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

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Abstract

In recent decades, efforts have been made to understand how global warming affects biodiversity and in this regard butterflies have emerged as a model group. The most conspicuous sign that warming is affecting the ecology of butterflies are the phenological advances occurring in many species. Moreover, rising temperatures are having a notable impact – both negative and positive – on population abundances. To date, patterns have generally been analysed at species level without taking into account possible differences between populations, which, when they are noted, are mostly attributed to large-scale climate differences across a latitudinal gradient. In this work, we use a long-term database of butterflies from the island of Menorca (Balearic Islands, Spain) to investigate how phenology and population dynamics have been affected by climate warming during the past two decades. In addition, we assess how responses are modulated by habitat characteristics and by species' biological cycles. Our results show that species respond differently to warming at a local scale depending on season and habitat, and that coastal habitats in the Mediterranean region are particularly sensitive to the effects of climate change. Furthermore, our findings suggest that the effects of temperature could be partially offset in more inland habitats such as forests and deep ravines. The positive effect of temperature on ravine populations during the summer suggests that butterflies disperse across habitats as a response to rising temperatures during the season. This type of dispersal behaviour as a response to warming could be especially important in island ecosystems where the possibilities of modifying altitudinal or latitudinal distributions are often severely limited.

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

Introduction

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

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

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

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

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

Material and Methods

Study area

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

Butterfly data

We used butterfly abundance data collected in 2001–2018 within the framework of the Catalan Butterfly Monitoring Scheme (CBMS) (www.catalanbms.org). Butterfly abundances were recorded weekly from March to September along fixed transects of 2–3 km in length using the standard BMS methodology (Pollard and Yates, 1993; Schmucki *et al.*, 2016). Butterflies were counted and identified to species level in a 5×5 m area along transects (2.5 m to each side and 5 m in front of the recorder) whenever weather conditions met certain minimum standards (temperature over 15ºC, 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 studies (e.g. Roy & Sparks, 2000; Stefanescu *et al*., 2003: Gutierrez-Illán *et al*., 2012). The WMFP represents the date (i.e. the week in a range of 1–30) in which the mean of adult counts of a given species at a given locality occurs:

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

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

Temperature data

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

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

Given that some of the butterflies on Menorca are migratory species (e.g. *Colias crocea*, *Pieris rapae*, *Pieris brassicae*, *Vanessa atalanta* and *Vanessa cardui*) whose immature stages do not develop on the island, it was also necessary to obtain the mean temperatures in the 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°N < latitude < 36.75N°; 10.50°W < longitude < 10.50°E); Europe (32.25°N < latitude < 45.75°N; 10.50°W < longitude < 10.50°E); Mediterranean Europe (37.50°N < latitude < 45.75°N; 0.00° < longitude < 10.50°E); and Atlantic Europe (37.50°N < latitude < 45.75°N; 10.50°W < longitude < 0.75°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 population. In both cases, we analysed the differences between localities and seasonality (i.e. spring vs. summer generations). To compare temperature effects between localities and between seasons, we excluded the long-distance migrants *V. cardui* and *P. brassicae* given that the phenology and abundance of their populations are not related to local temperatures (see Table 1).

Results

Temporal trends in temperature

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

Phenological response to increasing temperatures

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

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

In multivoltine species with clearly distinct flight periods (*A. cramera*, *C. argiolus*, *C. pamphilus*, *C. crocea*, *P. brassicae*, *P. celina* and *V. cardui*), phenological advances were recorded in both spring and summer (four and five cases, respectively; Table 1). In the two long-distance migrants *V. cardui* and *P. brassicae*, WMFPs did not have significant relationships with local temperatures but with mainly temperatures in the presumed regions of origin of the recorded adults (i.e. North Africa for the spring generations of both species, and Mediterranean Europe for the late summer generation of *V. cardui*).

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

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

Spatial and seasonal variation of the WMFP-temperature relationship

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

Grau (coastal area, *P* = 0.0471) and Santa Catalina (Mediterranean forest, P = 0.0651) (Fig. 2). The latter two populations did not differ significantly.

Spatial and seasonal variation in the abundance-temperature relationship

The analysis of population abundance showed similar results for the two types of models, i.e. considering the temperatures during the CP before adult emergence and during the butterfly's flight period. Both models showed significant differences between localities (model 1: *P* = 0.001; model 2: *P* = 0.058) and between seasons (model 1: *P* = 0.09; model 2: *P* = 0.005). However, in the first model (i.e. for developmental periods) the spatial variable was more important than the seasonal variable, whereas in the second model (i.e. for adult flight periods) the reverse was true.

As for the spatial scale, it was clear from both models that butterfly populations in the ravine (Barranc d'Algendar) benefitted more from higher temperatures than in the two other sites (Fig. 3). This was particularly the case in summer, when higher temperatures led to more abundant butterfly populations in the ravine (beta coefficients were positive in both models) but gave rise to less abundant populations in the coastal and forest sites (beta coefficients were negative at both sites and in both models).

We found a consistent stronger temperature effect on population abundance in summer than in spring (Fig. 3). This was especially so at the coastal and forest sites (differences in beta coefficients between spring vs. summer: model 1 = 0.04; model 2 = 0.03) compared to the ravine site (differences in beta coefficients between spring vs. summer = model 1 = 0.02; model 2 = 0.009). Interestingly enough, in both the coastal and forest areas there was a reverse effect of the temperature on population abundance, with an almost neutral effect in spring but a very strong negative effect in summer. In the ravine area, by contrast, the effect was always positive and very similar in spring and summer.

Discussion

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

Despite the observed warming trends during the study period, however, we only detected phenological trends in three species. On the one hand, *Coenonympha pamphilus* advanced its phenology in spring, a finding consistent with other studies of this species in the UK (Roy & Sparks, 2000) and the continental Mediterranean region (Stefanescu *et al.*, 2003), whilst, on the other, *Celastrina argiolus* and *Pieris brassicae* showed phenological changes in the opposite direction, i.e. delayed phenologies. In *C. argiolus*, the apparent delay in their spring WMFP is probably an artefact related to an advance in the summer generation, which has many more individuals and may overlap with the spring generation in warmer years. For *P. brassicae*, the delay in the summer WMFP may have different causes. Firstly, this species has a complex life cycle in the Mediterranean region where it enters a summer diapause or aestivation phase that is not observed in other regions, as noted by Held & Spieth (1999) and Spieth *et al.* (2011); according to these authors, more severe drought conditions could lengthen the summer diapause period, resulting in a later emergence of the summer generation. Moreover, *P. brassicae* is migratory and many specimens move to higher latitudes to avoid the dry summer season (CS, pers. obs.). Conversely, in late summer, large numbers of *P. brassicae* from Central Europe migrate southward to breed in the Mediterranean region. The arrival of these specimens on Menorca, which in some cases is massive, could be delayed due to an extension of the summer season given that higher temperatures allow for an increase in the number of generations developed in Central Europe (Altermatt, 2009).

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

As hypothesized, we found evidence that the phenology of the long-distance migrants *Pieris brassicae* and *Vanessa cardui* is not influenced by local temperatures but, rather, by temperatures experienced in distant source areas. Interestingly, for the rest of the species affected by local temperatures we found that phenological patterns were also strongly dependent on both habitat and season, which implies that variation occurs between populations of the same species (Figs. 2, 3). On a temporal scale, the effects of temperature were not seasonally homogenous and, although advances did occur in both spring and summer, warming caused the strongest effects in the spring generations. This pattern, observed in numerous other studies of different groups of organisms (e.g. Walther *et al.*, 2002), is a consequence in the case of butterflies of how the metabolism of immature stages relates to environmental temperatures. It is well known that in insects the rate of development depends on body temperature, which in turn, as ectothermic organisms, is closely contingent on external temperature. Once a threshold of minimum temperature is exceeded, developmental rates increase linearly for a range of temperature until a decline occurs as an upper threshold is approached, beyond which no further development is possible (cf. Kingsolver, 1989). In the Mediterranean region, this means that temperature increases in the winter-spring transition, when average temperatures are commonly 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, these factors are minimized. In spite of this, our results showed significant differences in the effect of temperature on both the flight period and the abundance of different populations. Our results agree with those reported by Altermatt (2012), who showed that habitat (in his study due to anthropogenic changes in microclimate) can affect butterfly phenology. In our case, the strongest effects on phenology and abundance were observed at the coastal site. This suggests that in warmer years the effect of temperature could be more notable on coastal than in forested areas, where more stable climatic conditions are expected (cf. Suggitt *et al*., 2011).

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

Tables

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

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

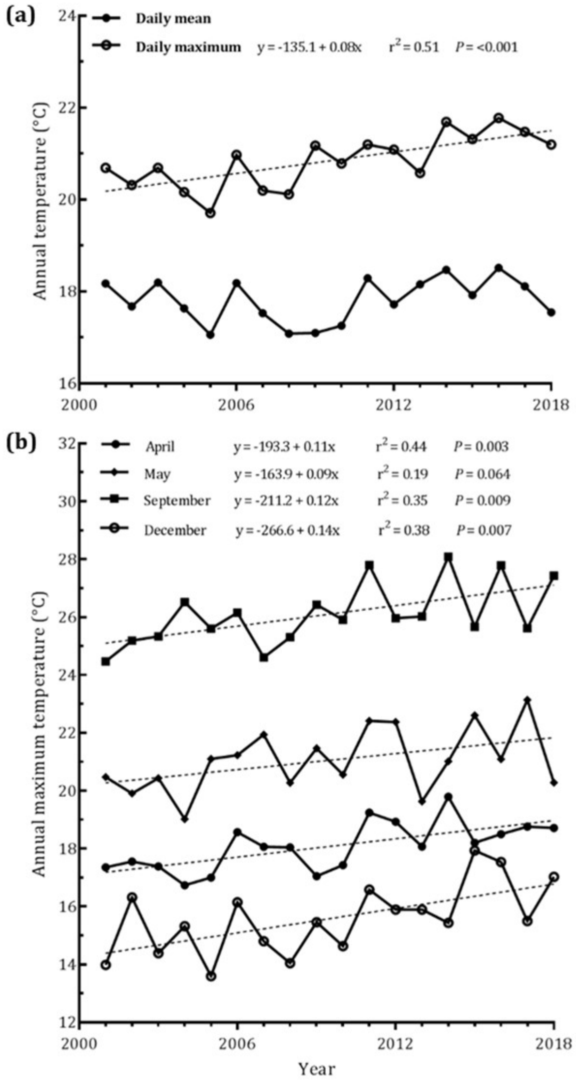
	(23 - 30)lsum	Menorca	July - September	0.041	-0.57	0.003	0.13
Pieris rapae	(1 - 30)over	North Africa	April - July	0.042	-0.89		
Polyommatus celina	(1 - 9)spr	-	-	-	-	-	-
	(11 - 24)sum	Menorca	May - August	<0.0001	-1.03	-	-
*Pyronia cecilia**	(10 - 30)sum	Menorca	May -June	0.001	-0.68	-	-
Vanessa atalanta	(1 - 17)spr	-	-	-	-	-	-
	(18 - 24)sum	-	-	-	-	-	-
Vanessa cardui	(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	-	-

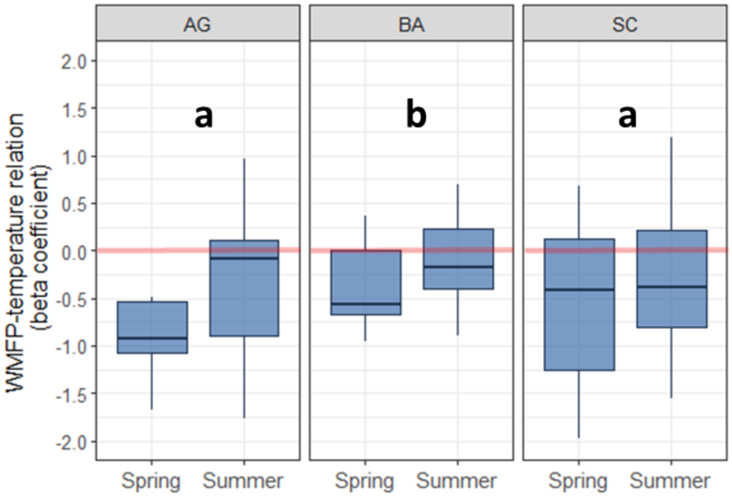
Figures

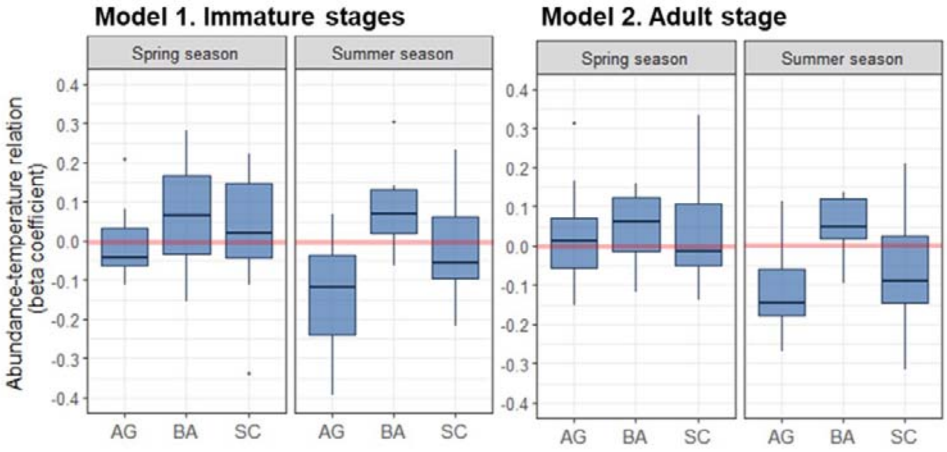
Figure 1. Climate trends in Menorca in 2001–2018. (a) Mean and maximum annual temperatures. (b) Mean monthly maximum temperatures from April, May, September and December. Dotted lines represent significant or marginally significant linear regressions ($P < 0.1$).

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

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


(a)
Daily mean
Daily maximum y = -135.1 + 0.08x r² = 0.51 P = <0.001
Annual temperature (°C)
24
22
20
18
16
2000
2006
2012
2018
(b)
April y = -193.3 + 0.11x r² = 0.44 P = 0.003
May y = -163.9 + 0.09x r² = 0.19 P = 0.064
September y = -211.2 + 0.12x r² = 0.35 P = 0.009
December y = -266.6 + 0.14x r² = 0.38 P = 0.007
Annual maximum temperature (°C)
32
30
28
26
24
22
20
18
16
14
12
2000
2006
2012
2018
Year


AG
BA
SC
a
b
a
WMFP-temperature relation
(beta coefficient)
2.0
1.5
1.0
0.5
0.0
-0.5
-1.0
-1.5
-2.0
Spring
Summer
Spring
Summer
Spring
Summer


Model 1. Immature stages
Model 2. Adult stage
Spring season
Summer season
Spring season
Summer season
Abundance-temperature relation (beta coefficient)
0.4
0.3
0.2
0.1
0.0
-0.1
-0.2
-0.3
-0.4
AG
BA
SC
AG
BA
SC
AG
BA
SC
AG
BA
SC

Acknowledgements

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References

Altermatt, F. (2009). Climatic warming increases voltinism in European butterflies and moths. *Proceedings of the Royal Society B: Biological Sciences*, 277(1685), 1281-1287. doi: 10.1098/rspb.2009.1910

Altermatt, F. (2012). Temperature□related shifts in butterfly phenology depend on the habitat. *Global Change Biology*, 18(8), 2429-2438. doi: 10.1111/j.1365-2486.2012.02727

Araújo, M. B., Rahbek, C. (2006). How does climate change affect biodiversity?. *Science*, 313(5792), 1396-1397. doi: 10.1126/science.1131758

Bartolini, G., Di Stefano, V., Maracchi, G., Orlandini, S. (2012). Mediterranean warming is especially due to summer season. *Theoretical and Applied Climatology*, *107*(1-2), 279-295. doi: 10.1007/s00704-011-0481-1

Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W., Courchamp, F. (2012). Impacts of climate change on the future of biodiversity. *Ecology Letters*, 15(4), 365-377. doi: 10.1111/j.1461-0248.2011.01736

Boggs, C. L., Inouye, D. W. (2012). A single climate driver has direct and indirect effects on insect population dynamics. *Ecology Letters*, 15(5), 502-508. doi: 10.1111/j.1461-0248.2012.01766

Caloiero, T., Coscarelli, R., Ferrari, E., Sirangelo, B. (2017). Trend analysis of monthly mean values and extreme indices of daily temperature in a region of southern Italy. *International Journal of Climatology*, 37, 284-297. doi: 10.1002/joc.5003

Carnicer, J., Stefanescu, C., Vives□Ingla, M., López, C., Cortizas, S., Wheat, C., ... Peñuelas, J. (2019). Phenotypic biomarkers of climatic impacts on declining insect populations: A key role for decadal drought, thermal buffering and amplification effects and host plant dynamics. *Journal of Animal Ecology*, 88(3), 376-391. doi: 10.1111/1365-2656.12933

Colom, P., Carreras, D., Stefanescu, C. (2019). Long-term monitoring of Menorcan butterfly populations reveals widespread insular biogeographical patterns and negative trends. *Biodiversity and Conservation*, 28(7), 1837-1851. doi: 10.1007/s10531-019-01764-1

Coumou, D., Rahmstorf, S. (2012). A decade of weather extremes. *Nature Climate Change*, 2(7), 491. doi: 10.1038/nclimate1452

Dee, D. P., Uppala, S. M., Simmons, A. J., Berrisford, P., Poli, P., Kobayashi, S., … Vitart, F. (2011). The ERA-Interim reanalysis: configuration and performance of the data assimilation system. *Quarterly Journal of the Royal Meteorological Society*, *137* (656), 553-597. doi: 10.1002/qj.828

Dennis, R. L. (1993). Butterflies and climate change. *Manchester University Press, Manchester.*

Devictor, V., Van Swaay, C., Brereton, T., Brotons, L., Chamberlain, D., Heliölä, J., ... Jiguet, F. (2012). Differences in the climatic debts of birds and butterflies at a continental scale. *Nature Climate Change*, 2(2), 121. doi: 10.1038/nclimate1347

Diamond, S. E., Frame, A. M., Martin, R. A., Buckley, L. B. (2011). Species' traits predict phenological responses to climate change in butterflies. *Ecology*, 92(5), 1005-1012. doi: 10.1890/10-1594.1

Easterling, D. R., Meehl, G. A., Parmesan, C., Changnon, S. A., Karl, T. R., Mearns, L. O. (2000). Climate extremes: observations, modeling, and impacts. *Science*, 289(5487), 2068-2074. doi: 10.1126/science.289.5487.2068

Forister, M. L., Shapiro, A. M. (2003). Climatic trends and advancing spring flight of butterflies in lowland California. *Global Change Biology*, 9(7), 1130-1135. doi: 10.1046/j.1365-2486.2003.00643

García, M. J. L. (2015). Recent warming in the Balearic Sea and Spanish Mediterranean coast. Towards an earlier and longer summer. *Atmósfera*, 28(3), 149-160. doi: 10.20937/ATM.2015.28.03.01

García-Barros, E., Munguira, M.L., Stefanescu, C. & Vives-Moreno, A. (2013). Lepidoptera: Papilionoidea. Fauna Ibérica, 37. *Museo Nacional de Ciencias Naturales-CSIC, Madrid.* 1213 pp.

Giorgi, F. (2006). Climate change hot□spots. *Geophysical Research Letters*, 33(8). doi: 10.1029/2006GL025734

Giorgi, F., Lionello, P. (2008). Climate change projections for the Mediterranean region. *Global and Planetary Change*, 63(2-3), 90-104. doi: 10.1016/j.gloplacha.2007.09.005

Gutierrez-Illan, J., Gutierrez, D., Diez, S. B., Wilson, R. J. (2012). Elevational trends in butterfly phenology: implications for species responses to climate change. *Ecological Entomology*, 37(2), 134-144. doi: 10.1111/j.1365-2311.2012.01345

Held, C., Spieth, H. R. (1999). First evidence of pupal summer diapause in Pieris brassicae L.: the evolution of local adaptedness. *Journal of Insect Physiology*, 45(6), 587-598. doi: 10.1016/S0022-1910(99)00042-6

Herrando, S., Titeux, N., Brotons, L., Anton, M., Ubach, A., Villero, D., … Stefanescu, C. (2019). Contrasting impacts of precipitation on Mediterranean birds and butterflies. *Scientific reports*, 9: 5680. doi: 10.1038/s41598-019-42171-4

Hodgson, J. A., Thomas, C. D., Oliver, T. H., Anderson, B. J., Brereton, T. M., Crone, E. E. (2011). Predicting insect phenology across space and time. *Global Change Biology*, 17(3), 1289-1300. doi: 10.1111/j.1365-2486.2010.02308

Jansa, A., Homar, V., Romero, R., Alonso, S., Guijarro, J. A., & Ramis, C. (2017). Extension of summer climatic conditions into spring in the Western Mediterranean area. *International Journal of Climatology*, 37(4), 1938-1950. doi: 10.1002/joc.4824

Jansa, A. & Gomis, D. (2018). *Series climáticas de interés para la evaluación de los impactos presentes del cambio climático sobre la biodiversidad*. Institut Menorquí d'Estudis.

Merrill, R. M., Gutiérrez, D., Lewis, O. T., Gutiérrez, J., Díez, S. B., Wilson, R. J. (2008). Combined effects of climate and biotic interactions on the elevational range of a phytophagous insect. *Journal of Animal Ecology*, 77(1), 145-155. doi: 10.1111/j.1365-2656.2007.01303

Mills, S. C., Oliver, T. H., Bradbury, R. B., Gregory, R. D., Brereton, T., Kühn, E., ... Evans, K. L. (2017). European butterfly populations vary in sensitivity to weather across their geographical ranges. *Global Ecology and Biogeography*, 26(12), 1374-1385. doi: 10.1111/geb.12659

Paaijmans, K. P., Heinig, R. L., Seliga, R. A., Blanford, J. I., Blanford, S., Murdock, C. C., Thomas, M. B. (2013). Temperature variation makes ectotherms more sensitive to climate change. *Global Change Biology*, 19(8), 2373-2380. doi: 10.1111/gcb.12240

Parmesan, C. 2003. Butterflies as bioindicators for climate change effects. In: Butterflies: ecology and evolution taking flight (Boggs, C.L., Watt, W.B. & Ehrlich, P.R. eds), *University of Chicago Press, Chicago.*

Parmesan, C., Ryrholm, N., Stefanescu, C., Hill, J. K., Thomas, C. D., Descimon, H., ... Warren, M. (1999). Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature*, 399(6736), 579. doi: 10.1038/21181

Parmesan, C., Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, 421(6918), 37. doi: 10.1038/nature01286

Pollard, E. (1979). Population ecology and change in range of the White Admiral butterfly Ladoga camilla L. in England. *Ecological Entomology*, 4(1), 61-74. doi: 10.1111/j.1365-2311.1979.tb00561

Pollard, E. (1991). Changes in the flight period of the hedge brown butterfly Pyronia tithonus during range expansion. *Journal of Animal Ecology*, 737-748. doi: 10.2307/5411

Pollard, E., Yates, T. (1993). Monitoring butterflies for ecology and conservation. *Chapman and Hall, London.*

Post, E., Steinman, B. A., Mann, M. E. (2018). Acceleration of phenological advance and warming with latitude over the past century. *Scientific reports*, 8(1), 3927. doi: 10.1038/s41598-018-22258-0

Radchuk, V., Turlure, C., Schtickzelle, N. (2013). Each life stage matters: the importance of assessing the response to climate change over the complete life cycle in butterflies. *Journal of Animal Ecology*, 82(1), 275-285. doi: 10.1111/j.1365-2656.2012.02029

Radchuk, V., Reed, T., Teplitsky, C., Van De Pol, M., Charmantier, A., Hassall, C., ... Kramer-Schadt, S. (2019). Adaptive responses of animals to climate change are most likely insufficient. *Nature communications*, 10(1), 1-14. doi: 10.1038/s41467-019-10924-4

Roy, D.B., Sparks. T.H. 2000. Phenology of British butterflies and climate change. *Global Change Biology*, 6, 407-416. doi: 10.1046/j.1365-2486.2000.00322

Roy, D. B., Rothery, P., Moss, D., Pollard, E., Thomas, J. A. (2001). Butterfly numbers and weather: predicting historical trends in abundance and the future effects of climate change. *Journal of Animal Ecology*, 70(2), 201-217. doi: 10.1111/j.1365-2656.2001.00480

Schmucki, R., Pe'Er, G., Roy, D. B., Stefanescu, C., Van Swaay, C. A., Oliver, T. H., ... Julliard, R. (2016). A regionally informed abundance index for supporting integrative analyses across butterfly monitoring schemes. *Journal of Applied Ecology*, 53(2), 501-510. doi: 10.1111/1365-2664.12561

Suggitt, A. J., Gillingham, P. K., Hill, J. K., Huntley, B., Kunin, W. E., Roy, D. B., Thomas, C. D. (2011). Habitat microclimates drive fine□scale variation in extreme temperatures. *Oikos*, 120(1), 1-8. doi: 10.1111/j.1600-0706.2010.18270

Scorzini, A. R., Di Bacco, M., Leopardi, M. (2018). Recent trends in daily temperature extremes over the central Adriatic region of Italy in a Mediterranean climatic context. *International Journal of Climatology*, 38, e741-e757. doi: 10.1002/joc.5403

Socolar, J. B., Epanchin, P. N., Beissinger, S. R., Tingley, M. W. (2017). Phenological shifts conserve thermal niches in North American birds and reshape expectations for climate-driven range shifts. *Proceedings of the National Academy of Sciences*, 114(49), 12976-12981. doi: 10.1073/pnas.1705897114

Spieth, H. R. (2002). Estivation and hibernation of Pieris brassicae (L.) in southern Spain: synchronization of two complex behavioral patterns. *Population Ecology*, 44(3), 273-280.

Spieth, H. R., Pörschmann, U., Teiwes, C. (2011). The occurrence of summer diapause in the large white butterfly Pieris brassicae (Lepidoptera: Pieridae): A geographical perspective. *European Journal of Entomology*, 108(3). doi: 10.1007/s101440200031

Stefanescu, C. (2001). The nature of migration in the red admiral butterfly Vanessa atalanta: evidence from the population ecology in its southern range. *Ecological Entomology*, 26(5), 525-536. doi: 10.1046/j.1365-2311.2001.00347

Stefanescu, C., Carnicer, J., Peñuelas, J. (2011). Determinants of species richness in generalist and specialist Mediterranean butterflies: the negative synergistic forces of climate and habitat change. *Ecography*, 34(3), 353-363. doi: 10.1111/j.1600-0587.2010.06264

Stefanescu, C., Peñuelas, J. Filella, I. (2003). Effects of climatic change on the phenology of butterflies in the northwest Mediterranean Basin. *Global Change Biology* 9, 1494-1506. doi: 10.1046/j.1365-2486.2003.00682

Thackeray, S. J., Henrys, P. A., Hemming, D., Bell, J. R., Botham, M. S., Burthe, S., ... Wanless, S. (2016). Phenological sensitivity to climate across taxa and trophic levels. *Nature*, 535(7611), 241. doi: 10.1038/nature18608

Thomas, C. D., Cameron, A., Green, R. E., Bakkenes, M., Beaumont, L. J., Collingham, Y. C., ... Williams, S.E. (2004). Extinction risk from climate change. *Nature*, 427(6970), 145. doi: 10.1038/nature02121

van Swaay, C.A.M., Nowicki, P., Settele, J. van Strien, A.J. 2008. Butterfly monitoring in Europe: methods, applications and perspectives. *Biodiversity and Conserv*ation, 17, 3455–3469. doi: 10.1007/s10531-008-9491-4

Vila, R., Stefanescu, C., Sesma, JM. (2018). Guia de les papallones diürnes de Catalunya. *Lynx edicions, Barcelona*.

WallisDeVries, M. F., van Swaay, C. A. (2006). Global warming and excess nitrogen may induce butterfly decline by microclimatic cooling. *Global Change Biology*, 12(9), 1620-1626. doi: 10.1111/j.1365-2486.2006.01202

WallisDeVries, M. F., Baxter, W., van Vliet, A. J. (2011). Beyond climate envelopes: effects of weather on regional population trends in butterflies. *Oecologia*, 167(2), 559. doi: 10.1007/s00442-011-2007-z

WallisDevries, M. F., van Swaay, C. A., Plate, C. L. (2012). Changes in nectar supply: a possible cause of widespread butterfly decline. *Current Zoology*, 58(3), 384-391. doi: 10.1093/czoolo/58.3.384

Walther, G. R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T. J., ... Bairlein, F. (2002). Ecological responses to recent climate change. *Nature*, 416(6879), 389. doi: 10.1038/416389a

Wilson, R. J., Gutiérrez, D., Gutiérrez, J., Martínez, D., Agudo, R., Monserrat, V. J. (2005). Changes to the elevational limits and extent of species ranges associated with climate change. *Ecology Letters*, 8(11), 1138-1146. doi: 10.1111/j.1461-0248.2005.00824x

Zografou, K., Kati, V., Grill, A., Wilson, R. J., Tzirkalli, E., Pamperis, L. N., Halley, J. M. (2014). Signals of climate change in butterfly communities in a Mediterranean protected area. *PLoS One*, 9(1), e87245. doi: 10.1371/journal.pone.0087245

Supporting Information

Figures

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

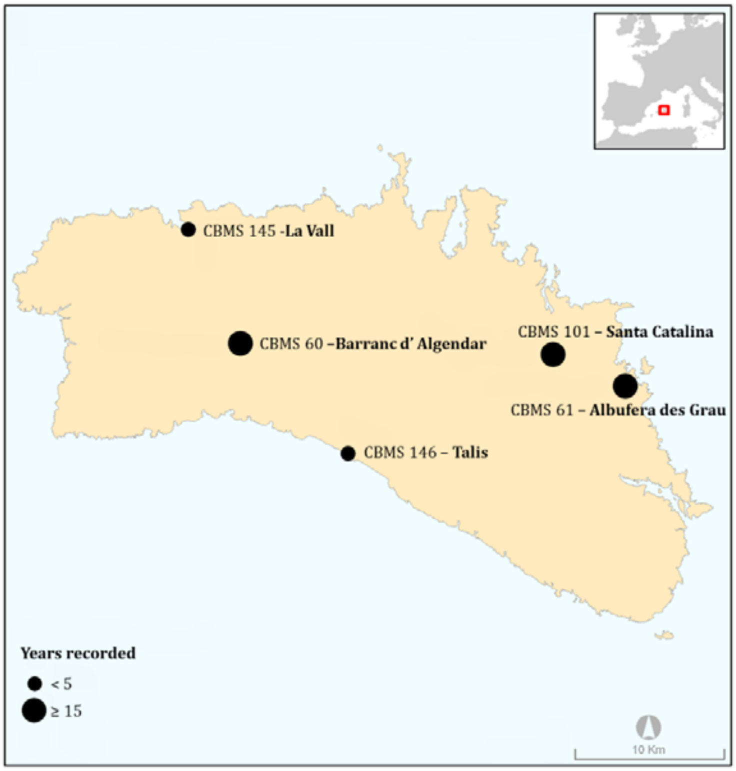
Figure S2. Details of the five CBMS transects used in the study.

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

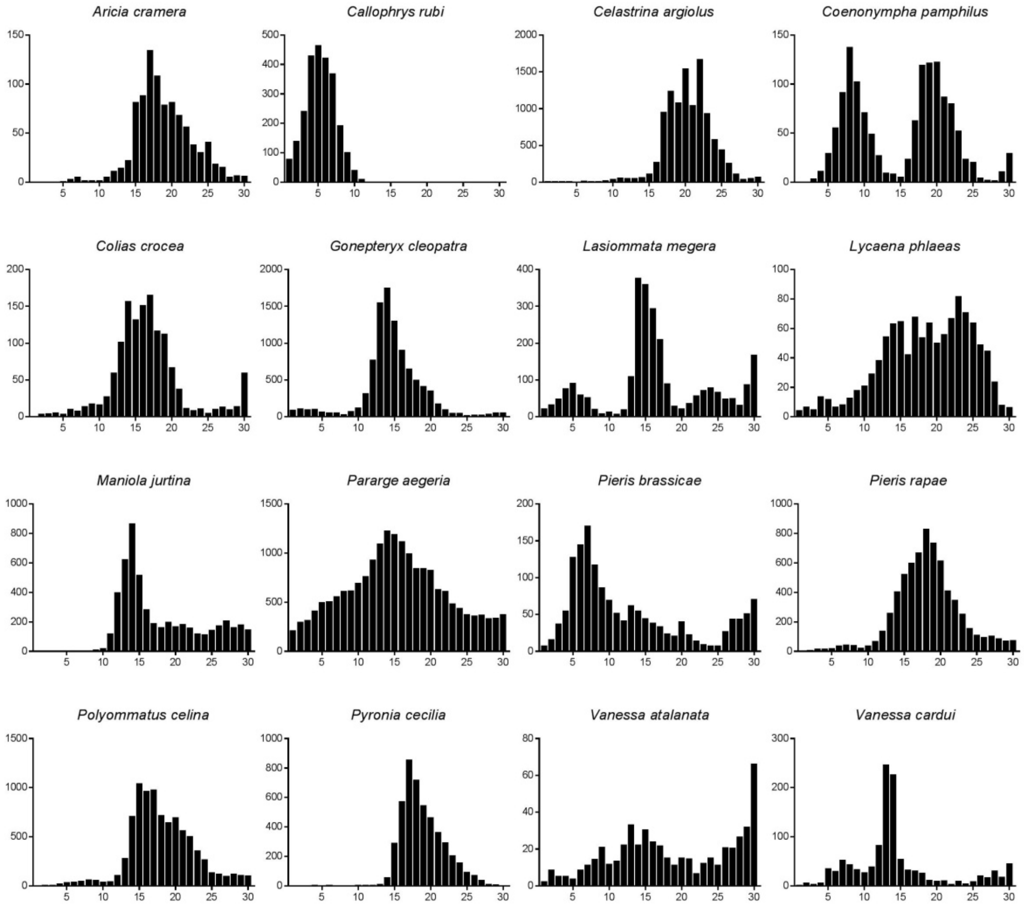
Tables

Table S1. Ecological traits of the analysed butterfly species.

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


CBMS 145 -La Vall
CBMS 60 –Barranc d' Algendar
CBMS 101 – Santa Catalina
CBMS 61 – Albufera des Grau
CBMS 146 – Talis
Years recorded
● < 5
● ≥ 15
10 Km

	**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


Aricia cramera
0
50
100
150
Callophrys rubi
0
100
200
300
400
500
Celastrina argiolus
0
500
1000
1500
2000
Coenonympha pamphilus
0
50
100
150
Colias crocea
0
50
100
150
200
Gonepteryx cleopatra
0
500
1000
1500
2000
Lasiommata megera
0
100
200
300
400
Lycaena phlaeas
0
20
40
60
80
100
Maniola jurtina
0
200
400
600
800
1000
Pararge aegeria
0
500
1000
1500
Pieris brassicae
0
50
100
150
200
Pieris rapae
0
200
400
600
800
1000
Polyommatus celina
0
500
1000
1500
Pyronia cecilia
0
200
400
600
800
1000
Vanessa atalanata
0
20
40
60
80
Vanessa cardui
0
100
200
300
5
10
15
20
25
30

Species	Voltinism	Migratory behaviour	Hibernating phase
Aricia cramera	Polivoltine	Sedentary	Larva
Callophrys rubi	Univoltine	Sedentary	Pupa
Celastrina argiolus	Polivoltine	Sedentary	Pupa
Coenonympha pamphilus	Polivoltine	Sedentary	Larva
Colias crocea	Polivoltine	Migratory	Larva
Gonepteryx cleopatra	Univoltine*	Sedentary	Adult
Lasiommata megera	Polivoltine	Sedentary	Larva
Lycaena phlaeas	Polivoltine	Sedentary	Larva
Maniola jurtina	Univoltine	Sedentary	Larva
Pararge aegeria	Polivoltine	Sedentary	Larva, pupa
Pieris brassicae	Polivoltine	Migratory	Pupa
Pieris rapae	Polivoltine	Migratory	Pupa
Polyommatus celina	Polivoltine	Sedentary	Larva
Pyronia cecilia	Univoltine	Sedentary	Larva
Vanessa atalanta	Polivoltine	Migratory	Larva, adult
Vanessa cardui	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
Aricia cramera	11-26	Menorca	January - March
			April - June
			May - July
Callophrys rubi	1-12	Menorca	January - April
			February - April
			March - April
Celastrina argiolus	1-14	Menorca	January - April
			February - April
			March - April
	15-26	Menorca	April- August
			May - August
			June - August
Coenonympha pamphilus	1-13	Menorca	January - April
			February - April
			March - April
	14-26	Menorca	March - August
			April - August
			May - August
Colias crocea	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
Gonepteryx cleopatra	1-9	Menorca	January - April
			February - April
			March - April

	10-30	Menorca	April - May
			April - June
			April - July
Lasiommata megera	1-9	Menorca	January - April
			February - April
			March - April
	10-22	Menorca	March - July
			April - July
			May - July
Lycaena phlaeas	1-15	Menorca	February - May
			March - May
			April - May
	16-30	Menorca	April - September
			May - September
			June - September
Maniola jurtina	1-17	Menorca	March - June
			April - June
			May - June
	18-30	Menorca	March - September
			April - September
			May - September
Pararge aegeria	1-30	Menorca	January - March
			March - May
			April - June
			May - July
Pieris brassicae	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
Pieris rapae	1-30	Menorca	March - May
			June - July
			May - July
			June - July
		North Africa	March - May
			June - July
			May - July
			June - July
Polyommatus celina	1-9	Menorca	January - April
			February - April
			March - April
	11-24	Menorca	March - August
			April - August
			May - August
Pyronia cecilia	10-30	Menorca	March - September
			April - September
			May - September
Vanessa atalanta	1-17	Menorca	February - May
			March - May
			April - May
	23-30	Europe	June - September

			July – September
			August - September
		Mediterranean E.	June - September
			July – September
			August - September
		Atlantic E.	June - September
			July – September
			August - September
Vanessa cardui	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
		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