

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

Article

Published Version

Creative Commons: Attribution 4.0 (CC-BY)

Open access

Wyver, C., Potts, S. G. ORCID: <https://orcid.org/0000-0002-2045-980X>, Edwards, R., Edwards, M. and Senapathi, D. ORCID: <https://orcid.org/0000-0002-8883-1583> (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. ISSN 0168-1923 doi: 10.1016/j.agrformet.2022.109281 Available at <https://centaur.reading.ac.uk/109264/>

It is advisable to refer to the publisher's version if you intend to cite from the work. See [Guidance on citing](#).

To link to this article DOI: <http://dx.doi.org/10.1016/j.agrformet.2022.109281>

Publisher: Elsevier

All outputs in CentAUR are protected by Intellectual Property Rights law, including copyright law. Copyright and IPR is retained by the creators or other copyright holders. Terms and conditions for use of this material are defined in

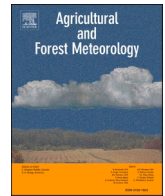
the [End User Agreement](#).

www.reading.ac.uk/centaur

CentAUR

Central Archive at the University of Reading

Reading's research outputs online



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

Chris Wyver^{a,*}, Simon G. Potts^a, Rowan Edwards^b, Mike Edwards^b, Deepa Senapathi^a

^a Centre for Agri-Environmental Research, School of Agriculture, Policy and Development, University of Reading RG6 6AR, United Kingdom

^b Bees, Wasps and Ants Recording Society, Leaside, Carron Lane, West Sussex, GU29 9LB, United Kingdom

ARTICLE INFO

Keywords:

Climate change
Pollination
Phenology
Phenological mismatch

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) 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 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.

1. 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 (e.g., 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 and 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 and Ives, 2011). This can lead to lower seed production (Kudo and 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

* Corresponding author.

E-mail address: c.w.wyver@pgr.reading.ac.uk (C. Wyver).

<https://doi.org/10.1016/j.agrformet.2022.109281>

Received 15 July 2022; Received in revised form 13 October 2022; Accepted 5 December 2022

Available online 11 December 2022

0168-1923/© 2022 The Author(s). Published by Elsevier B.V. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

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 and Ida, 2013; Robbirt et al., 2014; Thomson, 2010). Trends in more generalist interactions were often less pronounced or more stable (Bartomeus et al., 2011, 2013).

Apple (*Malus x domestica* Borkh.) is highly dependant on insect pollination, primarily by bees including both wild and honeybees, and the contribution of insect pollinators is valued at £36.7 million per annum to UK apple production (Garratt et al., 2014). Most apple cultivars are self-incompatible (Ramírez and 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., 2013; Grab and 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 delaying budburst (Heide, 2003). While such delays are already notable in the Mediterranean (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.

Many wild pollinators including hoverflies, beetles and other flies have been recorded visiting apples (Pardo and Borges, 2020), the most frequent and largest contributors are wild bees, particularly *Bombus*, *Andrena*, and *Osmia* spp. (Garratt et al., 2016; Pardo and 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 pollinations is highly variable across regions, ranging from as little as 12.4% to 85.4% depending on variety (Burns and Stanley, 2022).

Bee phenology has been the subject of recent studies and climate-driven phenological advances have been seen in both observational (Bartomeus et al., 2013; Stemkovski et al., 2020) and experimental (Fründ et al., 2013) 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 and Cooper, 2019; Olliff-Yang and Mesler, 2018). However, advances in phenology may not be consistent across all bee species. Individual species traits, nest location, 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:

- 1) 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.
- 3) Any observed asynchrony between the phenology of apples and their pollinators is being driven by climatic variables.

2. Methods

2.1. NFC recording 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 (Department for Environment, Food and Rural Affairs, 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.

2.2. 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 S1, Figure S1). When considered as a group, these 19 species will be referred to as 'the community'.

2.3. 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.

2.4. Impact of climate on pollinator phenology

For the pollinator community and univoltine species (i.e. 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, any species x year combinations calculated using 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.

2.5. 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 (50th percentile estimate) of insect community recording, and the peak flowering date of apple (provided by the NFC at Brogdale). Additionally, as apple blossom may be an important early season resource for bees, the mismatch between bee emergence (10th percentile estimate) of insect community recording and peak flowering date of apple was calculated.

2.6. Statistical modelling

2.6.1. Climate

To test for changes in the climate variables (May-Sep, Oct-Dec, and Jan-Apr average temperature and total precipitation) initial Generalised Additive Models (GAMs) were used to test for trends over time. If the GAM showed no substantial non-linearity, and gave a smoothing term with less than two degree of freedom ($\text{edf} < 2$), 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)” (Wood, 2010)

2.6.2. Apple and Pollinator flight dates, flight duration, and peak mismatch metric

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 ($\text{edf} < 2$), it was replaced with a GLM.

GLMs were then run to test for the effect of climate on the same 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 test for an effect of dataset size.

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 and 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.

3. Results

3.1. Change in climate

A significant, non-linear, increase was seen in January to April temperature ($\text{edf} = 2.72$, $p(\text{edf}) = 0.008$). 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 $0.34 \pm 0.07^\circ\text{C}$ ($p < 0.001$) per decade. October to December temperatures experienced significant linear increases of $0.32 \pm 0.09^\circ\text{C}$ ($p = 0.001$) per decade. There was no significant change in total rainfall amount over time, either linear or non-linear. (Figure S2).

3.2. 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 – $\text{edf} = 3.975$, $p(\text{edf}) < 0.001$, peak flowering – $\text{edf} = 4.757$, $p(\text{edf}) < 0.001$) and was primarily seen between the early- and mid-periods (Table 1, Fig. 1).

Pollinator phenology also exhibited non-linear change over time in both phenological stages (flight onset – $\text{edf} = 2.891$, $p(\text{edf}) < 0.001$, peak flight – $\text{edf} = 2.914$, $p(\text{edf}) < 0.001$). 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 1, Fig. 1).

Not all pollinator species showed the same phenological patterns over time (Fig. 2, Table S2 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 species that showed a linear relationship with time 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 -

Table 1

Change in mean dates of flowering onset and peak flowering for early (1970–74), mid (1991–95) and late (2013–17) periods. For change over time, negative values indicate advancement in phenophase, positive values indicate delay.

		Date range			Change (days)	
		Early 1970–74	Mid 1991–95	Late 2013–17	Early - Mid	Mid - Late
Apple	Flower onset	128.6	117.2	115.8	–11.4	–1.4
	Flower peak	133.4	120.6	119.4	–12.8	–1.2
Pollinator	Flight onset	115.6	70.7	82.8	–44.9	+12.1
	Flight peak	194.3	157.2	170.4	–37.1	+13.2

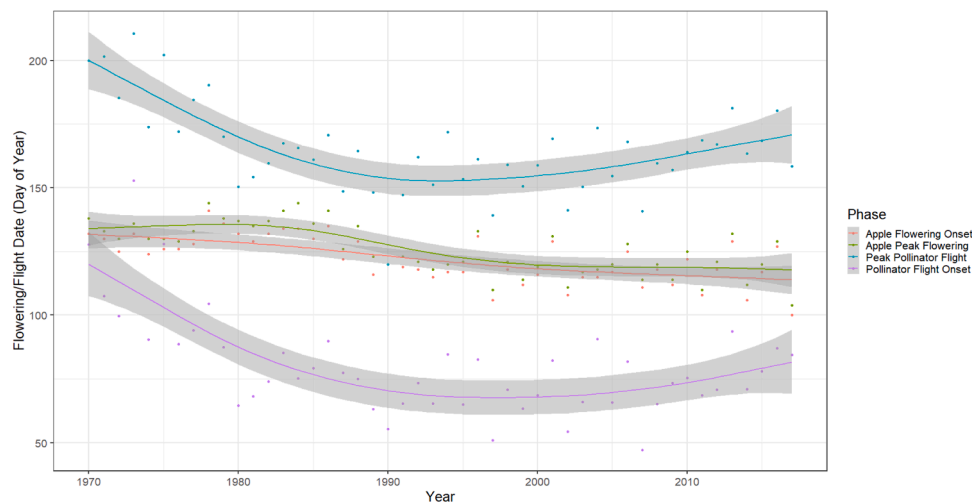


Fig. 1. Trends in apple flowering and pollinator flight dates over time. Shaded area indicates 95% confidence intervals.

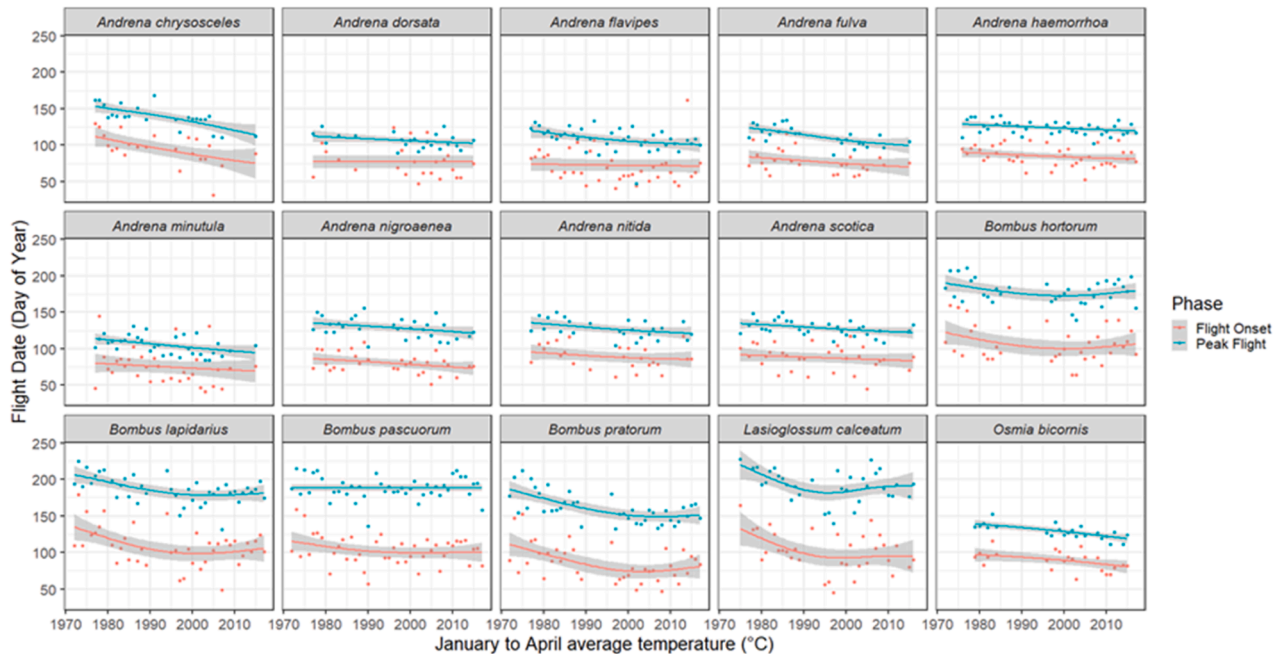


Fig. 2. Trends in apple-pollinating bee species' flight onset and peak flight dates over time. Shaded area indicates 95% confidence intervals'. Full model details available in Table S2.

11.3 days per decade. The other three species (*B. lapidarius*, *B. pratorum* and *Lasioglossum calceatum*) showed significant non-linearity in flight onset dates ($\text{edf} < 2$, $p(\text{edf}) < 0.05$).

Peak flight dates followed a similar pattern to first flight dates (Fig. 2, Table S2 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 ($\text{edf} < 2$, $p(\text{edf}) > 0.05$).

3.3. Impact of climate on phenology

All three 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 ($\text{Pr}(>|z|) < 0.001$) and 6.7 ± 0.9 ($\text{Pr}(>|z|) < 0.001$) days per 1°C warming respectively (Fig. 3, Table S3 for full model details).

By contrast increasing rainfall between January and April is linked to delayed phenology (Figure S3). Model averaging of the best performing models predicted estimates of a delay of 0.36 ± 0.12 ($\text{Pr}(>|z|) = 0.05$) and 0.42 ± 0.13 ($\text{Pr}(>|z|) = 0.002$) days per 10 mm additional rainfall during the period for flowering onset and peak flowering respectively (Table S3 for full model details).

Increased January to April temperature was the only significant variable in impacting onset and peak flight dates with linear models

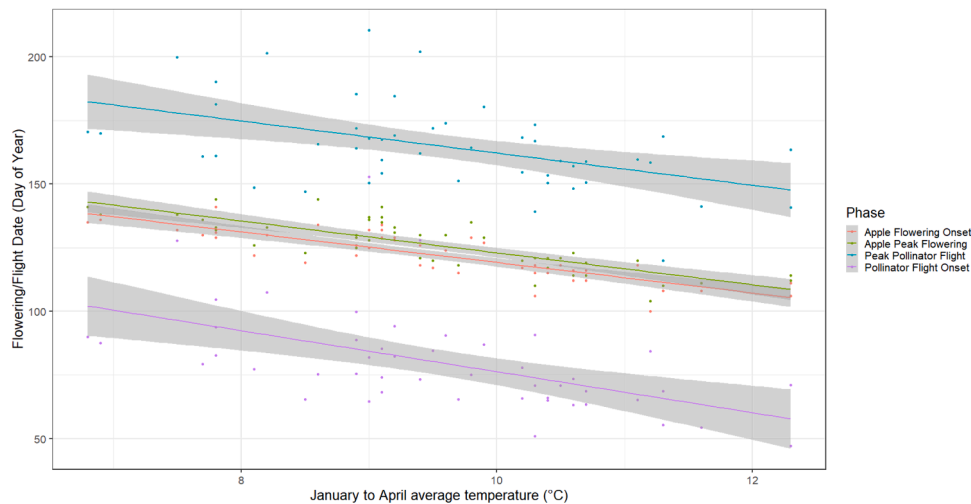


Fig. 3. Impact of January to April temperature on apple flowering and pollinator flight dates. Shaded area indicates 95% confidence intervals.

revealing an advancement of 8.5 ± 2.3 ($\text{Pr}(>|z|) < 0.001$) days per 1°C advancement for flight onset date and 6.5 ± 2.1 ($\text{Pr}(>|z|) = 0.003$) days per degree for peak flight date (Fig. 3, Table S3 for full model details). Dataset size did not significantly predict pollinator community phenology (Table S3 for full model details).

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 temperatures. 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 phenology, and these advances ranged from 4.0 to 9.6 days per 1°C rise. (Fig. 4, Table S4 for full model details).

3.4. 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 (Fig. 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 and pollinator community structure also did not significantly predict either mismatch.

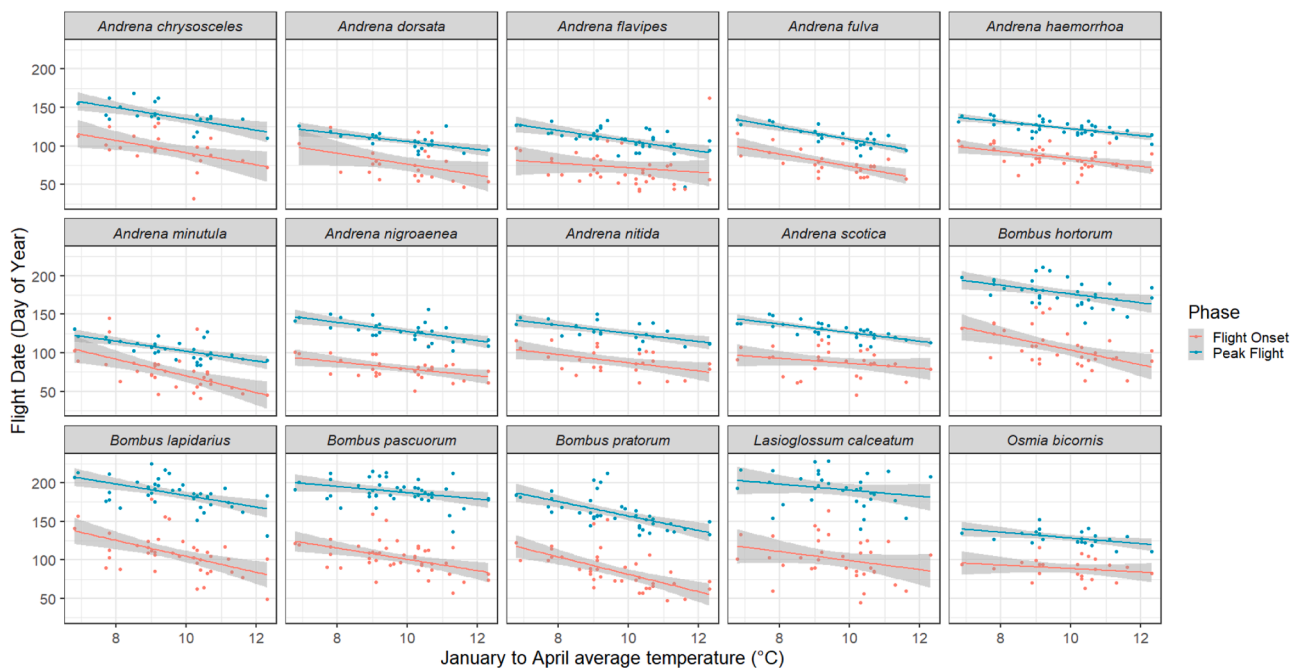


Fig. 4. Trends in apple-pollinating bee species' flight onset and peak flight dates against average January to April temperature. Shaded area indicates 95% confidence intervals. Full model details available in Table S4.

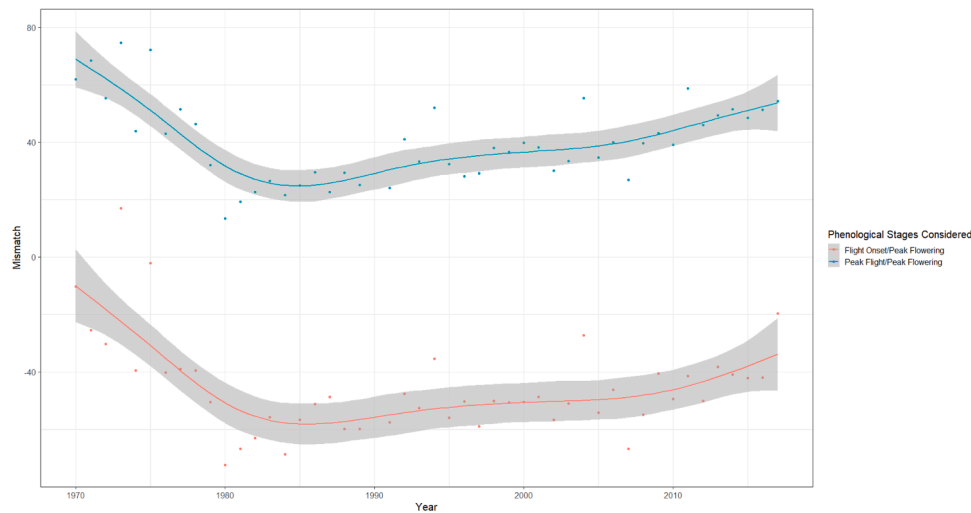


Fig. 5. Change in phenological mismatch (days) between peak apple flowering and peak pollinator flight dates (blue) and peak apple flowering and pollinator flight onset dates (red). Shaded area indicates 95% confidence intervals.

4. Discussion

This study provides evidence of differing patterns of changes in the phenology of bees and the apple crops they pollinate in 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.

4.1. 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 and Kobayashi, 2010; Kunz and Blanke, 2008). This indicates that the climate during the forcing period is the major driver of flowering phenology in the UK. Further warming, however, could cause chill delay 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). This could exacerbate the size of the mismatch between apple flowers and pollinators as well as lead to less synchronised and less dense budburst and ultimately reduced 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 and 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 for the insect, in this case the bee, 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. We found that there was no statistically significant trend over time for the community composition (proportion of yearly records of each species), however there was interannual variation in the dataset which could impact community flight date estimates (Figure S4). It may be possible to increase the size of the pollinator dataset to include data from multiple datasets such as iNaturalist, the Global Biodiversity Information Facility (GBIF) or the National Biodiversity Network (NBN), 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 we expect this number 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’.

4.2. 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.) 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 are 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.

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, we may expect to see increases 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 dependant 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.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgments

Thank you to the National Fruit Collection, especially Matt Ordidge and Lorinda Jewsbury at Brogdale for access to and advice regarding apple flowering records and to the Bees, Wasps & Ants Recording Society for sharing their long-term dataset. This project was funded by BBSRC (Grant number: BB/T508895/1) and Waitrose Agronomy Group as part of the Waitrose Collaborative Training Partnership. WorldWide Fruit Ltd contributed to the funding and development of this project.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.agrformet.2022.109281.

References

- Bartomeus, I., Ascher, J.S., Wagner, D., Danforth, B.N., Colla, S., Kornbluth, S., Winfree, R., 2011. Climate-associated phenological advances in bee pollinators and bee-pollinated plants. *Proc. Natl. Acad. Sci. U.S.A.* 108 (51), 20645–20649. <https://doi.org/10.1073/pnas.1115559108>.
- Bartomeus, I., Park, M.G., Gibbs, J., Danforth, B.N., Lakso, A.N., Winfree, R., 2013. Biodiversity ensures plant-pollinator phenological synchrony against climate change. *Ecol. Lett.* 16 (11), 1331–1338. <https://doi.org/10.1111/ele.12170>.
- Barton, K., 2020. MuMIn: Multi-Model Inference. R Package Version 1.43.17. <https://CRAN.R-project.org/package=MuMIn>.
- Belitz, M.W., Larsen, E.A., Ries, L., Guralnick, R.P., 2020. The accuracy of phenology estimators for use with sparsely sampled presence-only observations. *Methods Ecol. Evol.* 11 (10), 1273–1285. <https://doi.org/10.1111/2041-210X.13448>.
- Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W., Courchamp, F., 2012. Impacts of climate change on the future of biodiversity. *Ecol. Lett.* 15 (4), 365–377. <https://doi.org/10.1111/j.1461-0248.2011.01736.x>.
- Buckley, L.B., Nufio, C.R., Kirk, E.M., Kingsolver, J.G., 2015. Elevational differences in developmental plasticity determine phenological responses of grasshoppers to recent climate warming. *Proc. R. Soc. B* (1809), 282. <https://doi.org/10.1098/rspb.2015.0441>.
- Büntgen, U., Piermattei, A., Krusic, P.J., Esper, J., Sparks, T., Crivellaro, A., 2022. Plants in the UK flower a month earlier under recent warming. *Proc. R. Soc. B* (1968), 289. <https://doi.org/10.1098/rspb.2021.2456>.
- Burns, K.L.W., Stanley, D.A., 2022. The importance and value of insect pollination to apples: a regional case study of key cultivars. *Agric. Ecosyst. Environ.* 331 <https://doi.org/10.1016/j.agee.2022.107911>.
- Chen, I.-C., Hill, J.K., Ohlemüller, R., Roy, D.B., Thomas, C.D., 2011. Rapid range shifts of species associated with high levels of climate warming. *Science* 333 (6045), 1024–1026. <https://doi.org/10.1126/science.1206432>.
- Chmielewski, F.M., Müller, A., Bruns, E., 2004. Climate changes and trends in phenology of fruit trees and field crops in Germany, 1961–2000. *Agric. For. Meteorol.* 121 (1–2), 69–78. [https://doi.org/10.1016/S0168-1923\(03\)00161-8](https://doi.org/10.1016/S0168-1923(03)00161-8).
- Cho, J.G., Kumar, S., Kim, S.H., Han, J.H., Durso, C.S., Martin, P.H., 2021. Apple phenology occurs earlier across South Korea with higher temperatures and increased precipitation. *Int. J. Biometeorol.* 65, 265–276. <https://doi.org/10.1007/s00484-020-02029-1>.
- Darbyshire, R., Webb, L., Goodwin, I., Barlow, E.W.R., 2013. Evaluation of recent trends in Australian pome fruit spring phenology. *Int. J. Biometeorol.* 57 (3), 409–421. <https://doi.org/10.1007/s00484-012-0567-1>.
- Davison, P.J., Field, J., 2018. Limited social plasticity in the socially polymorphic sweat bee *Lasioglossum calceatum*. *Behav. Ecol. Sociobiol.* (Print) 72 (3). <https://doi.org/10.1007/s00265-018-2475-9>.
- Drepper, B., Gobin, A., Remy, S., van Orshoven, J., 2020. Comparing apple and pear phenology and model performance: what seven decades of observations reveal. *Agronomy* 10 (1). <https://doi.org/10.3390/agronomy10010073>.
- Faust, M., 1989. *Physiology of Temperate Zone Fruit Trees*. John Wiley & Sons, Inc.
- Fitter, A.H., Fitter, R.S.R., 2002. Rapid changes in flowering time in British plants. *Science* 296 (5573), 1689–1691. <https://doi.org/10.1126/science.1071617>.
- Fründ, J., Zieger, S.L., Tscharnkte, T., 2013. Response diversity of wild bees to overwintering temperatures. *Oecologia* 173 (4), 1639–1648. <https://doi.org/10.1007/s00442-013-2729-1>.
- Fujisawa, M., Kobayashi, K., 2010. Apple (*Malus pumila* var. domestica) phenology is advancing due to rising air temperature in northern Japan. *Glob. Change Biol.* 16, 2651–2660. <https://doi.org/10.1111/j.1365-2486.2009.02126.x>.
- Funes, I., Aranda, X., Biel, C., Carbó, J., Camps, F., Molina, A.J., de Herralde, F., Grau, B., Savé, R., 2016. Future climate change impacts on apple flowering date in a Mediterranean basin. *Agric. Water Manag.* 164, 19–27. <https://doi.org/10.1016/j.agwat.2015.06.013>.
- Garratt, M.P.D., Breeze, T.D., Boreux, V., Fountain, M.T., McKerchar, M., Webber, S.M., Coston, D.J., Jenner, N., Dean, R., Westbury, D.B., Biesmeijer, J.C., Potts, S.G., 2016. Apple pollination: demand depends on variety and supply depends on pollinator identity. *PLoS ONE* (5), 11. <https://doi.org/10.1371/journal.pone.0153889>.
- Garratt, M.P.D., Breeze, T.D., Jenner, N., Polce, C., Biesmeijer, J.C., Potts, S.G., 2014. Avoiding a bad apple: insect pollination enhances fruit quality and economic value. *Agric. Ecosyst. Environ.* 184, 34–40. <https://doi.org/10.1016/j.agee.2013.10.032>.
- Grab, S., Craparo, A., 2011. Advance of apple and pear tree full bloom dates in response to climate change in the southwestern Cape, South Africa: 1973–2009. *Agric. For. Meteorol.* 151 (3), 406–413. <https://doi.org/10.1016/j.agrformet.2010.11.001>.
- Heide, O.M., 2003. High autumn temperature delays spring bud burst in boreal trees, counterbalancing the effect of climatic warming. *Tree Physiol.* 23, 931–936. <https://doi.org/10.1093/treephys/23.13.931>.
- Hunsicker, M.E., Kappel, C.V., Selkoe, K.A., Halpern, B.S., Scarborough, C., Mease, L., Amrhein, A., 2016. Characterizing driver-response relationships in marine pelagic ecosystems for improved ocean management. *Ecol. Appl.* 26 (3), 651–663. <https://doi.org/10.1890/14-2200/supinfo>.
- Hurvich, C.M., Tsai, C.-L., 1989. Regression and time series model selection in small samples. *Biometrika* 76 (2), 297–307.
- Hutchinson, L.A., Oliver, T.H., Breeze, T.D., Bailes, E.J., Brünjes, L., Campbell, A.J., Erhardt, A., de Groot, G.A., Földesi, R., García, D., Goulson, D., Hainaut, H., Hambäck, P.A., Holzschuh, A., Jauker, F., Klatt, B.K., Klein, A.M., Kleijn, D., Kovács-Hostyánszki, A., Garratt, M.P.D., 2021. Using ecological and field survey data to establish a national list of the wild bee pollinators of crops. *Agric. For. Meteorol.* 315 <https://doi.org/10.1016/j.agee.2021.107447>.
- Jacobs, J.N., Jacobs, G., Cook, N.C., 2002. Chilling period influences the progression of bud dormancy more than does chilling temperature in apple and pear shoots.

- J. Hort. Sci. Biotechnol. 77 (3), 333–339. <https://doi.org/10.1080/14620316.2002.11511502>.
- Juknys, R., Kanapickas, A., Šveikauskaitė, I., Sujetovienė, G., 2016. Response of deciduous trees spring phenology to recent and projected climate change in Central Lithuania. *Int. J. Biometeorol.* 60 (10), 1589–1602. <https://doi.org/10.1007/s00484-016-1149-4>.
- Kehrerberger, S., Holzschuh, A., 2019. Warmer temperatures advance flowering in a spring plant more strongly than emergence of two solitary spring bee species. *PLoS ONE* 14 (6), e0218824. <https://doi.org/10.1371/journal.pone.0218824>.
- Kudo, G., Cooper, E.J., 2019. When spring ephemerals fail to meet pollinators: mechanism of phenological mismatch and its impact on plant reproduction. *Proc. R. Soc. B* 286 (1904), 1–9. <https://doi.org/10.1098/rspb.2019.0573>.
- Kudo, G., Ida, T.Y., 2013. Early onset of spring increases the phenological mismatch between plants and pollinators. *Ecology* 94 (10), 2311–2320. <https://doi.org/10.1890/12-2003.1>.
- Kunz, A., Blanke, M.M., 2008. Effects of global climate change on apple “golden delicious” phenology-based on 50 years of meteorological and phenological data in Klein-Altendorf. *ISHS Acta Hort.* 903, 1121–1126. <https://doi.org/10.1016/j.agrformet.2017.02.017>.
- Martínez-Lüscher, J., Hadley, P., Ordidge, M., Xu, X., Luedeling, E., 2017. Delayed chilling appears to counteract flowering advances of apricot in southern UK. *Agric. For. Meteorol.* 237, 209–218.
- Meier, U., Graf, H., Hack, H., Heß, M., Kennel, W., Klose, R., Mappes, D., Seipp, D., Stauß, R., 1994. Codierung und Beschreibung nach der erweiterten BBCH-Skala, mit Abbildungen. *Nachr Dtsch Pflanzenschutz* 46 (7), 141–153.
- Olliff-Yang, R.L., Mesler, M.R., 2018. The potential for phenological mismatch between a perennial herb and its ground-nesting bee pollinator. *AoB Plants* 10 (4). <https://doi.org/10.1093/aobpla/ply040>.
- Pardo, A., Borges, P.A.V., 2020. Worldwide importance of insect pollination in apple orchards: a review. *Agric. Ecosyst. Environ.* 293 <https://doi.org/10.1016/j.agee.2020.106839>.
- Peñuelas, J., Filella, I., Comas, P., 2002. Changed plant and animal life cycles from 1952 to 2000 in the Mediterranean region. *Glob. Change Biol.* 8, 531–544. <https://doi.org/10.1046/j.1365-2486.2002.00489.x>.
- R Core Team, 2020. R: A language and environment for Statistical Computing. R Foundation for Statistical Computing. <https://www.R-project.org/>.
- Rafferty, N.E., Ives, A.R., 2011. Effects of experimental shifts in flowering phenology on plant-pollinator interactions. *Ecol. Lett.* 14, 67–74. <https://doi.org/10.1111/j.1461-0248.2010.01557.x>.
- Ramírez, F., Davenport, T.L., 2013. Apple pollination: a review. *Sci. Hortic.* 162, 188–203. <https://doi.org/10.1016/j.scienta.2013.08.007>.
- Reid, P.C., Hari, R.E., Beaugrand, G., Livingstone, D.M., Marty, C., Straile, D., Barichivich, J., Goberville, E., Adrian, R., Aono, Y., Brown, R., Foster, J., Groisman, P., Hélaouët, P., Hsu, H.H., Kirby, R., Knight, J., Kraberg, A., Li, J., Zhu, Z., 2016. Global impacts of the 1980s regime shift. *Glob. Change Biol.* 22 (2), 682–703. <https://doi.org/10.1111/gcb.13106>.
- Robbirt, K.M., Roberts, D.L., Hutchings, M.J., Davy, A.J., 2014. Potential disruption of pollination in a sexually deceptive orchid by climatic change. *Curr. Biol.* 24 (23), 2845–2849. <https://doi.org/10.1016/j.cub.2014.10.033>.
- Rucker, R.R., Thurman, W.N., Burgett, M., 2012. Honey Bee pollination markets and the internalization of reciprocal benefits. *Am. J. Agric. Econ.* 94 (4), 956–977. <https://doi.org/10.1093/ajae/aas031>.
- Sparks, T.H., Croxton, P.J., Collinson, N., Taylor, P.W., 2005. Examples of phenological change, past and present, in UK farming. *Ann. Appl. Biol.* 146 (4), 531–537. <https://doi.org/10.1111/j.1744-7348.2005.050016.x>.
- Steele, T.N., Schürch, R., Ohlinger, B.D., Couvillon, M.J., 2022. Apple orchards feed honey bees during, but even more so after, bloom. *Ecosphere* (9), 13. <https://doi.org/10.1002/ecs2.4228>.
- Stemkovski, M., Pearse, W.D., Griffin, S.R., Pardee, G.L., Gibbs, J., Griswold, T., Neff, J. L., Oram, R., Rightmyer, M.G., Sheffield, C.S., Wright, K., Inouye, B.D., Inouye, D.W., Irwin, R.E., 2020. Bee phenology is predicted by climatic variation and functional traits. *Ecol. Lett.* 23 (11), 1589–1598. <https://doi.org/10.1111/ele.13583>.
- Thomson, J.D., 2010. Flowering phenology, fruiting success and progressive deterioration of pollination in an early-flowering geophyte. *Philos. Trans. R. Soc. B* 365 (1555), 3187–3199. <https://doi.org/10.1098/rstb.2010.0115>.
- Timberlake, T.P., Vaughan, I.P., Memmott, J., 2019. Phenology of farmland floral resources reveals seasonal gaps in nectar availability for bumblebees. *J. Appl. Ecol.* 56 (7), 1585–1596. <https://doi.org/10.1111/1365-2664.13403>.
- White, J., Son, Y., Park, Y.-L., 2009. Temperature-dependent emergence of Osmia cornifrons (Hymenoptera: megachilidae) adults. *J. Econ. Entomol.* 102 (6), 2026–2032. <https://doi.org/10.1603/029.102.0602>.
- Wood, S.N., 2010. Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *J. R. Stat. Soc. B* 73, 3–36. <https://doi.org/10.1111/j.1467-9868.2010.00749.x>.