

# Contrasting impacts of climate-driven flowering phenology on changes in alien and native plant species distributions

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## Summary

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- Plant phenology is particularly sensitive to climate and a key indicator of environmental change. Globally, first flowering dates (FFDs) have advanced by several days per decade in response to recent climate warming, but, while earlier flowering should allow plant distributions to increase, a link between FFD and range changes has not been observed.

- Here I show for 347 species that the extent to which FFD has responded to climate warming is linked to the degree to which their relative distributions have changed over 30 yr across the British Isles.

- Native plant species whose phenology did not track climate change declined in distribution, whereas species that became more widespread all exhibited earlier flowering. In contrast, alien neophytes showed both a stronger phenological response to warming and a more marked increase in distribution, but no link between the two.

- These trends were consistent both for relative changes in the national distribution and for local abundance. At the national scale, the more recently an alien species became established in Britain, the more likely it was to increase in distribution irrespective of FFD, suggesting that recent changes in alien species distributions are decoupled from climate and driven by other factors.

## Introduction

Species shifts in latitude and altitude provide strong evidence of the impact of recent climate warming on biodiversity (Kelly & Goulden, 2008; Lenoir *et al.*, 2008; Rosenzweig *et al.*, 2008). Yet climate impacts may be underestimated where limited dispersal retards population expansion (Parmesan & Yohe, 2003) or where land-use constrains species ranges (Davis & Shaw, 2001). Alternatively, climate impacts may be overestimated where changes in species distributions are driven by human transport that facilitates the spread of alien species (Hulme *et al.*, 2009). Thus differences in dispersal and/or land-use change could obscure distribution changes in responses to climate. Instead, measures of plant performance such as phenological shifts, particularly in first flowering date (FFD), may be better indicators of the potential impact of climate change (Peñuelas & Filella, 2001; Root *et al.*, 2005; Parmesan, 2007).

Plant phenology is particularly sensitive to climate and a key indicator of environmental change (Badeck *et al.*, 2004; Estrella *et al.*, 2007; Peñuelas *et al.*, 2009; Yang & Rudolf, 2010), but while earlier flowering should allow plant distributions to increase (Hegland *et al.*, 2009; Miller-Rushing & Weltzin, 2009; Steltzer & Post, 2009), a link between FFD and changes in species distributions has not been observed. Such a link would enable phenological changes to be more rigorously used as early warning systems of potential climate impacts on species distributions (Menzel *et al.*, 2006; Cleland *et al.*, 2007; Crimmins *et al.*, 2009). Process-based models predict such a link (Chuine & Beaubien, 2001; Morin *et al.*, 2007) under the assumption that phenology governs reproductive success, growth and survivorship which ultimately determines the probability of species occurrence under particular climatic conditions (Cleland *et al.*, 2007; Steltzer & Post, 2009). Finding such a link is a significant challenge as few long-term studies have examined temperature-related changes in FFD for more

than a handful of species in natural populations (Abu-Asab *et al.*, 2001; Fitter & Fitter, 2002; Peñuelas *et al.*, 2002; Willis *et al.*, 2008; Gordo & Sanz, 2009) and thus any test requires correspondence between several scarce data sets: long-term records of FFD, climate and distribution change.

Under what circumstances might we expect the response of flowering phenology and species distributions to climate to be linked? A widely held belief is that species from warmer climates are pre-adapted to respond rapidly to increasing temperatures and this could be facilitated by flowering phenology tracking climate change (Walther *et al.*, 2009). Alternatively, the flowering phenology of life-forms with short generation times, such as annual weeds and opportunistic woody species, may be less constrained by photoperiod and more responsive to temperature (Körner & Basler, 2010), resulting in rapid spread. Warmer regions of species origin and opportunistic life-histories are likely to coincide in the case of many alien plant species (Hulme, 2009) and such taxa might reveal a stronger link between flowering phenology and increases in distribution than natives. However, against these synergistic effects of flowering phenology, life-history and climate change, species distributions may be constrained by edaphic conditions less immediately influenced by variation in temperature such as soil fertility, moisture, pH or disturbance. Furthermore, these drivers and constraints are only likely to act where species are already at equilibrium with the current climate. The distribution of recently introduced alien plant species appears to reflect the length of time a species has had to expand its range since it was first introduced (Williamson *et al.*, 2009) and potentially may not be at equilibrium with climate.

Clearly an assessment of a link between flowering phenology and species distributions is much needed as it will be crucial to gauge the potential impact of global warming on plants and address whether alien species pose a greater threat under climate change (Walther *et al.*, 2002). To test for a link between flowering phenology and species distributions, the FFDs of 347 terrestrial plant species recorded from 1970 to 2000 in Chinnor, south-central England (Fitter & Fitter, 2002) were analysed in relation to their change in distribution in Britain over the same period. Variation in the number of days FFD occurred earlier per 1°C warming and the Change Index (CI), a measure of the relative change in species distribution between 1969 and 1999 (Preston *et al.*, 2002a; Hill *et al.*, 2004), was examined in relation to a set of plant attributes that might strengthen or weaken any link between flowering phenology and species distributions.

To assess whether alien species and/or opportunistic life-forms were more likely to exhibit a link between flowering response and distribution, analyses examined the importance of life-form (annual, herbaceous or woody perennial) and species status (native, archaeophyte (alien introduced before 1500 AD) or neophyte (alien introduced after

1500 AD)) for flowering response and distribution change. Within each status group, more detailed analyses examined whether species from warmer climates showed the most marked response in phenology and distribution change using a measure of a species' current bioclimatic niche in the UK. These analyses also accounted for measures that reflected a species response to less temperature-dependent factors (important environmental gradients of light, soil moisture, pH and fertility) in constraining phenology or distribution change. Finally, to assess whether recent changes in distribution simply reflect progressive range expansion rather than a response to the environment, for neophytes the date of introduction to the British Isles was included in these models. The results indicate that, at least for native species, a link between FFD and the CI exists, with species exhibiting delayed flowering undergoing relative distribution declines. Yet earlier flowering did not guarantee range increase and no such relationship was found for neophytes.

## Materials and Methods

### Study location

Each year between 1970 and 2000, FFDs were recorded by a single observer (the naturalist and author Richard Fitter) on a more or less daily basis within a few kilometres of a single locality in south-central England (Chinnor, Oxfordshire; National Grid reference SU 7599; 0°42'9W 51°42'9N). Most records are from this locality, which is rural and has not experienced substantial land-use change in recent years; however, records within counties adjacent to Oxfordshire were also used (Fitter & Fitter, 2002). Most of the 347 species were recorded each year (the median number of species recorded per year is 272) and individual species were recorded in most years (the median number of years per species is 25). There was no difference in the frequency of years in which native (mean  $\pm$  SE =  $24.08 \pm 0.28$ ), archaeophyte ( $23.55 \pm 0.65$ ) or neophyte ( $23.00 \pm 0.72$ ) species were recorded over this period ( $F_{2,344} = 1.03$ ,  $P = 0.358$ ), but woody species were recorded in more years ( $25.89 \pm 0.49$ ) than either annual ( $22.80 \pm 0.63$ ) or perennial herbaceous ( $23.76 \pm 0.29$ ) species ( $F_{2,344} = 6.52$ ,  $P = 0.002$ ). Similarly, there was no systematic trend in the number of species recorded over time (correlation coefficient  $r = -0.316$ , df 29,  $P > 0.05$ ) or in relation to annual temperature ( $r = -0.353$ , df 29,  $P > 0.05$ ). Thus, although not systematic, the phenology surveys are unlikely to have suffered temporal or spatial sampling bias (Fitter *et al.*, 1995).

### Climate data

The mean minimum monthly temperatures for the period December to May, a key period for flower initiation

(Abu-Asab *et al.*, 2001; Fitter & Fitter, 2002), were drawn from monthly summaries of the Central England Temperature (CET). The CET interpolated data are representative of a triangular area of Britain enclosed by Bristol, Lancashire and London, in which the study location is found (UK Meteorological Office, Hadley Centre, 2006). These interpolations have received considerable and detailed attention to reduce error and improve spatio-temporal homogeneity (Parker & Horton, 2005); in addition, the CET is representative of the major temperature trends across England and Wales (Croxtan *et al.*, 2006). The UK has experienced marked warming since 1970 (Hulme *et al.*, 2002) and, even over this short time-span, several taxa have exhibited range increases (Hickling *et al.*, 2005, 2006).

### Species traits

Only terrestrial taxa were considered in the analyses and comprised Magnoliopsida (340 species), Pteropsida (two species), Equisetopsida (three species) and Pinopsida (two species). Casual and planted species as well as those with uncertain status were not included in the analysis. Thus, while Fitter & Fitter (2002) report results for 385 species, analyses described here are for a subset of 347 species (Supporting Information Table S1). For the Pteropsida and Equisetopsida, mature sporangia were taken as equivalent to flowers. Data on the native status, plant height, species bioclimatic profiles, life-form, Ellenberg scores and the CI were derived from the PLANTATT database (Hill *et al.*, 2004). Mean January ( $T_{\text{jan}}$ ) and July ( $T_{\text{jul}}$ ) temperatures ( $^{\circ}\text{C}$ ) are commonly used to describe the climate space occupied by plant species and reflect the boundaries on species distributions imposed by cold temperatures and annual heat sums (Woodward, 1988). To assess whether species differed in relation to their bioclimatic range, a bioclimatic profile for each species was calculated as the  $T_{\text{jan}}$  and  $T_{\text{jul}}$  of the current 10 km  $\times$  10 km grid cells where the species occurs in Britain, Ireland and the Channel Islands, averaging over the cells enumerated for the counts.  $T_{\text{jan}}$  and  $T_{\text{jul}}$  for the grid cells were constructed by interpolation of daily weather measurements from individual meteorological stations, averaged over the 30-yr period 1961–1990 (Hill *et al.*, 2004). It is important to stress that these climate variables are used to describe a simple 'bioclimatic profile' of each species based on their distribution recorded during 1987–1999 (Preston *et al.*, 2002a). These climate profiles are used as an indicator as to whether species occur in cooler or warmer bioclimates and are included in subsequent analyses to examine whether bioclimate has any influence on the magnitude of a species' flowering response to temperature change over the 30-yr period. Information on dates of when a neophyte was first recorded as naturalizing in the wild was taken from Preston *et al.* (2002b).

### Change Index

The CI measures the relative magnitude of change in the number of 10 km  $\times$  10 km grid cells in which a species was recorded in the British Isles, comparing the period 1930–1969 with 1987–1999 (Preston *et al.*, 2002a). These two periods coincide with the dates for inclusion of records in two major atlases of the distribution of the British flora. Although the duration of the assessment periods for each atlas differed, so did the effort employed during these two periods and the CI, as a relative measure, has been designed to be robust to differential effort between surveys. For example, most data from the 1987–1999 period were gathered via an intensive 4-yr survey between 1996 and 1999 that involved 1600 recorders (Preston *et al.*, 2002b). For each species, counts of grid cells were expressed as proportions of the total survey area, and then logit-transformed (where  $\text{logit} = \log [p/(1-p)]$  for the proportion  $p$ ). Species that were recorded in five or fewer grid cells in the earlier plant atlas were excluded from the analysis. A weighted linear regression model that further accounts for the undue influence of rare species in the initial survey period was then fitted to the relationship between logit-transformed proportions in 1930–1969 and 1987–1999 (Telfer *et al.*, 2002). The standardized residual of this relationship for each species is an index of its change in range size relative to the trend in the whole flora. The robustness of this analytical approach has seen the CI becoming increasingly used for comparisons of distribution change between vegetation surveys in Europe and the USA (Aronson *et al.*, 2007; Van Calster *et al.*, 2008; Van Landuyt *et al.*, 2008). The CI values used for the species in this study are derived from regressions using 1524 taxa for which this calculation was possible (Preston *et al.*, 2002b). Although the CI is proportional to relative change in actual range size, it is a relative measure and thus it is not possible to decide whether a species with a CI of zero has increased, remained stable or declined in absolute terms.

### Analysis

Previous analyses by Fitter & Fitter (2002) highlighted the impact of life-form and first flowering date on the difference in FFD between two different time periods: 1954–1990 and 1991–2000. These authors also indicated that there was no taxonomic pattern to the data above the genus level in the 13 families (in two subclasses) that were represented by at least two genera each with more than one species, and that differences among subclasses, superorders, and families were not significant (Fitter & Fitter, 2002). The current study explored the phenological data further by calculating a species-specific rate of flowering response over the period 1970–2000. Flowering response, the number of days FFD occurred earlier per  $1^{\circ}\text{C}$  warming, was estimated by the

slope of the linear regression between FFD and the mean minimum monthly temperature between December and May (Abu-Asab *et al.*, 2001; Peñuelas *et al.*, 2002; Willis *et al.*, 2008). For ease of interpretation, as these regressions present negative values for earlier flowering as temperature increases, the sign of the slopes was reversed so that flowering response reflected the number of days a species flowered earlier for a 1°C increase in temperature. Thus negative scores indicate a species that is failing to track climate change and flowering later as temperature increases. Subsequently, variation in flowering response was examined in relation to species status, traits and its association with the relative change in species distribution since 1970. Initially an overall general linear model (GLM) assessed the effect of species status, life-form and their interaction on flowering response (with first flowering date as covariate) and CI. Subsequently, separate multiple regressions were undertaken for each of the three status groups and examined the strength of the relationships of flowering response and CI with plant height (to account for differences among life-forms); Ellenberg scores for light, soil moisture, pH and fertility; and the species' two bioclimatic profiles. Interpretation of multiple regressions was carried out in three steps (Whittingham *et al.*, 2006). First, full models were examined to identify the contribution of all independent variables in explaining variation in flowering response and CI. Secondly, backward elimination of variables from the full model was used to identify whether at least one minimum adequate model (MAM) existed. Thirdly, an information theoretic approach to model selection was used to identify the subset of equivalent and alternative models to the MAM. Because of the small sample sizes for archaeophyte and neophyte models, the difference in the second-order Akaike information criterion ( $\Delta_{AICc}$ ) from the minimum model was used to identify a set of models that could be viewed as equivalent to the minimum model ( $\Delta_{AICc} < 2$ ; Burnham & Anderson, 2002). Comparison of variables retained in the MAM with the consistent occurrence of individual or groups of variables in subsets of equivalent AICc models was used to identify a parsimonious set of predictors. All statistical analyses were undertaken using SAS 9.1 (Statistical Analysis System Institute Inc, 2003).

## Results

A flowering response was most evident for earlier flowering species in all status groups (Table 1, Fig. 1). Independently of flowering date, neophytes flowered on average mean  $\pm$  SE =  $2.20 \pm 0.87$  d earlier than natives per 1°C warming (by analysis of covariance (ANCOVA);  $F_{2,337} = 3.52$ ,  $P = 0.031$ ; Fig. 2a), with no significant difference between archaeophytes and natives. The magnitude of flowering response was also greater for annuals than for other life-forms ( $F_{2,337} = 8.98$ ,  $P < 0.0001$ ; Fig. 2b) and

this was consistent for all status groups (two-way interaction;  $F_{4,337} = 2.25$ ,  $P = 0.064$ ). Significant MAMs (all  $P < 0.001$ ) were found for natives ( $R^2 = 0.424$ ), archaeophytes ( $R^2 = 0.163$ ), and neophytes ( $R^2 = 0.306$ ), and there was good correspondence between variables in the MAM and those most commonly found in the 'best' subset models using AICc (Table 1). Mean first flowering date was the single variable with greatest explanatory power in the MAM for natives, archaeophytes and neophytes and in all the 'best' subset AICc models. For natives, flowering response was greater for shade-tolerant species (e.g. with low Ellenberg light scores), reflecting the response of the spring-flowering woodland flora, whereas short-statured archaeophytes of more fertile sites, mostly arable weeds, exhibited a greater advance (Table 1). Species from warmer climates were expected to respond more markedly to climate change. No bioclimatic variables were retained in the MAM but  $T_{jan}$  was included in the minimum AICc model for both natives and archaeophytes. Nevertheless,  $T_{jan}$  has less support than the other variables in the minimum AICc model as it was not consistently found in the AICc models identified in the 'best' subset. Furthermore, while native species encountering warmer winter temperatures exhibited the greatest advance, the opposite was true for archaeophytes.

Although the FFD of natives and archaeophytes occurred c. 6 d earlier for every 1°C rise in temperature, overall there was only limited evidence for any significant increase or decrease in the CI since 1970; in contrast, neophytes exhibited a relative increase in their distribution over the same period ( $F_{2,338} = 27.30$ ,  $P < 0.0001$ ; Fig. 2a). Differences were found among life-forms ( $F_{2,338} = 4.71$ ,  $P = 0.010$ ; Fig. 2b), where woody perennials revealed a relative increase in distribution, whereas the CI for annuals and herbaceous perennials was not significantly different from zero. This trend among life-forms was similar across all status groups (two-way interaction;  $F_{2,338} = 1.50$ ,  $P = 0.203$ ) but was the opposite to that found for flowering response.

There was only partial evidence that changes in flowering phenology fed back to changes in species distribution. For archaeophytes, soil fertility was the only variable retained in the MAM ( $R^2 = 0.130$ ,  $P = 0.019$ ), and was included in all 'best' AICc subset models (Table 1). A further variable,  $T_{jul}$ , was also included in most of the 'best' subset AICc models, implying that species of fertile and warm environments exhibited the greatest increase in CI. The CI for neophytes was not significantly related to flowering response or any other environmental covariate. However, there was a positive relationship between the date of naturalization in the wild and relative change in distribution since 1970 (Fig. 3a, full model beta = 0.483,  $P = 0.004$ ). Only date of naturalization was retained in the MAM ( $R^2 = 0.210$ ,  $P = 0.007$ ) and was the only variable consistently found in all the 'best' subset AICc models.



**Table 1** Parameters in the full models from separate general linear model (GLM) analyses for native ( $N = 271$ ), archaeophyte ( $N = 42$ ) and neophyte ( $N = 34$ ) taxa summarizing the strength (beta) and statistical significance ( $P$ ) of plant height, bioclimatic profile ( $T_{jan}$  and  $T_{jul}$ ) and response to environmental gradients (Ellenberg scores for light, moisture, pH and fertility)

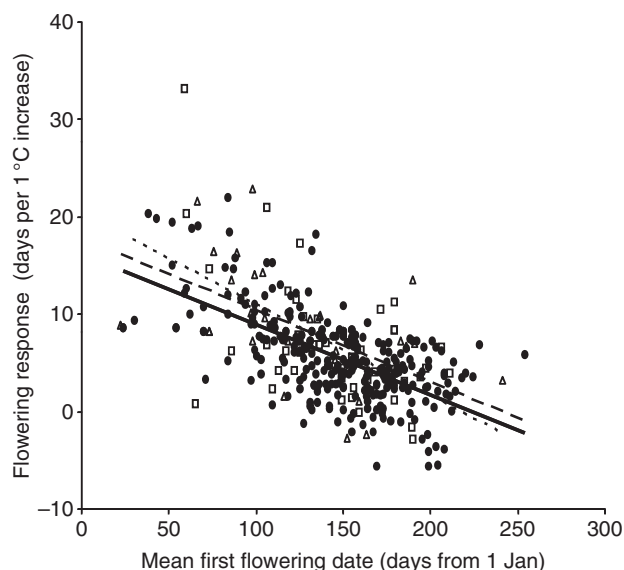
	Native		Neophyte		Archaeophyte	
	Beta	$P$	Beta	$P$	Beta	$P$
(a) Response						
Mean FFD	<b>-0.568</b>	<b>0.000</b>	<b>-0.525</b>	<b>0.006</b>	<b>-0.657</b>	<b>0.000</b>
Height	-0.049	0.320	-0.042	0.839	<b>-0.347</b>	<b>0.030</b>
$T_{jan}$	<u>0.097</u>	<u>0.098</u>	-0.144	0.531	<u>-0.251</u>	<u>0.106</u>
$T_{jul}$	-0.106	0.117	0.136	0.547	0.171	0.252
Light	<b>-0.219</b>	<b>0.000</b>	0.097	0.684	0.029	0.841
Moisture	0.025	0.634	-0.125	0.525	-0.063	0.701
pH	0.038	0.541	-0.035	0.852	-0.139	0.300
Fertility	0.030	0.599	0.321	0.151	<b>0.303</b>	<b>0.016</b>
$R^2$		0.440		0.395		0.557
$F$		25.722		2.040		5.195
$P$		0.000		0.083		0.000
(b) Change Index						
Response	<b>0.185</b>	<b>0.005</b>	-0.105	0.615	-0.077	0.671
Height	<u>0.105</u>	<u>0.096</u>	0.044	0.854	0.064	0.760
$T_{jan}$	-0.033	<u>0.657</u>	0.043	0.873	-0.108	0.576
$T_{jul}$	0.090	0.299	-0.012	0.964	<u>0.313</u>	<u>0.100</u>
Light	<b>0.212</b>	<b>0.004</b>	0.208	0.472	0.011	0.952
Moisture	0.025	0.708	0.142	0.550	0.107	0.607
pH	-0.150	0.061	-0.279	0.220	-0.065	0.713
Fertility	<b>0.199</b>	<b>0.007</b>	0.064	0.815	<b>0.351</b>	<b>0.044</b>
$R^2$		0.090		0.127		0.247
$F$		3.236		0.456		1.355
$P$		0.002		0.875		0.252

Separate full models are presented for (a) flowering response ('Response') and (b) distribution change (Change Index). Flowering response is included as an explanatory variable in the distribution change models. Values in bold have strong support from both regression and information theoretic approaches to model selection (included in the minimum adequate model and best Akaike information criterion (AICc) model), while underlined values have moderate support (included in most high-ranking AICc models). FFD, first flowering date.

In contrast to the alien taxa, flowering response was related to the relative changes in distribution of natives. Native species that showed the greatest flowering response, persisted in shaded habitats and benefited from fertile soils exhibited increases in relative distribution (Table 1, Fig. 3b). These three variables were found in the MAM ( $R^2 = 0.061$ ,  $P < 0.001$ ) and all equivalent 'best' AICc subsets. Two other variables, height and pH, were included in all but one of the 'best' subset models but not the MAM. Taller species and those of more acid soils exhibited greater increases in CI. There was no support for the view that species from warmer regions of the UK might exhibit the greatest relative change in distribution, with neither bioclimatic variable included in the 'best' subset AICc models or the MAM. Of those native species where FFD did not initiate earlier with warming, all but one declined in distribution, whereas species whose distributions showed a relative increase had a greater response. However, an earlier flowering response was not by itself a guarantee of a relative increase in distribution. Almost two-thirds of native species exhibiting earlier flowering in response to warming also showed relative

declines in distribution, probably in response to other environmental pressures related to variation in light and soil fertility (Table 1).

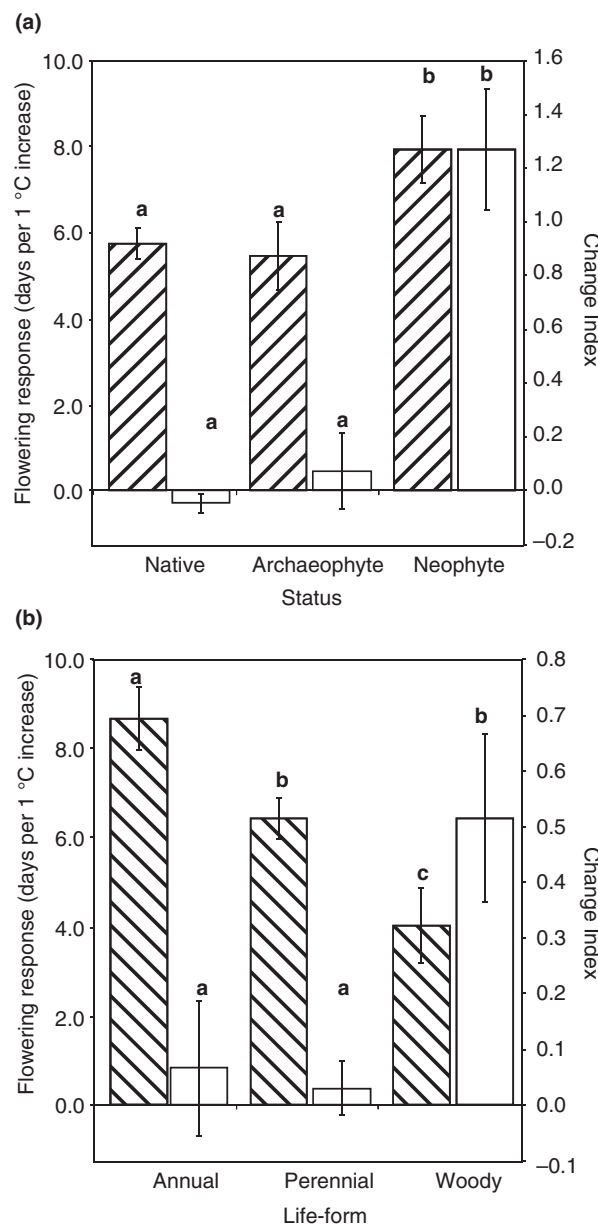
Could these national scale results translate to patterns at the local scale? There are no data on the local abundance of species in the vicinity of Chinnor but it might be assumed that species increasing in the local area may be more likely to be recorded in any one year. Thus a proxy for abundance may be the frequency with which a species was recorded in the phenological time series. At this local scale, a positive relationship did exist between flowering response and the frequency with which a species was recorded, but again this was only for native species (beta = 0.301,  $P < 0.001$ ). Native species whose FFD failed to respond significantly to warming tended to be under-recorded in the Chinnor data set (Fig. 4). As at the national scale, no relationship was found for either archaeophytes (beta = -0.077,  $P = 0.630$ ) or neophytes (beta = 0.287,  $P = 0.099$ ). These results are consistent with the interpretation that changes in flowering phenology subsequently impact upon local abundance.



**Fig. 1** Negative relationship between flowering response (positive scores reflect earlier flowering) and the mean date of first flowering for native, archaeophyte and neophyte species. Neither the slopes nor intercepts derived from linear regressions differed significantly among status groups: native (closed circle, dashed line)  $y = -0.073x + 16.18$ , adjusted  $R^2 = 0.39$ ,  $P < 0.001$ ; archaeophyte (open triangle, continuous line)  $y = -0.074x + 17.86$ ,  $R^2 = 0.29$ ,  $P < 0.001$ ; neophyte (open square, dotted line)  $y = -0.094x + 20.42$ ,  $R^2 = 0.28$ ,  $P < 0.001$ .

## Discussion

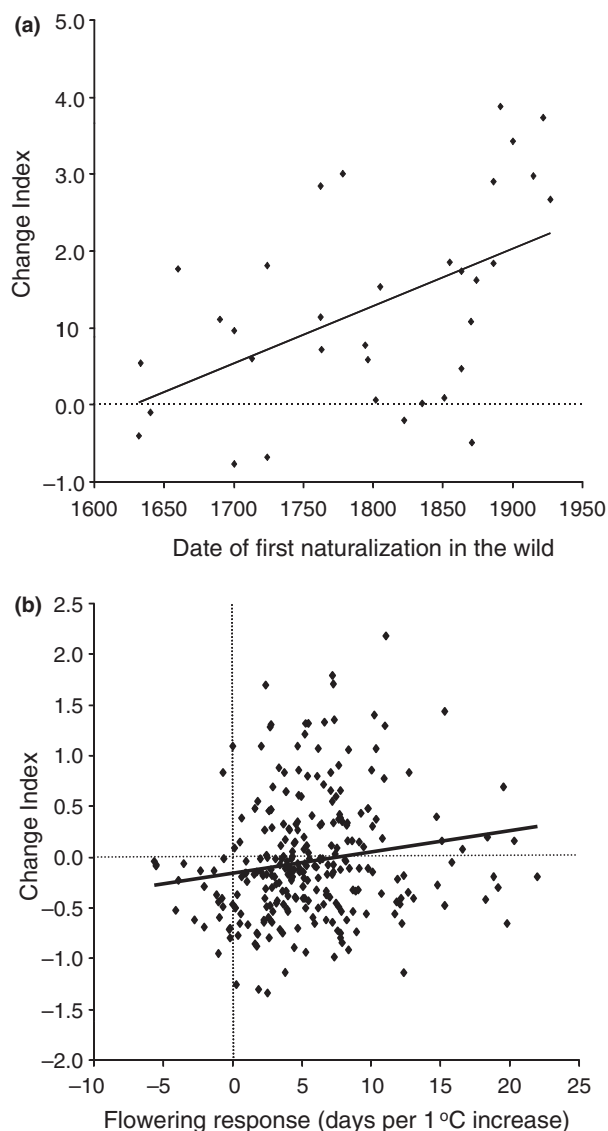
The primary causes of change in the distribution of the British flora over the last 30 yr have been land-use transformation (Preston *et al.*, 2002a,b) and eutrophication (Smart *et al.*, 2005) rather than climate change (Haines-Young *et al.*, 2003; Hulme, 2009). The results of the present study suggest that, while many species have shown relative declines in response to these pressures, there is still a detectable climate signal. The response in FFD explained only a small proportion of the variation in native CI and thus this result should not be over-interpreted. The explanatory power of the analysis is limited by changes in FFD being only one component of plant phenology that influences plant demography (Morin *et al.*, 2007). Even under experimental warming, plants respond in idiosyncratic and unpredictable ways as a result of different combinations of changes in organ size and physiological rates (Lambrecht *et al.*, 2007). In addition, while flower phenology at a single site may parallel patterns at a national scale, such correlations are not perfect (Sparks *et al.*, 2000; Menzel *et al.*, 2001), although phenological models fitted locally can predict regional phenology (Chuine *et al.*, 2000). Finally, additional environmental drivers impose further constraints on distribution change (Hulme, 2009). Under such circumstances the explanatory power of the responsiveness of FFD to warming may be of less interest than how its effect ranks



**Fig. 2** Variation in flowering response (shaded bars) and the Change Index (open bars) for (a) species status and (b) life-form. The significance of the post hoc comparisons refer to Bonferroni-type simultaneous confidence intervals based on Student's *t* distribution and bars labelled with the same letter are not statistically different from each other at  $P = 0.05$ .

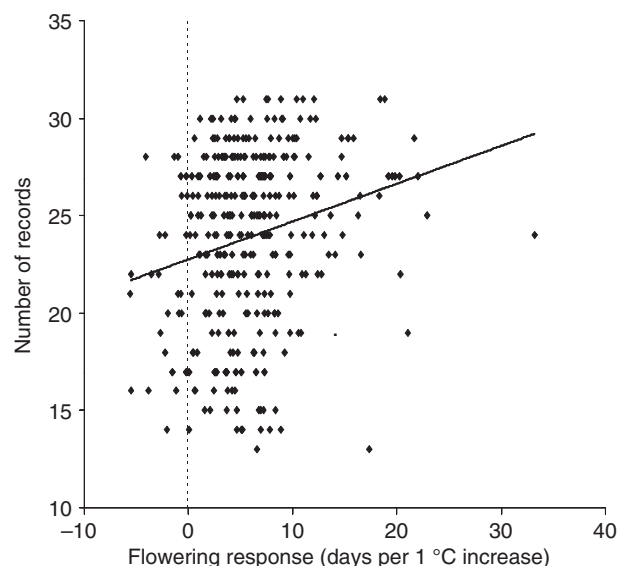
against other explanatory variables (Freckleton, 2009). Thus the significance of the relationship may be better reflected by the variation explained by flowering response being similar in magnitude to the light and soil fertility covariates, which are likely indicators of the response of the British flora to land-use change (Preston *et al.*, 2002b) and eutrophication (Smart *et al.*, 2005).

Native plants whose phenology did not respond significantly to climate warming revealed a relative decline in



**Fig. 3** Positive relationships between the Change Index and (a) date of first naturalization in the wild for neophyte species ( $y = 0.007x - 11.329$ , adjusted  $R^2 = 0.213$ ,  $P = 0.004$ ); (b) flowering response for native species ( $y = 0.021x - 0.159$ , adjusted  $R^2 = 0.023$ ,  $P = 0.007$ ).

distribution (e.g. *Stachys officinalis* and *Scabiosa columbaria*). Later flowering may impair plant performance and reproductive output (Suttle *et al.*, 2007), especially if plant species that respond to temperature change may better maintain interactions with pollinators (Willis *et al.*, 2008; Walther *et al.*, 2009). Later flowering may also result in a shorter growing season and potentially lower productivity either in absolute terms (Steltzer & Post, 2009) or relative to competitors that flower earlier. A combination of a shorter growing season, decreased productivity, reduced competitive ability, and lower fecundity could result in reduced local abundance and distribution range as well as



**Fig. 4** Positive relationship between the frequency with which phenological records were obtained for species between 1970 and 2000 in the vicinity of Chinnor and the flowering response over the same period ( $y = 0.296x + 22.451$ , adjusted  $R^2 = 0.087$ ,  $P < 0.001$ ).

making species less able to deal with other environmental pressures such as disturbance, habitat fragmentation and eutrophication. Partial support for such a hypothesis is found in observed changes in local abundance at Chinnor that appeared to mirror trends at the national scale.

However, it is important to distinguish cause and effect because declines in population size may result in sampling later FFD, irrespective of any role of climate (Miller-Rushing *et al.*, 2008). Are these changes in local abundance a result of differences in flowering phenology translating into changes in plant demography or simply a sampling artefact arising from a higher likelihood of picking up earlier flowering dates in larger populations? While changes in plant population size may have occurred in Chinnor, this seems an unlikely determinant of the changes in FFD. First, if the relationship is a sampling artefact it would not generate a strong relationship between first flowering date and the magnitude of the response to warming, as this would assume that the magnitude of the sampling artefact was strongly correlated with the mean date of flowering. In contrast, there is a sound physiological basis to expect spring-flowering species to respond more strongly to temperature changes (Lapointe, 2001). Secondly, a sampling artefact should be observed for all species irrespective of status, rather than only natives. If the magnitude of advance is an artefact of changes in abundance, then a strong relationship between the two variables should have been observed for neophytes as these species exhibited the most marked increase in both variables. Thirdly, the phenological records reveal high interannual variation in FFD (mean CVs:

native, 9.36; archaeophyte, 13.09; neophyte, 13.61) that is more consistent with changes in flowering responses to annual temperature differences than dramatic changes in plant population size. Thus, while it is important to recognize the potential effect of a sampling artefact, the evidence above suggests that such an artefact may play only a minor role in the patterns observed. This interpretation is consistent with the conclusions drawn regarding the role of delayed phenological response and the declining local abundance of woodland species in Massachusetts (Willis *et al.*, 2008).

Even improved plant performance as a result of earlier flowering may be no guarantee of population persistence in the face of these environmental pressures. Archaeophytes of fertile soils, mainly arable weeds (e.g. *Viola arvensis* and *Lamium album*), exhibited earlier flowering but they have also shown the strongest relative declines in their distributions in the British Isles as a result of the intensification of agriculture (Preston *et al.*, 2002b). Similarly, the FFD of native species typical of shaded habitats (with Ellenberg light scores < 5; e.g. *Mercurialis perennis* and *Viola hirta*) showed the strongest response to warming, yet native species best suited to open conditions (with Ellenberg light scores > 5; e.g. *Plantago lanceolata* and *Rumex acetosa*), such as might result from disturbance, showed greater relative increases in distribution (Table 1).

Given their marked earlier flowering and increase in distribution, the absence of a significant association between flowering response and CI for neophytes is in stark contrast to native species. However, the populations and hence ranges of invasive alien species may be expected to increase irrespective of changes in climate and most models of their spread have not required a specific climate driver (Hastings *et al.*, 2005). Under these circumstances, change would be greatest for more recently introduced species which are potentially furthest away from reaching any limits imposed by climate. For example, the distribution of *Acer pseudoplatanus* introduced in 1635 has shown little relative change in the UK between 1969 and 1999, whereas the relative distribution of *Cerastium tomentosum*, first recorded in the wild in 1915, has increased fivefold over the same period. This study has shown that time since naturalization, even after > 100 yr, appears to have a strong effect on the relative change in neophyte distributions since the 1970s, more so than recent environmental pressures such as climate-induced early flowering or eutrophication. This suggests that many alien species distributions have yet to reach equilibrium with the environment (Williamson *et al.*, 2009). Nevertheless, the higher proportion of alien species that exhibited earlier flowering in response to warming compared with native species indicates that these taxa may be better adapted to higher temperatures and is consistent with their bioclimate profiles being significantly warmer and drier than those of natives (Hulme, 2009).

This study highlights that changes in flowering phenology are not only a sign of climate change (Peñuelas & Filella, 2001; Root *et al.*, 2005; Peñuelas *et al.*, 2009; Steltzer & Post, 2009; Walther *et al.*, 2009) but, at least for native species, could be viewed as an indicator of the potential impacts of global warming on plant species distributions. While species from warmer climates (at least natives) and opportunistic species (e.g. annuals) exhibited a more marked flowering response, this did not appear to be directly translated in greater relative distribution change. It appears that environmental constraints, particularly relating to soil fertility and pH, mediate the magnitude of distribution change for species whose ranges are most likely to be in equilibrium with current climate. For species whose ranges are not in equilibrium with current climate (e.g. neophytes), there is no evidence of a relationship between flowering response and distribution change.

Three important caveats emerge from this study. First, most emphasis in phenological studies has been placed on identifying species showing a positive response to climate change rather than those that have shown delayed or no change in phenology (Parmesan & Yohe, 2003; Root *et al.*, 2005; Parmesan, 2006; Rosenzweig *et al.*, 2008). Yet it is the species that fail to track climate change that are of particular concern as they may decline as a result of reduced productivity, shorter growing seasons and/or phenological mismatch (Parmesan, 2006; Suttle *et al.*, 2007; Willis *et al.*, 2008; Steltzer & Post, 2009; Walther *et al.*, 2009). Over 20% of species across Europe may be failing to track climate change (Menzel *et al.*, 2006). Secondly, many phenological networks utilize alien ornamental species as a basis for their observations (Sparks *et al.*, 2000; Menzel *et al.*, 2006; Cleland *et al.*, 2007; Morissette *et al.*, 2009) and, while their responsiveness to temperature makes them suitable indicators, aliens may not be representative of phenological changes in native communities, particularly given their tendency for earlier FFD (Miller-Rushing & Primack, 2008; Peñuelas *et al.*, 2009). Thirdly, current distributions of alien species and also certain native species (Davis & Shaw, 2001; Svenning & Skov, 2004) may reflect dispersal limitation rather than climatic limits and may exhibit only limited tracking of future climate. Thus, while a link between phenological response and distribution change may exist, this study warns against the uncritical extrapolation of such data to predictions of future changes in species distributions (Walther *et al.*, 2009).

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## Supporting Information

Additional supporting information may be found in the online version of this article.

**Table S1** The 347 species examined in the phenology study

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