

Changes in first flowering dates and flowering duration of 232 plant species on the island of Guernsey

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Abstract

Climate change has affected plant phenology; increasing temperatures are associated with advancing first flowering dates. The impact on flowering duration, however, has rarely been studied. In this study, we analysed first flowering dates and flowering durations from a 27 year dataset of weekly flower observations on 232 plant species from the island of Guernsey in the English Channel. The aim of this study was to explore variation in trends and relationships between first flowering dates, flowering duration and temperature. We specifically looked for evidence that traits, such as life forms and phylogenetic groups, explained variation in sensitivity of first flowering and flowering duration among species. Overall trends revealed significantly earlier flowering over time, by an average of 5.2 days decade⁻¹ since 1985. A highly significant shortening of flowering duration was observed by an average of 10 days decade⁻¹. Correlations between first flowering, flowering duration and year varied between different species, traits and flowering periods. Significant differences among traits were observed for first flowering and to a lesser degree for flowering duration. Overall, in comparison to first flowering, more species had significant trends in flowering duration. Temperature relationships revealed large differences in strength and direction of response. 55% of the species revealed a significant negative relationship of first flowering dates and temperature. In contrast, only 19% of flowering durations had a significant negative temperature relationship. The advance in first flowering date together with a shortening of flowering duration suggests potentially serious impacts on pollinators, which might pose a major threat to biodiversity, agriculture and horticulture. Human health, in terms of pollen allergies, however, might benefit from a shortening of specific plant pollen seasons.

Keywords: climate change, first flowering date, flowering duration, long-term data, phenology, temperature relationship

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Introduction

Understanding species' response to climate change is an important challenge in ecology. Phenological data, derived from professional or private observations, confirm an overall advance in phenological phases across the Northern Hemisphere due to increasing temperatures (Parmesan & Yohe, 2003; Menzel *et al.*, 2006a; Wolkovich *et al.*, 2012; Bolmgren *et al.*, 2013). Across all taxa, a mean phenological response in the Northern Hemisphere of between 2.3 and 2.8 days decade⁻¹ in the advance of spring events has been estimated (Parmesan, 2007). In a recent meta-analysis of trends among Southern Hemisphere species, dominant patterns were found to be consistent with findings from the Northern Hemisphere. However, large data deficiencies and

biases, e.g. in terms of data availability were acknowledged in the south (Chambers *et al.*, 2013). Other studies have explained further variation in phenology using location (Rötzer & Chmielewski, 2001; Estrella *et al.*, 2009) or by traits such as season of flowering and life forms (Fitter & Fitter, 2002; Peñuelas *et al.*, 2002; Menzel *et al.*, 2006b; Miller-Rushing & Primack, 2008).

In contrast, fewer studies have examined changes in the length of phenological phases. Concerning pollination, changes in flowering duration could have serious ecological and agronomic impacts (Menzel *et al.*, 2006c), and furthermore affect human health via modified exposure to allergenic pollen (Ziello *et al.*, 2012b; Newnham *et al.*, 2013). Moreover, flowering seasons for ornamental plants may have aesthetic and economic benefits for some regions (Sparks *et al.*, 2012), a prominent example being the Japanese cherry festivals, which are of major cultural importance (Sakurai *et al.*, 2011). While several studies suggested that warmer

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temperatures would shorten the average length of flowering (Arroyo *et al.*, 1981; Črepinšek *et al.*, 2012), other studies have found the reverse (Dunne *et al.*, 2003; Miller-Rushing *et al.*, 2007). These apparently contradictory results might be explained by the use of different methods of estimating flowering duration, different species analysed and different climates examined. Working with continuous flowering observations, we were able to determine the exact flowering duration from the beginning to the end of flowering. Generally, lengthening of flowering is associated with longer periods of pollination. Therefore, the viability of pollinators is improved and, thus the chance of successful pollination of plant species is enhanced (Zhao *et al.*, 2013). However, more comprehensive studies particularly on flowering duration, are needed to examine phenological trends and predict the consequences of a changing climate.

In this study, we use a 27 year record of over 160 000 flowering observations from the island of Guernsey, a British Crown dependency in the English Channel. Within a single location, first flowering date (FFD) and flowering duration (FD) of 470 plant species (trees, shrubs, herbaceous plants and geophytes) were generated from flowering records observed by the same person (NJ) from 1985 to 2011. From this dataset, 232 plant species were selected for the present study. In comparison to other long-term studies (Fitter & Fitter, 2002; Peñuelas *et al.*, 2002; Bolmgren *et al.*, 2013), this maritime study area is located within a region of high precipitation with temperate summers and few, if any, frost events in winter.

The dataset was examined for trends over time and relationships between FFD and FD. We analysed variations in trends among species and by traits. Furthermore, temperature effects on first flowering dates and duration were evaluated. Thus, our research demonstrates the value of assessing not only FFD but also including FD. We furthermore discuss the potential future impacts of changes on ecology, economy and human health.

Material and methods

Flower data

We analysed a dataset of 160 433 phenological observations on flowering of 470 plant species for the period 1985 to 2011. The dataset consists of dates on which flowering was observed. Flowering was defined as anthers visible and at least some flowers not senesced. Observations were conducted within a single location in Guernsey (49°27'48.4" N, 2°35'48" W, elevation: 26 m). The island covers 63 km² and has a maximum elevation of 111 m, thus all areas are close to the sea.

The study site is located in the centre of the island in the large extensive garden of a farmhouse, including an adjoining meadow (0.63 ha). The large variety of species observed were mostly managed garden plants (annual and perennial herbaceous and woody species). Records consist of mainly weekly observations by a single observer (NJ). Due to the large number of species flowering and to make the task manageable, recording in the summer months (approximately May till November) was reduced by the observer, starting in 1998, to continued weekly observations for plants coming into flower for the first time (i.e. FFD) but a complete inventory of continuing flowering only every second week. Occasional gaps in the record occurred due to absence of the recorder for holidays (a maximum of 2 weeks in May/June and 2 weeks in September/October nearly every year).

For each year FFD and FD of each species were extracted from the dataset as, respectively, the first observed date of flowering, and the interval between the first and last flowering observation dates. We coded the individual time series of FFD according to the recording interval of observations: (i) every week or; (ii) every second week. FD was coded in observations made (i) every week; (ii) every second week; (iii) every third week or (iv) every 4 weeks, respectively. From this dataset, we selected plant species of the first two categories (i and ii). We furthermore refined the records by selecting species with a minimum of 15 years of observational data. Plants that had second flowering periods or which flowered for, on average, more than 9 months per year were excluded from the analysis. On this basis, FFD and FD for 232 of 470 species were analysed. Furthermore, the average FFD and FD were calculated for each year across all 232 species.

Plants species were assigned to a simplified version of Raunkiaer life forms (Raunkiaer, 1937), the Angiosperm Phylogeny Group system (Bremer *et al.*, 2009) and to flowering period (early and late flowering species). Life forms and phylogenetic groups with less than 10 species (epiphyt and gymnosperm) were not analysed (Table 1). Early flowering was defined as the majority of flowering occurring from January to June; late flowering was defined as the majority of flowering occurring from July to December.

Climate data

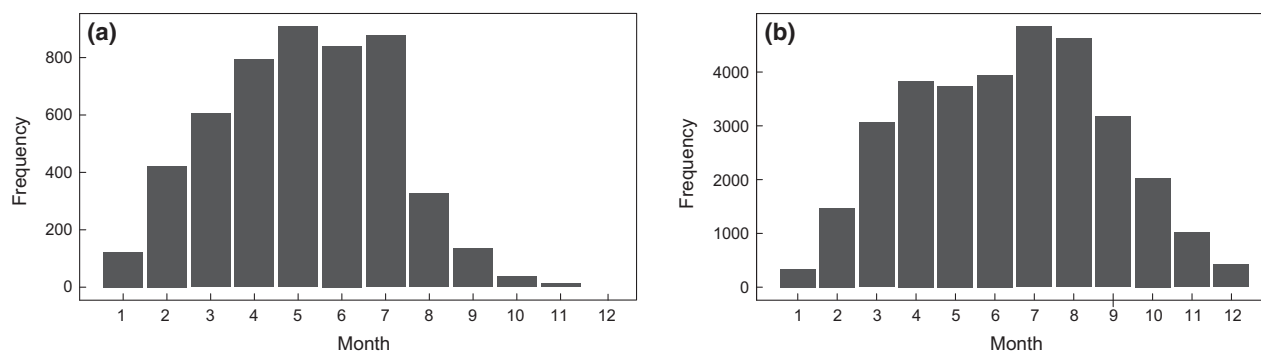
Climate data were obtained from the local climate station (Meteorological Observatory of Guernsey Airport), which is located approximately 3.3 km south of the study area at an elevation of 108 m. The data consist of daily mean temperature (°C) for the period 1985–2011, that were aggregated to monthly mean temperatures (°C). Mean annual temperature in the observation period was 11.4 °C, mean temperature of the coldest month (February) was 6.6 °C, mean temperature of the warmest month (August) was 16.9 °C. There were 31 days with daily mean temperature below 0 °C.

Statistical analysis

All calculations were performed with the program R 2.13.1 (R Development Core Team, 2011). Dates were converted to day

Table 1 Description of traits analysed and number of species observed

Description		Number of species
Life form		
Geophytes	Herbaceous perennial plants with buds in the soil below ground on underground bulbs, tubers, rhizomes or corms.	79
Hemicytrophytes	Herbaceous perennials with overwintering buds at soil level.	71
Trees and shrubs	Woody perennials with buds above soil level (phanerophytes, nanophanerophytes, chamaephytes).	69
Therophytes	Annual herbaceous plants with buds at soil level.	12
Epiphyte	Plant that grows upon another plant nonparasitically.	1
Phylogenetic Group		
Eudicots	Monophyletic clade of angiosperms including most of the dicots.	143
Magnoliids	Classification of angiosperms, characterized by trimerous flowers, pollen with one pore and usually branching-veined leaves.	11
Monocots	Angiosperm with one embryonic leaf in their seeds, trimerous flowers. Flower parts in threes or in multiples of three – having three, six, or nine petals. Usually with leaves with parallel veins.	77
Gymnosperm	A group of seed-producing plants that include conifers, cycads, Ginkgo and Gnetales. Unenclosed condition of seeds.	1
Flower type		
Early flowering	Species with majority of flowering events from January to 31 June.	131
Late flowering	Species with majority of flowering events from July to December.	101

**Fig. 1** (a) Number of species first flowering (FFD) by month; (b) Number of species in flower by month.

of the year (DOY, 1 = Jan 1, etc.) prior to analysis. Due to departures from the weekly observations (fortnightly observations) and occasional gaps in the records (absence of the observer), we checked the dataset for reliability. Nonweekly recording may have affected 10% of FFD observations and 33% of FD observations. Because of this potential issue, we compared FFD and FD of (i) the unmodified; (ii) an adjusted and (iii) a reduced dataset. The unmodified dataset consists of the complete dataset as recorded by the observer. The adjusted dataset uses the earliest possible FFD (–6 to –13 days) and the maximum possible FD (+6 to +24 days) that could be achieved from weekly or fortnightly recordings. The reduced dataset consists of species recorded solely on a weekly basis (FFD: 212, FD: 90 species). We henceforth refer to results from these datasets as ‘unmodified’, ‘adjusted’ or ‘reduced’.

Due to species-specific characteristics, analyses were done for each species and for each trait separately. Linear regression

techniques were used to relate FFD and FD to each other, to year and to temperature variables. Residuals from regressions were tested to confirm normality (results not shown). Depending on the number of groups, differences in changes in FFD and FD among traits were tested using a *t*-test or ANOVA followed by the Tukey HSD test. Equality of trends over time were tested using ANCOVA (Draper & Smith, 1998). The threshold for statistical significance was taken as $P = 0.05$.

Results

First flowering date

During the observation period, FFD ranged from January 1 to November 26. The earliest mean FFD was January 25 (*Galanthus nivalis* ‘Atkinsii’), the latest

November 11 (*Chrysanthemum* sp.). The largest number of FFD was in May (Fig. 1a), while July was the month with the maximum number of species in flower (Fig. 1b). No first flowering was recorded in December, otherwise the month with the least flower occurrence was January.

Overall, regression coefficients of FFD on year were negative. Using the unmodified dataset, 63% of the species advanced their FFD, 16% significantly with an advance of 13 days decade⁻¹. 37% of species delayed their FFD, 7% significantly. Neither the adjusted dataset (61% advancing, 14% significantly; 39% delaying, 7% significantly) nor the reduced dataset (63% advancing, 15% significantly; 37% delaying, 7% significantly) showed any substantial difference from the unmodified dataset (Fig. 2a–c).

Averaged across all species, FFD advanced significantly by approximately 5.2 days decade⁻¹ for the unmodified dataset (4.9 days decade⁻¹ for the adjusted and 5.6 days decade⁻¹ for the reduced dataset). No significant differences in trends over time, intercepts or means were found between the unmodified, the adjusted or reduced datasets (Fig. 3a; Table 2). Thus, in the following analysis of trends in FFD by trait and

temperature relationships, the unmodified dataset was used. For comparison, the results of the adjusted and reduced datasets are also summarized in Table 2. Trends over time (regression coefficients) ranged from -5.0 days decade⁻¹ (*Geranium lucidum*) to $+3.8$ days decade⁻¹ (*Arabis* sp.). There were significant differences among species and traits (results not shown). Trends through time and means differed significantly between life forms. Herbaceous perennials (geophytes and hemicryptophytes) showed stronger and more significant trends towards earlier flowering dates, on average, than woody species (trees and shrubs) or annuals (therophytes). Geophytes displayed the strongest trend to earliness with FFD advancing by approximately 7 days decade⁻¹ ($R^2 = 0.19$, $P < 0.05$). Therophytes showed positive trends (towards later FFD), though not significant. There were no significant trends overall for either woody species or deciduous woody species. However, evergreen woody species had a significant ($P < 0.01$) negative trend ($R^2 = 0.35$), with FFD advancing approximately 8 days decade⁻¹ (Table 2). Trends through time between phylogenetic groups, as well as between early and late flowering species did not differ. All phylogenetic groups had negative trends

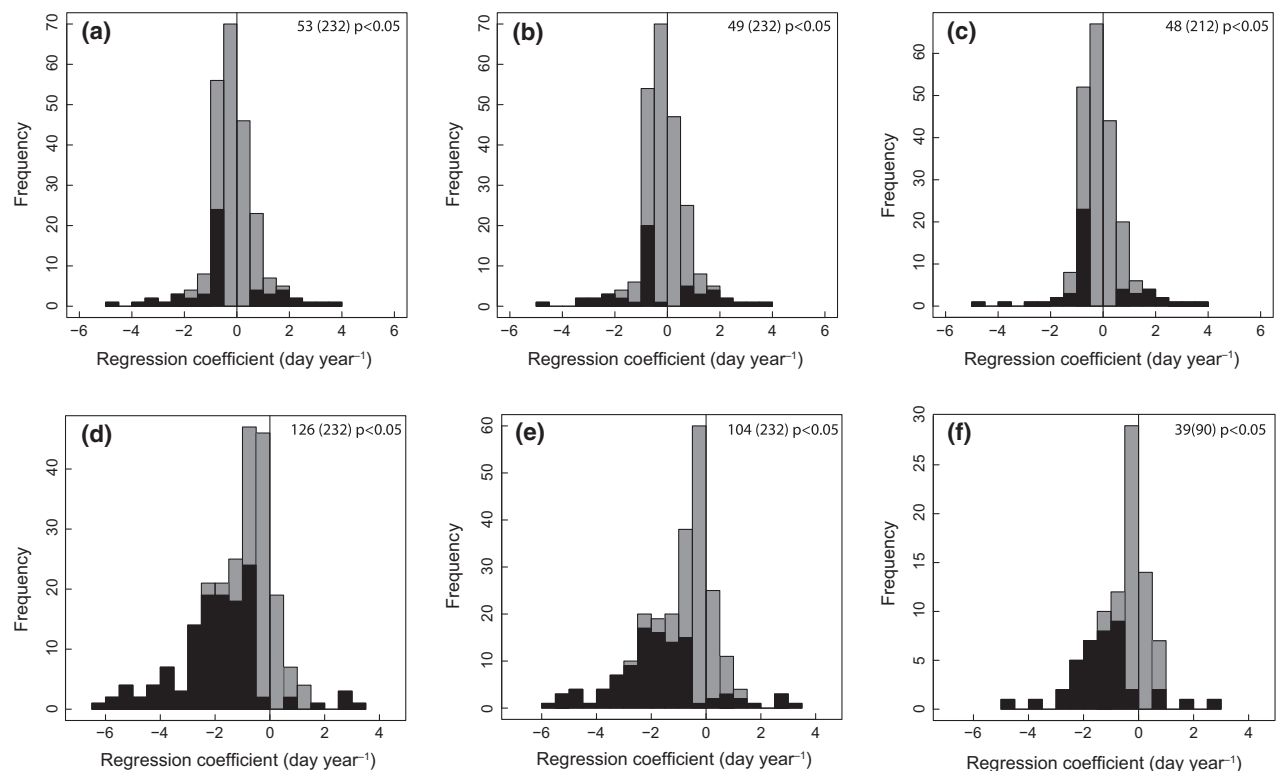


Fig. 2 Histograms of time trends of FFD in the upper row (a–c) and FD and the lower row (d–f), using differently adjusted datasets (1985–2011). Significant coefficients are presented in black. (a and d) flowering dates as recorded, (b and e) adjusted earliest possible FFD and longest possible FD, (c and f) records of weekly recorded species only. In the top right corner is shown the number of significant species (total species in brackets). Time trends estimated as linear regression coefficients (days yr⁻¹).

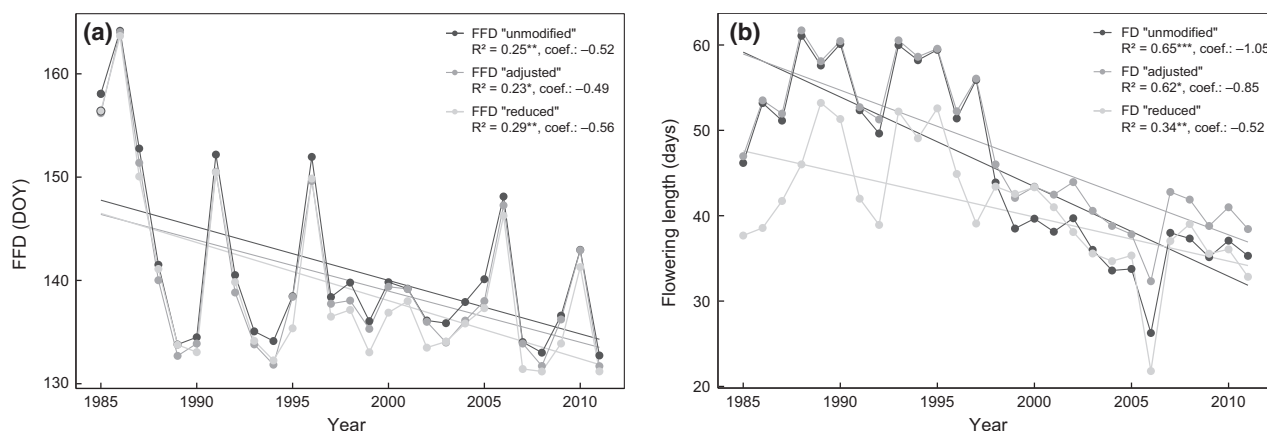


Fig. 3 Time series of the average FFD (a) and FD (b) of all species, using the data as recorded (black), the 'adjusted' data (dark grey) and the 'reduced' data (light grey). FFD = First flowering; DOY = day of year; FD = Flowering duration; regression lines superimposed.

(towards earlier flowering), though not significant for magnoliids (Table 2). No substantial difference in trends, intercepts or means of traits were found between the unmodified and adjusted datasets (results not shown).

Flowering duration

Across the dataset, FD ranged between 7 and 217 days. The shortest average FD was 13 and 16 days (*Robinia pseudoacacia*), the longest 140 and 144 days (*Abelia grandiflora*) for the unmodified and adjusted datasets, respectively. For the reduced dataset, the shortest duration was 17 days (*Ornithogalum umbellatum*), the longest 87 days (*Euphorbia mellifera*).

Overall, regression coefficients of FD on year were clearly negative. Using the unmodified dataset, 85% of the species shortened FD, 51% significantly by a mean of approximately 21 days decade⁻¹. 15% of the species lengthened FD, 3% significantly. There were similar findings in the adjusted (81% shortening, 40% significantly; 19% lengthening, 5% significantly) and reduced (74% shortening, 38% significantly; 26% lengthening, 4% significantly) datasets (Fig. 2d–f).

Trends over time (regression coefficients) ranged from -6.3 to -5.8 days yr⁻¹ (*Lavandula angustifolia* 'Hidcote') to $+3.0$ to $+3.1$ days yr⁻¹ (*Crassula multicava*) using the unmodified and adjusted dataset, respectively, and from -4.6 days yr⁻¹ (*Arabis* sp.) to $+3.0$ days yr⁻¹ (*Camellia* × *williamsii* 'Donation') using the reduced dataset.

FD averaged across all species significantly ($P < 0.001$) shortened by approximately 10 days decade⁻¹ (8 days decade⁻¹ for the adjusted and 5 days decade⁻¹ for the reduced dataset; Table 3; Fig. 3b). While the overall trend was negative for all datasets, significant

differences ($P < 0.05$) in trends over time for FD were found between the unmodified and the reduced dataset. Trends were homogeneous between the other paired comparison datasets ($P > 0.05$; Fig. 3b). Given this difference in trends, the adjusted dataset is used in the following analysis of traits and climate relationships. For reasons of comparability, due to the differences in trends over time between the datasets, the results of the unmodified and reduced datasets are also summarized in Table 3.

All traits had very significant ($P < 0.01$) trends towards a shortening of FD, however, significant differences in trends were found among phylogenetic groups, life forms and early and late flowering species. Geophytes had the weakest trend towards a shortening of FD ($R^2 = 0.42$, $P < 0.001$) by approximately 4 days decade⁻¹. There were differences in trends between deciduous and evergreen woody species with FD of deciduous species shortening more ($R^2 = 0.62$, $P < 0.001$) than evergreen species ($R^2 = 0.39$, $P < 0.001$; Table 3). Monocots differed from eudicots and magnoliids, while hemicryptophytes and therophytes were the only life forms displaying similar trends ($P > 0.05$; results not shown). A trend over time accounted for 68% of the variation in FD for late flowering species, with a highly significant shortening by approximately 14 days decade⁻¹. In contrast, only 33% of the variation in early flowering species could be explained by a trend over time, with FD significantly shortening by approximately 4 days decade⁻¹. No significant difference in trends over time, intercepts or means of traits were found between the unmodified and adjusted datasets (results not shown).

Averaged across all species, Pearson's correlations between FFD and FD were significant, but the magnitudes of correlation coefficients were less than 0.1.

Table 2 Mean dates and trends through time in first flowering date (FFD) for 1985–2011. In the first three rows, overall trends were estimated using the ‘unmodified’ data (*u*), ‘adjusted’ data (*a*) with the earliest flowering date (FFD) and the ‘reduced’ dataset (*r*), with weekly recorded species only. Subsequently, data are presented separately for each life form, phylogenetic group and time of flowering (early and late flowering). Traits with <11 species are indicated in italics. The trend over the study period is summarized as regressions on year. *N*: number of species. *b*: slope of regression coefficients. Key to significance: **P* < 0.05, ***P* < 0.01, ****P* < 0.001. Results in bold are significant (*P* < 0.05)

FFD		<i>N</i> species	Min (DOY)	Max (DOY)	Mean (DOY)	SD (days)	<i>R</i> ²	<i>b</i> (days yr ⁻¹)
Overall	<i>u</i>	232	1	330	140	59.3	0.25**	-0.52
	<i>a</i>	232	1	330	139	58.9	0.23*	-0.49
	<i>r</i>	212	1	330	136	60.3	0.29**	-0.56
Life Form†								
Geophytes	<i>u</i>	79	1	293	111	64.3	0.19*	-0.72
	<i>a</i>	79	1	293	110	63.6	0.19*	-0.72
	<i>r</i>	75	1	293	109	63.1	0.22*	-0.75
Hemicryptophytes	<i>u</i>	71	1	330	167	49.2	0.47***	-0.56
	<i>a</i>	71	1	330	166	49.2	0.47***	-0.56
	<i>r</i>	65	1	330	168	49.1	0.40***	-0.50
Trees and shrubs	<i>u</i>	69	5	302	143	48.4	0.04	-0.21
	<i>a</i>	69	5	302	142	48.0	0.04	-0.20
	<i>r</i>	60	5	284	140	47.8	0.08	-0.31
Deciduous	<i>u</i>	43	7	238	132	41.4	0.01	0.09
	<i>a</i>	43	7	238	131	41.0	0.01	0.11
	<i>r</i>	40	7	238	130	40.9	0.01	0.13
Evergreen	<i>u</i>	26	5	302	163	53.3	0.35**	-0.85
	<i>a</i>	26	5	302	161	53.2	0.33**	-0.85
	<i>r</i>	20	5	284	159	54.3	0.53***	-1.37
Therophytes	<i>u</i>	12	26	264	162	44.2	0.04	0.15
	<i>a</i>	12	26	264	160	44.1	0.04	0.15
	<i>r</i>	12	26	264	160	44.1	0.07	0.23
Phylogenetic Group‡								
Eudicots	<i>u</i>	143	5	330	162	49.7	0.13*	-0.26
	<i>a</i>	143	5	330	160	49.5	0.11*	-0.24
	<i>r</i>	128	5	330	160	49.2	0.17*	-0.29
Magnoliids	<i>u</i>	11	1	238	121	56.4	0.08	-0.55
	<i>a</i>	11	1	238	121	56.0	0.07	-0.53
	<i>r</i>	10	1	238	121	58.1	0.07	-0.56
Monocots	<i>u</i>	77	1	293	105	57.9	0.28**	-0.87
	<i>a</i>	77	1	293	104	57.3	0.27**	-0.84
	<i>r</i>	73	1	293	104	58.6	0.29**	-0.90
Flowering type								
Early flowering	<i>u</i>	131	1	210	100	39.1	0.18*	-0.54
	<i>a</i>	131	1	210	100	39.1	0.17*	-0.51
	<i>r</i>	122	1	210	98	38.9	0.19*	-0.56
Late flowering	<i>u</i>	101	98	330	193	34.1	0.23*	-0.39
	<i>a</i>	101	1	210	193	34.1	0.21*	-0.37
	<i>r</i>	90	106	330	193	32.7	0.26**	-0.42

†Epiphyt (*n* = 1) not listed.

‡Gymnosperm (*n* = 1) not listed.

Among life forms and phylogenetic groups, correlations varied in significance, magnitude and sign. Among the unmodified, adjusted and reduced dataset (90 species), the signs per trait were mainly identical, however, the magnitude and significance was highest overall for the reduced dataset (Table 3, last column).

Climate relationships

During the observation period (1985–2011) mean annual temperature significantly (*P* < 0.05) increased by 0.5 °C in Guernsey. Months with significant increases in temperature were April (0.06 °C yr⁻¹),

Table 3 Mean dates and trends through time in flowering duration (FD) for 1985–2011. In the first three rows, overall trends were estimated using the unmodified data (*u*), the adjusted data (*a*) with longest flowering duration (FD) possible and the reduced data-set (*r*), with weekly recorded species only. Subsequently, data are presented separately for each life form, phylogenetic group and time of flowering (early and late flowering). Traits with <11 species are indicated in italics. The trend over the study period is summarized as regressions on year. *N*: number of species; *b*: slope of regression coefficients. *r*: Pearson correlations between average FFD and average FD. Key to significance: **P* < 0.05, ***P* < 0.01 ****P* < 0.001. Results in bold are significant (*P* < 0.05)

FD		N species	Min (days)	Max (days)	Mean (days)	SD (days)	<i>R</i> ²	<i>b</i> (days yr ⁻¹)	<i>r</i>
Overall	<i>u</i>	232	7	217	44.9	30.6	0.65***	-1.05	0.14
	<i>a</i>	232	7	217	47.5	30.1	0.62***	-0.85	0.12
	<i>r</i>	90	7	147	40.9	23.3	0.34**	-0.52	-0.14
Life Form†									
Geophytes	<i>u</i>	79	7	189	40.0	24.0	0.47***	-0.54	-0.15
	<i>a</i>	79	7	189	41.7	23.7	0.42***	-0.43	-0.27
	<i>r</i>	52	7	147	39.2	10.0	0.08	-0.22	-0.52**
Hemicryptophytes	<i>u</i>	71	7	168	50.6	31.8	0.65***	-1.55	-0.45*
	<i>a</i>	71	7	175	53.9	30.8	0.62***	-1.27	-0.33
	<i>r</i>	11	7	140	49.4	25.8	0.56***	-1.76	0.59**
Trees and shrubs	<i>u</i>	69	7	217	43.0	33.9	0.57***	-0.98	-0.19
	<i>a</i>	69	7	217	45.9	33.4	0.51***	-0.76	-0.16
	<i>r</i>	26	7	140	40.1	27.0	0.20*	-0.48	-0.37
Deciduous	<i>u</i>	43	7	210	39.8	32.6	0.62***	-0.16	-0.38*
	<i>a</i>	43	7	210	32.6	32.0	0.57***	-0.13	-0.38
	<i>r</i>	21	7	133	36.1	24.0	0.40***	-0.77	-0.44*
Evergreen	<i>u</i>	26	7	217	48.6	35.6	0.39***	-0.10	0.12
	<i>a</i>	26	7	217	52.0	34.8	0.26**	-0.06	0.00
	<i>r</i>	5	7	140	56.1	32.4	0.14*	0.64	-0.62***
Therophytes	<i>u</i>	12	7	196	57.7	35.7	0.72***	-1.82	-0.30
	<i>a</i>	12	7	196	60.6	34.6	0.69***	-1.53	-0.28
	<i>r</i>	1	28	105	55.2	22.2	0.21*	-1.29	-0.59**
Phylogenetic Group‡									
Eudicots	<i>u</i>	143	7	217	48.1	33.7	0.66***	-1.32	0.11
	<i>a</i>	143	7	217	51.3	32.9	0.62***	-1.05	0.12
	<i>r</i>	33	7	140	42.3	26.3	0.60***	-0.94	0.23
Magnoliids	<i>u</i>	11	7	196	58.4	31.6	0.62***	-1.55	-0.01
	<i>a</i>	11	7	196	60.7	31.0	0.59***	-1.38	-0.03
	<i>r</i>	5	7	147	60.2	28.7	0.42***	-1.55	-0.52**
Monocots	<i>u</i>	77	7	189	37.6	22.0	0.34**	-0.48	-0.19
	<i>a</i>	77	7	189	39.2	21.3	0.29**	-0.38	-0.27
	<i>r</i>	51	7	140	38.4	19.4	0.20	-0.11	-0.57**
Flowering type									
Early flowering	<i>u</i>	131	7	147	37.2	22.4	0.40***	-0.52	-0.24
	<i>a</i>	131	7	161	38.9	21.5	0.33**	-0.41	-0.34
	<i>r</i>	84	7	140	40.2	23.1	0.28**	-0.47	-0.37
Late flowering	<i>u</i>	101	7	217	55.1	36.6	0.70***	-1.74	0.22
	<i>a</i>	101	7	217	58.9	35.5	0.68***	-1.41	0.27
	<i>r</i>	6	7	112	50.1	23.8	0.19*	0.63	0.32

†Epiphyt (*n* = 1) not listed.

‡Gymnosperm (*n* = 1) not listed.

June (0.05 °C yr⁻¹) and November (0.05 °C yr⁻¹). There were no significant changes in precipitation. Stepwise linear regressions of FFD and FD on mean monthly temperatures preceding the phenological event showed that the month of the species' mean FFD and the preceding 2 months were the ones with the strongest relationships. Thus, the average temperature

of these 3 months was used as the independent variable in the model for FFD and FD. After testing the reliability of the three datasets, the unmodified dataset was used in the following analysis.

Most of the temperature responses of FFD (regression coefficients) had a negative sign (88% advancing, 55% significantly; 12% delaying, none significantly), with

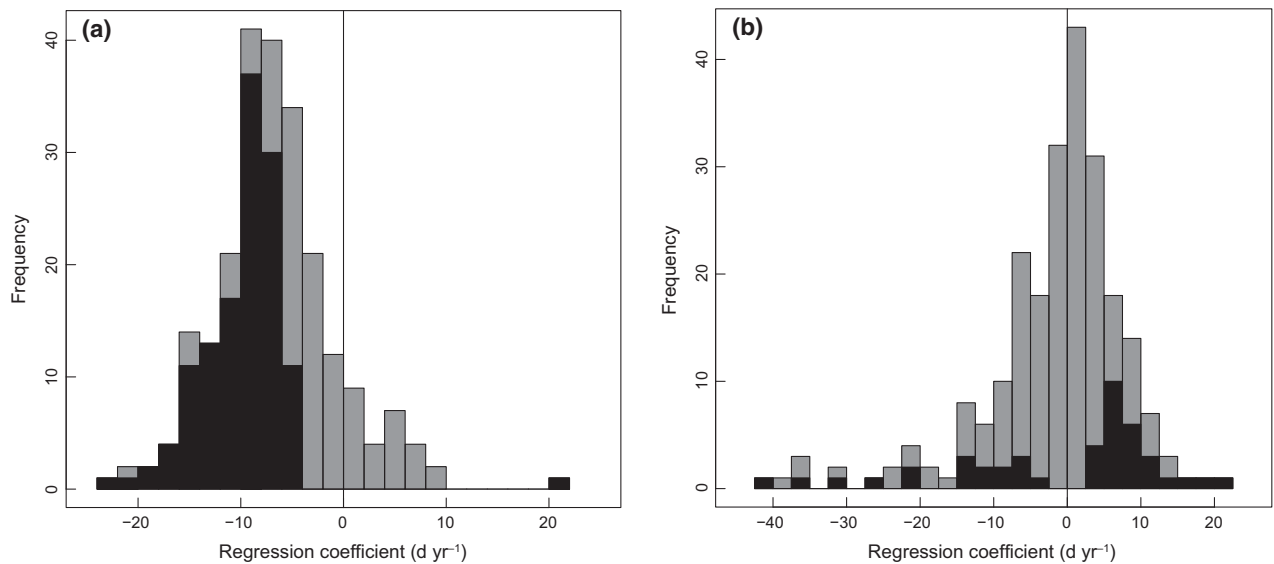


Fig. 4 Histograms of temperature relationships of FFD (a) and FD (b) for each species (1985–2011), $n = 232$. Temperature relationships estimated as linear regression coefficients (days °C⁻¹).

warmer temperatures resulting in earlier FFD (Fig. 4a). Averaged across all species with significant temperature relationships (55%), mean temperature explained approximately 37% of the variation in FFD, the overall mean response was -9.7 days °C⁻¹, ranging from

-22.6 days °C⁻¹ (*Iris* 'Pacific Coast') to $+8.6$ days °C⁻¹ (*Alchemilla mollis*; Table 4). For species with significant relationships, temperature explained between 15% and 80% of the variation in FFD. While 73% of all geophytes were significantly responsive to temperature, only 34%

Table 4 Regression model and regression coefficients of FFD and FD (1985–2011) on mean monthly temperature in the mean month of FFD and the preceding 2 months for each species. Significant ($P < 0.05$) coefficients of determination (R^2) and regression coefficients of the individual species were averaged (overall and for each trait). N: number of species. sig: percentage of species with significant relationships; mn R^2 : average of significant coefficients of determination; mn b : average of significant trends over time of regression coefficients (days °C⁻¹), average trend for all species in brackets

	N	FFD unmodified			FD adjusted		
		sig	mn R^2	mn b	sig	mn R^2	mn b
Overall	232	55%	0.37	-9.7 (-6.7)	19%	0.26	-0.9 (-1.7)
Life forms*							
Geophytes	79	73%	0.39	-8.9 (-7.4)	34%	0.27	0.9 (0.6)
Hemicryptophytes	71	34%	0.32	-10.1 (-4.8)	11%	0.23	-7.7 (-3.5)
Trees and shrubs	69	56%	0.39	-10.5 (-7.8)	10%	0.24	0.7 (-2.7)
Therophytes	12	50%	0.26	-10.0 (-4.7)	17%	0.23	-3.4 (-3.0)
Leaf type							
Deciduous trees and shrubs	43	58%	0.39	-10.2 (-7.5)	5%	0.25	5.9 (-1.1)
Evergreen trees and shrubs	26	54%	0.38	-10.9 (-8.5)	19%	0.24	-1.4 (-3.9)
Phylogenetic group†							
Eudicots	143	44%	0.35	-9.7 (-5.7)	12%	0.25	-5.7 (-3.5)
Magnoliids	11	54%	0.40	-10.8 (-8.1)	9%	0.20	-25.5 (0.7)
Monocots	77	75%	0.37	-9.5 (-8.4)	15%	0.27	3.2 (1.4)
Flowering type							
Early flowering	131	69%	0.40	-9.9 (-7.9)	22%	0.27	6.9 (2.3)
Late flowering	101	38%	0.31	-9.3 (-6.7)	15%	0.23	-16.0 (-6.7)

*Epiphyt ($n = 1$) not listed.

†Gymnosperm ($n = 1$) not listed.

of all hemicryptophytes were significant. Including the species displaying no significant relationship resulted in a general weakening of the relationship by approximately 1.4–5.3 days °C⁻¹ (Table 4).

Regression coefficients of FD on temperature did not show any obvious pattern (49% shortening, 8% significantly; 51% delaying, 12% significantly; Fig. 4b). Averaged across all species with significant temperature relationships (19%), mean temperature explained 26% of the variation in FD, with a significant shortening of the flowering period by 0.9 days °C⁻¹. The response ranged from -41.0 days °C⁻¹ (*Dahlia* sp.) to +22.5 days °C⁻¹ (*Zantedeschia aethiopica*). For species with significant relationships, temperature explained 15–55% of the variation in FD.

Temperature relationships were significantly different between traits. Traits with fewer than 10% significant ($P < 0.05$) temperature relationships of FD were trees and shrubs, deciduous trees and shrubs and magnoliids. 34% of all geophytes, 15% of monocots and 22% of early flowering species displayed a significant response of FD (+0.9 to +6.9 days °C⁻¹) to increasing temperatures. The remaining traits overall had negative temperature relationships (i.e. a shortening of FD by approximately 1.4–16.0 days °C⁻¹). Including the species with no significant relationship resulted in a marked weakening of the coefficients, however, the overall trend was still negative (Table 4).

Discussion

Most studies on phenology have focused primarily on onset dates of phenological phases. Despite its importance, especially concerning pollination, long-term datasets on the duration of phenological phases rarely exist. This is likely due to the time and effort needed to conduct continuous observations over a long period. Thus, the uniqueness of the dataset analysed in our study is based on continuous weekly flowering observations. Therefore, observed beginning and end of flowering could be extracted, resulting in a dataset of first flowering and flowering duration of 232 plant species within a specific location. This paper is thus based on one of the most comprehensive phenological datasets on flowering duration.

Although a reduced observation frequency was considered as a potentially confounding factor, we showed that this did not have a significant impact on the analysis of FFD. We did not find any significant differences in trends, means or variances between the unmodified, adjusted or reduced time series. For FD, however, there was a significant difference in trends between the unmodified and the reduced dataset. The reduced dataset had the weakest, however, still significantly

negative trend of all three datasets. This dataset, consisting only of 90 (39%) species from the entire dataset, is not as representative since it mainly consists of early flowering species. Therefore, the adjusted version was considered as the most valid dataset for analysing changes and responses in duration of flowering. It also generates conservative estimates of change in FD.

Trends varied greatly among species. Overall, we found a significant advancing trend in FFD and a significant shortening of FD over our recording period on the island of Guernsey. Among traits, correlations between FFD and FD varied in magnitude and sign and were not significant for the adjusted dataset. For the reduced dataset, the magnitude and significance of the correlation increased. They predominantly indicated a negative relationship, i.e. earlier FFD is associated with longer FD. However, this is most likely due to the reduced number of species, predominantly early flowering ones, and are thus not comparable with the remaining results of this study.

Trends through time of FFD are comparable with other multi-species studies (Fitter & Fitter, 2002; Peñuelas *et al.*, 2002; Bolmgren *et al.*, 2013), advancing approximately 5.2 days decade⁻¹. Trends in FD towards an overall shortening by approximately 10 days decade⁻¹, however, appear to be more complex and will be discussed in greater detail below.

There were significant differences in trends of FFD and FD between species and traits, although geophytes (i.e. herbaceous perennials) showed the strongest advance in FFD (7.2 days decade⁻¹) among life forms, they also had the least shortening of FD (4.3 days decade⁻¹). Therophytes (i.e. herbaceous annuals), on the other hand, did not show a significant trend in FFD. In contrast, Fitter & Fitter (2002) revealed a stronger advance in FFD for annuals than for perennials for south-central England. For the Mediterranean region, Peñuelas *et al.* (2002) did not find any differences among life forms, and thus assumed a general advancing trend. Our results add to the inconsistency of findings, pointing out the complexity of factors that might have an influence. We furthermore found differences between deciduous and evergreen woody species with only evergreen species showing a significant advance in FFD, with both groups showing equal trends towards a shortening of flowering of 0.6–1.3 days decade⁻¹. Early season species are reported to be more responsive than later species (Menzel *et al.*, 2006a; Pau *et al.*, 2011). However, Høye *et al.* (2013) discovered in a 14 year (1996–2009) study from the high-Arctic, that late flowering plants changed their flowering dates to a greater extent than early flowering plants. In our study, we found that trends in FFD between early and late flowering species did not differ. Nevertheless, there were significant differences in

FD between early and late flowering species. Late flowering species had a shortening of flowering duration by 14 days decade⁻¹ ($R^2 = 0.68$), while the flowering period of early species only shortened by 4.1 days decade⁻¹ ($R^2 = 0.33$). Furthermore, there is a moderate negative correlation between FFD and FD of early flowering species ($r = -0.34$), indicating that later FFD is associated with shorter FD. Late flowering species, on the other hand, have a moderate positive relationship ($r = 0.27$), i.e. later FFD is associated with longer FD. In contrast to other long-term studies (Fitter *et al.*, 1995; Peñuelas *et al.*, 2002; Nordli *et al.*, 2008; Bolmgren *et al.*, 2013), the setting of our study is quite different. The study site, being located on a small island, is surrounded completely by the sea, and lies within a maritime region, characterized by rainfall throughout the year with temperate summers and hardly any frosts in winter. Phenological responses to climate change may differ among different environments.

FFD was significantly influenced by temperature of the month of the species' mean FFD and the preceding 2 months. 55% of all observed species were significantly negatively related to temperature. Our findings correspond to other studies (Fitter & Fitter, 2002; Peñuelas *et al.*, 2002; Parmesan & Yohe, 2003; Menzel *et al.*, 2006a; Estrella *et al.*, 2009), confirming that FFD is sensitive to temperature. Among traits, the highest percentage of species with significant temperature relationships were geophytes, which also had the strongest trend towards earlier flowering ($R^2 = 0.39$). The lowest coefficient of determination was found for therophytes ($R^2 = 0.26$). These findings are consistent with Fitter *et al.* (1995), who found strongest temperature relationships for geophytes and woody species ($R^2 = 0.46/0.47$). The R^2 of FFD for therophytes was the lowest ($R^2 = 0.31$). While there were significant differences in FFD trends over time for deciduous and evergreen trees and shrubs, both traits were equally responsive to temperature. This result suggests that other factors, which are not considered in this study, may have been responsible for this effect.

For FD, temperature relationships were much weaker. While 81% (40% significant) of all species shortened FD, only 19% were significantly responsive to temperature during the preceding months, reducing FD by approximately -0.9 days °C⁻¹. However, including the species that did not show significant temperature relationships still resulted in an overall negative trend with a shortening of FD by approximately -1.7 days °C⁻¹. These findings are consistent with Arroyo *et al.* (1981) and Primack (1985) who found the longevity of a flower was usually shorter in warm than in cold environments. Other recent studies show a more inconsistent picture of flowering duration. In a

long-term (1981–2005) study on flowering phenology of cherry trees (*Cerasus* sp. or *Prunus* sp.) in Japan, Miller-Rushing *et al.* (2007) found that flowering durations were greater in warm years than in cold years. This conclusion was confirmed by Ziello *et al.* (2012a), who also found a lengthening of flowering duration in general. However, this inconsistency might be explained by different definitions and approximations of flowering duration. The recording of flowering duration of plant species is time consuming, since a continuous observation of the plant is necessary throughout the flowering season. Thus, most long-term studies on flowering duration use approximate values. Both studies (Miller-Rushing *et al.*, 2007; Ziello *et al.*, 2012a) estimated the flowering duration as the time between first and full flowering, thus implicitly assuming a strong correlation with the remainder of flowering, i.e. between full flowering and end of flowering. However, while the first 'half' of flowering might lengthen with warming, this cannot automatically be assumed to apply to the whole flowering duration. Another long-term (1970–2011) study on grapevine phenology in Germany, which estimated flowering duration as the time between beginning and end of flowering, revealed *inter alia* no significant trend in flowering duration (Bock *et al.*, 2011). Črepinšek *et al.* (2012), on the other hand, found a tendency towards a shorter flowering duration with warming for Hazel (*Corylus avellana*) in Maribor, Slovenia since 1969. In this study, flowering duration was recorded as first flowers open to last flowers open for male and female flowers, respectively. The latter relationships were confirmed by a study in a tropical climate in Asia on tropical plant species. Increasing temperatures were associated with an overall shortening of flowering duration, with 24% (5 of 21 species) revealing significant ($P < 0.05$) negative trends (Zhao *et al.*, 2013).

However, the drivers of FD appear to be more complex than for FFD. The present analysis was a broad-brush approach, solely taking monthly mean temperatures into account. To disentangle the factors that might influence FD, other influences (e.g. soil moisture, accumulated heat or chilling units) need to be considered. Pau *et al.* (2011), for example, found that in areas with long growing seasons and relatively low interannual variability (e.g. Guernsey), biotic rather than abiotic forces are expected to drive phenology. Furthermore, exotic species with flexible phenologies are supposed to be more successful than native species (Matesanz *et al.*, 2010; Wolkovich *et al.*, 2013). These factors may further enhance the variability in FFD and FD of the species analysed in this study, especially since they consist largely of managed garden cultivars (i.e. nonnative species).

Our study demonstrates that there has been a change in flowering phenology in Guernsey during the last 27 years. Despite differences among species, FFD is getting earlier while FD is getting shorter. Our findings imply that the general assumption that increasing temperatures result in longer flowering duration did not apply to this study. An explanation might be that flowering duration in most studies derived from approximations of flowering duration. Moreover, factors additional to mean air temperature may have had a major influence on flowering. What are the consequences of earlier FFD and shorter FD? Shorter flowering duration shortens the period of pollination and thus may reduce the chance of successful pollination. Therefore, the natural reproduction of these species may be impacted, which elsewhere might lead to declines in agricultural and horticultural crop production. Furthermore, a reduction in flowering duration will reduce the unquantified but aesthetic value of flowering, one aspect of ecosystem services often overlooked. Previously an advance and prolongation of the grass pollen season was found (Rasmussen, 2002; Bartra *et al.*, 2007) especially for summer and late flowering species (Emberlin, 1994), which suggests a serious threat to human health in terms of allergenicity. However, the estimation of the pollen season was derived from pollen counts of a larger region. Since, spatial variability in spring phenophases are expected to increase in a warming climate (Menzel *et al.*, 2006b), this may be the reason for a prolonged pollen season, and not an actual lengthening of the flowering period. A significant shortening of flowering for the majority of species due to increased temperatures may actually reduce human exposure time to pollen of specific allergenic species. Therefore, allergic sufferers might benefit. However, further research is needed to identify further potential drivers of change, especially for FD.

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