AIC to test for the "best" model as this penalizes for overly complex models. All modelling was undertaken in R with R version 4.2.2 (2022-10-31 ucrt) (R Core Team, 2020) and the following packages for analyses: tidyverse, nlme, lavaan (Wickham et al., 2019; Pinheiro et al., 2023).

Table 3.1: The phenological variables included as fixed effects in the linear mixed effects models.

Environmental variables	Description
Cumulative Mean Temperature	a cumulative mean temperature value that represents the temperature over a 365 day period, averaged for a VC. This was calculated for every rolling 365-day period from 1970-2019.
Year	The year of the moth occurrence was recorded.

Table 3.2: Seven life history traits used for the included in the analyses, with description from Cook (2022) and Henwood, Sterling & Lewington (2020). We hypothesised that these traits would be phenologically relevent and thus have an influence on the way moth species respond to changes in their environment due to global climatic change.

Life History Traits	Description
Communal	Larvae that feed or bask communally or inhabit a communal nest.
Daily Activity Period	Listed as either Diurnal, Nocturnal or Both if at least one sex of the species is described as being active during that period.
Hostplant Category	Each species has single or multiple broad hostplant categories assigned depending on hostplants listed in Henwood, Sterling & Lewington (2020).
Number of Hostplants	The number of main and occasional hostplants the species is known to feed on as a larve, according to Henwood, Sterling and Lewington (2020).
Overwinter Stage	The life stage each species adopts as their overwintering strategy.
Pupa location	The location in which species form a pupa (e.g. below ground, external hostplant, dead wood).
Specificity	The phylognenetic variation in hostplants for each species.

3.2.3 *Phenological variables*

The rate of phenological change for moths may vary throughout the season, depending on the measure used, and with space, as phenological variables can vary depending on location.

Accordingly, three emergence variables were derived for each species from the recorded data:

- First Emergence – (FE) the day of year on which the first 25% of First Emergences had been observed for each species each year in each VC (*sensu* van Strien et al. (2008)).
- Peak Emergence (PE) – the average day with the highest number of records for each species each year in each VC.
- Emergence Standard Deviation (ESD) – the standard deviation of the average peak emergence. As the standard deviation is the spread of records around the peak emergence it represents the length of the flight period for each species each year in each VC.

3.3 Results

3.3.1 *Data Structure and model selection*

Cumulative mean temperatures for a location were averaged across a VC for each day in each year where data was available. Average cumulative mean temperatures for a VC (hereafter CMT) were matched to the day of year of FE and PE for each VC each year. Thus, for every VC each moth species would have two CMT values associated each year, one matched to FE and one to PE. As ESD is the spread of days around PE there are no CMT values associated with it. Hostplant Categories were simplified into whether the moth species fed on "Woody" or "Herbaceous" plants, or neither. We considered the importance of Pupa Location to be based on whether a species was exposed to the environment during the pupal stage. Accordingly, we also simplified Pupa Location to whether a species pupates in "Exposed" or "Covered" locations, or both. The number of species in each classification as well as number of species per subfamily are in Appendix B. The "Year" covariable was altered to be a scale of 1-50 as larger numbers can influence model output (Pinheiro & Bates, 2006). The overall distribution of each of the phenological variables and the distribution of overwintering stages can be seen in (Figure 3.1).

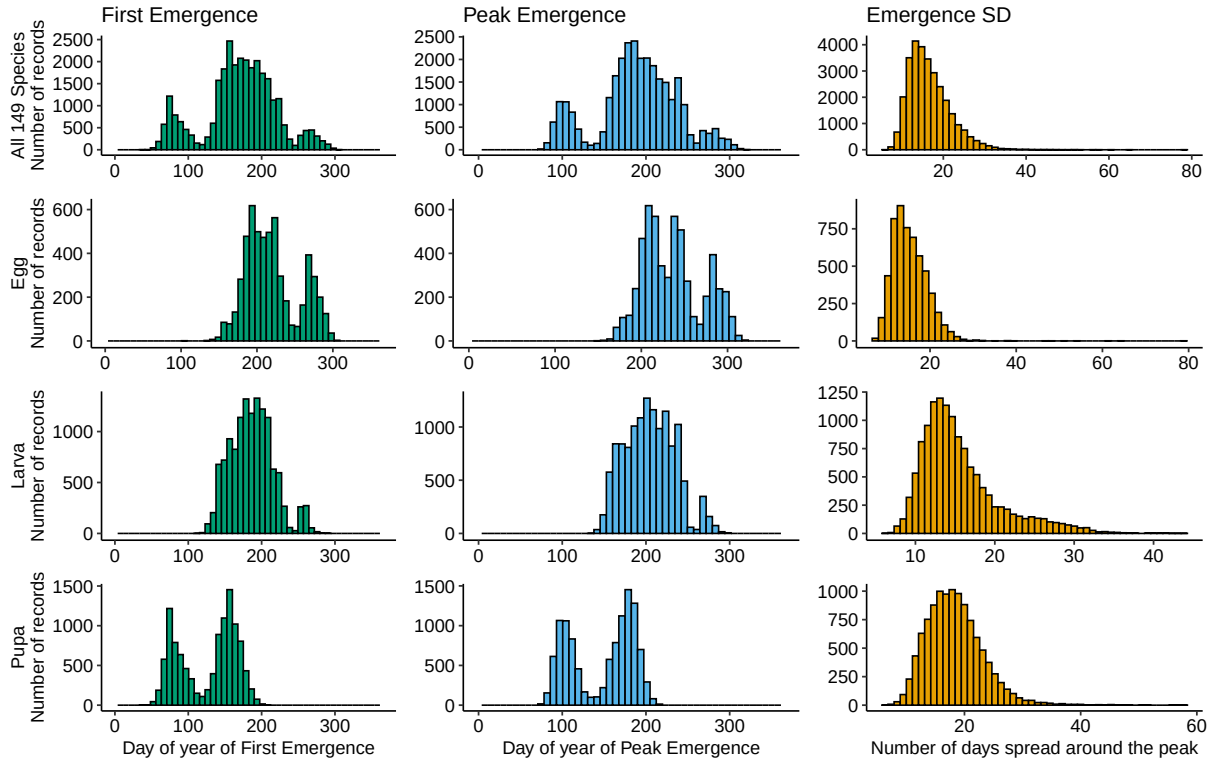


Figure 3.1: The number of First Emergence and Peak Emergence records on each day of year, and the number of Emergence SD records of number of days spread, for all 149 species and for each overwintering stage category.

We determined that we could not analyse all the species at once, as their phenology was highly influenced by their overwintering stage (Figure 3.1). Thus, we chose to limit the data to the species that overwinter as either an egg (40 species), larva (65 species) or pupa (44 species) as their main strategy. To confirm we could not include these three overwinter stages in the same model, we ran lme models for each emergence variable to see whether the groups were significantly different. For First Emergence (Table 3.3) and Peak Emergence (Table 3.3) the three overwintering stages were significantly different. The overwintering stage Larva was not significantly different from Egg for Emergence SD (Table 3.3), but we did not consider this an issue as both the First Emergence and Peak Emergence were significantly different for these overwinter stages. This indicates that although the length of the flight period is not significantly different for the egg and larva overwintering stage, the timing of the flight period is significantly different. As such, we considered them different enough that we could not include them in a model as one group.

Table 3.3: The results from the best LME model for each of the three phenological metrics when testing for significant difference between each of the overwintering stage categories.

Phenological Metric	Best Model	Variables	Value	Std.Error	DF	t-value	p-value
First Emergence	FE ~ Overwintering Stage + Year, random effect = Year per Watsonian Vice County nested in Species	(Intercept)	227.282	4.959	28,448	45.833	<0.001***
		Larva	-42.659	6.301	146	-6.771	<0.001***
		Pupa	-92.208	6.852	146	-13.458	<0.001***
Peak Emergence	PE ~ Overwintering Stage + Year, random effect = Year per Watsonian Vice County nested in Species	(Intercept)	243.133	4.972	28,448	48.897	<0.001***
		Larva	-42.141	6.318	146	-6.670	<0.001***
		Pupa	-88.948	6.870	146	-12.947	<0.001***
Emergence SD	ESD ~ Overwintering Stage + Year, random effect = Year per Watsonian Vice County nested in Species	(Intercept)	14.901	0.499	28,448	29.883	<0.001***
		Larva	-0.115	0.630	146	-0.182	0.856 NS
		Pupa	2.346	0.688	146	3.410	0.001**

3.3.2 *Egg overwintering species*

The best linear mixed effects models for the 40 species that overwinter as an egg included Year and CMTVC for both FE and PE and Year for ESD, no traits were significant. The slope of change for Year was the largest for FE at -0.17, compared to -0.04 for PE and 0.016 for ESD (Tables 3.4, 3.4 and 3.4). However, temperature affected PE the most as this had the larger slope of -3.44 compared to -3.13 for FE (Tables 3.4 and 3.4).

Table 3.4: The results from the best LME model for Egg overwintering species for each of the three phenological metrics.

Phenological Metric	Best Model	Variables	Value	Std.Error	DF	t-value	p-value
First Emergence	FE ~ Year + Cumulative Mean Temperature, random effect = Watsonian Vice County nested in Species	(Intercept)	275.795	5.839	5,319	47.230	<0.001***
		Year	-0.172	0.009	5,319	-18.484	<0.001***
		Cumulative Mean Temperature	-3.132	0.144	5,319	-21.788	<0.001***
Peak Emergence	PE ~ Year + Cumulative Mean Temperature, random effect = Watsonian Vice County nested in Species	(Intercept)	291.391	5.691	5,319	51.205	<0.001***
		Year	-0.040	0.008	5,319	-5.159	<0.001***
		Cumulative Mean Temperature	-3.438	0.125	5,319	-27.435	<0.001***
Emergence SD	ESD ~ Year, random effect = Watsonian Vice County nested in Species	(Intercept)	14.351	0.475	5,320	30.238	<0.001***
		Year	0.016	0.004	5,320	4.368	<0.001***

3.3.3 *Larva overwintering species*

The best LME model for each emergence variable was not as consistent for larva overwintering stage as it was for egg. For both FE and PE the best model included Year, CMTVC, and the Hostplant Category trait. There were no traits significant for ESD so only Year was included. The woody hostplant category was significant and had the largest slope for both FE and PE, but the herbaceous hostplant category was not (Tables 3.5 and 3.5). Temperature had a larger slope for FE at -3.28, compared to -3.03 for PE. There was a large difference in the slope for Year for each emergence variable, with FE advancing much quicker than PE and ESD (Tables 3.5, 3.5 and 3.5).

Table 3.5: The results from the best LME model for Larva Overwintering species

Phenological Metric	Best Model	Variables	Value	Std.Error	DF	t-value	p-value
First Emergence	FE ~ Year + Cumulative Mean Temperature + Woody + Herbaceous, random effect = Watsonian Vice County nested in Species	(Intercept)	236.219	8.679	12,452	27.218	
		Year	-0.179	0.006	12,452	-28.137	
		Cumulative Mean Temperature	-3.276	0.084	12,452	-38.896	
		Hostplant Category: Woody	17.165	7.394	62	2.321	
		Hostplant Category: Herbaceous	-6.230	8.988	62	-0.693	
Peak Emergence	PE ~ Year + Cumulative Mean Temperature + Woody + Herbaceous, random effect = Watsonian Vice County nested in Species	(Intercept)	241.971	8.727	12,452	27.728	
		Year	0.020	0.005	12,452	3.804	
		Cumulative Mean Temperature	-3.033	0.075	12,452	-40.325	
		Hostplant Category: Woody	17.628	7.447	62	2.367	
		Hostplant Category: Herbaceous	-6.234	9.053	62	-0.689	

Table 3.5: The results from the best LME model for Larva Overwintering species

Phenological Metric	Best Model	Variables	Value	Std.Error	DF	t-value	p-value
Emergence SD	ESD ~ Year, random effect = Watsonian Vice County nested in Species	(Intercept)	13.508	0.415	12,453	32.538	
		Year	0.035	0.003	12,453	13.833	

3.3.4 *Pupa overwintering species*

The best LME models for species that overwinter as pupa were the same as for egg species, with Year and CMTVC included for FE and PE and Year for ESD. In comparison with the other overwintering stages, pupa had a much stronger response to temperature overall, but particularly for FE (Table 3.6). Further, the year response was also the strongest for all phenological variables for pupa species, but particularly for FE as the slope was almost double the equivalent slope for egg and larva species (Tables 3.6, 3.4 and 3.5).

Table 3.6: The results from the best LME model for Pupa Overwintering species

Phenological Metric	Best Model	Variables	Value	Std.Error	DF	t-value	p-value
First Emergence	FE ~ Year + Cumulative Mean Temperature, random effect = Watsonian Vice County nested in Species	(Intercept)	210.645	5.374	10,671	39.198	<0.001***
		Year	-0.308	0.009	10,671	-35.572	<0.001***
		Cumulative Mean Temperature	-4.613	0.110	10,671	-42.008	<0.001***
		(Intercept)	213.509	5.330	10,671	40.060	<0.001***
		Year	-0.049	0.007	10,671	-7.051	<0.001***

Table 3.6: The results from the best LME model for Pupa Overwintering species

Phenological Metric	Best Model	Variables	Value	Std.Error	DF	t-value	p-value
Peak Emergence	PE ~ Year + Cumulative Mean Temperature, random effect = Watsonian Vice County nested in Species	Cumulative Mean Temperature	-4.126	0.093	10,671	-44.466	<0.001***
Emergence SD	ESD ~ Year, random effect = Watsonian Vice County nested in Species	(Intercept)	15.291	0.489	10,672	31.285	<0.001***
		Year	0.053	0.003	10,672	15.254	<0.001***

3.4 Discussion

Our results showed that phenological shifts for moths are different depending on the overwintering stage of the species measured. Species overwintering as pupa have the earliest First Emergence and Peak Emergence, followed by larva species and finally egg overwintering species, with approximately 40 days difference between each of these categories. Further, pupa overwintering species had a significantly longer flight period than egg and larva overwintering species, which further confirms the results in O'Neill et al. (2012), Végvári et al. (2015) and Hällfors et al. (2021). However, this variation in response depending on overwintering stage makes investigating the drivers of species' phenology challenging. The interspecific variation between each of the overwintering stages could not be captured in one model with the hypothesised error distribution, which would result in inaccurate measures of phenological shifts and their drivers. Thus, by running the model sepearetely for each overwintering stage we could more accurately determine the drivers of phenological shifts. Overall, there is a strong indication from the LME models that temperature is an important driver of phenology. As well as this, the type of vegetation utilised by species can influence phenology, but the strength of this driver varies depending on the phenological measure and overwintering stage. Here, we have confirmed and expanded on previous studies on the impact of species' traits on phenology (Altermatt, 2010b; Hällfors et al., 2021; Teder, 2020).

All of the overwintering stages followed predominantly the same trend of traits not being included in the best model, with the exception of Hostplant Category for the larva overwintering stage. This is likely due to the inclusion of species in the random effects of each model. In essence, a species traits are the parts that make up the sum that is the species itself, so by including both the traits as fixed effects and species as the random effects we were including the "species" explanatory variable twice. However, the models with species included as a random effect were a better fit to the data than the models including the traits as fixed effects. Individual life history traits are not good predictors of phenological change in moths because of interspecific variation. In other words, the individualistic responses of moth species outweigh the predictive value of particular traits. As such, the only variables that were consistently significant across all the models were the environmental variables Year and Cumulative Mean Temperature. Furthermore, the best model for all phenological metrics and overwintering stages included Vice County as a random effect. This demonstrates that averaging phenology to large areas, such as England for example, may be problematic as the variation in environmental cues over such a large area leads to variation in phenology. Thus, by calculating the phenological metrics and Cumulative Mean Temperature at the Vice County level we included this spatial variation in our models.

It has been shown that phenological measures at the beginning of the season can be highly variable, dependent on recording effort and population changes (van Strien et al. (2008); Miller-Rushing et al. (2008)). Here, we attempted to mitigate this using the First Emergence measure recommended by van Strien et al. (2008). However, this does not take into account changes in species distribution that may have occurred over the study period. Many species have altered their distribution over the last 50 years (Randle et al., 2019), which could be due to species tracking their ideal climate in response to temperature changes (Lenoir et al., 2020). Furthermore, a change in the timing of phenology for species with an altered distribution could be due to more records where the species previously was not present, but could also represent species responding to phenological variables such as lower temperatures compared to where they were previously distributed. Population changes could also impact measures early in the season, as a large increase in abundance could lead to the appearance of earlier phenology due to there being more individuals to record, but could also be a real change in phenology. Similar problems can be seen with increased recording effort.

First Emergence changed the most for pupa overwintering species, which had the largest slope for both year and Cumulative Mean Temperature, followed by species that overwinter as larva,

and then egg. For all overwintering stage categories the slopes were negative, indicating an overall phenological shift towards earlier emergence for the species in each category. Additionally, contrary to Végvári et al. (2015), we found that the hostplant category "woody" was significant for species that overwinter as larva, instead in agreement with Altermatt (2010b). This is intuitive, as there is expected to be strong selection pressure on the phenology of moth caterpillars to coincide with the narrow window in which the freshly emerged leaves of woody plants are edible, and indeed such phenological flexibility and significant temporal trends has previously been demonstrated (Visser et al., 2006; Altermatt, 2010b; Burgess et al., 2018).

Compared to First Emergence, there was a much more varied response in Peak Emergence phenology across the three overwintering stages. The slope for year for Peak Emergence was positive, indicating delayed phenology, for larva overwintering species. However, for egg and pupa overwintering species the slope was negative, with the strongest response again for pupa species as with First Emergence, in agreement with previous studies such as Bonoan et al. (2021) and Prior et al. (2009). This disparity may be due to Hostplant Category "woody" being significant for larva overwintering species' Peak Emergence phenology, with a larger slope than for First Emergence, along with a smaller slope for temperature. However, it is possible that due to only 4 of the 65 larva species specialising in woody hostplants and 15 of the 65 having both woody and herbaceous, this result of woody being important for larva overwintering species' phenology is unreliable, and instead represents the different phenological strategies between species that feed on woody and herbaceous plants. This could explain why there was no significance for Hostplant Category for the egg and pupa overwintering species, as the majority have woody hostplants. Evidently, the three overwintering stage categories respond to the same variables differently at different parts of the season. There is an overall larger change across years for Peak Emergence than for First Emergence. However, temperature is more important for early season phenology for both the larva and pupa species, but not for the egg species. This may be due to the reliance of larva and pupa species on food sources in the early season and thus utilising temperature as a way to fine-tune their phenology, in contrast to egg species which in spring need to continue to develop before food sources become important, hence the much larger slope for temperature for egg species' Peak Emergence phenology.

The slope for year for Emergence Standard Deviation was positive for all three overwintering stage categories, indicating they are on the wing for longer, following the trend of lengthening

seasons due to a delay in winter onset (Keret et al., 2020). This is in contrast to Bonoan et al. (2021) who found that Peak Emergence shifted but overall flight period did not. Species that overwinter as an egg had the smallest change in flight period over time, whereas the slope for year was the largest for larva and pupa species. However, when compared to the overall response, larva overwintering species were increasing their flight period a lot faster in relation to their change in First and Peak Emergence than the egg and pupa overwintering species. This implies the possibility of a developmental trap; if the flight period does not change at the same rate as the rest of the species' phenology there could be extra generations or species may be present when their hostplant is unavailable (Van Dyck et al., 2015).

3.5 Conclusion

In summary, the phenology of our three phenological variables varied considerably between the overwintering stage categories, and responded differently in the models. This illustrates the importance of the choice of phenological measure when investigating impacts of climate change on phenology, as the response of the moths depends on their stage of development through the seasons. Further, it is only when the whole season is taken into account do we get a clearer picture of how species are responding to climate change. While previous studies have studied Lepidoptera species together in phenological analyses, here we have illustrated this may not be appropriate. Different overwintering life stages had significantly different phenology and thus could not be considered in the same model, and grouping them together could impact the reliability of measured phenological shifts. Further, the resources utilised for the main period of growth in the larval stages has important consequences for how changes in temperature influenced changes in phenology. Thus, future studies on Lepidopteran phenology should carefully consider how species are analysed as one group, as different life history strategies play a large part in how species react to any changes in their environment.

Chapter 4

Drivers of Plant Phenology in England and Wales

4.1 Introduction

Plants undergo measurable changes with seasonality, known as their phenology, the timing of their life history traits. Climate change is altering the phenology of many species, including plants (Thackeray et al., 2010; Menzel & Dose, 2005; Memmott et al., 2007; Geissler et al., 2023; Menzel et al., 2020). Temperature is a key driver of plant phenology, with many studies consistently finding that increasing temperatures due to climate change can advance plant phenology, both in observational and experimental studies (Geissler et al. (2023); Menzel et al. (2020); Büntgen et al. (2022); de Manincor et al. (2023)). However, for many plant species the warmer winter temperatures are leading to delayed dormancy and/or lack of chilling for germination, resulting in delayed spring phenology (Cook et al., 2012; Grossman, 2023; Gu et al., 2023; Menzel et al., 2020; Tansey et al., 2017). Warming also has consequential effects on plant fitness, and can lead to a reduced seed output and fewer pollinator interactions (de Manincor et al. (2023)).

Davies et al. (2013) demonstrated that the timing of leafing out and flowering is more similar in closely related plant species, and Davis et al. (2010) showed that this similarity extended to closely related species' phenology responding in a similar way to climate change. Phylogenetic conservatism, where closely related species are more likely to have similar traits, may elucidate how multiple species will respond to climate change. However, when assessing both *why* species are responding as well as *how*, we need to determine the degree to which phylogeny

plays a part in phenological changes, as this could be crucial to predicting future impacts of climate change. One method for assessing this is through trait-based approaches, as traits are more similar in closely related species. Trait-based approaches can be a powerful way of investigating large-scale changes in systems, as they are a representation of how a species has adapted to survive (Chaudhary et al., 2022). For example, if a plant has a mycorrhizal symbiosis their life history strategies tend to vary from those without, which in turn can impact their phenological response (Chaudhary et al., 2022). One of the main ways of separating groups of plants is into herbaceous and woody. These two distinct groups have very different life history strategies, with herbaceous species investing resources quickly over a short period of time compared to woody species. These two systems of growth have been shown to impact the way their phenology is responding to climate change, for example Geissler et al. (2023) found that woody plants had a much stronger association between flowering and warming than herbaceous plants, contradicting their hypothesis that woody species would be more responsive to photoperiod. As well as having different responses to warming, woody and herbaceous species have different cues for key phenological metrics; while leaf senescence in trees is regulated mostly by temperature and global radiation and occurs later in the year, herbaceous plant leaf senescence is driven by species-specific characteristics (Horbach et al., 2023). Herbaceous plants also tend to be more variable in their early season phenology than woody plants, with insect-pollinated herbaceous plants not advancing their phenology as much as wind-pollinated species (Horbach et al., 2023; Menzel et al., 2020). Furthermore, the same trait for woody and herbaceous plants may have different functional implications when applied to phenology, such as vegetative height (Geissler et al., 2023). Indeed, Horbach et al. (2023) found that vegetative height had a much stronger relationship with phenology for herbaceous plants, possibly due to the concurrent relationship between height and competitive ability.

A leading measure of plant life history strategies is Grime's CSR theory (Grime et al., 1988), where their competitive (C) ability, stress (S) tolerance, and level of ruderalism (R) represent the trait combinations of plant species (Pierce et al., 2017). The CSR classification of a species is thus a useful metric where the strategy of a species is an average calculated from individuals and thus can represent how an individual might respond, e.g. in terms of their phenology, to climate change (Pierce et al., 2017). As there is potential for phylogeny and traits to influence the phenological response of plant species to climate change, the CSR metric offers an alternative measure that encapsulates these two variables and is potentially more informative. The ability of a plant species to compete with other individuals and tolerate

stress are potentially crucial traits that could impact their survivability with ongoing climate change. For example, an individual with a high stress tolerance may not need to alter its phenology as it can cope with higher temperatures, or a competitive individual may be able to take advantage of the environmental changes that accompany climate change and outcompete others. Thus, there is potential that a simple metric such as CSR could be useful in the analyses of phenological changes of plants and how they might respond to climate change. Here, we use a combination of environmental variables and plant life history traits and CSR metrics to determine the main drivers of plant species first flowering dates, from 1969-2019. We have three objectives:

1. Identify whether plant life history traits and CSR metrics will have a large influence on their phenological response to climate change.
2. Identify whether the CSR metric will influence phenological response more than individual life history traits
3. Assess the dependency of plant phenology on the phenology of the previous year

To examine these objectives, we conduct a series of Linear Mixed Effects (LME) models with environmental, life history trait and CSR variables as fixed effects to determine which are the main drivers of phenological changes (Objective 1 and 2). As part of the LME model selection, we will include autocorrelation and autocovariance to account for phenology in previous years (Objective 3).

4.2 Methods

4.2.1 *Data sources*

Plant phenological data was sourced from the Woodland Trust Nature's Calendar (Accessed 08/09/2020: www.naturescalendar.org.uk), which contained phenological data for 532 plant species in the UK. We narrowed down the species to those for which there was data from Grime et al. (1988) and Hodgson et al. (1995), and for which there were CSR percentages available from Pierce et al. (2017), leaving 216 species. We then calculated the average phenology in each Watsonian Vice County each year for species that had at least 20 years of data in that vice county following the methods of van Strien et al. (2008) and Chapter 3. We

then removed any species that did not have any trait data available. Thus, we were left with 185 species that had both trait data and enough data in at least one vice county. Temperature data were obtained from the Met Office (Met Office et al., 2018), and a cumulative mean temperature variable was calculated for every 365 day period for every coarse Easting and Northing (1km grid square) for 50 years from 1969. All cumulative mean temperature values within a vice county were averaged, leaving a single cumulative mean temperature value for each vice county for each day of year for a 50 year period. We used the CSR database from Grime et al. (1988) and Pierce et al. (2017) which included many life history traits. We chose life history traits we hypothesized (Table 4.1) would be most phenologically relevant and could impact a plant species' ability to alter their phenology in response to climate change (Obj. 1). The traits "story", "woody/herbaceous", and "annual/perennial" were determined from what is known about the species included. The full list of traits and where their sources are is in Table 4.1.

Table 4.1: The life history trait variables included in the analyses.

Life History Traits	Description	Origin
Soil pH	Modal pH class for each species (i.e. species with soil pH 7 would be most frequent in the range 7.0-7.9)	Grime, Hodgson and Hunt (1988)
Soil pH Range	Number of pH classes in which the frequency of the species exceeds 50% of that in their modal class (soilph)	Grime, Hodgson and Hunt (1988)
Mycorrhizas	Whether a species has a mycorrhizal assocation of the following: Vesicular-Arbuscular (VA); Ectomycorrhizas (EC); Intermediate (26-74% record report infection with VA mycorrhizas); no mycorrhiza	Grime, Hodgson and Hunt (1988)

Table 4.1: The life history trait variables included in the analyses.

Life History Traits	Description	Origin
Leaf Phenology	Whether a species had leaf phenology in one of the following: Canopy evergreen (always evergreen); Canopy evergreen (partially evergeen); Canopy seasonal (aestival); Canopy seasonal (hibernal); Canopy seasonal (vernal)	Grime, Hodgson and Hunt (1988)
Life Form	Whether a speices is one of the following: Chamaephyte; Geophyte; Hemicryptophyte; Phanerophyte	Grime, Hodgson and Hunt (1988)
SC percentage	Combined percentages of Stressor and Competitor from the functional matrix in Pierce et al. (2017).	Pierce et al. (2017)
Story	Whether a species is generally "Overstory" or "Understory"	Defined based on literature search
Woody / Herbaceous	Whether a species is "Woody" or "Herbaceous"	Defined based on literature search
Annual / Perennial	A measure of whether a species experiences multiple seasons. We grouped Biennial and Perennial species into the "Perennial" group, as all Annual species were removed from analyses. Any species that were variable, e.g. listed as Annual and Perennial depending on conditions, were included in Perennial.	Defined based on literature search

4.2.2 *Modelling strategy*

We used the same methodology as Chapter 3 for these analyses: stepwise model selection with Liner Mixed Effects (LME) models including the enviornmental variables (Table 4.2)) and traits variables (Table 4.1) as fixed effects, with species, Watsonian Vice County (VC) and family as random effects. The response variable for the LME models was the average first flowering in each VC, so for each year in the data we had a single first flowering record for each VC for each species. We analysed by VC to account for any spatial variation in first flowering phenological shifts, but we had to remove Scotland due to too few records. All modelling was undertaken in R with R version 4.2.2 (2022-10-31 ucrt) (R Core Team, 2020) and the following packages for analyses: tidyverse, nlme, lavaan (Wickham et al., 2019; Pinheiro et al., 2023; Rosseel, 2012).

Table 4.2: The environmental variables included in the analyses.

Environmental variables	Description
Cumulative Mean Temperature	The cumulative mean temperature each day each year, averaged across a Watsonian Vice County.
Year	The year of the moth occurrence was recorded.

The Nature's Calendar data contained several phenological variables, but these were not measured for all species. As we were primarily assessing drivers of phenology we only included the phenolgical variable "First Flowering", the day of year when a plant species first flowers at a specific location, which had data for the most species. We excluded "annual" species due to the likelihood of any shifts in their phenology being on a year-by-year basis, rather than reflecting the long-term changes caused by GCC. We also excluded "woody" species, as there was not a sufficient number (11 species) to include in a LME model separately, and their phenology was different enough from "herbaceous" species that they could not be modelled together (Figure 4.1). As with Chapter 3, we could not analyse the remaining species together due to the difference in the phenologies of different Leaf Phenology categories (Figure 4.2).

Leaf Phenology categories "Seasonal - Hibernal" and "Seasonal - Vernal" were excluded due to there being fewer than 10 species. A plot of the distribution of the traits selected among these three Leaf Phenology categories, as well as density plots of the CSR values, and list of species included in the analyses, are in Appendix C.

The following model selection process was conducted for each of the three remaining Leaf Phenology categories. LME models with all fixed effects (Tables 4.2, 4.1) included and species and VC as the random effect were the starting point for each of the Leaf Phenology categories. Fixed effects were removed if the model without them either had a lower AIC and explained the same amount of variation (R^2), or if the AIC only increased a small amount (e.g. 2567 to 2569) and the R^2 only decreased by a small amount (e.g. 0.12 to 0.10). Using the same model selection method we also tested the combination of random effects for each of the Leaf Phenology categories, with each one always having species nested in VC as the best model. Once we obtained the best model for the fixed and random effects, we tested the model for autocovariance and autocorrelation. If there was significance, we then included a Autoregressive Moving Average (ARMA) correlation structure using the "corARMA" function in the LME, and tested for the best AR(p) and MA(q) values using AIC. The AR(p) and MA(q) model with the lowest AIC was taken as the best and final model. Thus, we aimed to obtain the simplest model using this process. Normality was checked for all models and fixed effects that caused the models to be less normal were also removed. After the best model was obtained, extreme outliers were removed to improve normality.

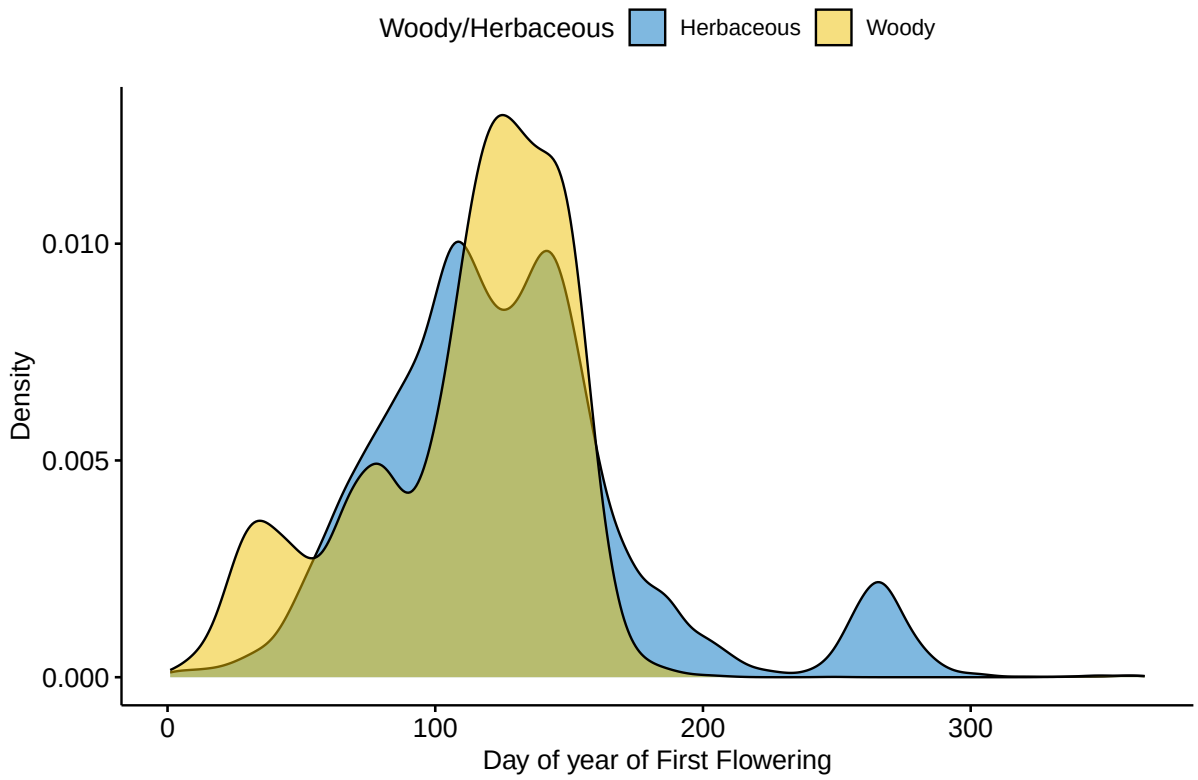


Figure 4.1: The density distribution of all the first flowering dates for the categories Woody and Herbaceous.

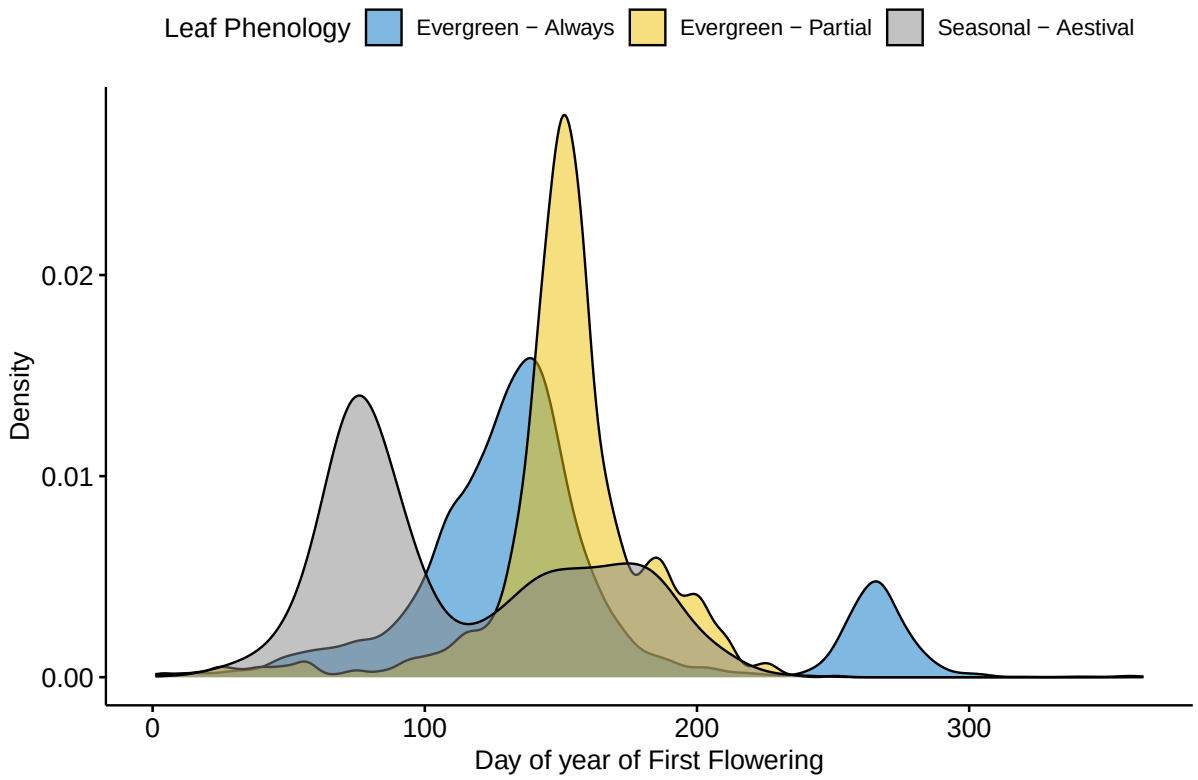


Figure 4.2: The density distribution of all the first flowering dates of annual species for the categories in Leaf Phenology for which there are more than 5 species.

4.3 Results

There were no plant traits significant for any of the three Leaf Phenology categories. Plants with different Leaf Phenologies had significantly different first flowering phenology (Table 4.3), so we could not model all species together. Overall, "Seasonal - Aestival" species were the most responsive to temperature, followed by "Evergreen - Partial" species and finally "Evergreen - Always" species. Further,the First Flowering phenology of both "Seasonal - Aestival" and "Evergreen - Always" species was dependent on the phenology of previous years, as the best model for both of these Leaf Phenology categories included the corARMA structure.

Table 4.3: The results of the fixed effects for the linear mixed effect model for First Flowering and Leaf Phenology: First Flowering ~ Leaf Phenology, random effects = Watsonian Vice County nested in Species.

Variables	Value	Std.Error	DF	t-value	p-value
(Intercept)	140.373	3.851	14,850	36.448	<0.001***
Evergreen - Partial	19.080	8.500	129	2.245	0.026*
Seasonal - Aestival	17.940	6.975	129	2.572	0.011*

4.3.1 *Model selection*

We tested whether the different regeneration strategies in each of the remaining Leaf Phenology categories were significant, but there was no significant difference in the flowering phenology of species with different strategies. After this filtering process, we had 132 species remaining in the analyses, with the species split into the following Leaf Phenology categories: 20 "Evergeen - Partial (EP)" species, 34 "Seasonal - Aestival (SA)" species and 78 "Evergreen - Always (EA)" species. Only 8 of the 132 species were present in all 70 VCs, one was present in 20 VCs, and the remaining species were present in less than 10 VCs. We tested these remaining Leaf Phenology categories using an LME and they were significantly different (Table 4.3). While the Leaf Phenology categories were significantly different to each other, within the categories there was still variation in first flowering with no single "true peak" (Figure 4.2). Due to this variability in first flowering within each of the Leaf Phenology categories, models never reached perfect normality. This is understandable and does not decrease the value of the model, as we are amalgamating over 100 species into a single model, they will never respond in the same way. Indeed, the significance of species as a random effect illustrates this point, as family never explained the variation as well as the species themselves, indicating there is species-species variation that cannot be accounted for in any other way.

4.3.2 *Leaf Phenology: Seasonal - Aestival*

Year and CMT had a significant effect on the day of First Flowering for "Seasonal - Aestival" (Table 4.4). Year had a much smaller slope than CMT and the marginal R^2 was 0.04, whereas the conditional R^2 that included the random effects was 0.85. Thus, although both Year and CMT were highly significant, it was the random effect of species and VC that explained the most amount of variation in the model. When we repeated the model with a correlation ARMA (corARMA) structure, an AR(p) of 6 and MA(q) of 2 had a lower AIC value than the model not including this structure. As a result of the correlation structure the R^2 changed, with the marginal R^2 now 0.03 and the conditional R^2 now 0.76. Further, the slope for temperature increased with the corARMA model from -5.86 to -6.05, and year decreased from 0.45 to 0.30 (Table 4.4). Thus, once the temporal correlation with previous years was accounted for with the corARMA structure, the impact of Year decreased with a smaller marginal R^2 and slope, and the random effect of species and VC explained less variation. The marginal R^2 also decreased with the corARMA structure for CMT, but unlike Year the slope increased.

Table 4.4: The results of the fixed effects for the linear mixed effect model for the Leaf Phenology category Seasonal - Aestival: First Flowering $\sim$ Year $+$ Cumulative Mean Temperature, random effects $=$ Watsonian Vice County nested in Species, correlation structure: Autoregressive order ($p = 6$), Moving average order ($q = 2$).

Variables	Value	Std.Error	DF	t-value	p-value
(Intercept)	234.945	6.817	2,620	34.466	<0.001***
Year	0.305	0.055	2,620	5.572	<0.001***
Cumulative Mean Temperature	-6.046	0.348	2,620	-17.381	<0.001***

4.3.3 *Leaf Phenology: Evergreen - Always*

The Leaf Phenology category "Evergreen - Always" was the only one of the three categories to just have CMT as the fixed effect in the best model. Further, the slope for CMT for

"Evergreen - Always" was the smallest of the three categories (Table 4.5). However, the variation explained by CMT was twice as much for "Evergreen - Always" than it was for the other categories, with the marginal $R^2 = 0.022$. The conditional R^2 was similar to "Seasonal - Aestival" at 0.86. The correlation ARMA structure was also significant for "Evergreen - Always", at AR(p) = 2 and MA(q) = 2 having a lower AIC than the model not including the correlation structure. With the correlation structure the marginal R^2 increased slightly to 0.23 and the conditional R^2 decreased to 0.80. Hence, the response of "Evergreen - Always" to the inclusion of the corARMA structure was different to the "Seasonal - Aestival" category in that the impact of CMT increased, indicating the importance of temperature for "Evergreen - Always" First Flowering phenology.

Table 4.5: The results of the fixed effects for the linear mixed effect model for the Leaf Phenology category Evergreen - Always: First Flowering ~ Cumulative Mean Temperature, random effects = Watsonian Vice County nested in Species, correlation structure: Autoregressive order (p = 2), Moving average order (q = 2).

Variables	Value	Std.Error	DF	t-value	p-value
(Intercept)	203.510	4.377	6,743	46.496	<0.001***
Cumulative Mean Temperature	-4.681	0.195	6,743	-24.034	<0.001***

4.3.4 *Leaf Phenology: Evergreen - Partial*

As with "Seasonal - Aestival", the Leaf Phenology category "Evergreen - Partial" also had Year and CMT as fixed effects in the best model (Table 4.6). The fixed effects were the least effective at explaining variation in the model for "Evergreen - Partial", as the marginal $R^2 = 0.026$. However, the conditional $R^2 = 0.92$, the largest of the three categories. Although both Year and CMT were included in the best model, Year had a much smaller slope at around one third of the slope for year for "Seasonal - Aestival", and the CMT was also smaller for "Evergreen - Partial". The ACF plot indicated no requirement for a correlation structure for "Evergreen - Partial" (Appendix C).

Table 4.6: The results of the fixed effects for the linear mixed effect model for the Leaf Phenology category Evergreen - Partial: First Flowering $\sim$ Year $+$ Cumulative Mean Temperature, random effects $=$ Watsonian Vice County nested in Species.

Variables	Value	Std.Error	DF	t-value	p-value
(Intercept)	229.305	9.345	1,761	24.539	$<$0.001***
Year	-0.159	0.038	1,761	-4.200	$<$0.001***
Cumulative Mean Temperature	-4.862	0.379	1,761	-12.815	$<$0.001***

4.4 Discussion

The inclusion of the correlation structure in the best LME models for the two Leaf Phenology categories "Seasonal - Aestival" and "Evergreen - Always" indicated the phenology of these species has dependence on the First Flowering phenology of previous years. This finding demonstrates the importance of considering different life history strategies in phenological analyses. However, neither traits nor CSR percentages were significant for any of the Leaf Phenology categories. Instead, the importance of temperature was consistent across all models, but the slope for temperature varied across the Leaf Phenology categories. For two categories, "Seasonal - Aestival" and "Evergreen - Partial", Year was also significant, indicating a consistent change in First Flowering phenology for these categories across the study period. However, although temperature and year were significant, most of the variation was captured by the random effects of species and vice counties (VC), which suggests a spatial impact on First Flowering phenology. Further, as species and VC were the best random effects and not family, our findings do no corroborate previous studies such as Davies et al. (2013) and Davis et al. (2010) that phylogeny is important for phenology.

4.4.1 Aestival plant species

The Leaf Phenology category "Seasonal - Aestival" contained 34 species, all of which leaf out between spring and autumn. This category had the largest slope for temperature, indicating a high reliance on temperature in determining phenology. The negative slope for temperature is consistent with the findings of previous studies, as this indicates that an increase in temperature results in earlier flowering phenology for species in this category (Menzel et al., 2020). There was also a significant effect of Year for this category with a slope twice that of Year for "Evergreen - Partial", suggesting the rate at which phenology is shifting for "Seasonal - Aestival" species is much faster than the Evergreen species. Although the slope for Year did decrease when the correlation structure was included, likely due to the correlation structure explaining some of the variation previously captured by year, it was still highly significant so there was a still a shift in phenology over the study period.

The significance of the corARMA correlation structure in the best model for "Seasonal - Aestival" suggests that the First Flowering phenology of "Seasonal - Aestival" species each year was (best model AR(p) value of 6) influenced by the flowering phenology up 6 years prior, which was the longest temporal dependence of the three Leaf Phenology categories. Further, there was a correlation in the error term for the model for up to 2 years, as MA(q) in the best model was 2. As this correlation structure captured the temporal autocorrelation in flowering phenology, it is possible the remaining effect of Year represents changes not captured by temperature, such as other environmental variables also changing with climate change but not included in the model or a particular time window within which temperature changes are more important. Interestingly, once the correlation structure was included both the marginal and the conditional R^2 decreased as well as the slope for year, as the temporal correlation was captured by the AR(p) and MA(q) structure, and the slope for temperature also increased. As the slope for temperature was negative, even though the effect was small compared to the marginal R^2, this indicates that with higher temperatures led to earlier First Flowering phenology. With the inclusion of the correlation structure, the larger slope for temperature indicates that once the previous 6 years are taken into account "Seasonal - Aestival" species are even more responsive to temperature and will advance their phenology faster. Thus, by being more responsive to temperature when the previous years are taken into account, "Seasonal - Aestival" species may be faster at adapting to climate change than expected if we were to just examine a single year. Thus, there is potential for a lag in the impacts of climate change for seasonal species, as they are influenced by their phenology of several years before the current

year.

4.4.2 Evergreen plant species

The Leaf Phenology category "Evergreen - Always" was the largest category containing 67 species that maintain a canopy throughout the seasons. The only significant fixed effect for this category was temperature, which had a negative effect, indicating that an increase in temperature results in earlier First Flowering phenology for evergreen species. The "Evergreen - Always" category also had a correlation structure but over a smaller time period than "Seasonal - Aestival" of up to two years, as AR(p) was 2. Similarly, MA(q) was also 2, indicating that the temporal correlation for "Evergreen - Always" for both the flowering phenology and error terms was a maximum of 2 years. The marginal R^2 increased when the correlation structure was included, unlike with "Seasonal - Aestival", but the conditional R^2 did decrease. This indicates that the fixed effect of temperature became more important once we accounted for the temporal correlation in the data, represented by the larger negative slope. This suggests that temperature is more important for "Evergreen - Always" species' flowering phenology than "Seasonal - Aestival" due to the larger marginal R^2. The decrease in the conditional R^2 for both "Seasonal - Aestival" and "Evergreen - Always" once the correlation structure was included is likely due to the variation previously being captured by species, which were dependent on their own previous flowering phenology, now being captured by the correlation structure included in each model.

The Leaf Phenology category "Evergreen - Partial" was the smallest with 20 species and was the only category to have no correlation structure in the model with the lowest AIC, which included the fixed effects Year and temperature. The marginal R^2 was also comparatively the smallest, but the conditional R^2 was by far the highest of the three Leaf Phenology categories. These results indicate that most of the variation in First Flowering phenology for the 20 "Evergreen - Partial" species is due to both spatial variation and the fact that being different species they have different strategies. The "Evergreen - Partial" category encapsulates all species that are evergreen at times, but this timing is not consistent across species. As a result, the inclusion of species in the random effects explained most of the variation in First Flowering phenology. Regardless, these species' flowering phenology is still influenced by temperature, which as with the other two categories results in earlier phenology as temperature increases. However, the slope for Year was negative for "Evergreen - Partial" species, the opposite of the Year slope for "Seasonal - Aestival", which indicates that the flowering phenology for these

species is getting earlier over the study period.

4.5 Conclusions

Overall, the models for the three Leaf Phenology categories illustrated the importance of temperature for determining the timing of flowering phenology, corroborating findings in a previous study on Nature's Calendar by Tansey et al. (2017). However, the models also emphasized the different dependencies of each of the three groups, as plant species with seasonal phenology had relatively long-term dependence on flowering phenology of up to 6 years previous, whereas species that are always evergreen had a shorter dependence of up to 2 years, and species that are partially evergreen had no dependence on previous years. Along with the consistent significance of temperature, this variation in temporal correlation between plant species with different leaf phenologies implies vastly different strategies for responding to their environment, and as a result ongoing climate change. Future studies should consider temporal correlation in plant phenology studies, as well as being aware that species in different life history categories may respond in a similar way.

Chapter 5

Spatial variation in Moth and Plant phenology and the synchrony of their phenologies

5.1 Introduction

Phenological changes as a result of climate change have been consistently found over the last 20 years (Menzel et al., 2020; Burgess et al., 2018; Thackeray et al., 2016). Altered timing of species' life history traits could result in loss of fitness and impact species' survival (Damien & Tougeron, 2019). However, discerning the drivers of phenological change is more complicated, as species vary in both the direction (advance or delay) and degree of phenological change (Damien & Tougeron, 2019). This variation in species' response to climate change has led to the match-mismatch hypothesis, first developed by Cushing (1973) in relation to fisheries, to be investigated as part of phenological research, as proposed by Harrington et al. (1999). Such trophic asynchrony is more likely to happen in seasonal habitats, where the consumer relies on an ephemeral food source (Kharouba & Wolkovich, 2023). If species that used to have synchronised phenology diverge, such as in a predator-prey system, or if intraspecific variation leads to mismatched phenology within a species' population, this could also have impacts on fitness (Cushing, 1973). The type of interaction, for example a mutualistic or antagoninstic relationship, will confer different pressures on survival and reproduction which impact fitness directly (Renner & Zohner, 2018). A classic example of this is the bird predator-prey stystem studied by Both & Marvelde (2007), where advanced food phenology led to population declines,

and when plants were considered in a tri-trophic system by Burgess et al. (2018) there was significant spatial variation in the phenology of the three species considered.

While experimental studies on phenological mismatch have shown that warming can lead to asynchrony (Chen et al. (2023); de Manincor et al. (2023); Gronchi et al. (2023); Liu et al. (2011)), a drawback is applicability (in situ) to the natural world. Firstly, such enclosed systems usually are not capable of examining a whole food web, and thus any conclusions are difficult to reliably extrapolate to in situ species responses and fitness consequences (Pardikes et al., 2022). This is also a drawback with many mismatch studies on observational data, as many focus on pairwise interactions, a scoping issue that is difficult to overcome when such studies rely on available data (Damien & Tougeron, 2019). Secondly, spatial variation could be crucial to species' response, as many variables that can influence species' phenology can also vary in space(Anderson et al., 2023). This seems to particularly be something seen in Lepidoptera, as Phillimore et al. (2012) found significant spatial variation in the phenology of *Anthocharis cardamines*, which they determined was in response to temperature and not the flowering time of it's hostplants. Similarly, a review by Zhemchuzhnikov et al. (2021) found little latitudinal variation in bird phenology, but the timing of when food was most abundant advanced significantly faster at more northerly latitudes. Spatial variation in elevation can also impact phenology, as higher elevations can delay phenology, possibly due to cooler temperatures (Shutt et al., 2019). Furthermore, host availability to Lepidoptera could influence the duration of their "food peak" for bird species, as Shutt et al. (2019) also found that the caterpillar peak was longer on Willow than Oak. For the lowest trophic level, plants, spatial variation in nutrient availability and rainfall may be just as important as temperature in influencing plant phenology (Thuma et al., 2023). However, a synthesis by Kharouba & Wolkovich (2023) demonstrated that in many studies the plant phenological variables considered were too coarse to allow investigation of the ecological processes underlying asynchrony. In this context, a crude measure of phenology such as the Normalised Difference Vegetation Index (NDVI) cannot be used to resolve differences in synchrony. Thus, it is evident that phenological asychrony is likely to vary in space, with individuals closer together more likely to shift their phenology in a similar way due to similarities in environmental variables. It is therefore important to consider asychrony in a spatial context and account for differences in asychrony between individuals and populations closer together and further apart.

As suggested by Kharouba & Wolkovich (2023), here we test the match-mismatch hypothesis in a spatial context, including species-specific data on both the hostplant and the consumer for

various moth species and different hostplants. We utilise Bayesian methodology via Integrated Nested Laplace Approximations (INLA) in R which enables the inclusion of a spatial structure in the form of a Besag-York-Mollié model to address the following objectives:

1. Determine whether spatial variation in environmental variables will influence the phenology of moths, resulting in spatial variation in phenology.
2. Assess whether asynchrony is increasing or decreasing for the interactions between the moths and their hostplants

5.2 Methods

5.2.1 *Data*

Data from the National Moth Recording Scheme (Butterfly Conservation, 2022), Garden Moth Scheme (Passey, 2020), and Woodland Trust Nature's Calendar (Accessed 08/09/2020: www.naturescalendar.org.uk) were used and prepared for in Chapters 3 (Moth data) and 4 (Plant data), respectively. There was not enough spatial coverage data for species that overwinter as an egg for them to be included in these analyses, and diet was not significant for these species in Chapter 3. The moth species chosen for these analyses (Table 5.1) had the highest spatial coverage data and number of records for both the overwinter stages and specificities (Oligophagous/Polyphagous), while also having hostplants with comparable spatial coverage data and number of records (Table 5.2). Respective phenological variables for moth and plant data (Table 5.3) were calculated at the Watsonian Vice County (VC) level, as with Chapters 3 and 4. Each phenological variable for the moth and hostplants was assigned a mean Cumulative Mean Temperature for each Vice County (CMTVC) for each year. This CMTVC value represented the average cumulative mean temperature for the VC for the year previous to the day of year of the phenological variable.

Table 5.1: Moth species included in the INLA analyses, based on data availability, and key life history traits.

Species	Overwinter stage	Specificity	Pupation	Habitats	Abundance change	Distribution Change	Hostplant species	Number of records	Years covered
Lunar Underwing (Omphaloscelis lunosa)	Larva	Oligophagous (Family)	Ground	A range of grassy places	Increased	-	Yorkshire Fog (Holcus lanatus)	345	1999-2016
Lesser Broad-Bordered Yellow Underwing (Noctua janthe)	Larva	Polyphagous	Ground	Wide variety	-	Increased	Primrose (Primula vulgaris); Blackthorn (Prunus spinosa)	795	1990-2018
Clouded border (Lomaspilis marginata)	Pupa	Oligophagous (Family)	Ground ; Spun leaves	Wide variety	-	Increased	Hazel (Corylus avellana)	576	1996-2016

Table 5.1: Moth species included in the INLA analyses, based on data availability, and key life history traits.

Species	Overwinter stage	Specificity	Pupation	Habitats	Abundance change	Distribution Change	Hostplant species	Number of records	Years covered
Buff Ermine (Spilosoma lutea)	Pupa	Polyphagous	Ground (In cocoon)	Wide variety	Decreased	Increased	Ivy (Hedera helix) ; Blackthorn (Prunus spinosa)	751	1995-2018

Table 5.2: Hostplants included in the INLA analyses, based on data availability.

Moth Species	Herbaceous hostplants	Woody hostplants
Lunar Underwing (*Omphaloscelis lunosa*)	Yorkshire Fog (*Holcus lanatus*)	-
Lesser Broad-Bordered Yellow Underwing (*Noctua janthe*)	Primrose (*Primula vulgaris*)	Blackthorn (*Prunus spinosa*)
Clouded Border (*Lomaspilis marginata*)	-	-
Buff Ermine (*Spilosoma lutea*)	Ivy (*Hedera helix*)	Blackthorn (*Prunus spinosa*)

Table 5.3: The phenological variables for the moths and hostplants in the analyses and their definition.

Category	Phenological variable
Moths	First Emergence - the day of year on which the first 25% of First Emergences had been observed for each species each year in each vice county
	Peak Emergence - the average day with the highest number of records for each species each year in each vice county
	Emergence SD - the standard deviation of the average peak emergence. As the standard deviation is the spread of records around the peak emergence it represents the length of the flight period for each species each year in each vice county.

Table 5.3: The phenological variables for the moths and hostplants in the analyses and their definition.

Category	Phenological variable
Hostplants	First Flowering - the day of year on which the plant first flowered

5.2.2 *Modelling strategy*

Modelling was conducted in three stages: 1) Moth models: test for spatial changes over time in moth phenology, 2) Hostplant models: test for spatial changes over time in plant phenology, 3) Comparison models: test for spatial changes over time in the relationship between the Peak Emergence of moth species and the First Flowering of their hostplants. We utilised a Bayesian methodology via Integrated Nested Laplace Approximations with the R-INLA package version 22.05.07 set with default priors. This method enabled the inclusion of a spatial structure to determine whether there was spatial variation in phenology. The spatial structure was specified using shapefiles of VCs and the Besag-York-Mollié (BYM) model method in the R-INLA formula. The BYM model accounts for neighbouring VCs as these observations may be more similar than VCs further away, and thus can account for spatial correlation in the data. Each stage of the modelling strategy utilised the same model structure, the full list of models are in (Table 5.3). Additionally, the Cumulative Mean Temperature for the last day of year (365 or 366 on leap years) for each VC was also modelled against Year to investigate any spatial changes in the CMTVC during the study period. The best model, either Null, Non-Spatial or Spatial, was chosen using Deviance Information Criteria (DIC). DIC is a goodness-of-fit measure for assessing the performance of Bayesian models, developed by Spiegelhalter et al. (2002).

Table 5.4: The models run for each stage of the analyses. The models in each stage were repeated for each of the four moth and two hostplant species, as well as each combination of moth and hostplant (See Tables 1 and 2).

Modelling stage	Phenological measure	Models
1: Moths	First Emergence	Null model: First Emergence ~ 1
		Non-Spatial model: First Emergence ~ 1 + year + Cumulative Mean Temperature
		Spatial model: First Emergence ~ 1 + year + Cumulative Mean Temperature + Spatial BYM Structure
	Peak Emergence	Null model: Peak Emergence ~ 1
		Non-Spatial model: Peak Emergence ~ 1 + year + Cumulative Mean Temperature
		Spatial model: Peak Emergence ~ 1 + year + Cumulative Mean Temperature + Spatial BYM Structure
	Emergence SD	Null model: Emergence SD ~ 1
		Non-Spatial model: Emergence SD ~ 1 + year
		Spatial model: Emergence SD ~ 1 + year + Spatial BYM Structure
2: Hostplants	First Flowering	Null model: First Flowering ~ 1
		Non-Spatial model: First Flowering ~ 1 + year + Cumulative Mean Temperature
		Spatial model: First Flowering ~ 1 + year + Cumulative Mean Temperature + Spatial BYM Structure
		Null model: Sync Measure ~ 1

Table 5.4: The models run for each stage of the analyses. The models in each stage were repeated for each of the four moth and two hostplant species, as well as each combination of moth and hostplant (See Tables 1 and 2).

Modelling stage	Phenological measure	Models
3: Combined	Sync Measure (Peak Emergence - First Flowering)	Non-Spatial model: Sync Measure ~ 1 + year
		Spatial model: Sync Measure ~ 1 + year + Spatial BYM Structure

It was not possible to assign the phenological variables Emergence SD and Sync Measure a CMTVC value as they represent a range of days, so only year was included as a covariate for these variables (Table 5.4). The time over which species were analysed varied per group based on data availability of both the moth and the hostplant. The years covered for each moth species analysed are in Table 5.1, and hostplants were matched to these ranges.

5.3 Results

5.3.1 *Average Cumulative Mean Temperature per Vice County*

There was significant spatial variation in mean Cumulative Mean Temperature for each vice county (CMTVC), with the spatial model (DIC: 6085.74) performing far better than the non-spatial (DIC: 10533.91) and null models (DIC: 11182.00). There was an overall significant increase in CMTVC over the study period (Table 5.5).

Table 5.5: The results of the spatial model for Cumulative Mean Temperature: cumulative mean temperature ~ 1 + year + f(vice county, model = bym, graph = vc adj).

Variables	mean	sd	0.025quant	0.5quant	0.975quant	kld
(Intercept)	12.564	0.020	12.526	12.564	12.603	0
Year	0.032	0.001	0.031	0.032	0.033	0

5.3.2 *Moth and hostplant models*

Models with fixed effects including the spatial BYM stucture performed the best overall based on DIC for moth phenology (Table 5.5). Models with fixed effects but with no spatial structure were the best for all hostplants (Table 5.5). Of the six comparison models, only one of the *S. lutea* spatial models were better than the null model (Table 5.5). These results are considered more fully below.

Table 5.6: The results of the analyses summarised. The Best Model column refers to the model with the lowest DIC: Spatial refers to the model including a spatial Besag-York-Mollié model structure, Non-spatial is the model including covariates without the spatial structure, and Null is the Null model. The blue highlight in the DIC columns refers to the accepted model (Null, Non-Spatial or Spatial), with grey indicating that although this DIC is lower, it was not different enough to accept it as the best model. In the Year and Temperature columns: S is significant, with green indicating positive slope and red indicating negative slope, NS is not significant, and - is not measured.

Class of species	Species	Phenological measure	DIC			Year			Cumulative Mean Temperature		
			Null	Spatial	Non-Spatial	Mean	0.025 quant	0.975 quant	Mean	0.025 quant	0.975 quant
Larva	Oligophagous -Lunar Underwing (*Omphaloscelis lunosa*)	First Emergence	5829.8	5521.69	5674.08	-0.035	-0.098	0.028	0.774	0.207	1.34
		Peak Emergence	5287.31	5221.69	5222.95	0.071	-0.026	0.168	0.894	0.197	1.591
		Emergence SD	4243.56	4057.12	4233.61	-0.027	-0.027	0.094	NA	NA	NA
	Polyphagous - Lesser Broad-Bordered Yellow Underwing (*Noctua janthe*)	First Emergence	4864.45	4588.25	4761.76	-0.262	-0.309	-0.214	-1.303	-1.768	-0.845
		Peak Emergence	4238.74	3919.36	4211.93	0.106	0.075	0.137	-0.99	-1.319	-0.661
		Emergence SD	3765.99	3454.6	3722.08	0.082	0.059	0.105	NA	NA	NA
Pupa	Oligophagous - Clouded Border (*Lomaspilis marginata*)	First Emergence	4337.46	3903.44	4193.06	-0.186	-0.321	-0.051	-4.733	-5.458	-4.007
		Peak Emergence	3920.17	3712.2	3802.09	0.174	0.084	0.265	3.49	-4.176	-2.823
		Emergence SD	3187.85	3039.16	3185.49	-0.063	-0.114	-0.013	NA	NA	NA
	Polyphagous - Buff Ermine (*Spilosoma lutea*)	First Emergence	5379.54	5225.28	5364.77	-0.162	-0.271	-0.053	-2.977	-1.68	-0.438
		Peak Emergence	5441.69	4941.62	5381.29	0.545	0.461	0.63	-3.025	-3.75	-2.297
		Emergence SD	4271.43	3751.7	4224.65	0.199	0.161	0.237	NA	NA	NA
Herbaceous	Yorkshire fog (*Holcus lanatus*)	First Flowering	9245.16	9161.13	9163.86	-0.059	-0.17	0.051	-2.752	-3.339	-2.165
	Ivy (*Hedera helix*)	First Flowering	10944.52	10748.85	10749.01	-0.072	-0.191	0.046	-4.963	-5.63	-3.768
	Primrose (*Primula vulgaris*)	First Flowering	5952.11	5940.27	5939.81	-1.493	-2.474	-0.511	-4.767	-8.532	-4.295
Woody	Blackthorn (*Prunus spinosa*)	First Flowering	12352.04	11752.15	11752.88	0.18	0.09	0.269	-7.445	-7.984	-6.906
	Hazel (*Corylus avellana*)	First Flowering	13425.14	13414.36	13414.89	0.411	0.184	0.638	-0.965	-2.259	0.33
Larva	Oligophagous - Lunar Underwing (Omphaloscelis lunosa) and Yorkshire fog (*Holcus lanatus*)	Peak Emergence - First Flowering	4860.49	4860.53	4861.45	NULL	NULL	NULL	NA	NA	NA
	Polyphagous - Lesser Broad-Bordered Yellow Underwing (Noctua janthe) and Blackthorn (*Prunus spinosa*)	Peak Emergence - First Flowering	5768.82	5677.33	5770.81	NULL	NULL	NULL	NA	NA	NA
	Polyphagous - Lesser Broad-Bordered Yellow Underwing (Noctua janthe) and Primrose (*Primula vularis*)	Peak Emergence - First Flowering	2061.11	2058.66	2059.25	NULL	NULL	NULL	NA	NA	NA
Pupa	Oligophagous - Clouded Border (*Lomaspilis marginata*) and Hazel (*Corylus avellana*)	Peak Emergence - First Flowering	4763.06	4764.15	4764.77	NULL	NULL	NULL	NA	NA	NA
	Polyphagous - Buff Ermine (*Spilosoma lutea*) and Blackthorn (*Prunus spinosa*)	Peak Emergence - First Flowering	5872.28	5868.75	5869.68	NULL	NULL	NULL	NA	NA	NA
	Polyphagous - Buff Ermine (*Spilosoma lutea*) and Ivy (*Hedera Helix*)	Peak Emergence - First Flowering	5432.88	4817.91	5392.45	0.851	0.718	0.983	NA	NA	NA

5.3.2.1 Larva Overwintering, Oligophagous: Lunar Underwing (*Omphaloscelis lunosa*) and hostplant Yorkshire Fog (*Holcus lanatus*)

The First Emergence and Emergence SD (representing the flight period) of *O. lunosa* varied in space, but the Peak Emergence phenology of *O. lunosa* did not (Table 5.5). As a difference of ~5 in DIC is the smallest considered noteworthy (Adrion & Mansmann, 2012), the simpler non-spatial model was accepted for Peak Emergence. The phenological variables were not affected by Year, but First Emergence and Peak Emergence were positively impacted by temperature increases, indicating a delay (Table 5.5). The DIC for the spatial and non-spatial models were again not different enough for the First Flowering of *H. lanatus*, leading to the simpler non-spatial model being accepted as best. Year was not significant in the non-spatial model for *H. lanatus*, but CMTVC was significant with a negative slope (Table 5.5). The comparison model DIC for the spatial and non-spatial models of the Sync Measure were too similar to the null model, so no effect of Year or CMTVC was found.

5.3.2.2 Larva Overwintering, Polyphagous: Lesser Broad-Bordered Yellow Underwing (*Noctua janthe*) and hostplants Blackthorn (*Prunus spinosa*) and Primrose (*Primula vulgaris*)

The spatial model performed the best for all three phenological variables for *N. janthe*, with both Year and CMTVC being significant (Table 5.5). There was a negative impact of CMTVC on both First Emergence and Peak Emergence (Table 5.5). Year had a negative impact on First Emergence, but positive for both Peak Emergence and Emergence SD (Table 5.5). *P. spinosa* and *P. vulgaris* were similar to *H. lanatus* in that the spatial and non-spatial model DICs were very close, resulting in the non-spatial model being accepted as best. For both the hostplants of *N. janthe* CMTVC was significant with a negative slope. However, while *P. spinosa* had a significant positive slope for year indicating later flowering, *P. vulgaris* had a significant negative slope indicating earlier flowering. The comparison models were not significant due to similarity in DIC between the null, spatial and non-spatial models.

5.3.2.3 Pupa Overwintering: Oligophagous: Clouded Border (*Lomaspilis marginata*) and hostplant Hazel (*Corylus avellana*)

As opposed to the Larva Oligophagous species *O. lunosa*, the spatial models performed the best for all phenological variables for *L. marginata* (Table 5.5). Year and was significant for all

three phenological variables with negative slope for First Emergence and Emergence SD and a positive slope for Peak Emergence. CMTVC was significant with a negative slope for both First Emergence and Peak Emergence. The DIC was again less than 5 different between the spatial and non-spatial models for *C. avellana*, so the non-spatial model was accepted as best, with only Year significant with a positive slope (Table 5.5). The comparison models were not significant (Table 5.5).

5.3.2.4 Pupa Overwintering, Polyphagous: Buff Ermine (*Spilosoma lutea*) and hostplants Blackthorn (*Prunus spinosa*) and Ivy (*Hedera helix*)

The spatial models were significant for all phenological variables for *S. lutea* (Table 5.5). The First Emergence response was similar to *N. janthe* and *L. marginata* as both Year and CMTVC were significant with a negative slope. Additionally, also similar to *N. janthe*, both Peak Emergence and Emergence SD had a significant positive slope for Year, and Peak Emergence had a significant negative slope for CMTVC (Table 5.5). The difference in DIC was too small to accept the spatial model, so the non-spatial model was accepted for *H. helix*, with only CMTVC having a significant negative slope. As with *N. janthe*, there was no significant comparison model for *S. lutea* and *P. spinosa*. However, the spatial comparison model for *S. lutea* and *H. helix* was significant, with a positive slope for Year (Table 5.5). This spatial variation can be seen in Figures 5.1 and 5.2, which display the actual synchrony for *S. lutea* and *H. helix* for each VC each year and the mean synchrony predicted by the model, respectively. Similar plots for each moth and plant species model can be seen in Appendix D.

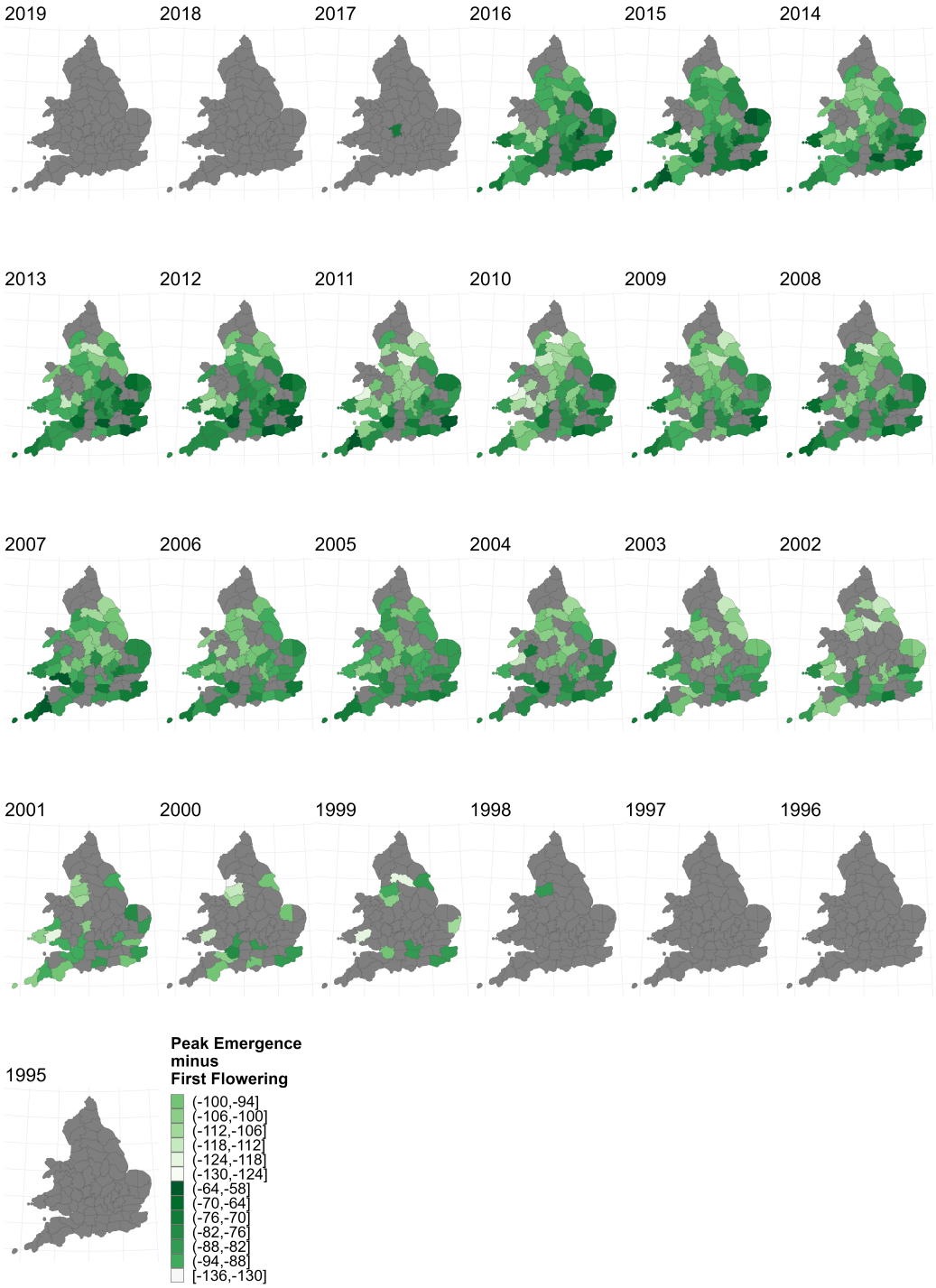


Figure 5.1: Comparison model for Spilosoma lutea Peak Emergence day of year and Hedera helix First Flowering day of year: sync ~ 1 + year + f(Watsonian Vice County, model=bym, graph=vc adj)

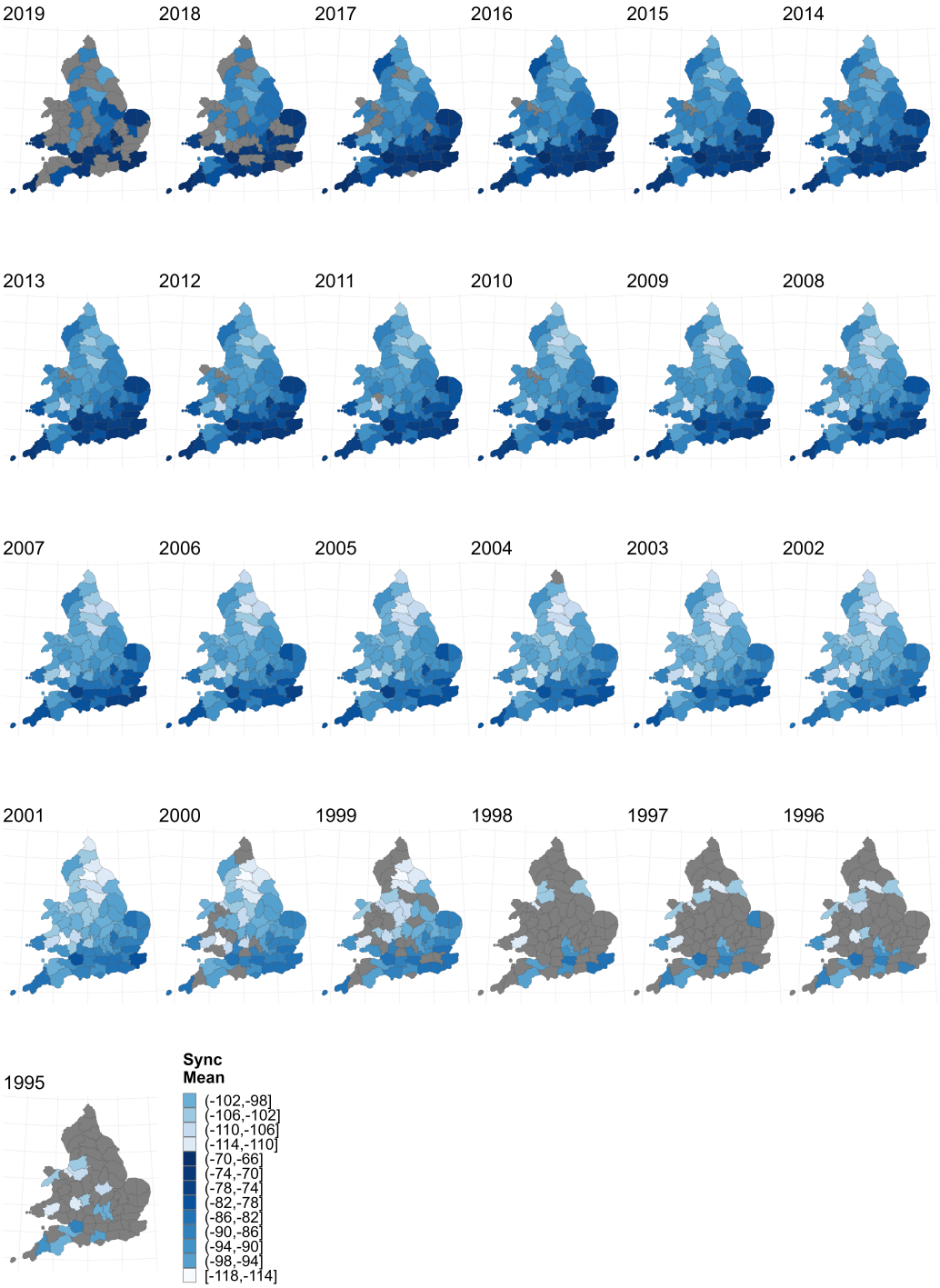


Figure 5.2: Comparison model for Spilosoma lutea Peak Emergence day of year and Hedera helix First Flowering day of year mean from model: sync ~ 1 + year + f(Watsonian Vice County, model=bym, graph=vc adj)

5.4 Discussion

There was spatial variation in phenology in the best models for each of the four moth species, indicating that the timing of moth phenology was more similar in vice counties that were closer to each other. The model for temperature also demonstrated that increases in temperature varied across England and Wales, with southern vice counties warming faster than the northern vice counties (Kendon et al., 2023). These results explain why environmental, habitat, and landscape changes can lead to phenological changes varying in space. Higher latitudes have less sunlight which results in shorter seasons and lower temperatures, which can be exacerbated by higher altitudes and coastal areas, which generally have lower temperatures. Further, this spatial dependency reflects the variation in Global Climatic Change (GCC) impacts on environmental variables; although we found uneven increases in temperature across England and Wales, other environmental variables such as rainfall and humidity will also vary in space as a result of GCC and impact plants and insects. We have demonstrated that the vice counties utilised in these analyses are suitable for examining spatial changes in phenology, but they are still a coarse measure. Within vice counties there can be large changes in habitat availability, altitude and even soil type, which could impact host plant availability and severity of phenological changes on a smaller scale than the vice county level. Thus, although we were able to capture spatial variation in our models, there will undoubtedly be variation within vice counties. Further, although utilised as a measure for change through time in phenology, Year can also represent differences in variables not captured by temperature, as it encapsulates other forms of variation that are also changing with time.

The larva overwintering species *Omphaloscelis lunosa* had a spatial variation in its First Emergence and Emergence SD phenology, but not the Peak Emergence. This was the only moth species that did not have a significant spatial model as well as no effect of Year for any of the *O. lunosa* phenological variables. While lack of a Year effect could indicate that there have been no long-term changes in phenology for this species, it is worth noting that this is the most data-deficient of the four species in the study, leading to the shortest study period of 17 years. Further, this species has increased in abundance over the time of the study period (Henwood et al., 2020), which may result in the phenology trend being masked by the abundance trend in the data. This could explain the divergent response of this species to Cumulative Mean Temperature, as unlike the other species, *O. lunosa* is delaying as temperature increases for both First Emergence and Peak Emergence. This delay could be due to the flight period of *O. lunosa* being towards the end of the growing season, which studies have shown is being

delayed (Menzel et al., 2020), which may indicate that *O. lunosa* is responding to more than just temperature if it is tracking the end of the growing season. Further, a delay in First Emergence and Peak Emergence could be indicative of a whole flight period shift to later in the year. It is possible that an increase in abundance is overshadowing this delay, as there would be a higher chance of being captured and recorded earlier in the season with more individuals present, despite the flight period shifting. In contrast to this, the hostplant for *O. lunosa*, *Holcus lanatus* had no spatial impact and was advancing it's First Flowering phenology in response to increases in Cumulative Mean Temperature, but still with no effect of Year. This lack of spatial response in the Peak Phenology of *O. lunosa* and *H. lanatus* is likely why the comparison model of their phenology was not significant for either the non-spatial or spatial models.

The spatial models for second larva overwintering species *Noctua janthe* were the best for all three phenological variables. As opposed to *O. lunosa*, Year was significant, with a negative slope for First Emergence and a positive slope for both Peak Emergence and Emergence SD. This would indicate that there is a move towards a longer flight period for *N. janthe* over the study period, with First Emergence moving earlier and Peak Emergence delaying. However, this could also be related to an increase in distribution for *N. janthe* (Randle et al., 2019). The response to Cumulative Mean Temperature may corroborate this, as there was a significant negative slope similar to or larger than that for Year for both First Emergence and Peak Emergence, indicating these phenological variables advanced with increasing temperatures. It is possible that these are two halves of the same story; as rising temperatures enable the distribution of *N. janthe* to increase there will be more records where there were previously very few, which may in turn lead to earlier records as there are more individuals to sample, thus giving the impression of a longer flight period. The spatial model for First Flowering was not significant for either of the two *N. janthe* hostplants. The non-spatial model for the herbaceous *P. vulgaris* had a significant negative slope for both Year and Cumulative Mean Temperature, whereas the non-spatial model for *Prunus spinosa* was also significant with a negative slope for Cumulative Mean Temperature, but with a positive slope for Year. Both of these species follow the general trend of earlier flowering in the UK in response to rising temperatures (Büntgen et al., 2022). Despite the clear impacts of space on both *N. janthe*, as well as the consistent impact of Year and Cumulative Mean Temperature on the moth and both hostplants, the comparison models for both hostplants were not significant, which could indicate that being a polyphagous species *N. janthe* does not have to synchronise with it's

hostplants.

The oligophagous pupa overwintering species *Lomaspilis marginata* responded differently to oligophagous *O. lunosa* in that the spatial models were significant for all three phenological variables with a significant slope for Year. However, *L. marginata* was the only moth species with a significant negative slope for Year for Emergence SD. This seems to indicate that *L. marginata* is emerging earlier in the year, but with decreased flight period length indicated by a negative Emergence SD trend; it is possible the distance between the First Emergence and Peak Emergence is getting longer, but after the peak the species is not on the wing for as long. This result could also be explained by the increased distribution of this species over the study period (Randle et al., 2019). As with *N. janthe*, an increased distribution could lead to the appearance of an earlier emergence, and if this were the case, these results could instead indicate a delayed and contracted flight period of L. marginata. The hostplant for *L. marginata*, *Corylus avellana*, had no effect of space and was the only plant to have no impact of Cumulative Mean Temperature on the First Flowering phenology, but with a significant positive slope for Year. As with *N. janthe* despite the spatial variation in Peak Emergence phenology for *L. marginata* the comparison model with *C. avellana* First Flowering phenology was not significant.

The results for the pupa overwintering polyphagous *Spilosoma lutea* were largely similar to the larva polyphagous species *N. janthe*, as all spatial models were significant with the same slope direction for both Year and Cumulative Mean Temperature: First Emergence had a significant negative slope for Year, while Peak Emergence and Emergence SD had a significant positive slope for Year. For all phenological variables Cumulative Mean Temperature was significant with a negative slope. Thus, the results of both *N. janthe* and *S. lutea* may be also demonstrating the impacts of an increased distribution, as they both have earlier emergence with an increased length of the flight period (Randle et al., 2019). The hostplant *Hedera helix* was the only other hostplant with no significant slope for Year, and similar to the other hostplant for *S. lutea*, *P. spinosa*, had a significant negative slope for Cumulative mean temperature. Interestingly, *S. lutea* was the only moth species for which one of the spatial comparison models was significant for the hostplant *H. helix*, with a significant positive slope for Year. This positive slope indicates that the Peak Emergence of *S. lutea* and the First Flowering of its hostplant *H. helix* are getting further apart, implying loss of synchrony. This could be due to the response of *S. lutea*, as Peak Emergence has a significant positive slope, indicating it is getting later, but there is no significant slope for Year for *H. helix*. Thus, it

is possible that the significant comparison model for *S. lutea* indicates a loss of synchrony, which could explain the decrease in abundance of *S. lutea* of almost 50% over the study period (Randle et al., 2019).

Although the life history strategies of the species analysed were different, with different overwintering stages and specificity in diet, the overall response of species was broadly similar. All four species were responsive to temperature for all phenological variables, with the dominant response being a shift to earlier phenology as a result. However, there was some correlation in the response of the two polyphagous species, both of which were emerging earlier over time with later peaks and longer flight periods. Despite diet being significant for larva species in Chapter 4, it was the pupa overwintering polyphagous species *S. lutea* that had a significant relationship with one of it's hostplants *H. helix*. This may corroborate the results of Kharouba & Wolkovich (2023) that phenological asychrony may be less common in terrestrial systems than previously hypothesised. These results also further confirm those of Kharouba & Wolkovich (2023) that resource specialisation does not necessarily lead to higher levels of phenological asynchrony, as it was only the polyphagous species *S. lutea* that was significant. Further, the decrease in abundance of *S. lutea* in recent decades does lend weight to the hypothesised fitness impacts of asynchrony (Damien & Tougeron, 2019). The lack of significant spatial models for any of the hostplants further demonstrates the difference in strategies between moths and their hostplants. However, in the tritrophic system studied by Burgess et al. (2018), there was an impact of space on the phenology of oak first leafing. It is possible that the impact of space on plants is species-dependent, thus leading to these conflicting results. As such, any broad-scale conclusions about phenological mismatch may be difficult. While it is possible to discern the overall trend for groups of species, such as the moths and plants in these analyses, discerining the risk of mismatch at the group level will likely be challenging. The interactions between trophic levels evidently vary on a species-by-species basis and the interaction itself may not be enough to accurately predict mismatch.

5.5 Conclusion

The results for the four moth species demonstrated spatial variation in at least two phenological variables. However, there were no significant spatial models for First Flowering phenology of the five hostplants, in contrast to findings of a spatial effect by Tansey et al. (2017). This lack of a spatial effect could indicate loss of synchrony, particularly as the two oligophagous

moth species' hostplants had no spatial effect, but this was not the case with the comparison models. In fact, we found no support for loss of synchrony for species with more specific diets such as *O. lunosa* and *L. marginata*. The only significant comparison model was for the pupa overwintering polyphagous species *S. lutea*. The large difference in DIC between the spatial and non-spatial models for *S. lutea* and it's hostplant *H. helix* illustrates the strength of this spatial effect, with the slope for Year larger in the comparison model than the slope for Year for *S. lutea* Peak Emergence. While there is potential for this loss of synchrony to be an artifact of the changes in abundance and distribution for *S. lutea*, it is also possible that the decline in abundance for *S. lutea* could be due to it losing synchrony with it's hostplants. Thus, it is possible that polyphagous species are more at risk than previously thought, and should not be overlooked when investigating the implications of phenological changes and asynchrony due to climate change.

Chapter 6

Discussion

6.1 *Overview*

The research into phenology has increased substantially over the last 30 years. In Chapter 1 topic modelling was used to identify research topics and themes in phenological research over a 30 year period. The utility of phenological research for monitoring the impacts of Global Climatic Change (GCC) has led to a rapid increase in the varitety of organisms studied as well as the various methodologies used. However, the topic model found that although research has increased it's scope, there are still only a few organisms that have been the focus of phenological research, with research primarily focused in the Northern hemisphere. Further, while research has expanded, the connectivity between different spheres of research has not developed, and organisms are usually only studied in isolation or a pair-wise manner. Phenological changes will have implications for the whole ecosystem, and research must follow suit, but there are many challenges to be addressed before an ecosystem-level phenological analysis is possible. Firstly, the availability of data is a consistent problem, as long-term data on the phenological variable of interest for a species is required to monitor for phenological changes. This level of data would then be required for all species in the ecosystem to analyse whether phenological changes will impact their interactions. Secondly, the drivers of phenology are not well understood, as the variety of environmental, abiotic and biotic variables a species experiences are vast and could all impact their phenological response to GCC. Lastly, an in depth knowledge of the interactions between the species in an ecosystem is required, so the interpretation of the impacts of phenological changes on their interactions can be assessed. Such requirements are difficult to obtain and may never be possible, but the analyses presented here have endeavored

to answer some of the questions relating to the first two points by analysing the phenology of Lepidoptera and their hostplants in the UK. The UK has a rich entomological and botanical history, resulting in numerous records for both Lepidoptera and their hostplants, as well as a good understanding of their life history traits. Further, the UK has experienced an increase in temperature as a result of GCC at a slightly faster rate than the global average, so is a good study location for the impacts of GCC on phenology (Kendon et al., 2023).

6.2 *Moth Phenology*

The phenology of Lepidoptera has been well studied in the UK due to the vast number of records available, but the drivers of the phenological response of moths to GCC are less well known. In Chapter 3, Linear Mixed Effects (LME) modelling was used to identify drivers of moth phenology in England and Wales, utilising citizen science data on the occurrence of 149 moth species with life history data from the National Moth Recording Scheme (Butterfly Conservation, 2022) and temperature data from the Met Office (Met Office et al., 2018). As opposed to previous studies (e.g. O'Neill et al. (2012)), analysing all moth species together was not possible due to the significantly different phenology of moths with different overwintering life stages, corroborating previous work (Végvári et al., 2015). Thus, we conducted our analyses on three overwintering stage categories: Egg, Larva and Pupa. This finding clearly indicates that life history strategy plays an important part in determining moth phenology, and could impact their response to GCC. However, no other traits were significant in the LME models conducted for each of the overwintering stage categories. This is likely due to the inclusion of "species" in the random effects of the LME, which accounted for any variation not encapsulated by the traits included in the model. Despite this, diet was significant for the Larva overwintering category, which further emphasises the role of the lower trophic level in the phenology of moths, corroborating previous studies (e.g. Burgess et al. (2018)). By examining phenology at the beginning of the season (First Emergence), the peak (Peak Emergence) and the spread (Emergence SD, representing the flight period), it was possible to determine whether phenology is changing at different rates depending on the measure used. Indeed, while First Emergence consistently advanced over time and with higher temperatures, Peak Emergence varied across the overwintering stage categories, and Emergence SD consistently increased for all overwintering stages, indicating a longer flight period. This general trend was mostly reflected in the results for four individual species in Chapter 5, although one of the four

species had no effect of Year for any of the phenological variables. For the remaining three species the pattern was the same for First Emergence (advance) and Peak Emergence (delay), with Emergence SD increasing (i.e. longer flight period) for the two polyphagous species and decreasing (i.e. shorter flight period) for the significant oligophagous speices. Throughout all the models from both Chapters 3 and 5 there has been the significance of temperature in impacting phenology, again corroborating previous studies on the sensitivity of insects to GCC temperature changes (e.g. Visser & Holleman (2001); Sparks et al. (2005); Altermatt (2010a); de Manincor et al. (2023)). Indeed, for all the models in Chapter 3 and the three species with a significance of Year in Chapter 5, an increase in temperature lead to earlier phenology. Peak Emergence delayed with Year for the larva overwintering stage category in Chapter 3 and all species with a significance of Year in Chapter 5, while also advancing with increases in temperature. This suggests that there are drivers that are changing over time that were not included in the models, resulting in these divergent responses of Peak Emergence. With the UK climate has getting wetter over the study period (Kendon et al., 2023), it is possible that precipitation is impacting phenology.

The impact of space on moth phenology was evident across the models in both Chapters 3 and 5. The phenological variables were calculated at the level of Watsonian Vice Counties (VC), and when vice county was included as a random effect in the LME models in Chapter 3 the AIC was lower than a model without this included. For Chapter 5, the spatial models were significant for all three phenological variables for the three species with an impact of Year, and for the last species *Omphaloscelis lunosa*, the spatial model was significant for First Emergence and Emergence SD. These results demonstrate the need for moth phenological analyses to include space, as this evidently impacts their phenology, and it is possible that studies that have previously amalgamated moth phenology for an area may not have captured the true trends in phenological shifts. Indeed, even within the VC measure utilised in Chapters 3-5, there will undoubtedly be variation in the phenological response of moths *within* the VCs, which would not have been captured by the phenological variables used in Chapters 3 and 5. Additionally, the presence of urban areas will likely have influenced phenology as temperatures are higher due to the urban heat island effect, which may have resulted in more populated VCs not being as accurate (Diamond et al., 2014). However, conducting analyses at a finer spatial scale would take much longer and require higher computing power, which were not within the scope of this thesis. Future studies in moth phenology in the UK would benefit from this finer spatial scale, as well as the inclusion of additional environmental variables such

as precipitation, altitude, habitat type and distance from urban areas.

6.3 *Plant Phenology*

As with Lepidoptera phenology, plant phenology has been frequently studied in the UK, but the impact of plant life history traits on their phenology is less clear. Plants are incredibly diverse, and moths utilise many different kinds of plant as their hostplant. Thus, in Chapter 4, the significantly different First Flowering phenologies meant the analyses were conducted on 132 species in the following three Leaf Phenology categories: "Seasonal - Aestival", "Evergreen - Always" and "Evergreen - Partial". There were no traits significant for any of Leaf Phenology categories, which was unexpected. Instead, there was a consistent impact of temperature on First Flowering phenology, with Year only impacting "Seaonsal - Aestival" and "Evergreen - Partial" phenology. Furthermore, in the Chapter 4 LME models the categories "Seasonal - Aestival" and "Evergreen - Always" were correlated with First Flowering phenology in the previous years. Due to different life history strategies, it is likely that the categories "Seasonal - Aestival" and "Evergreen - Always" had different drivers for this correlation with previous years. The "Evergreen - Always" category contains species that invest resources over time, so it is intuitive that the amount of resources collected the previous year will impact the current year. However, the "Seasonal - Aestival" category species are more ephemeral and generally have shorter generation times, which can lead to faster microevolution and adaptation to GCC (Compagnoni et al., 2021). This is likely why, once the corARMA correlation structure was included in the LMEs, the slope for temperature for "Seasonal - Aestival" species got steeper, indicating a faster advancement with higher temperatures. This dependence on previous seasons means these species may be more able to adapt to a changing climate, corroborating the study by Franks et al. (2007) on inheritability of flowering time. However, while "Seasonal - Aestival" species may be more adaptable to temperature, it is possible that "Evergreen - Always" species are more influenced by it, as the impact of temperature increased (due to a higher marginal R^2) with the inclusion of the corARMA correlation structure.

The importance of temperature for herbaceous species was corroborated in Chapter 5, as all herbaceous species had a significant impact of temperature. Conversely, only one woody species was influenced by temperature, which lends weight to the generation theory, as woody species are much longer lived and appear to be less responsive to temperature. This could be why the Hostplant Category "woody" was significant for larva in Chapter 3; if the phenology

of woody plants is less influenced by temperature than herbaceous plants, then moth species that utilise woody species as hostplants will need to synchronise more closely to woody plant phenology, instead of relying on their response to temperature. However, an alternative explanation is that it is the *timing* of temperature that is important for woody species; Tansey et al. (2017) found that woody species with an early flowering window were more sensitive to a chilling window in the winter period. Thus, it is possible that, although relevant for moths due to growing degree days, our measure of cumulative mean temperature was less applicable to plants, and the timing of temperature extremes needed to be considered. This would corroborate the results of Chapter 5, as the two woody species flower early in the year: *Prunus spinosa* in March - April and *Corylus avellana* in January - April, and both have a positive slope for Year. Thus, it is possible that the very early flowering window for *C. avellana* is why temperature was not significant. With winters generally getting warmer, it is possible that a lack of chilling has resulted in a delay in First Flowering for these woody species. In terms of the lack of a spatial effect, this could again be due to the ability of plants, especially long-lived ones such as *P. spinosa* and *C. avellana*, to adapt in-situ. Unlike moths, plants are not able to move away from extreme temperatures, and as such may be more tolerant to GCC due to their ability to plastically respond to temperature (Tansey et al., 2017). The time period over which the species were analysed in chapter 5 may not sufficient to see spatial changes in phenology, as the LME models in Chapter 4 demonstrated plant phenology each year may be dependent on the previous year for some categories. This may explain why all five plant species in Chapter 5 had no impact of space on their First Flowering phenology, when an impact of space was found in Chapter 4 with the inclusion of vice counties in the random effects. Chapters 4 and 5 demonstrated the dependency of plants on previous years, as well as the different phenological responses of plants with different Leaf Phenologies. Future studies in plant phenology should consider the dependence of plant phenology the phenology of previous years, which combined with the impacts of forcing and chilling (e.g. Tansey et al. (2017); Phillimore et al. (2012)), might elucidate more specific drivers of plant phenology.

6.4 *Asynchrony*

In Chapter 5 a comparison of moth Peak Emergence and their hostplant First Flowering was used to ascertain whether the number of days between the peaks was changing. Although larva species had a significance of diet in Chapter 3, the significant comparison models were instead

for the pupa overwintering polyphagous moth species *Spilosoma lutea* and it's hostplant *Hedera helix*. There was spatial variation in the relationship between the *S. lutea* Peak Emergence phenology and the First Flowering phenology of *H. helix*, with an increase in the number of days between these peaks over the course of the study period. This positive slope for Year for the significant comparison model indicates that this relationship may be losing synchrony. However, it may be due to this species attempting to synchronise with other hostplants it is reliant upon, as *S lutea* has been recorded as an egg and first instar larvae on broadleaf trees such as *P. spinosa* (Henwood et al., 2020). An analysis of the famous Marsham record of plant phenology by Roberts et al. (2015) projected that the order of spring events might change, with the specific hostplants for *S. lutea* Hawthorn and Rowan delaying their first leaf phenology, whereas Oak first leafing advanced. The divergent responses of these important hostplants for *S. lutea* could be responsible for the decrease in abundance of nearly 50% of *S. lutea* over the study period (Henwood et al., 2020; Randle et al., 2019). This could partly explain *S. lutea* losing synchrony with *H. helix,* as the flight period for *S. lutea* ends and the feeding period begins when *H. helix* starts to come into flower (Henwood et al., 2020). Thus, although the Peak Emergence was delaying and the flight period was increasing in length for *S. lutea*, it could be the earlier First Emergence that is leading to loss of synchrony with *H. helix*. Further, it is possible that the peak for *H. helix* is shifting also, as there was a much larger negative slope for Cumulative Mean Temperature for *H. helix* than for *S. lutea*. Nevertheless, it is evident that another variable must be impacting the relationship between *S. lutea* and *H. helix*. Thus, the Chapter 5 INLA models demonstrated that loss of synchrony may even be happening for polyphagous species such as *S. lutea*, as despite having an abundance of possible hostplants, the dependence of different life stages on particular plants may result in loss of abundance.

6.5 *Limitations*

The phenological shifts presented in this thesis are in accordance with previous studies, but there are limitations to using citizen science data that need to be acknowledged. Citizen science data suffers from recorder bias, with individual recorders having different levels of proficiency at identification and sampling bias when recording (Dickinson et al., 2012; Dickinson et al., 2010). This is mitigated somewhat as records in the National Moth Recording Scheme and Garden Moth Scheme data are verified (Butterfly Conservation, 2022; Passey, 2020). However

the sampling bias is still present, as trap type can impact the diversity of the catch (Bates et al., 2013), and recorders are much more likely to sample in an area nearer their home (Dickinson et al., 2010), which results in spatial gaps in the data. This may have led to the records in Scotland being removed from the analyses in this thesis, as there were too few records to calculate a reliable phenological variable. Further, common species are much more likely to be sampled, and even with many records it is possible there is not enough to calculate a reliable response. For example, the lack of response for Year for the fourth moth species (*Omphaloscelis lunosa*) in Chapter 5 could be evidence of no phenological shift over the study period, but considering that it was the most data deficient of the four species and has increased in abundance over the study period (Henwood et al., 2020), this result may instead represent there not being enough data to see a trend. Further, although moths do feed on flowers, it would have been useful to also include First Leafing in the chapter 5 analyses, as some moths species are more reliant on this timing, but there was no enough data to do so. The analyses of large sets of data also comes with limitations. In Chapters 3 to 5, the scale of the models had to be considered in relation to time and computing power. For example, in Chapter 5 a finer spatial scale might have enabled a better idea of spatial trends in the species analysed. Similarly, in Chapter 1 due to the vast literature on phenology a topic model was a convenient method to achieve a synthesis of phenological research within the scope of this thesis, but a more in-depth synthesis would enable better identification of knowledge gaps.

6.6 *Future work*

This research has provided important insights into the drivers of moth and plant phenology and how they vary in space. However, there remains many avenues of research outside the scope of this thesis. In Chapter 3, the phenology of moths with different overwintering stages was found to be significantly different, but this was only for univoltine species due to the difficulty in obtaining phenological variables for moth species with multiple generations a year. However, it is possible that moth species are increasing the number of generations per year in response to higher temperatures and a longer growing season, which could lead to a developmental trap (Van Dyck et al., 2015). This could lead to declines in moths populations, along with asynchrony. Thus, while this research has identified drivers for univoltine species, there remains the question of what drives multivoltine speices, and what drives species to have more generations in a year in response to GCC. In terms of drivers, there are many

environmental variables that could influence moth and plant phenology. Although Büntgen et al. (2022) found no effect of precipitation on plant phenology, western parts the UK are wetter and could result in different phenology if considered within a spatial model. As well as this, variation in soil type could influence plant distribution and therefore their phenology. Further, the spatial models could be developed at a finer scale, for example by utilising species' exact locations rather than averaging to the vice county level. This would enable the inclusion of records excluded from this research due to too few records in a vice county, as well as the inclusion of variables such as altitude and proximity to urban areas, both of which impact temperature. Moreover, the models in Chapter 5 could be developed further for more moths and their hostplants, and used to predict into the future, which would enable prediction of asynchrony.

6.7 *Conclusions*

The results of this thesis have contributed to the current state of knowledge for phenological shifts of moths and plants in England and Wales. In Chapters 3 and 4 the LME models identified that drivers of moths and plant phenology are different depending on the life history strategy of the species. In particular, these Chapters demonstrated the need for future research on phenological shifts to consider whether species included in analyses need to be separated based on their life history traits, as they may have significantly different phenologies. In Chapter 5 the INLA models identified spatial variation in moth phenology but not their hostplants, indicating different strategies when responding to GCC. These analyses demonstrated the possibility for polyphagous moths to lose synchrony with their hostplants and as such future studies on asynchrony in Lepidoptera should not discount polyphagous species as low risk.

Appendix A

Chapter 2: Additional plots and topic table

Table A.1: The 20 highest weighted words for the 40 topics.

No.	Topic 1	Topic 2	Topic 3	Topic 4	Topic 5	Topic 6	Topic 7	Topic 8	Topic 9	Topic 10
1	season	leaf	growth	warm	event	precipit	migrat	factor	time	ecosystem
2	grow	forest	bud	plant	increas	veget	arriv	respons	sea	product
3	length	tree	tree	respons	frost	studi	bird	climat	bloom	carbon
4	end	decidu	burst	treatment	extrem	grassland	time	import	water	dynam
5	start	temper	differ	experi	risk	region	migratori	understand	phytoplankton	atmospher
6	period	senesc	condit	experiment	damag	signific	migrant	environment	peak	cycl
7	longer	observ	proven	increas	frequenc	delay	distanc	role	abund	result
8	begin	fall	seedl	growth	sever	correl	speci	influenc	spawn	primari
9	day	leav	break	effect	weather	zone	breed	photoperiod	fish	terrestri
10	extend	canopi	spruce	control	reduc	sos	ground	driver	marin	global
11	earlier	unfold	shoot	shrub	occur	plateau	spring	mechan	zooplankton	activ

Table A.1: The 20 highest weighted words for the 40 topics.

No.	Topic 1	Topic 2	Topic 3	Topic 4	Topic 5	Topic 6	Topic 7	Topic 8	Topic 9	Topic 10
12	durat	color	format	plot	may	differ	winter	process	ocean	increas
13	increas	autumn	rate	field	decreas	area	date	key	coastal	net
14	onset	oak	wood	ambient	due	show	earlier	limit	atlant	function
15	lengthen	studi	stem	manipul	occurr	china	long	studi	concentr	annual
16	result	time	pine	open	caus	advanc	nao	well	biomass	process
17	later	evergreen	height	signific	potenti	trend	advanc	determin	earlier	system
18	extens	result	cessat	year	like	chang	departur	critic	chang	flux
19	shorter	found	xylem	biomass	result	climat	short	suggest	nutrient	season
20	prolong	show	boreal	suggest	lead	alpin	condit	play	river	level

Table A.2: The 20 highest weighted words for the 40 topics.

No.Topic 11	Topic 12	Topic 13	Topic 14	Topic 15	Topic 16	Topic 17	Topic 18	Topic 19	Topic 20
1northern	data	spring	ecolog	insect	chill	ice	flower	effect	trend
2north	observ	winter	impact	develop	requir	lake	plant	affect	term
3latitud	use	warm	research	emerg	temperatur	snow	time	interact	long
4region	studi	summer	system	host	pollen	cover	fruit	impact	show
5rang	record	temperatur	includ	generat	accumul	arctic	pollin	direct	chang
6southern	provid	onset	biolog	temperatur	dormanc	durat	reproduct	import	decad
7south	collect	autumn	chang	pest	forc	chang	seed	negat	period
8europ	monitor	earlier	manag	adult	budburst	freez	result	may	signific
9distribut	detect	warmer	particular	butterfli	heat	melt	may	combin	year
10central	research	delay	need	may	differ	depth	earlier	howev	observ
11eastern	inform	advanc	review	flight	birch	air	set	relat	increas

Table A.2: The 20 highest weighted words for the 40 topics.

No.Topic 11	Topic 12	Topic 13	Topic 14	Topic 15	Topic 16	Topic 17	Topic 18	Topic 19	Topic 20
12across	network	climat	current	rate	bloom	result	bee	depend	recent
13western	measur	cold	ecosystem	larval	period	increas	speci	addit	studi
14similar	indic	suggest	discuss	thermal	phase	region	floral	posit	analyz
15geograph	avail	previous	global	development	tree	decreas	durat	climat	last
16america	sampl	may	divers	larva	date	free	affect	studi	toward
17hemispher	present	result	mani	affect	determin	use	alter	non	past
18state	first	less	import	diapaus	studi	surfac	success	consid	earlier
19locat	histor	later	focus	stage	releas	break	visit	differ	howev
20part	assess	contrast	major	moth	cherri	strong	fungal	indirect	record

Table A.3: The 20 highest weighted words for the 40 topics.

No.	Topic 21	Topic 22	Topic 23	Topic 24	Topic 25	Topic 26	Topic 27	Topic 28	Topic 29	Topic 30
1	develop	annual	climat	popul	use	model	chang	breed	veget	water
2	seed	climat	futur	resourc	time	predict	shift	nest	green	soil
3	stage	year	scenario	mismatch	analyzi	use	respons	lay	land	drought
4	studi	variabl	region	declin	analyz	simul	time	time	ndvi	increas
5	delay	rainfal	project	size	method	base	advanc	egg	use	product
6	harvest	period	use	abund	seri	data	consequ	food	index	growth
7	germin	weather	impact	level	data	develop	recent	date	satellit	condit
8	compar	tropic	condit	habitat	correl	observ	caus	success	deriv	stress
9	condit	variat	current	densiti	linear	paramet	report	hatch	base	root
10	matur	influenc	model	rate	regress	estim	suggest	bird	resolut	reduc
11	result	relat	assess	predat	relationship	accur	evid	clutch	surfac	dri

Table A.3: The 20 highest weighted words for the 40 topics.

No.	Topic 21	Topic 22	Topic 23	Topic 24	Topic 25	Topic 26	Topic 27	Topic 28	Topic 29	Topic 30
12	qualiti	correl	expect	trophic	statist	improv	studi	peak	data	avail
13	aim	month	potenti	bodi	indic	valid	find	reproduct	remot	decreas
14	produc	pattern	centuri	may	variabl	evalu	mani	size	sens	moistur
15	time	inter	rcp	avail	phase	perform	whether	tit	sos	plant
16	signific	studi	general	prey	estim	approach	document	relat	differ	biomass
17	varieti	posit	simul	food	mean	daili	investig	avail	modi	mediterranean
18	number	indic	suitabl	high	result	appli	like	earlier	imag	nitrogen
19	evalu	cycl	indic	dynam	show	process	examin	brood	spatial	limit
20	Higher	fluctuat	repres	forag	approach	calibr	although	may	normal	precipit

Table A.4: The 20 highest weighted words for the 40 topics.

No.Topic 31	Topic 32	Topic 33	Topic 34	Topic 35	Topic 36	Topic 37	Topic 38	Topic 39	Topic 40
1reproduct	speci	studi	crop	popul	site	variat	year	temperatur	day
2time	communiti	area	yield	adapt	elev	time	earli	degre	date
3life	respons	differ	wheat	trait	high	pattern	late	increas	advanc
4condit	among	urban	period	select	snowmelt	across	period	air	signific
5histori	distribut	result	increas	plastic	gradient	spatial	may	mean	year
6environment	shift	signific	cultivar	genet	low	scale	month	sensit	mean
7individu	group	show	growth	respons	higher	tempor	april	thermal	averag
8femal	rang	found	impact	variat	along	variabl	occur	day	per
9behavior	nativ	compar	product	phenotyp	lower	larg	mid	maximum	first
10environ	relat	type	rice	environment	differ	local	appear	rise	phenophas
11organ	composit	influenc	matur	fit	altitud	climat	first	daili	decad

Table A.4: The 20 highest weighted words for the 40 topics.

No.Topic 31	Topic 32	Topic 33	Topic 34	Topic 35	Topic 36	Topic 37	Topic 38	Topic 39	Topic 40
12male	specif	use	agricultur	differ	mountain	within	march	minimum	period
13cycl	invas	intens	maiz	local	alpin	vari	number	higher	respect
14may	respond	investig	use	evolutionari	limit	respons	time	rate	observ
15influenc	across	import	sow	individu	less	relationship	averag	averag	earlier
16predict	mani	island	adapt	potenti	relat	among	mean	respons	station
17activ	predict	small	decreas	environ	howev	explain	later	night	correl
18strategi	common	previous	stage	among	occur	differ	earlier	cool	delay
19sex	greater	citi	grain	genotyp	altitudin	geograph	week	warmer	gdd
20anim	ecolog	local	durat	natur	found	consist	june	effect	show

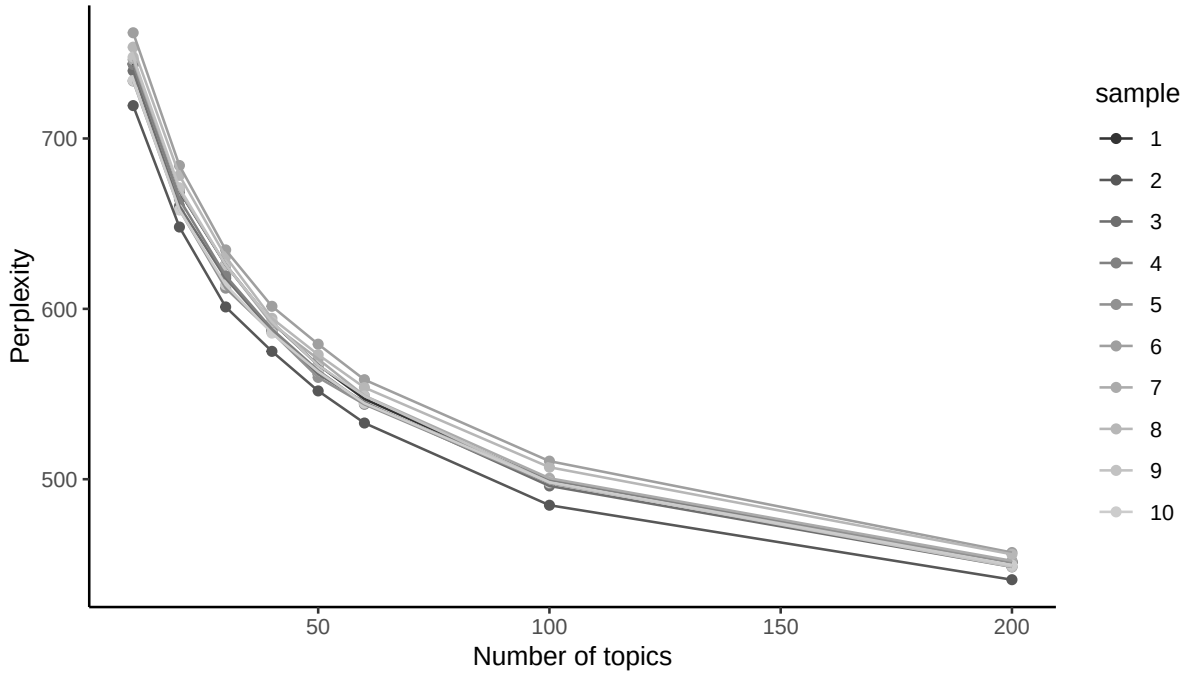


Figure A.1: The perplexity (uncertainty in predicting a single word) against the number of topics for a 10-fold block cross-validation.

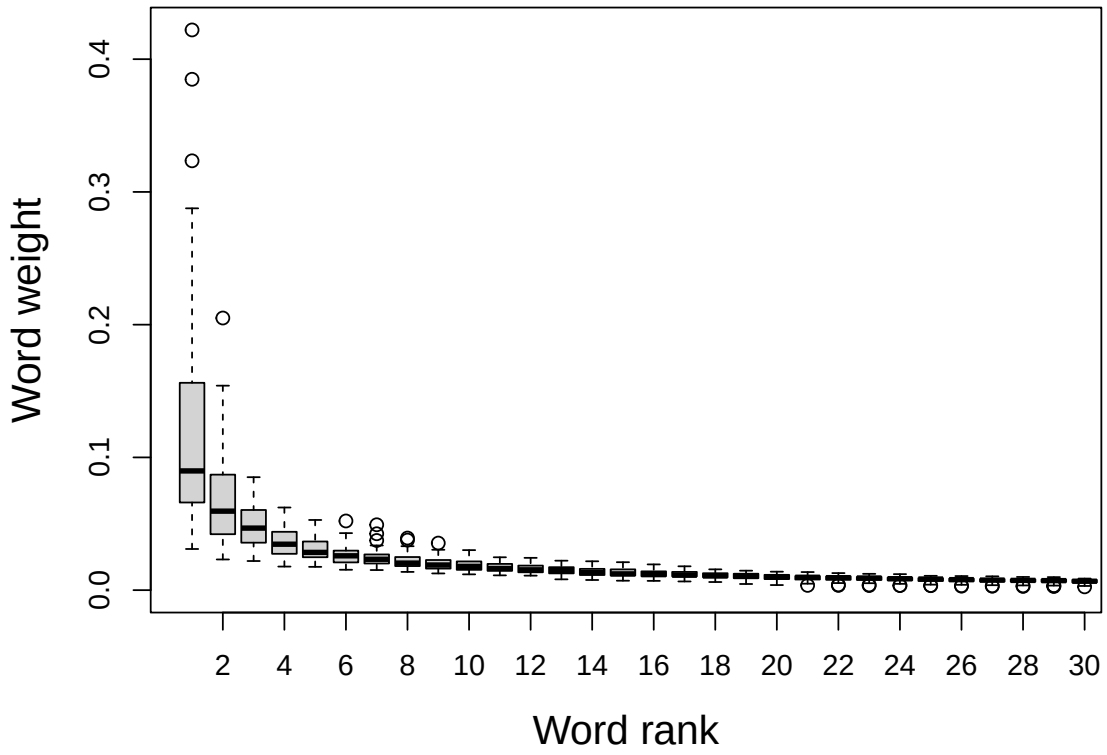


Figure A.2: The weight of each word against word rank for the 30 highest weighted words within each of the 40 topics.

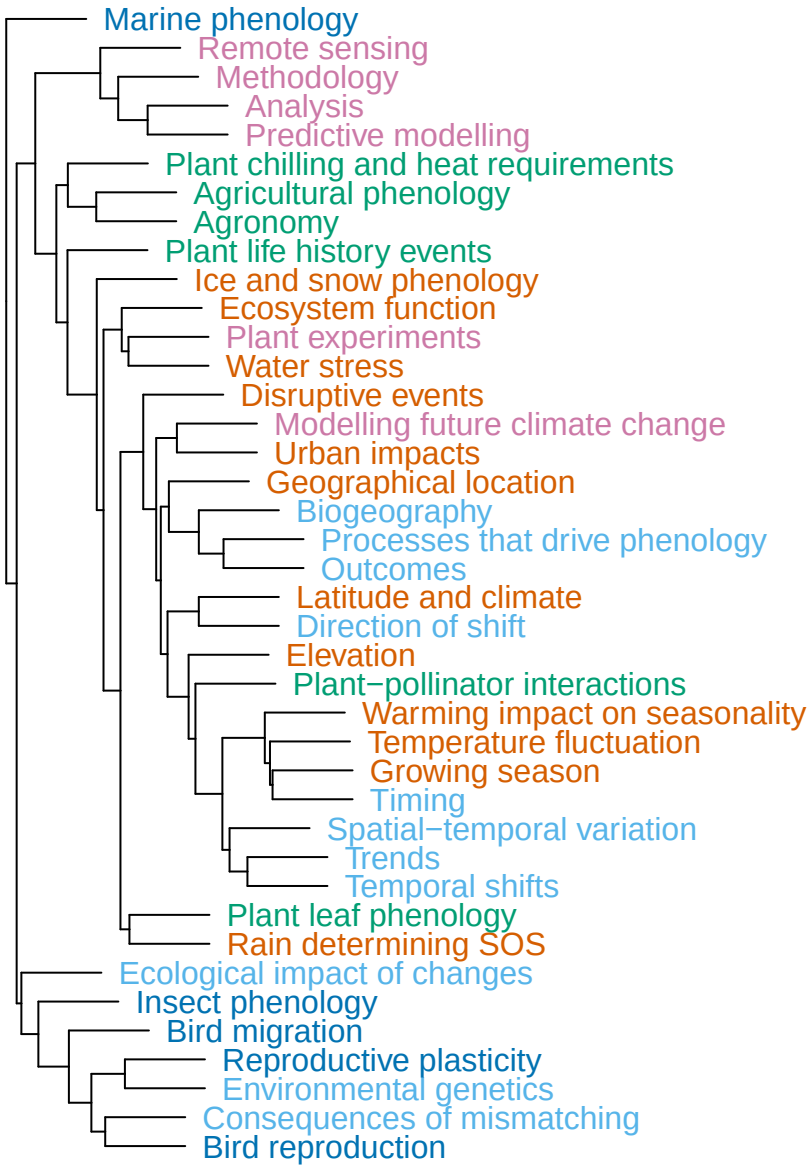


Figure A.3: Dendrogram showing topic similarity based on shared occurrence of words.

A.1 Journal plots

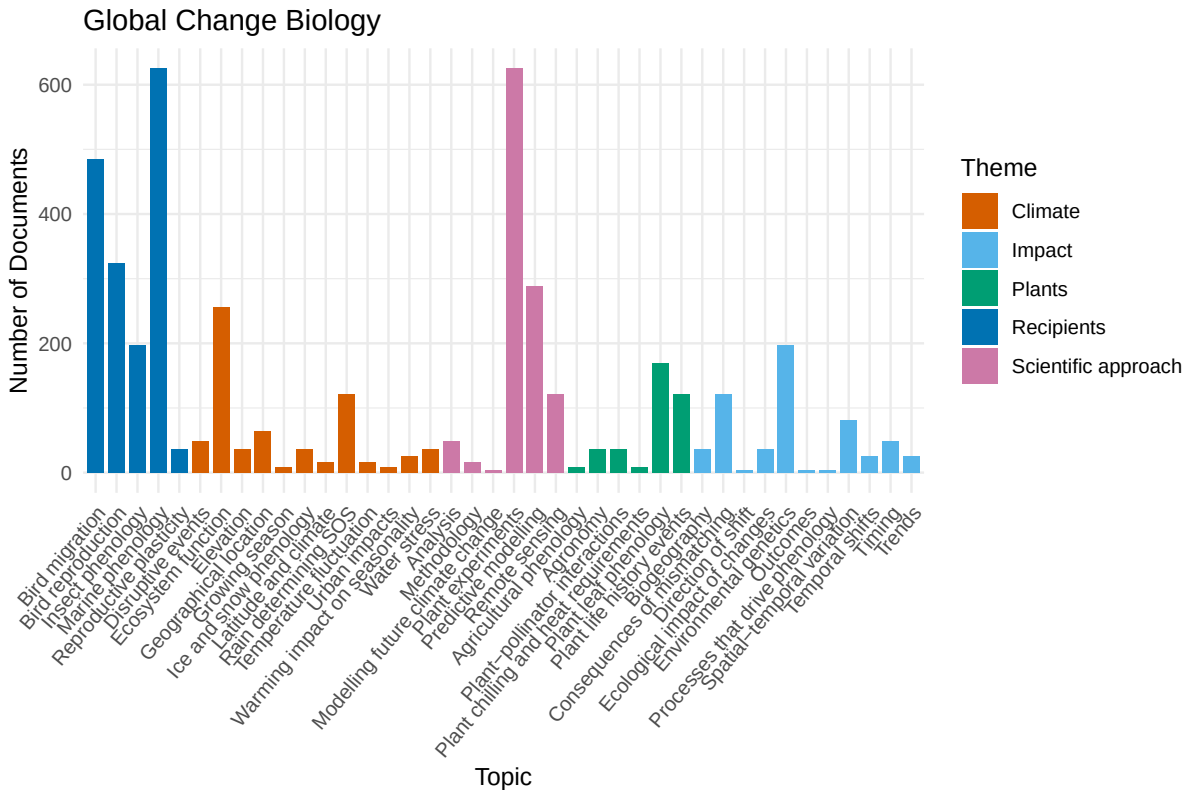


Figure A.4: The distribution of topics and themes among 341 documents for the journal Global Change Biology.

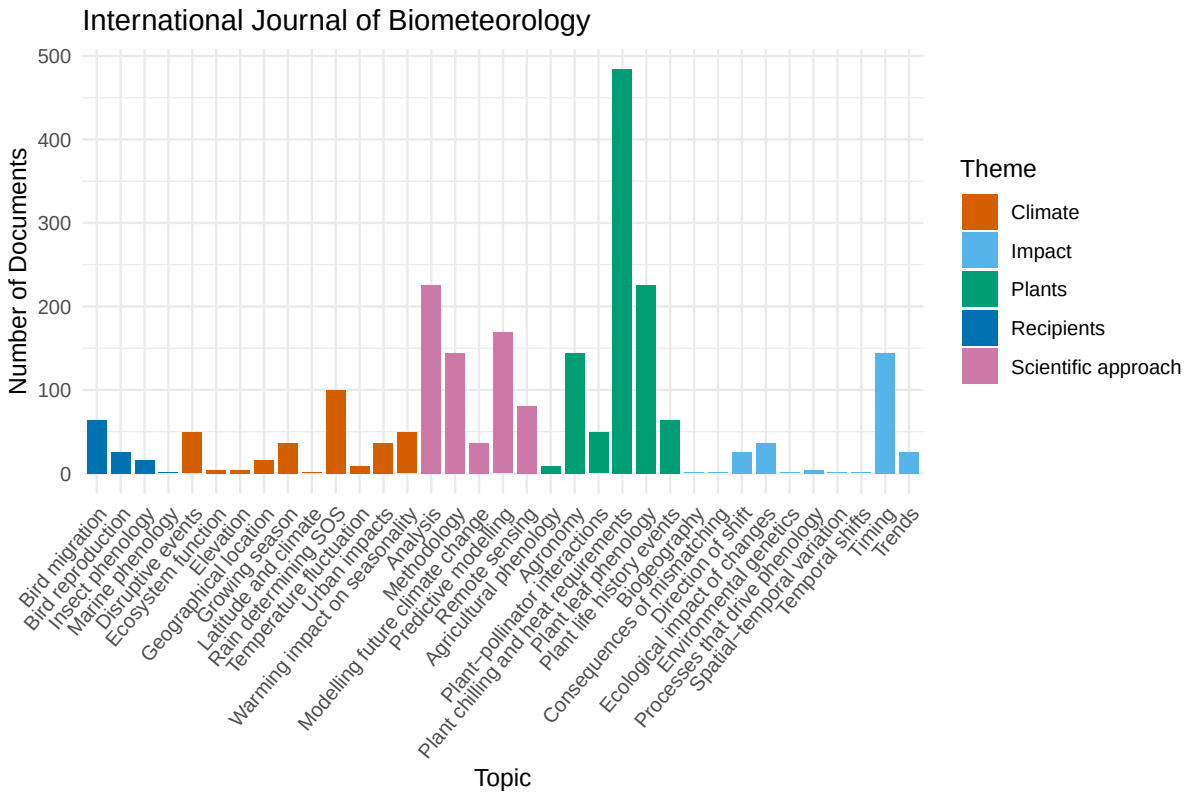


Figure A.5: The distribution of topics and themes among 223 documents for the International Journal of Biometeorology.

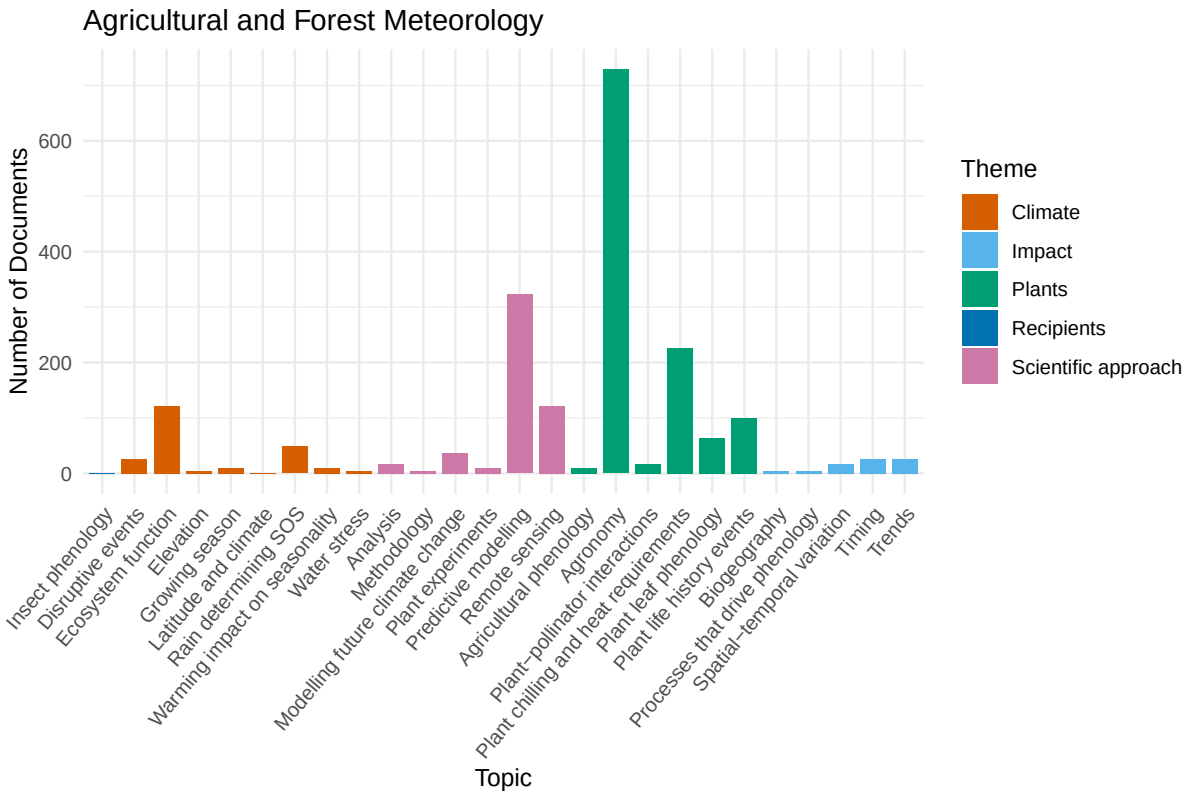


Figure A.6: The distribution of topics and themes among 164 documents for the journal Agricultural and Forest Meteorology.

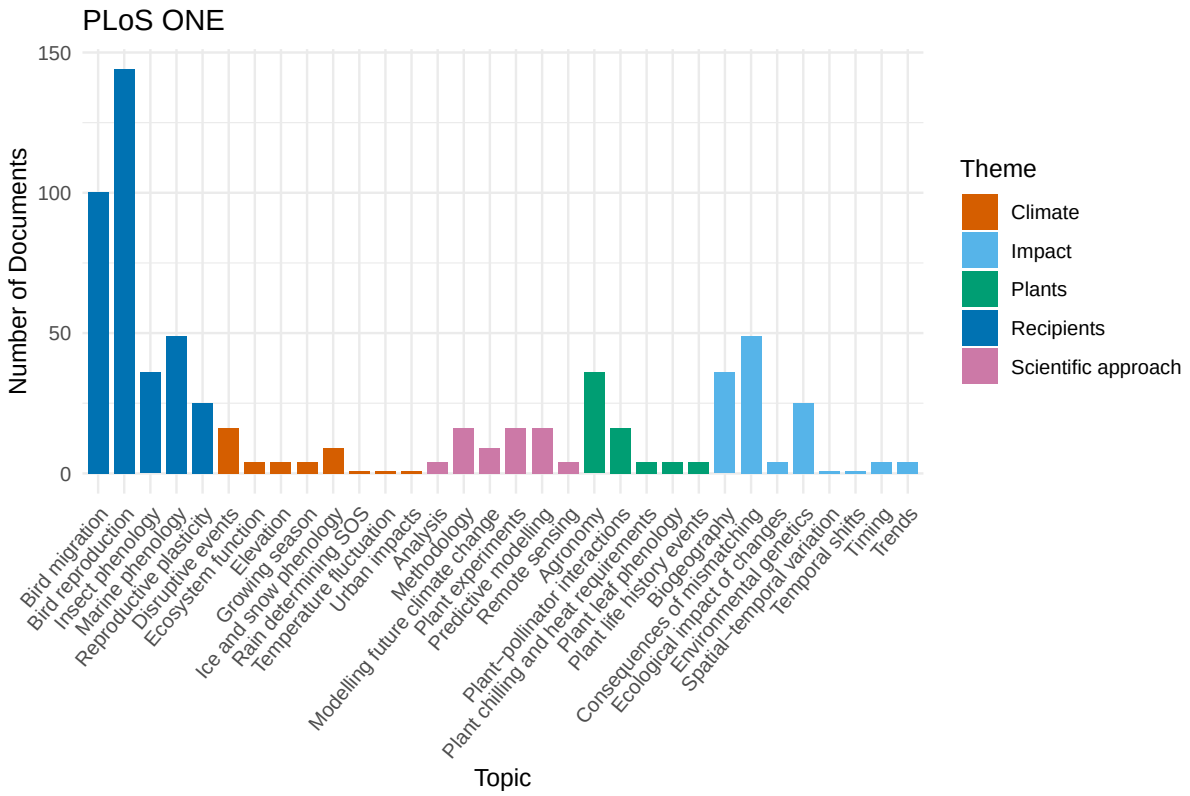


Figure A.7: The distribution of topics and themes among 117 documents for the journal PLoS ONE.

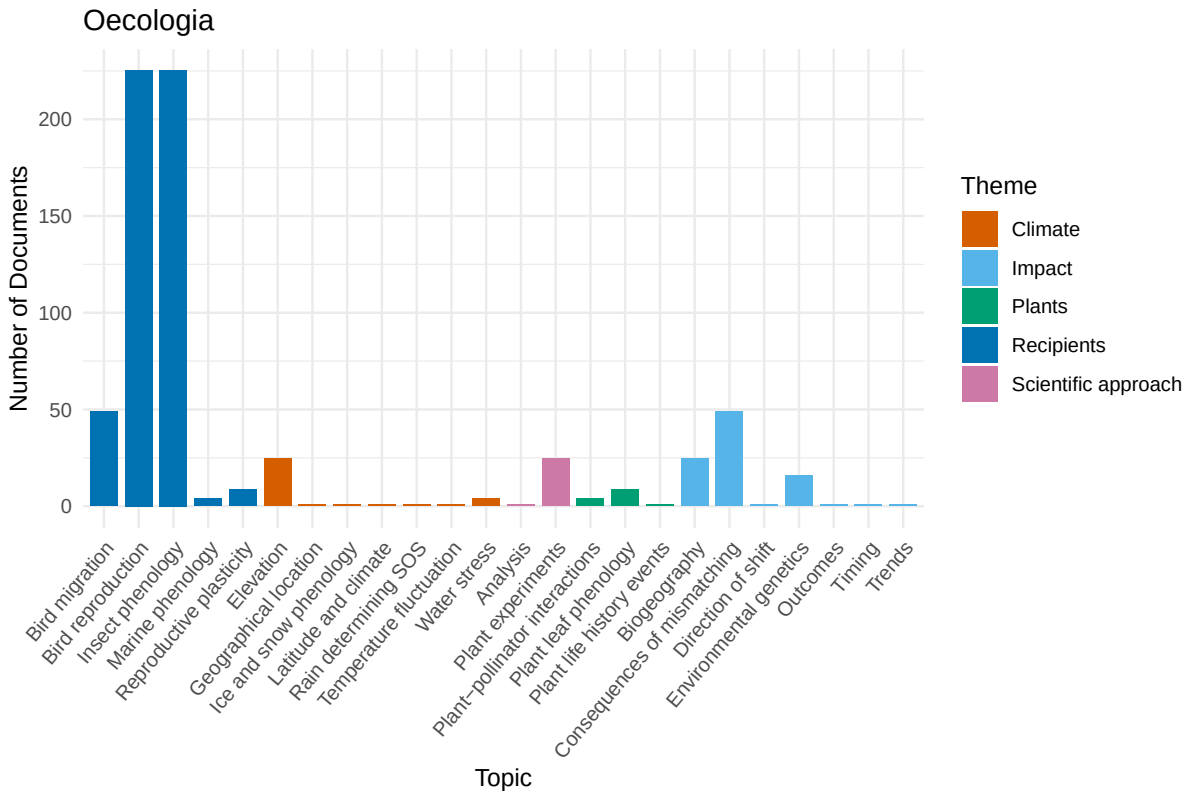


Figure A.8: The distribution of topics and themes among 86 documents for the journal Oecologia.

Appendix B

Chapter 3: Data cleaning, species included and normality plots

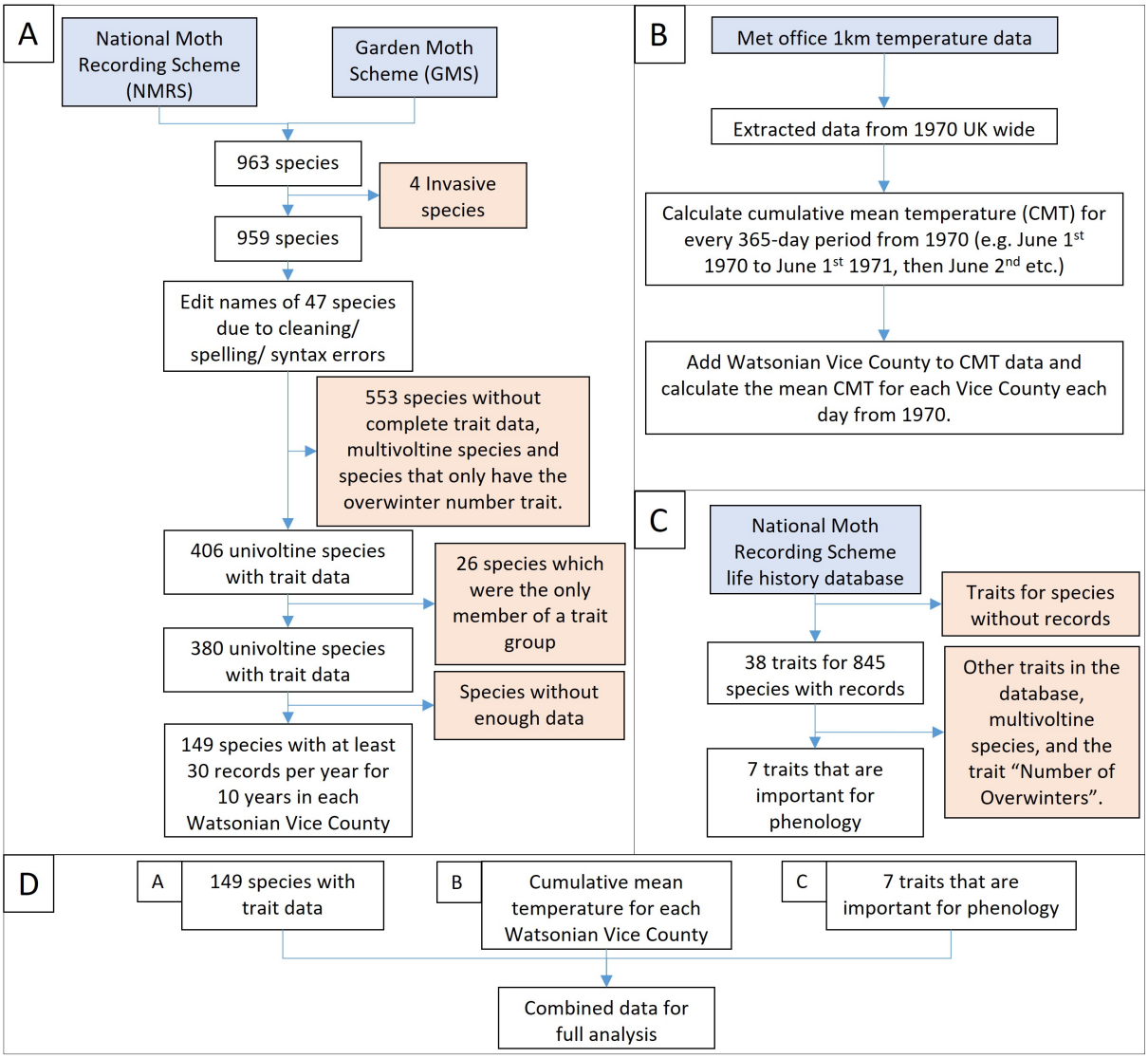


Figure B.1: The process by which data were cleaned and species were narrowed down to those included in the final analyses.

B.1 Species included

Table B.1: The number of records from the National Moth Recording Scheme (NMRS) and Garden Moth Scheme (GMS) datasets for the moth species included in the analyses.

Species	Subfamily	Family	Number of GMS records	Number of NMRS records
Habrosyne pyritoides	Acronictinae	Drepanidae	5,678	67,419
Cybosia mesomella	Amphipyrinae	Erebidae	0	9,130
Diaphora mendica	Amphipyrinae	Erebidae	4,393	43,709
Eilema depressa	Amphipyrinae	Erebidae	2,529	27,138
Eilema griseola	Arctiinae	Erebidae	6,821	75,718
Eilema sororcula	Arctiinae	Erebidae	797	15,384
Euplagia quadripunctaria	Arctiinae	Erebidae	545	5,284
Lithosia quadra	Arctiinae	Erebidae	675	6,035
Nudaria mundana	Arctiinae	Erebidae	485	14,409
Spilosoma lubricipeda	Arctiinae	Erebidae	9,094	129,218
Spilosoma lutea	Arctiinae	Erebidae	15,009	169,052
Tyria jacobaeae	Arctiinae	Erebidae	1,702	56,673
Herminia grisealis	Arctiinae	Erebidae	2,677	40,286
Calliteara pudibunda	Arctiinae	Erebidae	4,094	45,995
Euproctis chrysorrhoea	Arctiinae	Erebidae	394	11,735

Table B.1: The number of records from the National Moth Recording Scheme (NMRS) and Garden Moth Scheme (GMS) datasets for the moth species included in the analyses.

Species	Subfamily	Family	Number of GMS records	Number of NMRS records
Lymantria monacha	Bryophilinae	Erebidae	849	27,202
Abraxas grossulariata	Bryophilinae	Geometridae	3,188	48,967
Alcis repandata	Dicranurinae	Geometridae	6,861	96,182
Biston betularia	Dilobinae	Geometridae	8,525	108,271
Colotois pennaria	Ennominae	Geometridae	3,732	47,555
Crocallis elinguaria	Ennominae	Geometridae	9,071	102,778
Ennomos alniaria	Ennominae	Geometridae	3,968	52,668
Ennomos erosaria	Ennominae	Geometridae	511	12,696
Ennomos fuscantaria	Ennominae	Geometridae	3,630	36,541
Ennomos quercinaria	Ennominae	Geometridae	0	9,281
Epione repandaria	Ennominae	Geometridae	0	10,442
Lomaspilis marginata	Ennominae	Geometridae	7,098	100,200
Lomographa bimaculata	Ennominae	Geometridae	533	13,465
Lomographa temerata	Ennominae	Geometridae	5,622	64,039
Plagodis dolabraria	Ennominae	Geometridae	860	29,869
Hemithea aestivaria	Ennominae	Geometridae	2,993	44,556

Table B.1: The number of records from the National Moth Recording Scheme (NMRS) and Garden Moth Scheme (GMS) datasets for the moth species included in the analyses.

Species	Subfamily	Family	Number of GMS records	Number of NMRS records
Camptogramma bilineata	Ennominae	Geometridae	4,036	60,425
Dysstroma citrata	Ennominae	Geometridae	456	21,689
Earophila badiata	Eustrotiinae	Geometridae	1,392	24,552
Epirrita dilutata	Geometrinae	Geometridae	0	19,345
Eulithis populata	Hadeninae	Geometridae	422	15,004
Eulithis testata	Hadeninae	Geometridae	188	14,584
Eupithecia abbreviata	Hadeninae	Geometridae	506	45,415
Eupithecia absinthiata	Hadeninae	Geometridae	0	19,863
Eupithecia exiguata	Hadeninae	Geometridae	231	37,343
Eupithecia intricata	Hadeninae	Geometridae	0	21,255
Eupithecia phoeniceata	Hadeninae	Geometridae	803	6,498
Eupithecia pulchellata	Hadeninae	Geometridae	1,145	33,270
Eupithecia vulgata	Hadeninae	Geometridae	505	96,772
Gandaritis pyraliata	Hadeninae	Geometridae	3,570	68,512
Hydriomena furcata	Hadeninae	Geometridae	5,169	83,125
Hydriomena impluviata	Hadeninae	Geometridae	51	14,193

Table B.1: The number of records from the National Moth Recording Scheme (NMRS) and Garden Moth Scheme (GMS) datasets for the moth species included in the analyses.

Species	Subfamily	Family	Number of GMS records	Number of NMRS records
Lampropteryx suffumata	Hadeninae	Geometridae	431	20,801
Pasiphila rectangulata	Hadeninae	Geometridae	4,596	60,223
Perizoma alchemillata	Hadeninae	Geometridae	3,032	46,561
Perizoma flavofasciata	Hadeninae	Geometridae	556	23,892
Scotopteryx chenopodiata	Hadeninae	Geometridae	2,135	43,872
Xanthorhoe montanata	Hepialidae	Geometridae	6,132	119,796
Idaea dimidiata	Hepialidae	Geometridae	7,306	106,985
Idaea rusticata	Herminiinae	Geometridae	2,173	19,110
Scopula floslactata	Larentiinae	Geometridae	0	9,322
Hepialus humuli	Larentiinae	Hepialidae	1,634	24,332
Korscheltellus lupulina	Larentiinae	Hepialidae	3,958	68,464
Malacosoma neustria	Larentiinae	Lasiocampidae	570	25,384
Euthrix potatoria	Larentiinae	Lasiocampidae	2,291	54,176
Craniophora ligustri	Larentiinae	Noctuidae	2,061	28,326
Amphipyra berbera	Larentiinae	Noctuidae	0	16,148
Amphipyra pyramidea	Larentiinae	Noctuidae	0	43,791

Table B.1: The number of records from the National Moth Recording Scheme (NMRS) and Garden Moth Scheme (GMS) datasets for the moth species included in the analyses.

Species	Subfamily	Family	Number of GMS records	Number of NMRS records
Amphipyra tragopoginis	Larentiinae	Noctuidae	2,500	49,626
Bryophila domestica	Larentiinae	Noctuidae	7,905	96,904
Nyctobrya muralis	Larentiinae	Noctuidae	657	9,054
Diloba caeruleocephala	Larentiinae	Noctuidae	328	9,272
Deltote pygarga	Larentiinae	Noctuidae	941	19,204
Anorthoa munda	Larentiinae	Noctuidae	4,022	37,201
Ceramica pisi	Larentiinae	Noctuidae	1,370	24,005
Cerapteryx graminis	Larentiinae	Noctuidae	2,245	39,526
Leucania comma	Larentiinae	Noctuidae	2,989	31,929
Melanchra persicariae	Larentiinae	Noctuidae	5,181	60,744
Mythimna conigera	Larentiinae	Noctuidae	1,626	18,547
Mythimna ferrago	Larentiinae	Noctuidae	6,559	81,814
Mythimna pudorina	Larentiinae	Noctuidae	0	4,166
Mythimna straminea	Larentiinae	Noctuidae	0	9,444
Mythimna turca	Lymantriinae	Noctuidae	43	4,308
Orthosia cerasi	Lymantriinae	Noctuidae	20,226	170,266

Table B.1: The number of records from the National Moth Recording Scheme (NMRS) and Garden Moth Scheme (GMS) datasets for the moth species included in the analyses.

Species	Subfamily	Family	Number of GMS records	Number of NMRS records
Orthosia cruda	Lymantriinae	Noctuidae	8,594	83,524
Orthosia gothica	Macroglossinae	Noctuidae	26,235	258,636
Orthosia gracilis	Macroglossinae	Noctuidae	2,606	29,819
Orthosia incerta	Malacosomatinae	Noctuidae	13,874	126,235
Panolis flammea	Noctuinae	Noctuidae	468	11,404
Lacanobia w-latinum	Noctuinae	Noctuidae	516	10,176
Agrotis vestigialis	Noctuinae	Noctuidae	85	6,807
Cerastis rubricosa	Noctuinae	Noctuidae	1,627	33,082
Diarsia brunnea	Noctuinae	Noctuidae	1,812	31,784
Diarsia mendica	Noctuinae	Noctuidae	5,843	85,539
Euxoa nigricans	Noctuinae	Noctuidae	188	5,366
Euxoa tritici	Noctuinae	Noctuidae	257	12,262
Naenia typica	Noctuinae	Noctuidae	1,333	18,693
Noctua comes	Noctuinae	Noctuidae	22,044	221,225
Noctua fimbriata	Noctuinae	Noctuidae	5,816	59,045
Noctua interjecta	Noctuinae	Noctuidae	2,361	28,925

Table B.1: The number of records from the National Moth Recording Scheme (NMRS) and Garden Moth Scheme (GMS) datasets for the moth species included in the analyses.

Species	Subfamily	Family	Number of GMS records	Number of NMRS records
Noctua janthe	Noctuinae	Noctuidae	18,122	167,608
Xestia baja	Noctuinae	Noctuidae	3,000	34,900
Xestia ditrapezium	Noctuinae	Noctuidae	1,186	11,776
Xestia sexstrigata	Nolinae	Noctuidae	3,341	45,209
Xestia triangulum	Phalerinae	Noctuidae	9,852	109,438
Autographa jota	Pinarinae	Noctuidae	2,800	34,951
Autographa pulchrina	Plusiinae	Noctuidae	4,013	47,112
Allophyes oxyacanthae	Plusiinae	Noctuidae	4,039	43,842
Xylocampa areola	Psaphidinae	Noctuidae	10,516	87,176
Agrochola circellaris	Psaphidinae	Noctuidae	1,478	22,781
Agrochola litura	Sphinginae	Noctuidae	2,084	24,698
Agrochola lota	Sphinginae	Noctuidae	4,489	41,698
Agrochola lychnidis	Sterrhinae	Noctuidae	4,724	55,681
Agrochola macilenta	Sterrhinae	Noctuidae	4,812	47,731
Apamea anceps	Sterrhinae	Noctuidae	339	18,279
Apamea crenata	Thyatirinae	Noctuidae	4,282	51,155

Table B.1: The number of records from the National Moth Recording Scheme (NMRS) and Garden Moth Scheme (GMS) datasets for the moth species included in the analyses.

Species	Subfamily	Family	Number of GMS records	Number of NMRS records
Apamea lithoxylaea	Xyleninae	Noctuidae	3,660	55,730
Apamea oblonga	Xyleninae	Noctuidae	0	2,086
Apamea remissa	Xyleninae	Noctuidae	2,634	36,807
Apamea sordens	Xyleninae	Noctuidae	4,203	58,598
Apamea unanimis	Xyleninae	Noctuidae	119	10,940
Aporophyla nigra	Xyleninae	Noctuidae	6,228	50,058
Brachylomia viminalis	Xyleninae	Noctuidae	63	10,718
Charanyca trigrammica	Xyleninae	Noctuidae	5,795	58,251
Cirrhia icteritia	Xyleninae	Noctuidae	2,884	33,764
Cosmia trapezina	Xyleninae	Noctuidae	7,853	93,468
Denticucullus pygmina	Xyleninae	Noctuidae	1,144	25,087
Eremobia ochroleuca	Xyleninae	Noctuidae	855	20,826
Gortyna flavago	Xyleninae	Noctuidae	2,060	27,648
Hydraecia micacea	Xyleninae	Noctuidae	8,512	101,197
Lithophane leautieri	Xyleninae	Noctuidae	5,435	46,857
Litoligia literosa	Xyleninae	Noctuidae	364	17,609

Table B.1: The number of records from the National Moth Recording Scheme (NMRS) and Garden Moth Scheme (GMS) datasets for the moth species included in the analyses.

Species	Subfamily	Family	Number of GMS records	Number of NMRS records
Longalatedes elymi	Xyleninae	Noctuidae	0	3,212
Luperina testacea	Xyleninae	Noctuidae	9,405	132,840
Mesapamea secalis	Xyleninae	Noctuidae	0	43,293
Mesoligia furuncula	Xyleninae	Noctuidae	1,613	41,449
Oligia fasciuncula	Xyleninae	Noctuidae	4,845	65,449
Oligia latruncula	Xyleninae	Noctuidae	0	21,895
Oligia strigilis	Xyleninae	Noctuidae	0	23,807
Omphaloscelis lunosa	Xyleninae	Noctuidae	8,277	95,552
Photedes minima	Xyleninae	Noctuidae	504	27,928
Polymixis lichenea	Xyleninae	Noctuidae	2,862	21,196
Rhizedra lutosa	Xyleninae	Noctuidae	517	18,853
Rusina ferruginea	Xyleninae	Noctuidae	2,144	52,130
Thalpophila matura	Xyleninae	Noctuidae	2,595	36,371
Tiliacea aurago	Xyleninae	Noctuidae	2,500	21,170
Xanthia togata	Xyleninae	Noctuidae	2,286	28,458
Nola confusalis	Xyleninae	Nolidae	1,234	20,989

Table B.1: The number of records from the National Moth Recording Scheme (NMRS) and Garden Moth Scheme (GMS) datasets for the moth species included in the analyses.

Species	Subfamily	Family	Number of GMS records	Number of NMRS records
Stauropus fagi	Xyleninae	Notodontidae	198	12,462
Phalera bucephala	Xyleninae	Notodontidae	6,358	75,207
Deilephila elpenor	Xyleninae	Sphingidae	9,282	88,735
Deilephila porcellus	Xyleninae	Sphingidae	789	16,391
Sphinx ligustri	Xyleninae	Sphingidae	1,519	24,625
Sphinx pinastri	Xyleninae	Sphingidae	439	10,802

B.2 Traits plots

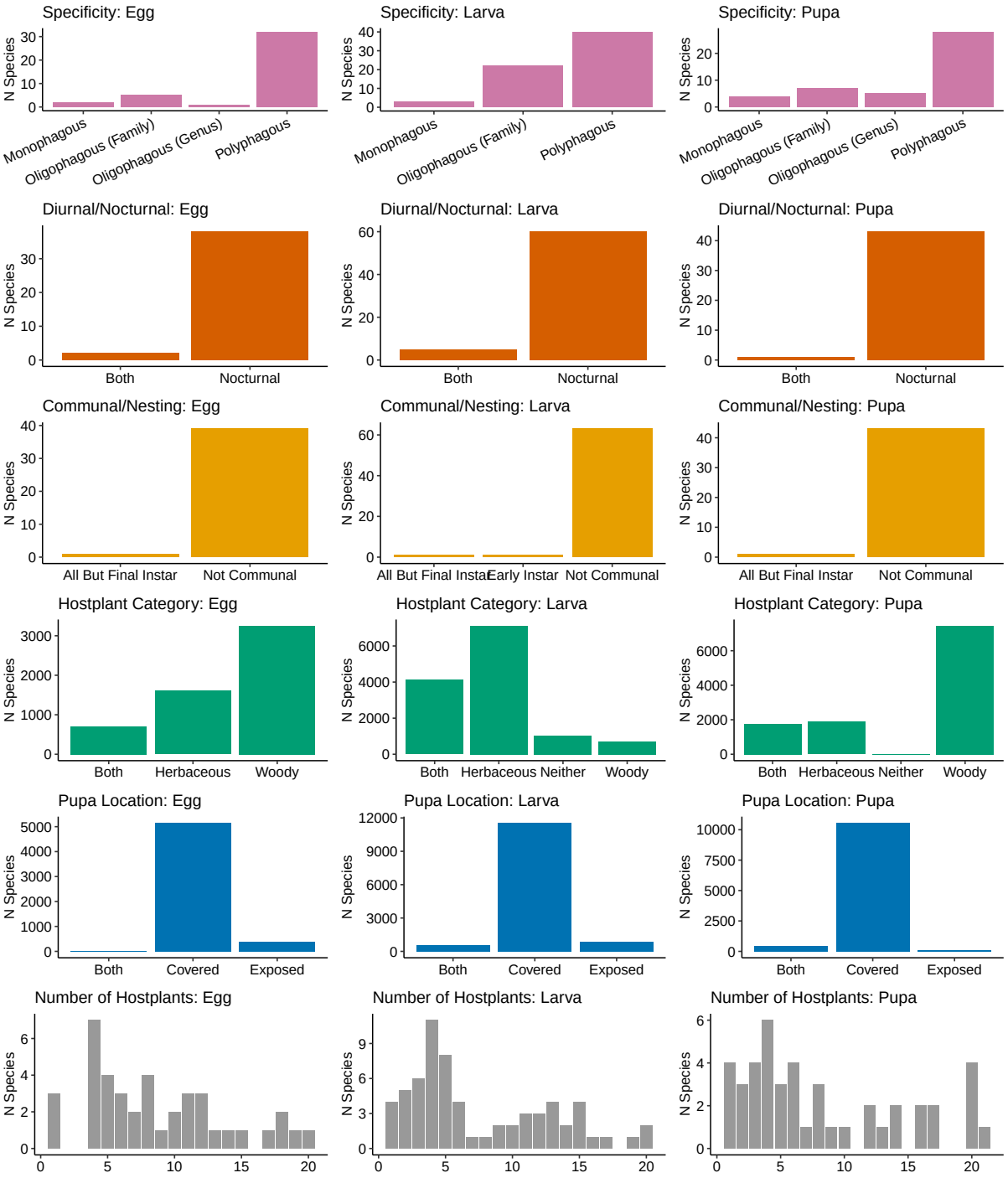


Figure B.2: The number of species in each trait category for each overwintering stage.

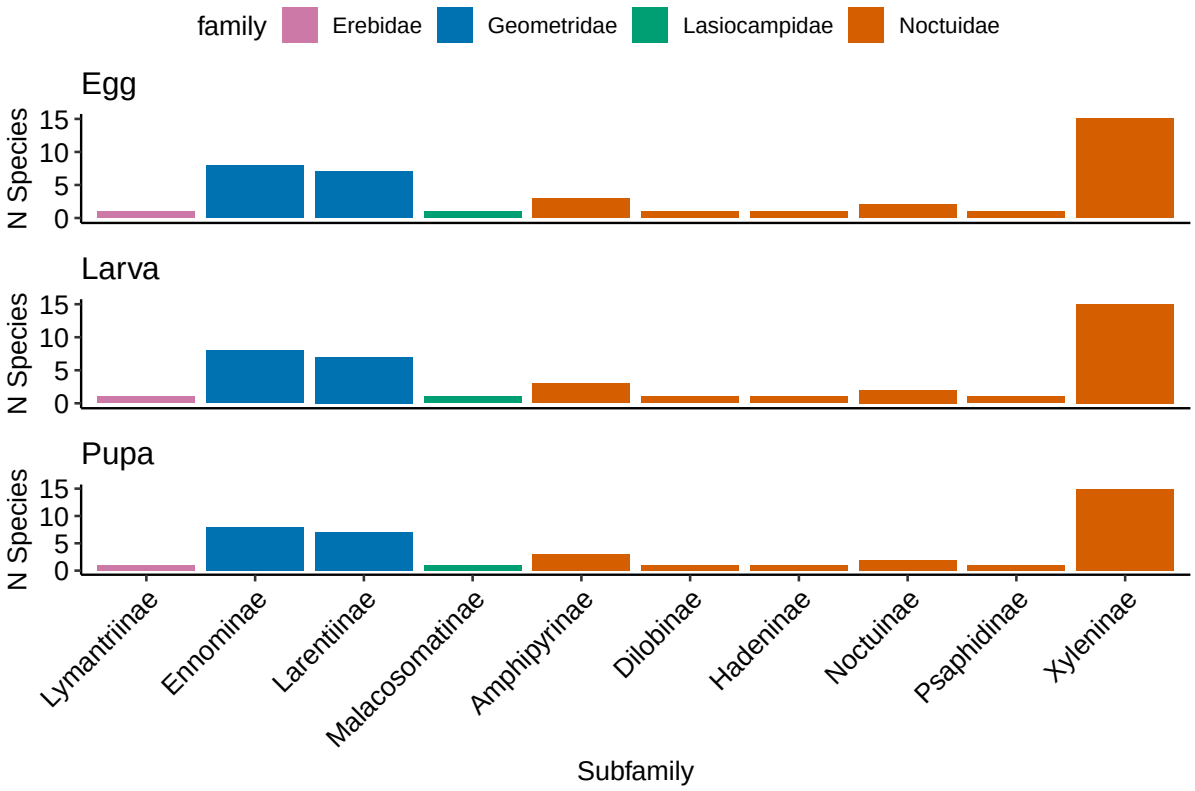


Figure B.3: The number of species per subfamily for each overwintering stage.

B.3 Normality plots

B.3.1 Egg overwintering species

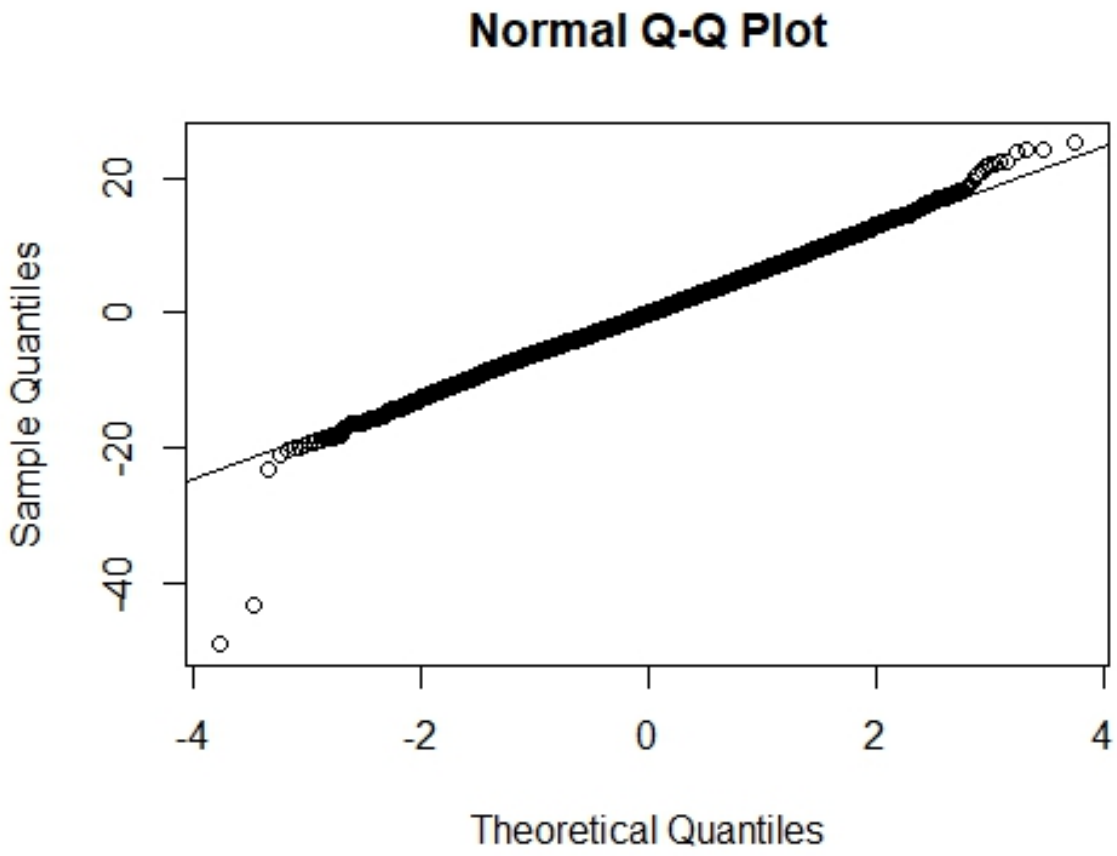


Figure B.4: The QQ plot for the best model for the First Emergence of species that overwinter in the egg stage: First Emergence ~ Year + Cumulative Mean Temperature, random effects = Watsonian Vice County nested in Species.

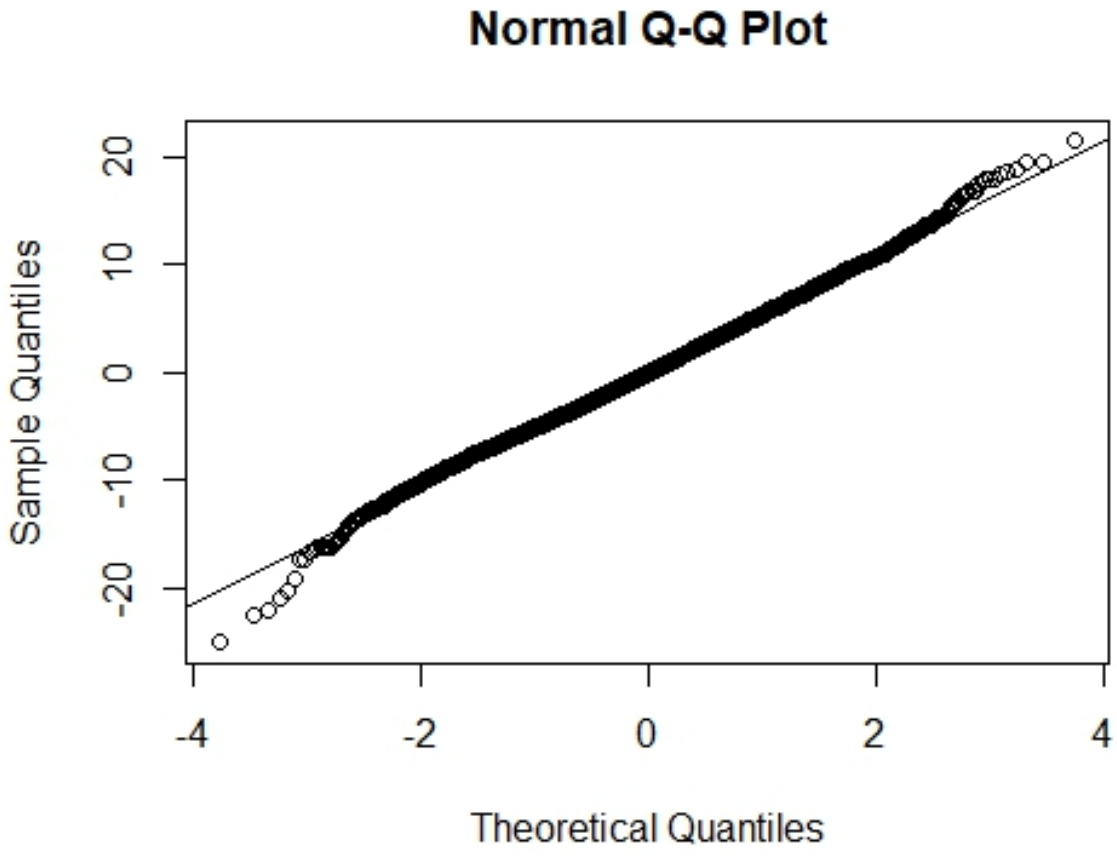


Figure B.5: The QQ plot for the best model for the Peak Emergence of species that overwinter in the egg stage: Peak Emergence $\sim$ Year + Cumulative Mean Temperature, random effects = Watsonian Vice County nested in Species.

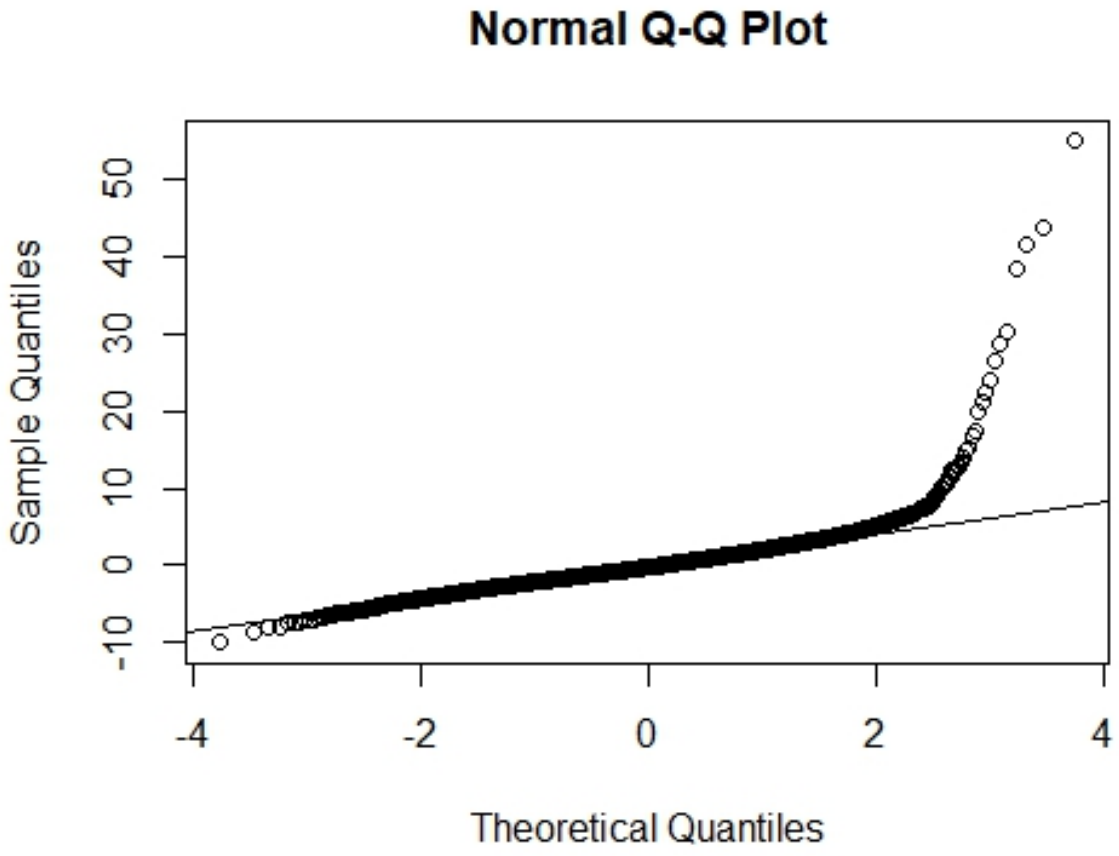


Figure B.6: The QQ plot for the best model for the Emergence SD of species that overwinter in the egg stage: Emergence SD ~ Year, random effects = Watsonian Vice County nested in Species.

B.3.2 Larva overwintering species

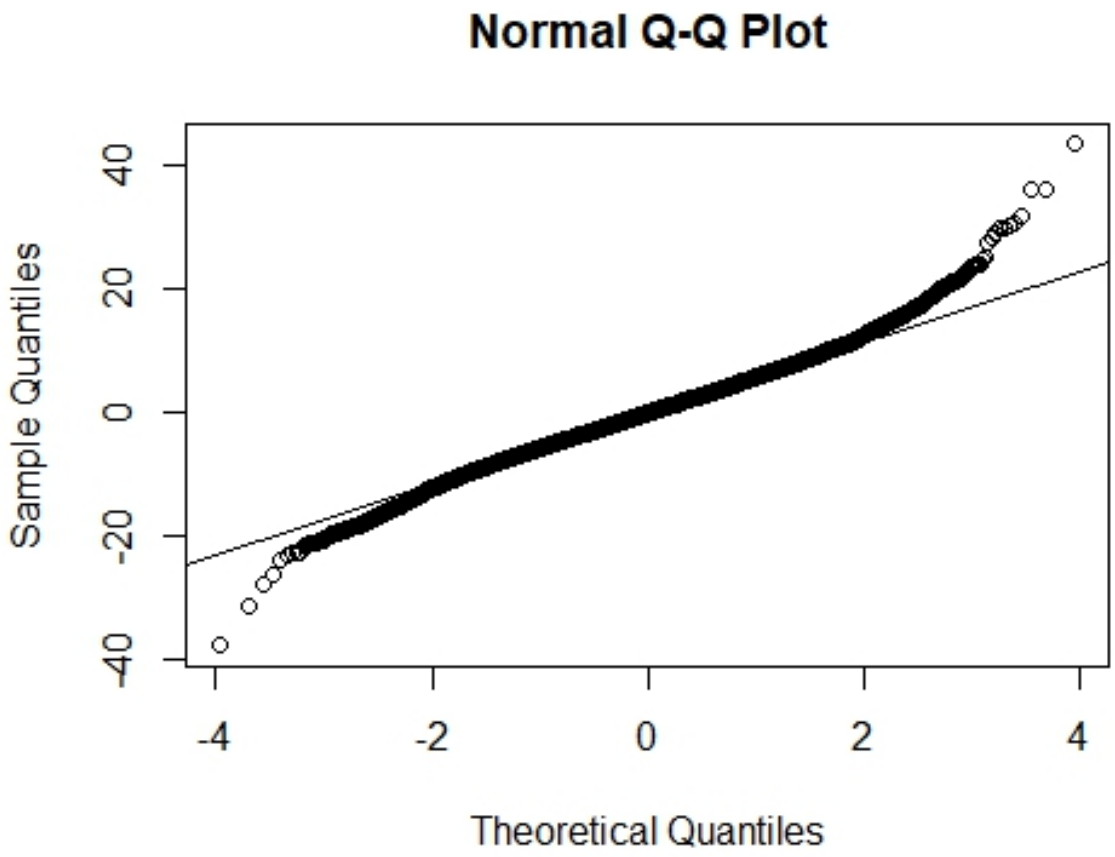


Figure B.7: The QQ plot for the best model for the First Emergence of species that overwinter in the larva stage: First Emergence ~ Year + Cumulative Mean Temperature + Hostplant Category: Woody + Hostplant Category: Herbaceous, random effects = Watsonian Vice County nested in Species.

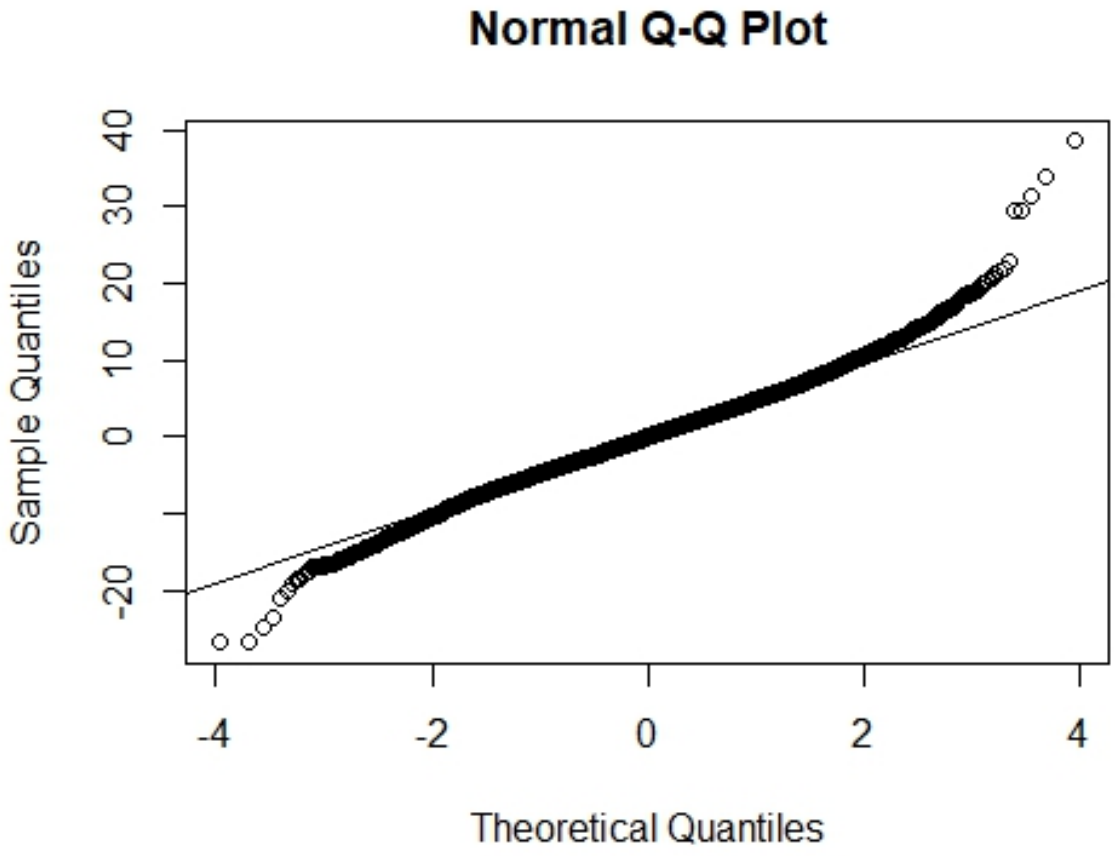


Figure B.8: The QQ plot for the best model for the Peak Emergence of species that overwinter in the larva stage: Peak Emergence ~ Year + Cumulative Mean Temperature + Hostplant Category: Woody + Hostplant Category: Herbaceous, random effects = Watsonian Vice County nested in Species.

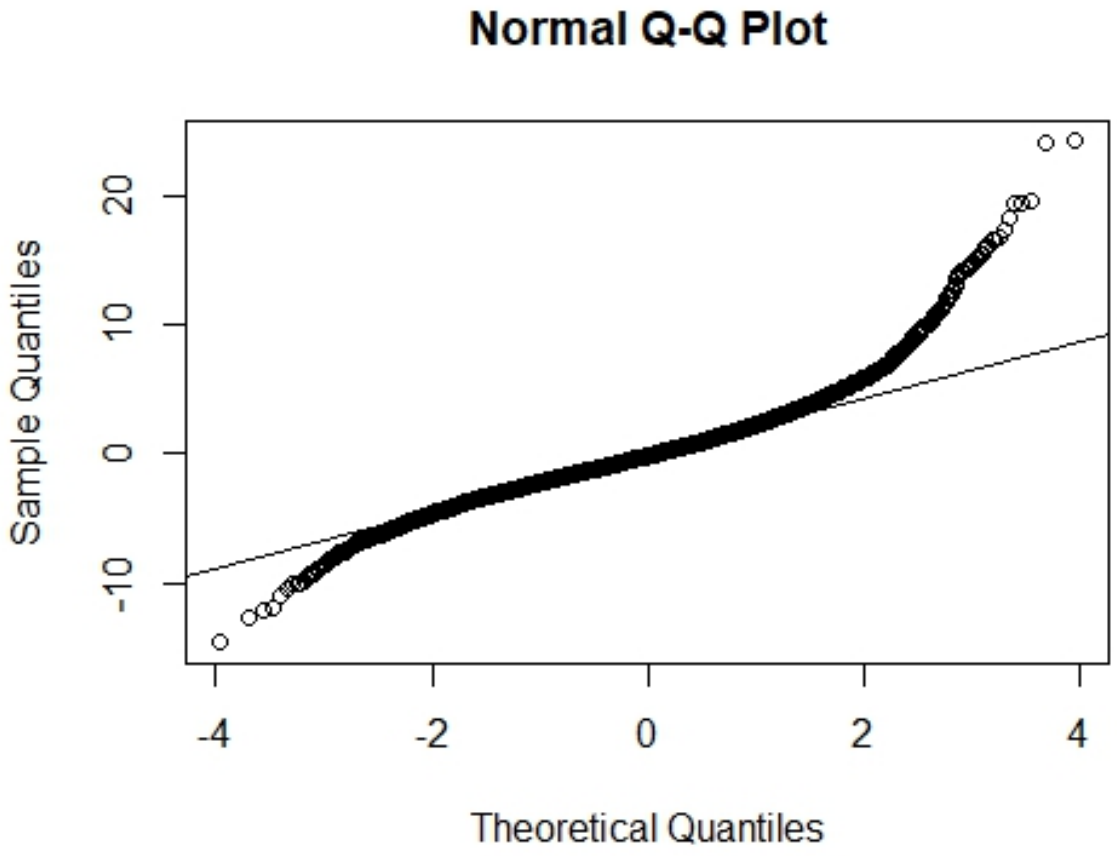


Figure B.9: The QQ plot for the best model for the Emergence SD of species that overwinter in the larva stage: Emergence SD ~ Year, random effects = Watsonian Vice County nested in Species.

B.3.3 Pupa overwintering species

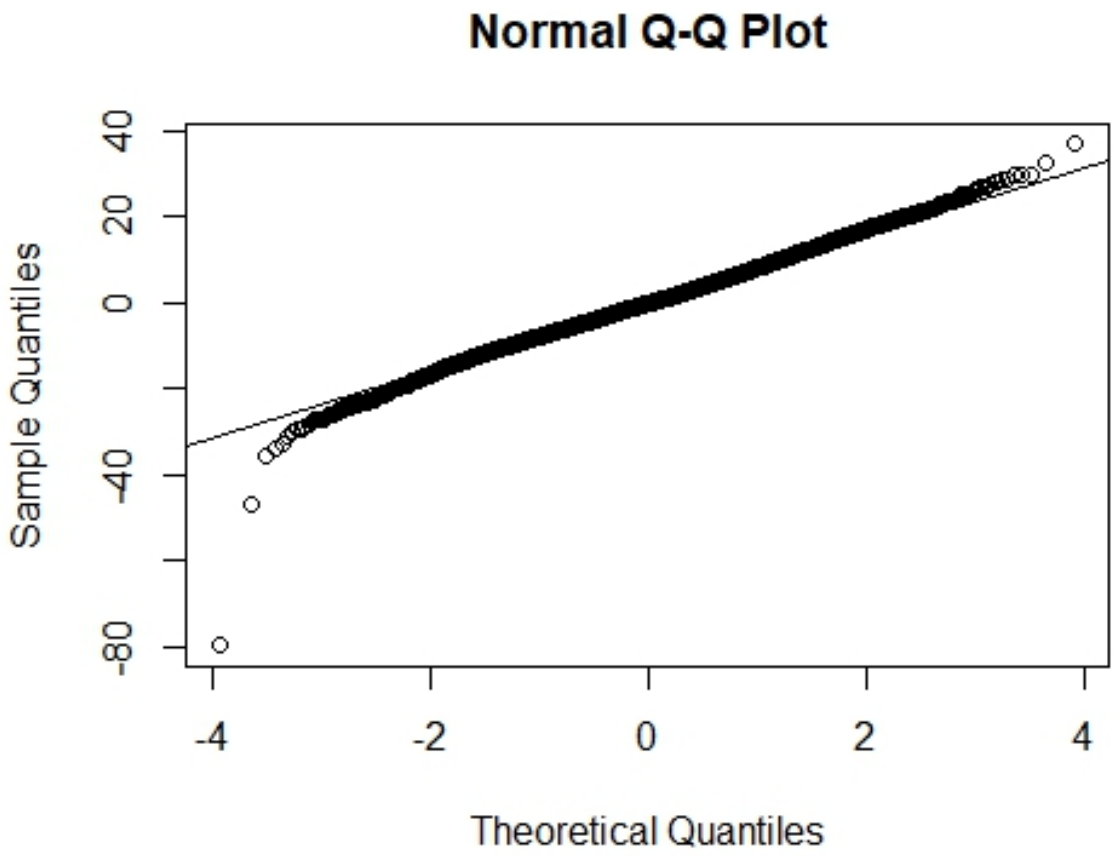


Figure B.10: The QQ plot for the best model for the First Emergence of species that overwinter in the pupa stage: First Emergence $\sim$ Year + Cumulative Mean Temperature, random effects = Watsonian Vice County nested in Species.

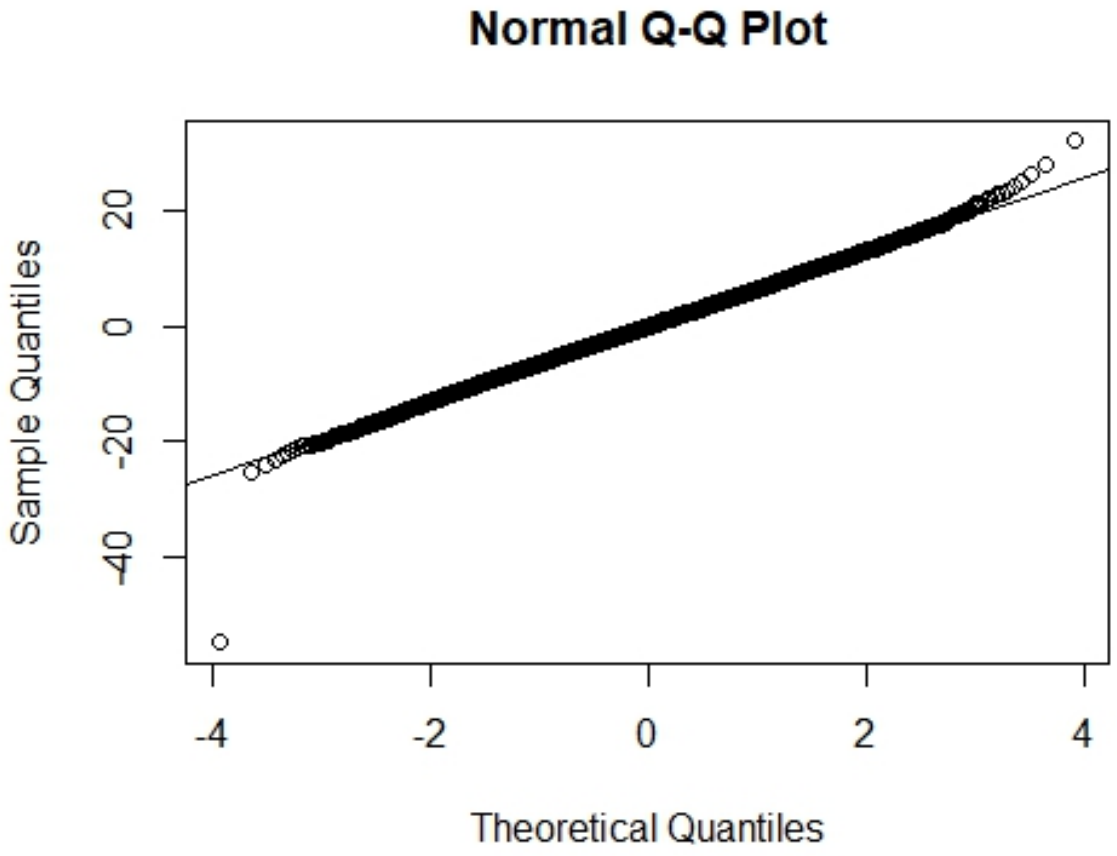


Figure B.11: The QQ plot for the best model for the Peak Emergence of species that overwinter in the pupa stage: Peak Emergence ~ Year + Cumulative Mean Temperature, random effects = Watsonian Vice County nested in Species.

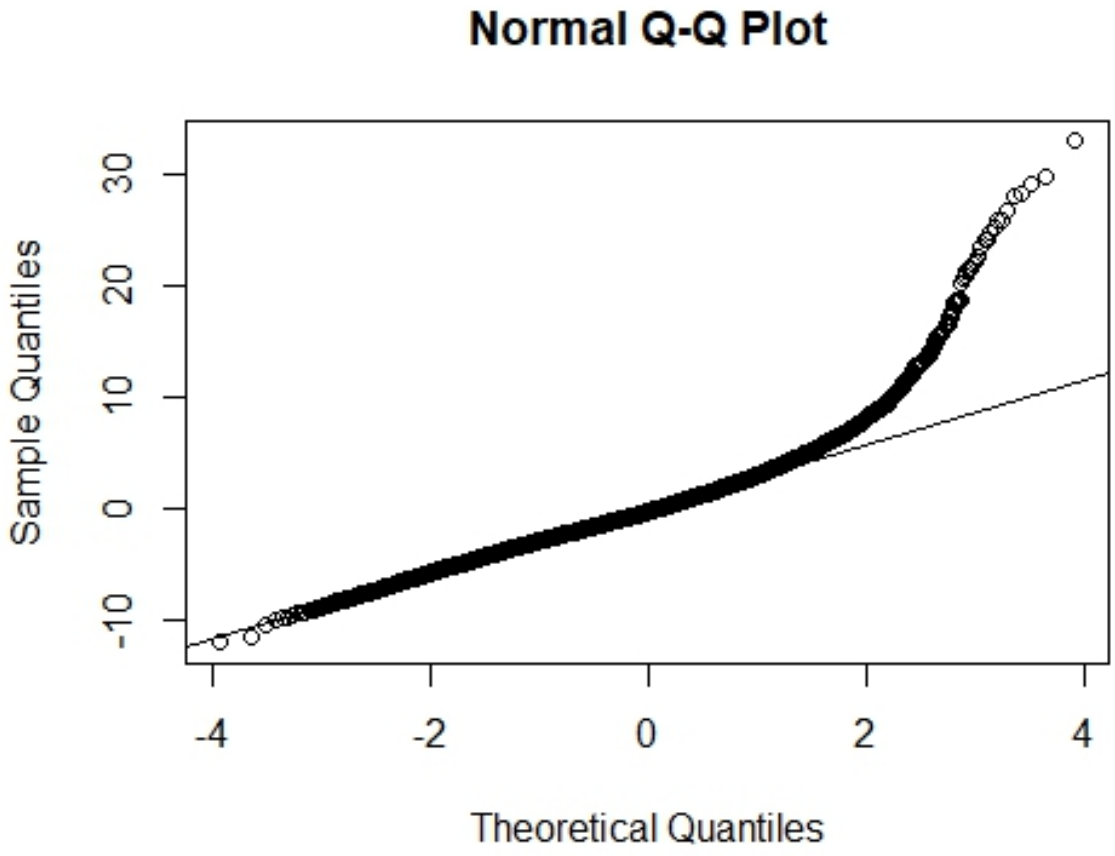


Figure B.12: The QQ plot for the best model for the Emergence SD of species that overwinter in the pupa stage: Emergence SD ~ Year, random effects = Watsonian Vice County nested in Species.

Appendix C

Chapter 4: Plant species included, Trait and ACF plots

C.1 Plant species included

Table C.1: The number of records for the plant species included in the analyses.

Species	Family	Number of Records
Centaurea nigra	Apiaceae	50
Tussilago farfara	Apiaceae	1,578
Hedera helix	Apiaceae	1,412
Primula vulgaris	Apiaceae	657
Cardamine pratensis	Apiaceae	1,521
Alopecurus pratensis	Araliacae	1,315
Dactylis glomerata	Asteraceae	1,280
Holcus lanatus	Asteraceae	1,201

Table C.1: The number of records for the plant species included in the analyses.

Species	Family	Number of Records
Rubus fruticosus agg.	Asteraceae	41
Primula veris	Asteraceae	88
Phleum pratense	Asteraceae	998
Leucanthemum vulgare	Asteraceae	1,529
Achillea millefolium	Asteraceae	38
Aegopodium podagraria	Asteraceae	29
Aethusa cynapium	Asteraceae	31
Ajuga reptans	Asteraceae	45
Alopecurus geniculatus	Asteraceae	20
Anacamptis pyramidalis	Asteraceae	29
Anthoxanthum odoratum	Asteraceae	21
Arctium minus	Asteraceae	43
Arrhenatherum elatius	Asteraceae	32
Artemisia vulgaris	Asteraceae	52
Barbarea vulgaris	Asteraceae	34
Brachypodium sylvaticum	Boraginaceae	26
Briza media	Boraginaceae	29
Caltha palustris	Brassicaceae	37

Table C.1: The number of records for the plant species included in the analyses.

Species	Family	Number of Records
Carex acutiformis	Brassicaceae	27
Carex caryophyllea	Brassicaceae	27
Carex hirta	Caprifoliaceae	25
Carex panicea	Caprifoliaceae	25
Carlina vulgaris	Caryophyllaceae	24
Centaurea scabiosa	Caryophyllaceae	50
Cerastium fontanum	Caryophyllaceae	36
Chamerion angustifolium	Caryophyllaceae	70
Chelidonium majus	Cistaceae	37
Circaea lutetiana	Cyperaceae	30
Cirsium vulgare	Cyperaceae	43
Clinopodium vulgare	Cyperaceae	28
Conium maculatum	Cyperaceae	37
Cymbalaria muralis	Dennstaedtiaceae	28
Cynosurus cristatus	Dryopteridaceae	36
Daucus carota subsp. carota	Dryopteridaceae	45
Deschampsia cespitosa	Euphorbiaceae	23
Deschampsia flexuosa	Fabaceae	29

Table C.1: The number of records for the plant species included in the analyses.

Species	Family	Number of Records
Dryopteris dilatata	Fabaceae	20
Dryopteris filix-mas	Fabaceae	26
Epilobium ciliatum	Fabaceae	27
Epilobium hirsutum	Fabaceae	29
Epilobium montanum	Fabaceae	31
Eupatorium cannabinum	Hypericaceae	37
Festuca arundinacea	Hypericaceae	26
Festuca gigantea	Iridaceae	27
Festuca rubra	Junaceae	33
Filipendula ulmaria	Junaceae	57
Galium odoratum	Junaceae	33
Galium saxatile	Junaceae	22
Glechoma hederacea	Lamiaceae	48
Gymnadenia conopsea	Lamiaceae	24
Helianthemum nummularium	Lamiaceae	30
Heracleum sphondylium	Lamiaceae	29
Hesperis matronalis	Lamiaceae	27
Hypericum hirsutum	Lamiaceae	41

Table C.1: The number of records for the plant species included in the analyses.

Species	Family	Number of Records
Hypericum perforatum	Lamiaceae	32
Iris pseudacorus	Lamiaceae	35
Juncus effusus	Lamiaceae	20
Juncus inflexus	Lamiaceae	27
Lamium album	Lamiaceae	47
Lapsana communis	Malvaceae	49
Leontodon hispidus	Onagraceae	41
Linaria vulgaris	Onagraceae	47
Lonicera periclymenum	Onagraceae	47
Lotus corniculatus	Onagraceae	55
Luzula campestris	Onagraceae	27
Luzula pilosa	Orchidaceae	28
Lycopus europaeus	Orchidaceae	22
Malva sylvestris	Oxalidaceae	66
Medicago lupulina	Papaveraceae	53
Melica uniflora	Plantaginaceae	29
Mentha aquatica	Plantaginaceae	28
Mentha arvensis	Plantaginaceae	31

Table C.1: The number of records for the plant species included in the analyses.

Species	Family	Number of Records
Mercurialis perennis	Plantaginaceae	69
Milium effusum	Plantaginaceae	21
Mycelis muralis	Plantaginaceae	35
Ononis repens	Poaceae	42
Origanum vulgare	Poaceae	42
Oxalis acetosella	Poaceae	36
Pentaglottis sempervirens	Poaceae	29
Plantago lanceolata	Poaceae	39
Plantago major	Poaceae	34
Poa nemoralis	Poaceae	31
Poa pratensis	Poaceae	32
Poa trivialis	Poaceae	29
Polygala serpyllifolia	Poaceae	25
Polygala vulgaris	Poaceae	30
Polygonum aviculare	Poaceae	37
Potentilla anserina	Poaceae	48
Potentilla erecta	Poaceae	45
Potentilla reptans	Poaceae	21

Table C.1: The number of records for the plant species included in the analyses.

Species	Family	Number of Records
Prunella vulgaris	Poaceae	38
Pteridium aquilinum	Poaceae	25
Ranunculus acris	Poaceae	42
Ranunculus repens	Poaceae	33
Reseda luteola	Poaceae	30
Rubus caesius	Poaceae	30
Rubus idaeus	Polygalaceae	29
Rumex acetosa	Polygalaceae	39
Rumex acetosella	Polygonaceae	28
Rumex crispus	Polygonaceae	40
Scabiosa columbaria	Polygonaceae	24
Scrophularia nodosa	Polygonaceae	23
Senecio squalidus	Primulaceae	55
Silene dioica	Primulaceae	44
Silene vulgaris	Ranunculaceae	40
Solanum dulcamara	Ranunculaceae	37
Sonchus arvensis	Ranunculaceae	31
Stachys officinalis	Resedaceae	28

Table C.1: The number of records for the plant species included in the analyses.

Species	Family	Number of Records
Stachys sylvatica	Rosaceae	40
Stellaria graminea	Rosaceae	22
Symphytum officinale	Rosaceae	30
Tanacetum parthenium	Rosaceae	35
Tragopogon pratensis	Rosaceae	56
Trifolium pratense	Rosaceae	34
Trifolium repens	Rosaceae	42
Trisetum flavescens	Rubiaceae	29
Urtica dioica	Rubiaceae	42
Verbascum thapsus	Scrophulariaceae	22
Veronica beccabunga	Scrophulariaceae	25
Veronica chamaedrys	Solanaceae	35
Vicia cracca	Urticaceae	33
Viola hirta	Violaceae	32
Viola odorata	Violaceae	46
Viola riviniana	Violaceae	75

C.2 Trait plots

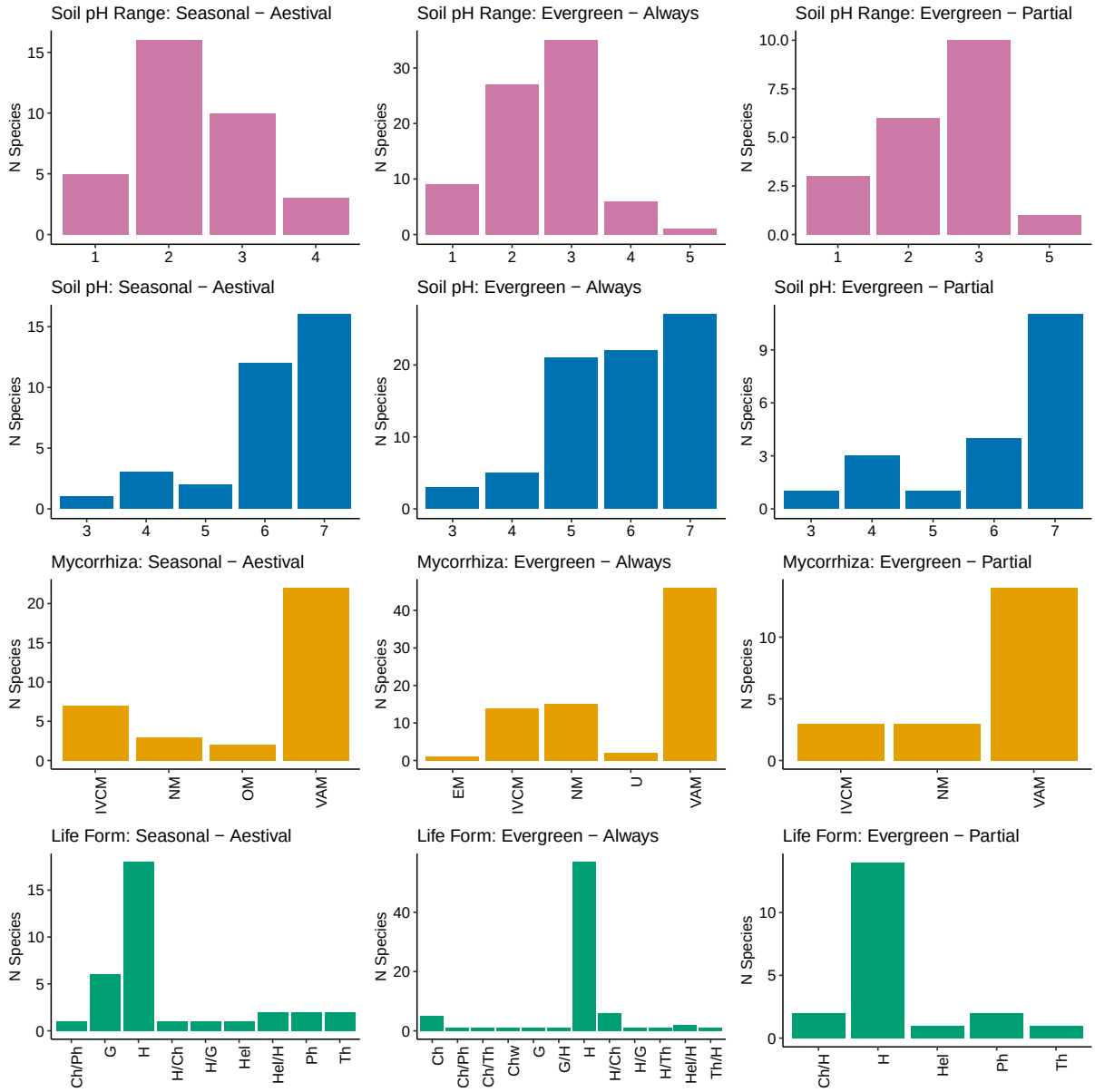


Figure C.1: The number of species for each of the life history traits categories for all herbaceous perennial species included in the analyses. Mycorrhiza plot: IVCM = Intermediate VA mycorrhiza; NM = No mycorrhiza; OM = Orchid mycorrhiza; VAM = Vesicular-Arbuscular mycorrhiza; EM = Ectomycorrhiza; U = Uncertain. Life form plot: Ch/Ph = Chamaephyte/Phanerophyte; G = Geophyte; Hel = Helophyte; H = Hemicryptophyte; H/Ch = Hemicryptophyte/Chamaephyte; H/Hel = Hemicryptophyte/Helophyte; Ph = Phanerophyte; Th = Therophyte; Ch = Chamaephyte; Chw = Chamaephyte (woody); Ch/Th = Chamaephyte/Therophyte; G/H = Geophyte/Hemicryptophyte; H/Th = Hemicryptophyte/Therophyte; Th/H = Therophyte/Hemicryptophyte; Ch/H = Chamaephyte/Hemicryptophyte.

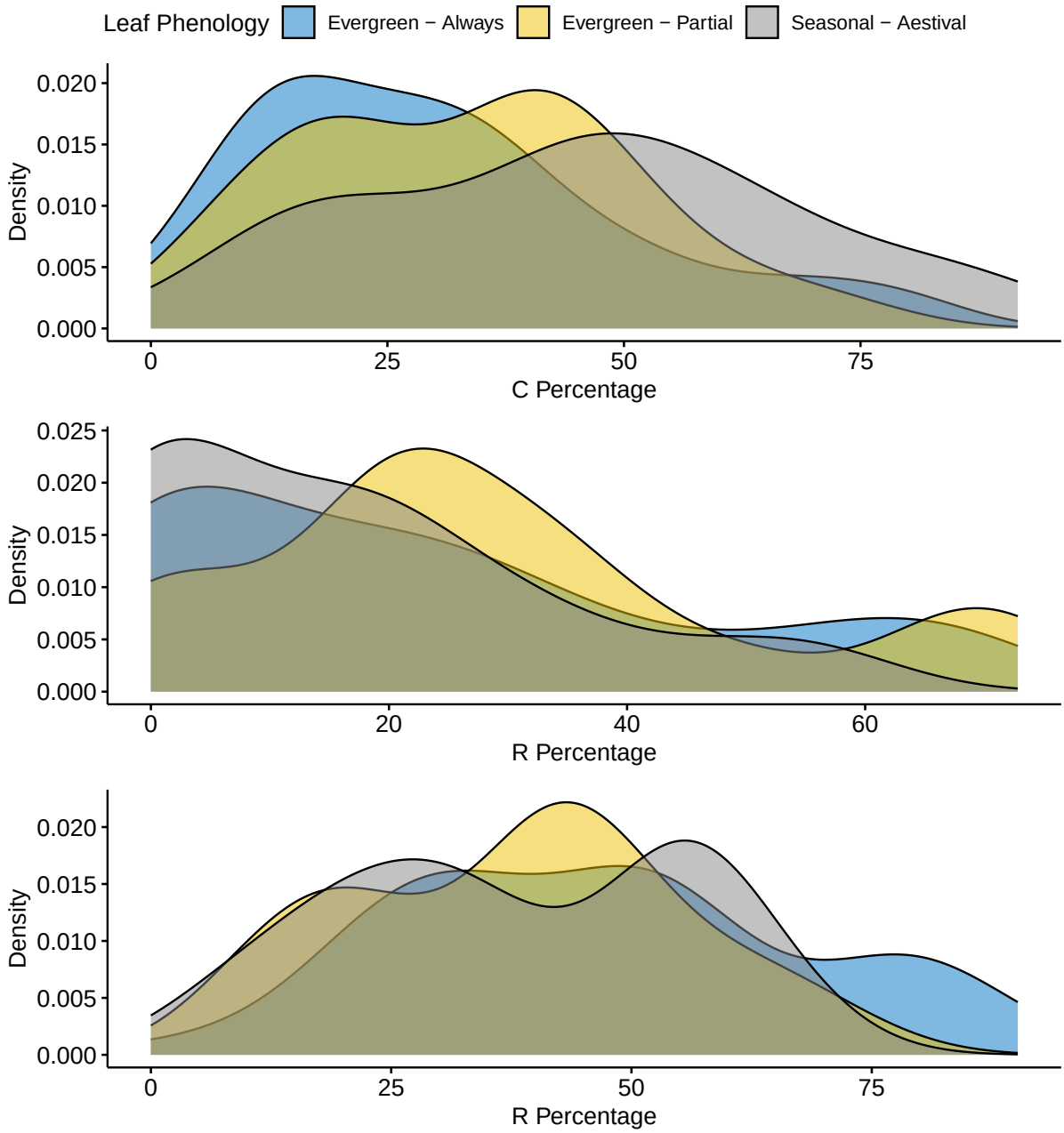


Figure C.2: The density distribution of the C, S and R percentages for each of the three Leaf Phenology categories.

C.3 ACF plots

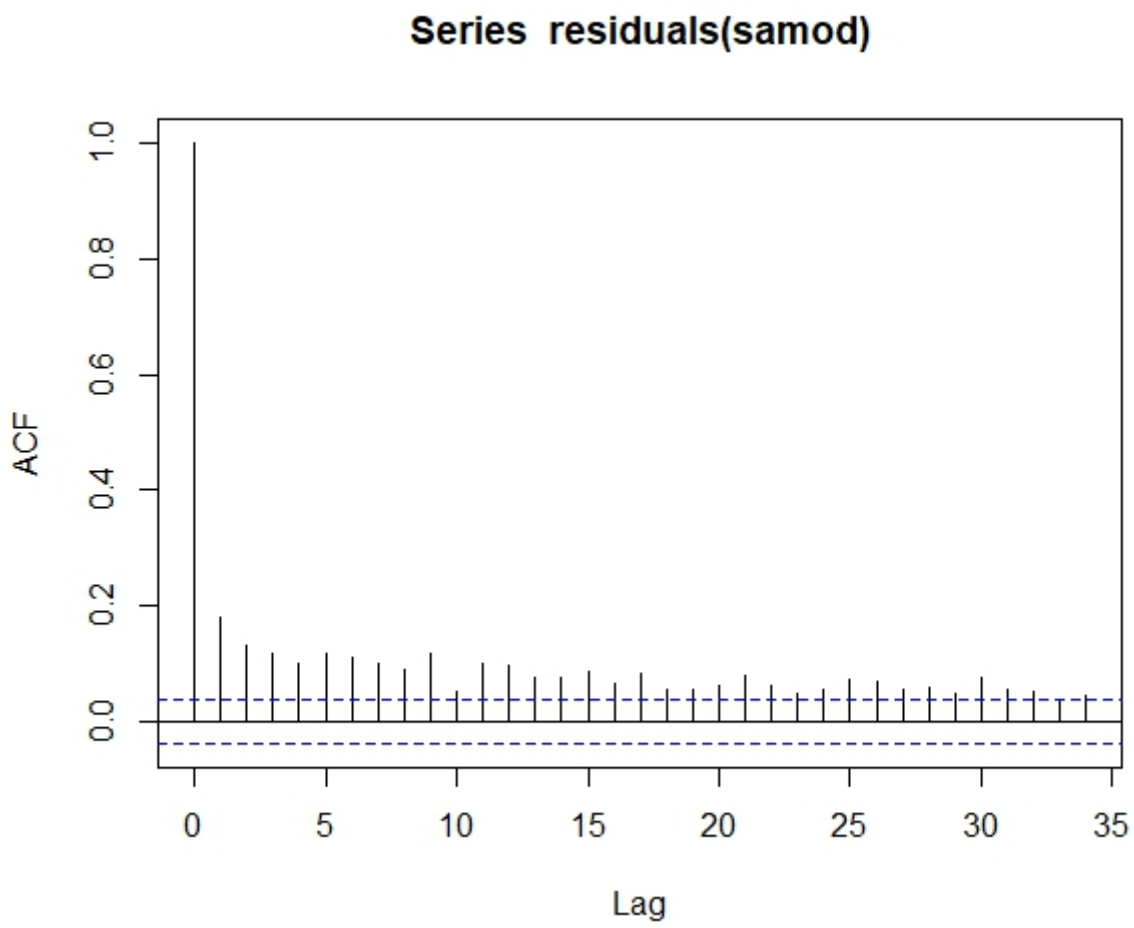


Figure C.3: The autocovariance and autocorrelation of the Seasonal Aestival model: first flowering $\sim$ Year $+$ Cumulative Mean Temperature, random effects $=$ Watsonian Vice County nexted in plant species.

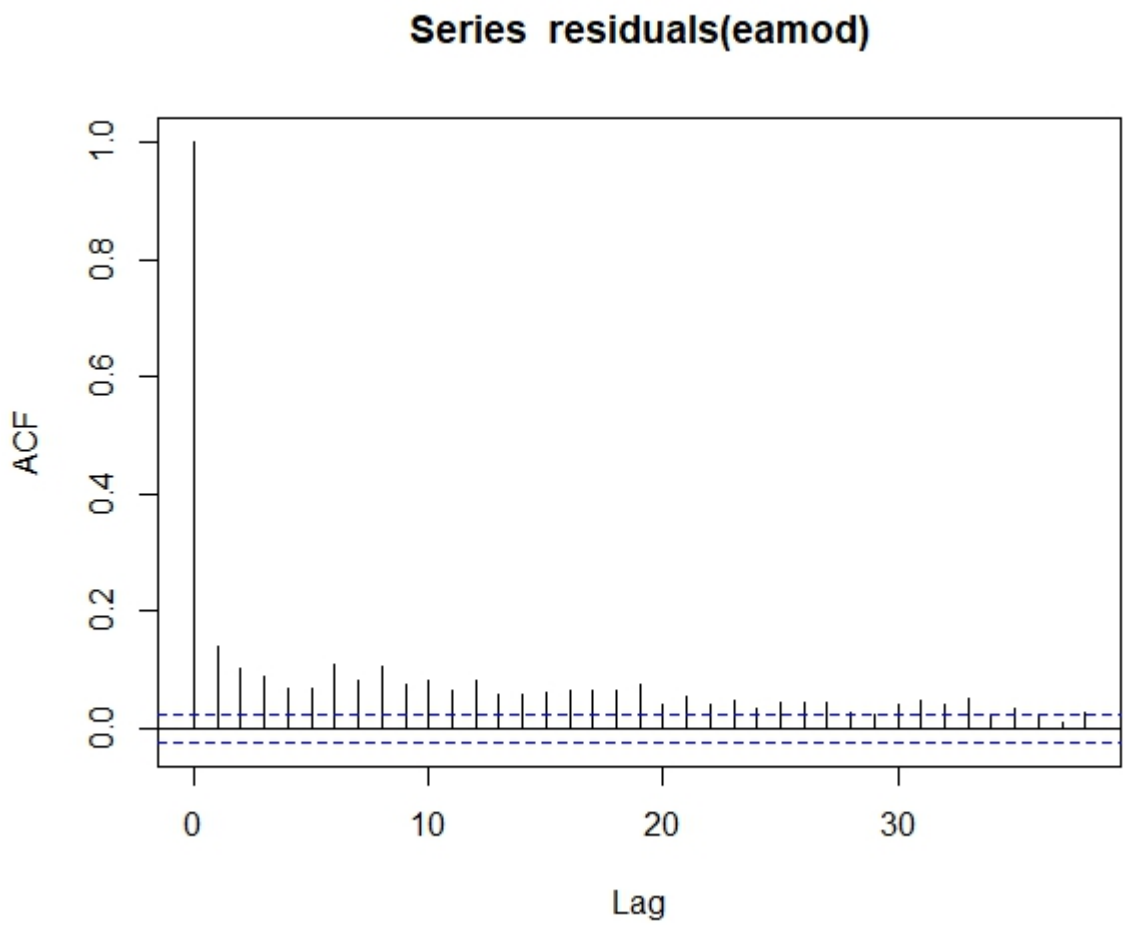


Figure C.4: The autocovariance and autocorrelation of the Evergreen Always model: first flowering ~ Cumulative Mean Temperature, random effects = Watsonian Vice County nexted in plant species.

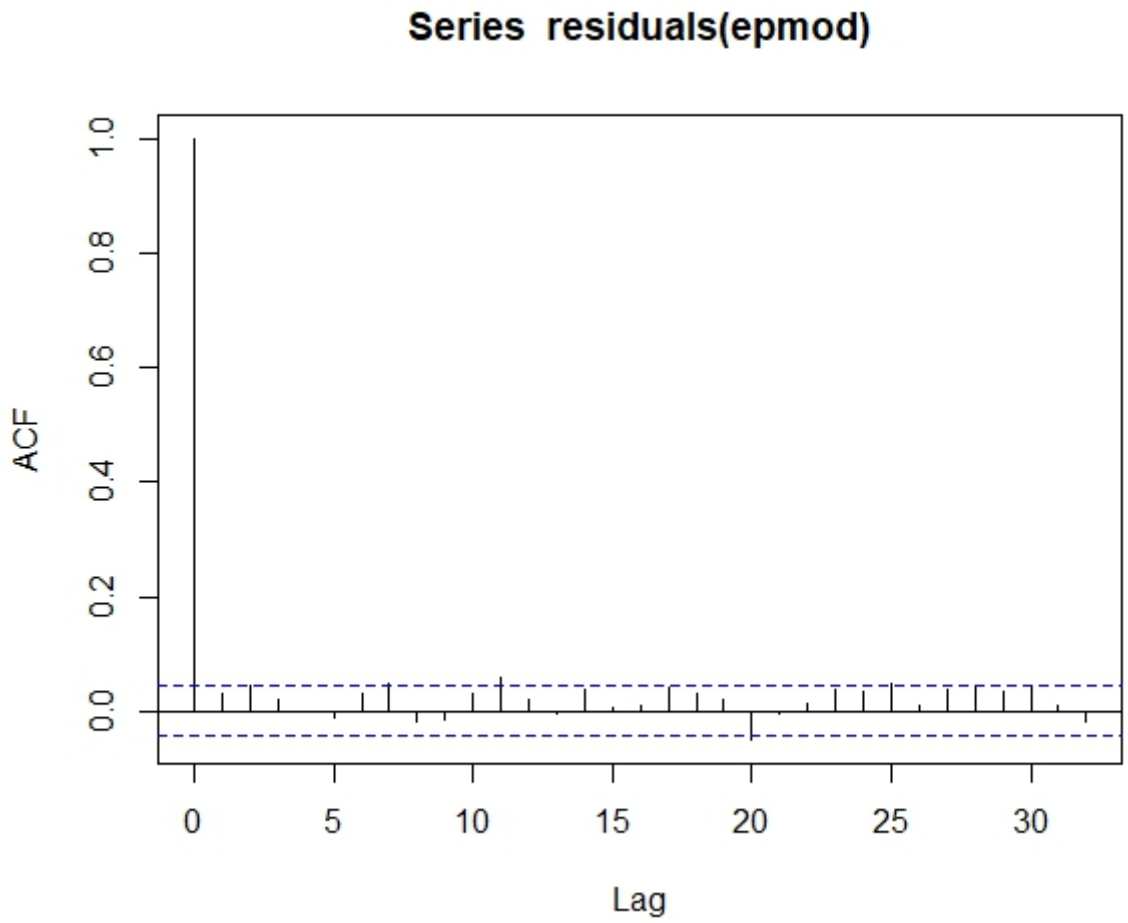


Figure C.5: The autocovariance and autocorrelation of the Evergreen Partial model: first flowering ~ Year + Cumulative Mean Temperature, random effects = Watsonian Vice County nexted in plant species

Appendix D

Chapter 5: Results tables and maps

D.1 Larva results tables

D.1.1 Oligophagous (Family): Lunar underwing (*Omphaloscelis lunosa*). Foodplant: Yorkshire fog (*Holcus lanatus*).

Table D.1: Omphaloscelis lunosa: First Emergence ~ 1 + Year + Cumulative Mean Temperature + f(Watsonian Vice County, model=bym, graph=vc adj)

Variables	mean	sd	0.025quant	0.5quant	0.975quant
(Intercept)	245.010	4.200	236.768	245.010	253.252
Year	-0.035	0.032	-0.098	-0.035	0.028
Cumulative Mean Temperature	0.774	0.289	0.207	0.774	1.340

Table D.2: Omphaloscelis lunosa: Peak Emergence ~ 1 + Year + Cumulative Mean Temperature

Variables	mean	sd	0.025quant	0.5quant	0.975quant
(Intercept)	256.527	5.158	246.406	256.527	266.648
Year	0.071	0.050	-0.026	0.071	0.168
Cumulative Mean Temperature	0.894	0.355	0.197	0.894	1.591

Table D.3: Omphaloscelis lunosa: Emergence SD ~ 1 + Year + f(Watsonian Vice County, model=bym, graph=vc adj)

Variables	mean	sd	0.025quant	0.5quant	0.975quant
(Intercept)	10.397	0.478	9.459	10.396	11.337
Year	0.033	0.031	-0.027	0.033	0.094

Table D.4: Holcus lanatus: First Flowering ~ 1 + Year + Cumulative Mean Temperature

Variables	mean	sd	0.025quant	0.5quant	0.975quant
(Intercept)	189.387	4.201	181.147	189.387	197.627
Year	-0.059	0.056	-0.170	-0.059	0.051
Cumulative Mean Temperature	-2.752	0.299	-3.339	-2.752	-2.165

D.1.2 Polyphagous: Lesser Broad-bordered Yellow Underwing (*Noctua janthe*). Foodplants: Blackthorn (*Prunus spinosa*) and Primrose (*Primula vulgaris*).

Table D.5: Noctua janthe: First Emergence ~ 1 + Year + Cumulative Mean Temperature + f(Watsonian Vice County, model=bym, graph=vc adj)

Variables	mean	sd	0.025quant	0.5quant	0.975quant
(Intercept)	229.587	3.259	223.236	229.572	236.023
Year	-0.262	0.024	-0.309	-0.262	-0.214
Cumulative Mean Temperature	-1.303	0.235	-1.768	-1.302	-0.845

Table D.6: Noctua janthe: Peak Emergence ~ 1 + Year + Cumulative Mean Temperature + f(Watsonian Vice County, model=bym, graph=vc adj)

Variables	mean	sd	0.025quant	0.5quant	0.975quant
(Intercept)	236.916	2.315	232.378	236.915	241.456
Year	0.106	0.016	0.075	0.106	0.137
Cumulative Mean Temperature	-0.988	0.168	-1.317	-0.988	-0.658

Table D.7: Noctua janthe: Emergence SD ~ 1 + Year + f(Watsonian Vice County, model=bym, graph=vc adj)

Variables	mean	sd	0.025quant	0.5quant	0.975quant
(Intercept)	12.826	0.315	12.207	12.826	13.446
Year	0.082	0.012	0.059	0.082	0.105

Table D.8: Prunus spinosa: First Flowering ~ 1 + Year + Cumulative Mean Temperature

Variables	mean	sd	0.025quant	0.5quant	0.975quant
(Intercept)	180.890	3.889	173.262	180.889	188.517
Year	0.180	0.046	0.090	0.180	0.269
Cumulative Mean Temperature	-7.446	0.275	-7.985	-7.446	-6.906

Table D.9: Primula vulgaris: First Flowering ~ 1 + Year + Cumulative Mean Temperature

Variables	mean	sd	0.025quant	0.5quant	0.975quant
(Intercept)	156.551	26.797	103.975	156.552	209.120
Year	-1.493	0.501	-2.475	-1.493	-0.511
Cumulative Mean Temperature	-4.763	1.919	-8.529	-4.763	-0.997

D.2 Pupa results tables

D.2.1 Oligophagous (Family): Clouded border (*Lomaspilis marginata*). Foodplant: Hazel (*Corylus avellana*).

Table D.10: Lomaspilis marginata: First Emergence ~ 1 + Year + Cumulative Mean Temperature + f(Watsonian Vice County, model=bym, graph=vc adj)

Variables	mean	sd	0.025quant	0.5quant	0.975quant
(Intercept)	231.977	5.215	221.757	231.977	242.198
Year	-0.186	0.068	-0.320	-0.186	-0.052
Cumulative Mean Temperature	-4.733	0.368	-5.454	-4.733	-4.012

Table D.11: Lomaspilis marginata: Peak Emergence ~ 1 + Year + Cumulative Mean Temperature + f(Watsonian Vice County, model=bym, graph=vc adj)

Variables	mean	sd	0.025quant	0.5quant	0.975quant
(Intercept)	231.967	5.242	221.683	231.967	242.252
Year	-0.186	0.069	-0.322	-0.186	-0.051
Cumulative Mean Temperature	-4.732	0.370	-5.457	-4.732	-4.007

Table D.12: Lomaspilis marginata: Emergence SD ~ 1 + Year + f(Watsonian Vice County, model=bym, graph=vc adj)

Variables	mean	sd	0.025quant	0.5quant	0.975quant
(Intercept)	22.032	0.487	21.076	22.032	22.988
Year	-0.063	0.026	-0.114	-0.063	-0.013

Table D.13: Corylus avellana: First Flowering ~ 1 + Year + Cumulative Mean Temperature

Variables	mean	sd	0.025quant	0.5quant	0.975quant
(Intercept)	245.010	4.200	236.768	245.010	253.252
Year	-0.035	0.032	-0.098	-0.035	0.028
Cumulative Mean Temperature	0.774	0.289	0.207	0.774	1.340

D.2.2 Polyphagous: Buff Ermine (*Spilosoma lutea*). Foodplants: Blackthorn (*Prunus spinosa*) and Ivy (*Hedera helix*).

Table D.14: Spilosoma lutea: First Emergence ~ 1 + Year + Cumulative Mean Temperature + f(Watsonian Vice County, model=bym, graph=vc adj)

Variables	mean	sd	0.025quant	0.5quant	0.975quant
(Intercept)	198.000	5.943	186.411	197.978	209.718
Year	-0.141	0.052	-0.242	-0.141	-0.040
Cumulative Mean Temperature	-2.977	0.422	-3.808	-2.975	-2.154

Table D.15: Spilosoma lutea: Peak Emergence ~ 1 + Year + Cumulative Mean Temperature + f(Watsonian Vice County, model=bym, graph=vc adj)

Variables	mean	sd	0.025quant	0.5quant	0.975quant
(Intercept)	211.046	5.174	200.882	211.051	221.187
Year	0.545	0.043	0.461	0.545	0.630

Table D.15: Spilosoma lutea: Peak Emergence ~ 1 + Year + Cumulative Mean Temperature + f(Watsonian Vice County, model=bym, graph=vc adj)

Variables	mean	sd	0.025quant	0.5quant	0.975quant
Cumulative Mean Temperature	-3.025	0.370	-3.750	-3.025	-2.297

Table D.16: Spilosoma lutea: Emergence SD ~ 1 + Year + f(Watsonian Vice County, model=bym, graph=vc adj)

Variables	mean	sd	0.025quant	0.5quant	0.975quant
(Intercept)	15.706	0.489	14.745	15.706	16.666
Year	0.199	0.019	0.161	0.199	0.237

see *Prunus spinosa* table under Lesser broad bordered yellow underwing - same analysis

Table D.17: Hedera helix: First Flowering ~ 1 + Year + Cumulative Mean Temperature

Variables	mean	sd	0.025quant	0.5quant	0.975quant
(Intercept)	336.851	4.785	327.464	336.851	346.237
Year	-0.072	0.060	-0.191	-0.072	0.046
Cumulative Mean Temperature	-4.961	0.340	-5.628	-4.961	-4.294

Table D.18: Spilosoma lutea and Hedera helix: Peak Emergence minus First Flowering ~ 1 + Year + f(Watsonian Vice County, model=bym, graph=vc adj)

Variables	mean	sd	0.025quant	0.5quant	0.975quant
(Intercept)	-102.303	1.240	-104.740	-102.302	-99.873
Year	0.851	0.068	0.718	0.851	0.983

D.3 Larva spatial model maps

D.3.1 Oligophagous (Family): Lunar underwing (*Omphaloscelis lunosa*)

D.3.1.1 First Emergence

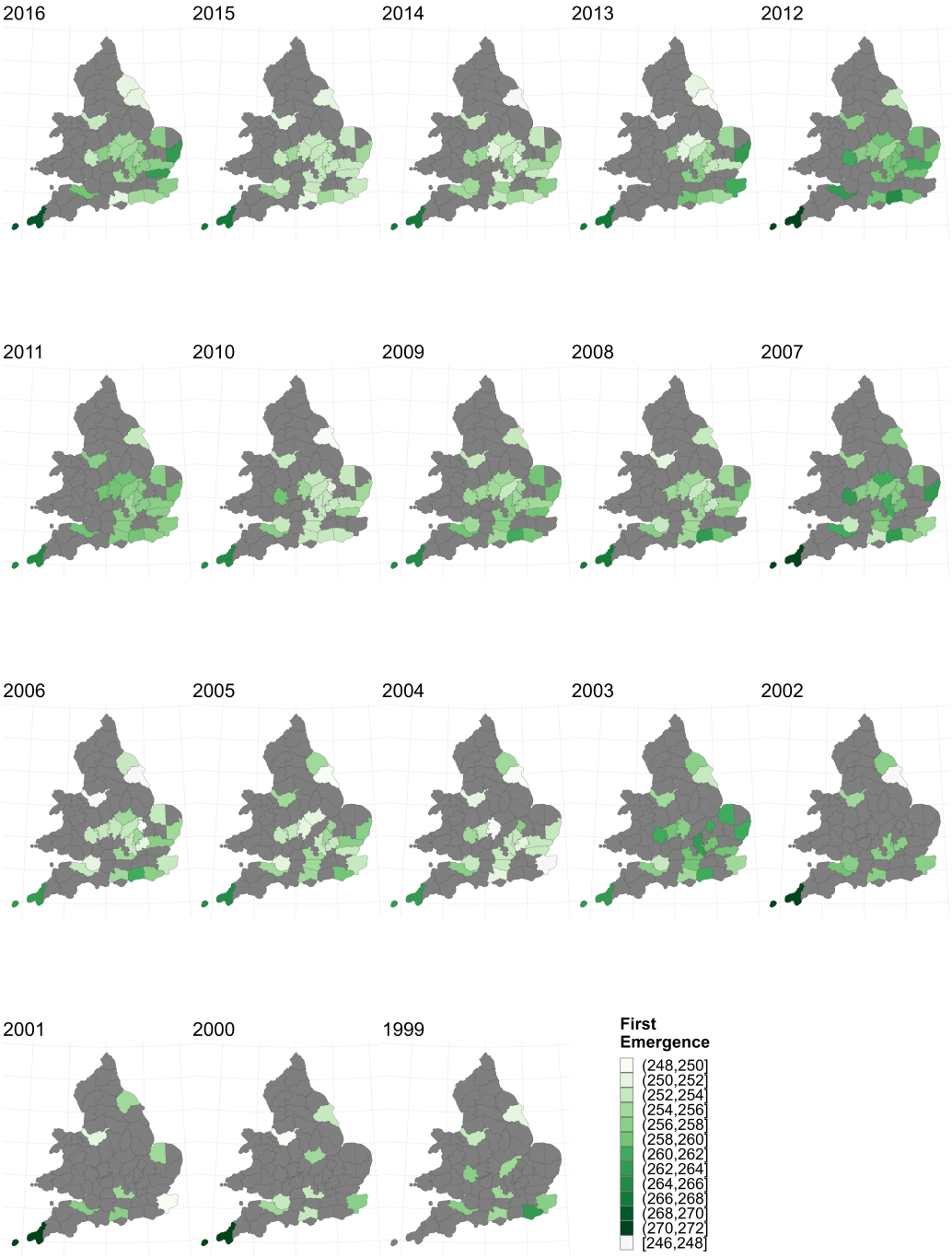


Figure D.1: Omphaloscelis lunosa First Emergence day of year: First Emergence ~ 1 + Year + Cumulative Mean Temperature + f(Watsonian Vice County, model=bym, graph=vc adj)

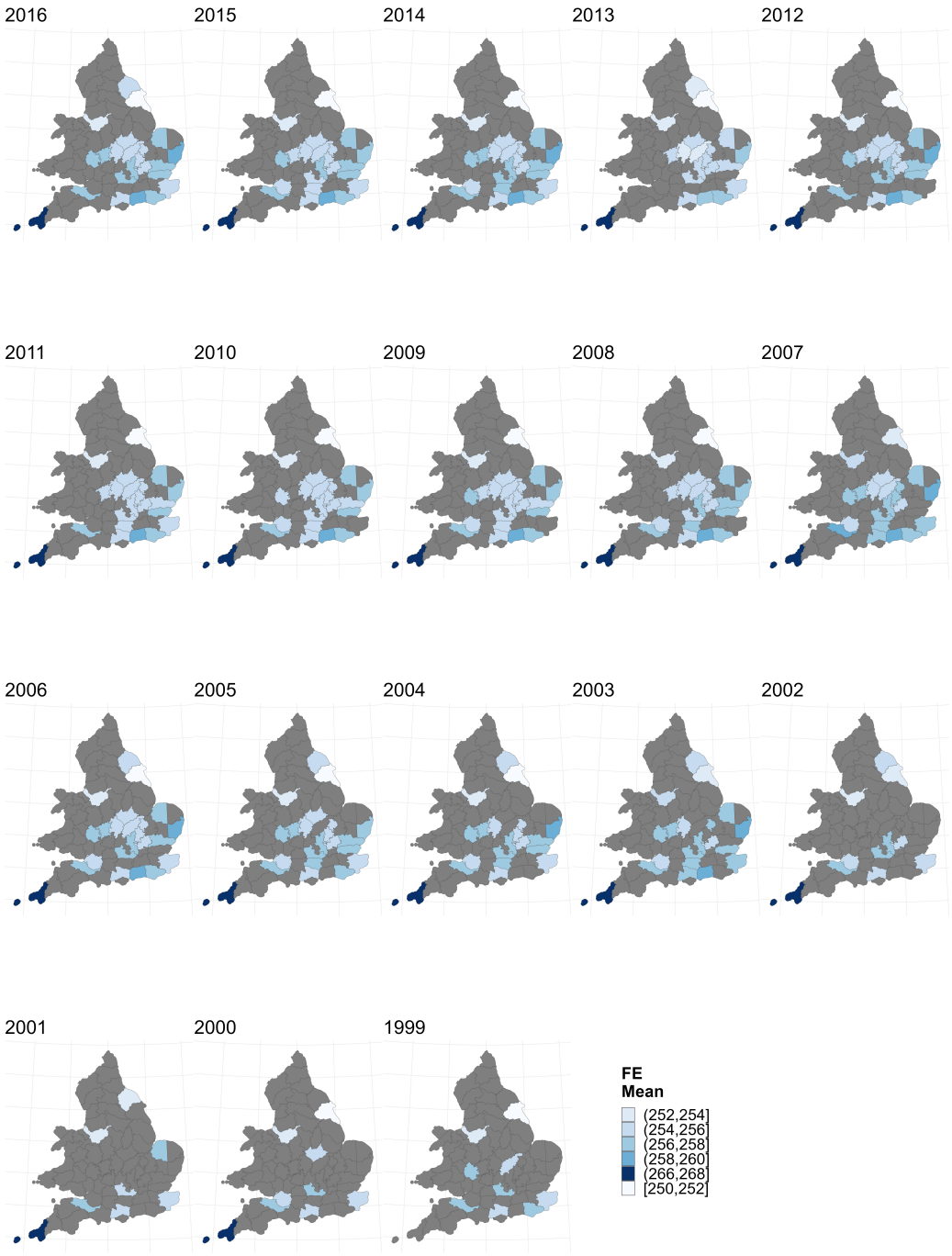


Figure D.2: Omphaloscelis lunosa First Emergence mean day of year from model: First Emergence ~ 1 + Year + Cumulative Mean Temperature + f(Watsonian Vice County, model=bym, graph=vc adj)

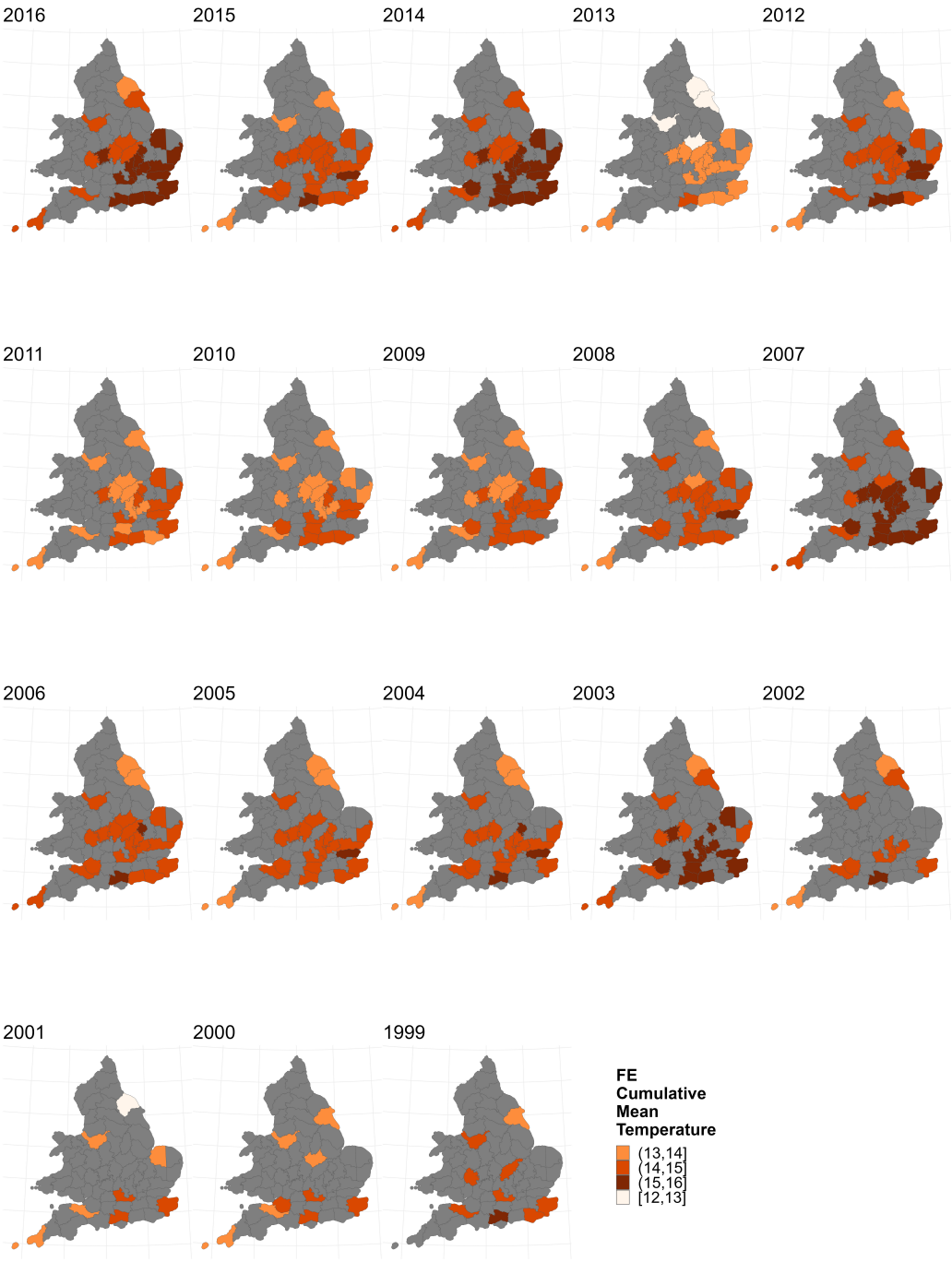


Figure D.3: Omphaloscelis lunosa First Emergence day of year cumulative mean temperature: First Emergence ~ 1 + Year + Cumulative Mean Temperature + f(Watsonian Vice County, model=bym, graph=vc adj)

D.3.1.2 Emergence SD



Figure D.4: Omphaloscelis lunosa Emergence SD: Emergence SD ~ 1 + Year + f(Watsonian Vice County, model=bym, graph=vc adj)

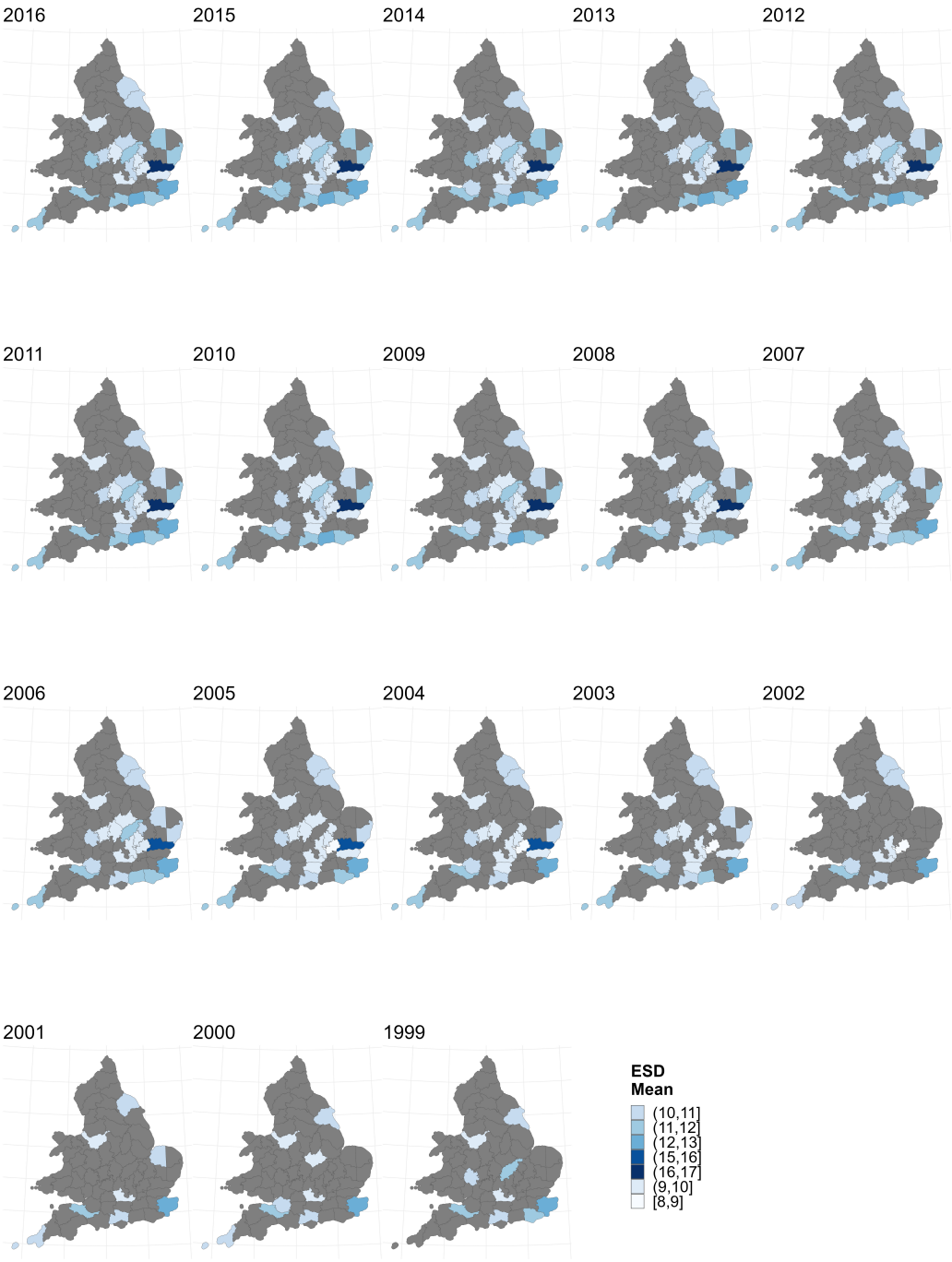


Figure D.5: Omphaloscelis lunosa Emergence SD mean from model: Emergence SD ~ 1 + Year + f(Watsonian Vice County, model=bym, graph=vc adj)

D.3.2 Polyphagous: Lesser Broad-bordered Yellow Underwing (*Noctua janthe*)

D.3.2.1 First Emergence

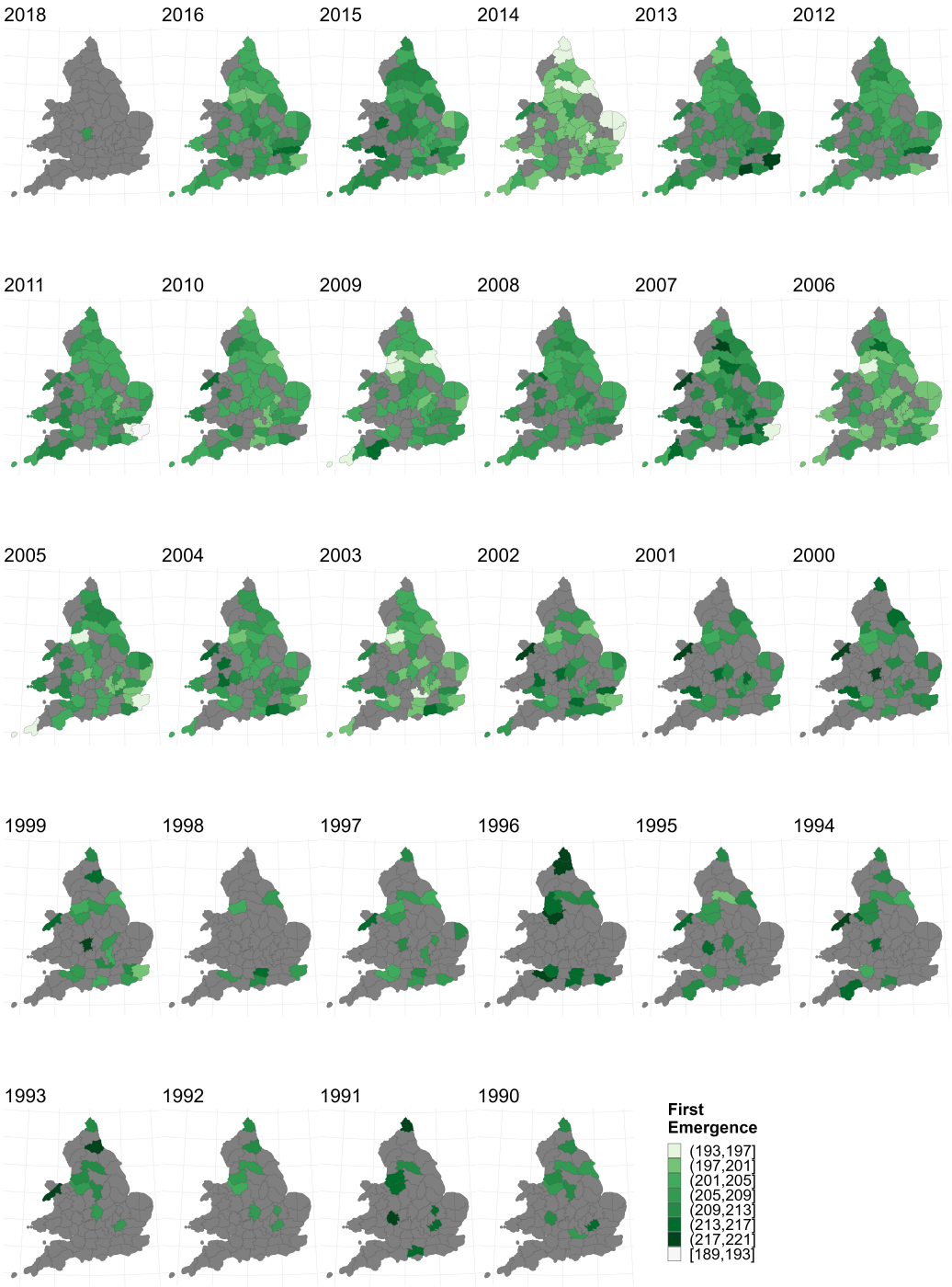


Figure D.6: Noctua janthe First Emergence day of year: First Emergence ~ 1 + Year + Cumulative Mean Temperature + f(Watsonian Vice County, model=bym, graph=vc adj)

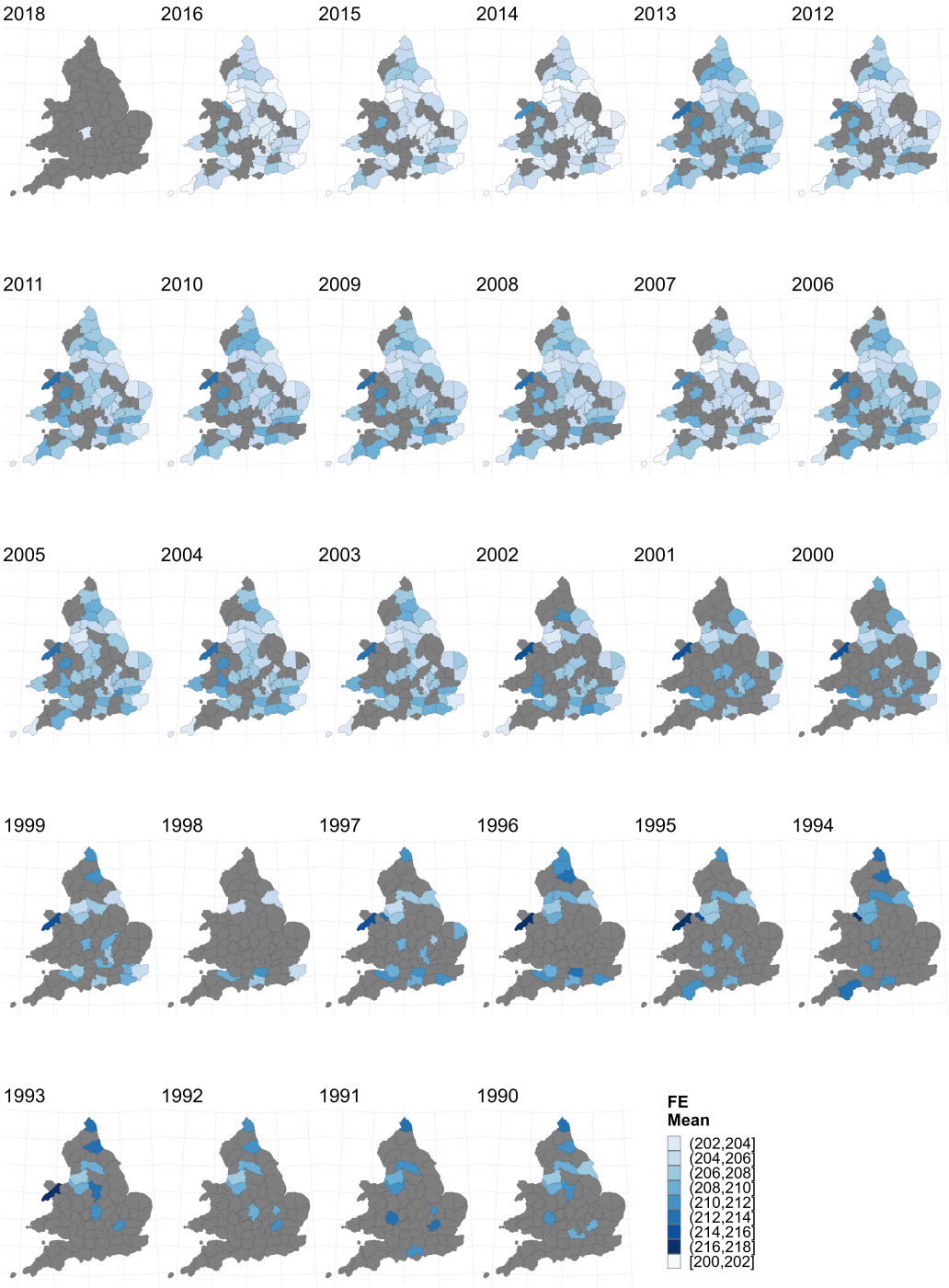


Figure D.7: Noctua janthe First Emergence mean day of year from model: First Emergence ~ 1 + Year + Cumulative Mean Temperature + f(Watsonian Vice County, model=bym, graph=vc adj)

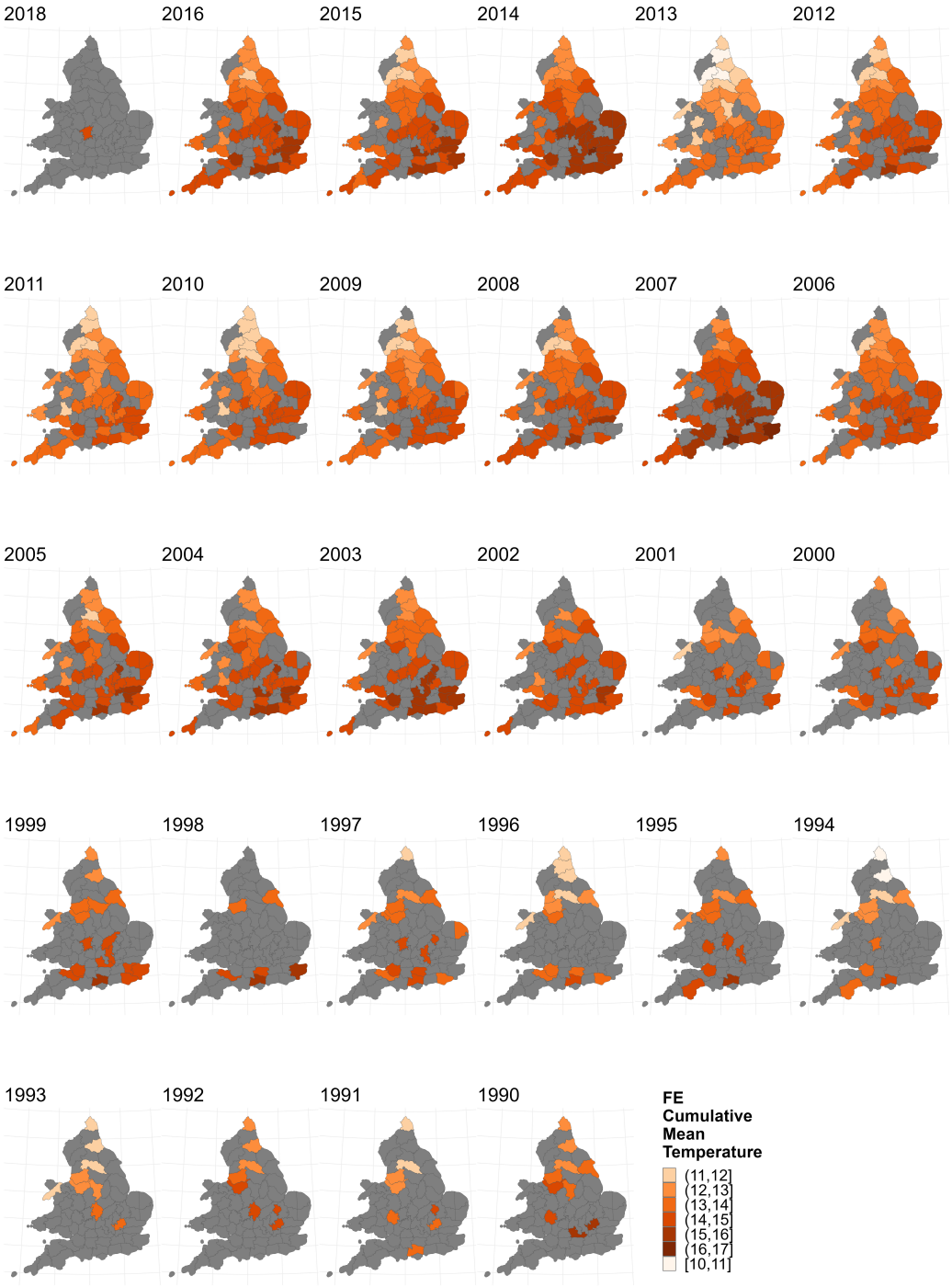


Figure D.8: Noctua janthe First Emergence day of year cumulative mean temperature: First Emergence ~ 1 + Year + Cumulative Mean Temperature + f(Watsonian Vice County, model=bym, graph=vc adj)

D.3.2.2 Peak Emergence

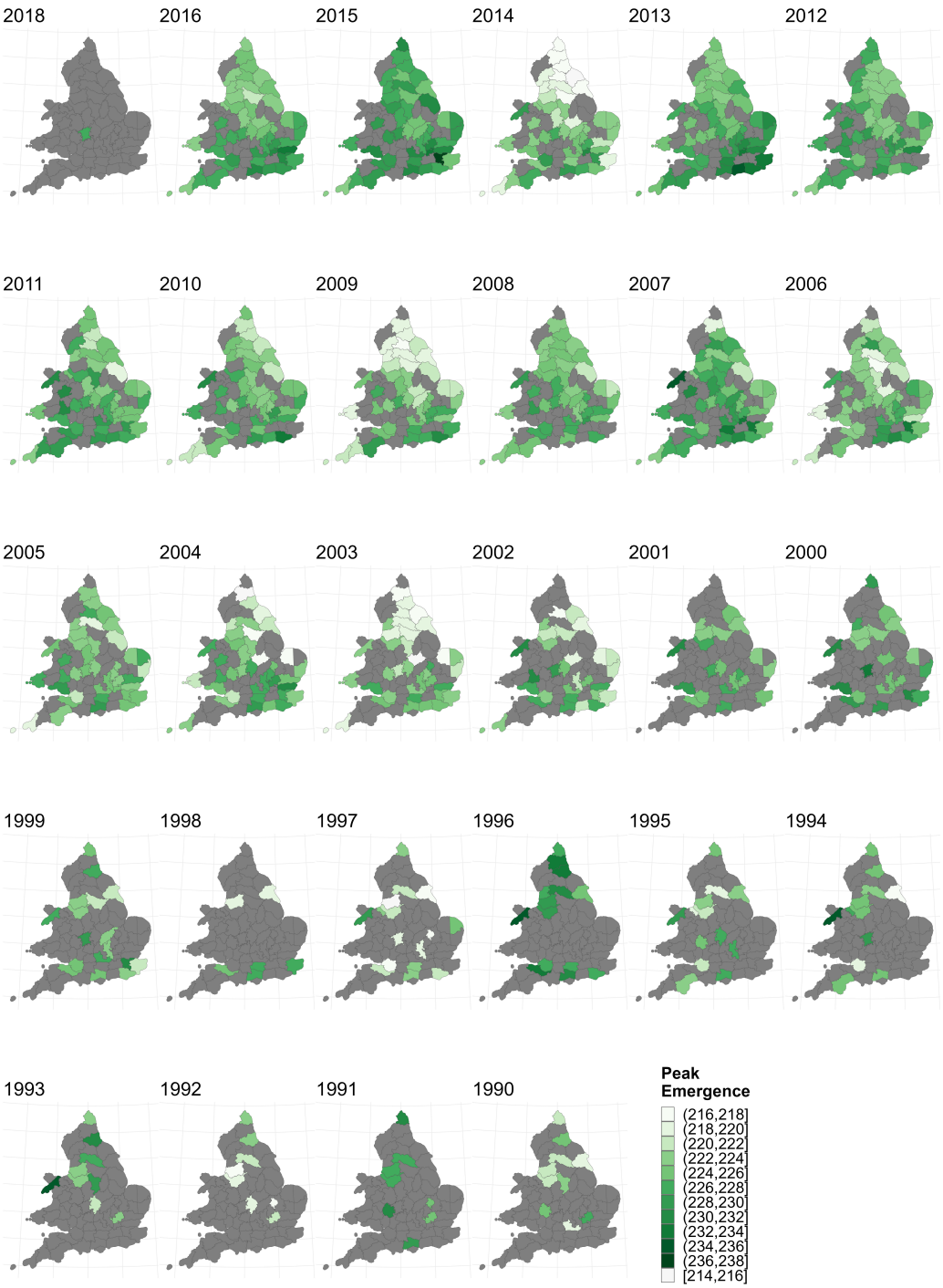


Figure D.9: Noctua janthe Peak Emergence day of year: Peak Emergence ~ 1 + Year + Cumulative Mean Temperature + f(Watsonian Vice County, model=bym, graph=vc adj)

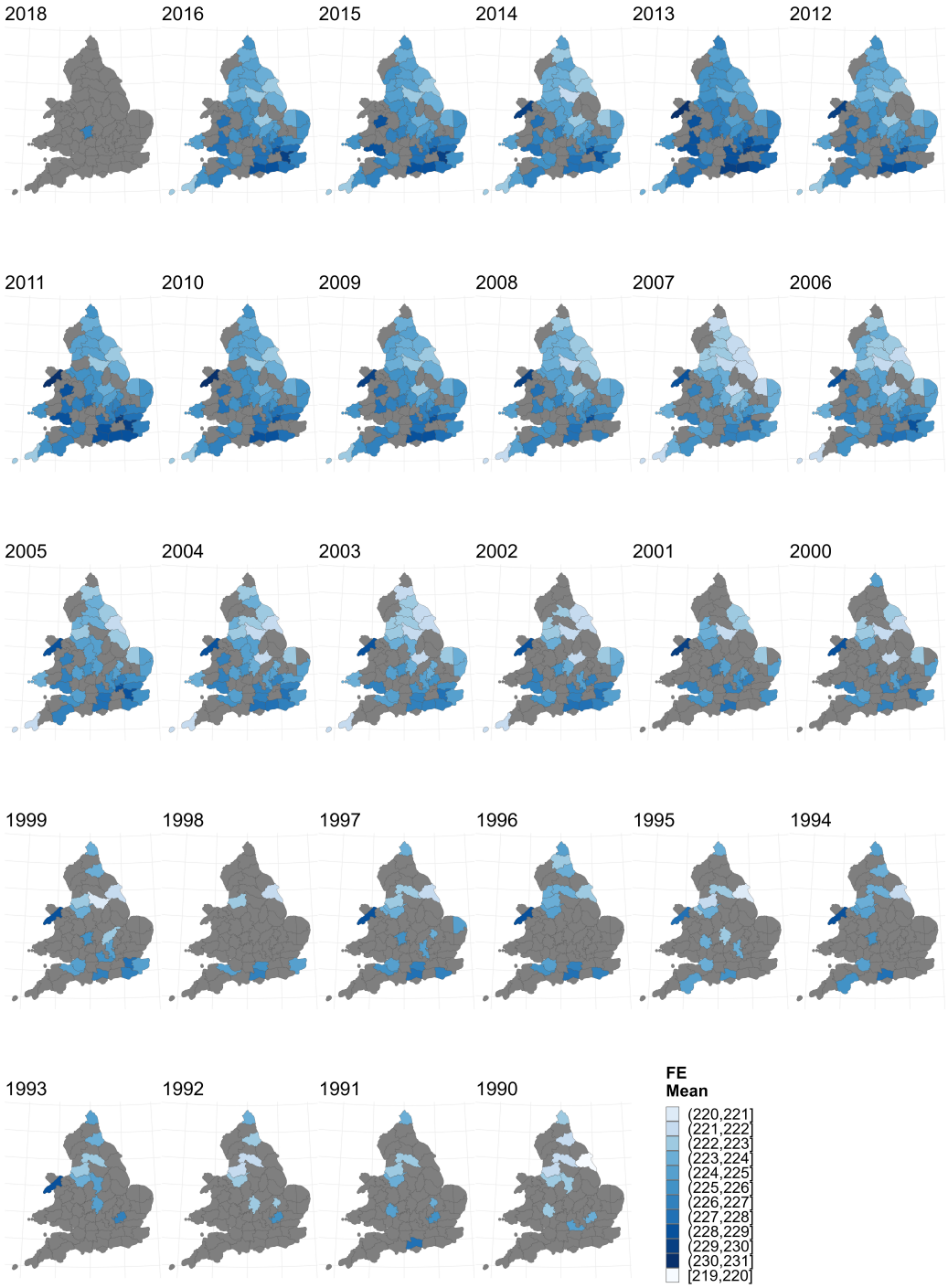


Figure D.10: Noctua janthe Peak Emergence mean day of year from model: Peak Emergence ~ 1 + Year + Cumulative Mean Temperature + f(Watsonian Vice County, model=bym, graph=vc adj)

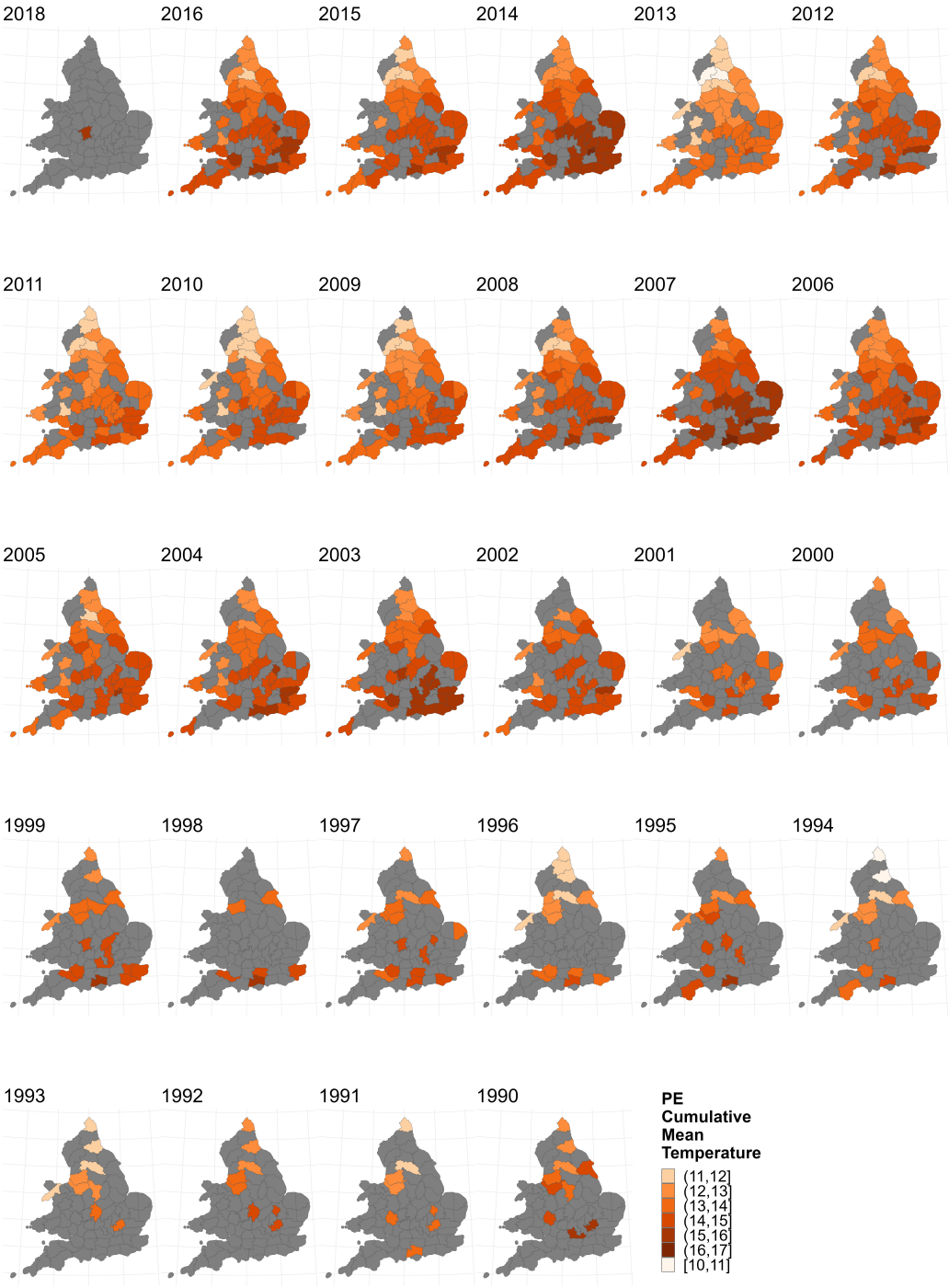


Figure D.11: Noctua janthe Peak Emergence day of year cumulative mean temperature: Peak Emergence ~ 1 + Year + Cumulative Mean Temperature + f(Watsonian Vice County, model=bym, graph=vc adj)

D.3.2.3 Emergence SD

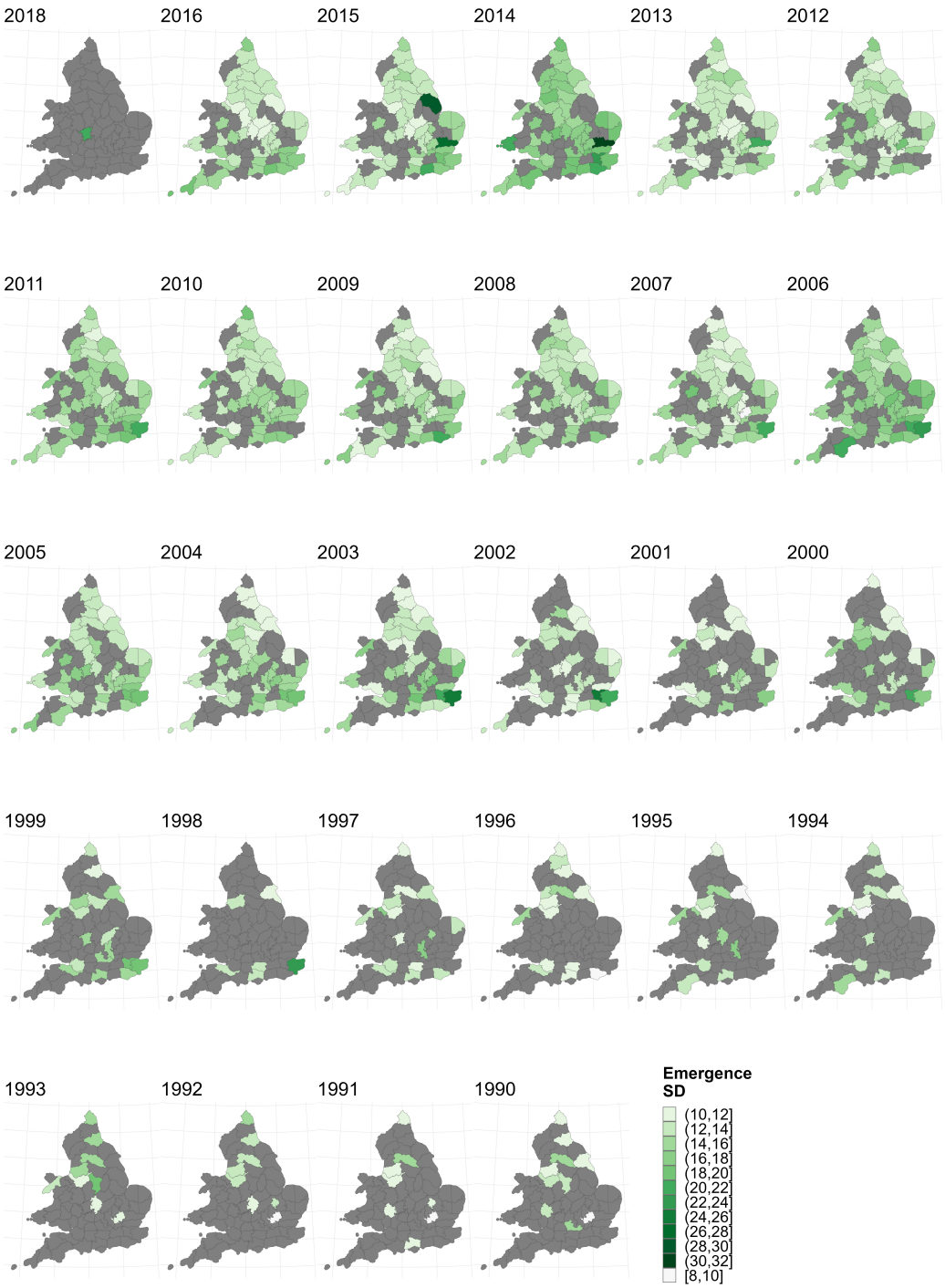


Figure D.12: Noctua janthe Emergence SD: Emergence SD ~ 1 + Year + f(Watsonian Vice County, model=bym, graph=vc adj)

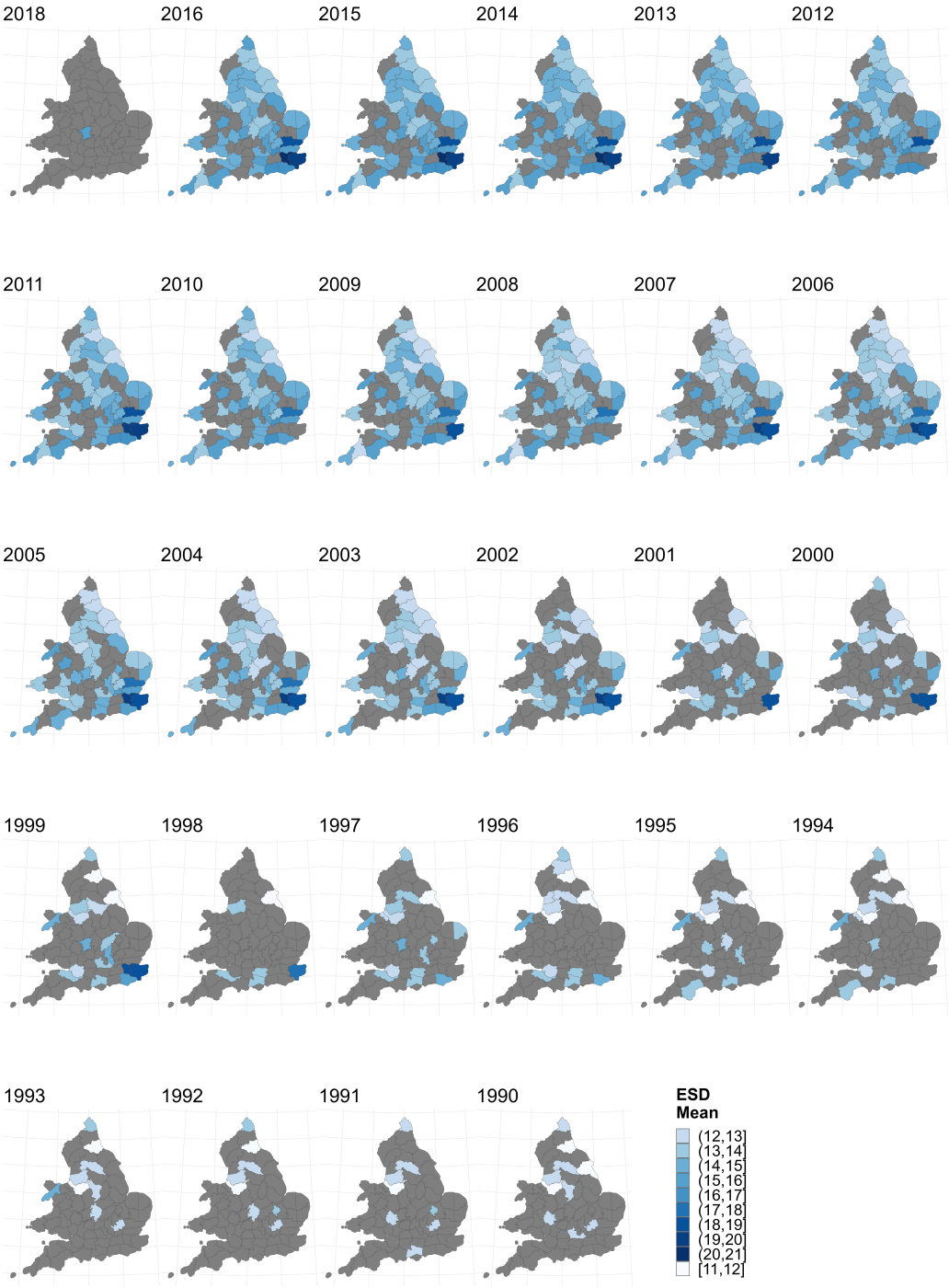


Figure D.13: Noctua janthe Emergence SD mean from model: Emergence SD ~ 1 + Year + f(Watsonian Vice County, model=bym, graph=vc adj)

D.4 Pupa spatial model maps

D.4.1 Oligophagous (Family): Clouded border (*Lomaspilis marginata*)

D.4.1.1 First Emergence

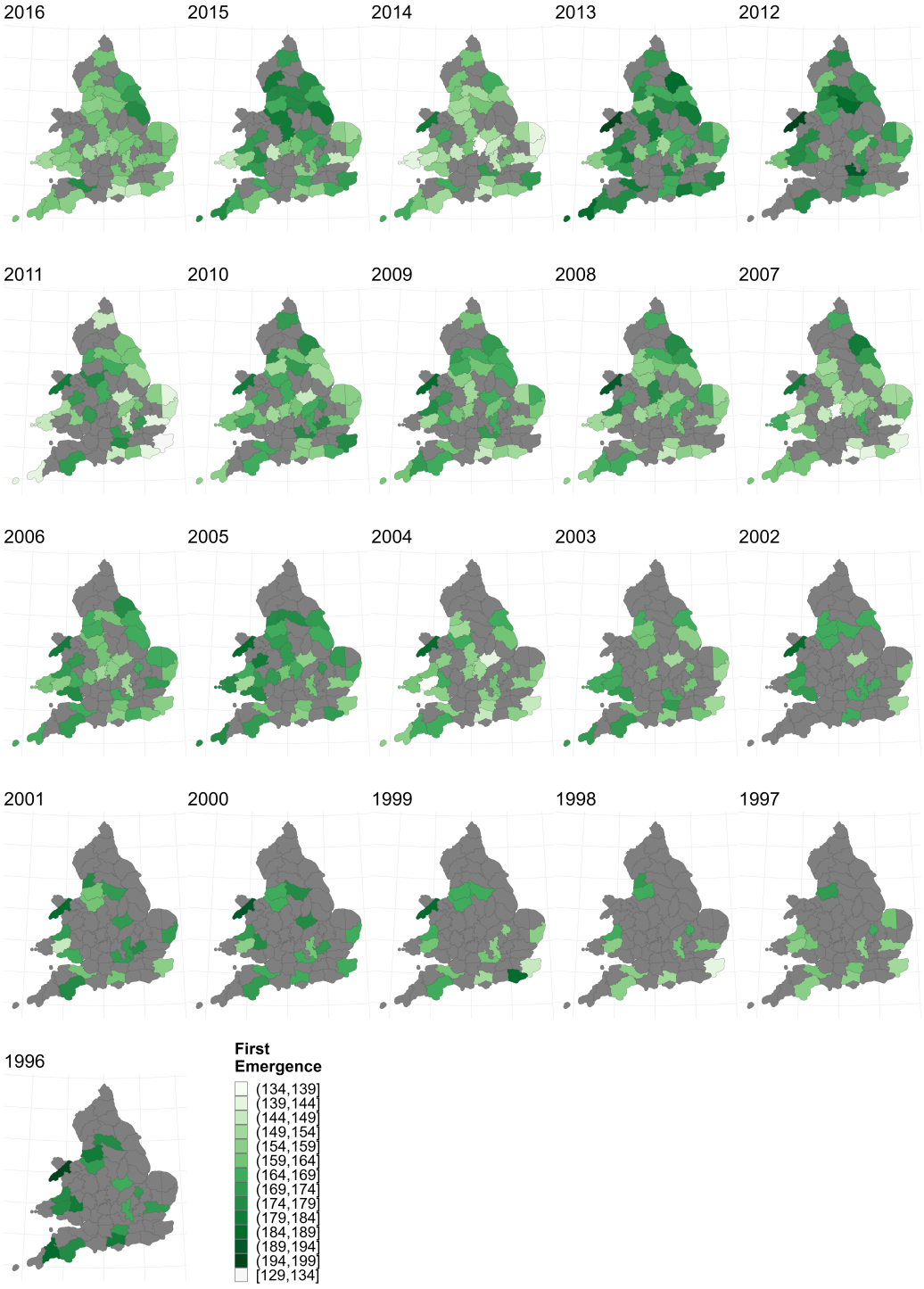


Figure D.14: Lomaspilis marginata First Emergence day of year: First Emergence ~ 1 + Year + Cumulative Mean Temperature + f(Watsonian Vice County, model=bym, graph=vc adj)

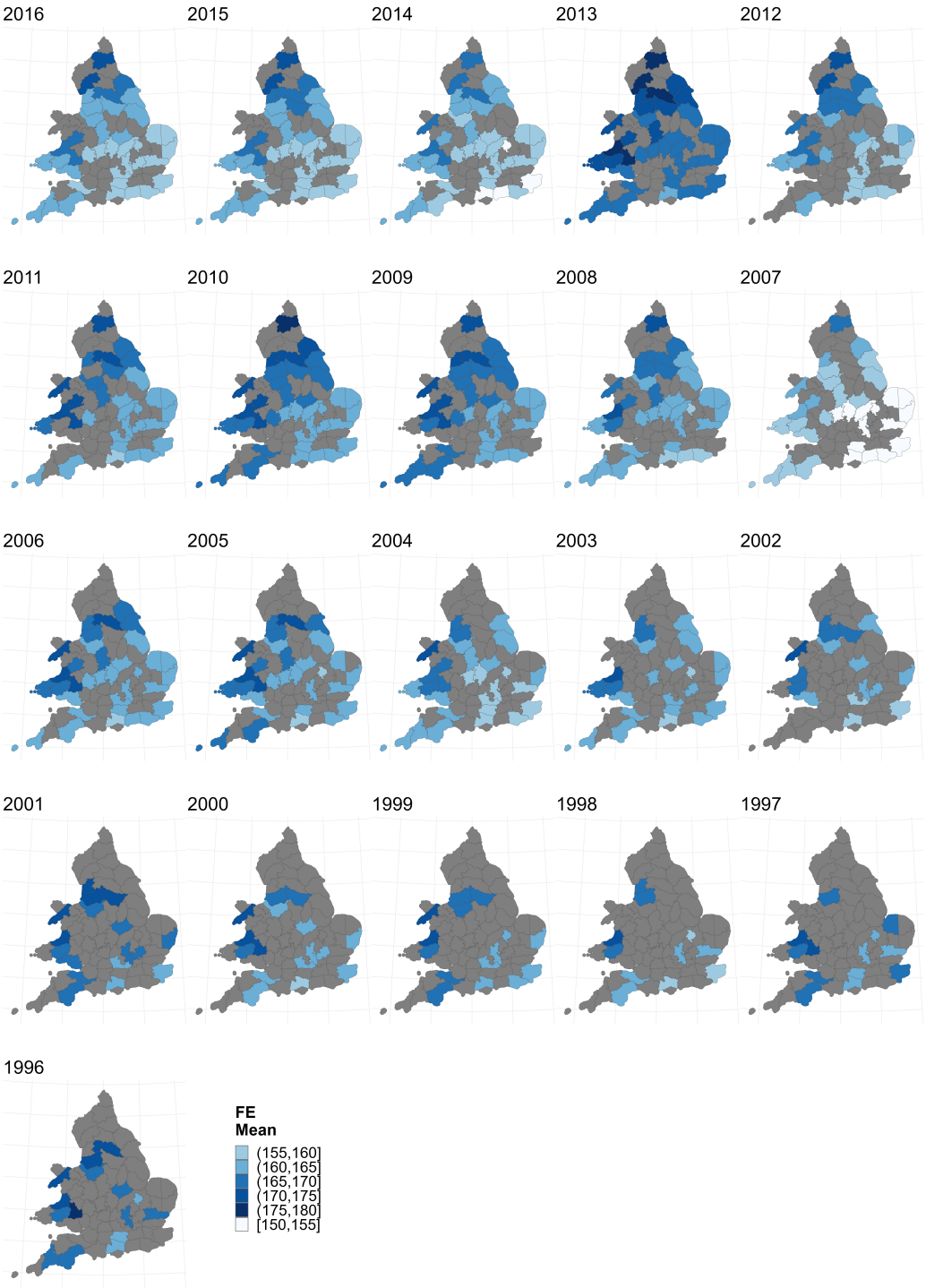


Figure D.15: Lomaspilis marginata First Emergence mean day of year from model: First Emergence ~ 1 + Year + Cumulative Mean Temperature + f(Watsonian Vice County, model=bym, graph=vc adj)

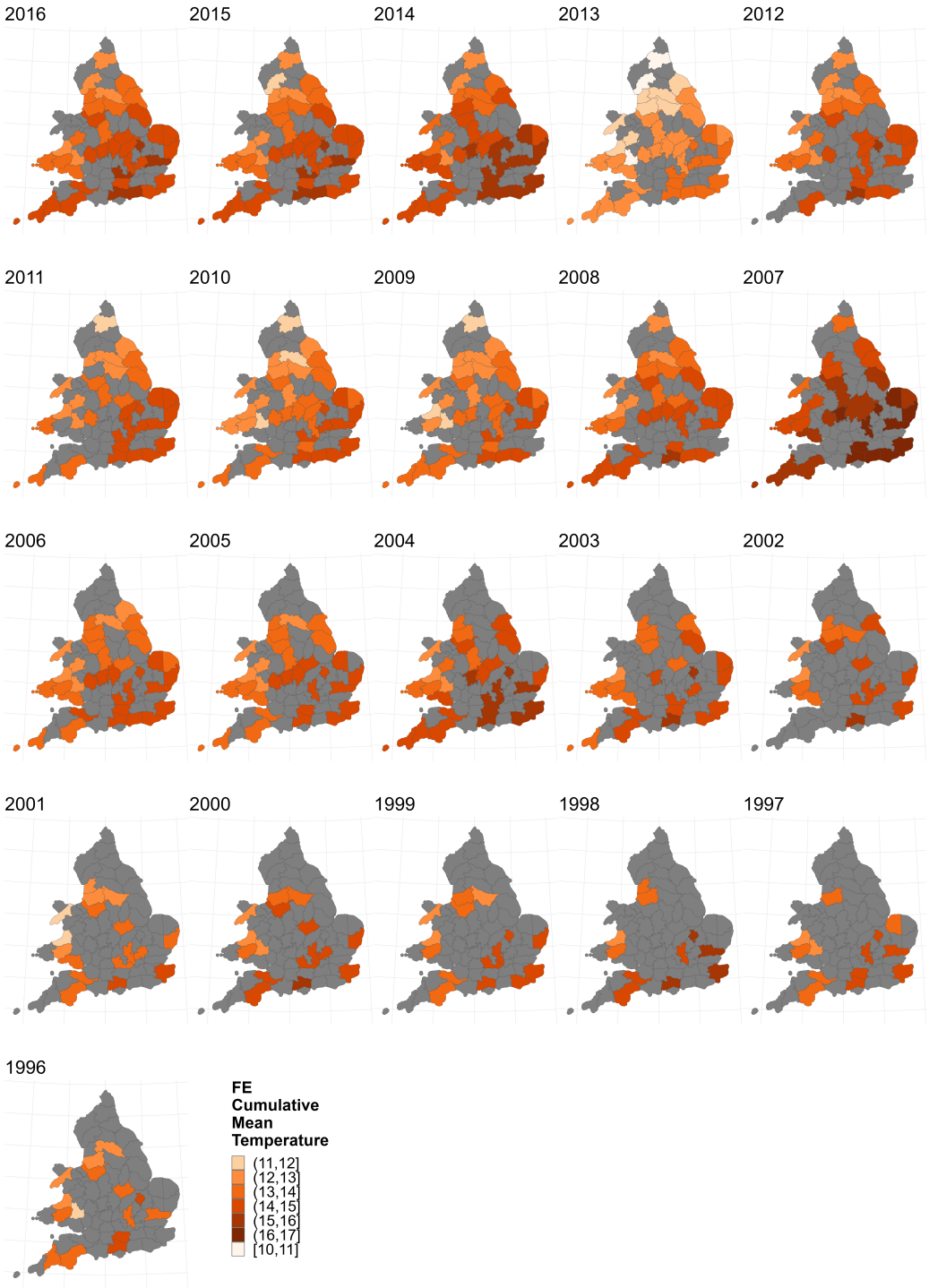


Figure D.16: Lomaspilis marginata First Emergence day of year cumulative mean temperature: First Emergence ~ 1 + Year + Cumulative Mean Temperature + f(Watsonian Vice County, model=bym, graph=vc adj)

D.4.1.2 Peak Emergence



Figure D.17: Lomaspilis marginata Peak Emergence day of year: Peak Emergence ~ 1 + Year + Cumulative Mean Temperature

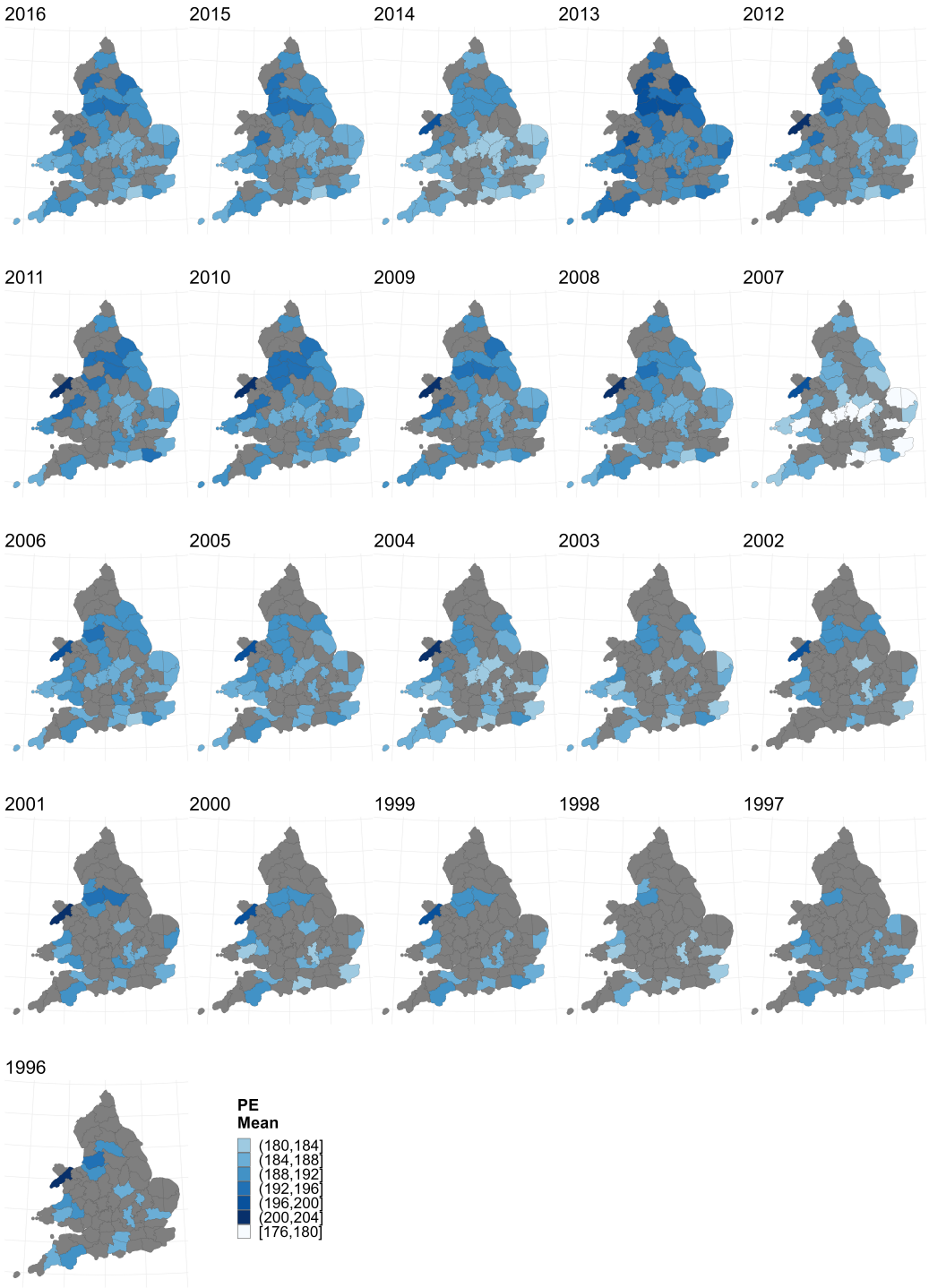


Figure D.18: Lomaspilis marginata Peak Emergence mean day of year from model: Peak Emergence ~ 1 + Year + Cumulative Mean Temperature

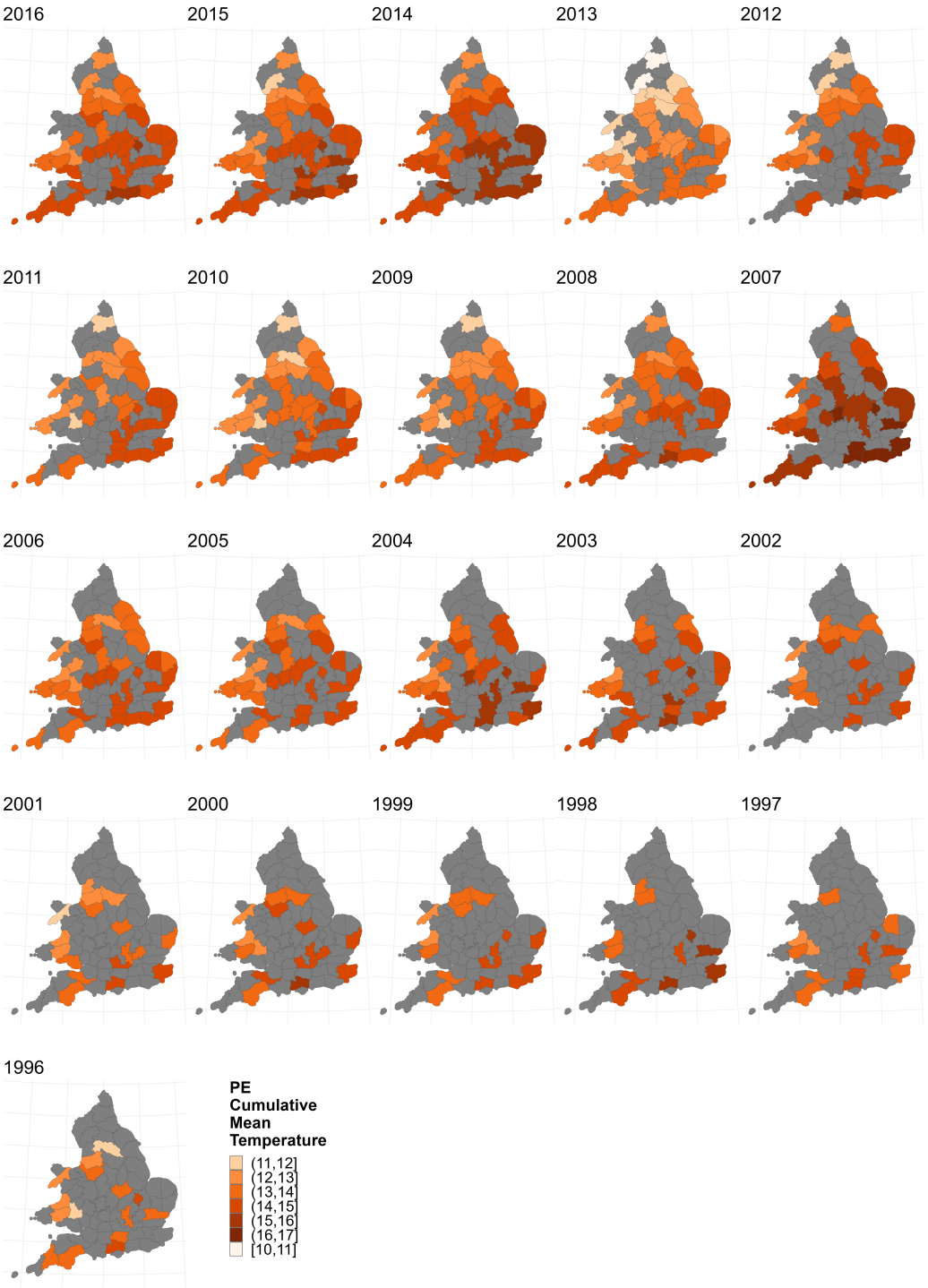


Figure D.19: Lomaspilis marginata Peak Emergence day of year cumulative mean temperature: Peak Emergence ~ 1 + Year + Cumulative Mean Temperature

D.4.1.3 Emergence SD

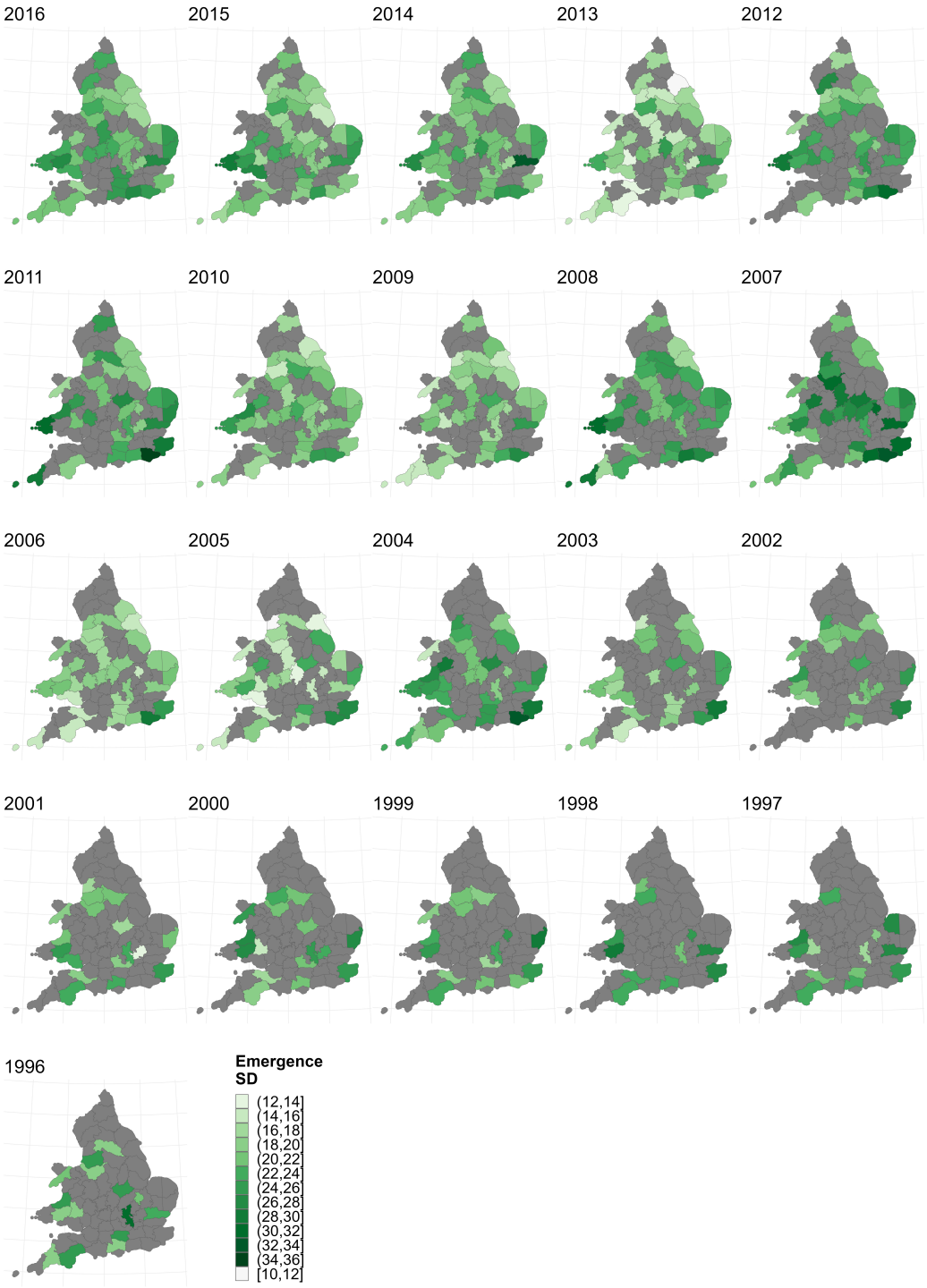


Figure D.20: Lomaspilis marginata Emergence SD: Emergence SD ~ 1 + Year + f(Watsonian Vice County, model=bym, graph=vc adj)

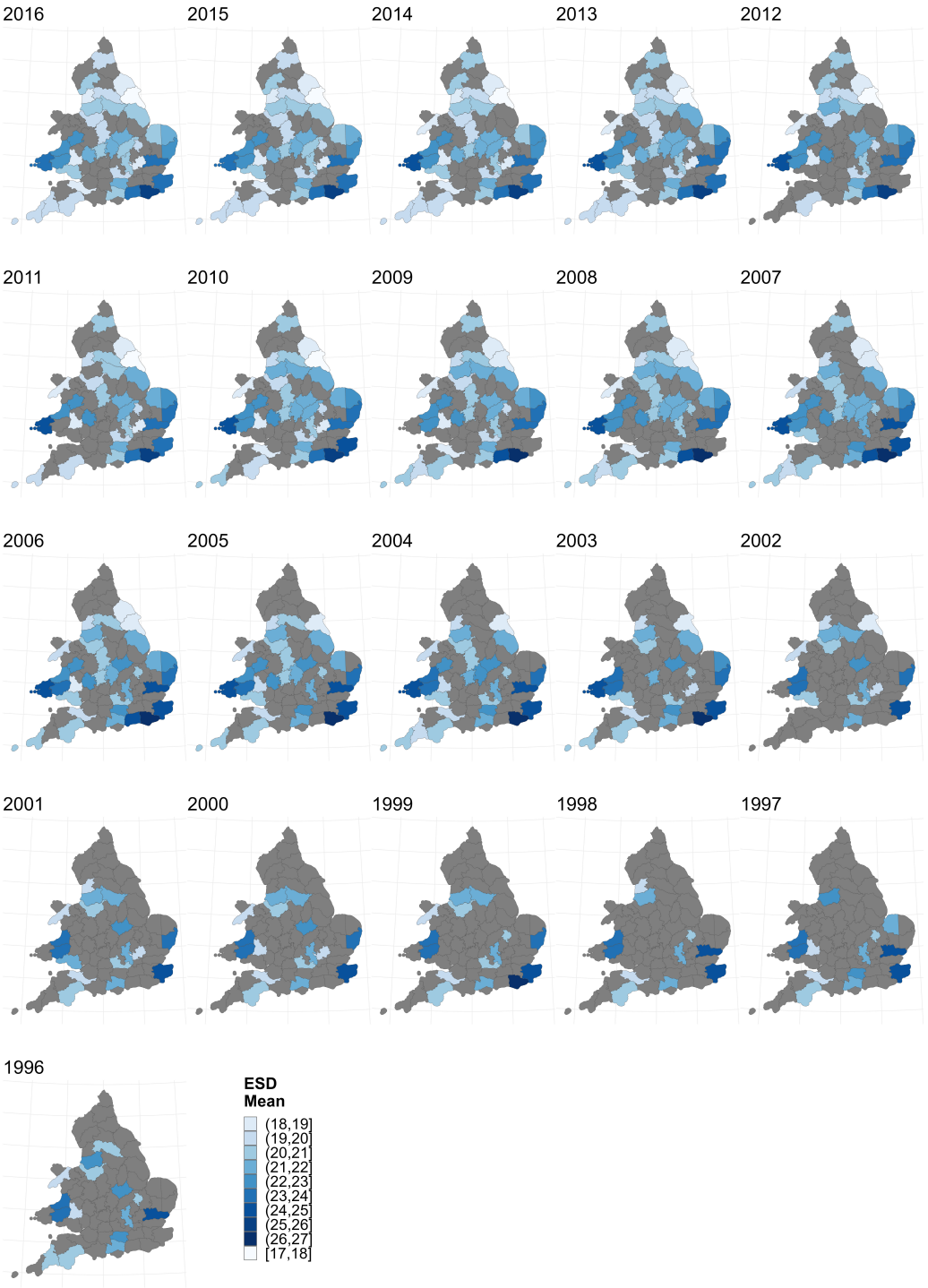


Figure D.21: Lomaspilis marginata Emergence SD mean from model: Emergence SD ~ 1 + Year + f(Watsonian Vice County, model=bym, graph=vc adj)

D.4.2 Polyphagous: Buff Ermine (*Spilosoma lutea*)

D.4.2.1 First Emergence

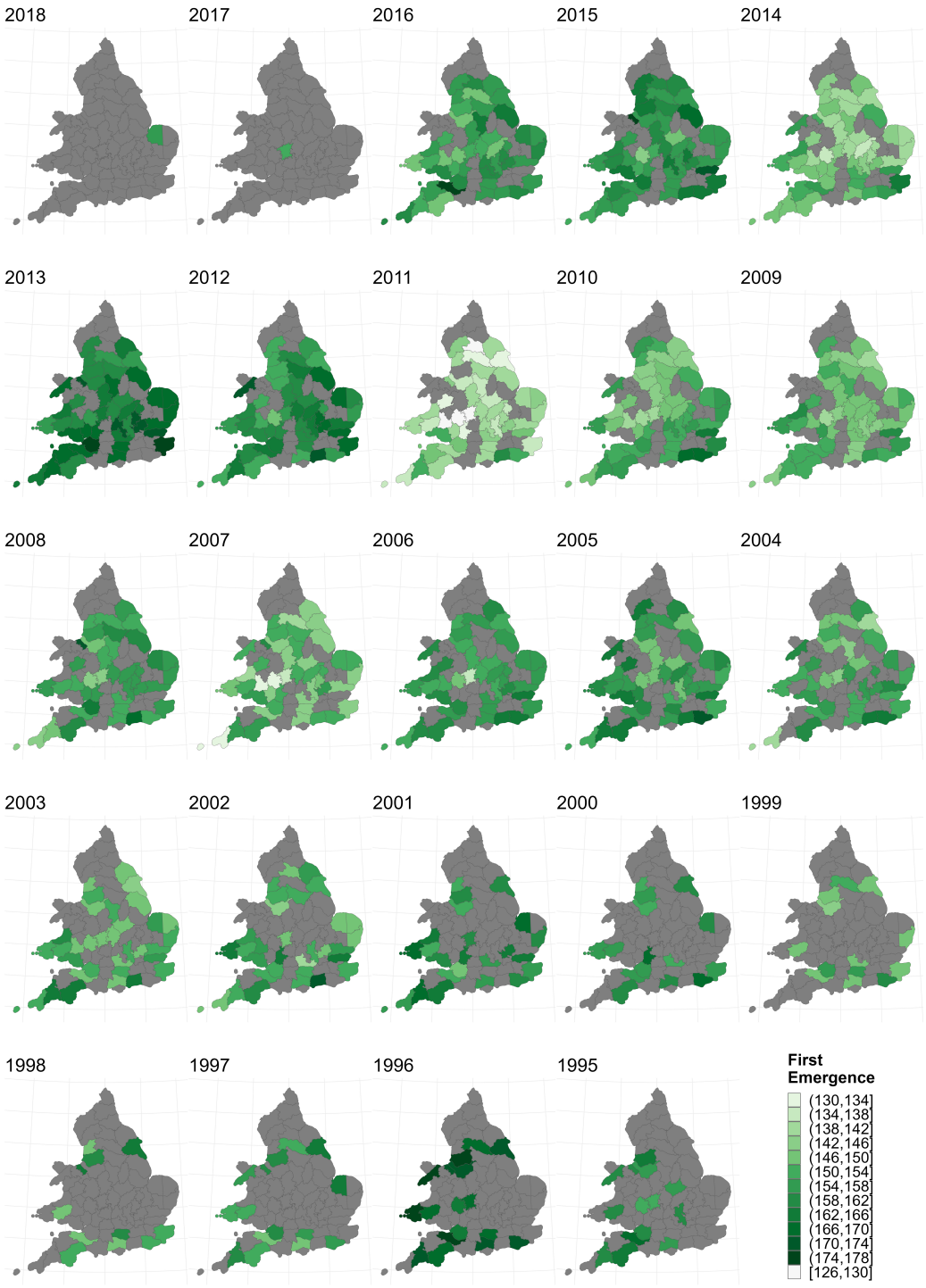


Figure D.22: Spilosoma lutea First Emergence day of year: First Emergence ~ 1 + Year + Cumulative Mean Temperature + f(Watsonian Vice County, model=bym, graph=vc adj)

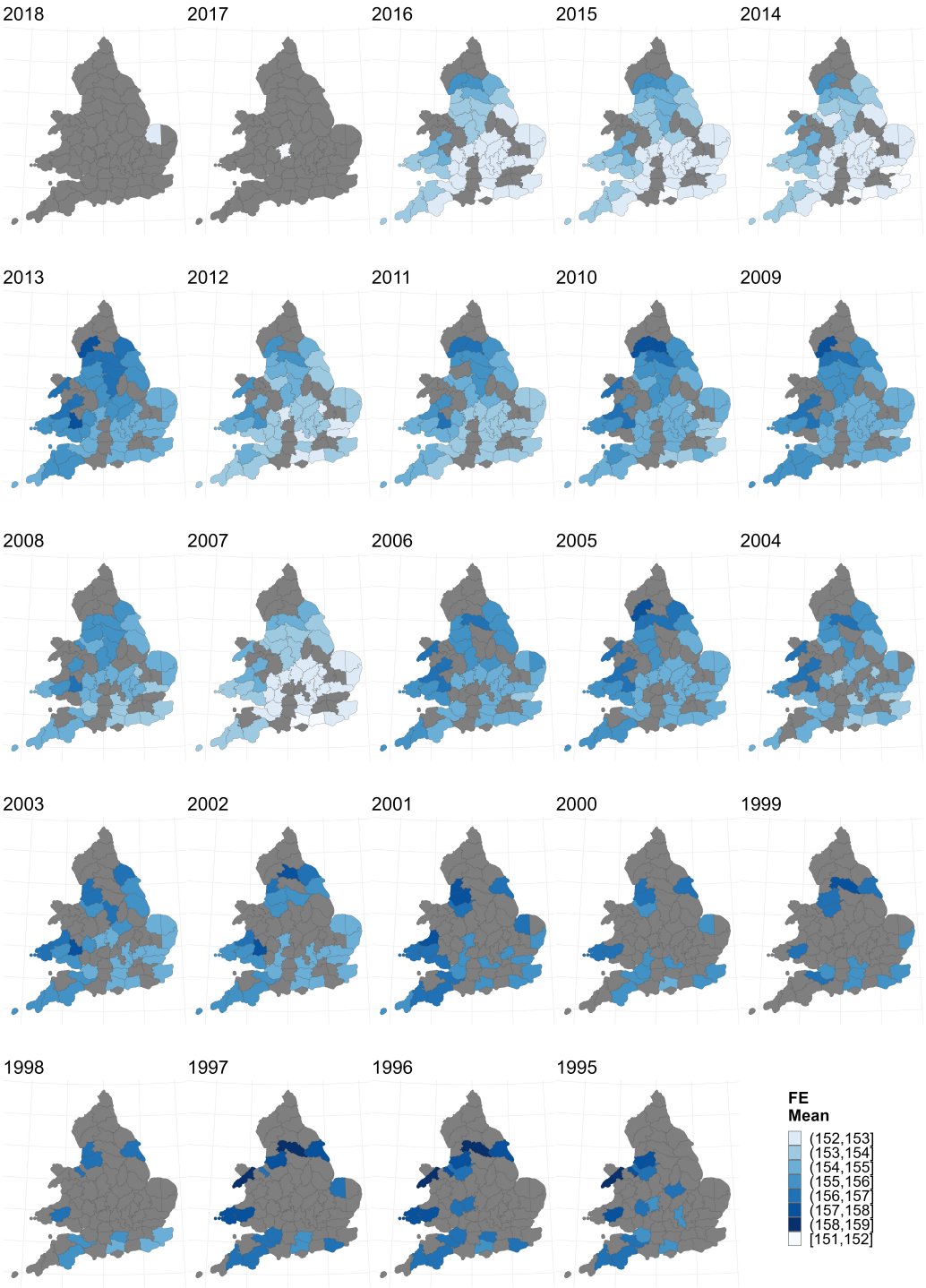


Figure D.23: Spilosoma lutea First Emergence mean day of year from model: First Emergence ~ 1 + Year + Cumulative Mean Temperature + f(Watsonian Vice County, model=bym, graph=vc adj)

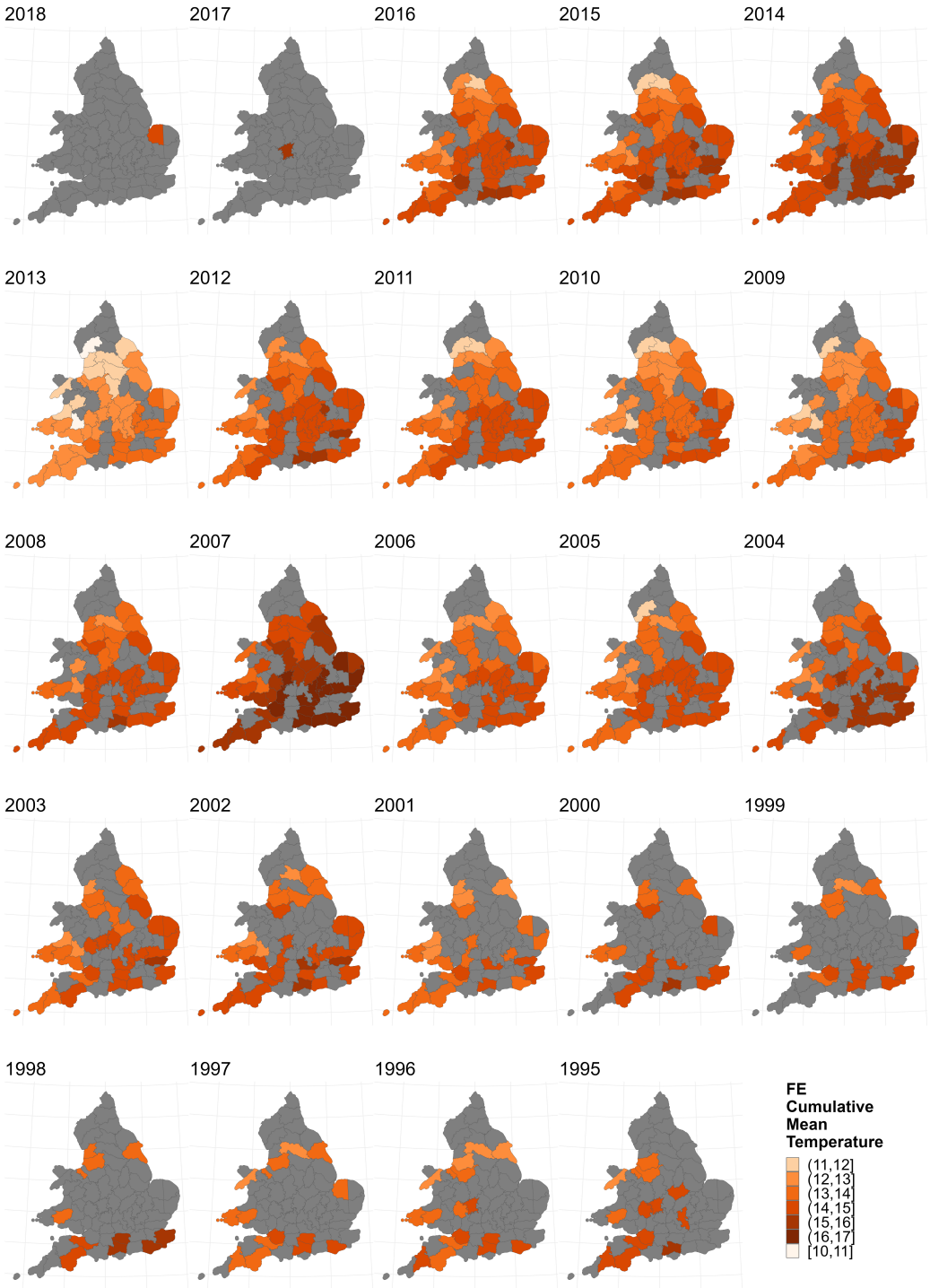


Figure D.24: Spilosoma lutea First Emergence day of year cumulative mean temperature: First Emergence ~ 1 + Year + Cumulative Mean Temperature + f(Watsonian Vice County, model=bym, graph=vc adj)

D.4.2.2 Peak Emergence

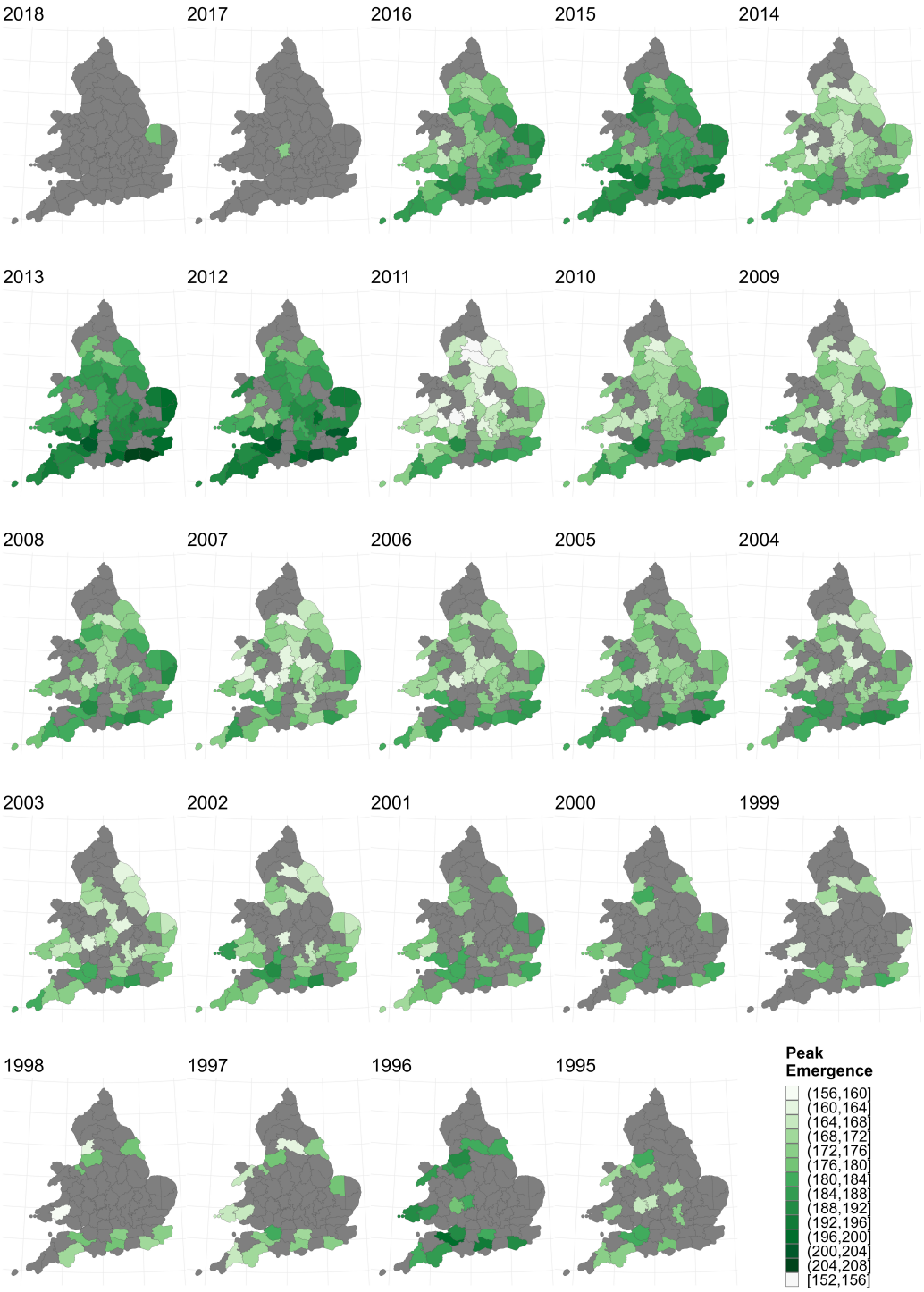


Figure D.25: Spilosoma lutea Peak Emergence day of year: Peak Emergence ~ 1 + Year + Cumulative Mean Temperature + f(Watsonian Vice County, model=bym, graph=vc adj)

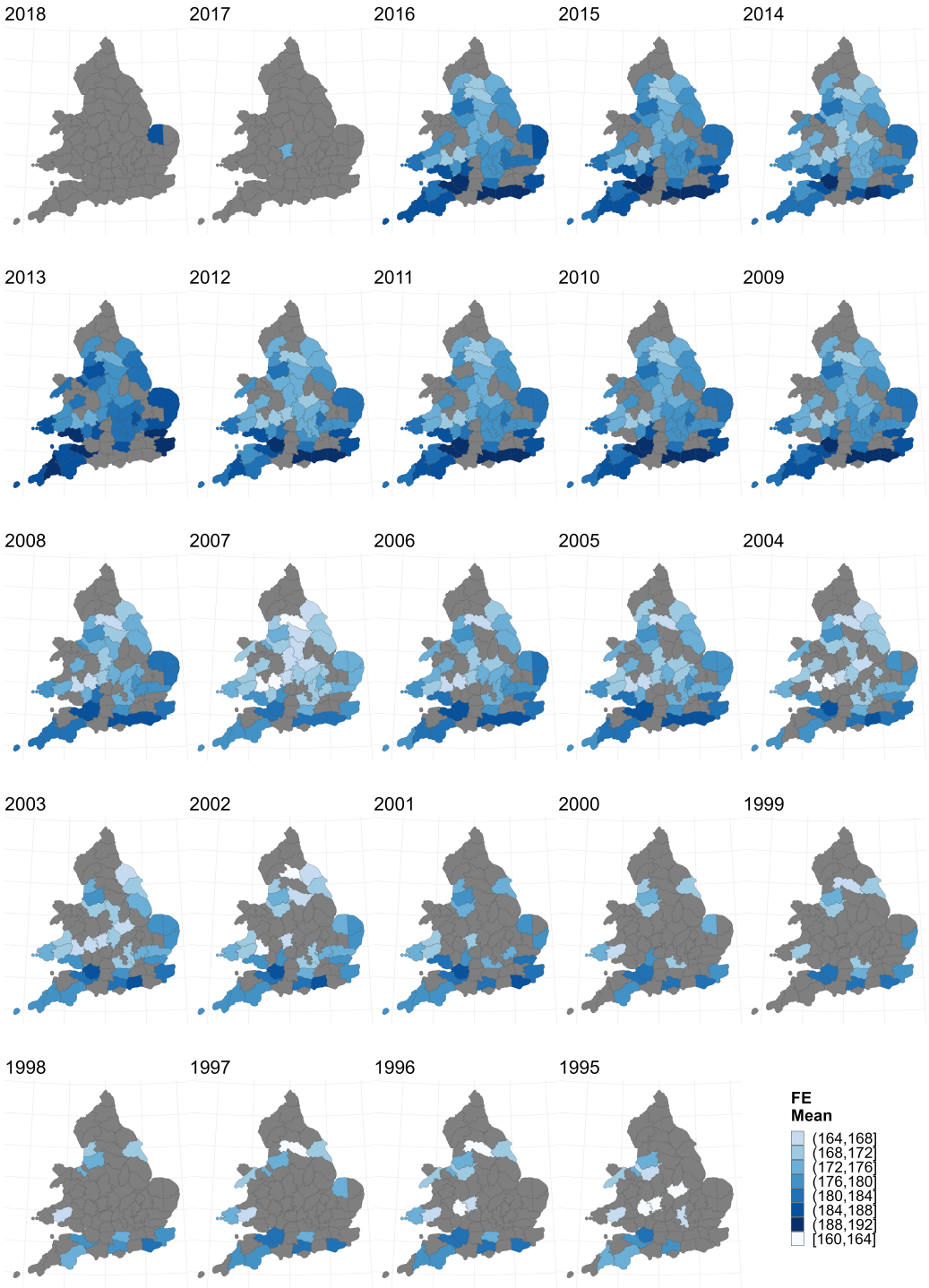


Figure D.26: Spilosoma lutea Peak Emergence mean day of year from model: Peak Emergence ~ 1 + Year + Cumulative Mean Temperature + f(Watsonian Vice County, model=bym, graph=vc adj)

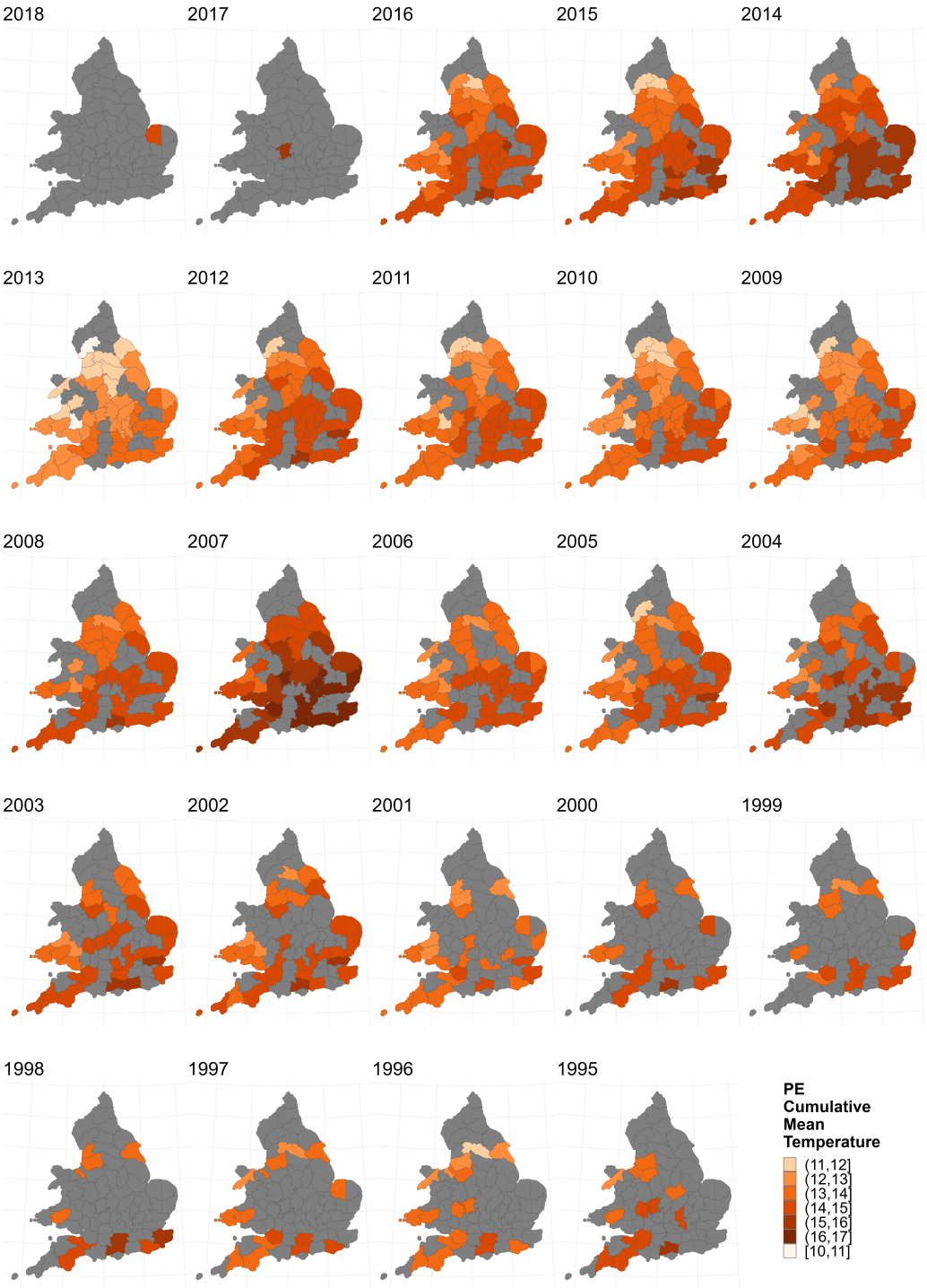


Figure D.27: Spilosoma lutea Peak Emergence day of year cumulative mean temperature: Peak Emergence ~ 1 + Year + Cumulative Mean Temperature + f(Watsonian Vice County, model=bym, graph=vc adj)

D.4.2.3 Emergence SD

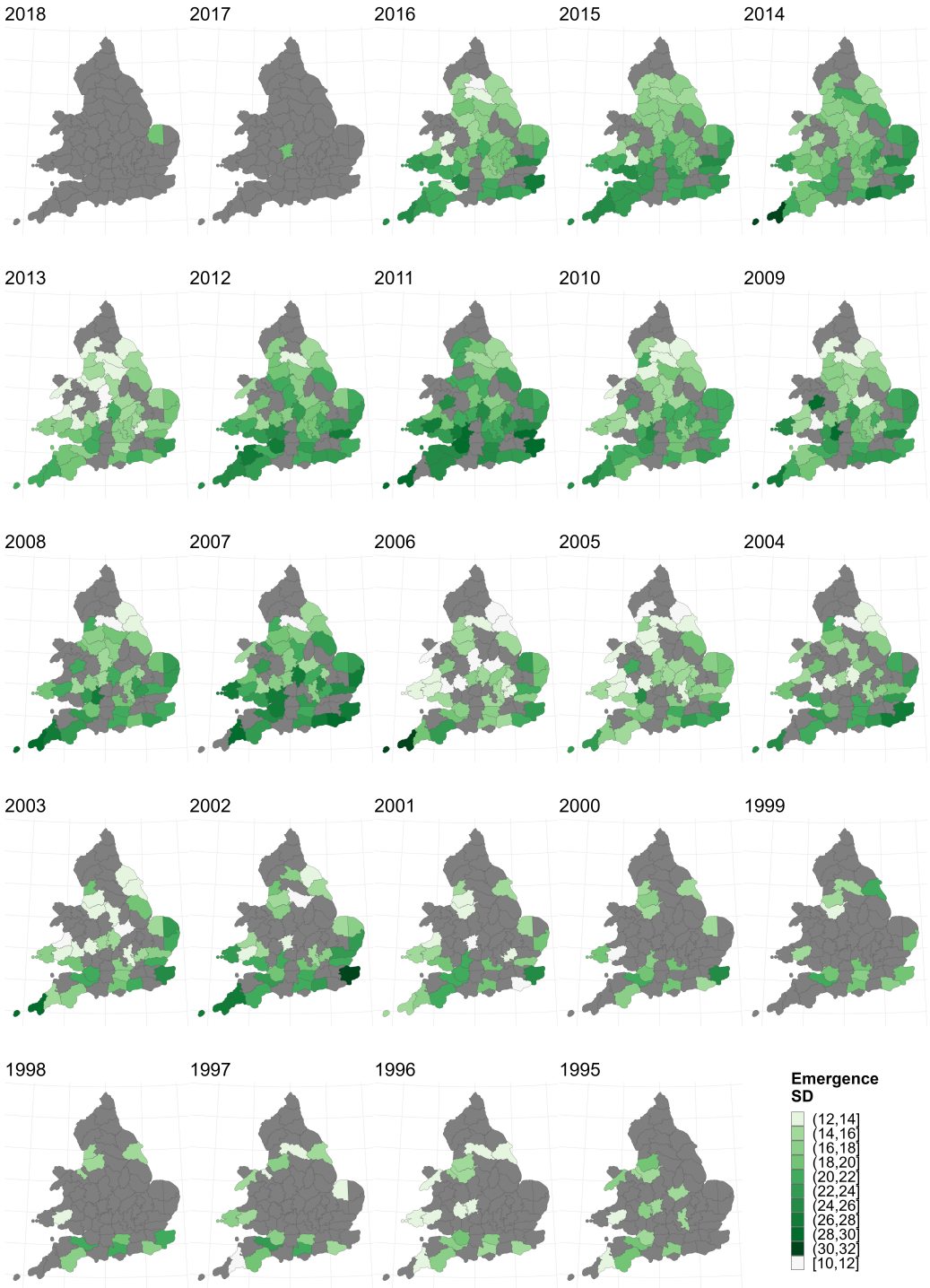


Figure D.28: Spilosoma lutea Emergence SD: Emergence SD ~ 1 + Year + f(Watsonian Vice County, model=bym, graph=vc adj)

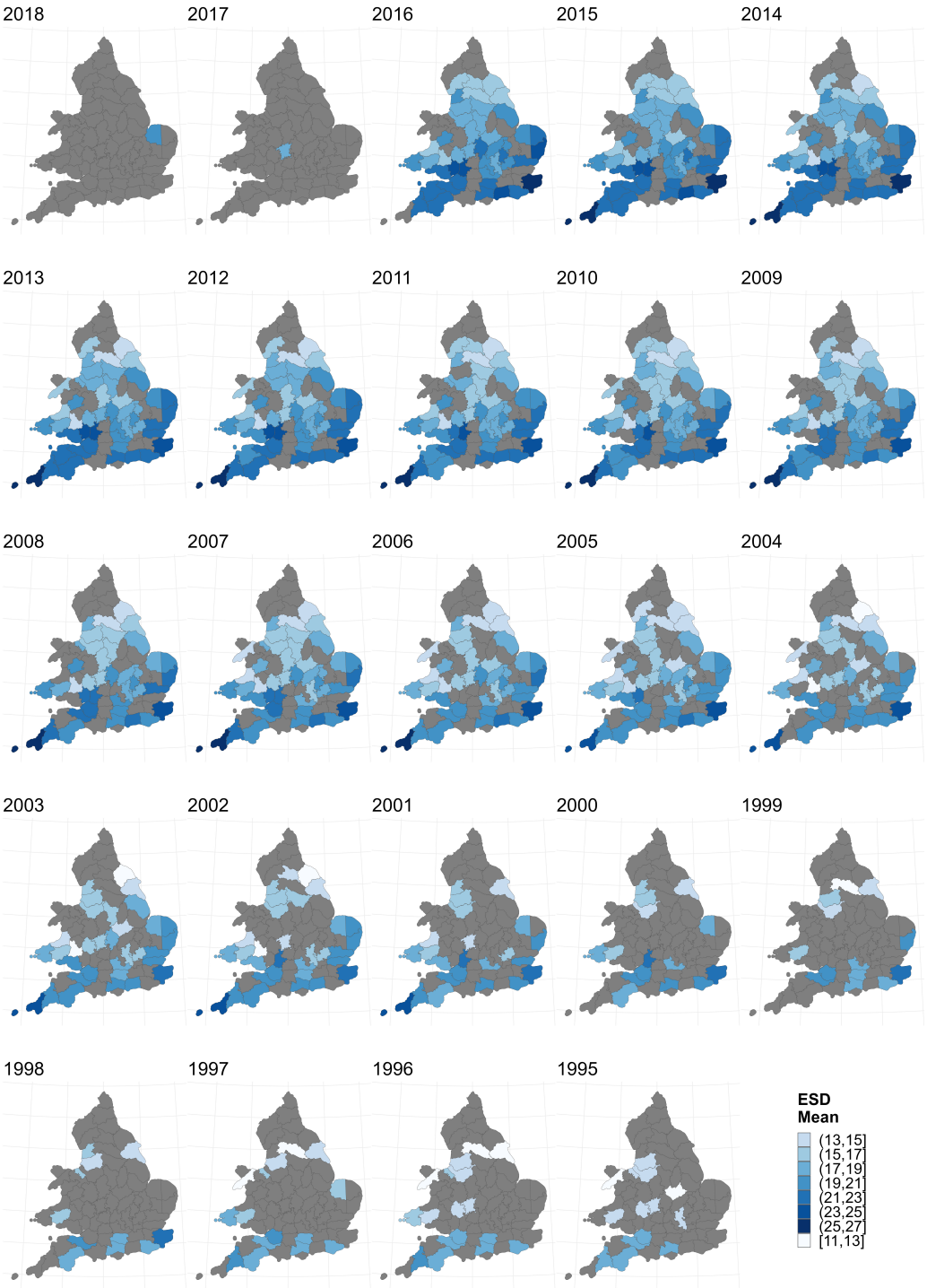


Figure D.29: Spilosoma lutea Emergence SD mean from model: Emergence SD ~ 1 + Year + f(Watsonian Vice County, model=bym, graph=vc adj)

D.4.2.4 Cumulative Mean Temperature

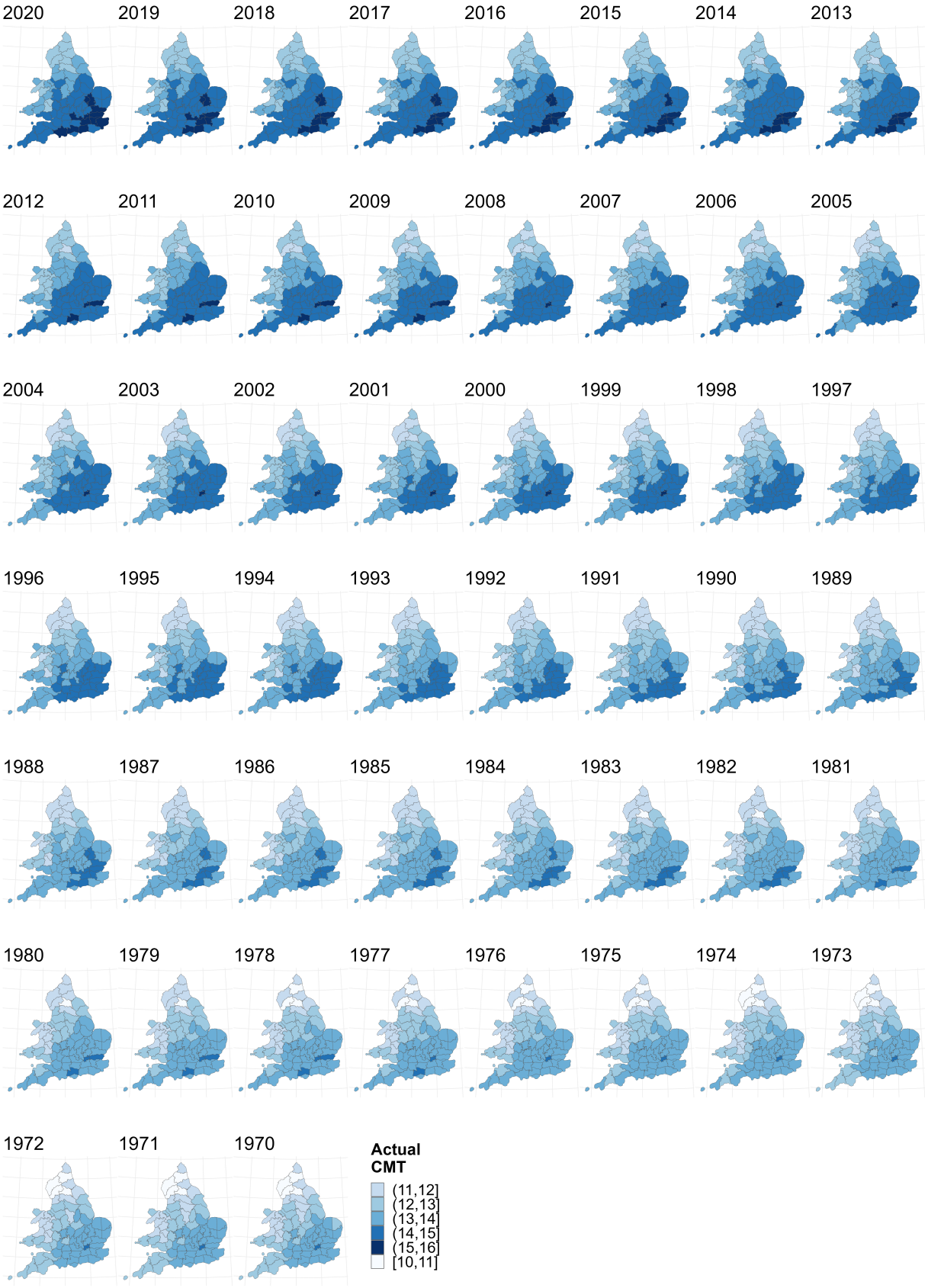


Figure D.30: The mean cumulative mean temperature plotted for each vice county each year from the posterior distribution of the INLA spatial model: cumulative mean temperature ~ 1 + year + f(vice county, model = bym, graph = vc adj).

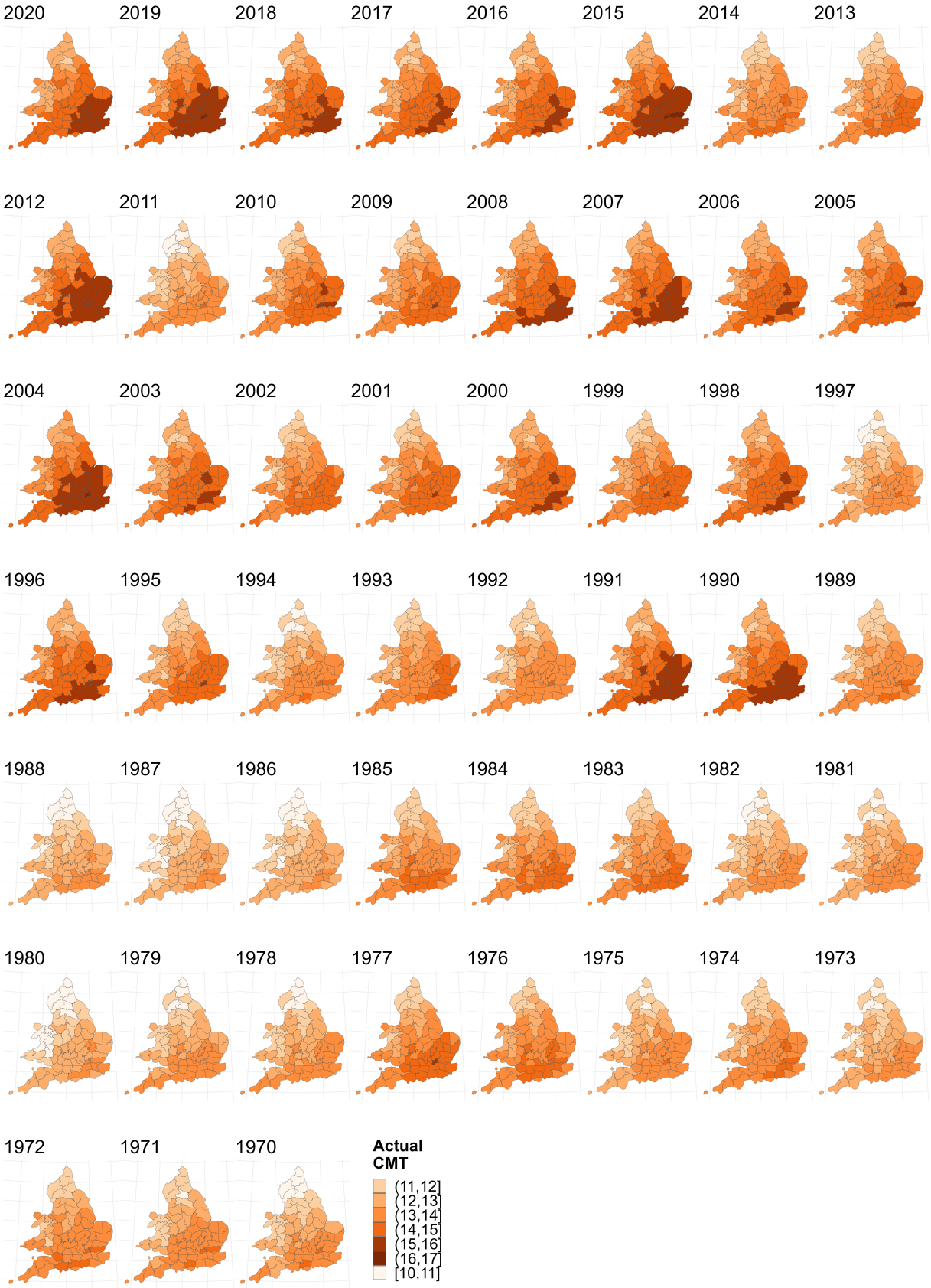


Figure D.31: The actual cumulative mean temperature plotted for each vice county each year: cumulative mean temperature ~1 + year + f(vice county, model = bym, graph = vc adj).

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