The cues, responses to temperature and potential for mismatch in UK plant phenology

Christine Tansey

Thesis for the degree of Doctor of Philosophy

The University of Edinburgh

2016

Abstract

Changes in phenology are often cited as a key biotic impact of climate change. Consequently, understanding the major environmental cues and responses to those cues in different species is important for making predictions about the future impacts and ecological implications of changing phenology. In this thesis, I set out to explore the phenological cues, mechanisms of response to temperature and the potential for interacting species to experience phenological mismatch in a range of UK plants. To do this, I utilised phenological records from two citizen science schemes; the well-established Nature's Calendar, which collects observations for the UK Phenology Network (UKPN), and Track a Tree, a novel project I set up specifically to examine the phenology of interacting plant species in UK woodlands.

I first assessed the ability of plasticity to track shifts in the optimum phenology for 22 plant species. I employed a statistical approach to estimate the plasticity and temperature sensitivity of the phenological optimum for leafing and flowering dates obtained from the UKPN. In identifying the most important cues I found that all species are sensitive to spring forcing temperatures, with plastic responses ranging from -3 to -8 days $°C^{-1}$. Chilling temperatures in autumn/winter and photoperiod were important in species with early and late phenology, respectively. In seven species, plasticity was sufficient to track geographic variation in the optimum phenology. In four species, plasticity did not track the optimum, which is consistent with clinal local adaptation to temperature, and which could place phenology under directional selection in a changing climate. I then performed a phylogenetic comparative analysis on the median phenology and estimates of plasticity and local adaptation for the 22 species analysed previously. I found that phenological event (leafing or flowering) and growth form (woody or herbaceous perennial) predicted plasticity in phenological response. These traits may help inform future predictions of phenological responses to temperature. In contrast, the median date of phenology and clinal local adaptation over latitude were not predicted by any of the ecological traits considered.

I next used records from the Track a Tree project to examine the relative phenology of canopy tree and understorey flowering species across UK woodlands. I found that first leafing and peak flowering of focal species pairs were correlated over space, and that the time between canopy leafing and the ground flora flowering (relative phenology) was spatially consistent. Relative phenology of two canopy tree species pairs was spatially consistent, but for a native versus non-native tree species pair the relationship varied over space (with a slope close to 0). If temperature-mediated plasticity determines these species' phenology, my results suggest understorey flowering may be able to track canopy leafing in future, maintaining shading interactions. Finally, I used the Track a Tree data to partition the variance in phenology for seven tree species, and test what predicts variation in oak and birch. I found that the contributors to variance differ among tree species, with spatial variables important, and within site variance low, for all species except sycamore. The low intraspecific within-site variance suggests that some species may have a limited capacity for phenological buffering. These findings contribute to understanding what impacts on the phenological distribution of different species, an important requirement for assessing the phenological buffering of mismatch.

In this thesis, I broadened the range of approaches that can be used to understand plant phenology in a changing climate. I demonstrated the value of employing novel statistical methods to analyse existing phenology data and the utility of hypothesis driven citizen science for predicting phenological shifts and the subsequent ecological implications for interacting species.

Lay summary

The seasonal timing of growth and development in plants and animals is called phenology, and includes events such as the flowering of plants and the nesting of birds. Changes in the timing of phenological events are recognised as one of the key biological impacts of climate change. To understand and predict how these changes will affect species in future, we need to know how phenology responds to aspects of the environment such as temperature. In this work, I explored the role of temperature on the flowering and leafing times of a range of UK plants, as well as examining how changes to their phenology could affect other species that they interact with. To do this, I used phenological records from two citizen science schemes; the well-established Nature's Calendar, which collects observations for the UK Phenology Network (UKPN), and Track a Tree, a new project I set up to specifically monitor interacting plant species in UK woodlands.

The phenological optimum is the timing that will lead to the most successful growth and reproduction, and it depends on environmental conditions such as temperature. If long-term temperatures change, it might alter the optimum timing for plants to produce leaves and flowers. I first tested whether 22 plant species would be able to keep up with changes in their optimum phenological timing that might arise as a consequence of climate change. I identified the most important cues for leafing or flowering spring events in these species. All species were sensitive to the warming temperatures of spring, and I found that their spring events would get earlier by between 3-8 days for each 1°C increase in temperature. For some species, cooler temperatures in autumn or winter, or day-length, were also important cues. I found that seven species are likely to be able to keep up with, or track, future changes in their optimum timing, but four species will not be able to track the rate of change. The remaining 11 species did not show a consistent pattern, so I could not draw any conclusions about their ability to keep up with their optimum timing.

For the same 22 species, I then tested whether they had any characteristics that could help predict how their phenology responds to temperature. I found that the ability to keep up with different temperatures depends on whether the event type is flowering or leafing, and whether the plant is a woody or herbaceous perennial. These traits may help make predictions about how the phenology of different species with similar traits could respond to future changes in temperature.

The Track a Tree project was set up to examine the effect of shading on the competition for light between canopy trees and flowering plants in woodlands. Participants collect unique phenology observations of plant species that interact with one another. I used records from the Track a Tree project to examine the relative timing of canopy tree leafing and the flowering of ground flora species in UK woodlands. I found that first leafing and peak flowering of several trees and flowering plants was consistent across the UK. For example, wood anemone peak flowering was around 22 days earlier than the first leafing of oak trees wherever they occurred. The timing of oaks versus birch, and oaks versus ash, was also consistent across the UK, but was different in different places for oak versus the non-native species, sycamore. In colder parts of the UK, oak leafing happens later, but sycamore leafing is very similar all over the UK. These results suggest that the flowering of species on the woodland floor may be able to track canopy leafing times of native tree species in future conditions, this would maintain patterns of shading and competition for light in woodlands. Finally, I used the Track a Tree data to test how variable tree leafing phenology is, both for different tree species and the same species in different woodlands. I found that tree leafing varies by different extents for different species, but there was little variation observed within a species in the same woodland. This means that species that depend on the leafing of woodland trees, such as caterpillars, only have a narrow window of opportunity to interact with them during spring. This finding will help us understand how the leafing of different trees will affect species they interact with in future.

In this work, I have broadened the range of approaches that can be used to understand plant phenology in a changing climate. Using new statistical methods and question-driven citizen science may continue to improve predictions of how phenological shifts in plants will affect the other species that rely upon them.

Declaration

I composed this thesis with guidance from my supervisor.

The work described in this thesis was carried out by me, or as acknowledged below.

Analyses performed throughout this thesis utilised data collected by citizen scientists who contribute to the Nature's Calendar and Track a Tree recording schemes.

Chapter 2: I conducted the analyses here with support from Albert Phillimore and Jarrod Hadfield, who developed the theoretical and statistical framework. This chapter was prepared as a manuscript, I wrote the first draft and co-authors contributed to subsequent drafts. To address reviewer comments Albert Phillimore prepared portions of Appendix A including A.2, Table A1 and Fig. A2.

Chapters 4 and 5: Analyses in these chapters include phenology data collected on a Scottish transect of 40 sites by Albert Phillimore, Jack Shutt, Edward Ivimey-Cook and Irene Benedicto-Cabello.

This work has not, in whole or part, been submitted for any other degree or professional qualification.

[redacted]

Acknowledgements

It was somewhat to my own surprise that I found myself undertaking a PhD, and my decision to do so was determined by the appeal of this project and the incredible enthusiasm (from the outset), of my supervisor, Ally Phillimore. Your constant support, knowledge, patience (especially throughout my struggles with R), and sheer love of science, has contributed vastly to this thesis. I have a huge amount of respect for you, and am incredibly grateful for all you have taught me over the last four years; about research, cursing at computers, and how to fall over on fieldwork. My deepest thanks.

Thank you to NERC, for funding me to complete this project. I am also indebted to my CASE partner, the Woodland Trust, for their ongoing support and for allowing me to work with phenology data collected via the Nature's Calendar scheme. I would particularly like to thank Kate Lewthwaite, who has shared her extensive citizen science expertise and offered useful guidance on many occasions. Thanks also to Sian Atkinson, who has helped review my work with the Woodland Trust over the last few years, and Tim Sparks, founder of the current UK Phenology Network (UKPN).

I, and many other researchers before me, owe a great deal to the tens of thousands of citizen scientists who have collected the millions of phenology observations held by the UKPN. I am especially grateful to the participants of the Track a Tree scheme, without whom I would have had but half a thesis, and who it has been a pleasure to interact with. As a participant in Track a Tree myself, I'd also like to mention the oak and birch trees of King's Buildings and Roslin Glen, trees that I've spent a lot of time with during my PhD!

From the Institute of Evolutionary Biology, I owe thanks to my unofficial supervisor Jarrod Hadfield, whose theoretical and statistical knowledge underpins this thesis. My official second supervisor, Graham Stone, allowed me to join lab group meetings for many interesting debates over the years. Both he and Sarah Reese are also due thanks for their exceptionally helpful discussion in the early stages of my project.

The proof-readers who gave their time during the last stage of writing were brilliant, thanks to Rachel Tansey, Annie McKee, Lucy Wilshaw and Jude Frankau. I would also like to mention Agatha Christie (yes, the Queen of Crime). The voices of her characters (via radio dramas), have been my most consistent companions through hours of tedious tasks.

The thought of how to acknowledge everyone else who has been important to me in the last four years of PhD life is somewhat overwhelming. So, rather than list those who have not only been academically supportive, life-enriching, and who helped me through moments of uncertainty and confusion, I will do my best to thank them in real life. The various cohorts of Ashworth PhDs, my flatmates and friends outside of academia who kept me sane, the posters of encouraging cards; all of you have made my life immeasurably better.

To my family I owe the greatest thanks. Geoff and Kath Tansey, you have loved and supported me through every decision and blind alley I have taken in pursuit of work and education, and I cannot thank you enough. Rachel Tansey, without your sistership there is a chance I would forget to be silly, or that I am short, and I am always grateful when you remind me.

Contents

Chapter 1

General introduction

1.1 Climate change and phenology

Climate change influences different biological processes through the impacts of changing abiotic conditions such as temperature, precipitation and ocean acidification (Walther *et al.* 2002; Parmesan 2006; Settele *et al.* 2014), and may in turn affect the fitness and survival of many species (Hoffmann & Sgrò 2011; Chevin, Collins & Lefèvre 2013). The most commonly recorded biotic impacts of climate change are shifts in the phenological timing of numerous taxa (Fitter & Fitter 2002; Parmesan & Yohe 2003; Thackeray *et al.* 2010), and latitudinal and altitudinal range shifts (Root *et al.* 2003; Perry *et al.* 2005; Hickling *et al.* 2006; Chen *et al.* 2011; Devictor *et al.* 2012). Climate change may also impact species through changes to disease (Harvell *et al.* 2002; Garrett *et al.* 2006; Bruno *et al.* 2007; Rohr & Raffel 2010), recruitment success (Durant *et al.* 2005) and species interactions (Menéndez *et al.* 2008; Schweiger *et al.* 2008).

A variety of approaches have been taken to projecting the fates of species under climate change, whether through modelling species distributions based on changes to their inferred climatic niche (e.g. Engler *et al.* 2011) or examining the impact species interactions may have on abundance and distributions (Brooker *et al.* 2007; Van der Putten, Macel & Visser 2010). Phenological change is an important aspect of species' response to climate, and is strongly linked to temperature. Timing influences the growth and reproduction of individuals within a population and therefore shifts in phenology may have fitness consequences (Gienapp, Reed & Visser 2014). This is particularly important in temperate plant species, as the timing of vegetative growth and flowering determines the environmental conditions (e.g. early year frosts), and the biotic interactions (e.g. availability of pollinators), that individuals will be exposed to (Durant *et al.* 2005, 2007; Miller-Rushing *et al.* 2010). The fitness consequences of phenology could influence future species distributions (Chuine 2010) and the invasion success of exotic species, especially in terrestrial plants (Wolkovich & Cleland 2011). The combined effects of phenological change on fitness and other ecological processes, such as soil nutrient cycles (Nord & Lynch 2009), will inform the future impacts of a changing climate on community structure and function. A fuller understanding of interspecific differences in how climate influences phenological response will also aid our ability to predict the consequences of phenological shifts on populations (Buckley & Kingsolver 2011) and the associated impacts on species distributions (Chuine 2010).

Changes in phenology that are thought to be a response to changing climate variables have been well documented across different ecosystems and many taxa (e.g. Menzel *et al.* 2006a; Parmesan 2006; Cook *et al.* 2012a, b). Phenological shifts are changes in the timing of phenological events over time and have been associated with warming temperature trends (Root *et al.* 2003; Menzel *et al.* 2006a; Menéndez 2007; Devictor *et al.* 2008). Examples of earlier spring events and an extended growing season at high latitudes include earlier flowering in plants (Fitter & Fitter 2002; Amano *et al.* 2010; Cook *et al.* 2012b); earlier migration and laying dates in birds (Cotton 2003; Both *et al.* 2004; Hurlbert & Liang 2012); earlier nesting at higher latitudes in sea turtles (Mazaris *et al.* 2013); earlier emergence in Lepidoptera (Roy & Sparks 2000; Stefanescu, Penuelas & Filella 2003; Dell, Sparks & Dennis 2005; O'Neill *et al.* 2012); and earlier fruiting in fungi (Kauserud *et al.* 2010). Species that delay their spring phenology and those that do not exhibit a directional response, have also been identified (e. g. Cook *et al.* 2012). Phenological events at other times of the year and those outside of arctic and temperate regions have been less well studied (Gallinat, Primack & Wagner 2015), however there are examples of shifting autumnal events in temperate areas(Ibáñez *et al.* 2010; Fridley 2012). Autumn phenology may be affected by spring phenology (Keenan & Richardson 2015) and in turn affect the subsequent spring, as sequential events can be constrained by development (Wolkovich & Ettinger 2014).

1.2 Temperate deciduous woodland

Temperate deciduous woodlands are some of the most common plant communities in the UK and support a range of biodiversity (e.g. Southwood *et al.* 1979, 1986). Understanding the influence of warming temperatures on their phenology will shed light on how woodlands will fare under climate change (Polgar & Primack 2011). In such seasonal systems, phenology impacts on growth and reproduction in different species (e.g. Emborg 1998), and influences the availability of resources, for example, the flowering phenology of woodland herbs has a short-lived spring peak to benefit from high light levels (Whigham 2004), and determines the biotic interactions that occur in the community (e.g. Schemske *et al.* 1978; van Asch & Visser 2007; Kudo *et al.* 2008). Such interactions could become mismatched if there are interspecific differences in climate related phenological shifts (e.g. Both *et al.* 2009). Intraspecific variation in phenology may be able to buffer such mismatches within a population, or over space, if not all individuals experience the same degree of phenological shift.

The vegetative phenology of woodland communities is usually ordered by competition for light, progressing through herbaceous ground flora species, shrubs and canopy trees (Salisbury 1921). Canopy shading limits light at the woodland floor (Anderson 1964) and thus influences growth and reproduction in herbs (Blackman & Rutter 1946; Whigham 2004; Dahlgren, von Zeipel & Ehrlen 2007) and woody species (Augspurger, Cheeseman & Salk 2005). The composition of the understorey can be affected by light availability (Sparks *et al.* 1996; Thomsen, Svenning & Balslev 2005), and light influences the distribution and density of ground flora species, such as bluebells (Blackman & Rutter 1946). Understorey plants in woodlands may be structured according to their shade tolerance (Sparling 1967; Henry & Aarssen 1997), and light availability can affect fitness via seed set (Kudo *et al.* 2008), and population growth rate (Valverde & Silvertown 1998), in herbs, and regeneration in woody species (Emborg 1998).

By understanding the effect of spring temperatures on different plant species, we will be better able to project their response to future temperature change, and gain insight into how ecological communities such as woodlands may be affected. To project the future phenological responses of species or populations we need to i) identify the phenological cues involved, ii) estimate the plastic response to a change in temperature, iii) identify the contribution that adaptation will need to make, and iv) infer the degree to which phenological species interactions may be maintained or disrupted.

1.3 Phenological cues

Plant phenology is strongly influenced by environmental cues, particularly temperature and photoperiod (Rathcke & Lacey 1985; Tooke & Battey 2010; Polgar & Primack 2011). Phenological shifts as a result of climate warming may lead to advances (e.g. Fitter & Fitter 2002) or delays (e.g. Yu, Luedeling, & Xu 2010) in event occurrence.

Much of the evidence for the importance of different cues in plant phenology comes from experiments that manipulate temperature and light conditions (e.g. Caffarra &

Donnelly 2011). Temperatures may act as a cue at different times of the year, with forcing (via thermal accumulation) and chilling effects recognised as important to stimulate tissue development and break dormancy, respectively (Polgar & Primack 2011). Strong correlations between spring temperatures and phenological events provide evidence of when forcing temperatures are important (e.g. Sparks *et al.* 2000; Thackeray *et al.* 2016). The role of photoperiod is less well understood, with its importance as a cue for tree leafing still debated. Some studies suggest that it is a particularly important cue in late successional species (Basler & Körner 2012, 2014), while others have found that chilling effects may outweigh the influence of photoperiod (Laube *et al.* 2014). It may be that the interplay between photoperiod and temperature cues is complex (Vitasse & Basler 2013) and varies among species. Photoperiod has also been shown to act as a cue in non-woody species, including herbs (Kudoh, Ishiguri & Kawano 1995; Chew *et al.* 2012) and grasses (Hay 1990).

In the context of a changing climate, it is especially important to identify the role of temperature, and several methods have been used to model its influence (reviewed in Cleland *et al.* 2007; Chuine *et al.* 2013; Zhao *et al.* 2013). There is evidence that chilling, forcing and photoperiod cues vary among species (e.g. Morin *et al.* 2009; Basler & Körner 2012, 2014; Laube *et al.* 2014), but there remains a dearth of knowledge about how they differ across a wide range of plants because much of the existing work has been conducted on trees. In order to improve projections of phenological responses it is therefore important to broaden the range of plant species for which we have model estimates of the most important temperature and photoperiod cues.

1.4 Plasticity and adaptation

Temperature varies in space and time and this may generate variation in the optimal timing (i.e. that which maximises growth and successful reproduction under amenable environmental conditions). Phenology also varies over both space and time (e.g. Menzel *et al.* 2006; Tooke & Battey 2010; Polgar & Primack 2011; Hurlbert & Liang 2012), arising via plasticity and adaptation (Anderson *et al.* 2012), which are ways in which a population can track the optimum. Phenological plasticity with respect to temperature describes the ability of a single genotype or individual to exhibit a different phenology at different temperatures. Adaptation to temperature through natural selection leads to genetic change to the mean phenology of a population, with adaptation over space known as local adaptation. Throughout this work adaptation will be used to imply genetic change.

Theory suggests that populations able to track changes in the optimum phenology via plasticity do not require adaptation to future conditions such as temperature changes (Chevin, Lande & Mace 2010). A population that is unable to track the optimum via plasticity and needs to adapt in order to do so will be at greater risk of extinction if it has insufficient additive genetic variation, and thus fails to adapt. Relatively few attempts have been made to disentangle the contributions of plasticity and adaptation in the ability to track optimum phenology (but see examples exploring passerine phenology in Gienapp *et al.* 2013; Vedder *et al.* 2013; Phillimore *et al.* 2016). Integrating evolutionary processes into predictions of species response has been identified as an important way to improve projections of the fates of populations (Chevin *et al.* 2010), as well as the assessment of broader climate change impacts on biodiversity (McMahon *et al.* 2011).

Plasticity is an important mechanism in plant responses to changing temperature (Nicotra *et al.* 2010). Plasticity can itself be adaptive, with similar plastic reaction norms in different populations (Palacio-López *et al.* 2015), although there is limited evidence for this in plants (van Kleunen & Fischer 2005; De Kort *et al.* 2015). Plasticity may be an important factor in short term plant persistence under climate change, as in other taxa where it does not perfectly track a shifting optimum, adaptive plasticity has been found to act as a buffer to rapid environmental change through partial tracking (Kovach-Orr & Fussmann 2013; Phillimore *et al.* 2016). It may also provide longer-lived species with the opportunity for genetic adaptation through ensuring their short term persistence (Nicotra *et al.* 2010). Temperature-mediated plasticity in the spring phenological responses of temperate plants has been documented in a number of ways, including longitudinal studies of individual trees (Vitasse *et al.* 2010), geographic transplants of trees (Kramer 1995) and manipulative experiments on various plant species (Franks, Weber & Aitken 2014). Recent modelling work suggests that plasticity contributes substantially to spatial as well as temporal variation in leafing times of *Quercus robur* in response to temperature (Phillimore *et al.* 2013).

Relatively few studies have examined adaptation in phenology over time, but there is some evidence of rapid evolutionary changes in flowering of members of the

Brassicaceae (Franks, Sim & Weis 2007; Franks & Weis 2008; Anderson *et al.* 2012). Other work has highlighted evidence of local adaptation along spatial environmental gradients in various tree species (Alberto *et al.* 2013). Recent reviews have examined the evidence for evolutionary responses to climate change, and describe numerous examples of plasticity to temperature in terrestrial plants (Donnelly *et al.* 2012; Franks *et al.* 2014). Fewer studies were found to provide evidence of genetic adaptation to temperature (but see Alberto *et al.* 2013).

Understanding interspecific differences in the influence of plasticity and adaptation on the phenology of temperate plants will improve projections of how populations may fare under climate change. For example, if certain species require adaptation in order to track the optimum they may be more likely to struggle. Differences in how the populations of interacting species in woodland communities may respond could also shed light on whether existing species interactions may face changes.

1.5 Species interactions and phenological mismatch

Species interactions that are dependent on synchronous phenological timing could become mismatched if there is variation in the degree of phenological shift among different species, or individuals of the same species (Cushing 1990; Durant *et al.* 2007). Such mismatches may impact on demography and population dynamics (Miller-Rushing *et al.* 2010). Examples of increasing mismatch include the relationships between a lily, *Erythronium grandiflorum* and its pollinator community (Thomson 2010); a pollinating butterfly, *Pieris rapae* and *Prunus* tree species flowering (Doi, Gordo & Katano 2008); and a tri-trophic food chain of oak (*Quercus robur*), winter moth (*Opheroptera brumata*) and great tit (*Parus major*) (Visser & Both 2005). Other work has reviewed a wider range of potentially interacting species and found differences in the degree of phenological shift between particular species (Visser & Both 2005; Burkle, Marlin & Knight 2013) or at broad trophic levels (Thackeray *et al.* 2010). In contrast, the rates of phenological change in some pollinators and insect pollinated plants have been similar, implying that the degree of matching in some systems is unchanging (Hegland *et al.* 2009; Bartomeus *et al.* 2011).

In forest communities, phenology affects the fitness of leaf feeding herbivores, and any mismatch between the leafing of host trees and emergence of caterpillars can seriously affect caterpillar growth and survival (van Asch & Visser 2007; Foster, Townsend & Mladenoff 2013). Chemical leaf defence also affects the fitness of such herbivores and narrows their window of optimum synchrony (Tikkanen & Julkunen-Tiitto 2003). Tree-dependent herbivores may be particularly affected, since trees can exhibit great phenological plasticity and may respond to different phenological cues to their herbivore community, as climate sensitivity potentially varies among trophic levels (Thackeray *et al.* 2016). Understanding the effect of asynchrony on tree-herbivore interactions has an important application, as it may help predict disturbances caused by tree pest species and plan forest management strategies under altered climatic conditions. For example, recent modelling suggests that gypsy moth (*Lymantria dispar L.)* population expansion may be limited by increasing asynchrony with forest phenology in the US (Foster *et al.* 2013).

A variety of studies have examined other interacting woodland species across trophic levels, for example, plant-pollinator networks have been shown to be sensitive to phenological shifts (Kudo *et al.* 2008; Burkle *et al.* 2013). Less attention has been given to the disruption of other phenological interactions, such as those within trophic levels. Such intraguild interactions may also be at risk of mismatch under a changing climate (Brooker 2006; Miller-Rushing *et al.* 2010), which could affect processes important for community dynamics, such as competition (Nakazawa & Doi 2012) and intraguild predation (Revilla, Encinas-Viso & Loreau 2014). Some studies have shown increased intraguild predation as a result of shifting phenologies amongst frogs and newts (Walther *et al.* 2002), salamanders (Anderson *et al.* 2015) and dragonflies (Rasmussen, Van Allen & Rudolf 2014). There is also evidence for intraguild competition for resources being affected, such as for nesting sites in penguins (Lynch *et al.* 2012) and for abiotic resources and pollination in a plant community (CaraDonna, Iler & Inouye 2014). It is therefore clear that intraguild interactions may provide insights into the effects of phenological shifts on community structure (e.g. via competition) and community level responses to climate change. Nevertheless, the potential for mismatch in competitive intraguild relationships among plants remains underexplored; despite, for example, the recognition that canopy leafing in woodlands affects the competition for light and can constrain phenology in understorey herbs (Whigham 2004; Dahlgren *et al.* 2007).

In order to predict future phenological match or mismatch in community interactions, it is necessary to understand the phenological response of the different species involved. Each species may respond to different phenological cues, exhibit different plasticity or be able to adapt or disperse at different speeds. The opportunity for species to interact with one another is also dependent on the overlap of the distribution of phenological events in different populations (Miller-Rushing *et al.* 2010), rather than the central tendency or first date; measures that are often used in studies of phenological mismatch (e.g. Doi *et al.* 2008). Variance in the distribution of phenological events in a population may also help buffer important species interactions, such as pollination (e.g. Forrest & Thomson 2010). It is therefore necessary to identify the cues, contributions of plasticity and adaptation, and the variance in phenological responses to make more accurate phenological predictions. Integrating knowledge of species interactions driven by phenology into projections of species abundances and geographic distributions will improve our overall understanding of the ecological consequences of climate-driven ecological change (Van der Putten *et al.* 2010).

1.6 Tools for studying phenology

1.6.1 Citizen science

Integrating large scale data into models will improve predictions of changing phenology (Morisette *et al.* 2009), and one of the most effective ways of obtaining such data is through citizen science (Mayer 2010; Dickinson, Zuckerberg & Bonter 2010; Dickinson *et al.* 2012; Amano, Lamming & Sutherland 2016). Phenology lends itself very well to citizen science recording, as encountering seasonal change is part of our everyday lives. Internationally, there are various schemes that record phenological data for different taxa (See Table 1 for selected examples); these include Project Budburst in the US and eBird, which covers the globe.

Table 1. A selection of phenology based citizen science projects from around the globe.

Scheme	Region	Taxa
PlantWatch www.naturewatch.ca/plantwatch/	Canada	Plants
Project Budburst www.budburst.org/	USA	Plants
Naturens kalender www.naturenskalender.se/	Sweden	Plants
PhaenoNet www.phaenonet.ch/de/	Switzerland	Plants
Season Watch www.seasonwatch.in/	India	Plants
Nature's Notebook www.usanpn.org/natures_notebook	USA	Plants, mammals, fish, reptiles, amphibians, birds, insects
Nature's Calendar www.naturescalendar.org.uk/	UK	Plants, fungi, insects, birds, amphibians
UK Butterfly Monitoring scheme www.ukbms.org/	UK	Insects
Queen Quest www.bumbleboosters.unl.edu/queenquest	USA	Insects
FrogWatch www.naturewatch.ca/frogwatch/	Canada	Amphibians
eBird www.ebird.org/	Global	Birds
The Nest Record Scheme www.bto.org/volunteer-surveys/nrs	UK	Birds

In the UK, phenology recording has a long history, from Robert Marsham's 27 'indications of spring', which he and his descendants recorded between 1736 and 1947 on his Norfolk estate; to The Royal Meteorological Society's national phenology recording scheme that ran between 1875 and 1947. Building upon this foundation of long-term data sets, the UK Phenology Network (UKPN) was set up in 1998 by the Centre for Ecology and Hydrology, and The Woodland Trust became the network's custodian of historic and modern phenology observations in 2000.

Nature's Calendar, the scheme that collects phenology data for the UKPN, now has over 16 years of data from across the UK. This scheme records observations of spring and autumn phenology in a range of common plants, insects, birds, amphibians and fungi.

Events include first leafing, flowering and leaf fall in plants, first sighting of insects and migratory birds, first frogspawn and first fungi fruiting bodies. These data have been analysed in various studies and work published on shifting first flowering dates (Amano *et al.* 2010); climatic niche conservatism (Amano *et al.* 2014); asynchronous phenological change across trophic levels (Thackeray *et al.* 2010, 2016); and, the contribution of plasticity and local adaptation to the phenology of the common frog, the orange tip butterfly, garlic mustard, cuckooflower and pedunculate oak (Phillimore *et al.* 2010, 2012, 2013).

While existing work has contributed a great deal to understanding the cues and processes affecting phenology in the UK, the data collected by the UKPN is deficient in some aspects. For instance, the phenology of interacting species is not monitored directly, limiting opportunities for in-depth analysis of phenological interactions. The risk of phenological mismatch is dependent on the overlap of the phenological distributions of interacting species (Miller-Rushing *et al.* 2010), which cannot be assessed using UKPN observations that are based upon the first date of events. To learn something about the full phenological distribution, phenological observations for multiple individuals in a population are required. In addition, to quantify phenological variation within and between individuals requires repeat monitoring of the same individual organism, and this information is not currently captured by Nature's Calendar. Projects such as Nature's Notebook in the USA and PlantWatch in Canada advocate monitoring the same plant throughout multiple phenophases, but this approach has so far been lacking in UK phenology monitoring. Greater collaboration between research and citizen science communities could help address such shortcomings in citizen science collected data (Theobald *et al.* 2015).

1.6.2 Space-for-time substitution

To understand possible future changes in phenological response, some methods rely on projections based on historical responses to varying conditions. However, temporal data are often lacking and space-for-time substitution can be employed when a range of environmental conditions, including temperature, are experienced by a species over its range. Assuming that conditions have remained relatively similar across multiple millennia, biotic patterns over space may be informative about processes at equilibrium. Observations across environmental gradients (e.g. over latitudes) can therefore indicate phenological responses under different conditions, which can be used as a substitute for projected future climates (Dunne *et al.* 2004).

Using short-term space-for-time substitution to predict phenology is simplest when species respond solely via plasticity (Phillimore *et al.* 2013). Where there is evidence of local adaptation in populations, space may be a prediction of a longer term evolutionary response (Phillimore *et al.* 2010). Where biotic interactions are studied, space-for-time substitution may only be applicable to part of the interaction, illustrating the difficulty of making meaningful predictions. For example, evidence of local adaptation in orange-tip butterfly (*Anthocharis cardamines*) phenology, but not in its host plant species *Cardamine pratensis* and *Alliaria petiolata,* means that using space-for-time to model phenological response is only acceptable for the hosts (Phillimore *et al.* 2012). More recently, statistical methods to estimate how optimal phenologies change as the environment changes (termed the environmental sensitivity of selection, *B,* by Chevin *et al.* 2010), using large spatial data sets have been developed (Hadfield 2016). This is particularly useful due to the difficulty of obtaining data to estimate *B* over time, therefore spatial data can be used in lieu of temporal data. Using the relationship between temperature and optimum phenology to project future phenological responses assumes that the relationship between temperature and optimum timing is the same over space and time. This approach was used to infer that plasticity may be able to track shifts in optimum nesting phenology in passerines (Phillimore *et al.* 2016). Applying the same methods to spatial phenology data from citizen science schemes would enable estimates of *B* (inferred on the basis of clinal local adaptation) to be made for a greater number of species across different taxa.

1.6.3 Comparative analyses

Analysing citizen science data and using space-for-time substitution can shed light on the phenological cues, responses, and potential for mismatch in species for which phenology data is available. In order to make inferences for a wider range of species for which data are unavailable, comparative approaches can assess whether phylogenetic signal or certain traits predict such cues or responses (Buckley & Kingsolver 2011; Pau *et al.* 2011).

Currently, phylogenetic relationships have been found in phenological responses to temperature (Willis *et al.* 2008; Davis *et al.* 2010; Mazer *et al.* 2013), and it has been suggested that such phylogenetic signal is a conserved response to abiotic cues (Davies *et al.* 2013), although this has not been explicitly tested. There have been some attempts to use plant traits as a predictor of phenological responses (e.g. Jia *et al.* 2011; Hensel & Sargent 2012; Panchen *et al.* 2014); however, such studies have not specifically explored cue use.

Phylogenetic patterns in the ability of plant phenology to track short-term variation in temperature (likely reflecting plasticity) have been found and linked to extinction risk in Thoreau's Woods (Willis *et al.* 2008). Phylogenetic signal in plastic responses has also been found in plant communities in the USA and UK (Davis *et al.* 2010), and there is evidence that taxonomic families which flower early in the year advance most in response to warming temperatures (Mazer *et al.* 2013). Phylogenetic signal in evolutionary response to temperature may not have been examined directly, but a study that suggested flowering time shift could reflect an evolutionary response found no signal (Davis *et al.* 2010), although the assumption that it indicates an evolutionary response, and not plasticity is questionable. Where plastic phenological responses to temperature in non-native species are similar to those of native communities, it may cause phylogenetically biased patterns of success (Davis *et al.* 2010), and similar flowering shifts in closely related species could affect gene flow and pollination (Miller-Rushing *et al.* 2007).

With respect to plant traits, growth form (Iversen *et al.* 2009), seed size (Jia *et al.* 2011) and pollination strategy (Fitter & Fitter 2002) have been shown to predict the date of phenological events. Few attempts have been made to test whether traits can predict plasticity or adaptation in phenological response, yet understanding this could help predict the potential for future evolutionary responses to climate change (Franks *et al.* 2014).

1.7 Aims

The overall aim of this thesis is to help guide predictions about how UK plant species will fare under climate change. To do this I address a series of specific aims about phenological variation across two distinct strands.

Macroecological analyses

These analyses will use data for 22 UK species provided by the UKPN and weather data from the UK Met Office. Phenological records from the 'Nature's Calendar' scheme and interpolated daily mean temperatures will be analysed using a mixed modelling approach to address the following aims:

i) To determine the temperature and photoperiod cues that best predict phenological events in different UK plant species.

ii) To establish whether plasticity will be able to keep up with changes in the optimum phenology for these species.

Estimates of plasticity and clinal local adaptation from these analyses will then be used in a comparative analysis to test:

iii) Whether plant traits predict variation in median phenology, plasticity and non-clinal local adaptation across species.

iv) Whether there is a phylogenetic signal in different aspects of the phenological response.

Track a Tree

The Track a Tree citizen science scheme was developed as part of this thesis. It gathered phenological records for individual trees and their associated understorey flowering plants in order to address the following aims:

v) To determine whether the relative phenology of woodland trees and selected ground flora species is correlated and spatially consistent.

vi) To identify the sources that contribute to phenological variation in UK woodland trees, within sites, between sites and over time.

Chapter 2

The roles of plasticity and microevolution in tracking temperature-mediated phenological optima in plants

2.1 Abstract

Changes in phenology are a key biotic impact of climate change, and as a consequence of changing temperatures the optimum phenology for temperate plants may shift. The fates of populations can be projected if the shift in the optimum, and the ability of plasticity to track this optimum, can be quantified. Here I used a statistical method to estimate the temperature-sensitivity of the phenological optimum and plasticity. I applied this approach to the first leafing and flowering dates of 22 UK plant species collected via the Nature's Calendar citizen science project, which contributes observations to the UK Phenology Network (UKPN). I found that all species were sensitive to forcing temperatures, with plastic responses to forcing ranging between -3 and -8 days°C^{-1}. Chilling temperatures and photoperiod tended to be important cues for species with early and late phenology, respectively. For most species I found that plasticity was adaptive and for seven species plasticity was sufficient to track geographic variation in the optimum phenology, suggesting they may adjust well to changing temperatures. In four species plasticity did not track the optimum, which is consistent with clinal local adaptation to temperature and could place the phenology of these species under directional selection in a changing climate. For the remaining species, the results were inconsistent and no conclusions could be drawn about the degree to which plasticity may track their optimum phenology.

2.2 Introduction

Shifts in phenology are among the most widely reported ecological responses to changing climate across different ecosystems and taxa (Walther *et al*. 2002; Parmesan & Yohe 2003; Settele *et al.* 2014). For temperate plants, the timing of spring events, such as leafing and flowering have been especially well-recorded by both professional and citizen scientists, and analysis of the resultant longitudinal datasets reveals that as temperatures have risen spring phenology has advanced in many species (Fitter & Fitter 2002; Amano *et al.* 2010). Some of the advancement in phenology will be due to microevolutionary change (Franks *et al.* 2014), but direct, plastic responses to a changing climate probably dominate (Nicotra *et al.* 2010). Temperate plants often exhibit pronounced temperature-mediated plasticity in their spring phenology, as documented via longitudinal studies of individuals (Vitasse *et al.* 2010, www.trackatree.org.uk), geographic transplants (Kramer 1995) and experimental approaches (Franks *et al.* 2014).

Plastic phenological responses to a changing climate are often thought to be adaptive. Consequently, the observed advance in phenology strongly suggests that the optimal phenology has advanced as the climate has warmed. However, little information is available as to whether observed phenologies are advancing at the same rate as optimal phenologies, and what the demographic consequences of any shortfall are (see Wilczek *et al.* 2014 for an exception). This paucity of information reflects the difficulty in measuring how optimal phenologies change per unit change in the environment; termed the environmental sensitivity of selection (B) by Chevin *et al*. (2010).

The standard approach for estimating B requires that the phenology-fitness surface be estimated in several different environments, and the relationship between the fitness peak and the driving aspect(s) of the environment characterised (Chevin, Visser & Tufto 2015). The logistical challenge this poses is unfortunate given the importance of B in estimating the maximum rate of environmental change under which a population can persist (Chevin *et al.* 2010). In the context of climate change and temperature, B can be taken to map temporal changes in a temperature cue to temporal changes in the optimal phenology. However, in a spatial context B also maps spatial changes in the temperature cue to spatial changes in the optimal phenology. In a simple model where temperature varies clinally (with, for example, latitude) and phenotypic optimums depend linearly on temperature, spatial differences in the observed phenology would quickly equilibrate to spatial differences in the optimal phenology, if there is no spatial variation in population density and dispersal is symmetric (Felsenstein 1977; Slatkin 1978). This means the spatial relationship between phenology and the temperature cue could be used as an estimator of B. When spatial changes in temperature also have a stochastic component then this estimator is biased towards zero, but an unbiased estimator of B can be obtained from the ratio of the rate at which phenology changes with latitude with the rate at which the temperature cue changes with latitude (Hadfield 2016). Where the environment of selection and development (the cue) are the same, this estimate of B will correspond to the optimal slope of phenology on temperature. If the correlation between the two environments is < 1, this estimate of B will correspond to the optimal phenological response to the environment of development, which is shallower than the optimal phenological response to the environment of selection (Tufto 2015). Where the correlation between the environment of development and selection is the same over time as it is over space, the spatially-derived estimate of B will represent the optimal phenological response to year-to-year variation in the environment of development (Hadfield 2016).

Regression-based estimation of B from observational data relies on the correct phenological cue(s) having been identified. In most temperate plants the primary drivers of spring phenology are temperature and photoperiod (Rathcke & Lacey 1985; Polgar & Primack 2011), though the relative importance of these cues will vary among species (Laube *et al.* 2014) and continues to be a source of disagreement (Chuine, Morin & Bugmann 2010; Körner & Basler 2010). Temperatures at different times of the year can have opposing effects, with the forcing effect of warm springs usually advancing phenology, whilst warm conditions in autumn/winter may delay phenology via effects on dormancy induction, breaking dormancy and stimulating growth (Murray, Cannell & Smith 1989; Polgar & Primack 2011; Laube *et al.* 2014; Roberts *et al.* 2015). Experimental studies demonstrate a role for photoperiod in some species (Caffarra & Donnelly 2011), though the precise nature of any interactions between photoperiod and the response to forcing and/or chilling temperatures is not well understood (Polgar & Primack 2011; Vitasse & Basler 2013). While longitudinal data from a single site are not informative about any effect that photoperiod may have, spatiotemporal data, as collected by many citizen science phenology schemes, may be (Phillimore *et al.* 2013).

The UK Phenology Network (UKPN) was set up in 1998 and now comprises hundreds of thousands of plant phenology records collected by citizen scientists that are replicated over space and time. In this study I apply a recently developed statistical framework (Hadfield 2016; Phillimore *et al.* 2016) to the spring phenology (first leafing and first flowering) of 22 plant species. My main aims are to estimate (i) the temperature sensitivity of the phenological optimum (B), and (ii) the degree to which phenological plasticity is adaptive and tracks geographic variation in the optimal phenotype. I include three non-native species (horse chestnut, sycamore and larch), which I predict will show no local adaptation and respond solely through plasticity. This analysis relies on having identified the correct phenological cues, and a secondary aim is therefore to identify the time windows during which forcing temperatures have an effect and to identify the relative importance of chilling temperatures versus photoperiod. While the temperature sensitivity of plant phenology is often modelled using growing degree day mechanistic models (e.g. Chuine 2000), here I adopt a reaction norm approach due to its amenability to linear statistical modelling and to facilitate comparisons with theoretical models of quantitative trait evolution (e.g. Chevin *et al.* 2010; Hadfield 2016). Where growing degree day and linear reaction norm approaches have been applied to the same datasets, insights into phenological cues and responses are similar (Phillimore *et al.* 2013; Roberts *et al.* 2015).

2.3 Methods

2.3.1 Spatiotemporal data

I used phenological data collected by citizen scientists from the UKPN (www.naturescalendar.org.uk). I focused on spring events (first flowering and first leafing) collected over the period 1998-2014 for 22 species (see Table 1 for details), excluding species for which I anticipated greater data quality issues (see Appendix A.1 for selection criteria). Prior to any analysis, I visually inspected histograms and removed extreme outliers for each species. Extreme outliers were classified as those outside the expected 95% distribution that were likely to have been caused by observer error. In order to minimise measurement errors introduced by novice recorders, for each species I excluded all data collected by participants who only contributed records for a single year. The number of filtered observations ranged between 2,805 for sessile oak to 22,177 for lesser celandine (Table 1).

Each phenological observation was assigned to the 5 x 5km grid cell (hereafter 5km grid cell) in which it was reported, and matched to daily air temperature data interpolated between recording stations on the same grid for the appropriate year (Perry & Hollis 2005; Perry *et al.* 2009; www.metoffice.gov.uk/climatechange/science/monitoring/ukcp09/). Based on average Central England Temperatures for the period Feb – May (Parker, Legg & Folland 1992), there has been little directional trend in UK spring temperatures over the focal years (slope = -0.06 ± 0.03).

To calculate the day-length (time from sunrise to sunset) in minutes for each day, sunrise and sunset equations (Meeus 1991) were applied to the centroid of each 5km grid cell. Each 5km grid was assigned to a 150 x 150km grid cell (hereafter 150km grid cell), which was treated as an arbitrary definition of a population in subsequent analyses, as in earlier studies using a similar approach (Phillimore *et al.* 2010, 2016). Data were stored in a spatial relational database PostgreSQL, version 8.3.5 (PostgreSQL Global Development Group). The database was queried via the RpostgreSQL R package.

Table 1. Species records selected for analyses from the UKPN data set.

Species	**Binomial**	**Event**	**Collection period**	**Unfiltered records**	**Filtered records**	**% of original data**
Alder	*Alnus glutinosa*	Leafing	2000-2014	6405	4988	78
Ash	*Fraxinus excelsior*	Leafing	1998-2014	12350	10165	82
Beech	*Fagus sylvatica*	Leafing	1998-2014	12586	10281	82
Blackthorn	*Prunus spinosa*	Flowering	1998-2014	20782	16913	81
Bluebell	*Hyacinthoides non-scripta*	Flowering	1998-2014	26591	21362	80
Cocks-foot	*Dactylis glomerata*	Flowering	1999-2014	5049	4013	79
Cuckooflower	*Cardamine pratensis*	Flowering	1998-2014	13883	11533	83
Dog rose	*Rosa canina*	Flowering	1998-2014	13529	11163	83
Elder	*Sambucus nigra*	Leafing	1998-2014	15048	12267	82
Field maple	*Acer campestre*	Leafing	1999-2014	5353	4445	83
Garlic mustard	*Alliaria petiolata*	Flowering	1998-2014	13835	11620	84
Hawthorn	*Crataegus monogyna*	Leafing	1998-2014	20486	16813	82
Horse chestnut	*Aesculus hippocastanum*	Leafing	1998-2014	16983	13979	82
Larch	*Larix decidua*	Leafing	1998-2014	5045	3808	75
Lesser celandine	*Ranunuculus ficaria*	Flowering	1998-2014	26555	22177	84
Meadow foxtail	*Alopecurus pratensis*	Flowering	1999-2014	5006	4001	80
Pedunculate oak	*Quercus robur*	Leafing	1998-2014	11285	9219	82
Rowan	*Sorbus aucuparia*	Leafing	1998-2014	12026	9754	81
Sessile oak	*Quercus petraea*	Leafing	1998-2014	3688	2805	76
Silver birch	*Betula pendula*	Leafing	1998-2014	14892	12161	82
Sycamore	*Acer pseudoplatanus*	Leafing	1998-2014	13358	10929	82
Wood anemone	*Anemone nemorosa*	Flowering	1998-2014	15419	12471	81

2.3.2 Statistical analyses

I fitted a series of linear mixed models designed to identify the environmental cues that best explain the spatiotemporal variation in phenology of each species. Models were fitted in ASReml-R (Butler *et al.* 2009; Gilmour *et al.* 2009).

All models (parameters summarised in Table 2) treated the ordinal date of the phenological observation as a response variable and included 150km grid cell, year, 25km:year and a residual term as random effects (Table 2). The motivation for including the 25km:year term was to account for pseudoreplication of interpolated temperatures within a 5km grid cell and year, which occurs when multiple phenology observations are made in the same 5km grid square. A 5km:year term was not used as this would have resulted in zero residual temperature variation.

The **null** model included only the intercept as a fixed effect. I also considered geographic and temporal cline models in order to (i) identify broad spatial and temporal trends, and (ii) act as an additional baseline against which the performance of cue based models can be compared. The simple clinal model included year (as a numeric variable), and latitude and longitude as fixed effects (**geo1**). A more complex clinal model also included the interaction between latitude and longitude, as well as quadratic terms of latitude and longitude (**geo2**).

All subsequent models included environmental cues (Fig. 1). The first was consistent with a photoperiod threshold triggering phenology (**photo**). The ordinal date at which the specified minutes of daylight (I considered values between 486 and 980 minutes at intervals of 4 minutes) was first reached in each 5km grid cell was used as an offset in the model, which made the response the time lag between a specified photoperiod being reached and the date of the phenological event. The only fixed effect in this model was the intercept.

For models that incorporated an effect of temperature I followed Phillimore *et al.* (2010; 2016) and fitted both phenology and temperature as a bivariate response. By using a bivariate response I was able to separately model the relationship between phenology and temperature over space (across locations) versus time (within locations). The temperature response in the **temp** model was the mean temperature during a predefined sliding-window. The start and end dates for the sliding-windows were the same for all locations, and I tested windows by varying the start date (from ordinal days -59 to 100 in 2 day intervals) and duration (from 4 to 120 days in 2 day intervals). Each time window was constrained, so it did not extend beyond ordinal day 150 (30th May). The end of the time window was included as an offset for the phenology response, which generated a model that predicted whether temperature within a time window predicts the lag time until the phenological response is observed.

To model the combined effects of temperature and photoperiod (**phototemp**), I allowed sliding-windows of thermal sensitivity to be initiated once a specified day length (using the same range of values as the photo model) had been reached. This date then became the start of the local time window and I considered the same range of window durations as in the temp model.

The final model included two sliding-windows during which mean temperatures predict phenological response (**doubletemp**), with both temperature variables and the phenological lag (between the end of the second time window and the phenological event) fitted in a trivariate response. The time window immediately preceding the event (the forcing window) was identical to the best performing temp model for each species. I then explored mean temperatures over a pre-forcing time window during the autumn/winter preceding the phenological event. For simplicity, this window is referred to as the “chilling” window, although the timing of this window could reflect temperatures that impact on phenology through a mechanism other than chilling, such as dormancy induction (Heide 2003). I varied start dates (from ordinal day -120 up to the beginning of the forcing window in 2 day intervals) and durations (from 4 to 120 days in 2 day intervals) in all combinations.

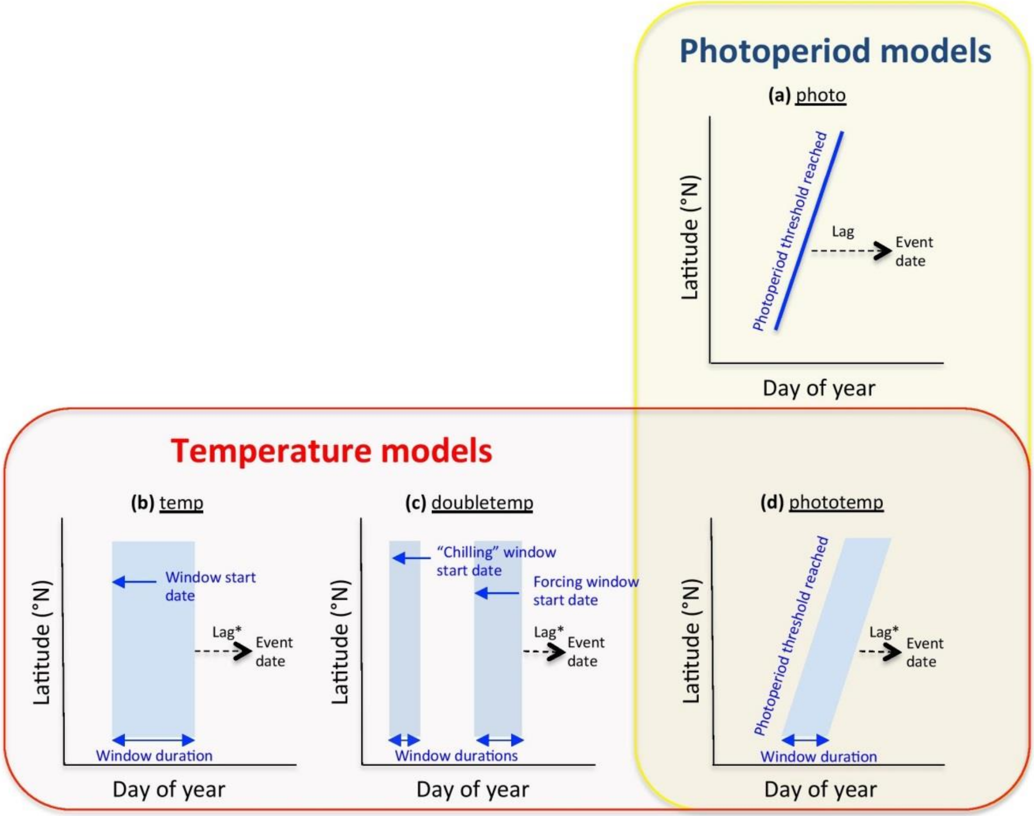


Figure 1. A schematic depicting parameters pertaining to cues under models that include (a, d) photoperiod and (b – d) average temperature in a sliding-window. Parameters that are optimized via iterative searches are in blue. Lag* indicates models where the lag duration is a linear response to spatial and temporal variation in the mean temperature during the time window.

Table 2. Parameters included in mixed effect models and in the calculation of AICs.

Model	**Mixed model terms**				
	Response(s)	Fixed effects	Random effects	Additional parameters used to generate the model offset	K used in AIC based on conditional likelihood[§]
null	Phenology	Intercept	150km grid cell, year, 25km:year, residual		5
geo1	Phenology	Intercept, Year, latitude, longitude	150km grid cell, year, 25km:year, residual		8
geo2	Phenology	Intercept, Year, latitude, longitude, latitude:longitude, latitude^2, longitude^2	150km grid cell, year, 25km:year, residual		11
photo	Phenological lag	Intercept	150km grid cell, year, 25km:year, residual	Photoperiod threshold	6
temp	Phenological lag, temperature	Intercepts, latitude, longitude	150km grid cell, year, 25km:year, residual	Temperature window start and end dates	13
phototemp	Phenological lag, temperature	Intercepts, latitude, longitude	150km grid cell, year, 25km:year, residual	Temperature window start and end dates	13
doubletemp	Phenological lag, “chilling” temperature, forcing temperature	Intercepts, latitude, longitude	150km grid cell, year, 25km:year, residual	“Chilling” and forcing temperature window start and end dates	23

[§] For the conditional likelihood each fixed term contributed 1 parameter and each random term contributed 2 parameters.

I used Akaike Information Criteria (AIC) and AIC weights (Burnham & Anderson 2004) to compare the best models of each class (see Table 2 for the parameters included in the AIC calculation for each model). ASReml outputs the restricted maximum likelihood, therefore in order to compare models with different fixed effects, this was converted to a normal likelihood (Phillimore *et al.* 2016). For bivariate models I calculated the likelihood of phenology (y_P) conditional on forcing temperature (y_F) and parameters from the bivariate model ($\hat{\theta}$)

$$\mathrm{L}(y_P\,|\,y_F,\hat{\theta}) = \mathrm{L}\big(y_P, y_F\big|\hat{\theta}\big)/\mathrm{L}(y_F\,|\,\hat{\theta})$$

Here the likelihood of the bivariate model ($\mathrm{L}\big(y_P, y_F\big|\hat{\theta}\big)$) was required as well as the likelihood of temperature conditional on the relevant model parameters from the bivariate model ($\mathrm{L}(y_F|\hat{\theta})$).

For models with a trivariate response, I calculated the likelihood of phenology (y_P) conditional on forcing temperature (y_F) and "chilling" temperature (y_C) and parameters from the trivariate model ($\hat{\theta}$)

$$\mathrm{L}(y_P|y_F, y_C, \hat{\theta}) = \mathrm{L}\big(y_P, y_F, y_C\big|\hat{\theta}\big)/\mathrm{L}(y_F, y_C|\hat{\theta})$$

The sliding-window method involves multiple testing which inflates type I errors, though the very high autocorrelation in daily temperatures served to reduce the severity of this problem (M. Morrissey pers comm).

I obtained an estimate of the variance-covariance between response variables for each random effect (r):

$$\begin{bmatrix} v_{Pr} & \mathbf{v}'_{Pr,Tr} \\ \mathbf{v}_{Pr,Tr} & \mathbf{V}_{Tr} \end{bmatrix}$$

v_{Pr} is the variance in phenology, $\mathbf{v}_{Pr,Tr}$is a vector of covariance(s) between phenology and the temperature cue(s) and $\mathbf{V}_{Tr}$ is a matrix of (co)variances between the temperature cue(s). In the bivariate model $\mathbf{v}_{Pr,Tr}$ and $\mathbf{V}_{Tr}$ are scalars.

The slope estimate(s) of the phenological lag on the temperature cue(s) was obtained as $\mathbf{V}_{Tr}^{-1}\mathbf{v}_{Pr,Tr}$ for each random term (Phillimore *et al.* 2012). When year was the random effect I obtained a temporal slope (i.e. the change in phenology in response to year-to-year variation in temperature), and when 150km grid was the random effect I obtained a de-trended spatial slope (i.e. the change in phenology in response to non-clinal spatial variation in temperature).

I assumed that temporal slopes were primarily due to the mean population-level temperature-mediated phenological plasticity (b) (for detailed discussion of the validity of assumptions required by the theory and statistical models see Table A1 in Appendix A). Following the approach of Phillimore *et al.* (2016) I estimated the temperature sensitivity of selection over latitude and longitude, which I refer to as B_{lat} and B_{lon}. Assuming that the temperatures in the selected thermal window cue phenology, that populations are at migration-selection equilibrium and that population density is constant in space, B can be estimated by dividing the slope of phenological lag on latitude (or longitude) by the slope of temperature on latitude (or longitude) (Hadfield 2016). In the absence of confounding variables, I anticipated that $B_{\mathrm{lat}}=B_{\mathrm{lon}}$. Assuming that plasticity is constant among populations, $B–b$ can be used to estimate the contribution made by clinal local adaptation. When $|B - b| < |B|$ then plasticity partially tracks the optimum and can be said to be adaptive, and $B = b$ indicates perfect adaptive plasticity.

In addition to clinal local adaptation, non-clinal local adaptation can be estimated as the difference between the de-trended spatial slope and b (Phillimore *et al.* 2010, 2016). When $|B - b| > 0$, migration is expected to reduce the efficiency of adaptation to track B across temperatures that vary stochastically across grid cells (Hadfield 2016). Therefore, I predicted that the de-trended spatial slope will lie between B and b.

To get credible intervals for slopes and slope differences I selected the lowest AIC model for each species and re-estimated the parameters in a Bayesian setting using MCMCglmm (Hadfield 2010). For species where the phenological response was best explained by the temp or phototemp models I ran MCMCglmm using forcing windows from the best performing model. For species where phenology was best predicted by the doubletemp model, I tested the correlation of mean temperatures across the two time windows over time and space and found that temperatures in the two time windows were highly correlated over space (but not time, r over space varies in the range 0.57 – 0.99, Table A4 in Appendix A). I interpreted this as meaning that the model was effective at identifying the time windows during which temperature is most important as a phenological cue, but that multicolinearity precludes interpretation of forcing and “chilling” slopes estimated across spatially varying temperatures. For these species I focused solely on parameter estimates for the forcing window, and re-estimated parameters from the best performing temp or phototemp model.

I ran models for 60,000 iterations, discarding the first 10,000 as burn-in and sampled every 10th iteration to get posterior sample sizes of 5000 for each species. I visually inspected traces of the posterior distributions of focal parameters to check for model convergence. I used priors for the (co)variance components which were drawn from the inverse Wishart distribution with $V = I$ and $\nu = 0.002$. All statistical analyses were conducted in R (R Core Team 2012).

2.4 Results

2.4.1 Spatiotemporal trends

Phenology varied among 150km grid cells for all focal species (Fig. 2), with species such as lesser celandine, wood anemone and meadow foxtail showing substantially greater variation over space than others such as field maple and beech. Variance among years was of similar magnitude to the variance among 150km grid cells, and tended to be higher for species with earlier phenology such as lesser celandine, hawthorn and blackthorn. For all species, residual variance within a single 25km grid cell and year was considerably larger than other variance components (Fig. 2).

Of the basic spatiotemporal models, geo1 was preferred for two species (field maple and garlic mustard), with geo2 the best performing for the remaining twenty species. The geo2 model describes a geographical scenario where the effects of latitude and longitude interact and are subject to quadratic relationships. For most species, phenology was delayed as latitude increased (Fig. 3), though the magnitude of the gradient varied, being steepest in bluebell and pedunculate oak and shallow in hawthorn, horse chestnut and beech. For elder, sycamore, rowan, garlic mustard and field maple, phenology advanced as latitude increased. Longitudinal trends were more variable, with some species being most advanced in the west and others in the east. Several species showed longitudinal clines that changed sign with latitude (most where the east was earliest in the south and the west was earliest in the north). Directional temporal shifts (estimated using the geo models) in phenology during the period 1998-2014 were non-significant for all species, consistent with the weak temporal temperature trend over this period.

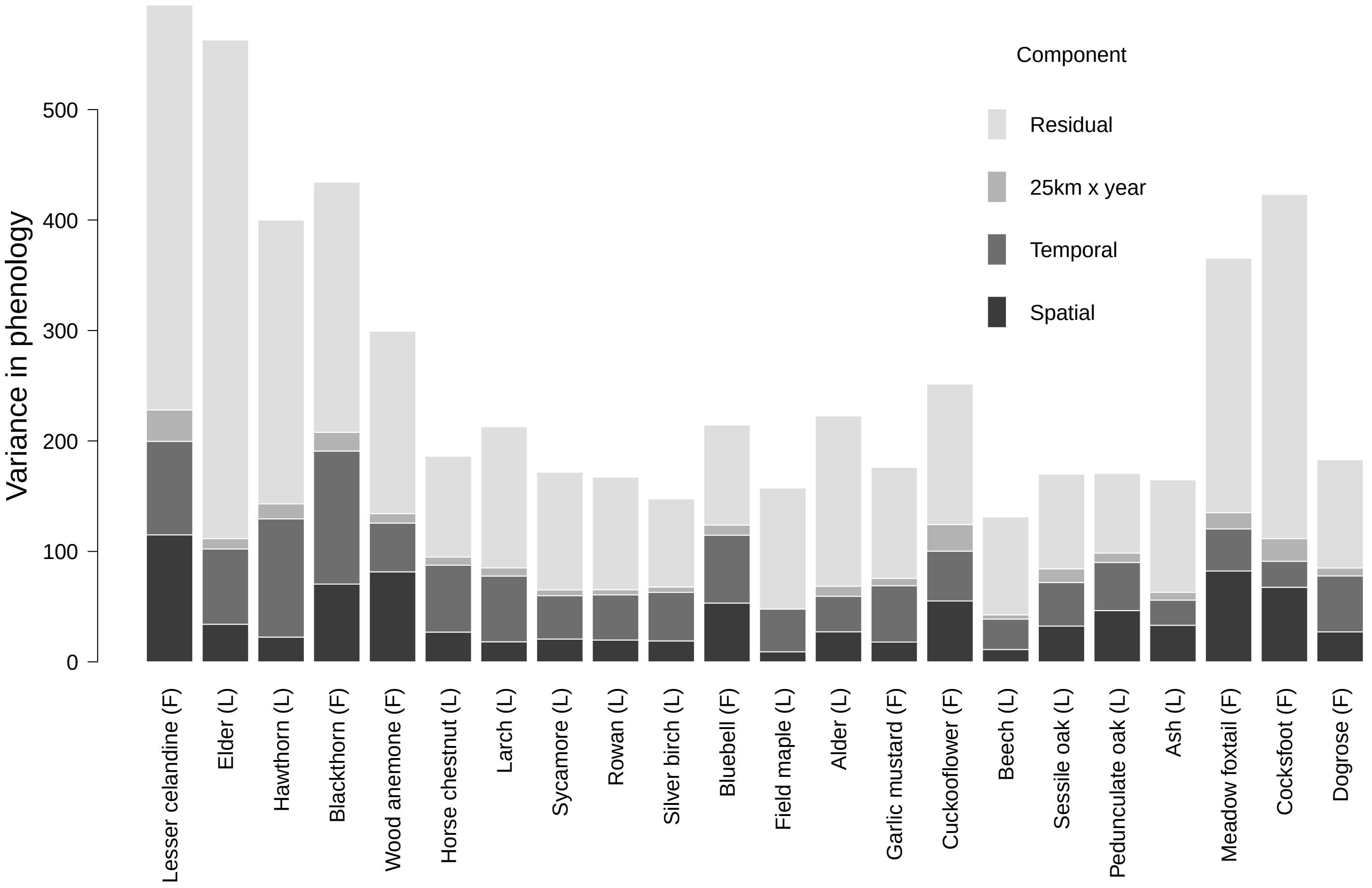
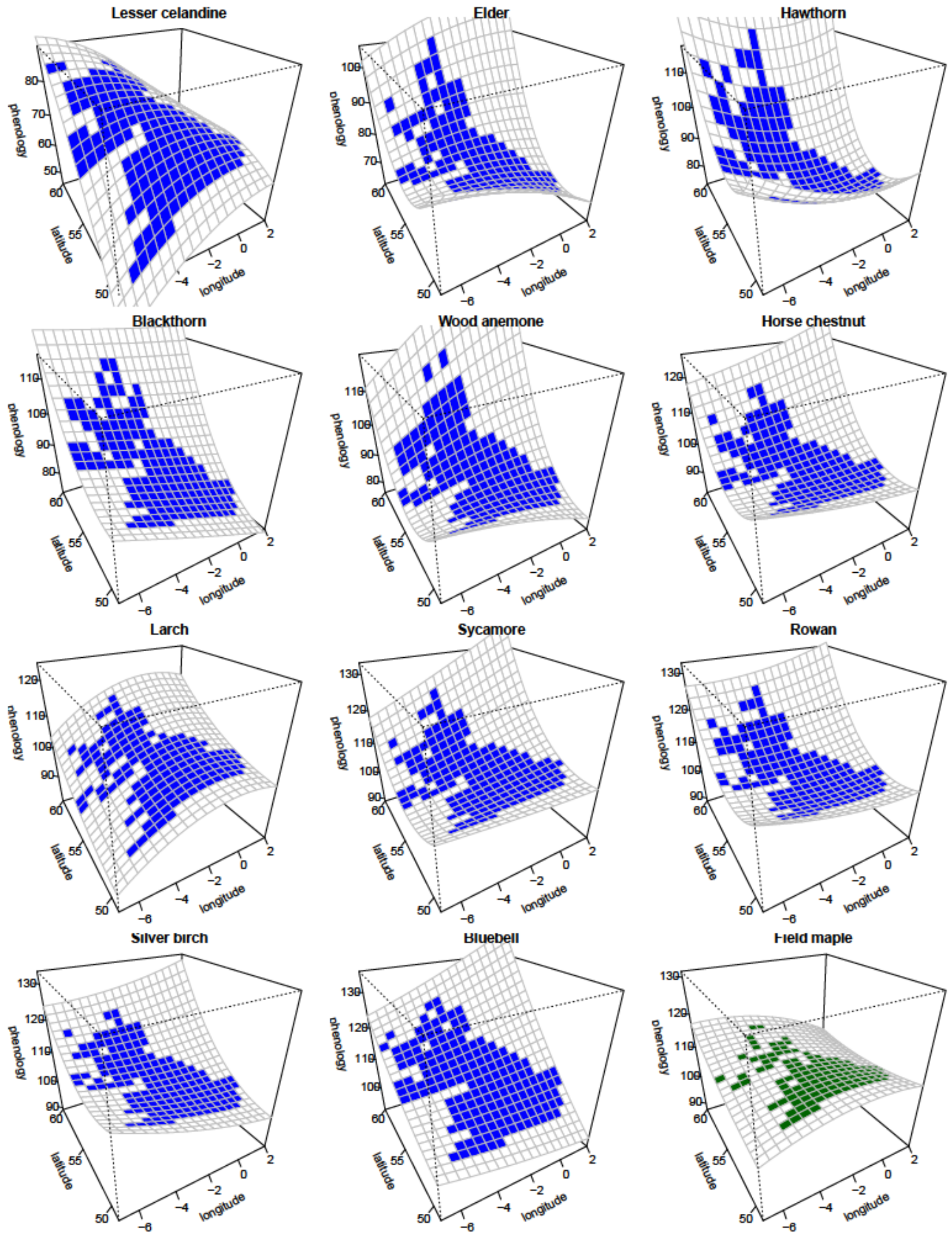


Figure 2. Variance components of the null model for each species, where bars represent variance components. Species are plotted in ascending order of mean phenology from left to right.


Lesser celandine
Elder
Hawthorn
Blackthorn
Wood anemone
Horse chestnut
Larch
Sycamore
Rowan
Silver birch
Bluebell
Field maple
phenology
latitude
longitude

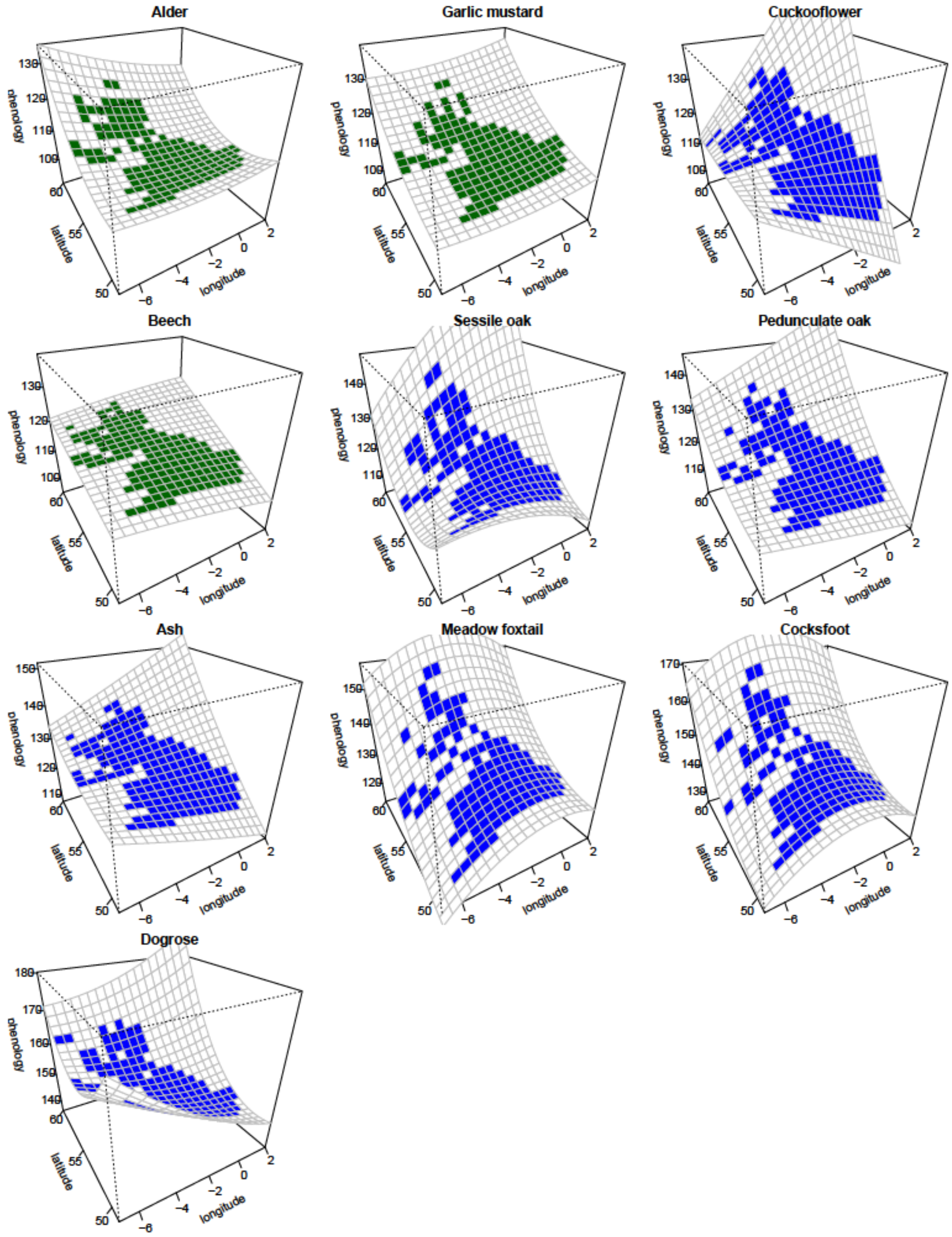


Figure 3. Latitudinal and longitudinal trends in phenology. Slope estimates obtained from the lowest AIC simple clinal model (geo1 = green or geo2 = blue). Filled grid cells represent locations with records available. Species are plotted in ascending order of mean phenology.

2.4.2 Cues

All focal species were sensitive to spring forcing (Fig. 4), but they varied in whether they were sensitive to “chilling” or photoperiod and in the parameters defining the sliding-windows. The single sliding-window temp model was preferred for meadow foxtail, whilst the more complex doubletemp model performed best for thirteen species, most of which are typified by early phenology. For eight predominantly late spring species, the phototemp model, wherein the window of thermal sensitivity comes into effect once a threshold number of minutes of daylight has been met, performed best.

For all species, the spring forcing windows preceded and overlapped with spatiotemporal variation in the event itself. Forcing windows were earlier for species with earlier phenology; however there were no clear trends in the length of forcing window according to best model type or timing of phenological event (Fig. 5). For species with phenology best predicted by the phototemp model, forcing windows were delayed further north (Fig. 5). The difference in the timing of photoperiod threshold being met at 50°N versus 56°N varied from three days in alder to 11 days in sycamore and field maple, with the latitudinal gradient in the start of the window becoming shallower toward the equinox. For species whose phenology was best predicted by the doubletemp model, the pre-forcing or “chilling” temperature sensitivity window was generally found during the latter part of the year prior to the phenological event itself (Fig. 5). Sessile oak was an exception, where the “chilling” window was in the year of the phenological event, between ordinal days 16 - 19.

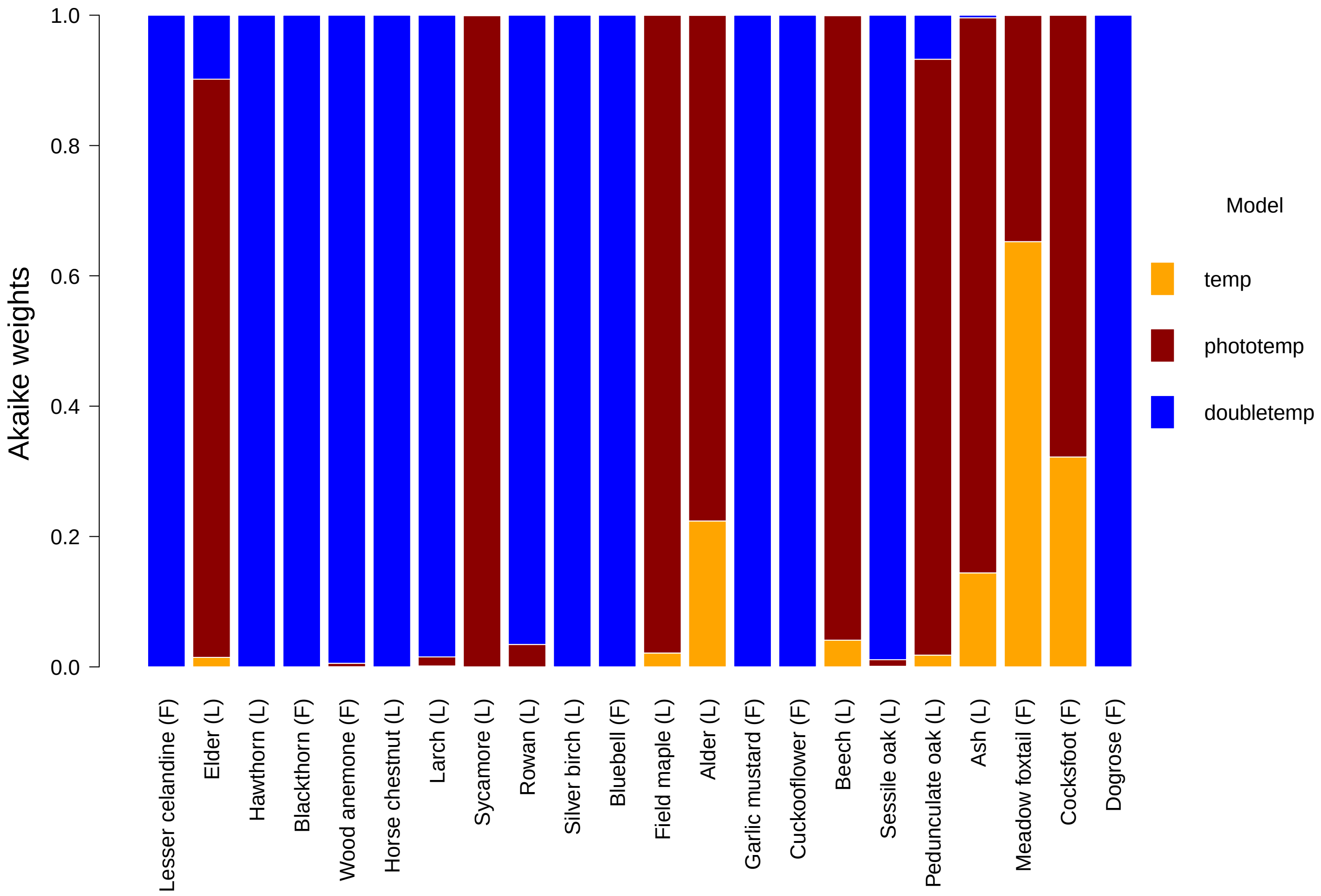


Figure 4. AIC weights across the minimum AIC candidate of each model type. Models with AIC weights <0.01 are not visible. Species are in ascending order of mean phenology from left to right.

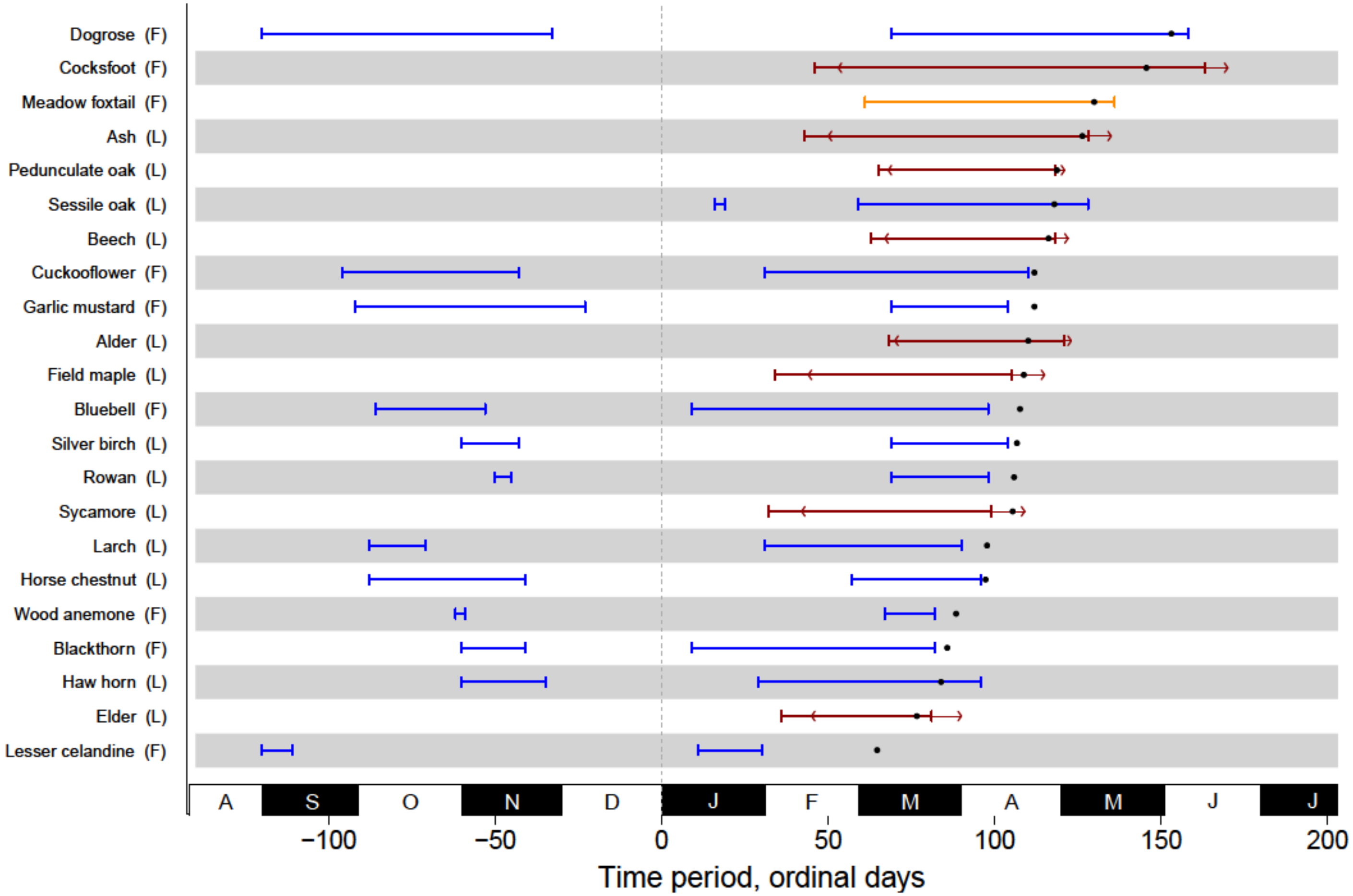


Figure 5. Time windows during which mean temperatures best predict the phenological events (median date of event shown as filled circle) for each species. Species are plotted in ascending order of mean phenology from bottom to top. Event type is reported in parentheses, where F = flowering and L = leafing. Bars are coloured according to the lowest AIC model; orange = temp, red = phototemp and blue = doubletemp. Time windows for the phototemp model covary with latitude; the bar depicts the time window at 50°N and the arrow head the time window at 56°N.

2.4.3 Temperature as a predictor of phenology

The temporal slope of phenology on temperature during the forcing window, which I assume to estimate the population mean temperature-mediated plasticity (b), was significantly negative for all focal species (Fig. 6a), with posterior median estimates that varied from -3 to -10 days°C^{-1}. In general I found little evidence of spatial variance in b among 150km grid cells (Fig. A2 in Appendix A), except in lesser celandine, for which plasticity was estimated to be shallower at the temperature extremes. This is most likely attributable to the sliding-window partially missing the window of thermal sensitivity at the latitudinal extremes, causing the slopes to be underestimated. Temporal slopes of phenology on temperature during the "chilling" window were close to 0 in most cases, though positive for larch, horse chestnut and sessile oak (Table A4 in Appendix A). The temporal "chilling" slopes were shallower than the forcing slopes, and ranged from -2 to 2 days°C^{-1}.

Due to multicolinearity over space (but not time) between forcing and "chilling" temperatures in the doubletemp model (see methods) I did not interpret the latitudinal, longitudinal or the de-trended spatial slope estimates from this model and instead used the forcing parameters from the next best performing model (temp or phototemp). The temperature sensitivity of the optimum across latitudes (B_{lat}) and longitudes (B_{lon}) was significantly negative in most cases (Fig. 7a, b), with a median gradient of ~ -3 days°C^{-1}. Sycamore, which showed a significant positive gradient across both spatial clines was a notable exception. In 16 of 22 cases B_{lat} and B_{lon} were of the same sign (Fig. 7a, b, Tables A2 & A3 in Appendix A). The among 150km grid cell de-trended spatial slopes of phenology on temperature were negative for all species other than garlic mustard and sycamore, and significantly so for ten species (Fig. 7c, Tables A2 & A3 in Appendix A). The de-trended spatial forcing slopes varied from around 0 in cuckooflower and dogrose to around -6 days°C^{-1} in lesser celandine and field maple.

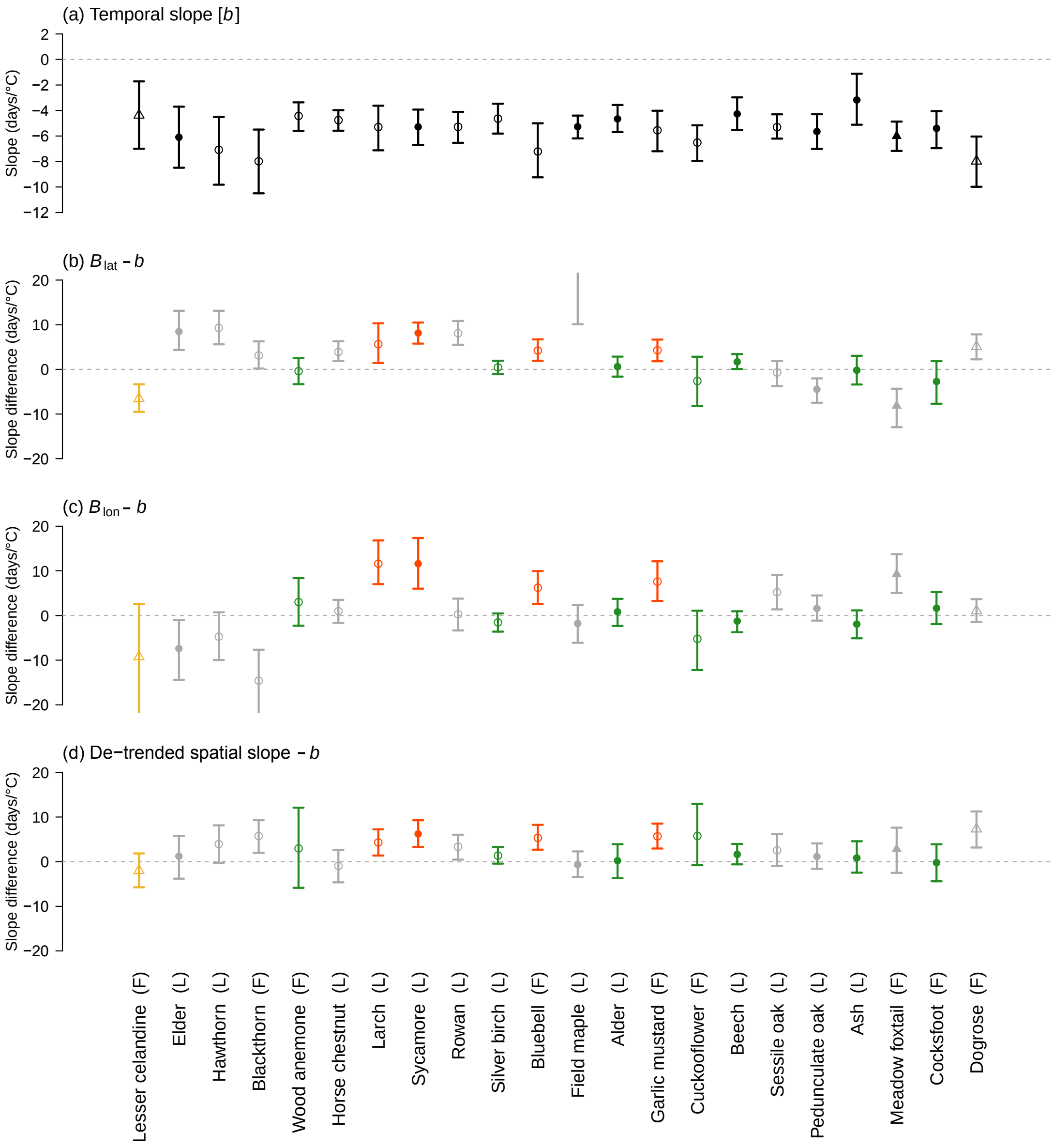


Figure 6. Posterior medians and 95% credible intervals for parameters estimated over the forcing time window. (a) Temporal slope of phenology regressed on temperature, assumed to estimate plasticity, *b*, (b) B_{lat}-*b*, (c) B_{lon}-*b,* and, (d) the de-trended spatial slope (across 150km grid cells) of phenology on temperature minus *b*. Bars are coloured according to the ability of plasticity to track the optimum $|B - b|$: grey = inconsistent signal, gold = consistent in direction, orange = consistently significant, and, green = consistent with the hypothesis that plasticity tracks the optimum $|B - b| = 0$. Slopes for species whose phenology was best predicted by the doubletemp model were plotted using results from the lowest AIC alternative model and are represented by unfilled datapoints. Species are in ascending order of mean phenology from left to right.

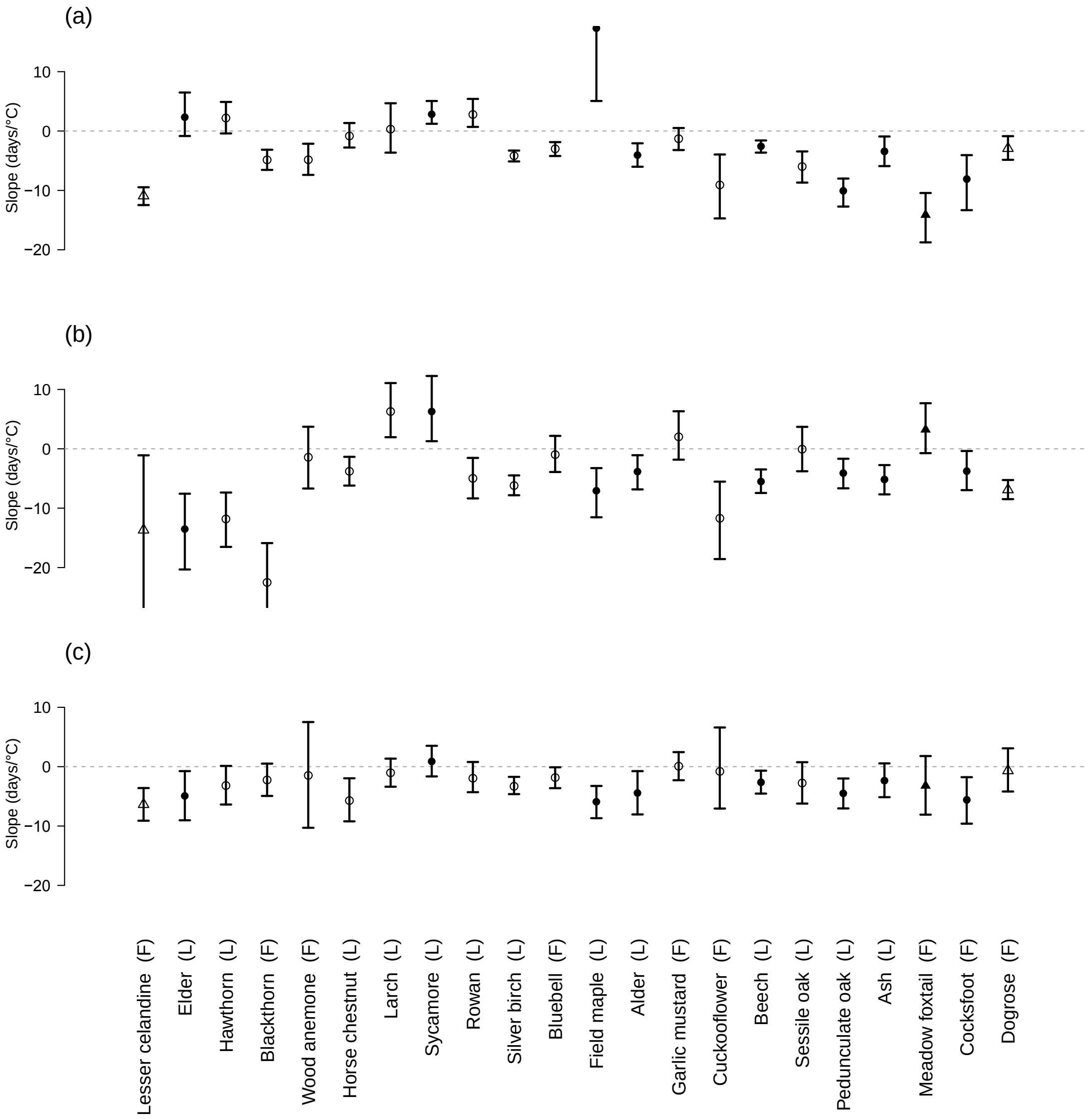


Figure 7. Posterior medians and 95% credible intervals for slopes of phenology on forcing temperature that correspond to the temperature sensitivity of the optimum phenology across (a) latitude = B_{lat}, (b) longitude = B_{lon} and (c) the de-trended spatial slope across 150km grid cells. Slopes for species whose phenology was best predicted by the doubletemp model were plotted using results from the lowest AIC alternative model and are represented by unfilled datapoints. Species are in ascending order of mean phenology from left to right.

2.4.4 The contributions of plasticity and local adaptation to spatial variation

Focusing solely on responses to forcing, four species, larch, sycamore, bluebell and garlic mustard, showed significant $B - b$ differences that are qualitatively consistent when B is estimated as B_{lat} or B_{lon} (Fig. 6b, c). For each of these species the gradient of the optimum (B) was shallower than the plastic slope b, consistent with countergradient local adaptation (i.e., temperature mediated local adaptation acting in the opposite direction to plasticity), or the effect of a third variable on the optimum (Chevin & Lande 2015). For lesser celandine alone, B was more steeply negative than b, consistent with co-gradient local adaptation (i.e., temperature-mediated local adaptation acting in the same direction as plasticity), although the credible interval for $B_{\text{lon}} - b$ includes zero.

For seven species, the two estimates of $B - b$ did not depart significantly from zero, consistent with temperature-mediated plasticity tracking clinal variation in the phenological optimum (Fig. 6b, c). In a further three species (horse chestnut, pedunculate and sessile oak), while there was a significant difference between $B - b$ over either latitude or longitude, the point estimate didn't depart greatly from 0, implying that plasticity is adaptive and partially tracks the optimum in these species. For the remaining seven species $B - b$ estimates over latitudes and longitudes were inconsistent. I found forcing plasticity to be adaptive (inferred as where point estimates of $|B\text{-}b|<|B|$) for 12/22 species when B is estimated as B_{lat}, and 16/22 species when B is estimated as B_{lon}. Plasticity was found to be consistently maladaptive for bluebell, garlic mustard, larch and sycamore.

In the species for which $B - b$ estimated across both latitude and longitude was different from zero, the difference between the de-trended spatial (among 150km grid cell) slope and b (corresponding to an estimate of non-clinal local adaption) also exhibited a countergradient pattern (Fig. 6d). Consistent with theoretical expectations (Hadfield 2016), the de-trended spatial slopes were intermediate between B and b (Fig. 7c). More generally there was a tendency for the de-trended spatial slope minus b to be closer to zero than the $B - b$ slope differences. In fifteen cases the slope difference was non-significant, meaning that I cannot reject the null hypothesis that the de-trended spatial slope of phenology on forcing temperature is attributable to plasticity alone.

2.5 Discussion

The absolute difference between the temperature sensitivity of the optimum B (across latitude and longitude) and plasticity (b) reveals the contribution that genetic adaptation must make in order to track the optimum (Chevin *et al.* 2010). For wood anemone, silver birch, alder, cuckooflower, beech, ash and cocksfoot, the difference between these slopes was small and non-significant. Plasticity also closely tracked gradients of thermal optima for the leafing of horse chestnut (as predicted for this non-native species), pedunculate and sessile oak and dogrose, though a small but significant slope difference existed across latitude or longitude for each of these. Adopting space-for-time substitution I project that these populations will be able to track temperature-mediated changes in the phenological optima, and, all else being equal, climate change should pose least threat to such populations (Chevin *et al.* 2010). In more than half of species I found plasticity to be adaptive.

For five species I found consistent evidence that $|B - b|$ differed significantly from zero, i.e., plasticity does not track the temperature sensitivity of the optimum. In four species, which include woodland trees and flowers, the plastic response was steeper and more negative than the temperature sensitivity of the optimum, consistent with countergradient local adaptation (Conover & Schultz 1995; Phillimore *et al.* 2012), or potentially due to B being underestimated due to maladaptation at the range edges (Table A1 in Appendix A). The spring phenology of temperate plants is expected to be exposed to opposing selection pressures; for later phenology to reduce frost damage and early phenology to take advantage of the growing season (e.g. Augspurger & Salk 2016). Countergradient variation may arise where a latitudinal (or altitudinal) decline in growing season duration also affects the optimum phenology. If spring temperatures rise, species exhibiting countergradient variation may experience selection for delayed phenology. Evidence for countergradient variation in spring phenology from common garden experiments on plants is quite limited, though examples do exist (Alberto *et al.* 2013; Kremer, Potts & Delzon 2014; Toftegaard *et al.* 2016). Unexpectedly, I found that sycamore, a species first introduced to the UK in the sixteenth century, shows a pronounced countergradient pattern and the latitudinal trend in leafing time of this species is negative. Larch, a non-native conifer species introduced in the seventeenth century, was also found to have a countergradient pattern. For these species, my inference of countergradient adaptation is likely to have arisen from the confounding effects of a third variable (possibly an effect of chilling that I did not detect) generating a different relationship between temperature and phenology in space versus time (Chevin & Lande 2015). A single species, the early flowering lesser celandine, exhibited a co-gradient local adaptation pattern, where the effect of adaptation on the trait is in the same direction as plasticity.

For the remaining ten species, my estimate of the temperature sensitivity of the optimum differed over latitude versus longitude, which is inconsistent with the underlying theory (Hadfield 2016). This may reflect the influence of a third variable, such as the frequency of late frosts or precipitation, which covaries with temperature and phenology differently over latitude versus longitude (see Table A1 in Appendix A). For several species for which spatial slope estimates were not consistent, such as hawthorn, blackthorn and rowan, the timing of temperature sensitivity sliding-windows was estimated with a higher degree of uncertainty (Fig. A1 in Appendix A). Both the statistical approach I employed, and the underlying theory, rely upon a large number of assumptions; for a full discussion of whether they are biologically reasonable, see Table A1 in Appendix A.

These analyses revealed a broad trend in cue use; species with earlier mean phenology were better predicted by two temperature time windows, while photoperiod tended to be an important cue for species with later phenology. Exposure to late frosts and the damage that incurs can impair new growth and reproductive success (Inouye 2000). The positive phenological response to temperatures during a “chilling” window identified for 11/13 species (for which the doubletemp model was preferred), may therefore be an adaptation to reduce the chances of initiating new growth during a warm winter spell. A reliance on temperature rather than photoperiod cues may also enable these early phenology species to respond more quickly to warm forcing temperatures early in the year (Polgar & Primack 2011). Chilling requirements have been demonstrated for numerous woody species (Laube *et al.* 2014) and flowering annuals (Kim *et al.* 2009). My finding that early spring species were generally more sensitive to a “chilling” window agrees with inferences drawn for an overlapping set of species by an analysis of the well-known Marsham phenological time-series (Roberts *et al.* 2015).

The precise timing of all forcing and “chilling” windows varied amongst species. Forcing windows were important in cuing the phenology of all focal species and directly preceded the mean phenology. In comparison, the timing of "chilling" windows varied more among species. This may reflect different processes that constitute a "chilling" signal in these analyses, such as autumn dormancy induction or winter chilling accumulation for dormancy release (Hänninen & Tanino 2011; Polgar & Primack 2011). Species that show a positive phenological response to temperature during a "chilling" window (i.e. delay their phenology) may advance their phenology by less than chilling insensitive species if temperatures rise throughout the year (Murray *et al.* 1989). Some evidence indicates that advancing leaf phenology of European tree species in response to climate change is slowing, which may be due to chilling requirements no longer being met (Fu *et al.* 2015). This is however, still debated (Wang *et al.* 2016), therefore integrating the effect of chilling into predictive models is increasingly important (Vitasse *et al.* 2011; Roberts *et al.* 2015).

For species with phenological events later in the spring, photoperiod assumes a greater influence than "chilling" as a predictor of a species' spatiotemporal phenological variation. I included photoperiod as a threshold, but recent experimental and modelling work on trees finds that photoperiod and chilling interact, and that photoperiod may assume a greater importance when chilling requirements are not fully met (Caffarra, Donnelly & Chuine 2011a; Caffarra *et al.* 2011b; Laube *et al.* 2014). The models in these analyses, while able to identify species where "chilling" or photoperiod was a stronger predictive cue for phenology, did not capture these more subtle effects. It may be possible to extend this approach to incorporate such complexity, though expanding the parameter space would present a substantial computational challenge, and multicolinearity of cues in space is a considerable obstacle.

Three of the species included here, pedunculate oak, garlic mustard and cuckooflower, have been subject to earlier work in a simpler version of this framework (Phillimore *et al.* 2012, 2013). My temporal slope estimates were similar to those obtained in previous studies. However, in contrast to my finding that garlic mustard may exhibit countergradient local adaptation, Phillimore *et al*. (2012) reported no evidence for this and found that plasticity could account for the spatiotemporal covariation between temperature and phenology. This discrepancy may be due to the earlier study relying on a measure of model fit that took only the temporal relationship between temperature and phenology into account. This instance highlights the risks of a correlation-based approach arriving at incorrect inferences regarding local adaptation.

Particular caution is required when interpreting *B* for species best predicted by the doubletemp model, as my estimates may have been biased upwards by correlations between forcing and "chilling" effects. In addition, other than photoperiod and temperature, the approach taken here does not capture spatially varying variables that may contribute to geographic variation in the phenological response. For these reasons, I recommend that these findings be viewed as hypotheses requiring validation via transplant experiments, rather than as strong evidence.

There are two existing opportunities that can be used to explore the validity of aspects of my inferences. The first is the Marsham record, which allows a comparison of estimates of plasticity (or more accurately, the temporal slope of phenology on forcing temperature), for ten taxa at a single site within the same region estimated over a non-overlapping time period (Table S1b in Roberts *et al.* 2015). I identified similar forcing sliding-windows and estimated plasticity of the same sign and of similar magnitude, but all my estimates are shallower, with the average difference ~1.65 days°C^{-1}. This discrepancy may reflect a true difference in the phenological response to temperatures during the two time periods, but is more likely due to methodological biases. For instance, enforcing a single sliding-window across the UK might underestimate the true local responses to forcing temperatures, or the spatially interpolated temperature data may include more measurement error.

Secondly, several tree species have been subject to extensive transplant experiments in the Pyrenees, providing an opportunity to test the validity of my inferences regarding plasticity and local adaptation. Vitasse *et al.*'s (2010) estimates of the plasticity of leaf unfolding with respect to spring temperatures ranged from ~ -4.9 – -5.8 days°C^{-1} in beech and -5.7 – -6.3 days°C^{-1} in sessile oak, similar to my temporal slope estimates of -4.27 and -5.30 days°C^{-1} (Tables A3 & A4 in Appendix A), respectively. A common garden study of tree provenances from different elevations revealed countergradient local adaptation of flushing in beech, co-gradient variation in ash, and no local adaptation in sessile oak and sycamore (Vitasse *et al.* 2009a). In contrast, I found no local adaptation in beech (albeit with a marginal countergradient tendency), no local adaptation in ash, weak/absent countergradient variation in sessile oak and strong countergradient variation in sycamore (Fig. 6). Such limited agreement between this work and reciprocal transplant experiments regarding the presence and direction of local adaptation may reflect true biological differences in the nature of adaptation to elevation versus meso-scale geographic clines. Nonetheless, they underpin the need to interpret these findings with caution.

A corollary of my finding that plant species respond to different cues, with different plasticity and exhibit different degrees and directions of local adaptation, is that the sequence of spring events may vary geographically. Furthermore, under climate change local phenological sequences may be subject to re-ordering (Roberts *et al.* 2015), the nature of which may itself vary geographically, making extrapolation especially challenging. For example, in the south of the UK, elevated winter temperatures may mean that the “chilling” requirement is not met for some species (Laube *et al.* 2014; Roberts *et al.* 2015), thereby causing them to advance by less than chilling-insensitive species. The implications of any phenological re-orderings that may arise for the absolute fitness of individual populations and community composition are currently unknown and require further investigation.

In summary, I have shown that for several UK plant species phenological plasticity is sufficient to adaptively adjust to changing spring conditions. I highlight several species for which plasticity does not track geographic variation in the optimum phenology as potential candidates to face directional selection on their phenology under climate change.

Chapter 3

A comparative analysis of aspects of the phenological response of UK plant species

3.1 Abstract

The fates of plant species and populations under climate change will be influenced by their phenological response to changing conditions. Predicting phenological responses of different species under warming temperatures requires us to know i) how plastic their response is and ii) how well plasticity can track the optimum. Estimates of both aspects of phenological response exist for a limited number of species, and these can be used in a comparative framework to draw inferences regarding the responses of species for which we lack direct phenological observations. Using estimates of these parameters for 22 plant species from Chapter 2, I tested whether ecological traits predict i) median phenology, ii) plasticity (b), and, iii) $|B\text{-}b|$, a measure of the degree of (non-clinal) local adaptation. I estimated phylogenetic signal for each of these aspects of phenological response and found that phenological event (leafing or flowering) and growth form (woody or herbaceous perennial) predicted plasticity in phenological response. These traits could help inform predictions of plasticity in phenological response to temperature. In contrast, the median date of phenology and local adaptation over latitude were not predicted by any of the ecological traits considered. Point estimates of phylogenetic signal for median phenology and plasticity were high, but estimates were non-significant for all responses considered. The power of these analyses to identify significant predictors and estimate phylogenetic signal was limited by the number of species and phenological events analysed.

3.2 Introduction

Phenological shifts in response to climate change are well-documented across many taxa (Walther *et al.* 2002; Parmesan 2007; Settele *et al.* 2014). These shifts include advances (e.g. Both *et al.* 2004; Bartomeus *et al.* 2011) and delays (e.g. Yu *et al.* 2010) in spring phenology. Some species do not exhibit a significant trend in their phenology, although an apparent non-response may mask differing responses to spring and autumn/winter temperatures within the same species (Cook *et al.* 2012b). Phenological trends are less clear for autumn events, in part due to fewer studies on this season (Gallinat *et al.* 2015). Some evidence suggests delays may be common (Sparks & Menzel 2002; Ibáñez *et al.* 2010), and that autumn senescence is influenced by spring phenology (Keenan & Richardson 2015) as sequential phenological events may be constrained by development (Wolkovich & Ettinger 2014).

By understanding the phenological temperature cues of different species, and how plastic their response to those cues is, it is possible to project how those species may respond to warming temperatures under climate change. Plastic responses to temperature may enable populations to persist in the medium term (e.g. Willis *et al.* 2008) and recent work has found that species with weaker responses to temperature were less able to phenologically track their climatic niches (Amano *et al.* 2014). In order to predict how a species or population will respond under warming temperatures, we need to know i) how much their optimum phenology will shift, ii) how able they are to track that shift, and, iii) what phenological cue they respond to. In Chapter 2, I estimated these parameters for 22 UK plant species, and this provides an opportunity to examine whether any generalities can be gleaned for these aspects of plant phenological response.

Comparative analyses can be used to test whether certain traits predict different aspects of species' phenological responses (Roy *et al.* 2015). If they do, these relationships can be used to draw inferences regarding the responses of species for which we lack direct phenological observations. There have been some attempts to apply comparative approaches to different taxa (reviewed in Buckley & Kingsolver 2011). For example, certain traits predict flight period shift (reflecting plastic responses to temporal variation in environmental conditions such as temperature) (Altermatt 2010), and the date of first appearance in Lepidoptera (Diamond *et al.*

2011). In birds, traits have been found that predict the temporal shift and response to temperature in first singing date (Rubolini, Saino & Møller 2010), and the shift in migratory arrival date in response to temperature (Hurlbert & Liang 2012).

In plants, growth form (Iversen *et al.* 2009) and seed size (Jia *et al.* 2011) have been shown to predict phenological timing in alpine species, while pollination strategy has been identified as a predictor of flowering date in an analysis of British species (Fitter & Fitter 2002). Spring flowering has been correlated with understorey occupancy, perennial reproductive schedules, herbaceous growth forms and light coloured corollas in forest species (Hensel & Sargent 2012). Leaf out times have also been correlated with traits including growth form and ring porosity in woody species (Panchen *et al.* 2014). To what extent traits can inform plasticity and local adaptation in phenological response is less well studied, yet is important to understand as mating systems and gene flow affect the potential for evolutionary responses (Franks *et al.* 2014).

Phylogenetic signal measures the degree to which pattern in species traits is due to their phylogenetic relationship (Revell, Harmon & Collar 2008). We can use modern phylogenetic comparative methods to estimate phylogenetic signal in species traits (Freckleton, Harvey & Pagel 2002; Hadfield & Nakagawa 2010). The timing of phenological events is determined by i) the environment, and the response to the environment via, ii) plasticity and iii) adaptation, each of which may be phylogenetically conserved. In plants there is evidence for phylogenetic signal in first flowering dates (Lessard-Therrien, Davies & Bolmgren 2014), peak flowering (Jia *et al.* 2011) and leaf out times of woody species (Panchen *et al.* 2014). Previous work has suggested that phylogenetic signal in phenological timing reveals a conserved phenological response to abiotic cues (Davies *et al.* 2013), although this has not yet been explicitly explored. Some studies have identified phylogenetic patterns in the plasticity of phenological responses, both in plants (Willis *et al.* 2008; Davis *et al.* 2010), for example where earlier flowering families have advanced more in response to temperatures (Mazer *et al.* 2013), and in other taxa such as butterflies (Roy *et al.* 2015).

Few studies have looked at phylogenetic signal in the evolutionary response to climate change or local adaptation to phenological cues, but, where they have been examined (directly or indirectly), no significant patterns were observed (Davis *et al.* 2010; Roy *et al.* 2015). Previous work has not examined the ability of a taxon to track the optimum phenology via plasticity, which is an important measure as its magnitude can be viewed as a sign of the potential difficulty a species may face in responding to temperature shifts under climate change. The degree of phylogenetic signal in these different aspects of phenological response, and the extent to which traits affect such responses in different species, may therefore be crucial to predicting long-term phenological trends and how species will fare under climate change. Phylogenetic comparative methods have already contributed to determining the extinction risk for plant species in Thoreau's woods (Willis *et al.* 2008), and predicting the success of invasive plants (Davis *et al.* 2010). By using comparative methods it is possible to start making wider predictions about phenological responses in other species.

Using phenology observations from the UK Phenology Network (UKPN) and the estimates of plasticity and local adaptation from Chapter 2, I conducted a comparative analysis to ask: what are the predictors of i) median phenology; ii) plasticity; and, iii) non-clinal local adaptation for 22 UK plant species? I will also estimate phylogenetic signal in each of these aspects of phenological response.

3.3 Methods

3.3.1 Phenology data

I used citizen science collected phenological data from the UKPN (www.naturescalendar.org.uk), as described in Chapter 2. These comprised first leafing and flowering dates for 22 species; collected during the period 1998-2014 (Chapter 2, Table 1). The focus of this chapter was interspecific variation in the estimates obtained in Chapter 2's analyses for (i) plasticity in response to forcing (b), and, (ii) the absolute slope difference between plasticity and the gradient between temperature and optimum phenology over latitude ($|B_{lat}-b|$). The estimates over latitude were chosen instead of those over longitude, as latitude is thought to be a better gradient to observe local adaptation to temperature in Europe, where natural selection can act on larger populations across a greater temperature gradient (Savolainen, Pyhäjärvi & Knürr 2007). I used the absolute values of these estimates of local adaptation as response variables, where 0 = no local adaptation, and, >0 = local adaptation. For b and $|B_{lat}-b|$ I used the variance of the relevant posterior distribution to estimate measurement variance. My measure of average timing was the median date of phenological event from the UKPN data.

3.3.2 Phylogeny

I used the recent species level dated ‘*Daphne*’ phylogeny (Durka & Michalski 2012) of European flora, the topology of which was based on the family level phylogeny of the Angiosperm Phylogeny Group III (APG III 2009) and incorporated 518 recent molecular phylogenies (Durka & Michalski 2012). I pruned the phylogenetic supertree to include only the 22 focal species (Fig. 1). I plotted the best cue type for each species (identified in Chapter 2) onto the phylogeny to visually inspect it for any phylogenetic clustering of preferred environmental cues (Fig. 1), as species replication was insufficient to allow a formal test.

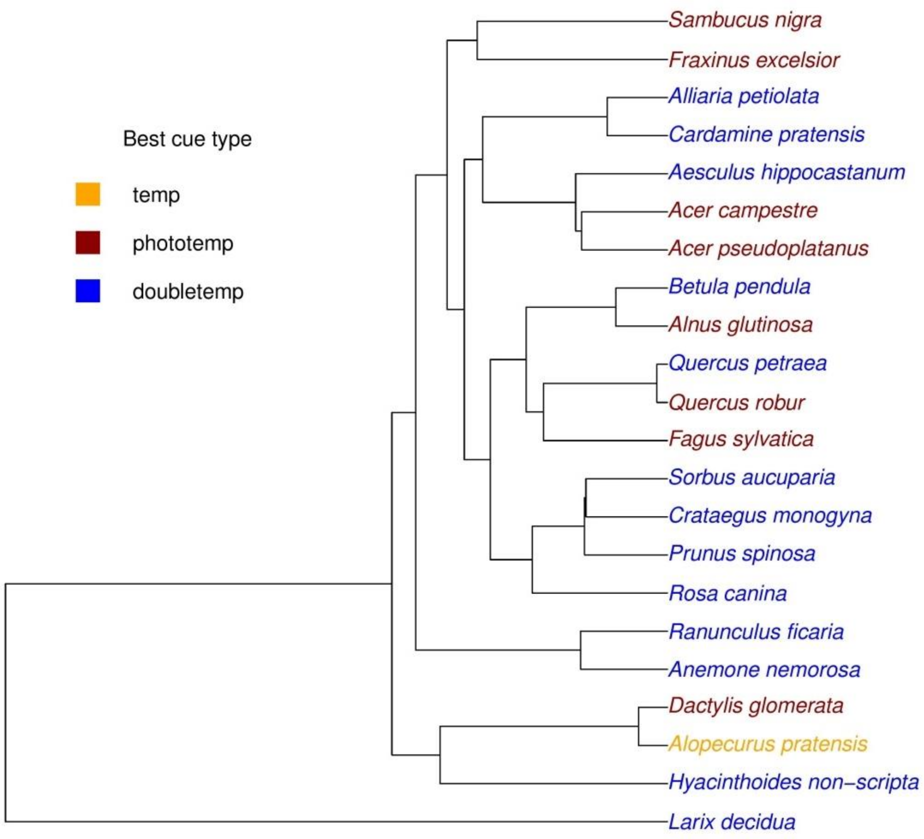


Figure 1. Phylogenetic tree of 22 species analysed, based on the *Daphne* phylogeny. Tip labels are colour coded according to the best performing cue type identified in Chapter 2.

3.3.3 Ecological traits

I selected six plant traits from the PLANTATT (Hill, Preston & Roy 2004), LEDA (Kleyer *et al.* 2008), and ECOFLORA (Fitter & Peat 1994) databases (Table 1), for which there are strong *a priori* hypotheses that they could affect each of my response variables. Selected traits had either been previously linked to phenology in earlier comparative analyses on plants, or there was a strong hypothesis that they correlated with the focal response variable, and were subject to the constraint that complete data was available for our study species. Data for most traits was obtained from a single source, except for minimum age at first flowering, for which I compiled several sources to obtain information for all species (see Table 1 for the variables and their predicted effects on each response variable).

Table 1. Plant traits, ecological variables and their hypothesised effects that were included as explanatory variables in the analyses of phenological response.

Variable	**Source**	**Measures**	**Predicted effect(s) on responses**		
			Date of phenology	**Plasticity**	**Local adaptation**
Event type	UKPN	Flowering Leafing	Flowering is fast in forbs and vegetative growth slower. Vegetative growth is fast in deciduous shrubs, and flowering slower (Iversen *et al.* 2009).	Both first flowering and first leafing can advance under warming temperatures (Wolfe *et al.* 2005; Gordo & Sanz 2009), but correlated responses between events may vary (Davies *et al.* 2013). This could be due to different rates of plasticity in response, but this requires further investigation.	The correlation between leafing and flowering events can vary between locations (Davies *et al.* 2013). This could be evidence of adaptation to different temperature cues in different phenological events, but this requires further investigation.
Median date of phenology	UKPN	Ordinal day		Species with earlier leafing (Morin *et al.* 2009) and flowering (Mazer *et al.* 2013) phenology have been shown to be more plastic/exhibit a greater response to temperature (Fitter & Fitter 2002; Pau *et al.* 2011; Davies *et al.* 2013).	Early phenology species with high levels of plasticity (Pau *et al.* 2011),may exhibit less local adaptation. They are both mechanisms for tracking optimum timing, and higher plasticity may be enough to do so.
Growth form	Plantatt	Woody perennial Herbaceous perennial*	Species with perennial aboveground parts may have earlier phenology than those that have to re-grow vegetative parts, as resources are more easily available to them (Iversen *et al.* 2009).	Woody species with longer generation times and life spans may require high levels of plasticity to deal with inter-annual variation in temperature cues (Vitasse *et al.* 2013).	
Ellenberg light value	Plantatt	Ellenberg indicator value for light preference: 1 = deep shade 9 = full light	Species with a higher shade tolerance may have later phenology, as they can successfully grow and reproduce under the lower light levels of a canopy (Kudo *et al.* 2008; Hensel & Sargent 2012).	Species with lower shade tolerance may need to be more plastic to make the most of early year growing conditions, when there is less competition for light (Kudo *et al.* 2008).	

Pollen vector	Ecoflora	Wind Insect	Abiotic (wind) pollinated species may have earlier phenology, to maximise pollen dispersal when it is least impeded by vegetative growth (Rathcke & Lacey 1985; Jia *et al.* 2011).		Biotic (insect) pollinated species may be adapted to temperature cues in order to coincide phenology with availability of pollinators (Willis *et al.* 2008; Franks *et al.* 2014). Conversely, wind pollinated species may be more likely to show countergradient local adaptation to allow for gene flow over greater areas.
Habitat breadth	Plantatt	Number of broad habitat types a species occurs in, based on 23 categories.		Generalist species (those which occur in a broader variety of habitats) may have a wider spatial distribution and be more plastic in order to respond to cues across their range (Morin *et al.* 2009).	Generalist species whose niche breadth is wide may be less likely to be locally adapted.
Mean seed mass	Ecoflora	mg			Smaller seeds may be more widely dispersed (e.g. through wind)(Primack 1987; Jakobsson & Eriksson 2000). This may promote greater gene flow, making local adaptation less likely.
Minimum age at first flowering	LEDA except for: Larch - Ecoflora Alder - Claessens *et al.* 2010	< 1 year 1-5 years > 5 years			Species with longer generation times are expected to adapt less quickly to changing temperature cues (Chevin et al. 2010; Franks *et al.* 2014).

*Perennial classification includes any species with more than one growing season, such as the biennial Garlic mustard.

3.3.4 Statistical analyses

I fitted phylogenetic mixed models (Hadfield & Nakagawa 2010) to identify the relationship between the explanatory variables and the different measures of phenological response, taking the phylogenetic relationship among species into account. Models were fitted in a Bayesian setting using MCMCglmm (Hadfield 2010). The response variable and the selected plant trait predictors were different for different models (Table 2). Where the responses were estimates of plasticity or local adaptation from Chapter 2's analyses, I included a measure of variance (obtained from the response's posterior distribution) in the models as a measurement error term (Roy *et al.* 2015). I estimated phylogenetic signal as phylogenetic heritability, applying the following formula to each sample of the posterior distribution:

$$h^2 = V_P / V_P+V_R$$

Where V_P is the phylogenetic variance component and V_R is the residual variance component.

The **DateNull, PlasNull, and BlatNull** models included only the intercept as a fixed effect and phylogeny as a random effect. The **Date, Plas, and Blat** models included additional fixed effects (Table 2). I ran models for 1,030,000 iterations, discarding the first 30,000 as burn-in. I sampled every 100th iteration to get posterior sample sizes of 10,000 for each species. A high iteration number and sampling interval were selected in order to provide an acceptable effective sample size from the small data set. I visually inspected traces of the posterior distributions of focal parameters to check for model convergence. I used priors for the (co)variance components which were drawn from the inverse Wishart distribution with $V = 1$ and $\nu = 0.002$.

All statistical analyses were conducted in R (R Core Team 2012).

Table 2. Parameters included in mixed effect models.

Model	**Mixed model terms**		
	Response(s)	***Fixed effects***	***Random effects***
DateNull	Median date of phenology	Intercept	Phylogeny, residual
Date	Median date of phenology	Intercept, Event type, Growth form, Ellenberg light value, Pollen vector	Phylogeny, residual
PlasNull	Plasticity (b)	Intercept	Phylogeny, residual
Plas	Plasticity (b)	Intercept, Median date of phenology, Event type, Habitat breadth, Growth form, Ellenberg light value, Mean seed mass	Phylogeny, residual
BlatNull	Absolute B_{lat}-b	Intercept	Phylogeny, residual
Blat	Absolute B_{lat}-b	Intercept, Median date of phenology, Event type, Habitat breadth, Minimum age at first flowering, Pollen vector	Phylogeny, residual

3.4 Results

3.4.1 Median phenology

While the median date of phenological events showed a strong phylogenetic signal (h^2 = 0.93), the lower 95% credible interval (CI) was close to 0. None of the plant traits significantly predicted interspecific variation in the median date of phenology (Table 3 & Fig. 2).

Table 3. Parameters for the *Date* model estimated via MCMCglmm. Asterisks indicate significance, CIs = credible intervals.

	Posterior mean (95% CIs)	*pMCMC*
Intercept[1]	123.45 (49.93, 194.11)	<0.01**
Event (leafing)	-13.60 (-49.80, 24.74)	0.45
Growth form (woody)	9.71 (-28.98, 50.49)	0.60
Ellenberg light value	-3.19 (-14.47, 8.06)	0.59
Pollen vector (wind)	8.73 (-16.75, 34.42)	0.48

[1] Corresponds to flowering (event), herbaceous perennial (growth form) and insect (pollen vector).

Median phylogenetic variance = 17.43, median residual variance = 351.95.

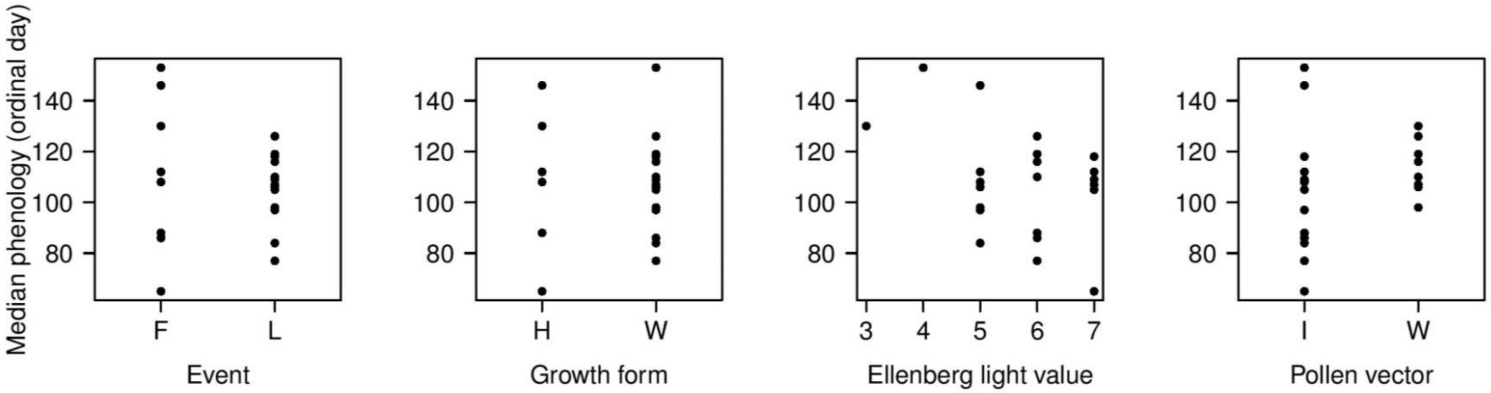


Figure 2. The relationship between plant traits tested as predictors and the median date of phenology. From left to right: event (F = first flowering and L = first leafing); growth form (H = herbaceous perennial and W = woody perennial); Ellenberg light value; pollen vector (I = insect and W = wind).

3.4.2 Plasticity

Phylogenetic signal in species plasticity to forcing temperature cues (b) was non-significant, though the point estimate was high ($h^2 = 0.80$, CI = 0.01 – 0.99). I found phenological event and growth form to be significant predictors for plastic response to forcing temperatures (Table 4). Leafing events were 2.83 days°C^{-1} less plastic than flowering, whilst a woody growth form predicted a higher degree of plasticity (steeper by -2.27 days°C^{-1}) (Fig 3). However, only two species (blackthorn and dogrose) were informative in testing the influence of event and growth form, as they were the only woody species for which flowering event data was analysed. This suggests that the two terms were quite confounded.

Table 4. Parameters for the *Plas* model estimated via MCMCglmm. Asterisks indicate significance, CIs = credible intervals.

	Posterior mean (95% CIs)	*pMCMC*
Intercept[1]	-5.60 (-9.77, -1.81)	<0.01**
Median phenology	0.00 (-0.02, 0.02)	0.90
Habitats	-0.35 (-0.94, 0.24)	0.23
Event (leafing)	2.83 (0.96, 4.63)	<0.01**
Growth form (woody)	-2.27 (-4.04, -0.40)	0.02*
Ellenberg light value	0.14 (-0.32, 0.55)	0.52
Mean seed mass	0.00 (<-0.01, <0.01)	0.93

[1] Corresponds to flowering (event) and herbaceous perennial (growth form).
Median phylogenetic variance = 0.06, median residual variance = 0.02.

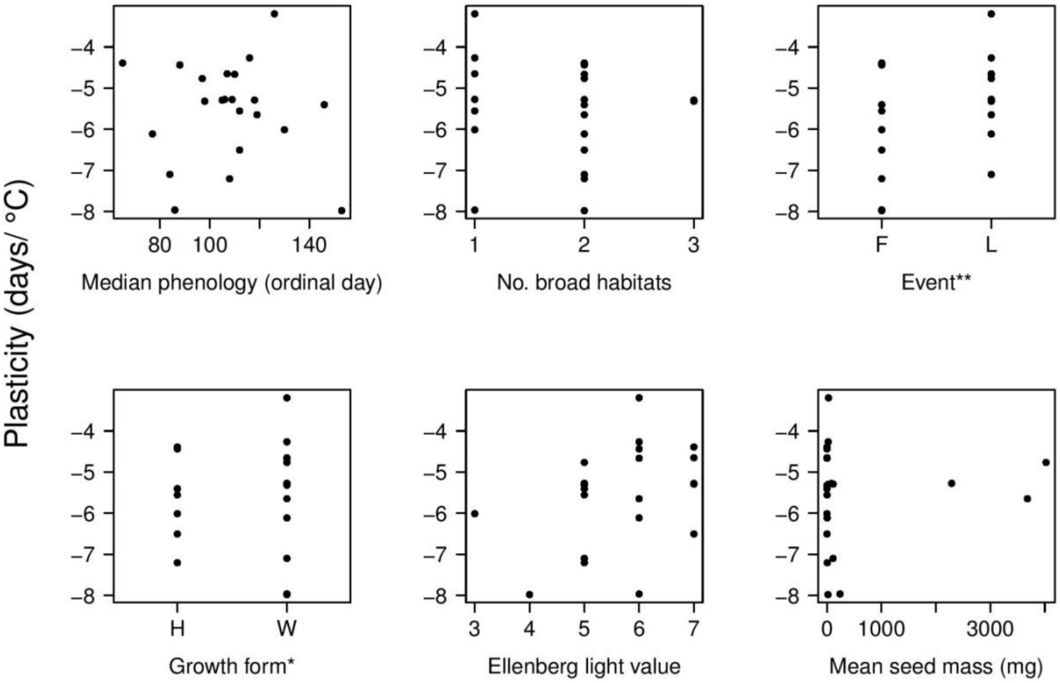


Figure 3. The relationship between plant traits tested as predictors and phenological plasticity. Top from left to right: median date of phenological event; number of broad habitat types; event (F = first flowering and L = first leafing). Bottom from left to right: growth form (H = herbaceous perennial and W = woody perennial); Ellenberg light value; mean seed mass. Significant predictors are indicated by asterisks.

3.4.3 Local adaptation

The absolute value of B_{lat}-b was found to have low phylogenetic signal (h^2 = 0.02, CI = 0 – 0.97). None of the predictors considered were significant (Table 5, Fig 4), but minimum age at first flowering was closest to significance. The direction of this relationship indicated that where $|B_{lat}$-$b|$ was higher, the minimum age at first flowering was lower. This non-significant result may be influenced by $|B_{lat}$-$b|$ for field maple, which is considerably higher (29.05, see Fig 4) than any of the other species in the analysis.

Table 5. Parameters for the *Blat* model estimated via MCMCglmm. Asterisks indicate significance, CIs = credible intervals.

	Posterior mean (95% CIs)	*pMCMC*
Intercept[1]	10.60 (0.21, 22.22)	0.05*
Median phenology	-0.03 (-0.11, 0.05)	0.39
Habitats	0.18 (-2.40, 2.74)	0.89
Event (leafing)	1.21 (-3.08, 5.50)	0.56
Min age 1st flowering	-1.43 (-3.41, 0.57)	0.15
Pollen vector (wind)	-0.51 (-5.13, 3.95)	0.81

[1] Corresponds to flowering (event) and insect (pollen vector).

Median phylogenetic variance = 1.46, median residual variance = 4.81.

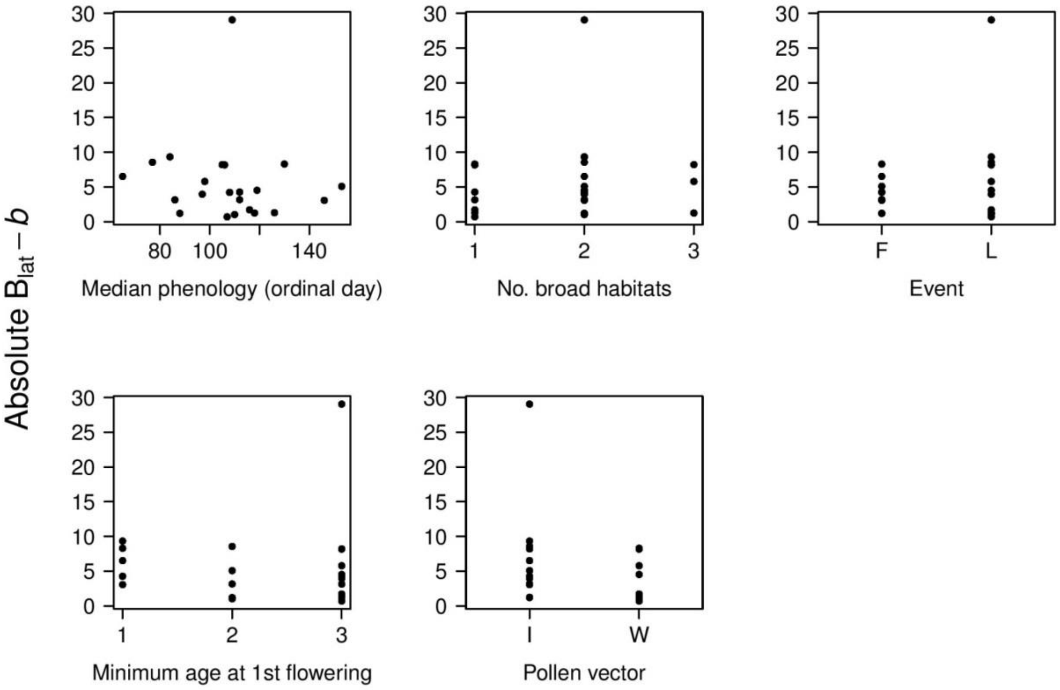


Figure 4. The relationship between plant traits tested as predictors and a measure of local adaptation over latitude. Top from left to right: median date of phenological event; number of broad habitat types; event (F = first flowering and L = first leafing). Bottom from left to right: minimum age at 1st flowering (1 = < 1 year, 2 = 1-5 years and 3 = > 5 years); pollen vector (I = insect and W = wind).

3.4.4 Cues

I mapped the best cue type identified by the models in Chapter 2 (i.e. temp, phototemp or doubletemp) on the pruned plant phylogeny. The pattern showed some clades where all species use either phototemp or doubletemp cues, indicating that there is some phylogenetic clustering in the type of cue that best explains variation in phenological responses (see Fig 1). However, with so few species there is insufficient power to further test the best cue type in these analyses.

3.5 Discussion

I found high point estimates for phylogenetic signal in median date of phenology and plasticity, but the low levels of species replication meant there was considerable uncertainty in these estimates and I cannot discount the possibility that phylogenetic signal is low. The point estimate for phylogenetic signal in $|B_{lat}-b|$ was low. I found that event type and growth form predicted variation in plasticity in phenological response, but that none of the ecological variables were significant predictors of variation in median date of phenology or $|B_{lat}-b|$. The comparative analyses conducted here lacked power, as they were limited by the number of species for which flowering and leafing data were available.

In contrast to previous work (e.g. Fitter & Fitter 2002; Iversen *et al.* 2009; Jia *et al.* 2011; Panchen *et al.* 2014), I did not identify any significant predictors of the median date of phenology. In addition to the number of species, the mixture of leafing and flowering phenology may have limited the ability of this approach to detect the influence of predictors. The posterior means from the *Date* model suggested that woody species had later phenology, leafing was earlier, wind pollinated species later and less shade tolerant species later, although all had very wide credible intervals. None of the herbaceous species included in this analysis used vegetative phenology data, so the influence of growth form, a predictor in earlier work (Iversen *et al.* 2009; Hensel & Sargent 2012), may be confounded with event type. Similarly, while pollination strategy has previously been found to predict flowering time (Fitter & Fitter 2002), leafing phenology was used for most of the woody, wind-pollinated species in these analyses. This means that though wind-pollinated trees may flower early (Rathcke & Lacey 1985), their leafing phenology is driving the results here. An expanded approach, examining the leafing and flowering phenology of more species in the UKPN data, may be better able to detect predictors of phenological timing.

The type of phenological event, i.e. whether it was flowering or leafing, was found to be a significant predictor of the estimates of phenological plasticity, with flowering substantially more plastic than leafing. It has been suggested that plastic responses to temperature may vary for different events as they respond to different temperature cues (Davies *et al.* 2013). If the degree of plasticity differs among phenophases of a species, it could have implications for plant fitness, particularly through impacts on pollination. For example, wind pollinated trees often flower before leaf emergence, when pollen dispersal is least impeded (Rathcke & Lacey 1985). Highly plastic flowering responses in such species could be advantageous if early flowering enables them to take advantage of early season conditions. If flowering responses are delayed under some conditions, then pollen movement may be impeded as flowers coincide with leafing phenology. Plasticity in flowering may also affect interactions with insect pollinators (e.g. Kudo & Suzuki 2002; Rafferty & Ives 2013), or change the timing available for seed development. In some temperate plants therefore, there may be advantages to highly plastic responses in flowering. In contrast, for areas of high inter-annual climate variability such as the Mediterranean, phenological plasticity in vegetative growth may be more important for plant fitness through impacts on survival (Milla, Castro-Díez & Montserrat-Martí 2010).

Other studies have found that the plasticity of flowering and vegetative growth events (Sola & Ehrlén 2007; Davies *et al.* 2013) and other phenophases such as flowering and fruiting correlate positively (Rathcke & Lacey 1985; Primack 1987; Kudo & Suzuki 2002). The species for which I used flowering observations may be more responsive than those with leafing observations, and so conclusions about the plasticity of different phenophases cannot be made from this analysis alone. Further work on species for which both flowering and leafing records are available from the UKPN data would enable this result to be tested, and the correlation between flowering plasticity and leafing plasticity assessed.

Species with woody growth were found to be more plastic than herbaceous species, which could be linked to the longer life spans and generation times of woody plants. They are exposed to more temporal variation in selection for the ability to respond to environmental cues like temperature than shorter-lived herbaceous species (Chevin *et al.* 2013; Duputié *et al.* 2015). Woody growth forms have been linked to spring flowering strategies (Hensel & Sargent 2012), and species of this form may be able to use their stored resources and pre-developed aboveground parts to respond more speedily to temperature cues than herbaceous species. My results indicate that prior knowledge of the focal phenological event and a species' growth form may be useful in making predictions about plastic responses to temperature cues under climate change. Contrary to other work (Fitter & Fitter 2002; Davies *et al.* 2013; Mazer *et al.* 2013), I found no evidence that species with earlier phenological events showed greater plasticity in their phenological responses to temperature cues.

Although event type and growth form were identified as predictors of plasticity in this analysis, they are likely to be highly confounded with one another, and therefore these results should be interpreted very cautiously. The majority of species for which leafing phenology was used were woody perennials, and most flowering data was for herbaceous species. Only two species were truly informative for these predictors in the *Plas* model; blackthorn and dogrose, both woody species for which I used flowering data. To test the effect of having limited informative data I re-ran the plasticity model with *either* growth form *or* event type. In these models only event type was nearing significance, suggesting that colinearity may be a problem in the full model. Future analyses that estimate rates of plasticity across a wider range of species and events could be used to better investigate these ecological predictors.

No significant predictors of $|B_{lat}\text{-}b|$, a measure of the degree of local adaptation, were found. The directions of the relationships indicated by the posterior mean estimates in the *Blat* model were very shallow for median phenology, habitat breadth and pollen vector. The results indicated that leafing may have higher $|B_{lat}\text{-}b|$, as may those with a higher minimum age at first flowering. However, the variance passed to the model may not capture measurement error very well due to absolute $B_{lat}\text{-}b$'s non-Gaussian distribution. Across all species the median measurement variance for $|B_{lat}\text{-}b|$ was 1.91, higher than that of plasticity alone (median variance = 0.49); therefore, there was in effect less information for each species with which to perform the comparative analysis.

If further analyses were to reveal that leafing events have a greater degree of local adaptation to temperature than flowering, it may indicate that some phenophases are more likely to respond to temperature through microevolutionary processes over latitudinal gradients. Similarly, if flowering were found to respond more plastically to forcing cues in future work (as indicated here), it would suggest that different phenological events respond differently to changes in temperature cues under climate change. It should be noted however that many studies have demonstrated that plastic and locally adapted responses are not mutually exclusive (reviewed in Franks *et al.* 2014), therefore the same phenological event may exhibit both.

A major limitation of the analyses performed here is that I did not conduct a full exploration of the cues. A multinomial phylogenetic model that explored predictors of cue type (e.g. the temp, phototemp or doubletemp cues from Chapter 2) would be an informative approach to analysing interspecific differences in cues. In particular, understanding what predicts the importance of photoperiod versus chilling cues would be interesting, as there is still debate over their relative importance (e.g. Basler & Körner 2012, 2014; Laube *et al.* 2014). There was not enough power to test this with cue information for only 22 species, so further work in this area would be beneficial.

The approach utilised here to estimate slopes, accounting for measurement error, has not been previously used for phenological studies of plant species (but see Roy *et al.* 2015 for an example using butterfly data). Expanding the analyses to include more species could provide more informative estimates of phylogenetic signal. It should be noted however, that even when phylogenetic signal is detected in plant phenology, it may not mean that phenological sensitivity to abiotic variation (and thus response to climate change), is phylogenetically conserved. Closely related species may occupy different abiotic environments that they respond to, despite having similar physiological mechanisms underpinning timing of phenology (CaraDonna & Inouye 2015).

In this work, I found some evidence that traits such as growth form may be important for predicting phenological responses to temperature cues across species, and that these responses may vary depending on the phenological event. Understanding the influences on plasticity and local adaptation for different aspects of phenological response is important, as there is evidence that these processes impact on the conservation of climatic niches in plants. Whether climatic niches can be conserved through plasticity may also help determine which species require geographical range shifts to persist under climate change (Amano *et al.* 2014). While these analyses had insufficient power to reveal significant phylogenetic signal in the species responses tested, further work including more species could determine whether there are any phylogenetic patterns in these responses.

Chapter 4

Do understorey flowering plants track spatial variation in the leaf out phenology of woodland trees?

4.1 Abstract

Species interactions between and within trophic levels may be affected by shifting phenologies under climate change. Intraguild phenological interactions that could be affected include competitive and facilitative relationships, yet the potential for such interactions to be disrupted is relatively unstudied and poorly understood. In temperate deciduous woodlands few attempts have been made to project how intraguild interactions, such as the competition for light among plants, could change. I set up Track a Tree; a novel citizen science project to examine the spring phenology of interacting plant species in UK woodlands. Citizen scientists collected repeat observations of tree leafing phenology and the flowering of selected understorey species, during springs 2013-2015. I used these records to examine the relative phenology of i) oak versus three ground flora species; (ii) birch versus bluebell and iii) oak versus three other canopy tree species. I found that first leafing and peak flowering of oaks versus wood anemone, lesser celandine and bluebell were correlated over space. The time between canopy leafing and flowering in these species was spatially consistent (major axis slopes did not differ significantly from 1). If temperature-mediated plasticity determines these species' phenological responses, my results suggest that understorey flowering may be able to track canopy leafing under future conditions, maintaining shading interactions in UK woodlands. The relative phenology of oaks versus birch and ash was also spatially consistent, but varied for oaks versus sycamore. This finding suggests that the order of leafing in oaks and sycamore may change in future, thus altering the competitive relationship between the two species. My results indicate that many native woodland plant shading interactions may be resilient in the face of climate change. However, these patterns were observed over space and further work would be needed to see whether they are transferable to the relative phenology of woodland species over time.

4.2 Introduction

Phenological timing determines not only the environmental conditions that individuals are exposed to, but also the biological interactions they experience, interactions which in turn influence selection on phenological timing (Elzinga *et al.* 2007). The well documented shifts in phenology resulting from changes to the climate (Settele *et al.* 2014) do not affect different species, or individuals of the same species uniformly (Fitter & Fitter 2002). Consequently, where biotic interactions are dependent on synchronous timing, variation in the degree of phenological shift could lead to mismatch (Durant *et al.* 2007). Understanding if and how phenological mismatch occurs is important, as mismatches could affect the demography and population dynamics of species (Miller-Rushing *et al.* 2010).

Existing work on how differing phenological responses to climate may affect interacting species has primarily focussed on trophic interactions (Harrington, Woiwod & Sparks 1999; Donnelly, Caffarra & O'Neill 2011). A major analysis of phenological time series across numerous taxa, found a difference in the rate of phenological change over time at different trophic levels (Thackeray *et al.* 2010). Differences in the rate of phenological response to temperature between, or within, trophic levels could arise through different mechanisms. Species may respond to different temperature cues (see Chapter 2; Ovaskainen *et al.* 2013; Roberts *et al.* 2015) or exhibit differing slopes of plasticity in response to such cues (see Chapter 2;Vitasse *et al.* 2010; Donnelly *et al.* 2012), leading to species shifting their phenology by different degrees in response to climate change. The range of phenological shifts species exhibit may include delays in addition to advances, or there may be no clearly discernible shift in response to temperature (Cook *et al.* 2012b). An incomplete understanding of the type of phenological shift (e.g. an advance or delay) a species will experience, may make detecting *potential* phenological mismatches more difficult. This could apply especially to mismatches within the same trophic level (CaraDonna *et al.* 2014) where shifting phenology may lead to changes in competition for resources, and for which an appropriate 'yardstick' measure (as advocated by Visser & Both 2005) may be lacking.

Most studies that have investigated the impact of phenology on species interactions have done so by examining a specific interaction between particular species (e.g. predator-prey, see Durant *et al.* 2005) at a single site over time, to test whether they might be maintained or disrupted as environmental conditions alter under climate change. Broader studies have shown that the phenology of plants and generalist pollinators exhibit similar rates of advance (Bartomeus *et al.* 2011), yet other work has suggested that plant-pollinator interaction network structure may be disrupted by phenological mismatch in bee and forest understorey communities (Burkle *et al.* 2013). In herbivorous insect-plant interactions, the degree of phenological synchrony can be crucial for the fitness of the herbivore (van Asch & Visser 2007) or affect the severity of defoliation of the host plant (Foster *et al.* 2013), therefore shifts in phenology may lead to deleterious mismatch on either side of the interaction.

The disruption of other types of phenological interaction, particularly within trophic levels, has received little attention, bar some work to investigate intraguild predation in various taxa (Walther *et al.* 2002; Rasmussen *et al.* 2014; Anderson *et al.* 2015), and nesting competition in penguins (Lynch *et al.* 2012). However, it is well recognised that intraguild interactions may also depend on temporal synchrony and so be subject to potential mismatch (Miller-Rushing *et al.* 2010). Recent work on the variation of phenological responses in a plant community (CaraDonna *et al.* 2014) highlighted the importance of studying such neglected interactions to gain insight into how competition for resources, or pollination patterns between interacting species, may be affected. Intraguild interactions between plants may provide insights into the effects of phenological shifts on community structure (e.g. via competition) and community level responses to climate change (Brooker 2006).

Amongst plants, the phenological timing of different species impacts competition for resources (Rathcke & Lacey 1985), which may be abiotic, such as light or soil resources (Dunnett & Grime 1999), or biotic, such as pollinator availability (Campbell & Motten 1985; Mitchell *et al.* 2009). In deciduous woodland systems, the competition for light during spring influences the relative phenology of plant species in the community, with the characteristic vegetative development progressing from herbaceous species to shrubs and then canopy trees (Salisbury 1921). The light available at the woodland floor is influenced by canopy leafing phenology (Anderson 1964) and is important for the successful vegetative growth and reproduction of woodland herbs (Blackman & Rutter 1946; Valverde & Silvertown 1998; Whigham 2004; Dahlgren *et al.* 2007), orchids (Shefferson *et al.* 2006), understorey woody species (Augspurger *et al.* 2005) and juvenile trees (Vitasse 2013).

Light availability also contributes to the composition of the understorey (Thomsen *et al.* 2005), as shading impacts on the fitness and survival of particular species in different light environments. Work during the mid-twentieth century found that variation in the density of bluebells in mixed deciduous woodland is correlated with light intensity at the forest floor (Blackman & Rutter 1946), demonstrating the influence of light on geographic variation in understorey plant communities. Woodland understorey species have been categorised according to their degree of shade tolerance (Sparling 1967) and different strategies impose trade-offs on growth under varying light conditions (Henry & Aarssen 1997; Augspurger & Salk 2016).These strategies may also contribute to woodland understorey composition via their effects on plant fitness. In advanced shade, some understorey species may exhibit a reduction in successful seed set, as fruit production may be dependent on the photosynthetic activity during high irradiance levels before canopy closure (Kudo *et al.* 2008). Low light intensity has also been shown to limit the regeneration of different canopy tree species in woodland, including Ash (*Fraxinus excelsior*) and Beech (*Fagus sylvatica*) (Emborg 1998).

Changes in climate may result in shifting relative phenologies of plant species in mixed deciduous woodland. This could affect shading relationships and competition for light, leading to the success of one species relative to another and ultimately affecting the species composition of such systems (Kramer, Leinonen & Loustau 2000). A recent analysis of the historic Marsham dataset indicated that the order of spring leafing in UK tree species may shift under projected climate scenarios (Roberts *et al.* 2015), in part due to chilling cues (such as those identified in Chapter 2) no longer being met for some species, such as birch. Such shifts could alter the competition for light amongst trees and seedlings and, in the absence of other limiting factors, lead to shade trees with high growth rates and long life spans (e.g. beech, ash and sycamore) dominating (Ellenberg, 1986). Although intraspecific variation in phenological response has been demonstrated over space for some species (Menzel *et al.* 2006b; Primack *et al.* 2009), little is known about the relative phenology of species across UK plant communities, which would tell us about any spatial variation in their phenological relationships.

Intra-trophic phenological interactions across space may expose geographic variation that can be used to predict changing patterns in the future. Assuming that the cues and plasticity underpinning phenology are transferable from space to time, the relative phenology of different species can be used to help predict whether the order of spring events is likely to shift under climate change. Examining the relative phenology of canopy and understorey species across the UK will help test whether shading interactions in woodlands will be maintained under climate change. Box 1 shows scenarios of how the relative phenology of woodland species could vary over space, and hypotheses associated with such patterns.

Box 1. Relative phenology over space

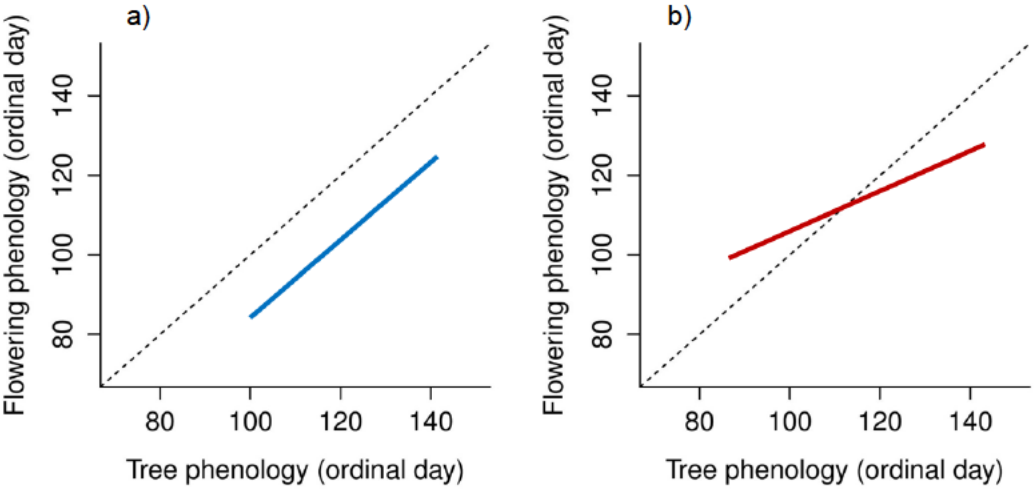


Figure 1. Example patterns of how phenology could vary across space where a) relative phenology is not significantly different across space and b) relative phenology differs significantly across space. Coloured lines represent slope of phenology across geographical space.

Fig. 1 depicts two scenarios of how relative phenology could vary across space. These scenarios were used to develop hypotheses about woodland shading relationships under climate change.

Hypothesis a

The pattern of relative phenology across UK sites is geographically invariant (Fig. 1a), and space-for-time substitution suggests that understorey species may be able to track the timing of canopy phenology under environmental conditions that change over time to reflect the conditions currently experienced over space. This could preserve shading relationships in the future.

Hypothesis b

The pattern of relative phenology across UK sites varies over space (Fig. 1b), space-for-time substitution suggests that understorey species may not track the timing of canopy phenology under environmental conditions that change over time to reflect the conditions currently experienced over space. Changes to relative phenology under climate change could lead to a shift in the order of spring events in some woodlands in years where phenology is advanced. This may alter future shading relationships and competition for light, affecting the long term fitness and survival of some species.

Citizen science has proven to be an effective method for conducting ecological monitoring over large geographic areas (Schmeller *et al.* 2009; Dickinson *et al.* 2010). The UK Phenology Network (UKPN) collects data via the Nature's Calendar (www.naturescalendar.org.uk), citizen science project, and its records have been widely used to document shifts in phenology (e.g. Amano *et al.* 2010) and to identify the environmental cues and spatial variation in the responses of different species (e.g. Chapter 2; Phillimore *et al.* 2012, 2013). The existing UKPN dataset has many advantages including a very large number of observations spanning a wide range of common UK species over 15 years. However, it does not hold information on the phenology of interacting species, the phenology of individuals or the habitat where a phenological event was observed. Therefore, investigation of phenological interactions and the shading relationships of woodland plants across the UK would benefit from a new approach. Any new citizen science project should build upon the experiences of previous plant phenology schemes, such as PlantWatch in Canada (Beaubien & Hamann 2011). In addition, it should take into account general issues faced by citizen science approaches, including observer error (Dickinson *et al.* 2010), and recorder effort, such as weekend bias (Courter *et al.* 2013).

To address the lack of *in situ* observations of phenological interactions over space and time I developed Track a Tree, a novel UK-wide citizen science project. Participants in Track a Tree monitor the spring phenology of an individual tree (or several trees) within woodland and the associated flowering phenology of selected understorey species. The project focuses on plant species that compete for light during spring in order to explore how shading relationships in woodland plants may be affected by climate change. In this chapter I use Track a Tree to test, i) whether canopy and understorey phenology is correlated in space? ii) Whether the relative phenology of different species pairs is consistent over space? iii) Whether the order of phenological events is geographically consistent? Where spatial replication permits, I will address the same questions considering the relative phenology of selected tree species. To supplement sparse data from the North of Scotland, in the analysis of tree species pairs I will include observations of tree leafing collected on a 40 site transect between Edinburgh (55°97'N -3°39'W) and Dornoch (57°89'N -4°08'W).

4.3 Methods

4.3.1 Phenology data

The Track a Tree project

The Track a Tree citizen science project was piloted in 2013 and launched across the UK in 2014 (www.trackatree.org.uk). Details that follow refer to 2014 onwards, and I will highlight where this represents a change from 2013 pilot protocols.

Volunteers were asked to take part in two stages of data collection for Track a Tree. First, participants selected a tree within woodland and recorded information about the site and the tree itself. Trees were located in woodland of a minimum size 100m x 100m and participants selected the focal tree(s) at random using a die to choose between candidates. Additional measures were taken including the girth at breast height (m) of the tree, the aspect of the tree's location, and density of the woodland. The precise location of the site (including latitude and longitude) was obtained via a Google Earth based mapping tool on the Track a Tree website.

For the second stage of data collection volunteers revisited and monitored the phenology of the tree and a range of understorey flowering plants (see Table 1) on a regular basis, with weekly visits recommended from the time of selection until the tree was entirely in leaf. On each visit the phenological stage of the tree was observed and recorded as one of the following; no budburst, first budburst, partial budburst, entire tree budburst, first leaf, partial leaf and entire tree in leaf. Any flowers present beneath the canopy were counted and allocated to a flowering number category (1-5, 6-10, 11-25, 26-50, 51-100, over 100). Flowers were only counted once the petals had opened enough to see inside the flower itself, and each flowering stem was counted as one flower. On each repeat visit the date was recorded, which meant that I could obtain upper and lower bounds on when the different phenological events occurred. Uncertainty in the precise date of events such as first leafing could then be taken account of in the analyses.

The complete protocols that Track a Tree observers followed can be seen in Appendix B, which includes the field guide, field workbook and field recording forms that were made available to participants. Recorders were asked to enter observations into the database via the Track a Tree website. After the pilot study in 2013, the protocols were revised to exclude one of the initial understorey species (Dog's mercury – *Mercurialis perennis*) and instructions improved for clarity. At the end of the first full season in 2014, existing recorders were invited to nominate and vote upon an additional flower to include in the project. As a result of this vote and other feedback from 2014, one new understorey flowering plant (Red Campion – *Silene dioica*) and one new tree species (Beech – *Fagus sylvatica*) were included in the 2015 flowering season. The final list of species that were monitored for Track a Tree can be seen in Table 1.

During the three years of data collection for Track a Tree, Roslin Glen (55°85'N, 2°84'W) acted as a core site, where Dr Albert Phillimore and I monitored multiple trees (fifteen and seven respectively), which contributed to the overall dataset and allowed us to refine the recording protocols. Some data from the project were excluded due to incomplete records being submitted.

The mean Central England Temperature (CET) (Parker *et al.* 1992) and temperature anomaly with respect to the 1961-1990 average for March, April and May for the years 2013 - 2015 varied. In 2013, mean CET for these months was 6.9°C (anomaly = -1.4°C); in 2014 mean CET = 10°C (anomaly = 1.8°C); and in 2015 mean CET = 8.7°C (anomaly = 0.47°C).

Table 1. Species included in the Track a Tree woodland phenology monitoring citizen science scheme. * represents species added to the project for the 2015 recording season. Species highlighted in grey were selected for analysis in this chapter.

	Species	**Binomial**
Canopy tree species	Pedunculate oak	*Quercus robur*
	Sessile oak	*Quercus petraea*
	Silver birch	*Betula pendula*
	Ash	*Fraxinus excelsior*
	Sycamore	*Acer pseudoplatanus*
	Rowan	*Sorbus aucuparia*
	Hazel	*Corylus avellana*
	Beech*	*Fagus sylvatica**
Understorey flowering species	Lesser celandine	*Ranunculus ficaria*
	Primrose	*Primula vulgaris*
	Wood anemone	*Anemone nemorosa*
	Wood sorrel	*Oxalis acetosella*
	Greater stitchwort	*Stellaria holostea*
	Ramsons	*Allium ursinum*
	Bluebell	*Hyacinthoides non-scripta*
	Red campion*	*Silene dioica**

Scottish transect data

Additional tree phenology observations were obtained from a 40 site transect running between Edinburgh (55°97'N, 3°39'W) and Dornoch (57°89'N, 4°08'W) in Scotland (see Appendix C for a map of these sites). Each site was visited every two days between mid-March and June in 2014 and 2015, as part of a larger project, and the phenology of 8-10 trees recorded. Tree first leafing was defined in the same way as Track a Tree, and therefore I used these observations to supplement the sparse data available from Track a Tree in the North of Scotland.

4.3.2 Statistical analyses

Relative phenology of canopy and understorey species

To examine the relationship between the phenology of selected tree and understorey species (highlighted in Table 1) I considered both as a bivariate response in a Bayesian generalised linear mixed model (Hadfield 2010). Uncertainty in the date of tree and flower phenology was accounted for by treating observation upper and lower bounds as interval-censored Gaussian (Hadfield *et al.* 2013; Bjorkman *et al.* 2015), meaning that it was equally probable for the event to have occurred at any point in this interval. The mixed model included site, year of observation (as a factor), individual tree ID and a residual term as random effects and I estimated the variances and co-variances for these terms.

Models were run for 60,000 iterations, discarding the first 10,000 as burn-in and sampling every 100th iteration to get posterior sample sizes of 5,000. I visually inspected traces of the posterior distributions of focal parameters to check for model convergence. Parameter expanded priors were used for the (co)variance components and priors for the residual term were drawn from the inverse Wishart distribution with V = I and v = 0.002.

The model intercepts estimate mean phenology of each species in space and time, and the (co)variances estimated across sites were used to calculate the correlation between each two species over space. The major axis slope estimate was calculated on the basis of (co)variance components to investigate trends in relative phenology over space. The same approach could be used to estimate slopes over time (e.g. Phillimore *et al.* 2012), but temporal replication in Track a Tree records was insufficient to do so. This was deemed more appropriate than the standard regression slope as the aim of these analyses was not to determine whether the phenology of one species predicted the phenology of another, but rather whether the phenology of the two species is coincident (Warton *et al.* 2006). I used 95% confidence intervals to assess whether slope estimates were < 1.

I used the bivariate modelling framework to compare a limited selection of species for which data was collected via the Track a Tree project. For tree phenology records to be informative, the event date needed to have lower and upper bounds; upper bound = the date a phenological event was observed, and lower bound = the date when the event was last not observed. For the tree species, the phenological event used for analysis was first leafing. This phenophase was selected over others (e.g. first budburst), as field experience suggested it would be less prone to observer error, particularly when monitoring mature trees. The primary tree species analysed were silver birch and the two oak species. Pedunculate and sessile oak observations were combined as they occupy a similar niche, have similar responses to their phenological cues (see Chapter 2) and can be difficult to distinguish from one another in the field when their characteristics overlap. Silver birch records from Track a Tree were analysed as ‘birch’, which is how this species was recorded on the Scottish transect. This decision was taken due to the difficulty distinguishing silver birch (*Betula pendula*) and downy birch (*Betula pubescens*) and their hybrids from one another in the field when their characteristics overlap. As a result of this, my findings cannot be ascribed to a single oak or single birch species, but must be assumed to describe closely related species that occupy similar niches. There is also some evidence that silver and downy birch also exhibit similar phenological responses to temperature (Myking & Heide 1995; Junttila, Nilsen & Igeland 2003; Heide 2003). I compared the relative phenology of the oak species and a measure of peak flowering of bluebell, wood anemone and lesser celandine, and silver birch and peak flowering of bluebell. These were the species deemed to have an adequate replication of records across the UK. I took peak flowering to be the date when the highest flowering category was reached. This measure was chosen in order to minimise the sensitivity of the flowering phenology records of individual early-flowering plants, which may bear little relation to the population trend of a particular species at a site.

Relative phenology of canopy species

In addition to the tree-understorey flowering plant comparisons, I analysed the relative phenology of several tree versus tree combinations: oaks versus, i) birch, ii) ash, and, iii) sycamore. Additional data obtained from a transect of Scottish sites supplemented the tree phenology observations from Track a Tree in these models. Tree phenology was a bivariate response and site, tree ID, year and a residual term as random effects. For site and year, I also estimated the covariance in the phenology of the two tree species. Priors were the same as the canopy tree versus understorey relative phenology models.

Latitudinal trends in phenology

The latitudinal trends in phenology for each species in the canopy tree versus understorey analyses were examined with the phenology of each individual species as the response (interval censored Gaussian), latitude of the site as a fixed effect, and site and year as random effects. I estimated the intercept and regression slope for each species. Priors were drawn from the inverse Wishart distribution with V = 1 and v = 0.002.

All statistical analyses were conducted in R (R Core Team 2012), using the MCMCglmm mixed model package (Hadfield 2010).

4.4 Results

4.4.1 Track a Tree

Excluding the records from the core site at Roslin Glen, the total number of sites (which serves as a proxy for number of active recorders, assuming a 1:1 ratio between recorders and sites) at which trees were monitored over the three years was 109. In total 224 trees were monitored across these sites with an average of two trees per site and a maximum of seven. The number of sites varied between years. In the pilot year of 2013, 21 sites (in addition to Roslin Glen) were monitored. In 2014 (the project launch year), 97 sites were monitored, and this dropped to 51 in 2015.

For the focal species analysed in this chapter, informative records were obtained for 73 pedunculate, 28 sessile oaks and 58 birches observed between 2013-15. The focal ground flora were observed under 27 oaks and 7 birch trees for wood anemone, 27 oaks and 11 birch trees for lesser celandine and 56 oaks and 18 birch trees for bluebell. As wood anemone and lesser celandine were observed under fewer than 15 birch trees, these species pairs were not analysed further as there was insufficient replication.

Additional records of birch, ash and sycamore were obtained from the Scottish phenology transect data, and comprised 58 oaks from 22 sites, 134 birch from 38 sites, 14 ash from 10 sites and 40 sycamore from 17 sites.

4.4.2 Relative phenology

The number and spatial distribution of flowering and leafing records varied between the focal species selected for the canopy tree versus understorey analysis (Fig 1).

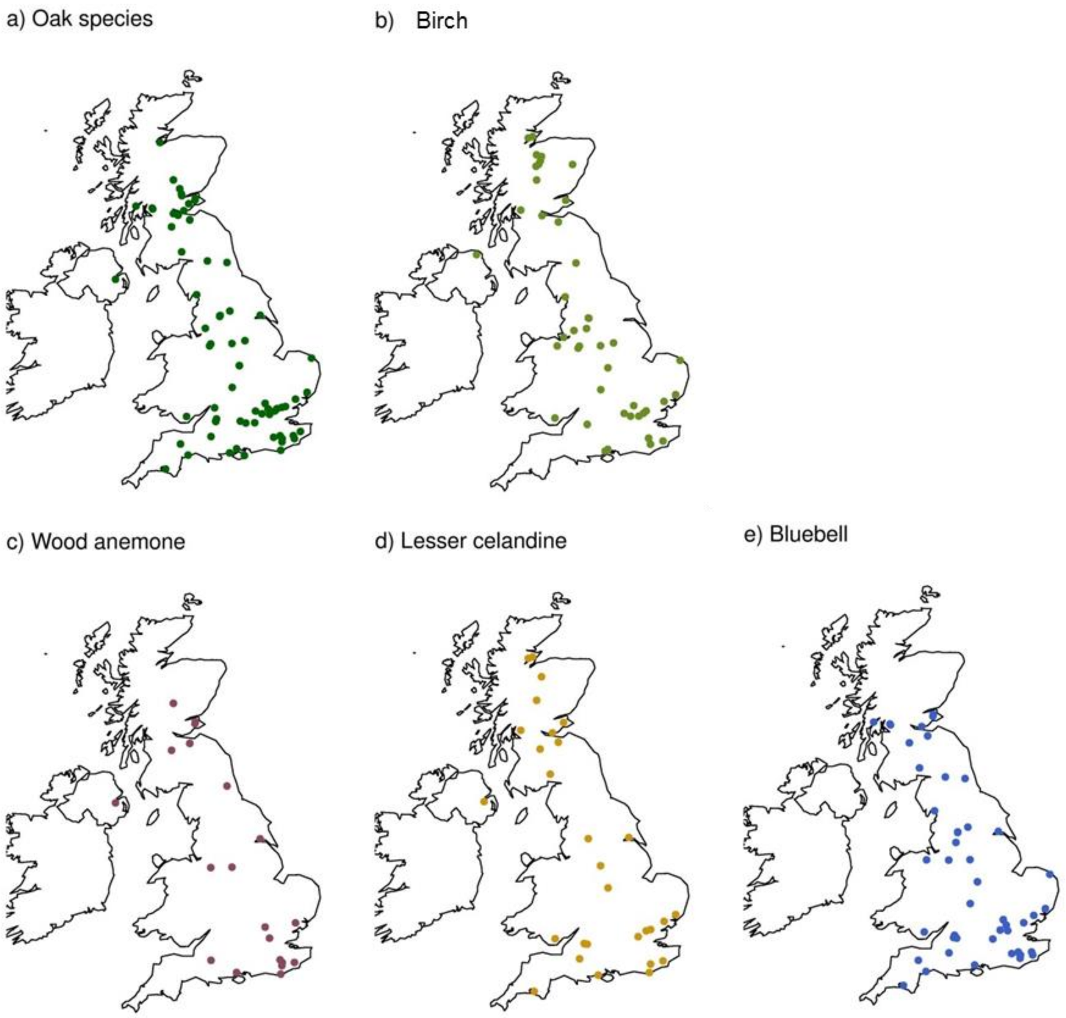


Figure 1. Spatial distribution for Track a Tree records of, a) oaks (pedunculate and sessile), and, b) birch, first leafing. Distributions of, c) wood anemone, d) lesser celandine, and, e) bluebell, peak flowering are limited to records that occur under one of the above tree species.

Records for the two oak species were the most numerous and associated with the least uncertainty in the analyses, therefore I first consider the phenology of the oaks relative to the three understorey flowering species. Peak flowering of wood anemone was found to occur approximately 22 days earlier than the oaks first leafing (oaks mean first leafing day 119.55, 95% CIs = 89.15 – 146.86 and wood anemone mean peak flowering day 97.74, 95% CIs = 81.18 – 114.65). Their phenology was highly correlated in space (r=0.73). The median major axis slope indicated that relative phenology shows some variation across space, being considerably shallower than 1, but was marginally non-significant (Table 2, Fig. 2a). In this case, the more limited spatial coverage and replication of wood anemone records (Fig. 1c) may have affected the ability of the analysis to accurately detect spatial patterns in relative phenology.

The peak flowering of lesser celandine was also found to occur before the oaks first leafing dates by approximately two weeks (oaks mean first leafing day 116.25, 95% CIs = 93.58 – 141.90 and lesser celandine mean peak flowering day 102.09, 95% CIs = 73.10 – 134.97). Their phenology was significantly correlated over space (r= 0.63) and relative phenology did not depart from constancy (slope = 1) (Table 2, Fig. 2b).

The mean timing of the oak species first leafing and bluebell peak flowering was found to be highly synchronous (oaks mean first leafing day 118.67, 95% CIs = 87.33 – 148.59 and bluebell mean peak flowering day 118.37, 95% CIs = 89.81 – 152.49). Their phenology was highly correlated across space (r= 0.78, Table 2). The relative phenology did not differ significantly and the major axis slope was close to 1, with credible intervals overlapping 1 (Table 2, Fig. 2c).

Table 2. Correlations and median major axis slopes between the first leafing and peak flowering phenology of species pairs in space. 95% credible intervals in parentheses.

Species pair	Correlation	Major axis slope
Oaks/wood anemone	0.73 (0.03, 0.995)	0.39 (-0.09, 1.02)
Oaks/lesser celandine	0.63 (0.14, 0.97)	0.69(-0.08, 1.93)
Oaks/bluebell	0.78 (0.55, 0.95)	0.81 (0.51, 1.16)
Birch/bluebell	0.58 (-0.49, 0.99)	0.66 (-9.81, 19.18)

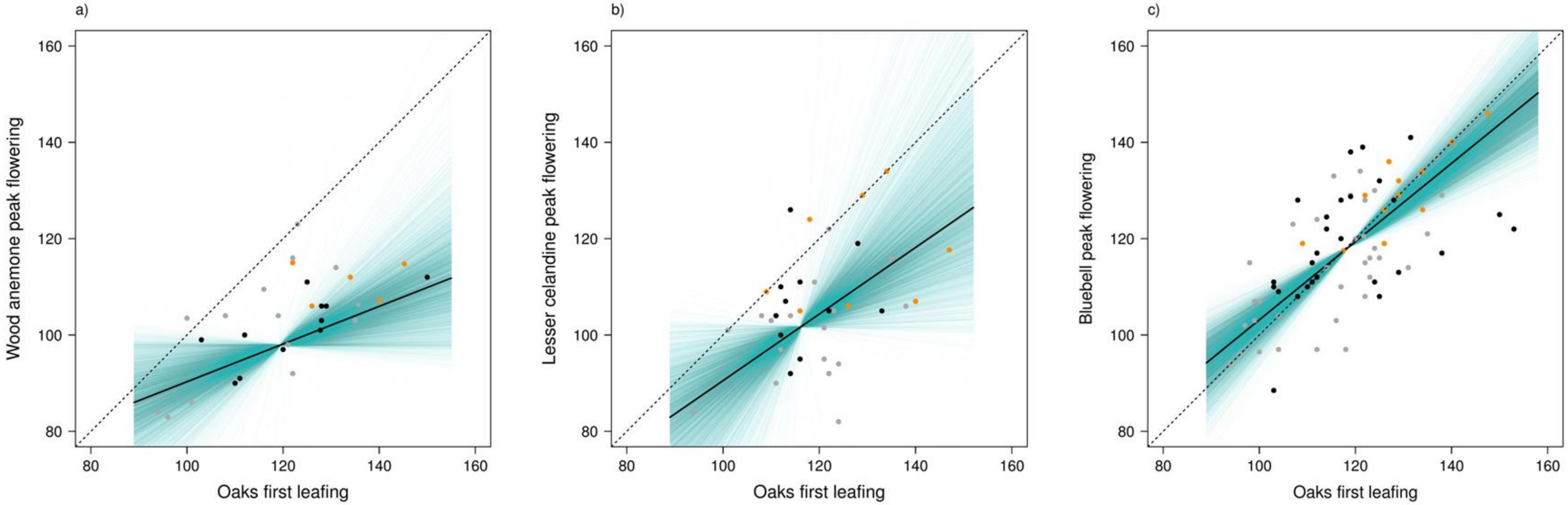


Figure 2. Major axis slopes for oaks first leafing vs a) wood anemone, b) lesser celandine and c) bluebell peak flowering. Median major axis slope = black. Major axis slopes for remaining posteriors = turquoise. Dashed line corresponds to phenological synchrony. Points represent the mean phenology at each site in each year where 2013 = orange, 2014 = grey and 2015 = black.

Birch records from Track a Tree had a similar geographic distribution to the oaks, but spatial patterns in relative phenology were estimated with less precision. Only the relative phenology of birch and bluebell was analysed, and mean first leafing of birch was found to occur approximately 11 days before peak flowering of bluebell (birch mean first leafing day 106.65, 95% CIs = 73.83 – 134.11 and bluebell mean peak flowering day 117.25, CIs = 94.59 – 142.83). Birch first leafing and the peak flowering of bluebell were not significantly correlated across space (Table 2). The median major axis slope was below 1, but not significantly so, which means that there is no evidence that relative phenology differs over space (Table 2, Fig. 3). There is however, a great deal of uncertainty in the major axis slopes.

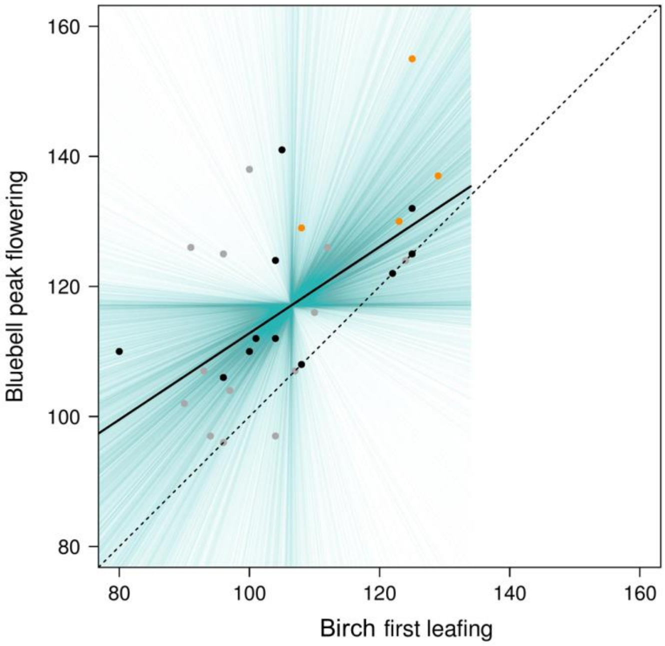


Figure 3. Major axis slopes for birch first leafing vs bluebell peak flowering. Median major axis slope = black. Major axis slopes for remaining posteriors = turquoise. Dashed line corresponds to phenological synchrony. Points represent the mean phenology at each sitein each year where 2013 = orange, 2014 = grey and 2015 = black.

The relative phenology of oaks versus birch, ash and sycamore revealed differences in their mean first leafing phenology. Birch exhibited earlier leafing phenology than the oak species by approximately 10 days (oaks mean first leafing day 122.97, 95% CIs = 96.62 – 148.42 and birch mean first leafing day 112.75, CIs = 82.98 – 143.11). Ash first leafing was approximately 8 days later than the oak species (oaks mean first leafing day

120.24, 95% CIs = 90.11 – 150.74 and ash mean first leafing day 128.09, CIs = 110.16 – 147.61) and sycamore was earlier by approximately 11 days (oaks mean first leafing day 120.37, 95% CIs = 96.52 – 144.08 and sycamore mean first leafing day 109.44, CIs = 65.09 – 165.89).

Phenology of the oak species and birch was highly correlated over space (r= 0.78), as was the phenology of the oaks and ash (r= 0.81). In contrast, the oak species and sycamore phenology was not correlated over space (Table 3).

The major axis slopes of the oak species versus birch and ash show that their relative phenology did not depart from constancy (Table 3, Fig. 4). The relative phenology of the oaks and sycamore varied over space, with the median major axis slope below 1 (0.04), and credible intervals did not overlap 1 (Table 3, Fig. 4), implying that as oak phenology changes over space, sycamore phenology shows no change.

Table 3. Correlations and median major axis slopes between the first leafing phenology of tree species pairs in space. 95% credible intervals in parentheses.

Species pair	Correlation	Major axis slope
Oaks/birch	0.78 (0.55, 0.94)	0.96 (0.71, 1.31)
Oaks/ash	0.81 (0.45, 0.99)	1.04(0.52, 1.63)
Oaks/sycamore	0.17 (-0.66, 0.90)	0.04 (-0.29, 0.52)

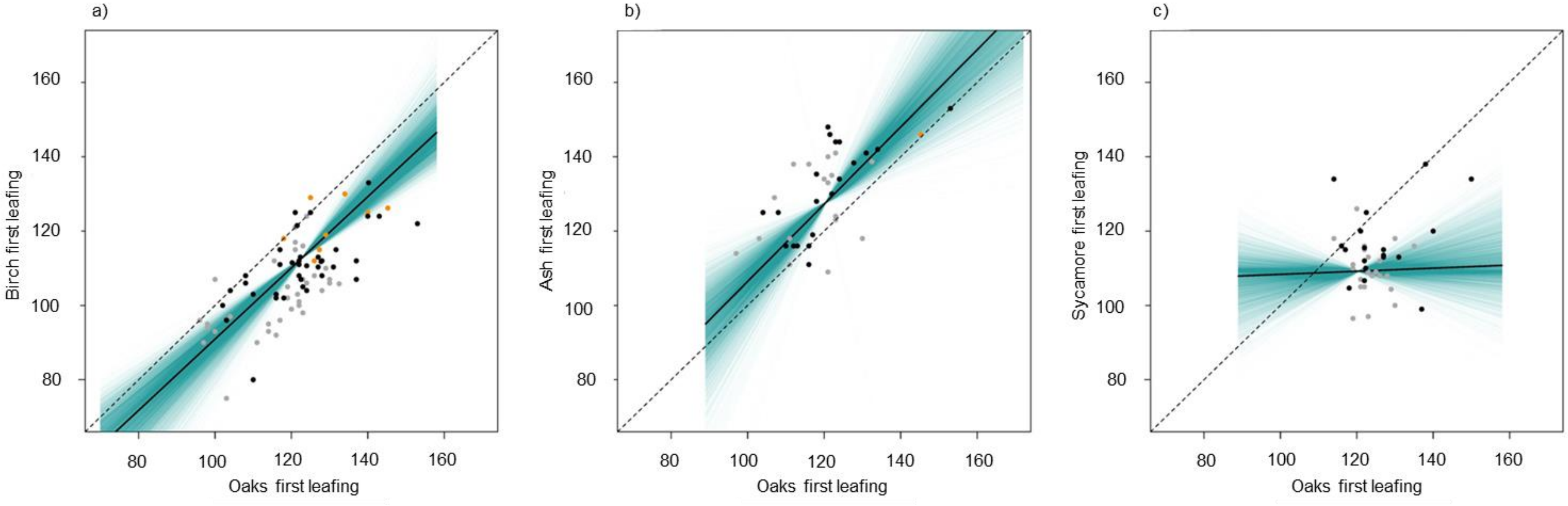


Figure 4. Major axis slopes for oaks first leafing vs the first leafing of a) birch, b) ash and c) sycamore. Median major axis slope = black. Major axis slopes for remaining posteriors = turquoise. Dashed line corresponds to phenological synchrony. Points represent the mean phenology at each site in each year where 2013 = orange, 2014 = grey and 2015 = black.

4.4.3 Latitudinal trends in phenology

Latitudinal trends in the phenology of the species in the tree-understorey analyses were detected (Fig. 5). The slopes for each species report the estimated delay in phenology for an increase of one degree of latitude. All species showed a significant tendency for later phenology further north and slopes ranged from 2.29 days/°N in lesser celandine to 3.31 days/°N in the oak species. The slopes for the oak species and bluebell indicate that at different latitudes the order of oak first leafing and bluebell peak flowering may differ (Fig. 5).

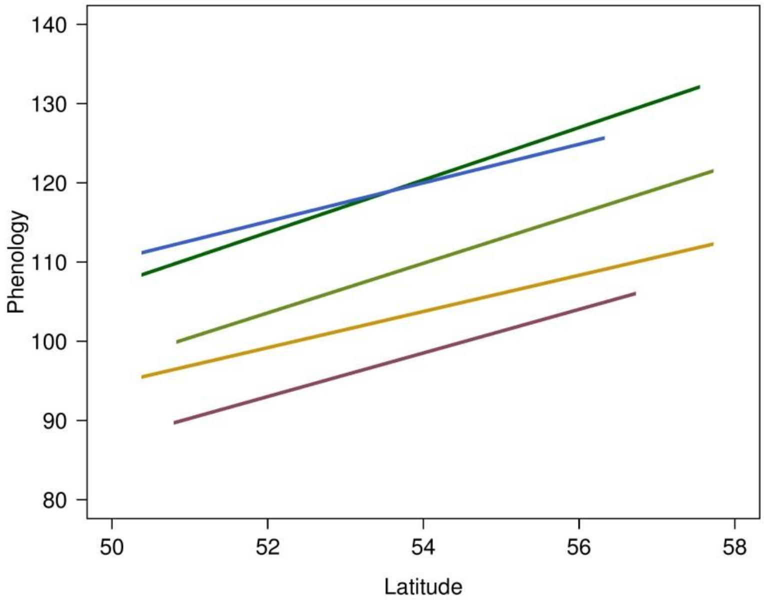


Figure 5. Latitudinal trends in the phenology of oaks (dark green), birch (light green) first leafing and wood anemone (dark pink), lesser celandine (gold) and bluebell (blue) peak flowering. Length of each line corresponds to the latitudinal range for which there are records of each species.

4.5 Discussion

First leafing of the oak species was correlated with peak flowering of wood anemone, lesser celandine and bluebell over space. The major axis slopes of all tree-understorey species pairs did not depart from constancy, suggesting that relative phenology did not differ over space for any of these interactions. The spatially consistent relative phenology between the canopy trees and understorey species in this analysis suggests that woodland ground flora phenology tracks that of the canopy species over space. If this phenological tracking is due to plasticity in response to phenological temperature cues, for which there is evidence in plants (e.g. Chapter 2, Kramer 1995; Vitasse *et al.* 2010; Franks *et al.* 2014) and other species (e.g. Phillimore *et al.* 2010; Hodgson *et al.* 2011; Roy *et al.* 2015) then a space-for-time substitution approach may be predictive. Assuming that this is the case (as Chapter 2's analyses suggested may be reasonable for a number of UK species), phenological tracking over space indicates that phenological interactions between these species may be maintained under future climate conditions. In particular, it suggests that shading relationships may not be disrupted.

Of the tree species pairs examined, oaks versus birch and ash were correlated over space, and their major axis slopes did not depart from constancy. Phenology of the oak species and sycamore was not correlated over space and the major axis slope was significantly below 1. Again, assuming that plasticity is the major determinant of phenological shifts, this finding suggests that while oak leafing may change in future, sycamore leafing may not. This could change the order of spring events where the species co-exist (as projected for some tree species in Roberts *et al.* 2015), and alter competitive relationships between them. Examining relative phenology over space might therefore be a useful indicator of future intra-guild phenological relationships.

In the canopy tree versus understorey analysis based on Track a Tree observations, the model intercepts for each species represent the mean phenological timing of an event and indicate the order of spring events in these woodland species. The mean timing of peak flowering of wood anemone and lesser celandine were both well before the oaks first leafing, and for bluebell peak flowering was found to occur at approximately the same time as the oaks first leafing. Peak flowering occurring consistently earlier, or at the same time as oaks coming into leaf is a strategy to optimise light levels available to these flowering plants, and corresponds to earlier findings (Salisbury 1921; Henry & Aarssen 1997). This is in contrast to the peak flowering of bluebell and first leafing of birch, the timings of which were found to overlap. Birch species have an open and light canopy structure (Beck et al, 2016a), and as light levels are higher under birch, it may not be a limiting factor that understorey flowering species need to track in order to achieve successful growth and reproduction.

The relative phenology of the canopy tree versus canopy tree combinations is consistent across space for two sets of species pairs, as birch first leafing occurs 11 days earlier and ash first leafing eight days later than the first leafing of the oak species. These differences in phenological timing may reflect the shade tolerance of the different tree species, with ash exhibiting a greater tolerance than the light demanding birch (Ellenberg, 1986). The UK forms part of the native range of these species, and the consistent phenological sequence may also arise out of their differing successional position in temperate woodland communities (Beck *et al.* 2016a; b; Eaton *et al.* 2016). Birch species are regarded as pioneer species that can colonise open areas of poorer soil that are subsequently overtaken by the climax shade trees such as ash (Ellenberg, 1986), and birch species have historically leafed earlier than both oak and ash (Roberts *et al.* 2015). Given a chilling requirement in birch (identified in Chapter 2 and Roberts *et al.* 2015), one may predict the relative phenology to be different in the south where temperatures are warmer. However, the tracking of oaks and birch identified here may suggest that chilling is adequate in the south, or that birch and oak species respond to broadly similar cues.

In contrast to the above tree species pairs, relative phenology of the oak species and sycamore is not consistent across sites. Unlike the oak species, sycamore leafing shows little geographic variation, which is consistent with the lack of latitudinal gradient found for this species in Chapter 2 (see Fig 3, Chapter 2). The spatial variation in relative phenology could arise in several ways. Although I found photoperiod and forcing temperature to be cues for sycamore leafing (Chapter 2), sycamore has previously been regarded as a photoperiod insensitive species (Basler & Körner 2014) and recent model evidence suggests that it responds to a chilling cue (Roberts *et al.* 2015). If this chilling cue were not being met in parts of the UK, it could help to explain the spatial variation in the relative phenology of sycamore and the oak species. However, sycamore is usually regarded as a naturalised non-native species whose native range is central and southern Europe (Pasta, de Rigo & Caudullo 2016), where, due to the continental climate, chilling may be greater than that experienced in the oceanic climate of the UK. Other variables such as soil moisture could also be affecting the phenological cues used by sycamore. In addition, little is known about the genetic origin of sycamore populations initially planted in the UK (Hubert & Cundall 2006) and so it is possible that its current phenological variation across space may be influenced by the phenological variation of the source population.

The approach taken in these analyses was restricted by the available data from the Track a Tree project. Data were only drawn from three years and the analyses based on the informative records submitted to the project. This meant that the spatial coverage of phenology observations of the selected species was limited. For example, the number of records for wood anemone is close to the minimum required for analyses to be informative. With further years of observations at an increased number of sites, spatial relationships may be estimated with greater precision for the species included in this study. The method of analysis may also influence the accuracy of these findings. Sites are treated independently in the modelling framework, but are themselves spatially structured, which at present the models do not capture. The key consequence of ignoring spatial autocorrelation is that credible intervals will be underestimated in the analyses.

Thus far, attempts to investigate the relative phenology of interacting woodland species have been limited, but work across different trophic levels (tree-caterpillar-passerine-avian predator) has demonstrated differences in phenological correlations over time (Both *et al.* 2009). With additional years of data, Track a Tree observations could be used to test how correlated the phenology of canopy trees and understorey flowering plants are over time. Gaining insight into the relative phenology of other woodland species interactions would require additional monitoring across trophic levels in future years of the Track a Tree project. This would enable further exploration of how phenological relationships in woodland communities may change.

The Track a Tree protocol was designed to address a number of the deficiencies of existing phenology based citizen science schemes. Repeated visits made by recorders to the same individual trees meant that the uncertainty in the timing of events could be captured as upper and lower bounds. The species selected for monitoring provided informative data on the relative phenology (and associated shading interactions) of UK woodland communities, as well as the phenology of randomly selected individuals. Track a Tree data therefore addressed some of the requirements for general good practice to account for observer bias in citizen science projects (Devictor, Whittaker & Beltrame 2010; Dickinson *et al.* 2010) as well as approaches advocated for plant phenology schemes based on the experiences of PlantWatch in Canada (Beaubien & Hamann 2011).

The spatially consistent relative phenology of the canopy tree and ground flora species included in this analysis suggests that if temperature-mediated plasticity is the major determinant of each species' phenology, understorey flowering may be able to track the timing of canopy leafing under future climate conditions. This indicates that some of the shading interactions that take place in UK woodlands may be resilient in the face of temperature change. Such interactions are affected by additional factors which are not captured in this analysis (such as moisture and soil), and understanding the impact of other influential ecological processes is essential for making further predictions.

Chapter 5

Interspecific differences in the components of variance in phenology of UK tree species

5.1 Abstract

Species interactions may be affected by shifting phenologies under climate change, with mismatch occurring when the temporal overlap of interacting species is low. The degree of mismatch may be buffered by variance in the phenology of interacting species, both in local populations and over space. Here, I define such buffering as the situation where variance in phenology leads to some overlap in the temporal distribution of two events, while the means are substantially mismatched. The capacity of temperate deciduous woodland trees for buffering mismatch has not been widely studied, due to limited data on full phenological distributions. Participants in the citizen science project; Track a Tree, monitor the spring phenology of interacting tree species in UK woodlands. Using phenology observations from Track a Tree I examined the contributors to variance in leafing for seven tree species. I first partitioned the variance in phenology over space, between years and between individual trees and found that contributors differed among species. Spatial variables were important, whereas the variance within a site and year was low for all species except sycamore. Low intraspecific within site variance suggests that for most species, their capacity to buffer phenological interactions at a particular site may be limited. I then examined whether three ecological variables; aspect, woodland density and girth at breast height (gbh), predicted variation in oak and birch species. Aspect was found to be a significant predictor for birch, but with an effect that was counter to my prediction, and no other variables were significant. These findings contribute to the understanding of factors that influence phenological distributions in different tree species. Interspecific differences in the amount of variance among years, and between sites, suggests that the degree of mismatch and buffering of species that interact with trees is likely to vary among tree species.

5.2 Introduction

Some biotic interactions are dependent on synchronous timing of phenological events. Variation in the degree of phenological shift as a result of a changing climate (Fitter & Fitter 2002; Settele *et al.* 2014) could lead to mismatch in these interactions (Durant *et al.* 2005, 2007). Concerns about phenological mismatch (e.g. Thackeray *et al.* 2010, as discussed in Chapter 4), rely on the assumption that the means, variances and skewness of phenological distributions of species will impact on interspecific interactions (Fig. 1, Miller-Rushing *et al.* 2010). Most studies have used the difference between a mean measure of two phenological distributions (e.g. first or peak dates of an event) to assess the opportunity for interaction (e.g. Doi *et al.* 2008). However, the opportunity for species to interact with one another is dependent on the overlap in their temporal distributions and other characteristics of the distribution such as variance or skew (CaraDonna *et al.* 2014), species abundances (Durant *et al.* 2005, 2007) or ontogeny (Yang & Rudolf 2010) may be important influences. These influences have not been extensively investigated, in part due to a paucity of relevant data. Phenology observations of randomly selected individuals from populations of different UK tree species, collected via the Track a Tree project (see Chapter 4); provide an opportunity to explore the variance as well as the mean of phenological distributions.

Understanding the phenological distributions of different species, and the extent to which they could change is important not only for examining specific cases of mismatch, but for understanding wider community responses to changing conditions (Forrest & Miller-Rushing 2010; Revilla *et al.* 2014). As the degree of overlap between phenological distributions is affected by their variances (Fig. 1c & d), examining the variance in phenology may therefore help determine how much a population could be buffered from mismatch with interacting species *in situ.* I define buffering by variance as the situation where variance in phenology leads to some overlap in the temporal distribution of two events, while the means are substantially mismatched. The degree of variance in a phenological distribution may also enable buffering with respect to variation in the abiotic environment, i.e., high variance may allow some individuals to experience benign abiotic conditions even if the mean timing is mismatched. Phenological buffering of interactions could occur among individuals in very close proximity, or on a within site scale, e.g. mismatch occurring in a population on one side of a valley but not the other, or over larger scales, e.g. mismatch occurring in one population but not another. Temporal buffering may also occur, when the degree of matching is greater in some years than others. Furthermore, how intraspecific distributions of phenological events vary over different spatial scales can tell us about how a species' phenology behaves under different environmental conditions (see also Chapter 2). This can provide insights into how future climate changes could affect phenological interactions within and between populations.

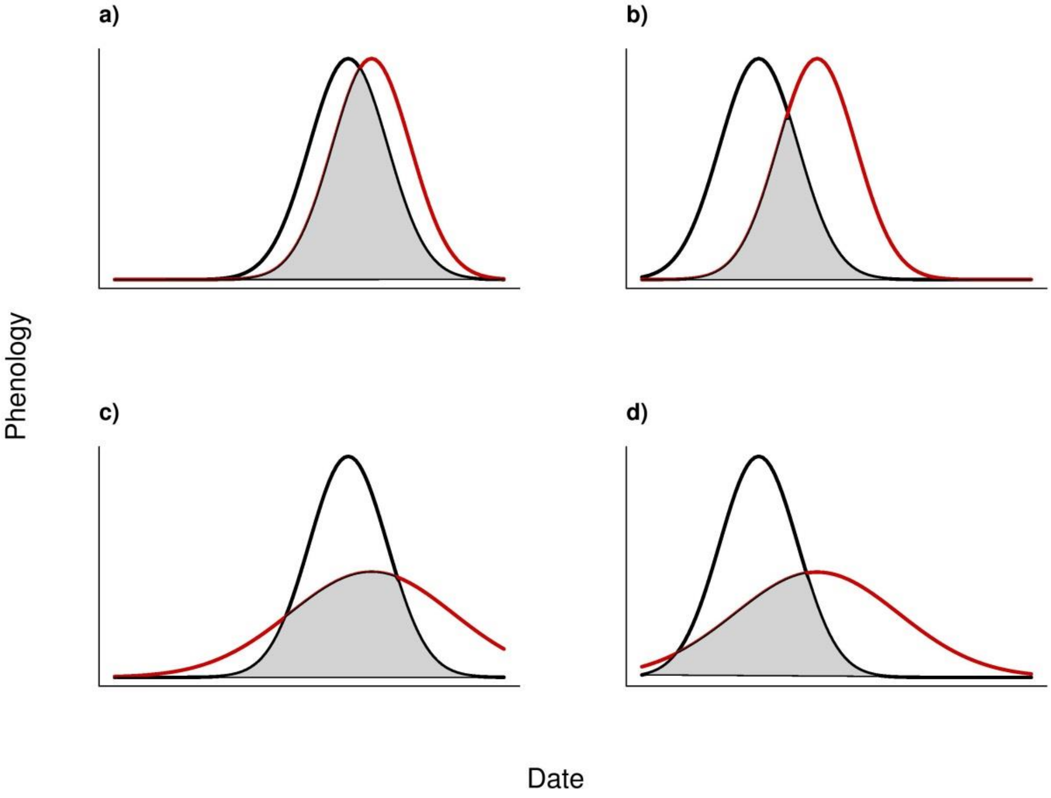


Figure 1. A schematic of the phenological distributions of interacting species where species 1 = black, species 2 = red and phenological overlap = grey. a) Phenologies are synchronised, and distributions largely overlap, b) the phenological distribution of species 1 has shifted to a greater extent than the distribution of species 2, c) peak phenology is synchronised but variance in species 2 is greater and d) species 1 has shifted to a greater extent than species 2, but the greater variance in species 2 means a greater proportion of their distributions overlap than in situation b). Adapted from Both *et al.* 2009 and Miller-Rushing *et al.* 2010.

The within year variation in the phenological records of a species in the same location, or across multiple locations describes the phenological distribution under similar or differing conditions. Information about phenological variance may improve our ability to identify potential mismatch, or phenological buffering between interacting species.

Variance in phenology may act as a buffer at different scales. Within a particular community, variance between species may be important for generalists that interact with multiple species. Within a species, the variance of a population at a site in a particular year may be an important buffer for more specialist interacting species. For example, an extended flowering period has been found to increase resilience to short term pollinator deficits in *Mertensia fusiformis* (Forrest & Thomson 2010).

A common criticism of many existing phenology datasets is that records have traditionally focussed on the first events observed in a population (Forrest & Miller-Rushing 2010), such as those recorded by the Nature's Calendar project (see Chapters 2 and 3). While first dates may be informative about spatial and year-to-year variance in phenology (Chapter 2), they do not contain information about the within year variance within a population. In order to examine the distribution of phenological events within a species, observations of random individuals within a population are necessary (Miller-Rushing *et al.* 2010). The protocols for the Track a Tree project (Chapter 4) require recorders to randomly select individual trees in UK woodlands. This means that Track a Tree observations can tell us about the phenological distributions of the tree species in the project by assessing the variation within the records.

Within woodland communities the impacts of canopy tree phenology on species they interact with is a consequence of the variation both within and between tree species, as well as other variables. Understanding the factors that affect the phenological distribution of woodland tree species could therefore shed light on potential future impacts on, for example, the successful growth and reproduction of ground flora species (Chapter 4), the abundance of herbivorous invertebrates (e.g. Tikkanen & Julkunen-Tiitto 2003; Foster *et al.* 2013) and subsequent food availability for nesting passerines (Both *et al.* 2009). In addition, other factors such as woodland management through coppicing can also strongly influence flowering dates of ground flora species (Salisbury 1921).

The variance in leafing phenology of a woodland in any particular year is a result of the phenological variation in the tree species that make up the woodland, and of variation between individuals of the same species. Within site and intraspecific variation may be influenced by ontogenetic, genetic, microsite or microclimatic factors, and is important as it determines the level of potential phenological buffering at a particular location. Such local scale effects will influence the degree of mismatch that may be experienced by interacting species within a population in a particular year. Track a Tree records include observations of multiple individuals of the same species at a number of sites over several years, which will allow within site, within year variation to be estimated.

Spatial variance in phenology across different woodlands may result from the different environmental conditions they experience, as phenological timing is influenced by certain temperature and photoperiod cues being met in different species, as well as the contributions of plasticity and local adaptation to phenological responses (see Chapter 2). Within a particular year, spatial variation in phenology could mean phenological buffering occurs in some woodland communities but not others. UK wide monitoring of woodland tree phenology will allow spatial variation to be estimated, and provide insight into the potential for spatial buffering.

Among year variance in phenology reflects the ability of individuals in a population to respond to different environmental conditions (that act as phenological cues) in different years. In plants, especially long lived species like trees, phenotypic plasticity is thought to be an important mechanism in responding to different conditions (Donnelly *et al.* 2012; Alberto *et al.* 2013; Franks *et al.* 2014). For this reason, we may predict that tree species exhibit higher variation between years (or between sites that experience different conditions) than within a year or site. The Track a Tree project provides a novel opportunity to test this by utilizing *in situ* phenology observations at multiple sites over several years, collected by citizen scientists. Additionally, as Track a Tree participants monitor the same individual trees over successive years, it provides data on how an individual varies over time, an important source of variation that has been recognised for decades (Salisbury 1921; Miller-Rushing *et al.* 2010). This is a key parameter in models of how populations may respond to climate change (Chevin et al. 2010), yet remains under-recorded for trees.

The variance in phenology among different tree species may reflect differences in cue use and strategy. This variance is important, as the phenological distributions of different tree species that make up woodland communities will influence potential buffering (either at a single site or in different woodlands). For generalist species that interact with woodland trees, the phenological variance among species within a site may act as an important buffer. For specialist interacting species, the variance in phenology of specific tree species may determine the degree of mismatch that they may experience within a woodland in a given year. Species that have a stronger plastic response to environmental variables (e.g. temperature, as estimated in Chapter 2), might be expected to exhibit greater variance in phenology than those with a weaker plastic response. Track a Tree participants record eight tree species therefore this dataset will allow the phenology of different species to be compared.

Investigating phenological variation within tree species has traditionally used common garden scenarios (provenance trials), where trees from different origins are grown at the same location (e.g. Vitasse *et al.* 2009) or an observational approach based on population means (Chapter 2), therefore studies of individuals in nature are rare (Franks *et al.* 2014). The Track a Tree project takes a citizen science approach to gathering *in situ* observations in order to quantify sources of variation. As well as recording phenological observations, participants in the Track a Tree project collect additional information about the trees and sites they monitor. These variables can therefore be tested as predictors of phenological variation. While citizen science projects can vastly increase the spatial range of phenological records available, a drawback is that there may be under-sampled areas (Dickinson *et al.* 2010; Beaubien & Hamann 2011). Track a Tree had fewer participants in the North of Scotland, therefore to maximise the geographical spread of records, tree phenology observations from a Scottish transect of 40 sites will supplement those from the citizen science scheme.

The main aim of this chapter is quantify sources of phenological variation among individuals, and over time and space, for eight tree species across the UK. I will address this by, i) partitioning the variance in phenology of trees monitored by the Track a Tree project and a Scottish transect of 40 sites, focussing on the variation across space (between both grid cells and sites), variation between years and variation among individuals within a site and year, and, ii) testing the factors that predict variation in phenology in addition to the key spatial variables, using information collected for the Track a Tree project. This chapter will identify whether there are differences among tree species in the contributors to phenological variance.

5.3 Methods

5.3.1 Phenology data

Tree phenology data was obtained via the Track a Tree project (www.trackatree.org.uk), from 2013-15, and supplemented by records from a 40 site Scottish transect in 2014 and 2015. For full collection protocols for Track a Tree and the transect see Chapter 4 methods and Appendix B. The analyses in this chapter were based on records of the tree species listed in Table 1.

Table 1. Tree species included in the Track a Tree scheme and monitored on the Scottish transect.

Tree species	Binomial	Total number of trees†
Pedunculate oak	*Quercus robur*	159
Sessile oak	*Quercus petraea*	
Birch species	*Betula pendula/Betula pubescens*	192
Ash	*Fraxinus excelsior*	46
Sycamore	*Acer pseudoplatanus*	66
Rowan	*Sorbus aucuparia*	14
Hazel	*Corylus avellana*	23
Beech	*Fagus sylvatica*	26

†Combined number of trees recorded via Track a Tree and on the Scottish transect. Note that numbers of the oak species are combined as per the analyses.

5.3.2 Statistical analyses

For tree phenology records to be informative about uncertainty, the event date needed to have lower and upper bounds, as described in the methods of Chapter 4. The phenological event used for analysis was first leafing, as it was less prone to observer error than first budburst. Pedunculate and sessile oak observations were combined, and silver birch records from Track a Tree analysed as 'birch', for the reasons stated in Chapter 4.

Variance partitioning

To partition the variance in phenology of the tree species highlighted in Table 1, I considered tree leafing observation upper and lower bounds as interval-censored Gaussian response (Hadfield *et al.* 2013; Bjorkman *et al.* 2015, Chapter 4) in a Bayesian generalised linear mixed model (Hadfield 2010). This means that the precise timing of an event was treated as being equally probable at any time within the interval. Additional data obtained from the transect of Scottish sites supplemented the tree phenology observations from Track a Tree in this model.

The mixed model included the intercept (estimating the grand mean) for each species as the sole fixed effect and grid cell (each 1°cell of latitude and longitude), site, year of observation (as a factor), individual tree ID, the interaction between grid cell and year (to assess any geographical differences in among year variation) and a residual term as random effects. I allowed the variances for each random term to differ among species. Models were run for 600,000 iterations, discarding the first 100,000 as burn-in and sampling every 50th iteration to get a posterior sample size of 10,000. I visually inspected traces of the posterior distributions of focal parameters to check for model convergence. Parameter expanded priors were used for the variance components and priors for the residual term were drawn from the inverse Wishart distribution with $V = I$ and $v = 0.002$.

Predicting variation in phenology

To attempt to identify variables that affect the phenology of the tree species highlighted in Table 1, I took a two stage approach, firstly exploring the contribution of spatial variables for all species. The **Spatial** model used data obtained from the transect of Scottish sites in addition to the tree phenology observations from Track a Tree.

In a mixed model framework with tree leafing as the response (interval-censored Gaussian), species and the interactions between species and latitude, longitude and elevation of the site were included as fixed effects. Grid cell, site, year of observation (as a factor), tree ID and a residual term were included as random effects. Due to the small contribution to variance of the grid cell:year term in the variance partitioning model, it was excluded here for simplicity. Variances were allowed to differ among species. The model was run as above, using the same priors as the variance partitioning model.

The **Ecological** model used phenology observations from the Track a Tree project only, as additional variables recorded as part of the project protocols were available. In this model, only records for silver birch and the two oak species were included, as these focal tree species had the greatest spatial coverage and number of observations.

I used the same mixed model framework with tree leafing as the response. In addition to latitude, longitude and elevation, girth at breast height (gbh) of the tree, aspect of the tree's location and density of the woodland were included as fixed effects. Girth at breast height was included to indicate tree maturity, aspect to indicate the temperature microclimate and density of the woodland to indicate the level of competition for light. Random effects were grid cell, site, year (as a factor), tree ID and a residual term, and variances were allowed to differ for 'birch' and 'oak' categories. The model was run as above, using parameter expanded priors for the variance components and priors for the residual drawn from the inverse Wishart distribution with V = I and v = 0.002.

All statistical analyses were conducted in R (R Core Team 2012), using the MCMCglmm mixed model package (Hadfield 2010).

5.4 Results

5.4.1 Variance partitioning

Mean dates of phenology were estimated using the intercepts of each species in the variance partitioning model (Fig. 2). Mean date of phenology is reported here, but medians are reported for the subsequent variance results, as means were a poor measure of central tendency for the variance components due to long-tailed posterior distributions. The model estimated the greatest uncertainty in UK-wide mean leafing date for rowan (day 118.97, 95% CIs = 79.28 – 155.39), and least for ash (day 127.17, 95% CIs = 111.92 – 144.19), with uncertainty affected by both sample size and intraspecific variation.

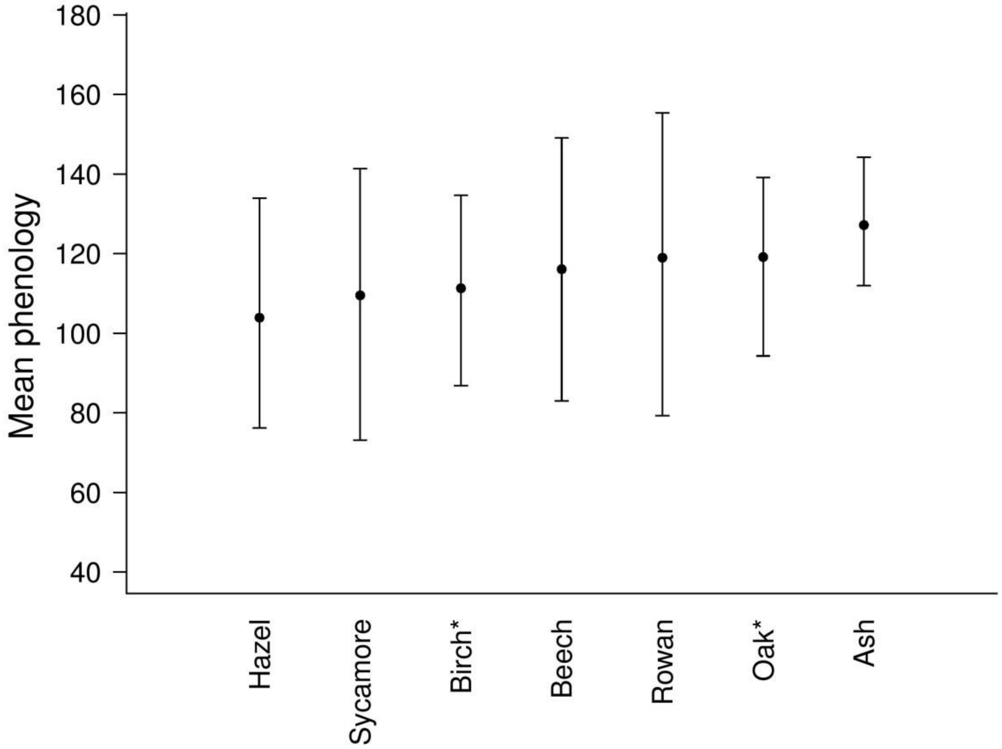


Figure 2. UK-wide Mean tree leafing phenology estimated by the variance partitioning model. Species are plotted in order of mean phenology and bars represent 95% CIs. *denotes focal tree species.

Variance in phenology differed among species (Fig. 3). To aid interpretation, a variance of 1, 10 or 100 would imply that 95% of the observations lie within an approximate range +/- 2, 6 or 20 days. For rowan, some random effects were estimated poorly, with lower effective sample sizes (<1000) across grid cell, site, year and grid cell:year. The model's ability to estimate these effects was likely influenced by the sparse data available for rowan. Caution should therefore be taken when interpreting these variances.

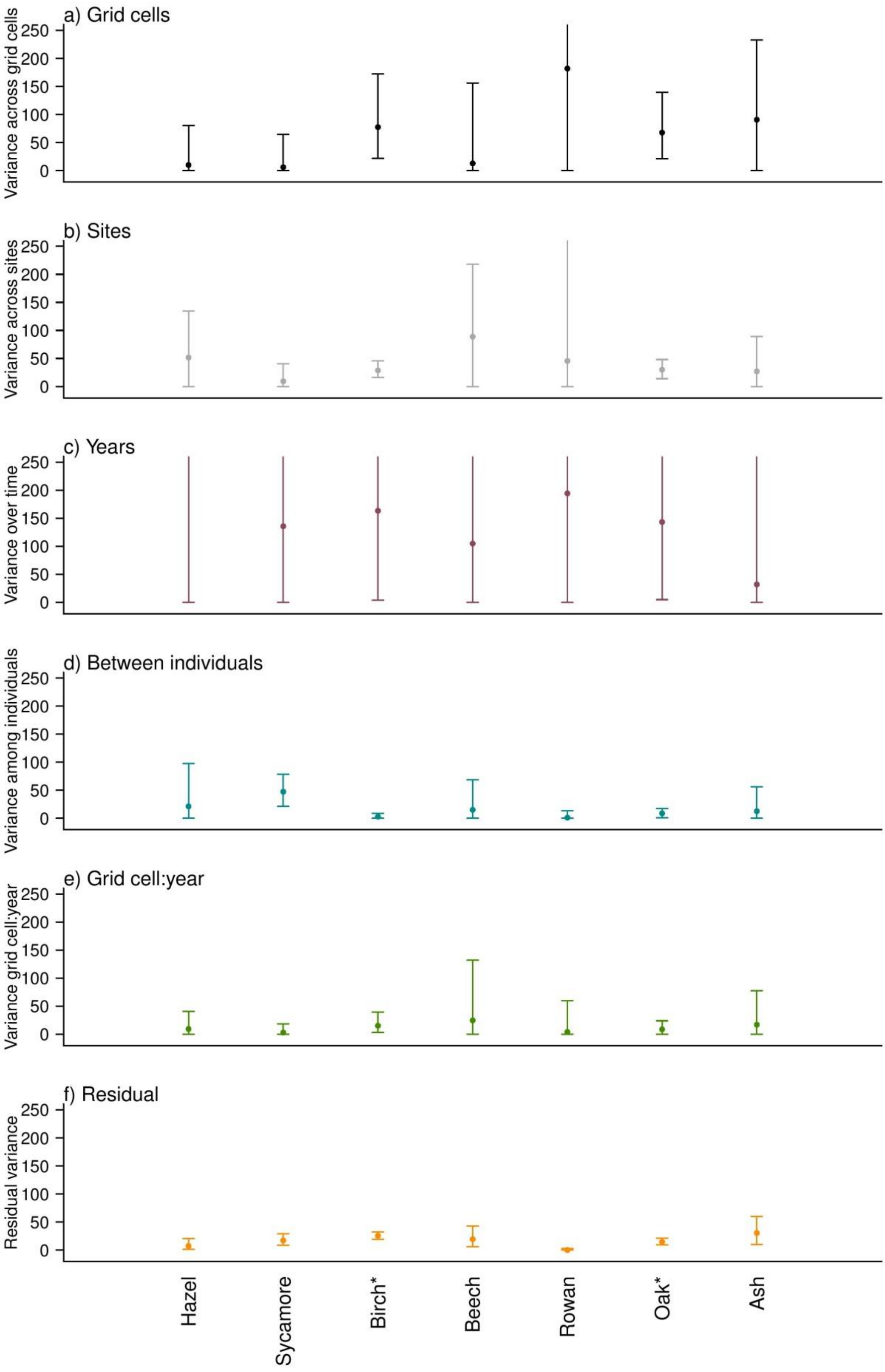


Figure 3. Posterior estimates of variance in phenology a) across 1°grid cells, b) across sites within grid cells, c) between years, d) among individual trees, e) for grid cell:year and f) residual variance estimated by the variance partitioning model. Species are plotted in order of mean phenology. Dots represent medians and bars represent 95% CIs. *denotes focal tree species.

Species differed greatly in the total variance in phenology and how it was partitioned (Figs. 3 and 4). The total variance was lowest in sycamore and ash, and greatest in rowan and hazel (Fig. 4). Across 1° grid cells variance in phenology differed widely between species (Fig. 3a). Spatial (among grid cell) variance was low for hazel, sycamore and beech, with medians below 13 for all three and the narrowest CIs found for hazel and sycamore. The median variance for the remaining species was between 67.78 for oak and 182.00 for rowan, which also exhibited the greatest uncertainty associated with the estimate (Fig. 3a).

Variance across sites was more consistent across species (Fig. 3b), with the median estimated to be less than 50 for all species bar hazel (median = 51.60), and beech (median = 88.75). It was lowest for sycamore, which was also associated with less uncertainty (median = 9.30, Fig. 3b). Birch and oak exhibited a similar variance and had small CIs across sites (birch median = 28.67 and oak median = 29.99, Fig. 3b), while the estimate for rowan was associated with the highest uncertainty (Fig. 3b).

The variance over time (between years) differed widely among species, but was associated with high levels of uncertainty for all (Fig. 3c). The median estimate was lowest for ash (median = 32.02, Fig. 3c) and highest for hazel (median = 268.42). The grid cell:year variance (which corresponds to geographical differences in the among year variance) was small (under 17) for all species except beech (median = 24.68), which was also associated with the greatest uncertainty (Fig. 3e).

Among individual trees, median variances were generally low (Fig. 3d), being under ten for birch, oak and rowan, while sycamore had the highest (median = 47.35, Fig. 3d). CIs were fairly narrow across all species. Median residual variances were mostly below 26 and had small CIs (Fig. 3f), with 0.06 for rowan the lowest and 30.47 for ash the greatest (Fig. 3f).

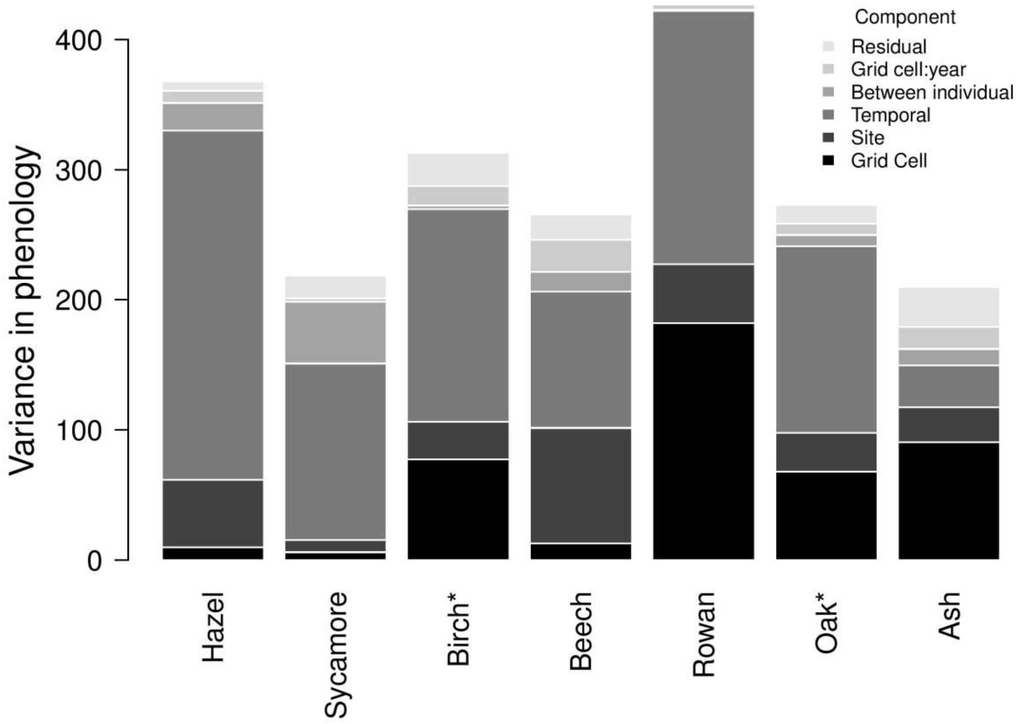


Figure 4. Variance components from the variance partitioning model (calculated as median estimates from the posterior distributions). Species are plotted in order of mean phenology. *denotes focal tree species.

5.4.2 Testing other sources of variation

The *Spatial* model estimated the influence of latitude, longitude and elevation on variation in tree leafing of all seven species and spatial trends differed among them (Table 2 and Fig. 5). For latitude, longitude and elevation, the trends estimated for rowan were dramatically different from the other species, both in terms of magnitude (Figs. 5a and b) and direction (Fig. 5c), which may be ascribable to colinearity between latitude and elevation data for this species.

For all species except hazel, more Northerly latitudes delayed phenology (Fig. 5a), and latitude was a highly significant predictor for birch, rowan, oak and ash. For three of these species the mean delay in phenology lay between 2.84 – 3.21 days/°N, while for rowan the posterior estimate was noticeably higher (mean = 21.18 days/°N, Table 2,

Fig. 5a). Of the species where Northerly latitudes delayed phenology, the shallowest slope was estimated for sycamore (mean = 1.23 days/°N, Table 2, Fig. 5a).

Trends across longitude exhibited the greatest variation among species. More Easterly longitudes were estimated to advance phenology for hazel, oak and ash, and delay it for the remaining species. Longitude was not a significant predictor for any of the tree species, but was close to significance for rowan, which also had the highest mean estimate of 10.18 days/°E (Table 2, Fig. 5b).

Increasing elevation delayed phenology in all species except rowan (mean = -9 days/100m, Table 2, Fig. 5c). It was a significant predictor for birch, beech, rowan and oak. For species where elevation predicted a delay to phenology this ranged between 1 – 6 days/100m, with the shallowest slope estimated for sycamore.

Variances from the *Spatial* model show that it accounted for most of the variance in phenology across grid cells (median = 2.33 – 32.13) for all species. The variance across sites was also reduced for all species (median = 3.79 – 45.18), though the reduction was smallest for hazel and beech. Temporal variance remained high for most species.

Table 2. Coefficients for the *Spatial* model estimated via MCMCglmm. Asterisks indicates significance, CIs = credible intervals, † denotes focal tree species.

Coefficient	**Hazel**		**Sycamore**		**Birch**†		**Beech**		**Rowan**		**Oak**†		**Ash**	
	Posterior mean (95% CIs)	***pMCMC***	**Posterior mean (95% CIs)**	***pMCMC***	**Posterior mean (95% CIs)**	***pMCMC***	**Posterior mean (95% CIs)**	***pMCMC***	**Posterior mean (95% CIs)**	***pMCMC***	**Posterior mean (95% CIs)**	***pMCMC***	**Posterior mean (95% CIs)**	***pMCMC***
Intercept	171.70 (-43.31, 403.20)	0.12	41.92 (-113.70, 204.30)	0.59	-51.01 (-134.30, 27.72)	0.20	-131.4 (-589.1, 334)	0.55	-1014 (-1605, -462.40)	<0.01**	-41.00 (-102.70, 18.00)	0.18	-51.74 (-131.40, 56.92)	0.37
Latitude	-1.49 (-5.77, 2.83)	0.47	1.23 (-1.67, 4.30)	0.39	2.89 (1.46, 4.42)	<0.01***	4.56 (-4.37, 13.54)	0.26	21.18 (10.27, 31.70)	<0.01***	2.84 (1.74, 3.89)	<0.01***	3.21 (1.09, 5.58)	<0.01**
Longitude	-3.75 (-8.84, 0.45)	0.09	0.53 (-3.58, 4.51)	0.78	0.63 (-1.42, 2.63)	0.53	4.12 (-7.68, 16.83)	0.47	10.18 (-0.33, 21.03)	0.05	-1.33 (-2.79, 0.10)	0.07	-1.45 (-4.09, 1.39)	0.28
Elevation	0.04 (-0.04, 0.12)	0.42	0.01 (-0.03, 0.06)	0.55	0.06 (0.04, 0.07)	<0.01***	0.06 (0.01, 0.11)	0.03*	-0.09 (-0.15, -0.03)	0.01*	0.06 (0.03, 0.08)	<0.01***	0.04 (<0.01, 0.09)	0.06

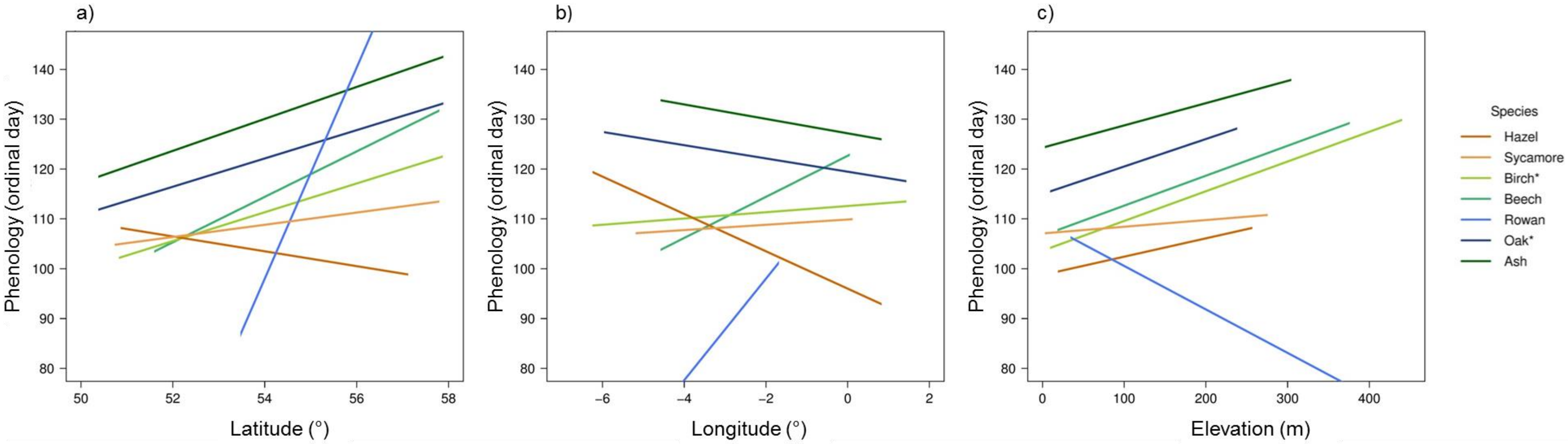


Figure 5. Spatial trends in the posterior mean of tree leafing phenology estimated across a) latitude, b) longitude and c) elevation by the *Spatial* model. Length of each line corresponds to the range of the spatial variable for which there are records of each species. Phenology as ordinal day. *denotes focal tree species.

The *Ecological* model tested additional variables collected by the Track a Tree project as predictors of phenological variation in birch and oak, the focal tree species for which records had the greatest spatial and temporal replication (Table 3). As in the *Spatial* model, latitude and elevation were found to be significant predictors for these species, but only one of the additional variables was significant and only for birch. For birch, a South facing slope significantly delayed phenology (mean = 4.86, Table 3). Like the *Spatial* model, variances in the *Ecological* model were reduced across grid cells and sites, but remained high across years.

Table 3. Parameters for the Additional Variables model estimated via MCMCglmm. Asterisks indicates significance, CIs = credible intervals.

Coefficient	**Birch**		**Oak**	
	Posterior mean (95% CIs)	***pMCMC***	**Posterior mean (95% CIs)**	***pMCMC***
Intercept[1]	-46.94 (-145.80, 50.74)	0.35	-22.59 (-93.32, 55.23)	0.54
Latitude	2.79 (0.91, 4.55)	<0.01**	2.54 (1.14, 3.85)	<0.01**
Longitude	0.18 (-2.09, 2.67)	0.87	-1.20 (-2.77, 0.44)	0.14
Elevation	0.04 (<0.01, 0.08)	0.03*	0.04 (0.01, 0.08)	0.02*
Girth	0.68 (-4.79, 6.59)	0.80	-0.27 (-0.88, 0.36)	0.40
Aspect (slope EW)	4.79 (-0.62, 9.71)	0.07	0.48 (-3.53, 4.53)	0.81
Aspect (slope N)	2.54 (-3.39, 8.00)	0.37	-0.10 (-4.51, 4.24)	0.96
Aspect (slope S)	4.86 (0.41, 9.29)	0.03*	-1.04 (-5.19, 3.17)	0.61
Density (open/varied)	-0.56 (-5.53, 4.49)	0.83	-0.36 (-4.52, 3.79)	0.87

[1] Corresponds to level ground (aspect) and dense woodland (density)

5.5 Discussion

The degree of, and major contributors to, variance in phenology differed widely among the tree species analysed. A key finding was that variance across individuals (within a site and year) was low for all species bar sycamore. This suggests that within most species, there is a low capacity for variance to act as a buffer for phenological interactions within a particular site and year, or may only act at a small scale. The contribution of spatial variables to variance in phenology indicates that buffering may operate over space for these species, but such buffering will also depend on the spatial covariance between interacting species (see Chapter 4).

Relatively low among individual variance was found for six of the seven taxa. For the oak species I found among individual variance that corresponds to approximately 95% of the within site and year leafing observations falling within a 10 day range (with an upper CI of 17). This result, and the associated expectation of limited within site and year phenological buffering, contrasts with previous findings where budburst dates of 36 pedunculate oaks varied by up to 25 days at a single site (Crawley & Akhteruzzaman 1988). The lower among individual variance in this analysis may be partly due to the accuracy with which it was measured. Far fewer trees of the same species were monitored at any single site, with a maximum of seven observed at Track a Tree sites, and 10 at transect sites. For some species this maximum was much less, and so increasing the number of individuals of the same species observed at different sites would improve estimates of among individual variance. It is possible that among individual variance within a site may be non-constant over time, if the phenological plasticity of individual trees differs. This could be explored with more data from individuals at the same site over a number of years.

Further work to explore within site variance in phenology is required to better assess the ability of individuals of the same species to buffer phenological mismatch of specialists. The spatial scale at which consumers of different trophic levels experience trees in their environment will also influence the impact of among individual phenological variation. The differing phenology of individual trees has been demonstrated to affect the abundance and composition of invertebrate herbivores they support (Crawley & Akhteruzzaman 1988), and although this work suggested that ovipositing female insects may be able to select between trees of different phenological stages, the scale at which this occurs remains underexplored. Within site phenological variation of tree leafing has also been shown to correlate with tit breeding times, with tree phenology and food availability important at local scales for individual birds (Cole *et al.* 2015; Hinks *et al.* 2015). Phenological synchrony among trees within a site may therefore reduce opportunities for buffering at several trophic levels, and emphasises the importance of not only understanding variance at a site scale, but also recognising the spatial scale at which species interactions take place. It should also be noted that buffering of generalists at a site may be largely determined by the among species variance in phenology, so community composition may play an important role in phenological buffering.

Sycamore, a non-native naturalized species in the UK, exhibited a noticeably higher among individual variance. This could be a result of high levels of genetic variance influencing its phenology in environments outside its original range. Previous work has examined the spring phenological response of non-native and invasive species and found that successful invaders may be those that are most able to track seasonal temperatures via plasticity (Willis *et al.* 2010; Davis *et al.* 2010) and exploit early or late seasonal niches (Wolkovich & Cleland 2011; Wolkovich *et al.* 2013). Higher levels of among individual phenological variance may also influence the success of non-natives under climate change, and impact not only on the buffering of interacting generalist species, but the long term composition of woodland communities if they are able to exploit a broader temporal niche than other species. Predicting how phenology may affect plant invasions under climate change has become increasingly important (Wolkovich & Cleland 2014), and further exploring the phenological variance of non-natives may help contribute to understanding of the role of phenological niche breadth in their success.

The differing degree of temporal (among year) variance found for the tree species in this analysis is likely to be attributable to plasticity (Donnelly *et al.* 2012). Plasticity plays an important role in the phenological buffering (Nicotra *et al.* 2010) of an individual's response to changes in environmental conditions. There is evidence that some species with early year phenology exhibit greater temporal variability (Fitter & Fitter 2002; Sparks & Menzel 2002; Menzel *et al.* 2006b; a). Assuming that temporal variance is largely attributable to temperature-mediated plasticity (comparable to the approach described in Chapter 2), plasticity was most pronounced in hazel, a woody species with early mean phenology (Fig. 2), and weakest in ash, which had the latest mean phenology of the species analysed here. My finding that the smallest contribution of temporal variance was for ash concurs with the lowest estimate of plasticity in response to forcing temperature in Chapter 2 also being found for ash (-3.18 days/°C). All species exhibited low levels of grid cell:year variance, which suggests that temporal variance, and thus plasticity (following my assumption above), does not differ geographically. Further evidence that plasticity is relatively constant across the UK was found in Chapter 2 (Fig. A3 in Appendix A).

In the variance partitioning analysis I found residual variance in phenology to be relatively small for all species, although it was highest for ash. The residual variance may include the influence of microsite effects (e.g. through soil or microclimate) that vary among species, and non-directional observer effects (directional observer effects are likely to be contained in the grid cell and site spatial variances). Observer error is often thought to be a major issue with data collected by citizen scientists. However, in testing the contribution of observer error to residual variance in Canadian phenology records, Beaubien and Hamann (2011) found that records from experienced observers are only slightly less variable than those from novices, and so observer effects may not account for much variance in this analysis. In addition, the residual variance will include any within individual among year variation, i.e. how much an individual differs from the general temporal (across year) variance.

Results from the *Spatial* model showed that significant spatial predictors differed among species (Table 1) but that latitude, longitude and elevation explained almost all variance across grid cells and most between sites, except for hazel. No spatial variables were significant for sycamore, which was reflected in shallow slopes across latitude, longitude and elevation, both in this analysis (Fig. 5), and that of Chapter 2 (Fig. A1 in Appendix A). In contrast, trends for hazel leafing in Fig. 5 included a negative trend across latitude and a steep slope across longitude, with later leafing predicted in the West, despite these variables not being significant. Previous work modelling hazel flowering across Europe found a strong W-E gradient in date of onset (Schleip *et al.* 2009). The result here may reflect a difference in the impact of longitudinal gradients on different phenological events, or be due to a lack of power in these analyses to detect the true trends. Trends across longitude showed the most variation among the tree species (Fig. 5), which could reflect non-linearity in the relationship between longitude and phenology. Longitude only neared significance in rowan, for which the *Spatial* model did not appear to successfully disentangle the colinearity between predictors. In addition, fewest observations were available for rowan, so the smaller geographic spread of this species may have impacted on the ability of the analysis to effectively model spatial predictors.

The *Spatial* model was limited in its use of linear terms for gradients over latitude and longitude. In Chapter 2, I looked at the spatiotemporal trends of phenology using records from the Nature's Calendar project for all the tree species, bar hazel, analysed here. For all species except beech, a model that included the interaction between latitude and longitude, and where they were subject to quadratic relationships performed better than one which did not include these more complex terms (see Fig. 3 in Chapter 2). My analysis in Chapter 2 found more variable patterns in phenology over longitude, which is also seen in the results from the *Spatial* model and may reflect more complex temperature clines over longitude. However, my previous findings suggest that this analysis may have been limited in its ability to fully detect spatial trends.

Elevation predicted a delay in phenology for all species except rowan, where the trend was likely affected by the limited range of elevations for which records were available. For the remaining species, the delay in phenology ranged between 1 days/100m for sycamore to 6 days/100m for birch, beech and oak. The delay likely reflects the altitudinal temperature gradient, which has been shown to influence leaf unfolding in deciduous tree species through phenological plasticity (Vitasse *et al.* 2013). The among species differences in the trends across latitude, longitude and elevation may arise through the varying contribution of phenotypic plasticity and local adaptation to temperature across space, for which there is evidence from common garden experiments and provenance trials (e.g. Ducousso *et al.* 1996; Vitasse *et al.* 2013).

Of the additional predictors included in the *Ecological* model, only South-facing slopes were found to be a significant predictor, for birch. Seemingly counter-intuitively, South-facing slopes were found to delay phenology in birch species. However, birch leafing requires a chilling cue to be met (identified in Chapter 2; Caffarra *et al.* 2011) and this may be reached more slowly on South-facing slopes. Although earlier work detected a six day difference in flowering phenology on opposing slopes at a single site (Jackson 1966), in an analysis based on widespread Canadian phenology observations, exposure (both slope and aspect) did not contribute to phenological variation. The authors suggested this may be due to the microclimatic effects arising through exposure being less detectable at larger scales (Beaubien & Hamann 2011). My result for oak could therefore be evidence (see also Iversen *et al.* 2009) that small scale, within site environmental variation may not be a major influence on the phenological distribution of some species at particular sites.

The main limitation of the analyses conducted here was the number of records available. Records were limited by the spatial distribution of some species, especially rowan, and the number of years for which observations were available. This influenced how robust some of the model estimates were, and may have affected the ability of the models to detect the influence of some predictors, particularly in the *Ecological* model. Future analyses that include observations from subsequent years and of multiple individual trees within the same site would improve confidence in some of the model findings.

Quantifying the phenological plasticity of individual trees was one of the initial aims of the Track a Tree project. I have been unable to test the within individual, between year variance in phenology explicitly in these analyses, as including this interaction in the variance partitioning model was confounded with the residual variance. With more years of data more robust estimates of this source of phenological variation will be possible. Variance in phenology has been examined for tree species alone in this work. Investigating the phenological variance of ground flora, or other interacting species would allow a more direct assessment of how the distributions of phenology may affect potential future mismatch. Expanding the approach taken here to more plant species may also enable a comparative analysis to test whether certain plant traits predict different types of variance.

The differing degree of overall variance among the tree species (Fig. 4) suggests that the phenological distributions of different species may vary in their ability to act to buffer potential mismatch. Species exhibiting less variance, such as beech and sycamore, could have a smaller impact in decreasing the risk of mismatch in communities of interacting species, although how the variance is partitioned may be more important than the overall variance. Low within site, within year variance may mean that the ability of individual species to buffer mismatch at a particular site may be limited, with phenological buffering more likely to occur across larger spatial scales. The analyses undertaken here reveal that understanding the influences on the phenological distribution of trees in woodland requires a species by species approach.

Chapter 6

General discussion

6.1 Overview

Shifting phenology may affect how populations and communities respond to climate change, and therefore understanding phenological change is important for projecting the fates of species under future conditions. The aim of my thesis was to enhance our ability to project the consequences of temperature change for UK plants by: i) identifying the phenological cues used by different species, ii) estimating whether plasticity in response to these cues will be able to keep up with changes in their optimum phenology, iii) using space-for-time substitution to predict whether shading interactions in woodland plants will be maintained, and, iv) investigating the capacity for the phenological distributions of woodland trees to buffer potential mismatches. Citizen science collected data was central to my research and this gave me an opportunity to reflect upon and start to evaluate the role of citizen science as a tool available to researchers. I have been able to explore the potential for different citizen science approaches to address new questions about phenology.

6.2 Phenological cues

In modelling the temperature and photoperiod cues for 22 UK plant species for which phenology observations were available from the UK Phenology Network (UKPN) (Chapter 2), I found that there was considerable among-species variation in the time window during which they were most sensitive to forcing temperatures. The importance of ‘chilling’ versus photoperiod cues also varied between species, where those with later year phenology tended to be more sensitive to photoperiod and those with earlier year phenology tended to be more sensitive to ‘chilling’ temperatures. These findings lend support to the evidence that cue use varies among plant species (e.g. Morin *et al.* 2009; Basler & Körner 2012, 2014; Laube *et al.* 2014), but takes a finer scale time-window approach than previous work that has used mean monthly temperatures (e.g. Yu *et al.* 2010). Other recent work has also attempted to more accurately identify periods of climate sensitivity in multiple taxa (Thackeray *et al.* 2016). My results also provide some support to the theory that ‘chilling’ cues may be more important to species with early year phenology, while interannually stable photoperiod cues may be particularly important in species with later phenology

(Polgar & Primack 2011). The degree of temperature change is projected to vary both spatially and temporally (throughout the year) under climate change. By contributing to the evidence for differences in the way species use phenological cues at different times of the year, this work indicates that there may be considerable variation in how plants will continue to respond to warming temperatures under climate change.

The methods used to obtain the forcing and ‘chilling’ windows in Chapter 2 searched a greater parameter space than many previous approaches. This meant I was able to test a wider variety of time windows, and identify differences in important periods that may not be captured when looking at mean monthly temperatures. A shortcoming of this approach however, was that due to time constraints, I was unable to run a model that included both forcing and ‘chilling’ temperatures, and photoperiod. It may be that this combination would better reflect the cue use of some species. If this is the case, the accuracy of the subsequent estimates of plasticity, and the temperature sensitivity of the optimum (B_{lat} and B_{lon}) in Chapter 2 may have been affected, as the approach assumes that the correct cue has been identified (Hadfield 2016). Nevertheless, the modelling here provided a method with which to determine species for which including a photoperiod or chilling cue explains more of the spatiotemporal variation in phenology. The other key limitation of the linear modelling in this analysis is that it included photoperiod as a threshold to a period of forcing and was therefore unable to capture any more complex role that photoperiod might play. For example, photoperiod may only become an important cue when a period of chilling is inadequate (Caffarra *et al.* 2011a; Caffarra *et al.* 2011b; Laube *et al.* 2014).

Future work to model the cues of a broad range of plant species could develop the approach here by integrating forcing and ‘chilling’ temperatures and photoperiod into the same model. It may also be advantageous to compare the findings of different modelling approaches, to see whether the same cues are consistently found (see Phillimore *et al.* 2013; Roberts *et al.* 2015 for previous attempts). To further test the pattern of cue use in early and late phenology species it would also be beneficial to expand future analyses to include more species for which the phenological timing is recorded.

6.3 Plasticity and adaptation

In completing an analysis of the responses to the phenological cues identified in Chapter 2, I found that all species respond to forcing plastically in the range of -3 to -8 days °C^{-1}. This is in accordance with evidence of phenological plasticity from experimental work (e.g. Kramer 1995; Vitasse *et al.* 2010), and demonstrates the primary mechanism for the well documented shifts in phenology as climate warms (Nicotra *et al.* 2010). My finding that plasticity is likely to be able to track the optimum phenology in seven species utilises a new method to estimating Chevin *et al's* (2010) environmental sensitivity of selection, *B*. In four species, plasticity did not track the optimum, and this finding was consistent with evidence for clinal local adaptation to temperature which could place their phenology under directional selection in a changing climate. This demonstrated that species may exhibit both plastic and locally adapted responses to temperature, a finding that has previously been documented in a number of different studies (reviewed in Franks *et al.* 2014). Using phenology observations to estimate the ability of a species to keep up with changes in optimum phenology has rarely been attempted (but see Phillimore *et al.* 2016), due to the difficulty of estimating how optimal phenologies change as the environment does (known as the environmental sensitivity of selection, *B* in Chevin *et al.* 2010). The analyses here therefore provide an important demonstration of a recently developed approach to estimating *B* that could be applied more widely.

The analyses I conducted in Chapter 2 also revealed some challenges in estimating *B* from spatial phenological data. Estimating *B* using the approach taken here relies on the correct phenological cues having been identified. As discussed in the previous section, the accuracy of the cues may have been compromised as I did not allow for a more complex model including 'chilling', forcing and photoperiod. Some of the species in the analysis may respond to a combination of these cues that I was unable to capture to pass on to the model of their responses. In addition, for some species, the direction of the estimates for B_{lat} and B_{lon} were different and inconsistent with the underlying theory (Hadfield 2016), which suggests that an additional third variable could covary with phenology and temperature differently over latitudes versus longitudes. This limited any conclusions about the ability of plasticity to track the optimum phenology in these species. Because of these limitations to the model, my findings should be viewed as hypotheses about the future phenological responses of the species tested.

Further experimental work would provide greater insights into species responses, as well as acting as a check on the robustness of my model estimates.

Despite the challenges of using these methods to estimate phenological responses, the statistical approach I employ here has the potential to be applied to other existing phenology datasets of plants and other taxa. It could prove a useful tool for identifying species which may be less likely to keep up with their optimum phenology and that would benefit from further experimental exploration. As well as utilising this method more widely, attempting to integrate more complex cues would enable a greater degree of confidence in the ability of the models to estimate *B*.

6.4 Species interactions

My analyses addressing the relative phenology of woodland canopy tree and ground flora species in Chapter 4 provide one of the first attempts to look at the future of intraguild phenological interactions in woodland communities. I found that first leafing and peak flowering of focal canopy tree/ground flora species pairs were correlated over space and that their relative phenology was spatially consistent. For two native canopy tree species pairs, relative phenology was also spatially consistent, but it varied for one native versus non-native tree species pair. If the phenology of these species is determined by temperature-mediated plasticity, understorey flowering may be able to track canopy leafing in the future and shading interactions could be maintained. There has been a good deal of work exploring temperate deciduous woodland communities (e.g. Salisbury 1921; Blackman & Rutter 1946; Anderson 1964; Sparling 1967; Emborg 1998; Whigham 2004; Augspurger *et al.* 2005), as well as some exploration of species interactions across trophic levels in such woodlands (e.g. Kudo *et al.* 2008). However, the degree to which phenological interactions between plant species could be affected by climate change has not been much examined, yet it is an important aspect of understanding the long term fate of these communities. My finding that the shading interactions of deciduous woodland canopy and understorey species may be maintained in future indicates that there may be some resilience of UK woodland plants to climate change. This inference is based on substituting spatial trends in the relative phenology of these species pairs for temporal ones. This is a useful approach for phenology data without adequate temporal replication, such as Track a Tree's records.

However, it assumes that the driver of spatial trends also drives temporal patterns in phenology, an assumption that is not tested here.

The analysis of variance in tree leafing that I conducted in Chapter 5 provides an insight into the phenological distributions of different tree species. This is important because both inter- and intraspecific variation in tree phenology could buffer the effect of potential mismatches with interacting species (such as herbivorous insects). I found that the contributors to variance differed among tree species but that spatial variables were important, and within site variance was low for all species except sycamore. This finding suggests that the phenological distributions of tree species are affected by differing variables, and that this may affect their ability to buffer mismatch with interacting species. Thus far, the data from Track a Tree has not been enough to robustly estimate the landscape and biogeographic drivers of phenology for the species analysed, and more observations from multiple individual trees (of a single or several species) at the same site would be required to address this.

The records from Track a Tree have succeeded in indicating how interacting plant species may respond, although the short time-scale for achieving a research outcome from the Track a Tree project during a PhD limited the amount of data that could be collected. In addition, using a citizen science approach meant a trade-off between the complexity of the protocol and the amount of participation in Track a Tree. A clear progression of the project would be to expand to include other types of phenological interaction. Additional data could be collected for other taxa, and could for example, explore the relationship of canopy trees and herbivorous insects.

Further work on phenological interactions in woodlands could expand on the citizen science approach taken here, as it enables spatial variation in phenology to be used as a tool to predict future responses. In particular, development of Track a Tree would benefit from, i) an expansion of the range of phenological interactions it monitors, and, ii) a focus on recording inter- and intraspecific variation in leafing phenology in woodlands, to explore the potential for local intraspecifc variation in timing to buffer mismatched interactions.

6.5 Comparative analyses

I conducted phylogenetic comparative analyses on the date of phenology, estimates of plasticity and the ability of plasticity to track the optimum (an indicator of the degree of local adaptation) in Chapter 3. These analyses were underpowered due to an insufficient number of species and phenological events analyses. This prevented the phylogenetic signal and role of ecological predictors in these responses being estimated accurately. Despite this, the analyses were a useful exercise in identifying potentially useful predictors, and highlighted event type (leafing or flowering) and growth form (woody or herbaceous perennial) as variables that might predict the degree of plasticity in phenological response. The key difficulty in separating their influence arose from the fact that most woody species included only had leafing records available, and most herbaceous species only had flowering records available. A greater sample size would be required to disentangle the influence of these predictors, and any others that may be confounded. I did not identify any ecological variables that predicted the median date of phenology or my indicator of clinal local adaptation. Nevertheless, conducting comparative analyses on multiple elements of phenological response has thus far been understudied, and my approach demonstrates how this could be tackled. Future comparative analyses would therefore benefit from being based on the phenological records of, i) a greater number of species, and, ii) species that have more than one phenophase recorded. Estimates of plasticity and local adaptation for multiple phenological events could then be made for those species, and predictors for these aspects of their response investigated.

6.6 Citizen science

In using observations from the UKPN, collected by the Nature's Calendar citizen science scheme, I employed recently developed statistical methods to explore questions that have rarely been addressed using this type of spatiotemporal phenology data. The techniques that I used could be applied to other datasets (e.g. from the schemes listed in Chapter 1) in order to assess the ability of plasticity to keep up with changes in the optimum phenology in more plant species, or other taxa (e.g. birds, see Phillimore *et al.* 2016). The Nature's Calendar data has clear strengths for conducting this type of analysis, as it holds tens of thousands of records for a variety of common UK species, collected over 16 years. It monitors several phenological events throughout the year and has a good spatial coverage, all of which allows both spatial and temporal patterns to be analysed. Undertaking work using Nature's Calendar also allowed me to assess some of the limitations that may be encountered by researchers using these data, which I have summarised in Table 1.

The second part of my thesis (Chapters 4 and 5) relied on records from the Track a Tree scheme. In Table 2 I have highlighted the challenges faced by the project and the type of data collection it requires. From its inception it was clear that Track a Tree would require a greater level of commitment and knowledge than previous phenology citizen science schemes in the UK. The complexity of the protocols and the repeat visits required to obtain informative records meant that the potential audience for the project was limited from the outset. This is reflected in the number of recorders that participated in the project in 2014-15. The number of sites which were monitored and provided informative data dropped off from 97 to 51 over these two years. While the overall spatial coverage for some species was reasonable (see Chapter 4, Fig. 1), the limited number of sites meant that informative records were not obtained for a number of species monitored in Track a Tree. One of the major challenges in obtaining records via the project was ensuring that it reached an appropriate audience of potential participants. Improving links with organisations with woodland volunteer networks, interested individuals and educators may help increase the level of participation in future. For existing repeat Track a Tree recorders however, an important aspect of engaging them in the project was regular communication via the Track a Tree blog and social media accounts. Throughout the duration of the project 35 blog posts were written, and regular updates posted on Twitter (>850 followers) and Facebook (>460 page likes). In addition, Track a Tree featured in several Nature's Calendar newsletters, Woodland Trust publications and blog posts.

There have been some attempts to draw up recommendations from plant phenology citizen science before, in particular by the Canadian PlantWatch scheme (Beaubien & Hamann 2011).These previous findings and the work I conducted using Nature's Calendar data highlighted existing deficiencies in the Nature's Calendar scheme (Table 1), which I attempted to address when developing the Track a Tree project. While I succeeded in examining interacting species in woodland communities, monitoring random individuals in a population and capturing recorder effort, I encountered a number of challenges in running the project (Table 2). To address these issues and to further develop Track a Tree, the project would benefit from establishing research partnerships with institutions such as the Centre for Ecology and Hydrology and Forest Research. Despite the challenges in setting up Track a Tree, I have demonstrated that during the course of a PhD it is possible to focus small-scale citizen science schemes on specific questions that will advance our understanding of phenological responses under climate change. Over short time-scales, the ability to use space as a substitute for time is particularly valuable. Although three years of records allowed me to examine year to year variance, it was not enough to estimate a slope over time. An additional and unexpected outcome of the project has been the research links made with the Sustainable Places Research Institute (SPRI) at the University of Cardiff. Dr Ria Dunkley from SPRI has conducted interviews with Track a Tree participants to examine their experiences of and motivations for taking part in the project. This work was presented at the European Citizen Science conference in May 2016, and is likely to be developed in future, continuing to contribute to an expanding body of work on the motivations and rewards associated with citizen science (e.g. Everett & Geoghegan 2015).

Table 1. Deficiencies and challenges in the Nature's Calendar scheme, recommendations to address these and potential future research links associated with the recommendations.

Deficiency or challenge	Recommendation	Potential research links
No measure of recorder effort.	Include an optional field for recorders to submit a date the event was last 'not observed'. This would mean each record was associated with a time window during which the event occurred. A similar approach has been taken by US project Nature's Notebook.	This date would provide a measure of error associated with each phenology record. This date could be passed to models used in research to take account of the uncertainty in the analyses.
No environmental information (e.g. the type of habitat) is associated with phenological records.	Include a field to describe the habitat category where a phenology observation was made. Categories could include the following: Garden Hedge Park Woodland Urban area Field/Pasture	Collecting environmental information would allow the phenology of the same species in different habitats to be examined. This has recently been attempted for urban areas, where the influence of light pollution was studied (Ffrench-Constant *et al.* 2016). Including more habitat information would allow research to focus on one, or compare several, habitat types.
No information on whether the same individual or habitat patch (e.g. pond) is recorded throughout the year, or between years.	Include optional fields for recorders to submit this information. Project Budburst in the US and PlantWatch in Canada both have protocols for monitoring individual plants.	The information could be used to examine how the phenology of individual organisms (e.g. trees) responds over time, which could be used to quantify plasticity and/or carry-over effects between seasons. Using habitat patch information could provide insight into how phenology at specific geographic locations varies.
The geographical location of records is at a coarse resolution and is limited by the use of post-codes to define a recording site.	Include an optional field for a more accurate grid-reference or GPS location. Alternatively, users could be asked to draw a polygon on a base map (as in Track a Tree) to designate their usual recording area. Any records outside this area could be submitted using additional location data.	Accurate location data could be used obtain site characteristics. For studies examining species that interact with one another, detailed location data would allow an assessment of the likelihood of interactions between them. Accurate location data would improve record matching

	Any future app for the scheme would automatically associate records with accurate location data.	with accurate temperature models; this may be especially important where elevation affects temperature.
A limited number of phenophases are recorded, focussed on the first events during spring.	Include the option to record additional phenophases (e.g. full leaf, seed set) in order to monitor phenological progression.	Additional phenophase records would allow a more in-depth exploration of through-year phenology (either at the same location or in the same individual). This could include a better assessment of growing season length in plants.
Records comprise first dates of event occurrence, and therefore only reflect one tail of the phenological distribution of a population.	Addressing this would require a fundamental change in the way observations are collected, so I do not offer any immediate recommendations.	Researchers have often assumed that first dates reflect the mean phenology of a population or species. This assumption may be a problem for species that exhibit a greater variance in phenology, and so caution may be required when interpreting first dates.

Table 2. Deficiencies and challenges in the Track a Tree scheme, recommendations to address these and potential future research links associated with the recommendations.

Deficiency or challenge	**Recommendation**	**Potential research links**
Methodological		
Validation of records limited to manual checks by project co-ordinators.	Include automated processes to help validate accuracy, e.g. outliers could be identified via the website, a quiz to test ID skills and phenophase scoring of recorders could flag up records that need manual checks.	Better validation of records may improve the robustness of results and how research outcomes are viewed in academic settings (e.g. Rose *et al.* 2015).
Only one tree phenophase able to be recorded on a single visit.	Allow recorders to submit multiple phenophases for a single visit, e.g. partial budburst and partial leaf.	Recording multiple phenophases could be used to quantify the phenological progression in individual trees.
Flowering categories provide only rough estimation of peak flowering.	Include a free count of flowers up to a certain number, e.g. ≤50.	The phenological distribution of flowering could be better quantified.
Recorders may miss peak flowering by ending observations after leafing is reached.	Change guidelines to end recording after ground flora species have started to go over/set seed.	The phenological distribution of flowering could be better quantified.
Limited species interactions monitored	Develop additional optional recording modules for	Examining more species interactions would enable a

	participants. This could include a survey of herbivore damage to tree leafing, or recording the presence of early season pollinators.	better assessment of the potential community response to climate change in woodlands.
Estimation of within site variation in tree phenology limited by records. Protocols do not focus on recording multiple trees at a site.	Establish core-sites across the UK where local participants are asked to monitor multiple individuals of the same tree species.	The intraspecific variation in phenology could be quantified within sites and years and used to assess the potential to buffer mismatches.
Recording limited to spring events	Include the option for participants to record additional phenophases e.g. autumn leaf fall and seed set of ground flora species.	Additional phenophases could be used to examine inter-season effects on phenology.
Other		
A limited number of records were collected, leading to geographic gaps in the data available.	Target promotion of project in focus areas, and through making links with woodland sites that have regular friends, volunteer or schools groups.	A better coverage of observations would encompass woodlands exposed to a greater gradient of environmental conditions (e.g. temperature). This would improve any forecasts that employ space-for-time substitution.
A drop-off in repeat recorders i.e. those that make observation of the same tree(s) in multiple years.	Provide better support for recorders who stop recording through difficulties with project protocols. Provide a motivation for those that commit to recording for >1 year. For example, employ a Track a Tree reward system.	Repeat observations of the same trees will allow a better estimation of temperature-mediated plasticity of the phenological response of individual trees and at the same sites.
Difficult to promote Track a Tree to the most appropriate target audience for the project.	Improve promotion via relationship with the Woodland Trust and other potential partners. Target particular groups by running training events or providing supporting materials.	Successful promotion to more participants will increase the number of records available for future analysis.
Lack of direct contact with participants for training and motivation.	Investigate possibility of running training events with interested groups at relevant sites.	This will increase the number of records available and lead to the establishment of core sites.

6.7 Conclusions

The work outlined in this thesis contributes both to the current state of knowledge of UK plant phenology, and to the breadth of approaches that can be used in phenological research. The analyses of Chapters 2 could be used to help identify further hypotheses about the contributions of plasticity and local adaptation that could be explored experimentally. The findings in Chapter 3 indicated that applying a consistent method to many species would enable more robust comparative analyses to be conducted in future. In particular, these chapters highlighted the need for estimates of plasticity and local adaptation to be made for a wider variety of species and for successive phenophases in the same species. This work also provided an example of how recent statistical tools can be employed to draw new conclusions from existing spatiotemporal phenology datasets. The development of the Track a Tree project and the analyses conducted in Chapters 3 and 4 demonstrated how novel citizen science projects can be used to examine and predict possible phenological mismatches. While new schemes may not necessarily be the best approach in a crowded market place for citizen science, developing existing schemes to include optional recording tasks or challenges would provide a tiered level of involvement that addressed specific questions. This is an area that has been previously neglected in phenology based citizen science, yet it has great potential to be a valuable tool in addressing pressing questions about phenology under climate change.

Bibliography

Alberto, F.J., Aitken, S.N., Alía, R., González-Martínez, S.C., Hänninen, H., Kremer, A., Lefèvre, F., Lenormand, T., Yeaman, S., Whetten, R. & Savolainen, O. (2013) Potential for evolutionary responses to climate change - evidence from tree populations. *Global Change Biology*, **19**, 1645–1661.

Altermatt, F. (2010) Tell me what you eat and I'll tell you when you fly: diet can predict phenological changes in response to climate change. *Ecology Letters*, **13**, 1475–1484.

Amano, T., Freckleton, R.P., Queenborough, S.A., Doxford, S.W., Smithers, R.J., Sparks, T.H. & Sutherland, W.J. (2014) Links between plant species' spatial and temporal responses to a warming climate. *Proceedings of the Royal Society B: Biological Sciences*, **281**, 20133017.

Amano, T., Lamming, J. & Sutherland, W.J. (2016) Spatial gaps in global biodiversity information and the role of citizen science. *BioScience*, **66**, 393–400.

Amano, T., Smithers, R.J., Sparks, T.H. & Sutherland, W.J. (2010) A 250-year index of first flowering dates and its response to temperature changes. *Proceedings of the Royal Society B: Biological Sciences*, **277**, 2451–2457.

Anderson, M.C. (1964) Studies of the Woodland Light Climate: II Seasonal Variation in the Light Climate. *Journal of Ecology*, **52**, 643–663.

Anderson, T.L., Hocking, D.J., Conner, C.A., Earl, J.E., Harper, E.B., Osbourn, M.S., Peterman, W.E., Rittenhouse, T.A.G. & Semlitsch, R.D. (2015) Abundance and phenology patterns of two pond-breeding salamanders determine species interactions in natural populations. *Oecologia*, **177**, 761–773.

Anderson, J.T., Inouye, D.W., McKinney, A.M., Colautti, R.I. & Mitchell-Olds, T. (2012) Phenotypic plasticity and adaptive evolution contribute to advancing flowering phenology in response to climate change. *Proceedings of the Royal Society B: Biological Sciences*, **279**, 3843–3852.

APG III. (2009) An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG III. *Botanical Journal of the Linnean Society*, **161**, 105–121.

van Asch, M. & Visser, M.E. (2007) Phenology of forest caterpillars and their host trees: the importance of synchrony. *Annual Review of Entomology*, **52**, 37–55.

Augspurger, C.K., Cheeseman, J.M. & Salk, C.F. (2005) Light gains and physiological capacity of understorey woody plants during phenological avoidance of canopy shade. *Functional Ecology*, **19**, 537–546.

Augspurger, C.K. & Salk, C.F. (2016) Constraints of cold and shade on the phenology of spring ephemeral herb species. *Journal of Ecology*, **Accepted A**, doi:10.1111/1365-2745.12651.

Bartomeus, I., Ascher, J.S., Wagner, D., Danforth, B.N., Colla, S., Kornbluth, S. & Winfree, R. (2011) Climate-associated phenological advances in bee pollinators and bee-pollinated plants. *Proceedings of the National Academy of Sciences of the United States of America*, **108**, 20645–20649.

Basler, D. & Körner, C. (2012) Photoperiod sensitivity of bud burst in 14 temperate forest tree species. *Agricultural and Forest Meteorology*, **165**, 73–81.

Basler, D. & Körner, C. (2014) Photoperiod and temperature responses of bud swelling and bud burst in four temperate forest tree species. *Tree Physiology*, **34**, 377–388.

Beaubien, E.G. & Hamann, A. (2011) Plant phenology networks of citizen scientists: recommendations from two decades of experience in Canada. *International Journal of Biometeorology*, **55**, 833–841.

Beck, P., Caudullo, G., de Rigo, D. & Tinner, W. (2016a) Betula pendula, Betula pubescens and other birches in Europe: distribution, habitat, usage and threats. *European Atlas of Forest Tree Species* (eds J. San-Miguel-Ayanz),, D. de Rigo),, G. Caudullo),, T. Houston Durrant), & A. Mauri), p. e010226. Publication Office of the European Union, Luxembourg.

Beck, P., Caudullo, G., Tinner, W. & de Rigo, D. (2016b) Fraxinus excelsior in Europe: distribution, habitat, usage and threats. *European Atlas of Forest Tree Species* (eds J. San-Miguel-Ayanz),, D. de Rigo),, G. Caudullo),, T. Houston Durrant), & A. Mauri), p. e0181c0. Publication Office of the European Union, Luxembourg.

Bjorkman, A.D., Elmendorf, S.C., Beamish, A.L., Vellend, M. & Henry, G.H.R. (2015) Contrasting effects of warming and increased snowfall on Arctic tundra plant phenology over the past two decades. *Global Change Biology*, **21**, 4651–4661.

Blackman, G.E. & Rutter, A.J. (1946) Physiological and Ecological Studies in the Analysis of Plant Environment 1. The Light Factor and the Distribution of the Bluebell (Scilla non-scripta) in Woodland Communities. *Annals of Botany*, **10**, 361–390.

Both, C., Artemyev, A. V, Blaauw, B., Cowie, R.J., Dekhuijzen, A.J., Eeva, T., Enemar, A., Gustafsson, L., Ivankina, E. V, Järvinen, A., Metcalfe, N.B., Nyholm, N.E.I., Potti, J., Ravussin, P.-A., Sanz, J.J., Silverin, B., Slater, F.M., Sokolov, L. V, Török, J., Winkel, W., Wright, J., Zang, H. & Visser, M.E. (2004) Large-scale geographical variation confirms that climate change causes birds to lay earlier. *Proceedings of the Royal Society B: Biological Sciences*, **271**, 1657–1662.

Both, C., Van Asch, M., Bijlsma, R.G., Van Den Burg, A.B. & Visser, M.E. (2009) Climate change and unequal phenological changes across four trophic levels: Constraints or adaptations? *Journal of Animal Ecology*, **78**, 73–83.

Brooker, R.W. (2006) Plant-plant interactions and environmental change. *The New Phytologist*, **171**, 271–284.

Brooker, R.W., Travis, J.M.J., Clark, E.J. & Dytham, C. (2007) Modelling species' range shifts in a changing climate: The impacts of biotic interactions, dispersal distance and the rate of climate change. *Journal of Theoretical Biology*, **245**, 59–65.

Bruno, J.F., Selig, E.R., Casey, K.S., Page, C.A., Willis, B.L., Harvell, C.D., Sweatman, H. & Melendy, A.M. (2007) Thermal stress and coral cover as drivers of coral disease outbreaks. *PLoS Biology*, **5**, 1220–1227.

Buckley, L.B. & Kingsolver, J.G. (2011) Functional and Phylogenetic Approaches to Forecasting Species' Responses to Climate Change. *Annual Review of Ecology, Evolution, and Systematics*, **43**, 205–226.

Burkle, L.A., Marlin, J.C. & Knight, T.M. (2013) Plant-Pollinator Interactions over 120 Years: Loss of Species, Co-Occurrence and Function. *Science*, **339**, 1611–1615.

Burnham, K.P. & Anderson, D.R. (2004) Multimodel Inference: Understanding AIC and BIC in Model Selection. *Sociological Methods & Research*, **33**, 261–304.

Butler, D.G., Cullis, B.R., Gilmour, A.R. & Gogel, B.J. (2009) *ASReml-R Reference Manual*. The State of Queensland, Department of Primary Industries and Fisheries, Brisbane.

Caffarra, A. & Donnelly, A. (2011) The ecological significance of phenology in four different tree species: Effects of light and temperature on bud burst. *International Journal of Biometeorology*, **55**, 711–721.

Caffarra, A., Donnelly, A. & Chuine, I. (2011a) Modelling the timing of Betula pubescens budburst. II. Integrating complex effects of photoperiod into process-based models. *Climate Research*, **46**, 159–170.

Caffarra, A., Donnelly, A., Chuine, I. & Jones, M.B. (2011b) Modelling the timing of Betula pubescens budburst. I. Temperature and photoperiod: a conceptual model. *Climate Research*, **46**, 147–157.

Campbell, D.R. & Motten, A.F. (1985) The Mechanism of Competition for Pollination between Two Forest Herbs. *Ecology*, **66**, 554–563.

CaraDonna, P.J., Iler, A.M. & Inouye, D.W. (2014) Shifts in flowering phenology reshape a subalpine plant community. *Proceedings of the National Academy of Sciences of the United States of America*, **111**, 4916–4921.

CaraDonna, P.J. & Inouye, D.W. (2015) Phenological responses to climate change do not exhibit phylogenetic signal in a subalpine plant community. *Ecology*, **96**, 355–361.

Chen, I., Hill, J.K., Ohlemüller, R., Roy, D.B. & Thomas, C.D. (2011) Rapid range shifts of species of climate warming. *Science*, **333**, 1024–1026.

Chevin, L.-M., Collins, S. & Lefèvre, F. (2013) Phenotypic plasticity and evolutionary demographic responses to climate change: taking theory out to the field. *Functional Ecology*, **27**, 967–979.

Chevin, L.-M. & Lande, R. (2015) Evolution of environmental cues for phenotypic plasticity. *Evolution*, **69**, 2767–2775.

Chevin, L.-M., Lande, R. & Mace, G.M. (2010) Adaptation, plasticity, and extinction in a changing environment: towards a predictive theory. *PLoS Biology*, **8**, e1000357.

Chevin, L.M., Visser, M.E. & Tufto, J. (2015) Estimating the variation, autocorrelation, and environmental sensitivity of phenotypic selection. *Evolution*, **69**, 2319–2332.

Chew, Y.H., Wilczek, A.M., Williams, M., Welch, S.M., Schmitt, J. & Halliday, K.J. (2012) An augmented Arabidopsis phenology model reveals seasonal temperature control of flowering time. *The New Phytologist*, **194**, 654–665.

Chuine, I. (2000) A unified model for budburst of trees. *Journal of Theoretical Biology*, **207**, 337–347.

Chuine, I. (2010) Why does phenology drive species distribution? *Philosophical Transactions of the Royal Society of London . Series B, Biological Sciences*, **365**, 3149–3160.

Chuine, I., Garcia de Cortazar-Atauri, I., Kramer, K. & Hänninen, H. (2013) Plant Development Models. *Phenology: An Integrative Environmental Science*, Second Edi (ed M.D. Schwartz), pp. 275–294. Springer.

Chuine, I., Morin, X. & Bugmann, H. (2010) Warming, Photoperiods and Tree Phenology. *Science*, **329**, 277–278.

Claessens, H., Oosterbaan, A., Savill, P. & Rondeux, J. (2010) A review of the characteristics of black alder (Alnus glutinosa (L.) Gaertn.) and their implications for silvicultural practices. *Forestry*, **83**, 163–175.

Cleland, E.E., Chuine, I., Menzel, A., Mooney, H.A. & Schwartz, M.D. (2007) Shifting plant phenology in response to global change. *Trends in Ecology & Evolution*, **22**, 357–365.

Cole, E.F., Long, P.R., Zelazowski, P., Szulkin, M. & Sheldon, B.C. (2015) Predicting bird phenology from space: Satellite-derived vegetation green-up signal uncovers spatial variation in phenological synchrony between birds and their environment. *Ecology and Evolution*, **5**, 5057–5074.

Conover, D.O. & Schultz, E.T. (1995) Phenotypic similarity and the evolutionary significance of countergradient variation. *Trends in Ecology & Evolution*, **10**, 248–252.

Cook, B.I., Wolkovich, E.M., Davies, T.J., Ault, T.R., Betancourt, J.L., Allen, J.M., Bolmgren, K., Cleland, E.E., Crimmins, T.M., Kraft, N.J.B., Lancaster, L.T., Mazer, S.J., McCabe, G.J., McGill, B.J., Parmesan, C., Pau, S., Regetz, J., Salamin, N., Schwartz, M.D. & Travers, S.E. (2012a) Sensitivity of Spring Phenology to Warming Across Temporal and Spatial Climate Gradients in Two Independent Databases. *Ecosystems*, **15**, 1283–1294.

Cook, B.I., Wolkovich, E.M. & Parmesan, C. (2012b) Divergent responses to spring and winter warming drive community level flowering trends. *Proceedings of the National Academy of Sciences of the United States of America*, **109**, 9000–9005.

Cotton, P.A. (2003) Avian migration phenology and global climate change. *Proceedings of the National Academy of Sciences of the United States of America*, **100**, 12219–22.

Courter, J.R., Johnson, R.J., Stuyck, C.M., Lang, B.A. & Kaiser, E.W. (2013) Weekend bias in Citizen Science data reporting: implications for phenology studies. *International Journal of Biometeorology*, **57**, 715–720.

Crawley, M.J. & Akhteruzzaman, M. (1988) Individual variation in the phenology of oak trees and its consequences for herbivorous insects. *Functional Ecology*, **2**, 409–415.

Cushing, D.H. (1990) Plankton Production and Year-class Strength in Fish Populations: an Update of the Match/Mismatch Hypothesis. *Advances in Marine Biology*, **26**, 249–293.

Dahlgren, J.P., von Zeipel, H. & Ehrlen, J. (2007) Variation in vegetative and flowering phenology in a forest herb caused by environmental heterogeneity. *American Journal of Botany*, **94**, 1570–1576.

Davies, T.J., Wolkovich, E.M., Kraft, N.J.B., Salamin, N., Allen, J.M., Ault, T.R., Betancourt, J.L., Bolmgren, K., Cleland, E.E., Cook, B.I., Crimmins, T.M., Mazer, S.J., McCabe, G.J., Pau, S., Regetz, J., Schwartz, M.D. & Travers, S.E. (2013) Phylogenetic conservatism in plant phenology. *Journal of Ecology*, **101**, 1520–1530.

Davis, C.C., Willis, C.G., Primack, R.B. & Miller-Rushing, A.J. (2010) The importance of phylogeny to the study of phenological response to global climate change. *Philosophical Transactions of the Royal Society of London . Series B, Biological Sciences*, **365**, 3201–3213.

Dell, D., Sparks, T.H. & Dennis, R.L.H. (2005) Climate change and the effect of increasing spring temperatures on emergence dates of the butterfly Apatura iris (Lepidoptera : Nymphalidae). *European Journal of Entomology*, **102**, 161–167.

Devictor, V., Julliard, R., Couvet, D. & Jiguet, F. (2008) Birds are tracking climate warming, but not fast enough. *Proceedings of the Royal Society B: Biological Sciences*, **275**, 2743–2748.

Devictor, V., van Swaay, C., Brereton, T., Brotons, L., Chamberlain, D., Heliölä, J., Herrando, S., Julliard, R., Kuussaari, M., Lindström, Å., Reif, J., Roy, D.B., Schweiger, O., Settele, J., Stefanescu, C., Van Strien, A., Van Turnhout, C., Vermouzek, Z., WallisDeVries, M., Wynhoff, I. & Jiguet, F. (2012) Differences in the climatic debts of birds and butterflies at a continental scale. *Nature Climate Change*, **2**, 121–124.

Devictor, V., Whittaker, R.J. & Beltrame, C. (2010) Beyond scarcity: citizen science programmes as useful tools for conservation biogeography. *Diversity and Distributions*, **16**, 354–362.

Diamond, S.E., Frame, A.M., Martin, R.A. & Buckley, L.B. (2011) Species' traits predict phenological responses to climate change in butterflies. *Ecology*, **92**, 1005–1012.

Dickinson, J.L., Shirk, J., Bonter, D., Bonney, R., Crain, R.L., Martin, J., Phillips, T. & Purcell, K. (2012) The current state of citizen science as a tool for ecological research and public engagement. *Frontiers in Ecology and the Environment*, **10**, 291–297.

Dickinson, J.L., Zuckerberg, B. & Bonter, D.N. (2010) Citizen Science as an Ecological Research Tool: Challenges and Benefits. *Annual Review of Ecology, Evolution, and Systematics*, **41**, 149–172.

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

Donnelly, A., Caffarra, A., Kelleher, C.T., O'Neill, B.F., Diskin, E., Pletsers, A., Proctor, H., Stirnemann, R., O'Halloran, J., Peñuelas, J., Hodkinson, T.R. & Sparks, T.H. (2012) Surviving in a warmer world: environmental and genetic responses. *Climate Research*, **53**, 245–262.

Donnelly, A., Caffarra, A. & O'Neill, B.F. (2011) A review of climate-driven mismatches between interdependent phenophases in terrestrial and aquatic ecosystems. *International Journal of Biometeorology*, **55**, 805–817.

Ducousso, A., Guyon, J.P. & Kremer, A. (1996) Latitudinal and altitudinal variation of bud burst in western populations of sessile oak (Quercus petraea (Matt) Liebl). *Annales des Sciences Forestieres*, **53**, 775–782.

Dunne, J.A., Saleska, S.R., Fischer, M.L. & Harte, J. (2004) Integrating experimental and gradient methods in ecological climate change research. *Ecology*, **85**, 904–916.

Dunnett, N.P. & Grime, J.P. (1999) Competition as an amplifier of short-term vegetation responses to climate: An experimental test. *Functional Ecology*, **13**, 388–395.

Duputié, A., Rutschmann, A., Ronce, O. & Chuine, I. (2015) Phenological plasticity will not help all species adapt to climate change. *Global Change Biology*, **21**, 3062–3073.

Durant, J.M., Hjermann, D., Anker-Nilssen, T., Beaugrand, G., Mysterud, A., Pettorelli, N. & Stenseth, N.C. (2005) Timing and abundance as key mechanisms affecting trophic interactions in variable environments. *Ecology Letters*, **8**, 952–958.

Durant, J.M., Hjermann, D., Ottersen, G. & Stenseth, N.C. (2007) Climate and the match or mismatch between predator requirements and resource availability. *Climate Research*, **33**, 271–283.

Durka, W. & Michalski, S.G. (2012) Daphne: a dated phylogeny of a large European flora for phylogenetically informed ecological analyses. *Ecology*, **93**, 2297–2297.

Eaton, E., Caudullo, G., Oliveira, S. & de Rigo, D. (2016) Quercus robur and Quercus petraea in Europe: distribution, habitat, usage and threats. *European Atlas of Forest Tree Species* (eds J. San-Miguel-Ayanz),, D. de Rigo),, G. Caudullo),, T. Houston Durrant), & A. Mauri), p. e01c6df. Publication Office of the European Union, Luxembourg.

Elzinga, J.A., Atlan, A., Biere, A., Gigord, L., Weis, A.E. & Bernasconi, G. (2007) Time after time: flowering phenology and biotic interactions. *Trends in Ecology and Evolution*, **22**, 432–439.

Emborg, J. (1998) Understorey light conditions and regeneration with respect to the structural dynamics of a near-natural temperate deciduous forest in Denmark. *Forest Ecology and Management*, **106**, 83–95.

Engler, R., Randin, C.F., Thuiller, W., Dullinger, S., Zimmermann, N.E., Araújo, M.B., Pearman, P.B., Le Lay, G., Piedallu, C., Albert, C.H., Choler, P., Coldea, G., De LAMO, X., Dirnböck, T., Gégout, J.-C., Gómez-García, D., Grytnes, J.-A., Heegaard, E., Høistad, F., Nogués-Bravo, D., Normand, S., Puşcaş, M., Sebastià, M.-T., Stanisci, A., Theurillat, J.-P., Trivedi, M.R., Vittoz, P. & Guisan, A. (2011) 21st century climate change threatens mountain flora unequally across Europe. *Global Change Biology*, **17**, 2330–2341.

Everett, G. & Geoghegan, H. (2015) Initiating and continuing participation in citizen science for natural history. *BMC Ecology*, **16**, 15–22.

Felsenstein, J. (1977) *Multivariate Normal Genetic Models with a Finite Number of Loci.* Washington Univ., Seattle (USA). Dept. of Genetics.

Ffrench-Constant, R.H., Somers-yeates, R., Bennie, J., Economou, T., Hodgson, D., Spalding, A. & Mcgregor, P.K. (2016) Light pollution is associated with earlier tree budburst across the United Kingdom. *Proceedings of the Royal Society B: Biological Sciences*, **283**, 20160813.

Fitter, A.H. & Fitter, R.S.R. (2002) Rapid changes in flowering time in British plants. *Science*, **296**, 1689–1691.

Fitter, A.H. & Peat, H.J. (1994) The Ecological Flora Database. *Journal of Ecology*, **82**, 415–425.

Forrest, J. & Miller-Rushing, A.J. (2010) Toward a synthetic understanding of the role of phenology in ecology and evolution. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, **365**, 3101–3112.

Forrest, J. & Thomson, J.D. (2010) Consequences of variation in flowering time within and among individuals of Mertensia fusiformis (Boraginaceae), an early spring wildflower. *American Journal of Botany*, **97**, 38–48.

Foster, J.R., Townsend, P.A. & Mladenoff, D.J. (2013) Mapping asynchrony between gypsy moth egg-hatch and forest leaf-out: Putting the phenological window hypothesis in a spatial context. *Forest Ecology and Management*, **287**, 67–76.

Franks, S.J., Sim, S. & Weis, A.E. (2007) Rapid evolution of flowering time by an annual plant in response to a climate fluctuation. *Proceedings of the National Academy of Sciences of the United States of America*, **104**, 1278–1282.

Franks, S.J., Weber, J.J. & Aitken, S.N. (2014) Evolutionary and plastic responses to climate change in terrestrial plant populations. *Evolutionary Applications*, **7**, 123–139.

Franks, S.J. & Weis, A.E. (2008) A change in climate causes rapid evolution of multiple life-history traits and their interactions in an annual plant. *Journal of Evolutionary Biology*, **21**, 1321–1334.

Freckleton, R.P., Harvey, P.H. & Pagel, M. (2002) Phylogenetic analysis and comparative data: A test and review of evidence. *American Naturalist*, **160**, 712–726.

Fridley, J.D. (2012) Extended leaf phenology and the autumn niche in deciduous forest invasions. *Nature*, **485**, 359–362.

Fu, Y.H., Zhao, H., Piao, S., Peaucelle, M., Peng, S., Zhou, G., Ciais, P., Song, Y., Vitasse, Y., Zeng, Z., Janssens, I.A., Huang, M., Menzel, A. & Penuelas, J. (2015) Declining global warming effects on the phenology of spring leaf unfolding. *Nature*, **526**, 104–107.

Gallinat, A.S., Primack, R.B. & Wagner, D.L. (2015) Autumn, the neglected season in climate change research. *Trends in Ecology and Evolution*, **30**, 169–176.

García-Ramos, G. & Kirkpatrick, M. (1997) Genetic Models of Adaptation and Gene Flow in Peripheral Populations. *Evolution*, **51**, 21–28.

Garrett, K.A., Dendy, S.P., Frank, E.E., Rouse, M.N. & Travers, S.E. (2006) Climate change effects on plant disease: Genomes to ecosystems. *Annual Review of Phytopathology*, **44**, 489–509.

Gienapp, P., Lof, M., Reed, T.E., McNamara, J., Verhulst, S. & Visser, M.E. (2013) Predicting demographically sustainable rates of adaptation: can great tit breeding time keep pace with climate change? *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, **368**, 20120289.

Gienapp, P., Reed, T.E. & Visser, M.E. (2014) Why climate change will invariably alter selection pressures on phenology. *Proceedings of the Royal Society B: Biological Sciences*, **281**, 20141611.

Gilmour, A.R., Gogel, B.J., Cullis, B.R. & Thompson, R. (2009) *ASReml User Guide Release 3.0*. VSN International Ltd, Hemel Hempstead, HP1 1ES, UK www.vsni.co.uk.

Gordo, O. & Sanz, J.J. (2009) Long-term temporal changes of plant phenology in the Western Mediterranean. *Global Change Biology*, **15**, 1930–1948.

Hadfield, J. (2010) MCMC Methods for Multi-response Generalized Linear Mixed Models : The MCMCglmm R Package. *Journal of Statistical Software*, **33**, 1–22.

Hadfield, J.D. (2016) The spatial scale of local adaptation in a stochastic environment. *Ecology Letters*, 780–788.

Hadfield, J.D., Heap, E.A., Bayer, F., Mittell, E.A. & Crouch, N.M.A. (2013) Intraclutch differences in egg characteristics mitigate the consequences of age-related hierarchies in a wild passerine. *Evolution*, **67**, 2688–2700.

Hadfield, J.D. & Nakagawa, S. (2010) General quantitative genetic methods for comparative biology: Phylogenies, taxonomies and multi-trait models for continuous and categorical characters. *Journal of Evolutionary Biology*, **23**, 494–508.

Hänninen, H. & Tanino, K. (2011) Tree seasonality in a warming climate. *Trends in Plant Science*, **16**, 412–416.

Harrington, R., Woiwod, I. & Sparks, T. (1999) Climate change and trophic interactions. *Trends in Ecology & Evolution*, **14**, 146–150.

Harvell, C.D., E.Mitchell, C., Jessica, R.W., Sonia, A., Andrew, P.D., S.Ostfeld, R. & Michael, D.S. (2002) Climate Warming and Disease Risks for Terrestrial and Marine Biota. *Science*, **296**, 2158–2162.

Hay, R.K.M. (1990) The influence of photoperiod on the dry matter production of grasses and cereals. *New Phytologist*, **116**, 233–254.

Hegland, S.J., Nielsen, A., Lázaro, A., Bjerknes, A.-L. & Totland, Ø. (2009) How does climate warming affect plant-pollinator interactions? *Ecology Letters*, **12**, 184–195.

Heide, O.M. (2003) High autumn temperature delays spring bud burst in boreal trees, counterbalancing the effect of climatic warming. *Tree Physiology*, **23**, 931–936.

Henry, H.A.L. & Aarssen, L.W. (1997) On the relationship between shade tolerance and shade avoidance strategies in woodland plants. *Oikos*, **80**, 575–582.

Hensel, L.E. & Sargent, R.D. (2012) A phylogenetic analysis of trait convergence in the spring flora. *Botany*, **90**, 557–564.

Hickling, R., Roy, D.B., Hill, J.K., Fox, R. & Thomas, C.D. (2006) The distributions of a wide range of taxonomic groups are expanding polewards. *Global Change Biology*, **12**, 450–455.

Hill, M.O., Preston, C.D. & Roy, D.B. (2004) *PLANTATT - Attributes of British and Irish Plants: Status, Size, Life History, Geography and Habitats*. Biological Records Centre, NERC Centre for Ecology and Hydrology.

Hinks, A.E., Cole, E.F., Daniels, K.J., Wilkin, T.A., Nakagawa, S. & Sheldon, B.C. (2015) Scale-Dependent Phenological Synchrony between Songbirds and Their Caterpillar Food Source. *The American Naturalist*, **186**, 84–97.

Hodgson, J.A., Thomas, C.D., Oliver, T.H., Anderson, B.J., Brereton, T.M. & Crone, E.E. (2011) Predicting insect phenology across space and time. *Global Change Biology*, **17**, 1289–1300.

Hoffmann, A.A. & Sgrò, C.M. (2011) Climate change and evolutionary adaptation. *Nature*, **470**, 479–485.

Hubert, J. & Cundall, E. (2006) Choosing Provenance in Broadleaved Trees. *Forestry Commision Information Note*, 1–12.

Hurlbert, A.H. & Liang, Z. (2012) Spatiotemporal variation in avian migration phenology: citizen science reveals effects of climate change. *PLoS ONE*, **7**, e31662.

Ibáñez, I., Primack, R.B., Miller-Rushing, A.J., Ellwood, E., Higuchi, H., Lee, S.D., Kobori, H. & Silander, J.A. (2010) Forecasting phenology under global warming. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, **365**, 3247–3260.

Inouye, D.W. (2000) The ecological and evolutionary significance of frost in the context of climate change. *Ecology Letters*, **3**, 457–463.

Iversen, M., Brathen, K.A., Yoccoz, N.G. & Ims, R.A. (2009) Predictors of plant phenology in a diverse high-latitude alpine landscape: Growth forms and topography. *Journal of Vegetation Science*, **20**, 903–915.

Jackson, M.T. (1966) Effects of Microclimate on Spring Flowering Phenology. *Ecology*, **47**, 407–415.

Jakobsson, A. & Eriksson, O. (2000) A comparative study of seed number, seed size, seedling size and recruitment in grassland plants. *Oikos*, **88**, 494–502.

Jia, P., Bayaerta, T., Li, X. & Du, G. (2011) Relationships between Flowering Phenology and Functional Traits in Eastern Tibet Alpine Meadow. *Arctic, Antarctic, and Alpine Research*, **43**, 585–592.

Junttila, O., Nilsen, J. & Igeland, B. (2003) Effect of Temperature on the Induction of Bud Dormancy in Ecotypes of Betula pubescens and Betula pendula . *Scandinavian Journal of Forest Research*, **18**, 208–217.

Kauserud, H., Heegaard, E., Semenov, M.A., Boddy, L., Halvorsen, R., Stige, L.C., Sparks, T.H., Gange, A.C. & Stenseth, N.C. (2010) Climate change and spring-fruiting fungi. *Proceedings of the Royal Society B: Biological Sciences*, **277**, 1169–1177.

Keenan, T.F. & Richardson, A.D. (2015) The timing of autumn senescence is affected by the timing of spring phenology: Implications for predictive models. *Global Change Biology*, **21**, 2634–2641.

Kim, D.-H., Doyle, M.R., Sung, S. & Amasino, R.M. (2009) Vernalization: winter and the timing of flowering in plants. *Annual Review of Cell and Developmental Biology*, **25**, 277–299.

van Kleunen, M. & Fischer, M. (2005) Constraints on the evolution of adaptive phenotypic plasticity in plants. *New Phytologist*, **166**, 49–60.

Kleyer, M., Bekker, R.M., Knevel, I.C., Bakker, J.P., Thompson, K., Sonnenschein, M., Poschlod, P., van Groenendael, J.M., Klimeš, L., Klimešová, J., Klotz, S., Rusch, G.M., Hermy, M., Adriaens, D., Boedeltje, G., Bossuyt, B., Dannemann, A., Endels, P., Götzenberger, L., Hodgson, J.G., Jackel, A.-K., Kühn, I., Kunzmann, D., Ozinga, W.A., Römermann, C., Stadler, M., Schlegelmilch, J., Steendam, H.J., Tackenberg, O., Wilmann, B., Cornelissen, J.H.C., Eriksson, O., Garnier, E. & Peco, B. (2008) The LEDA Traitbase: a database of life-history traits of the Northwest European flora. *Journal of Ecology*, **96**, 1266–1274.

Körner, C. & Basler, D. (2010) Phenology under global warming. *Science*, **327**, 1461–1462.

De Kort, H., Vander Mijnsbrugge, K., Vandepitte, K., Mergeay, J., Ovaskainen, O. & Honnay, O. (2015) Evolution, plasticity and evolving plasticity of phenology in the tree species Alnus glutinosa. *Journal of Evolutionary Biology*, **29**, 253–264.

Kovach-Orr, C. & Fussmann, G.F. (2013) Evolutionary and plastic rescue in multitrophic model communities. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, **368**, 20120084.

Kramer, K. (1995) Phenotypic plasticity of the phenology of seven European tree species in relation to climatic warming. *Plant, Cell and Environment*, **18**, 93–104.

Kramer, K., Leinonen, I. & Loustau, D. (2000) The importance of phenology for the evaluation of impact of climate change on growth of boreal, temperate and Mediterranean forests ecosystems: an overview. *International Journal of Biometeorology*, **44**, 67–75.

Kremer, A., Potts, B.M. & Delzon, S. (2014) Genetic divergence in forest trees: understanding the consequences of climate change. *Functional Ecology*, **28**, 22–36.

Kudo, G., Ida, T.Y. & Tani, T. (2008) Linkages between phenology, pollination, photosynthesis and reproduction in deciduous forest understory plants. *Ecology*, **89**, 321–331.

Kudo, G. & Suzuki, S. (2002) Relationships Between Flowering Phenology and Fruit-set of Dwarf Shrubs between in Alpine Fellfields in Northern Japan: A Comparison with a Subarctic Heathland in Northern Sweden. *Arctic, Antarctic, and Alpine Research*, **34**, 185–190.

Kudoh, H., Ishiguri, Y. & Kawano, S. (1995) Phenotypic plasticity in Cardamine flexuosa : variation among populations in plastic response to chilling treatments and photoperiods. *Oecologia*, **103**, 148–156.

Laube, J., Sparks, T.H., Estrella, N., Höfler, J., Ankerst, D.P. & Menzel, A. (2014) Chilling outweighs photoperiod in preventing precocious spring development. *Global Change Biology*, **20**, 170–182.

Lessard-Therrien, M., Davies, T.J. & Bolmgren, K. (2014) A phylogenetic comparative study of flowering phenology along an elevational gradient in the Canadian subarctic. *International Journal of Biometeorology*, **58**, 455–462.

Lynch, H.J., Fagan, W.F., Naveen, R., Trivelpiece, S.G. & Trivelpiece, W.Z. (2012) Differential advancement of breeding phenology in response to climate may alter staggered breeding among sympatric pygoscelid penguins. *Marine Ecology Progress Series*, **454**, 135–145.

Mayer, A. (2010) Phenology and Citizen Science. *BioScience*, **60**, 172–175.

Mazaris, A.D., Kallimanis, A.S., Pantis, J.D. & Hays, G.C. (2013) Phenological response of sea turtles to environmental variation across a species â€™ northern range. *Proceedings of the Royal Society B: Biological Sciences*, **280**, 20122397.

Mazer, S.J., Travers, S.E., Cook, B.I., Jonathan Davies, T., Bolmgren, K., Kraft, N.J.B., Salamin, N. & Inouye, D.W. (2013) Flowering date of taxonomic families predicts phenological sensitivity to temperature: Implications for forecasting the effects of climate change on unstudied taxa. *American Journal of Botany*, **100**, 1381–1397.

McMahon, S.M., Harrison, S.P., Armbruster, W.S., Bartlein, P.J., Beale, C.M., Edwards, M.E., Kattge, J., Midgley, G., Morin, X. & Prentice, I.C. (2011) Improving assessment and modelling of climate change impacts on global terrestrial biodiversity. *Trends in Ecology & Evolution*, **26**, 249–259.

Meeus, J.H. (1991) *Astronomical Algorithms*. Willmann-Bell, Richmond, Virginia.

Menéndez, R. (2007) How are insects responding to global warming ? *Tijdschrift voor Entomologie*, **150**, 355–365.

Menéndez, R., González-Megías, A., Lewis, O.T., Shaw, M.R. & Thomas, C.D. (2008) Escape from natural enemies during climate-driven range expansion: a case study. *Ecological Entomology*, **33**, 413–421.

Menzel, A., Sparks, T.H., Estrella, N., Koch, E., Aasa, A., Ahas, R., Alm-Kübler, K., Bissolli, P., Braslavská, O., Briede, A., Chmielewski, F.M., Crepinsek, Z., Curnel, Y., Dahl, Å., Defila, C., Donnelly, A., Filella, Y., Jatczak, K., Måge, F., Mestre, A., Nordli, Ø., Peñuelas, J., Pirinen, P., Remišová, V., Scheifinger, H., Striz, M., Susnik, A., Van Vliet, A.J.H., Wielgolaski, F.-E., Zach, S. & Zust, A. (2006a) European phenological response to climate change matches the warming pattern. *Global Change Biology*, **12**, 1969–1976.

Menzel, A., Sparks, T.H., Estrella, N. & Roy, D.B. (2006b) Altered geographic and temporal variability in phenology in response to climate change. *Global Ecology and Biogeography*, **15**, 498–504.

Milla, R., Castro-Díez, P. & Montserrat-Martí, G. (2010) Phenology of Mediterranean woody plants from NE Spain: Synchrony, seasonality, and relationships among phenophases. *Flora*, **205**, 190–199.

Miller-Rushing, A.J., Høye, T.T., Inouye, D.W. & Post, E. (2010) The effects of phenological mismatches on demography. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, **365**, 3177–3186.

Miller-Rushing, A.J., Katsuki, T., Primack, R.B., Ishii, Y., Lee, S.D. & Higuchi, H. (2007) Impact of global warming on a group of related species and their hybrids: cherry tree (Rosaceae) flowering at Mt. Takao, Japan. *American Journal of Botany*, **94**, 1470–1478.

Mitchell, R.J., Flanagan, R.J., Brown, B.J., Waser, N.M. & Karron, J.D. (2009) New frontiers in competition for pollination. *Annals of Botany*, **103**, 1403–1413.

Morin, X., Lechowicz, M.J., Augspurger, C., O'Keefe, J., Viner, D. & Chuine, I. (2009) Leaf phenology in 22 North American tree species during the 21st century. *Global Change Biology*, **15**, 961–975.

Morisette, J.T., Richardson, A.D., Knapp, A.K., Fisher, J.I., Graham, E.A., Abatzoglou, J., Wilson, B.E., Breshears, D.D., Henebry, G.M., Hanes, J.M. & Liang, L. (2009) Tracking the rhythm of the seasons in the face of global change: phenological research in the 21st century. *Frontiers in Ecology and the Environment*, **7**, 253–260.

Murray, M.B., Cannell, M.G.R. & Smith, R.I. (1989) Date of Budburst of Fifteen Tree Species in Britain Following Climatic Warming. *Journal of Applied Ecology*, **26**, 693–700.

Myking, T. & Heide, O.M. (1995) Dormancy release and chilling requirement of buds of latitudinal ecotypes of Betula pendula and B. pubescens. *Tree physiology*, **15**, 697–704.

Nakazawa, T. & Doi, H. (2012) A perspective on match/mismatch of phenology in community contexts. *Oikos*, **121**, 489–495.

Nicotra, A.B., Atkin, O.K., Bonser, S.P., Davidson, A.M., Finnegan, E.J., Mathesius, U., Poot, P., Purugganan, M.D., Richards, C.L., Valladares, F. & van Kleunen, M. (2010) Plant phenotypic plasticity in a changing climate. *Trends in Plant Science*, **15**, 684–692.

Nord, E.A. & Lynch, J.P. (2009) Plant phenology: a critical controller of soil resource acquisition. *Journal of Experimental Botany*, **60**, 1927–1937.

O'Neill, B.F., Bond, K., Tyner, A., Sheppard, R., Bryant, T., Chapman, J., Bell, J. & Donnelly, A. (2012) Climatic change is advancing the phenology of moth species in Ireland. *Entomologia Experimentalis et Applicata*, **143**, 74–88.

Ovaskainen, O., Skorokhodova, S., Yakovleva, M., Sukhov, A., Kutenkov, A., Kutenkova, N., Shcherbakov, A., Meyke, E. & Delgado, M.D.M. (2013) Community-level phenological response to climate change. *Proceedings of the National Academy of Sciences of the United States of America*, **110**, 13434–13439.

Palacio-López, K., Beckage, B., Scheiner, S. & Molofsky, J. (2015) The ubiquity of phenotypic plasticity in plants: a synthesis. *Ecology and Evolution*, **5**, 3389–3400.

Panchen, Z.A., Primack, R.B., Nordt, B., Ellwood, E.R., Stevens, A.-D., Renner, S.S., Willis, C.G., Fahey, R., Whittemore, A., Du, Y. & Davis, C.C. (2014) Leaf out times of temperate woody plants are related to phylogeny, deciduousness, growth habit and wood anatomy. *The New Phytologist*, **203**, 1208–1219.

Parker, D.E., Legg, T.P. & Folland, C.K. (1992) A new daily central England temperature series, 1772-1991. *International Journal of Climatology*, **12**, 317–342.

Parmesan, C. (2006) Ecological and Evolutionary Responses to Recent Climate Change. *Annual Review of Ecology, Evolution, and Systematics*, **37**, 637–669.

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

Parmesan, C. & Yohe, G. (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, **421**, 37–42.

Pasta, S., de Rigo, D. & Caudullo, G. (2016) Acer pseudoplatanus in Europe: distribution, habitat, usage and threats. *European Atlas of Forest Tree Species* (eds J. San-Miguel-Ayanz),, D. de Rigo),, G. Caudullo),, T. Houston Durrant), & A. Mauri), p. e01665a. Publication Office of the European Union, Luxembourg.

Pau, S., Wolkovich, E.M., Cook, B.I., Davies, T.J., Kraft, N.J.B., Bolmgren, K., Betancourt, J.L. & Cleland, E.E. (2011) Predicting phenology by integrating ecology, evolution and climate science. *Global Change Biology*, **17**, 3633–3643.

Perry, M. & Hollis, D. (2005) The generation of monthly gridded datasets for a range of climatic variables over the UK. *International Journal of Climatology*, **25**, 1041–1054.

Perry, M., Hollis, D. & Elms, M. (2009) *Climate Memorandum No 24 The Generation of Daily Gridded Datasets of Temperature and Rainfall for the UK*. National Climate Information Centre, Met Office.

Perry, A.L., Low, P.J., Ellis, J.R. & Reynolds, J.D. (2005) Climate Change and Distribution Shifts in Marine Fishes. *Science*, **308**, 1912–1915.

Phillimore, A.B., Hadfield, J.D., Jones, O.R. & Smithers, R.J. (2010) Differences in spawning date between populations of common frog reveal local adaptation. *Proceedings of the National*

Academy of Sciences of the United States of America, **107**, 8292–8297.

Phillimore, A.B., Leech, D.I., Pearce-Higgins, J.W. & Hadfield, J.D. (2016) Passerines may be sufficiently plastic to track temperature-mediated shifts in optimum lay date. *Global Change Biology*, 1–14.

Phillimore, A.B., Proios, K., O'Mahony, N., Bernard, R., Lord, A.M., Atkinson, S. & Smithers, R.J. (2013) Inferring local processes from macro-scale phenological pattern: a comparison of two methods. *Journal of Ecology*, **101**, 774–783.

Phillimore, A.B., Stålhandske, S., Smithers, R.J. & Bernard, R. (2012) Dissecting the contributions of plasticity and local adaptation to the phenology of a butterfly and its host plants. *The American Naturalist*, **180**, 655–670.

Polgar, C.A. & Primack, R.B. (2011) Leaf-out phenology of temperate woody plants: from trees to ecosystems. *The New Phytologist*, **191**, 926–941.

Primack, R.B. (1987) Relationships Among Flowers, Fruits, and Seeds. *Annual Review of Ecology and Systematics*, **18**, 409–430.

Primack, R.B., Ibáñez, I., Higuchi, H., Lee, S.D., Miller-Rushing, A.J., Wilson, A.M. & Silander, J.A. (2009) Spatial and interspecific variability in phenological responses to warming temperatures. *Biological Conservation*, **142**, 2569–2577.

Van der Putten, W.H., Macel, M. & Visser, M.E. (2010) Predicting species distribution and abundance responses to climate change: why it is essential to include biotic interactions across trophic levels. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, **365**, 2025–2034.

Rafferty, N.E. & Ives, A.R. (2013) Phylogenetic trait-based analyses of ecological networks. *Ecology*, **94**, 2321–2333.

Rasmussen, N.L., Van Allen, B.G. & Rudolf, V.H.W. (2014) Linking phenological shifts to species interactions through size-mediated priority effects. *Journal of Animal Ecology*, **83**, 1206–1215.

Rathcke, B. & Lacey, E.P. (1985) Phenological Patterns of Terrestrial Plants. *Annual Review of Ecology and Systematics*, **16**, 179–214.

Revell, L., Harmon, L. & Collar, D. (2008) Phylogenetic Signal, Evolutionary Process, and Rate. *Systematic Biology*, **57**, 591–601.

Revilla, T.A., Encinas-Viso, F. & Loreau, M. (2014) (A bit) Earlier or later is always better: Phenological shifts in consumer-resource interactions. *Theoretical Ecology*, **7**, 149–162.

Roberts, A.M.I., Tansey, C., Smithers, R.J. & Phillimore, A.B. (2015) Predicting a change in the order of spring phenology in temperate forests. *Global Change Biology*, **21**, 2603–2611.

Rohr, J.R. & Raffel, T.R. (2010) Linking global climate and temperature variability to widespread amphibian declines putatively caused by disease. *Proceedings of the National Academy of Sciences of the United States of America*, **107**, 8269–8274.

Root, T.L., Price, J.T., Hall, K.R., Schneider, S.H., Rosenzweig, C. & Pounds, J.A. (2003) Fingerprints of global warming on wild animals and plants. *Nature*, **421**, 57–60.

Rose, N.L., Turner, S.D., Goldsmith, B., Gosling, L. & Davidson, T. (2015) Quality control in public participation assessments of water quality: The OPAL Water Survey. *BMC Ecology*, **16(Suppl 1**, S14.

Roy, D.B., Oliver, T.H., Botham, M.S., Beckmann, B., Brereton, T., Dennis, R.L.H., Harrower, C., Phillimore, A.B. & Thomas, J.A. (2015) Similarities in butterfly emergence dates among populations suggest local adaptation to climate. *Global Change Biology*, **9**, 3313–3322.

Roy, D.B. & Sparks, T.H. (2000) Phenology of British butterflies and climate change. *Global Change Biology*, **6**, 407–416.

Rubolini, D., Saino, N. & Møller, A.P. (2010) Migratory behaviour constrains the phenological response of birds to climate change. *Climate Research*, **42**, 45–55.

Salisbury, E.J. (1921) Phenology and habitat with special reference to the phenology of woodlands. *Quarterly Journal of the Royal Meteorological Society*, **47**, 251–260.

San-Miguel-Ayanz, J., de Rigo, D., Caudullo, G., Houston Durrant, T. & Mauri, A. (eds). (2016) *European Atlas of Forest Tree Species*. Publication Office of the European Union, Luxembourg.

Savolainen, O., Pyhäjärvi, T. & Knürr, T. (2007) Gene Flow and Local Adaptation in Trees. *Annual Review of Ecology, Evolution, and Systematics*, **38**, 595–619.

Schemske, D.W., Willson, M.F., Melampy, M.N., Miller, L.J., Verner, L., Schemske, K.M. & Best, L.B. (1978) Flowering Ecology of Some Spring Woodland Herbs. *Ecology*, **59**, 351–366.

Schleip, C., Sparks, T.H., Estrella, N. & Menzel, A. (2009) Spatial variation in onset dates and trends in phenology across Europe. *Climate Research*, **39**, 249–260.

Schmeller, D.S., Henry, P.-Y., Julliard, R., Gruber, B., Clobert, J., Dziock, F., Lengyel, S., Nowicki, P., Déri, E., Budrys, E., Kull, T., Tali, K., Bauch, B., Settele, J., Van Swaay, C., Kobler, A., Babij, V., Papastergiadou, E. & Henle, K. (2009) Advantages of volunteer-based biodiversity monitoring in Europe. *Conservation Biology*, **23**, 307–316.

Schweiger, O., Settele, J., Kudrna, O., Klotz, S. & Kühn, I. (2008) Climate change can cause spatial mismatch of trophically interacting species. *Ecology*, **89**, 3472–3479.

Settele, J., Scholes, R., Betts, R., Bunn, S., Leadley, P., Nepstad, D., Overpeck, J.T., Taboada, M.A. (2014) Terrestrial and inland water systems. In: Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part A: Global and Sectoral Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. (eds C.B. Field),, V.R. Barros),, D.J. Dokken),, K.J. Mach),, M.D. Mastrandrea),, T.E. Bilir),, M. Chatterjee),, K.L. Ebi),, Y.O. Estrada),, R.C. Genova),, B. Girma),, E.S. Kissel),, A.N. Levy),, S. MacCracken),, P.R. Mastrandrea), & L.. White), pp. 271–359. Cambridge University Press.

Shefferson, R.P., Kull, T. & Tali, K. (2006) Demographic response to shading and defoliation in two woodland orchids. *Folia Geobotanica*, **41**, 95–106.

Slatkin, M. (1978) Spatial patterns in the distributions of polygenic characters. *Journal of Theoretical Biology*, **70**, 213–228.

Sola, A.J. & Ehrlén, J. (2007) Vegetative phenology constrains the onset of flowering in the perennial herb Lathyrus vernus. *Journal of Ecology*, **95**, 208–216.

Southwood, T.R.E., Brown, V.K. & Reader, P.M. (1979) The relationships of plant and insect diversities in succession. *Biological Journal of the Linnean society*, **12**, 327–348.

Southwood, T.R.E., Brown, V.K., Reader, P.M. & Green, E.E. (1986) The use of different stages of a secondary succession. *Bird Study*, **33**, 159–163.

Sparks, T.H., Greatorex-Davies, J.N., Mountford, J.O., Hall, M.L. & Marrs, R.H. (1996) The effects of shade on the plant communities of rides in plantation woodland and implications for butterfly conservation. *Forest Ecology and Management*, **80**, 197–207.

Sparks, T.H., Jeffree, E.P. & Jeffree, C.E. (2000) An examination of the relationship between flowering times and temperature at the national scale using long-term phenological records from the UK. *International Journal of Biometeorology*, **44**, 82–87.

Sparks, T.H. & Menzel, A. (2002) Observed changes in seasons: an overview. *International Journal of Climatology*, **22**, 1715–1725.

Sparling, J.H. (1967) Assimilation Rates of Some Woodland Herbs in Ontario. *Botanical Gazette*, **128**, 160–168.

Stefanescu, C., Penuelas, J. & Filella, I. (2003) Effects of climatic change on the phenology of butterflies in the northwest Mediterranean Basin. *Global Change Biology*, **9**, 1494–1506.

Team, R.C. (2012) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.r-project.org/

Thackeray, S.J., Henrys, P.A., Hemming, D., Bell, J.R., Botham, M.S., Burthe, S., Helaouet, P., Johns, D.G., Jones, I.D., Leech, D.I., Mackay, E.B., Massimino, D., Atkinson, S., Bacon, P.J., Brereton, T.M., Carvalho, L., Clutton-Brock, T.H., Duck, C., Edwards, M., Elliott, J.M., Hall, S.J.G., Harrington, R., Pearce-Higgins, J.W., Høye, T.T., Kruuk, L.E.B., Pemberton, J.M., Sparks, T.H., Thompson, P.M., White, I., Winfield, I.J. & Wanless, S. (2016) Phenological sensitivity to climate across taxa and trophic levels. *Nature*, **535**, 241–245.

Thackeray, S.J., Sparks, T.H., Frederiksen, M., Burthe, S., Bacon, P.J., Bell, J.R., Botham, M.S., Brereton, T.M., Bright, P.W., Carvalho, L., Clutton-Brock, T., Dawson, A., Edwards, M., Elliott, J.M., Harrington, R., Johns, D., Jones, I.D., Jones, J.T., Leech, D.I., Roy, D.B., Scott, W.A., Smith, M., Smithers, R.J., Winfield, I.J. & Wanless, S. (2010) Trophic level asynchrony in rates of phenological change for marine, freshwater and terrestrial environments. *Global Change Biology*, **16**, 3304–3313.

Theobald, E.J., Ettinger, A.K., Burgess, H.K., DeBey, L.B., Schmidt, N.R., Froehlich, H.E., Wagner, C., HilleRisLambers, J., Tewksbury, J., Harsch, M.A. & Parrish, J.K. (2015) Global change and local solutions: Tapping the unrealized potential of citizen science for biodiversity research. *Biological Conservation*, **181**, 236–244.

Thomsen, R.P., Svenning, J.-C. & Balslev, H. (2005) Overstorey Control of Understorey Species Composition in a Near-natural Temperate Broadleaved Forest in Denmark. *Plant Ecology*, **181**, 113–126.

Thomson, J.D. (2010) Flowering phenology, fruiting success and progressive deterioration of pollination in an early-flowering geophyte. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, **365**, 3187–3199.

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

Toftegaard, T., Posledovich, D., Navarro-Cano, J.A., Wiklund, C., Gotthard, K. & Ehrlén, J. (2016) Variation in plant thermal reaction norms along a latitudinal gradient - more than adaptation to season length. *Oikos*, **125**, 622–628.

Tooke, F. & Battey, N.H. (2010) Temperate flowering phenology. *Journal of Experimental Botany*, **61**, 2853–2862.

Tufto, J. (2015) Genetic evolution, plasticity, and bet-hedging as adaptive responses to temporally autocorrelated fluctuating selection: A quantitative genetic model. *Evolution*,

69, 2034–2049.

Valverde, T. & Silvertown, J. (1998) Variation in the demography of a woodland understorey herb (Primula vulgaris) along the forest regeneration cycle: projection matrix analysis. *Journal of Ecology*, **86**, 545–562.

Vedder, O., Bouwhuis, S. & Sheldon, B.C. (2013) Quantitative assessment of the importance of phenotypic plasticity in adaptation to climate change in wild bird populations. *PLoS Biology*, **11**, e1001605.

Visser, M.E. & Both, C. (2005) Shifts in phenology due to global climate change: the need for a yardstick. *Proceedings of the Royal Society B: Biological Sciences*, **272**, 2561–2569.

Vitasse, Y. (2013) Ontogenic changes rather than difference in temperature cause understory trees to leaf out earlier. *The New Phytologist*, **198**, 149–155.

Vitasse, Y. & Basler, D. (2013) What role for photoperiod in the bud burst phenology of European beech. *European Journal of Forest Research*, **132**, 1–8.

Vitasse, Y., Bresson, C.C., Kremer, A., Michalet, R. & Delzon, S. (2010) Quantifying phenological plasticity to temperature in two temperate tree species. *Functional Ecology*, **24**, 1211–1218.

Vitasse, Y., Delzon, S., Bresson, C.C., Michalet, R. & Kremer, A. (2009a) Altitudinal differentiation in growth and phenology among populations of temperate-zone tree species growing in a common garden. *Canadian Journal of Forest Research*, **39**, 1259–1269.

Vitasse, Y., Delzon, S., Dufrêne, E., Pontailler, J.-Y., Louvet, J.-M., Kremer, A. & Michalet, R. (2009b) Leaf phenology sensitivity to temperature in European trees: Do within-species populations exhibit similar responses? *Agricultural and Forest Meteorology*, **149**, 735–744.

Vitasse, Y., François, C., Delpierre, N., Dufrêne, E., Kremer, A., Chuine, I. & Delzon, S. (2011) Assessing the effects of climate change on the phenology of European temperate trees. *Agricultural and Forest Meteorology*, **151**, 969–980.

Vitasse, Y., Hoch, G., Randin, C.F., Lenz, A., Kollas, C., Scheepens, J.F. & Körner, C. (2013) Elevational adaptation and plasticity in seedling phenology of temperate deciduous tree species. *Oecologia*, **171**, 663–678.

Walther, G., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin, J., Hoegh-guldberg, O. & Bairlein, F. (2002) Ecological responses to recent climate change. *Nature*, **416**, 389–395.

Wang, H., Rutishauser, T., Tao, Z., Zhong, S., Ge, Q. & Dai, J. (2016) Impacts of global warming on phenology of spring leaf unfolding remain stable in the long run. *International Journal of Biometeorology*, doi:10.1007/s00484-016-1210-3.

Warton, D.I., Wright, I.J., Falster, D.S. & Westoby, M. (2006) Bivariate line-fitting methods for allometry. *Biological Reviews*, **81**, 259–291.

Whigham, D.E. (2004) Ecology of Woodland Herbs in Temperate Deciduous Forests. *Annual Review of Ecology, Evolution, and Systematics*, **35**, 583–621.

Wilczek, A.M., Cooper, M.D., Korves, T.M. & Schmitt, J. (2014) Lagging adaptation to warming climate in Arabidopsis thaliana. *Proceedings of the National Academy of Sciences of the United States of America*, **111**, 7906–7913.

Willis, C.G., Ruhfel, B., Primack, R.B., Miller-Rushing, A.J. & Davis, C.C. (2008) Phylogenetic patterns of species loss in Thoreau's woods are driven by climate change. *Proceedings of* *the National Academy of Sciences of the United States of America*, **105**, 17029–17033.

Willis, C.G., Ruhfel, B.R., Primack, R.B., Miller-Rushing, A.J., Losos, J.B. & Davis, C.C. (2010) Favorable climate change response explains non-native species' success in Thoreau's Woods. *PLoS ONE*, **5**, e8878.

Wolfe, D.W., Schwartz, M.D., Lakso, A.N., Otsuki, Y., Pool, R.M. & Shaulis, N.J. (2005) Climate change and shifts in spring phenology of three horticultural woody perennials in northeastern USA. *International Journal of Biometeorology*, **49**, 303–309.

Wolkovich, E.M. & Cleland, E.E. (2011) The phenology of plant invasions: a community ecology perspective. *Frontiers in Ecology and the Environment*, **9**, 287–294.

Wolkovich, E.M. & Cleland, E.E. (2014) Phenological niches and the future of invaded ecosystems with climate change. *AoB Plants*, **6**, plu013.

Wolkovich, E.M. & Ettinger, A.K. (2014) Back to the future for plant phenology research. *New Phytologist*, **203**, 1021–1024.

Wolkovich, E.M., Jonathan Davies, T., Schaefer, H., Cleland, E.E., Cook, B.I., Travers, S.E., Willis, C.G. & Davis, C.C. (2013) Temperature-dependent shifts in phenology contribute to the success of exotic species with climate change. *American Journal of Botany*, **100**, 1407–1421.

Yang, L.H. & Rudolf, V.H.W. (2010) Phenology, ontogeny and the effects of climate change on the timing of species interactions. *Ecology Letters*, **13**, 1–10.

Yu, H., Luedeling, E. & Xu, J. (2010) Winter and spring warming result in delayed spring phenology on the Tibetan Plateau. *Proceedings of the National Academy of Sciences of the United States of America*, **107**, 22151–22156.

Zhao, M., Peng, C., Xiang, W., Deng, X., Tian, D., Zhou, X., Yu, G., He, H. & Zhao, Z. (2013) Plant phenological modeling and its application in global climate change research: overview and future challenges. *Environmental Reviews*, **21**, 1–14.

Appendix A

Supplementary material for Chapter 2

A.1. Species selection from UKPN

The UKPN holds data for a broad range of plant species and phenological events. Spring events were selected for this analysis because temperature's role as a cue is better understood for spring rather than autumn events. I selected species with > 3500 records and excluded taxa for which there were known issues associated with data collection. This included species with common cultivars (e.g., snowdrop and primrose) or easily confused alternative species. In addition to the flowering events, I selected first leafing events over first budburst to include in the analysis. First leaf dates were used because I have found this phenophase to be more straightforward to observe than first budburst, and preliminary analyses revealed that it was less subject to among recorder variance.

A.2. Assessing the impact of spatial variation in population heterogeneity on B_{lat} and B_{lon}

Although I do not have direct information on species population sizes, I can use the UKPN data to gain an insight into latitudinal and longitudinal clines in species abundances. For each species the latitudinal and longitudinal cline in the number of records will be a poor measure of change in abundance, as the number of records is greatly influenced by the density of recorders, which is greatest in the southeast of Britain and declines to the north and west. However, assuming that differences in the density of recorders are the same for all species, relative differences between species in the way their abundances change with latitude and/or longitude can be estimated. I estimated species-specific trends via a generalised linear mixed model, with the response variable as the number of records of each species per 5km grid cell, assuming Poisson family errors. Species, latitude, longitude and the interaction of species with latitude and longitude were included as fixed effects, and 150km grid cells as random effects.

Latitudinal trends in estimated species abundances were most positive for larch, rowan, silver birch and sessile oak, and most negative for blackthorn, garlic mustard, hazel and pedunculate oak. Longitudinal trends in estimated species abundances were most positive for field maple, dogrose, pedunculate oak and silver birch, and most negative for sessile oak, cuckooflower, larch and wood anemone.

If latitudinal variation in population size leads to B_{lat} underestimating B, across species this may give rise to a negative relationship between the absolute value of the species specific latitudinal abundance deviation and $|B_{\mathrm{lat}}|$. By the same token there should be a correlation between the deviations in longitudinal abundance trends $|B_{\mathrm{lon}}|$. I considered point estimates only, and excluded field maple and hazel as outliers from the latitudinal and longitudinal analysis, respectively. In both instances the correlation was weakly negative but non-significant ($|B_{\mathrm{lat}}|$r = -0.06, p = 0.80, $|B_{\mathrm{lon}}|$ r = -0.23, p = 0.32).

Table A1. Discussion of the validity of key theoretical (i-vi) and statistical (vii-ix) assumptions in estimating *B* and *b* from spatiotemporal data

Assumption	Comments
i. The temperature cue that determines plasticity has been correctly identified.	While the temperature sensitivity of plant phenology is often modelled using growing degree day mechanistic models (e.g. Chuine 2000), here a reaction norm approach is adopted due to its amenability to linear statistical modelling and to facilitate comparisons with theoretical models of quantitative trait evolution (e.g. Chevin *et al.* 2010; Hadfield 2016). Where growing degree day and linear reaction norm approaches have been applied to the same datasets, insights into phenological cues and responses are similar (Phillimore *et al.* 2013; Roberts *et al.* 2015). Here a sliding-window approach is used to identify the window during which mean temperature best predicts phenology. It is possible that the window of thermal sensitivity varies geographically, and the phototemp model allows for a latitudinal cline in the window of temperature sensitivity.
ii. The temperature cue that determines plasticity also determines the optimum (*B*).	Where the environment of selection and development (the cue) are the same, these estimates of *B* will correspond to the optimal slope of phenology on temperature. If the correlation between the two environments is < 1, these estimates of *B* will correspond to the optimal phenological response to the environment of development, which is shallower than the optimal phenological response to the environment of selection (Tufto 2015).
iii. The selected temperature variable is the sole determinant of the optimum.	While temperature may have a direct effect on the optimum for a species, it is quite likely that some of its effect is indirect, via the phenology of interacting species (e.g., forest tree and understorey species competing for light in spring, or flowers competing to attract pollinators). If the identity of interacting species varies clinally then this may cause B_{lat} or B_{lon} to overestimate or underestimate *B*. Similarly, other environmental variables that vary geographically and affect phenology, such as precipitation, may lead to B_{lat} or B_{lon} overestimating or underestimating *B.*
iv. Population density is constant in space	Violation of this assumption is anticipated to lead to underestimation of *B* (García-Ramos & Kirkpatrick 1997). Atlas data reveals little present-day geographic heterogeneity across Britain in the abundance of larch, rowan, silver birch, field maple (although this species is absent from the north of Britain) and alder. However, horse chestnut, beech, pedunculate oak and ash all appear about twice as frequently in plots in the south of Britain than they do further north, whereas, sycamore has elevated abundance at mid-latitudes (San-Miguel-Ayanz *et al.* 2016). If spatial heterogeneity in abundance leads to a severe underestimation of *B* across species one would expect to find a negative correlation between these estimates of $\vert B \vert$ and the absolute change in abundance with latitude or longitude, which has not been found here (Appendix A.2).
v. Migration is symmetric among populations.	At the range limits migration will be from a single direction and migration load is expected to perturb such populations from the optimum (Hadfield 2016). To assess whether this impacts on estimation of *B* here, the residuals and 150km grid cell best linear unbiased predictors (BLUPs) were plotted as a function of latitude and longitude. These were visually inspected to see whether there was a tendency for values to depart from 0 at the latitudinal and longitudinal extremes. Such deviations in BLUPs were observed at one or both latitudinal extremes for wood anemone, lesser celandine, sycamore, hazel and rowan, and for these

	species B_{lat} may be biased downward. Most species showed such departures in BLUPs over longitudes, implying that B_{lon} will tend to be biased downward.
vi. Populations are at migration-selection equilibrium.	Violation of this assumption would cause B_{lat} and B_{lon} to be biased away from B towards b. Introduced species, such as horse chestnut, larch and sycamore, will violate this assumption. Whether the other remaining species obey this assumption is unknown, but short-lived species (e.g. garlic mustard) are likely to have had more generations over which to adapt.
vii. The temporal slope of phenology regressed on temperature is attributable to mean population plasticity.	Based on average Central England Temperatures for Feb – May (Parker *et al.* 1992), there has been little directional trend in UK spring temperatures over the period 1998 – 2014 (slope = -0.06 ± 0.03). For long-lived species, such as the focal tree and shrub species, the contribution of microevolution to the temporal slope is likely to be negligible. For these species the assumption that this slope is attributable to plasticity is also supported by similar estimates obtained for individual trees (Vitasse *et al.* 2010). Several of the focal species are short-lived perennials (e.g. herbs, grasses) and for these species the possibility cannot be discounted that microevolution contributes to the temporal slope and biases the estimate of b toward B.
viii. Populations share the same plastic response.	When the temporal slope is estimated separately for each 150km grid cell, little evidence is found for intraspecific geographic variation in plasticity (Fig. A2). Plasticity has also been found to vary little between sites for a sample of European trees (Vitasse *et al.* 2009b).
ix. Observations are random samples from a population.	The UKPN observations are of first dates in a population, which means that the individuals sampled have more negative intercepts than the population they are drawn from. The bias that this will generate is likely to depend on the ratio of within year/grid cell variance to between year/grid cell variance. First dates are also sensitive to sampling effort and species abundance and if either co-varies with spring temperatures over time and/or space this can bias any of the slope estimates up or down (Phillimore *et al.* 2012, Appendix).

Table A2. Parameters for the temp model estimated via MCMCglmm. Species listed in ascending order of mean phenology, * indicates species for which temp is the best performing alternative to the doubletemp model, CI = credible interval.

Species	**Forcing window (ordinal days)**	**Forcing window spatial slope (95% CIs)**	**Forcing window temporal slope (95% CIs)**	**Forcing window de-trended spatial slope – b (95% CIs)**	**Forcing B_{lat} slope (95% CIs)**	**Forcing B_{lon} slope (95% CIs)**	**Forcing B_{lat} – b slope difference (95% CIs)**	**Forcing B_{lon} – b slope difference (95% CIs)**
Lesser celandine*	11 to 30	-6.37 (-9.11, 3.60)	-4.37 (-7.00, -1.72)	-1.99 (-5.73, 1.85)	-10.92 (-12.46, -9.48)	-13.67 (-29.77, -1.10)	-6.52 (-9.50, -3.35)	-9.25 (-26.20, 2.61)
Meadow foxtail	61 to 136	-3.20 (-8.08, 1.79)	-6.01 (-7.17, -4.87)	2.79 (-2.51, 7.61)	-14.12 (-18.76, -10.44)	3.25 (-0.73, 7.69)	-8.15 (-12.95, -4.32)	9.26 (5.07, 13.75)
Dogrose*	69 to 158	-0.67 (-4.19, 3.10)	-7.97 (-9.98, -6.04)	7.30 (3.17, 11.25)	-2.94 (-4.85, -0.86)	-6.90 (-8.49, -5.26)	5.09 (2.24, 7.86)	1.05 (-1.44, 3.68)

Table A3. Parameters for the phototemp model estimated via MCMCglmm. Species listed in ascending order of mean phenology, * indicates species for which phototemp is the best performing alternative to the doubletemp model, CI = credible interval.

Species	Forcing window at 50°N (ordinal days)	Forcing window at 56°N (ordinal days)	Photoperiod requirement (minutes)	Window duration (days)	Forcing window de-trended spatial slope (95% CIs)	Forcing window temporal slope (95% CIs)	Forcing window de-trended spatial slope - *b* (95% CIs)	Forcing B_{lat} slope (95% CIs)	Forcing B_{lon} slope (95% CIs)	Forcing $B_{lat} - b$ slope difference (95% CIs)	Forcing $B_{lon} - b$ slope difference (95% CIs)
Elder	36 to 81	45 to 90	558	46	-4.93	-6.10	1.21	2.32	-13.52	8.46	-7.39
					(-9.03, -0.75)	(-8.49, -3.70)	(-3.81, 5.77)	(-0.84, 6.49)	(-20.32, -7.56)	(4.34, 13.13)	(-14.39, -1.01)
Hawthorn*	37 to 94	46 to 103	562	58	-3.18	-7.08	3.93	2.19	-11.81	9.29	-4.73
					(-6.38, 0.12)	(-9.82, -4.51)	(-0.28, 8.14)	(-0.41, 4.90)	(-16.52, -7.36)	(5.61, 13.12)	(-9.97, 0.72)
Blackthorn*	37 to 82	46 to 91	562	46	-2.24	-7.98	5.73	-4.87	-22.51	3.12	-14.61
					(-4.94, 0.51)	(-10.50, -5.50)	(1.99, 9.29)	(-6.55, -3.15)	(-32.48, -15.88)	(0.19, 6.26)	(-25.01, -7.66)
Wood anemone*	59 to 84	63 to 88	642	26	-1.47	-4.43	2.96	-4.85	-1.42	-0.41	3.02
					(-10.29, 7.51)	(-5.60, -3.36)	(-5.87, 12.08)	(-7.39, -2.14)	(-6.68, 3.72)	(-3.32, 2.51)	(-2.28, 8.39)
Horse chestnut*	53 to 98	58 to 103	618	46	-5.71	-4.75	-0.94	-0.84	-3.79	3.90	0.97
					(-9.21, -1.96)	(-5.59, -3.97)	(-4.64, 2.63)	(-2.79, 1.36)	(-6.19, -1.35)	(1.88, 6.30)	(-1.66, 3.50)
Larch*	40 to 83	49 to 92	574	44	-1.03	-5.30	4.30	0.31	6.29	5.64	11.62
					(-3.37, 1.36)	(-7.12, -3.63)	(1.38, 7.23)	(-3.65, 4.68)	(1.97, 11.10)	(1.42, 10.33)	(7.04, 16.82)
Sycamore	32 to 99	42 to 109	546	68	0.88	-5.29	6.21	2.82	6.29	8.15	11.61
					(-1.65, 3.50)	(-6.70, -3.93)	(3.30, 9.25)	(1.22, 5.06)	(1.29, 12.28)	(5.78, 10.49)	(6.03, 17.39)
Rowan*	34 to 95	44 to 105	554	62	-1.95	-5.28	3.33	2.78	-4.97	8.09	0.27
					(-4.29, 0.78)	(-6.53, -4.11)	(0.46, 6.04)	(0.69, 5.41)	(-8.34, -1.54)	(5.53, 10.84)	(-3.36, 3.79)
Silver birch*	65 to 104	68 to 107	662	40	-3.31	-4.64	1.35	-4.18	-6.18	0.45	-1.56
					(-4.63, -1.72)	(-5.81, 3.47)	(-0.45, 3.29)	(-5.13, -3.29)	(-7.82, -4.47)	(-1.02, 1.94)	(-3.61, 0.47)
Bluebell*	25 to 104	38 to 117	526	80	-1.84	-7.22	5.34	-3.00	-0.97	4.21	6.22
					(-3.62, -0.11)	(-9.24, -5.00)	(2.69, 8.24)	(-4.22, -1.87)	(-3.90, 2.18)	(1.94, 6.73)	(2.59, 9.94)
Field maple	34 to 105	44 to 115	554	72	-5.91	-5.27	-0.65	17.31	-7.07	22.56	-1.80
					(-8.69, -3.26)	(-6.19, -4.40)	(-3.43, 2.28)	(5.07, 47.13)	(-11.53, -3.24)	(10.11, 52.37)	(-6.12, 2.37)
Alder	68 to121	70 to 123	674	54	-4.43	-4.66	0.23	-4.06	-3.84	0.62	0.83
					(-8.05, -0.75)	(-5.69, -3.57)	(-3.69, 3.93)	(-6.02, -2.08)	(-6.84, -1.07)	(-1.63, 2.86)	(-2.33, 3.75)

Garlic mustard*	38 to 105	47 to 114	566	68	0.08 (-2.28, 2.44)	-5.55 (-7.20, -4.02)	5.67 (2.95, 8.53)	-1.29 (-3.20, 0.51)	2.03 (-1.81, 6.33)	4.28 (1.81, 6.68)	7.59 (3.28, 12.16)
Cuckooflower*	28 to 105	40 to 117	534	78	-0.80 (-7.06, 6.60)	-6.51 (-7.95, -5.16)	5.77 (-0.80, 12.97)	-9.09 (-14.73, -3.95)	-11.70 (-18.57, -5.53)	-2.61 (-8.22, 2.84)	-5.23 (-12.22, 1.07)
Beech	63 to 118	67 to 122	658	56	-2.63 (-4.54, -0.69)	-4.27 (-5.52, -2.98)	1.63 (-0.61, 3.97)	-2.57 (-3.65, -1.60)	-5.51 (-7.44, -3.46)	1.69 (0.08, 3.42)	-1.24 (-3.75, 0.95)
Sessile oak*	62 to 117	66 to 121	654	56	-2.76 (-6.22, 0.74)	-5.30 (-6.20, -4.30)	2.53 (-0.94, 6.22)	-5.99 (-8.69, -3.44)	-0.06 (-3.77, 3.70)	-0.70 (-3.74, 1.91)	5.21 (1.39, 9.11)
Pedunculate oak	65 to 118	68 to 121	662	54	-4.50 (-7.04, -1.99)	-5.65 (-7.01, -4.30)	1.15 (-1.62, 4.08)	-10.08 (-12.73, -8.02)	-4.09 (-6.65, -1.67)	-4.45 (-7.50, -2.02)	1.58 (-1.13, 4.50)
Ash	43 to 128	50 to 135	582	86	-2.35 (-5.14, 0.55)	-3.18 (-5.12, -1.12)	0.83 (-2.47, 4.58)	-3.42 (-5.91, -0.92)	-5.16 (-7.67, -2.74)	-0.19 (-3.38, 3.04)	-1.94 (-5.10, 1.15)
Cocksfoot	46 to 163	53 to 170	594	118	-5.59 (-9.60, -1.78)	-5.40 (-6.95, -4.05)	-0.23 (-4.39, 3.89)	-8.10 (-13.33, -4.06)	-3.76 (-6.96, -0.37)	-2.72 (-7.70, 1.85)	1.63 (-1.92, 5.24)

Table A4. Parameters for the doubletemp model estimated via MCMCglmm for forcing window and "chilling" windows. Species listed in ascending order of mean phenology, CIs = credible intervals. Note that B_{lat}, B_{lon} and slope differences are not reported due to the issues of multicolinearity in the doubletemp model.

Species	**Forcing window (ordinal days)**	**Forcing window de-trended spatial slope (95% CIs)**	**Forcing window temporal slope (95% CIs)**	**"Chilling" window (ordinal days)**	**"Chilling" window spatial slope (95% CIs)**	**"Chilling" window temporal slope (95% CIs)**	**Temperature spatial correlation**	**Temperature temporal correlation**
Lesser celendine	11 to 30	-6.74 (-10.02, -2.85)	-4.52 (-7.01, -2.15)	-120 to -111	1.03 (-7.68, 8.79)	-2.09 (-5.26, 1.14)	0.57	-0.08
Hawthorn	29 to 96	-11.42 (-22.30, -0.72)	-7.83 (-10.60, -5.41)	-60 to -35	6.77 (-1.22, 14.92)	0.11 (-2.59, 2.84)	0.97	-0.02
Blackthorn	9 to 82	-9.37 (-24.22, 4.85)	-9.19 (-11.08, -7.37)	-60 to -41	6.52 (-6.10, 19.17)	-0.32 (-2.08, 1.74)	0.98	0.03
Wood anemone	67 to 82	37.63 (15.77, 72.83)	-3.78 (-4.95, -2.49)	-62 to -59	-30.08 (-56.24, -14.09)	0.29 (-0.46, 1.08)	0.92	0.11
Horse chestnut	57 to 96	-15.03 (-29.64, -2.03)	-5.15 (-5.82, -4.41)	-88 to -41	6.75 (-2.30, 16.06)	1.25 (0.12, 2.26)	0.95	0.27
Larch	31 to 90	15.36 (5.21, 28.45)	-7.41 (-8.75, -6.03)	-88 to -71	-17.88 (-30.50, -7.76)	1.73 (0.77, 2.78)	0.99	0.43
Rowan	69 to 98	-5.44 (-13.66, 2.33)	-3.38 (-4.47, -2.12)	-50 to -45	1.16 (-3.25, 6.09)	0.18 (-1.18, 1.50)	0.94	-0.03
Silver birch	69 to 104	-6.02 (-9.30, -3.13)	-4.15 (-5.42, -2.88)	-60 to -43	2.00 (0.27, 3.96)	0.62 (-1.08, 2.37)	0.94	0.21
Bluebell	9 to 98	-0.79 (-7.46, 6.06)	-6.83 (-8.37, -5.16)	-86 to -53	-1.10 (-7.70, 4.61)	1.10 (-0.32, 2.65)	0.97	0.30
Garlic mustard	69 to 104	0.64 (-7.31, 8.24)	-3.95 (-5.49, -2.54)	-92 to -23	-0.19 (-4.60, 5.29)	1.90 (-0.06, 3.92)	0.93	0.12
Cuckooflower	31 to 110	-12.30 (-45.61, 21.42)	-6.61 (-8.06, -5.16)	-96 to -43	10.24 (-18.24, 37.45)	0.61 (-0.78, 2.18)	0.98	0.30
Sessile oak	59 to 128	-12.37 (-20.36, -5.61)	-6.75 (-7.47, -6.09)	16 to 19	8.17 (2.88, 15.02)	0.44 (0.13, 0.76)	0.93	0.72
Dogrose	69 to 158	-5.11 (-12.01, 2.25)	-8.16 (-10.08, -6.35)	-120 to -33	3.76 (-0.67, 9.12)	1.40 (-0.47, 3.45)	0.84	0.15

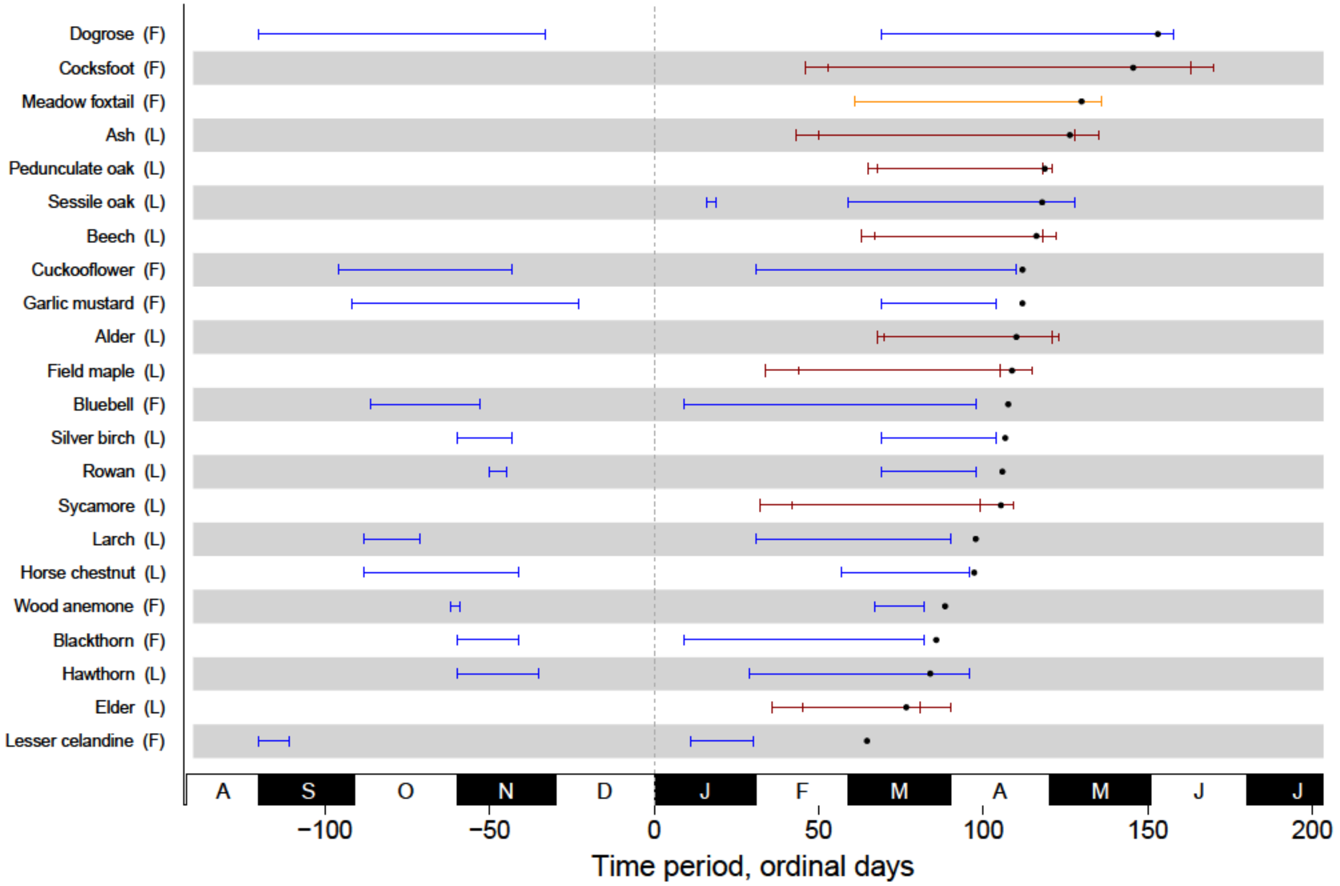
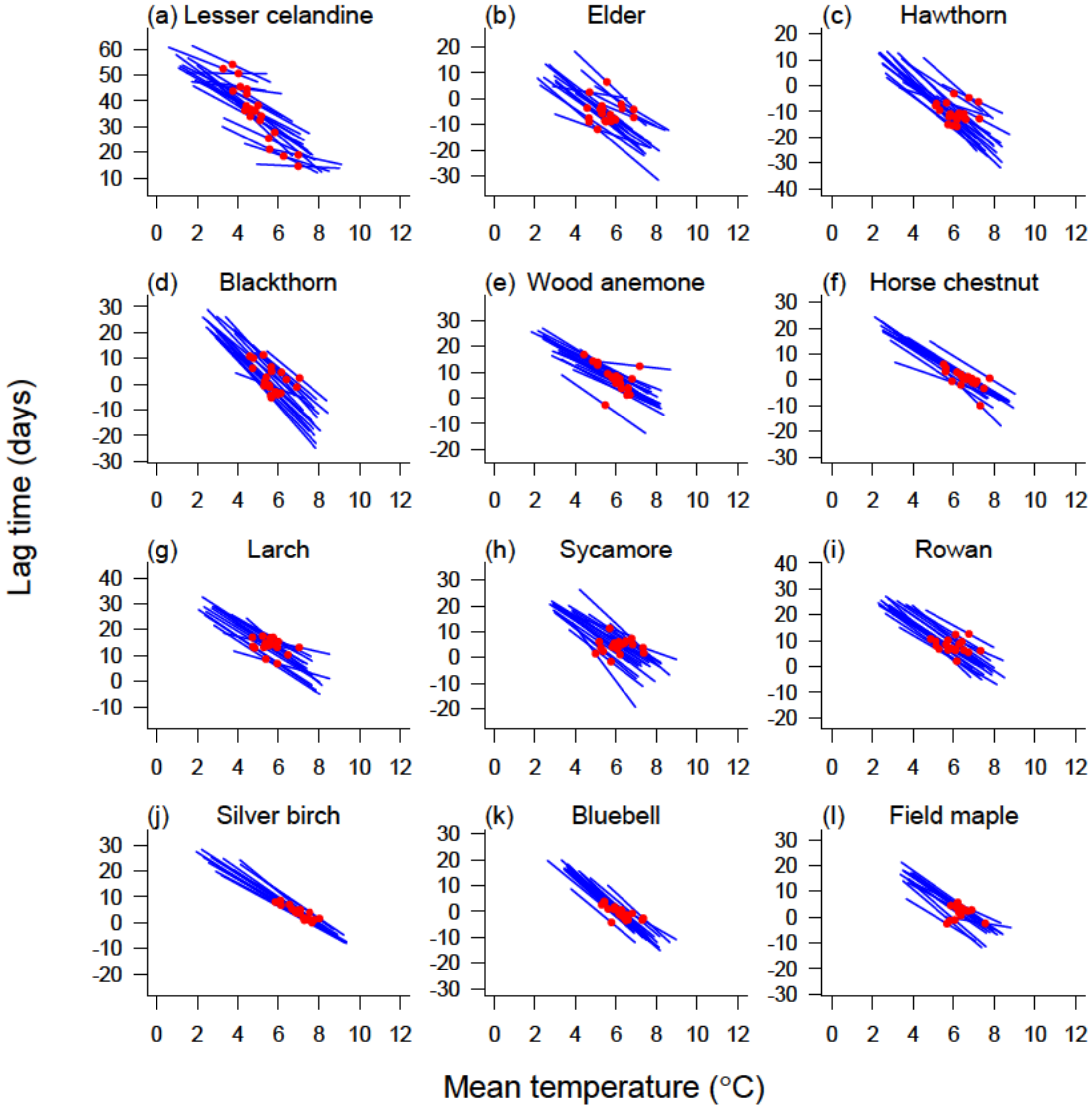


Figure A1. Time windows that received substantial support (AIC_i - AIC_{min}<2 for a model type), during which mean temperatures best predict the phenological events (median phenology shown as filled circle) for each species. Windows corresponding to AIC_{min} appear as bold bars, with other windows that received substantial AIC support appearing as translucent bars. Species are plotted in ascending order of mean phenology from bottom to top. Event type is reported in parentheses, where F = flowering and L = leafing. Bars are coloured according to the AIC_{min} model type: orange = temp, red = phototemp and blue = doubletemp. Time windows for the phototemp model covary with latitude; the thick bar depicts the time window at 50°N and the thin bar the time window at 56°N.


(a) Lesser celandine
(b) Elder
(c) Hawthorn
(d) Blackthorn
(e) Wood anemone
(f) Horse chestnut
(g) Larch
(h) Sycamore
(i) Rowan
(j) Silver birch
(k) Bluebell
(l) Field maple
Lag time (days)
Mean temperature (°C)
0 2 4 6 8 10 12
60 50 40 30 20 10
20 10 0 -10 -20 -30
20 10 0 -10 -20 -30 -40
30 20 10 0 -10 -20 -30
30 20 10 0 -10 -20
30 20 10 0 -10 -20 -30
40 30 20 10 0 -10
30 20 10 0 -10 -20
40 30 20 10 0 -10 -20
30 20 10 0 -10 -20
30 20 10 0 -10 -20 -30
30 20 10 0 -10 -20 -30

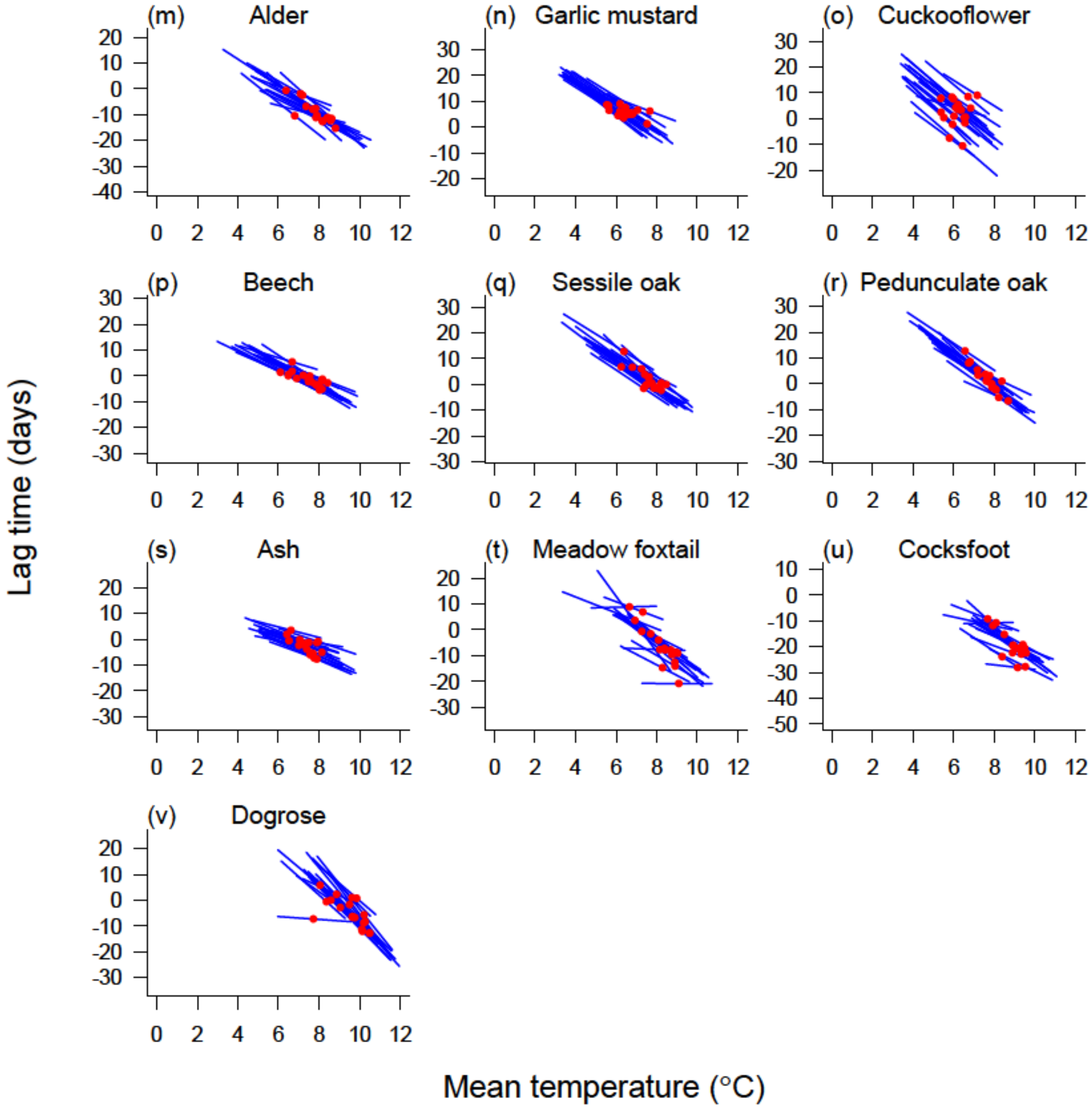


Figure A2. Temporal slopes across 150km grid cells calculated for the forcing time window that was identified by the best temp or phototemp model for each species (a – v). Only grid cells with at least 20 records and spanning a minimum of 10 years were included. Species are listed in ascending order of mean phenology.

Appendix B

Supplementary material for Chapters 4 and 5

B1. Track a Tree field guide

TRACK A TREE

recording spring
in the woods

Field Guide

Introduction to the project

How to record

THE UNIVERSITY
of EDINBURGH

WOODLAND
TRUST

NERC
SCIENCE OF THE
ENVIRONMENT

Contents

What is Track a Tree?

Track a Tree is a new project that will record the **spring phenology**, or seasonal timing, of individual **woodland trees** and the **flowering plants** that make up the woodland understorey or ground flora.

Phenology is the study of recurring seasonal events in plants and animals, and the timing of these events in relation to weather and climate.

Why is phenology important?

Timing determines the environmental conditions a plant or animal is exposed to, as well as its interactions with members of the same or other species. If this timing changes too much, individuals may be mismatched with important resources such as food or sunlight, or miss out on the opportunity to mate.

The timing of spring in woodlands is sensitive to spring temperatures. Collecting detailed seasonal observations of the UK's woodland trees and flowering plants will allow researchers to explore the response of important woodland habitats to different climate conditions.

As a Track a Tree recorder you will adopt one or more *individual* trees in your local woodland, and observe their phenology over the spring season, ideally revisiting the same tree in future years. In addition, you'll monitor the flowering of several key understorey species beneath the canopy of your chosen trees.

Track a Tree is a sister project to **Nature's Calendar**, the phenology recording scheme run by the Woodland Trust.

What is special about Track a Tree?

Track a Tree recorders will collect important *new* information on the phenology of woodland trees and flowering plants. These records will become part of a national network monitoring our woodlands over this and future springs.

Four key features make Track a Tree a unique project:

1. It follows **individual trees**. This means we can find out how much trees are able to adjust their phenology from year to year as climate conditions vary. Scientists call this flexibility *phenotypic plasticity*.
2. It follows **randomly selected trees** in woodland. Selecting trees randomly reduces bias in our observations. It also means we can record the range of dates that different species reach budburst or come into leaf, rather than recording only the individual trees with the earliest spring phenology.
3. It follows **interacting species**. By observing the flowering of plants beneath individual trees, we can see whether these ground flora species are able to shift their phenology to keep up with changes in the timing of shading under climate change.
4. It follows **woodland communities**. Through recording the phenology of UK woodland communities, we can find out how seasonal timing varies across some of our most important habitats.

You can read more about these features in the 'Start recording' section of this guide.

What do we already know?

Nature's Calendar records show that the phenology of many tree and flowering species varies across the UK, and between years. These observations show **earlier spring** growth and flowering when and where conditions are warmer.

What could happen in the future?

One possible effect of rising spring temperatures is **phenological mismatch**, where the interactions among species are altered. For instance, earlier leafing of the canopy may lead to a change in the species making up the understorey.

Why do we need your observations?

Investigating the relationship between spring temperatures and the phenology of individual trees and their understorey flowering species is the main objective of Track a Tree.

By understanding how woodland communities respond to different spring temperatures at different locations, we can project how the same communities might be affected by a change in spring temperatures. This is where you come in.

The best way to collect high quality data with the spatial coverage needed to explore this relationship is to ask for your help. By participating in Track a Tree you will become a **citizen ecologist** and we hope that insights arising from this research will help to inform the future adaptive management of our woodlands.

How to become a Track a Tree recorder

To take part in Track a Tree, you will need to do the following:

- Select one or more individual trees within a *woodland*.
- Re-visit and observe your trees and their understorey flowering plants on an approximately *weekly* basis from selection until they reach leafing.
- Enter your results on the Track a Tree website: **www.trackatree.org.uk/startRecording**

If possible, we'd like you to record the same tree over *two* or more spring seasons. This will allow us to assess how flexible the spring timing of individual trees can be in different years.

Important points to remember

Track a Tree will focus on **trees within woodlands** only, therefore isolated individuals and those in gardens are not suitable candidates.

If you are unsure whether you are able to commit to tracking a tree over two springs, data you collect over one season is still of great value.

Choosing your woodland

It is important you choose a tree or trees in **publicly accessible woodland**, where there is an established right of way. Please ensure you do not trespass. This will make it easy to re-access the tree throughout the spring and in future years.

The woodland you choose should be made up of mainly broadleaved or **deciduous species**. It may be mixed if there are sparse conifers, but please avoid predominantly conifer woodland.

Which tree species can you track?

There are eight species of tree you can choose to monitor for Track a Tree. Species identification resources are listed on the Track a Tree website. You will be recording the **budburst** and **first leaf** phenology of these species.

You may choose to follow *any one* or *any combination* of these species, but you do not have to follow all of them to take part. For instance, you could follow 3 Pedunculate oaks, or 1 Pedunculate oak and 2 Silver birch or a single Ash. The number of trees you track and which species they are is up to you.

Pedunculate Oak *(Quercus robur)*: Also known as English or common oak. Bark is thick and fissured in mature trees. Buds are oval, orange-brown and scaly, leaves are deeply lobed. Leaves have short stalks up to 0.5cm long. The acorns are on long stalks, which distinguish it from sessile oak.

Sessile Oak *(Quercus petraea)*: Buds are oval, buff-brown and scaly. Leaves are lobed and unlike Pedunculate oak, are on stalks 1-2.5cm long. The acorns are stalkless.

Silver birch *(Betula pendula)*: Slender tree with distinctive bark that is orange-red in young trees, becoming smooth silvery white and developing deep dark fissures with age. Oval leaves have double-toothed serrations along edges. Buds, leaf stems and leaves are hairless. NB: Downy birch twigs and buds are covered in downy white hairs. See the Track a Tree workbook for tips on identifying birch species.

Ash *(Fraxinus excelsior)*: Smooth grey bark that becomes fissured with age. Grey twigs are tipped with conical black buds. Leaves have 7-13 pointed leaflets. NB: Distinctive coral-like flowers appear before the leaves, please ensure you record leaf budburst only.

Sycamore *(Acer pseudoplatanus)*: Grey-brown bark is smooth in young trees and becomes scaly with age. Fat reddish buds produce large maple-like leaves with five pointed lobes.

Rowan *(Sorbus aucuparia)*: Also known as Mountain Ash. Silvery-grey bark is sometimes ridged. Twigs are hairy and purplish; buds are oval with curved tips, also purplish and covered with greyish hairs. Leaves are made up of 11-17 long toothed leaflets.

Hazel *(Corylus avellana)*: Shrubby, multi-stemmed tree with smooth often shiny brown-grey bark that splits and peels with age. Catkins and tiny red flowers appear before budburst. Twigs are covered in stiff hairs; buds are green, oval and smooth. Leaves are rounded with a heart shaped base and pointed tip, and a slightly hairy upper surface.

Beech *(Fagus sylvatica)*: Smooth grey bark that becomes rougher with age. Slender greyish-brown twigs that zig-zag at buds. Reddish brown buds are 1-2cm long, thin and pointed with a criss-cross pattern. Leaves up to 10cm long are oval and pointed. Newly opened leaves are bright green with a fringe of silky hairs; they darken and lose their hairs as they mature.

Please use these definitions to judge the tree phenology

Budburst: The green of new leaves is seen protruding from between the scales of the swollen and elongated bud.

NB: Judging tree budburst from the ground can be tricky, especially in poor light conditions. Aim to record budburst when you can see a clear change in bud shape that reflects the protruding leaves.

First leaf: When the first leaf is fully open and is recognisably the shape, if not the full size, of the adult leaf. For compound leaves like Ash the leaf must be erect but the leaflets don't need to be.

Which flowering plants can you monitor?

There are eight flowering species we'd like you to look out for and we have listed identification resources on the Track a Tree website. If these species are present, you will be recording the approximate **number of flowers** beneath the canopy of your selected trees. Don't worry if few or none of these flowers are present, as we can learn a lot from species absences.

Count flowers once the **petals have opened sufficiently** for you to see **inside the flower**. For the number of flowers, please count each **flowering stem** as 'one flower', even if it is composed of many flower heads (e.g. Bluebell).

Lesser Celandine *(Ranunculus ficaria)*
An early flowering species. Flowers have 8-12 shiny yellow petals, opening in sunshine. Dark green leaves are glossy and heart-shaped.

WTPL/Margaret Barton

Primrose *(Primula vulgaris)*
An early flowering species. A single pale yellow 5-lobed flower with a dark yellow centre on a downy stem. Tongue-shaped leaves are broad and wrinkled.

Wood anemone *(Anemone nemorosa)*

An early flowering species. Flowers are usually white with 5-8 petal-like sepals, which are often pink on the back. Leaves are divided into 3 deep lobes with serrated edges.

Wood sorrel *(Oxalis acetosella)*

White flowers with five petals and small purple veins. Leaves have three heart shaped lobes. Both flowers and leaves close at night.

Greater stitchwort *(Stellaria holostea)*

WTPL/F Hitchinson

White flowers are 2-3cm in size with 5 deeply lobed petals. Leaves are narrow, pointed and grass-like. Stems are brittle and rough-edged.

Ramsons *(Allium ursinum)*

Also known as Wild garlic, the whole plant smells garlicky. Rounded clusters of white star-like flowers grow on 3-sided stems. Leaves are long and oval, growing from base of stem.

Bluebell *(Hyacinthoides non-scripta)*

Deep blue flowers are narrow and tube-like with up-rolled tips. Flowers are scented and grow on a tall stem which often bends with their weight. Leaves are long, 1-2cm wide and drooping.

NB: The Spanish bluebell is a garden escape
and has broader leaves and wider bell-shaped flowers.
See the Track a Tree workbook for tips on identifying the Spanish bluebell.

Red campion *(Silene dioica)*

A late spring flowering species. Bright reddish-pink flowers are 2-3cm in size with 5 deeply notched petals. Leaves and stems are hairy and leaves grow in opposite pairs on the stem.

NB: Where White campion (*Silene latifolia*) grows alongside Red campion they can produce hybrids with light pinky-white flowers. Do not record plants that may be hybrids.

Safe Fieldwork Guidelines

Woodlands are usually safe places, but use your common sense while recording, and be aware of potential risks when visiting the woods. Please remember you are responsible for your own safety when participating in Track a Tree.

- **Wear weatherproof clothing and appropriate footwear.** Check the weather forecast before going out, and do not record in stormy conditions or high winds.
- **Go recording with another person or ensure someone knows where you are.** Carry a charged mobile phone if possible.
- **Take care on uneven terrain.** Familiarise yourself with your site and be aware of obstacles such as dead wood or low-hanging branches that may cause trips and injuries. Follow instructions on any warning signs.
- **Beware of broken and hanging branches.** Assess trees with broken branches from a distance.
- **Avoid handling potential hazards.** Wash your hands thoroughly and check for ticks on your return from the woods. Avoid contact with prickly or stinging plants and toxic hairy caterpillars, which can irritate skin. Ensure cuts and scratches are covered and new injuries treated.
- **Be considerate of other woodland users.** Be aware of activities going on around you. Do not record when woodland management is taking place.
- **Look after the woodland.** Avoid disturbing any wildlife. Clean your footwear thoroughly afterwards to avoid spreading pests and diseases.

Start Recording

When to start recording

We suggest you select your trees in early to mid March. You may start recording sooner if you wish. If you are unable to select your trees by this time you can still participate, just ensure you record your first visit date. Depending on temperatures and your location, you may see little or no signs of budburst or flowering on your early visits. Please still submit these records.

What you need to take part

- This field guide, the Track a Tree workbook and recording forms.
- A soft tape measure.
- Dice.
- A compass.

What you might find useful

- Binoculars. We recommend using binoculars to observe your trees.
- A mobile phone.
- A camera.
- A GPS device or OS map. You will be able to record your location using an online map when you submit your records.

Remember that Track a Tree is interested in records from **trees within woodlands** only. Our recommended minimum size for **woodland** in this project is an area of approximately **100m x 100m.** Woodlands come in many shapes; so for example, a 25m wide woodland along 400m of stream would still qualify.

Part 1: Your site and tree information

Use these instructions to start recording for Track a Tree. You can complete the Track a Tree recording sheets while out in the woods.

To submit your records please register as a recorder and sign in to the Track a Tree website:

www.trackatree.org.uk/startRecording

Some of the information we ask you to record for Track a Tree is *essential* and some is *optional*. The essential information appears below marked by an asterisk *. The more information we have, the more we can find out about our woodlands, so please complete as much as you are able to.

Complete the site information

You only need to complete this information **once** for the woodland where you record trees. Use the downloadable *site and tree information* recording form.

Site name*: Choose an appropriate name for your site, such as the name of the woodland where your tree is.

Location*: You may wish to include an optional OS map grid reference or GPS reading on the paper form for your own records. When you enter your site on the Track a Tree website, the location is essential and will be automatically completed as you select the site on the interactive map.

Choose your tree

On your **first visit** to your woodland, you will need to select the tree or trees you will be monitoring.

When you are selecting trees please ensure you are confident with the species identification, and make use of identification guides if necessary. You can find more tree species information in the Track a Tree workbook and through the links to additional identification resources found on the website.

An important feature of Track a Tree is to monitor **randomly chosen trees** and you can do this by following the steps outlined below.

How to randomly select a tree

1. Select your trees **as soon as possible**, ideally before you observe budburst. Try not to choose trees that you know from past experience have particularly early or late budburst.

2. Use the **girth at breast height criteria** in the next information box to find several candidate trees to choose from. Although we are particularly interested in data from more mature trees, try not to choose only the oldest individuals, but select your tree from a range of ages.

3. Use the **dice method** for your final selection. To do this, please choose 6 potential trees. Number these 1-6, and roll a die to select the one you will track. If you do not have 6 candidates, you can still use this method for 2-5 individuals. Either assign more than one number to each tree or simply roll again if one of the assigned numbers does not come up.

By following random trees we can build up a picture of how phenology varies **within** a woodland as well as **between** different woodlands. If you are unable to use the dice method, use a different random selection method, or only find one suitable tree to follow in your woodland, you will be able to specify this on the recording form.

Girth at breast height (GBH) is the circumference of the tree trunk at 1.5m above ground.

Track a Tree is especially interested in phenology records from mature trees. When looking for candidate trees please use the following **minimum girth at breast height** measures to guide you:

Silver birch	**0.6m (60cm)**
Rowan	**0.6m (60cm)**
Pedunculate oak	**0.8m (80cm)**
Sessile oak	**0.8m (80cm)**
Ash	**0.8m (80cm)**
Sycamore	**0.8m (80cm)**
Beech	**0.8m (80cm)**
Hazel	**No minimum GBH**

NB: Please choose Hazel with a minimum height of approximately 2m, and record the GBH of the thickest trunk.

If there are no trees available that reach these GBH measures, you can still take part in Track a Tree, but please make sure you record the GBH measure of any tree you select.

A few more tips to help you find the best trees to track:

- Exclude individuals that have lost a large portion of their canopy through severely broken limbs or trunks.
- Exclude trees with several trunks from the same base that all meet the minimum girth at breast height. Note that this does not apply to Hazel.
- Trees with smaller trunks emerging from above 1.5m on the main trunk are suitable candidates.
- To minimise the disturbance of the ground flora by trampling from other woodland visitors, try to select trees that are not directly by a large path or clearing.

Once you have chosen your tree you may wish to make additional notes on its exact location. You can also take a photo to upload to the Track a Tree website. It is very important to record the **same individual tree** on your repeat visits, throughout this spring and in future years. This information will ensure you always record the same tree.

Complete the tree information

You only need to complete this information **once** for each tree you wish to track.

Date*: Record the date that you selected your tree.

Tree ID*: Please complete this column with a Tree ID that will be memorable to you. This is particularly important if you record multiple trees in the same woodland, or in different woodlands. Please make sure your records from each visit are assigned to the right tree ID.

Tree location*: When you submit your records on the Track a Tree website you will be able to select the approximate location of your tree on the interactive map of your site. It is optional to record this on the paper form.

Tree species*: Record the species of each individual tree you track. More information on tree identification can be found in the Track a Tree workbook and list of additional resources on our website.

Recorder name*: Please record your name here. This is particularly important if you are recording with another person in the same woodland, as we need to assign each tree to a particular observer.

How you selected your tree*: Please choose the category that describes the method you used to select your tree. Although we would prefer you to use the *dice method*, we realise this may not always be suitable. You can select one of the following:

- Selected randomly using the dice method
- Selected randomly using another method
- The tree chosen was the only suitable candidate of that species
- Selected non-randomly

Distance to edge of woodland: Estimate the distance (in metres) of your chosen tree to the edge of the woodland and choose one of these categories:

- Less than 50m
- 50-100m
- 100m+

Characteristics: Using the codes provided below, please record some information on the characteristics of the woodland within approximately 25m of your chosen tree.

Woodland density*: On your recording form please tick one of the following codes to describe the density of the woodland structure:

- **OW:** Open woodland structure. Individual trees are well spaced, receive some direct sunlight and tree canopies are spread out and not seriously constrained by neighbouring trees.

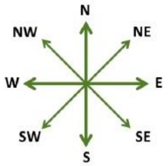
- **DW:** Dense woodland structure. Individual trees in complete shade and tree canopies of neighbouring trees are packed closely together.
- **VW:** Woodland structure varied. Some individual trees receive direct sunlight.

Other characteristics: Tick any of the below characteristics that apply to your woodland, you may need to select more than one of these codes:

- **WM:** Woodland is mainly comprised of mixed deciduous species, with few conifers present.
- **WD:** Woodland is dominated by a single species. This is where one species makes up over 50% of the trees present in the area you are assessing. If you select this category, you can record the dominant tree species if you wish, but this is optional.
- **WP:** Woodland has been planted within the last 30 years. If this is the case, and you know when the woodland was planted, please include the date.
- **RC:** Evidence of recent coppicing in woodland.
- **HC:** Evidence of historical coppicing in woodland.

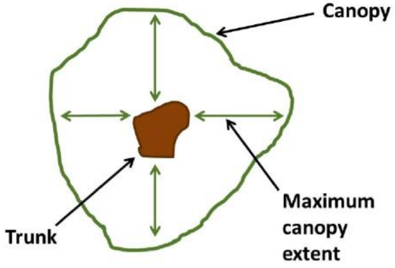
Aspect*: If your chosen tree is on a slope, this is the compass direction that the slope is facing. This direction can strongly affect the temperatures a tree and its understorey flora are exposed to. If the tree is on level ground please select that category.

If the tree is on a slope, use a compass or GPS to select the option that best describes the direction it faces. Please choose one of the following compass directions:



Girth of tree at breast height (GBH)*: This is a commonly used measure that is used to estimate the maturity of individual trees, and is described in the 'Choose your tree' section. Use a soft tape measure around the tree trunk at approximately 1.5m high to obtain the GBH. If your tree is on a slope, please stand on the uphill side of the trunk to measure it. Make sure you hold the tape measure level around the trunk of the tree to ensure the measurement is accurate. If you do not have a tape measure with you, you can use string and measure it later.

Canopy size measures: Measure the extent of the canopy in four directions from the trunk. Start with the side where the branches of the canopy extend the furthest, then take the 3 other measures around the tree as in the diagram below:



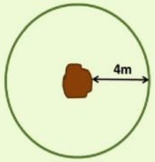
If these measurements are less than 5m, please provide the exact distance. If they are greater than 5m an exact measure is not required, please record the distance as '5'. If you cannot tell the direction of the maximum canopy extent, please record any four equally spaced measures around the tree.

Safe fieldwork: If the canopy extends over a steep slope or other hazard, please do not put yourself in danger, and do not record these canopy measures.

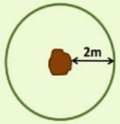
Monitoring the understorey area

When you monitor the understorey flowering of your tree, you will be **surveying inside a circle** that falls around the trunk of your chosen tree. The radius of this circle will depend on the tree species.

This will be a **4m radius** for:
Pedunculate oak
Sessile oak
Ash
Sycamore
Beech



This will be a **2m radius** for:
Rowan
Silver birch
Hazel



Number of trees/young trees/young coppice in understorey area: Count the number of trees that fall within the circle around your chosen tree, and record how many can be categorised as:

- 'Trees', individuals with a GBH of 0.5m or greater
- 'Young trees', individuals with a GBH of less than 0.5m. Please include young trees of approximately 10cm GBH (about 'broom-handle' size) and above. If the young trees are shorter than 1.5m, which is the height that GBH is measured, please exclude them from your count.
- 'Young coppice', trees in coppice management are periodically cut back to ground level. If there is evidence of young coppiced trees please give your best estimate of how many are present.

Optional external scheme IDs: If you later choose to record this tree as part of another citizen science project, please submit the tree ID assigned by that scheme. This will help us share information about the trees you monitor. You can submit IDs online for the Ancient Tree Hunt, Treezilla, and the OPAL Tree Health Survey.

Additional information: You can use this space in the online form for additional details about your site and tree. You may wish to include information on the ownership of the woodland or your own notes on the tree's location and other features of your woodland.

Part 2: Your phenology observations

During Track a Tree we would like you to record the phenology of your chosen tree and **selected flowering plant species** present in the 2m or 4m radius circle around it. If the flowering species listed do not appear under your tree, the tree information alone is still useful so please submit all records you collect.

Further information on the identification of the understorey species can be found in the Track a Tree workbook and through the links to additional identification resources on the website.

Complete the tree phenology

You will need to complete this information on **each visit** you make to your chosen tree. Use the downloadable *phenology observations* recording form.

Site name*: Record the site name where your tree is located.

Tree ID*: Record the ID you have assigned your chosen tree.

Date of visit*: It is very important to record the date of each visit you make to your tree to record phenology.

Tree phenology*: Record the tree phenology you observe on each visit to your tree. Select one of the following categories to describe the phenology:

- **No budburst observed**.
- **First budburst**: Where you observe budburst anywhere on your chosen tree.
- **Partial budburst**: Where you have observed first budburst on an earlier visit, but budburst is not yet present across the entire tree.
- **Entire tree budburst**: Where budburst appears to be present on all observed branches of your chosen tree.
- **First leaf**: Where you observe first leafing anywhere on your chosen tree.
- **Partial leaf**: Where you have observed first leafing on an earlier visit, but leafing not yet present across the entire tree.
- **Entire tree in leaf**: Where all branches observed have reached leafing.

How much of the tree you observed: Different trees have branches at different levels and while some may be accessible by hand others may only be visible from a distance. On each visit please select the category that describes how much of the tree you were able to observe:

- **Lower branches**: Only those branches within reach were observed.
- **The whole tree:** The lower branches within reach AND the upper branches observed using binoculars.
- **Upper branches:** Only the upper branches were observed using binoculars.

Complete the flowering plant phenology

You will need to complete this information on **each visit** you make to your chosen tree.

Flowering plant phenology*: On the paper recording form, if the species is absent, please leave the box blank. When you submit your records online, if any of the flowering species were *present* you will need to tick a box to say so. You will then be able to complete the flowering category for that species. If you observed *none* of the flowering species, or if the understorey area was not visible due to snow cover, you will be able to select these options online.

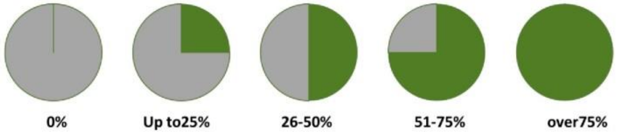
For each of the species present below your chosen tree, tell us approximately how many flowers there are using these categories:

- **0**
- **1-5**
- **6-10**
- **11-25**
- **26-50**
- **51-100**
- **Over 100**

Count flowers once the **petals have opened sufficiently** for you to see **inside the flower**.

Remember to count each **flowering stem** as **'one flower'**. Count stems once the petals of the **first individual flower** have opened.

Bramble coverage*: Estimate the percentage cover of bramble in the understorey survey area around your chosen tree trunk. Bramble thickets can shade the woodland floor, so it is useful to know how much is present. Choose from the following categories:



Field notebook: You may wish to record additional observations of your visits online. This could include interesting wildlife sightings or records of other flowering plants. Please consider using this area as your own field notebook. When you enter your notes online, you will be able to look back at the diary of your visits. This information will not be analysed for the project, but we hope the notebook will prove useful to you.

When to stop tracking your trees

Please continue your visits until you observe **'Entire tree in leaf'**. Of course, you are welcome to continue visiting your tree beyond this point if you wish!

Please submit all records on our website:
www.trackatree.org.uk/startRecording

We recommend you submit records online regularly throughout spring so that:

- You'll have fewer records to submit all at once.
- You'll be able to compare your observations with other records of spring's progress across the UK.
- The records will be safely stored in case of damage or loss.
- If you need to stop recording at any point, we can still use your observations up to that time.

We realise that submitting records throughout the season may not always be possible. If you cannot do so, please fill in our online forms when you can.

Finally, a huge **thank you** for being part of Track a Tree.

TRACK A TREE

B2. Track a Tree field workbook

TRACK A TREE
recording spring
in the woods

Field Workbook

Identification and fieldwork tips

Example field recording forms

THE UNIVERSITY
of EDINBURGH

WOODLAND
TRUST

NERC
SCIENCE OF THE
ENVIRONMENT

Contents

In this workbook you will find:

- **Tips for species identification and recording**
- **Safe fieldwork guidelines**
- **An example site and tree information recording form**
- **An example phenology observations recording form**

Tips for species identification

The tree and flowering species you can record are described in the Track a Tree field guide. For further information we suggest you check out the list of **online resources** that can be found on our website links page:

www.trackatree.org.uk/resources

You may also wish to use species identification **guidebooks** to help improve your knowledge of the plants found in your local woodland.

iSpot We also recommend **iSpot**, which is an excellent online identification tool. You can upload a picture of an unknown plant (or animal) via the iSpot website or smartphone app and the community of iSpot users will help identify it.

Things to look out for

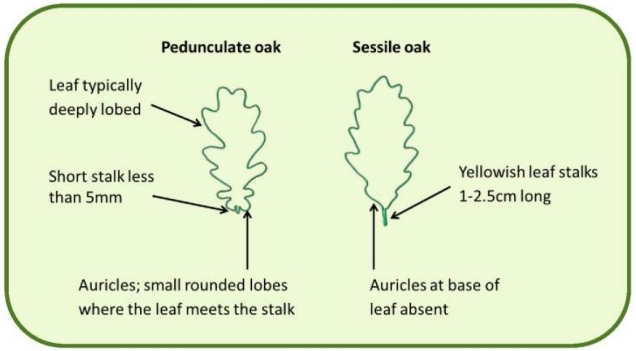
The species that feature in Track a Tree have been chosen to reflect different types of tree and relatively common and easily identifiable flowering species. You can see the full list of these species in the Track a Tree field guide.

There are however, a few species that are more easily confused with other similar species. Here are a few extra things to look out for when you are identifying your trees and flowering plants.

Oak species identification

It can be difficult to tell the difference between Pedunculate and Sessile oaks in winter. If there are any **dead leaves** or **acorns** remaining on or directly beneath the tree these can help you identify your oak.

Pedunculate oak leaves have very **short stalks** and are **deeply lobed**, while Sessile oak leaves have **long stalks**. The diagram below shows some typical oak leaf shapes to look out for.



The **acorns** of Pedunculate oak are on **long stalks**, while those of Sessile oak are **stalkless**. If you find old acorns on or under your tree, the length of their stalk may also help with identification.

Please note: Pedunculate and Sessile oaks can **hybridise**, and hybrids may have characteristics of each species. If your candidate tree shows signs of hybridisation and you are not confident of its species, please select another candidate tree to track.

Remember you can edit the tree species in the online form after you have first submitted it. You may wish to check your initial identification after the tree's leaves emerge later in the spring.

Silver birch identification

Silver birch can be confused with the similar species Downy birch (*Betula pubescens*). The twigs of Silver birch are **hairless** with small dark warts, while Downy birch twigs are smooth but covered in **fine hairs**, as seen in the pictures below.

Silver birch

Downy birch

Please note: Silver and Downy birch can also **hybridise**. If you think a candidate tree may be a Downy birch or a hybrid, please choose another tree.

Recording Ash budburst

Be careful when recording Ash budburst. Its coral like flowers burst before the leaves. Please look carefully to make sure you record **leaf budburst** only.

Leaf budburst

Flower budburst

Ash flowers are striking and appear from black buds like those that produce the leaves.

Please note: If you are selecting an Ash tree be careful not to confuse its flowers with those of **Elm species**. Elms also produce reddish-purple flowers before their leaves during February and March.

Remember to use these definitions for the tree phenology

Budburst: The green of new leaves is seen protruding from between the scales of the swollen and elongated bud.

NB: Judging tree budburst from the ground can be tricky, especially in poor light conditions. Aim to record budburst when you can see a clear change in bud shape that reflects the protruding leaves.

First leaf: When the first leaf is fully open and is recognisably the shape, if not the full size, of the adult leaf. For compound leaves like Ash the leaf must be erect but the leaflets don't need to be.

Recording damaged leaves

If you continue visiting your trees after they have come into leaf, you may notice that **caterpillars** and other insect herbivores have eaten many of the new leaves.

If you have already scored **first leaf** or **partial leaf** and you start to see many damaged leaves, it may be difficult to judge when **entire tree in leaf** is reached. In this situation, please continue to use the **partial leaf** tree phenology category.

Bluebell identification

Our native Bluebell can sometimes be confused with a common garden escape, the Spanish bluebell (*Hyacinthoides hispanica*). Please **record native Bluebells only** during Track a Tree.

Native Bluebells have **deep blue**, narrow **tube-like** flowers that are **heavily scented**. Their pollen is a **creamy white**. Spanish bluebells are often a **paler blue**, and have wider **bell-shaped** flowers with **little/no scent**. The pollen of Spanish bluebells is usually **pale blue or green**, but not white.

Bluebell

Spanish bluebell

Photo by Schnobby / CC BY-SA 3.0

Please note: Bluebell and Spanish bluebell can **hybridise**, and hybrids show characteristics of both species. If you find Spanish bluebells or what may be hybrids, please **do not record** them.

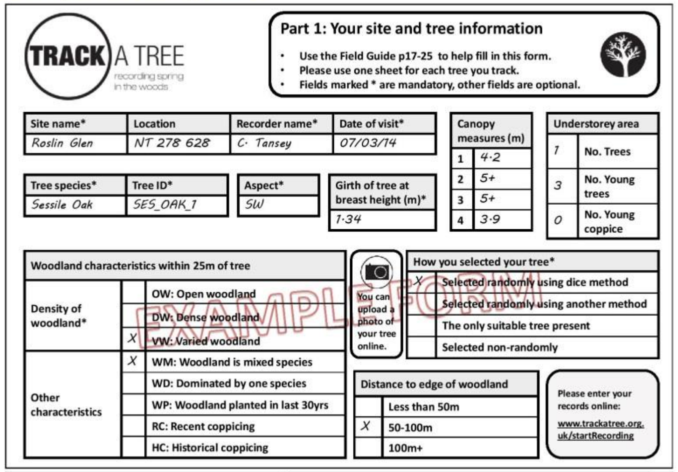
Remember to count each **flowering stem** as 'one flower', even if it is composed of many flower heads like Bluebells.

Safe Fieldwork Guidelines

Woodlands are usually safe places, but use your common sense while recording, and be aware of potential risks when visiting the woods. Please remember you are responsible for your own safety when participating in Track a Tree.

- **Wear weatherproof clothing and appropriate footwear.** Check the weather forecast before going out, and do not record in stormy conditions or high winds.
- **Go recording with another person or ensure someone knows where you are.** Carry a charged mobile phone if possible.
- **Take care on uneven terrain.** Familiarise yourself with your site and be aware of obstacles such as dead wood or low-hanging branches that may cause trips and injuries. Follow instructions on any warning signs.
- **Beware of broken and hanging branches.** Assess trees with broken branches from a distance.
- **Avoid handling potential hazards.** Wash your hands thoroughly and check for ticks on your return from the woods. Avoid contact with prickly or stinging plants and toxic hairy caterpillars, which can irritate skin. Ensure cuts and scratches are covered and new injuries treated.
- **Be considerate of other woodland users.** Be aware of activities going on around you. Do not record when woodland management is taking place.
- **Look after the woodland.** Avoid disturbing any wildlife. Clean your footwear thoroughly afterwards to avoid spreading pests and diseases.

Example recording forms



TRACK A TREE
recording spring in the woods

Part 1: Your site and tree information

- Use the Field Guide p17-25 to help fill in this form.
- Please use one sheet for each tree you track.
- Fields marked * are mandatory, other fields are optional.

Site name*	Location	Recorder name*	Date of visit*
Roslin Glen	NT 278 628	C. Tansey	07/03/14

Tree species*	Tree ID*
Sessile Oak	SES_OAK_1

Aspect*
SW

Girth of tree at breast height (m)*
1.34

Canopy measures (m)	
1	4.2
2	5+
3	5+
4	3.9

Understorey area	
1	No. Trees
3	No. Young trees
0	No. Young coppice

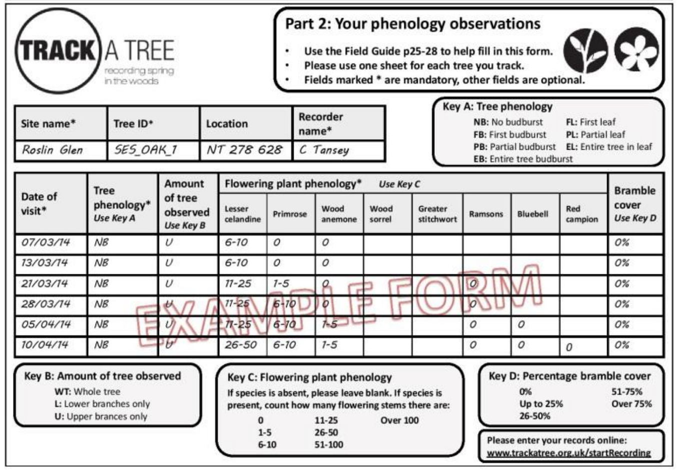
Woodland characteristics within 25m of tree		
Density of woodland*	☐	OW: Open woodland
	☐	DW: Dense woodland
	☒	VW: Varied woodland
Other characteristics	☒	WM: Woodland is mixed species
	☐	WD: Dominated by one species
	☐	WP: Woodland planted in last 30yrs
	☐	RC: Recent coppicing
	☐	HC: Historical coppicing

You can upload a photo of your tree online.

How you selected your tree*	
☒	Selected randomly using dice method
☐	Selected randomly using another method
☐	The only suitable tree present
☐	Selected non-randomly

Distance to edge of woodland	
☐	Less than 50m
☒	50-100m
☐	100m+

Please enter your records online:
www.trackatree.org.uk/startRecording



TRACK A TREE
recording spring in the woods

Part 2: Your phenology observations

- Use the Field Guide p25-28 to help fill in this form.
- Please use one sheet for each tree you track.
- Fields marked * are mandatory, other fields are optional.

Site name*	Tree ID*	Location	Recorder name*
Roslin Glen	SES_OAK_1	NT 278 628	C Tansey

Key A: Tree phenology
NB: No budburst
FB: First budburst
PB: Partial budburst
EB: Entire tree budburst
FL: First leaf
PL: Partial leaf
EL: Entire tree in leaf

Date of visit*	Tree phenology* *Use Key A*	Amount of tree observed *Use Key B*	Flowering plant phenology* *Use Key C*								Bramble cover *Use Key D*
			Lesser celandine	Primrose	Wood anemone	Wood sorrel	Greater stitchwort	Ramsons	Bluebell	Red campion	
07/03/14	NB	U	6-10	0	0						0%
13/03/14	NB	U	6-10	0	0						0%
21/03/14	NB	U	11-25	1-5	0			0			0%
28/03/14	NB	U	11-25	6-10	0			0			0%
05/04/14	NB	U	11-25	6-10	1-5			0	0		0%
10/04/14	NB	U	26-50	6-10	1-5			0	0	0	0%

Key B: Amount of tree observed
WT: Whole tree
L: Lower branches only
U: Upper brances only

Key C: Flowering plant phenology
If species is absent, please leave blank. If species is present, count how many flowering stems there are:
0
1-5
6-10
11-25
26-50
51-100
Over 100

Key D: Percentage bramble cover
0%
Up to 25%
26-50%
51-75%
Over 75%

Please enter your records online:
www.trackatree.org.uk/startRecording

B3. Track a Tree recording forms

TRACK A TREE
recording spring
in the woods

Part 1: Your site and tree information

- Use the Field Guide p17-25 to help fill in this form.
- Please use one sheet for each tree you track.
- Fields marked * are mandatory, other fields are optional.

Site name*	Location	Recorder name*	Date of visit*

Tree species*	Tree ID*

Aspect*

Girth of tree at breast height (m)*

Canopy measures (m)	
1	
2	
3	
4	

Understorey area	
	No. Trees
	No. Young trees
	No. Young coppice

Woodland characteristics within 25m of tree		
Density of woodland*		OW: Open woodland
		DW: Dense woodland
		VW: Varied woodland
Other characteristics		WM: Woodland is mixed species
		WD: Dominated by one species
		WP: Woodland planted in last 30yrs
		RC: Recent coppicing
		HC: Historical coppicing

You can upload a photo of your tree online.

How you selected your tree*	
	Selected randomly using dice method
	Selected randomly using another method
	The only suitable tree present
	Selected non-randomly

Distance to edge of woodland	
	Less than 50m
	50-100m
	100m+

Please enter your records online:

www.trackatree.org.uk/startRecording

TRACK A TREE
recording spring
in the woods

Part 2: Your phenology observations

- Use the Field Guide p25-28 to help fill in this form.
- Please use one sheet for each tree you track.
- Fields marked * are mandatory, other fields are optional.

Site name*	Tree ID*	Location	Recorder name*

Key A: Tree phenology

NB: No budburst
FB: First budburst
PB: Partial budburst
EB: Entire tree budburst
FL: First leaf
PL: Partial leaf
EL: Entire tree in leaf

Date of visit*	Tree phenology* *Use Key A*	Amount of tree observed *Use Key B*	Flowering plant phenology* *Use Key C*								Bramble cover *Use Key D*
			Lesser celandine	Primrose	Wood anemone	Wood sorrel	Greater stitchwort	Ramsons	Bluebell	Red campion	

Key B: Amount of tree observed

WT: Whole tree
L: Lower branches only
U: Upper brances only

Key C: Flowering plant phenology

If species is absent, please leave blank. If species is present, count how many flowering stems there are:

0
1-5
6-10
11-25
26-50
51-100
Over 100

Key D: Percentage bramble cover

0%
Up to 25%
26-50%
51-75%
Over 75%

Please enter your records online:
www.trackatree.org.uk/startRecording

Appendix C

Supplementary material for Chapters 4 and 5

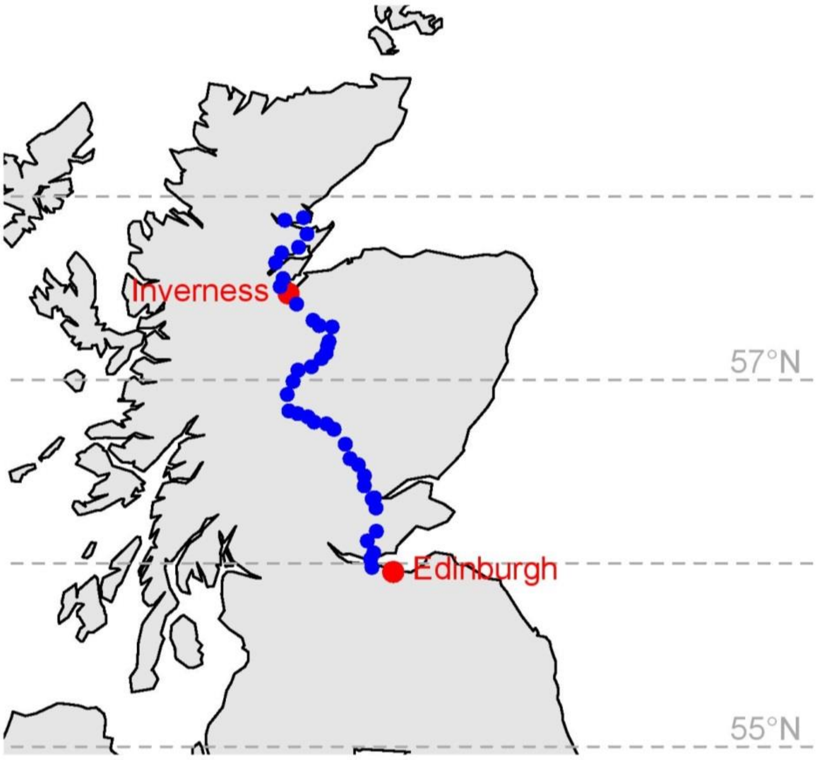


Figure C1. Sites monitored on the Scottish transect between Edinburgh and Dornoch.