

Spatio-Temporal Responses of British Wild Bees and Fruit Trees to Climate Change

Submitted for the Degree of Doctor of Philosophy

Centre for Agri-Environmental Research, School of Agriculture, Policy, and Development

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Declaration

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

Chris Wyver, January 2024

Contributions to co-authored papers

Chapter 2 was co-authored with Simon Potts, Rowan Edwards, Mike Edwards and Deepa Senapathi. I conceived the idea, carried out analysis and wrote the manuscript. Simon Potts and Deepa Senapathi provided support with conceptualisation and manuscript revisions. Rowan Edwards and Mike Edwards provided access to data used in the analysis. All co-authors provided comments on various drafts of the manuscript.

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i

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iii

Abstract

Biodiversity is under immense pressure from a range of threats, including land-use change, pollution, overexploitation, and climate change. Climate change significantly impacts species' ranges, physiology, and phenology (the timing of recurring biological events). Species-specific responses to climate change may alter the synchrony of inter-species interactions, potentially affecting the provision of important ecosystem services such as pollination. This thesis explores the impact of climate change on wild bees (including many important pollinator species) and their interaction with economically important pome and stone fruits. Focussing on Great Britain, it assesses historic patterns and predicts potential future spatio-temporal trends in fruit, wild bees, and the synchrony between them.

Analysis of apple blossom and wild bee pollinator phenology revealed different patterns of change over time, although both emerged earlier in warmer years. Many wild bee species are advancing their emergence dates in response to temperature, however shifts were species-specific. The climate envelopes of many British wild bee species were predicted to shift poleward under future climate scenarios. The ability of a species to fill its climate envelope was found to be influenced by its life-history traits, specifically foraging behaviour, body size, and overwintering strategy. Finally, an important spatial data gap in fruit tree phenology recording was uncovered. Consequently, this thesis developed a citizen science project, FruitWatch, to collect blossom dates of fruit trees across Great Britain. Blossom predictions based on these records showed a strong link to temperature, with earliest dates predicted in the warmest locations.

These results have direct implications for fruit growers, showing changing spatio-temporal dynamics of fruit crops and wild bee pollinators. Understanding these shifts is crucial to maintaining effective pollination of orchards. More broadly, this thesis provides a framework for assessing spatio-temporal shifts in many taxa, highlighting citizen science as a powerful tool for monitoring spatio-temporal shifts.

iv

1. Introduction	1
1.1. Impact of climate change on biodiversity - individual species	2
1.1.1. Spatial changes	2
1.1.2. Temporal changes	3
1.1.3. Behavioural changes	4
1.2. Impact of climate change on interactions between species	4
1.3. Impact of climate change on ecosystem services	6
1.4. Impact of climate change on insect pollinators	6
1.4.1. Spatial changes in insect pollinators	6
1.4.2. Temporal changes in insect pollinators	8
1.4.3. Other changes in insect pollinators	9
1.4.3.1. Size	9
1.4.3.2. Reproduction	9
1.4.3.3. Activity period	10
1.4.3.4 Behaviour	10
1.4.3.5. Pests and pathogens	10
1.4.4. Changes in community composition	11
1.5. Plant-pollinator interactions and climate-driven mismatches	12
1.5.1. Impacts of mismatches on crop pollination	13
1.6. Case Study: Apples and their pollinators	15
1.6.1. Importance of pollination to apple production	16
1.6.2. Insect pollinators of apple orchards	16
1.6.3. Impact of climate change on fruit trees	18
1.7. Aims and structure of the thesis	20
1.7.1. Summary of knowledge gaps	20
1.7.2 Research questions	22
1.7.3 Approach and structure	23
2. Climate driven shifts in the synchrony of apple (Malus x domestica Borkh.)	26
flowering and pollinating bee flight phenology.	20
2.1. Abstract	26
2.2. Introduction	27
2.3. Methods	29
2.3.1. Apple flowering data	29
2.3.2. Pollinator data	30
2.3.3. Climate data	31

2.3.4. Impact of climate on pollinator phenology	31
2.3.5. Calculating mismatch	32
2.3.6. Statistical analysis	32
2.3.6.1. Climate	32
2.3.6.2. Apple and Pollinator flight dates, flight duration, and peak mismatch	33
2.4. Results	34
2.4.1. Change in climate	34
2.4.2. Change in phenology over time	34
2.4.3. Impact of climate on phenology	36
2.4.4. Phenological synchrony between apples and pollinators	38
2.5. Discussion	39
2.5.1. Change in apple and pollinator phenology	39
2.5.2. Mismatch	41
2.6. Acknowledgements	43
. Climate-driven phenological shifts in emergence dates of British bees	44
3.1. Abstract	44
3.2. Introduction	45
3.3. Methods	48
3.3.1. Bee data	48
3.3.2. Climate data	49
3.3.3. Statistical analysis	50
3.3.3.1. Phenological shift over time	50
3.3.3.2. Phenological sensitivity to climate change	51
3.3.3.3. Impacts of traits on phenological sensitivity to climate change	51
3.4. Results	53
3.4.1. How have the emergence dates of British bee species changed over the past 40 years?	53
3.4.2. Does temperature play a role in any changes observed in emergence dates?	55
3.4.3. Do specific traits influence temporal shifts in bee emergence dates?	56
3.5. Discussion	58
3.6. Acknowledgements	61
. Spatio-temporal shifts in British wild bees in response to changing climate	62
4.1. Abstract	62
4.2. Introduction	63
4.3. Methods	67
4.3.1. Bee data	67
4.3.2. Temporal shifts	68

4.3.2.1. Sliding window analysis	68
4.3.2.2. Predicting future emergence	69
4.3.3. Spatial shifts	69
4.3.3.1. Modelling current climate envelopes	69
4.3.3.2. Modelling historic and future climate envelopes	71
4.4. Results	71
4.4.1. Temporal shifts	71
4.4.1.1. Sliding window analysis	71
4.4.1.2. Potential changes in future phenology	72
4.4.2. Spatial shifts	74
4.4.2.1. Current distribution of suitable climate envelopes	74
4.4.2.2. Predicted changes in suitable climate envelopes	75
4.5. Discussion	78
4.5.1. Temporal shifts	78
4.5.2. Spatial shifts	79
4.5.3. Implications for pollination and conservation	82
4.6. Acknowledgements	83
5. Biological traits predict ability of British wild bees to occupy their climate	94
envelopes.	84
5.1. Abstract	84
5.2. Introduction	85
5.3. Methods	88
5.4. Results	91
5.5. Discussion	94
5.6. Acknowledgements	98
6. New citizen science initiative enhances blossom phenology predictions for fruit	00
trees in Great Britain	99
6.1. Abstract	99
6.2. Introduction	100
6.3. Methods	103
6.3.1. The FruitWatch platform	103
6.3.2. Data cleaning	104
6.3.3. Statistical analysis	105
6.3.3.1 Cultivar selection	105
6.3.3.2. Does blossom phenology shift across a latitudinal gradient in Great	105
Britain, across a single year?	103

6.3.3.3. Can citizen science data be used to parameterize existing phenology	106
models in a space-for-time substitution?	100
6.3.3.4. How well can models parameterized using a single year of citizen	100
science data predict blossom dates across orchard-growing areas in that year?	109
6.4. Results	110
6.4.1. Does blossom phenology shift across a latitudinal gradient in Great Britain,	110
across a single year?	110
6.4.2. Can citizen science data be used to parameterize existing phenology models	110
in a space-for-time substitution?	112
6.4.3. How well can models parameterized using a single year of citizen science	114
data predict blossom dates across orchard-growing areas in that year?	114
6.5. Discussion	116
6.5.1. Does blossom phenology shift across a latitudinal gradient in Great Britain,	116
across a single year?	110
6.5.2. Can citizen science data be used to parameterize existing phenology models	117
in a space-for-time substitution?	110
6.5.3. How well can models parameterized using a single year of citizen science	117
data predict blossom dates across orchard-growing areas in that year?	11/
6.5.4. Implications for growers	118
6.5.4. Implications for growers6.6. Acknowledgements	118 120
6.5.4. Implications for growers6.6. Acknowledgements7. General discussion	118120121
6.5.4. Implications for growers 6.6. Acknowledgements 7. General discussion 7.1. Overview	 118 120 121 121
6.5.4. Implications for growers 6.6. Acknowledgements 7. General discussion 7.1. Overview 7.2. Synthesis of key findings	 118 120 121 121 122
 6.5.4. Implications for growers 6.6. Acknowledgements 7. General discussion 7.1. Overview 7.2. Synthesis of key findings 7.2.1. How has the phenology of apple trees and their pollinators at the National 	 118 120 121 121 122
 6.5.4. Implications for growers 6.6. Acknowledgements 7. General discussion 7.1. Overview 7.2. Synthesis of key findings 7.2.1. How has the phenology of apple trees and their pollinators at the National Fruit Collection (Kent, GB) shifted over time, and is a phenological mismatch 	 118 120 121 121 122 122
 6.5.4. Implications for growers 6.6. Acknowledgements 7. General discussion 7.1. Overview 7.2. Synthesis of key findings 7.2.1. How has the phenology of apple trees and their pollinators at the National Fruit Collection (Kent, GB) shifted over time, and is a phenological mismatch developing? 	 118 120 121 121 122 122
 6.5.4. Implications for growers 6.6. Acknowledgements 7. General discussion 7.1. Overview 7.2. Synthesis of key findings 7.2.1. How has the phenology of apple trees and their pollinators at the National Fruit Collection (Kent, GB) shifted over time, and is a phenological mismatch developing? 7.2.2. How has the phenology of wild bee pollinators of apple (and the wider wild 	 118 120 121 121 122 122
 6.5.4. Implications for growers 6.6. Acknowledgements 7. General discussion 7.1. Overview 7.2. Synthesis of key findings 7.2.1. How has the phenology of apple trees and their pollinators at the National Fruit Collection (Kent, GB) shifted over time, and is a phenological mismatch developing? 7.2.2. How has the phenology of wild bee pollinators of apple (and the wider wild bee fauna) shifted over time across Great Britain, and what might phenology look 	 118 120 121 121 122 122 123
 6.5.4. Implications for growers 6.6. Acknowledgements 7. General discussion 7.1. Overview 7.2. Synthesis of key findings 7.2.1. How has the phenology of apple trees and their pollinators at the National Fruit Collection (Kent, GB) shifted over time, and is a phenological mismatch developing? 7.2.2. How has the phenology of wild bee pollinators of apple (and the wider wild bee fauna) shifted over time across Great Britain, and what might phenology look like under future climate scenarios? 	 118 120 121 121 122 122 123
 6.5.4. Implications for growers 6.6. Acknowledgements 7. General discussion 7.1. Overview 7.2. Synthesis of key findings 7.2.1. How has the phenology of apple trees and their pollinators at the National Fruit Collection (Kent, GB) shifted over time, and is a phenological mismatch developing? 7.2.2. How has the phenology of wild bee pollinators of apple (and the wider wild bee fauna) shifted over time across Great Britain, and what might phenology look like under future climate scenarios? 7.2.3. How has the suitable climate envelope (area with climate suitable for 	 118 120 121 121 122 122 123
 6.5.4. Implications for growers 6.6. Acknowledgements 7. General discussion 7.1. Overview 7.2. Synthesis of key findings 7.2.1. How has the phenology of apple trees and their pollinators at the National Fruit Collection (Kent, GB) shifted over time, and is a phenological mismatch developing? 7.2.2. How has the phenology of wild bee pollinators of apple (and the wider wild bee fauna) shifted over time across Great Britain, and what might phenology look like under future climate scenarios? 7.2.3. How has the suitable climate envelope (area with climate suitable for persistence) of wild bee pollinators of apple (and the wider wild bee fauna) 	 118 120 121 121 122 122 123
 6.5.4. Implications for growers 6.6. Acknowledgements 7. General discussion 7.1. Overview 7.2. Synthesis of key findings 7.2.1. How has the phenology of apple trees and their pollinators at the National Fruit Collection (Kent, GB) shifted over time, and is a phenological mismatch developing? 7.2.2. How has the phenology of wild bee pollinators of apple (and the wider wild bee fauna) shifted over time across Great Britain, and what might phenology look like under future climate scenarios? 7.2.3. How has the suitable climate envelope (area with climate suitable for persistence) of wild bee pollinators of apple (and the wider wild bee fauna) shifted over time, and what might climate envelopes look like under future 	 118 120 121 121 122 122 123 125
 6.5.4. Implications for growers 6.6. Acknowledgements 7. General discussion 7.1. Overview 7.2. Synthesis of key findings 7.2.1. How has the phenology of apple trees and their pollinators at the National Fruit Collection (Kent, GB) shifted over time, and is a phenological mismatch developing? 7.2.2. How has the phenology of wild bee pollinators of apple (and the wider wild bee fauna) shifted over time across Great Britain, and what might phenology look like under future climate scenarios? 7.2.3. How has the suitable climate envelope (area with climate suitable for persistence) of wild bee pollinators of apple (and the wider wild bee fauna) shifted over time, and what might climate envelopes look like under future climate scenarios? 	 118 120 121 121 122 122 123 125
 6.5.4. Implications for growers 6.6. Acknowledgements 7. General discussion 7.1. Overview 7.2. Synthesis of key findings 7.2.1. How has the phenology of apple trees and their pollinators at the National Fruit Collection (Kent, GB) shifted over time, and is a phenological mismatch developing? 7.2.2. How has the phenology of wild bee pollinators of apple (and the wider wild bee fauna) shifted over time across Great Britain, and what might phenology look like under future climate scenarios? 7.2.3. How has the suitable climate envelope (area with climate suitable for persistence) of wild bee pollinators of apple (and the wider future climate scenarios? 7.2.4. How well are wild bee pollinators of apple (and the wider wild bee fauna) 	 118 120 121 121 122 122 123 125
 6.5.4. Implications for growers 6.6. Acknowledgements 7. General discussion 7.1. Overview 7.2. Synthesis of key findings 7.2.1. How has the phenology of apple trees and their pollinators at the National Fruit Collection (Kent, GB) shifted over time, and is a phenological mismatch developing? 7.2.2. How has the phenology of wild bee pollinators of apple (and the wider wild bee fauna) shifted over time across Great Britain, and what might phenology look like under future climate scenarios? 7.2.3. How has the suitable climate envelope (area with climate suitable for persistence) of wild bee pollinators of apple (and the wider wild bee fauna) shifted over time, and what might climate envelopes look like under future climate scenarios? 7.2.4. How well are wild bee pollinators of apple (and the wider wild bee fauna) currently filling their climate envelopes, and are differences in range filling 	 118 120 121 121 122 122 123 125 126

7.2.5. Is it possible to produce reliable predictions blossom dates of fruit trees	107
from data submitted to Citizen Science platforms?	127
7.3. Wider implications	128
7.3.1. Implications for society	128
7.3.2. Implications for biodiversity management	130
7.4. Methodological limitations	132
7.4.1. Data limitations	132
7.4.2. Use of citizen science in agro-ecology	132
7.5. Recommendations for future research, policy, and practice	133
7.6. Concluding remarks	135
8. References	136
9. Supplementary material	165
9.1. Climate driven shifts in the synchrony of apple (Malus x domestica Borkh.)	165
flowering and pollinating bee flight phenology.	105
9.2. Climate-driven phenological shifts in emergence dates of British bees	171
9.3. Spatio-temporal shifts in British wild bees in response to changing climate	190
9.4. Biological traits predict ability of British wild bees to occupy their climate	240
envelopes.	247
9.5. New citizen science initiative enhances blossom phenology predictions for	254
fruit trees in Great Britain	234

1. Introduction

"Nature is declining globally at rates unprecedented in human history" – This was the warning from a recent report from the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES, 2019). Human impacts influencing this decline in species abundance and diversity include anthropogenic climate change, both directly through impacting species' thermal tolerances and indirectly through land use change driven by climate change. Other anthropogenic impacts include habitat fragmentation, agricultural expansion and intensification, pollution, over-fishing and hunting as well as movement of invasive species either accidentally or deliberately facilitated by humans (Tilman et al., 2017).

The impact of climate change on biodiversity is seen as a major threat and is an area of research that has become increasingly important, with a Web of Science search for 'Biodiversity AND Climate Change' revealing only one paper published in 1990 compared with 4,096 published in 2022 (Figure 1.1). There are a complex range of impacts that changing climate can have on biodiversity. These work at a range of spatial scales, from individual to biome, and temporal scales, from days to decades. These are all impacted by several aspects of the climate that can change, including temperature, rainfall, the frequency and intensity of extreme climatic events, CO₂ concentration and ocean dynamics (Bellard et al., 2012).



Figure 1.1. Number of papers per year for a Web of Science search for papers containing Biodiversity AND Climate Change. Accessed 15/01/2024

Traditionally there have been considered three responses to climate change by species: "(1) persistence in situ if changing climate remains within the species' tolerance limits; (2) range shifts (migration) to regions where climate is within the species' tolerance limits; or (3) extinction" (Davis et al., 2005). Recently a fourth acclimatization response has been added to this group of responses, where species can modify their behaviour and timing of biological events to cope with climatic changes (Beever et al., 2017).

1.1. Impact of climate change on biodiversity - individual species

1.1.1. Spatial changes

One of the most well-studied responses of biodiversity to climate change is shifts in species ranges. As the climate changes, new areas fit the climatic requirements of a species' niche, or the "set of physical conditions that allow individuals to live and grow" (Sax et al., 2013). Most evidence suggests this movement is poleward and there has been evidence in insects - with 63% of British butterflies studied by Parmesan et al. (1999) shifting poleward; fish - with juveniles of 30 tropical reef fishes being found further poleward in 2016 than 2006 (Fowler et al., 2018); and mammals - with the Mediterranean water shrew moving poleward (Balčiauskas et al., 2016). Birds have also been demonstrated to shift their ranges poleward. A study of British birds has shown an average poleward range shift of 13.5km in 2008-11 compared with 1988-91 (Gillings et al., 2015). There is less evidence to suggest widespread poleward movement of plants, however, there is evidence that some species are shifting their ranges (Groom, 2013).

This poleward shift was theorized before climate-induced latitudinal shifts were noticed by Wright (1983) who stated that "as the available resources in more northern areas increases with a warming climate, so should the variety of resource types and therefore also the abundance and diversity of species that are able to exist in increasingly poleward areas". Most of the evidence supporting this theory comes from the northern hemisphere, and although projections suggest species in the southern hemisphere should experience similar range shifts (e.g. Krüger et al., 2018; Péron et al., 2012), there is currently less empirical evidence to support these predictions (Lenoir & Svenning, 2015).

Range shifts have not only been seen latitudinally but also in terms of elevation. Historically, higher altitudes have been subject to colder temperatures, resulting in heat and energy deficiencies that limit species' ability to develop, reproduce and survive (Körner & Paulsen, 2004). As higher altitudes warm, they become more suitable for species adapted to warmer temperatures (Gottfried et al., 2012). Analysis of 171 forest plant species shows a mean 29m uphill shift in elevation/decade (Lenoir et al., 2008). This is also seen in insects, with the bumblebees in the Pyrenees migrating uphill by an average of 129m over a 115-year period (Marshall et al., 2020). This uphill shift is being complemented by in some cases by extinctions at lower elevations (Kerr et al., 2015; Ploquin et al., 2013).

1.1.2. Temporal changes

Climate also plays a role in phenology, defined as **"the timing of recurring biological events"** (Buisson et al., 2017). Example of phenological events include life history traits in both plants and animals, such as emergence, budburst, flowering, fruiting, migration, and egg laying, which are all influenced by climate. Temperature is regarded as the key driver of phenological shifts (Gordo & Sanz, 2005) and changes in phenology caused by warming temperatures are well documented, but often vary in magnitude and direction (Chmura et al., 2019). Other climatic factors also drive phenology, such as rainfall, which is linked to fruiting phenology in tropical rainforests (Dunham et al., 2018) and wind is thought to be an important explanatory factor in phenology of dry forests in Bolivia (Justiniano & Fredericksen, 2000).

Phenology has been monitored by humans for centuries, beginning in Japanese cherry orchards in the 9th Century (Aono & Kazui, 2008). In Great Britain, phenological records date as far back as 1736 (Margary, 1926) with the discovery of the Marsham phenological record, a record of the 'onset of spring' collected by five generations of the same family in Norfolk (Sparks & Carey, 1995). Since then, phenological recording has remained a long-established feature of amateur natural history (Lawrence, 2009), and recent collaborations have attempted to bring a more systematic approach to phenological recording in the Great Britain, such as between the

Centre for Ecology and Hydrology and the Woodland Trust saw the creation of the UK phenology network, better known as "Nature's Calendar" (Lawrence, 2009).

Plant phenology has been particularly well studied in comparison to other taxa, and results show a general advancement in the average date of flowering (Menzel, 2003; Vitasse et al., 2022) with these studies showing an average advancement of 4-5 days per 1°C warming. Fitter and Fitter (2002) showed the average first date of flowering in 385 British plant species advanced by 4.5 days in the 1990s compared with the four decades previously, with only 3% of species exhibiting significantly delayed phenology, although high individual variability surrounding this mean exists and suggests that not all plants exhibit the same trends in phenology.

1.1.3. Behavioural changes

Organisms can also respond to climate change in other ways. Individuals can acclimatize or alter behaviour to escape conditions that fall outside its optimum range whilst remaining within its habitat (Sassi et al., 2015). Behavioural flexibility allows organisms to cope with ever changing conditions and is an important component of species' adaptive capacity (Beever et al., 2017). Research on this topic is limited to a small range of taxa, behaviours, and climatic stimuli (Beever et al., 2017), however the research conducted to date shows that some species have been altering their active periods depending on the climatic conditions (Dias et al., 2012).

Whilst this generally comes with benefits to the individual, in some cases behavioural adaptation comes with fitness costs. Extremely warm temperature can restrict activity and has been linked to local extinctions of Mexican *Sceloporus* lizards through severely reduced activity periods leading to insufficient food intake (Kearney, 2013).

1.2. Impact of climate change on interactions between species

Species do not live in isolation from other species, with organisms living within ecological communities, which are defined "as an assemblage of populations of at least two different species that interact directly and indirectly within a defined geographic area" (Lang & Benbow,

2013). These can be predator-prey interactions (Burthe et al., 2012), host-parasitoid (Evans et al., 2013), host plant- larvae (Visser & Holleman, 2001) and plant-pollinator (Kudo & Ida, 2013). Mismatches can occur at a range of levels and include spatial, temporal, morphological and recognition mismatches (Gérard et al., 2020).

Changes in the ranges, timings and behaviour of individual species have knock-on impacts on these inter-species interactions. Where interacting species respond to the same environmental cues with different magnitudes or in different directions, or to different cues altogether there becomes a risk of these interactions becoming decoupled. This decoupling reduces the capacity of the ecological community to maintain existing levels of the ecosystem processes and services it provides. Mismatches have already been seen across all three axes of species' adaptation to climate change. This includes spatial mismatches, with differential shifts in ranges between giant pandas (*Ailuropoda melanoleuca*) and bamboo (*Bambusa* spp.) between 1980 and 2010 in China (Zang et al., 2020) as an example.

Temporal mismatches have also been observed, such as between oak (*Quercus* spp.) leafing, peak caterpillar (Lepidoptera) biomass and peak nesting activity of pied flycatchers (*Ficedula hypoleuca*), blue tits (*Cyanistes caeruleus*) and great tits (*Parus major*) in the UK. This is especially noticeable in warm springs and the interaction is projected to become increasingly mismatched under future climates (Burgess et al., 2018). There is also evidence of asynchrony in a host-parasitoid system, with warmer springs having a greater effect on the life cycle of the cereal leaf beetle than its parasitoid *Tetrastichus julis*, resulting in reduced biological control of this pest in warmer springs (Evans et al., 2013). Finally, there have been reports of behavioural and morphological mismatches, a 'camouflage mismatch' has been seen in weasels *Mustela nivalis*. These animals moult seasonally, although with limited plasticity, resulting in extended periods of camouflage mismatch as snow days reduce due to a warming climate. This results in significantly higher risk of detection by predators for the weasels (Atmeh et al., 2018).

Shifts in synchrony are not always detrimental to all interacting parties, with asynchrony potentially releasing prey from predators (Lindén, 2018). Shifts can also lead to the creation of

novel interactions, where species that did not previously overlap (either spatially, temporally, or morphologically) begin to interact with each other (Gilman et al., 2010).

1.3. Impact of climate change on ecosystem services

The interactions between species, providing ecosystem services such as pollination and pest regulation, and between species and the physical environment, providing services such as carbon capture, movement of water and recycling of minerals create functioning ecosystems that deliver services that benefit society (Mooney et al., 2009). As the spatio-temporal dynamics of these interactions change as the climate changes, so does the capacity of ecosystems to deliver these services (Scholes, 2016). A range of services are likely to be impacted by climate change, including food production (Fezzi et al., 2014), nutrient cycling (Montoya & Raffaelli, 2010), pest regulation (Civantos et al., 2012) and pollination (Settele et al., 2016). These changes are likely to vary in the magnitude and direction of their effect across the globe, for example food production in the United Kingdom expected to increase in the northern parts of the nation and decrease in the south-east by 2060 under future climate scenarios (Fezzi et al., 2014), whereas nations such as India may see declines in agricultural production under climate change (Mahato, 2014)

1.4. Impact of climate change on insect pollinators

1.4.1. Spatial changes in insect pollinators

Pollination of crops is a key ecosystem service for provisioning both food crops and wild plants, - 87 out of 124 of the leading global food crops (Klein et al., 2007) and 85% of wild plants (Ollerton et al., 2011) are dependent on animal pollination - with the service valued at between US\$267–657 billion annually (adjusted for inflation in March 2020) (Porto et al., 2020). The most diverse and abundant group of animal pollinators are invertebrates (Katumo et al., 2022), and invertebrates provide a large proportion of the overall pollination service provided by animals.

Insect pollinators face many challenges also faced by wider biodiversity, including land use change, issues relating to land management decisions, pesticide use and climate change (Dicks et al., 2021). One of the major impacts of global change, including climate change, are changes in the distributions of pollinator species. Kerr et al. (2015) show that historical ranges of many bumblebees have contracted on the equatorward edge faster than it is expanding on the poleward edge, effectively placing some bumblebees species in a "climatic vice" (Figure 1.2) (Kerr et al., 2015).



Figure 1.2. Impact of climate change on bumble bee ranges in Europe (Kerr et al., 2015 - infographic by Ann Sanderson)

The exact mechanism for range contraction at the equatorward edge is hypothesised to be due to increased temperatures, which demands increased thermoregulatory behaviour and therefore an increased energy demand (Buckley et al., 2015). In some cases, this contraction can be severe, with equatorward edges contracting by as much as 300km in some species (Kerr et al., 2015). In addition to species being placed in a "climatic vice", some species' range shifts are not keeping pace with climate change, resulting in range shift lags (Bedford et al., 2012). There are several potential explanations for the observed climatic vices and range shift lags, including poor dispersal ability or geographical and/or other environmental barriers to dispersal. Poor colonisation of poleward sites has also been attributed to the fact that the poleward population is not large enough to colonise new sites successfully (Ash et al., 2017). There have also been uphill shifts in the distributions of some species of pollinators. Wilson et al. (2005) found that

the lower elevational limits of 16 species of butterfly have moved uphill by an average of 212m over 30 years in response to a 1.3°C degree warming. A significant uphill shift in 15 species of butterfly in the Czech Republic was also seen in the period 1995-2001 compared with 1950-80 (Konvicka et al., 2003).

However, like the lags in latitudinal range shifts, there is also evidence to suggest that elevational range shifts are also not keeping pace with climate change. Pyke et al. (2016) looked at bumble bee species in the Rocky Mountains and found the altitudinal change in most species was less than the altitudinal change required to track warming in the period 1974-2007. In Spain, although over half of species studies by Ploquin et al. (2013) shifted uphill between 1989 and 2009, the lower limit shifted uphill faster than the upper limit, resulting in contracting altitudinal ranges. The same trend has been seen in *Bombus alpinus*, with an upward shift in lower limit of 479m between 1984 and 2014, with no change in upper limit, resulting in a range contraction (Biella et al., 2017).

Some pollinator species are likely to benefit from the predicted changes in climate. In Australia, *Ceratina australensis* is predicted to expand its range under future climatic scenarios (Dew et al., 2019), primarily linked to an expansion of suitable habitat linked to increasing aridity (although some of this projected habitat is the most densely populated by humans in the country). This is consistent with projections for other arid adapted species (Silva et al., 2018).

1.4.2. Temporal Changes in insect pollinators

Another way pollinators adapt is to alter their phenology. The magnitude and direction of phenological shifts vary between species and locations. Many butterfly species have shown advancing phenology, with first spring flight in California, advancing by 24 days over 31 years (Forister & Shapiro, 2003). This is consistent with Roy and Sparks (2000) who found that 26 of 35 species studied in the UK have also advanced first flight dates, and with Peñuelas et al. (2002), who found that *Peris rapae* appeared earlier in a Mediterranean climate (11.4 days in 48 years). Conversely, some species are predicted to delay phenology. *Osmia ribifloris* studied in the Southwestern USA exhibited delayed emergence from black (warmer) nest boxes when

compared with white (cooler) nest boxes as well as up to 5.5x more variation in emergence date (CaraDonna et al., 2018). Although much of the current research highlights phenological shifts in many pollinator species, these shifts are often species specific. Indeed, not all species appear to show any temporal shift in relation to climate change, with no significant trend found in most bumblebee species studied by (Pyke et al., 2016).

1.4.3. Other changes in insect pollinators

1.4.3.1. Size

Warmer overwintering temperatures have been shown to decrease body size at emergence in two species of spring-emerging solitary bee, *Osmia cornuta* and *O. bicornis* (Schenk et al., 2018a). As large individuals have more offspring than smaller individuals, this reduction in body weight can also be perceived as a reduction in fitness (Kim, 1997). Comparison of museum specimens of four *Bombus* species also shows smaller body size compared with 100 years ago (Nooten & Rehan, 2020) This is also seen in high-Arctic butterflies (Bowden et al., 2015). This could be a factor in species poor colonization of poleward sites, as smaller body and wing size impact dispersal ability (Stevens et al., 2012).

1.4.3.2. Reproduction

Some pollinator species' mating signals are influenced by temperature. Male *O. bicornis* mating signals appear to be impacted by temperature to different levels between individuals (Conrad et al., 2017). Males who were rejected by females were those whose thorax vibrations were influenced by air temperature, which had a different frequency and pulse duration to those that were unaffected. If the climate warms sufficiently, the authors find it conceivable that *O. bicornis* could see climate change caused mating disruption. Some species may also encounter difficulty with reproductive diapause, for example in Brazil, *Plebeia droryana* may not experience temperatures cold enough to enter diapause (Dos Santos et al., 2016), potentially creating a shortage of pollen and nectar during the winter months as more bees are active and foraging.

1.4.3.3. Activity period

Flight activity in *Plebia remota*, a stingless bee native to southern Brazil, was influenced by a range of climatic factors. Throughout the activity period, rainfall negatively impacted flight activity and cold temperatures resulted in shorter, more concentrated flight periods (Hilário et al., 2012). This reduces the amount of nectar pollinators are able to obtain, potentially reducing ability to provide for their brood. Rainfall has the secondary effect of improving conditions for fungal infections in soil nesting bees (Drummond et al., 2017), particularly fungus of the genus *Aspergillus* (Batra et al., 1973).

1.4.3.4. Behaviour

Pollinators may also adapt to climate change by adapting behaviours to allow them to survive in changing conditions. Examples of this include sociality in *Halictus rubicundus*, a socially polymorphic bee, which is either solitary or social, dependent on the length of the growing season (Eickwort et al., 1996). With the growing season projected to increase, switches from a solitary to a social lifestyle should increase, increasing worker numbers and ability to collect more floral resources (Schürch et al., 2016). Another example is a change in nectar preference dependent on temperature in Australian stingless bee *Trigona carbonaria* (Norgate et al., 2010), however this area is relatively under-reported, and little is known about if and how pollinator behavioural plasticity may facilitate acclimatization to changes in climate (Shrestha et al., 2018).

1.4.3.5. Pests and pathogens

The changing climate may also bring secondary threats to pollinators such as increased pest and pathogen abundance. Much of the work in this area has been through modelling of pest population cycles. *Chaetodactylus krombeini*, a cleptoparasitic pest mite associated with *Osmia* bees which is at sufficient density, can reduce a bee population by half from the previous year's population (Batra, 1998) is projected to have 14 to 16 generations per year by 2100, up from 8-10 in 2015 (Ahn et al., 2016). The varroa mite, *Varroa destructor*, is a parasitic mite of

honeybee colonies across the globe (Le Conte & Navajas, 2008) and can diminish immune response of bees as well as being vectors for bacteria and viruses (Le Conte & Navajas, 2008). Under the future climate, *Varroa* populations could become 135% bigger requiring 1-3 times more suppression by beekeepers to stay under the threshold of 5% mite infestation to adult bees (Jung, 2015). One study exists modelling the range of a pollinator pest. The small hive beetle (*Aethina tumida*) is a parasite of social bee species, and models predict that the area suitable for this species is likely to expand poleward into northern temperate regions, as soil temperature and moisture become more suitable for pupal survival (Cornelissen et al., 2019).

1.4.4. Changes in community composition

Species turnover is likely to be higher at habitat extremes, it is possible that climate-driven poleward expansion of more generalized species is masking the declines of more specialized species (Carvalheiro et al., 2013; Pradervand et al., 2014). This is projected along an altitudinal gradient, with species that occupy cold, high-altitude habitats projected to decline in range and replaced by species from warmer, lower altitude habitats (Pradervand et al., 2014).

Community homogenization and declines in species richness have been identified or predicted in many taxa (Davey et al., 2012; Stewart et al., 2018), and may also be occurring in insect pollinators. In terms of changes in insect pollinator species richness, Papanikolaou et al. (2017) uesd bee monitoring data from 6 sites across Germany over 2 years and found a strong negative relationship between bee species richness and temperature. The authors argue that future increasing temperatures will lead to a decrease in species richness. Similar declines in species richness of *Bombus* have also been reported in the Netherlands (Van Dooren, 2019) and Sweden (Bommarco et al., 2012). Recent work published by Zattara & Aizen (2021) also highlight this decline in the number of bee species recorded on the Global Biodiversity Information Facility (GBIF, 2024a), with a 25% decline in the number of species recorded between 2006 and 2015, compared with 1990.

1.5. Plant-pollinator interactions and climate-driven mismatches

If plants and their pollinators respond to different environmental cues or respond in different directions or magnitudes to the same cue, there becomes the risk of a spatial, temporal, morphological or recognition mismatch (Gérard et al., 2020) (Figure 1.3).



Figure 1.3. Potential impacts of climate change on plant-pollinator interactions. (Gérard et al., 2020)

Evidence for spatial, morphological, and recognition mismatches between plants and pollinators is scarce, although Marshall et al. (2023) predict spatial mismatches between apple orchards and wild bee pollinators across Europe and (Miller-Struttmann et al., 2015) found that decreases in bumblebee tongue length have not been matched by changes in the depth of corolla tubes of in an alpine ecosystem.

There are far more studies focussing on temporal mismatches. Plants have been shown to respond to both climatic factors such as temperature and moisture (Leopold & Kriedemann,

1975), and non-climatic factors, such as photoperiod (Flynn & Wolkovich, 2018), whereas pollinators appear to be more strongly influenced by climatic factors (Bosch & Kemp, 2003). Historically, climatic, and non-climatic factors such as temperature and photoperiod have been closely linked, however more recent evidence suggests a decoupling of these drivers (Wadgymar et al., 2015), and this may be a cause of phenological mismatch between plants and their insect pollinators.

Evidence for temporal mismatches is mixed. In an analysis of 14 papers providing details on either experimental, modelled or observed changes in phenology of one or more plant-pollinator interaction, 5 papers showed evidence of a potential mismatch, 5 found no evidence of a mismatch and the remaining 4 returned insufficient or mixed evidence (Bartomeus et al., 2011; Benadi et al., 2014; Burkle et al., 2013; Forrest & Thomson, 2011; Gezon et al., 2016; Gillespie et al., 2016; Iler et al., 2013; Kőrösi et al., 2018; Kudo, 2014; Kudo & Cooper, 2019; Kudo & Ida, 2013; Olliff-Yang & Mesler, 2018; Petanidou et al., 2014; Schmidt et al., 2016).

Interestingly, the papers that suggested a mismatch were all focussed on an interaction between a single plant and single pollinator, whereas those that suggested no evidence for a mismatch looked at multiple interactions. This would indicate that diversity is important in maintaining plant-pollinator interactions at a broad scale (Bartomeus et al., 2013), however at the individual interaction scale mismatches may exist, and have been shown to have fitness costs on the individuals involved (Schenk et al., 2018b).

1.5.1. Impacts of mismatches on crop pollination

There is strong evidence that agriculture is becoming more pollinator dependent due to shifts in crop selection (Aizen et al., 2008) and diversity (Aizen et al., 2019). It is estimated that there has been a greater than 300% increase in the proportion of agriculture dependent on pollinators over the last 50 years (Aizen & Harder, 2009). When this is coupled with reports of insect decline (Raven & Wagner, 2021) and more specifically pollinator decline (Biesmeijer et al., 2006; Powney et al., 2019) concerns have been raised about a potential pollination deficit. It is

thought that globally, 3-5% of fruit, vegetable and nut production is lost because of inadequate pollination (Smith et al., 2022).

As a result of different regions relying on pollinator dependent crops to different levels, there is regional variation in vulnerability to potential pollinator deficits. In Europe, as an example, vulnerability to pollination shortfalls is suggested to be greater in southern Europe than northern Europe (Leonhardt et al., 2013) as growth of pollinator dependent fruits and nuts such as peaches, citrus fruits, watermelons, and almonds is better suited to warmer, southern European, climates than colder, more northerly climates.

There is also variation in vulnerability to pollination deficits between individual crops. Some crops are more dependent on insect pollination than others (Aizen et al., 2009). In the UK, Cox apples set significantly less fruit on open pollinated branches compared with hand pollinated branches, with a fruit set deficit of up to 75% (Garratt et al., 2014a). Conversely, courgettes in the UK see an average pollination deficit of just 3% in a study that compared open and hand pollinated crops, and used yield (length, circumference, and weight) as a measure of this deficit (Knapp & Osborne, 2017).

Spatial changes in crops and their wild pollinators could be a driver of a potential mismatch, and projections from some areas predict a large enough spatial mismatch between crops and their insect pollinators to impact production. Bezerra et al. (2019) estimate that there may be a reduction in overlap between the area suitable for passion fruit growth and area suitable for pollinators of up to 54.9% by 2080 under the strongest climate projections in the Neotropics. In Brazil it is projected that the probability of pollinator occurrence will decline by up to 13% across 13 crops grown in the country, with tomato crops projected to see this probability drop by 25% by 2050 through spatial mismatches (Millard et al., 2023). The risk from pollinator loss is likely to be greatest in the tropics, meaning crops such as coffee, cocoa, mango and watermelon could be at the greatest risk (Millard et al., 2023).

Pollinators also rely on non-crop habitat on farmland for resources (Carvalheiro et al., 2011; Decourtye et al., 2010). This resource is also shifting phenology, and in conjunction with

bumblebee phenology has created a 'hunger gap' in March and much of August and September in the Northern Hemisphere, where low floral resources are unlikely to meet demand of bumblebee species (Timberlake et al., 2019).

1.6. Case Study: Apples and their pollinators

Climate-driven changes in spatio-temporal distributions of both crops and pollinators mean that changes in spatio-temporal synchrony in the pollination interaction are possible. Couple this with societies increasing dependency on insect pollinated crops (Aizen et al., 2008) and it becomes clear investigations into historic, current and future spatio-temporal dynamics of crop-pollinator interactions are needed. To do this at a global scale requires significant amounts of data relating to crop distributions and phenologies, insect distributions and phenologies, and knowledge of which insects visit which crops in which regions. For many crops and many regions, this data doesn't currently exist, making assessment of spatio-temporal trends difficult. However, in specific locations and for specific crops, the required data and knowledge of insect pollinator exist, and can be used as a model system to begin to understand these trends.

One such system is apples in Great Britain. Apple growing is heavily reliant on pollinators, both managed and wild. Globally it is the most widespread temperate fruit (Ramírez & Davenport, 2013), and the most abundant pollinator dependent crop in Europe (Leonhardt et al., 2013). In Great Britain, over 400,000 tonnes of apples (including cider apples) were produced in 2022 (DEFRA, 2023). Long term phenology data exists for apples from the National Fruit Collection (www.nationalfruitcollection.org.uk), in Kent, South-East Great Britian, for a range of cultivars since the 1960s, and recent work has identified which wild bee species visit apple blossom (Hutchinson et al., 2021). Long-term bee recording data exists for these species, collected primarily by citizen observers, is held by the Bees, Wasps and Ants Recording Society (BWARS – www.bwars.com), and dates to the 19th Century. This richness of data therefore makes apples in Great Britain an ideal model system to assess climate-driven shifts in spatio-temporal synchrony of crop pollination delivery.

1.6.1. Importance of pollination to apple production

Most apple cultivars are self- incompatible (Ramírez & Davenport, 2013), meaning crosspollination is important in producing a financially viable crop. This requires pollen transfer from a different cultivar, known as a "polliniser" (Delaplane & Meyer, 2000) and this is usually facilitated by insect pollinators. Insect pollination has been shown to increase yields of apple crops, with reports of up to a 100% increase in yield when managed honeybees are introduced sequentially (Stern et al., 2001). Wild bees are also important contributors to apple pollination, with 67% of the 70 papers studied by (Pardo & Borges, 2020) finding wild bees more important pollinators than honeybees

Across the globe, it is estimated that there is a pollination deficit in apple orchards, with fruit set 41% higher when flowers are hand pollinated compared with insect pollination (Olhnuud et al., 2022). The UK is no different, with Garratt et al. (2014a) finding between 0-75% deficits, at an 8% average, in fruit set of 'Cox' apples across eight Kentish orchards using a comparison between hand pollinated, insect pollinated, and pollinator excluded branches. Questions have also been raised about future spatial overlap between areas suitable for apple orchards and areas suitable for survival of important wild bee pollinators of apple. At the European scale, Marshall et al. (2023) reported an average decline in suitable area for 33 species of wild bee known to pollinate apple orchards across Europe of 7.3% (RCP 2.6) to 24.9% (RCP 8.5) by 2080. Additionally, this study reports potential loss of overlap between areas suitable for pollinators and areas suitable for apple orchards, by as much as 13% across Europe by 2080. In Great Britain spatial overlap between orchards and pollinators may be at risk due to climate change, with Polce et al., (2014) reporting that by 2050, the most suitable areas for orchard growth will correspond to low pollinator availability.

1.6.2. Insect pollinators of apple orchards

Managed honeybees are often used in apple orchards to overcome this self-incompatibility and reduce pollination deficits. They are often the dominant pollinator species in apple orchards (Park et al., 2016). Geslin et al. (2017) add that honeybee colony quality, as well as quantity,

was a factor in the quality of the pollination service provided, and suggest that in Argentina, pome fruit production relied solely on honeybees to provide pollination. There is, however, growing concern that the recommended number of managed honeybee colonies required in Europe is outstripping supply by as much as 4.9 times (Breeze et al., 2011).

Beyond managed honeybees there are a suite of wild pollinators that visit apple crops, and these differ between locations. Bartomeus et al. (2013) found that 26 bee species visited an apple orchard in New York State, whereas Hutchinson et al. (2021) found 20 different bee species visiting apple blossom in the United Kingdom. Bees are not the only wild insect pollinators, however, and various species of Diptera, Lepidoptera, Coleoptera and Hemiptera also being recorded on apple blossom (Pardo & Borges, 2020). Although wild pollinators contribution to apple pollination can be difficult to quantify, it is thought that wild insect pollinators add £70.7 million in additional production value across four key cultivars in the UK, with the vast majority of this (£70 million) added by solitary and bumble bees and the remainder by hoverflies (Garratt et al., 2016). This study also shows that honeybees, are estimated to add £21.4 million in additional production, which highlights the relative importance of wild pollinators – particularly wild bees, to apple production. Visitation rates by wild bees vary between orchards, wild bees can provide the majority of visits to apple blossom with 77% of visits made to apple orchards in Virginia, US, made by wild bees again highlighting that wild, native bees play a major role in apple pollination (Adamson et al., 2012).

There are several reasons that wild bees may contribute more to apple pollination than managed honeybees in some cases. There is growing evidence to suggest that honeybees are not the most efficient pollinators of apple orchards with Park et al. (2016) showing that more pollen was transferred to stigmas during wild bee visits than honeybee visits (although the higher abundance of honeybees meant they made the most important contribution to apple pollination during this study). Additionally, honeybees have been shown to forage selectively for nectar, avoiding contact with the stigma therefore carrying less pollen (Kendall & Solomon, 1973; Woodcock et al., 2013), and mainly forage within an apple variety during a single foraging trip,

reducing the potential for cross-pollination (Kendall & Smith, 1975). (Boyle & Philogène, 1983), Boyle-Makowski (1987) and Vicens and Bosch (2000) also add that wild bees are particularly important pollinators in adverse weather conditions, able to forage in less optimal conditions that honeybees. Wild pollinators are also not sensitive to floral density on apple trees, with Mallinger & Gratton (2015) finding that honeybees preferred foraging on more densely blooming trees whereas wild bees showed no preference. Additionally, in the presence of crops such as oilseed rape, which flower at a similar time to apple blossom, honeybees may switch away from apple orchards. This has been observed in strawberries, with fewer honeybees found in strawberry crops when oilseed rape is present and flowering, compared to when it is absent (Bänsch et al., 2020).

1.6.3. Impact of climate change on fruit trees

Fruit trees are not immune to the changes in climate that impact the various aspects of biodiversity mentioned previously. Elevated CO₂ levels can have a range of positive and negative impacts on fruit trees, through factors such as increased rates of photosynthesis, increased light-use efficiency (Drake et al., 1997) reduced or insufficient nitrogen uptake (Stitt & Krapp, 1999) and reduced nutritional value of fruit (Schaffer et al., 1997).

Temporal changes in the phenology of fruit trees are also well documented, and studies generally show an advance in blossom phenology in temperate regions, including apples (e.g. Chmielewski et al., 2004; Cho et al., 2021; Guédon & Legave, 2008), pears (e.g. Grab & Craparo, 2011; Reeves et al., 2022), cherries (e.g. Primack et al., 2009) and plum (e.g. Cosmulescu et al., 2010). The cherry blossom record from Primack et al. (2009) is particularly interesting as it contains over 1100 years of data from Japan, and analysis shows a sharp advancement in flowering date corresponding with the sharp rise in temperature suggesting that anthropogenic climate change is linked with phenological advancements.

Fruit trees require a period of cold weather in order to break dormancy and subsequently blossom (Luedeling, 2012). The amount of "chilling" required varies between variety, and it is important this "chilling requirement" or "winter chill" is met in order for the tree to blossom,

ensuring consistent flower and fruit set and economically viable yields (Luedeling, 2012). As the temperature warms, the amount of winter chill is reduced (Baldocchi & Wong, 2008; Luedeling et al., 2009). This has been projected to have negative impacts on yields, especially in already warm areas such as California (Baldocchi & Wong, 2008) and Tunisia (Benmoussa et al., 2020) where winter chill is already limited. In the UK there is some evidence of delayed onset and accumulation of winter chill delaying budburst of apricot crops (Martínez-Lüscher et al., 2017). Interestingly, this delayed onset appeared to counteract the flowering advances of apricot caused by the warming temperatures during the heat accumulation period, consistent with findings from the Alps (Asse et al., 2018).

Another possible risk caused by advancing phenologies of fruit trees is an increased risk of spring frosts. Maximum temperatures have increased more than minimum temperatures, and spring phenologies are advancing, in some places, faster than the date of last frost (Vitasse et al., 2018). This poses the risk of freeze damage to xylem, bark, roots, and buds, and can result in death of the trees which can be costly to replace (Palonen & Buszard, 1997). As an example, in Canada it is estimated that if temperatures drop below -25°C more than 1 in 7 years, fruit growing ceases to be profitable (Quamme, 1987).

1.7. Aims and structure of the thesis

1.7.1. Summary of knowledge gaps

Despite extensive recent work on climate-driven shifts in spatio-temporal distributions of species across the globe, gaps remain in our understanding of the scale and direction of shifts for many taxa, and how these shifts might impact interactions between species. This includes shifts in many important pollinator species and food crops important for human consumption. There have been recent attempts to make global estimations of the potential changes in pollination delivery, with Smith et al. (2022) forecasting losses in production of 5% across fruit, vegetable, and nut crops, however, the impacts of this loss will not be felt equally across regions and crops. Different regions rely on different insect pollinators to pollinate different crop types, and as such, individual crop-pollinator systems will be impacted differently by climate change. This highlights the need for more localised study (e.g. national instead of global) to assess the impacts of climate change in specific, regionally important interactions.

Given the importance of apples to the agricultural sector in Great Britain, and their reliance on pollinators to set viable amounts of fruit, understanding historic and future spatio-temporal synchrony between fruit trees and their pollinators is vital to assessing the security of the pollination service to apple orchards and by extension apple production. Spatially, while changes in potential distributions of apple orchards have been relatively well documented (Marshall et al., 2023; Polce et al., 2013), knowledge of changes in apple pollinator distributions (and the wider bee fauna) in Great Britain is less well understood, creating uncertainty from a spatial mismatch viewpoint.

Temporally, although there have been several studies on the phenology of apple blossom, most of these studies do not link any advances to wild pollinators, and thus inferences about plantpollinator temporal synchrony cannot be made. One notable exception comes from Bartomeus et al. (2013), from an Agricultural Experiment station in New York State, US. However, the pollinator community from this study is different to that known to visit apple orchards in Great Britain (Hutchinson et al., 2021), and combined with reports of differing shifts in apple blossom

phenology between locations and cultivars (Table 1.1) mean that the results found in the US may not be the same as in Great Britain.

Authors	Location	Study	Voniety	Phenological	Temporal	Temperature
Autions	Location	Period	v al lety	stage	change	change
Grab & Craparo, 2011	, South Africa	1973- 2009	Golden Delicious Sayaka Granny Smith	Full Bloom	-1.9d/decade (-4.2d/°C) -1.4d/decade (-2.4d/°C)	+0.45°C /decade
Chmielewski et al., 2004	Germany	1961- 2000	Early season varieties	Blossom Onset	-2.2d/decade (-4.6d/°C)	+0.36°C /decade
Blanke & Kunz, 2010	Germany	1958- 2007	Cox's Orange Pippin	Full Bloom	-4d (88-07 vs 58-87)	+0.29°C /decade
Wolfe et al., 2005	NE USA	1965- 2001	Mean of Delicious & Empire	Mid Bloom	-2d/decade	+0.18°C /decade
Fujisawa & Kobayashi, 2010	Japan)	1977- 2004	Fuji	Flowering	-1.1- 1.4d/decade (-3.8- 4.7d/°C)	+0.25-0.27°C /decade
Peñuelas et al., 2002	Spain	1952- 2000	Unspecified	Flowering	-26d (52-00)	+0.28°C /decade

 Table 1.1. Summary of studies looking at the phenological shift of apple crops throughout the world (negative values indicate advancement in phenology)

A common characteristic of apple phenology studies is that phenological shifts are limited to records from a single focal orchard, which raises issues about the applicability of these results to wider geographic areas. Identifying other suitable sources of data for blossom recordings is a key knowledge gap, which, if filled could provide a wealth of data to make more spatially relevant conclusions about blossom phenology across space as well as time. Citizen science, or "scientific work undertaken by members of the general public" (Oxford English Dictionary, 2023), is one potential data source that may provide data to increase the spatial applicability of investigation into spatio-temporal dynamics of pollination.

Both systematic and citizen science data undoubtably have value for answering different questions, with long-term systematically collected data lending itself towards assessing temporal trends and opportunistically collected citizen science data predominantly being used to assess spatial trends. This thesis will look to use both at different points to answer questions relating to spatial and temporal dynamics of apple pollination in Great Britain.

While it is important to understand spatio-temporal dynamics of important pollinator species, gaps also exist in the knowledge of range and phenology shifts of the wider British wild bee fauna. The methods used to identify spatio-temporal shifts in wild bee pollinators are also applicable to wider bee fauna, and this thesis will also look to provide information about range and phenology shifts of wild bee species beyond those that pollinate apple crops.

1.7.2. Research questions

This study intends to make use of existing, nationwide biological recording schemes and introduce a new scheme, to build on knowledge of spatio-temporal dynamics of bees and fruit trees to answer the following questions:

- How has the phenology of apple trees and their pollinators at the National Fruit Collection (Kent, GB) shifted over time, and is a phenological mismatch developing with known insect pollinators?
- 2. How has the phenology of wild bee pollinators of apple (and the wider wild bee fauna) shifted over time across Great Britain, and what might phenology look like under future climate scenarios?
- 3. How has the suitable climate envelope (area with climate suitable for persistence) of wild bee pollinators of apple (and the wider wild bee fauna) shifted over time, and what might climate envelopes look like under future climate scenarios?

- 4. How well are wild bee pollinators of apple (and the wider wild bee fauna) currently filling their climate envelopes, and are differences in range filling ability driven by life history traits?
- 5. Is it possible to produce reliable predictions of blossom dates of fruit trees from data submitted to Citizen Science platforms?

1.7.3. Approach and structure

The remainder of this thesis consists of five chapters, each a distinct study to answer the five questions listed above.

Chapter 2 looks at phenological shifts in the "Bramley" apple at the National Fruit Collection in Kent, both over time and in relation to seasonal temperature. It also looks at phenological shifts in 15 species of wild bee known to pollinate apple crops in Kent, using data from a citizen science dataset collated by the Bees, Wasps and Ants Recording Society (BWARS). Subsequently, it compares the phenological shifts of both apple blossom and their pollinators and provides an initial overview of the changes in phenological synchrony between them. Chapter 2 is published in *Agricultural and Forest Meteorology* as: Wyver, C., Potts, S. G., Edwards, R., Edwards, M., & Senapathi, D. (2023). Climate driven shifts in the synchrony of apple (Malus x domestica Borkh.) flowering and pollinating bee flight phenology. *Agricultural and Forest Meteorology, 329, 109281*. https://doi.org/10.1016/j.agrformet.2022.10928. The manuscript has been reformatted to conform to the format of the thesis.

Chapter 3 digs deeper into phenological shifts in emergence dates of wild bees, encompassing 88 data-rich species. It looks for species-level changes in emergence dates in relation to temperature around the period of emergence. It also groups species into "trait-groups", with each group containing species which share the same combination of four life-history traits and looks to isolate the impact of a single trait on the sensitivity of emergence dates to climate change by comparing groups that differ by only a single trait. Chapter 3 is published in *Ecology and Evolution* as: Wyver, C., Potts, S. G., Edwards, R., Edwards, M., Roberts, S., & Senapathi, D. (2023). Climate-driven phenological shifts in emergence dates of British bees. *Ecology and*

Evolution, 13(7), e10284. https://doi.org/10.1002/ece3.10284. The manuscript has been reformatted to conform to the format of the thesis.

Chapter 4 looks to build on the phenological shift models presented in the previous chapter, by incorporating a sliding window analysis to refine climate window selection and to help overcome the arbitrary selection of a climate window. Using "middle-of-the-road" (RCP 4.5) and "worst-case" (RCP 8.5) future climate projections, emergence dates were predicted for the period 2070-79. This chapter also looks at spatial changes in climate envelopes (area of Great Britain climatically suitable for persistence) of wild bees. Using fine scale climate date, Climate Envelope Models (CEMs) were calculated for a historic (1980-89), current (2010-19) and future (2070-79) time period, and shifts in climate envelope size and the position of northern and southern range boundaries were analysed. Chapter 4 is published in *Ecology and Evolution* as: Wyver, C., Potts, S. G., Edwards, R., Edwards, M., & Senapathi, D. (2023). Spatio-temporal shifts in British wild bees in response to changing climate. *Ecology and Evolution*, *13(11)*, *e10705*. https://doi.org/10.1002/ece3.10705. The manuscript has been reformatted to conform to the format of the thesis.

Chapter 5 is a study building on the CEMs developed in Chapter 4. It looks to assess whether species' life-history traits impact the species ability to fill its climate envelope. Using presence records from the BWARS dataset for the period 2010-19, and the climate envelope models created for the same period, the range filling ability was calculated (proportion of climate envelope containing presence records). This was then analysed in relation to life-history traits. This is currently being prepared for submission to *Journal of Applied Ecology* as: Wyver, C., Potts, S. G., Roberts, S., & Senapathi, D. (2023). Biological traits predict ability of British wild bees to occupy their climate envelopes. *Journal of Applied Ecology, In prep.*

Chapter 6 introduces a new Citizen Science initiative called FruitWatch (www.fruitwatch.org), a citizen science platform aiming to collect information about blossom dates of four types of fruit tree (apple, cherry, pear and plum) across Great Britain. This chapter details the submission process, and then takes the most recorded cultivar across each fruit to provide data to for use

with an existing phenology model with the aim of assessing the suitability of citizen science data to parameterize such models and make blossom phenology predictions across Great Britain for a single year. This chapter aims to address the issue faced my many phenology studies of a lack of geographic variation in data and uses a space-for-time framework (as FruitWatch has been running for two blossom seasons) to do so. Chapter 6 is under review at *Horticulture Research* as: Wyver, C., Potts, S. G., Pitts, R., Riley, M., Janetzko, G., & Senapathi, D. (2024). New citizen science initiative enhances blossom phenology predictions for fruit trees in Great Britain. *Horticulture Research. Under Review.* Reviewer comments have not been received at the time of submission of this thesis.

Finally, **Chapter 7** summarises key findings of the preceding five chapters and discusses their implications both from biodiversity conservation and orchard management viewpoints.

2. Climate driven shifts in the synchrony of apple (*Malus x domestica* Borkh.) flowering and pollinating bee flight phenology.

2.1. Abstract

The phenology, or timing of key life-history events, of many globally important crops and the insects that pollinate them are shifting because of the changing climate. Where these temporal shifts occur at different rates or in different directions, it induces a risk of phenological mismatch, potentially reducing the quality and quantity of crop production. This study makes use of 48 years of UK citizen science (pollinating bee records) and systematic (apple flowering records) data to report phenological shifts of apples and their bee-pollinator community. It quantifies the mismatches between peak flowering and flight dates which could potentially cause pollination deficits.

Flowering onset and peak flowering dates of Bramley apples advanced throughout the study period. This advance was primarily driven by increasing early spring temperatures, with peak flowering dates advancing by 6.7 ± 0.9 per 1 °C warming. In addition, increasing spring rainfall significantly delayed flowering dates by 0.4 ± 0.1 days per 10 mm additional rainfall. By contrast, bee phenology shifted in a non-linear manner, advancing from 1970 to 1985 before plateauing until the end of the study period. The peak flight date of the apple pollinating bee community appears to be similarly sensitive to spring temperatures, experiencing an advance of 6.5 ± 2.1 days per 1 °C warming, although individual bee species responses to climate varied.

Furthermore, this study compared the phenological trends to assess the potential risk of asynchrony between crop and pollinator phenology. The different response patterns in the phenology of apples and bees led to shifting patterns of temporal mismatch between peak flowering and peak flight over time. Differences in sensitivity to climate do not appear to directly contribute to the phenological mismatch. Finally, this study highlights the potential value of citizen science data (with sufficient quality control) in understanding phenological shifts and mismatches and highlights potentially increasing temporal mismatch between apple trees and their bee pollinators.
2.2. Introduction

Climate change has been shown to have impacts on species over both space and time (Bellard et al., 2012). For crops and the insects that pollinate them, these impacts can include where and when they occur, with evidence indicating a trend of poleward (latitudinal) and uphill (altitudinal) spatial shifts in both plants and animals (Chen et al., 2011). Climate change also influences phenology, or the timing of key life-history events, causing events such as insect first flight date and flowering plant budburst, to occur increasingly early in the year (e.g. Bartomeus et al., 2011; Fitter & Fitter, 2002).

These spatiotemporal changes induced by climate change can lead to the phenology of interacting species becoming mismatched. Temporal mismatches can have impacts on a range of interactions including plant-pollinator relationships. In the worst case, temporal mismatches, where activity periods of interacting species either do not or only partially overlap can, in the case of plants and pollinators, have negative impacts on plants through reduced visitation by pollinators (Rafferty & Ives, 2011). This can lead to lower seed production (Kudo & Cooper, 2019) and ultimately a reduction in fitness. Pollinators may also suffer due to a lack of floral resources reducing the amount of pollen and nectar available, and in some cases, creating seasonal gaps in resource availability (Timberlake et al., 2019).

Temporal mismatches may arise if the interacting organisms respond at different magnitudes or in different directions to the same climatic cues, or different climatic cues altogether. Current evidence for temporal mismatches is mixed, especially in plant-pollinator interactions. Where phenological mismatch has been found it is in specific, often specialist, plant-pollinator interactions (Kudo & Ida, 2013; Robbirt et al., 2014; Thomson, 2010). Trends in more generalist interactions were often less pronounced or more stable (Bartomeus et al., 2013).

Apple (*Malus x domestica Borkh.*) production is highly dependent on insect pollination, primarily by bees including both wild and honeybees, and the contribution of insect pollinators is valued at £92.1 million per annum to UK apple production (Garratt et al., 2016). Most apple cultivars are self-incompatible (Ramírez & Davenport, 2013), meaning cross-pollination,

predominantly by insects, is important in producing a financially viable crop. Therefore, temporal mismatches between apple and apple-pollinators, and the potential resulting reduction in pollination service, could impact the quality and quantity of apple production.

Various studies have quantified the phenological shift in apple crops, in a range of locations and of different apple varieties, and the vast majority highlight advances across all stages relating to budburst and full bloom. These shifts in phenology are often attributed to annual (Peñuelas et al., 2002) or spring temperature increases (e.g. Chmielewski et al., 2004; Darbyshire et al., 2016; Grab & Craparo, 2011; Sparks et al., 2005). Rainfall has also been linked with advances in spring phenology in trees (Juknys et al., 2016), including apples in South Korea (Cho et al., 2021).

In addition to spring temperatures, apple trees require a period of chilling during winter to break dormancy (Faust, 1989), with insufficient chilling often leading to delayed budburst (Heide, 2003). While such delays are already notable in Mediterranean apple orchards (Funes et al., 2016), there's little evidence to suggest this is currently an issue in the UK. Future climate projections, however, suggest that insufficient winter chill may have a detrimental impact on flowering phenology, as is already being seen in apricot orchards in the UK (Martínez-Lüscher et al., 2017).

Many wild pollinators including hoverflies, beetles and other flies have been recorded visiting apples (Pardo & Borges, 2020), the most frequent and largest wild contributors are wild bees, particularly *Bombus*, *Andrena*, and *Osmia* spp. (Garratt et al., 2016; Pardo & Borges, 2020). Although this study focuses on exclusively on wild bees, the contribution of honeybees (*Apis mellifera*) to apple pollination must also be noted. Honeybee contribution to apple pollination is highly variable across regions, ranging from as little as 12.4% to 85.4% depending on variety (Burns & Stanley, 2022) and in many places wild bees make the greatest contribution to pollination to pollination to pollinators (Pardo & Borges, 2020).

Bee phenology has been the subject of recent studies and climate-driven phenological advances have been seen in both observational (Bartomeus et al., 2011; Stemkovski et al., 2020) and

experimental (Fründ et al., 2013a) studies. Alongside changes in air temperature, changes in soil temperature have also been linked to changes in bee phenology, especially those that nest underground (Kudo & Cooper, 2019; Olliff-Yang & Mesler, 2018). However, advances in phenology may not be consistent across all bee species. Individual species traits such as nesting strategy, and overwintering stage also all have significant effects on bee phenology (Stemkovski et al., 2020).

This study aims to quantify both historical trends in apple and pollinating bee phenology, to add to the growing body of evidence pointing towards phenological shifts of species. It also looks to quantify trends in the temporal mismatch between apples and the pollinator community in Great Britain and attempts to understand how these phenological shifts and interactions are influenced by climate.

Three specific hypotheses tested in this study were:

- Both apple crops and their bee pollinators are shifting their phenology, and this advancement is at least partially due to changing climate.
- 2) Changes in the phenology of apples and bees track each other.
- Any observed asynchrony between the phenology of apples and their pollinators is being driven by climatic variables.

2.3. Methods

2.3.1. Apple flowering data

Apple flowering data was obtained from the National Fruit Collection (NFC), at Brogdale, Faversham, Kent. This contained a list of varieties and the dates of flowering onset and full bloom dates. From this list, Bramley was selected for use in this analysis. This was selected as it is historically amongst the most widely grown varieties in the UK (DEFRA, 2019), and has a near-complete dataset for the chosen study period. Data from 1970 to 2017 was selected to overlap with the period of most abundant pollinator records. Bramley flowering records were available for all years in this period, except for 1990. The flowering onset date, estimated as the date 10% of flowers were open (BBCH scale for pome-fruit code 61 (Meier et al., 1994)) and the peak flowering date, taken to be the date of full bloom (BBCH code 65) were used in this analysis. Average peak flowering dates for early (1970–1974), mid (1990–1994), and late (2013–2017) periods were also extracted.

2.3.2. Pollinator data

The Bees, Wasps, and Ants Recording Society (BWARS) recording scheme was used to provide pollinator data for this study. This dataset collates records from as many sources as possible, largely submitted by experts in the taxonomy of aculeate Hymenoptera. This dataset has no formal survey protocol and includes data sourced from both field observations and microscope identification of collected specimens. Photographic records from public sources are not incorporated into this collection. Data must be trusted by a network of taxonomic experts for inclusion in the dataset. Each record consists of a species, the recording date, and a grid location, with a resolution equal to, or finer than, 10 km.

A total of 20 bee species have been recorded visiting apple flowers in the UK (Hutchinson et al., 2021). All except *Bombus lucorum* were included in this analysis, as modern taxonomy has revealed the presence of a cryptic complex of *B. lucorum*, *magnus*, and *cryptarum* within the UK fauna. These species have different flight periods, but cannot be reliably separated from each other, and have been confounded in both historic and modern recording.

Records from Kent (defined as being within the boundaries of Watsonian vice-counties 15 -East Kent and 16 - West Kent, which have remained unchanged throughout the study period) between 1970 and 2017 were extracted for the selected species. The BWARS dataset contained 54,348 records for the 19 species for the study period (Table S2.1, Figure S2.1). When considered as a group, these 19 species will be referred to as 'the community'.

2.3.3. Climate data

Daily mean temperatures and daily total precipitation were obtained at a 0.25° gridded resolution from the E-Obs dataset (v25.0e) (Cornes et al., 2018), and the mean value of all grid squares covering Kent were extracted.

The year was split into three periods, beginning with May to September before the year of apple flowering and pollinator emergence, followed by the chilling period in apple trees, October to December, and finally the forcing period in apple trees, January to April of the year of flowering and emergence (Drepper et al., 2020).

The mean temperature of each period was derived from the average of daily mean temperatures, and total rainfall of each period was derived from the sum of daily total rainfall.

2.3.4. Impact of climate on pollinator phenology

Pollinator flight dates (flight onset and peak flight) was calculated in two parts, firstly for the community as a whole, with a single estimate generated from all pollinator records and secondly for individual species, with individual flight dates calculated for each species. For the whole pollinator community and for univoltine species (i.e. species with unimodal seasonal abundance curves), the package "phenesse" (v0.1.2) (Belitz et al., 2020) was used in RStudio v1.3.1073 (R Core Team, 2020), to estimate the 10th and 50th percentile flight dates. These were used as a proxy for flight onset and peak flight dates. For bivoltine species (i.e. with bimodal seasonal abundance curves) flight onset date was calculated above, peak flight was calculated as the date of the first peak, estimated from the smoothed density distribution for each year. In all cases, the first peak is closer to apple flowering than any subsequent peaks. Early (1970–1974), mid (1990–1994), and late (2013–2017) period means were also calculated as above.

To calculate species-specific trends, estimates of dates of flight onset and peak flight were calculated and thresholds were set to ensure only data-rich species were used in the species-level analysis. Any species x year combinations with less than 20 records were excluded.

Additionally, any species with fewer than 20 years of flight date estimates were excluded. This resulted in 3 known apple pollinator species, *Andrena cineraria*, *Bombus hypnorum*, and *Lasioglossum pauxillum* being excluded from further analysis, containing only 3, 9, and 17 years of suitable estimates respectively. Annual flight date estimates for *B. terrestris* were also not calculated due to difficulties separating yearly cycles, as this species can be active year-round.

2.3.5. Calculating mismatch

To test whether a mismatch between apple flowering and pollinator flight exists or is developing, peak mismatch was calculated. Peak mismatch was taken to be the difference in days between the peak flight date of the insect community recording, and the peak flowering date of apple. Additionally, as apple blossom may be an important early season resource for bees, the mismatch between flight onset of the pollinator community and peak flowering date of apple was calculated.

2.3.6. Statistical analysis

2.3.6.1. Climate

To test for changes in the climate initial Generalised Additive Models (GAMs) were used to test for trends over time for each climate variable (May-Sep, Oct-Dec, and Jan-Apr average temperature and total precipitation). If the GAM showed no substantial non-linearity and gave a smoothing term with less than two degree of freedom (edf < 2), a generalized linear model (GLM) was run instead. This was done so as not to assume a linear trend during exploratory data analysis. This follows Hunsicker et al. (2016) who state that "... in the absence of evidence for a linear relationship, it is safer to assume a relationship is non-linear."

All analysis was run using in RStudio v1.3.1073 (R Core Team, 2020) and GAMs using the package "mgcv (v1.8–36)" (S. N. Wood, 2010).

2.3.6.2. Apple and Pollinator flight dates, flight duration, and peak mismatch

Initial GAMs were used to test for trends in the following groups:

- 1) Onset and peak apple flowering dates.
- 2) Onset and peak flight dates of the pollinator community.
- 3) Onset and peak flight dates of individual bee species.
- 4) The mismatch between peak flowering and peak flight dates.

Again, if the GAM relationship gave a smoothing term with less than two degrees of freedom (edf < 2), it was replaced with a GLM.

GLMs were then run to test for the effect of climate on the phenology of groups 1,2 and 4 as listed above. Independent variables were temperature and rainfall from May to September and October to December preceding the year of flowering, and January to April of the year of flowering. For pollinator phenology, the number of records per year was also included in models to account for variation in sampling effort.

A model averaging approach was taken, using the model.avg function in the package "MuMin (v1.43–17)" (Barton, 2020). Models with all combinations of climate predictors were generated, and those within 2 AICc units of the best model were averaged using the model.avg function within "MuMin". Model averaging was used as in cases where two or more models achieve similarly high levels of support (in this case within 2 AIC units of the best model), model averaging of this 'top model set' can provide a robust means of obtaining parameter estimates and making predictions (Burnham & Anderson, 2002). AICc was preferred over AIC to rank candidate models to account for the small sample size (Hurvich & Tsai, 1989).

Individual species responses (Group 3) to spring climate were also tested using GLMs, with January to April temperature used as the explanatory variable and the day of the year of each phenophase as the response variable.

2.4. Results

2.4.1. Change in climate

A significant, non-linear, increase was seen in January to April temperature (edf = 2.72, p(edf) = 0.008). There was a less severe increase in temperature experienced in the latter part of the study period (c. 1995–2017) compared with the earlier period (1970-c.1995). May to September temperature experienced significant linear increases of 0.34 ± 0.07 °C (p < 0.001) per decade. October to December temperatures experienced significant linear increases of 0.32 ± 0.09 °C (p = 0.001) per decade. There was no significant change in total rainfall amount over time, either linear or non-linear. (Figure S2.2).

2.4.2. Change in phenology over time

The flowering onset and peak flowering dates of Bramley significantly advanced throughout the study period and did so at similar rates. This advance was non-linear (flowering onset – edf = 3.975, p(edf) < 0.001, peak flowering – edf = 4.757, p(edf) < 0.001) and was primarily seen between the early- and mid-periods (Table 2.1, Figure 2.1).

Pollinator phenology also exhibited non-linear change over time in both phenological stages (flight onset – edf = 2.891, p(edf) < 0.001, peak flight – edf = 2.914, p(edf) < 0.001). There were initial advances in dates of flight onset and peak flight dates. This lasted until approximately 1990 for all stages. After this period, bee phenology experienced a plateau where flight phenology remained stable (Table 2.1, Fig. 2.1).

 Table 2.1. Mean dates of flowering onset and peak flowering for early (1970–74), mid

 (1991–95) and late (2013–17) periods, and change over time between early - mid, and mid - late periods. For change over time, negative values indicate advancement in phenophase, positive values indicate delay.

		Change (days)				
Time period(s)		Early	Mid	Late	Early –	Mid –
		1970-74	1991-95	2013-17	Mid	Late
Apple	Flowering	128.6	117.2	115.8	-11.4	-1.4
	Onset					
	Peak	133.4	120.6	119.4	-12.8	-1.2
	Flowering					
Pollinator	Flight	115.6	70.7	82.8	-44.9	+12.1
	Onset					
	Peak	194.3	157.2	170.4	-37.1	+13.2
	Flight					



Figure 2.1. Trends in apple flowering and pollinator flight dates over time. Shaded area indicates 95% confidence intervals.

Not all pollinator species showed the same phenological patterns over time (Figure 2.2, Table S2.2 for full model details). 12 species showed statistically significant linear advances in flight onset dates over time (p < 0.05). Subsequent linear models of those 12 species revealed only

three species showed significant advances in flight onset date over time (*A. chrysosceles*, *A. nigroaenea*, and *O. bicornis*) with advances in emergence dates ranging from 4.6 - 11.3 days per decade. The other three species (*B. lapidarius*, *B. pratorum* and *Lasioglossum calceatum*) showed significant non-linearity in flight onset dates (edf < 2, p(edf) < 0.05).

Peak flight dates followed a similar pattern to first flight dates (Figure 2.2, Table S2.2 for full model details). Most solitary bee species (*Andrena* sp. and *Osmia bicornis*) showed linear trends over time, with the exceptions of *A. fulva* and *A. scotica*. Seven of the species showing a linear relationship between peak flight date and time showed a significant advancement (p < 0.05) of this date, ranging from 2.8 - 10.4 days per decade. Six species, all primitively eusocial (All *Bombus* sp. except *B. pascuorum*, and *L. calceatum* in the study area (Davison and Field, 2018) showed significant non-linearity over time (edf < 2, p(edf) > 0.05).



Figure 2.2. Trends in apple-pollinating bee species' flight onset and peak flight dates over time. Shaded area indicates 95% confidence intervals. Full model details available in Table S2.2.

2.4.3. Impact of climate on phenology

Both Bramley phenological stages were significantly predicted by both temperature and rainfall between January and April. Warmer temperatures were linked to advanced flowering onset and peak flowering phenology by 6.5 ± 0.8 (Pr(>|z|) < 0.001) and 6.7 ± 0.9 (Pr(>|z|) < 0.001) days per 1 °C warming respectively (Figure 2.3, Table S2.3 for full model details).

By contrast increasing rainfall between January and April is linked to delayed phenology (Figure S2.3). Model averaging of the best performing models predicted estimates of a delay of 0.36 ± 0.12 (Pr(>|z|) = 0.05) and 0.42 ± 0.13 (Pr(>|z|) = 0.002) days per 10 mm additional rainfall during the period for flowering onset and peak flowering respectively (Table S2.3 for full model details).

Increased January to April temperature was the only significant variable in impacting onset and peak flight dates with linear models revealing an advancement of 8.5 ± 2.3 (Pr(>|z|) < 0.001) days per 1 °C advancement for flight onset date and 6.5 ± 2.1 (Pr(>|z|) = 0.003) days per degree for peak flight date (Figure 2.3, Table S2.3 for full model details). Dataset size did not appear to significantly impact pollinator community phenology (Table S2.3 for full model details).



Figure 2.2. Impact of January to April temperature on apple flowering and pollinator flight dates. Shaded area indicates 95% confidence intervals.

GLMs with flight onset date, and subsequently peak flight date as the response variable and spring temperature as the explanatory variable revealed variation in species' responses to spring temperature change. 10 out of 15 species showed a significant advance in flight onset phenology, with advances ranging from 5.8 to 12.5 days per 1 °C rise in temperature. All but one of the species tested for advances in peak flight showed a significant advance in peak





Figure 2.3. Trends in apple-pollinating bee species' flight onset and peak flight dates against average January to April temperature. Shaded area indicates 95% confidence intervals. Full model details available in Table S2.4.

2.4.4. Phenological synchrony between apples and pollinators

Different temporal patterns of phenology over time between apple flowering and pollinator flight led to differing patterns of phenological synchrony between them (Figure 2.5). There was an improvement in peak synchrony between the start of the study period, as pollinator flight dates advanced more rapidly than apple flowering dates. This lasted until approximately 1985, where pollinator flight dates began to plateau and apple flowering dates continued to advance, resulting in increasingly reduced synchrony until the end of the study period. No climatic variables were found to have a significant direct impact on the degree of peak mismatch between the pollinator community and flowering dates of either apple variety.

When comparing flight onset date to peak flowering date, it is apparent that at least a subset of apple pollinating bee species are emerging before peak flowering and are present to provide pollination. This followed a similar trend to peak mismatch. Unlike peak mismatch, however, the latter part of the study period saw peak blossom occur increasingly close to insect emergence. Dataset size did not significantly impact either mismatch.



Figure 2.4. Change in phenological mismatch (days) between peak apple flowering and peak pollinator flight dates (blue) and peak apple flowering and pollinator flight onset dates (red). Shaded area indicates 95% confidence intervals.

2.5. Discussion

This study provides evidence of differing patterns of changes in the phenology of wild bees and the apple crops they pollinate in a major apple growing region of the UK. This pattern could be being driven by differing sensitivity to the same spring temperatures, which appear to be a slightly stronger driver of apple flowering phenology than pollinating bee flight phenology. Additionally, this trend in phenology could be being influenced by the sensitivity of apple flowering dates to spring rainfall, compared with the apparent insensitivity of pollinator phenology to this variable.

2.5.1. Change in apple and pollinator phenology

This study reports an advancement in apple flowering dates consistent with other studies from the temperate region, which also show a strong impact of early spring climate on flowering phenology (Chmielewski et al., 2004; Fujisawa & Kobayashi, 2010; Kunz & Blanke, 2008). This indicates that the temperature during the forcing period is the primary driver of flowering phenology in the UK, and should spring temperatures continue to increase, further advances are likely to be seen. Warming winter temperatures, however, could lead to insufficient chill accumulation and counter advances caused by warming in the forcing period, as is already being seen in Apricot crops in the UK (Martínez-Lüscher et al., 2017). Although historically blossom dates have advanced, Future delays caused by insufficient chill accumulation could exacerbate the size of the mismatch between apple flowers and pollinators as well causing synchronised and less dense budburst and ultimately reducing yield (Jacobs et al., 2002).

The utilisation of GAMs highlights a non-linear trend in bee phenology between 1970 and 2017, with an initial advance followed by a plateau in the latter part of this period. This non-linear trend over time was predicted by early spring temperatures (January to April), with the plateau coinciding with less severe warming seen in the latter part of the study period. This suggests that bee emergence may have a degree-day requirement as reported by White et al. (2009).

This work also provides new insight into the phenological shift of Kentish populations of bees. While previous research on bees in other regions has shown advances throughout the study period (e.g. Bartomeus et al., 2011; Kehrberger & Holzschuh, 2019), the pattern of a plateau in flight phenology in the latter part of this study has not previously been reported in bees. It could be that the elongated period of favourable conditions brought by warmer temperatures relaxes selection pressure and allows individuals to develop over a longer time and emerge larger and fitter, a trend found especially in early emerging species (Buckley et al., 2015), a category in which several important apple pollinators fall.

Although this study found no impact of dataset size on pollinator phenology, this type of opportunistic data with no standardized protocol can also be subject to temporal issues. There was some interannual variation in the community composition (Figure S2.4) which could impact community flight date estimates. However, by using data from only the most data-rich period (1970-2017), the pollinator community phenology estimates are likely to be robust. It may be possible to increase the size of the pollinator dataset to include data from multiple

datasets such as the Global Biodiversity Information Facility (GBIF, 2024a), although this would require significant quality control.

Additionally, two of the species that make up the pollinator community are managed for their use as pollinators in apple orchards (*B. terrestris* and *O. bicornis*) when required. It is possible that some managed specimens are recorded in the BWARS dataset, although this number is expected to be small and have a negligible effect on the phenological estimates. Managed individuals may also be introduced to orchards should phenological mismatches between wild pollinators and apple flowering lead to pollination deficits.

Despite this potential limitation, the phenological shifts in both apple crops and their bee pollinators observed in this study, both of which are influenced by climate, is in line with hypothesis 1, that 'Both apple crops and their bee pollinators are shifting their phenology, and this advancement is at least partially explained by climate'.

2.5.2. Mismatch

This study found variable mismatch between peak pollinator flight and peak flowering dates over time. This finding is contrary to the work of Bartomeus et al. (2013) who show similar temporal advances in both phenologies of apples and their bee pollinators. The utilization of GAMs here has also shown potential non-linearity in both bee flight and apple flowering phenology, which has not been reported previously. Additionally, other factors, such as estimation method of phenological stages and the differences in the bee pollinator community (19 species here vs 26 used by Bartomeus et al., 2013) between the two studies, could play a role in the different trends of phenological synchrony between studies.

There is a shift from improving to worsening phenological synchrony over time, with a tipping point in the mid-1980s. During this time, apple flowering dates began to experience a more rapid advancement in flowering dates, whereas pollinator phenology remained stable. This could be due to differing responses to the change in the mode of the North Atlantic Oscillation (NAO) around this period (Reid et al., 2016). This phenomenon has been linked to rapid

advances in flowering plant phenology (Büntgen et al., 2022), and it is possible that the same response was not seen in the phenology of the pollinator community.

The finding that insect emergence is becoming increasingly close to peak blossom, coupled with the relatively short flowering window of apple flowering, could be a concern should this trend continue. Mass flowering crops often present a "feast or famine" scenario for insect pollinators (Steele et al., 2022), where resources provided by the crop are only abundant for a short period of time (i.e. during flowering), and then almost non-existent. Should insect emergence occur after peak flowering, there is a risk of bees emerging during the "famine" period, which could negatively impact fitness of wild bees, as has been shown in honeybees (Dolezal et al., 2019).

Wild bees missing the peak blossom window may not only have fitness costs for the bees, but also an economic cost for the grower. Without wild pollinators, growers may need to rely more heavily on managed honeybees to ensure an economically viable fruit set. Should demand for managed honeybees increase, it is expected that there will beincreases in production costs related to managed pollinators, a cost which has been steadily increasing since the 1990s (Rucker et al., 2012).

As well as climate, bee phenology is dependent on functional traits such as nest location and the life stage in which bees overwinter (Stemkovski et al., 2020). These are factors which could also be contributing to the changes in phenological synchrony over time. Further work is required to provide more insight into the drivers of this change, and the differing trends in phenology over time suggests that both hypotheses 2 'Changes in the phenology of apples and pollinators tracking each other' and 3 'Climatic factors are driving change in phenological synchrony between apples and pollinators' cannot be fully supported.

In conclusion, spring climate predicts the phenology of apple blossom and its bee pollinators. The phenologies of these two groupings are changing at slightly different rates, potentially indirectly changing peak synchrony between flowering and flight. The difference in sensitivity to spring climate was small, however, and as a result, further work is recommended to better understand the non-climate drivers of the trends in phenological mismatch observed here. Finally, this work provides a framework for utilising citizen science and other opportunistic recording data to quantify temporal mismatches between crops and their pollinators and has the potential to extend to any location, crop, or taxa of interest where recording datasets exist.

2.6. Acknowledgements

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3. Climate-driven phenological shifts in emergence dates of British bees

3.1. Abstract

Climate change has a diverse range of impacts on wild bees, including their phenology or timing of life history events. Climate-driven phenological shifts can not only impact individuals at species level but also threaten the vital pollination service that wild bees provide to both wild plants and cultivated crops. Despite their involvement in pollination, for most bee species, especially in Great Britain, little is known about phenological shifts. This study makes use of 40 years of presence-only data for 88 species of wild bees to analyse shifts in emergence dates, both over time and in relation to temperature.

The analyses reveal widespread advances in emergence dates of British wild bees, at an average rate of 0.40 ± 0.02 days per year since 1980 across all species in the study data set. Temperature is a key driver of this shift, with an average advance of 6.5 ± 0.2 days per 1°C warming. For change in emergence dates both over time and in relation to temperature, there was significant species-specific variation, with 14 species showing significant advances over time and 67 showing significant advances in relation to temperature.

Traits did not appear to explain variation in individual species' responses, with overwintering stage, lecty, emergence period and voltinism considered as possible explanatory traits. Pairwise comparisons showed no differences in sensitivity of emergence dates to increasing temperature between trait groups (groups of species which share all four traits) that differed by only one trait. These results highlight not only a direct impact of temperature on the phenology of wild bees themselves but also the species-specific shifts highlight a possible impact on the temporal structure of bee communities and the pollination networks for which the wild bees are so crucial.

3.2 Introduction

Many taxa, including plants (Büntgen et al., 2022), birds (Crick & Sparks, 1999) and insects (Hassall et al., 2017) have been shown to shift their phenologies in response to the changing climate. For example, in the UK, the first flowering dates of plants are advancing by an average of 5.4 days per decade (Büntgen et al., 2022), and the emergence dates of hoverflies are advancing at an average rate of 12.5 days per 1°C temperature increase (Hassall et al., 2017). Wild bees in the US have also been shown to be impacted, with evidence of climate-driven phenological shifts in emergence dates of 10.4 days over the last 130 years (Bartomeus et al., 2011) and 0.43 days per decade (Dorian et al., 2023). While it might seem sensible to predict widespread advances in phenology under warmer conditions through increased rates of metabolic processes, these mechanisms and the impact of climate change on them remain poorly quantified (Fründ et al., 2013a). Advances in phenology are also not guaranteed, with warmer temperatures linked to slower completion of the prepupal stage in *Osmia bicornis* (Radmacher & Strohm, 2011). In either case, the impact of climate on phenological shifts in bee emergence for many species, particularly in Great Britain, is yet to be studied in depth.

Phenological shifts can impact not only the individual species but also the ecosystem services they provide such as pollination. Globally, animals, including wild bees contribute significantly to the pollination of plants. This includes up to 87.5% of angiosperms (Ollerton et al., 2011) and around 75% of cultivated crop species (Klein et al., 2007). Great Britain is home to some 270 species of wild bees (Falk, 2019), and they increase agricultural productivity in the region by an estimated £630 million (Breeze et al., 2021). The list of crops where yield and/or quality is improved when insect pollination occurs includes many fruits and vegetables such as apples (Garratt et al., 2014b) and pears (Fountain et al., 2019), both of which are commonly cultivated in Great Britain.

Phenological shifts could have mixed repercussions for bee fitness. Earlier emergence, for example, could benefit a particular species, by reducing competition for forage should the phenologies of competitors not keep pace. The same species may benefit more generally from

an elongated growing season. Conversely, the same species could also experience an increased risk of exposure to suboptimal temperatures (Iler et al., 2021) both directly and indirectly, through damage to the plants on which they forage.

Bee species exhibit a wide range of life-history strategies, which influence the timing of emergence dates (Stemkovski et al., 2020). These strategies may also influence their phenological sensitivity to climate change, as shown in solitary bees in the US (Dorian et al., 2023) and Canadian butterflies (Kharouba et al., 2014). There are a range of traits that could influence the sensitivity of emergence dates to climate change. For example, butterflies that overwinter as adults tend to advance their phenologies more than those butterflies that overwinter as larvae or pupae (Diamond et al., 2011). This is possibly because by overwintering as adults, these butterflies can respond to favourable temperatures without further development (Dennis, 1993), in comparison to species that overwinter as larvae or pupae, which require additional time to reach maturity. More generally, there is also evidence from solitary bees to suggest that early emerging species' phenology is more sensitive to climate change, compared with those that emerge later in the year (Dorian et al., 2023).

Other life history traits may also play a role in determining bee emergence. Lecty, for example, may impact sensitivity. Lecty 'determines the breadth of resources that a bee exploits: oligolectic bees collect pollen from a narrow range of (usually related) plant genera, while polylectic bees have a broader diet' (Ogilvie & Forrest, 2017). Oligolectic species must remain in temporal synchrony with the plants they forage on, which in the case of some species is restricted to plants that only flower for a short duration. These oligolectic bees could have different phenological sensitivities to climate change than polylectic species (Minckley et al., 2013), which are adapted to forage on a range of plants and are therefore under less pressure to track the flowering dates of a particular plant or group of plants.

Alongside species-specific or trait-specific phenological responses to climate change, interactions between different species and taxa at a range of trophic scales may also be impacted. Especially relevant to bees are plant–pollinator interactions. Temporal mismatches

between wild bees and the plants on which they depend may arise for several reasons, each relating to differential impacts of climatic variability on two species (Stenseth & Mysterud, 2002). This can include interacting species responding (1) to different climatic cues (e.g. temperature vs. rainfall), (2) to the same climatic cue at different times (e.g. March temperature vs. May temperature) or (3) with different magnitudes to the same climatic cue during the same window. Loss of floral resources, such as pollen, has been proposed as one of the major drivers of wild bee decline (Biesmeijer et al., 2006; Scheper et al., 2014), and temporal mismatches have been shown to reduce flower visitation. In turn, this could possibly impact offspring size - which may negatively impact offspring survival (Slominski & Burkle, 2021) and potentially longer term population persistence. Current evidence for phenological mismatches in plant–pollinator interactions is mixed, with the majority of interactions tracking each other temporally. There are, however, certain interacting partners, especially in early-season interactions, that show independent shifts in phenology, such as seen between the flowering plant *Corydalis ambigua* and its bumblebee pollinators in northern Japan, which show different phenological shifts in response to changes in the timing of snowmelt (Kudo & Ida, 2013).

Long-term, ad hoc records of bee sightings may provide a useful proxy for phenology and have been used to generate estimates for emergence dates in numerous other studies (Brooks et al., 2014; Olsen et al., 2020). Ad hoc hoverfly recording schemes produce similar phenological estimates to those produced by standardized hoverfly recording schemes (Hassall et al., 2017), suggesting ad-hoc data may be suitable for phenological studies. As with hoverflies, a long-term database of bee records exists in Great Britain, collected and verified for accuracy by expert taxonomists of aculeate Hymenoptera, by the Bees, Wasps and Ants Recording Society (BWARS, www.bwars.com), which holds records dating back over 100 years.

Understanding the impact of temperature on phenology not only provides a picture of the past but may also allow for predictions of future flight dates, which in turn can help inform future conservation efforts through 'phenological matching' of bee flight and suitable forage plants (Russo et al., 2013). It is predicted that emergence dates of British bees will (1) be gradually

becoming earlier in the year, and that (2) emergence dates are earlier in warmer years compared with cooler ones. It may also be the case that (3) specific life-history traits determine sensitivity of emergence dates to temperature increases. Therefore, this study looks to make use of this long-term data set to answer the following questions:

- 1) How have the emergence dates of British bee species changed over the past 40 years?
- 2) Does temperature play a role in any changes observed in emergence dates?
- 3) Do specific life-history traits influence temporal shifts in bee emergence dates?

3.3. Methods

3.3.1. Bee data

The BWARS of Great Britain and Ireland provided records of bee sightings - although only records from Great Britain were used. This comprises an opportunistic, predominantly observational data set, where contributors can submit records containing a species, a sighting date and a location. While anyone could submit records to this database, to be eligible for inclusion in this data set records must meet a data quality threshold, where the data is checked and verified by experts within BWARS for taxonomic accuracy. BWARS coordinates a network of regional coordinators, usually an expert entomologist specialising in Hymenopteran species (Sumner et al., 2019). In cases where species identification is questionable, consultation between the observer and coordinator takes place, and if the record cannot be verified to the satisfaction of the coordinator, it is not included in the data set.

To ensure robust estimates of bee emergence dates, only species that met a minimum threshold of 20 years of data with 20 or more records per year were included in the analysis. This threshold was met by 88 species of bees. Records for these species were extracted for the period 1980–2019 (Table S3.1), as this period provides the most abundant data, for a total of 363,724 records. For univoltine species (71 species) the fifth percentile flight date for each species, in each year, was calculated and is hereafter referred to as the 'emergence date' and is 5% of the distance between the first and last record. For the 7 bivoltine and 10 species with variable voltinism, a k-means clustering analysis was used to identify which generation each record belonged to, and only those records in the earlier generation were used in the fifth percentile estimation. This was done to reduce the influence of the second generation on the predicted emergence date.

Traits data were obtained from the European Bee Traits Database held by S.P.M. Roberts. Data for four traits were extracted for the 88 bee species and are listed in Table 3.1. These were the 'Emergence period', 'Voltinism', 'Lecty' and 'Overwintering stage'. Species were then grouped into trait groups, with each group comprising species with the same characteristics across all four traits.

Trait	Levels				
Emorgonce Period	"Spring" - Mean emergence (1980-2019) in March, April or May				
Entergence i criou	"Summer" - Mean emergence (1980-2019) in June, July or August				
	"Univoltine" – Species has one generation per year				
Voltinism	"Bivoltine" – Species has two generations per year				
v orthinshi	"Variable" – Species varies in the number of generations per year				
	across the study period.				
	"Polylectic" – Visits a wide range of unrelated plant species for				
	pollen				
Lasta	"Oligolectic" – Visits a narrow range of plant species from a single				
Lecty	plant family for pollen				
	"Clepto- and social parasites" – Cleptoparasites and Social				
	parasites. Do not visit plants for pollen				
	"Adult (female only)" – Females overwinter as adults				
Overwintering Stage	"Adult within nest" – Overwinter as adults within cocoon				
	"Prepupa" – Overwinters as prepupa				

 Table 3.1. Traits selected for phenological sensitivity analysis.

3.3.2. Climate data

The mean daily temperature from 1979 to 2019 was obtained at a 0.25° gridded resolution from the ensemble mean of the E-Obs data set v26.0e (Cornes et al., 2018), and the mean value of all grid squares covering Great Britain was extracted.

A temperature record was then assigned to each phenophase record. The timing of this window varied on a species-by-species basis. For each species, first, the mean emergence date across all years was calculated. This was termed the 'reference date'. The climate window ran from the 90 days leading up to and including the reference dates. For example, for a species with a mean emergence date across all years of 17 April, the temperature window would begin to run on 18 January (17th in leap years), and end on 17 April.

3.3.3. Statistical analysis

3.3.3.1. Phenological shift over time

A two-step process, similar to that employed by Bartomeus et al. (2011), was used to estimate phenological trends over time. This included looking at community (all 88 species considered as a group) and species (all 88 species considered individually) level trends. First, the shift in emergence dates of all bee species over time was tested using a linear mixed model regressing emergence date as a function of year, with the number of records making up each estimate (*n*) and the mean northing of each emergence estimate (*northing*) also included as fixed effects, to take into account issues related to sampling effort and sampling distribution. Species was included as a random effect. Mixed models were run using the package 'nlme' (Pinheiro et al., 2017), and marginal and conditional R² were calculated using the 'performance' package (Lüdecke et al., 2021).

Subsequently, the data set was split into individual species, and species-level linear models were run regressing emergence date against year, while again accounting *n* and *northing* to estimate the shift in emergence dates over time for each species. The estimate of these models was taken to be the temporal shift in emergence dates (days per year). These models were run with a Benjamini–Hochberg correction for multiple tests to avoid Type I errors (q = 0.05) (Benjamini & Hochberg, 1995).

3.3.3.2. Phenological sensitivity to climate change

A similar approach was used to estimate the sensitivity of bee emergence dates to temperature change. First, a linear mixed model was run with emergence date as a function of mean temperature during the 90-day window, also with *n* and *northing* as fixed effects, and again accounting for variation between species by including it as a random factor. The estimate was once again taken to be the sensitivity of each phenophase to increasing temperature (days per °C). Second, species-level linear models were run with the regressing emergence date against mean temperature for the 90 days prior to the reference date, including again n and northing in order to estimate the shift in emergence dates in relation to temperature for each species. Once again, species-level models were run with a Benjamini–Hochberg correction for multiple tests to avoid Type I errors (q = 0.05).

3.3.3.3. Impact of traits on phenological sensitivity to climate change

The Kruskal–Wallis test (Kruskal & Wallis, 1952) was used to test for differences in phenological sensitivity of emergence dates to temperature change between 'trait groups' that differed by only one trait. Trait groups are defined as species which share all four traits (Table 3.2).

Table 3.2. Trait groupings, and number of species within each trait group. Groups in **bold**

 were used to test for differences in phenological sensitivity of emergence dates to climate change.

Trait								
Group	Lecty	Overwintering Stage	Emergence Period	Voltinism	Species			
Α	Polylectic	Adult within cocoon	Spring	Univoltine	15			
В	Polylectic	Adult within cocoon	Spring	Bivoltine	5			
С	Polylectic	Adult within cocoon	Spring	Variable	4			
D	Oligolectic	Adult within cocoon	Spring	Univoltine	3			
Е	Polylectic	Prepupa	Summer	Univoltine	10			
F	Oligolectic	Prepupa	Spring	Univoltine	1			
G	Polylectic	Prepupa	Spring	Univoltine	1			
Н	Oligolectic	Prepupa	Summer	Univoltine	2			
Ι	Oligolectic	Adult within cocoon	Spring	Variable	1			
J	Clepto- and Social Parasite	Adult (female only)	Spring	Univoltine	12			
Κ	Polylectic	Adult (female only)	Summer	Univoltine	1			
L	Polylectic	Adult (female only)	Spring	Univoltine	22			
М	Polylectic	Adult (female only)	Spring	Multivoltine	2			
Ν	Clepto- and Social Parasite	Prepupa	Summer	Univoltine	2			
0	Polylectic	Prepupa	Summer	Variable	4			
Р	Polylectic	Adult (female only)	Spring	Variable	1			
Q	Oligolectic	Adult within cocoon	Summer	Univoltine	2			

Grouping species into trait groups helps to overcome the fact that many traits often overlap (e.g. all species that overwinter as adults within a cocoon are also spring emerging species). By comparing trait groups that differ by only one trait, it isolates the effects of an individual trait on sensitivity of emergence dates to temperature change (Dorian et al., 2023). Phenological sensitivity of emergence dates to temperature change was taken as the species-level estimates from the linear models described in the previous section. Where the Kruskal–Wallis test

indicated significant differences between groups, the Dunn test (Dunn, 1964) was used to identify which pairs significantly differ from each other, again using a Benjamini–Hochberg correction for multiple comparisons (q = 0.05). This test was carried out using the package 'FSA' (Ogle & Ogle, 2017).

Only trait groups containing a minimum of three species were used in this analysis, resulting in a total of eight trait groups available for comparison. Groups A (univoltine), B (bivoltine) and C (variable) were compared, which differ only in voltinism. These groups share the same traits for the other three trait categories, all being polylectic, spring emerging species which overwinter as adults within a cocoon. Second, Groups A (polylectic) and D (oligolectic) were compared, which differed only in lecty, with both groups containing spring emerging, univoltine species which overwinter as adults within a cocoon. Finally, Groups A (adult within cocoon) and L (adult—female only) were compared, these groups differ only in overwintering stage, containing species which shared the other three traits—containing spring emerging, univoltine, polylectic species.

Additionally, to test for a taxonomic trend, a Kruskal–Wallis test and subsequent Dunn test with Benjamini–Hochberg correction for multiple comparisons were run to compare sensitivity of emergence dates to temperature change at the genus level. Again, only genera containing 3 or more species were included, allowing for comparisons between seven genera (*Andrena*, *Bombus*, *Hylaeus*, *Lasioglossum*, *Megachile*, *Osmia* and *Sphecodes*).

3.4. Results

3.4.1. How have the emergence dates of British bee species changed over the past 40 years?

When considered as a group, emergence dates showed a significant advance throughout the study period $(0.40 \pm 0.02 \text{ days per year}, p < 0.001)$. There was also a significant effect of n on emergence phenology, with increasing records also linked to earlier emergence estimates $(0.005 \pm 0.002 \text{ days per additional record}, p = 0.018)$. Northing did not have a significant effect

in the community time model (p = 0.972). The fixed effects explained relatively little of the variation in this model (marginal $R^2 = 0.018$, conditional $R^2 = 0.857$).

At the species level, 14 species (15.9%) showed a significant advance in emergence dates over time, ranging from 0.50 ± 0.15 days per year (*Andrena barbilabris*, p = 0.021) to 1.56 ± 0.48 days per year (*Sphecodes crassus*, p = 0.028) (Figure 3.1). R² values from the species-level models ranged from 0.009 to 0.485, with a mean of 0.231. Full model results are available in Table S3.2 and species' level plots in Figure S3.1.



Change in emergence date (days/year)

Figure 3.1. Change in species' emergence dates per year. Error bars indicate standard error.

3.4.2. Does temperature play a role in any changes observed in emergence dates?

Emergence dates were significantly earlier in years with warmer average temperatures (90 days preceding mean emergence date), at a rate of 6.5 ± 0.2 days per 1°C temperature increase (p < 0.001) across all species as a group. Neither n (p = 0.139) nor northing (p = 0.402) had a significant effect on emergence dates in the community temperature model. Again, the fixed effects accounted for relatively little of the variation in this model (marginal R² = 0.092, conditional R² = 0.940). There was variation in individual species' responses to temperature change, with emergence dates of 67 species (76.1%) showing a significant advancement in warmer years. Sensitivity ranged from a 4.2 ± 1.2 -day advance in emergence date per 1°C temperature increase (*O. bicornis*, p = 0.029) to a 21.7 ± 4.4 -day advance in emergence date per 1°C temperature increase (*S. crassus*, p = 0.029) (Figure 3.2). R² values of species level models ranged from 0.029 to 0.722, with a mean of 0.371. Full model results are available in Table S3.3, and species' level plots in Figure S3.2.



Figure 3.2. Change in species' emergence dates per °C temperature increase. Error bars indicate standard error.

3.4.3. Do specific traits influence temporal shifts in bee emergence dates?

Separate Kruskal–Wallis tests were conducted to assess whether there were significant differences in the median values of phenological sensitivity of emergence dates to temperature warming (estimates of linear models calculated in previous section) between three sets of groups, each of which differ by a single trait (A, B and C—voltinism, A and D—lecty, A and L—overwintering stage) and between different genera.

None of these comparisons yielded significant differences in phenological sensitivity of emergence dates to temperature warming. This included the comparison between different

levels of voltinism in spring emerging, polylectic species, which overwinter as adults within a cocoon (Groups A, B and C) ($\chi 2 = 2.63$, df = 2, p = 0.269, Figure 3.3A). There was also no significant difference in sensitivity of emergence dates to temperature change between oligolectic and polylectic species in spring emerging, univoltine species, which overwinter as adults within a cocoon (Groups A and D) ($\chi 2 = 2.19$, df = 1, p = 0.139, Figure 3.3B). Finally, no significant difference in sensitivity of emergence dates between different overwintering stages in spring emerging, univoltine, polylectic species (Groups A and L) ($\chi 2 = 0.16$, df = 1, p = 0.688, Figure 3.3C). Significant differences were found between Genera, ($\chi 2 = 15.93$, df = 6, p = 0.014, Figure 3.3D). Pairwise comparisons using a post-hoc Dunn test revealed significant differences only between *Andrena* and *Sphecodes* (p = 0.045) and *Hylaeus* and *Sphecodes* (p = 0.019).



Figure 3.3. Comparison of sensitivity of emergence dates to temperature increase of trait groups sharing three traits and differing by (A) voltinism, (B) lecty and (C) overwintering stage, and comparison of sensitivity of emergence dates to temperature increase of different genera (D). Brackets indicate significant pairwise differences between groups.

3.5. Discussion

This study utilises 40 years of presence-only data to present evidence of climate-driven temporal shifts in the phenology of a wide range of British bees. When all 88 species are considered as a group, the mean emergence date has advanced an average by 0.40 ± 0.02 days per year, with species-level linear models revealing significant species-level variation in this advance. The scale of the advancements here are over twice as severe as similar studies from different parts of the globe, with Bartomeus et al. (2011) reporting a 0.18 ± 0.05 days per year advance in bee phenology in the US between 1970 and 2010 and with Dorian et al. (2022), who reported a shift of 0.16 ± 0.06 days per year between 1970 and 2022, also in the US.

We also add to the growing body of evidence that phenological shifts are linked to climate, in this case, temperature, with an average advance of 6.5 ± 0.2 days per 1°C rise in temperature, across all species as a group. Again, these advances were species-specific, with individual advances of up to 21.7 ± 4.4 days per 1°C rise in temperature (*Sphecodes geofrellus*). This advance is also more severe than the findings of Bartomeus et al. (2011), who found the average collection day of museum specimens advanced by 3.6 ± 0.2 days per 1°C temperature increase in mean April temperatures. However, the findings of both this study and Bartomeus et al. (2011) point to changing climatic conditions being a major driver of bee phenology, while also indicating potential regional differences in phenological responses to temperature. The differences in findings could also be due, in part, to differences in bee communities, as none of the species studied by Bartomeus et al. (2011) were used in this study.

This study also adds to the growing body of evidence that phenological shifts are not uniform and vary between species, although shifts in emergence dates do not appear to be driven to any great degree by specific life history traits. Pairwise comparisons of changes in emergence dates of different groups of species that differed by only one trait showed no significant difference between any pairs. This finding is contrary to results from Dorian et al. (2022), who found differences in phenological sensitivity between species with different activity periods and

nesting preferences, a trait not tested here due to lack of variation in nesting preference between species.

While this study was not able to isolate a specific trait that impacts sensitivity of emergence dates to temperature, not all traits were tested. Other traits, such as sociality or body size may impact sensitivity of emergence dates to temperature change. Sociality may impact the emergence estimates themselves, most of the *Bombus* species in this analysis are primitively eusocial, and the queens emerge before workers and males. Evidence for sociality as an important trait in determining phenological sensitivity to climate change is limited, with a non-significant difference in rates of phenological change found between eusocial and solitary species (Bartomeus et al., 2011). Additionally, while this study did not explicitly account for a phylogenetic signal, comparing sensitivity of emergence dates to temperature by genera showed limited differences, with only two pairs of genera showing any significant differences (*Halictus* and *Sphecodes*). Again, this confirms findings by Bartomeus et al. (2011) that most of the variability in phenological shifts are at the species level rather than at higher taxonomic ranks.

The earlier emergence of bees highlighted here is likely to come with a range of consequences. For example, despite the warming climate, incidences of late-spring frosts are increasing in Europe (Lamichhane, 2021; Zohner et al., 2020). While the direct impact of late frost on bees is somewhat buffered by their ability to insulate themselves from cold temperatures in their nests, especially for ground-nesters, the plants they forage on do not have such ability and are at greater risk of damage. This may impact their attractiveness to bees by reducing the number of flowers and flower size (Pardee et al., 2018) or through a reduction or alteration of the chemical composition of the rewards they offer (Akšić et al., 2015). Some plant groups have also been shown to receive fewer visits by pollinators after experiencing frost (Pardee et al., 2018). Although bees spent longer working frost-damaged flowers compared with undamaged flowers, this could be because they are having to work harder to extract rewards, reducing their net energy gain. There is evidence that these plants are indeed undergoing shifts in flowering dates

which could potentially expose them to this late frost risk (Büntgen et al., 2022; Fitter & Fitter, 2002).

Recent estimates suggest that plants in the UK are advancing first flowering dates by an average of 5.4 days per decade (Büntgen et al., 2022). Although there is significant species-level variation in these shifts in plant phenology, plant phenological shifts are generally more pronounced than the average of a 4.0 day per decade advance in bee emergence reported in this study. Even seemingly small phenological mismatches between bee emergence and plant flowering can have severe implications for bee survival (Schenk et al., 2018b; Slominski & Burkle, 2021). The evidence we present here, coupled with evidence of shifts in plant phenology, highlight the potential for phenological mismatches.

While this study shows that climate plays a role in determining bee phenology, it is probable that temperatures over a fixed 90 day window are not the most biologically meaningful predictor of emergence dates at the species level (van de Pol et al., 2016). Bee emergence can likely be better predicted using a species-specific time window, through the implementation of a sliding window or climate window analysis (van de Pol et al., 2016). Future work is therefore recommended to refine the exploratory models presented here to find more biologically meaningful climate windows for explaining phenological trends of species of interest. Additionally, exploration of other potential climatic factors and extreme events that may influence bee emergence dates, such as rainfall, drought or frost may also be an important area of future research. This is recommended as understanding which climatic factors and time windows are good predictors of emergence dates. In turn, this could allow for better-timed conservation interventions (Russo et al., 2013), ensuring resources are available at the period around bee emergence under future climate scenarios.

While more work is required to refine the temporal windows of the models presented here, it provides a framework for utilising long-term citizen science data to assess phenological shifts in British bees. To conclude, analysis of this long-term data set reveals that many British bee

species are advancing their emergence dates, and that these advances are likely to continue with further climate warming. Comparison with similar analyses on flowering plants suggests that bee emergence is less sensitive to climate change than flowering dates, highlighting a potential risk of phenological mismatch, which could lead to major disruption of vital pollination networks. Finally, we recommend investigating the development of more refined models to better predict bee emergence dates to further our understanding of climate-induced shifts in bee emergence to evaluate potential risks of future phenological mismatches.

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4. Spatio-temporal shifts in British wild bees in response to changing climate

4.1. Abstract

Climate plays a major role in determining where species occur, and when they are active throughout the year. In the face of a changing climate, many species are shifting their ranges poleward. Many species are also shifting their emergence phenology. Wild bees in Great Britain are susceptible to changes in climatic conditions but little is known about historic or potential future spatio-temporal trends of many species. This study utilized a sliding window approach to assess the impacts of climate on bee emergence dates, estimating the best temperature window for predicting emergence dates for 88 species of wild bees. Using a 'middle-of-the-road' (RCP 4.5) and 'worst-case' (RCP 8.5) climate scenario for the period 2070–2079, predictions of future emergence dates were made. In general, the best predicting climate window occurred in the 0–3 months preceding emergence. Across the 40 species that showed a shift in emergence dates in response to a climate window, the mean advance was 13.4 days under RCP 4.5 and 24.9 days under RCP 8.5.

Climate Envelope models (CEMs) were used to predict suitable climate envelopes under historic (1980–1989), current (2010–2019) and future (2070–2079 under RCP 4.5 and RCP 8.5 scenarios) climate conditions. These models predict that the climate envelope for 92% of studied species has increased since the 1980s. For 97% and 93% of species under RCP 4.5 and RCP 8.5 respectively, climate envelope expansion is predicted to continue, due to poleward movement of the northern range boundary. While any actual range changes will be moderated by habitat and resource availability, it highlights that Great Britain will likely experience northward shifts of bee populations in the future. By combining spatial and temporal trends, this work provides an important step towards informing conservation measures suitable for future climates, directing how interventions can be provided in the right place at the right time.
4.2. Introduction

Wild bees in Great Britain comprise over 270 species (Falk, 2019). Many of these species provide important pollination services to numerous crops widely grown in Great Britain (Breeze et al., 2011; Hutchinson et al., 2021). They are expected to need to provide this service to an even greater extent in the future as the area of land cultivated with pollinator-dependent crops continues to increase (Aizen et al., 2019). Although the majority of crop pollination is carried out by a very small proportion of the overall bee fauna (Hutchinson et al., 2021; Kleijn et al., 2015), widespread reports of declines in many species of wild bees in the United Kingdom (Biesmeijer et al., 2006; Powney et al., 2019) mean that this important ecosystem service is potentially under threat. Pollination deficits are already being reported in apple crops (Garratt et al., 2014a), and other crops such as sweet cherry, blueberry and highland coffee show increased yield when visited by insect pollinators (Klein et al., 2003; Nicholson & Ricketts, 2019; Osterman et al., 2023). Additionally, wild bees contribute to the pollination of many non-crop flowering plants, up to 87.5% globally (Ollerton et al., 2011). This includes many rare and threatened flowering plants in Great Britain, such as the late flowering *Gentianopsis ciliata*, classed as Critically Endangered in England (Stroh et al., 2014), but highly dependent on insect pollination to produce seeds, likely to be carried out by bumblebees (Oostermeijer et al., 2002). There are a range of threats to wild bees and their associated pollination service. One of the major threats is climate change (Dicks et al., 2021), which has been shown to alter both spatial (i.e. range boundaries) (Nooten & Rehan, 2020) and temporal (i.e. activity periods) (Bartomeus et al., 2011) distributions of wild bees. Historically, bumblebee species show mixed spatial responses to climate change in the United Kingdom, with common bumblebees generally becoming more widely distributed, and rarer bees seeing range contractions, although these trends appear to have stabilized in recent years (Casey et al., 2015). Despite these historic changes, relatively little data exists on potential future climate-driven changes in wild bee distributions in Great Britain. Reports from the United States predict widespread range losses of bumblebees under future climate conditions, with gains at more northerly latitudes and losses in

the south (Sirois-Delisle & Kerr, 2018). In many cases, in both the United States and Europe, poleward range gains are not keeping pace with equatorward range losses, effectively placing many species in a 'climatic vice' (Kerr et al., 2015). With Great Britain sitting at the northern edge of many wild bee species ranges (Ollerton et al., 2014), and the projections of northwards movement shown in the United States and hypothesized in Great Britain, climate change could present an opportunity for wild bees to see range expansions in Great Britain.

Climate, however, is not the only determinant of species ranges. Habitat fragmentation and loss of habitat and floral resources through land use change are also contributing to changes in the distributions of wild bee species in the United Kingdom (Senapathi et al., 2015a). This is largely attributed to large-scale changes in agricultural policy and practices linked to agricultural expansion and intensification in the periods post-First and Second World Wars (Raven & Wagner, 2021). Indeed, significant declines in bumblebees in Great Britain were seen in the post-World War II period. Although these declines appeared to have slowed in recent decades the resultant communities are much more homogenized as many of the most sensitive species have been lost (Carvalheiro et al., 2013; Powney et al., 2019). More recently, the improvement of land considered economically unviable for agricultural production (Ollerton et al., 2014) has threatened bee populations. These changes in agricultural practices, such as increased use of mechanization and synthetic fertilizers and pesticides, coupled with increasing adoption of monocultures and loss of boundary features are likely to have contributed to rapid local extinctions of wild bees and wasps (Powney et al., 2019). This simplification of agricultural landscapes also reduces the amount of available forage for those species that persist, exacerbating risk, especially for species that do not forage on flowers found in these crop monocultures, such as Rosaceae, Brassicaceae and Asteraceae species (Scheper et al., 2014).

Alongside the spatial changes, many species of wild bees in Britain and further afield are also experiencing earlier emergence dates over time, and these advances are linked to warming climates (Bartomeus et al., 2011; Chapter 3). These shifts are species-specific, but at least in

part explained by life-history traits, namely nesting habits (spring emerging above-ground nesters showed greater phenological sensitivity to climate change than below-ground nesters) and general activity period (spring emergers generally experienced phenological advancements whereas autumn emergers generally experienced delays) (Dorian et al., 2023). The major drivers of these changes are known to be temperature (Bartomeus et al., 2011; Chapter 3) and/or rainfall (Fründ et al., 2013a; Stemkovski et al., 2020). The exact mechanisms controlling this process are not fully understood, although it is likely linked to increased metabolic rates, especially under increased temperatures (Fründ et al., 2013a). Usually, however, the climate window chosen to test for phenological shifts is often the same for all species (i.e. 'spring' or 'April') and may not be directly relevant to the ecology of each species. This approach may fail to identify a window of greater sensitivity which could provide a better estimate of phenological sensitivity to climate change.

These combinations of spatial and temporal changes pose clear threats, but also potential opportunities for both species' persistence and the pollination services they provide. To minimize the threats and maximize opportunities, policymakers and land managers have a range of response options that can provide suitable habitats and resources for wild bees. In the United Kingdom, encompassing Great Britain and Northern Ireland, 69% of all land is classed as utilized agricultural area (DEFRA, 2022a), encompassing arable, horticultural and pastoral land, and as a result, perhaps the largest opportunity for providing for wild bees comes from biodiversity-friendly management of farmland. These schemes, such as England's Environmental Land Management Scheme (ELMs), often provide benefits to pollinators by including interventions such as sowing or managing flower-rich habitats and non-crop plants, and reductions in agricultural inputs (DEFRA, 2023a). Flower-rich interventions have been shown to locally benefit some groups of pollinators, dependent on the diversity of non-crop plants present (Carvell et al., 2007; Crowther & Gilbert, 2020; McHugh et al., 2022; Wood et al., 2015), which currently may not be optimal for promoting bee diversity (Wood et al., 2015). Whilst evidence suggests that agri-environment schemes may provide some benefits to pollinators (Breeze et al., 2014), it is likely that these benefits are not being maximized due to

limited considerations of target species phenology, especially for floral interventions (Image et al., 2022; Timberlake et al., 2019).

Additionally, management for wild bees can take the form of protected areas, and in Great Britain, these come at a range of scales ranging from regional (e.g. National Parks) to local (e.g. local nature reserves). With a finite budget for nature conservation in the United Kingdom (Great Britain and Northern Ireland), £624 million in public money and £243 million of private sector money attributed to biodiversity protection in 2020/2021 (DEFRA, 2022b), maximizing value for money by incorporating both spatial and temporal ecology of wild bees, targeting the most beneficial areas, with the most beneficial implementations at the most beneficial time is crucial to ensure bees can persist and provide pollination services to both crops and wildflowers.

To effectively do this, understanding where and when bees currently occur, where and when they could potentially occur under future climate scenarios, is vital to understanding where and when management interventions are needed. In Great Britain, there is an extensive database of where bees occur, curated by the Bees, Wasps and Ants Recording Society (BWARS), however, for many species, climate suitability modelling has not been undertaken, with notable exceptions studied by Polce et al. (2014), who used Species Distribution Models (SDMs) to assess changes in the spatial overlap between apple crops and their pollinators between current and 2050 climates. This study predicted possible changes in the ranges of bees (increases for 20 species and contractions for 10 species), and ultimately a potential decline in the spatial overlap between apple orchards and their pollinators by 2050. Additionally, utilizing SDMs to predict future ranges and activity periods can help conservation planners to forward plan for specific goals, either to prevent further loss, attract potentially suitable species or simply maintain or improve the pollination service provided by a wild bee community.

This study looks to combine both spatial and temporal trend analyses of bee populations by asking:

- What temperature window (generated through sliding window analysis) best predict bee emergence dates, and what might emergence dates look like under future climate scenarios?
- 2) What are the current climate envelopes of British wild bee species, and how are these projected to change under a future climate scenario?

4.3. Methods

4.3.1. Bee data

Bee data was obtained from the Bees, Wasps and Ants Recording Society (BWARS www.bwars.com) within Great Britain. This is a dataset comprised of opportunistic records, each with a species, recording date and location. Although there is no formal protocol, records must meet a data quality threshold, where the data is checked by experts within BWARS for taxonomic accuracy for inclusion. Data were extracted for the period 1980–2019.

A species was eligible for inclusion in analysis provided it had 20 or more years of records, with each year containing a minimum of 20 records. This resulted in a total of 88 (out of a potential total of 270) species being available for analysis. A full list of species can be found in Table S4.1. Emergence dates of each of these species x year combinations were calculated as the 5th percentile flight date, taken as being 5% of the distance between the first and last recorded observations, and is independent of abundance of records. For univoltine species (species with one generation per year), this was simply taken as the 5th percentile of all records for any given year. For bivoltine species (two generations per year), or species exhibiting variable voltinism throughout the study area (partial second generation in some years), a k-means clustering method was used to identify records belonging to the first generation. Only records shown to be in the first generation were used in the calculation of the 5th percentile flight date in these instances. Outlying emergence dates were identified for each species individually, using the interquartile range (IQR) method (Barbato et al., 2011), whereby the IQR is calculated as the range between the 25th (Q1) and 75th (Q3) percentile values. Values lower than Q1 - 1.5*IQR or higher than Q3 + 1.5*IQR were removed.

4.3.2. Temporal shifts

4.3.2.1. Sliding window analysis

To overcome the often-arbitrary selection of the best predicting climate window, a sliding window approach using the R package 'Climwin' (Bailey & Van De Pol, 2016) was implemented. This approach allows for all climate windows within a set range to be tested, and allows for fine-resolution data, in this case daily mean temperature, to be used.

Historic daily temperature data came from the e-Obs dataset (v26.0) (Cornes et al., 2018) at $0.25^{\circ} \times 0.25^{\circ}$ gridded resolution. Data for all grid squares covering Great Britain were extracted and averaged to generate mean daily temperature for the study region.

An absolute window was selected, meaning to climate window for each year is relative to a fixed 'reference day', rather than being relative to yearly emergence date, which varies between years. The reference day was set as the mean date of emergence for each species across the whole study period. Possible time windows were restricted to allow the timing of the window to fall at any point within the 365 days before the reference date, with a minimum window duration of 14 days. The inclusion of very short climate windows is often not biologically plausible and can produce statistical artefacts (van de Pol et al., 2016).

The best predicting window was chosen as the window with the largest decrease in AICc from the null model, and the randomization function within the Climwin package was used to calculate the probability the best predicting window was chosen by chance ('false positives'). Ten randomizations were used for this purpose, which has been shown to balance a suitable detection rate of false positives and reduce large computing time, as this process is computationally intensive. A climate window was considered a 'true' cue if p Δ AICc was <0.05 (i.e. the probability of such a result occurring in a randomized dataset was <5%). The raw data from the best supported 'true' window was extracted, and used in a linear model to assess change in emergence date linked to climate:

Emergence Date ~ Mean temperature during best 'true' temperature window

4.3.2.2. Predicting future emergence

To predict future emergence dates, daily climate projections between 2070 and 2079 were obtained from CMIP5 climate projections under RCP 4.5 and RCP 8.5, also available from the E-Obs dataset and selected to provide assessments of temporal shifts under a 'middle-of-the-road' and 'worst-case' future climate scenario. Mean projected temperature for each of the selected climate windows for the period 2070–2079 was calculated and models were re-fitted using the 'predict()' function in R to generate future emergence dates for both scenarios.

4.3.3. Spatial shifts

4.3.3.1. Modelling current climate envelopes

Historic and future changes in potential climate envelopes were estimated using Climate Envelope Models (CEMs) created using MaxEnt version 3.3.4 (Phillips et al., 2008). This a commonly used tool in species distribution modelling where presence-only data, such as that provided by BWARS, are available. Raw bee records were passed through two filter stages to be included in the spatial analysis. Initially, records with imprecise grid coordinates (<1 km scale) were removed, and subsequently, duplicate records within the same species and 1 km square were also removed. The bioclimatic variables used in this analysis are the same as those used in pollinator distribution models in Great Britain (Polce et al., 2013). These were derived using the 'biovars' function from the 'dismo' package (Hijmans et al., 2017) using maximum and minimum monthly temperature, and monthly precipitation, which were obtained from CHESS-SCAPE at a 1 km2 resolution (Robinson et al., 2023) (Table 4.1).

Predictor	Description
Bio3	Isothermality
Bio7	Temperature Annual Range
Bio9	Mean Temperature of Driest Quarter
Bio11	Mean Temperature of Coldest Quarter
Bio15	Precipitation Seasonality
Bio19	Precipitation of Coldest Quarter

Table 4.1. Predictors used in the wild bee distribution models.

To create the models for each species, 75% of the data was used for training and 25% for testing. CEMs for each species were run 10 times, using the 'sub-sample' method. The convergence threshold was set to 10-5 with 5000 iterations, and with a maximum of 10,000 background points. The selection of the functions for the predictor variables (feature type) was carried out automatically, following the default options depending on the number of occurrences: 'linear + quadratic + hinge' if there are from 15 to 79 points (2 species) and 'all' if there are >80 points (86 species) (Urbani et al., 2015).

The cloglog output was used, and this provides continuous values for each grid cell from 0 (unsuitable) to 1 (most suitable). These values can be interpreted as the probability of presence of suitable climate conditions for the target species (Veloz, 2009). The '10th percentile training presence cloglog threshold' was selected to covert the continuous score to a binary output. This threshold selects the value above which 90% of the training locations are correctly classified (Zarzo-Arias et al., 2019). This threshold is a recommended for datasets collected with non-standardized methods or by different collectors or observers over a long time, as the BWARS dataset is (Rebelo & Jones, 2010; Urbani et al., 2015), and is commonly used in species distribution and climate envelope modelling exercises (e.g. Barik et al., 2022; Crawshaw et al., 2021).

Validation of CEMs was done by testing whether the area under the curve (AUC) of the receiver operating characteristic (ROC) significantly differed from a random expectation using bias-

corrected null models (Raes & Ter Steege, 2007). Ninety-nine null models were created for each species, run using the same MaxEnt settings, except the random test percentage, which was set to 0. with the number of 'records' equal to the actual number of records of each species. These were drawn randomly without replacement from a list of grid squares containing records for the whole dataset, to account for potential geographic sampling bias. If a species observed AUC (mean of 10 replicate runs) ranked above the upper 95% confidence interval of the null models (above the 95th highest AUC value of the 99 null models), then the modelled distribution was considered acceptable, with a <5% chance that a random set of records could produce an equally good model (Table S4.2).

4.3.3.2. Modelling historic and future climate envelopes

To test for changes in climate envelopes, each CEM that proved significantly better than null models was re-fitted, with future bioclimatic variables for the period 1980–1989 and 2070–2079 (under both RCP 4.5 and RCP 8.5), again obtained from CHESS-SCAPE. Change in the climate envelope was calculated as the change in the number of grid cells classed as suitable. Finally, to test for the movement of climatically suitable area, the latitude of the northern range boundary (90th percentile latitude), range centroid (50th percentile latitude) and southern range boundary (10th percentile latitude) of the climate envelope was calculated under historic, current and future climate conditions. The distance and bearings between the historic and current, and current and future range boundaries were calculated using the 'geosphere' package (Hijmans et al., 2019).

4.4. Results

4.4.1. Temporal shifts

4.4.1.1. Sliding window analysis

In total, 40 of the 88 (45.5%) species showed a significant phenological response to a 'true' climate window (i.e. a climate window, greater than 14 days, that performed better than a null model and $p\Delta AICc < 0.05$). The timing of these windows generally was within 0–3 months of the mean date of emergence for each species (Figure 4.1A, Table S4.3).

All 40 species showing significant phenological shifts related to temperature experienced earlier emergence dates in warmer years. These ranged from 4.1 ± 1.1 (*Halictus rubicundus*, p < 0.001) to 14.2 ± 3.2 (*Sphecodes crassus*, p < .001) days per °C temperature increase during the bestexplaining temperature window (Table S4.4).

4.4.1.2. Potential changes in future phenology

For the 40 species that showed a significant phenological response to a climate window, potential emergence dates under 'middle-of-the-road' (RCP 4.5) and 'worst-case' (RCP 8.5) scenarios for the period 2070–2079 were estimated. All 40 species are projected to emerge earlier in the future under both climate scenarios, compared with baseline (1980–2020) dates. Under RCP 4.5, changes range from a 5.6 ± 3.1 -day advance (*Anthophora plumipes*) to a 34.7 ± 11.2 day advance (*Megachile willughbiella*). Under RCP 8.5, changes range from a 14.2 ± 4.1 -day advance (*Andrena nigroaenea*) to a 54.4 ± 17.2 day advance (*M. willughbiella*) (Figure 4.1B, Table S4.5).



1980-2020 mean compared with 2070-2079 predicted mean

Figure 4.1. (A) Locations of best predicting climate windows for wild bee emergence. All windows presented here were statistically unlikely to occur by chance ($p\Delta AICc < 0.05$), and linear models of emergence date regressed against mean temperature during the highlighted window show a significant effect. (B) Predicted shift in emergence between current (1980–2020) and future (2070–2079) emergence dates. Negative values indicate advancement of emergence dates. Bars indicate 95% confidence intervals.

4.4.2. Spatial shifts

4.4.2.1. Current distribution of suitable climate envelope

SDMs for 76 of the species performed significantly better than the bias-corrected null models and were used in further analysis (Table S4.2). This included both rare and widespread species ranging from *Bombus distinguendus* (2489 grid squares, classed as suitable climate under current climate conditions) to *Bombus hortorum* (Figure 4.2) (80,300 pixels classed as suitable climate under current climate conditions). The predicted accuracy of models was high, with the mean AUC across all 76 species at 0.860.



Unsuitable Suitable

Figure 4.2. MaxEnt climate maps for *Bombus hortorum*. Showing climate envelope for 1980–1989 (A), 2010–2019 (B) and 2070–2079 under RCP 4.5 (C) and RCP 8.5 (D). 10th percentile training presence threshold = 0.3167. Plots for all other species can be found in Figure S4.1

4.4.2.2. Predicted changes in suitable climate envelopes

Of the 76 species with CEMs significantly better than the bias-corrected null models, the area of the suitable climate envelope increased between the 1980s and 2010s for 91% of species, with the mean climate envelope being 43.6% smaller in the 1980–1989 period compared with the 2010–2019 period.

The climate envelope was predicted to continue to increase under both RCP 4.5 and RCP 8.5 into the 2070–2079 period for 74 and 71 species, respectively. Under RCP 4.5 the mean climate envelope increased in size by 113% in the 2070s compared with the present day, and these changes ranged from a 637% increase (*Andrena florea*) to a 100% decrease—complete loss of climate suitable for persistence (*B. distinguendus*). Under RCP 8.5, the mean increase in climate envelope area was 200% in the 2070s compared with present day conditions. The same species showed the largest positive and negative potential changes (1091% increase for *A. florea* and 100% decrease for *B. distinguendus*) (Figure 4.3, Table S4.6).



Figure 4.3. Predicted change in area of suitable climate envelope under historic and future

climate scenarios. 0 represents the climate envelope under current (2010–2019) conditions.

There was clear evidence of poleward movement of species climate envelopes, with the northern range boundary of most species' potentially suitable climate envelope shifting northwards. Between the 1980s and current period, the northern range boundary shifted northwards by an average of 29.4 km, and between the current period and the 2070s, the current period, the northern range boundary shifted by a mean of 206.0 km (RCP 4.5) and 371.4 km (RCP 8.5) (Figure 4.4, Table S4.7).



Figure 4.4. Distance and bearing of shifts in northern climate envelope boundary, climate envelope centroid and southern climate envelope boundary area under historic and future climate conditions. The centre of each plot indicates the position during the current period, and the points indicate the position during the historic or future period.

For most species, the southern range boundary stayed relatively static between the 1980s to the current period (mean = -5.0 km) and the current period to the 2070s under both RCP 4.5 (mean = 18.5 km) and RCP 8.5 (mean = 44.0 km). However, for *Bombus monticola*, which shows a reduced climate envelope under RCP 4.5 and the four species showing reduced climate envelopes under RCP 8.5 (*B. distinguendus* is predicted to have no suitable climate range under both scenarios, so is not included in this group), the southern range boundary moves northwards at a much greater rate than their northern range boundary. *B. monticola*, for example, sees its southern range edge move northwards by 26.4 and 243.4 km under RCP 4.5 and RCP 8.5

respectively, whereas the northern range boundary moves northwards by less—17.4 km under RCP 4.5 and 27.9 km under RCP 8.5, indicating that these species may be caught in a climatic vice in the future. Climate envelope maps for each species can be found in Figure S4.1.

4.5. Discussion

4.5.1. Temporal shifts

This study presents the first quantitative analysis of the projected spatial and temporal changes of British wild bees and provides important insights into the impacts of future climate change on their phenology and distribution. The study found that many bee species analysed (45.5%) showed a significant phenological response to a specific temperature window. Additionally, potential emergence dates for all 40 species that responded to climate windows were projected to advance (mean = 13.4 days under 'middle-of-the-road' RCP 4.5, 24.9 days under 'worst-case' RCP 8.5) from 2070 to 2079 compared to baseline dates from 1980 to 2020. The phenological aspect of this study, predicting earlier emergence in warmer years, conforms to the general trend of phenological advances found in other studies on wild bees (Bartomeus et al., 2011; Chapter 3), however, the inclusion of species-specific climate windows again highlights the individual nature of species responses to climate change.

Using a sliding window analysis to produce species-specific phenology models shows that in Great Britain, temperatures in the period directly before emergence appear to be the best predictor of emergence dates. This conforms with many studies stating spring temperatures are the main driver of temperate bee emergence phenology (Bartomeus et al., 2011; Gordo & Sanz, 2005). However, even species-specific models still do not explain all the variation in emergence dates, indicating other unexplained factors are still important to some degree in determining emergence phenology. These unexplained drivers could include winter temperatures. Although not as important as spring temperatures, winter temperatures have been shown to play a role in the timing of the emergence dates of several solitary bee species (Fründ et al., 2013a), and so are also a likely source of some unexplained variation from the sliding window models. Additionally, the timing of the end of the previous generations flight season may be one source

of this variation and has been shown to influence emergence dates in other studies (Stemkovski et al., 2020).

Microhabitat conditions could also be influencing phenology estimates. The emergence phenology of the codling moth (*Cydia pomonella*) is influenced by microhabitat temperatures (Kührt et al., 2006), and bees could experience a similar phenomenon, emerging earlier in warmer microhabitats. In the case of this study, the emergence dates may be influenced by the proportion of records from different habitats (i.e. an emergence estimate comprising 90% of records from agricultural land may be different from an estimate comprising 90% of records from semi-natural habitat, providing different emergence estimates despite the same mean temperature). While the BWARS dataset does not incorporate habitat type in its recording structure, making it difficult to test for an effect of microhabitat on emergence phenology in this study, it is plausible that this may be the cause of at least some of the unexplained variation in the phenology models.

4.5.2. Spatial shifts

In terms of spatial shifts, this study provides evidence for significant historic latitudinal shifts in the climate envelopes of many of the species included in this study. Specifically, an average northward shift of 29.4 km in the northern range boundary across all species. Other studies investigating latitudinal shifts in bee distributions report similar shifts, although the magnitude differs. Aguirre-Gutiérrez et al. (2016), for example reported a 22 km northward shift in Dutch bees. These differences could be due to a range of factors, for example, this study shows strong species-specific variation in shifts, and differential results could be caused by different study species, and in different study areas.

This study also used SDMs to evaluate the current and future distribution of suitable climates for 76 of the 88 total study species. The SDMs were found to have a high level of predicted accuracy, with a mean AUC of 0.860 across all 76 species. The study found that the suitable climate envelope was predicted to increase for almost all species under future climate scenarios (74 species under RCP 4.5 and 71 species under RCP 8.5). The magnitude of change varied between species and climate scenario, ranging from a 637% increase to a 100% decrease (mean = 113% increase) under RCP 4.5 and a 1091% increase to a 100% decrease (mean = 200% increase) under RCP 8.5. While this is consistent with other distribution and climate envelope modelling exercises focusing on bees, which show both range expansions and shrinkages dependent on the species (Kuhlmann et al., 2012; Sirois-Delisle & Kerr, 2018), the magnitude of predicted range increases are much greater here than in these studies.

The historic and future shifts in climate envelopes presented here also appear similar to many large-scale studies, such as the Climatic Risk and Distribution Atlas of European Bumblebees (Ollerton et al., 2014; Rasmont et al., 2015). This work predicts the widespread poleward movement of many bumblebee species, with large range expansions in northern Europe, including in Great Britain. Great Britain sits in a potentially advantageous position for many wild bee species, relative to much of mainland Europe, as it is close to the northern boundary of the ranges of many species' geographic ranges (Ollerton et al., 2014). This may be a contributing factor to the large northward shifts seen in this study. For many species it was expected that the northern edge of potentially suitable climate would shift further north under future climate scenarios as the temperature move away from species' minimum thermal tolerances towards more favourable conditions for survival, thus allowing for northward colonization.

Conversely, for species already constrained to northern parts of England and Scotland or highaltitude areas such as *B. distinguendus* and *B. monticola*, climate change has been projected to leave them with nowhere to migrate within Great Britain, resulting in large net range losses. The CEMs for these two species confirm this projection, with range losses of 100% (i.e. complete loss from Great Britain) under both climate scenarios for *B. distinguendus* and losses of 20.5% (RCP 4.5) and 64.6% (RCP 8.5) for *B. monticola*. This study focusses primarily on data-rich species, and therefore rare species, many of which already inhabit marginal habitats are likely to see similar trends to *B. distinguendus* and *B. monticola*. However, it is important to note that while future climate may allow for many species to expand northwards, they are likely to be constrained by a lack of suitable habitat. Many of the species exhibiting the largest increases in suitable climate envelopes are constrained to specific, often rare, habitats, and climate is a major constraint in shaping distributions in Great Britain. *A. florea*, which exhibited the largest potential increase in suitable climate envelope is narrowly oligolectic, and almost exclusively visits plants from the genus *Bryonia* (Polidori & Federici, 2019), and is therefore constrained to areas where these plants are also present and in practice is extremely unlikely to fill its entire predicted climate envelope.

Species' not filling their full predicted climate envelope will not be unique to *A. florea*. Many other species will be constrained to varying degrees (depending on the habitat specificity of each bee species), by non-climatic factors. Life-history traits such as habitat breadth (variety of habitats a species can survive in) can be a key factor in realized range shifts (proportion of climate envelope filled) in both mammals and birds (Estrada et al., 2018) and is likely to play a similar role in realized range shifts of bees, although to date this has not been explicitly tested.

Loss of suitable habitat from existing ranges, or lack of suitable habitat in future climate envelopes means that other biological factors such as dispersal ability, voltinism and lecty could play a role in the colonization of new sites. The maps presented here assumes dispersal ability is unlimited, and a species can fill all suitable habitat, however, in practice, there are often barriers that prevent dispersal ability, for example, large areas of intensive farming decreasing habitat connectivity. This again highlights the importance of considering habitat provision, alongside climate, when planning future conservation strategies.

Reduced dispersal ability has been shown to exacerbate range declines in bumblebees in the United States (Sirois-Delisle & Kerr, 2018). One of the major barriers to the colonization of new areas is increasing habitat fragmentation and a lack of connecting corridors with adequate resources to allow for survival. Conversion of land to intense agricultural or urban land often provides such fragmentation, and expansion of these land uses, something that was not included in future projections in the MaxEnt models, could lead to species not filling all areas identified

as being potentially suitable under future climate conditions. In light of this, it could be that the main conservation priority is to reduce or reverse existing fragmentation, to allow for localized dispersion from existing habitats.

4.5.3. Implications for pollination and conservation

Whether caused by changes in climate, habitat or by a combination, changing spatio-temporal bee distributions are also likely to have a knock-on impact on the pollination of many flowering crops and plants. Much of the pollination service, particularly of crops, is predominantly carried out by a small proportion of wild bee species such as *Bombus lapidarius* and *Andrena chrysosceles* (Kleijn et al., 2015). Both of these species are likely to expand their ranges under future climate scenarios, and this could present new opportunities for the growth of pollinator-dependent crops such as apple and oilseed rape. However, studies have also shown that increasing functional complementarity within the pollinator community can lead to increased seed set (Fründ et al., 2013), increased fruit quality and improved long-term storability (Samnegård et al., 2019). The expansion of generalist species may, however, increase competition for floral resources and nesting space, ultimately having a detrimental impact on overall species diversity as sensitive species are replaced in a continuation of the trend found by Powney et al. (2019).

Any assessment of potential benefits to crop pollination services under future climate scenarios needs to be considered in conjunction with potential changes in areas suitable for the growth of pollinator-dependent crops. Currently, distribution modelling of crops in Great Britain is limited to a restricted range of bioenergy crops and orchard fruit (Bellarby et al., 2010; Polce et al., 2014), and although beyond the scope of this study, modelling the potential distributions of pollinator-dependent crops, alongside their pollinators, may provide insights into where best to target interventions to boost wild pollinators for crop pollination.

However, this work presents complex patterns of spatial and temporal changes in wild bees, so planning is not as simple as looking at spatial or temporal overlap between crops and pollinators separately. From a crop pollination perspective, it is important to consider spatial and temporal changes together when attempting to identify areas suitable for pollinator-dependent crops and with high insect pollination potential. This is currently a potential missing link in predicting future crop suitability and is an area recommended for future research.

Projecting spatio-temporal distributions into the future naturally comes with some uncertainty and should be treated with some caution. There are likely to be obstacles to spatio-temporal adaptation that are very difficult to predict and may influence the future projections in this study. Species may reach the limits to the phenotypic plasticity or genetic variability that prevents them continuing to adapt to changing climate conditions. Species which are unable to overcome such obstacles may, in practice, exhibit different phenological responses, or not fill their climate envelopes as presented here.

In spite of these potential issues, these results highlight the significant impact of future climate change on bee phenology and distribution in Great Britain, with implications for both bee populations and the pollination service they provide. The findings suggest that conservation efforts may need to focus on maintaining suitable local habitats for bee species as they shift their distribution in response to changing climatic conditions.

4.6. Acknowledgements

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5. Biological traits predict ability of British wild bees to occupy their climate envelopes.

5.1. Abstract

Understanding a species' ability to fill its climate envelope is crucial to understanding barriers to dispersal, and for predicting capacity to respond to climate change. If a species is not present in its climate envelope, its absence is likely due to non-climatic environmental factors, including 1) Disperal Limitations; 2) Unsuitable Habitat and Resources and 3) Insufficient Data.

This study investigates the relationship between British wild bees' life-history traits and their ability to occupy their suitable climate envelopes. Across 64 species of wild bee this study reveals large species with polylectic pollen foraging behaviour and that overwinter in more advanced developmental stages filled a greater proportion of their climatic envelope than smaller bees with more restricted foraging preferences and that take a longer time to reach maturity.

These results suggest that while larger, generalist species are relatively more successful at filling their climate envelopes, many species appear not to fill the entirety of their potential climate envelopes due the synergistic effects of dispersal limitations, unsuitable habitat and resources and insufficient data. This study also identifies and discusses barriers to range filling, namely large distances between areas of suitable habitat and a lack of foraging and nesting resources within suitable habitat.

Given that many species do not fill their climate envelopes, it is clear that Great Britain's conservation mantra of "Bigger, better, more joined up" will be crucial for helping wild bees to maximise range filling success. Finally, this study also raises the issue that Great Britain may experience a homogenization of future bee communities, dominated by widespread generalist species, which could replace specialist species, who this study shows are less able to overcome the non-climatic barriers to filling their climate envelope.

5.2. Introduction

Climate plays a large role in determining species' distributions (Thomas, 2010), and understanding a species' suitable climate envelope is an important tool for predicting these distributions. Most species, however, do not fill their entire potential climate envelope. This can be for a range of reasons, including limited dispersal ability and insufficient habitat, and forage availability (Pearson & Dawson, 2003). One group of species where knowledge of climate envelopes are of particular importance is wild bees. In Great Britain, wild bees comprise 270 species (Falk, 2019), many of which provide important pollination services to a wide range of wild and cultivated plants valued at approximately £630m/year (Breeze et al., 2021).

Many species, including bees, are undergoing range shifts in response to changing climate (Buckner & Danforth, 2022), and understanding where species currently occur, and are likely to occur in the future is important from both species' conservation and ecosystem service perspectives (Senapathi et al., 2021a). If a species is not present in a climatically suitable area, its absence may be due to other environmental factors, such as unsuitable habitat type, geographic barriers, or dispersal limitations (Estrada et al., 2018), with species that fill greater proportions of their climate envelope better able to overcome these barriers.

There are a range of non-climatic factors that influence range filling ability, and these can be grouped into three primary categories. Where bees, and biodiversity more generally, do not fill their climate envelopes, it is likely caused by a combination of these three factors:

- Dispersal Limitation a species cannot disperse far enough to reach a new site. This can include intrinsic (species' ability to disperse) and extrinsic (barriers to dispersal) dispersal (Baselga et al., 2012).
- Unsuitable Habitat and Resources a species can reach a new site, but the new site contains unsuitable or insufficient nesting and/or foraging resources.
- Insufficient Data a species may already exist in a new area, but there is insufficient data to adequately document it.

Dispersal limitation, both intrinsic (Baselga et al., 2012) and extrinsic (Munguía et al., 2008), has been shown to be a major driver of range filling in a wide variety of taxa including plants (e.g. Arnell & Eriksson, 2022; Seliger et al., 2021) and mammals (Munguía et al., 2008). Relatively little is known about the intrinsic dispersal capabilities of wild bees in Great Britain (Torné-Noguera et al., 2014), however there is evidence to suggest that extrinsic barriers to bee dispersal are increasing. Loss of suitable habitat and increasing habitat fragmentation has occurred in Great Britain, with marked declines in heathland and grassland, and increases in urban and arable areas occurring since 1950 (Senapathi et al., 2015a), and increases in barriers to dispersal such as roads (Fitch & Vaidya, 2021). Given these increases in habitat fragmentation and barriers to dispersal, it is likely that dispersal limitation plays a role in bee range filling success.

The loss of suitable habitat also has impacts on bee range filling ability even if a species can reach new areas. Given the historic loss of important habitats such as heathland and grassland (Senapathi et al., 2015a), there are likely to be fewer resources available in the landscape, increasing competition and ultimately resulting in landscapes capable of supporting fewer bees. The increase of monocultures of mass flowering crops in the landscape often create "feast or famine" scenarios for bees (Dolezal et al., 2019). Much of the current research into feast or famine scenarios focusses on honeybees (Dolezal et al., 2019), with health declines seen away from the flowering period of the mass-flowering crop. While this is not directly applicable to wild bees, which have different life history strategies to honeybees, the fitness costs away from the mass flowering period are likely to be similar if alternative forage is not provided, and this is another potential reason why wild bees may not fill their entire climate envelope.

Finally, incomplete, or insufficient data may be a cause of perceived range underfilling. Much of the data used in range filling exercises come from presence-only observations from publicly accessible databases such as GBIF (GBIF, 2024) or datasets held by organizations such as the Bees, Wasps, and Ants Recording Society (BWARS - www.bwars.com). These datasets often come with biases towards easy to detect species in easy to access locations (Cretois et al.,

2021), meaning that a species not being found in an area could be due to a lack of sampling effort. Couple this with the fact that many species of bee are only accurately identifiable under a microscope, and it is clear that detectability and sampling effort must be accounted for in any range filling analysis.

Life-history traits may explain differences in species' abilities to fill their climate envelopes. Indeed, life-history traits across different taxa, including mammals, birds, and plants have been shown to influence range filling ability. These traits include habitat breadth (Estrada et al., 2015), lecty (pollen foraging specialization) (Morimoto, 2020), overwintering stage (Pöyry et al., 2009) and body size. These traits were selected as they have been shown to influence geographic distributions (Morimoto, 2020), range filling (Estrada et al., 2015) and/or range shifts (Pöyry et al., 2009) in other taxa and may therefore impact the ability of bees to fill their climate envelopes. Additionally, lecty has been shown to modulate the responses of wild bees to habitat loss (Bommarco et al., 2010), and may consequently also be a driver of range filling ability.

Choosing between conservation priorities, such as focussing on reversing habitat fragmentation or improving existing habitat is an important part of conservation planning. Add to this there may not even be sufficient data to make an informed conservation decision and the synergistic nature of the three drivers of range filling success pose challenges for policy makers and conservation practitioners, especially it is difficult to tease apart the individual effects of each impact. Chapter 4 predicted that the climate envelopes of wild bees will change under future climate scenarios, and understanding the influence of life-history traits on range filling will give important insights to which species may require additional help to overcome the barriers to range filling success.

This study looks to build on Chapter 4, which attempted to understand climate envelopes for a range of British bee species but did not explore how well species can fill their ranges. Understanding range filling ability, and whether it is influenced by specific traits is crucial to revealing barriers to wild bee dispersal and help inform policy and practice to help species

overcome these barriers. This chapter attempts to fill this knowledge gap by answering the question "Do life-history traits of British wild bees influence range filling ability?".

5.3. Methods

This study combined the four traits (lecty, overwintering stage, habitat breadth and body size) with range filling ability for 64 species of wild bee in Great Britain, selected as they have existing climate envelope models and are well represented in the dataset used to calculate range filling. Climate envelopes were taken from the previously developed climate envelope models derived from a long-term database of bee recordings held by the Bees, Wasps, and Ants Recording Society (www.bwars.com) at 0.0155° gridded resolution, developed in Chapter 4 using six bioclimatic variables derived from the UK CHESS-SCAPE project (Robinson et al., 2023) and produced using the MaxEnt modelling software (Phillips et al., 2008). Detailed descriptions of the previously developed climate envelope models can be found in Chapter 4. The resolution of the climate envelope models was rescaled to 0.155° gridded resolution. Presence records were obtained from the Global Biodiversity Information Facility (GBIF, 2024a), with observations for all Hymenoptera (excluding the managed honeybee, *Apis mellifera*) in Great Britain between 2010-2019 downloaded (GBIF, 2024b). Each record was assigned to a grid square (on the same grid scale as the rescaled climate envelope model) based on its latitude and longitude. No BWARS data is included in the GBIF dataset, and vice versa.

To improve the probability that cells without observations are true absences, all data analyses were carried out only for areas with high sampling effort – also known as "low ignorance" areas (Ruete, 2015). This method helps overcome issues related to sampling effort and the detectability of rare and small species which are often underrepresented in opportunistic citizen science data (Callaghan et al., 2021). This was carried out according to Arnell & Eriksson (2022), who implemented low ignorance maps, to identify areas with high sampling effort in Swedish woody plants. Data for all Hymenoptera (excluding *A. mellifera* – 1569 species, 347,731 records) were used to produce a low ignorance map for Hymenoptera within Great Britain. The number of species present in each grid cell was counted, and only grid cells with

20 or more species recorded were used in the range filling analysis (Figure 5.1). A bee species was considered if it had 80 or more presence records in the GBIF dataset, resulting in a total of 64 species available for analysis (Note: *Bombus distiguendus* met this threshold but was also removed from analysis due to its extremely restricted suitable climate envelope).



Low Ignorance Area

Figure 5.1. Map of Low Ignorance Areas for Hymenoptera recording in Great Britain 2010-2019. Area in grey is the area used in range filling analysis.

Range filling ability was calculated as the percentage of cells classed as climatically suitable from the climate envelope models derived from BWARS data containing a bee observation from the GBIF dataset. This percentage was log transformed, to conform with the assumption of normality (indicated using a Shapiro–Wilk test (Shapiro & Wilk, 1965)) and used as the dependent variable in a phylogenetic generalized least squares (PGLS) model, with bee lifehistory traits used as fixed factors. Habitat breadth, lecty (foraging specialization), overwintering stage and body size were the four traits tested as potential explanatory traits. Habitat breadth was classed as the number of habitats suitable for each species, as categorized in the European Red List of Bees (Nieto et al., 2014). Lecty and Overwintering Stage were obtained from a database curated by S.P.M. Roberts. Traits for each species can be found in Table S5.1.

The issue of imperfect detectability of small and rare species is accounted for, in part, by the use of low ignorance maps previously described. An additional method of accounting for detectability is to include traits relating to ease of detection into any modelling. Body size, has been linked to detectability in a range of taxa (Johnston et al., 2014; Kéry & Schmid, 2004), and may also account, at least in part, for the issue of imperfect detectability. Therefore, intertegular distance (ITD - defined as the distance between the bases of the wings on the thorax (Raiol et al., 2021)) was used as a proxy for body size (Cane, 1987) and incorporated into the model to account for detectability. This metric is noted as "body size" throughout the rest of this text.

To account for any phylogenetic signal, where closely related species resemble each other more than a species randomly drawn from the same phylogenetic tree (Blomberg et al., 2003), a phylogenetic generalized least squares (PGLS) model was run. The logged range filling percentage as the dependent variable, with lecty, overwintering stage, habitat breadth and ITD as independent variables (Table 5.1). The model.dredge function from the package "MuMin" (Barton, 2020) was used to identify the best model. Models containing all combinations of explanatory variables were produced and compared using AICc value. One model performed significantly better (>2 AICc units) than the rest (Table S5.2), so was used for final analysis. This model included Lecty, Overwintering Stage, and Body Size as explanatory variables. Habitat Breadth was excluded from this model.

Three phylogenetic correlation structures were assessed (corMartins, corBrownian and corPagel) and performance compared using AICc values. A Pagel correlation structure provided the lowest AICc value and was used in the final model. Information about the phylogenies of each species was downloaded from the Bee Tree of Life (Figure S5.1) (Hedtke et al., 2013), and analysis was run using the "ape" package (Paradis et al., 2004).

Trait	Levels				
Lecty	 "Polylectic" – Forages on a wide range of plants "Oligolectic" – Forages on a restricted range of plants "Clepto- and social parasites" – Does not visit plants to forage 				
Overwintering Stage	 "Adult (female only)" – Females overwinter as adults "Adult within nest" – Overwinter as adults within cocoon "Prepupa" – Overwinters as prepupa 				
Habitat Breadth	Continuous – number of suitable habitats according to the European Red List of Bees (Nieto et al., 2014)				
Body Size	Continuous – mean intertegular distance, measured in mm.				

 Table 5.1. Traits selected for range filling analysis

To test for significant differences between levels of the two categorical variables (Lecty and Overwintering Stage), a Kruskal-Wallis test (Kruskal & Wallis, 1952), followed by a post-hoc Dunn test (Dunn, 1964), with a Benjamini-Hochberg correction for multiple comparisons (q = 0.05) (Benjamini & Hochberg, 1995) was implemented.

5.4. Results

Range filling varied between species, ranging from 9.7% (*Epeolus cruciger*) to 128.3% (*Bombus lapidarius*) of suitable climate cells within the low ignorance area containing an observation (Figure 2). Mean range filling was 43.8% of suitable climate cells containing an observation.



Figure 5.2. Range filling ability of 64 species of bee. Range filling ability is calculated as a percentage of the suitable climate cells containing a presence record (restricted to only include low ignorance areas)

Species traits appear to have a significant impact on the ability of a species to fill its climate envelope (Table 5.2). Polylectic species appeared to fill significantly more of their climate envelope than those that have a restricted foraging breadth, and those species reliant on other species to survive (i.e., clepto- and social parasites). Additionally, Bees that overwinter as adults tended to be better at filling their climate envelope than those that overwintered as prepupae.

A Kruskal-Wallace test also revealed significant differences in range filling ability between levels of Lecty ($\chi 2 = 7.99$, df = 2, p = 0.018), and Dunn's test with Benjamini-Hochberg

correction for multiple comparisons revealed significant differences between polylectic bees and clepto- and social parasites (p = 0.043). A Kruskal-Wallace test also revealed significant differences in range filling ability between different levels of Overwintering Stage ($\chi 2 = 6.94$, df = 2, p = 0.034), with bees overwintering as adults within a cocoon filling significantly more of their ranges than those that overwinter as prepupa (p = 0.001) (Figure 5.3).

Term	Estimate	SE	t value	Pr(> z)	
Lecty: Oligolectic	-0.68	0.22	-3.05	0.003	**
Lecty: Clepto- and social parasites	-0.46	0.19	-2.43	0.018	*
Overwintering Stage: Adult within cocoon	0.64	0.14	4.55	< 0.001	***
Overwintering Stage: Adult (female only)	0.29	0.15	1.91	0.060	
Body Size	0.31	0.03	10.13	< 0.001	***

 Table 5.2. PGLS model output showing influence of species' life-history traits on range

 filling ability



Figure 5.3. **A)** Boxplot showing impact of Lecty on range filling ability. Bar indicates significant differences between levels. **B)** Boxplot showing impact of Overwintering Stage on range filling ability. Bar indicates significant differences between levels. **C)** Impact of Body Size on range filling ability. Shaded area indicates 95% confidence interval.

5.5. Discussion

This study makes use of two separate datasets of British wild bees to produce the first quantitative analysis of bee range filling ability, and the extent to which range filling ability is driven by life-history traits. Whilst the results here may seem unsurprising – that traits relating to generalism, more advanced developmental stages and body size are determinants of

successful range filling – they provide important insights into some of the challenges faced by wild bees in Great Britain.

Lecty, or pollen foraging specialization, was found to be important in determining a species' range filling ability. Alongside being able to access a new area, it is important that suitable forage plants and nesting resources are available. For many generalist species, this is of minimal concern, however for bees that depend on a restricted range of plants the issue of unsuitable habitat and resources is of far greater concern, with distributions limited to the distribution of suitable forage. Narrow foraging specialisation may also increase the risk caused by competition for resources. Generalist species may be able to shift to other plant species for resources when under competition pressure (Walther-Hellwig et al. 2006) but more specialist species may not have this flexibility and therefore be at greater risk of competition for resources. Given this, it is clear that interactions between bee species will undoubtably also influence range filling ability. Similarly with the bees in the "clepto- and social parasites" group, which also limited to their hosts' ranges, who must be present for the parasites to lay eggs.

Overwintering stage also appears to impact range filling ability. Bees that overwinter in later developmental stages (i.e., adults) appear better able to fill their ranges than those that overwinter in early developmental stages (i.e., prepupae). This could be linked to phenology, with species distributions linked to the ability to complete at least one full annual life cycle (Chuine, 2010). It is possible that bees could exhibit a similar trend, and that species overwintering in more advanced stages are better able to respond to favourable conditions, giving them both more time to complete their life cycles and a head start on exploiting available resources. These advantages will likely increase the ability of a species to survive in a greater proportion of their climate envelope. This also implies that having suitable nesting habitat is an important factor for wild bees to be able to fill their ranges.

Body size was also a significant determinant of range filling success, with range filling higher in larger bees. This can be attributed to a range of factors. Firstly, although there is currently

little empirical evidence relating to dispersal distances (Torné-Noguera et al., 2014), it is likely that larger bees have better intrinsic dispersal abilities (i.e. able to fly further) and better abilities to overcome extrinsic dispersal limitations. Larger bees have indeed been found to fly over greater distances when foraging (Greenleaf et al., 2007), and therefore it could be that they can also disperse further. If this is the case, it means larger bees will be able overcome larger physical distance between suitable habitat patches and more substantial physical barriers to dispersal, and therefore can access a larger part of their climate envelope. The finding that body size is a predictor of range filling ability could also be related to data limitations. Larger species are often easier to spot and identify (Callaghan et al., 2021), and as a result larger species could be overrepresented in the BWARS and GBIF datasets, although this is controlled to a certain extent in this study through the use of only data-rich species in low ignorance areas.

When considering these results in the context of the three challenges presented earlier in this study (dispersal limitation, unsuitable habitat and resources and insufficient data), it is clear that all three factors are influencing the range filling success of British wild bees to some degree. These results have important consequences for current and potential future biodiversity and ecosystem services bees provide. If range filling can be a proxy for capacity to undergo range shifts in the face of a changing climate, as has been suggested (Estrada et al., 2018), generalist species appear to be better equipped to fill their climate envelopes and therefore to colonize new areas in the future. Many of these generalist species also visit crops and are provide a large proportion of the pollination service (Kleijn et al., 2015). This work indicates that there is likely to be changes in pollinator community structure, with large, generalist species dominating. This will mean that there could be changes in the geographic areas of the delivery of pollination services, potentially providing new opportunities for crop growth of pollinator dependent crops in more northerly or upland areas, as climate envelopes are predicted to expand northwards under future climate scenarios (Chapter 4).

Large, generalist species are better equipped to fill their current climate envelopes, and this includes some species that already occur outside of their 'suitable' climate envelope such as

Bombus lapidarius and *Bombus pascuorum* – possibly an artefact of the resolution of the climate data missing localised microclimates within a pixel which act as climate refugia for these species, despite the overall pixel being classed as unsuitable. Should climate envelopes change in the future, which is predicted in Chapter 4, Great Britain may experience a homogenization of bee communities. Generalist species, which can better fill their climate envelopes could outcome rarer, more specialist bees for forage and nesting resources. Recent work on a range of taxa, including bees, suggests that higher annual temperatures harbour more homogeneous communities (Ganuza et al., 2022). Smaller, specialist bees, in particular those that feed on specific plants or that take a longer time to reach maturity are less able to fill their climate envelope, which could lead to replacement of these species with more adaptable, generalist species.

The issue of community homogenization by species better equipped to fill their ranges is a complex topic in the context of conservation. From an ecosystem service perspective, community homogenization may be beneficial, especially for pollination, given that much of the pollination service is carried out by a small subset of the overall bee fauna (Kleijn et al., 2015) including generalists such as *Bombus lapidarius* and *Bombus pascuorum*. The fact that these two species already exist in areas outside of their climate envelope (more than 100% range filling) indicate high levels of adaptability to climate conditions and habitat and resource requirements. The loss of species diversity, however, can lead to less resilient communities and less stable interannual pollination supply (Senapathi et al., 2021b). Another school of thought is that species have a right to live, and that every species is a "natural share-holder of the biosphere with an inherent right to survival" (Kassas, 2002), In this case, ecosystem service provision alone is an insufficient argument for conservation, and a more holistic approach should be encouraged (Senapathi et al., 2015b).

Whilst recommending conservation priorities is beyond the scope of this study, it does highlight the difficult decisions conservation planners will have to make regarding which species to target for support. Certain species are better placed than others to overcome barriers to range filling,

them and careful consideration will need to be given to prioritizing which species are given conservation attention. This study presents an initial view of bee range filling ability, and further research, ideally using systematically collected data to better overcome the inherent biases present in presence-only data, is needed to refine the models presented here and to begin to tease apart the individual challenges of dispersal limitation, unsuitable habitat and resources and insufficient data.

In conclusion, this study highlights the importance of life-history traits in determining the ability of British wild bees to fill their climate envelopes. It shows that large-bodied generalists overwintering in more advanced stages are in a better position to fill their climate envelope and that careful conservation planning is needed to determine the future wild bee community in Great Britain. Whatever the conservation priority, be it ecosystem service based or a more holistic approach, providing more, bigger, better-connected patches of habitat targeted to the conservation goal will be important to help facilitate the movement of wild bees. "Bigger, better, more joined up" has long been a conservation target for wildlife sites in Great Britain (Lawton, 2010), and with habitat and resource availability both constraining factors in bee range filling, clearly all three of these targets will need to be met to allow wild bees to respond, at least spatially, to uncertain future climates.

5.6. Acknowledgements

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6. New citizen science initiative enhances blossom phenology predictions for fruit trees in Great Britain

6.1. Abstract

To enable timely introductions of pest and pathogen treatments and introduction of managed pollinators, it is critical to accurately predict blossom phenology in fruit tree orchards. Making such predictions requires large datasets of blossom dates. However, these datasets are scarce and often limited to single locations. Consequently, resulting phenology predictions are often not representative across larger geographic areas. One potential untapped data source for increasing the spatial applicability of phenology predictions is citizen science, with millions of biological records across a wide range of taxa recorded annually. Here, a new citizen science platform called "FruitWatch" is introduced, which records blossom dates of fruit trees in Great Britain. This study assesses the suitability of FruitWatch submissions for parameterizing existing phenology modelling frameworks to ultimately make predictions of blossom dates across Great Britain for a single year.

Using data for four cultivars from 2022, modelling frameworks performed well, with rootmean-square Error values of predictions from validation datasets ranging between 4.6 and 8.0 days. This shows that models generated using citizen science data can perform comparably to models developed with single-site, standardized data collection procedures. The parameterized models are also used to predict blossom onset dates for known locations of orchards across Great Britain for 2022, with earlier blossom dates predicted in warmer areas (lower latitudes and altitudes, and urban areas). Overall, this study provides an important breakthrough in predicting blossom phenology, highlighting the potential of citizen science to increase spatial applicability of phenology predictions and providing growers with cultivar specific phenology predictions to incorporate into orchard management plans.

6.2. Introduction

It is well documented that climate change is having a diverse range of impacts on many taxa. One of these impacts is changes in phenology, defined here as the 'timing of recurrent biological events' (Badeck et al., 2004) and there is mounting evidence to suggest that many species have exhibited phenological shifts in in response to the changing climate. These shifts have been reported across a range of taxa, including plants (Büntgen et al., 2022), insects (Bartomeus et al., 2011) and birds (Socolar et al., 2017).

Plants, particularly fruit trees are of both commercial and public interest in Great Britain, including pome fruits such as apples (*Malus domestica*) and pears (*Pyrus communis*), and stone fruits such as cherries (*Prunus avium*) and plums (*Prunus domestica*). Pome and stone fruits are an economically important horticultural crop in Great Britain, with 239,300 tonnes of apples, 17,900 tonnes of pears, 6,300 tonnes of plums and 4,100 tonnes of cherries (plus an additional 170,100 tonnes of cider apples and perry pears) grown in the United Kingdom (encompassing Great Britain and Northern Ireland) in 2022 (DEFRA, 2023b). This production has an estimated total value of over £600 million (DEFRA, 2023b), making pome and stone fruit growth a very important sector in Great Britain's agricultural industry, emphasizing the importance of understanding the impacts of any climate driven shifts in fruit tree phenology.

Identifying phenological shifts across flora and fauna usually requires long-term datasets, collected either through systematic or opportunistic observations, or through analysis of museum collections. The current knowledge of phenological shifts of pome and stone fruit crops in Great Britain is limited. Long-term data that does exist comes primarily from single focal orchards. This includes the National Fruit Collection, located in Brogdale, Kent, UK, which holds phenological records for a wide range of cultivars dating back to the 1960s. Data from this collection shows advances in blossom dates of both apples (Chapter 2) and pears (Reeves et al., 2022), likely linked to changing climatic conditions. From further afield, cherries and plums have also been shown to be advancing blossom phenology. Research carried out in German sweet cherry orchards highlights advances in blossom onset dates of 2.0 days per

decade (Chmielewski et al., 2004), and Norwegian plums exhibit a 3.2 day per decade advance in full bloom dates (Woznicki et al., 2019).

While these long-term, single-, or few-location datasets provide valuable insights into phenological shifts within these specific locations, they come with the trade-off that they may not be representative of phenological trends over space. Phenology may be influenced by specific local environmental and management conditions unique to a location, including cultivar selection (Reeves et al., 2022), soil composition (Arend et al., 2015) and microclimate (Jackson, 1996). These different influences may be disentangled by incorporating citizen science to increase the spatial scale of the dataset, and therefore increase its geographical applicability.

Citizen science, defined as "the involvement of non-professionals in scientific investigations" (Bison et al., 2019), can be either systematically (with a standardised survey procedure) or opportunistically (ad-hoc recordings) collected. Citizen science data has often been used in place of data collected by traditional scientific protocols to detect phenological change in a wide range of taxa, including forest trees (Elmore et al., 2016), bumblebees (Blasi et al., 2023), plants (Klinger et al., 2023) and birds (Newson et al., 2016).

Citizen science and biological recording are popular activities for many people, especially in Great Britain. This includes both systematic schemes, such as the Butterfly Monitoring Scheme (www.ukbms.org), and ad-hoc schemes such as Nature's Calendar (www. naturescalendar.woodlandtrust.org.uk). As a result, large citizen science datasets - both systematically and opportunistically collected - exist for a wide range of taxa, including bees, hoverflies, birds and many plant and tree species. A notable exception to this list is pome and stone fruits, including apples, pears, cherries and plums. All four of these trees are grown extensively across Great Britain, both for commercial and non-commercial purposes and can be found in many public (e.g., community orchards, stately homes) and private (e.g., commercial orchards, private gardens) places.

Given the prevalence of these fruit trees in the British landscape, there arises a potential opportunity to recruit citizen scientists to record blossom dates, and to begin to understand

phenological patterns beyond the focal orchards with long-term data for many cultivars. Additionally, as pome and stone fruits are grown across Great Britain, in a wide variety of climate conditions, they provide a good system for a space-for-time substitution study, allowing for testing of the sensitivity of blossom dates to different climate conditions in the absence of a long-term dataset.

Understanding the phenology of pome and stone fruit trees, particularly during the blossom stage is key to assessing phenological synchrony, and identifying any mismatches that are arising with pollinators and pests. Maintaining synchrony with pollinators is of particular importance for apples, pears, cherries, and plums, as they depend on insect pollination to set fruit (Garratt et al., 2014b). Many cultivars of all four crops require cross-pollination from a suitable "polliniser" cultivar to produce more and/or higher quality fruit (Fountain et al., 2019; Lech et al., 2008; Ramírez & Davenport, 2013). Much of this cross-pollination is carried out by insects, with managed honeybees, bumblebees, solitary bees and hoverflies being often cited as major contributors(Fountain et al., 2019; Garratt et al., 2016). Therefore, maintaining temporal synchrony, both with the polliniser cultivars and the insect pollinators is crucial to maximise fruit set, quality, and ultimately economic value. Recent reports have shown phenological shifts in pollinators, such as wild bees (Bartomeus et al., 2011; Chapters 3 & 4) and hoverflies (Hassall et al., 2017), and therefore understanding phenological trends fruit tree blossom is critical for understanding potential disruptions in temporal synchrony between blossom and insect pollinators.

This study introduces a novel citizen science platform, called FruitWatch (www.fruitwatch.org) – a collaborative effort between researchers at the University of Reading and Oracle for Research, which was launched at the beginning the British fruit tree blossom season in 2022, and asks citizen scientists to record blossom dates of apple, pear, cherry and plum trees. This study uses data submitted to the FruitWatch platform to track spatial phenological trends in the four focal crops, using space-for-time substitution to assess the effect of temperature (known to be a major driver of blossom dates in temperate orchards (Chmielewski et al., 2004)) on blossom dates. Additionally, using a case study of the most recorded cultivar of each tree type, assessments of whether blossom dates of cultivars show different sensitivities to climate are also made, ultimately resulting in predictions of blossom dates being made across Great Britain at fine spatial resolutions. The specific research questions addressed here are:

- Does blossom phenology shift across a latitudinal gradient in Great Britain, across a single year?
- 2) Can citizen science data be used to parameterize existing phenology models in a spacefor-time substitution?
- 3) How well can models parameterized using a single year of citizen science data predict blossom dates across orchard-growing areas in that year?

6.3. Methods

6.3.1. The FruitWatch platform

The FruitWatch platform was built using Oracle Application Express (APEX) (Van Der Plas & Van Zoest, 2013) and consists of a website (www.fruitwatch.org) containing project information and a simple recording form. The recording form consists of three stages. Firstly, information regarding the date and location of the record is collected. This can either be done automatically through a phone GPS, entering a postcode which is then converted to latitude and longitude, or through dropping a pin on a map. Secondly, information about the tree is collected. This involves recorders selecting the tree type (apple, pear, cherry or plum) from a drop-down menu, and information about the cultivar (if known) is entered. At this point, recorders also input the phenological stage of the fruit tree, based on the well-established BBCH Scale for Pome and Stone Fruits (Meier et al., 1994). This contains five categories: A (first flowers open, BBCH code 65), D (Flowers fading, BBCH code 67) and E (End of flowering, BBCH code 69). Finally, the recorders are asked to upload two photographs, firstly of the tree, and secondly of a cluster of flowers representative of the tree. This is currently an optional step and can be skipped if the recorder wishes to do so.

6.3.2. Data cleaning

The recording scheme has been open since February 2022, and in that time 6,696 records have been submitted. These records were passed through a filtering process. Initially, as uploading photographs was an optional step in the recording process, some records were uploaded without photographs, and as such the phenological stage could not be independently verified. Therefore, records without photographs were removed. Secondly, records from 19th March 2022 were removed. FruitWatch was featured in a national newspaper on this date, and as a result, a disproportionately large number of records were received on this day, potentially skewing the results towards this date. Finally, records containing pictures without trees were removed and records containing locations that were either outside Great Britain or with postcodes that could not be converted to latitude and longitude were removed.

Deciding which phenological stage a tree is at requires the recorder to make a subjective decision and this can vary between recorders (Fuccillo et al., 2015). This is a common issue where subjective questions are included in citizen science, and recorder identity has been shown to explain almost 20% of the variance in vegetation percentage cover surveys, also a subjective measure (Bergstedt et al., 2009). Where records contain pictures, it is often possible to overcome this obstacle by having submitted records re-classified by a single person and comparing the consensus between the original records and the independent assessor.

To assess the accuracy of recordings, a random subsample of 1,000 sets of photographs were assessed and re-classified by a single individual, a commonly used method for quality control in citizen science projects (McDonough MacKenzie et al., 2017). Of these 1,000 records, 67.6% were classified as belonging to the same phenological stage by both the initial observer and the independent observer. 28% of results differed by only one phenological stage (i.e., A to B), with only 4.1% differing by more than one phenological stage (i.e., A to C), and the remaining 0.3% contained unusable images (Figure S6.1A).

As a result of this lack of consensus between recorders and the independent verifier, especially when differentiating between adjacent phenological stages, records were reclassified into

"Start" (original codes A and B), "Full" (original code C) and "End" (original codes D and E). This resulted in a greater consensus of results, with 81.3% of results classified as the same by the original recorders and the independent recorder. This classification scheme was taken forward into further analyses, and the original recorders' observations were used, excluding those with no or unusable pictures (Figure S6.1B).

Finally, an outlier removal process was used. The interquartile range (IQR) method was used to identify outlying observations (Barbato et al., 2011) within each cultivar and flowering stage. The IQR is calculated as the range between the 25th (Q1) and 75th (Q3) percentile values. Values lower than Q1 - 1.5*IQR or higher than Q3 + 1.5*IQR were removed.

Cultivar spelling and synonyms were standardized using a range of online sources, primarily from the databases of the National Fruit Collection (www.nationalfruitcollection.org.uk) and Pomiferous (www.pomiferous.com).

6.3.3. Statistical analysis

6.3.3.1. Cultivar selection

Data for the most recorded cultivar of each fruit type for the year 2022 was selected for further analysis. This included the apple 'Bramley', cherry 'Stella', pear 'Conference' and plum 'Victoria'. To model the spatial variation on blossom onset, records classed as "Onset" were selected for each cultivar. Where multiple records for a cultivar exist within the same grid square, the mean blossom date was calculated and used.

6.3.3.2. Does blossom phenology shift across a latitudinal gradient in Great Britain, across a single year?

Using data for 2022 for the four selected cultivars, separate cultivar-level linear models were run, with latitude as the independent variable and recording date as the dependent variable to assess change in blossom onset date in relation to latitude. A Benjamini-Hochberg correction for multiple tests was applied to these models to help avoid Type I errors (q=0.05) (Benjamini & Hochberg, 1995).

6.3.3.3. Can citizen science data be used to parameterize existing phenology models in a space-for-time substitution?

Fruit trees' relationship with temperature is somewhat complex, and trees require exposure to cool temperatures (known as the "chilling" period), followed by warm temperatures (known as the "forcing" period) to break dormancy. A recently developed modelling framework, called "PhenoFlex" (Luedeling et al., 2021) incorporates two commonly used models to predict bloom dates. It uses the Dynamic Model (Fishman et al., 1987) to account for chill accumulation, and the Growing Degree Hours Model (Anderson et al., 1985) to account for the heat accumulation. A detailed description of the PhenoFlex framework can be found in Luedeling et al. (2021), and this framework has performed well in predicting blossom dates in temporal phenology series.

The PhenoFlex framework requires hourly maximum and minimum temperature data, and so daily minimum and maximum temperature for the period between 01/01/2021 and 30/06/2023 was obtained at 0.1° gridded resolution from the ensemble mean of the E-Obs database version 27.0e (Cornes et al., 2018), and downscaled using the 'stack_hourly_temps' function within the 'chillR' package (Luedeling et al., 2023). Each phenology submission was then assigned to its corresponding grid square, so it could be linked to temperature records.

The PhenoFlex framework allows for many parameters (Table 6.1) to be set which allows for high flexibility when forecasting phenology across different cultivars. Each cultivar was analysed separately, allowing for cultivar-specific parameter estimates.

Table 6.1. List and descriptions of parameters used in the PhenoFlex modelling framework,

 and their initial values used in the parameter fitting procedure

Parameter	Description	Starting Value (lower, upper)	
yc	Chilling requirement: critical value of y,	10 (20, 90)	
	which defines the end of chill accumulation.	40 (20, 80)	
70	Heating requirement: critical value of z,	100 (100 500)	
ZC	which defines the end of heat accumulation.	190 (100, 500)	
e1	Slope parameter that determines the transition		
51	from the chill accumulation to the heat	0.5 (0.1, 1.0)	
	accumulation period in PhenoFlex.		
Tu	Optimal temperature of the growing degree	25(0,20)	
Iu	hours (GDH) model.	23 (0, 30)	
EO	Time-independent activation energy of		
LU	forming the precursor to the dormancy-	3372.8 (3000.0, 4000.0)	
	breaking factor (PDBF).		
	Time-independent activation energy of		
E1	destroying the precursor to the dormancy-	9900.3 (9000.0, 10000.0)	
	breaking factor (PDBF).		
40	Amplitude of the process involved in forming		
110	the precursor to the dormancy-breaking factor	6319.5 (6000.0, 7000.0)	
	in the dynamic model.		
	Amplitude of the process involved in		
Α1	destroying the precursor to the dormancy-	5 939917e13 (5e13 6e13)	
711	breaking factor (PDBF) in the dynamic	5.557717015 (5015, 6015)	
	model.		
	Transition temperature parameter of the		
Tf	sigmoidal function in the dynamic model, also	4 (0, 10)	
	involved in converting the PDBF to chill		
	portions.		
Tc	Upper threshold in the GDH model.	36 (0, 40)	
Tb	Base temperature of the GDH model.	4 (0, 10)	
slope	Slope parameter of the sigmoidal function in		
	the dynamic model, which determines what	1.60(0.05,50,00)	
	fraction of the PDBF is converted to chill	1.00 (0.05, 50.00)	
	portions.		

Initially, the dataset was ordered by latitude and split into calibration and validation subsets. 75% of records for each cultivar were used to calibrate the model, with the remaining 25% used for validation, in a repeating pattern of 'v', 'c', 'c', 'c' (where 'v' = validation, 'c' = calibration). This was split in this way so as to to capture a range of latitudes, and therefore temperature profiles, within both the calibration and validation datasets.

The GenSA algorithm (Xiang et al., 2013) was used to parameterize the PhenoFlex model, using the calibration dataset as phenological records and using the starting values and parameter ranges set in Table 6.1. These parameters are deliberately wide following initial parameter bounds used in similar PhenoFlex studies (Fernandez et al., 2022). A maximum of 1,000 iterations of the algorithm were run, and the process was stopped when there was no further improvement in model fit after 250 consecutive iterations.

To assess the suitability of the citizen science phenology recordings for use in the PhenoFlex framework, and for making predictions of blossom dates, the model for each cultivar was evaluated by calculating the root-mean-square Error (RMSE) and mean absolute error (MAE) of both the calibration and validation datasets. As an additional step, temperature response curves (chill and heat accumulation) were fitted using the final parameters, and visually inspected for plausibility.

In similar studies, the best-fitting parameters were only obtained after multiple iterations of the optimization procedure (Fernandez et al., 2022). Therefore, the optimization process was run multiple times in an attempt to further refine models and reduce error. The parameter values were changed in each iteration to reflect the values provided by the previous iteration. This process of refining only stopped after two consecutive unsuccessful iterations (i.e. no improvement in RMSE or MAE), and the parameter estimates from the final model showing improvement were taken forwards as the best parameter estimates.

Standard errors of the best parameter estimates were calculated using a bootstrapping technique, which was repeated 10 times. Bootstrapping was carried out following the methods described by Fernandez et al. (2022) and Luedeling et al. (2021), as Fernandez et al. (2022) describe it, it

involves randomly sampling the residuals for the blossom onset dates calculated during the calibration phase of the PhenoFlex model and adding the randomly sampled residuals to the original blossom onset dates, effectively creating a new dataset. Secondly, the parameter fitting procedure was re-run, generating a new set of parameters. This procedure was repeated ten times, and the standard deviation across the bootstrapping iterations was calculated as a measure of uncertainty in the parameter estimates. Finally, the 16th and 84th percentiles were calculated, which can be used to characterize the standard error in non-normally distributed data (Fernandez et al., 2022). The blossom onset dates for the validation dataset were estimated using the parameters generated by each of the ten bootstrapped replicates, and uncertainty was expressed as the standard deviation of the ten replications.

6.3.3.4. How well can models parameterized using a single year of citizen science data predict blossom dates across orchard-growing areas in that year?

To attempt to understand how blossom onset phenology changes across Great Britain, the parameter estimates generated in the previous section were used to estimate blossom onset dates for grid squares without records. Temperature data for grid squares known to contain orchards, based on a map of known orchard locations in 2016, from the Ordnance Survey MasterMap (www.ordnancesurvey.co.uk), were extracted, and converted to hourly series using the stack_hourly_temps function from the chillR package (Luedeling et al., 2023) as described previously. Blossom dates were modelled using the parameter estimates generated from the parameter estimates of each of the bootstrapping procedures. To assess uncertainty in these estimates, the standard deviation of the predictions across each of the bootstrapping replications was calculated, as well as the 16th and 84th percentiles, which represent the standard error in non-normally distributed samples. The 'blossom onset period' was also calculated for each cultivar, as being between the 25th and 75th percentile predicted blossom dates.

6.4. Results

6.4.1. Does blossom phenology shift across a latitudinal gradient in Great Britain, across a single year?

Across the four cultivars, a total of 449 verified and validated records were received in 2022. These records had a good geographical spread across Great Britain. The split of these records can be found in Table 6.2 and the locations in Figure 6.1.

Cultivar	Total Records	Unique grid squares	Model calibration records	Model validation records
Apple 'Bramley'	64	54	41	13
Cherry 'Stella'	25	20	15	5
Pear 'Conference'	118	92	69	23
Plum 'Victoria'	242	178	133	45

Table 6.2. Number of records of each cultivar used in the analysis.



Figure 6.1. Geographic location of blossom onset record submissions for each cultivar

Linear mixed-effects models to assess geographical trends in phenology revealed significantly delayed blossom onset phenology at more northerly latitudes for 'Stella', 'Conference' and 'Victoria', ranging from 1.22 ± 0.18 days per ° of latitude further north ('Victoria') to 1.49 ± 0.63 days ('Conference'). (Table 6.3, Figure 6.2).

 Table 6.3. Linear model output assessing the change in blossom onset date against latitude.

 Positive estimates indicate delayed phenology at higher latitudes

Cultivor	Estimato	SF	statistia	Corrected p-
Cultival	LSumate	SE	statistic	value
Apple 'Bramley'	0.79	0.52	1.51	0.135
Cherry 'Stella'	1.39	0.48	2.88	0.017
Pear 'Conference'	1.49	0.63	2.37	0.025
Plum 'Victoria'	1.22	0.18	6.65	< 0.001



Figure 6.2. Relationship between latitude and blossom onset date for 2022. Shaded area represents 95% confidence interval

6.4.2. Can citizen science data be used to parameterize existing phenology models in a space-for-time substitution?

The PhenoFlex modelling framework produced RMSE values for the calibration dataset of between 2.4 (Stella) and 8.0 days (Conference), and MAE values of between 1.9 days (Stella) and 6.3 days (Conference). RMSE values for the validation dataset also varied, ranging from between 4.6 days (Victoria) and 8.0 days (Conference), and MAE values of between 3.5 days (Victoria) and 6.4 days (Conference) (Figure 6.3).



Figure 6.3. Observed versus predicted blossom onset dates for calibration and validation data sets and model performance metrics for each cultivar. Black line indicates perfect agreement between observed and predicted blossom dates

Parameter values, and their uncertainty, used in the PhenoFlex modelling framework are presented in Table 6.4, and the values and uncertainty varied between cultivars. These parameters produced temperature response curves of which appeared plausible for all four fruits, with chill responses stopping between 8°C-12°C depending on the fruits, with optimum chilling temperatures around 7.5°C for all four fruits. Heat accumulation curves also appeared plausible, with optimum temperatures for all four fruits around 15°C-18°C (Figure 6.4).

Parameter	Apple	Cherry	Pear	Plum
	'Bramley'	'Stella'	'Conference'	'Victoria'
yc	70.34 ± 11.68	28.84 ± 2.48	32.40 ± 1.67	60.74 ± 3.15
ZC	223.59 ± 46.13	165.93 ± 21.19	271.76 ± 9.13	122.08 ± 9.67
s1	0.99 ± 0.26	0.80 ± 0.19	1.00 ± 0.20	0.80 ± 0.14
Tu	17.82 ± 3.58	17.18 ± 1.19	16.62 ± 1.41	14.80 ± 0.35
E0	3209.96 ± 43.21	3348.03 ± 26.08	3391.97 ± 1.41	3369.83 ± 0.46
E1	9720.66 ± 47.32	9831.58 ± 25.91	9902.75 ± 1.06	9893.16 ± 0.58
A0	6021.25 ± 53.99	6067.81 ± 67.13	6092.49 ± 32.98	6673.28 ± 28.71
A1	$5.93\text{E}{+}13~\pm$	$5.94\text{E}{+}13~\pm$	$5.94\text{E}{+}13~\pm$	$5.94\text{E}{+}13~\pm$
	1.90E+8	1.93E+8	2.49E+8	2.15E+8
Tf	6.55 ± 0.40	7.86 ± 1.63	7.13 ± 0.17	7.03 ± 0.76
Tc	20.59 ± 8.49	20.02 ± 2.62	42.94 ± 20.55	36.09 ± 7.62
Tb	6.87 ± 0.84	7.43 ± 0.87	3.90 ± 0.96	6.66 ± 0.23
slope	14.80 ± 4.07	10.32 ± 6.22	5.02 ± 2.03	4.32 ± 7.28

 Table 6.4. Best fitting parameters for each cultivar. ± values indicate standard deviation

 following the bootstrapping procedure.



Figure 6.4. Chill and heat response plots for each cultivar. The chill response (blue dashed line) shows chill effectiveness over a time period of 1200 hours assuming constant temperature. The heat response (red solid line) represents heat efficiency for constant temperatures.

6.4.3. How well can models parameterized using a single year of citizen science data predict blossom dates across orchard-growing areas in that year?

Projections across known orchard-growing areas of Great Britain for all four fruits revealed delayed blossom onset in more northerly and higher latitudes. The earliest blossom dates in 2022 were predicted to be found in urban areas, and this is especially noticeable in the projections for 'Conference' (Figure 6.5). The uncertainty of these estimates also varied between varieties, with the lowest uncertainty produced in 'Victoria' (Figure 6.6A). The blossom onset period also varied between varieties, with 'Victoria' being the earliest, starting on March 25th and ending on March 28th. The blossom onset period was longer and later in the year for the other three varieties (6 days for 'Stella' and 7 days for 'Bramley' and 'Conference) (Figure 6.6B).



Figure 6.5. Maps showing predictions of blossom onset dates for known orchard locations within Great Britain.



Figure 6.6. A) Boxplot showing distribution of blossom onset dates (the box highlights the main blossom onset period). B) Boxplot showing distribution of standard errors of the blossom onset predictions

6.5. Discussion

It is well documented that citizen science recordings of the natural world may provide a good proxy for estimating dates of key phenological stages, and this study looks to utilize citizen science data to parameterize tree phenology models and ultimately to provide a national scale prediction of patterns of blossom across a blossom season.

6.5.1. Does blossom phenology shift across a latitudinal gradient in Great Britain, across a single year?

Perhaps unsurprisingly, given the evidence from a study in the United Kingdom pointing towards delayed blossom phenology at higher latitudes in plants (Büntgen et al., 2022), analysis of the FruitWatch submissions highlighted significant delays in flowering at more northerly sites for three of the four cultivars. It is well documented that temperature plays a large role in determining blossom dates (Reeves et al., 2022) and given the gradient of temperature across Great Britian, with warmest temperatures generally in the South-West, gradually decreasing at increasingly northerly latitudes (Fox & Jönsson, 2019), this result is much to be expected.

6.5.2. Can citizen science data be used to parameterize existing phenology models in a space-for-time substitution?

Here, root-mean-square Error (RMSE) values varied, ranging from 2.4 to 8.0 days. In comparison to similar studies utilizing the PhenoFlex framework, the citizen science informed models perform similarly to models collected through either standardized data collection schemes (RMSE 14-18 days in various Italian olive cultivars (Didevarasl et al., 2023)), experimental systems simulating different temperature conditions (RMSE 2.3-5.5 days in experimentally managed apple trees (Fernandez et al., 2022)) or other proxies for estimating blossom (RMSE 4.56 days using airborne pollen data from trees in the *Platanus* genus (Picornell et al., 2024)).

The PhenoFlex framework is not the only modelling framework in existence for predicting blossom onset dates, and there are a range of different models that are commonly used. When

considered alongside other fruit tree blossom onset models produced using different modelling frameworks, the RMSE values presented here were also comparable. Legave et al. (2013) found RMSE values of between 3.6 and 5.3 days in western European 'Golden Delicious' apples using the Sequential Model, whereas Darbyshire et al. (2016) found better performance using the Chill Overlap model in 'Cripps Pink' apples in Australia. These comparisons, therefore, provide a promising outlook for using citizen science data to parameterize relatively complex phenology models.

Visual inspections of the temperature response curves revealed an optimum chilling temperature of around 7.5°C for all four fruits, and this optimum value is around the values reported in experimental systems on apple and cherry (Guak & Neilsen, 2013). Whilst the varieties differed between this study and the experimental study, the optimum chilling temperatures found here are in the same ballpark, again indicating that data generated through FruitWatch appears to be suitable for use with the PhenoFlex modelling framework. When considering the heat accumulation response, the optimum values for all four fruits are around 15°C, in keeping with the early spring temperatures around the flowering period, and again is similar to reported values from other studies (Luedeling et al., 2021).

6.5.3. How well can models parameterized using a single year of citizen science data predict blossom dates across orchard-growing areas in that year?

A major benefit of citizen science data is that it can come from multiple locations, covering a large geographic area and therefore capturing a wide range of temperature profiles. With plenty of evidence showing variable blossom phenology in different locations (Legave et al., 2015), as well as variable phenology of pollinators (Chapter 2), pests and natural enemies (Wearing et al., 2013), understanding how blossom dates vary across the country is important. With models produced by the PhenoFlex framework shown to perform adequately, coupled with the good geographic spread of records submitted to the FruitWatch platform, this study also looked to present a picture of the spatial variation in blossom onset dates across Great Britain for the 2022 blossom season.

By providing the models with temperature data for grid squares known to contain orchards, phenological gradients appear in multiple directions for all four fruits tested. Perhaps unsurprisingly given the well-established links between temperate fruit tree phenology and temperature, we see gradients related to latitude (delayed phenology at more northerly latitudes), elevation (delayed phenology at higher altitudes) and urbanization (advanced phenology in large urban areas such as London and Manchester).

The presence of urban heat islands (UHIs) is well established in Great Britain (Howard, 1833) and Great Britain is also seeing the UHI effect increase in intensity (Levermore et al., 2018). The effect of UHIs on phenology is also relatively well understood (Neil & Wu, 2006). (Jochner & Menzel, 2015) provide a comprehensive review of 45 studies on the phenology of a range of taxa in UHIs, and the majority of these studies show strong advances in phenological events. In the context of fruit tree phenology, Roetzer et al. (2000) show earlier blossom dates in urban compared with rural areas in central Europe in both apple and sweet cherry. Again, this evidence backs up the findings presented here, with clusters of early blossom onset concentrated around areas projected to suffer from the UHI effect (Chowienczyk et al., 2020) and this finding provides confidence that the predicted results fit with well-established ecological and phenological principles.

6.5.4. Implications for growers

The suitability of FruitWatch (and more generally, citizen science) recordings for predicting blossom dates of fruit trees comes with a number of real-world applications, ranging from climate change detection to informing precision management of fruit crops and their pests and pollinators. It is well known that climate influences phenology of fruit trees (Chmielewski et al., 2004; Reeves et al., 2022), and fruit tree pollinators (Chapters 2, 3 & 4). By building a long-term, spatially diverse set of records at the cultivar level, it is possible to detect local shifts in local phenology across a geographic area.

Whilst this study focusses explicitly on four types of fruit tree within Great Britain, it provides a framework for collecting citizen science data suitable for modelling spatial variation in blossom

phenology. The tree selection can be expanded, to include fruits such as apricots and peaches, and the spatial scale of the FruitWatch platform can easily be increased, to accept records from a wider geographic range. With reports of declining winter chill coming from growing regions warmer than Great Britian, such as northern Africa (Fernandez et al., 2023) and California (Luedeling et al., 2009), coupled with future predictions of further declines in winter chill in the same studies, finding cultivars with suitable chill requirements for a given area is crucial for maintaining commercially viable orchards. The FruitWatch project aims to build an open access, long-term database of flowering dates of various fruit types and cultivars across a large spatial scale, and the blossom data generated through this project could help to inform localised cultivar selection.

Given the importance of phenological synchrony between fruit tree blossom and pollination, the spatial understanding of blossom dates could be a vital tool in localised decision-making, which could influence, for example, whether particular species of non-crop flowering plants are sown between rows in an orchard. This can be done to plug "hungry gaps", or periods of low resource availability, by planting crops that flower at different periods to the main blossom period. Knowing when an orchard is likely to blossom is also important if managed pollinators are to be introduced. Managed pollinators cost money to introduce to an orchard, costing US growers an estimated \$350 million across all crops in 2009 (Rucker et al., 2012), so understanding when they are likely to be needed could result in a better targeted – and more cost-effective – intervention.

Whilst there can be confidence in the results presented here, both in terms of model parameterization and performance and spatial predictions, it is important to note that citizen science undeniably comes with challenges, especially opportunistic programs. Amongst concerns are that participants often have no scientific background, that submissions are biased towards easily accessible locations and non-working days (i.e. weekends and public holidays) (Courter et al., 2013), and that taxa may be misidentified. However, in the case of this study,

there did not appear to be large differences between the number of records submitted on each day, with fewer records submitted on Saturday than on every other day except Wednesday.

To conclude, the results presented here provide a promising outlook for the use of citizen science to inform blossom phenology models, and the potential positive benefits of this work are wide-ranging. Firstly, with appropriate quality control checks, both in terms of the data being used and the models themselves, this study shows citizen science data can be suitable for use in phenology modelling frameworks. Secondly, these models may inform growers of past, present, and with enough temporal resolution (which was unfortunately not available for this study), potential future trends in phenology. Looking to the future, this data could be used to support fine resolution and local decision-making across a national scale with relation to phenological synchrony with wild pollinators, and the timing of deployment of managed pollinators and pest and disease treatments.

6.6. Acknowledgements

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7. General discussion

7.1. Overview

Pome and stone fruit orchards form a sizeable proportion of Great Britain's agricultural sector, and their reliance on insect pollination, including both managed and wild pollinators, is well known. The effects of climate change on spatio-temporal dynamics of the crops, insect pollinators and the interactions between them need to be understood to safeguard production in the face of an uncertain climate future.

There are gaps in knowledge of spatio-temporal trends in both fruit crop and pollinators, and this thesis is an attempt to begin to fill some of these gaps. In terms of pollinators, focussing specifically on wild bees (the largest contributing group to pollination value of four British apple varieties), significant gaps remain around how climate change has impacted, and will continue to impact where bees will be able to survive and when they will be active. Chapter 2, 3 and 4 look to answer these questions, incorporating a wide range of Great Britain's bee fauna beyond apple pollinating species with Chapter 2 providing an initial look at temporal synchrony between apple blossom from a long-term, systematically collected blossom dataset, and pollinators from the surrounding area, and Chapters 3 and 4 exploring nationwide spatio-temporal shifts in British wild bee fauna, including many important apple pollinators. The climate envelope models generated in Chapter 4 are used in Chapter 5, alongside presence only data from the Global Biodiversity Information Facility (GBIF, 2024a) to assess the extent to which bees are actually filling these envelopes, and whether life-history traits can be used to predict range filling success.

For fruit crops, whilst climate driven spatial trends, particularly around apple crops, have been recently predicted (Marshall et al., 2023; Polce et al., 2014), issues still remain around the spatial replicability of temporal trends and predictions derived from observations from single orchards. Therefore, Chapter 6 looked to the public to help fill this data gap and provide data to inform more geographically relevant blossom predictions.

This section summarises the findings of each chapter and provides recommendations for safeguarding wild pollination of pome and stone fruit crops, as well as conserving wider wild bee diversity. The methodological limitations of the overall study will be subsequently discussed and used to direct recommendations for further investigations in the future.

7.2. Synthesis of key findings

7.2.1.How has the phenology of apple trees and their pollinators at the National Fruit Collection (Kent, GB) shifted over time, and is a phenological mismatch developing?

Summary of Key Findings

- Blossom onset, full bloom, pollinator emergence and pollinator peak flight dates all advanced throughout the study period, with most the extreme advance happening before 1990.
- Pollinating wild bee species showed species-specific shifts in phenology, ranging from 5.8 to 12.5 days per 1 °C rise in average Jan-Apr temperature.
- This advance was primarily driven by early spring temperatures, but apple blossom
 (6.7 ± 0.9 day advance per 1 °C rise in average Jan-Apr temperature) and pollinator
 flight phenologies (6.7 ± 0.9 day advance per 1 °C rise in average Jan-Apr
 temperature) have different sensitivities to temperature change potentially driving
 shifts in synchrony between apple blossom and pollinating wild bee species.

The study described in Chapter 2 intended to give an initial overview of temporal synchrony between apple blossom at a focal orchard (the National Fruit Collection, Kent) and pollinating wild bee phenology (from citizen science records from Kent) both over time and in relation to temperature. It found that both apple blossom and pollinator phenology had advanced significantly, and importantly at different rates, over time and in relation to climate, with apple blossom dates appearing to be more sensitive to changes in spring temperature than pollinator phenology. Across the whole pollinating community, there did not appear to be a significant decoupling of the plant-pollinator interaction. It is known that increasing pollinator diversity provides a buffer against temporal mismatches in apple orchards through temporal partitioning of pollinator flight periods (Bartomeus et al., 2013), however, the finding of species-specific shifts in wild bee pollinator phenology does raise questions about the future of the diversity of bee pollinators. Some species such, as *Bombus pratorum*, are advancing their emergence phenology almost twice as quickly as apple blossom, raising questions about the sustainability of some interactions between apple blossom and individual pollinator species. This may be offset by new species entering the wild 'pollination workforce', as has been seen as recently as 2001 with *Bombus hypnorum* being discovered in Great Britain for the first time (Goulson & Williams, 2001).

7.2.2.How has the phenology of wild bee pollinators of apple (and the wider wild bee fauna) shifted over time across Great Britain, and what might phenology look like under future climate scenarios?



Chapter 3 looked to dig deeper into phenological trends of apple pollinating wild bee species, given the species-specific responses to temperature change found in Chapter 2, alongside a larger section of Great Britain's bee fauna. It included 88 of the most data-rich species (out of

the 270 of species found in Britain) for the period 1980-2019 and provided novel insights into phenological trends in British wild bees. The results found in this chapter were concurrent with other studies, showing advances in bee phenology in warmer years and over time (Bartomeus et al., 2011; Chapter 2).

There was also significant variation in the scale of species responses, with advances of as much as 21.7 ± 4.4 days per 1°C rise in temperature (*Sphecodes geofrellus*) in a fixed 90-day window prior to emergence. Whilst these results are therefore not entirely surprising given the speciesspecific responses shown in Chapter 2, it again raises questions about the potential temporal community composition of wild bees. Furthermore, it raises questions as to whether there will be sufficient resources to provide for an ever earlier emerging populations of bees, or whether "hungry gaps" might occur under future climate scenarios, where there are insufficient resources to support newly emerged bees.

The sliding-window section from Chapter 4 attempted to refine these models. Where Chapter 3 looked at a temperature during a fixed, 90-day time window, Chapter 4 looked at species' responses to temperature species-specific time windows, varying in duration and placement. This study also showed that the phenological responses to climate change to be species-specific, with variation in timing and duration of the best time window, and differential magnitude of response to temperature changes during this window.

7.2.3. How has the suitable climate envelope (area with climate suitable for persistence) of wild bee pollinators of apple (and the wider wild bee fauna) shifted over time, and what might climate envelopes look like under future climate scenarios?



The latter part of Chapter 4 investigated spatial shifts in suitable climate area for 88 species of wild bee in Great Britain, through implementation of Species Distribution Models using climate data from a historic, current and future (under two different climate scenarios). Poleward movement of northern range boundaries is unsurprising as the climate becomes increasingly hospitable between time periods, and this trend is similar to a number of other studies. The scale of the shift in the northern range boundary are similar to other studies (e.g. Aguirre-Gutiérrez et al., 2016; Rasmont et al., 2015), given that, for many species, the northern range boundary is in southern or central Great Britain, and there is often plenty of room for expansion.

This work implies that a northward shift should be expected, and that there will be changes in community composition in the future. However, unlike Kerr et al. (2015), most species were not expected to be caught in a "climatic vice", with limited evidence for species southern range boundary moving faster than its northern range boundary. This is likely because much of the British bee fauna is currently found in warmer climates in continental Europe and as a result can tolerate the temperatures that Great Britain is predicted to experience even under extreme future climate change. This work does not necessarily mean that the full climate envelope will be

filled simply because the climate becomes suitable. There are a range of other barriers that may prevent species' fully filling their ranges. Such barriers include lack of suitable forage and nesting habitat and impassable geographic barriers, which have both been shown to influence realised distributions of wild bees (Andersson et al., 2017; Antoine & Forrest, 2021).

7.2.4. How well are wild bee pollinators of apple (and the wider wild bee fauna) currently filling their climate envelopes, and are differences in range filling ability driven by life history traits?

Summary of Key Findings

envelopes.

- Range filling varied between species, ranging from 9.7% (*Epeolus cruciger*) to
 128.3% (*Bombus lapidarius*) of suitable climate cells. Mean range filling was 43.8%
 of suitable climate cells containing an observation.
 Large species with polylectic foraging behaviour and that overwinter in more
 advanced developmental stages filled a greater proportion of their climate
 - Highlights significant barriers to range filling for many species, namely a lack of, or fragmented areas of, suitable forage and nesting habitat.

The main findings of Chapter 5 were that traits relating to generalism (polylectic foraging behaviour), dispersal (and possibly detectability) (larger body size) and developmental stage were all traits related to successful range filling. This result is perhaps unsurprising, with similar findings coming from studies on other taxonomic groups (Estrada et al., 2018; Seliger et al., 2021), however, provides important insight into some of the barriers faced by many species to successfully fill their climate envelopes.

This work suggests that Great Britain's conservation mantra of "bigger, better and more joined up" (Burns et al., 2023; Lawton, 2010) will be vital to ensuring bees can successfully keep pace with climate change, and potentially promote Great Britain as a centre of bee diversity. Conversely, Chapter 5 also raises concerns that generalist species that are better able to fill their ranges might be able to outcompete rarer, specialist species, and as a result there may be a homogenization of Great Britain's wild bee fauna dominated by generalist species. It also has implications for pollination. With a particular focus on fruit tree crops, the areas with suitable wild bee pollination provision are likely to change and may bring about changes in suitable growing areas beyond traditional growing hotspots.

7.2.5.Is it possible to produce reliable predictions blossom dates of fruit trees from data submitted to Citizen Science platforms?

Summary of Key Findings		
•	Linear models show significant latitudinal delays in flowering onset of 1.49±0.63	
	days per degree latitude further north (Pear 'Conference'), with significant delays	
	also seen in Cherry 'Stella' (1.39±0.48 days) and Plum 'Victoria' (1.22±0.18 days).	
•	The models produced using citizen science data performed comparably to models	
	generated from systematically collected data, indicating suitability of citizen science	
	data.	
•	Predictions for 2022 showed a wave of blossom across Great Britain, with earlier	
	blossom onset at southerly, lower elevation, urban areas.	

With Chapters 2, 3 and 4 showing changes in wild bee phenology, Chapters 4 and 5 showing likely changes in the distributions of wild bees (including many that can pollinate pome and stone fruit crops in Great Britain), and other studies highlighting changes in areas suitable for orchard growth (Marshall et al., 2023; Polce et al., 2014) understanding variation in blossom dates across the country is vital. Knowing when a crop is likely to flower in a particular area is key to assessing whether blossom dates of any potential newly suitable areas for pome and stone fruit crops are likely to be in synchrony with pollinator activity. In order to do this, blossom dates of fruit trees from across Great Britain are needed. Systematically collected apple

blossom phenology data is sparse, so Chapter 6 looks to assess the suitability of citizen science data for making cultivar-specific blossom phenology predictions.

Using records submitted to a new recording scheme, FruitWatch, Chapter 6 shows that citizen science has the potential to be a powerful tool in creating blossom predictions across Great Britain, with models performing similarly to studies using systematically collected data using the same modelling framework (Didevarasl et al., 2023; Picornell et al., 2024). Predictions for blossom dates across a single growing season, 2022, revealed several, unsurprising, patterns in blossom dates of four popular cultivars. Blossom appeared to occur earlier more southerly, lower elevation and urban locations, all of which are linked to warmer temperatures.

7.3. Wider implications

Overall, this thesis presents evidence to support the overarching scientific consensus that biodiversity is shifting and will continue to shift both spatially and temporally in response to climate change. The changes in spatio-temporal distributions of wild bee pollinators shown in this study, and of fruit crops shown elsewhere (Marshall et al., 2023) will inevitably mean changes in the pollination supply to existing orchards and may create sufficient supply in new locations within Great Britain. The implications of this work are wide ranging, from ecosystem functioning, service provisioning and resilience to financial implications for growers to large scale societal issues related to nutrition.

7.3.1.Implications for society

There are a range of stakeholders within society who are likely to be impacted by changing spatio-temporal synchrony between fruit orchards and wild bee pollinators. Pome and stone fruit production in Great Britain was valued at over £375 million in 2022 (DEFRA, 2023b) so naturally, any changes in potential productivity of orchards are of primary interest to fruit growers. Production, and by extension growers' livelihoods depend, at least partially, on synchrony between fruit tree blossom and wild bee pollinators. While this thesis does not look to predict scale and magnitude of change in the actual amount of wild bee pollination that will

be available to growers, which could indeed be positive as well as negative, it shows changes are likely to occur and should prompt further research into specific impacts of these changes. It is not only the growers who will feel the impact of any changes in wild pollination supply to fruit orchards in Great Britain. There are a range of other stakeholders dependent on fruit as a source of income. These range from the approximately 38,000 seasonal labourers (McKinney et al., 2023) to export companies, who exported £14 million worth of orchard fruit in 2022 (DEFRA, 2023b).

The inevitable spatio-temporal reshuffling of the bee communities is likely to pose growers with difficult questions concerning conserving wild bee diversity in the face of climate change. Whilst, at face value, warmer climate leading to a greater number of species being able to survive in more northerly areas seems like a positive, especially with increased biodiversity shown to safeguard apple pollination (Bartomeus et al., 2013; Blitzer et al., 2016), whether species diversity will actually increase in more northerly areas remains to be seen. Many of the species predicted to move north are generalist species, capable of nesting in a variety of different habitats and foraging on a range of plants, and while generalists are often good pollinators of apple (Hutchinson et al., 2021; Kleijn et al., 2015), community homogenization may lead to loss of resilience of the pollination services, with the Biodiversity Insurance Hypothesis stating that "biodiversity insures ecosystems against declines in their functioning because many species provide greater guarantees that some will maintain functioning even if others fail" (Yachi & Loreau, 1999). Indeed, inter-annual stability in crop pollination is shown to be greater in more diverse communities (Senapathi, et al., 2021a),

From a global societal viewpoint, any potential changes in synchrony between pollinatordependent crops and their pollinators are likely to also have knock-on impacts on fruit consumption and public health. It is estimated that globally, 3-5% of fruit, vegetable, and nut production is lost due to inadequate pollination, resulting in 427,000 excess deaths annually from lack of healthy food consumption (Smith et al., 2022).

While this thesis focusses on fruit pollination in Great Britain, the impact of climate-driven phenological asynchrony between other pollinator-dependent crops and their pollinators is unlikely to be evenly distributed across the globe and is likely to disproportionately impact low-income countries such as Somalia, Guinea Bissau and the Philippines (Millard et al., 2023). This is attributed to the fact that low-income countries are often both less resilient to yield losses and more reliant on the micronutrients provided by insect pollinated crops (University of Bristol, 2020). Complete loss of the pollination service could see over 70 million people from low-income countries become newly deficient in vitamin A, and global fruit supplies could be reduced by 22.9% should this complete loss occur (Smith et al., 2015). While this thesis cannot make explicit predictions about loss of spatio-temporal synchrony between other crops and pollinators in other regions of the globe, it can highlight the area as being worthy of further research.

7.3.2.Implications for biodiversity management

Great Britain sits in a potentially advantageous position to provide areas with suitable climate for many species (Ollerton et al., 2014), and climate change could present an opportunity for the nation to position itself as a hotspot for wild bee diversity with thermal constraints likely to be released at species' northern range boundaries. The research presented in this thesis conforms with this theory and predicts widespread northward shifts in suitable climate areas. There is already evidence of bees moving northwards, such as *Bombus hypnorum*, which since its discovery in Great Britain in 2001 (Goulson & Williams, 2001) is now found as far north as the highlands of Scotland. It is not just species currently present in Great Britain that might benefit from future climate change, but there is evidence to suggest that many species are crossing the channel from continental Europe and establishing nesting populations in southern areas of Great Britain. As recently as April 2023, a new species, *Andrena ventralis*, was discovered nesting in Hampshire (Else, 2023). Since 2000, at least nine species of wild bee have been newly discovered nesting in Great Britain (Roberts, 2024, pers. comm.).

The spatio-temporal reshuffling of the bee communities is also likely to ask questions of policy makers and conservation practitioners. Prioritising choices in conservation management is a complex topic, and there are a range of reasons that a species might be considered for conservation (Habel et al., 2020). This ranges from an individual species level, where at-risk species are prioritised to global scale, with the creation of "global hotspots" of biodiversity, where sites with high species diversity are prioritised (Cadotte & Tucker, 2018). Conservation can also be based on the potential for an area, and the species living within it to provide ecosystem services that benefit society (Chan et al., 2006).

Therefore, deciding on the motivation for providing conservation intervention is vital to best tailoring any interventions to the specific goal. If the aim is to conserve an ecosystem service provision, such as pollination, then prioritising those species which contribute most to pollination is critical. In this case, community homogenization may be an overall benefit, with crop pollination predominantly carried out by a small subset of the overall bee fauna (Kleijn et al., 2015), comprising mainly generalist species expected to benefit from community homogenization. An alternative school of thought is that every species is a "natural share-holder of the biosphere with an inherent right to survival" (Kassas, 2002), and thus more conservation effort should be given to species that are at greater risk, which often include specialist species constrained to certain habitats or energy sources (Biesmeijer et al., 2006).

The arguments presented above highlight one of the many complex decisions conservation planners and practitioners have to make when deciding where to prioritise. Whether or not community homogenisation is a good thing (increase in pollinators of crops) or a bad thing (loss of specialist species), many traditional metrics of measuring the impact of biodiversity management fail to account for the impacts of homogenization (Filippi-Codaccioni et al., 2010) and therefore the impact of climate change on the most sensitive individual species is sometimes missed. Filippi-Codaccioni et al. (2010) recommend monitoring population trends in specialist species as part of any biodiversity management interventions, and this is something that must be done to understand what impact climate change is having on wild bee populations at the species level. Additionally, the 2023 State of Nature report (Burns et al., 2023) showed that wild bees are not the only species that will require conservation attention in Great Britain, with 16% of flora and fauna in the country are at risk of being lost. Efforts to mitigate the impacts of climate change (as well as other drivers of change) will also need to focus on taxa beyond wild bees, creating further difficult management decisions for policy makers and practitioners.

7.4. Methodological limitations

7.4.1. Data limitations

This thesis has relied on a variety of data sources to reach conclusions about climate-driven shifts in spatio-temporal dynamics of apple pollination and general wild bee diversity, and analyses were restricted to the data contained within the BWARS (www.bwars.com), FruitWatch (www.fruitwatch.org), GBIF (www.gbif.org) and National Fruit Collection datasets (www.nationalfruitcollection.org.uk).

7.4.2.Use of citizen science in agro-ecology

A key theme that runs throughout this thesis is the use of citizen science data. The BWARS, GBIF and FruitWatch datasets, which form essential datasets for analyses in every analytical chapter, are examples of how public engagement can help scientists detect trends in biodiversity and ecosystem service provision. Currently, citizen science is well established in biodiversity monitoring, but a potentially underused source in agricultural planning. As with most data types, citizen science comes with a range of benefits and costs. Citizen science, as was shown with the FruitWatch project, has the potential to unlock trends across a large spatial scale, without the need for often costly standardized monitoring schemes run by paid experts, and there are numerous studies highlighting the value of citizen science in answering a variety of ecological questions (Adler et al., 2020). Recording accuracy varies between studies, and depends on many factors, including the difficulty of identifying taxa of interest, complexity of methodology and training provision (Kosmala et al., 2016). This thesis shows that for studies such as FruitWatch, asking a distinct scientific question while asking recorders to submit

relatively straightforward data from a narrow range of familiar taxa, citizen science can be a powerful tool.

However, even simple recording schemes such as FruitWatch come with challenges. Firstly, and perhaps most importantly, it is extremely difficult to verify the accuracy of the cultivar submitted by the recorder (i.e. is the cultivar given by the recorder actually the cultivar of the tree) given the visual similarity of trees of the same fruit type (i.e. between two different cultivars of apple trees). This means that cultivar was taken at face value, and therefore there may be a small subset of records incorrectly classified. There are several other minor concerns with the FruitWatch platform, discussed in greater detail in Chapter 6, such as the variability between recorders when determining flowering stages. Initially, the five phenological stages encompassing the flowering period were too narrow, and consensus between recorders and an individual recorder looking at the same pictures was poor. This was overcome by combining similar stages, resulting in a much greater level of agreement. Despite these issues this thesis has shown that citizen science data may still be a powerful tool in assessing agro-ecological trends.

7.5. Recommendations for future research, policy, and practice

Great Britain, particularly England, is currently undergoing a transition away from the existing "Countryside Stewardship" (CS) schemes for funding environmental protection measures to a new scheme, known as "Environmental Land Management" schemes (ELMs) (DEFRA, 2023). Existing CS schemes make no provision for phenology monitoring or mitigation of phenological shifts. Given the scale of historic phenological shifts in fruit crops shown in chapter 2 of this thesis, it is recommended that crop phenology monitoring should be included in any payment schemes under the new ELMs schemes. Whilst demands placed on growers by environmental schemes can be considerable, resulting in many growers showing a reluctance to participate in environmental management schemes (Hejnowicz et al., 2016), the FruitWatch app has shown it can be a simple process to record blossom phenology. This thesis recommends that growers, for whom synchrony between fruit tree blossom and pollinators is of greatest concern,

should be encouraged to keep records and begin to build a nationwide picture of commercial orchard phenology to complement the citizen science data held by FruitWatch.

This research could also be expanded to include other wild pollinating insects. Hoverflies also play a role in fruit tree pollination, valued at £700,000 per year across four cultivars of apple in Great Britain (Garratt et al., 2016), and pollination of crops more generally (Hodgkiss et al., 2018; Jauker & Wolters, 2008; Sánchez et al., 2022) and large citizen science datasets also exist documenting observations of hoverflies in Great Britain, held by the Hoverfly Recording Scheme (www.hoverfly.uk). Phenological shifts revealed by this dataset are relatively well understood (Hassall et al., 2017), however the impact of climate on spatial distributions of hoverflies is less clear, and the methods used in Chapter 4 and 5 of this thesis could be implemented to better understand how hoverfly distribution might change in the future.

While this thesis presents findings relating fruit tree pollination within Great Britain, this is only an example system, and the methods presented here could be applied to interactions between pollinators and other pollinator dependent crops and regions. This would, however, require the creation and curation of large pollinator record and crop phenology datasets. Global citizen science records of many taxa exist in various recording schemes, most notably the Global Biodiversity Information Facility (GBIF – www.gbif.org) (GBIF, 2024), but these datasets are not spread equally across the globe. Invertebrate records, for example, are concentrated predominantly in industrialised countries (Deacon et al., 2023) and pollinator dependent crop growth spread across the globe. The spatial mismatch in data sources will need to be addressed to fully maximise the potential of the methods applied in this thesis to have a truly global application.
7.6. Concluding remarks

This thesis provides new perspectives on climate-driven spatio-temporal shifts on wild bees, and their ability to provide pollination services to fruit crops in Great Britain. The findings presented here provide new insights into spatio-temporal dynamics of wild bees and fruit crops, presenting historic trends, current positions, and future projections. This thesis demonstrates for the first time that Great Britain, could potentially become a regional hotspot in bee diversity provided the right management regimes are implemented, and discusses the potential impact of the likely spatial reshuffling of wild bee populations from both pollination and species diversity perspectives. The knowledge and discussion provided in this thesis provides a baseline for further work, highlights key gaps in available data, and provides recommendations for policymakers and practitioners that will help safeguard both crop pollination and wider bee diversity in the face of an uncertain climate.

8. References

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9. Supplementary material

9.1. Climate driven shifts in the synchrony of apple (*Malus x domestica* Borkh.) flowering and pollinating bee flight phenology.

Table S2.1. List of pollinator species used in the analysis* Not included in species level analysis**Species x year combination with at least 20 records

Spacios	Total number of records	Number of data rich		
Species	Total number of records	years**		
Andrena chrysosceles	1172	23		
Andrena cineraria*	257	3		
Andrena dorsata	1587	23		
Andrena flavipes	3510	39		
Andrena fulva	1163	25		
Andrena haemorrhoa	2177	39		
Andrena minutula	2299	32		
Andrena nigroaenea	1366	30		
Andrena nitida	1414	25		
Andrena scotica	1850	31		
Bombus hortorum	3497	36		
Bombus hypnorum*	960	9		
Bombus lapidarius	6614	41		
Bombus pascuorum	8796	44		
Bombus pratorum	4227	40		
Bombus terrestris*	8840	41		
Lasioglossum calceatum	2585	34		
Lasioglossum pauxillum*	881	17		
Osmia bicornis	1153	23		



Figure S2.1. Trends in number of pollinator records over time



Figure S2.2. Average temperature (top) and total rainfall (bottom), for each period (Jan-Apr, May-Sep, Oct-Dec) between 1970-2017 in Kent. Shaded area indicates 95% confidence intervals.



Figure S2.3. Impact of rainfall between January and April on peak apple flowering date. Shaded area indicates 95% confidence intervals.



Figure S2.4. Trends in composition of pollinator records, split by Genus, over time.

 Table S2.2. Change in flight dates (in days) of individual species over time. GAM tests for non-linear trends, where no significant non-linear trend was found, LM was used to test for change per year.

 Negative values indicate advancement in phenology, positive values indicate delay.

 *, **, ***, indicates significance at 0.05, 0.01 and <0.01 respectively</td>

^B indicates species is bivoltine in the study area, and 'peak' refers to the peak of the first generation

 $^{\rm E}$ indicates species is primitively eusocial in the study area

$\begin{array}{rrrr} 0.21 & -4.914 & < 0.001^{***} \\ 0.19 & -1.925 & 0.068 \end{array}$).19 -2.831 0.007**) d significant non-linear trend 111 -2 548 0.015*	0.19 -2.831 0.007*** d significant non-linear trend 0.11 -2.548 0.015* 0.20 -2.968 0.006** 0.20 -2.354 0.026* 0.19 -2.532 0.019*	0.19 -2.831 0.007** d significant non-linear trend 0.11 -2.548 0.015* 0.20 -2.968 0.006** 0.20 -2.954 0.006** 0.20 -2.354 0.026* 0.19 -2.532 0.019* 0.19 -2.532 0.019* d significant non-linear trend d significant non-linear trend	0.19 -2.831 0.007** d significant non-linear trend 0.11 -2.548 0.015* 0.20 -2.968 0.006** 0.20 -2.968 0.006** 0.20 -2.354 0.026* 0.19 -2.532 0.019* 19 -2.532 0.019* 3 significant non-linear trend d significant non-linear trend d significant non-linear trend d significant non-linear trend d significant non-linear trend 0.18 0.18 -0.444 0.659
-1.04 0.1 -0.36 0.1 -0.55 0.1	GAM showed	GAM showed : -0.28 0.1 -0.59 0.2 -0.46 0.2 -0.48 0.1	GAM showed s -0.28 0.1 -0.59 0.2 -0.46 0.2 -0.48 0.1 GAM showed GAM showed	GAM showed s -0.28 0.1 -0.59 0.2 -0.46 0.2 -0.48 0.1 GAM showed i GAM showed i GAM showed i -0.08 0.1 GAM showed
<0.001***	0.001**	0.001** 0.004** 0.003** 0.012* 0.009*	0.001** 0.004** 0.003** 0.012* 0.012* 0.026* 0.031*	0.001** 0.001** 0.003** 0.012* 0.012* 0.009* 0.009* 0.031* 0.031* 0.031* 0.209
27.480 * 4.892 6.990	7.093	7.093 9.711 10.450 7.190 8.211	7.093 9.711 10.450 7.190 8.211 3.389 3.655 8.864 •	7.093 9.711 10.450 7.190 8.211 3.389 3.665 8.864 8.864 1.555 14.250
1.00 1.00 1.70	3.65 1.00	3.65 1.00 1.00 1.00 1.00	3.65 1.00 1.00 1.00 1.00 3.71 2.57 2.57	3.65 1.00 1.00 1.00 1.00 2.57 2.57 2.57 2.57 2.57
1.00 1.00 1.40	2.94	2.94 1.00 1.00 1.00 1.00	2.94 1.00 1.00 1.00 1.00 2.99 2.06	2.94 1.00 1.00 1.00 2.99 2.06 2.06 2.44 2.08
0.003** 0.329 0.308	0.065	0.065 0.068 0.167 0.030* 0.134	0.065 0.068 0.167 0.134 0.134 0.139 0.143	0.065 0.068 0.167 0.139 0.139 0.139 0.139 0.143 inear trend 0.129 inear trend
-3.300 -1.000 -1.035	-1.939	-1.939 -1.884 -1.417 -2.287 -1.553	-1.939 -1.884 -1.417 -2.287 -1.553 -1.521 -1.501 cont hon-lin	-1.939 -1.884 -1.417 -2.287 -1.553 -1.521 -1.501 icant non-lii icant non-lii
0.34 0.42 0.33	0.27	0.27 0.17 0.43 0.20 0.27	0.27 0.17 0.43 0.20 0.27 0.26	0.27 0.17 0.43 0.20 0.26 0.26 0.27 0.27 owed signif
-1.13 -0.42 -0.34	-0.31	-0.52 -0.31 -0.60 -0.46 -0.42	-0.52 -0.31 -0.60 -0.46 -0.42 -0.42 -0.41 -0.41	-0.52 -0.31 -0.60 -0.46 -0.46 -0.40 -0.40 -0.41 GAM sh
0.002** 0.351 0.262	0.140	0.140 0.078 0.143 0.019* 0.149	0.140 0.078 0.143 0.149 0.149 0.149 0.102 0.066	0.140 0.078 0.143 0.149 0.149 0.149 0.102 0.066 0.066 0.006
11.810 0.776 1.448	1.965 3 580	1.965 3.580 2.267 6.188 2.116	1.965 3.580 2.267 6.188 6.188 2.116 2.856 2.759 5.162	1.965 3.580 2.267 6.188 6.188 2.116 2.116 2.759 5.162 5.162 5.162 6.936
1.00 1.26 2.12	3.18	3.18 1.72 1.00 1.00 2.05	3.18 1.72 1.00 1.00 2.05 2.05 1.00 2.46 2.46	3.18 1.72 1.00 1.00 2.05 1.00 2.46 2.54 2.54 2.54 2.54
1.00 1.14 1.70	2.55	2.55 1.41 1.00 1.00 1.65	2.55 1.41 1.41 1.00 1.00 1.65 1.97 1.97 2.04	2.55 1.41 1.00 1.00 1.00 1.00 1.97 2.04 2.04 2.11
Andrena chrysosceles Andrena dorsata ^B Andrena flavipes ^B	Andrena fulva Andrena haemorroha	Andrena fulva Andrena haemorroha Andrena minutula ^B Andrena nigroaenea Andrena nitida	Andrema fulva Andrema haemorroha Andrena minutula ^B Andrena nitida Andrena scotica Bombus hortorum E	Andrema fulva Andrema haemorroha Andrema mimutula ^B Andrema nitida Andrema scotica Bombus hortorum E Bombus lapidarius E Bombus pascuorum E Bombus pascuorum E

Model	Significant Variables	estimate	std.error	z value	Pr(> Z)
Bramley First Flowering	Jan-Apr Rain (mm)	0.036	0.012	2.84	0.005 **
	Jan-Apr Temp (°C)	-6.463	0.755	8.333	<0.001 ***
	Oct-Dec Temp (°C)	-0.219	0.559	0.387	0.699
	May-Sep Temp (°C)	-0.297	0.771	0.38	0.704
	May-Sep Rain (mm)	0.011	0.015	0.241	0.809
Bramley Peak Flowering	Jan-Apr Rain (mm)	0.042	0.013	3.095	0.002 **
	Jan-Apr Temp (°C)	-6.713	0.856	7.649	<0.001 ***
	Oct-Dec Temp (°C)	0.233	0.601	0.382	0.702
	May-Sep Temp (°C)	0.657	1.14	0.569	0.569
Pollinator First Flight	Jan-Apr Rain (mm)	0.011	0.028	0.402	0.688
	Jan-Apr Temp (°C)	-8.511	2.312	3.586	<0.001 ***
	May-Sep Temp (°C)	-0.706	2.132	0.326	0.744
	May-Sep Rain (mm)	0.008	0.026	0.299	0.755
Pollinator Peak Flight	Jan-Apr Rain (mm)	0.027	0.037	0.724	0.469
	Jan-Apr Temp (°C)	-6.496	2.129	2.972	0.003 ***
	May-Sep Temp (°C)	0.801	2.167	0.363	0.717
Peak Fight - Peak Flowering Mismatch		No significat	nt variables		
Flight Onset - Peak Flowering Mismatch		No significat	nt variables		

Table S2.3. Full model results following model averaging procedure for each of the phenology/climate model	ls
*. ** and *** indicate significance at 0.05, 0.01 and <0.001 respectively	
Table S2.4. Change in flight dates (in days) of individual species per 1°C rise in average Jan-Apr temperatu	re
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Negative values indicate advancement in phenology, positive values indicate delay.	
*, **, *** indicates significance at 0.05, 0.01 and <0.001 respectively	

*, **, *** indicates significance at 0.05, 0.01 and <0.001 respectively
 ^B indicates species is bivoltine in the study area, and 'peak' refers to the peak of the first generation
 ^E indicates species is primitively eusocial in the study area

Servering	Flight Onset				Peak Flight					
Species	estimate	std.error	t value	p.val	ue	estimate	std.error	t value	p.val	ue
Andrena chrysosceles	-8.27	3.64	-2.272	0.034	*	-7.96	2.44	-3.266	0.004	**
Andrena dorsata ^B	-7.28	4.02	-1.812	0.084		-5.34	1.65	-3.243	0.004	**
Andrena flavipes ^B	-3.05	3.28	-0.931	0.358		-6.83	1.84	-3.721	< 0.001	***
Andrena fulva	-8.63	2.19	-3.948	< 0.001	***	-8.45	1.45	-5.833	< 0.001	***
Andrena haemorroha	-5.25	1.59	-3.291	0.002	**	-5.03	0.92	-5.481	< 0.001	***
Andrena minutula ^B	-11.17	3.19	-3.499	0.001	**	-6.75	1.52	-4.451	< 0.001	***
Andrena nigroaenea	-5.15	1.79	-2.879	0.008	**	-6.74	1.57	-4.295	< 0.001	***
Andrena nitida	-5.77	2.18	-2.650	0.014	*	-5.70	1.48	-3.848	< 0.001	***
Andrena scotica	-2.68	2.57	-1.043	0.306		-6.00	1.11	-5.428	< 0.001	***
Bombus hortorum ^E	-9.96	3.27	-3.048	0.004	**	-5.73	2.31	-2.484	0.018	*
Bombus lapidarius ^E	-11.05	3.14	-3.515	0.001	**	-7.68	2.19	-3.509	0.001	**
Bombus pascuorum ^E	-7.83	2.38	-3.293	0.002	**	-4.30	1.97	-2.188	0.034	*
Bombus pratorum ^E	-12.53	2.73	-4.594	< 0.001	***	-9.59	2.30	-4.175	< 0.001	***
Lasioglossum calceatum ^{B,E}	-5.25	4.01	-1.309	0.200		-3.45	3.21	-1.076	0.290	
Osmia bicornis	-1.89	2.71	-0.698	0.493		-4.04	1.78	-2.270	0.034	*

9.2. Climate-driven phenological shifts in emergence dates of British bees

Species	Number of Records	Number of Years**	Lecty	Overwintering Stage	Emergence Period	Voltinism	Trait Group
Andrena barbilabris	2936	38	Polylectic	Adult within cocoon	Spring	Univoltine	А
Andrena bicolor	7508	40	Polylectic	Adult within cocoon	Spring	Bivoltine	В
Andrena chrysosceles	5014	40	Polylectic	Adult within cocoon	Spring	Univoltine	А
Andrena cineraria	3849	34	Polylectic	Adult within cocoon	Spring	Variable	С
Andrena clarkella	2797	40	Oligolectic	Adult within cocoon	Spring	Univoltine	D
Andrena denticulata	1150	27	Polylectic	Prepupa	Summer	Univoltine	Е
Andrena dorsata	6549	38	Polylectic	Adult within cocoon	Spring	Bivoltine	В
Andrena flavipes	10853	40	Polylectic	Adult within cocoon	Spring	Bivoltine	В
Andrena florea	713	20	Oligolectic	Prepupa	Spring	Univoltine	F
Andrena fucata	1174	30	Polylectic	Prepupa	Spring	Univoltine	G
Andrena fulva	5293	40	Polylectic	Adult within cocoon	Spring	Univoltine	А
Andrena fuscipes	1802	33	Oligolectic	Prepupa	Summer	Univoltine	Н
Andrena haemorrhoa	10941	40	Polylectic	Adult within cocoon	Spring	Univoltine	А
Andrena helvola	1213	28	Polylectic	Adult within cocoon	Spring	Univoltine	А
Andrena humilis	709	21	Oligolectic	Adult within cocoon	Spring	Univoltine	D
Andrena labialis	900	21	Oligolectic	Adult within cocoon	Spring	Variable	Ι
Andrena labiata	1308	25	Polylectic	Adult within cocoon	Spring	Univoltine	А
Andrena minutula	7298	40	Polylectic	Adult within cocoon	Spring	Bivoltine	В
Andrena nigroaenea	6709	40	Polylectic	Adult within cocoon	Spring	Univoltine	А
Andrena nitida	6043	39	Polylectic	Adult within cocoon	Spring	Univoltine	А
Andrena ovatula	2027	34	Polylectic	Adult within cocoon	Spring	Univoltine	А
Andrena praecox	1425	34	Oligolectic	Adult within cocoon	Spring	Univoltine	D
Andrena scotica	7926	40	Polylectic	Adult within cocoon	Spring	Univoltine	А
Andrena subopaca	4141	40	Polylectic	Adult within cocoon	Spring	Variable	С
Andrena synadelpha	678	24	Polylectic	Adult within cocoon	Spring	Univoltine	А
Andrena thoracica	1672	32	Polylectic	Adult within cocoon	Spring	Variable	С
Andrena trimmerana	1311	32	Polylectic	Adult within cocoon	Spring	Bivoltine	В

Table S2.1. Species included in this analysis, and their life history traits** Species x year combination with at least 20 records

Anthidium manicatum	1787	30	Polylectic	Prepupa	Summer	Univoltine	Е
Anthophora bimaculata	1963	32	Polylectic	Prepupa	Summer	Univoltine	Е
Anthophora plumipes	6349	36	Polylectic	Adult within cocoon	Spring	Univoltine	А
Bombus bohemicus	2186	32	No Lectic Status	Adult (female only)	Spring	Univoltine	J
Bombus campestris	1528	33	No Lectic Status	Adult (female only)	Spring	Univoltine	J
Bombus distinguendus	1061	20	Polylectic	Adult (female only)	Summer	Univoltine	Κ
Bombus hortorum	13773	40	Polylectic	Adult (female only)	Spring	Univoltine	L
Bombus humilis	3438	27	Polylectic	Adult (female only)	Spring	Univoltine	L
Bombus jonellus	3573	32	Polylectic	Adult (female only)	Spring	Bivoltine	М
Bombus lapidarius	27935	40	Polylectic	Adult (female only)	Spring	Univoltine	L
Bombus monticola	1890	34	Polylectic	Adult (female only)	Spring	Univoltine	L
Bombus pascuorum	39605	40	Polylectic	only)	Spring	Univoltine	L
Bombus pratorum	16749	40	Polylectic	Adult (female only)	Spring	Bivoltine	М
Bombus ruderarius	797	24	Polylectic	Adult (female only)	Spring	Univoltine	L
Bombus rupestris	1680	23	No Lectic Status	Adult (female only)	Spring	Univoltine	J
Bombus sylvestris	3148	39	No Lectic Status	Adult (female only)	Spring	Univoltine	J
Dasypoda hirtipes	1190	31	Oligolectic	Prepupa	Summer	Univoltine	Н
Epeolus cruciger	1454	33	No Lectic Status	Prepupa	Summer	Univoltine	Ν
Epeolus variegatus	1571	34	No Lectic Status	Prepupa	Summer	Univoltine	Ν
Halictus rubicundus	4300	40	Polylectic	Adult (female only)	Spring	Univoltine	L
Halictus tumulorum	7413	40	Polylectic	Adult (female only)	Spring	Univoltine	L
Hylaeus brevicornis	1697	35	Polylectic	Prepupa	Summer	Variable	0
Hylaeus communis	5326	40	Polylectic	Prepupa	Summer	Variable	0
Hylaeus confusus	1408	36	Polylectic	Prepupa	Summer	Variable	0
Hylaeus dilatatus	1810	35	Polylectic	Prepupa	Summer	Univoltine	Е
Hylaeus hyalinatus	2443	39	Polylectic	Prepupa	Summer	Variable	0
Lasioglossum albipes	4047	40	Polylectic	Adult (female only)	Spring	Univoltine	L
Lasioglossum calceatum	10436	40	Polylectic	Adult (female only)	Spring	Univoltine	L
Lasioglossum fulvicorne	3202	39	Polylectic	Adult (female only)	Spring	Univoltine	L
Lasioglossum laevigatum	695	20	Polylectic	Adult (female only)	Spring	Univoltine	L
Lasioglossum lativentre	1516	27	Polylectic	Adult (female only)	Spring	Univoltine	L
Lasioglossum leucopus	3247	40	Polylectic	Adult (female only)	Spring	Univoltine	L

Lasioglossum leucozonium	6158	40	Polylectic	Adult (female only)	Spring	Univoltine	L
Lasioglossum malachurum	4856	40	Polylectic	Adult (female only)	Spring	Univoltine	L
Lasioglossum minutissimum	2335	40	Polylectic	Adult (female only)	Spring	Univoltine	L
Lasioglossum morio	9084	40	Polylectic	Adult (female only)	Spring	Univoltine	L
Lasioglossum parvulum	2754	39	Polylectic	Adult (female only)	Spring	Univoltine	L
Lasioglossum pauxillum	2939	27	Polylectic	Adult (female only)	Spring	Univoltine	L
Lasioglossum smeathmanellum	3142	40	Polylectic	Adult (female only)	Spring	Univoltine	L
Lasioglossum villosulum	5854	40	Polylectic	Adult (female only)	Spring	Variable	Р
Lasioglossum zonulum	1951	36	Polylectic	Adult (female only)	Spring	Univoltine	L
Megachile centuncularis	1954	36	Polylectic	Prepupa	Summer	Univoltine	Е
Megachile leachella	1175	28	Polylectic	Prepupa	Summer	Univoltine	Е
Megachile ligniseca	1566	29	Polylectic	Prepupa	Summer	Univoltine	Е
Megachile maritima	1019	26	Polylectic	Prepupa	Summer	Univoltine	Е
Megachile versicolor	1804	34	Polylectic	Prepupa	Summer	Univoltine	Е
Megachile willughbiella	2836	36	Polylectic	Prepupa	Summer	Univoltine	Е
Melitta leporina	1055	24	Oligolectic	Adult within cocoon	Summer	Univoltine	Q
Melitta tricincta	823	24	Oligolectic	Adult within cocoon	Summer	Univoltine	Q
Osmia aurulenta	1439	29	Polylectic	Adult within cocoon	Spring	Univoltine	А
Osmia bicolor	1784	26	Polylectic	Adult within cocoon	Spring	Univoltine	А
Osmia bicornis	6012	40	Polylectic	Adult within cocoon	Spring	Univoltine	А
Osmia caerulescens	2306	34	Polylectic	Adult within cocoon	Spring	Variable	С
Sphecodes crassus	1134	23	No Lectic Status	Adult (female only)	Spring	Univoltine	J
Sphecodes ephippius	4182	40	No Lectic Status	Adult (female only)	Spring	Univoltine	J
Sphecodes geoffrellus	3209	40	No Lectic Status	Adult (female only)	Spring	Univoltine	J
Sphecodes gibbus	1329	32	No Lectic Status	Adult (female only)	Spring	Univoltine	J
Sphecodes hyalinatus	715	22	No Lectic Status	Adult (female only)	Spring	Univoltine	J
Sphecodes monilicornis	3452	37	No Lectic Status	Adult (female only)	Spring	Univoltine	J
Sphecodes pellucidus	2388	39	No Lectic Status	Adult (female only)	Spring	Univoltine	J
Sphecodes puncticeps	1313	26	No Lectic Status	Adult (female only)	Spring	Univoltine	J

Species	term	estimate	std.error	statistic	p.value
	Year	-0.51	0.15	-3.31	0.018
Andrena barbilabris	n	-0.03	0.05	-0.76	0.707
	Northing	-7.46E-06	1.19E-05	-0.63	0.874
	Year	-0.29	0.13	-2.17	0.124
Andrena bicolor	n	-0.06	0.02	-2.73	0.192
	Northing	3.85E-06	9.57E-06	0.40	0.897
	Year	-0.27	0.13	-2.12	0.124
Andrena chrysosceles	n	-0.05	0.02	-2.45	0.214
	Northing	5.64E-05	5.49E-05	1.03	0.856
	Year	-0.48	0.29	-1.69	0.212
Andrena cineraria	n	-0.01	0.04	-0.16	0.970
	Northing	2.54E-06	6.57E-06	0.39	0.897
	Year	-0.30	0.20	-1.49	0.272
Andrena clarkella	n	-0.10	0.07	-1.52	0.450
	Northing	-1.33E-05	4.75E-05	-0.28	0.902
	Year	-0.32	0.13	-2.35	0.109
Andrena denticulata	n	-0.08	0.07	-1.12	0.585
	Northing	5.43E-06	2.25E-05	0.24	0.904
	Year	-0.20	0.17	-1.20	0.394
Andrena dorsata	n	-0.03	0.01	-2.23	0.230
	Northing	7.95E-06	2.95E-05	0.27	0.902
	Year	-0.29	0.13	-2.24	0.114
Andrena flavipes	n	-0.03	0.01	-2.95	0.192
	Northing	-4.87E-06	4.05E-06	-1.20	0.856
	Year	-0.37	0.35	-1.03	0.445
Andrena florea	n	0.32	0.22	1.45	0.489
	Northing	-1.61E-04	1.75E-04	-0.92	0.874
	Year	-0.56	0.23	-2.42	0.097
Andrena fucata	n	-0.23	0.18	-1.29	0.514
	Northing	-2.52E-05	3.59E-05	-0.70	0.874
	Year	0.03	0.21	0.15	0.923
Andrena fulva	n	-0.08	0.04	-1.94	0.295
	Northing	7.75E-06	1.91E-05	0.41	0.897
	Year	-0.10	0.16	-0.61	0.648
Andrena fuscipes	n	-0.05	0.06	-0.75	0.707
	Northing	-1.31E-05	5.33E-06	-2.47	0.382
Andrena haemorrhoa	Year	-0.15	0.15	-1.01	0.445

Table S3.2. Species-level models with emergence date (day of year) as a function of time (year).

	n	-0.01	0.01	-1.05	0.602
	Northing	-1.24E-05	1.89E-05	-0.66	0.874
	Year	0.27	0.33	0.82	0.543
Andrena helvola	n	-0.14	0.10	-1.43	0.489
	Northing	-1.19E-04	8.34E-05	-1.43	0.762
	Year	-0.36	0.30	-1.18	0.401
Andrena humilis	n	-0.27	0.22	-1.22	0.529
	Northing	-4.65E-06	5.14E-06	-0.90	0.874
	Year	-0.33	0.18	-1.81	0.192
Andrena labialis	n	-0.03	0.11	-0.33	0.911
	Northing	-4.43E-05	7.77E-05	-0.57	0.874
	Year	-0.34	0.18	-1.85	0.177
Andrena labiata	n	-0.22	0.08	-2.63	0.197
	Northing	-1.63E-05	6.17E-06	-2.65	0.382
	Year	-0.15	0.14	-1.09	0.424
Andrena minutula	n	-0.04	0.02	-2.30	0.230
	Northing	-4.43E-05	3.25E-05	-1.36	0.762
Andrena nigroaenea	Year	-0.18	0.16	-1.16	0.401
	n	0.00	0.02	0.02	0.984
	Northing	-5.77E-06	9.29E-06	-0.62	0.874
	Year	-0.19	0.18	-1.04	0.445
Andrena nitida	n	-0.03	0.02	-1.64	0.406
	Northing	-7.56E-06	7.88E-05	-0.10	0.950
	Year	-0.70	0.23	-3.08	0.028
Andrena ovatula	n	-0.05	0.10	-0.52	0.863
	Northing	-2.27E-07	4.09E-06	-0.06	0.967
	Year	-0.30	0.17	-1.84	0.175
Andrena praecox	n	-0.16	0.11	-1.47	0.477
	Northing	7.44E-05	5.55E-05	1.34	0.762
	Year	-0.20	0.14	-1.45	0.281
Andrena scotica	n	-0.04	0.02	-2.21	0.230
	Northing	-1.21E-06	1.35E-05	-0.09	0.950
	Year	-0.07	0.17	-0.41	0.779
Andrena subopaca	n	-0.05	0.03	-1.76	0.348
	Northing	-9.57E-06	3.10E-05	-0.31	0.902
	Year	-0.19	0.24	-0.79	0.562
Andrena synadelpha	n	-0.73	0.41	-1.80	0.348
	Northing	-5.12E-06	4.68E-06	-1.09	0.856
Andrena thoracica	Year	-0.49	0.18	-2.75	0.050
	n	0.08	0.07	1.01	0.602

	Northing	5.22E-09	2.09E-06	0.00	0.998
	Year	-0.20	0.12	-1.74	0.201
Andrena trimmerana	n	-0.19	0.07	-2.73	0.192
	Northing	1.88E-06	4.39E-06	0.43	0.897
	Year	-0.36	0.18	-2.07	0.125
Anthidium manicatum	n	-0.08	0.08	-1.03	0.602
	Northing	-3.82E-06	6.45E-06	-0.59	0.874
	Year	-0.33	0.15	-2.13	0.124
Anthophora bimaculata	n	-0.09	0.05	-1.80	0.348
	Northing	9.96E-07	3.15E-06	0.32	0.902
	Year	-0.26	0.35	-0.73	0.580
Anthophora plumipes	n	-0.01	0.03	-0.43	0.878
	Northing	-4.69E-06	1.72E-05	-0.27	0.902
	Year	-0.57	0.23	-2.43	0.097
Bombus bohemicus	n	-0.09	0.04	-2.04	0.281
	Northing	3.05E-05	1.89E-05	1.61	0.762
	Year	-0.37	0.31	-1.19	0.394
Bombus campestris	n	-0.22	0.13	-1.75	0.348
	Northing	-2.07E-05	5.37E-05	-0.38	0.897
	Year	-1.16	0.69	-1.68	0.223
Bombus distinguendus	n	0.05	0.12	0.38	0.890
	Northing	-1.91E-04	8.10E-05	-2.36	0.392
	Year	0.00	0.20	0.00	0.997
Bombus hortorum	n	-0.01	0.01	-0.97	0.616
	Northing	2.63E-05	1.95E-05	1.35	0.762
	Year	-0.29	0.42	-0.69	0.605
Bombus humilis	n	0.07	0.04	1.79	0.348
	Northing	-1.24E-04	1.48E-04	-0.84	0.874
	Year	-0.88	0.36	-2.42	0.097
Bombus jonellus	n	0.00	0.04	-0.12	0.971
	Northing	2.08E-05	2.70E-05	0.77	0.874
	Year	-0.06	0.21	-0.28	0.846
Bombus lapidarius	n	0.00	0.01	-0.37	0.890
	Northing	-2.40E-05	2.39E-05	-1.00	0.858
	Year	-0.55	0.24	-2.30	0.109
Bombus monticola	n	-0.06	0.05	-1.23	0.528
	Northing	4.95E-06	3.12E-05	0.16	0.950
	Year	-0.11	0.20	-0.55	0.684
Bombus pascuorum	n	0.00	0.00	0.18	0.970
	Northing	-2.53E-05	3.23E-05	-0.78	0.874

	Year	-0.43	0.22	-1.96	0.140
Bombus pratorum	n	-0.01	0.01	-1.31	0.514
	Northing	-4.03E-06	3.30E-05	-0.12	0.950
	Year	-0.56	0.66	-0.85	0.531
Bombus ruderarius	n	-0.05	0.50	-0.10	0.971
	Northing	1.97E-05	2.91E-05	0.68	0.874
	Year	0.11	0.41	0.27	0.846
Bombus rupestris	n	-0.24	0.07	-3.21	0.192
	Northing	-2.42E-04	8.89E-05	-2.72	0.382
	Year	-0.40	0.26	-1.55	0.247
Bombus sylvestris	n	-0.01	0.06	-0.09	0.971
	Northing	6.40E-05	3.78E-05	1.69	0.762
	Year	-0.03	0.27	-0.11	0.947
Dasypoda hirtipes	n	-0.15	0.16	-0.95	0.616
	Northing	-3.29E-06	6.65E-06	-0.49	0.897
	Year	-0.03	0.20	-0.17	0.916
Epeolus cruciger	n	0.01	0.08	0.14	0.971
	Northing	-1.68E-04	6.54E-05	-2.56	0.382
	Year	-0.61	0.17	-3.59	0.011
Epeolus variegatus	n	-0.08	0.08	-1.02	0.602
	Northing	5.34E-06	2.48E-06	2.15	0.435
	Year	-0.54	0.15	-3.60	0.010
Halictus rubicundus	n	0.01	0.06	0.21	0.969
	Northing	-7.51E-06	1.32E-05	-0.57	0.874
	Year	-0.70	0.14	-4.88	0.001
Halictus tumulorum	n	0.00	0.02	0.06	0.973
	Northing	-3.54E-06	1.01E-05	-0.35	0.897
	Year	-0.11	0.26	-0.40	0.780
Hylaeus brevicornis	n	0.08	0.15	0.55	0.856
	Northing	3.64E-05	2.88E-05	1.26	0.826
	Year	-0.05	0.16	-0.30	0.846
Hylaeus communis	n	-0.04	0.03	-1.37	0.496
	Northing	-4.14E-05	2.82E-05	-1.47	0.762
	Year	-0.17	0.15	-1.14	0.404
Hylaeus confusus	n	-0.22	0.11	-1.97	0.295
	Northing	-7.49E-05	4.68E-05	-1.60	0.762
	Year	-0.30	0.32	-0.95	0.469
Hylaeus dilatatus	n	-0.01	0.15	-0.07	0.973
	Northing	-2.40E-04	2.13E-04	-1.13	0.856
Hylaeus hyalinatus	Year	-0.50	0.15	-3.32	0.018

	n	0.03	0.06	0.43	0.878
	Northing	9.93E-06	8.42E-06	1.18	0.856
	Year	-0.68	0.23	-3.01	0.028
Lasioglossum albipes	n	-0.02	0.05	-0.48	0.876
	Northing	7.10E-06	2.87E-05	0.25	0.904
	Year	-0.18	0.15	-1.24	0.380
Lasioglossum calceatum	n	-0.02	0.01	-1.28	0.514
	Northing	8.48E-06	1.12E-05	0.76	0.874
	Year	-0.49	0.18	-2.73	0.050
Lasioglossum fulvicorne	n	-0.07	0.04	-1.57	0.427
	Northing	8.31E-06	7.51E-05	0.11	0.950
	Year	0.21	0.43	0.49	0.730
Lasioglossum laevigatum	n	-0.25	0.23	-1.06	0.602
	Northing	4.82E-04	3.51E-04	1.37	0.762
	Year	-0.01	0.45	-0.02	0.996
Lasioglossum lativentre	n	-0.26	0.12	-2.13	0.280
	Northing	-1.41E-04	6.88E-05	-2.05	0.506
Lasioglossum leucopus	Year	-0.21	0.17	-1.24	0.380
	n	-0.09	0.07	-1.30	0.514
	Northing	-2.25E-05	2.07E-05	-1.09	0.856
	Year	-0.11	0.18	-0.62	0.648
Lasioglossum leucozonium	n	-0.04	0.02	-1.59	0.427
	Northing	7.88E-06	1.07E-05	0.74	0.874
	Year	-0.37	0.17	-2.22	0.115
Lasioglossum malachurum	n	-0.04	0.02	-2.26	0.230
	Northing	2.66E-04	1.17E-04	2.26	0.392
	Year	-0.21	0.21	-0.97	0.461
Lasioglossum minutissimum	n	-0.03	0.09	-0.29	0.919
	Northing	1.20E-06	1.03E-05	0.12	0.950
	Year	-0.34	0.16	-2.08	0.125
Lasioglossum morio	n	0.02	0.01	1.07	0.602
	Northing	4.32E-06	6.61E-06	0.65	0.874
	Year	-0.26	0.18	-1.43	0.283
Lasioglossum parvulum	n	0.01	0.06	0.19	0.969
	Northing	-1.77E-05	1.64E-05	-1.08	0.856
	Year	-0.46	0.31	-1.49	0.274
Lasioglossum pauxillum	n	-0.02	0.04	-0.56	0.856
	Northing	3.23E-05	4.88E-05	0.66	0.874
Lasioglossum	Year	-0.43	0.22	-1.93	0.147
smeathmanellum	n	0.06	0.07	0.87	0.652

	Northing	6.84E-06	7.53E-06	0.91	0.874
	Year	-0.37	0.18	-2.06	0.125
Lasioglossum villosulum	n	0.00	0.03	0.02	0.984
	Northing	-5.20E-06	1.16E-05	-0.45	0.897
	Year	-0.54	0.27	-2.04	0.125
Lasioglossum zonulum	n	-0.33	0.13	-2.63	0.192
	Northing	-1.47E-05	8.53E-05	-0.17	0.950
	Year	-0.26	0.23	-1.11	0.416
Megachile centuncularis	n	-0.09	0.11	-0.78	0.706
	Northing	3.31E-06	9.12E-06	0.36	0.897
	Year	-0.02	0.26	-0.09	0.947
Megachile leachella	n	-0.22	0.18	-1.22	0.529
	Northing	-3.91E-06	4.31E-06	-0.91	0.874
	Year	-1.05	1.01	-1.04	0.445
Megachile ligniseca	n	-0.15	0.36	-0.41	0.890
	Northing	2.08E-04	2.56E-04	0.81	0.874
	Year	-0.56	0.27	-2.08	0.125
Megachile maritima	n	0.09	0.17	0.53	0.863
	Northing	4.96E-06	4.70E-06	1.06	0.856
	Year	-1.40	0.48	-2.90	0.038
Megachile versicolor	n	0.06	0.16	0.36	0.890
	Northing	3.41E-04	1.41E-04	2.42	0.382
	Year	-0.67	0.16	-4.21	0.003
Megachile willughbiella	n	-0.01	0.04	-0.21	0.969
	Northing	1.34E-05	9.81E-06	1.37	0.762
	Year	-0.37	0.17	-2.18	0.124
Melitta leporina	n	-0.03	0.10	-0.30	0.919
	Northing	-1.70E-06	4.73E-06	-0.36	0.897
	Year	-0.27	0.16	-1.70	0.212
Melitta tricincta	n	-0.06	0.12	-0.51	0.864
	Northing	4.52E-05	6.16E-05	0.73	0.874
	Year	-0.21	0.21	-0.97	0.461
Osmia aurulenta	n	0.03	0.08	0.44	0.878
	Northing	8.01E-06	7.75E-06	1.03	0.856
	Year	-0.33	0.44	-0.75	0.580
Osmia bicolor	n	-0.01	0.10	-0.11	0.971
	Northing	4.63E-05	1.26E-04	0.37	0.897
	Year	-0.06	0.22	-0.28	0.846
Osmia bicornis	n	-0.07	0.02	-2.81	0.192
	Northing	1.63E-05	3.12E-05	0.52	0.897

	Year	-0.99	0.32	-3.11	0.028
Osmia caerulescens	n	-0.13	0.09	-1.37	0.496
	Northing	1.21E-04	8.65E-05	1.40	0.762
	Year	-1.56	0.48	-3.26	0.028
Sphecodes crassus	n	-0.42	0.20	-2.09	0.281
	Northing	-2.37E-05	1.42E-05	-1.67	0.762
	Year	-0.76	0.17	-4.56	0.002
Sphecodes ephippius	n	-0.03	0.03	-1.25	0.525
	Northing	4.12E-06	1.20E-05	0.34	0.897
	Year	-0.81	0.20	-4.13	0.003
Sphecodes geoffrellus	n	-0.15	0.06	-2.32	0.230
	Northing	8.41E-06	1.41E-05	0.60	0.874
	Year	-0.97	0.24	-3.98	0.006
Sphecodes gibbus	n	-0.14	0.14	-0.95	0.616
	Northing	-6.45E-06	1.11E-05	-0.58	0.874
	Year	-0.50	0.31	-1.60	0.247
Sphecodes hyalinatus	n	0.24	0.26	0.93	0.629
	Northing	-5.30E-05	8.10E-05	-0.65	0.874
	Year	-0.90	0.21	-4.28	0.003
Sphecodes monilicornis	n	-0.04	0.05	-0.84	0.664
	Northing	-5.66E-06	9.30E-06	-0.61	0.874
	Year	-0.70	0.14	-4.93	0.001
Sphecodes pellucidus	n	-0.03	0.05	-0.58	0.856
	Northing	-7.99E-06	1.64E-05	-0.49	0.897
	Year	-0.71	0.32	-2.20	0.124
Sphecodes puncticeps	n	-0.14	0.16	-0.89	0.651
	Northing	1.20E-05	8.64E-06	1.38	0.762

	Andrena barbilabris	Andrena bicolor	Andrena chrysosceles	Andrena cineraria	Andrena clarkella	Andrena denticulata	Andrena dorsata	Andrena flavipes	Andrena florea	Andrena fucata
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	Andrena fulva	Andrena fuscipes	Andrena haemorrhoa	Andrena helvola	Andrena humilis	Andrena labialis	Andrena labiata	Andrena minutula	Andrena nigroaenea	Andrena nitida
200 150 - 200	*****									
-	Andrena ovatula	Andrena praecox	Andrena scotica	Andrena subopaca	Andrena synadelpha	Andrena thoracica	Andrena trimmerana	Anthidium manicatum	Anthophora bimaculata	Anthophora plumipes
8 2 8 9 9		***					*****		****	
	Bombus bohemicus	Bombus campestris	Bombus distinguendus	Bombus hortorum	Bombus humilis	Bombus jonellus	Bombus lapidarius	Bombus monticola	Bombus pascuorum	Bombus pratorum
- 55 55 S			<u>.</u>	******	*****	******	*****	******		*******
•	Bombus ruderarius	Bombus rupestris	Bombus sylvestris	Dasypoda hirtipes	Epeolus cruciger	Epeolus variegatus	Halictus rubicundus	Halictus tumulorum	Hylaeus brevicornis	Hylaeus communis
8 8 8 8		,	·····	****		•••••••••••••••••••••••••••••••••••••••		******		
-	Hylaeus confusus	Hylaeus dilatatus	Hylaeus hyalinatus	Lasioglossum albipes	Lasioglossum calceatum	Lasioglossum fulvicorne	Lasioglossum laevigatum	Lasioglossum lativentre	Lasioglossum leucopus	Lasioglossum leucozonium
		•							*********	
-	Lasiogiossum malachurum	Lasioglossum minutissimum	Lasioglossum morio	Lasioglossum parvulum	Lasioglossum pauxillum	Lasioglossum smeathmanellum	Lasioglossum villosulum	Lasioglossum zonulum	Megachile centuncularis	Megachile leachella
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-	Megachile ligniseca	Megachile maritima	Megachile versicolor	Megachile willughbiella	Melitta leporina	Mellitta tricincta	Osmia aurulenta	Osmia bicolor	Osmia bicornis	Osmia caerulescens
20 15 15 15 15 15 15 15 15 15 15 15 15 15	.		****					1		
• •	Sphecodes crassus	Sphecodes ephippius	Sphecodes geoffrellus	Sphecodes gibbus	Sphecodes hyalinatus	Sphecodes monificornis	Sphecodes pellucidus	Sphecodes puncticeps	1960 1990 2000 2010 2020	1980 1990 2000 2010 2020
200 150 100			~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~	÷****						
	1980 2000 2010 2023	0 1980 1990 2000 2010 202	20 1980 2000 2010 2020	1980 1980 2000 2010 2020	1960 1960 2000 2010 2020	1880 1890 2000 2010 2020	1800 1990 2000 2010 2020	1980 1990 2000 2010 2020		

Figure S3.1. Trends in bee emergence dates over time. Shaded area represents 95% confidence intervals.

Emergence Date (Day of Year)

182

Species	term	estimate	std.error	statistic	p.value
	Temp	-10.79	2.75	-3.92	0.010
Andrena barbilabris	n	-0.02	0.04	-0.49	0.819
	Northing	-2.52E-05	1.13E-05	-2.24	0.400
	Temp	-7.83	3.10	-2.53	0.063
Andrena bicolor	n	-0.04	0.02	-1.56	0.546
	Northing	2.03E-06	9.28E-06	0.22	0.916
	Temp	-7.22	2.25	-3.21	0.029
Andrena chrysosceles	n	-0.04	0.02	-2.10	0.546
	Northing	3.75E-05	4.93E-05	0.76	0.834
	Temp	-6.31	2.70	-2.34	0.075
Andrena cineraria	n	-0.04	0.02	-1.87	0.546
	Northing	3.79E-06	6.25E-06	0.61	0.834
	Temp	-10.45	3.70	-2.82	0.058
Andrena clarkella	n	-0.05	0.06	-0.82	0.693
	Northing	-2.05E-05	3.94E-05	-0.52	0.834
	Temp	-3.77	2.69	-1.40	0.268
Andrena denticulata	n	-0.07	0.07	-0.90	0.684
	Northing	-6.15E-06	2.34E-05	-0.26	0.909
	Temp	-6.20	3.10	-2.00	0.112
Andrena dorsata	n	-0.02	0.02	-1.29	0.563
	Northing	7.16E-06	2.60E-05	0.28	0.909
	Temp	-10.46	2.34	-4.48	0.006
Andrena flavipes	n	-0.01	0.01	-1.75	0.546
	Northing	-4.38E-06	3.47E-06	-1.26	0.786
	Temp	-11.34	3.76	-3.02	0.058
Andrena florea	n	0.43	0.18	2.35	0.546
	Northing	-8.04E-05	1.27E-04	-0.64	0.834
	Temp	-10.18	4.23	-2.41	0.069
Andrena fucata	n	-0.15	0.17	-0.85	0.684
	Northing	-3.80E-05	3.64E-05	-1.05	0.834
	Temp	-7.28	3.00	-2.43	0.066
Andrena fulva	n	-0.04	0.03	-1.15	0.608
	Northing	7.33E-06	1.77E-05	0.41	0.866
	Temp	1.46	3.24	0.45	0.746
Andrena fuscipes	n	-0.05	0.06	-0.85	0.684
	Northing	-1.34E-05	5.31E-06	-2.52	0.382
Andrena haemorrhoa	Temp	-5.99	2.37	-2.52	0.063

Table S2.3. Species-level models with emergence date (day of year) as a function of temperature.

	n	-0.01	0.01	-0.63	0.769
	Northing	-2.25E-05	1.72E-05	-1.31	0.764
	Temp	-0.56	3.82	-0.15	0.895
Andrena helvola	n	-0.13	0.10	-1.29	0.563
	Northing	-5.96E-05	5.08E-05	-1.17	0.821
	Temp	-7.28	4.72	-1.54	0.222
Andrena humilis	n	-0.20	0.20	-0.97	0.684
	Northing	-2.96E-06	5.16E-06	-0.57	0.834
	Temp	-6.24	4.52	-1.38	0.281
Andrena labialis	n	0.07	0.14	0.49	0.819
	Northing	-3.00E-05	8.34E-05	-0.36	0.872
	Temp	-4.76	3.08	-1.55	0.219
Andrena labiata	n	-0.17	0.09	-2.00	0.546
	Northing	-1.99E-05	6.49E-06	-3.06	0.175
	Temp	-5.95	2.45	-2.42	0.066
Andrena minutula	n	-0.03	0.02	-1.47	0.546
	Northing	-5.12E-05	2.55E-05	-2.01	0.575
	Temp	-7.27	2.61	-2.78	0.058
Andrena nigroaenea	n	0.02	0.02	0.88	0.684
	Northing	-1.20E-05	8.31E-06	-1.45	0.748
	Temp	-4.54	2.20	-2.07	0.104
Andrena nitida	n	-0.02	0.01	-1.60	0.546
	Northing	-4.59E-05	5.20E-05	-0.88	0.834
	Temp	-11.80	4.72	-2.50	0.066
Andrena ovatula	n	0.04	0.11	0.39	0.865
	Northing	-2.87E-06	4.19E-06	-0.69	0.834
	Temp	-6.15	3.26	-1.88	0.130
Andrena praecox	n	-0.14	0.11	-1.30	0.563
	Northing	4.65E-05	5.02E-05	0.93	0.834
	Temp	-5.25	2.63	-2.00	0.112
Andrena scotica	n	-0.03	0.02	-1.57	0.546
	Northing	-7.98E-06	1.26E-05	-0.64	0.834
	Temp	-3.34	2.65	-1.26	0.310
Andrena subopaca	n	-0.05	0.03	-1.47	0.546
	Northing	-1.09E-05	2.48E-05	-0.44	0.866
	Temp	-0.95	4.91	-0.19	0.878
Andrena synadelpha	n	-0.73	0.44	-1.64	0.546
	Northing	-5.65E-06	5.25E-06	-1.07	0.834
Andrena thoracica	Temp	-3.32	4.37	-0.76	0.555
	n	0.08	0.09	0.90	0.684

	Northing	1.32E-07	2.35E-06	0.06	0.998
	Temp	-4.80	2.46	-1.95	0.121
Andrena trimmerana	n	-0.16	0.07	-2.23	0.546
	Northing	2.63E-06	4.37E-06	0.60	0.834
	Temp	-5.43	2.97	-1.83	0.143
Anthidium manicatum	n	-0.11	0.08	-1.44	0.546
	Northing	-3.69E-06	6.56E-06	-0.56	0.834
	Temp	-5.37	3.25	-1.65	0.185
Anthophora bimaculata	n	-0.07	0.06	-1.29	0.563
	Northing	-8.64E-07	3.14E-06	-0.27	0.909
	Temp	-8.18	3.18	-2.58	0.063
Anthophora plumipes	n	-0.02	0.01	-1.30	0.563
	Northing	-6.14E-06	1.57E-05	-0.39	0.866
	Temp	-8.86	3.32	-2.67	0.063
Bombus bohemicus	n	-0.05	0.04	-1.18	0.608
	Northing	1.37E-05	1.54E-05	0.89	0.834
	Temp	-7.46	5.61	-1.33	0.289
Bombus campestris	n	-0.19	0.13	-1.43	0.546
	Northing	-3.29E-05	4.94E-05	-0.66	0.834
	Temp	3.26	10.12	0.32	0.803
Bombus distinguendus	n	0.05	0.13	0.39	0.865
	Northing	-2.33E-04	9.78E-05	-2.38	0.400
	Temp	-6.86	3.18	-2.16	0.087
Bombus hortorum	n	0.00	0.01	0.03	0.981
	Northing	3.13E-05	1.85E-05	1.69	0.748
	Temp	-8.95	5.09	-1.76	0.159
Bombus humilis	n	0.07	0.03	2.13	0.546
	Northing	-1.03E-04	1.33E-04	-0.77	0.834
	Temp	-12.07	6.50	-1.86	0.136
Bombus jonellus	n	0.00	0.04	0.06	0.971
	Northing	2.58E-05	2.78E-05	0.93	0.834
	Temp	-6.82	2.68	-2.54	0.063
Bombus lapidarius	n	0.00	0.00	0.49	0.819
	Northing	-1.67E-05	2.22E-05	-0.75	0.834
	Temp	-6.28	5.07	-1.24	0.319
Bombus monticola	n	-0.06	0.05	-1.12	0.608
	Northing	5.00E-07	3.39E-05	0.01	0.998
	Temp	-7.01	3.05	-2.30	0.075
Bombus pascuorum	n	0.00	0.00	1.02	0.656
	Northing	-2.84E-05	3.03E-05	-0.94	0.834

	Temp	-11.80	3.00	-3.94	0.010
Bombus pratorum	n	-0.01	0.01	-1.74	0.546
	Northing	1.57E-05	2.90E-05	0.54	0.834
	Temp	-2.85	10.08	-0.28	0.817
Bombus ruderarius	n	-0.18	0.48	-0.37	0.865
	Northing	9.53E-06	2.66E-05	0.36	0.872
	Temp	-9.61	3.51	-2.74	0.063
Bombus rupestris	n	-0.21	0.06	-3.34	0.151
	Northing	-2.01E-04	5.34E-05	-3.76	0.116
	Temp	-8.47	4.19	-2.02	0.112
Bombus sylvestris	n	-0.03	0.05	-0.57	0.803
	Northing	5.05E-05	3.43E-05	1.47	0.748
	Temp	-1.93	6.19	-0.31	0.803
Dasypoda hirtipes	n	-0.13	0.17	-0.78	0.707
	Northing	-3.85E-06	6.91E-06	-0.56	0.834
	Temp	0.53	3.51	0.15	0.895
Epeolus cruciger	n	0.01	0.08	0.11	0.958
	Northing	-1.78E-04	5.56E-05	-3.20	0.145
	Temp	-4.74	4.18	-1.13	0.365
Epeolus variegatus	n	-0.02	0.09	-0.21	0.926
	Northing	4.36E-06	2.96E-06	1.47	0.748
	Temp	-7.11	3.19	-2.23	0.081
Halictus rubicundus	n	0.00	0.06	0.02	0.981
	Northing	-1.55E-05	1.41E-05	-1.10	0.834
	Temp	-11.37	3.26	-3.49	0.016
Halictus tumulorum	n	0.01	0.02	0.35	0.865
	Northing	-7.48E-06	1.12E-05	-0.67	0.834
	Temp	-1.33	4.16	-0.32	0.803
Hylaeus brevicornis	n	0.11	0.13	0.80	0.698
	Northing	3.26E-05	2.68E-05	1.22	0.819
	Temp	-1.53	3.20	-0.48	0.746
Hylaeus communis	n	-0.04	0.04	-1.06	0.633
	Northing	-4.17E-05	2.66E-05	-1.56	0.748
	Temp	-2.01	2.91	-0.69	0.587
Hylaeus confusus	n	-0.20	0.12	-1.65	0.546
	Northing	-8.33E-05	4.84E-05	-1.72	0.748
	Temp	-4.01	5.58	-0.72	0.575
Hylaeus dilatatus	n	0.02	0.15	0.11	0.958
	Northing	-2.83E-04	2.02E-04	-1.41	0.748
Hylaeus hyalinatus	Temp	-7.84	3.11	-2.52	0.063

	n	0.02	0.07	0.36	0.865
	Northing	8.92E-06	8.92E-06	1.00	0.834
	Temp	-9.16	4.04	-2.27	0.079
Lasioglossum albipes	n	-0.03	0.05	-0.55	0.803
	Northing	-3.62E-05	2.54E-05	-1.43	0.748
	Temp	-6.15	2.75	-2.24	0.081
Lasioglossum calceatum	n	-0.01	0.01	-0.88	0.684
	Northing	8.08E-06	1.06E-05	0.76	0.834
	Temp	-8.69	3.63	-2.40	0.067
Lasioglossum fulvicorne	n	-0.04	0.05	-0.92	0.684
	Northing	-1.86E-05	7.51E-05	-0.25	0.909
	Temp	2.55	5.55	0.46	0.746
Lasioglossum laevigatum	n	-0.27	0.24	-1.16	0.608
	Northing	4.51E-04	3.23E-04	1.40	0.763
	Temp	3.63	9.01	0.40	0.760
Lasioglossum lativentre	n	-0.29	0.14	-2.09	0.546
	Northing	-1.51E-04	6.38E-05	-2.36	0.400
	Temp	-2.72	3.40	-0.80	0.547
Lasioglossum leucopus	n	-0.08	0.07	-1.19	0.608
	Northing	-2.80E-05	2.00E-05	-1.40	0.748
	Temp	-1.60	3.61	-0.44	0.746
Lasioglossum leucozonium	n	-0.03	0.02	-1.46	0.546
	Northing	7.76E-06	1.07E-05	0.73	0.834
	Temp	-4.93	3.13	-1.58	0.201
Lasioglossum malachurum	n	-0.03	0.02	-1.64	0.546
	Northing	1.63E-04	1.05E-04	1.55	0.748
	Temp	-7.34	4.20	-1.74	0.158
Lasioglossum minutissimum	n	0.03	0.10	0.26	0.920
	Northing	2.03E-06	9.98E-06	0.20	0.916
	Temp	-11.01	2.85	-3.86	0.010
Lasioglossum morio	n	0.03	0.01	1.93	0.546
	Northing	2.40E-06	5.84E-06	0.41	0.866
	Temp	-7.96	3.27	-2.44	0.066
Lasioglossum parvulum	n	0.04	0.06	0.73	0.730
	Northing	-2.21E-05	1.55E-05	-1.43	0.748
	Temp	-11.47	5.19	-2.21	0.087
Lasioglossum pauxillum	n	-0.01	0.04	-0.19	0.926
	Northing	2.96E-06	4.28E-05	0.07	0.998
Lasioglossum	Temp	-5.02	4.58	-1.10	0.380
smeathmanellum	n	0.06	0.07	0.87	0.684

	Northing	6.20E-06	7.78E-06	0.80	0.834
	Temp	-8.99	3.47	-2.59	0.063
Lasioglossum villosulum	n	0.02	0.03	0.55	0.803
	Northing	-5.10E-06	1.12E-05	-0.45	0.866
	Temp	-11.53	5.29	-2.18	0.087
Lasioglossum zonulum	n	-0.25	0.13	-1.95	0.546
	Northing	1.78E-06	8.43E-05	0.02	0.998
	Temp	-2.86	3.58	-0.80	0.547
Megachile centuncularis	n	-0.14	0.10	-1.46	0.546
	Northing	3.77E-06	9.37E-06	0.40	0.866
	Temp	-1.93	4.47	-0.43	0.746
Megachile leachella	n	-0.20	0.17	-1.16	0.608
	Northing	-3.92E-06	4.21E-06	-0.93	0.834
	Temp	0.88	9.86	0.09	0.930
Megachile ligniseca	n	-0.41	0.30	-1.40	0.549
	Northing	-3.25E-07	1.68E-04	0.00	0.998
	Temp	-5.10	5.08	-1.00	0.435
Megachile maritima	n	0.14	0.18	0.76	0.712
	Northing	2.68E-06	5.09E-06	0.53	0.834
	Temp	-13.09	8.19	-1.60	0.200
Megachile versicolor	n	0.07	0.19	0.35	0.865
	Northing	1.47E-04	1.23E-04	1.19	0.821
	Temp	-11.29	3.09	-3.65	0.016
Megachile willughbiella	n	0.00	0.04	0.09	0.965
	Northing	1.89E-06	9.78E-06	0.19	0.916
	Temp	-7.85	3.96	-1.98	0.121
Melitta leporina	n	0.02	0.11	0.17	0.933
	Northing	-4.52E-06	4.73E-06	-0.96	0.834
	Temp	-2.40	3.06	-0.79	0.547
Melitta tricincta	n	-0.03	0.13	-0.20	0.926
	Northing	2.77E-05	6.39E-05	0.43	0.866
	Temp	-7.06	3.65	-1.93	0.124
Osmia aurulenta	n	0.05	0.08	0.68	0.735
	Northing	4.75E-06	7.25E-06	0.66	0.834
	Temp	-12.52	4.63	-2.71	0.063
Osmia bicolor	n	-0.02	0.08	-0.24	0.925
	Northing	-2.36E-06	9.58E-05	-0.02	0.998
	Temp	-2.79	2.92	-0.96	0.453
Osmia bicornis	n	-0.07	0.02	-3.68	0.068
	Northing	1.86E-05	2.94E-05	0.63	0.834

	Temp	-7.22	5.57	-1.30	0.300
Osmia caerulescens	n	-0.16	0.11	-1.41	0.546
	Northing	-2.29E-05	7.86E-05	-0.29	0.909
	Temp	-24.77	12.48	-1.99	0.121
Sphecodes crassus	n	-0.28	0.25	-1.12	0.608
	Northing	-3.21E-05	1.73E-05	-1.86	0.748
	Temp	-12.36	3.52	-3.51	0.016
Sphecodes ephippius	n	-0.02	0.03	-0.70	0.732
	Northing	-1.11E-05	1.26E-05	-0.88	0.834
	Temp	-12.98	4.08	-3.18	0.029
Sphecodes geoffrellus	n	-0.11	0.07	-1.52	0.546
	Northing	-2.76E-06	1.48E-05	-0.19	0.916
	Temp	-13.41	5.09	-2.64	0.063
Sphecodes gibbus	n	-0.04	0.16	-0.22	0.926
	Northing	-7.42E-06	1.25E-05	-0.60	0.834
	Temp	-5.66	4.82	-1.17	0.357
Sphecodes hyalinatus	n	0.27	0.28	0.96	0.684
	Northing	-7.17E-05	8.32E-05	-0.86	0.834
Sphecodes monilicornis	Temp	-13.40	4.54	-2.95	0.051
	n	-0.02	0.06	-0.33	0.870
	Northing	-7.41E-06	1.03E-05	-0.72	0.834
	Temp	-8.15	3.37	-2.42	0.066
Sphecodes pellucidus	n	-0.03	0.07	-0.51	0.819
	Northing	-1.04E-05	1.98E-05	-0.53	0.834
	Temp	-5.30	6.72	-0.79	0.547
Sphecodes puncticeps	n	-0.13	0.18	-0.71	0.732
	Northing	1.27E-05	9.43E-06	1.35	0.764



Figure S3.2. Trends in bee emergence dates against temperature. Shaded area represents 95% confidence intervals.

9.3. Spatio-temporal shifts in British wild bees in response to changing climate

 Table S4.1. Species included in this analysis

** Number of years with over 20 records

Encoing	Number of	Number of
Species	Records	Years**
Andrena barbilabris	2936	38
Andrena bicolor	7508	40
Andrena chrysosceles	5014	40
Andrena cineraria	3849	34
Andrena clarkella	2797	40
Andrena denticulata	1150	27
Andrena dorsata	6549	38
Andrena flavipes	10853	40
Andrena florea	713	20
Andrena fucata	1174	30
Andrena fulva	5293	40
Andrena fuscipes	1802	33
Andrena haemorrhoa	10941	40
Andrena helvola	1213	28
Andrena humilis	709	21
Andrena labialis	900	21
Andrena labiata	1308	25
Andrena minutula	7298	40
Andrena nigroaenea	6709	40
Andrena nitida	6043	39
Andrena ovatula	2027	34
Andrena praecox	1425	34
Andrena scotica	7926	40
Andrena subopaca	4141	40
Andrena synadelpha	678	24
Andrena thoracica	1672	32
Andrena trimmerana	1311	32

Anthidium manicatum	1787	30
Anthophora bimaculata	1963	32
Anthophora plumipes	6349	36
Bombus bohemicus	2186	32
Bombus campestris	1528	33
Bombus distinguendus	1061	20
Bombus hortorum	13773	40
Bombus humilis	3438	27
Bombus jonellus	3573	32
Bombus lapidarius	27935	40
Bombus monticola	1890	34
Bombus pascuorum	39605	40
Bombus pratorum	16749	40
Bombus ruderarius	797	24
Bombus rupestris	1680	23
Bombus sylvestris	3148	39
Dasypoda hirtipes	1190	31
Epeolus cruciger	1454	33
Epeolus variegatus	1571	34
Halictus rubicundus	4300	40
Halictus tumulorum	7413	40
Hylaeus brevicornis	1697	35
Hylaeus communis	5326	40
Hylaeus confusus	1408	36
Hylaeus dilatatus	1810	35
Hylaeus hyalinatus	2443	39
Lasioglossum albipes	4047	40
Lasioglossum calceatum	10436	40
Lasioglossum fulvicorne	3202	39
Lasioglossum laevigatum	695	20
Lasioglossum lativentre	1516	27
Lasioglossum leucopus	3247	40

Lasioglossum leucozonium	6158	40
Lasioglossum malachurum	4856	40
Lasioglossum minutissimum	2335	40
Lasioglossum morio	9084	40
Lasioglossum parvulum	2754	39
Lasioglossum pauxillum	2939	27
Lasioglossum smeathmanellum	3142	40
Lasioglossum villosulum	5854	40
Lasioglossum zonulum	1951	36
Megachile centuncularis	1954	36
Megachile leachella	1175	28
Megachile ligniseca	1566	29
Megachile maritima	1019	26
Megachile versicolor	1804	34
Megachile willughbiella	2836	36
Melitta leporina	1055	24
Melitta tricincta	823	24
Osmia aurulenta	1439	29
Osmia bicolor	1784	26
Osmia bicornis	6012	40
Osmia caerulescens	2306	34
Sphecodes crassus	1134	23
Sphecodes ephippius	4182	40
Sphecodes geoffrellus	3209	40
Sphecodes gibbus	1329	32
Sphecodes hyalinatus	715	22
Sphecodes monilicornis	3452	37
Sphecodes pellucidus	2388	39
Sphecodes puncticeps	1313	26

Species	Number of Grid	AUC Null	AUC CEM	Difference
	Squares	0.776	0.026	0.070
Andrena barbilabris	313	0.776	0.836	0.060
Andrena bicolor	851	0.748	0.793	0.045
Andrena chrysosceles	518	0.764	0.810	0.046
Andrena cineraria	941	0.745	0.804	0.059
Andrena clarkella	343	0.767	0.762	-0.005
Andrena denticulata	152	0.799	0.833	0.034
Andrena dorsata	829	0.750	0.882	0.132
Andrena flavipes	879	0.745	0.880	0.135
Andrena florea	66	0.841	0.969	0.128
Andrena fucata	157	0.799	0.736	-0.063
Andrena fulva	797	0.750	0.796	0.046
Andrena fuscipes	156	0.803	0.865	0.062
Andrena haemorrhoa	1501	0.735	0.749	0.014
Andrena helvola	121	0.809	0.796	-0.013
Andrena humilis	116	0.824	0.867	0.043
Andrena labialis	108	0.814	0.937	0.123
Andrena labiata	206	0.790	0.888	0.098
Andrena minutula	801	0.748	0.838	0.090
Andrena nigroaenea	893	0.747	0.817	0.070
Andrena nitida	811	0.750	0.835	0.085
Andrena ovatula	211	0.788	0.892	0.104
Andrena praecox	218	0.796	0.863	0.067
Andrena scotica	1067	0.739	0.752	0.013
Andrena subopaca	439	0.765	0.736	-0.029
Andrena synadelpha	119	0.820	0.875	0.055
Andrena thoracica	170	0.794	0.950	0.156
Andrena trimmerana	154	0.796	0.920	0.124
Anthidium manicatum	252	0.790	0.833	0.043

Table S4.2. Results for the 88 Climate Envelope Models. Species with a positive value for

 "Difference" indicate CEMs performed better than bias corrected null models

Anthophora bimaculata	215	0.799	0.952	0.153
Anthophora plumipes	778	0.749	0.856	0.107
Bombus bohemicus	200	0.792	0.747	-0.045
Bombus campestris	173	0.793	0.772	-0.021
Bombus distinguendus	218	0.795	0.986	0.191
Bombus hortorum	1765	0.729	0.733	0.004
Bombus humilis	408	0.766	0.950	0.184
Bombus jonellus	437	0.768	0.746	-0.022
Bombus lapidarius	3561	0.709	0.743	0.034
Bombus monticola	260	0.783	0.872	0.089
Bombus pascuorum	4218	0.703	0.705	0.002
Bombus pratorum	2123	0.724	0.732	0.008
Bombus ruderarius	117	0.811	0.913	0.102
Bombus rupestris	392	0.766	0.838	0.072
Bombus sylvestris	609	0.761	0.748	-0.013
Dasypoda hirtipes	185	0.807	0.945	0.138
Epeolus cruciger	151	0.811	0.857	0.046
Epeolus variegatus	164	0.803	0.919	0.116
Halictus rubicundus	628	0.755	0.731	-0.025
Halictus tumulorum	805	0.750	0.815	0.065
Hylaeus brevicornis	169	0.805	0.860	0.055
Hylaeus communis	604	0.758	0.840	0.082
Hylaeus confusus	170	0.797	0.845	0.048
Hylaeus dilatatus	194	0.798	0.925	0.127
Hylaeus hyalinatus	315	0.777	0.847	0.070
Lasioglossum albipes	489	0.767	0.765	-0.002
Lasioglossum calceatum	1208	0.744	0.775	0.031
Lasioglossum fulvicorne	253	0.791	0.839	0.048
Lasioglossum laevigatum	81	0.836	0.899	0.063
Lasioglossum lativentre	224	0.788	0.853	0.065
Lasioglossum leucopus	400	0.772	0.786	0.014
Lasioglossum leucozonium	627	0.759	0.861	0.102

Lasioglossum malachurum	387	0.774	0.904	0.130
Lasioglossum minutissimum	243	0.781	0.903	0.122
Lasioglossum morio	868	0.751	0.835	0.084
Lasioglossum parvulum	214	0.795	0.884	0.089
Lasioglossum pauxillum	367	0.776	0.912	0.136
Lasioglossum smeathmanellum	296	0.780	0.842	0.062
Lasioglossum villosulum	555	0.762	0.840	0.078
Lasioglossum zonulum	162	0.808	0.951	0.143
Megachile centuncularis	333	0.778	0.821	0.043
Megachile leachella	192	0.795	0.964	0.169
Megachile ligniseca	285	0.778	0.859	0.081
Megachile maritima	135	0.821	0.949	0.128
Megachile versicolor	240	0.785	0.826	0.041
Megachile willughbiella	368	0.766	0.812	0.046
Melitta leporina	127	0.817	0.922	0.105
Melitta tricincta	98	0.825	0.935	0.110
Osmia aurulenta	160	0.799	0.964	0.165
Osmia bicolor	309	0.783	0.909	0.126
Osmia bicornis	839	0.754	0.799	0.045
Osmia caerulescens	311	0.784	0.845	0.061
Sphecodes crassus	145	0.802	0.875	0.073
Sphecodes ephippius	485	0.761	0.833	0.072
Sphecodes geoffrellus	358	0.781	0.796	0.015
Sphecodes gibbus	148	0.806	0.799	-0.007
Sphecodes hyalinatus	73	0.840	0.755	-0.085
Sphecodes monilicornis	455	0.766	0.826	0.060
Sphecodes pellucidus	240	0.798	0.865	0.067
Sphecodes puncticeps	128	0.814	0.876	0.062

Species	Reference	AAICc from	Days l referen	oefore ce date	PΔAICc	
	Date	model	Open	Close	Duration	
Andrena barbilabris	16/4	-20.28	50	50	0	0.001
Andrena bicolor	15/3	-22.09	2	0	2	0.000
Andrena chrysosceles	13/4	-37.86	75	0	75	0.000
Andrena cineraria	07/4	-15.94	18	12	6	0.120
Andrena clarkella	15/3	-35.13	65	0	65	0.000
Andrena denticulata	05/7	-21.91	106	94	12	0.001
Andrena dorsata	31/3	-45.79	78	0	78	0.000
Andrena flavipes	26/3	-36.67	50	3	47	0.000
Andrena florea	19/5	-12.40	133	109	24	0.242
Andrena fucata	08/5	-12.13	15	9	6	0.658
Andrena fulva	01/4	-51.47	66	0	66	0.000
Andrena fuscipes	22/7	-7.60	210	210	0	0.902
Andrena haemorrhoa	08/4	-45.74	50	0	50	0.000
Andrena helvola	19/4	-21.53	19	18	1	0.001
Andrena humilis	08/5	-10.38	129	129	0	0.679
Andrena labialis	13/5	-17.91	15	2	13	0.005
Andrena labiata	28/4	-14.99	31	3	28	0.308
Andrena minutula	25/3	-35.99	70	0	70	0.000
Andrena nigroaenea	04/4	-36.88	46	0	46	0.000
Andrena nitida	09/4	-50.13	61	0	61	0.000
Andrena ovatula	11/4	-14.84	59	1	58	0.000
Andrena praecox	22/3	-36.62	13	4	9	0.000
Andrena scotica	07/4	-35.32	57	0	57	0.000
Andrena subopaca	10/4	-25.17	86	0	86	0.000
Andrena synadelpha	23/4	-8.46	22	22	0	0.635
Andrena thoracica	20/3	-8.36	181	181	0	0.872
Andrena trimmerana	23/3	-26.10	70	0	70	0.000

 Table S4.3. Best predicting temperature windows for each species. Reference Date is the mean emergence date across the study period.

Anthidium manicatum	12/6	-25.52	92	21	71	0.001
Anthophora bimaculata	23/6	-18.75	75	20	55	0.000
Anthophora plumipes	16/3	-25.38	41	0	41	0.000
Bombus bohemicus	24/4	-19.76	33	9	24	0.000
Bombus campestris	21/5	-17.60	52	50	2	0.008
Bombus distinguendus	01/6	-10.05	58	56	2	0.736
Bombus hortorum	11/4	-27.83	20	9	11	0.000
Bombus humilis	20/5	-7.84	136	102	34	0.817
Bombus jonellus	11/4	-14.34	41	0	41	0.049
Bombus lapidarius	06/4	-43.95	48	0	48	0.000
Bombus monticola	28/4	-30.25	52	13	39	0.000
Bombus pascuorum	12/4	-29.85	84	0	84	0.000
Bombus pratorum	21/3	-32.19	42	0	42	0.000
Bombus ruderarius	17/4	-10.25	354	352	2	0.628
Bombus rupestris	13/5	-16.53	21	21	0	0.243
Bombus sylvestris	22/4	-20.40	27	27	0	0.001
Dasypoda hirtipes	28/6	-15.14	93	0	93	0.001
Epeolus cruciger	15/7	-5.03	123	123	0	0.921
Epeolus variegatus	28/6	-15.72	100	0	100	0.001
Halictus rubicundus	22/4	-19.56	66	0	66	0.000
Halictus tumulorum	28/4	-27.23	46	0	46	0.000
Hylaeus brevicornis	11/6	-13.83	67	0	67	0.008
Hylaeus communis	02/6	-18.66	42	31	11	0.001
Hylaeus confusus	31/5	-11.37	54	54	0	0.428
Hylaeus dilatatus	17/6	-16.05	151	151	0	0.034
Hylaeus hyalinatus	27/5	-7.38	76	73	3	0.880
Lasioglossum albipes	28/4	-9.02	308	308	0	0.699
Lasioglossum calceatum	16/4	-16.11	74	1	73	0.008
Lasioglossum fulvicorne	16/4	-11.43	237	0	237	0.072
Lasioglossum laevigatum	25/4	-7.28	345	332	13	0.756
Lasioglossum lativentre	09/4	-5.94	210	210	0	0.915

Lasioglossum leucopus	11/5	-11.60	27	0	27	0.630
Lasioglossum leucozonium	23/5	-21.20	51	47	4	0.003
Lasioglossum malachurum	05/4	-19.10	14	11	3	0.051
Lasioglossum minutissimum	20/4	-19.76	312	308	4	0.031
Lasioglossum morio	11/4	-25.86	82	0	82	0.000
Lasioglossum parvulum	09/4	-16.49	22	13	9	0.000
Lasioglossum pauxillum	24/4	-15.75	249	249	0	0.486
Lasioglossum smeathmanellum	25/4	-7.60	237	237	0	0.961
Lasioglossum villosulum	02/5	-12.99	20	20	0	0.039
Lasioglossum zonulum	17/5	-15.23	41	41	0	0.048
Megachile centuncularis	04/6	-15.86	42	0	42	0.002
Megachile leachella	12/6	-13.57	43	38	5	0.581
Megachile ligniseca	17/6	-11.45	85	57	28	0.019
Megachile maritima	16/6	-16.15	279	277	2	0.080
Megachile versicolor	11/6	-14.56	103	30	73	0.002
Megachile willughbiella	08/6	-26.59	62	0	62	0.000
Melitta leporina	24/6	-18.27	80	15	65	0.002
Melitta tricincta	24/7	-13.37	243	242	1	0.709
Osmia aurulenta	30/4	-14.17	30	15	15	0.467
Osmia bicolor	04/4	-18.94	37	8	29	0.001
Osmia bicornis	10/4	-27.34	18	16	2	0.000
Osmia caerulescens	29/4	-21.31	49	4	45	0.001
Sphecodes crassus	04/5	-12.37	104	0	104	0.018
Sphecodes ephippius	21/4	-26.57	65	0	65	0.000
Sphecodes geoffrellus	02/5	-15.44	42	2	40	0.046
Sphecodes gibbus	07/5	-16.77	29	28	1	0.583
Sphecodes hyalinatus	07/5	-14.51	340	339	1	0.708
Sphecodes monilicornis	26/4	-27.83	58	0	58	0.000
Sphecodes pellucidus	24/4	-20.52	34	0	34	0.001
Sphecodes puncticeps	29/5	-12.15	27	25	2	0.626

Species	Reference Date	Days refer da	before ence ate	Estimate	Std Error	Statistic	P Value
		Open	Close				
Andrena barbilabris	17/4		No	significant c	limate w	vindow	
Andrena bicolor	17/3		No	significant c	limate w	vindow	
Andrena chrysosceles	13/4	75	0	-6.99	0.86	-8.11	0.000
Andrena cineraria	07/4		No	significant c	limate w	vindow	
Andrena clarkella	13/3	65	0	-7.74	0.99	-7.78	0.000
Andrena denticulata	05/7		No	significant c	limate w	vindow	
Andrena dorsata	31/3	78	0	-7.08	0.74	-9.58	0.000
Andrena flavipes	25/3	50	3	-7.64	0.96	-7.98	0.000
Andrena florea	19/5		No	significant c	limate w	vindow	
Andrena fucata	06/5		No	significant c	limate w	vindow	
Andrena fulva	01/4	66	0	-8.16	0.79	-10.39	0.000
Andrena fuscipes	21/7		No	significant c	limate w	vindow	
Andrena haemorrhoa	08/4	50	0	-5.45	0.58	-9.40	0.000
Andrena helvola	19/4		No	significant c	limate w	vindow	
Andrena humilis	07/5		No	significant c	limate w	vindow	
Andrena labialis	09/5		No	significant c	limate w	vindow	
Andrena labiata	28/4		No	significant c	limate w	vindow	
Andrena minutula	25/3	70	0	-6.23	0.79	-7.87	0.000
Andrena nigroaenea	04/4	46	0	-5.50	0.69	-7.96	0.000
Andrena nitida	09/4	61	0	-5.37	0.52	-10.25	0.000
Andrena ovatula	13/4	59	1	-7.15	1.54	-4.63	0.000
Andrena praecox	23/3		No	significant c	limate w	vindow	
Andrena scotica	07/4	57	0	-5.74	0.74	-7.71	0.000
Andrena subopaca	10/4	86	0	-6.96	1.14	-6.13	0.000
Andrena synadelpha	22/4		No	significant c	limate w	vindow	

 Table S4.4. Linear model output for best predicting temperature windows. Reference Date is the mean

emergence date across the study period.

Andrena thoracica	20/3		No	significant o	climate w	vindow			
Andrena trimmerana	23/3	70	0	-6.12	0.93	-6.57	0.000		
Anthidium manicatum	12/6	92	21	-7.95	1.21	-6.57	0.000		
Anthophora bimaculata	24/6	75	20	-7.78	1.46	-5.34	0.000		
Anthophora plumipes	16/3	41	0	-6.57	1.05	-6.29	0.000		
Bombus bohemicus	25/4	33	9	-5.59	1.01	-5.55	0.000		
Bombus campestris	21/5	5 No significant climate window							
Bombus distinguendus	05/6		No	significant o	climate w	vindow			
Bombus hortorum	11/4	No significant climate window							
Bombus humilis	20/5		No	significant o	climate w	vindow			
Bombus jonellus	13/4	41	0	-10.46	2.29	-4.57	0.000		
Bombus lapidarius	06/4	48	0	-6.32	0.69	-9.10	0.000		
Bombus monticola	29/4	52	13	-9.32	1.28	-7.30	0.000		
Bombus pascuorum	12/4	84	0	-6.75	0.98	-6.85	0.000		
Bombus pratorum	21/3	42	0	-8.11	1.12	-7.22	0.000		
Bombus ruderarius	23/4	/4 No significant climate window							
Bombus rupestris	13/5		No	significant o	climate w	vindow			
Bombus sylvestris	23/4		No	significant o	climate w	vindow			
Dasypoda hirtipes	25/6	93	0	-7.59	1.60	-4.75	0.000		
Epeolus cruciger	15/7		No	significant o	climate w	vindow			
Epeolus variegatus	29/6	100	0	-7.09	1.47	-4.81	0.000		
Halictus rubicundus	23/4	66	0	-5.96	1.13	-5.28	0.000		
Halictus tumulorum	27/4	46	0	-7.80	1.20	-6.48	0.000		
Hylaeus brevicornis	05/6	67	0	-8.44	1.87	-4.52	0.000		
Hylaeus communis	31/5		No	significant o	climate w	vindow			
Hylaeus confusus	31/5		No	significant o	climate w	vindow			
Hylaeus dilatatus	16/6		No	significant o	climate w	vindow			
Hylaeus hyalinatus	27/5		No	significant o	climate w	vindow			
Lasioglossum albipes	29/4		No	significant o	climate w	vindow			
Lasioglossum calceatum	16/4	74	1	-5.95	1.26	-4.72	0.000		
Lasioglossum fulvicorne	17/4		No	significant o	climate w	vindow			

Lasioglossum laevigatum	27/4		No	significant c	limate w	vindow	
Lasioglossum lativentre	11/4		No	significant c	limate w	vindow	
Lasioglossum leucopus	11/5		No	significant c	limate w	vindow	
Lasioglossum leucozonium	21/5		No	significant c	limate w	vindow	
Lasioglossum malachurum	06/4		No	significant c	limate w	vindow	
Lasioglossum minutissimum	19/4		No	significant c	limate w	vindow	
Lasioglossum morio	11/4	82	0	-7.51	1.20	-6.24	0.000
Lasioglossum parvulum	09/4		No	significant c	limate w	vindow	
Lasioglossum pauxillum	27/4		No	significant c	limate w	vindow	
Lasioglossum smeathmanellum	25/4		No	significant c	limate w	vindow	
Lasioglossum villosulum	30/4		No	significant c	limate w	vindow	
Lasioglossum zonulum	18/5		No	significant c	limate w	vindow	
Megachile centuncularis	02/6	42	0	-7.84	1.64	-4.77	0.000
Megachile leachella	11/6		No	significant c	limate w	vindow	
Megachile ligniseca	13/6	85	57	-4.96	1.21	-4.10	0.000
Megachile maritima	14/6		No	significant c	limate w	vindow	
Megachile versicolor	09/6			-8.47	1.85	-4.59	0.000
Megachile willughbiella	08/6	62	0	-10.47	1.61	-6.52	0.000
Melitta leporina	24/6	80	15	-10.44	1.89	-5.53	0.000
Melitta tricincta	24/7		No	significant c	limate w	vindow	
Osmia aurulenta	30/4		No	significant c	limate w	vindow	
Osmia bicolor	04/4			-7.48	1.33	-5.61	0.000
Osmia bicornis	10/4		No	significant c	limate w	vindow	
Osmia caerulescens	24/4	37	8	-7.39	1.28	-5.78	0.000
Sphecodes crassus	11/5	104	0	-14.17	3.17	-4.47	0.000
Sphecodes ephippius	21/4	65	0	-9.25	1.46	-6.35	0.000
Sphecodes geoffrellus	05/5	42	2	-7.62	1.64	-4.65	0.000
Sphecodes gibbus	11/5		No	significant c	limate w	vindow	
Sphecodes hyalinatus	08/5		No	significant o	limate w	vindow	

Sphecodes monilicornis	28/4	58	0	-9.71	1.44	-6.73	0.000
Sphecodes pellucidus	24/4	34	0	-7.34	1.35	-5.43	0.000
Sphecodes puncticeps	29/5		No	significant	climate w	vindow	

Table S4.5. Predicted change in emergence dates (days) under RCP 4.5 and RCP 8.5 for t	the
period 2070-2079. Negative values indicate advancements	

	RCP 4.5 RCP 8.						
Species	Change	Lower CI	Upper CI	Change	Lower CI	Upper CI	
Andrena barbilabris		No sig	gnificant c	limate win	dow		
Andrena bicolor		No sig	gnificant o	limate win	dow		
Andrena chrysosceles	-8.3	-11.3	-5.3	-19.1	-24.4	-13.8	
Andrena cineraria		No sig	gnificant c	limate win	dow		
Andrena clarkella	-8.4	-12.0	-4.8	-21.6	-28.1	-15.1	
Andrena denticulata	No significant climate window						
Andrena dorsata	-9.0	-11.6	-6.4	-18.8	-23.1	-14.4	
Andrena flavipes	-10.0	-13.7	-6.4	-21.6	-27.5	-15.6	
Andrena florea		No sig	gnificant c	limate win	dow		
Andrena fucata		No sig	gnificant o	limate win	dow		
Andrena fulva	-9.8	-12.5	-7.2	-22.1	-26.7	-17.4	
Andrena fuscipes		No sig	gnificant c	limate win	dow		
Andrena haemorrhoa	-7.9	-10.2	-5.6	-14.3	-17.7	-10.8	
Andrena helvola		No sig	gnificant o	limate win	dow		
Andrena humilis		No sig	gnificant c	limate win	dow		
Andrena labialis		No sig	gnificant o	limate win	dow		
Andrena labiata		No sig	gnificant o	limate win	dow		
Andrena minutula	-7.6	-10.2	-5.0	-17.2	-21.7	-12.7	
Andrena nigroaenea	-7.8	-10.6	-5.1	-14.2	-18.3	-10.0	
Andrena nitida	-7.6	-9.7	-5.5	-14.4	-17.6	-11.1	
Andrena ovatula	-10.3	-16.5	-4.1	-21.1	-30.9	-11.2	

Andrena praecox		No sig	gnificant c	limate win	dow				
Andrena scotica	-8.1	-11.1	-5.0	-14.4	-18.9	-10.0			
Andrena subopaca	-7.9	-11.8	-4.0	-18.0	-24.7	-11.2			
Andrena synadelpha	No significant climate window								
Andrena thoracica		No sig	gnificant c	limate wir	dow				
Andrena trimmerana	-7.4	-10.7	-4.2	-15.8	-21.3	-10.4			
Anthidium manicatum	-18.5	-24.9	-12.2	-32.0	-42.3	-21.6			
Anthophora bimaculata	-28.2	-39.2	-17.2	-44.9	-62.0	-27.8			
Anthophora plumipes	-5.6	-8.7	-2.5	-16.0	-21.8	-10.2			
Bombus bohemicus	-9.9	-15.0	-4.9	-19.7	-28.3	-11.2			
Bombus campestris		No sig	gnificant c	limate win	dow				
Bombus distinguendus		No sig	gnificant c	limate wir	dow				
Bombus hortorum		No sig	gnificant c	limate win	dow				
Bombus humilis	No significant climate window								
Bombus jonellus	-14.2	-24.4	-3.9	-29.8	-47.5	-12.1			
Bombus lapidarius	-9.0	-11.8	-6.2	-16.1	-20.2	-12.0			
Bombus monticola	-12.8	-20.4	-5.2	-24.8	-37.5	-12.1			
Bombus pascuorum	-8.1	-11.5	-4.8	-18.1	-24.1	-12.2			
Bombus pratorum	-10.4	-14.8	-5.9	-19.8	-26.4	-13.2			
Bombus ruderarius		No sig	gnificant c	limate wir	dow				
Bombus rupestris		No sig	gnificant o	limate win	dow				
Bombus sylvestris		No sig	gnificant c	limate win	dow				
Dasypoda hirtipes	-12.9	-39.2	13.5	-21.0	-62.3	20.3			
Epeolus cruciger		No sig	gnificant c	limate wir	dow				
Epeolus variegatus	-29.1	-49.9	-8.3	-45.5	-77.5	-13.6			
Halictus rubicundus	-10.6	-15.8	-5.4	-19.8	-28.3	-11.4			
Halictus tumulorum	-14.4	-20.4	-8.3	-26.8	-37.0	-16.7			
Hylaeus brevicornis	-6.4	-30.6	17.8	-10.5	-48.6	27.6			
Hylaeus communis		No sig	gnificant o	limate win	dow				
Hylaeus confusus		No sig	gnificant c	limate wir	dow				
Hylaeus dilatatus		No sig	gnificant c	limate win	dow				
Hylaeus hyalinatus		No sig	gnificant c	climate wir	dow				

Lasioglossum albipes	No significant climate window						
Lasioglossum calceatum	-7.8	-12.3	-3.4	-16.9	-24.8	-9.0	
Lasioglossum fulvicorne	No significant climate window						
Lasioglossum laevigatum	No significant climate window						
Lasioglossum lativentre	No significant climate window						
Lasioglossum leucopus	No significant climate window						
Lasioglossum leucozonium	No significant climate window						
Lasioglossum malachurum	No significant climate window						
Lasioglossum minutissimum	No significant climate window						
Lasioglossum morio	-8.9	-13.0	-4.8	-20.0	-27.2	-12.7	
Lasioglossum parvulum	No significant climate window						
Lasioglossum pauxillum	No significant climate window						
Lasioglossum smeathmanellum	No significant climate window						
Lasioglossum villosulum	No significant climate window						
Lasioglossum zonulum	No significant climate window						
Megachile centuncularis	-30.6	-44.1	-17.0	-47.0	-67.3	-26.7	
Megachile leachella	No significant climate window						
Megachile ligniseca	-9.0	-20.7	2.7	-17.7	-36.6	1.2	
Megachile maritima	No significant climate window						
Megachile versicolor	-11.3	-21.3	-1.4	-21.6	-38.8	-4.5	
Megachile willughbiella	-34.7	-45.8	-23.5	-54.4	-71.6	-37.2	
Melitta leporina	-31.9	-44.2	-19.6	-51.1	-70.6	-31.7	
Melitta tricincta	No significant climate window						
Osmia aurulenta	No significant climate window						
Osmia bicolor	-8.7	-13.7	-3.8	-17.8	-25.3	-10.2	
Osmia bicornis	No significant climate window						
Osmia caerulescens	-7.8	-23.2	7.6	-15.7	-41.5	10.1	
Sphecodes crassus	-34.2	-51.7	-16.8	-71.2	-103.4	-38.9	
Sphecodes ephippius	-14.6	-20.3	-8.9	-26.4	-35.5	-17.3	
Sphecodes geoffrellus	No significant climate window						
Sphecodes gibbus	No significant climate window						
Sphecodes hyalinatus	No significant climate window						

Sphecodes monilicornis	-19.1	-26.8	-11.5	-38.6	-52.3	-25.0	
Sphecodes pellucidus	-14.2	-20.3	-8.0	-26.2	-36.6	-15.9	
Sphecodes puncticeps	No significant climate window						

Speeding	1980-89	2070-79	2070-79
Species		RCP 4.5	RCP 8.5
Andrena barbilabris	-36.4	17.3	-17.3
Andrena bicolor	-31.4	54.0	104.0
Andrena chrysosceles	-43.0	19.7	79.7
Andrena cineraria	-83.9	54.8	104.2
Andrena denticulata	-60.5	75.4	100.3
Andrena dorsata	-81.0	154.1	264.5
Andrena flavipes	-58.6	143.8	249.1
Andrena florea	6.1	636.6	1091.2
Andrena fulva	-75.8	26.5	-19.4
Andrena fuscipes	-38.6	119.7	206.8
Andrena haemorrhoa	-15.5	51.5	84.8
Andrena humilis	-80.8	53.3	77.3
Andrena labialis	-37.2	300.1	483.2
Andrena labiata	-43.8	28.9	164.1
Andrena minutula	-31.9	82.8	154.0
Andrena nigroaenea	-46.9	41.5	98.0
Andrena nitida	-77.4	91.2	154.0
Andrena ovatula	-73.3	170.4	274.8
Andrena praecox	-56.9	86.1	142.8
Andrena scotica	-39.5	57.8	84.5

Table S4.6. Percentage change in suitable climate envelopecompared with 2010-19 area.
Andrena synadelpha	-61.5	76.5	28.1
Andrena thoracica	-93.9	310.3	593.1
Andrena trimmerana	-91.5	169.6	297.1
Anthidium manicatum	-68.5	58.7	95.8
Anthophora bimaculata	-95.0	384.8	709.6
Anthophora plumipes	-69.2	94.9	170.0
Bombus distinguendus	-96.2	-100.0	-100.0
Bombus hortorum	-4.0	43.0	60.0
Bombus humilis	-91.3	71.1	367.1
Bombus lapidarius	-5.0	58.5	95.1
Bombus monticola	47.1	-20.5	-64.6
Bombus pascuorum	-5.1	53.3	71.1
Bombus pratorum	-2.1	48.9	69.9
Bombus ruderarius	-4.0	89.8	217.7
Bombus rupestris	-91.1	18.5	53.6
Dasypoda hirtipes	-87.3	208.0	486.0
Epeolus cruciger	-21.9	76.0	121.2
Epeolus variegatus	-58.5	169.4	294.8
Halictus tumulorum	-59.6	61.0	124.3
Hylaeus brevicornis	-26.2	85.7	149.5
Hylaeus communis	-44.0	81.9	149.9
Hylaeus confusus	-43.4	84.0	144.8
Hylaeus dilatatus	-49.7	198.9	342.7
Hylaeus hyalinatus	-21.3	84.0	143.8
Lasioglossum calceatum	-12.5	64.3	95.2
Lasioglossum fulvicorne	3.5	102.4	143.4
Lasioglossum laevigatum	21.4	174.9	218.1
Lasioglossum lativentre	-59.5	71.7	129.2
Lasioglossum leucopus	-26.3	39.2	78.2
Lasioglossum leucozonium	-31.4	101.4	175.4
Lasioglossum malachurum	-91.2	105.9	209.5

Lasioglossum minutissimum	-86.8	77.2	148.5
Lasioglossum morio	-55.4	85.0	153.0
Lasioglossum parvulum	-44.4	80.8	164.7
Lasioglossum pauxillum	-67.3	185.8	318.5
Lasioglossum smeathmanellum	-33.9	54.1	124.0
Lasioglossum villosulum	-14.3	70.8	131.7
Lasioglossum zonulum	47.0	326.8	629.7
Megachile centuncularis	-37.7	80.0	116.8
Megachile leachella	-87.3	239.0	534.0
Megachile ligniseca	-27.4	94.1	166.5
Megachile maritima	-57.4	339.7	557.0
Megachile versicolor	-64.3	57.4	120.0
Megachile willughbiella	-44.9	69.6	111.4
Melitta leporina	-41.0	182.7	319.9
Melitta tricincta	23.5	328.4	466.8
Osmia aurulenta	-16.7	224.2	472.3
Osmia bicolor	5.1	176.7	316.9
Osmia bicornis	-38.0	69.2	94.4
Osmia caerulescens	-39.1	95.7	151.9
Sphecodes crassus	-52.0	107.1	166.7
Sphecodes ephippius	-83.8	38.6	54.5
Sphecodes geoffrellus	-21.8	57.9	88.2
Sphecodes monilicornis	-26.2	80.6	120.7
Sphecodes pellucidus	-51.9	42.8	-32.2
Sphecodes puncticeps	-53.6	86.8	152.1

Table S4.7. Latitudinal shifts in the northern range boundary, range centroid and southern range boundary, compared with 2010-19 latitudes. Positive values indicate northward shift, negative values indicate southward shift.

	Nor F	orthern Range Boundary R		Ran	Range Centroid			Southern Range Boundary		
Species	1980 -89	2070 -79 RCP 4.5	2070 -79 RCP 8.5	1980 -89	2070 -79 RCP 4.5	2070 -79 RCP 8.5	1980 -89	2070 -79 RCP 4.5	2070 -79 RCP 8.5	
Andrena barbilabris	88.3	308.5	370.5	43.4	110.1	364.3	10.8	60.5	254.2	
Andrena bicolor	37.2	229.4	386.0	10.8	57.3	122.5	-3.1	12.4	24.8	
Andrena chrysosceles	-3.1	138.0	324.0	-32.5	41.9	86.8	-63.6	17.0	17.0	
Andrena cineraria	21.7	170.5	345.7	-38.8	46.5	108.5	-3.1	7.8	20.2	
Andrena denticulata	128. 7	255.8	275.9	66.6	79.1	114.7	23.3	18.6	24.8	
Andrena dorsata	54.2	213.9	440.2	7.8	85.2	161.2	-20.1	12.4	27.9	
Andrena flavipes	54.6	193.8	429.3	31.0	82.1	153.4	2.8	10.8	26.3	
Andrena florea	-51.1	167.4	390.6	-26.4	93.0	164.3	-17.0	6.2	23.2	
Andrena fulva	4.6	200.0	382.9	-48.0	46.5	277.5	-23.2	23.2	195.3	
Andrena fuscipes	24.8	175.2	390.6	-46.5	72.9	145.7	-52.7	9.3	24.8	
Andrena haemorrhoa	32.5	231.0	351.9	4.6	60.5	114.7	-3.1	13.9	23.3	
Andrena humilis	-35.7	240.3	412.3	-33.3	116.3	297.6	-34.1	65.1	37.2	
Andrena labialis	45.0	187.6	361.2	9.3	97.7	150.4	3.1	11.6	20.1	
Andrena labiata	-34.1	269.7	375.1	12.4	147.3	124.0	0.0	-10.8	23.3	
Andrena minutula	46.5	203.1	401.5	15.5	57.3	131.8	-1.6	6.2	21.7	
Andrena nigroaenea	-18.6	203.1	356.5	-40.3	37.2	77.5	-35.7	0.0	6.2	
Andrena nitida	17.0	251.1	418.5	26.3	77.5	150.4	-7.8	13.9	27.9	
Andrena ovatula	113. 2	261.9	443.3	29.4	107.0	182.9	40.3	21.7	37.2	
Andrena praecox	-3.1	238.7	399.9	-43.4	69.7	133.3	-63.6	10.8	24.8	
Andrena scotica	31.0	283.7	347.2	26.3	76.0	125.6	7.8	17.0	24.8	
Andrena synadelpha	41.8	262.0	413.9	-20.1	75.9	347.2	-58.9	38.7	190.6	
Andrena thoracica	189. 1	71.3	392.2	51.1	69.7	142.6	40.3	80.6	88.4	
Andrena trimmerana	63.6	207.7	452.6	3.1	96.1	170.5	51.1	20.1	34.1	
Anthidium manicatum	-21.7	227.9	373.6	-10.8	57.4	97.7	6.2	12.4	21.7	
Anthophora bimaculata	43.4	207.7	452.6	-20.1	93.0	172.0	-23.3	17.0	35.7	

Anthophora plumipes	0.9	195.3	410.8	-55.8	58.9	133.3	-38.8	9.3	23.3
Bombus distinguendus	-21.7	NA	NA	156. 6	NA	NA	134. 1	NA	NA
Bombus hortorum	10.8	158.1	167.4	1.5	52.7	88.4	-1.6	9.3	15.5
Bombus humilis	99.2	232.5	485.2	71.3	136.4	257.3	49.6	14.0	103.9
Bombus lapidarius	7.8	215.5	347.2	3.1	46.5	94.5	0.0	4.7	15.5
Bombus monticola	-17.1	17.4	27.9	13.9	72.9	117.8	20.2	26.4	243.4
Bombus pascuorum	23.3	223.2	234.1	4.7	63.6	99.2	0.0	10.8	17.0
Bombus pratorum	-35.6	240.3	268.2	-10.8	65.1	107.0	-4.7	14.0	20.2
Bombus ruderarius	23.3	178.3	401.5	21.7	86.8	153.4	10.8	37.2	43.4
Bombus rupestris	-27.9	117.8	251.1	-83.7	54.3	113.2	- 158. 1	34.1	40.3
Dasypoda hirtipes	65.1	122.5	415.4	7.8	82.1	142.6	29.5	15.5	29.4
Epeolus cruciger	7.8	235.6	379.8	-7.7	65.1	120.9	1.6	10.8	21.7
Epeolus variegatus	41.9	184.5	435.6	6.2	82.2	148.8	1.5	17.1	29.4
Halictus tumulorum	26.3	178.3	389.1	34.1	49.6	119.4	-1.6	9.3	23.3
Hylaeus brevicornis	52.7	237.2	403.0	27.9	68.2	131.8	6.2	10.8	24.8
Hylaeus communis	49.6	175.2	381.3	49.6	55.8	120.9	7.8	6.2	20.1
Hylaeus confusus	21.7	254.2	412.3	27.9	77.5	148.8	-3.1	15.5	29.4
Hylaeus dilatatus	15.5	158.1	358.1	-1.6	72.9	133.3	-4.6	4.6	15.5
Hylaeus hyalinatus	46.5	232.5	372.0	29.5	69.7	127.1	6.2	13.9	26.4
Lasioglossum calceatum	12.4	283.7	370.5	0.0	80.6	136.4	-4.7	18.6	26.4
Lasioglossum fulvicorne	-12.9	259.3	370.9	-9.3	77.5	130.2	-1.5	7.8	15.5
Lasioglossum laevigatum	-24.8	282.1	364.3	-29.5	111.6	148.8	-7.8	15.5	21.7
Lasioglossum lativentre	40.3	136.4	279.0	17.0	38.8	89.9	0.0	0.0	10.9
Lasioglossum leucopus	83.7	262.0	324.0	38.7	68.2	99.2	9.3	10.8	18.6
Lasioglossum leucozonium	57.4	207.7	404.6	18.6	74.4	142.6	-1.5	12.4	26.4
Lasioglossum malachurum	-35.7	147.3	299.2	- 107. 0	80.6	117.8	- 138. 0	27.9	23.3
Lasioglossum minutissimum	49.6	127.1	348.8	-48.0	85.2	169.0	-63.6	35.6	69.7
Lasioglossum morio	31.0	229.4	406.1	52.7	62.0	142.6	4.6	10.8	24.8
Lasioglossum parvulum	65.1	172.1	302.3	29.4	93.0	139.5	3.1	40.3	32.5

Lasiogiossum pauxillum	-12.4	167.4	365.8	6.2	82.1	151.9	-7.8	12.4	27.9
Lasioglossum smeathmanellum	23.2	192.2	404.6	10.8	54.2	130.2	-6.2	9.3	26.4
Lasioglossum villosulum	23.3	206.2	376.6	0.0	52.7	113.2	-4.7	4.7	17.0
Lasioglossum zonulum	-74.4	224.8	511.5	-48.0	110.1	198.4	-35.7	34.1	51.2
Megachile centuncularis	34.1	297.6	362.7	46.5	82.2	130.2	10.8	17.1	26.4
Megachile leachella	86.8	34.1	393.7	17.1	96.1	179.8	21.7	94.5	116.3
Megachile ligniseca	41.9	170.5	348.8	35.7	46.5	107.0	10.8	-1.6	10.8
Megachile maritima	134. 9	153.5	386.0	1.5	97.7	161.2	17.1	26.4	40.3
Megachile versicolor	9.3	203.1	392.2	-12.4	48.0	114.7	-1.6	9.3	21.7
Megachile willughbiella	63.6	272.8	359.6	66.6	60.5	113.2	15.5	12.4	21.7
Melitta leporina	71.3	203.1	449.5	-4.7	103.9	178.3	-7.8	20.1	35.6
Melitta tricincta	-18.6	243.4	412.3	-21.7	114.7	175.2	-3.1	12.4	26.3
Osmia aurulenta	181. 4	142.6	353.4	3.1	116.3	184.5	-1.5	55.8	71.3
Osmia bicolor	-10.8	210.8	434.0	-13.9	83.7	155.0	-3.1	12.4	20.1
Osmia bicornis	29.4	221.7	372.0	49.6	52.7	148.8	15.5	6.2	48.0
Osmia caerulescens	41.9	212.4	375.1	55.8	57.3	117.8	10.8	6.2	18.6
Sphecodes crassus	-35.7	213.9	370.5	-62.0	58.9	124.0	-9.3	4.7	17.1
Sphecodes ephippius	-24.8	192.2	393.7	-83.7	60.5	113.2	-57.4	15.5	9.3
Sphecodes geoffrellus	34.1	297.6	316.2	15.5	80.6	111.6	4.7	17.1	23.3
Sphecodes monilicornis	13.9	258.9	386.0	31.0	79.1	130.2	4.6	15.5	26.4
Sphecodes pellucidus	0.0	285.2	454.2	6.2	97.7	440.2	4.7	54.2	359.6
Sphecodes puncticeps	96.1	187.6	337.9	72.9	58.9	107.0	13.9	7.8	15.5



Figure S4.1. MaxEnt climate envelope maps for Andrena barbilabris. Showing climate envelope for 1980-89 (A), 2010-19 (B), and 2070-79 under RCP 4.5 (C) and RCP 8.5 (D). 10th percentile training presence cloglog threshold = 0.3007



Figure S4.1. MaxEnt climate envelope maps for Andrena bicolor. Showing climate envelope for 1980-89 (A), 2010-19 (B), and 2070-79 under RCP 4.5 (C) and RCP 8.5 (D). 10th percentile training presence cloglog threshold = 0.3007



Figure 54.1. MaxEnt climate envelope maps for Andrena chrysosceles. Showing climate envelope for 1980-89 (A), 2010-19 (B), and 2070-79 under RCP 4.5 (C) and RCP 8.5 (D). 10th percentile training presence cloglog threshold = 0.3007



Figure 54.1. MaxEnt climate envelope maps for *Andrena cineraria*. Showing climate envelope for 1980-89 (A), 2010-19 (B), and 2070-79 under RCP 4.5 (C) and RCP 8.5 (D). 10th percentile training presence cloglog threshold = 0.3007



Figure 54.1. MaxEnt climate envelope maps for Andrena denticulata. Showing climate envelope for 1980-89 (A), 2010-19 (B), and 2070-79 under RCP 4.5 (C) and RCP 8.5 (D). 10th percentile training presence cloglog threshold = 0.3007



Figure S4.1. MaxEnt climate envelope maps for Andrena dorsata. Showing climate envelope for 1980-89 (A), 2010-19 (B), and 2070-79 under RCP 4.5 (C) and RCP 8.5 (D). 10th percentile training presence cloglog threshold = 0.3007



Figure 54.1. MaxEnt climate envelope maps for Andrena flavipes. Showing climate envelope for 1980-89 (A), 2010-19 (B), and 2070-79 under RCP 4.5 (C) and RCP 8.5 (D). 10th percentile training presence cloglog threshold = 0.3007



Figure S4.1. MaxEnt climate envelope maps for Andrena florea. Showing climate envelope for 1980-89 (A), 2010-19 (B), and 2070-79 under RCP 4.5 (C) and RCP 8.5 (D). 10th percentile training presence cloglog threshold = 0.3007



Figure 54.1. MaxEnt climate envelope maps for Andrena futva. Showing climate envelope for 1980-89 (A), 2010-19 (B), and 2070-79 under RCP 4.5 (C) and RCP 8.5 (D). 10th percentile training presence cloglog threshold = 0.3007



Figure S4.1. MaxEnt climate envelope maps for *Andrena fuscipes*. Showing climate envelope for 1980-89 (A), 2010-19 (B), and 2070-79 under RCP 4.5 (C) and RCP 8.5 (D). 10th percentile training presence cloglog threshold = 0.3007



Figure 54.1. MaxEnt climate envelope maps for Andrena haemorrhoa. Showing climate envelope for 1980-89 (A), 2010-19 (B), and 2070-79 under RCP 4.5 (C) and RCP 8.5 (D). 10th percentile training presence cloglog threshold = 0.3007



Figure S4.1. MaxEnt climate envelope maps for Andrena humilis. Showing climate envelope for 1980-89 (A), 2010-19 (B), and 2070-79 under RCP 4.5 (C) and RCP 8.5 (D). 10th percentile training presence cloglog threshold = 0.3007



Figure S4.1. MaxEnt climate envelope maps for Andrena labialis. Showing climate envelope for 1980-89 (A), 2010-19 (B), and 2070-79 under RCP 4.5 (C) and RCP 8.5 (D). 10th percentile training presence cloglog threshold = 0.3007



Figure S4.1. MaxEnt climate envelope maps for Andrena labiata. Showing climate envelope for 1980-89 (A), 2010-19 (B), and 2070-79 under RCP 4.5 (C) and RCP 8.5 (D). 10th percentile training presence cloglog threshold = 0.3007



Figure 54.1. MaxEnt climate envelope maps for Andrena minutula. Showing climate envelope for 1980-89 (A), 2010-19 (B), and 2070-79 under RCP 4.5 (C) and RCP 8.5 (D). 10th percentile training presence cloglog threshold = 0.3007



Figure S4.1. MaxEnt climate envelope maps for Andrena nigroaenea. Showing climate envelope for 1980-89 (A), 2010-19 (B), and 2070-79 under RCP 4.5 (C) and RCP 8.5 (D). 10th percentile training presence cloglog threshold = 0.3007



Figure 54.1. MaxEnt climate envelope maps for *Andrena nitida*. Showing climate envelope for 1980-89 (A), 2010-19 (B), and 2070-79 under RCP 4.5 (C) and RCP 8.5 (D). 10th percentile training presence cloglog threshold = 0.3007



Figure S4.1. MaxEnt climate envelope maps for Andrena ovatula. Showing climate envelope for 1980-89 (A), 2010-19 (B), and 2070-79 under RCP 4.5 (C) and RCP 8.5 (D). 10th percentile training presence cloglog threshold = 0.3007



Figure 54.1. MaxEnt climate envelope maps for Andrena praecox. Showing climate envelope for 1980-89 (A), 2010-19 (B), and 2070-79 under RCP 4.5 (C) and RCP 8.5 (D). 10th percentile training presence cloglog threshold = 0.3007



Figure S4.1. MaxEnt climate envelope maps for Andrena scotica. Showing climate envelope for 1980-89 (A), 2010-19 (B), and 2070-79 under RCP 4.5 (C) and RCP 8.5 (D). 10th percentile training presence cloglog threshold = 0.3007



Figure 54.1. MaxEnt climate envelope maps for Andrena synadelpha. Showing climate envelope for 1980-89 (A), 2010-19 (B), and 2070-79 under RCP 4.5 (C) and RCP 8.5 (D). 10th percentile training presence cloglog threshold = 0.3007



Figure S4.1. MaxEnt climate envelope maps for *Andrena thoracica*. Showing climate envelope for 1980-89 (A), 2010-19 (B), and 2070-79 under RCP 4.5 (C) and RCP 8.5 (D). 10th percentile training presence cloglog threshold = 0.3007



Figure 54.1. MaxEnt climate envelope maps for Andrena trimmerana. Showing climate envelope for 1980-89 (A), 2010-19 (B), and 2070-79 under RCP 4.5 (C) and RCP 8.5 (D). 10th percentile training presence cloglog threshold = 0.3007



Figure S4.1. MaxEnt climate envelope maps for Anthidium manicatum, Showing climate envelope for 1980-89 (A), 2010-19 (B), and 2070-79 under RCP 4.5 (C) and RCP 8.5 (D). 10th percentile training presence cloglog threshold = 0.3007



Figure 54.1. MaxEnt climate envelope maps for *Anthophora bimaculata*. Showing climate envelope for 1980-89 (A), 2010-19 (B), and 2070-79 under RCP 4.5 (C) and RCP 8.5 (D). 10th percentile training presence cloglog threshold = 0.3007



Figure S4.1. MaxEnt climate envelope maps for Anthophora plumipes. Showing climate envelope for 1980-89 (A), 2010-19 (B), and 2070-79 under RCP 4.5 (C) and RCP 8.5 (D). 10th percentile training presence cloglog threshold = 0.3007



Figure S4.1. MaxEnt climate envelope maps for *Bombus distinguendus*. Showing climate envelope for 1980-89 (A), 2010-19 (B), and 2070-79 under RCP 4.5 (C) and RCP 8.5 (D). 10th percentile training presence cloglog threshold = 0.3007



Figure S4.1. MaxEnt climate envelope maps for *Bombus hortorum*. Showing climate envelope for 1980-89 (A), 2010-19 (B), and 2070-79 under RCP 4.5 (C) and RCP 8.5 (D). 10th percentile training presence cloglog threshold = 0.3007



Figure S4.1. MaxEnt climate envelope maps for *Bombus humilis*. Showing climate envelope for 1980-89 (A), 2010-19 (B), and 2070-79 under RCP 4.5 (C) and RCP 8.5 (D). 10th percentile training presence cloglog threshold = 0.3007



Figure 54.1. MaxEnt climate envelope maps for *Bombus lapidarius*. Showing climate envelope for 1980-89 (A), 2010-19 (B), and 2070-79 under RCP 4.5 (C) and RCP 8.5 (D). 10th percentile training presence cloglog threshold = 0.3007



Figure 54.1. MaxEnt climate envelope maps for *Bombus monticola*. Showing climate envelope for 1980-89 (A), 2010-19 (B), and 2070-79 under RCP 4.5 (C) and RCP 8.5 (D). 10th percentile training presence cloglog threshold = 0.3007



Figure S4.1. MaxEnt climate envelope maps for *Bombus pascuorum*. Showing climate envelope for 1980-89 (A), 2010-19 (B), and 2070-79 under RCP 4.5 (C) and RCP 8.5 (D). 10th percentile training presence cloglog threshold = 0.3007



Figure 54.1. MaxEnt climate envelope maps for *Bombus pratorum*. Showing climate envelope for 1980-89 (A), 2010-19 (B), and 2070-79 under RCP 4.5 (C) and RCP 8.5 (D). 10th percentile training presence cloglog threshold = 0.3007



Figure S4.1. MaxEnt climate envelope maps for *Bombus ruderarius*. Showing climate envelope for 1980-89 (A), 2010-19 (B), and 2070-79 under RCP 4.5 (C) and RCP 8.5 (D). 10th percentile training presence cloglog threshold = 0.3007



Figure 54.1. MaxEnt climate envelope maps for *Bombus rupestris*. Showing climate envelope for 1980-89 (A), 2010-19 (B), and 2070-79 under RCP 4.5 (C) and RCP 8.5 (D). 10th percentile training presence cloglog threshold = 0.3007



Figure S4.1. MaxEnt climate envelope maps for *Dasypoda hirtipes*. Showing climate envelope for 1980-89 (A), 2010-19 (B), and 2070-79 under RCP 4.5 (C) and RCP 8.5 (D). 10th percentile training presence cloglog threshold = 0.3007



Figure S4.1. MaxEnt climate envelope maps for *Epeolus cruciger*. Showing climate envelope for 1980-89 (A), 2010-19 (B), and 2070-79 under RCP 4.5 (C) and RCP 8.5 (D). 10th percentile training presence cloglog threshold = 0.3007



Figure S4.1. MaxEnt climate envelope maps for *Epeolus variegatus*. Showing climate envelope for 1980-89 (A), 2010-19 (B), and 2070-79 under RCP 4.5 (C) and RCP 8.5 (D). 10th percentile training presence cloglog threshold = 0.3007



Figure S4.1. MaxEnt climate envelope maps for *Halictus tumulorum*. Showing climate envelope for 1980-89 (A), 2010-19 (B), and 2070-79 under RCP 4.5 (C) and RCP 8.5 (D). 10th percentile training presence cloglog threshold = 0.3007



Figure S4.1. MaxEnt climate envelope maps for *Hylaeus brevicornis*. Showing climate envelope for 1980-89 (A), 2010-19 (B), and 2070-79 under RCP 4.5 (C) and RCP 8.5 (D). 10th percentile training presence cloglog threshold = 0.3007



Figure 54.1. MaxEnt climate envelope maps for *Hylaeus communis*. Showing climate envelope for 1980-89 (A), 2010-19 (B), and 2070-79 under RCP 4.5 (C) and RCP 8.5 (D). 10th percentile training presence cloglog threshold = 0.3007



Figure S4.1. MaxEnt climate envelope maps for *Hylaeus confusus*. Showing climate envelope for 1980-89 (A), 2010-19 (B), and 2070-79 under RCP 4.5 (C) and RCP 8.5 (D). 10th percentile training presence cloglog threshold = 0.3007



Figure S4.1. MaxEnt climate envelope maps for *Hylaeus dilatatus*. Showing climate envelope for 1980-89 (A), 2010-19 (B), and 2070-79 under RCP 4.5 (C) and RCP 8.5 (D). 10th percentile training presence cloglog threshold = 0.3007



Figure S4.1. MaxEnt climate envelope maps for *Hylaeus hyalinatus*. Showing climate envelope for 1980-89 (A), 2010-19 (B), and 2070-79 under RCP 4.5 (C) and RCP 8.5 (D). 10th percentile training presence cloglog threshold = 0.3007



Figure S4.1. MaxEnt climate envelope maps for *Lasioglossum calceatum*. Showing climate envelope for 1980-89 (A), 2010-19 (B), and 2070-79 under RCP 4.5 (C) and RCP 8.5 (D). 10th percentile training presence cloglog threshold = 0.3007



Figure S4.1. MaxEnt climate envelope maps for *Lasioglossum fulvicorne*. Showing climate envelope for 1980-89 (A), 2010-19 (B), and 2070-79 under RCP 4.5 (C) and RCP 8.5 (D). 10th percentile training presence cloglog threshold = 0.3007



Figure S4.1. MaxEnt climate envelope maps for *Lasioglossum laevigatum*. Showing climate envelope for 1980-89 (A), 2010-19 (B), and 2070-79 under RCP 4.5 (C) and RCP 8.5 (D). 10th percentile training presence cloglog threshold = 0.3007



Figure S4.1. MaxEnt climate envelope maps for *Lasioglossum lativentre*. Showing climate envelope for 1980-89 (A), 2010-19 (B), and 2070-79 under RCP 4.5 (C) and RCP 8.5 (D). 10th percentile training presence cloglog threshold = 0.3007



Figure S4.1. MaxEnt climate envelope maps for *Lasioglossum leucopus*. Showing climate envelope for 1980-89 (A), 2010-19 (B), and 2070-79 under RCP 4.5 (C) and RCP 8.5 (D). 10th percentile training presence cloglog threshold = 0.3007



Figure S4.1. MaxEnt climate envelope maps for *Lasioglossum leucozonium*. Showing climate envelope for 1980-89 (A), 2010-19 (B), and 2070-79 under RCP 4.5 (C) and RCP 8.5 (D). 10th percentile training presence cloglog threshold = 0.3007



Figure 54.1. MaxEnt climate envelope maps for *Lasioglossum malachurum*. Showing climate envelope for 1980-89 (A), 2010-19 (B), and 2070-79 under RCP 4.5 (C) and RCP 8.5 (D). 10th percentile training presence cloglog threshold = 0.3007



Figure S4.1. MaxEnt climate envelope maps for *Lasioglossum minutissimum*. Showing climate envelope for 1980-89 (A), 2010-19 (B), and 2070-79 under RCP 4.5 (C) and RCP 8.5 (D). 10th percentile training presence cloglog threshold = 0.3007



Figure S4.1. MaxEnt climate envelope maps for *Lasioglossum morio*. Showing climate envelope for 1980-89 (A), 2010-19 (B), and 2070-79 under RCP 4.5 (C) and RCP 8.5 (D). 10th percentile training presence cloglog threshold = 0.3007



Figure S4.1. MaxEnt climate envelope maps for Lasioglossum parvulum. Showing climate envelope for 1980-89 (A), 2010-19 (B), and 2070-79 under RCP 4.5 (C) and RCP 8.5 (D). 10th percentile training presence cloglog threshold = 0.3007



Figure S4.1. MaxEnt climate envelope maps for *Lasioglossum pauxillum*. Showing climate envelope for 1980-89 (A), 2010-19 (B), and 2070-79 under RCP 4.5 (C) and RCP 8.5 (D). 10th percentile training presence cloglog threshold = 0.3007



Figure S4.1. MaxEnt climate envelope maps for *Lasioglossum smeathmanellum*. Showing climate envelope for 1980-89 (A), 2010-19 (B), and 2070-79 under RCP 4.5 (C) and RCP 8.5 (D). 10th percentile training presence cloglog threshold = 0.3007



Figure S4.1. MaxEnt climate envelope maps for *Lasioglossum villosulum*. Showing climate envelope for 1980-89 (A), 2010-19 (B), and 2070-79 under RCP 4.5 (C) and RCP 8.5 (D). 10th percentile training presence cloglog threshold = 0.3007



Figure S4.1. MaxEnt climate envelope maps for *Lasioglossum zonulum*. Showing climate envelope for 1980-89 (A), 2010-19 (B), and 2070-79 under RCP 4.5 (C) and RCP 8.5 (D). 10th percentile training presence cloglog threshold = 0.3007



Figure S4.1. MaxEnt climate envelope maps for *Megachile centuncularis*. Showing climate envelope for 1980-89 (A), 2010-19 (B), and 2070-79 under RCP 4.5 (C) and RCP 8.5 (D). 10th percentile training presence cloglog threshold = 0.3007



Figure S4.1. MaxEnt climate envelope maps for *Megachile leachella*. Showing climate envelope for 1980-89 (A), 2010-19 (B), and 2070-79 under RCP 4.5 (C) and RCP 8.5 (D). 10th percentile training presence cloglog threshold = 0.3007



Figure S4.1. MaxEnt climate envelope maps for *Megachile ligniseca*. Showing climate envelope for 1980-89 (A), 2010-19 (B), and 2070-79 under RCP 4.5 (C) and RCP 8.5 (D). 10th percentile training presence cloglog threshold = 0.3007



Figure S4.1. MaxEnt climate envelope maps for *Megachile maritima*. Showing climate envelope for 1980-89 (A), 2010-19 (B), and 2070-79 under RCP 4.5 (C) and RCP 8.5 (D). 10th percentile training presence cloglog threshold = 0.3007


Figure 54.1. MaxEnt climate envelope maps for *Megachile versicolor*. Showing climate envelope for 1980-89 (A), 2010-19 (B), and 2070-79 under RCP 4.5 (C) and RCP 8.5 (D). 10th percentile training presence cloglog threshold = 0.3007



Figure S4.1. MaxEnt climate envelope maps for *Megachile willughbiella*. Showing climate envelope for 1980-89 (A), 2010-19 (B), and 2070-79 under RCP 4.5 (C) and RCP 8.5 (D). 10th percentile training presence cloglog threshold = 0.3007



Figure S4.1. MaxEnt climate envelope maps for *Melitta leporina*. Showing climate envelope for 1980-89 (A), 2010-19 (B), and 2070-79 under RCP 4.5 (C) and RCP 8.5 (D). 10th percentile training presence cloglog threshold = 0.3007



Figure S4.1. MaxEnt climate envelope maps for *Melitta tricincta*. Showing climate envelope for 1980-89 (A), 2010-19 (B), and 2070-79 under RCP 4.5 (C) and RCP 8.5 (D). 10th percentile training presence cloglog threshold = 0.3007



Figure S4.1. MaxEnt climate envelope maps for *Osmia aurulenta*. Showing climate envelope for 1980-89 (A), 2010-19 (B), and 2070-79 under RCP 4.5 (C) and RCP 8.5 (D). 10th percentile training presence cloglog threshold = 0.3007



Figure S4.1. MaxEnt climate envelope maps for Osmia bicolor. Showing climate envelope for 1980-89 (A), 2010-19 (B), and 2070-79 under RCP 4.5 (C) and RCP 8.5 (D). 10th percentile training presence cloglog threshold = 0.3007



Figure S4.1. MaxEnt climate envelope maps for *Osmia bicornis*. Showing climate envelope for 1980-89 (A), 2010-19 (B), and 2070-79 under RCP 4.5 (C) and RCP 8.5 (D). 10th percentile training presence cloglog threshold = 0.3007



Figure S4.1. MaxEnt climate envelope maps for Osmia caerulescens. Showing climate envelope for 1980-89 (A), 2010-19 (B), and 2070-79 under RCP 4.5 (C) and RCP 8.5 (D). 10th percentile training presence cloglog threshold = 0.3007



Figure S4.1. MaxEnt climate envelope maps for *Sphecodes crassus*. Showing climate envelope for 1980-89 (A), 2010-19 (B), and 2070-79 under RCP 4.5 (C) and RCP 8.5 (D). 10th percentile training presence cloglog threshold = 0.3007



Figure S4.1. MaxEnt climate envelope maps for *Sphecodes ephippius*. Showing climate envelope for 1980-89 (A), 2010-19 (B), and 2070-79 under RCP 4.5 (C) and RCP 8.5 (D). 10th percentile training presence cloglog threshold = 0.3007



Figure S4.1. MaxEnt climate envelope maps for *Sphecodes geoffrellus*. Showing climate envelope for 1980-89 (A), 2010-19 (B), and 2070-79 under RCP 4.5 (C) and RCP 8.5 (D). 10th percentile training presence cloglog threshold = 0.3007



Figure S4.1. MaxEnt climate envelope maps for *Sphecodes monilicomis*. Showing climate envelope for 1980-89 (A), 2010-19 (B), and 2070-79 under RCP 4.5 (C) and RCP 8.5 (D). 10th percentile training presence cloglog threshold = 0.3007



Figure S4.1. MaxEnt climate envelope maps for *Sphecodes pellucidus*. Showing climate envelope for 1980-89 (A), 2010-19 (B), and 2070-79 under RCP 4.5 (C) and RCP 8.5 (D). 10th percentile training presence cloglog threshold = 0.3007



Figure S4.1. MaxEnt climate envelope maps for *Sphecodes puncticeps*. Showing climate envelope for 1980-89 (A), 2010-19 (B), and 2070-79 under RCP 4.5 (C) and RCP 8.5 (D). 10th percentile training presence cloglog threshold = 0.3007

9.4. Biological traits predict ability of British wild bees to occupy their climate envelopes.

Table S5.1. Traits of the 64 species used in the range filling analysis. Mean intertegular distance, measured in mm (Cane, 1987) is used as a proxy for body size

Species	Habitat Breadth	Body Size	Lecty	Overwintering Stage
Andrena barbilabris	4	2.32	Polylectic	Adult within cocoon
Andrena bicolor	3	1.97	Polylectic	Adult within cocoon
Andrena chrysosceles	3	1.87	Polylectic	Adult within cocoon
Andrena cineraria	4	2.86	Polylectic	Adult within cocoon
Andrena denticulata	3	2.13	Polylectic	Prepupa
Andrena dorsata	4	1.94	Polylectic	Adult within cocoon
Andrena flavipes	5	2.31	Polylectic	Adult within cocoon
Andrena fulva	3	2.68	Polylectic	Adult within cocoon
Andrena haemorrhoa	2	2.43	Polylectic	Adult within cocoon
Andrena labialis	3	2.7	Oligolectic	Adult within cocoon
Andrena labiata	2	1.78	Polylectic	Adult within cocoon
Andrena minutula	4	1.39	Polylectic	Adult within cocoon
Andrena nigroaenea	4	2.83	Polylectic	Adult within cocoon
Andrena nitida	3	2.88	Polylectic	Adult within cocoon
Andrena praecox	3	2.36	Oligolectic	Adult within cocoon
Andrena scotica	4	2.86	Polylectic	Adult within cocoon
Andrena thoracica	4	3.23	Polylectic	Adult within cocoon
Anthidium manicatum	4	3.6	Polylectic	Prepupa
Anthophora bimaculata	3	3.25	Polylectic	Prepupa
Anthophora plumipes	4	4.13	Polylectic	Adult within cocoon
Bombus hortorum	3	5.67	Polylectic	Adult (female only)
Bombus humilis	2	4.54	Polylectic	Adult (female only)
Bombus lapidarius	4	5.99	Polylectic	Adult (female only)

Bombus monticola	3	5.1	Polylectic	Adult (female only)
Bombus pascuorum	5	4.89	Polylectic	Adult (female only)
Bombus pratorum	4	5.09	Polylectic	Adult (female
Bombus ruderarius	4	4.77	Polylectic	Adult (female only)
Bombus rupestris	3	5.62	No Lectic Status	Adult (female only)
Dasypoda hirtipes	3	2.73	Oligolectic	Prepupa
Epeolus cruciger	1	1.86	No Lectic Status	Prepupa
Epeolus variegatus	2	1.87	No Lectic Status	Prepupa
Halictus tumulorum	4	1.45	Polylectic	Adult (female only)
Hylaeus brevicornis	3	0.98	Polylectic	Prepupa
Hylaeus communis	3	1.3	Polylectic	Prepupa
Hylaeus confusus	3	1.4	Polylectic	Prepupa
Hylaeus hyalinatus	5	1.31	Polylectic	Prepupa
Lasioglossum calceatum	3	1.74	Polylectic	Adult (female only)
Lasioglossum fulvicorne	2	1.34	Polylectic	Adult (female only)
Lasioglossum lativentre	1	1.51	Polylectic	Adult (female only)
Lasioglossum leucopus	3	1.11	Polylectic	Adult (female only)
Lasioglossum leucozonium	3	1.8	Polylectic	Adult (female only)
Lasioglossum malachurum	3	1.6	Polylectic	Adult (female only)
Lasioglossum minutissimum	2	0.88	Polylectic	Adult (female only)
Lasioglossum morio	3	1.05	Polylectic	Adult (female only)
Lasioglossum parvulum	3	1.29	Polylectic	Adult (female only)
Lasioglossum pauxillum	2	1.17	Polylectic	Adult (female only)
Lasioglossum smeathmanellum	1	1.26	Polylectic	Adult (female only)
Lasioglossum villosulum	3	1.37	Polylectic	Adult (female only)
Megachile centuncularis	2	2.7	Polylectic	Prepupa
Megachile leachella	1	2.71	Polylectic	Prepupa
Megachile ligniseca	1	3.52	Polylectic	Prepupa
Megachile maritima	3	3.72	Polylectic	Prepupa

Megachile versicolor	1	3.16	Polylectic	Prepupa
Megachile willughbiella	3	3.38	Polylectic	Prepupa
Melitta leporina	3	2.24	Oligolectic	Adult within cocoon
Melitta tricincta	2	2.71	Oligolectic	Adult within cocoon
Osmia aurulenta	3	2.83	Polylectic	Adult within cocoon
Osmia bicolor	3	2.72	Polylectic	Adult within cocoon
Osmia bicornis	3	2.98	Polylectic	Adult within cocoon
Osmia caerulescens	3	2.25	Polylectic	Adult within cocoon
Sphecodes ephippius	4	1.5	No Lectic Status	Adult (female only)
Sphecodes geoffrellus	4	1.07	No Lectic Status	Adult (female only)
Sphecodes monilicornis	2	1.48	No Lectic Status	Adult (female only)
Sphecodes pellucidus	1	1.61	No Lectic Status	Adult (female only)

(Intercept)	Habitat Breadth	Body Size	Lecty	Overwintering Stage	df	logLik	AICc	delta	weight
2.070		0.306	+	+	8	-48.92	116.5	0.00	0.674
1.831	0.115	0.295	+	+	9	-49.48	120.3	3.82	0.100
2.224		0.368	+		6	-53.47	120.4	3.96	0.093
1.922	0.161	0.308	+		7	-52.82	121.6	5.18	0.051
2.162	0.198	0.308			5	-57.77	122.6	6.11	0.032
2.061	0.149	0.301		+	7	-53.47	122.9	6.46	0.027
2.517		0.387			4	-57.39	123.5	7.00	0.020
2.634			+	+	7	-56.46	128.9	12.45	0.001
2.263	0.173		+	+	8	-55.46	129.5	13.07	0.001
2.512	0.211		+		6	-58.53	130.5	14.07	0.001
3.004				+	5	-60.42	131.9	15.41	0.000
2.480	0.218			+	6	-59.38	132.2	15.77	0.000
2.745	0.260				4	-61.99	132.7	16.20	0.000
3.034				+	5	-61.61	134.3	17.78	0.000
3.491					3	-65.41	137.2	20.76	0.000

Table S5.2. Model Selection Table following the "model.dredge" procedure for the PGLS regression analysis assessing the impact of life history traits on range filling ability



Figure S5.1. Phylogenetic tree of the 64 species used in the range filling analysis



9.5. New citizen science initiative enhances blossom phenology predictions for fruit trees in Great Britain

Figure S6.1. Sankey plot showing agreement between Citizen Scientists (CS) and an independent observer (I) between A) original flowering stages and B) simplified flowering stages. X indicates unusable picture

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