1 **Spatio-temporal responses of butterflies to global warming on a Mediterranean island** 2 **over two decades**

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13

14 **Abstract**

15 In recent decades, efforts have been made to understand how global warming affects
16 biodiversity and in this regard butterflies have emerged as a model group. The most
17 conspicuous sign that warming is affecting the ecology of butterflies are the phenological
18 advances occurring in many species. Moreover, rising temperatures are having a notable impact
19 – both negative and positive – on population abundances. To date, patterns have generally been
20 analysed at species level without taking into account possible differences between populations,
21 which, when they are noted, are mostly attributed to large-scale climate differences across a
22 latitudinal gradient. In this work, we use a long-term database of butterflies from the island of
23 Menorca (Balearic Islands, Spain) to investigate how phenology and population dynamics have
24 been affected by climate warming during the past two decades. In addition, we assess how
25 responses are modulated by habitat characteristics and by species' biological cycles. Our results
26 show that species respond differently to warming at a local scale depending on season and
27 habitat, and that coastal habitats in the Mediterranean region are particularly sensitive to the
28 effects of climate change. Furthermore, our findings suggest that the effects of temperature
29 could be partially offset in more inland habitats such as forests and deep ravines. The positive

30 effect of temperature on ravine populations during the summer suggests that butterflies disperse
 31 across habitats as a response to rising temperatures during the season. This type of dispersal
 32 behaviour as a response to warming could be especially important in island ecosystems where
 33 the possibilities of modifying altitudinal or latitudinal distributions are often severely limited.

34

35 **Keywords** climate change · phenology · population dynamics · habitat variability ·
 36 seasonality · biodiversity reservoirs · biodiversity monitoring · Mediterranean basin

37 Introduction

38

39 In recent decades, climate change has become a key factor in attempts to understand trends
 40 in biodiversity and in species' distribution, phenology and population dynamics (Parmesan &
 41 Yohe 2003, Thomas *et al.*, 2004, Araújo & Rahbek 2006, Bellard *et al.*, 2012, Thackeray *et al.*,
 42 2016). A wealth of data has been assembled that shows how different organisms are responding
 43 to climate change, how populations are adapting to novel conditions and what the limits are to
 44 such adaptations (e.g. Devictor *et al.*, 2012; Socolar *et al.*, 2017; Radchuk *et al.*, 2019). Of the
 45 model organisms on which much of this research has been focused, butterflies are ideal case
 46 studies for various reasons (Dennis, 1993; Parmesan, 2003). As ectothermic animals with short
 47 generation times, their development and activity are heavily constrained by environmental
 48 temperature; even so, rapid, noticeable responses at population level are commonly observed
 49 (e.g. Roy *et al.*, 2001). Moreover, the existence of precise data on butterfly phenology (e.g.
 50 through standard monitoring methods; van Swaay *et al.*, 1997; Schmucki *et al.*, 2016) has
 51 afforded this insect group a key position in climate change research.

52 Advances in the flight periods of butterfly species related to increasing temperatures are
 53 well-established phenomena that have been reported from areas as diverse as the UK (Roy &
 54 Sparks, 2000), Central Europe (Altermatt, 2009) and the Mediterranean region (Stefanescu *et*
 55 *al.*, 2003; Forister & Shapiro, 2003). Nevertheless, not all species respond to warming in the
 56 same way and different responses stemming from differences in species traits are known to
 57 occur. For instance, species with narrower dietary ranges in larval stages and more advanced
 58 overwintering stages have been found to exhibit greater advances in flight periods (Diamond *et*
 59 *al.*, 2011). In addition, the relationship between butterfly phenology and temperature has been
 60 shown to be affected by habitat (Altermatt, 2012), elevation gradient (Gutiérrez-Illán *et al.*,
 61 2012), microclimate (WallisDevries & Van Swaay, 2006) and seasonality (Walther *et al.*, 2002).
 62 Hence, phenological responses to warming will differ across populations of the same species.

63 The effects of warming on butterfly numbers are more difficult to predict as different factors
 64 may interact in complex ways in a context-dependent manner (e.g. Roy *et al.*, 2001;

65 WallisDeVries *et al.*, 2011; Boggs and Inouye, 2012). Moreover, different climate conditions
66 can have differing impacts on population dynamics depending on whether they act upon
67 immature or adult stages (Radchuk *et al.*, 2013).

68 In this work, we use a long-term database of butterflies from the island of Menorca (Balearic
69 Islands, Spain) to investigate how the phenology and the population dynamics of this insect
70 group have been affected by climate warming during the past two decades, and how their
71 responses have been modulated by habitat characteristics and species' biological cycles. As
72 expected for a small island with no important mountain ranges (maximum elevation 358 m
73 a.s.l.), the butterfly community is species poor and strongly dominated by common generalists.
74 Nevertheless, most butterfly populations on the island have undergone similar declines to those
75 reported from nearby continental areas where many more specialist species occur (Colom *et al.*,
76 2019). Climate warming has been suggested as a possible factor underlying these negative
77 trends; recent work has revealed the major role of climate in the dynamics of Mediterranean
78 butterflies and shown the negative impact of increasing temperatures and drought on certain
79 species (e.g. Merrill *et al.*, 2007; Zografou *et al.*, 2014; Mills *et al.*, 2017; Herrando *et al.*, 2019;
80 Carnicer *et al.*, 2019). Moreover, given its small surface area, its physical limits as an island and
81 the absence of high mountain ranges, species on Menorca are limited in their capacity to modify
82 their distributions in response to climate change, as occurs in other areas (e.g. Parmesan *et al.*,
83 1999; Wilson *et al.*, 2005). Likewise, in contrast to mountainous areas (e.g. Gutiérrez-Illán *et al.*,
84 2012), phenological variation between populations is expected to be weak or non-existent in
85 Menorca due to its relatively flat landscape. In spite of this, systematic butterfly recording from
86 Menorca for nearly two decades has revealed differences in phenology and population trends
87 between monitored sites. Here we investigate in detail the nature of such variation and how it
88 relates to topographical diversity on the island. The results are important for improving
89 knowledge of how local conditions buffer the negative impacts of climate change in
90 Mediterranean landscapes outside of mountain ranges, and provide guidelines as to which
91 habitats are most deserving of concerted conservation efforts focused on mitigation and
92 adjustment to climate change.

93 **Material and Methods**

94

95 *Study area*

96 Five sites on the island of Menorca were selected for study (Supplementary Figures S1 and
 97 S2), all close to the sea (1–10 km) and geographically separated by a minimum of 5 km from
 98 each other. They are at low altitude (0–50 m) and embrace in total 10 CORINE land-cover types
 99 (e.g. Mediterranean grassland, coastal marshland, coniferous Mediterranean forest and
 100 herbaceous crops). Although all five sites were used to define the overall phenology of the
 101 species on the island, we only used three with 15–18 years of data for comparisons: (1) Albufera
 102 des Grau, an open coastal area with dry meadows and Mediterranean scrub; (2) Santa Catalina,
 103 a forested area dominated by evergreen oak and pine forests; and (3) Barranc d'Alendar, a
 104 ravine in the south of the island with orchards at the beginning and thick undergrowth further
 105 inland. Although the climate is typically Mediterranean throughout the island, with hot-dry
 106 summers and mild-wet winters (Jansà et al., 2017), the geomorphology of its ravines generates
 107 moister microclimatic conditions that set Barranc d'Alendar apart from the other studied
 108 localities.

109

110 *Butterfly data*

111 We used butterfly abundance data collected in 2001–2018 within the framework of the
 112 Catalan Butterfly Monitoring Scheme (CBMS) (www.catalanbms.org). Butterfly abundances
 113 were recorded weekly from March to September along fixed transects of 2–3 km in length using
 114 the standard BMS methodology (Pollard and Yates, 1993; Schmucki *et al.*, 2016). Butterflies
 115 were counted and identified to species level in a 5×5 m area along transects (2.5 m to each side
 116 and 5 m in front of the recorder) whenever weather conditions met certain minimum standards
 117 (temperature over 15°C, preferably under a sunny sky).

Analyses focused on 16 of the 25 butterfly species recorded on Menorca that in all five localities have an annual frequency of occurrence of >0.5 and an annual mean abundance of over five individuals. After applying these criteria, we were left with data for 80 populations that had been monitored for 4–18 years. The 16 species selected are all habitat generalists (Colom *et al.*, 2019) but still differed in certain ecological traits related to their voltinism (i.e. number of generations per year), migratory behaviour and hibernation phases, which were taken into account when analyzing phenological and population trends (Supplementary Table S1).

Butterfly phenology

The flight periods of each species were identified and characterised after pooling abundance data for all five study sites for 2001–2018 (Supplementary Figure S3). This information, together with published data on the ecology of the species in Spain (García-Barros *et al.*, 2013; Vila *et al.*, 2018), allowed us to interpret the life cycle of these species on Menorca (Supplementary Table S1) and define periods on their flight curves that correspond to different generations (Table 1). Four species in our dataset are univoltine (*Callophrys rubi*, *Gonepteryx cleopatra*, *Maniola jurtina* and *Pyronia cecilia*), the remaining 12 being multivoltine. For each species, we established a *critical period* (CP, hereafter) into which the development of the immature stages – i.e. before adult emergence and after the diapause stage – was concentrated. We assumed that the temperature experienced during the CPs is crucial for accounting for annual variations in the flight period. According to knowledge of the biology of these species and a close examination of their flight curves on Menorca, we proposed a maximum of three possible variations in the CP for each species (i.e. a variable extended period before adult emergence) for which the mean temperature was calculated (Supplementary Table S2). For *G. cleopatra*, the CP in winter-spring does not coincide with the development of immature stages but with the time when hibernating adults are most sensitive to temperature changes as a prelude to breaking diapause.

To estimate the annual flight period of a butterfly population, we used the Weighted Mean Flight Period (hereafter WMFP), which is a statistic widely used in butterfly phenological

146 studies (e.g. Roy & Sparks, 2000; Stefanescu *et al.*, 2003; Gutierrez-Illán *et al.*, 2012). The
147 WMFP represents the date (i.e. the week in a range of 1–30) in which the mean of adult counts
148 of a given species at a given locality occurs:

$$WMFP = \frac{\sum \text{Abundance of butterflies} \times \text{week number}}{\text{Annual total abundance of butterflies}}$$

149 As in other studies (Pollard *et al.*, 1991, Stefanescu *et al.*, 2003), the recording weeks rather
150 than the day of the counts were used as the time unit. For multivoltine species, we calculated
151 two or three WMFPs corresponding to spring and summer (in some cases early-summer or late-
152 summer) generations (see Table 1 for the WMFPs calculated for each species). As an exception,
153 we calculated a single WMFP for two multivoltine species with overlapping generations
154 (*Pararge aegeria* and *Pieris rapae*) given that their overall flight curves were better rendered by
155 a unimodal pattern.

156

157 *Temperature data*

158 Detailed climatic records for Menorca are available for the last 48 years from various
159 meteorological stations run by the Spanish Meteorological Agency (AEMET). During this
160 period, the mean temperature on Menorca has increased 0.34°C/decade (0.41°C/decade for
161 maximum temperatures). This increase, however, was not uniform over the seasons as the late-
162 spring months (April, May and June) were the greatest contributors to the overall annual
163 warming (Jansà & Gomis, 2018).

164 To investigate the relationship between temperature and phenology, we associated butterfly
165 recording sites with the closest meteorological station with data available for 2001–2018. At
166 each site, the WMFP of a given species was then related to the mean temperatures of the months
167 covering its critical period of development (Supplementary Table S2).

168 Given that some of the butterflies on Menorca are migratory species (e.g. *Colias crocea*,
169 *Pieris rapae*, *Pieris brassicae*, *Vanessa atalanta* and *Vanessa cardui*) whose immature stages
170 do not develop on the island, it was also necessary to obtain the mean temperatures in the
171 regions where these species originate. Specifically, through ERA-interim, a global atmospheric

reanalysis updated in real time by the European Centre for Medium-Range Weather Forecasts (www.ecmwf.int), the monthly mean temperatures of four domains were obtained: North Africa ($32.25^{\circ}\text{N} < \text{latitude} < 36.75^{\circ}\text{N}$; $10.50^{\circ}\text{W} < \text{longitude} < 10.50^{\circ}\text{E}$); Europe ($32.25^{\circ}\text{N} < \text{latitude} < 45.75^{\circ}\text{N}$; $10.50^{\circ}\text{W} < \text{longitude} < 10.50^{\circ}\text{E}$); Mediterranean Europe ($37.50^{\circ}\text{N} < \text{latitude} < 45.75^{\circ}\text{N}$; $0.00^{\circ} < \text{longitude} < 10.50^{\circ}\text{E}$); and Atlantic Europe ($37.50^{\circ}\text{N} < \text{latitude} < 45.75^{\circ}\text{N}$; $10.50^{\circ}\text{W} < \text{longitude} < 0.75^{\circ}\text{W}$).

Statistical analyses

Phenological analysis: We used Generalised Linear Mixed Models (GLMM) to test whether or not species advanced their phenologies in warmer years (i.e. warmer critical periods) and whether or not there were any related trends during the study period (2001–2018). Tests were conducted for the different flight periods of each species (except for *Pararge aegeria* and *Pieris rapae*, for which it was impossible to distinguish between individual generations due to overlaps; see above). The mean temperatures in the various combinations of the critical months (as defined previously) were used as the explanatory variable in the different models, with ‘site’ used as a random factor (Supplementary Table S2). The best models were selected based on the lowest AIC value (Akaike Information Criterion).

We used the results of these first analyses to examine with linear regressions the relationship between the WMFPs and the mean temperature of the relevant CPs. The strength of the relationship was quantified through the beta coefficient of the regression and was compared between localities (the three localities with >15 years of data) and seasonality (spring vs. summer generations) using a GLMM in which ‘site’ and ‘season’ were set as fixed factors and ‘species’ as a random factor.

Population dynamics analysis: We followed a similar approach to study the effects of temperature on population abundances in different generations. We examined separately the effect of temperature on immature stages and on adults by (1) using the mean temperatures of the CPs (for immatures) that were selected in the best models in the first analysis, and (2) using the mean temperatures of the flight time period in which butterflies were recorded in each

200 population. In both cases, we analysed the differences between localities and seasonality (i.e.
 201 spring vs. summer generations). To compare temperature effects between localities and between
 202 seasons, we excluded the long-distance migrants *V. cardui* and *P. brassicae* given that the
 203 phenology and abundance of their populations are not related to local temperatures (see Table
 204 1).

205 Results

206

207 *Temporal trends in temperature*

208 In spite of the general warming trend in Menorca since the 1970s, we did not detect any
 209 overall significant trend in mean annual temperatures in the study period (2001–2018). The only
 210 month with a marginally significant increase in mean temperature was April ($P = 0.084$, $R^2 =$
 211 0.18). Nevertheless, we did find a significant annual increase of 0.78 °C/decade in maximum
 212 temperatures ($P = 0.0009$, $R^2 = 0.51$). Moreover, when we restricted the analysis to individual
 213 months, there were significant warming trends in April ($P = 0.003$, $R^2 = 0.444$), May ($P = 0.066$,
 214 $R^2 = 0.15$), September ($P = 0.009$, $R^2 = 0.35$) and December ($P = 0.007$, $R^2 = 0.38$) (Fig. 1).

215

216 *Phenological response to increasing temperatures*

217 Three species changed the timing of their WMFPs during the study period (Table 1):
 218 *Coenonympha pamphilus* advanced the WMFP of its spring generation ($P = 0.04$), while there
 219 were significant delays in the spring WMFP of *Celastrina argiolus* ($P = 0.008$) and in the late
 220 summer WMFP of *Pieris brassicae* ($P = 0.03$). Despite these temporal delays, in both *C.*
 221 *argiolus* and *P. brassicae* there was a significant negative relationship between their WMFPs
 222 with temperature (Table 1).

223 In all, 80% of the analysed species showed the same negative WMFP-temperature
 224 relationship in some of their generations (Table 1). In fact, only three species (*Lasiommata*
 225 *megea*, *Vanessa atalanta* and *Lycaena phlaeas*) did not advance their phenology with
 226 increasing temperatures.

227 In multivoltine species with clearly distinct flight periods (*A. cramera*, *C. argiolus*, *C.*
 228 *pamphilus*, *C. crocea*, *P. brassicae*, *P. celina* and *V. cardui*), phenological advances were
 229 recorded in both spring and summer (four and five cases, respectively; Table 1). In the two
 230 long-distance migrants *V. cardui* and *P. brassicae*, WMFPs did not have significant
 231 relationships with local temperatures but with mainly temperatures in the presumed regions of

232 origin of the recorded adults (i.e. North Africa for the spring generations of both species, and
233 Mediterranean Europe for the late summer generation of *V. cardui*).

234 For two species, *Pararge aegeria* and *Pieris rapae*, the great overlap in their generations did
235 not allow us to analyse their spring and summer phenologies separately. Nevertheless, the
236 global unimodal flight curves of both species (weeks 1–30) showed a significant negative
237 relationship with late-spring–early-summer temperatures (April–July; Table 1).

238 The four univoltine species in our dataset also showed phenological advances with
239 increasing temperatures. As before, in the two species with unimodal flight curves, advances
240 were recorded in spring (*Callophrys rubi*) and in summer (*Pyronia cecilia*) (Table 1). Despite
241 having a single annual generation, the flight curves of the other two univoltine species were
242 approximately bimodal. In the case of *G. cleopatra*, a first small peak corresponds to adults
243 from the previous season that come out of hibernation in early spring, while a second and
244 stronger peak corresponds to the new annual generation. We found a significant negative
245 WMFP-temperature relationship in this second flight period. In *M. jurtina*, there was a strong
246 first peak in late spring that corresponds to the emergence of the annual generation, followed by
247 a much more prolonged but blurred second peak that mainly consists of the females that survive
248 through the summer but do not begin oviposition until September. Only the first flight period of
249 this species showed a significant relationship with temperature (Table 1).

250

251 *Spatial and seasonal variation of the WMFP-temperature relationship*

252 The WMFP-temperature relationship was explained both by the seasonal (i.e. spring and
253 summer flying periods) and spatial (i.e. the three individual sites) variables. For the 14 species
254 analysed, temperature had a greater negative effect in spring than in summer (-0.65 ± 0.86 vs. $-$
255 0.34 ± 0.84 ; $P = 0.0478$) (Fig. 2). The analysis also showed marginally significant differences
256 between localities ($P = 0.081$). Specifically, there was a weaker WMFP-temperature
257 relationship in Barranc d'Algendar (i.e. the ravine) than in the other two areas, Albufera des

258 Grau (coastal area, $P = 0.0471$) and Santa Catalina (Mediterranean forest, $P = 0.0651$) (Fig. 2).

259 The latter two populations did not differ significantly.

260

261 *Spatial and seasonal variation in the abundance-temperature relationship*

262 The analysis of population abundance showed similar results for the two types of models, i.e.

263 considering the temperatures during the CP before adult emergence and during the butterfly's

264 flight period. Both models showed significant differences between localities (model 1: $P =$

265 0.001; model 2: $P = 0.058$) and between seasons (model 1: $P = 0.09$; model 2: $P = 0.005$).

266 However, in the first model (i.e. for developmental periods) the spatial variable was more

267 important than the seasonal variable, whereas in the second model (i.e. for adult flight periods)

268 the reverse was true.

269 As for the spatial scale, it was clear from both models that butterfly populations in the ravine

270 (Barranc d'Algender) benefitted more from higher temperatures than in the two other sites (Fig.

271 3). This was particularly the case in summer, when higher temperatures led to more abundant

272 butterfly populations in the ravine (beta coefficients were positive in both models) but gave rise

273 to less abundant populations in the coastal and forest sites (beta coefficients were negative at

274 both sites and in both models).

275 We found a consistent stronger temperature effect on population abundance in summer than

276 in spring (Fig. 3). This was especially so at the coastal and forest sites (differences in beta

277 coefficients between spring vs. summer: model 1 = 0.04; model 2 = 0.03) compared to the

278 ravine site (differences in beta coefficients between spring vs. summer = model 1 = 0.02; model

279 2 = 0.009). Interestingly enough, in both the coastal and forest areas there was a reverse effect

280 of the temperature on population abundance, with an almost neutral effect in spring but a very

281 strong negative effect in summer. In the ravine area, by contrast, the effect was always positive

282 and very similar in spring and summer.

283 Discussion

284

285 Global warming is not spatially homogeneous and its effects vary widely across
 286 biogeographical areas (Post *et al.*, 2018), the Mediterranean region, in particular, being one of
 287 the most sensitive areas to this phenomenon (Giorgi, 2006). Likewise, warming is not
 288 homogeneous throughout the year and in the Mediterranean region the greatest contribution to
 289 annual warming occurs in the transition from spring to summer (Garcia, 2015). There is also
 290 strong evidence to suggest that summer seasons in the Mediterranean are becoming longer
 291 (Bartolini *et al.*, 2012; Jansà *et al.*, 2017). In this sense, despite the short climatic period
 292 analysed in our study, warming trends (with respect to maximum temperatures) were observed
 293 in April, September and December, and also marginally in May. Moreover, the annual increase
 294 in maximum temperature in the study period (0.78°C/decade) is higher than the annual increase
 295 reported recently for Menorca in the period 1971–2016 (0.41°C / decade) (Jansà & Gomis,
 296 2018). This trend may be related to the increase in the frequency of extreme climatic events (i.e.
 297 unusually high temperatures) observed in other parts of the Mediterranean, especially in the
 298 warm season (Caloiero *et al.*, 2017; Scorzini *et al.*, 2018).

299 Despite the observed warming trends during the study period, however, we only detected
 300 phenological trends in three species. On the one hand, *Coenonympha pamphilus* advanced its
 301 phenology in spring, a finding consistent with other studies of this species in the UK (Roy &
 302 Sparks, 2000) and the continental Mediterranean region (Stefanescu *et al.*, 2003), whilst, on the
 303 other, *Celastrina argiolus* and *Pieris brassicae* showed phenological changes in the opposite
 304 direction, i.e. delayed phenologies. In *C. argiolus*, the apparent delay in their spring WMFP is
 305 probably an artefact related to an advance in the summer generation, which has many more
 306 individuals and may overlap with the spring generation in warmer years. For *P. brassicae*, the
 307 delay in the summer WMFP may have different causes. Firstly, this species has a complex life
 308 cycle in the Mediterranean region where it enters a summer diapause or aestivation phase that is
 309 not observed in other regions, as noted by Held & Spieth (1999) and Spieth *et al.* (2011);
 310 according to these authors, more severe drought conditions could lengthen the summer diapause

311 period, resulting in a later emergence of the summer generation. Moreover, *P. brassicae* is
 312 migratory and many specimens move to higher latitudes to avoid the dry summer season (CS,
 313 pers. obs.). Conversely, in late summer, large numbers of *P. brassicae* from Central Europe
 314 migrate southward to breed in the Mediterranean region. The arrival of these specimens on
 315 Menorca, which in some cases is massive, could be delayed due to an extension of the summer
 316 season given that higher temperatures allow for an increase in the number of generations
 317 developed in Central Europe (Altermatt, 2009).

318 Overall, our findings are consistent with the idea that warming causes significant advances in
 319 the flight period of most butterflies. The only three species for which this pattern was not
 320 recorded are rare at some of the monitored localities and, therefore, their very low abundances
 321 probably precluded the detection of the expected advancement.

322 As hypothesized, we found evidence that the phenology of the long-distance migrants *Pieris*
 323 *brassicae* and *Vanessa cardui* is not influenced by local temperatures but, rather, by
 324 temperatures experienced in distant source areas. Interestingly, for the rest of the species
 325 affected by local temperatures we found that phenological patterns were also strongly dependent
 326 on both habitat and season, which implies that variation occurs between populations of the same
 327 species (Figs. 2, 3). On a temporal scale, the effects of temperature were not seasonally
 328 homogenous and, although advances did occur in both spring and summer, warming caused the
 329 strongest effects in the spring generations. This pattern, observed in numerous other studies of
 330 different groups of organisms (e.g. Walther *et al.*, 2002), is a consequence in the case of
 331 butterflies of how the metabolism of immature stages relates to environmental temperatures. It
 332 is well known that in insects the rate of development depends on body temperature, which in
 333 turn, as ectothermic organisms, is closely contingent on external temperature. Once a threshold
 334 of minimum temperature is exceeded, developmental rates increase linearly for a range of
 335 temperature until a decline occurs as an upper threshold is approached, beyond which no further
 336 development is possible (cf. Kingsolver, 1989). In the Mediterranean region, this means that
 337 temperature increases in the winter-spring transition, when average temperatures are commonly
 338 around minimum thresholds, provoke sharper developmental increases than when they occur in

summer, when temperatures may even reach the upper developmental thresholds. Moreover, in the current context of an increase in the frequency of extreme climatic events (Easterling *et al.*, 2000; Coumou & Rahmstorf, 2012), greater fluctuations in temperature (even if the average is constant) may mean a decrease in the developmental rate in warm conditions but an opposite effect at low temperatures (Paaijans *et al.*, 2013).

Our results also suggest a seasonal pattern for the effects of temperature on abundance (Fig. 3). While in the spring the effects of higher temperatures were very variable during both the development of immature stages and the adult flight period, in summer they clearly had a negative effect, except in the ravine. During summer, the increase in temperature generally implies an increase in aridity and a reduction in water availability, which has been identified as a key limiting factor for butterfly species in the Mediterranean (Stefanescu *et al.*, 2011; Herrando *et al.*, 2019) and for plant-butterfly interactions (Donoso *et al.*, 2016). In fact, the difference between this negative effect in summer and the neutral effect in spring was more noticeable when we considered the adult flight period (Fig. 3, model 2). During the summer season, a decrease in nectar supply under drought conditions could explain the negative effect of temperature on butterfly abundances (WallisDeVries *et al.*, 2012). On the other hand, in spring, which is the rainy season in the study region, temperature increases are not as strongly associated with drought. In spring, however, multiple causes could explain a negative or positive effect of temperature on the abundance of the first butterfly generations. On the one hand, faster development due to higher environmental temperatures could lessen mortality during larval and pupal stages as the exposure time to their predators and parasitoids is reduced (e.g. Pollard, 1979). But, on the other hand, an earlier emergence of butterflies is not necessarily accompanied by an advance in plant flowering. Consequently, asynchrony could occur between butterfly and plant phenologies, especially in dry springs (Donoso *et al.*, 2016), with a negative effect on butterfly abundances.

On a spatial scale, differences in phenology between populations of the same species have usually been attributed to adaptive or plastic responses to local day-length and temperatures (Hodgson *et al.*, 2011). However, for nearby populations with no marked altitudinal gradient,

367 these factors are minimized. In spite of this, our results showed significant differences in the
 368 effect of temperature on both the flight period and the abundance of different populations. Our
 369 results agree with those reported by Altermatt (2012), who showed that habitat (in his study due
 370 to anthropogenic changes in microclimate) can affect butterfly phenology. In our case, the
 371 strongest effects on phenology and abundance were observed at the coastal site. This suggests
 372 that in warmer years the effect of temperature could be more notable on coastal than in forested
 373 areas, where more stable climatic conditions are expected (cf. Suggitt *et al.*, 2011).

374 The case of Barranc d'Alendar area deserves special mention. The butterfly response to
 375 warming at this site is evidently different from that at the other two localities. The less marked
 376 effect of temperature on the phenology of ravine populations and the increase in their abundance
 377 in warmer summers could be explained by the particular environmental conditions of these
 378 habitats. The milder temperatures in summer in this and other ravines could favour the arrival of
 379 individuals of highly mobile species from other more arid environments on the island since in
 380 the ravines there is a greater abundance of both adult (i.e. nectar supply) and larval resources
 381 (i.e. host plants) due to greater humidity. On an island like Menorca, where species have a very
 382 narrow latitudinal and altitudinal range in which to respond to warming, dispersal into such
 383 environments may be a common response. The geomorphology of the ravines in Menorca could
 384 lead to a beneficial microclimate for butterfly species during certain critical periods, especially
 385 under extreme weather conditions. Consequently, the ravines constitute biodiversity reservoirs
 386 in Menorca due to their capacity to act as a buffer for extreme weather conditions.

387 **Tables**

388 **Table 1.** The Weighted Mean Flight Periods (WMFP) that were considered for each species and
389 the critical periods that were selected in the best models. Significant relationships between
390 WMFP and mean temperatures during the critical period (in the indicated region) are shown,
391 with Beta negative values corresponding to advances of the WMFP with greater temperatures.
392 Significant temporal trends in WMFP over the study period (2001–2018) are also shown
393 (significant *P*-values are provided). WMFP correspond to spring (spr), early summer (esum),
394 summer (sum), late summer (lsum), or to a succession of closely overlapping generations
395 (over). *: univoltine species.

Species	WMFP period (weeks)	Climatic region	Critical period	Temperature		Temporal	
				<i>P</i>	Beta	<i>P</i>	Beta
<i>Aricia cramera</i>	(11-26)sum	Menorca	May - July	0.017	-0.95	-	-
<i>Callophrys rubi</i> *	(1-12)spr	Menorca	January - April	0.023	-0.71	-	-
<i>Celastrina argiolus</i>	(1-14)spr	Menorca	March - April	0.032	-1.37	0.008	0.23
	(15-26)sum	-	-	-	-	-	-
<i>Coenonympha pamphilus</i>	(1-13)spr	Menorca	February - April	0.026	-0.59	0.04	-0.08
	(14-26)sum	Menorca		-	-	-	-
<i>Colias crocea</i>	(1-10)spr	-	-	-	-	-	-
	(11-20)sum	Menorca	May - July	<0.0001	-0.78	-	-
<i>Gonepteryx cleopatra</i> *	(1 - 9)spr	-	-	-	-	-	-
	(11 - 20)sum	Menorca	April - June	0.0004	-3.74	-	-
<i>Lasiommata megera</i>	(1 - 9)spr	-	-	-	-	-	-
	(10 - 22)sum	-	-	-	-	-	-
<i>Lycaena phlaeas</i>	(1 - 15)spr	-	-	-	-	-	-
	(16 - 30)sum	-	-	-	-	-	-
<i>Maniola jurtina</i> *	(1-17)spr	Menorca	March - June	0.011	-0.31	-	-
	(18 - 30)sum	-	-	-	-	-	-
<i>Pararge aegeria</i>	(1 - 30)over	Menorca	May - July	0.008	-1.02	-	-
<i>Pieris brassicae</i>	(1 - 22)spr-esum	North Africa	March - April	0.016	-2.49	-	-

	(23 - 30)lsum	Menorca	July - September	0.041	-0.57	0.003	0.13
<i>Pieris rapae</i>	(1 - 30)over	North Africa	April - July	0.042	-0.89		
<i>Polyommatus celina</i>	(1 - 9)spr	-	-	-	-	-	-
	(11 - 24)sum	Menorca	May - August	<0.0001	-1.03	-	-
<i>Pyronia cecilia</i> *	(10 - 30)sum	Menorca	May -June	0.001	-0.68	-	-
<i>Vanessa atalanta</i>	(1 - 17)spr	-	-	-	-	-	-
	(18 - 24)sum	-	-	-	-	-	-
<i>Vanessa cardui</i>	(1 - 10)spr	North Africa	January - April	0.044	-0.96		
	(11 - 20)esum	-	-	-	-	-	-
	(21 - 30)lsum	Med. Europe	July - September	0.007	-1.17	-	-

397 **Figures**

398

399 **Figure 1.** Climate trends in Menorca in 2001–2018. (a) Mean and maximum annual
400 temperatures. (b) Mean monthly maximum temperatures from April, May, September and
401 December. Dotted lines represent significant or marginally significant linear regressions ($P <$
402 0.1).

403 **Figure 2.** Beta coefficient of the regression of the Weighted Mean Flight Period (WMFP) and
404 temperature at different localities ($P = 0.081$) (AG: Albufera des Grau: coastal area; BA:
405 Barranc d'Algendar: ravine area; SC: Santa Catalina: Mediterranean forest) and seasons ($P =$
406 0.048) (spring and summer). Letters show significant differences between localities.

407 **Figure 3.** Beta coefficient of the regression of butterfly abundance and temperature at different
408 localities (AG: Albufera des Grau: coastal area; BA: Barranc d'Algendar: ravine area; SC: Santa
409 Catalina: Mediterranean forest) and seasons (spring and summer). Model 1 represents the effect
410 of temperature on the critical periods of the species (i.e. the immature stages). Model 2
411 represents the effect of temperature on the adult stages. Both models show significant
412 differences between seasons ((1) $P = 0.09$; (2) $P = 0.005$) and localities ((1) $P = 0.001$; (2) $P =$
413 0.058).

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417

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419

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598 **Supporting Information**

599

600 **Figures**

601 **Figure S1.** Map of the study area. The five sites form part of the CBMS network
 602 (www.catalanbms.org) and were used to characterize the phenology of the species. However,
 603 only the three sites with over 15 years of data were used in the analyses.

604 **Figure S2.** Details of the five CBMS transects used in the study.

605 **Figure S3.** Butterfly species flight curves. The x-axis represents the 30 weeks of monitoring
 606 running from the first week of March to the fourth week of September. The y-axis represents the
 607 mean abundance standardized to 100 m of transect length.

608

609 **Tables**

610 **Table S1.** Ecological traits of the analysed butterfly species.

611 **Table S2.** Different combinations of months and climatic regions used to analyse the critical
 612 periods of butterfly species in both spring and summer.

CBMS 61 – Albufera des Grau UTM: 39.94507, 4.24882 Transect longitude: 1856 m Altitude (a.s.l.): 9 m Years recorded: 18
CBMS 60 – Barranc d'Algendar UTM: 39.96691, 3.96648 Transect longitude: 1975 m Altitude (a.s.l.): 50 m Years recorded: 18
CBMS 145 – La Vall UTM: 40.05255, 3.92549 Transect longitude: 2980 m Altitude (a.s.l.): 22 m Years recorded: 4
CBMS 101 – Santa Catalina UTM: 39.96037, 4.20795 Transect longitude: 1914 m Altitude (a.s.l.): 12 m Years recorded: 15
CBMS 146 – Talis UTM: 39.90855, 4.06479 Transect longitude: 3072 m Altitude (a.s.l.): 5 m Years recorded: 4

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Species	Voltinism	Migratory behaviour	Hibernating phase
<i>Aricia cramera</i>	Polivoltine	Sedentary	Larva
<i>Callophrys rubi</i>	Univoltine	Sedentary	Pupa
<i>Celastrina argiolus</i>	Polivoltine	Sedentary	Pupa
<i>Coenonympha pamphilus</i>	Polivoltine	Sedentary	Larva
<i>Colias crocea</i>	Polivoltine	Migratory	Larva
<i>Gonepteryx cleopatra</i>	Univoltine*	Sedentary	Adult
<i>Lasiommata megera</i>	Polivoltine	Sedentary	Larva
<i>Lycaena phlaeas</i>	Polivoltine	Sedentary	Larva
<i>Maniola jurtina</i>	Univoltine	Sedentary	Larva
<i>Pararge aegeria</i>	Polivoltine	Sedentary	Larva, pupa
<i>Pieris brassicae</i>	Polivoltine	Migratory	Pupa
<i>Pieris rapae</i>	Polivoltine	Migratory	Pupa
<i>Polyommatus celina</i>	Polivoltine	Sedentary	Larva
<i>Pyronia cecilia</i>	Univoltine	Sedentary	Larva
<i>Vanessa atalanta</i>	Polivoltine	Migratory	Larva, adult
<i>Vanessa cardui</i>	Polivoltine	Migratory	Non hibernation

* Although some butterflies produce a second generation in early summer, the contribution of this second partial generation is negligible (pers. obs.).

Species	WMFP period (weeks)	Climatic region	Temperature period
<i>Aricia cramera</i>	11-26	Menorca	January - March April - June May - July
<i>Callophrys rubi</i>	1-12	Menorca	January - April February - April March - April
<i>Celastrina argiolus</i>	1-14	Menorca	January - April February - April March - April
	15-26	Menorca	April- August May - August June - August
<i>Coenonympha pamphilus</i>	1-13	Menorca	January - April February - April March - April
	14-26	Menorca	March - August April - August May - August
<i>Colias crocea</i>	1-10	Menorca	January - April February - April March - April
		North Africa	January - April February - April March - April
	11-20	Menorca	March - July April - July May - July
<i>Gonepteryx cleopatra</i>	1-9	Menorca	January - April February - April March - April

	10-30	Menorca	April - May April - June April - July
<i>Lasiommata megera</i>	1-9	Menorca	January - April February - April March - April
	10-22	Menorca	March - July April - July May - July
<i>Lycaena phlaeas</i>	1-15	Menorca	February - May March - May April - May
	16-30	Menorca	April - September May - September June - September
<i>Maniola jurtina</i>	1-17	Menorca	March - June April - June May - June
	18-30	Menorca	March - September April - September May - September
<i>Pararge aegeria</i>	1-30	Menorca	January - March March - May April - June May - July
<i>Pieris brassicae</i>	1-22	Menorca	March - June April - June May - June
		North Africa	March - June April - June May - June
	23-30	Menorca	June - September

			July - September
			August - September
		Europe	June - September
			July - September
			August - September
		Mediterranean E.	June - September
			July - September
			August - September
		Atlantic E.	June - September
			July - September
			August - September
<i>Pieris rapae</i>	1-30	Menorca	March - May
			June - July
			May - July
			June - July
		North Africa	March - May
			June - July
			May - July
			June - July
<i>Polyommatus celina</i>	1-9	Menorca	January - April
			February - April
			March - April
	11-24	Menorca	March - August
			April - August
			May - August
<i>Pyronia cecilia</i>	10-30	Menorca	March - September
			April - September
			May - September
<i>Vanessa atalanta</i>	1-17	Menorca	February - May
			March - May
			April - May
	23-30	Europe	June - September

<i>Vanessa cardui</i>	1-10	Mediterranean E.	July – September
			August - September
			June - September
		Atlantic E.	July – September
			August - September
			June - September
	11-20	Menorca	July – September
			August - September
			January - April
			February - April
			March - April
		North Africa	January - April
			February - April
			March - April
		Menorca	March - July
			April - July
			May - July
		North Africa	March - July
			April - July
			May - July
	21-30	Menorca	June - September
			July - September
			August - September
		Europe	June - September
			July - September
			August - September
		Mediterranean E.	June - September
			July - September
			August - September
		Atlantic E.	June - September
			July - September
			August - September