

1 Topographical variation reduces phenological mismatch between a
2 butterfly and its nectar source

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10

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.

29 **Keywords**

30 Insect-plant interactions; topographical diversity; asynchrony; *Melanargia galathea*; *Centaurea*
31 *scabiosa*

32 **Introduction**

33 Recent climate change has seen the advancement of biological events across many taxonomic
34 groups, including flowering in plants (Fitter and Fitter 2002; Menzel and Fabian 1999), egg
35 laying in birds (Crick et al. 1997; Crick and Sparks 1999) and the migration of a wide range of
36 taxonomic groups (Cherry et al. 2013; Marra et al. 2005). Whilst phenological responses to
37 climate change are common, the rates of change can differ across taxonomic groups (Parmesan
38 2007; Thackeray et al. 2010). Differences in the rate or direction of change between interacting
39 species can lead to phenological mismatches, with potential consequences for the abundance,
40 distribution and extinction risk of the interacting species (Fabina et al. 2010; Memmott et al.
41 2007; Parmesan 2007; van Asch and Visser 2007). Interacting species must be temporally, as
42 well as spatially, correlated for interactions to occur. Therefore, it is necessary to consider the
43 effects of changing conditions on inter-dependent species, including pollinators and their food
44 plants (Visser and Both 2005), when predicting the impacts of climate change and planning
45 appropriate conservation measures.

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

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

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

71 Here we examine the flight period of *M. galathea*, a generalist butterfly, over the period
72 2001-13 at three sites across the species' UK range. We relate the timing of *M. galathea*'s flight
73 period to the flowering period of one of its main nectar sources, *Centaurea scabiosa* (Linnaeus
74 1758) (Asher et al. 2001). In particular, we explore the possibility that *M. galathea*'s flight
75 period could be advancing more quickly than *C. scabiosa*'s flowering period, with the potential
76 for a phenological mismatch to occur. Finally, we consider whether the presence of
77 topographical diversity within a site alters the flowering period of this key nectar source, by
78 comparing flowering phenology across multiple aspects at a site on the species' northern range
79 margin.

80 **Methods**

81 *Study species and sites*

82 *M. galathea* is found primarily on calcareous grasslands; within the UK it is found
83 predominantly in the South, naturally occurring as far north as Yorkshire (Asher et al. 2001; Fox
84 et al. 2006). It has undergone rapid range expansions at its northern range boundary; a survey in
85 1995-9 found it present in 66% more 10km grid squares than in 1970-82 (Asher et al. 2001; Fox
86 et al. 2006). *C. scabiosa* is one of the species' main nectar sources although *Centaurea nigra*
87 (Linnaeus 1753) and other purple flowers such as *Scabiosa* spp. are also used (Asher et al.
88 2001). *C. scabiosa* is a perennial and flowers between June and September in the UK. It is
89 common within our study sites and across the natural range of *M. galathea* in the UK. At our
90 northernmost study site, at the species northern range limit, it is the dominant nectar source
91 during *M. galathea*'s flight period.

92 Data were collected at three study sites (Figure 1): Totternhoe Chalk Quarry Reserve,
93 Bedfordshire (Totternhoe; OS grid reference SP9722), Brockadale Nature Reserve, North
94 Yorkshire (Brockadale; OS grid reference SE5117) and Wingate Quarry Local Nature Reserve,
95 Co. Durham (Wingate; OS grid reference NZ3737). Totternhoe and Wingate are the sites of
96 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

$$131 \quad m(t) = y_{\max} \exp\left[-\frac{1}{\sigma} \frac{(t - \bar{t})^2}{\beta}\right], \quad (1)$$

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($y_{\max}[y] + \sigma[y]$)	24	Peak abundance and length of flight period differed between years	-639.7	155.4
M1($y_{\max}[y] + \bar{x}[y] + \sigma[y]$)	34	Peak abundance, day of peak abundance and flight period differ between years	-609.3	114.6
M1($y_{\max}[s] + \bar{x}[s] + \sigma[s]$)	13	Peak abundance, day of peak abundance and flight period differ between sites	-602.3	58.7
M1($y_{\max}[y,s] + \bar{x}[y,s] + \sigma[y,s]$)	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:

$$146 \quad \Pr(i | m, \bar{f}) = \frac{\Gamma(i+a) \phi^a b^{-a} \phi^{-i} \Gamma(1-\phi)^i}{\Gamma(i+1)\Gamma(a)\phi^{i+1} + b\phi^i \Gamma(1+b\phi)^i}, \quad (2)$$

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

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

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

$$171 \quad \Pr(N, n | p, \bar{f}) = \frac{\Gamma(N+1)\Gamma(a+b)\Gamma(n+a)\Gamma(N-n+b)}{\Gamma(n+1)\Gamma(N-n+1)\Gamma(a)\Gamma(b)\Gamma(N+a+b)}, \quad (4)$$

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*

185
 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

191 **Results**

192 *Flight period phenology*

193 Model selection suggested that the day of peak abundance, the peak abundance, and the length of
 194 the flight period differed among years and sites (Table 1). Wingate had the latest predicted day
 195 of peak abundance and the shortest predicted flight period (Table 4). At Wingate, the start
 196 (Linear regression; $R^2 < 0.01$, $F_{1,7} < 0.01$, $p = 0.96$) and the length (Linear regression; $R^2 < 0.01$,
 197 $F_{1,7} = 0.03$, $p = 0.86$) of the flight period have not changed significantly with year. Whilst the
 198 model generally appeared to fit the observed data well, this was not the case for all site-year
 199 combinations, particularly in 2009 and 2012 in Totternhoe and in 2008 in Brockadale (Table 4).

200
 201 **Table 4** Estimates of peak abundance (y_{max}), day of peak abundance (\bar{t}) and the length (FPL)
 202 and start date (FPS) of flight period for different years and sites, according to the best AIC model
 203 (Table 1). Flight period is calculated as the predicted number of days where ≥ 1 butterfly is
 204 expected to be observed on the wing

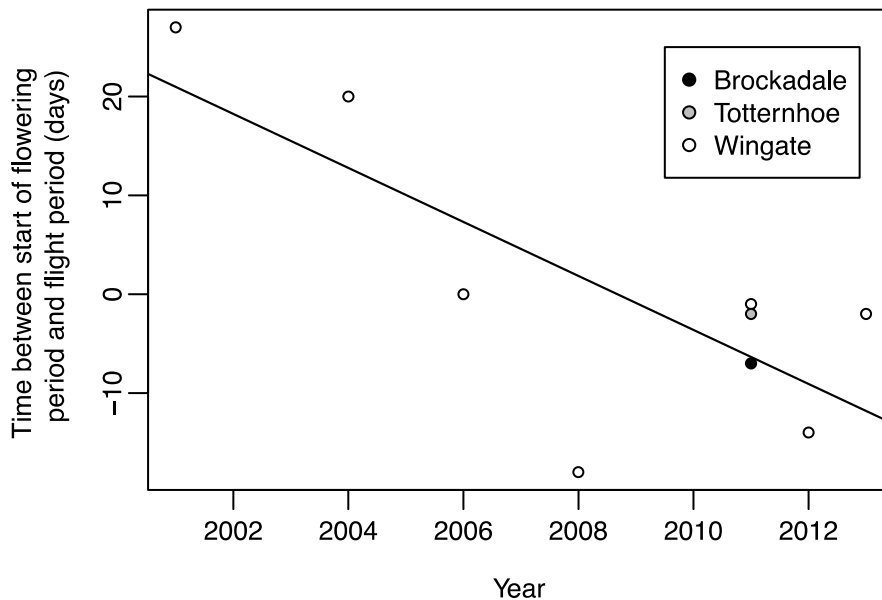
Year	Brockadale				Totternhoe				Wingate			
	Y_{max}	\bar{t}	FPS	FPL	Y_{max}	\bar{t}	FPS	FPL	Y_{max}	\bar{t}	FPS	FPL
2001	-	-	-	-	50	196	168	56	18	207	186	43
2002	-	-	-	-	-	-	-	-	18	202	185	35
2004	-	-	-	-	-	-	-	-	35	202	187	29
2006	-	-	-	-	88	193	163	60	56	204	179	51
2007	123	187	155	63	42	189	160	58	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

205
 206 *Flowering phenology*
 207 There was evidence that the timing and the length of the flowering period differed among years
 208 and between study sites (Table 2). Where data were available from all three sites (2011), the
 209 flowering period was earliest at the southernmost site (Totternhoe) and latest at the most
 210 northern site (Wingate; Table 5). At Wingate, where multiple years of data were available, over
 211 time the start of the flowering period generally shifted to later in the year (Linear regression;
 212 $\beta = 2.72$, $R^2 = 0.52$, $F_{1,7} = 7.68$, $p = 0.03$). There was also a general decrease in the length of the
 213 flowering period over time (Linear regression; $\beta = -3.20$, $R^2 = 0.59$, $F_{1,7} = 9.95$, $p = 0.02$).

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

218



219

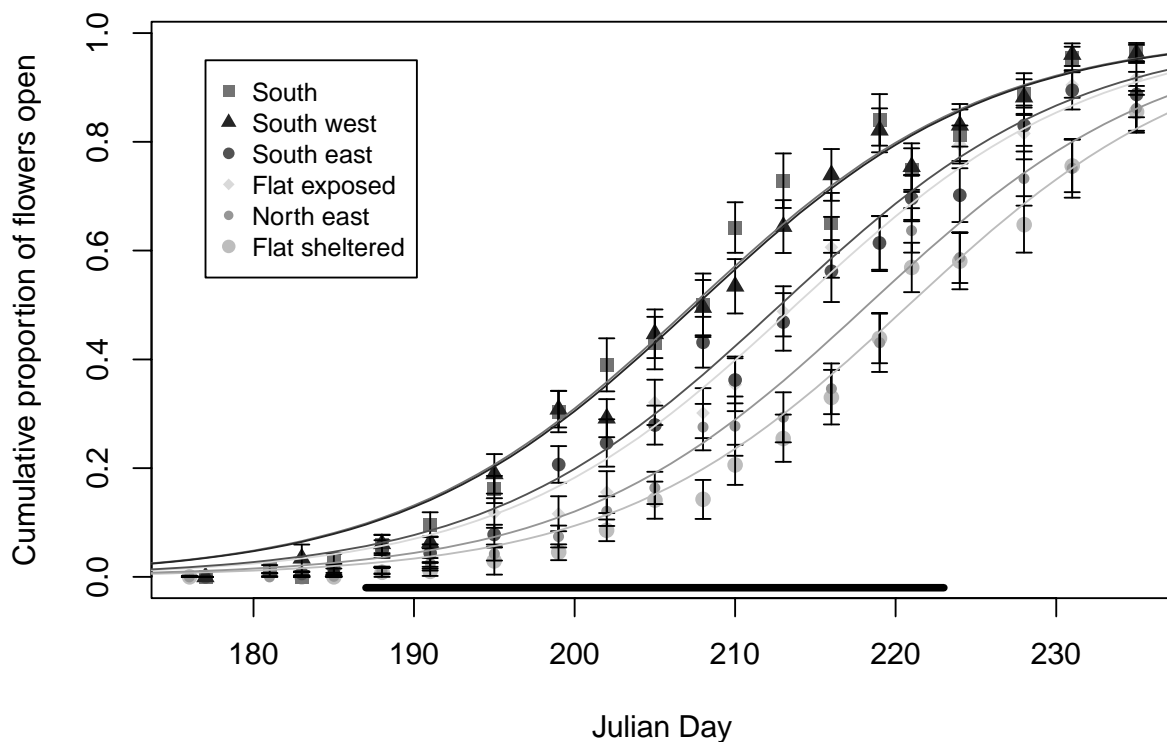
220 **Fig. 2** Difference between the start date of *M. galathea*'s flight period and *C. scabiosa*'s
 221 flowering period, each estimated from the fitted models. Each point represents one year's data at
 222 one of the three study sites. The line shows the linear regression fitted to the data.

223

224 There was evidence that the period between the start of *C. scabiosa* flowering and the start
 225 of *M. galathea* imago emergence had decreased over time (Figure 2; Linear regression; $\beta=-2.73$,
 226 $R^2=0.59$, $F_{1,7}=9.96$, $p=0.02$). There was no significant relationship between the length of *C.*
 227 *scabiosa*'s flowering period and *M. galathea*'s flight period (Linear regression; $R^2=0.12$,
 228 $F_{1,7}=0.93$, $p=0.37$).

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

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



240
 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 ($M3(\bar{x})$;
 244 Table 3). The solid horizontal line above the x-axis shows the estimated *M. galathea* flight
 245 period at Wingate in 2013.

246 **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.*

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.

373

374 **Acknowledgements**

375 Funding was provided by Grevillea Trust studentships to BJH and CLK, both supervised by
376 SGW and cosupervised by SAR and Dr Robert Baxter respectively. Data were supplied by the
377 UK Butterfly Monitoring Scheme (UKBMS) and Yorkshire Wildlife Trust. The UKBMS is
378 operated by the Centre for Ecology & Hydrology and Butterfly Conservation and funded by a
379 multi-agency consortium including the Countryside Council for Wales, Defra, the Joint Nature
380 Conservation Committee, Forestry Commission, Natural England, the Natural Environment
381 Research Council, and Scottish Natural Heritage. The UKBMS is indebted to all volunteers who
382 contribute data to the scheme. We thank Yorkshire Wildlife Trust, Durham City Council and the
383 Wildlife Trust for Bedfordshire, Cambridgeshire and Northamptonshire for access to their land
384 and numerous field assistants for their help in collecting data.

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