



# *Delayed chilling appears to counteract flowering advances of apricot in southern UK*

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1 **Delayed chilling appears to counteract flowering advances**  
2 **of apricot in southern UK**

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## 20 Abstract

21 Temperatures are rising across the globe, and the UK is no exception. Spring phenology of perennial  
22 fruit crops is to a large extent determined by temperature during effective chilling (endo-dormancy)  
23 and heat accumulation (eco-dormancy) periods. We used the apricot flowering records of the UK  
24 National Fruit Collections (NFC) to determine the influence of temperature trends over recent  
25 decades (1960 to 2014) on apricot (*Prunus armeniaca* L.) flowering time. Using Partial Least Squares  
26 (PLS) regression, we determined the respective periods for calculating chill and heat accumulation.  
27 Results suggested intervals between September 27<sup>th</sup> and February 26<sup>th</sup> and between December 31<sup>st</sup>  
28 and April 12<sup>th</sup> as the effective chilling and warming periods, respectively. Flowering time was  
29 correlated with temperature during both periods, with warming during chilling corresponding to  
30 flowering delays by  $4.82 \text{ d}^\circ\text{C}^{-1}$ , while warming during heat accumulation was associated with bloom  
31 advances by  $9.85 \text{ d}^\circ\text{C}^{-1}$ . Heat accumulation started after accumulating  $62.7 \pm 5.6$  Chill Portions, and  
32 flowering occurred after a further  $3744 \pm 1538$  Growing Degree Hours (above a base temperature of  
33  $4^\circ\text{C}$ , with optimal growth at  $26^\circ\text{C}$ ). When examining the time series, the increase in temperature  
34 during the chilling period did not appear to decrease overall chill accumulation during the chilling  
35 period but to delay the onset of chill accumulation and the completion of **the average chill**  
36 **accumulation necessary to start heat accumulation**. The resulting delay in heat responsiveness  
37 appeared to weaken the phenology-advancing effect of spring warming. These processes may  
38 explain why apricot flowering time remained relatively unchanged despite significant temperature  
39 increases. A consequence of this may be a reduction of frost risk for early flowering crops such as  
40 apricot in the UK.

41

42 Keywords: Climate warming; chilling; dormancy; spring phenology; frost risk; partial least squares  
43 regression

## 44 **1. Introduction**

45 Phenological records provide valuable data for characterizing the effect of variation in  
46 environmental conditions on plant development. Frequently, these records cover a longer time span  
47 than any defined experiment, making them one of the most valuable pieces of evidence of the  
48 impacts of global warming over past decades or even centuries (Fitchett et al., 2015; Menzel et al.,  
49 2008). Flowering time of fruit crops is one of the most widely used indicators of climate change,  
50 because of the availability of such records, but also because of the strong temperature dependence  
51 of the fruit crop life cycle (El Yaacoubi et al., 2014; Martínez-Lüscher et al., 2016). Although the vast  
52 majority of case studies have reported significant advances in flowering times over the years  
53 (Chmielewski et al., 2011; Chmielewski and Rotzer, 2001; Fitter and Fitter, 2002; Fu et al., 2015;  
54 Legave and Clauzel, 2006; Menzel et al., 2006; Parmesan, 2007; Parmesan and Yohe, 2003; Root et  
55 al., 2003; Wolfe et al., 2005), the literature includes a considerable number of records describing  
56 observations of flowering times that have remained unchanged or even experienced delays (Cook et  
57 al., 2012; Elloumi et al., 2013; Fitter and Fitter, 2002; Kozlov and Berlina, 2002; Legave et al., 2013;  
58 Menzel et al., 2006; Yu et al., 2010). Recent studies have indicated that the response of plant  
59 phenology to temperature is more complex than simply an advance due to warming (Andreini et al.,  
60 2014; Chuine et al., 2016; Cook et al., 2012; Guo et al., 2015; Pope et al., 2014).

61 Temperate deciduous trees enter a period of winter dormancy, during which they are leafless and  
62 their buds stay dormant awaiting suitable conditions to resume growth when temperatures rise.  
63 Apricots (*Prunus armeniaca* L.), like most temperate fruit crops, have an obligatory chilling  
64 requirement that must be fulfilled before trees can produce flowers (Campoy et al., 2011b;  
65 Luedeling, 2012). This means that they need a period of cool temperatures during the winter before  
66 normal budburst takes place (Campoy et al., 2011b; Campoy et al., 2013). The need to fulfil this chill  
67 requirement prevents these plants from flowering during short warm spells in winter, since flower

68 development is prevented even when temperatures are favourable. The time when the chill  
69 requirement has been met marks the end of endo-dormancy. Subsequently, during the eco-dormant  
70 period, budburst can be induced by warm temperatures (Lang et al., 1987). It occurs after sufficient  
71 accumulation of heat above a base temperature (measured in Growing Degree Days or Growing  
72 Degree Hours), which is often cultivar/species dependent (Campoy et al., 2011a; Luedeling, 2012).

73 For modelling purposes, chill and heat requirements have been conceptualized in different ways.  
74 The most common concept is one of sequential fulfilment of chilling and heat requirements, in  
75 which there is a period, before fulfilment of the chilling requirement, when buds are insensitive to  
76 heat accumulation, followed by the warming phase, when additional chilling has no effect. After  
77 sufficient heat has then accumulated to fulfil the heat requirement, bud burst occurs (Darbyshire et  
78 al., 2013; Guedon and Legave, 2008; Luedeling et al., 2009). A rather different concept proposes that  
79 chilling and heat accumulation start at a similar time and budburst is possible after a combination of  
80 chilling and heat accumulation. This indicates a trade-off between chill and heat accumulation, with  
81 abundant heat being able to compensate for low chilling, and vice versa (Harrington and Gould,  
82 2015; Harrington et al., 2010; Murray et al., 1989). This model assumes that plants with an  
83 obligatory chill requirement must first receive a minimum chilling dose (critical chilling units).  
84 Subsequently, high heat accumulation might induce bud burst. However, this heat requirement is  
85 reduced by exposure to additional chilling. Other modelling efforts for almonds have described this  
86 as an overlap between chilling and warming period, with a model assuming a budbreak-advancing  
87 effect of additional chilling until fulfilment of 75% of the heat requirement being best supported by  
88 field data (Pope et al., 2014). Experiments under controlled environment conditions also suggest  
89 that additional chilling during the early warming period may decrease the heat requirement  
90 (Couvillon and Erez, 1985). Since previous delineations between chilling and warming periods  
91 through PLS regression have also indicated an overlap between the phases, it seems plausible to  
92 differentiate between three temperature-responsive phases between the onset of bud dormancy  
93 and flowering: 1) only chilling accumulation has a flowering-advancing effect, 2) both chilling and

94 heat accumulation are effective, and 3) only heat accumulation may promote bud development  
95 (Guo et al., 2014; Guo et al., 2015; Luedeling et al., 2013).

96 Although the effects of temperature on the fulfilment of chilling and heat requirements have been  
97 addressed by a large number of studies (e.g. Anzanello et al., 2014; Campoy et al., 2013; Carew et  
98 al., 2001; Mahmood et al., 2000), at the mechanistic level, the process responsible for chill  
99 accumulation is not fully understood (Campoy et al., 2011a).

100 In climates such as those encountered in the United Kingdom (145 Chill Portions [CP] accumulated  
101 on average from 1<sup>st</sup> September to 31<sup>st</sup> April), chilling is not typically assumed to be a limiting factor  
102 of flowering or crop yield of apricots (Guo et al., 2015; Viti et al., 2010). In addition, a calculation of  
103 chilling according to the Dynamic Model for future climate projections did not forecast major  
104 changes in the seasonal number of accumulated Chill Portions in the UK (Luedeling et al., 2011).  
105 However, assuming sequential completion of chilling and heat requirements, the current trend of  
106 climate warming may have an effect on the timing of the initiation of chilling, fulfilment of chilling,  
107 initiation of heat accumulation and completion of heat requirement, with all these factors having  
108 potential for major impacts on flowering dates (Luedeling et al., 2009). This leaves significant  
109 uncertainty about future trends in spring flowering of fruit species in the UK. In fact, studies  
110 conducted on wild species show a change in the order of flowering among species as temperatures  
111 increase (Roberts et al., 2015). It is also worth considering that, at present, apricots in the UK already  
112 flower relatively early, so that their timing often coincides with low activity of pollinators during  
113 anthesis, whilst buds, flowers and fruitlets face substantial risk of frost damage (Else and Atkinson,  
114 2010). Further advances in apricot flowering dates may reduce their suitability for commercial  
115 plantings, whereas a delay in flowering may make them more suitable, particularly when associated  
116 with an increase in temperatures around flowering time (Cannell and Smith, 1986).

117 The aim of this study was to determine the influence of fluctuations in chill and heat accumulation  
118 on recorded flowering dates of apricots of the UK National Fruit Collections (NFC) in the SE England.

119 We used Partial Least Squares (PLS) regression to determine the start and end of the effective chill  
120 and warming periods and to give an outlook of how variation in daily chill and heat accumulation  
121 rates affect the flowering date.

## 122 **2. Materials and Methods**

### 123 **2.1 Phenology and climate data**

124 This study used a 35-year discontinuous record of the flowering dates of 14 apricot varieties at the  
125 UK NFC at Brogdale Farm, Faversham, UK (51.30° N, 0.87° E, 12 m a.s.l.) observed between 1960 and  
126 2014 (Table A1). Trees were generally monitored at least twice weekly (more frequently during  
127 particularly warm spells) and time of flowering was determined as the date when 10% of the flowers  
128 had fully opened. Dates were converted to Julian days (day of the year) for further analysis. There  
129 were no signs of any variety flowering earlier than the others (average range of 5.9 days; Fig. A.1).  
130 During several years, all varieties flowered on the same day or over a very short period (Fig. 1). The  
131 order in which different varieties flowered was not consistent throughout the record. For instance,  
132 the two varieties creating the largest flowering spread in the record (13 days in 1967 between Alfred and  
133 Sun-Glo), flowered only 2 days apart in the previous year. Another example is that Sun-Glo was the latest  
134 variety in 1981 but also the earliest three years later. Therefore, average flowering time for all varieties  
135 was used for the analyses. Among the 14 varieties, 'Alfred', 'Early Moorpark' and 'Farmingdale'  
136 were represented in most of the 35 years when flowering was recorded (Table A1), allowing  
137 meaningful trend analysis for these varieties.

138 Daily minimum and maximum temperatures were collected from a meteorological station located  
139 near the apricot orchard. A gap in the meteorological data, from March 1<sup>st</sup> of 1990 to April 30<sup>th</sup> of  
140 1998, was filled with data from the nearest weather station available (East Malling, 51.29° N; 0.45° E,  
141 78 m a.s.l., ca. 30 km away). These data were corrected for the 0.19 and -0.19°C difference in mean  
142 daily minimum and maximum temperatures determined by analysing differences between the  
143 records for overlapping periods. Minor gaps in the meteorological data were filled by linear



144 interpolation. These gaps were 14 recordings of daily maximum temperature and 29 of daily  
145 minimum temperature scattered throughout the whole time series.

## 146 **2.2 Chilling and heat accumulation models**

147 Most common chill and heat models require hourly temperature data as inputs. These were  
148 constructed using recorded (and gap-filled) daily minimum and maximum temperature records and  
149 following the recommendations of Linvill (1990) that the daily temperature curve can be composed  
150 of a sine curve for daytime warming and a logarithmic decay function for night-time cooling. Since  
151 these equations require daily data on sunrise, sunset and day length as inputs, these were modelled  
152 based on geographic latitude (Almorox et al., 2005; Spencer, 1971).

153 Daily chill accumulation was calculated according to the Dynamic Model (Erez et al., 1990; Fishman  
154 et al., 1987b), as it has consistently shown a better performance than other chill models in a wide  
155 range of circumstances (Campoy et al., 2011a; Darbyshire et al., 2011; Erez et al., 1990; Guo et al.,  
156 2013; Luedeling et al., 2013; Luedeling et al., 2009). Daily heat accumulation was calculated  
157 according to the Growing Degree Hours (GDH) Model (Anderson et al., 1986), a curvilinear model  
158 using a base temperature of 4°C and an optimum temperature of 26°C. The equations used for these  
159 chill and heat accumulation models are given in Luedeling and Brown (2011) and Luedeling et al.  
160 (2009), respectively. To facilitate the visual interpretation of the results, daily chill and heat values  
161 were subjected to an 11-day running mean procedure (Luedeling and Gassner, 2012; Luedeling et al.,  
162 2013). We illustrated variance of chill or heat accumulation over the periods of responsiveness using  
163 the standard deviation.

## 164 **2.3 Partial Least Squares regression**

165 Daily chill and heat accumulation were related to flowering dates for each year from 1<sup>st</sup> June to 25<sup>th</sup>  
166 April (latest flowering date recorded), creating 35 datasets consisting of 328 records of daily chill and  
167 heat accumulation (ignoring 25<sup>th</sup> April in leap years) and one flowering date each. PLS regression was

168 then used to find correlations between daily chill and heat accumulation rates (656 independent  
169 variables – 328 daily chill and 328 daily heat values) and flowering date (1 dependent variable). The  
170 Variable Importance in the Projection (VIP) statistic of PLS regression was used to highlight the most  
171 important among the large number of predictor variables. In contrast to other regression methods,  
172 PLS regression can effectively analyse effects of a large number of highly autocorrelated variables,  
173 even when they greatly outnumber the observations for the independent variables. For PLS  
174 regression, two latent factors were constructed from all the independent variables and used to  
175 perform a regression with the dependent variable, in line with the methods of Wold et al. (2001).  
176 We used the PLS implementation in the chillR package for R programming language (R version 3.2.0)  
177 (Luedeling, 2013). PLS regression gives two major outputs for each predictor variable: the VIP and a  
178 model coefficient. The VIP indicates how important variation in the value of a particular variable is  
179 for explaining variation in the dependent variable. As in previous studies, 0.8 was assumed to signify  
180 importance of a variable (Luedeling et al., 2013; Wold et al., 2001). For those independent variables  
181 with a significant VIP score, positive or negative PLS model coefficients indicate that a positive or  
182 negative deviation in the independent variable is correlated to an increase or decrease in the  
183 dependent variable, respectively. For our purposes, a negative coefficient on daily chill or heat  
184 accumulation indicates that high heat or chill accumulation on that particular day of the year is  
185 correlated to early spring flowering. Positive coefficients indicate correlation of high heat or chill  
186 accumulation with late flowering dates.

#### 187 **2.4 Interpretation of PLS output**

188 PLS regression highlights phases during which variation in independent variables (daily accumulation  
189 of chilling and heat) is correlated with variation in flowering date. Therefore, PLS regression analysis  
190 of a sufficiently long record of variable winter weather and the resulting flowering dates should  
191 allow delineation of relevant temperature response phases (Luedeling and Gassner, 2012; Luedeling  
192 et al., 2013). It should be kept in mind, however, that low VIP scores do not necessarily mean that

193 weather conditions on these days had no chilling or heat accumulation effect. It may simply mean  
194 that variation in weather conditions was not correlated with variation in flowering dates, which may  
195 also occur when, for example, temperatures varied only within a range that was optimal for chilling.

## 196 **2.5 Response of fruit tree flowering to conditions during the chilling and warming periods**

197 Once the chilling and warming periods were delineated, we determined heat accumulation during  
198 the warming phase (in GDH), chill accumulation during the chilling phase (in CP) and mean  
199 temperature during the chilling and warming periods. Other relevant parameters calculated were  
200 the day of the year when the first 5 CP (starting from 1<sup>st</sup> of July), the average chilling accumulation  
201 that enabled heat accumulation (first 62.7 CP starting from 1<sup>st</sup> of July) and the first 1000 GDH of the  
202 year (starting from 1<sup>st</sup> of January) had accumulated. The Kendall rank correlation coefficient ( $\tau$ , tau)  
203 was calculated for time series evaluation, and linear regression lines were plotted for chilling and  
204 warming period mean temperatures, chill and heat accumulation, completion date of the first 1000  
205 GDH, completion date of the first 5 CP and completion date of the **average chill accumulation that**  
206 **enabled heat accumulation**. Kendall's test is a non-parametric test where values are substituted by  
207 ranks, this means that no distribution or linear relationship is assumed. For this reasons Kendall's  
208 test is widely used for detecting trends in climatologic time series (Wilks, 2011). We used Pearson's  
209 correlation test for other data different from time series.

210 Through interpolation, we created a response surface illustrating the dependency of apricot  
211 flowering on chill and heat accumulation during the chilling and warming phases. For the  
212 interpolation, we used the Kriging technique, which is a Gaussian regression method commonly used  
213 in spatial statistics to estimate values at locations where no data are available (Oliver and Webster,  
214 1990). This illustration facilitated the interpretation of responses of flowering dates to multiple  
215 climatic drivers. In this case, the plot illustrated the direction and magnitude of the effects of chilling  
216 and heat accumulation on flowering dates (Guo et al., 2015). Guo et al. (2015) showed that as  
217 temperatures increase, temperatures during the chilling period may gain in relative influence on

218 bloom dates, compared to temperatures during the heat phase. However, within any single site, the  
219 relative importance of temperatures during these two phases appears to be relatively constant (Guo  
220 et al. 2015), unless temperatures increase very strongly, or the study site is already marginal for the  
221 species in terms of chilling. The kriging surface can be approximated by a bivariate linear model:  $y =$   
222  $a T_c + b T_h + c$ ; where  $T_c$  is temperature during the chilling period,  $a$  is the sensitivity of flowering date  
223 to chilling period temperature,  $T_h$  is temperature during the warming period, and  $b$  is the sensitivity  
224 of flowering date to warming period temperature. This method is often used with linear univariate  
225 models to estimate the sensitivity of phenology to changes in spring temperature (Fu et al., 2015).

## 226 **3. Results**

### 227 **3.1 Evolution of apricot flowering over time**

228 The average flowering date of apricots of the UK NFC showed a large degree of variability from year  
229 to year, being as early as 10<sup>th</sup> March in 1961 and 1989 and as late as 25<sup>th</sup> April in 1986 (Fig. 1), with  
230 46 days between earliest and latest flowering dates. Flowering time showed a slight trend towards  
231 earlier dates over the recording period (average advance by 0.238 days per year [ $d yr^{-1}$ ]), but this  
232 was not statistically significant ( $\tau=-0.13$ ;  $p=0.293$ ). The same results were observed for the three  
233 most frequently observed varieties; 'Alfred' ( $-0.092 [d yr^{-1}]$ ;  $\tau=-0.07$ ;  $p=0.621$ ), 'Early Moorpark' ( $-0.29$   
234 [ $d yr^{-1}$ ];  $\tau=-0.20$ ;  $p=0.149$ ) and 'Farmingdale' ( $-0.141 [d yr^{-1}]$ ;  $\tau=-0.09$ ;  $p=0.568$ ).

### 235 **3.2 Relevant periods for chill and heat accumulation**

236 Results from the PLS regression procedure indicated a period between 27<sup>th</sup> September and 26<sup>th</sup>  
237 February, which was characterized by high VIP scores ( $>0.8$ ) and negative model coefficients for the  
238 chill accumulation rate (Fig. 2). This phase was interrupted by a period between October and  
239 December, during which the correlation between variation in chill accumulation and flowering dates  
240 was not very pronounced. However, the daily chill accumulation rate during this time span was  
241 consistently high and varied relatively little, so that it seemed reasonable to us to interpret the

242 entire period between 27<sup>th</sup> September and 26<sup>th</sup> February as the chilling period. There were two  
243 additional periods of significant VIP scores for chill accumulation, where coefficients were  
244 alternating between positive and negative: 1) from 1<sup>st</sup> June to 4<sup>th</sup> July, and 2) from 10<sup>th</sup> March to 9<sup>th</sup>  
245 April. The fact that coefficients were not consistently positive or negative suggests that this pattern  
246 may not reflect the physiological processes commonly associated with dormancy progression.  
247 However, PLS analyses of mean temperatures (rather than chilling and forcing rates; Fig A. 2) also  
248 shows significant VIP scores and negative coefficients for both periods, which may indicate that  
249 apricot buds are truly responsive to temperatures during these periods.

250

251 The delineation of the warming period was clearer, with an almost uninterrupted period from 31<sup>st</sup>  
252 December to 12<sup>th</sup> April with negative model coefficients for daily heat accumulation rate, coupled  
253 with high VIP values. Chill accumulation over the chilling period was  $103.7 \pm 7.2$  CP, including  $41.7 \pm$   
254  $4.3$  CP in the period when chill and heat accumulation overlapped. This suggests that the difference,  
255  $62.7 \pm 5.6$  CP, accumulated from 27<sup>th</sup> September to 31<sup>st</sup> December, is the amount of chilling that  
256 these apricot trees received before starting to accumulate thermal time. The GDH accumulation  
257 during the overlapping period (from 1<sup>st</sup> January to 26<sup>th</sup> February) was  $1269 \pm 681$ , and this was  
258 followed by another  $2511 \pm 1062$  GDH between 26<sup>th</sup> February and 12<sup>th</sup> April, resulting in a total  
259 accumulation of  $3744 \pm 1538$  GDH accumulation in total (from 1<sup>st</sup> January to 12<sup>th</sup> April).

260 PLS results also indicated that the effects of heat accumulation depended strongly on when heat  
261 accumulation occurred (Fig. 2). Daily GDH showed also two periods of positive coefficients, when  
262 warm periods were correlated with late, rather than early, flowering dates: 1) from 4<sup>th</sup> to 16<sup>th</sup> of  
263 October, and 2) from 9<sup>th</sup> to 31<sup>st</sup> of December. During the first period, daily chilling accumulation was  
264 also correlated with flowering delays. This phase approximately coincided with the only period, for  
265 which high mean temperatures were associated with late flowering (Fig. A.2). In fact, the date of

266 completion of the first 5 CP was correlated with the heat accumulation required up to flowering (Fig.  
267 A.3).

### 268 **3.3 Relative importance of warming effects during the chilling and heat accumulation** 269 **phases**

270 Plotting flowering dates of apricot as a function of temperature during the chilling and warming  
271 periods predicted by PLS showed effects of both factors (Fig. 3A,  $R^2=0.74$ ). Cooler temperatures  
272 during the chilling period and warmer temperatures during the warming period appeared to induce  
273 earlier flowering. Since mean temperatures during the chilling and warming periods were positively  
274 correlated ( $r=0.79$ ;  $p<0.001$ ; data not shown), our dataset did not contain years with very warm  
275 chilling and cool heat accumulation phases, or vice versa (Fig. 3A). Had the data included such  
276 records, the bloom-advancing effect of cool temperatures would likely have featured more  
277 prominently in our results. Given that contour lines are nearly straight and parallel, the kriging  
278 surface could be approximated by a bivariate linear model ( $R^2=0.99$ ):  $y = 4.82 * T_c - 9.85 * T_w + 109.5$ ;  
279 where  $y$  is the flowering date (Julian Day),  $T_c$  is the mean temperature during the chilling period,  $T_w$  is  
280 the mean temperature during the warming period,  $4.82 \text{ days } ^\circ\text{C}^{-1}$  is the sensitivity to temperature  
281 during the warming period,  $-9.85 \text{ days } ^\circ\text{C}^{-1}$  is the sensitivity to temperature during the chilling  
282 period and  $109.5$  days is the model intercept (see methods for details). The angle of the contour  
283 lines, closer to parallel with the X axis than the Y axis and the greater sensitivity to temperatures  
284 during the warming period than the chilling period ( $-9.85$  vs  $4.82 \text{ days } ^\circ\text{C}^{-1}$ ) suggests that apricot  
285 flowering dates were influenced more strongly by temperature during the warming period than by  
286 temperature during the chilling phase. The combined effect of chill and heat accumulation described  
287 apricot flowering dates well (Fig. 3B,  $R^2=0.67$ ). The plot indicated a greater influence of variation in  
288 heat accumulation on flowering dates, but also showed a pronounced effect of chill accumulation  
289 rates, resulting in diagonal contour lines.

### 290 **3.4 Evolution of temperature-related variables over time**

291 Temperature during both chilling and warming periods increased significantly over time ( $\tau=0.35$ ;  
292  $p<0.001$ ; Fig. 4A and  $\tau=0.36$ ;  $p<0.001$ ; Fig. 4D). However, throughout the temperature record, mean  
293 temperature showed a slightly greater increase during the warming period ( $0.039\text{ }^{\circ}\text{C yr}^{-1}$ ) than during  
294 the chilling period ( $0.026\text{ }^{\circ}\text{C yr}^{-1}$ ). In contrast, heat accumulation showed a positive and significant  
295 trend over the period recorded ( $\tau=0.40$ ;  $p<0.001$ ; Fig 4B), but not chill accumulation ( $\tau=0.02$ ;  
296  $p=0.794$ ; Fig. 4E). Despite the lack of significant trend in chilling accumulation over time, the time to  
297 accumulate the first 5 CP of the season was significantly delayed over the years ( $0.28\text{ d yr}^{-1}$ ;  $\tau= 0.26$ ;  
298  $p=0.005$ ; Fig. 4F), leading to a delay in the time to complete the average chilling accumulation that  
299 enabled heat accumulation ( first 62.7 CP;  $0.21\text{ d yr}^{-1}$ ;  $\tau= 0.25$ ;  $p=0.006$ ; Fig. 4G). The time to  
300 accumulate the first 1000 GDH of the year shortened over the record ( $-0.45\text{ d yr}^{-1}$ ;  $\tau=-0.26$ ;  $p=0.006$ ;  
301 Fig. 4C). Mean temperatures around flowering showed a significant positive correlation with time  
302 ( $0.022\text{ }^{\circ}\text{C yr}^{-1}$ ;  $\tau=0.28$ ;  $p=0.02$ ; Fig. 5).

## 303 4. Discussion and conclusions

### 304 4.1 Identification of chilling and warming periods by PLS regression

305 Chilling and warming periods are often designated arbitrarily, based on intuition, or counting from  
306 the first day that chilling starts to accumulate (Darbyshire et al., 2011; Harrington and Gould, 2015;  
307 Harrington et al., 2010; Luedeling and Brown, 2011). In previous studies, PLS regression has been  
308 able to identify clearly the days of the year when accumulation of chilling or heat had an impact on  
309 spring phenology, so that chilling and warming periods could be defined (Guo et al., 2014; Guo et al.,  
310 2015; Luedeling and Gassner, 2012; Luedeling et al., 2013). This approach can also identify the  
311 chilling period for crops and places where the chilling requirement is easily satisfied (Guo et al.,  
312 2014) and variation in chilling accumulation has a small influence on flowering dates. In the present  
313 study, effective chilling and warming periods for apricots in the UK National Fruit Collection occurred  
314 from 27<sup>th</sup> September to 26<sup>th</sup> February and from 31<sup>st</sup> December to 12<sup>th</sup> April, respectively. Thus, the  
315 identified chilling and warming periods had a significant overlap of 58 days. This is in agreement with

316 studies on apricot and peach, which showed 1) an initial phase when heat accumulation cannot  
317 induce budburst, 2) a period when sufficient chill has accumulated to induce budburst by application  
318 of warm conditions, with the amount of required heat decreasing with additional chill accumulation  
319 and 3) a phase when additional chill has no effect and only heat is required for budburst (Campoy et  
320 al., 2011b; Campoy et al., 2013; Okie and Blackburn, 2011).

321 Guo et al. (2015) identified chilling and warming periods of apricots by PLS regression for several  
322 locations in China, among which results from our study were most similar to the analysis for Beijing,  
323 which was reported to have a chilling period from 17<sup>th</sup> September to 26<sup>th</sup> February. Considering the  
324 differences in temperature between locations at the start and end of the chilling period, this is a  
325 remarkable match (starting 10 days earlier and ending on the same day). Mean temperatures at UK  
326 NFC were approximately 5°C lower at the start of the chilling period and 4°C higher at the end of the  
327 chilling period than in Beijing. In fact, neither daily chill nor daily heat accumulation at these  
328 locations are within similar ranges or show a similar temporal pattern. However, both Beijing and  
329 the UK NFC, had similar mean temperatures during both the chilling and the warming periods, and  
330 PLS regression indicated similar chilling but also warming periods (from 9<sup>th</sup> January to 10<sup>th</sup> April in  
331 Beijing). Both locations were also similar in terms of the relative contributions of temperatures  
332 during the chilling and warming periods to variation in flowering dates (Fig. 3A). Therefore, in spite  
333 of big differences between the climates of Beijing and SE England, our results support the hypothesis  
334 of Guo et al. (2015), who proposed that, even though effects of spring warming have dominated  
335 phenological responses of temperate trees so far, continued warming may increase the importance  
336 of the phenology-delaying effects of warming in autumn/winter, which may slow and possibly  
337 reverse the advances in spring events that have been observed in recent decades.

338 In a study comparing the flowering dates of late varieties of apricot in Italy (Fideghelli et al., 1978),  
339 'Alfred' and 'Farmingdale' came out among the latest of the 146 varieties recorded, with the same  
340 flowering date as 'Bergeron', which is a common reference for late flowering apricots. 'Early



341 Moorpark', the third variety constituting the core of the data used for the analyses, flowered just 5  
342 days earlier than the other two. It must be noted that the late flowering of the varieties of the UK  
343 NFC led to the identification of the given chilling and warming periods and the use of varieties with  
344 lower chill requirements would have led to different periods (Guo et al., 2015).

345 The chilling accumulation before the period of heat accumulation at the study site (27<sup>th</sup> September  
346 to 31<sup>st</sup> December) and the subsequent heat accumulation was  $62.7 \pm 5.6$  CP and  $3744 \pm 1538$  GDH,  
347 respectively. This is similar to the requirements reported by Ruiz et al. (2007) for 'Bergeron' in a very  
348 different climate (SW Spain) of 64.8 CP for breaking dormancy and 4101 GDH from breaking  
349 dormancy to flowering. Similar accumulations were reported by Campoy et al. (2012) for 'Bergeron',  
350 together with a relatively high interannual variation in the estimation of both chilling and heat  
351 accumulations required to flower. The overlap between the chilling and warming periods found in  
352 this study and Guo et al. (2015) may offer the key to understanding the variability in the estimation  
353 of this important horticultural trait. In cold places, some years may not allow heat accumulation  
354 soon after buds have received enough chilling to break endo-dormancy. In this case, additional  
355 chilling may reduce the amount of heat required for flowering. In warmer places, however, in years  
356 with slightly lower chilling accumulation than the optimal required, additional heat can still trigger  
357 flowering (Harrington et al., 2010). This trade-off could be responsible for the interannual variability  
358 often reported in chill and heat requirement estimations. Assuming an overlap between chilling and  
359 warming periods has been shown to improve model fits (Darbyshire et al., 2016; Pope et al., 2014).  
360 Our approach to determining climatic needs, however, is based on calculating mean accumulation  
361 during the effective periods, so that interannual variation in the amount of chill and heat required,  
362 or interactions between chill and heat cannot be captured.

#### 363 **4.2 Impacts of chilling and heat accumulation conditions on flowering dates**

364 Apricot flowering dates were predominantly affected by mean temperature during the warming  
365 period (Fig. 3). Similar findings have previously been reported for apricots in China, France, Italy and

366 Spain (Andreini et al., 2014; Guo et al., 2015), chestnut and jujube in China (Guo et al., 2014), and  
367 apples and olives in France (El Yaacoubi et al., 2014). El Yaacoubi et al. (2014) analysed the spring  
368 phenology of different tree crops in different locations and noted that late flowering crops were  
369 more prone to earlier flowering in response to increasing temperature. The abundance of records  
370 showing a trend towards earliness may also be linked to the growers choosing species and cultivars  
371 with appropriate chilling requirements for their growing region. So far, it is only in very warm  
372 production regions, where available chill is barely sufficient for growing certain temperate species,  
373 that significant delays in spring flowering in response to warming have been observed (Elloumi et al.,  
374 2013; Luedeling et al., 2013).

375 PLS regression showed two periods when flowering was delayed by heat accumulation: 1) at the  
376 beginning of the chilling period, 2) and before the start of the warming period. For the first period,  
377 this effect may be related to the delaying impact of high summer/autumn temperature on growth  
378 cessation, which has been reported to potentially lead to delayed bud burst in the following year  
379 (Heide, 2003; Heide and Prestrud, 2005). In addition, the timing of the onset of chill accumulation  
380 (first 5 CP completion) appeared to increase the amount of heat required for flowering (Fig. A.3),  
381 suggesting that the timing of the first chill accumulation is important for counteracting the  
382 flowering-advancing effect of temperatures during the warming period. In the second case (i.e. the  
383 period of significant positive correlation for heat accumulation before the warming period, in the  
384 middle of the chilling period), controlled environment studies show that when heat is received too  
385 early, before critical chilling completion, it may not advance or even delay flowering (Anzanello et  
386 al., 2014). In the present study, the low heat accumulation during this period (i.e. right before the  
387 warming period) suggests that even though VIP scores were high, heat accumulation during this  
388 period probably had little effect. Chill accumulation also presented periods with high VIP that were  
389 outside the delineated chilling period (e.g. from 1<sup>st</sup> June to 4<sup>th</sup> July). Given that buds for the next year  
390 are not yet present at that time, this is probably not a biologically meaningful effect.

### 391 4.3 Impact of global warming on chilling and heat period conditions

392 In spite of global warming, in the UK, chill accumulation calculated using the Dynamic Model has  
393 decreased only slightly in recent decades, and no major decreases over the 21<sup>st</sup> century have been  
394 projected for future scenarios based on the CSIRO, HADCM3 and MIROC climate models (Luedeling  
395 et al., 2011). Our results show a significant increasing trend in mean temperatures during the chilling  
396 period of apricots, but no significant decrease in chill accumulation (Fig. 4D and E). It is worth noting  
397 that the Dynamic Model considers that, as long as temperatures during the day are not too high, 4  
398 hours at low temperature (i.e. 6°C) and 20 hours at moderate temperature (i.e. 14°C) per day are  
399 63% as effective as a regime with 24 hours at cold temperature (Fishman et al., 1987a). In  
400 consequence, the increase in mean temperature during the chilling period over the record did not  
401 correspond to a decrease in chill accumulation according to this model. In addition, for cold-  
402 temperate climates, increasing temperatures frequently shift temperatures to levels to which most  
403 chill models would assign higher—rather than lower—chilling effectiveness, resulting in no change or  
404 even increase in chilling (Luedeling et al., 2011). Even though according to the Dynamic Model,  
405 overall chill during the chilling period did not decrease ( $\tau= 0.02$ ,  $p=0.79$ ), the time to accumulate the  
406 first 5 CP and 62.7 CP (average chill accumulation that enabled heat accumulation) increased over  
407 the years. This may be an indication of a gradual shift of the chilling period. This delayed start of chill  
408 accumulation is unlikely to induce a reduction of chill accumulation *per se* in the short term, as the  
409 date identified as the end of the chilling period (26<sup>th</sup> February) is still succeeded by many days with  
410 high daily chill accumulation. However, this delay in chilling may delay chill requirement fulfilment  
411 and subsequent events, such as the start of the warming period, budburst and flowering.  
412 Simultaneously, heat accumulation increased and the time to accumulate the first 1000 GDH  
413 decreased over the years. If the start of the chilling and warming period continues to be delayed,  
414 while the accumulation of heat occurs earlier in the year, the net effect on spring event timing is  
415 difficult to predict. Possibilities then include continued advances (if additional heat accumulation is  
416 the dominant driver), unchanged flowering times (if effects cancel each other out) or even delays (if

417 delayed chill accumulation becomes dominant; Guo et al., 2015). In addition to the influence of  
418 conditions during the chilling and warming periods, our results highlight the relevance of the timing  
419 of multiple events for explaining variation in spring phenology.

420 As for the future suitability of this crop, temperatures before and after flowering are important for  
421 successful production, because of the need to synchronize bloom with pollinator activity (Else and  
422 Atkinson, 2010). Cannell and Smith (1986) found that future warming could increase the incidence of  
423 frost damage to the flowers of trees in Britain, but it could also cause the opposite, depending on  
424 the extent to which trees' chilling requirements are currently met. In this work we showed that  
425 warming likely delays chill accumulation, partially compensating for advances in response to warmer  
426 springs, resulting in warmer temperatures in the dates before and after flowering. If this trend is  
427 maintained, further warming may therefore reduce the frost risk for apricots in SE England rather  
428 than the opposite.

#### 429 **4.4 Conclusions**

430 In recent years, flowering in apricot has been experiencing an advancing effect related to increased  
431 temperature during the effective warming period. However, a delay in the onset of chill  
432 accumulation and completion of chill requirement necessary to start heat accumulation appear to  
433 moderate the effect of increasing heat during the warming period. Although the future trend in  
434 flowering dates of apricots in the UK is unclear, as temperature continues to increase during both  
435 chilling and warming periods, the trend to earliness in flowering induced by warming temperatures  
436 may continue being balanced by the apparent bloom-delaying effect of temperature during the  
437 chilling phase. Increases in temperatures around flowering time over the years, however, suggest  
438 that the southern UK may potentially become a more suitable region for apricots in the future due  
439 to the associated reduced risk of frost damage.

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646

647 **Figure captions**

648 Fig. 1. Average flowering date of apricots in the UK NFC between 1960 and 2014. Kendall's rank  
649 correlation coefficient ( $\tau$ ) and p value. Julian days are days from 1<sup>st</sup> January of each year flowering  
650 was analysed.

651

652 Fig. 2. Results of Partial Least Squares regression analysis for apricot flowering dates in the UK  
653 National Fruit Collection, using the Dynamic Model and the GDH Model for quantifying chill and heat  
654 accumulation, respectively. Colour bars in the figures indicate VIP above 0.8, the threshold for  
655 considering variables important. Green and red bars represent, besides importance, a positive and  
656 negative relationship, respectively, between flowering and daily chilling and heat accumulation. In  
657 the lower graphs (chill accumulation and heat accumulation), bars represent the standard deviation  
658 of daily chill and heat accumulation, with colours following the same pattern as for the VIP and  
659 model coefficients. Shaded areas and dashed lines represent the range in flowering dates and  
660 average flowering date, respectively. GDH stands for Growing Degree Hours; CP for Chill Portions;  
661 VIP for variable importance in the projection.

662

663 Fig. 3. Response of the average flowering date of apricot to average temperatures during the chilling  
664 and warming periods (27<sup>th</sup> Sep to 26<sup>th</sup> Feb and 31<sup>st</sup> Dec to 12<sup>th</sup> Apr, respectively (A); and response of  
665 flowering dates to chill accumulation during the chilling period and heat accumulation during the  
666 warming period (B). Colours and contour lines represent predicted flowering dates expressed in

667 Julian dates (days of the year) using observed data points of mean apricot flowering dates (black  
668 dots). GDH stands for Growing Degree Hours; CP for Chill Portions.

669 Fig. 4. Time trends for mean temperature during the warming period (A), heat accumulation during  
670 the warming period (B), completion date of the first 1000 GDH (C), mean temperature during the  
671 chilling period (D), chill accumulation during the chilling period (E), completion date of the first 5 CP  
672 (F) and completion date of average chill accumulation that enabled heat accumulation (i.e., first 62.7  
673 CP; G). GDH stands for Growing Degree Hours; CP for Chill Portions. Kendall's rank correlation  
674 coefficients ( $\tau$ ) and p values are also shown. Julian days are days from 1<sup>st</sup> January of each year  
675 flowering was analysed.

676 Fig. 5. Time trend of mean temperature during the 40 days before and after flowering for each  
677 season. Kendall's rank correlation coefficient ( $\tau$ ) and p value are given.

678

#### 679 **Appendix A. Supplementary information**

680

681 Table A.1. Summary of the UK's NFC apricot flowering dates archive.

682

683 Fig. A.1. Averages and box plots of the flowering date of apricot varieties in the UK NFC between  
684 1960 and 2014.

685 Fig A.2. Results of the partial squares regression of the average flowering dates of apricot varieties of  
686 the UK using daily mean temperatures as the predictor variable.

687 Fig A.3. Correlation between the date of completion of the first 5 CP of the season and the heat  
688 required for flowering.

689

Table A.1. Summary of the UK's NFC apricot flowering dates archive.

Season (end year)	Apricot varieties													
	Alfred	Bredase	Catherina	Early Moorpark	Farmingdale	Hemskirke	Kecskemeti	New Large Early	Old Cape	Puget Gold	Riland	Royale	Sun-Glo	Wilson's Delicious
1960	x													
1961	x												X	X
1962	x												X	X
1963	x												X	X
1964	x												X	X
1965	x												X	X
1966	x												X	X
1967														
1968														
1969														
1970														
1971														
1972														
1973														
1974			x	x	x		x		x		x			
1975														
1976				x	x		x		x		x			
1977														
1978														
1979				x	x		x		x		x		X	X
1980			x	x	x		x		x		x		X	
1981				x					x		x		X	
1982	x			x	x				x		x		X	
1983	x		x	x	x		x		x		x		X	X
1984	x		x	x	x		x		x		x		X	X
1985	x		x	x	x				x				X	
1986	x		x	x	x				x					X
1987	x		x	x	x									
1988	x		x	x	x									
1989	x		x	x	x									
1990														
1991	x		x	x	x									
1992														
1993	x			x	x									
1994	x			x	x									
1995														
1996	x			x	x							x		
1997														
1998														
1999	x			x	x				x		x			
2000														
2001	x			x	x				x		x			
2002														
2003				x					x					
2004														
2005	x			x										
2006	x			x	x				x		x			
2007		x		x	x	x					x			
2008														
2009														
2010	x	x		x	x	x		x			x			
2011	x	x		x	x	x		x			x			
2012	x	x		x	x	x		x			x			
2013	x	x		x	x	x		x			x			
2014	x	x		x		x		x			x			

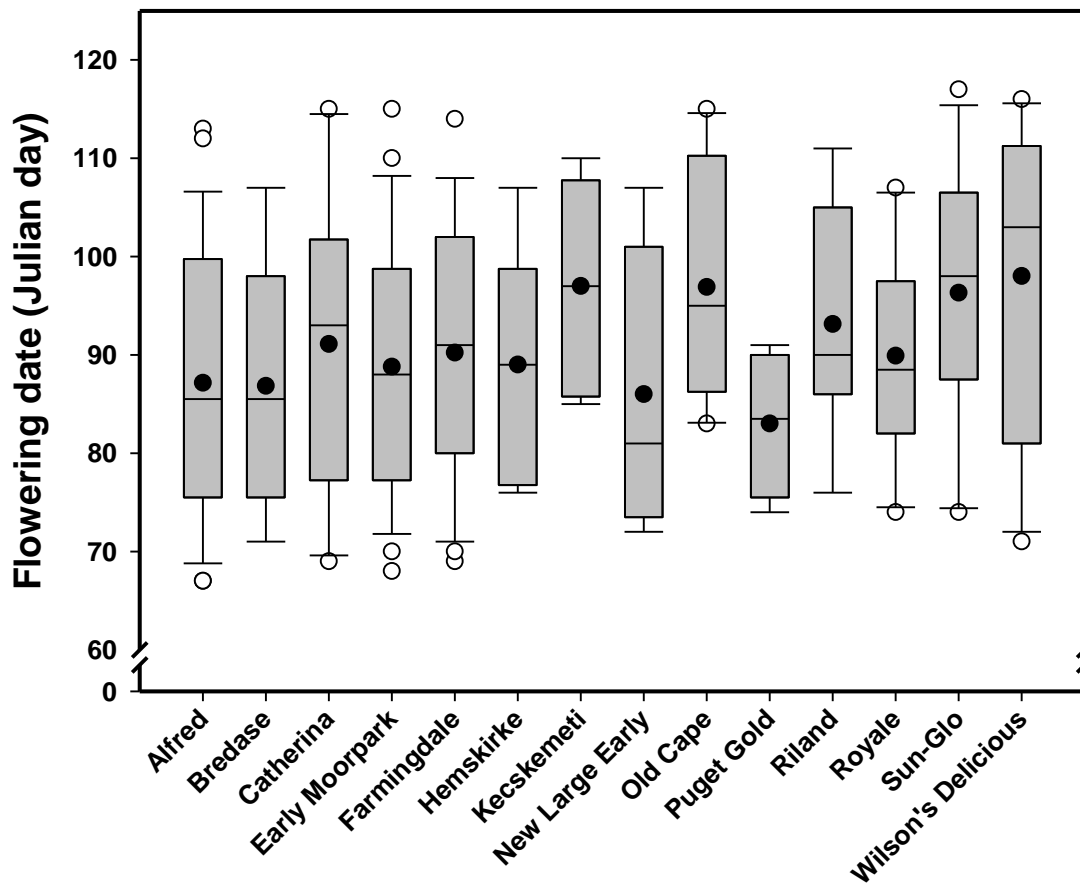


Fig. A.1. Averages (closed circles) and box plots of the flowering date of apricot varieties in the UK NFC between 1960 and 2014.



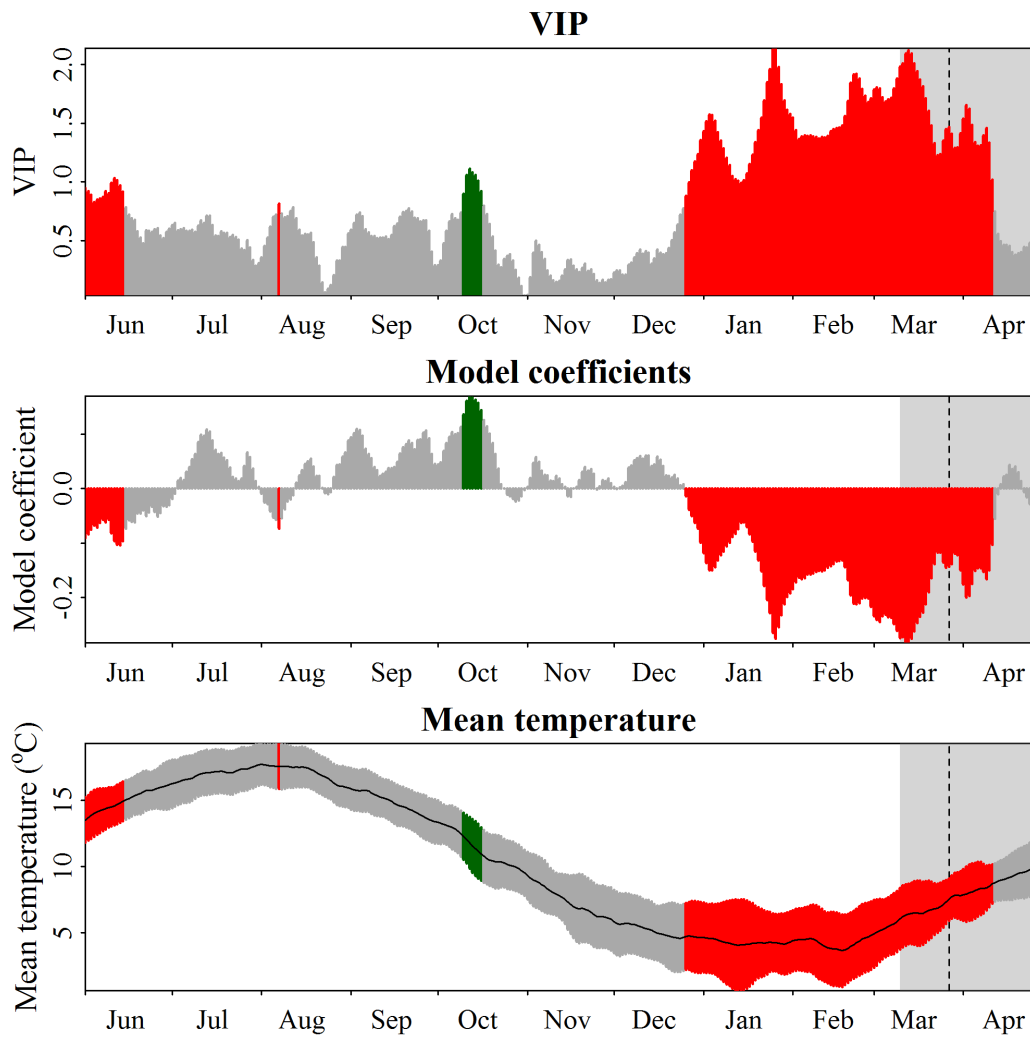


Figure A.2. Results of the PLS regression of the average flowering dates of apricot varieties of the UK using daily mean temperatures as the predictor variable. Colour bars in the figures indicate VIP above 0.8, the threshold for considering variables important. Green and red bars represent, besides importance, a positive and negative relationship, respectively, between flowering and temperatures. In the lower graphs (Mean temperature), bars represent the standard deviation of mean temperatures, with colours following the same pattern as for the VIP and model coefficients. Shaded areas and dashed lines represent the range in flowering dates and average flowering date, respectively. **VIP stands for variable importance in the projection.** Methods described in Luedeling et al., (2013).

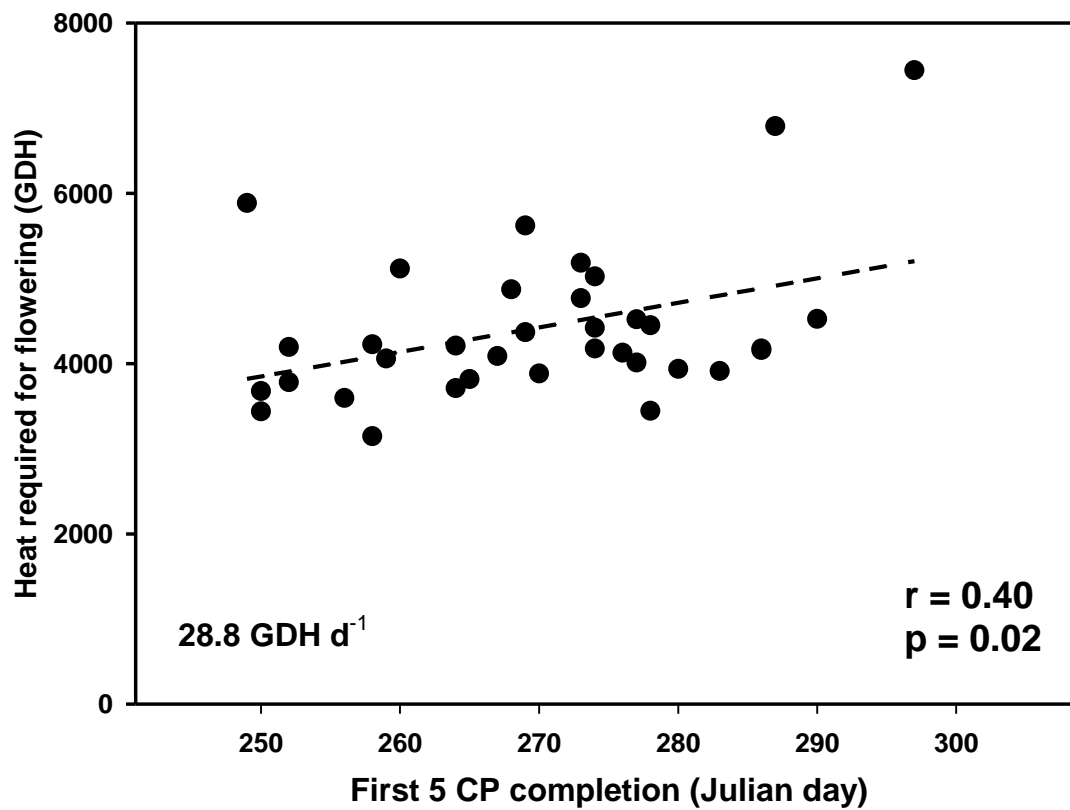
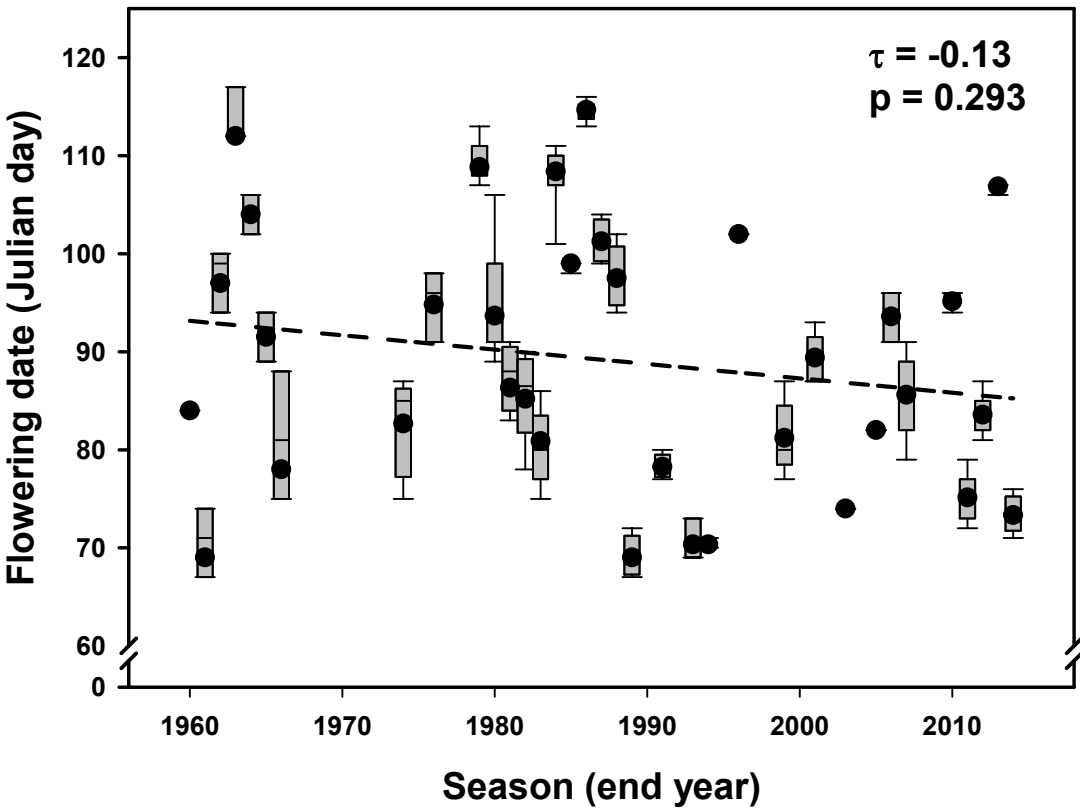


Figure A.3. Correlation between the date of completion of the first 5 CP of the season (starting the 1<sup>st</sup> July) and the heat required for flowering (GDH from onset of warming period to flowering) showing an increase in 28.8 GDH for each day the accumulation of chilling was delayed. GDH stands for Growing Degree Hours; CP for Chill Portions.

Figure 1



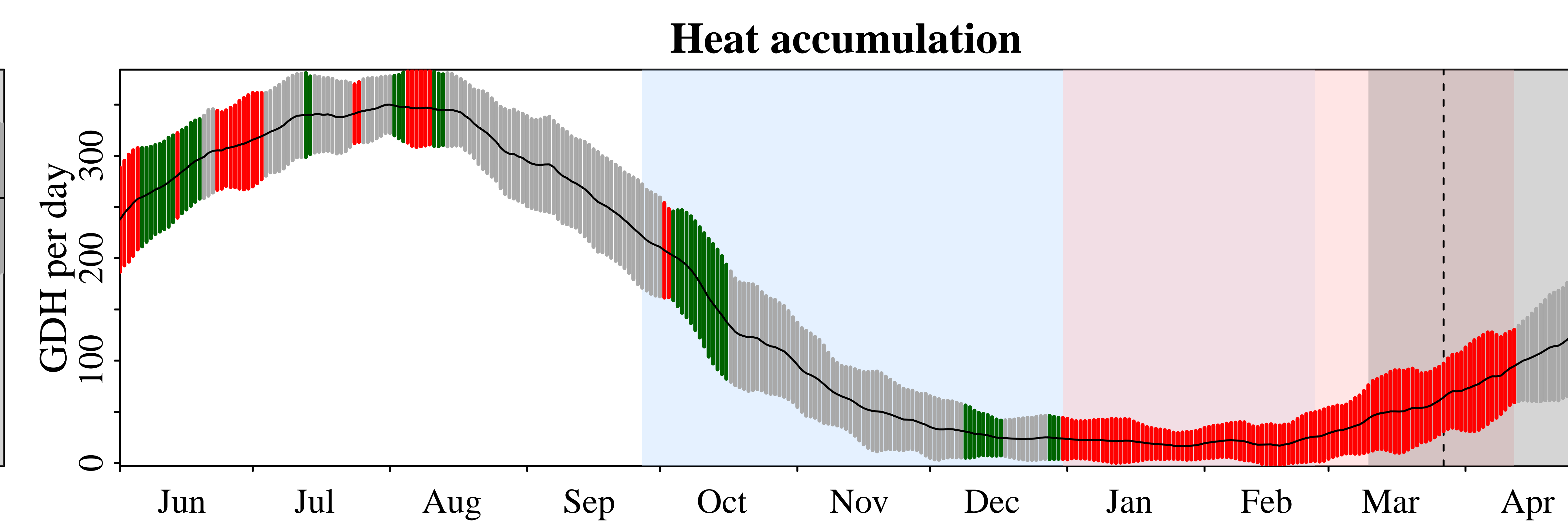
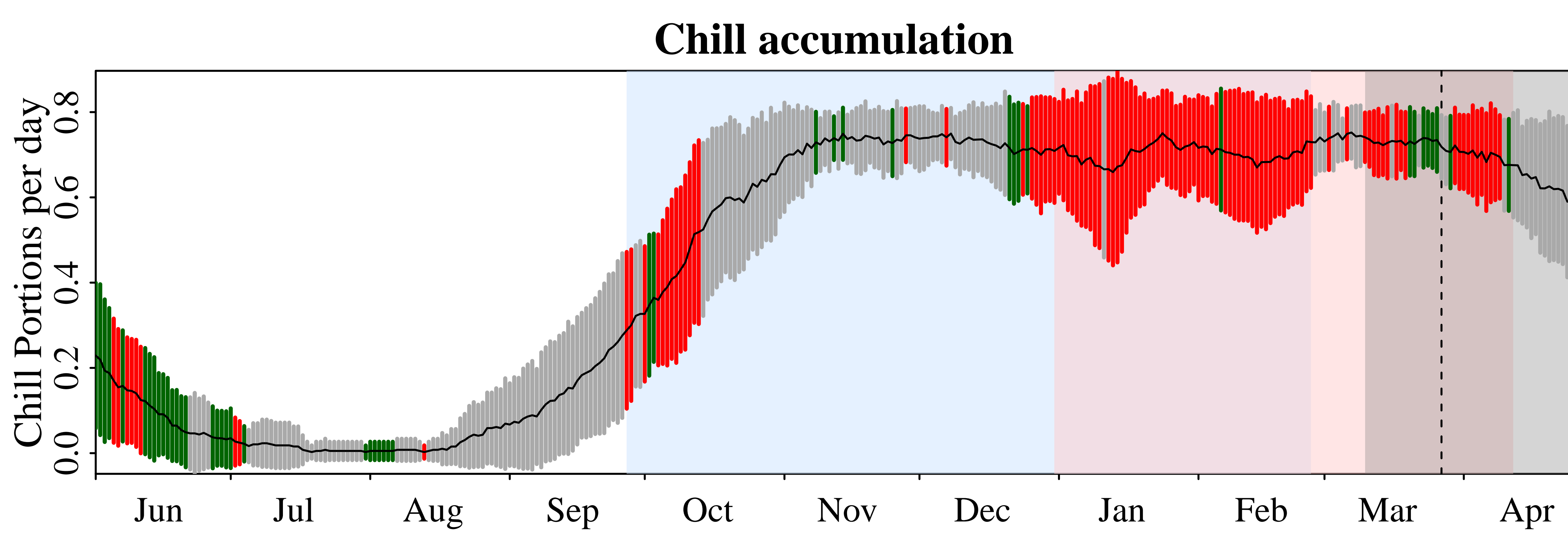
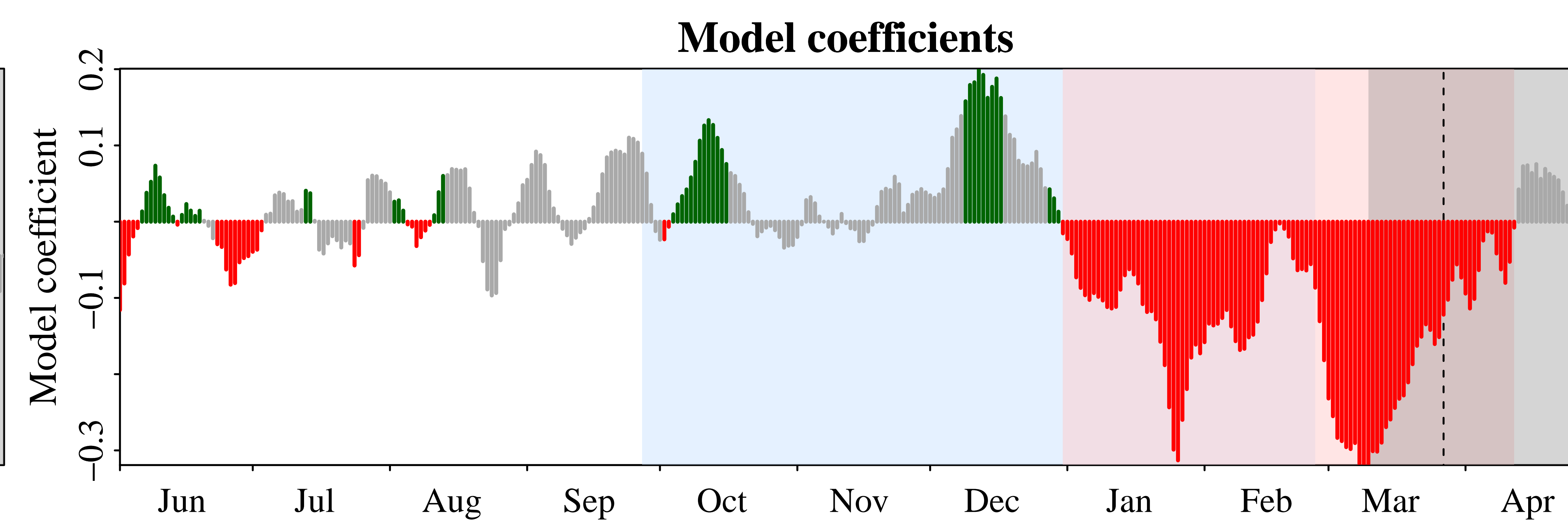
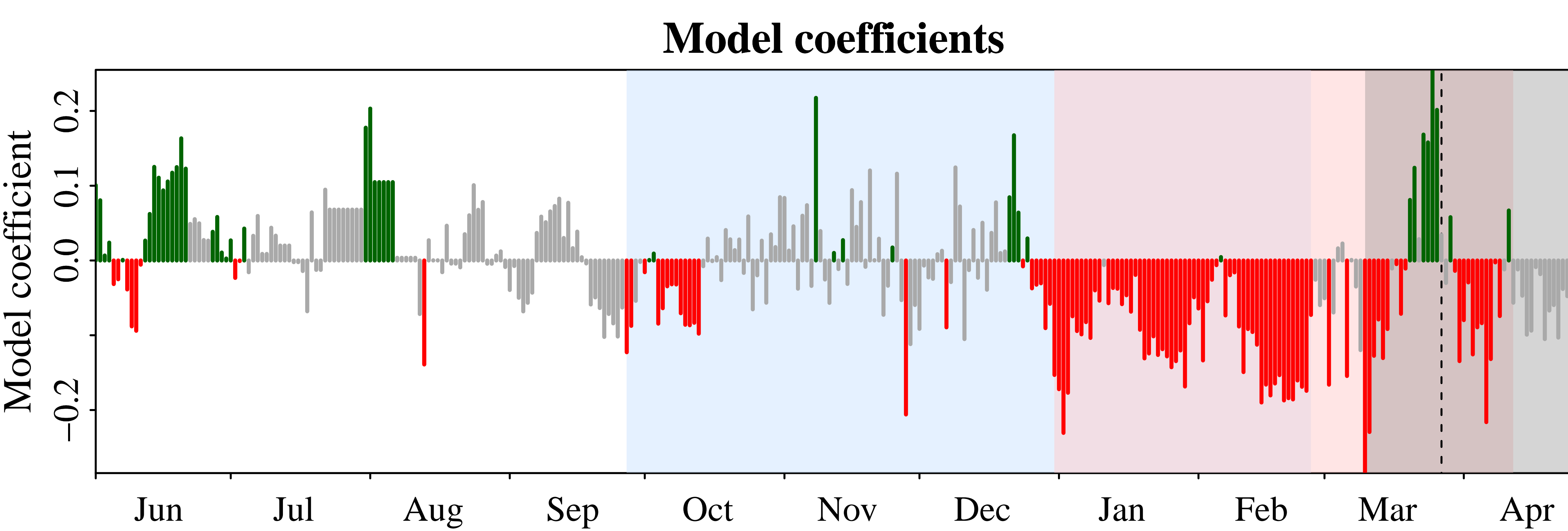
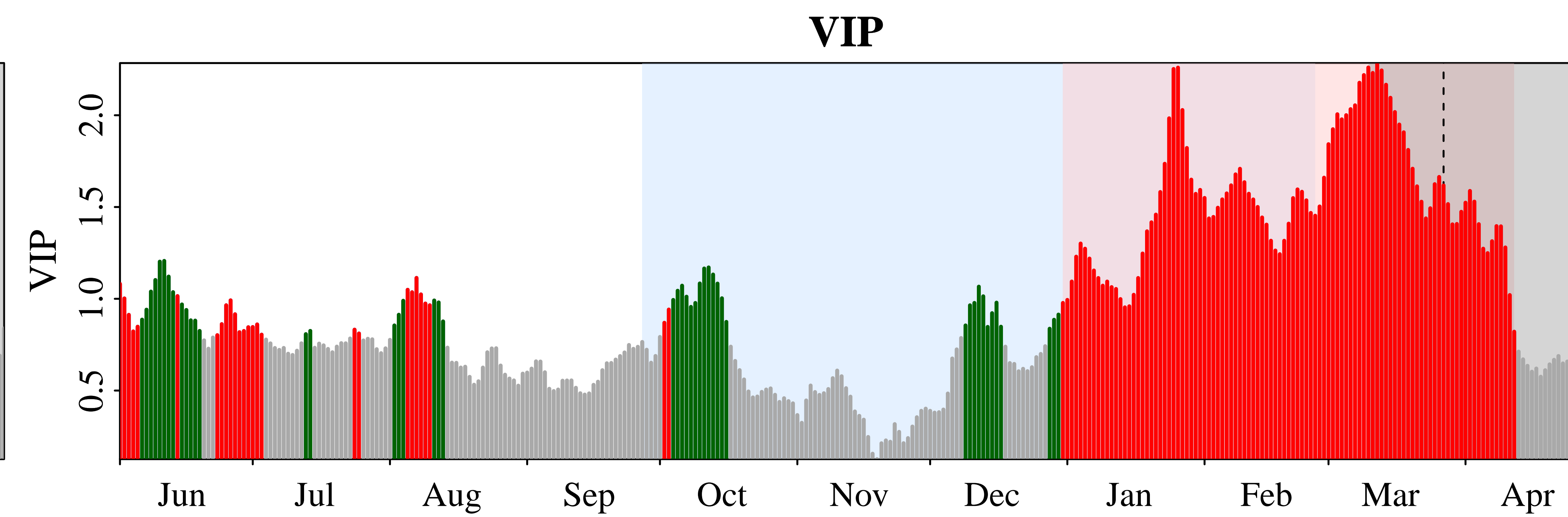
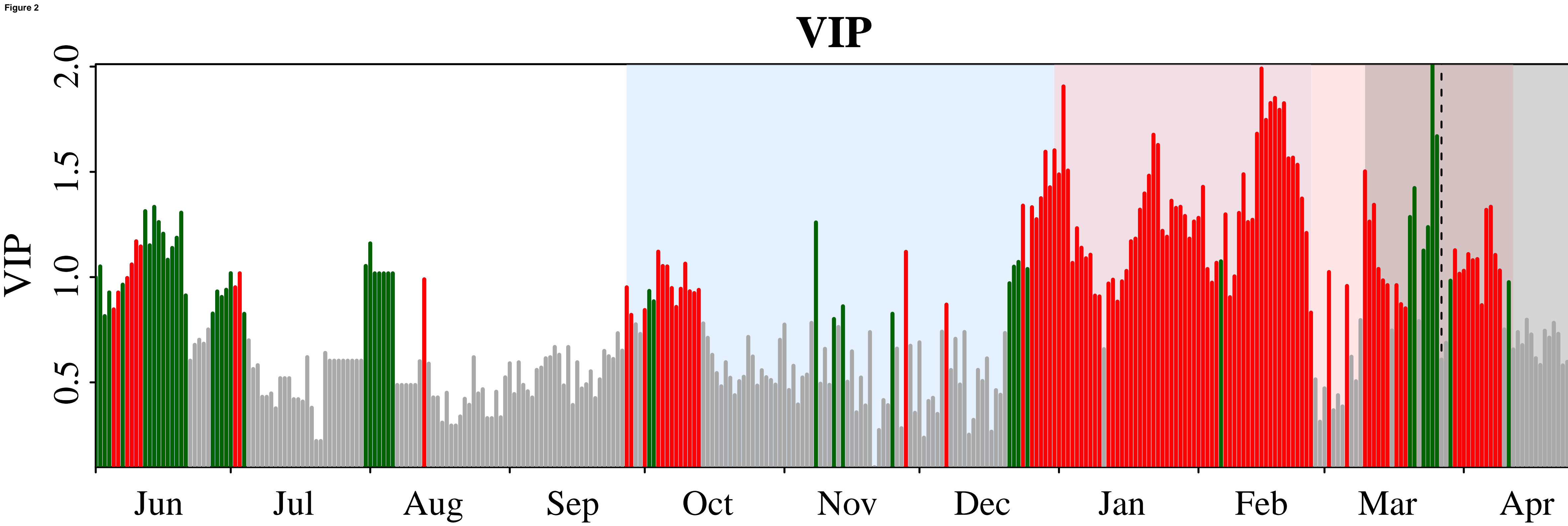


Figure 3

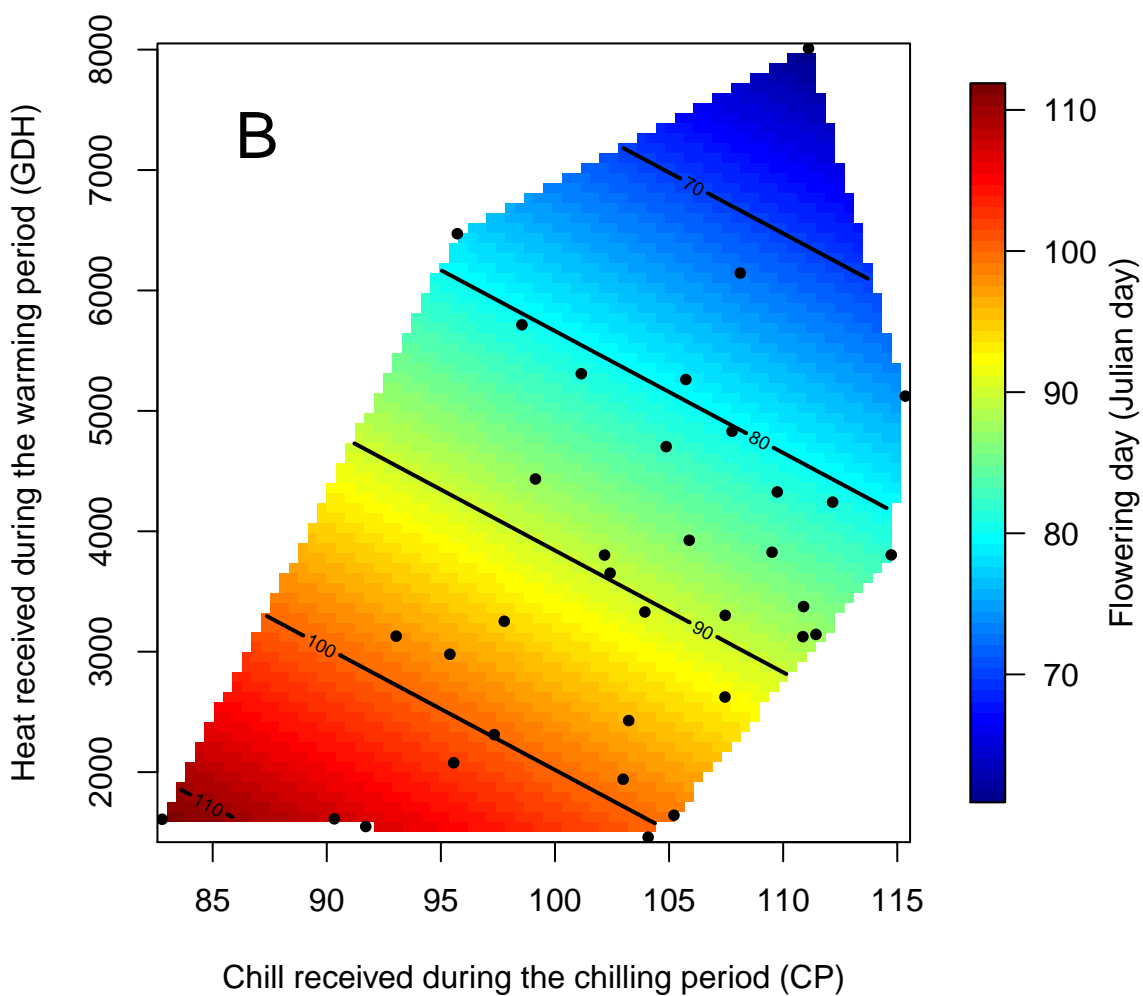
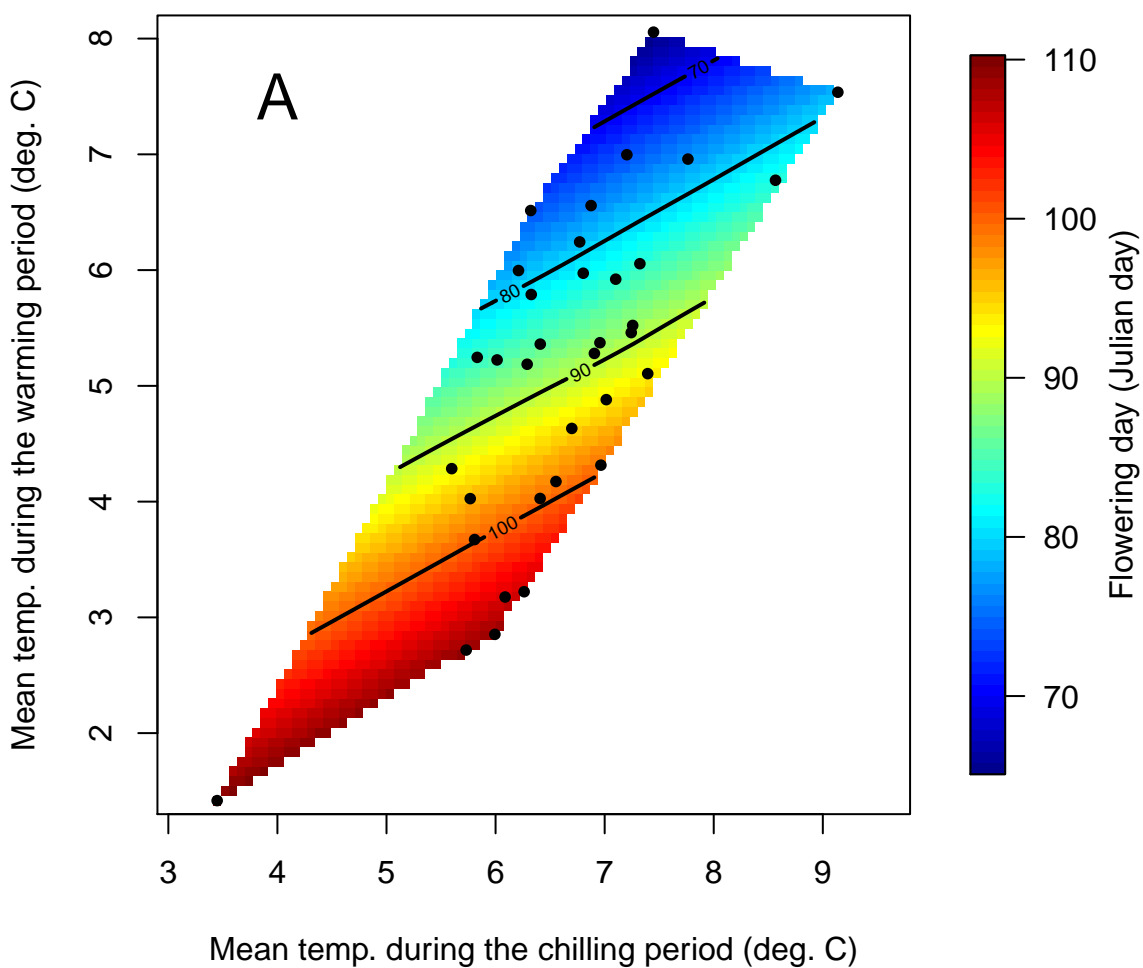


Figure 4

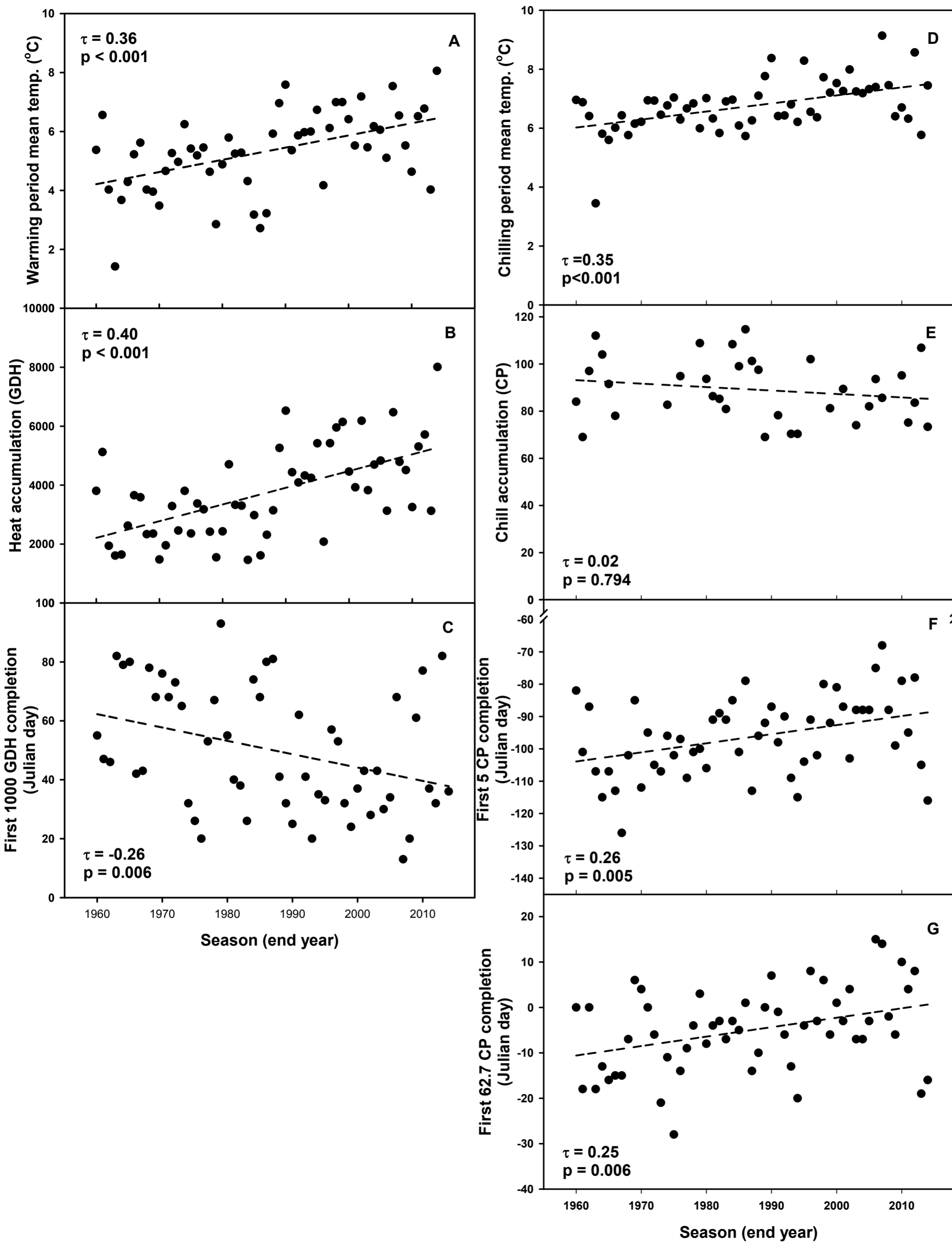


Figure 5

