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Climate effects on the onset of flowering in the United Kingdom

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Abstract

Background: A warmer climate has consequences for the timing of phenological events, as temperature is a key factor controlling plant development and flowering. In this study, we analyse the effects of the long-term climate change and an extreme weather event on the first flowering day (FFD) of five spring-flowering wild plant species in the United Kingdom. Citizen science data from the UK Woodland Trust were obtained for five species: *Tussilago farfara* (coltsfoot), *Anemone nemorosa* (wood anemone), *Hyacinthoides non-scripta* (bluebell), *Cardamine pratensis* (cuckooflower) and *Alliaria petiolate* (garlic mustard).

Results: Out of the 351 site-specific time series (≥ 15-years of FFD records), 74.6% showed significant negative response rates, i.e. earlier flowering in warmer years, ranging from − 5.6 to − 7.7 days °C^{-1}. 23.7% of the series had non-significant negative response rates, and 1.7% had non-significant positive response rates. For cuckooflower, the response rate was increasingly more negative with decreasing latitudes. The winter of 2007 reflects an extreme weather event, about 2 °C warmer compared to 2006, where the 2006 winter temperatures were similar to the 1961–1990 baseline average. The FFD of each species was compared between 2006 and 2007. The results showed that the mean FFD of all species significantly advanced between 13 and 18 days during the extreme warmer winter of 2007, confirming that FFD is affected by temperature.

Conclusion: Given that all species in the study significantly respond to ambient near-surface temperatures, they are suitable as climate-change indicators. However, the responses to a + 2 °C warmer winter were both more and less pronounced than expected from an analysis of ≥ 15-year time series. This may reflect non-linear responses, species-specific thresholds and cumulative temperature effects. It also indicates that knowledge on extreme weather events is needed for detailed projections of potential climate change effects.

Keywords: Bluebell, Citizen science, Climate change, Coltsfoot, Cuckooflower, Garlic mustard, Plant phenology, Wood anemone

Background

Human-induced global warming and associated environmental change is currently occurring [1, 2]. The timing of biological events and recurring plant and animal life cycle stages are linked to abiotic environmental factors [3], with many phenotypical characteristics being affected by temperature and precipitation [4–9]. Temperature is considered the most important factor controlling plant phenology at higher latitudes, with pronounced differences in temperature between the winter and summer seasons [10, 11].

A plant's first flowering day (FFD), defined as the 1st day of the year that flowers begin to emerge, may vary from year-to-year, and the FFD can act as a proxy that the surface temperature is rising due to global warming [12, 13]. Information on the species-specific temperature-dependent response may feed into climate change models, e.g. earth system and terrestrial ecosystem models that incorporate basic phenological factors [14], or be used to develop methods that control invasive species such as garlic mustard [15]. Regional assessments are needed since the phenological response is highly

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dependent on temperature conditions, with responses caused by both the cumulative temperature effects and the species-specific temperature thresholds [16–18]. Furthermore, the temperature response rate can be influenced by local climatic conditions and the length of the forcing period [19].

It is well documented that temperature is affected by geographical variables, and in the UK, lower latitudes, lower altitudes and westerly longitudes are relatively warmer than higher latitudes, higher altitudes and easterly longitudes [11, 17, 20]. Light intensity and photoperiod are influenced by latitude, where the solar angle, daylight length and sun intensity gradually increase as spring approaches. Elevation affects temperature through adiabatic pressure differences; with increasing elevation there is a corresponding decrease in air pressure, which leads to a reduction in temperature [20]. The westerly longitudinal temperature differences result from the warming effect of the North Atlantic Current feeding off the Gulf Stream subtropical gyre, which in turn affects atmospheric temperatures, bringing relatively warmer winters to the western side of the British Iles [20].

Climate change and extreme weather events may induce changes to various species' phenology. A study on 385 UK plant species indicated a mean FFD advancement of 4.5 days during the 1990s, compared to the three previous decades [21], and Tansey et al. [18] found a plastic response to forcing spring temperatures of -3 to -8 days °C^{-1} in 22 species studied, with early- and late-flowering species being influenced also by chilling and photoperiod, respectively. The immediate observable effects of an extreme weather event on phenology may provide an insight into the effects of subtler long-term climate variations on phenology [22]. Thus, not only is it important to assess the long-term impact of climate change on phenological events but also important to assess how plants react to extreme weather events [23, 24].

The aim of this study was to assess the relationship between temperature data from 1950 to 2017 and data on the FFD of five wild plant species in the United Kingdom. Citizen science data from the UK Woodland Trust were obtained for five species: *Hyacinthoides non-scripta* (bluebell), *Anemone nemorosa* (wood anemone), *Tussilago farfara* (coltsfoot), *Alliaria petiolate* (garlic mustard), and *Cardamine pratensis* (cuckooflower). We hypothesised that (1) the latter part of the study period is associated with warmer temperatures than the first part. (2) Warmer spring temperatures are associated with earlier FFD. (3) The geographical climatic temperature characteristics can explain observational variations in temperature response rate. (4) A warm winter would result in FFD advancement, compared to a winter with average temperature conditions.

Materials and methods

The UK study area, including England, Northern Ireland, Scotland and Wales, has an area of 248.5 thousand km^2. England consists mostly of low-lying terrain with some mountainous areas to the northwest of the country. Scotland is a mix of highland and lowland; the area is distinctly split between a geological fault line separating the two regions. Wales is predominantly mountainous with lower lying terrain in the south. Northern Ireland has a similar topography to Wales with some mountainous and hilly terrain and lowland flat areas. The climate of the UK is considered temperate (mesic), where generally the north of the country is cooler than the south. The Gulf Stream allows the UK to be relatively warm compared to other locations of similar latitude.

Data sources

Geographical outline maps were provided by the UK Ordnance Survey (http://www.ordnancesurvey.co.uk/business-and-government/products/opendata.html). Gridded mean elevation values and mean temperature at 2 m were obtained from the E-OBS daily gridded observational dataset version 18, covering the period 1 January 1950–31 December 2017 [25]. The E-OBS data, stored in NetCDF files (tg_ens_mean_0.25deg_reg_v18.0e.nc; elev_ens_0.25deg_reg_v18.0e.nc), had a spatial resolution of 0.25° regular lat–lon grid. This corresponds roughly to 28 km^2 per grid cell in the UK, covered by 601 grid cells. Precipitation was not included in this study since, in mesic temperate regions such as the UK, temperature data are regarded as an adequate variable in early spring plant phenological modelling studies [17].

Phenological records were provided by the UK Woodland Trust (http://www.woodlandtrust.org.uk/). These data were collected as part of a citizen science programme involving the general public to amass datasets over a large spatial and temporal range. For this study, FFD data covering the time period 1950–2017 were extracted. For this time period, the total number of FFD observations (all species) was 93,219 from 13,857 locations throughout the UK. FFD data from location points that were classified as sea grid cells according to the E-OBS land-sea mask were excluded due to a lack of temperature data. Further removals were made to eliminate outliers; FFD observations that exceeded three standard deviations from the mean FFD for each species were deleted, according to the method by Jochner et al. [17]. This left a dataset of 82,158 FFD observations from 11,865 locations (Fig. 1).

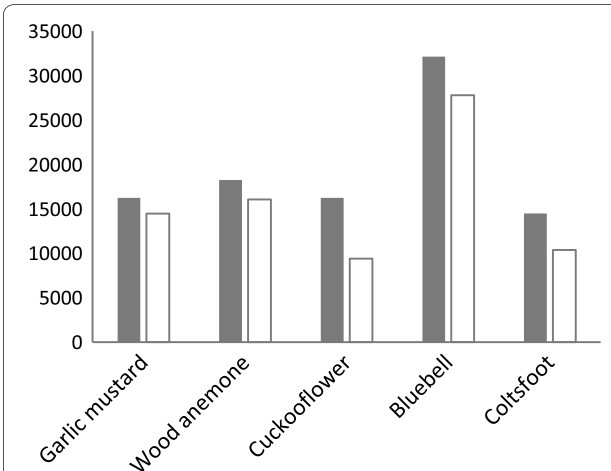

Fig. 1 Number of observations in the Woodland Trust FFD dataset, before (filled bars) and after (unfilled bars) removal of data points belonging to grid cells classified as sea and outliers (outside 3 standard deviations)

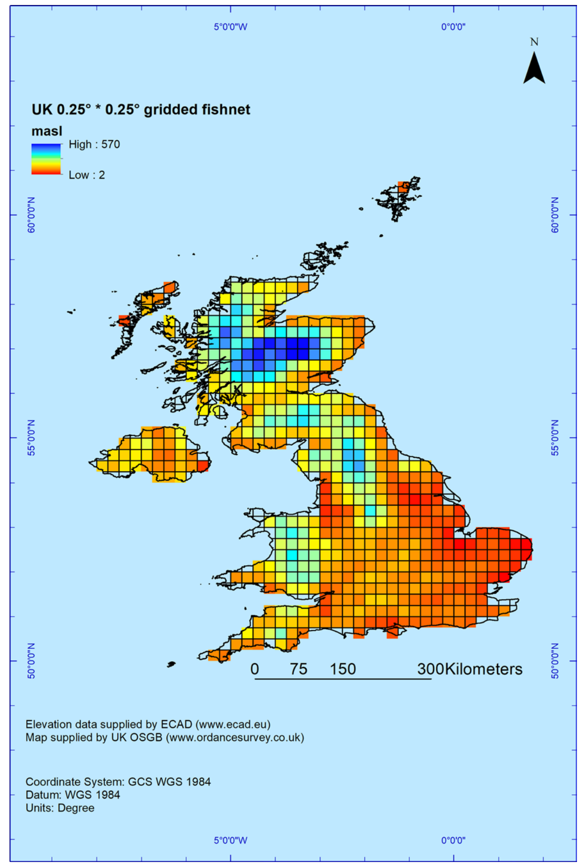

Fig. 2 The UK fishnet (0.25° regular lat–lon grid), with the E-OBS elevation data, overlaid to show that each fishnet grid is equal to that of the NetCDF file. Each grid represents the mean elevation value for the area

Merging of datasets

The FFD point location data and the gridded E-OBS data were imported in ArcGIS 10.6. Since the E-OBS data were defined in gridded squares, it was necessary to create a polygon shapefile so that this could be joined with the FFD point location data. This was achieved over a number of steps through the creation of a 'fishnet', with the cell size set at 0.25° (commensurate with the grid cell dimensions of the E-OBS elevation data). The site-specific elevation data were obtained for each FFD coordinate point using an online tool that adds elevation data to coordinate data (http://www.gpsvisualizer.com/elevation). The datasets were spatially joined, and a raster was created from this joined file, using the elevation grid codes, applying the WGS84 coordinate system. The raster file was converted to 0.25° grid cell polygons, then saved as a shapefile. Each 0.25° polygon represented a specific average elevation (masl) covering the whole of the UK (Fig. 2). The elevation file was joined with the FFD data file through a spatial join, to provide a table with each FFD data point (FFD, FFD elevation (masl) and FFD lat/lon data) and with information data on the corresponding E-OBS grid cell (mean elevation and mean annual temperature).

The point elevation data were used for refining the gridded temperature data to provide a better representation of temperature at each FFD location [26]. This was achieved by adjusting the gridded temperature data on the basis of the differences between the elevation of the observational site and the mean grid cell elevation. The environmental lapse rate (ELR) [27, 28] is a rate of decrease in temperature with altitude due to adiabatic effects and air becoming less dense with increasing altitude. The ELR is found to be -6.5 °C km^{-1} increase in elevation [29], and it has been applied in various phenological studies [26, 30, 31]. The adjusted FFD temperature was derived from the following calculation: FFD temperature $= dz * \Gamma + MGT$, where Γ is the lapse rate of 6.5 °C km^{-1}; dz the altitude difference (mean grid cell altitude − FFD altitude), and MGT the mean grid cell temperature (°C).

Analysis

To confirm that the climate of the study region is warming, commensurate with reports that the global climate is warming [2], the annual mean temperatures for each grid cell in UK were split into two time series (1950–1983 and 1984–2017) and statistically tested using a Student's *t* test.

The temperature during the two preceding months and the month of flowering is regarded as most appropriate for phenological studies [32]; coltsfoot and wood anemone flower in March; while bluebell, cuckooflower and garlic mustard flower in April. The gridded mean daily temperatures for January–March and February–April, respectively, were, therefore, calculated, and used in the analysis of the FFD temperature response rates. The temperature responses were analysed for time series with at least 15 observation years only, as shorter time series may not provide a statistically valid model in relation to climate change studies [17]. The FFD dataset was checked for duplicates, and when more than one FFD record existed for the same point location, year and species, only the first recorded observation was retained [33]. After removing short time series and duplicate FFD records, a total of 5718 FFD observations within 163 FFD locations were available for statistical analysis (Fig. 3; Table 1). Most of these time series represented observations made during the last decades.

The species-specific FFD temperature response rate (days °C^{-1}) was calculated through linear regression following the method by Jochner et al. [17]. For example, bluebell had 132 time series of 15 years or more. Thus, 132 bluebell linear regressions were calculated, where FFD was the dependent variable and FFD temperature was the independent variable. A negative regression coefficient represented an earlier FFD onset in days per °C increase, the opposite for a positive.

The FFD temperature response rate, calculated for each location and species, was further analysed using Spearman rank correlation to check for trends associated with latitude, longitude and altitude. The FFD temperature response rates were ranked in 5 equal ranks according to percentiles (20% in each group), with the values associated with higher temperature scoring the highest rank value of 5 (Table 2). The corresponding longitudinal values were ranked 1–5 moving east to west; latitudinal values were ranked 1–5 moving north to south; and the altitudes were ranked 1–5 moving from the highest to lowest altitude. The ranking of the variables negated problems associated with negative and positive values. For example, moving east to west, longitude values transform from positive values to negative values as they cross the Prime Meridian.

To assess the response to an extreme climate event, FFD data from 2006 and 2007 were compared. The winter of 2006 was selected as it represented the average temperature conditions of 1961–1990, which is the current, commonly used 30-year climate normal period (Fig. 4) [34]. The winter of 2007 was selected as it was an unusually warm winter [25], actually the warmest in over 500 years in Europe [31, 35]. The advantage of comparing two consecutive years was that data for both years were available from many sites. The 2006 and 2007 flowering data were, therefore, selected where pairs between the 2 years existed according to their longitudinal and latitudinal coordinates (Fig. 5), and analysed statistically using a paired *t* test. The mean grid cell temperature for the preceding 2 months and the month in which the mean FFD occurs was used in determining the FFD location temperature for each species.

Results

The mean annual temperature (MAT) in UK was significantly higher (0.62 °C ± 0.07) covering 1984–2017 compared with 1950–1983 (Fig. 6a), with an increase in MAT from 8.5 to 9.1 °C. The differences in mean daily temperatures during January–March (0.62 °C ± 0.15) and February–April (0.34 °C ± 0.03) were also significant, with an increase from 3.7 to 4.3 °C and 4.9 °C to 5.3 °C, respectively (Fig. 6b, c).

The linear regression analysis of the 351-time series ≥ 15 years showed a total of 98.3% of the temperature response rates were negative, of which 74.6% were significant ($p < 0.05$) (Table 3). However, the early flowering species had fewer significant series (44% and 53% for wood anemone and coltsfoot) than the later flowering species (ranging between 77 and 89%). Further, 1.7% of the responses were positive (5 of the wood anemone sites, and 1 bluebell), of which none were significant (Fig. 7). The temperature response rate (derived from linear regression) differed among the species, with wood anemone and garlic mustard having on average the smallest responses (−5.6 days °C^{-1}) and coltsfoot the largest (−7.7 days °C^{-1}) (Table 3). A rank analysis was carried out between the linear FFD temperature response rates and latitude, longitude and altitude. Most correlations were insignificant, but the temperature response rates of cuckooflower were larger at lower latitudes (Table 4, Fig. 7). The species-specific median r^2 values ranged from 0.32 to 0.51, with the lower degree of explanation being associated with the early-flowering species (coltsfoot and wood anemone), and the higher with the late-flowering species. For single sites, about 20–75% of the observed variation was explained by temperature conditions (Fig. 8).

The 2 years selected for analysis of an extreme event differed significantly ($p < 0.05$), with the 2007 mean daily temperature being higher in both January–March (+2.12 °C) and February–April (+2.09 °C). The daily mean temperatures during January–March and February–April in 2006 were slightly lower than the 1961–1990 baseline average (−0.05 °C ± 0.06 and −0.40 °C ± 0.02, respectively) and in 2007, significantly higher than the baseline average (2.07 °C ± 0.03 and 1.69 °C ± 0.06, respectively) (Fig. 9). For all species, most of the sites showed earlier FFDs in 2007 than in 2006 (Fig. 10), and a paired *t* test showed significant differences in mean FFD

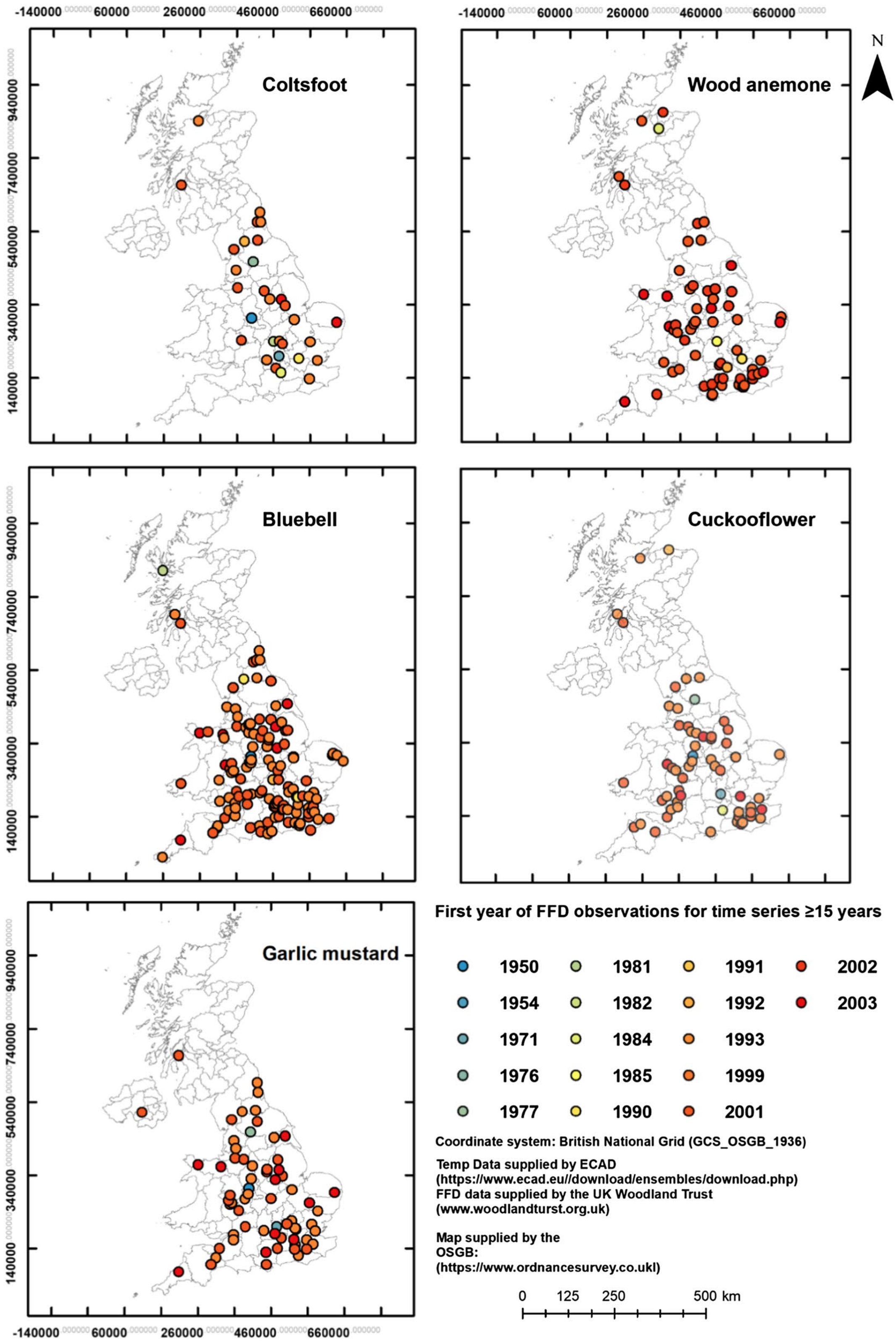

Fig. 3 Location of FFD sites in the UK ≥ 15-year time series. Each dot represents the FFD location for all species after the removal of time series with less than 15 years of FFD data collections (in total 163 sites containing 5718 FFD observations between 1950 and 2017; species-specific information is provided in Table 1)

Table 1 The plant species included in this study, sorted according to mean FFD in UK, include information on earliest and latest FFD, the total number of observations, and the number of FFD observations in time series (TS) ≥ 15 years

Species	Mean FFD ± SD	Earliest/latest FFD	No. of TS ≥ 15 years	No. of observations Total (TS ≥ 15 years)	Length of TS Mean ± SD
Coltsfoot	9 Mar ± 17 days	18 Jan–1 May	30	9390 (534)	18 ± 6.89
Wood anemone	27 Mar ± 13 days	13 Feb–9 May	64	16,053 (1016)	16 ± 1.44
Bluebell	15 Apr ± 13 days	7 Mar–25 May	132	27,787 (2117)	16 ± 2.44
Cuckooflower	16 Apr ± 15 days	1 Mar–30 May	60	14,475 (994)	17 ± 4.51
Garlic mustard	20 Apr ± 10 days	13 Mar–26 May	65	14,453 (1057)	16 ± 4.50

Table 2 Rank definitions for each variable used in the Spearman rank correlation analysis

Variable	Rank definitions
FFD temperature response rate (days °C^{-1})	1 = smallest, 5 = largest
FFD altitude (masl)	1 = highest, 5 = lowest
FFD longitude (degrees east to west)	1 = most easterly, 5 = most westerly
FFD latitude (degrees south to north)	1 = most northerly, 5 = most southerly

(Table 5). By way of example, the temperature response for bluebell showed a mean FFD advancement in 2007 of 17.8 days compared to 2006.

Discussion

The UK temperature has significantly increased between 1950–1983 and 1984–2017, both in terms of annual mean daily temperature and for the 3 monthly periods of key relevance for the onset of spring flowering, corresponding with the conclusions of the IPCC that the global temperature is warming [2, 36]. Over the period 1998–2014, the period during which most of the data included in this study were collected (Fig. 3), there has, however, been little directional trend in UK spring temperatures [18]. Even so, the observed inter-annual variation in FFD was correlated with the temperature, indicating a causal relation, in line with other studies where it was found that ambient temperature had an effect on FFD [11, 17, 21]. The analysis of an extreme event confirmed that the warm winter of 2007 was associated with a substantial advancement in FFD compared with average conditions, ranging between 2 to 3 weeks.

A small proportion of the time series had a starting year prior to 1998. The temperature responses of these series did in general not differ from series with a later start. However, non-significant positive linear regressions emerged for five series starting in 2002 and one in 2001. This may be due to the small sample sizes where 15-year time series may not have been sufficient, or to changes in local climate conditions, e.g. by growth or cutting of forest stands that were not captured by the adjusted local climate data (i.e. the species mainly affected was wood anemone). Uncertainties may also result from low accuracy of citizen science data [37]. For example, it is possible that the records are influenced by the visiting

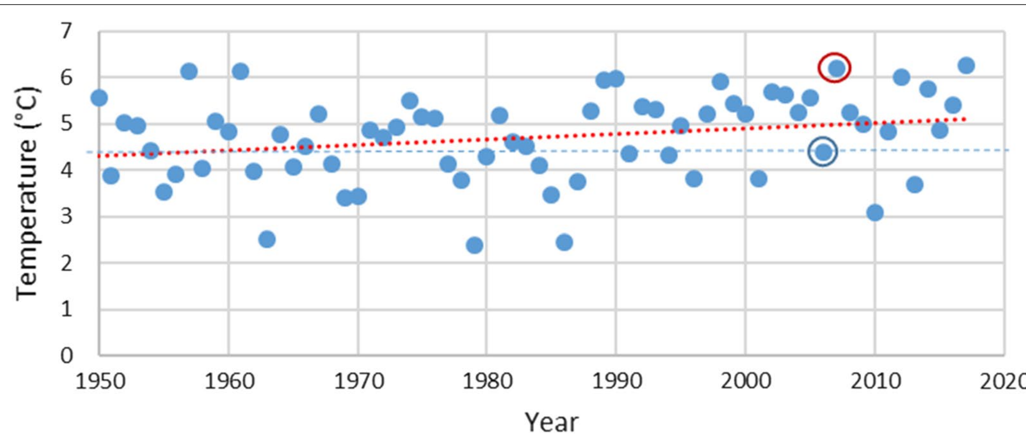

Fig. 4 UK mean daily temperatures of January–April for the period 1950–2017, with the annual averages (blue dots) based on E-OBS data from all UK gridcells (Fig. 2). The average of the climate normal period 1961–1990 is indicated by a blue dashed line, the trend over 1950–2017 as a red dashed line; 2006, representing the climate normal is indicated by a blue circle, and 2007, representing a warm spring, is indicated by a red circle

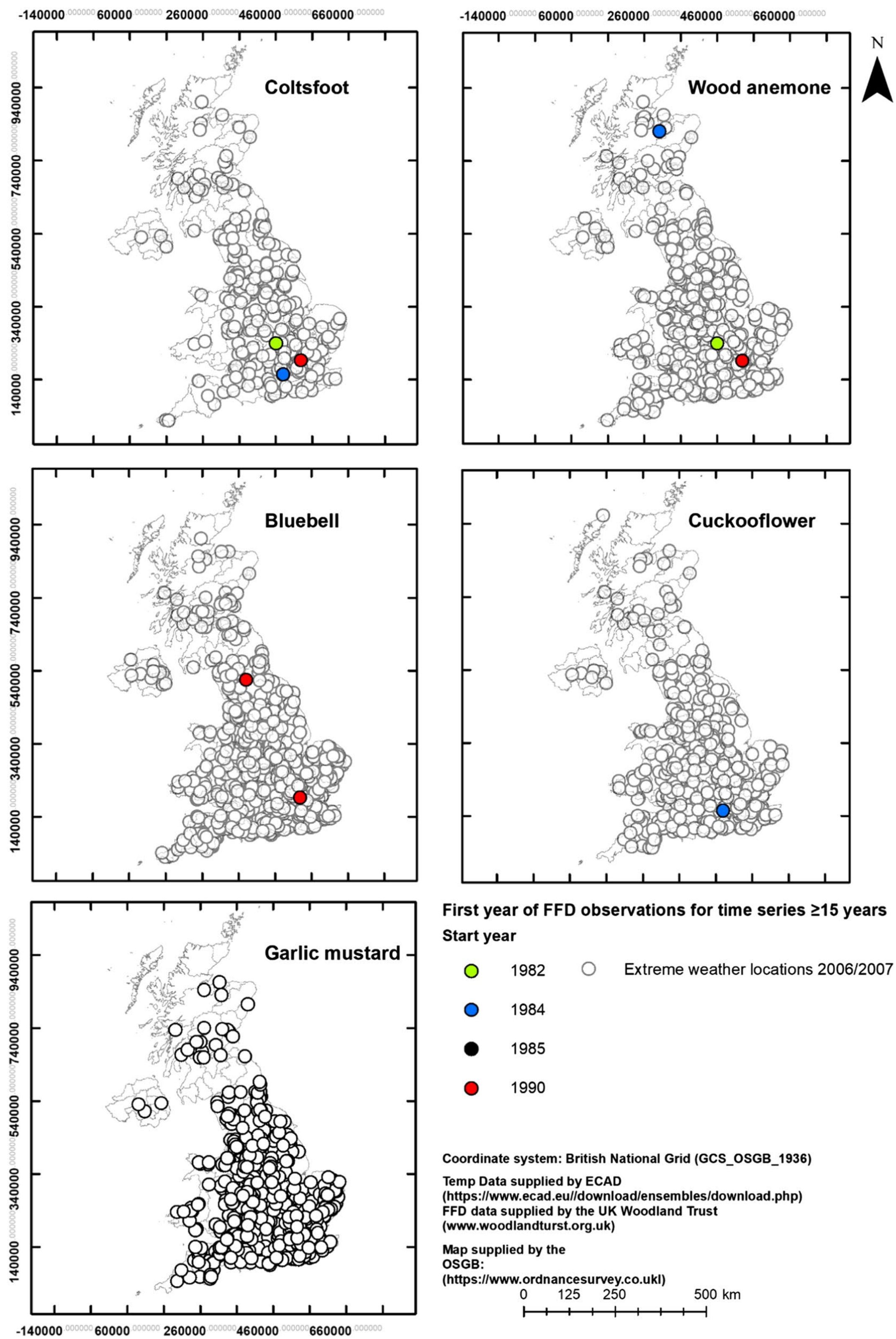

Fig. 5 Location of FFD sites used in the analysis of an extreme event, comparing data from 2006 (average winter) and 2007 (warm winter). Sites overlapping with the time series analysis (Fig. 3) are highlighted, in total 2583 sites; species-specific information is provided in Table 5

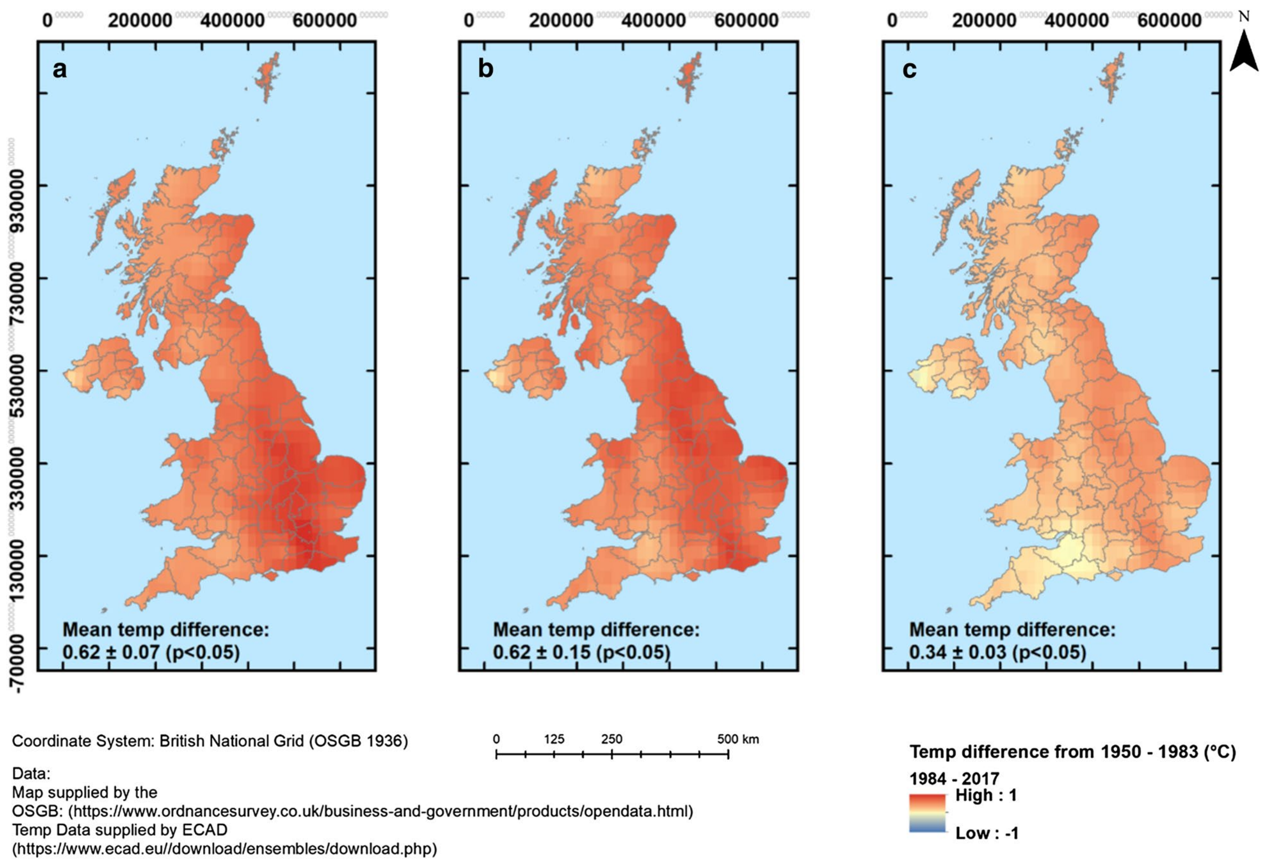

Fig. 6 Changes in temperature conditions in the UK between 1950–1983 and 1984–2017: **a** difference in annual mean temperature, **b** changes in mean daily temperature for the 3 months of January–March, **c** changes in mean daily temperature for the 3 months of February–April. The calculations were based on E-OBS gridded observational dataset. The spatial temperature characteristics that explain the observational variations in time and space in FFD

Table 3 Results from the time series linear regression analysis, including the number of significant negative responses (total number negative and positive responses in brackets), number of days per °C (significant responses only), and the average species-specific priming temperature, based on site-specific 3-month temperatures

Species	Temperature response rate			Mean 3-month temperature Months, °C ± SD
	Negative (total)	Positive	Days $°C^{-1} \pm$ SD	
Coltsfoot	14 (30)	(0)	−7.7 ± 1.7	January–March, 4.6 ± 1.3
Wood anemone	26 (59)	(5)	−5.6 ± 1.5	January–March, 5.0 ± 1.3
Bluebell	117 (131)	(1)	−6.2 ± 1.2	February–April, 6.1 ± 1.2
Cuckooflower	46 (60)	(0)	−6.7 ± 1.5	February–April, 5.9 ± 1.2
Garlic mustard	56 (65)	(0)	−5.6 ± 1.2	February–April, 6.0 ± 1.2

frequency and that citizen scientists may not work to a set standard when recording the emergence of a flower, with some recording the date when the flower is fully open, while others log the date just as the flower starts to open. One way further to reduce the effects of outliers is to use data within two instead of three standard deviations [38]; however, at the risk of removing true extreme values. For instance, water and nutrient availability is likely to differ among sites and may contribute to the observed variation in FFD, by way of example, UK lowland and upland areas have different habitats based on, among other things, soil types and climate [39, 40].

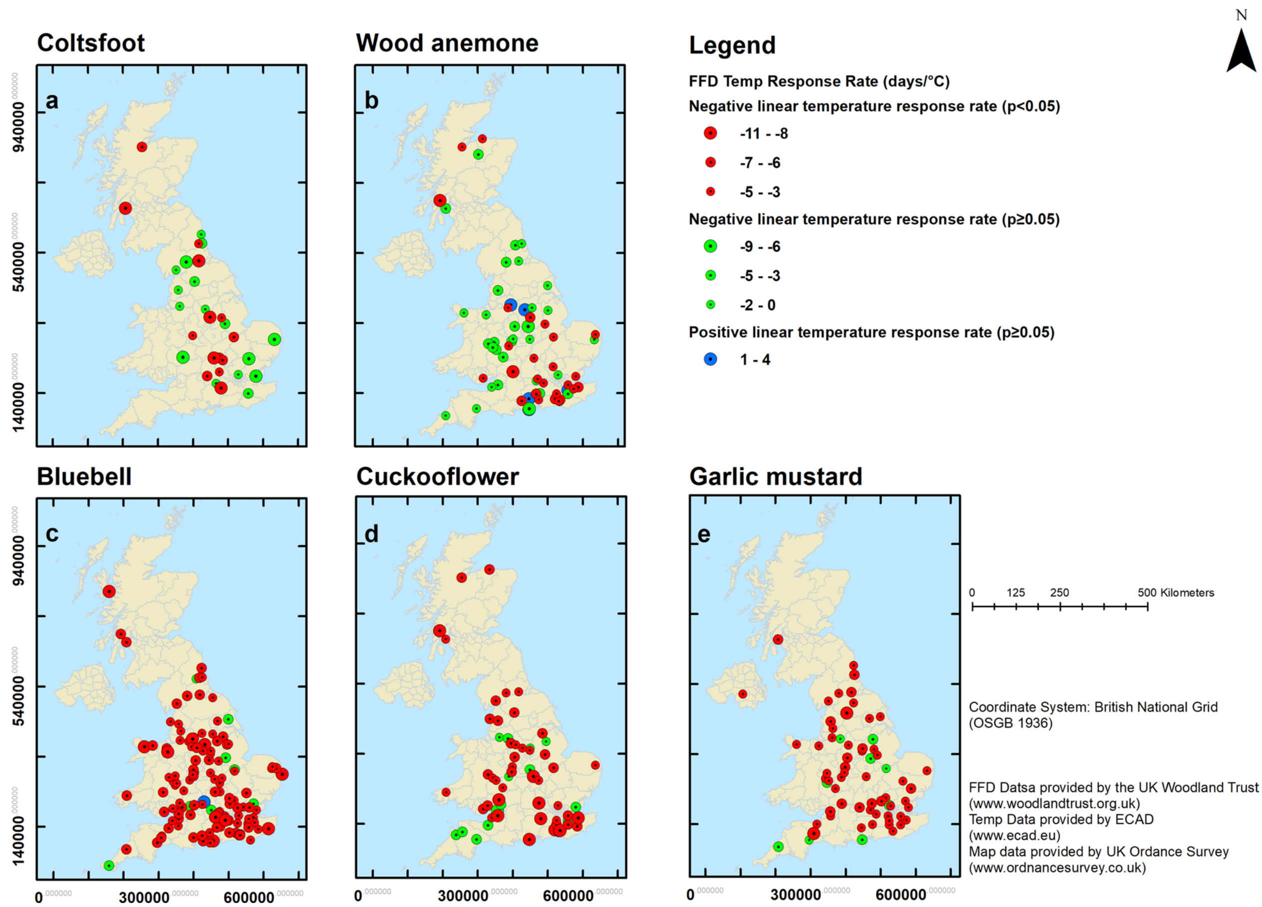

Fig. 7 The spatial distribution for each species in the study in relation to temperature response rates (days per °C); **a** coltsfoot, **b** wood anemone, **c** bluebell, **d** cuckooflower and **e** garlic mustard. The graduated symbol scheme is based on the mean temperature response rates across the UK and are classified according to natural breaks

Table 4 The correlation coefficients for the Spearman rank test, analysing the species-specific temperature response rates against latitude, longitude, and altitude

Species	*n*	Lat	Lon	Alt
Coltsfoot	14	− 0.063	0.219	0.235
Wood anemone	26	0.305	− 0.136	− 0.186
Bluebell	117	− 0.034	0.096	− 0.077
Cuckooflower	46	0.312*	− 0.076	0.170
Garlic mustard	56	− 0.194	0.141	− 0.055

*Correlation significant at the 0.05 level (two tailed)

Earlier springtime flowering events have been associated with stronger temperature responses [11, 17]. In this study, however, the early flowering of coltsfoot and wood anemone had fewer time series showing significant temperature responses than the three late-flowering species. Coltsfoot showed a temperature response rate of -4.8 days $°C^{-1}$ in Europe [17], whereas in the current study, it was -7.7 days $°C^{-1}$ (i.e. the largest temperature response and largest standard deviation). The European data indicated a strong influence of factors related to both latitude and longitude [17]. In this study, coltsfoot did not indicate any dependency on geographical climatic temperature characteristics, possibly because such relations are easier to detect given data from a larger region with more contrasting climate conditions (see Jochner et al. [17]). For the UK, only the temperature response rate of cuckooflower was associated with latitude. However, there are some values that warrant a follow-up study should more data become available over a greater number of years. For example, the wood anemone temperature response rate may become significantly dependent on latitude, given a greater dataset.

Regression analysis, a common method to compare FFD data and temperature data, allowed us to conceptualise and identify the effects of climate change in the form of FFD temperature response rates; however, non-linear

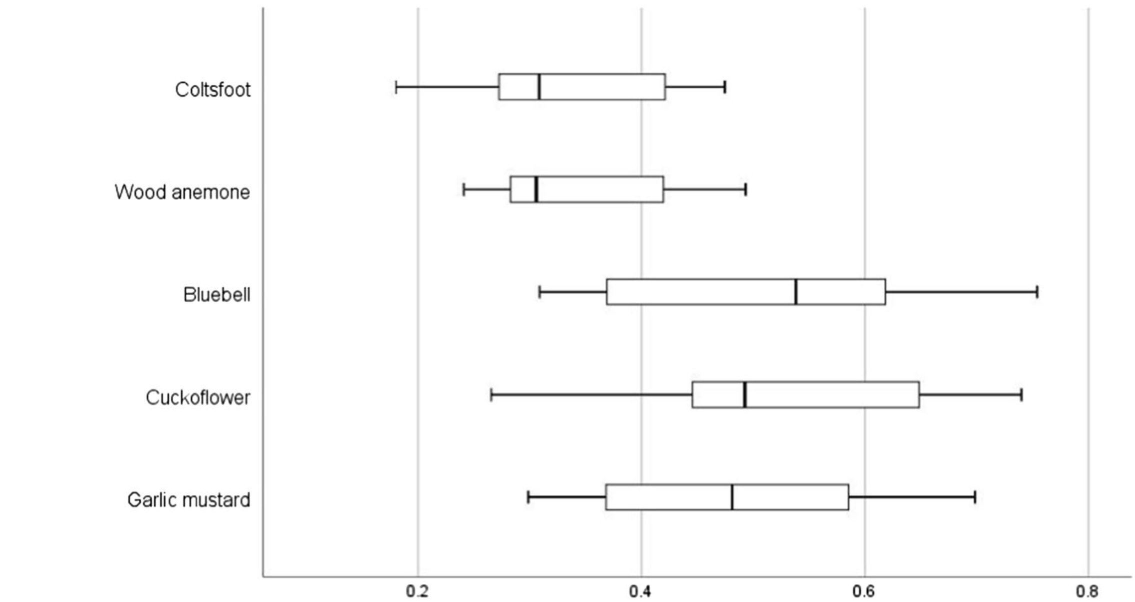

Fig. 8 Range of r^2 values of the temperature response rate for each species. The boxes indicate the median value, 25th and 75th percentiles, and the whiskers include all data points

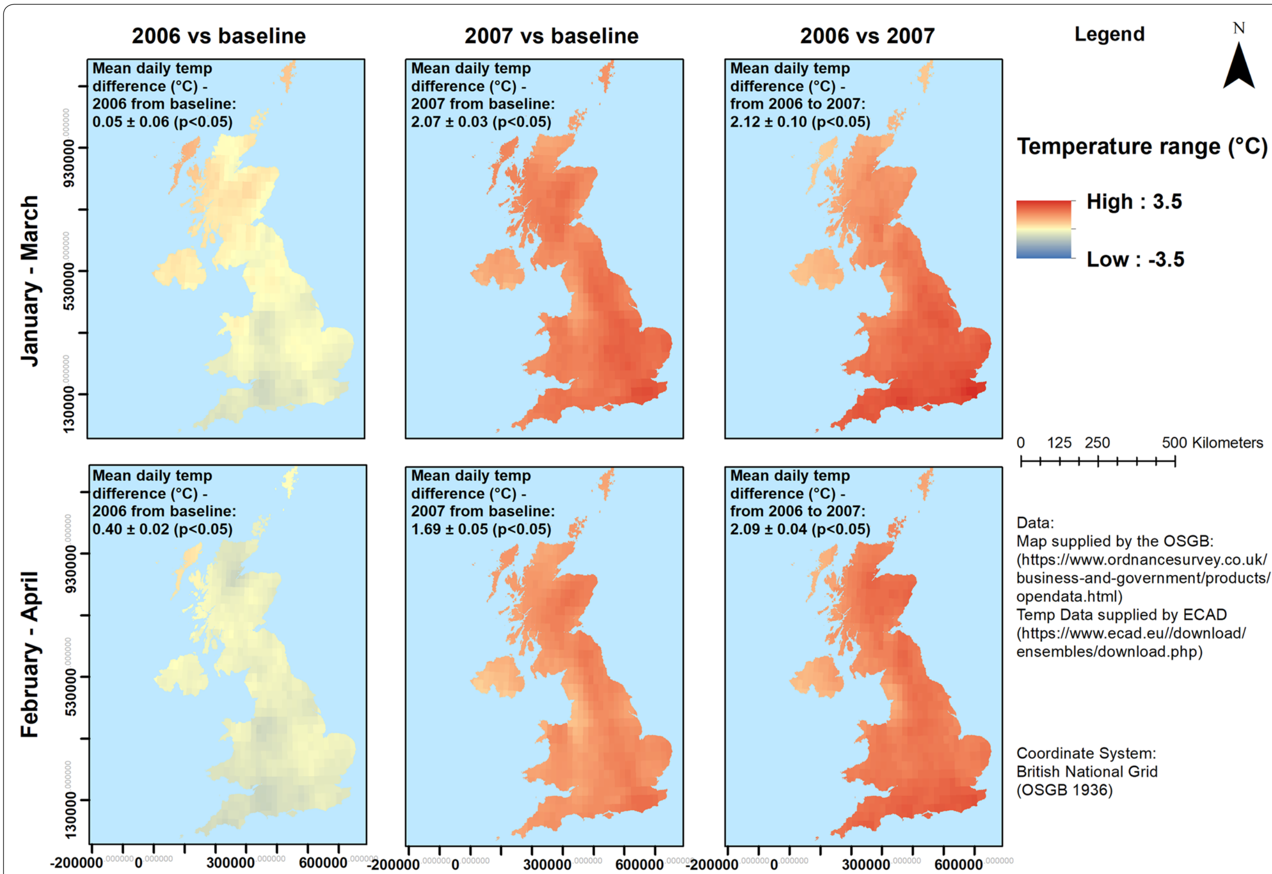

Fig. 9 Spring temperature anomalies of 2006 and 2007, in comparison with the 1961–1990 baseline temperature for the January–March mean daily temperature and the February–April mean daily temperature

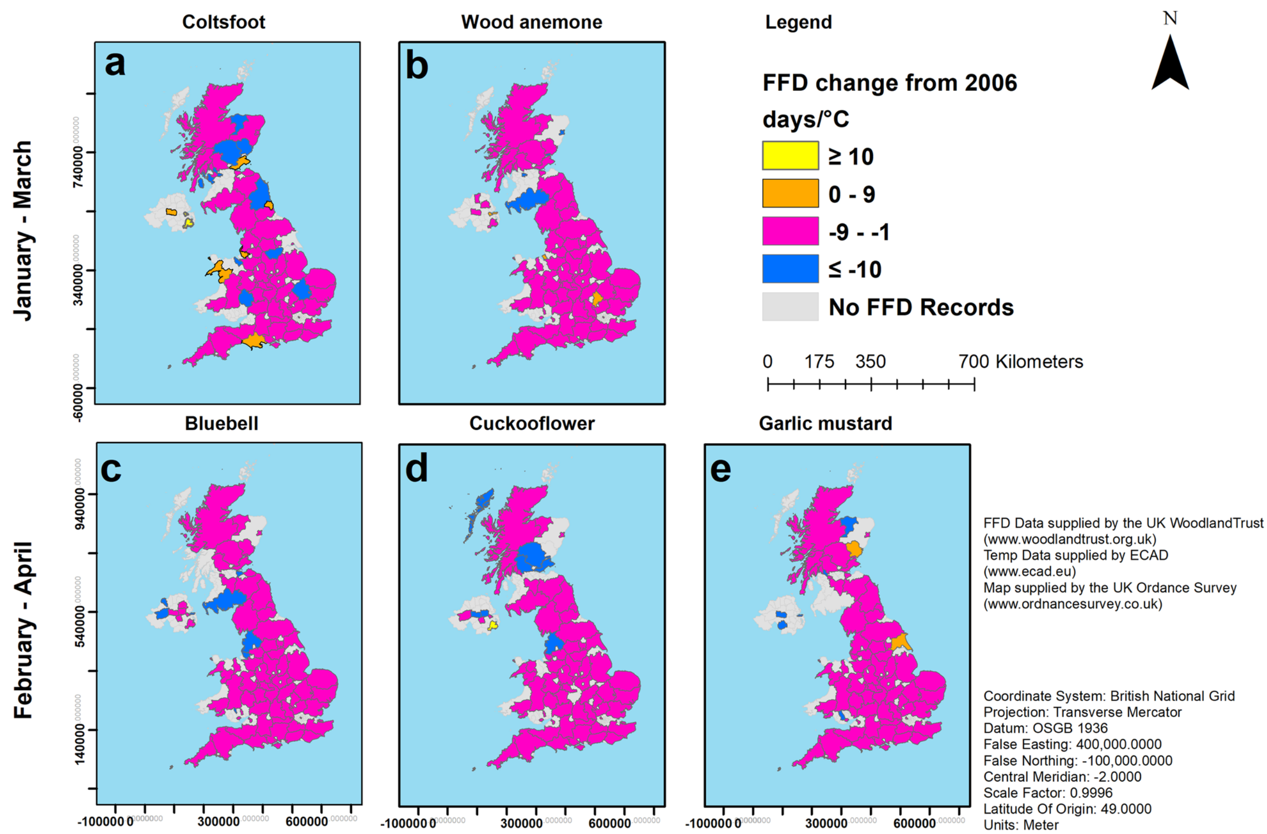

Fig. 10 The county FFD differences for each species between 2006 and 2007, with early-flowering species (**a**, **b**) dependent on temperature conditions during January–March at the top row and late-flowering species (**c**–**e**) dependent on temperature conditions during February–April below. The map colours correspond to ΔFFD per °C and, for the legend, a positive value represents a delay in the FFD calendar; the opposite for a negative value

Table 5 A comparison of the 2006 and 2007 mean FFD showed a significant advancement in FFD for all species in response to a ~2° warmer winter (i.e. negative values with Δ FFD = FFD_{2007} − FFD_{2006})

Species	Number of data pairs	FFD_{2006} ± SD	FFD_{2007} ± SD	Δ FFD ± 1SD	Days °C^{-1} ± 1 SD
Coltsfoot	274	86.0 ± 17.0	71.0 ± 17.1	− 15.0 ± 17.7	− 6.0 ± 7.5
Wood anemone	503	98.3 ± 10.5	85.6 ± 11.4	− 12.6 ± 13.3	− 5.0 ± 4.6
Bluebell	876	117.4 ± 8.0	99.6 ± 9.1	− 17.8 ± 8.5	− 7.6 ± 3.7
Cuckooflower	451	116.6 ± 11.3	102.0 ± 12.9	− 14.7 ± 10.4	− 6.3 ± 4.6
Garlic mustard	479	119.6 ± 8.5	106.9 ± 7.6	− 12.6 ± 10.0	− 5.5 ± 4.4

effects may emerge at the tail ends of sigmoid curves [17]. The extreme event analysis, with a pairwise comparison of data from multiple sites and 2 years representing the climate normal and a warm event, does, therefore, provide additional information in comparison with the regression analysis. Indeed, the wild plants investigated showed a significant mean advancement in FFD between the winters of 2006 and 2007, demonstrating the impact of a temperature extreme. For bluebell, the apparent response to a + 2 °C warmer winter was stronger than the response rate estimated from the ≥ 15-year time series, with an additional response of 1.4 days °C^{-1}. For cuckooflower and garlic mustard, the response was marginally weaker at 0.4 and 0.1 days °C^{-1}, respectively. Wood anemone and coltsfoot exhibited the weakest response rates at 0.6 and 1.7 days °C^{-1}, respectively. This may indicate the existence of non-linear responses, as identified for about 15% of the European time-series of coltsfoot

[17]. It may also be an effect of the warm winter as such, with the earliest flowering coltsfoot being more sensitive to an earlier and faster accumulation of forcing temperatures (c.f. Güsewell et al. [19]). Furthermore, many species are sensitive to specific temperature thresholds. For example, garlic mustard requires approximately 100 chilling days at temperatures between −1 and 6 °C before it breaks dormancy and germination occurs at temperatures between 6 and 15 °C [41]. Details regarding temperature thresholds, including population-specific adaptations, are unknown for most species, and more studies are needed on the effects of extreme weather to provide further evidence of the impact on flowering events [23], and their impact on ecosystems including potential phenological mismatching between co-dependent species [42–44].

Conclusion

This study showed that the early-spring-flowering species of bluebell, cuckooflower, coltsfoot, garlic mustard and wood anemone responded to increasing temperatures by advancing their FFD. However, the responses to a +2 °C warmer winter were both more and less pronounced than expected from an analysis of ≥15-year time series. This may reflect non-linear responses, species-specific thresholds and cumulative temperature effects, and indicates that knowledge on extreme weather events is needed for detailed projections of potential climate change effects.

Abbreviations

ELR: environmental lapse rate: used to calculate location-specific temperature; FFD: first flowering day.

Acknowledgements

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Authors' contributions

NF was responsible for gathering data, performing the analysis and writing a first version, presented as a Master Thesis, AMJ supervised the master thesis work and was responsible for revising the text from thesis to manuscript. Both authors read and approved the final manuscript.

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Availability of data and materials

All data sources (incl. links) are provided in "Material and methods", as well as in Acknowledgements.

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

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