1 Topographical variation reduces phenological mismatch between a

2 butterfly and its nectar source

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11 **Abstract**

12 The timing of many biological events, including butterfly imago emergence, has advanced under

13 climate change, with the rate of these phenological changes often differing among taxonomic

14 groups. Such inter-taxa variability can lead to phenological mismatches. For example, the timing

15 of a butterfly's flight period may become misaligned with a key nectar resource, potentially

16 increasing the extinction risk to both species. Here we fit statistical models to field data to

17 determine how the phenology of the marbled white butterfly, *Melanargia galathea*, and its main

18 nectar source, greater knapweed, *Centaurea scabiosa*, have changed over recent years at three

19 sites across the UK. We also consider whether topographical diversity affects *C. scabiosa*'s

20 flowering period. At our focal site, on the species northern range limit, we find that over a 13-

21 year period the onset of *C. scabiosa*'s flowering period has become later whilst there is no

22 obvious trend over time in the onset of *M. galathea*'s flight period. In recent years, butterflies

23 have started to emerge before their key nectar source was available across most of the site. This

24 raises the intriguing possibility that phenological mismatch could be an unrecognised

25 determinant of range limits for some species. However, the presence of topographical diversity

26 within the site decreased the chance of a mismatch occurring by increasing the length of the

27 flowering period by up to 14 days. We suggest that topographical diversity could be an important

28 component in minimising phenological mismatches under future climate change.

Introduction

Recent climate change has seen the advancement of biological events across many taxonomic groups, including flowering in plants (Fitter and Fitter 2002; Menzel and Fabian 1999), egg laying in birds (Crick et al. 1997; Crick and Sparks 1999) and the migration of a wide range of taxonomic groups (Cherry et al. 2013; Marra et al. 2005). Whilst phenological responses to climate change are common, the rates of change can differ across taxonomic groups (Parmesan 2007; Thackeray et al. 2010). Differences in the rate or direction of change between interacting species can lead to phenological mismatches, with potential consequences for the abundance, distribution and extinction risk of the interacting species (Fabina et al. 2010; Memmott et al. 2007; Parmesan 2007; van Asch and Visser 2007). Interacting species must be temporally, as well as spatially, correlated for interactions to occur. Therefore, it is necessary to consider the effects of changing conditions on inter-dependent species, including pollinators and their food plants (Visser and Both 2005), when predicting the impacts of climate change and planning appropriate conservation measures.

Despite the important roles insects play in ecosystem functioning and crop pollination there has been little research on potential phenological mismatches in this taxa, and the wider ecosystem impacts these could have (though see Bartomeus et al. 2011; Kudo and Ida 2013; Rafferty and Ives 2011). In butterflies, earlier and longer flight periods have been recorded across the United Kingdom (UK) and Europe (Diamond et al. 2011; Roy and Sparks 2000; Stefanescu et al. 2003) with evidence of correlations between temperature and appearance date (Diamond et al. 2011; Roy and Sparks 2000). A warming of 1°C could advance the first and the peak appearances of most British butterfly species by 2-10 days (Roy and Sparks 2000), whilst warming of 3°C could advance their appearance by as much as two or three weeks (Sparks and Yates 1997).

Many adult butterflies are dependent on a restricted number of plant species for nectar (Asher et al. 2001). Whilst the flowering periods of many plants have become earlier under climate change (Calinger et al. 2013; Fitter and Fitter 2002; Primack et al. 2004), there is evidence that butterflies flight periods are showing more rapid rates of advancement (Gordo and Sanz 2005; Parmesan 2007). Little is known about the physiological mechanisms controlling the phenology of imago emergence in butterflies; however, there is evidence in some species that the climatic cues used by butterflies differ from those used by plants (Doi et al. 2008), which may increase the chance of phenological mismatches. The phenology of sessile organisms such as plants will be affected by microclimate as well as larger scale climate changes. Plant

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phenologies, therefore, may be especially affected by topography (Pellerin et al. 2012) and, as a result, topographically heterogeneous sites may have longer site-wide flowering periods than homogeneous sites. This heterogeneity may help to minimise phenological mismatches between butterflies and their nectar sources, especially when the caterpillar food plant and the nectar plants for the imago occur in different microhabitats, as can be the case with *Melanargia galathea* (Linnaeus 1758) (Asher et al. 2001; Stace 1991; Wilson 1985).

Here we examine the flight period of *M. galathea,* a generalist butterfly, over the period 2001-13 at three sites across the species' UK range. We relate the timing of *M. galathea*'s flight period to the flowering period of one of its main nectar sources, *Centaurea scabiosa* (Linnaeus 1758) (Asher et al. 2001). In particular, we explore the possibility that *M. galathea*'s flight period could be advancing more quickly than *C. scabiosa*'s flowering period, with the potential for a phenological mismatch to occur. Finally, we consider whether the presence of topographical diversity within a site alters the flowering period of this key nectar source, by comparing flowering phenology across multiple aspects at a site on the species' northern range margin.

Methods

Study species and sites

M. galathea is found primarily on calcareous grasslands; within the UK it is found predominantly in the South, naturally occurring as far north as Yorkshire (Asher et al. 2001; Fox et al. 2006). It has undergone rapid range expansions at its northern range boundary; a survey in 1995-9 found it present in 66% more 10km grid squares than in 1970-82 (Asher et al. 2001; Fox et al. 2006). *C. scabiosa* is one of the species' main nectar sources although *Centaurea nigra* (Linneaus 1753) and other purple flowers such as *Scabiosa* spp. are also used (Asher et al. 2001). *C. scabiosa* is a perennial and flowers between June and September in the UK. It is common within our study sites and across the natural range of *M. galathea* in the UK. At our northernmost study site, at the species northern range limit, it is the dominant nectar source during *M. galathea*'s flight period.

Data were collected at three study sites (Figure 1): Totternhoe Chalk Quarry Reserve, Bedfordshire (Totternhoe; OS grid reference SP9722), Brockadale Nature Reserve, North Yorkshire (Brockadale; OS grid reference SE5117) and Wingate Quarry Local Nature Reserve, Co. Durham (Wingate; OS grid reference NZ3737). Totternhoe and Wingate are the sites of disused limestone quarries, whilst Brockadale is a narrow valley created by the River Went. All

97   three sites have been classified as Sites of Special Scientific Interest (SSSI) by Natural England.

98   As well as being topographically diverse they contain a variety of habitats, including calcareous

99   grasslands where *M. galathea* is found. Totternhoe is in the core of *M. galathea*'s UK range,

100   Brockadale is close to *M. galathea*'s natural northern range boundary and Wingate is beyond *M.*

101   *galathea*'s natural northern range limit. The Wingate study population was introduced in 2000 as

102   part of an assisted colonisation experiment (Willis et al. 2009).

103
104   **Fig. 1** Map showing the location of the three study sites, Totternhoe, Brockadale and Wingate
105   (from South to North)

106   *Flight period phenology*

107   Data on the abundance of *M. galathea* adults were collected using transects, following the

108   standard UK Butterfly Monitoring Scheme (UKBMS) guidelines (Pollard and Yates 1993). The

109   transects at each site run through calcareous grassland with diverse topographies. Transect data

110   from Wingate were collected at Wingate every 2-3 days from a 1,550m long and 5m wide

111   transect, for nine years between 2001 and 2013. Weekly transect data from Totternhoe and

112   Brockadale were collected by the Yorkshire Wildlife Trust and the UKBMS respectively. Eight

113   and five years of data were available from Totternhoe and Brockadale respectively.

114   *Flowering phenology*

115   Data on the flowering phenology of *C. scabiosa* were collected by counting the number of

116   developing (flower buds), flowering (bright inflorescences and pollen present) and spent

117   (withering flowers, and developing or spent seed capsules) flowers on each plant. A minimum of

118   30 plants were surveyed on ground of varying topography approximately every 3-4 days during

119   *M. galathea*'s flight period for nine non-consecutive years between 2001 and 2013 at Wingate

120   and in 2011 at Brockadale and Totternhoe. Plants were selected randomly from across the site.

121   In 2013, additional data on the effect of topography on the flowering phenology of *C.*
122   *scabiosa* were collected at Wingate. Four aspects were studied (north east (NE), south east (SE),
123   south west (SW) and south (S)). Data were also collected on two types of flat area: flat sheltered
124   (FS) sites were in low-lying quarry bottoms and were sheltered on all sides; whereas, flat
125   exposed (FE) sites were on the quarry tops, though still within the nature reserve, and were not
126   sheltered on any side. 30-40 randomly selected individuals were surveyed on each of the six
127   microhabitat types every 3-4 days.

128   *Statistical analysis of butterfly flight period phenology*
129   The expected number of *M. galathea* individuals seen on a transect on Julian day *t* was modelled
130   as

131
$$m(t) = y_{max} \exp\left(-\frac{1}{2}\left(\frac{t - \bar{t}}{s}\right)^2\right), \qquad (1)$$

132   where the peak abundance (y_{max}) is reached on day $\bar{t}$, and σ is positively related to the expected
133   duration of the flight period. When fitting this general model to the data we investigated possible
134   year and site effects on adult abundance by comparing fits for versions of the model that either
135   fixed or varied y_{max}, $\bar{t}$, or σ with respect to year and site, respectively (Table 1).

136

137   **Table 1** AIC analysis of the models that describe seasonal changes in adult *M. galathea* abundance
138   among three sites. Model names show whether the peak abundance (y_{max}), day of peak abundance ($\bar{t}$)
139   or flight period length (β) were allowed to vary between sites [s] or years [y]. *K* is the number of
140   parameters estimated in each model, *LL* is the maximum log-likelihood, and ΔAIC is the change in AIC
141   relative to the best AIC model. Parsimonious models are marked with an *. Total number of transects
142   across years and sites is 201.

Model	K	Description	LL	ΔAIC
M1(-)	4	Peak abundance, day of peak abundance and flight period constant between sites and years	-650.4	136.8
M1(y_{max}[y]+ $\bar{x}$ [y])	24	Peak abundance and day of peak abundance differed between years	-618.7	113.4
M1(y_{max}[y]+σ[y])	24	Peak abundance and length of flight period differed between years	-639.7	155.4
M1(y_{max}[y]+ $\bar{x}$ [y]+σ[y])	34	Peak abundance, day of peak abundance and flight period differ between years	-609.3	114.6
M1(y_{max}[s]+ $\bar{x}$ [s]+σ[s])	13	Peak abundance, day of peak abundance and flight period differ between sites	-602.3	58.7
M1(y_{max}[y,s]+ $\bar{x}$ [y,s]+σ[y,s])	43	Peak abundance, day of peak abundance and flight period differ between sites and years	-543.0	0*

143   Observed variation about the expected counts was assumed to have a negative-binomial

144   distribution as there was evidence of overdispersion in the data (i.e. the variance was higher than

145   the mean). The probability of observing i butterflies when μ were expected is:

146    $$\Pr(i \mid m, f) = \frac{G(i+a)}{G(i+1)G(a)} \left(\frac{b}{1+b}\right)^{a} \left(\frac{1}{1+b}\right)^{i},$$ (2)

147   where ϕ is a variance parameter, $a = \mu/\phi$ and $b = 1/\phi$. We assumed that ϕ was independent

148   of site and year. We performed model selection using AIC (Burnham and Anderson 2002).

149   Models were considered parsimonious if (1) they were associated with an AIC value within 6 of

150   the minimum calculated from the set, and (2) there were no simpler nested models having a

151   lower AIC value. This pair of selection rules prevents overly complex models from being

152   selected when applying AIC (Richards 2008). The flight period was defined as the number of

153   days during which more than one adult butterfly is expected to be observed alive during a

154   transect survey, and it was calculated using the best AIC model (lowest AIC value).

155   *Statistical analysis of flowering phenology*

156   Next, we sought evidence that the timing and length of the flowering period of *C. scabiosa*

157   differed across sites and years by modelling the expected cumulative proportion of flowers open

158   by Julian day x as

159    $$\text{logit } p(x) = b(x - \bar{x}),$$ (3)

160   where $\bar{x}$ is the day by which 50% of the flowers are expected to be open and β is negatively

161   related to the length of the flowering period. We compared the fit of the model that fixed $\bar{x}$ and

162   β, with the model that allowed these two parameters to differ among years (2001-2013) and

163   across the three sites (Table 2). We also used this general model formulation to determine

164   whether the timing ($\bar{x}$) and length (β) of the flowering period were affected by topography at

165   Wingate in 2013 (Table 3). In this case we compared model fits where $\bar{x}$ and β were allowed to

166   differ amongst the four aspects and two types of flat area.

167   For both of the flowering analyses we assumed that the variation in open flowers about the

168   expected proportion was described by a beta-binomial distribution, which accounts for variation

169   among plants caused by unknown covariates. The probability that n of the N flowers on a plant

170   had opened, given that fraction p were expected to have opened is

171    $$\Pr(N, n \mid p, f) = \frac{G(N+1)G(a+b)G(n+a)G(N-n+b)}{G(n+1)G(N-n+1)G(a)G(b)G(N+a+b)},$$ (4)

172 where $a = p/\phi$ and $b = (1-p)/\phi$ (Richards 2008). The data suggested that the degree of variation
173 among plants, quantified by ϕ, was similar between sites, years and microhabitats; as a result,
174 this term was kept constant in all of the models. Model selection was again performed using AIC
175 as above. The most parsimonious model (lowest AIC value) was then used to calculate the
176 flowering period, which was defined as the number of days during which between 5% and 95%
177 of the flowers had opened.

178

179 **Table 2** AIC analysis of the models that describe flowering phenology of *C. scabiosa* among
180 three sites. Model names show whether the timing ($\bar{x}$) or length (β) of the flowering period
181 were allowed to vary between sites [s] or years [y]. *K* is the number of parameters estimated in
182 each model, *LL* is the maximum log-likelihood, and ΔAIC is the change in AIC relative to the
183 best AIC model. Parsimonious models are marked with an *. Total number of plants across sites
184 and year is 10,042

Model	K	Description	LL	ΔAIC
M2(-)	3	Timing and length of flowering period (FP) constant between sites and years	-18863.0	4425.0
M2($\bar{x}$[s])	5	Timing of FP differs between sites	-17463.2	1629.3
M2($\bar{x}$[s]+β[s])	7	Timing and length of FP differ between sites	-17440.0	1587.0
M2($\bar{x}$[y]+β[y])	21	Timing and length of FP differ between years	-17089.6	914.2
M2($\bar{x}$[s,y])	14	Timing of FP differs between sites and years	-16676.6	74.2
M2($\bar{x}$[s,y]+β[s,y])	25	Timing and length of FP differ between sites and years	-16628.5	0*

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186 **Table 3** AIC analysis of the models that describe flowering phenology of *C. scabiosa* among
187 microhabitats at Wingate in 2013. Model names show which parameters ($\bar{x}$ or β) were allowed
188 to vary between microhabitats. *K* is the number of parameters estimated in each model, *LL* is the
189 maximum log-likelihood, and ΔAIC is the change in AIC relative to the best AIC model.
190 Parsimonious models are marked with an *. Total number of plants across microhabitats is 4569

Model	K	Description	LL	ΔAIC
M3(-)	3	Timing and length of flowering period (FP) and variation between plants constant between microhabitats	-5826.7	416.6
M3($\bar{x}$)	8	Timing of FP varied between microhabitats	-5613.4	0*
M3(β)	8	Length of FP varied between microhabitats	-5814.0	401.1
M3($\bar{x}$+β)	13	Timing and length of FP varied between microhabitats	-5610.8	4.8

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Results

Flight period phenology

Model selection suggested that the day of peak abundance, the peak abundance, and the length of the flight period differed among years and sites (Table 1). Wingate had the latest predicted day of peak abundance and the shortest predicted flight period (Table 4). At Wingate, the start (Linear regression; $R^2 < 0.01$, $F_{1,7} < 0.01$, $p = 0.96$) and the length (Linear regression; $R^2 < 0.01$, $F_{1,7} = 0.03$, $p = 0.86$) of the flight period have not changed significantly with year. Whilst the model generally appeared to fit the observed data well, this was not the case for all site-year combinations, particularly in 2009 and 2012 in Totternhoe and in 2008 in Brockadale (Table 4).

Table 4 Estimates of peak abundance (y_{max}), day of peak abundance ($\bar{t}$) and the length (FPL) and start date (FPS) of flight period for different years and sites, according to the best AIC model (Table 1). Flight period is calculated as the predicted number of days where ≥1 butterfly is expected to be observed on the wing

Year	Brockadale				Totternhoe				Wingate			
	Y_{max}	$\bar{t}$	FPS	FPL	Y_{max}	$\bar{t}$	FPS	FPL	Y_{max}	$\bar{t}$	FPS	FPL
2001	-	-	-	-	50	196	168	56	18	207	186	43
2002	-	-	-	-	-	-	-	-	18	202	185	35
2004	-	-	-	-	-	-	-	-	35	202	187	29
2006	-	-	-	-	88	193	163	60	56	204	179	51
2007	123	187	155	63	42	189	160	58	10	200	180	41
2008	129	195	159	72	48	197	164	67	16	209	183	52
2009	99	187	148	79	18	190	157	65	-	-	-	-
2010	175	189	164	49	94	191	166	49	-	-	-	-
2011	161	183	158	50	80	185	161	49	48	197	177	40
2012	-	-	-	-	46	196	173	46	14	207	191	33
2013	-	-	-	-	-	-	-	-	42	205	187	36

Flowering phenology

There was evidence that the timing and the length of the flowering period differed among years and between study sites (Table 2). Where data were available from all three sites (2011), the flowering period was earliest at the southernmost site (Totternhoe) and latest at the most northern site (Wingate; Table 5). At Wingate, where multiple years of data were available, over time the start of the flowering period generally shifted to later in the year (Linear regression; $\beta = 2.72$, $R^2 = 0.52$, $F_{1,7} = 7.68$, $p = 0.03$). There was also a general decrease in the length of the flowering period over time (Linear regression; $\beta = -3.20$, $R^2 = 0.59$, $F_{1,7} = 9.95$, $p = 0.02$).

Table 5 Julian day by which 5 and 50% of the flowers are expected to be open by, and the expected length of the flowering period (FP) for each year and site. Values are calculated using the best AIC model (M2($\bar{x}$[s,y]+β[s,y]); Table 2)

Year	Brockadale			Totternhoe			Wingate		
	5%	50%	FP	5%	50%	FP	5%	50%	FP
2001	-	-	-	-	-	-	159	207	97
2003	-	-	-	-	-	-	172	199	55
2004	-	-	-	-	-	-	167	208	83
2005	-	-	-	-	-	-	179	211	64
2006	-	-	-	-	-	-	179	205	53
2008	-	-	-	-	-	-	201	220	40
2011	165	190	52	163	186	47	178	203	51
2012	-	-	-	-	-	-	205	226	43
2013	-	-	-	-	-	-	189	214	52
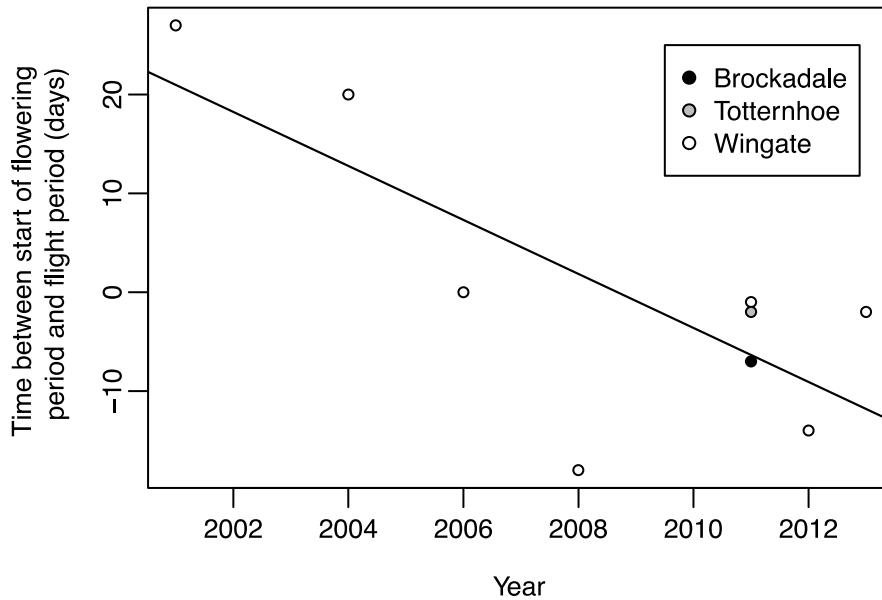
Fig. 2 Difference between the start date of *M. galathea*'s flight period and *C. scabiosa*'s flowering period, each estimated from the fitted models. Each point represents one year's data at one of the three study sites. The line shows the linear regression fitted to the data.

There was evidence that the period between the start of *C. scabiosa* flowering and the start of *M. galathea* imago emergence had decreased over time (Figure 2; Linear regression; β=-2.73, R^2=0.59, $F_{1,7}$=9.96, p=0.02). There was no significant relationship between the length of *C. scabiosa*'s flowering period and *M. galathea*'s flight period (Linear regression; R^2=0.12, $F_{1,7}$=0.93, p=0.37).

There was also evidence that at Wingate the timing, but not the length of the flowering period, varied among microhabitats (Table 3). Flowering was predicted to be earliest on south

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231   and south west facing slopes, where it occurred 14 days earlier than on the flat sheltered areas
232   (Figure 3). The flowering period in each microhabitat was estimated to be 54 days. Thus, the
233   presence of topographic diversity within the site lengthened the site-wide flowering period by
234   around 25% to 68 days across all six microhabitats. *M. galathea*'s flight period was estimated to
235   start at day 187 in Wingate in 2013, which is after the *C. scabiosa* flowering period was
236   estimated to start on three of the six microhabitats studied (Figure 3). The *M. galathea* flight
237   period was predicted to start on the same day as the *C. scabiosa* flowering period on flat exposed
238   areas and before the flowering period began on north-east slopes and in flat sheltered areas.
239
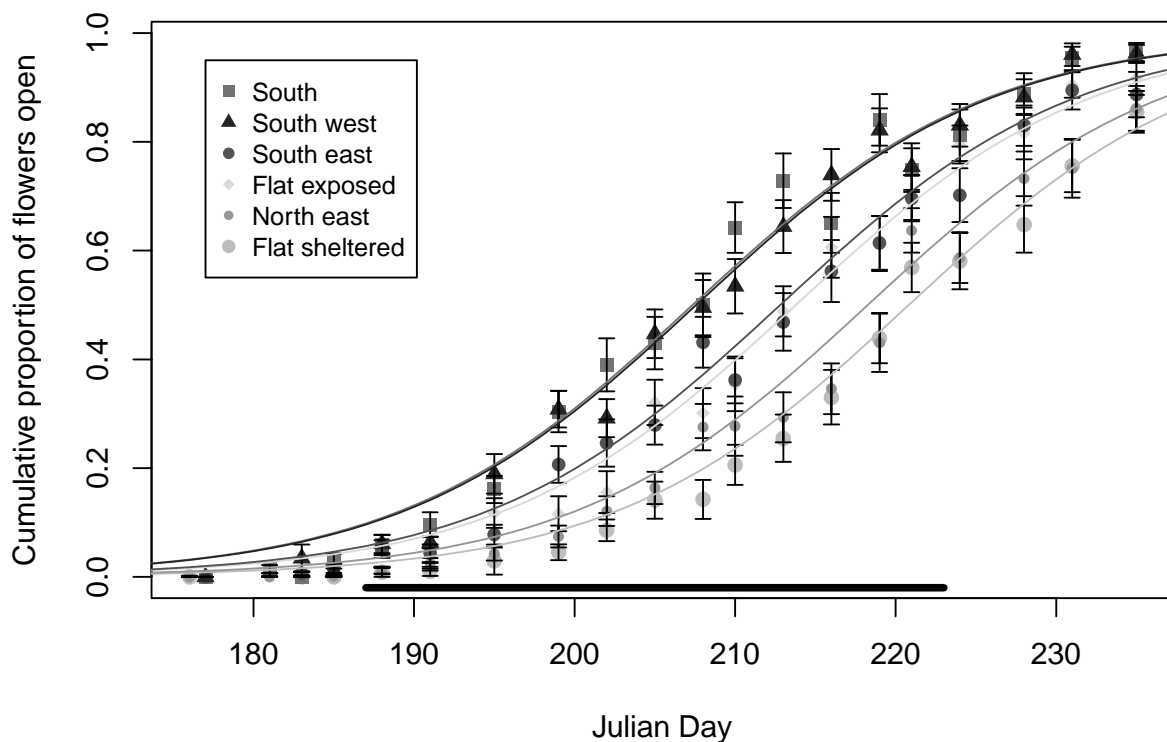
241   **Fig. 3** Mean cumulative proportion of flowers on each plant open in different microhabitats at
242   Wingate each day during the flowering period in 2013. The error bars show standard error of the
243   mean. The lines show the predicted number of open flowers according to the best model fit (M3(
244    $\bar{x}$); Table 3). The solid horizontal line above the x-axis shows the estimated *M. galathea* flight
245   period at Wingate in 2013.

Discussion

247   Over recent years, the start of *M. galathea*'s flight period has become much closer to, or even
248   preceded, the onset of flowering of a key nectar source, at least at its northernmost site in the
249   UK. This has resulted in some butterflies emerging before the start of *C. scabiosa*'s peak
250   flowering period. Whilst the majority of *M. galathea*'s flight period still overlaps with *C.*

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251 *scabiosa*'s flowering period, complete mismatches are not necessary for community effects to

252 occur (Fabina et al. 2010). The observed mismatch, if it continues, could have pronounced

253 effects for *M. galathea*, given that there appears to be a sexual phenological dimorphism, with

254 males emerging several days before females (personal observation by SGW, 2001-2014),

255 probably to maximise mating opportunities (Bulmer 1983; Wiklund and Solbreck 1982). Even

256 slight phenological mismatch in such a situation could result in substantial population declines, if

257 many males in the population fail to find sufficient nectar following emergence. This effect

258 could be particularly acute at the population margin at Wingate, as other key nectar sources

259 either do not exist (e.g. *Origanum majorana*), occur only in small numbers (e.g. *Knautia*

260 *arvensis*, *Scabiosa columbaria*), or are not yet flowering at the time of *M. galathea* butterfly

261 emergence (e.g. *C.nigra*).

262   The relatively poor model fit in some year and site combinations in the *M. galathea* model

263 suggests that site and year are not the only factors affecting the abundance of butterflies and the

264 timing of the flight period. Here, we do not link the phenology of either species directly to

265 climate. Further studies are needed to explain why the phenologies of both species have not

266 advanced as may be expected (Fitter and Fitter 2002; Roy et al. 2001), and such studies could

267 also predict how phenological patterns may change under projected rates of climate change

268 (Murphy et al. 2009). However, as the difference between the start of flowering period and flight

269 period has changed over time, it appears that these two species may use different climatic cues,

270 or possibly that one species may not be able to react as quickly to changes in the environment.

271 This suggests that future predicted climate change could lead to further phenological mismatch

272 between the species, probably to the greater detriment of *M. galathea*.

273   The increased length of *C. scabiosa*'s flowering period seen in the topographically diverse

274 Wingate site could help to reduce the chance of a phenological mismatch occurring between

275 these two species as their phenologies change under climate change. The phenology of

276 individuals may be affected by genetics and biotic or abiotic environmental factors. However,

277 here we suggest that the differences in *C. scabiosa*'s phenology within the site were most likely

278 to be caused by an abiotic factor, namely the aspect and its effect on microclimate, rather than

279 other factors. There is little chance of genetic differences in *C. scabiosa* between aspects given

280 their proximity to one another. As microclimate will also be affected by habitat type, this could

281 affect phenology (Altermatt 2012); however, as all of the aspects studied here were calcareous

282 grassland, habitat variability is also an unlikely driver of the observed phenological patterns.

283 Topography is likely to affect the phenology of sessile organisms, through changes to the

284   microclimate. It seems likely that these are not the only species for which topographically
285   diverse sites could help to ameliorate the potential for phenological mismatch under climate
286   change, at least in the short-term.

287   Mismatches between obligate plant-pollinator systems will obviously have severe impacts.
288   In the same way that pollinator biodiversity could buffer the effects of phenological asynchrony
289   in plants (Bartomeus et al. 2013), diversity in potential nectar sources may reduce the effects of
290   phenological asynchrony on butterfly abundance. Predicting whether generalist species will be
291   affected by phenological mismatches requires detailed studies of interactions with all possible
292   interacting species present, rather than simple paired interactions (Bartomeus et al. 2013). Whilst
293   specialist species are therefore more vulnerable to the effects of phenological mismatches,
294   impacts may still be pronounced for more generalist species that experience decreases in dietary
295   breadth, possibly leading to population declines (Memmott et al. 2007).

296   Consistent phenological shifts within broad taxonomic groups but that differ among
297   taxonomic groups (Parmesan 2007; Thackeray et al. 2010), e.g. insects versus flowering plants,
298   could result from different cueing systems for e.g. growth/emergence/flowering operating. This
299   could result in substantial changes in ecosystems, even among populations of e.g. generalist
300   butterfly species, if flowering is largely synchronous among nectar provisioning plants. The
301   general trend in flowering plants in the UK has been towards earlier flowering (Amano et al.
302   2010; Fitter and Fitter 2002), rather than the later flowering seen here in *C. scabiosa*. However,
303   the current study was over a relatively restricted period, during the latter part of which there
304   were several unusually late and wet summers. The decreasing length of flowering period seen in
305   *C. scabiosa* may also increase the likelihood of a phenological mismatch occurring with *M*
306   *.galathea*, and the effect of this may be exacerbated if shorter flowering periods occur in other
307   nectar sources. Although the negative effect of phenological mismatches are likely to be larger
308   for specialist species, which are unable to substitute resources, the impact of phenological
309   mismatching among generalist species is a field that merits future research. The potential for
310   multiple phenological mismatches in species such as Lepidoptera that use different plant
311   resources and species at different life stages must render them especially vulnerable. The ability
312   of butterflies to alter their flight period phenology under climate change may be affected by their
313   larval diet (Altermatt 2010).

314   The impacts of a plant-pollinator phenological mismatch will depend on whether nectar
315   sources are a limiting factor for that population. Despite one study suggesting that there is little
316   evidence that nectar limitation is causing population declines (Thomas et al. 2011), others have

317 found correlations between nectar abundance and butterfly density (e.g. Wallisdevries et al.
318 2012); nectar abundance may be more important for determining generalist species abundance,
319 whilst specialist species are more dependent on larval host plant abundance (Kraemer et al.
320 2012). Specifically, in the case of *M. galathea*, several studies have shown correlations between
321 the abundance of nectar sources such as *C. scabiosa* and this butterfly species (Lenda and Skorka
322 2010; Loertscher et al. 1995).

323   Climate change is expected to significantly impact many species, communities and
324 ecosystems (Parmesan and Yohe 2003), yet studies often focus on single species, without
325 considering the effects of biotic interactions. Phenological mismatches have the potential to
326 disrupt ecosystem functioning, with consequences not only for the species that have become
327 asynchronous (Fabina et al. 2010; Nakazawa and Doi 2012). Whilst biotic interactions are
328 slowly being included into models of climate impacts on species (Araujo and Luoto 2007;
329 Cormont et al. 2013), and in some cases are considered to exceed the importance of climate in
330 affecting distributions (Mason et al. 2014), there has been a lack of research on how the
331 phenologies of insects, and the species they interact with, will be affected. Phenological change
332 may affect the host plant preferences of generalist species, as growth rates on different host
333 plants may be affected by the time of season (Audusseau et al. 2013).

334   We have demonstrated here how heterogeneous habitats can serve to ameliorate
335 phenological mismatching, for species that can move between habitats/microclimates. We
336 suggest that sites of topographic heterogeneity might be prioritised for conserving similar species
337 under climate change. The diverse microclimates that such sites provide could also buffer
338 populations against the impacts of the extreme climatic events that are forecast to be more
339 frequent in future (Easterling et al. 2000; van Halder et al. 2011; Weiss et al. 1988). For sites
340 with little topographical diversity, management actions that increase the breadth of microclimatic
341 conditions could be encouraged (Hopkins 2007).

342   As the distributions of the majority of European butterflies appear to be lagging behind
343 climate change (Devictor et al. 2012; Warren et al. 2001), with specialist species particularly
344 vulnerable, conservation strategies are necessary to prevent widespread extinctions. Management
345 strategies such as increasing connectivity between protected areas may help to increase dispersal,
346 whilst assisted colonisations could be used for those species that are unlikely to be able to remain
347 within climatically suitable habitats (Loss et al. 2011; Vitt et al. 2009). Assisted colonisation
348 remains a controversial strategy, with risks of species potentially becoming invasive, and its cost
349 and feasibility questioned (Ricciardi and Simberloff 2009). However, it may be a necessary

350 conservation strategy if rare species with limited dispersal ability are to be conserved (Hoegh-
351 Guldberg et al. 2008; Thomas 2011) and could also be used to restore ecosystem function (Lunt
352 et al. 2013). The *M. galathea* population at our main study site is an example of a successful
353 translocation, and provides evidence that the distributions of even relatively mobile generalist
354 species may lag behind changes in suitable climate (Willis et al. 2009). Here we emphasise the
355 importance of considering species interactions before carrying out translocations, including the
356 possibility of temporal mismatch. Paired or multispecies assisted colonisations may be necessary
357 for specialist species that require particular host-plants (McLachlan et al. 2007); however, these
358 approaches may also be necessary for more generalist species. At Wingate, where potential
359 nectar sources from other parts of the range of *M. galathea* are absent, it may be beneficial to *M.*
360 *galathea* to introduce such species that might not otherwise reach the site, to minimise the
361 impact of phenological mismatch.

362   Here we demonstrate how the phenology of a generalist butterfly may lose synchronicity
363 with the flowering period of a key nectar source. However, this asynchrony may be reduced by
364 the presence of topographical diversity. The role of topography in egg-laying, caterpillar growth
365 and imago emergence in *M. galathea* has not been studied. Spatial preferences of adult
366 butterflies probably bear little relation to their natal area, apart from during egg-laying, and, as
367 such, could mask the role of habitat heterogeneity on phenology. Microhabitat choice is of
368 particular importance in ectothermic species such as butterflies, especially in the less mobile
369 larval stages, and may affect egg hatching and the survival and growth of the larval stages
370 (Bergman 2001; Bryant et al. 2002; Turlure and Van Dyck 2009; Weiss et al. 1988). Studies on
371 caterpillar topographic preferences could further our understanding of the mechanisms
372 explaining differential advancements in phenology of butterflies versus their nectar sources.

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